

# **Nassau Grouper, *Epinephelus striatus* (Bloch 1792)**

## **Biological Report**

### **PURPOSE**

This report summarizes and synthesizes biological information covering Nassau grouper, *Epinephelus striatus*, throughout its natural distribution. It seeks to present the best available information from published and unpublished sources, (e.g., literature searches, interviews).

## Table of Contents

<b>INTRODUCTION .....</b>	<b>3</b>
<b>1. NATURAL HISTORY.....</b>	<b>3</b>
<b>1.a. Description of species.....</b>	<b>3</b>
<b>1.b. Taxonomy and distinctive characteristics .....</b>	<b>20</b>
<b>1.c. Range wide distribution .....</b>	<b>22</b>
1.c.i. Historical Distribution .....	22
1.c.ii. Influences on Distribution .....	23
<b>1.d. Biological characteristics .....</b>	<b>23</b>
1.d.i. Age, growth and mortality.....	23
1.d.ii. Ecological Roles.....	27
1.d.iii. Population connectivity/population genetics.....	30
<b>2. THREATS OR STRESSORS .....</b>	<b>31</b>
<b>2.a. Anthropogenic Effects .....</b>	<b>31</b>
<b>2.b. Habitat loss or degradation .....</b>	<b>34</b>
<b>2.c. Climate change implications .....</b>	<b>35</b>
<b>2.d. Limits to recruitment/depensation .....</b>	<b>35</b>
<b>2.e. Disease, parasites, and abnormalities .....</b>	<b>37</b>
<b>2.f. Aquaculture – successes, failures, potential threats .....</b>	<b>37</b>
<b>3. DESCRIPTION OF FISHERIES AND FISHERIES MANAGEMENT AND CONSERVATION .....</b>	<b>38</b>
<b>3.a. Abundance indices and trends over time.....</b>	<b>39</b>
<b>3.b. COUNTRY ACCOUNTS.....</b>	<b>44</b>
ANGUILLA.....	46
BAHAMAS .....	47
BELIZE.....	55
BERMUDA .....	60
BRITISH VIRGIN ISLANDS.....	63
CAYMAN ISLANDS.....	64
COLOMBIA .....	68
CUBA .....	69
DOMINICAN REPUBLIC .....	72
HONDURAS .....	73
JAMAICA .....	75
LESSER ANTILLES, CENTRAL AMERICA, AND SOUTH AMERICA .....	77
MEXICO .....	79
TURKS AND CAICOS ISLANDS.....	82
UNITED STATES (FLORIDA).....	85
UNITED STATES (PUERTO RICO).....	89
UNITED STATES (VIRGIN ISLANDS).....	93
<b>LITERATURE CITED.....</b>	<b>97</b>

## INTRODUCTION

The Nassau grouper, *Epinephelus striatus*, is a large member of the family Serranidae (Sea Basses and Groupers). As with many serranids, the Nassau grouper is slow growing, long-lived and slow to mature. It is fished with spear, traps, and hook-and-line. The Nassau grouper migrates to predictable places at predictable times to spawn during only a few weeks each year. In many locations aggregation-fishing may produce the bulk of annual landings of the species.

Commercial and recreational landings data between 1986-91 shows that the Nassau grouper harvest in the US decreased both in terms of pounds landed and average size. As a result of this decrease in yield, the Caribbean (1990), South Atlantic (1991) and the Gulf of Mexico (1996) Fishery Management Councils and the state of Florida (1993) prohibited take and possession of Nassau grouper. Currently all three Councils classify them as “overfished.” In 1991, the National Marine Fisheries Service declared Nassau grouper to be a “species of concern” under the Endangered Species Act. Nassau grouper was classified as “Endangered” in the IUCN (World Conservation Union) Red list following a 2003 assessment that showed population declines of approximately 60% over the previous three generations (27-30 years). The American Fisheries Society (AFS) considers the Nassau grouper as “Threatened” in the US and Mexico (Musik *et al.* 2000).

This report is intended to document the current state of knowledge of Nassau grouper, throughout its biological range. It borrows sections generously from an earlier NOAA Technical Report (NMFS 146) by Sadovy and Eklund (1999), and a recent Caribbean Fishery Management Council report (Sadovy de Mitcheson 2012), with additional information added from other publications, reports and personal accounts. In an attempt to consolidate and streamline the relevant information some references to reports, communications, tables, and figures point to those two original reports; they are considered companions to this report. .

## 1. NATURAL HISTORY

### 1.a. Description of species

**General Overview.** The Nassau grouper is, primarily, a shallow-water, insular species that has long been valued as a major fishery resource throughout the wider Caribbean, South Florida, Bermuda and the Bahamas (Carter *et al.* 1994). As with many serranids, the Nassau grouper is slow-growing and long-lived; estimates range up to 29 years (Bush *et al.* 1996). The Nassau grouper is considered a reef fish, but it transitions through a series of ontogenetic shifts of both habitat and diet. As larvae they are planktonic. As juveniles, they are found in nearshore shallow waters in macroalgal and seagrass habitats. They shift progressively deeper with increasing size and maturation into predominantly reef habitat (e.g., forereef and reef crest). Adult Nassau grouper tend to be relatively sedentary and are found most abundantly on high

relief coral reefs or rocky substrate in clear waters (Sadovy and Eklund 1999), although they can be found from the shoreline to about 100-130 m. Larger adults tend to occupy deeper, more rugose, reef areas (Semmens *et al.* 2007a). Both adults and juveniles will use either natural or artificial reefs (Smith 1971, Beets and Hixon 1994, Colin *et al.* 1997).

As a top predator in reef ecosystems, the Nassau grouper serves ecological functions that are still being clarified (Mumby *et al.* 2006). Its presence maintains grazers and grazing pressure on reef alga providing an important benefit to stony corals (Mumby *et al.* 2006). The predatory Nassau grouper may help limit the impact of the invasive lionfish but the evidence is far from conclusive at this time (Mumby *et al.* 2011). Its absence has been speculated to effect ecological release for smaller predators, including small groupers, with resultant changes in the trophic relationships in reef ecosystems (Stallings 2008, Mumby *et al.* 2012).

As with most large marine reef fishes, Nassau grouper demonstrate a bi-partite life cycle with demersal juveniles and adults but pelagic eggs and larvae. Reproduction is only known to occur during annual aggregations, in which large numbers of Nassau grouper, ranging from dozens to tens of thousands, collectively spawn (Smith 1972, Olsen and LaPlace 1979, Colin *et al.* 1987, Fine 1990, Fine 1992, Colin 1992). Many fish travel long distances to arrive at predictable places during the few weeks, spread over several months, each year when spawning occurs and then return to their home reefs (Sadovy and Eklund 1999). Fertilization is external. Fertilized eggs hatch after 23 to 40 hours depending on environmental temperatures. After hatching, pelagic larval duration may range from 42-70 days with transformation from pelagic to demersal form occurring in less than one week (Powell and Tucker 1992, Tucker and Woodward 1994). Newly settled fish (mean= 31.7 mm Total Length (TL), standard deviation (SD) = 2.9, N = 31) near Exuma Cays, Bahamas, were found within coral clumps (*Porites* spp.) covered by masses of macroalgae (primarily the red alga *Laurencia* spp.).

### ***Nassau Grouper Juvenile Stages***

***Newly settled juveniles (~2.5 – 5 cm TL).*** Following settlement, Nassau grouper juveniles are reported to inhabit macroalgal clumps, seagrass beds, and coral (Eggleston 1995, Dahlgren 1998). Most of what is known about the earliest life stages comes from a series of studies conducted from 1987-1994 near Lee Stocking Island in the Exuma Cays in the Bahamas. The surveys and experiments in mangrove-lined lagoons and tidal creeks (1-4 m deep), seagrass beds and sand/patch reef habitats helped identify the Nassau grouper's series of ontogenetic habitat changes. Some variation exists in the exact body size at which habitat shifts occur but shifts are common across studies. Microhabitat of newly settled Nassau grouper was described as within coral clumps (*Porites* spp.) covered by masses of macroalgae (primarily *Laurencia* spp.) although often the habitat has simply been cited as *Laurencia*. The open lattice of the algal-covered coral clumps provided cover and facilitated the movement of individuals within the interstices of the clumps (Eggleston 1995). Several newly settled Nassau grouper (up to 8) were found close together in neighboring algal clumps. Abundance of late-larval to early-juvenile

Nassau grouper was substantially higher in *Laurencia* spp. habitats than in seagrass. Within the Barraterre Bay macroalgal system, percent algal cover was correlated with post-settlement grouper density; other habitat characteristics such as algal displacement volume, and the numbers of holes, ledges, and corals were not (Eggleston 1995). The functional relationship between percent algal cover and post-settlement density was linear and positive (Eggleston 1995). Recently settled Nassau grouper have also been collected from tilefish, *Malacanthus plumieri*, rubble mounds at 18m, with as many as 3 fish together (Colin et al. 1997). They have been reported as associated with discarded queen conch, *Strombus gigas*, shells and other debris around *Thalassia* beds (Claydon et al. 2010, Wicklund<sup>1</sup>, pers. comm.) in the Turks and Caicos Islands, although the exact fish sizes observed are not clear. Post-settlement survival in macroalgal habitats is higher than in seagrass beds, showing a likely adaptive advantage for the demonstrated habitat selection (Dahlgren and Eggleston 2000).

**Early juveniles (~4.5 – 15cm TL).** Small juvenile Nassau grouper are common in shallow seagrass beds, macroalgae, and around clumps of *Porites* spp. coral as they begin to shift from settlement habitats or microhabitats (Randall 1983, Eggleston 1995). The relationship between *Laurencia* and new settler and early juvenile densities was maintained until about 5 months after settlement. After that time, mortality as well as movement to patch reef habitat reflect changes in distribution and abundance (Eggleston 1995). Band transects performed near Lee Stocking Island, Bahamas, 4-5 months after the settlement period (June 1991-93) found that early juveniles demonstrated a subtle change in microhabitat; they were mainly solitary (88%) within or adjacent to algal-covered coral clumps. Reef habitats, including solution holes and ledges, took on comparatively greater importance as habitats for early juveniles as they grew. Repeated monthly censuses of a presumed cohort indicated that juvenile density decreased sharply after settlement, until fish emerged from algal habitat at several months of age, and thereafter remained relatively constant (Dahlgren 1998). On shallow constructed block reefs in the Virgin Islands, 30-80mm TL newly settled/early juveniles occupied small separate burrows beneath the reef while larger juveniles occupied holes in the reefs (Beets and Hixon 1994).

During the sampling period in 1993 around Lee Stocking Island, mean size increased from 31.7 to 85.0 mm TL (~ 10 mm/mo.). Growth rates were consistent with those reported for early juveniles inhabiting artificial patch reefs in the USVI (Beets and Hixon 1994). Habitat usage of newly settled juveniles reportedly maximizes survival while habitat shifts for early juveniles and juveniles facilitate increased growth rates (Dahlgren and Eggleston 2000).

**Juveniles (~15 – 35; 30 – 50cm TL).** Juvenile Nassau grouper are relatively solitary and, while they remain in specific areas for extended periods (Bardach 1958), they may exhibit distinct ontogenetic shifts in habitat and diet as sizes increase. Juveniles in the Bahamas shifted

---

<sup>1</sup> Wicklund, Bob. 1990. Caribbean Marine Research Center, Vero Beach Laboratory, 805 East 46th Place, Vero Beach, FL 32963.

from macroalgal habitats to natural and artificial patch reefs over a 3-month period at 120-150 mm TL (Eggleston 1995). A subsequent gradual shift appears to occur at between 300 and 350 mm TL from inshore patch reefs to forereef areas (Dahlgren et al. in prep) although all noted shifts are likely to be highly dependent on available habitat and the researchers' abilities to distinguish and test for them. As juveniles grow, they move progressively deeper, to deeper water banks and offshore reefs (Tucker et al. 1993, Colin et al. 1997). Schools of 30- 40 juveniles (250-350 mm TL) were observed at 8-10 m depths in the Cayman Islands (Tucker et al. 1993). Several of the juvenile stages show diversity in their tolerance for schooling versus a solitary existence. Recent work by Nemeth and coworkers in the USVI (ms, in prep) found that smaller juveniles tend to show overlapping home ranges but larger juveniles and adults tend to demonstrate more territoriality with larger home ranges.

Juveniles apparently have some familiarity with their surroundings and are able to home to residential reefs over short distances based on visual cues; blinded fish do not home (Bardach, 1958). Ten recaptures, out of 11 fish originally tagged in Bermuda, demonstrated homing between isolated patch reefs separated by 100 m of sandy substrate (Bardach, 1958). Over 12 months, in one area in Bermuda, a gradual turnover of individuals was detected until the original population had been replaced (Bardach 1958). In a classic tagging study in the USVI, the greatest distance traveled was 16 km in 12 days although this was a large juvenile and possibly a maturing adult (Randall 1962, 1963). In the Florida Keys and the Virgin Islands, tagged, translocated juveniles exhibited strong home-reef specificity (Beaumariage and Bullock 1976, Beets and Hixon 1994). Twenty-seven tagged, 31-month old fish (310-380mm TL), which had been raised from eggs in captivity, survived at least 200 days in the field with one fish moving 12 km in eight days (Roberts et al. 1995). In the Bahamas, juveniles moved from inshore areas offshore to natural and artificial reefs within a year of settling out of the plankton (Eggleston 1995).

No clear distinction can be made between types of adult and juvenile habitats, although a general size segregation with depth occurs with smaller fish in shallow inshore waters (2 to 9 fathoms) and larger individuals more common on deeper (10 to 30 fathoms) offshore banks (Bardach et al. 1958, Cervigón 1966, Silva Lee 1974, Radakov *et al.* 1975, Thompson and Munro 1978). Adults lead solitary lives outside of the spawning season, rarely venturing far from cover (Bohlke and Chaplin 1993, Smith 1971, Carter et al. 1994, Sluka *et al.* 1998).

### *Nassau Grouper Adult Stage*

*Size and age at maturity.* Male and female Nassau grouper typically mature between 400 and 450mm SL (440 and 504 mm TL), with most individuals attaining sexual maturity by about 500 mm SL (557 mm TL) and about 4-5 years of age (Table 1), although the smallest mature fish recorded in Cuba was a male in the 360-390mm TL size class (Claro et al. 1990). Olsen and LaPlace (1979) reported  $A_{95}$  (the age at which 95% of the asymptotic length is reached) is 15.9 years. In sampling fishery catches at Mahahual, southern Quintana Roo, Mexico, during 1991-3, and 1997, Aguilar-Perera (2004) reported the smallest male as 390 mm TL and the smallest female as 460 mm TL. Most individuals caught from a USVI spawning aggregation were between about 500 and 600 mm TL (Olsen and LaPlace 1979). Nemeth et al 2006 found that adult Nassau grouper at a different spawning aggregation site (Grammanik Bank) in the USVI ranged between 480 and 800 mm with average total length for males (603 mm, n=18) and

**Table 1. Summary of Age and Length Parameters for Nassau grouper, *Epinephelus striatus*. (from Table 3, Sadovy and Eklund 1999; “Bush et al., in press” refers to Bush et al. 2006)**

<i>Epinephelus striatus</i>	
Age and length at maturity	5 yrs, 580 mm SL (Virgin Islands) (Olsen and LaPlace, 1979)  420-450 mm SL females 400-450 mm SL males\4+ yrs (Cayman Islands) (Colin et al., 1987; Bush et al., in press) 500 mm TL (minimum size ripe males) (Cayman Islands) (Tucker et al., 1993) 425 mm SL females; 402 mm SL males, immatures are 3-6 yrs (otolith growth zones not validated) (Bahamas) (Sadovy and Colin, 1995) 483 mm TL (North Carolina-Florida) (SAFMC, text footnote 24) 480 mm TL (Jamaica) (Thompson and Munro, 1978)
Age and length at first capture	< 300 mm TL & 4-5 yrs (Virgin Islands) (Olsen and LaPlace, 1979; CFMC, text footnote 26) 6-7 yrs (Cayman Islands) (Bush et al., in press) 275-625 mm TL (mean = 570) (Jamaica) (Thompson and Munro, 1978) 300-500 mm TL depending on size limits (North Carolina-Florida) (SAFMC, text footnote 46) 450 mm TL (South Florida) (Bohnsack, 1990)
Maximum age and length	1200 mm TL (CFMC, text footnote 26) 9 yrs, 910-960 mm SL (Olsen and LaPlace, 1979) (Virgin Islands) 17 yrs, 710 mm TL, 6700 g (Cuba) (Claro et al., 1990) 755 mm SL (Bermuda) (Bardach et al., 1958) 840 mm TL (Jamaica) (Thompson and Munro, 1978) 640 mm TL (Netherlands Antilles) (Nagelkerken, 1981) 29 yrs, 850mm FL (Cayman Islands) (Bush et al., in press)

females (591 mm, n=44) being similar. From otolith ageing work, the minimum age at sexual maturity is between 4 and 8 years (Bush et al. 1996, 2006) with most fish spawning by age 7+ years (Bush et al. 2006). Nassau grouper raised from the egg in captivity matured at 27-28 months (400-450 mm SL/440-504 mm TL) (Tucker and Woodward 1994). Size, rather than age, may be the major determinant of sexual maturation (Sadovy and Eklund 1999).

### *Habitat and Home*

*Range.* Although there can be overlap between juvenile and adult habitats there is normally a positive correlation between size and depth. Nassau grouper are diurnal or crepuscular in their movements (Collette and Talbot 1972) and do not usually move far from

cover (Starck and Davis 1966). Three sonically tagged fish were most active in the hours prior to and following sunrise and sunset (Carter et al. 1994). Two of the fish moved randomly within a 160 m x 80 m rectangle during the day, returning in the evening to where they had initiated daily activities (Carter et al. 1994). Sullivan and de Garine-Wichatitsky (1994) estimated that individuals moved at least 400 m/day and 20 m or more from their home reefs. Mean home-range area was calculated at  $18,305\text{m}^2 \pm 5,806$  (SE) Bolden (2001). Nassau grouper had larger home ranges at less structurally complex reefs and resource availability (habitat and prey) influences home range size more than body size (Bolden 2001). Bolden (2001) investigated diel activity patterns via continuous acoustic telemetry and found Nassau groupers are more active diurnally and less active nocturnally with activity peaks at 1000 and 2000 hours. Nemeth and coworkers (UVI, ms. in prep) have found a significant positive relationship between body size and home range, for fish tagged in Lameshur Bay, St. John, with MCP variations from 89.5-9913.9  $\text{m}^2$ . Recent studies in a marine reserve in Cuba suggest that relative densities may control movements, changes in location, and, possibly, home range size (Amargós et al. 2010).

*Depth ranges.* Adult Nassau grouper are generally associated with shallow reef habitats to depths of 100 m. Reports from fishing activities in the Leeward Islands show that although Nassau grouper was fished to 130 m, the greatest trap catches were from 52-60 m (Brownell and Rainey 1971). In Venezuela, Nassau grouper were cited as common to 40 m in the Archipelago Los Roques, but rare in northeastern islands (Cervigón 1966). Recent tagging studies in Belize have shown that individuals regularly descend to depths of at least 255m (Starr et al. 2007). The shift in depth followed spawning and was synchronous to an average of  $71.9 \text{ m} \pm 0.1$  (SE), with a maximum depth of 255 m, and persisted about 3 months, throughout the winter spawning season in Belize. Starr and co-authors (2007) hypothesized that these deep migrations might facilitate physiological recovery and/or that spawning might continue at depth, but the true purpose requires future research.

*Sizes and size distribution.* Mean male and female sizes are similar within a given area, or at a specific aggregation site, with some indication that sizes of both sexes decline in areas within a specific region with higher exploitation (reviewed in Sadovy and Eklund, 1999). For example, in Belize, the average length of both sexes was 100 mm smaller in catches from exploited compared to unexploited aggregations (Carter et al. 1994). Individual Nassau grouper can live for almost three decades but most fish collected are substantially smaller and presumably younger. Bush et al. (2006) reported that the oldest Nassau grouper in their study in the Cayman Islands was 29 years, based on an ageing study using sagittal otoliths.

*Reproductive mode.* The Nassau grouper was originally considered to be a monandric protogynous hermaphrodite, like most other groupers, with all males deriving from the sex change of adult females (Smith 1971, Claro et al. 1990, Carter et al. 1994). Evidence of the change from adult female to adult male in the Nassau grouper (*i.e.*, fish undergoing sexual transformation whereby the gonads show degeneration of mature tissue of one sex and proliferation of reproductive tissue of the other), however, was weak (Sadovy and Shapiro 1987,

Shapiro 1987). Other characteristics were found to be inconsistent with a diagnosis of monandric protogyny such as the strong male/female size overlap, the presence of males that develop directly from the juvenile phase, and the mating system (Colin 1992, Sadovy and Colin 1995).

Nassau grouper pass through a juvenile bisexual phase (the gonads consist of both immature spermatogenic and immature ovarian tissue) (Table 2), and mature directly as male or female (Sadovy and Colin 1995). Although the Nassau grouper is capable of changing sex following hormone injection -- one Nassau grouper reproduced as a female and subsequently as a male approximately 6 months later, following an LHRH-a implant in captivity (Watanabe and Head<sup>2</sup>, Watanabe et al. 1995b) -- natural sex change has not been confirmed. The close affinity of this species with other hermaphroditic serranids accounts for the gonad structure of this species and although it may retain a capacity for natural sex change available evidence indicates that this is not typical and that the Nassau grouper is primarily gonochoristic (separate sexes) (Sadovy and Colin 1995).

**Table 2. Gonadal maturity according to size for Nassau grouper (from Sadovy and Eklund 1999).**

Stages of gonadal maturation for 230 *Epinephelus striatus* collected in the Bahamas between May 1988 and October 1990 (from Sadovy and Colin, 1995- Fig. 3). Bisexual fish are those in which the gonads contain both ovarian and testicular tissue and include both immature (both male and female tissue immature) and mature (in parentheses) bisexuals.

Size class (mm SL)	Female		Male		
	Bisexual	Immature	Mature	Immature	Mature
151-200	1	1			
201-250	2				
251-300	8	3			1
301-350	11	3			1
351-400	15	2			
401-450	4	1	2	1	1
451-500	9		10		23
501-550	4(1)		36		15
551-600	(3)		33		9
601-650			13		4
651-700			5		6
701-750			1		1
Total	58	10	100	1	61

*Spawning migrations.* The Nassau grouper aggregates in large numbers to spawn each year; the largest aggregation studied had an estimated 30,000-100,000 spawning fish (Smith 1972) in Bimini, Bahamas. As far as is known, all reproductive activity occurs in these aggregations that form consistently at specific sites ("grouper holes") and times. Aggregations have consisted of hundreds, thousands, or, historically, tens of thousands of individuals and have persisted at known locations for periods of 90 years or more (Smith 1972, Olsen and LaPlace 1979, Colin et al. 1987, Fine 1990, 1992, Colin 1992, Carter et al. 1994, Sadovy 1997, Claro<sup>3</sup> pers. comm.).

It is not known how Nassau grouper select and locate aggregation sites or why they aggregate to spawn. Aggregations are typically located near significant geomorphological features, such as the ends of islands or projections (promontories) of the reef seaward

from the general reef contour (Colin et al. 1987, Heyman and Kjerfve 2008). To locate a site,

<sup>2</sup> Watanabe, Wade, and William Head. 1992. Caribbean Marine Research Center, Vero Beach Laboratory. 805 East 46th Place. Vero Beach, FL 32963. Pers. comm.

<sup>3</sup> Claro, Rodolfo. 1991, Laboratory of Fish Ecology, Institute of Oceanology. #18406 Playa, Havana, Cuba.

grouper could swim up- or down-current along the shelf break to reach the most seaward up-current extension of the reef where aggregation sites are generally located (Carter 1986, Colin et al. 1987). The timing and synchronization of spawning may be determined by the necessity for widely dispersed adults to coordinate their reproductive activities, may facilitate egg dispersal, may minimize egg dispersal, or minimize predation on adults or eggs (Colin 1992).

Prior to spawning, fish migrate toward aggregation sites in groups numbering between 25 and 500, moving parallel to the coast or along the shelf edge (Colin 1992, Carter et al. 1994, Aguilar-Perera and Aguilar-Davila 1996). Over 5 years of observations (2002-2006) in the Cayman Islands, migrating Nassau grouper were reported at the shelf edge, typically at depths ranging from 20 to 33m. According to Whaylen *et al.* (2007): *Migrating grouper were mainly in the dark color phase, although the white belly phase was not uncommon. Peak numbers of migrating groupers were observed 2 to 3 days after full moon with clusters of up to 100 groupers traveling together along the wall towards the aggregation site.* Nassau grouper migrating to the Grammanik Bank spawning site off St. Thomas, USVI moved along a linear reef 300-500 m inshore rather than swimming along the actual shelf edge (Nemeth et al. 2009.)

“*Corridas de desove*” (spawning runs), which refers both to the migration of fish toward a spawning site and to the aggregation itself, were first described in Nassau grouper from Cuba in 1884 by Vilaro Diaz, and later by Guitart-Manday and Juarez-Fernandez (1966). All three workers noted that fishers reported spawning runs occurring mainly between November and February and at different moon phases. It is not known whether *corridas* are exclusively associated with spawning or occur at other times, unassociated with reproductive activity.

During the several-month spawning season each year, Nassau grouper move from their residential habitats to spawning aggregation habitats. Spawners appear to show some site fidelity to the same aggregation sites year after year. Movement away from resident reefs occurs as spawning time approaches and distances traveled vary depending on distance to aggregation site. Distance traveled is highly variable. Some fish move only a few kilometers but some individuals are known to travel up to several hundred kilometers to reproduce. Observations of migrating groups of fish, on or before the full moon of spawning, indicate that at least some fish travel to aggregation sites in groups ranging from a few fish up to about 500 individuals (Colin 1992). Several dozen fish were observed passing slowly along the 30-40 m shelf break contour at several localities along a reef in Belize in late October and early November (Carter et al. 1994), *i.e.*, a month or two before spawning was likely. In Honduras, groupers normally located 48 km from an aggregation site disappeared from resident reefs at spawning time (Fine 1992). One tagged fish in the Bahamas covered a distance of at least 110 km in two months to an aggregation site (Colin 1992). Another fish, tagged on an aggregation site in Belize, was recaptured 2 years later 240 km north of the tagging site (Carter et al. 1994). A Nassau grouper (58 cm TL) tagged with an external tag for a home range study in the central Bahamas was released in July 1997 and recaptured 185 days later by a fisherman at the Long Island spawning aggregation approximately 220 km from the release point (Bolden 2000). Ongoing research in

the Exuma Sound, Bahamas has tracked fish up to 200 km (125 mi) with likely estimates of up to 330 km (205 mi) as they move to spawning sites (C. Dahlgren pers. comm.). Spawners migrating along larger contiguous reef tracts seem to move greater distances to aggregate than those on small islands or atolls; the constraint is likely their reluctance or inability to navigate extreme water depths to reach suitable habitat (Starr et al 2007).

From acoustic tagging studies around Glover's Reef, Belize, Starr et al. (2007) measured average swimming speed of Nassau grouper migrating to and from the spawning site as  $1.90 \pm 0.05$  (SE) km/hour. The speed of movement to the spawning site was identical to the speed of travel away from the spawning site. They noted that several tagged groupers were recorded at receivers 30 km away from the spawning site and at the spawning site less than 24 hours later. They found sex based differences in swimming speed with mean speed of males,  $2.0 \pm 0.2$  (SE), being significantly faster than female groupers,  $1.8 \pm 0.2$  (SE) km/hr. They also used all swimming segments that were  $>5$  km to evaluate time of day of grouper movements to the spawning site by, and found that 16 tagged fish moved only during the day (defined as 1 h before sunrise through to sunset) and 8 fish moved both during the day and at night. Grouper swim speeds during the day averaged  $1.96 \pm 0.03$  (SE) km/hr and were significantly faster than mean grouper swim speeds at night ( $1.4 \pm 0.1$  km/hr).

Observations suggest that individuals can return to their original home reef following spawning. Several large adult Nassau grouper in the Bahamas, clearly swollen with gametes, disappeared from residential areas for periods ranging from 10 days before, to a few days after, the full moon of December 1989. They remained in home areas for the January 1990 full moon and were seen neither to swell with gametes nor to exhibit courtship behavior, suggesting that not all mature fish aggregate or spawn in every aggregation month in each reproductive season (Colin<sup>4</sup>). Sonic tracking studies around Little Cayman Island have demonstrated that spawners may return to the aggregation site in successive months with returns to or towards their residential reefs in between (Semmens et al. 2007). Larger fish are more likely to return and spawn in successive months than smaller fish (Semmens et al. 2007).

*Spawning habitat.* Spawning aggregation sites typically occur near the edge of insular platforms, as little as 50 m from the shore, and close to a drop-off into deep water over a wide (6-60 m) depth range and diversity of substrate types (Craig 1966, Smith 1972, Burnett-Herkes 1975, Olsen and LaPlace 1979, Colin et al. 1987, Carter 1989, Fine 1990, Beets and Friedlander 1992, Colin 1992, Aguilar-Perera 1994). Sites are characteristically small, highly circumscribed areas, measuring several hundred meters in diameter, with soft corals, sponges, stony coral outcrops, and sandy depressions (Craig 1966, Smith 1972, Burnett-Herkes 1975, Olsen and LaPlace 1979, Colin et al. 1987, Carter 1989, Fine 1990, Beets and Friedlander 1992, Colin 1992, Aguilar-Perera 1994). About 60-80 aggregation sites have been recorded, mostly from insular areas, although many no longer form. Recent work has identified geomorphological similarities in spawning sites that may be useful in applying remote sensing techniques to

---

<sup>4</sup> Colin, Pat. 1990. Coral Reef Research Foundation, P.O. Box 1765, Koror, Palau 96940. Pers. comm.

discover previously unknown spawning sites (Kobara and Heyman 2010). At spawning aggregation sites, Nassau grouper tend to meander around in a “staging area” adjacent to the core area where spawning activity actually takes place (Kadison *et al.* 2010, Nemeth 2012). These aggregation staging areas have been reported at depths of 6-50 m. As sunset approaches, the spawners typically move seaward, into slightly deeper water (30-60m). Spawning rushes have been described either as a column or cone of fish of different color phases rising to within 20-25m of the water surface or as a series of rushes by small groups of males following a single female (Olsen and LaPlace 1979, Carter 1986, Aguilar-Perera and Aguilar-Davila 1996).

All spawning, as far as is known, occurs in distinct aggregations at sites that remain consistent over long time periods. There are no reports of pair spawning. Spawning aggregations have been reported from the Bahamas, Belize, Bermuda, British Virgin Islands, Cayman Islands, Cuba, Honduras, Jamaica, Mexico, Puerto Rico, Turks and Caicos and the U.S. Virgin Islands (Olson and LaPlace 1979, Colin *et al.* 1987, Carter 1988, Colin 1992, Aguilar-Perera and Aguilar-Davila 1996, Paz and Grimshaw 2001). Suspected or anecdotal evidence also identifies spawning aggregations in Los Roques, Venezuela (Boomhower *et al.* 2010) and Old Providence (Prada *et al.* 2004) in Colombia’s San Andrés Archipelago. Neither aggregation nor spawning has been reported from South America although ripe Nassau groupers are frequently taken in certain areas (Cervigón<sup>5</sup>). Aggregation spawning is likewise unknown from the Lesser Antilles, from Central America south of Honduras, or from Florida. The environmental and social triggers that cause Nassau grouper to aggregate are not well understood, although changing lunar light conditions, water temperature, currents, learned behavior, or a combination of these or other factors are the postulated basis for aggregation formation (Colin *et al.* 1987, Carter 1989, Tucker *et al.* 1993, Domeier and Colin 1997, Sadovy and Eklund 1999, Paz and Grimshaw 2001).

*Spawning timing.* The Nassau grouper’s well-known reproductive mode of forming transient spawning aggregations is generally predictable within a prescribed area. Aggregations occur at predictable times and places each year around the time of the full moon, usually between December and March (reviewed in Sadovy and Eklund 1999), although in Bermuda aggregation spawning occurred in the northern summer period from May to July (Bardach *et al.* 1958). Olsen and LaPlace (1979) reported spawning occurring on the first full moon after the winter solstice. Working from gonad examinations, Munro and colleagues (1973) reported Nassau grouper from Jamaica’s offshore oceanic banks to be in spawning condition predominantly in February, but also to a lesser degree in April and May. Recent evidence suggests that spawning is also occurring at what appear to be reconstituted or novel spawning sites in both Puerto Rico and the USVI during June (R. Appeldoorn<sup>6</sup>, R. Nemeth<sup>7</sup>, D. Olsen<sup>8</sup>

---

<sup>5</sup> Cervigón, Fernando. 1991. Fundacion Cientifica Los Roques, Aptdo. 1139, Caracas 1010A, Venezuela. Personal commun.

<sup>6</sup> Appeldoorn, Richard S. University of Puerto Rico-Mayaguez, Department of Marine Science.

<sup>7</sup> Nemeth, Richard S. University of the Virgin Islands, Center for Marine and Environmental Studies.

<sup>8</sup> Olsen, David A., Chief Scientist, St. Thomas Fishermen’s Association

reporting the findings of R. Gomez VI DFW, pers. comm.) rather than during the winter months, although further work is needed to fully document these observations. Spawning occurs for up to 1.5 hours around the time of sunset for several days in each of several months (Whaylen et al. 2007). The gonadosomatic index (GSI) of females (*i.e.*, the relative ovary-to-body weight) is a good indicator of spawning seasonality (Fig. 1).

The reproductive season in the Nassau grouper is brief and evidently associated with temperature and moon phase, according to GSI, gonadal histology, macroscopic, and oocyte diameter analyses. At lower latitudes, reproductive activity lasts for about one week per month, for one to three months each year, between December and February (Fig. 1), either peaking in January (Smith

1972, Olsen and LaPlace 1979, Claro et al. 1990, Colin 1992, Powell and Tucker 1992,

Aguilar-Perera 1994, Miller<sup>9</sup>) or between January and April (Thompson and Munro 1978). In more northerly latitudes (*i.e.*, Bermuda), the reproductive season falls between May and August, peaking in July (La Gorce 1939, Smith 1971, Burnett-Herkes 1975). Exceptions to the possible latitudinal pattern were the capture of recently-spawned females in September in Cuba coupled with the observation, of a group of Nassau grouper at 29 m depth in the same location (Claro et al. 1990).

Spawning is highly synchronized and occurs briefly within about a week of full moon, or between full and new moon (Smith 1971, Colin 1992, Tucker et al. 1993, Aguilar-Perera 1994, Carter et al. 1994, Tucker and Woodward 1994), within the narrow temperature range of 25-26°C and over a wide range of day-lengths (Colin 1992, Tucker et al. 1993, Carter et al. 1994). Whaylen et al. (2007) have proposed a predictive guide for the Cayman Islands that if the span of time from the winter solstice to January's full moon is less than 30 days, then February was the major spawning month. Conversely, if it was greater than 30 days, January was the major spawning month. Other researchers have recognized that the timing of the full month, early or

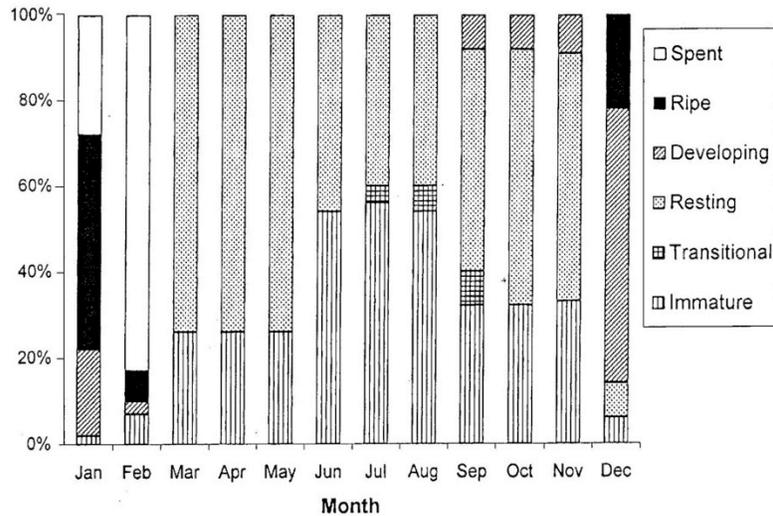


Figure 1. Percent frequency of different gonad development stages for female Nassau grouper by month collected from Belize from 1984-86 (n=1,232) [redrafted from Carter et al. 1994]

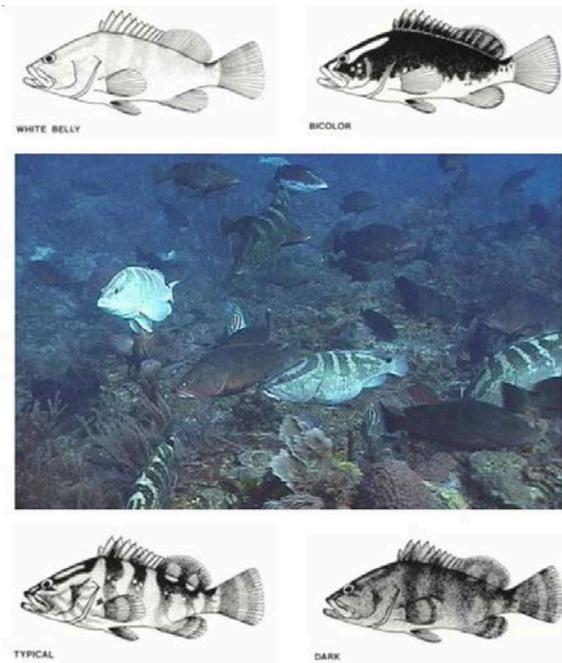
<sup>9</sup> Miller, W. 1984. Spawning aggregations of the Nassau grouper, *Epinephelus striatus*, and associated fishery in Belize. Advances in Reef Sciences, October 26- 28, 1984, University of Miami, Florida. Unpubl. data, p. 19.

late in the month, can give an indication of when the peak spawning will occur (Appeldoorn and Schärer, pers. comm.).

Sea surface temperature, as it falls beyond 26°C to seasonal lows, has also been proposed as a key control on spawning timing (Colin 1992). Similar associations between reproduction, temperature, and lunar phase were also noted in captive animals. Nassau grouper raised from egg to maturity in Florida and Bermuda under conditions of ambient light, temperature, and salinity, exhibited ovarian maturation, ovulation, behavior, and color changes characteristic of spawning, at 26°C, although no spawning was observed (Tucker and Woodward 1994).

Temperature is evidently a more important stimulus for spawning than day length, according to patterns of voluntary spawning in captive fish. While spawning occurred at temperatures ranging from 23.1-27.9°C, 24-27°C was the most suitable based on spawning frequency and volume, and egg and larval development (Tucker 1994, Watanabe et al. 1995a, Tucker et al. 1996). Nassau grouper spawned spontaneously one day prior to the new moon in April 1963 in an aquarium in Cuba under artificial light and water temperature of 24.9°C (Guitart-Manday and Juárez-Fernandez 1966).

*Spawning behavior.* Fish generally gather near the spawning site a day or two prior to initiation of spawning. Surveys can identify unusually high numbers of individuals either interacting or resting on/near the bottom. Prior to spawning, individuals mill around over the substrate exhibiting one of four distinctive color phases: (1) barred (normal); (2) bicolor; (3) white belly; or (4) dark phase (Fig. 2). There are intergradations of these patterns, with rapid



(Diagrams adapted from Sadovy & Eklund, 1999. Photograph by Andy Stockbridge)

**Figure 2. Color phases of Nassau grouper. From Paz and Grimshaw 2001b.**

changes among patterns possible (Colin 1992). The barred (typical) color phase is found among fish in the aggregation in the morning. The bicolor phase, first described by Smith (1972), occurs in both males and females and is dominant during the late afternoon with most fish becoming bicolored by dusk, when spawning occurs (Colin 1992). In this phase, the upper body and head become dark while the belly, lower sides, lips, and all fins but the dorsal are white. A white eyebar is prominent on the head (Colin 1992). In the white belly phase, seen among presumed females with bulging abdomens (probably full of ova), the normal color pattern is modified such that the abdominal area

is distinctly white (Colin 1992). The last pattern, the "dark" phase, is found in courting and spawning fish; the body and fins become dark gray to black with the barred pattern visible beneath the dark pigmentation. These fish are probably females ready to spawn since they appear to lead group-spawning events (Colin 1992).

Courtship is indicated by two behaviors which occur late in the afternoon: "following" and "circling" (Colin 1992): "following" occurs as one or more fish in the bicolor phase swim closely behind an apparent female; "circling" occurs as a bicolor phase fish circles a barred or dark phase fish. Progression from courtship to spawning may depend on aggregation size but generally occurs as follows. Towards the late afternoon fish move progressively higher in the water column, with an increasing number exhibiting the bicolor phase (Colin 1992, Carter et al. 1994). The aggregation then moves into deeper water shortly before spawning (Colin 1992, Tucker et al. 1993, Carter et al. 1994) by which time all individuals are either "dark phase" or "bicolor." Bicolor fish then follow dark phase fish closely and group-spawning occurs in sub-groups of 3-25 fish (Fig. 3). Similar accounts of spawning behavior from USVI described the aggregated fish as a cone (Fig 4.) in the water column rather than being dispersed across the bottom (Olsen and LaPlace 1979)

Smaller aggregations tend to include fewer bicolor phase fish and general activity and color changes are less intense (Colin 1992, Aguilar-Perera and Aguilar-Davila 1996). Spawning involves a rapid horizontal swim followed by a circling ascent of small sub-groups into the water column, with release of sperm and eggs and a rapid return of the fragmented sub-group to the substrate. Gamete release is well above the bottom. On the basis of observations of over 50 spawning events, the earliest and latest spawning occurred within 20 minutes of sunset and most within 10 minutes of sunset (Colin 1992). Hydration of vitellogenic eggs occurs in the afternoon shortly before spawning.

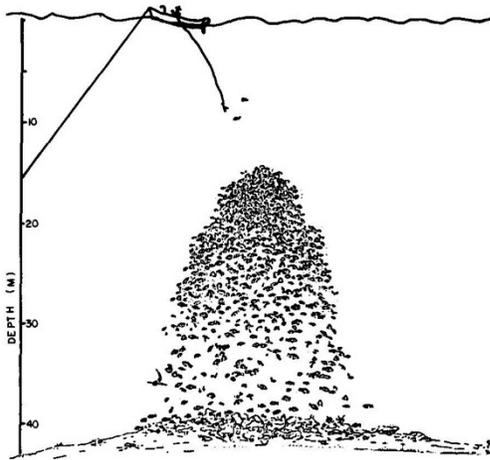
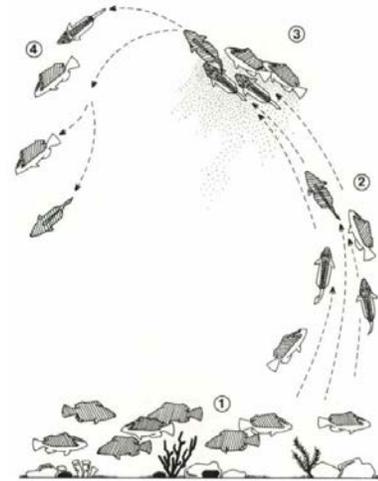


Figure 4. Depiction of spawning rush. From Olsen and LaPlace 1979.

Although aggregations form more than once at a particular site during a reproductive season, it is unclear whether the same individuals participate each time. However, several females from one aggregation contained ripe and sub-ripe oocytes together with post-ovulatory follicles (which remain after mature oocytes



Spawning Behavior of Nassau Grouper (Adapted from Sadovy & Eklund, 1999)

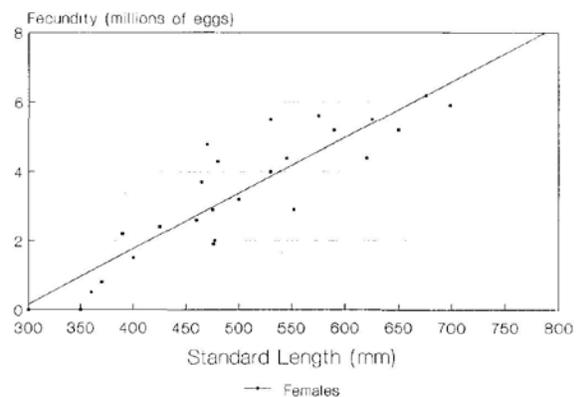
Figure 3. Depiction of spawning rush. From Sadovy and Eklund 1999.

have been released), suggesting that individual females spawn repeatedly on different days during one aggregation (Smith 1972, Sadovy pers. obs.). Moreover, examination of spawning on videotape indicated that during 3-4 successive gamete releases by a sub-group within a 15-20 second period, the same female led all spawning events, again indicating multiple egg releases in one evening (Colin 1992). No data are available, however, addressing whether each mature female spawns in every aggregation month, or indeed, each year.

In larger aggregations, a clear increase in the proportion of the bicolor phase to other color phases from 0.05 early in the aggregation to 0.40 on the day of spawning suggested the color phase indicated behavioral and physiological preparedness to spawn (Archer et al. 2012). While Nassau grouper in groups of as few as 20 fish were seen to spawn, Colin (1992) reported such small groups appeared to show substantially fewer fish in the bicolor phase that typically precedes spawning. In the Cayman Islands, fish in small aggregations gathered on site for longer than those in large groups (Brice Semmens pers. comm.) presumably extending or delaying spawning.

*Fecundity.* Fecundity estimates from wild-caught Nassau grouper are few and varied, but suggest a mean relative fecundity of between 3 and 5 eggs/mg of ripe ovary, depending on the method used, *i.e.*, which stages of oocytes are included in egg counts. Estimates from Belize (Fig. 5) yielded a mean relative fecundity of 4.1 eggs/mg ovary weight and a mean total number of oocytes (stage unspecified) of 4,200,000 (range = 350,000-6,500,000 for females from 300 to 700 mm SL) (Carter et al. 1994). Estimated number of eggs in the ripe ovary (90.7 g) of a 445 mm SL individual from Bermuda was 785,101 (Bardach et al. 1958). In the Virgin Islands, fecundity estimates made from 42 mature females gave a mean value of 4.97 eggs/mg of ovary (s.d.=2.32) with mean egg production of 4,800,000 eggs (Olsen and LaPlace 1979). However, since this latter estimate includes pre-vitellogenic oocytes, which may not recruit into the vitellogenic stock prior to spawning, it is considered to be an overestimate.

Fecundity estimates were also made, based on vitellogenic oocytes only, from Bahamas fish producing a mean relative fecundity of 2.9 eggs/mg ripe ovary (s.d.=1.09; n=64) and a mean fecundity of 716,664 (range= 11,724 - 4,327,440 for females, 475-686 mm SL). Estimates of oocyte production from animals induced to spawn in captivity are closer to those based solely on vitellogenic oocyte counts.



1984-1996

**Figure 5. Fecundity of female Nassau groupers as a function of size. (from Carter et al 1994).**

### ***Nassau Grouper Egg Stage***

Fertilized eggs are pelagic, measure about 1 mm in diameter, and have a single oil droplet about 0.22 mm in diameter (Guitart-Manday and Juárez-Fernandez 1966). Artificially fertilized eggs in seawater of 32 parts per thousand salinity or above are neutrally or positively buoyant and measure 0.86-1.0 (mean 0.92mm) in diameter, with a single oil globule averaging 0.24 mm (Colin 1992, Powell and Tucker 1992). Based on laboratory studies with a similar grouper egg, Colin (unpub. data, cited in Colin 1992) estimated an ascent rate of 110 mm/min for fertilized eggs. At this rate, eggs should reach the surface in 3-5 hours when released at 20-30 m deep. Following voluntary spawning under artificial conditions, sperm were collected and described as having a piriform (pear-shaped) cephalic portion and an extraordinarily long tail (Guitart-Manday and Juarez-Fernandez 1966).

Buoyant eggs hatch 23 to 40 hours following fertilization. Embryonic development of eggs produced in a Havana aquarium was followed from fertilization to absorption of the yolk sac at 2.8mm TL (72 hours); eggs hatched in about 40 hours at 25°C (Guitart-Manday and Juarez-Fernandez 1966). Artificially fertilized eggs hatched within 27-29 hours of fertilization at 25°C, 23-25 hours at 28°C (Powell and Tucker 1992), and 24 hours in ambient (25.2-26.2°C) water temperature (Colin 1992). The pelagic larvae begin feeding on zooplankton approximately 2 - 4 days after hatching (Tucker and Woodward 1994). The larvae develop elongate dorsal and pelvic fin spines for buoyancy and protection that are reabsorbed prior to transformation.

### ***Nassau Grouper Larval Stage***

Grouper larvae are usually rare in ichthyoplankton samples, but are characterized by having a very short and stout first dorsal spine; an elongate and serrate second dorsal spine with a modified and serially associated (first) pterygiophore; elongate and serrate pelvic-fin spines; a moderately-deep, laterally compressed body; and 24 myomeres. The third dorsal spine may be elongate in some species. Larvae have a small, triangular gut and pigmentation dorsally over the visceral mass varies. The head and mouth are large, and the eye round. Head pigmentation is sparse and generally confined to the mid and hind-brain areas. All members of the subfamily Epinephalinae have spines on the preopercle, posttemporal, and supracleithrum bones (Leis 1986), and all but the genus *Gonioplectrus* have spines on the interopercle and subopercle (Kendall & Fahay 1979, Baldwin et al. 1991). The spine at the angle of the preopercle is long and serrate. Larvae of some species have pigment laterally on the caudal peduncle, and those of the genus *Mycteroperca* and a few species of the genus *Epinephelus* also have pigment at the cleithral symphysis. The second and third spines of the dorsal fin, and pelvic spine have consistent spinelet morphology, which together with numbers of dorsal- and pectoral-fin elements, may be useful in identifying grouper larvae as small as 4-5 mm SL to genus and some of the genus *Epinephelus* to species (Johnson & Keener 1984).

Larvae of most specimens should be cleared and stained to assist in making accurate counts and characterizing spinelet morphology due to morphological similarity among taxa

(Richards et al. 2005). The long dorsal and pelvic spines are fragile and few specimens have spines intact, which makes identification problematic if meristics and spinelet morphology cannot be assessed. Richards et al. (2005) provide a provisional key to discriminate larvae of some to species or species groups.

Larval and early juvenile phases are well described for the Nassau grouper because of successful captive fertilization and spawning. Newly hatched larvae collected from induced spawning measured 1.7-1.8 mm notochord length (NL) (Powell and Tucker 1992). Larvae had pigmented eyes 48 hours post-hatching and began feeding within 60 hours (Tucker et al. 1991). Development has been described for laboratory-reared specimens from the egg to a 13.5mm SL larva approximately 40 days posthatching (Powell and Tucker 1992) (Figs. 13A- 13G in Sadovy and Eklund 1999). Fins develop in the order of pelvic, first dorsal, caudal, pectoral, anal, and second dorsal. The adult complement of principal caudal fin rays was attained at 6.0mm SL and of dorsal spines at the postflexion stage at approximately 6.6mm SL with completion of first and second dorsal and anal fins at 7.4mm SL. Preflexion larvae become flexion larvae over the range of 5.0- 5.4mm NL and flexion to postflexion occurs between 6.0 and 6.5mm NL (Powell and Tucker 1992). Larvae were planktonic until 42- 70 days post-hatching with transformation occurring in less than one week (Powell and Tucker 1992, Tucker and Woodward 1994).

Newly hatched larvae are inconspicuously pigmented and slightly curved around the yolk sac when artificially reared (Powell and Tucker 1992). Wild-caught larvae exhibit several small, dendritic melanophores on the snout (Smith 1971, Laroche<sup>10</sup>). Yolk-sac larvae with a developing mouth have a characteristic pigment pattern in the form of a distinct “inverted saddle” on the ventral midline and lateral surface of the caudal peduncle (Powell and Tucker 1992) and specimens <21 mm SL also lack the caudal peduncle blotch which is found in all fish >35 mm (Smith 1971). Pigment patterns change markedly during the flexion stage, and young postflexion larvae (<6.8 mm SL) are similar to late flexion larvae. In small juveniles there is a characteristic line of black spots along the bases of the dorsal rays posterior to the fifth spine (Smith 1961). The pattern of vertical bars seems to develop at about 40mm in specimens from the Bahamas (Smith 1961).

Preflexion and flexion epinephelinae larvae are difficult to identify positively as *Epinephelus striatus*, although certain combinations of pigment, fin spinelets, and spine lengths narrow down possibilities (Kendall 1979, Johnson and Keener 1984, Powell and Tucker 1992). With postflexion larvae greater than 7.4 mm SL it is possible to separate Nassau grouper from other groupers, except for *E. adscensionis*, on the basis of dorsal and anal fin ray counts, spinelet configuration, second first-dorsal-fin spine length relative to SL, and capture location (Powell and Tucker 1992).

Larvae attain a maximum size of 30 mm SL (average 23.4 mm) by 36 days after presumptive spawning (Shenker et al. 1993). Larvae collected 10 days after probable spawning

---

<sup>10</sup> Laroche, Wayne. Stonefish Environmental and Taxonomic Services, Box 216, Enosburg Falls, VT 05450. Unpubl. data.

measured 6-10 mm SL. Over a 15-day period, 8-22 days after the full moon, larval sizes increased from 5.7 to 10 mm SL (Greenwood 1991, Shenker et al. 1993). Pelagic juveniles were collected up to 46 days following a presumptive spawning moon, and benthic juveniles were first found on artificial and natural reefs at 47 days. Pelagic juveniles taken in channel nets just prior to settlement measured 22-27 mm SL (Colin 1992, Colin et al. 1997). Transition from larval to juvenile phases occurs at 6-7 weeks for wild fish and 6-10 weeks for fish raised under artificial conditions from induced spawns. The wild-caught larvae grew more slowly than larvae from induced spawns (Shenker et al. 1993, Tucker and Woodward 1994, Colin et al. 1997). From hatchery studies, larval duration is estimated to range between 25 and 75 days (Leis 1987, Tucker and Woodward 1994). Otolith analysis of newly settled juveniles in the Bahamas estimated pelagic larval duration as ranging from 37 to 45 days (Colin et al. 1997).

Presumptive daily increments in lapilli of wild-caught larvae indicate a larval period of 35- 40 days and support fertilization at the full moon. A mean larval period of 41.6 days was indicated from net-caught samples (Colin 1992, Colin et al. 1997). Presettlement otolith increments were distinct and easily counted, however, settlement marks were not as apparent. It was assumed that the first otolith increment forms after yolk absorption, at least 4 days post-fertilization and three days post-hatch, since larvae reared in aquaria up to the stage of yolk sac absorption showed no evidence of increment formation (Colin et al. 1997).

Larvae of *Epinephelus striatus* cannot be distinguished from *E. adscensionis* (rock hind) meristically as counts and pigmentation are nearly identical. Both *Epinephelus striatus* and *E. adscensionis* have small, simple, and straight spinelets, and cannot be separated from *E. morio* (red grouper), *E. guttatus* (red hind) and *E. drummondhayi* (speckled hind) until development of the anal fin is complete (Richards et al. 2005).

*Larval distribution and recruitment.* Nassau grouper larvae are rarely reported from offshore waters (Leis 1987) and little is known of their movements or distribution, other than limited data on settlement patterns. After a mean 35-40 day pelagic larval period, larvae recruit from an oceanic environment into demersal, bank habitats through tidal channels (Colin 1992). This recruitment process can be brief and intense, and is apparently driven by prevailing winds, currents, and lunar phase (Shenker et al. 1993). Pelagic larvae were collected 0.8-16 km off Lee Stocking Island, Bahamas, at night, at 2-50m depths and from tidal channels leading onto the Exuma Bank during the day (Greenwood 1991). However, the link between spawning sites and settlement sites is not well understood. Larval sampling adjacent to a spawning aggregation at Mahahual, Mexico (Vásquez-Yeomans et al. 1998) failed to capture even one Nassau grouper larvae. By way of explanation, the authors questioned both their methodology and the robustness of the local spawning as additional explanations.

The geomorphology of spawning sites has led researchers to assume that offshore transport was a desirable property of selected sites. However, currents in the vicinity of aggregation sites do not necessarily favor offshore egg transport, leaving open the possibility that some stocks are at least partially self-recruiting. For example, drogues (floats which drift with

water currents) deployed near the point of gamete release at eastern Long Island, Bahamas, moved little from the shelf edge for several days immediately following spawning and one ended up inshore (Colin 1992). In similar studies around a spawning aggregation site at Little Cayman, surface velocity profile drifters released on the night of peak spawning showed significant eddy formation so that drifters tended to remain near or return to the spawning reef but drifters released on the days preceding tended to move away in more of a straight line with the dominant currents (Heppell *et al.* 2011). Additional research is needed to understand these spatial dynamics.

Data on recruitment of larvae onto reefs suggest that their onshore transport can rely heavily on cross-shelf winds and currents and occurs in short pulses during highly limited periods each year (Shenker *et al.* 1993). Recruitment of Nassau grouper larvae occurs at an average of 32 mm TL (Eggleston 1995) and was monitored for a 75-day period from mid-December through February using channel nets suspended in tidal passes between islands on the edge of the Exuma Sound, Bahamas. Assuming that the full recruitment window was sampled, 86% of the total annual recruitment of Nassau grouper occurred in this area during a single 4-day storm, while another 10% recruited during a second storm event. During the sampling period, 13% of all larvae sampled were Nassau grouper, which recruited during particularly short, discrete pulses when compared to other taxa taken throughout the study. While early recruitment occurs into both coral-macroalgae and seagrass beds, subsequently higher abundances in coral-macroalgae are probably due to a combination of active selection for coral-macroalgae and high post-settlement predation in seagrass (Nadeau and Eggleston 1996).

### 1.b. Taxonomy and distinctive characteristics

**Phylum:** Chordata

**Class:** Actinopterygii

**Order:** Perciformes

**Family:** Serranidae

**Subfamily:** Epinephelinae

**Genus:** *Epinephelus*

**Species:** *striatus*

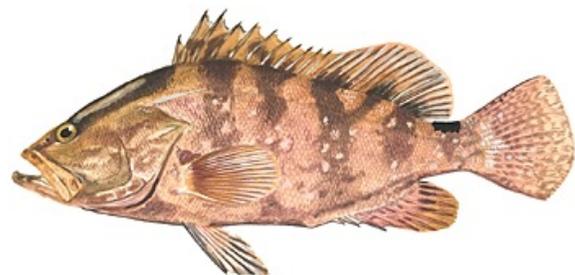


Figure 6. Nassau grouper adult

Recent genetic taxonomy suggests that family groupings may be challenged (Craig and Hastings 2007, Craig *et al.* 2001), however, previous descriptions are presented until modifications are widely accepted.

Reaching a maximum size of 122cm (48in) total length (TL) (Humann and Deloach 2002, Froese and Pauly 2010) and maximum weight of 25 kg (Heemstra and Randall 1993), the Nassau grouper is one of the larger serranids of the tropical Western Atlantic and Caribbean and can live for nearly 3 decades. Similar to many other grouper species, Nassau grouper juveniles

and adults are known for their large gapes and protruding jaws, which, when opened rapidly, produce suction that facilitates feeding. The Nassau grouper can be distinguished from other groupers at all life history phases by the characteristic vertical bar pattern and dark “saddle” coloration along the dorsal part of the caudal peduncle.

Smith (1971) identified an “*Epinephelus striatus* Species-Group” comprised of *E. striatus*, *E. guttatus* (red hind), *E. morio* (red grouper): “*E. striatus* and *E. guttatus* are so similar that sun-bleached display specimens are difficult to identify although there are several meristic characters that can be used to separate them. Red grouper (*E. morio*) differs in fin outlines but otherwise strongly resembles the other two species. They are all moderately large fishes with tapering and somewhat compressed body outlines. Red grouper has spotted and barred transient color phases and individuals in these color phases bear a remarkable resemblance to Nassau grouper. This is reflected in the Bermudan common name deer hamlet for *E. morio*, contrasting with hamlet (without a modifier) for *E. striatus*. These three species are certainly close to each other and well separated from other American groupers.”

The following descriptions are based predominantly on Smith (1971), Acero et al. (1991), and Heemstra and Randall (1993), as presented in Sadovy and Eklund 1999:

The Nassau grouper, *Epinephelus striatus* (Bloch 1792), is a moderate sized *Epinephelus* with large eyes and a robust body. Body depth is distinctly less than head length, depth contained 2.6 to 2.9 times in SL (for fish 160 to 330mm SL). Head length contained 2.4 to 2.6 times in SL; interorbital convex; preopercle evenly serrate, without salient angle; posterior nostrils somewhat enlarged and elongated or comma-shaped in large adults. Ground color generally buff, with 5 dark brown vertical bars and a large black saddle blotch on top of caudal peduncle; a row of black spots below and behind eye. Distinctive dark tuning-fork mark beginning at front of upper jaw, extending dorsally along interorbital region, and bifurcating on top of head behind the eyes; another dark band from tip of snout through eye and then curving upward to meet its fellow just before dorsal-fin origin. Some fish have irregular pale spots and blotches all over the head and body; specimens from deep water are somewhat pinkish or reddish ventrally. The inside of the mouth is red, the teeth are caniniform and villiform and are in two series in each jaw (Smith 1978). The range of color is wide. Color pattern can change within minutes from almost white to bicolored to uniformly dark brown, according to the behavioral state of the fish (Longley 1917, Colin 1992, Heemstra and Randall 1993, Carter et al. 1994). A distinctive bicolored pattern is seen when two adults or an adult and large juvenile meet and is frequently observed in spawning aggregations (Heemstra and Randall 1993). Only dots around the eyes and the blotch on the caudal peduncle do not change (Smith 1971). Juveniles exhibit a color pattern similar to adults (e.g., Silva Lee, 1977).

### 1.c. Range wide distribution

The Nassau grouper's confirmed distribution currently includes "Bermuda and Florida (USA), throughout the Bahamas and Caribbean Sea (Fig 7) (Smith 1971, Acero and Garzon-Ferreira 1991, Heemstra and Randall 1993, Cervigon 1994). The previous report of *E. striatus* from the Brazilian coast south of the equator (Fig. 414 (distribution map) in Heemstra and Randall 1993, p. 237) is unsubstantiated" (Craig et al. 2011). The Nassau grouper has been documented in the western Gulf of Mexico, to the west off the Yucatan Peninsula, Mexico, at Arrecife Alacranes (north of Progreso) (Hildebrand et al. 1964). It was cited as a rare or transient species in the northwestern Gulf of Mexico, off Texas (Gunter and Knapp 1951 in Hoese and Moore 1977) although this has not recently been verified. Nassau grouper is generally replaced ecologically in the eastern Gulf by *Epinephelus morio* (Smith 1971) in areas north of Key West or the Tortugas. Many of the earlier descriptions extend the range up the Atlantic coast to North Carolina but confirmation is currently lacking.

The Nassau grouper is listed as "Native" to the following countries/states (Cornish and Eklund 2003.): Anguilla; Antigua and Barbuda; Aruba; Bahamas; Barbados; Belize; Bermuda; Cayman Islands; Colombia; Costa Rica; Cuba; Curaçao; Dominica; Dominican Republic; French Guiana; Grenada; Guadeloupe; Guatemala; Guyana; Haiti; Honduras; Jamaica; Mexico; Montserrat; Netherlands Antilles (Curaçao); Nicaragua; Panama; Puerto Rico; Saint Kitts and Nevis; Saint Lucia; Saint Vincent and the Grenadines; Suriname; Trinidad and Tobago; Turks and Caicos Islands; United States (Florida); United States Minor Outlying Islands (Caribbean:

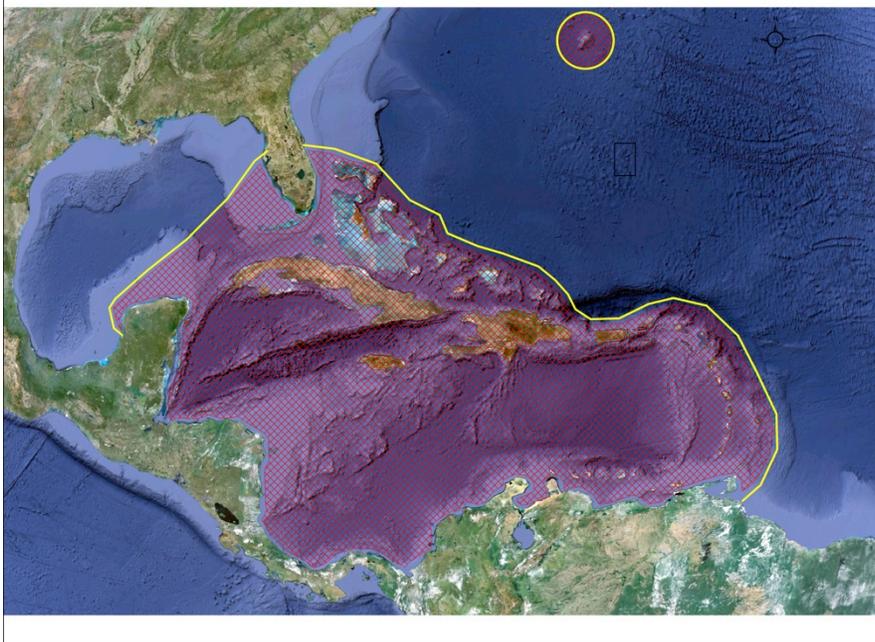


Figure 7. Range of Nassau grouper (*Epinephelus striatus*). Habitat zones include shoreline to insular or continental shelf throughout the indicated range.

i.e., Navassa Island); Venezuela; Virgin Islands, British; Virgin Islands, U.S.

#### 1.c.i. Historical Distribution

Nassau grouper otoliths have been retrieved from a variety of sites (middens) in prehistoric fishing communities of the Caribbean, and the species represented an

important component of these communities.

Otoliths were relatively

abundant at sites on eastern Antigua (AD 500-1150), in Grenada (AD 0-500, AD 1000-1500), San Salvador, Bahamas (AD 850-1100), St. John, Virgin Islands (AD 700-1200), Florida west coast (2000-1000 BC, AD 150-300, AD 400-1000), St. Lucia, West Indies (AD 0-1500) and on the north coast of Jamaica (no date) (Wing et al. 1968 and Wing and Reitz 1982, as cited in Sadovy and Eklund 1999).

### **1.c.ii. Influences on Distribution**

Primary determinants of distribution in Nassau grouper are not known although water clarity, habitat, and substrate type appear to be important (Smith 1971, Eggleston 1995). This species is most abundant in clear waters on high-relief coral or rocky reefs. Small juveniles are associated with macroalgae, seagrass beds, or *Porites* clumps. The mean depth range of the Nassau grouper (0-130 m) may be influenced more by the availability of suitable habitat than by food resources, since diet is highly varied and more a function of body size than of water depth.

Despite adults migrating long distances to reach spawning sites (Starr et al. 2007), proximity to these sites during non-reproductive periods is apparently not critical although the aggregation sites themselves may be essential for reproduction either because of physical characteristics of the substrate or because of the oceanographic conditions at the site. The loss of local stocks in a number of insular areas (e.g. Bermuda and Puerto Rico) suggests that some populations are partially self-recruiting, although further genetic studies are necessary to test this hypothesis (Sadovy 1993).

## **1.d. Biological characteristics**

### **1.d.i. Age, growth and mortality**

Growth in Nassau grouper has been examined by size-frequency analyses, tagging studies, field observations, and reading annular rings in sagittal otoliths (Table 3, Fig. 8). Most studies indicate rapid growth, about 10mm/month for small juveniles. Mean monthly growth of Nassau juveniles 30-270 mm TL on artificial and natural reefs in the Virgin Islands was 8.4 to 11.7 mm/month, determined during six visual censuses over 11 months, (Beets and Hixon 1994). Similarly, juveniles sampled at Lee Stocking Island in the Bahamas grew at about 10 mm/month between 32 and 85 mm TL (Eggleston, 1995). Near sexual maturity at about 4-7 years, growth slows to about 2mm/month, with lower rates in larger or sexually mature fish (Bush et al. 2006).

Marginal increment analysis of sagittal otoliths suggested that growth zones were formed annually and that annual increment deposition occurred from April to May in Cuba (Claro et al. 1990). The growth zones deposited in otoliths were validated as annual using oxytetracycline (OTC) marking techniques; otolith legibility was approximately 80- 95% (Bush et al. 1996).

Data from scales and otoliths indicate that fish reach 400-450 mm SL (*i.e.*, sexual maturity) in approximately 4-7 years. However, estimates of size-at-age derived from length-

frequency data (Table 3) suggest more rapid growth (Olsen and LaPlace 1979). This apparent discrepancy between otolith- and length-based methods of age determination could result from

**Table 3. Size at age data for Nassau grouper (from Sadovy and Eklund 1999; “Bush et al., in press” should refer to Bush et al. 2006).**

*Epinephelus striatus* size-at-age data for ages 1-13 years. All lengths are in mm (standard/SL or total/TL lengths as indicated). Ageing method is given.

Source	Age (years)												
	1	2	3	4	5	6	7	8	9	10	11	12	13
a	293	354	390	464	537	561	634	659	-	-	-	-	-
b	160	270	-	410	480	540	570	600	640	650	660	700	710
c	175	253	309	358	401	436	468	497	519	542	563	580	591
d	174	254	315	366	414	451	483	518	559	583	594	617	-
e	235	370	435	500	543	605	660	720	760	800	-	-	-

a: Buesa, 1987; Cuba, aged by scales/TL.

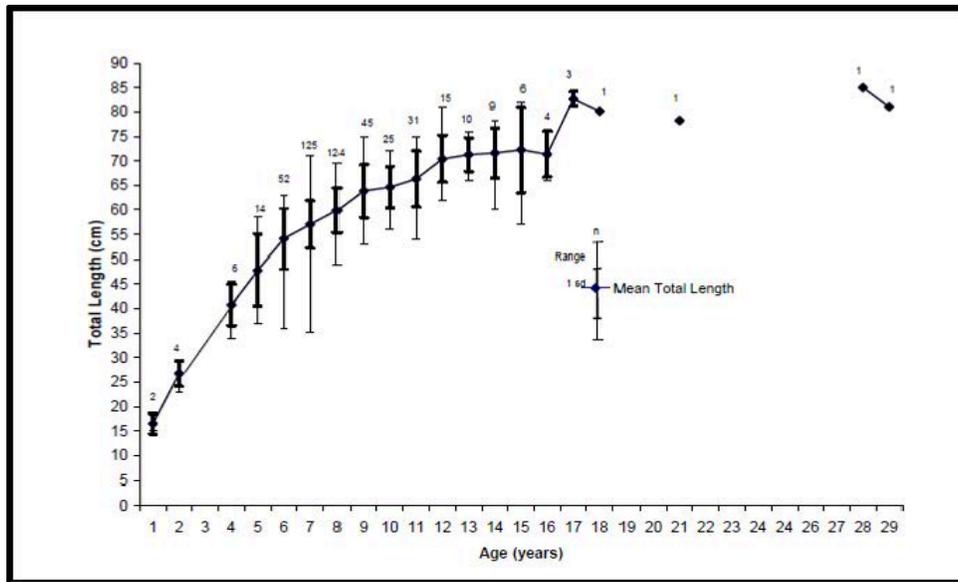
b: Bush et al., in press; Cayman Islands, aged by otoliths/TL lengths estimated from observed growth curve.

c & d: Claro et al., 1990; SW and NE Cuba, respectively, fish from both areas were aged by otoliths and backcalculation/TL.

e: Olsen and LaPlace, 1979; Jamaica, aged by length-frequency data/SL.

the unavailability of age class-1 individuals, resulting in older (*i.e.*, age 2+ years) individuals designated as age 1 year class (Sadovy and Eklund 1999). Moreover, length frequency analysis can be less reliable for long-lived species than otolith-based studies as older cohorts soon begin to merge into each other obscuring individual age classes.

Von Bertalanffy growth parameters derived for the Nassau grouper with the Brody growth coefficient (K) range from 0.063- 0.185 (Table 4).



**Figure 8. Growth curve for Nassau grouper sampled from aggregations between 1987 and 1992 in the Cayman Islands (from Bush et al, 2006)**

**Table 4. Von Bertalanffy growth equation parameters for Nassau grouper.**

Von Bertalanffy growth equation parameters for Nassau grouper, *Epinephelus striatus*. Standard equation for length-at-age is:  $L_t = L_\infty (1 - e^{-K(t-t_0)})$ . Lengths are in cm (length type indicated).

Source & method	Locality	Length type	Parameter		
			$L_\infty$	$t_0$	K
Olsen & LaPlace, 1979	Virgin Islands	SL	97.4	0.488 <sup>1</sup>	0.185
Claro et al., 1990	Cuba (SW)	TL	94.0	-3.27	0.063
	Cuba (NE)		76.0	-1.12 <sup>2</sup>	0.127
Thompson & Munro, 1978	Jamaica	TL	90.0 <sup>3</sup>	-	0.090
Baisre & Páez, 1981	Cuba	-	92.8	-	0.100

<sup>1</sup> Appears also as  $t_0 = -0.488$  in some places.

<sup>2</sup> Appears also as -4.13 in Abstract.

<sup>3</sup>  $L_\infty$  assumed, based on tagging data from Randall, 1962, 1963.

Growth rates were also determined in field observations and tagging studies. In the Virgin Islands, animals tagged for less than 300 days yielded the following growth rates: 175-250 mm TL grew about 4.55 mm/month; 251-325 mm TL about 3.5 mm/month; 326-451 mm

**Table 5. Age and size parameters for Nassau grouper. [excerpt from Sadovy and Eklund 1999: Bush et al, in press refers to Bush et al, 2006, CFMC footnote 26 refers to CFMC 1985, SAFMC footnote 24 refers to SAFMC 1983]**

<i>Epinephelus striatus</i>	
Age and length at maturity	5 yrs, 580 mm SL (Virgin Islands) (Olsen and LaPlace, 1979)  420-450 mm SL females 400-450 mm SL males 4+ yrs (Cayman Islands) (Colin et al., 1987; Bush et al., in press) 500 mm TL (minimum size ripe males) (Cayman Islands) (Tucker et al., 1993) 425 mm SL females; 402 mm SL males, immatures are 3-6 yrs (otolith growth zones not validated) (Bahamas) (Sadovy and Colin, 1995) 483 mm TL (North Carolina-Florida) (SAFMC, text footnote 24) 480 mm TL (Jamaica) (Thompson and Munro, 1978)
Age and length at first capture	< 300 mm TL & 4-5 yrs (Virgin Islands) (Olsen and LaPlace, 1979; CFMC, text footnote 26) 6-7 yrs (Cayman Islands) (Bush et al., in press) 275-625 mm TL (mean = 570) (Jamaica) (Thompson and Munro, 1978) 300-500 mm TL depending on size limits (North Carolina-Florida) (SAFMC, text footnote 46) 450 mm TL (South Florida) (Bohnsack, 1990)
Maximum age and length	1200 mm TL (CFMC, text footnote 26) 9 yrs, 910-960 mm SL (Olsen and LaPlace, 1979) (Virgin Islands) 17 yrs, 710 mm TL, 6700 g (Cuba) (Claro et al., 1990) 755 mm SL (Bermuda) (Bardach et al., 1958) 840 mm TL (Jamaica) (Thompson and Munro, 1978) 640 mm TL (Netherlands Antilles) (Nagelkerken, 1981) 29 yrs, 850mm FL (Cayman Islands) (Bush et al., in press)

TL about 1.92 mm/month (Randall 1962, 1963, Table 8 in Sadovy and Eklund 1999). However, growth rates were evidently underestimated because of growth suppression due to tagging (Thompson and Munro 1978). Fish that remained in the field for 313 to 737 days had higher growth rates, varying from 4 to 6.6 mm/month for fish in the 256-380 mm TL size. Growth in Nassau grouper was also measured by calculating weight increments of marked fish in the field: weight increase for 7 individuals in the 700 g size class was 20-50% per year with an average of 38% (Bardach and Menzel 1957) however, the authors suggested a decline in growth rate after jaw tags were applied when data were compared to dart-tagged fish. Age-size parameters are presented in Table 5 and length-weight relationships for standard, total, and fork lengths, and TL-SL relationships are shown in Table 6.

**Table 4. Length-weight and length-length conversion parameters for Nassau grouper (excerpt from Sadovy and Eklund 1999).**

Length-weight and length-length parameters for *Epinephelus striatus* and *E. itajara*. The length-weight relationship is defined as:  $W=aL^b$ , where L is length (standard/SL, fork/FL or total/TL, as indicated) in mm and W is body weight in grams (guttled, G, or unguttled, UG, as indicated- where known). The standard length-total length relationship is defined as:  $TL=a+bSL$ .

Locality	Restrictions <sup>1</sup>	Parameter		Source
		a	b	
<b>Length-weight</b>				
<i>Epinephelus striatus</i>				
Virgin Islands	180-760 (SL) n=241	0.0097	3.23	Olsen and LaPlace, 1979
(St. Thomas/St. John)	330-770 (SL) n=73	$1.43 \times 10^{-6}$	3.38	Bohnsack and Harper, 1988 (UG)
Puerto Rico	210-645 (FL) n=60	$1.26 \times 10^{-5}$	3.04	Bohnsack and Harper, 1988 (UG)
Cuba (NE)	n=75 (TL)	0.1980	2.98	Claro et al., 1990
Cuba (SW)	n=270 (TL)	0.0052	3.30	Claro et al., 1990
Jamaica	325-825 (TL) n=112	0.0107	3.11	Thompson and Munro, 1978 (UG)
Belize	180-802 (SL) n=930	0.0107	3.08	Carter et al., 1994 (UG implied)
Florida	203-516 (TL) n=9	$3.8 \times 10^{-6}$	3.23	Bohnsack and Harper, 1988 (UG)
Bahamas	174-724 (SL)	$2.14 \times 10^{-5}$	3.03	Sadovy and Colin, 1995 (UG)
<b>Total length-standard length</b>				
<i>Epinephelus striatus</i>				
Cuba	n=330	2.24	1.11	Claro et al., 1990
Jamaica	430-750 n=26	3.00	1.09	Thompson and Munro, 1978
Bahamas	174-695 n=33	2.81	1.13	Sadovy and Colin, 1995

<sup>1</sup> Restrictions are upper and lower sizes in samples analyzed.

**Longevity.** The maximum age recorded for Nassau grouper is 29 years, using sagittal otoliths from the Cayman Islands (Bush *et al.* 1996, 2006) (Fig. 8). Using length-frequency analysis, which tends to exclude younger animals, a theoretical maximum age at 95% asymptotic size is 16 years. Other maximum age estimates include individuals of up to 9 years in the heavily exploited Virgin Islands fishery (Olsen and LaPlace 1979), 12 years in northern Cuba, 17 years in southern Cuba (Claro *et al.* 1990), and 21 years from the Bahamas, assuming, as demonstrated in some locations, that rings are formed annually (Sadovy and Colin 1995). These differences in maximum age estimates are due to the samples available for aging and methodological differences. Individuals of more than 12 years of age are not common in fisheries, with more heavily fished areas yielding much younger fish on average. Generation time (the average age of parents in the population) is estimated as 9-10 years based on average fish size from an unexploited aggregation in Belize, the growth curve from the five Cayman Island spawning aggregations, and the SL-TL conversion curve from Sadovy and Colin (1995).

**Mortality rates.** Estimates of natural mortality (M), based on length-frequency data from Nassau grouper taken on unexploited banks in Jamaica, ranged from 0.17 to 0.30 (Thompson and

Munro 1978). Total mortality ( $Z$ ), using length frequency data, was estimated at 0.55 in Cuba. With a low natural mortality ( $M$ ) determined to be 0.18, this indicates a fishing mortality ( $F$ ) of 0.37 (Baisre and Paez 1981).

### **1.d.ii. Ecological Roles**

*As Prey.* Information on predation upon groupers is largely lacking, although sharks were reported to attack Nassau groupers at spawning aggregations in the Virgin Islands (Olsen and LaPlace 1979) and there is one report of cannibalism in this species (Silva Lee 1974). No predation was observed on spawning fish in the Bahamas, despite the presence of sharks in the area (Colin 1992). One mutilated fish was recovered, possibly attacked by a barracuda or shark following release of tagged, laboratory-reared, naive individuals onto a reef in the Virgin Islands (Roberts et al. 1995). Early post-settlement juvenile preferences for macroalgae rather than seagrass beds are probably related, in part, to higher levels of predation in seagrass beds (Nadeau and Eggleston 1996). Reports of lionfish predation on small reef fish and small life stages are a concern throughout the Caribbean as the invasive spread has widened (Albins and Hixon 2008).

*As Competitors.* Little is published on either intra- or inter-specific competition in Nassau grouper. Juveniles exhibit aggression towards similar-sized conspecifics and display interspecific aggression (Dunham<sup>11</sup>). When two non-reproductive adults, or an adult and large juvenile, encounter one another, the smaller fish acquires the bicolor pattern described for aggregating fish in apparent submission, then turns laterally and usually swims away (Colin 1992, Colin<sup>12</sup>).

*As Predators.* The Nassau grouper is a top-level predator on coral reefs. Nassau grouper are unspecialized-ambush-suction foragers (Randall 1965, Thompson and Munro 19778) that swallow prey whole (Werner 1974, 1977). Numerous studies describe Nassau grouper as piscivorous as adults (Randall and Brosk 1960, Randall 19645, Randall 1967, Parrish 1987, Carter et al. 1994, Eggleston et al. 1998). This species takes many types and sizes of food and moves among different habitats, such as seagrass beds and coral reefs, at different life-history stages or reproductive phases, or while hunting.

---

<sup>11</sup> Dunham, Jason. Caribbean Marine Research Center, c/o Florida State Marine Laboratory, Rte. 1. Box 456, Sopchoppy. FL 32358. Unpubl. report to the Caribbean Marine Research Center, 29 March, 1989.

<sup>12</sup> Colin, Pat. 1990. Coral Reef Research Foundation, P.O. Box 1765, Koror. Palau 96940. pers. comm.

Groupers are unspecialized, bottom-dwelling, solitary predators (Randall and Brock 1960, Randall 1965, 1967). Feeding takes place throughout the diel cycle although most fresh food is found in stomachs collected in the early morning and at dusk (Randall 1967). Empty stomachs were also noted throughout daylight hours (Silva Lee 1974). Individuals feed by

**Table 5. Food items recorded in the stomachs of Nassau grouper.**

Food items recorded in the stomachs of the Nassau grouper, *Epinephelus striatus* (from Randall, 1965, 1967; Silva Lee, 1974; Claro et al., 1990; Carter et al., 1994).

Nekton	Mullidae	Benthic animals
Fishes	<i>Pseudupeneus maculatus</i>	Molluscs
Acanthuridae	Muraenidae	Gastropods
<i>Acanthurus</i> sp.	<i>Gymnothorax moringa</i>	<i>Strombus gigas</i>
<i>Acanthurus coeruleus</i>	<i>Gymnothorax</i> sp.	<i>Strombus</i> sp.
Apogonidae	<i>Enchelycore nigricans</i>	<i>Fasciolaria tulipa</i>
Atherinidae	<i>Lycodontis moringa</i>	Bivalves
Balistidae	<i>Muraena miliaris</i>	<i>Barbatia cancellaria</i>
<i>Balistes vetula</i>	<i>Muraena</i> sp.	Pelecypods
Bothidae	Ostraciidae	Crustaceans
Carangidae	<i>Lactophrys</i> sp.	Isopods
<i>Caranx ruber</i>	Pomacentridae	Stomatopods
Clupeidae	<i>Chromis cyanea</i>	<i>Gonodactylus perstedii</i>
<i>Harengula humeralis</i>	<i>Chromis multilineata</i>	<i>Pseudosquilla ciliata</i>
<i>Harengula clupeola</i>	<i>Pomacentrus fuscus</i>	<i>Squilla</i> sp.
<i>Jenkinsia lamprotaenia</i>	<i>Pomacentrus</i> sp.	Shrimps/prawns
Gerreidae	<i>Abudefduf saxatilis</i>	Alpheids
<i>Gerres cinereus</i>	<i>Microspathodon chrysurus</i>	Carideans
Haemulidae	Priacanthidae	Penaeids
<i>Haemulon aurolineatum</i>	<i>Priacanthus cruentatus</i>	Lobsters
<i>Haemulon flavolineatum</i>	Scaridae	<i>Panulirus argus</i>
<i>Haemulon album</i>	<i>Sparisoma aurofrenatum</i>	<i>Panulirus guttatus</i>
<i>Haemulon sciurus</i>	<i>Sparisoma rubripinne</i>	<i>Justitia longimana</i>
<i>Haemulon plumieri</i>	<i>Sparisoma chrysopterum</i>	<i>Palinurellus gundlachi</i>
<i>Haemulon</i> sp.	<i>Sparisoma</i> sp.	Hermit crabs
Holocentridae	<i>Scarus vetula</i>	<i>Paguristes depressus</i>
<i>Sargocentron vexillarium</i>	<i>Scarus croicensis</i>	<i>Petrochirus diogenes</i>
<i>Myripristis jacobus</i>	<i>Scarus</i> sp.	Crabs
<i>Holocentrus rufus</i>	Serranidae	<i>Calappa flammea</i>
<i>Holocentrus</i> sp.	<i>Hypoplectrus puella</i>	<i>Calappa</i> sp.
Labridae	<i>Cephalopholis fulva</i>	<i>Stenorhynchus seticornis</i>
<i>Halichoeres garnoti</i>	<i>Epinephelus striatus</i>	<i>Mithrax verrucosus</i>
<i>Halichoeres bivittatus</i>	Synodontidae	<i>Mithrax cinctimanus</i>
<i>Halichoeres</i> sp.	<i>Synodus intermedius</i>	<i>Mithrax</i> sp.
<i>Hemipteronotus</i> sp.	<i>Synodus</i> sp.	<i>Macrocoelema</i> sp.
<i>Clepticus parrae</i>	Urolophidae	<i>Petrolisthes galathinus</i>
Lutjanidae	<i>Urolophus jamaicensis</i>	<i>Chronus ruber</i>
<i>Lutjanus synagris</i>	Molluscs	<i>Portunus sebae</i>
<i>Lutjanus</i> sp.	Squids	<i>Portunus</i> sp.
<i>Ocyurus chrysurus</i>	<i>Loligo</i> sp.	Xanthids
Monacanthidae	Cuttlefish/octopi	Grapsids
<i>Monacanthus ciliatus</i>		
<i>Monacanthus</i> sp.		
<i>Cantherines pullus</i>		

rapidly dilating the gill covers to engulf prey by suction (Thompson and Munro 1978, Carter 1986) and take a wide variety and size range of fishes and invertebrates, both benthic and pelagic (Tables 7 and 8). With increasing age, there is a shift from consuming crustaceans to taking fishes, larger bivalves, lobster, and gastropods (e.g. Eggleston et al. 1998). However, the relationship between fish size and prey size shows much variation, with large fish eating small prey and vice versa. One report documented a 580 mm FL Nassau grouper swallowing a 620

mm *Gymnothorax*; but overall, mean prey size was about 15% of the Nassau grouper FL (Silva Lee 1974). Four studies provide a feeding profile of the Nassau grouper (Table 7). Fish predominated, with scarids and labrids most commonly identified, possibly because the former can be readily recognized from stomach contents by their unique dentition (Randall 1965). Crabs were the most common invertebrates. Although hermit crabs and the operculae of *Strombus* and *Fasciolaria* were found, stomachs did not contain shells. In one Cuban study, the most abundant items (by weight) were grunts, parrotfishes, and octopus with a suggestion that more grunts were taken in winter months (Claro *et al.* 1990).

**Table 6. Comparison of 4 studies of stomach contents of Nassau grouper.**

Principal categories of food items encountered in the stomachs of Nassau grouper, *Epinephelus striatus*, in four studies: (A) Virgin Islands (Randall, 1965, percent by volume); (B) Cuba (Silva Lee, 1974, percent frequency occurrence); (C) Cuba (Claro *et al.*, 1990, percent by weight); (D) Belize (Carter *et al.*, 1994, percent frequency occurrence).

Food category	A	B	C	D
Nekton, fish	53	39	71	58
Benthic, crustaceans				
crabs	23	29	8	16
stomatopods	6	3	<1	1
shrimp/prawn	5	8	<1	3
spiny lobster	4	6	4	6
hermit crab	1	<1	-	1
isopod	<1	<1	-	-
unidentified	1	4	-	3
Nekton, molluscs				
cephalopods	5	9	15	6
Benthic, molluscs				
gastropods	2	2	2	1
Unidentified	-	-	-	5

predators and are defended by long venomous fin spines, such that, even when sharks or large grouper do attack, they have been observed immediately retreating without obvious injury to the lionfish (Sadovy, pers. obs.). Nonetheless, there is a published report of fishermen in the Bahamas capturing one tiger grouper (*Mycteroperca tigris*) and two Nassau grouper (*E. striatus*), each with a lionfish in its stomach (Maljković *et al.* 2008). Subsequently, five Nassau groupers, *E. striatus*, caught off Eleuthera Island at an approximate depth of 14 m on 5 March 2008, were dissected. Two of the stomachs contained red lionfish. The first grouper (477-mm SL) contained a partially digested lionfish, identifiable only by the morphology and multiplicity of the remaining fin rays. The second slightly larger grouper (482-mm SL) contained a red lionfish of 137-mm SL, which was in almost pristine condition. Some of this feeding may result from attempt to condition local predators to feed on the non-native species. Divers in the Cayman Islands have trained wild Nassau grouper to consume lionfish, without the grouper showing ill

In Belize, the predominant food, by percentage frequency of occurrence, was fish, with a high percentage of crustaceans, especially crabs, and a small number of gastropods, cephalopods, and pelecypods. The principal prey fish families were grunts and snappers (Carter *et al.* 1994). Like other groupers, Nassau follow and feed with other predators, such as triggerfish, octopus, or eel (Carter *et al.* 1994, Sullivan and de Garine-Wichatitsky 1994, Roberts *et al.* 1995, Sadovy pers. obs.) presumably benefiting from spoils made available directly, or from disturbance of prey species.

Some anecdotal and photographic evidence provided by fishers and divers suggests that native grouper species are preying on the invasive red lionfish with some regularity. Lionfish are generally unfamiliar to local

effects (Sadovy pers. comm., Heyman, pers. obs.). Much of this feeding likely results from attempts to condition local predators to feed on the non-native species. Divers in the Cayman Islands have trained wild Nassau grouper to consume lionfish, without the grouper showing ill effects (Sadovy pers. comm., Heyman, pers. obs.). It is, however, uncertain whether large Atlantic groupers can effectively predators on the invasive lionfish. As related in Albins and Hixon (2011): “one large Nassau grouper that ate a large lionfish tail first appeared to be literally stunned (authors [Albins and Hixon] pers. obs.). Additionally, large and clearly hungry Nassau grouper held in tanks will not eat small lionfish (M. Cook<sup>13</sup> and W. Raymond<sup>14</sup> unpubl. data). In controlled field experiments, Nassau grouper have no effect on the growth and survival of small lionfish (T. J. Pusack<sup>15</sup> unpubl. data).

Just as adult Nassau groupers are unspecialized predators, early life-history stages exhibit a high degree of trophic plasticity with evidence of filter feeding, particulate feeding, and piscivory (Grover 1993, 1994). Pelagic-phase Nassau grouper feed on pteropods, amphipods, and copepods (especially *Corycaeus* spp.), which comprised approximately 40% of identifiable items found in one study (Greenwood 1991, Grover *et al.* 1998). Pelagic early-juvenile Nassau grouper (20.2-27.2 mm SL) take food items ranging from dinoflagellates ( $\pm 99\%$  by number) to fish larvae and mysids (28-79% by volume).

### **1.d.iii. Population connectivity/population genetics**

Limited work on genetic variability in the Nassau grouper suggests that, while gene flow occurs throughout much of its geographic range, the relative contributions of local and foreign recruitment to particular populations have yet to be determined (Hinegardner and Rosen 1972, Hateley 2005). Cellular DNA in Nassau grouper was reported to be 1.3 picograms (haploid), similar to that of other serranids and similar to the average value of a wide diversity of other percomorph fishes (Hinegardner and Rosen 1972). Hateley (2005) presented preliminary results on genetic variability in the Nassau grouper, based on enzyme electrophoresis. Clearly resolved enzyme phenotypes were obtained at 20 loci, of which 5 exhibited polymorphisms. On the basis of a sample of 264 individuals taken from Belize, Bahamas, Turks and Caicos, and Cayman Islands, intermediate to low levels of genetic variability were indicated; mean heterozygosity per locus was 0.024; proportion of polymorphic loci = 0.15, and the mean effective number of alleles was 1.45. There was no evidence for population sub-structuring by sex or small-scale spatial distribution, or for macrogeographic stock separation. The results were interpreted as being consistent with a single panmictic population within the northern Caribbean basin and suggested high gene flow in the region. However, because gel electrophoresis can detect only differences among samples and not similarities; it may not detect real inter-stock differences and more sensitive methods must be applied to increase resolution (Hateley pers. comm.).

---

<sup>13</sup> Megan Cook, Oregon State Univ. (Hixon Lab)

<sup>14</sup> Wendel Raymond, Oregon State Univ. (Hixon Lab)

<sup>15</sup> Tim Pusack, Oregon State Univ. (Hixon Lab)

A study of genetic population structure in the Goliath grouper (*E. itajara*) and Nassau grouper, using PCR (Polymerase Chain Reaction)-amplified mtDNA genes and nuclear microsatellites, revealed no clearly defined population substructuring for either species at the geographic locations sampled, i.e. Belize, Cuba, Bahamas, Florida for Nassau grouper (Sedberry *et al.* 1996). These data indicate that spawning aggregations are not exclusively self-recruiting and that the larval stages can disperse over great distances, however the relative importance of self-recruitment and larval immigration to local populations was not clear (Sedberry *et al.* 1996). Recent advances might be applied to examine source or nursery areas and shifts in fish between habitats with contrasting microchemical signatures.

Results of both Hateley (2005) and Sedberry *et al.* (1996) indicate a single panmictic population of Nassau grouper in the northern Caribbean basin with high gene flow between Florida, Cuba, Belize and the Bahamas. However, they do not quantify the connection. Results of an ongoing PhD study using more fine-scale genetic techniques may provide a more detailed understanding of population structure. (Alexis Jackson, PhD research in progress, Department of Ecology & Evolutionary Biology, University of California Santa Cruz).

## **2. THREATS OR STRESSORS**

Key threats are presented although they are unlikely to be all that are possible.

### **2.a. Anthropogenic Effects**

*Fishing effects.* Two different aspects of fishing effect Nassau grouper stocks, fishing effort throughout the non-spawning months and fishing effort directed at spawning aggregations or migratory access to spawning aggregations.

Nassau grouper are fished commercially and recreationally throughout the year by handline, longline, fish traps, spear guns, and gillnets (NMFS General Canvas Landing System). Aggregations are mainly exploited by handlines or by fish traps, although gillnets were being used in Mexico in the early to mid-1990s (Aguilar-Perera 2004). Sadovy and Eklund (1999) show declines in landings, catch per unit effort (CPUE) and, by implication, abundance in the late 1980's and early 1990's throughout its range, which has led Nassau grouper to now be considered commercially extinct in a number of areas (Sadovy and Eklund 1999). Recent reports from throughout the Nassau grouper's range document continued population declines and loss of aggregations (Sadovy de Mitcheson 2012).

The aggregative reproduction style - gathering at predictable sites in large concentrations to spawn during a few weeks (over a few months) each year - makes the Nassau grouper vulnerable as a target of fishing like many other reef species that form large aggregations to spawn. In many places, aggregation-fishing once produced most of the annual landings of the species (e.g., Claro *et al.* 1990, Bush 1992). Because Nassau grouper are only known to reproduce in spawning aggregations, removing ripe individuals during spawning has the potential to greatly influence

population dynamics and future fishery yields (Shapiro 1987). The fact that much of the catch in many countries historically came from spawning aggregations (Olsen and LePlace 1978, Aguilar-Perera 1994, Sadovy and Eklund 1999) likely magnified the effects to the extent that targeted aggregations have collapsed in many countries (Sadovy de Mitcheson 2012). Its declines have compromised the ecological function of a major top predator in the reef ecosystem (Randall 1987, Mumby *et al.* 2006, Mumby *et al.* 2012).

Prior to regulations prohibiting the harvest and possession, the U.S. Virgin Islands and Puerto Rico's reef fisheries commonly took Nassau groupers at aggregation sites (SAFMC 1990, CFMC 1993). Nassau grouper have also been caught from several sites off the Jamaican coast and off the northern coast of the Dominican Republic (Thompson and Munro 1983, Sadovy 1997). In Mexico, at least seven aggregation sites have been fished along the Yucatan Peninsula since the beginning of the 20<sup>th</sup> century (1910-1920) (Aguilar-Perera 1994). Thompson (1945) described one large aggregation site off Cay Glory, Belize, that had been fished for many decades and postulated that other congregations occur, but had escaped detection because of their ephemeral nature; other sites have been identified since Thompson's work (Paz and Grimshaw 2001). In Cuba, 21 spawning aggregation sites were identified; only 10 of these aggregation sites were Nassau grouper spawning aggregation sites. Of the 10 Nassau grouper aggregation sites, two were "aggregation statuses" were identified as "declined" and eight were identified as "sharply declined" (Claro and Lindeman 2003). In Atlantic waters, Nassau grouper have been caught in the Florida Keys and the Bahamas (Bohnsack 2003). The Bahamian Department of Fisheries reported that in 1992, over 20 spawning locations were fished (Thompson<sup>16</sup>), although the current status of many is unknown. A research trip during the spawning season of 2013 (B. Erismas, SCRFA Newsletter 17, June 2013) failed to find any sign of Nassau groupers at the spawning aggregation site that was the original site described by Smith (1972). There are no known spawning aggregation sites in Florida waters. In the Gulf of Mexico, Nassau grouper were caught primarily off southwest Florida, with commercial and recreational catch reported from the southwest Florida Keys. Both recreational and commercial catches of Nassau grouper were higher from the Florida-Gulf of Mexico than from the Florida-Atlantic coast from 1986-1993 (NMFS General Canvass Landings System). After 1991, these differences were probably partially due to fishery regulations banning all capture of Nassau groupers from the U.S. Atlantic waters, though not from the Gulf of Mexico; harvest and possession are now banned in all U.S. waters (CFMC 1990, SAFMC 1991, GMFMC 1996, compiled in Sadovy and Eklund 1999).

*Age composition of fishery catches.* Nassau grouper sampled from catches at 5 spawning aggregations in the Cayman Island's from 1987-1992 generally fell within age classes 2-9 years and included many immature individuals (Bush *et al.* 2006). No size-at-age differences between males and females have generally been noted (Bush *et al.* 2006). Over 80% of the samples taken (n=816) from a known aggregation in the Virgin Islands between 1974 and 1978 were aged 4-6

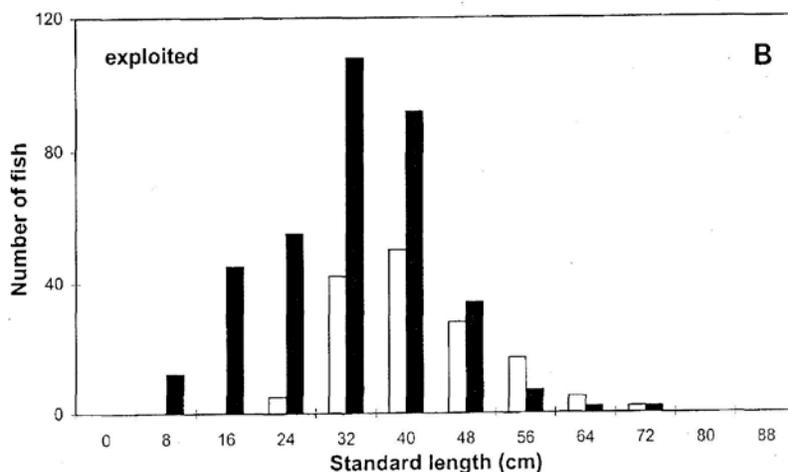
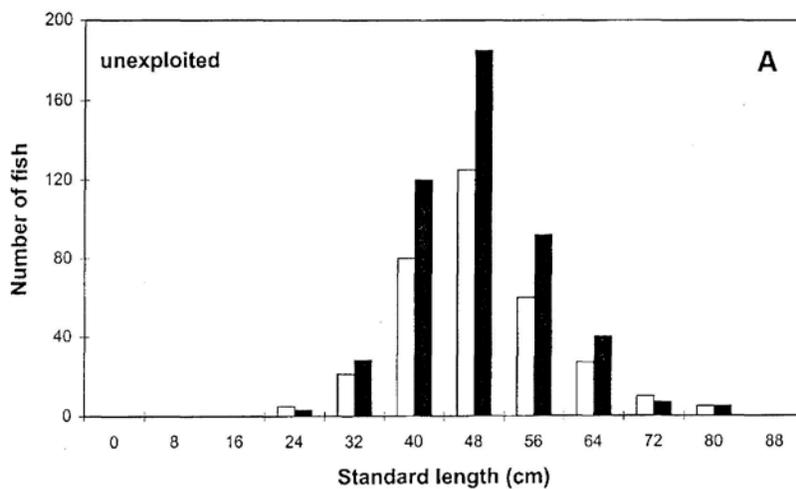
---

<sup>16</sup> Thompson, Ronald. 1992. Department of Fisheries, P.O. Box N 3028, Nassau, Bahamas. pers. comm.

years (as estimated by probit analysis) (Olsen and LaPlace 1979), while most fish landed from aggregations in the Cayman Islands from 1987-1992 were aged 7- 8 years (Bush *et al.* 2006). Age classes 6-9 dominated all landings in southwestern Cuba and 3-8 years in northeastern Cuba between the early 1960s and late 1980s with 50 percent of landings coming from aggregations (Claro *et al.* 1990).

*Size composition of fishery catches.* A maximum length of 1,220 mm TL and weight of 23-27 kg are recorded for the Nassau grouper (Evermann 1900, Randall 1963, Smith 1971, Buesa 1987). Most fish in markets, however, are considerably smaller (*i.e.*, 2-11 kg) (Smith 1971). Weights of aggregating fish ranged from 5-12 kg, with a maximum of 14 kg (Smith 1971, 1978, Aguilar-Perera 1994). Grouper up to 960 mm SL were taken in the Virgin Islands although fish larger than about 700 mm were uncommon (70 of 816 fish sampled) (Olsen and LaPlace 1979). Maximum theoretical mean length ( $L_{\infty}$  from the von Bertalanffy growth function - von Bertalanffy 1957) has been estimated at between 760-1,129 mm TL (Thompson and Munro 1978, Olsen and LaPlace 1979, Claro *et al.* 1990).

As stated previously, mean male and female sizes are similar within a given area, or at a



33

Figure 21

Length-frequency distributions of male and female Nassau grouper, *Epinephelus striatus*, taken from aggregations [males = white bars, females = black bars] in Belize: (A) unexploited site ( $n=694$ ); (B) exploited site ( $n=485$ ) (Carter *et al.*, 1994).

specific aggregation site. There is some indication that sizes of both sexes decline in areas of higher exploitation versus unexploited populations within a specific region (Carter *et al.* 1994) (Table 9).

When exploitation is high, catches are largely comprised of juveniles (growth overfishing). For example, in Belize, the average length of both sexes was 100 mm smaller in catches from exploited compared to unexploited aggregations (Fig. 9). In only two cases were females significantly longer than males, while males were never larger than females (Thompson and Munro 1978, Sadovy and Colin

Figure 9. Length-frequency distributions by sex for exploited and unexploited sites in Belize.

**Table 7. Mean sizes and sex ratio across a gradient of fishing pressure (excerpt from Sadovy and Eklund 1999).**

Mean sizes and sex ratios of aggregating and non-aggregating Nassau grouper, *Epinephelus striatus*, in the western Atlantic, from lightly (top of table) to heavily (bottom of table) exploited areas. Fishing intensity implied by descriptions of current and historic fishing activity (from Sadovy and Colin, 1995). Number in parentheses refers to references.

Sex ratio F:M	Mean SL in mm		Max SL in mm	Gear used <sup>1</sup>	Location and source <sup>2</sup>
	F	M			
0.57:1 (n=750)	526	529	750	T,H	Bermuda, offshore banks > 60 m deep (1)
0.72:1 (n=163)		554 <sup>3</sup>	718	H,T	Jamaica, offshore (3)
1.5:1 (n=694)	517	521	802	H,S	Belize, aggregation (4)
2.0:1 (n=42)	502	487	568	G	Mexico, aggregation (2)
0.67:1 (n=70)	514	503 <sup>4</sup>	657	G	Mexico, aggregation (2)
1.0:1 (n=940)	589	585	940	T,H	U.S.V.I., aggregation (5)
1.9:1 (n=95)	516	512	640	H	Caymans, aggregation (6)
2.0:1 (n=140)	506	538	772	H	Caymans, aggregation (7)
2.2:1 (n=717)	418	420	760	H,S	Belize, nonaggregated (4)
2.4:1 (n=485)	418	420	690	H,S	Belize, aggregation (4)
2.5:1 (n=216)	549	517 <sup>4</sup>	700	T	Bahamas, aggregation (8)
4.0:1 (n=319)		>500 <sup>3</sup>		710	S,T Cuba, (9) (only adults assessed)

<sup>1</sup> Gear used: T=trap; H=handline; S=spear; G=gillnet.

<sup>2</sup> Sources: (1) Bardach et al., 1958; (2) Sosa-Cordero & Cárdenas-Vidal, 1997; Aguilar-Perera, 1994; (3) Thompson & Munro, 1978; (4) Carter et al., 1994; (5) Olsen and LaPlace, 1979; (6) Colin et al., 1987; (7) Bush (text footnote 42); (8) Colin, 1992; (9) Claro et al., 1990.

<sup>3</sup> Males and females combined.

<sup>4</sup> Females significantly larger than males at  $p < 0.05$ , otherwise no sex difference in size.

Florida (Figs. 22 and 23 in Sadovy and Eklund 1999), and Cuba (Espinosa 1980), most catches consisted of juveniles.

## 2.b. Habitat loss or degradation

During its various life history stages, the Nassau grouper uses many different communities or habitat types within the coral reef ecosystem. The increase in urban, industrial, and tourist developments throughout the species' range impacts coastal mangroves, seagrass beds, estuaries, and live coral (Mahon 1990). Loss of juvenile habitat, such as macroalgae, seagrass beds, and mangrove channels is likely to negatively affect recruitment rates. As shown in the Bahamas (Dahlgren and Eggleston 2001), habitat preferences or selection may be key to early survival and subsequent population size and loss of those preferred coral-algal settlement habitats may pose a threat to grouper populations (Kaufman and Romero 2011). Poor water quality is a threat to both corals and macroalgae in nearshore areas. Increased sedimentation resulting from poor land development practices adds turbidity and pollutants into nearshore habitats and can change water flow patterns in creeks, where newly settled juveniles may be found. Dredging operations are also capable of destroying macroalgal beds that may be used as grouper nursery areas. Affects to Nassau grouper through habitat loss or degradation are summarized best by Semmens *et al.* 2008a:

*“While Nassau grouper are typically thought of as strictly a reef associated species, they transition through a series of ontogenetic shifts, from planktonic larvae, to nearshore sea-grass and algae habitat, to predominantly reef habitat (e.g. fore reef and reef crest). Even within reef habitat, there appears to be ontogenetic sorting, such that the larger individuals tend to occupy the deeper, more rugose reef areas. Each of these general habitats has undergone and continues to undergo change. Open-ocean larval habitat is being influenced by the ongoing increase in ocean sea-surface temperatures. These changes in temperature may influence habitat quality directly through physiological*

199  
5).  
In  
heav  
ily  
expl  
oite  
d  
area  
s of  
Puer  
to  
Rico

*stress, or indirectly through impacts to prey and predator densities (Anderson 1988). Seagrasses are in decline globally (Lotze et al. 2006); the decline of turtle grass in the Caribbean may reduce the amount of suitable habitat for newly settled Nassau grouper, and may influence the abundance of prey items for new recruits. Coral reef biogenic structure is in decline, owing in large part to the dramatic decline in Acroporid corals. Furthermore, the ongoing decrease in ocean acidity is likely to have a dramatic influence on the accretion rate of coral species in the future (Hoegh-Guldberg et al. 2007). It is possible that the ongoing and projected decline in biogenic structure on Caribbean coral reefs will have a dramatic impact on the availability and quality of reef habitat for mature Nassau grouper.”*

Suitable habitat for the Nassau grouper is also likely to be in decline (Semmens et al. 2008a, Lotze et al. 2006). Of the 20,000 km<sup>2</sup> of coral reef estimated for the Caribbean in the mid-1990s, 29% was estimated to be under high risk of degradation from human activities, 32% is at medium risk and 39% is at low risk (Bryant et al. 1998). A decade ago, Gardner and coworkers (2003) documented basin-wide losses of hard coral cover from about 50% to about 10%. With no indications of recovery of scleractinian coral cover, it is likely that many Caribbean reefs will continue to lose three-dimensional structure through uncompensated bioerosion and increases in macroalgal cover (McClanahan et al. 2002).

Under natural conditions the Nassau grouper appears to prefer clear waters (Albins et al. 2009), but is fairly tolerant of a range of water qualities: one adult survived for more than seven years in the old New York Aquarium in which the water at times became nearly fresh and was frequently quite polluted (Townsend 1905).

### **2.c. Climate change implications**

Nassau grouper have been found across a range of temperatures with the only implication being that spawning occurs when sea surface temperatures are about 25° C. If sea surface temperatures rise, the geographic range of the species may shift in response to any changes. One of the other potential effects of climate change could relate to the loss of structural habitat in the coral reef ecosystems (Munday et al. 2008). Ocean acidification is anticipated to affect the integrity of coral reefs and changing sea level could modify the depth regime with such rapidity that coral and coral reefs will be affected (Munday et al. 2008). Increased sea surface temperatures have been responsible for coral loss through bleaching and disease and bioerosion may reduce 3- dimensional structure in affected areas (Alvarez-filip et al. 2009), reducing adult habitat for Nassau grouper (Coleman and Koenig 2010, Rogers and Beets 2001). Changes in reproductive output or seasonal timing are also possible with unknown consequences for population abundance. Increased global temperatures are also predicted to change parasite-host relationships and may present unknown concerns (Harvell et al 2002, Marcogliese 2001).

### **2.d. Limits to recruitment/depensation**

Depensation, also referred to as the Allee effect, occurs when the abundance or density

of individuals drops below a critical threshold and reproduction becomes ineffective in sustaining the population. The different mechanisms hypothesized to cause depensation (after Semmens *et al.* 2008a) in Nassau grouper can be loosely classified as either 1) biological or ecological (e.g., low reproductive rates/low fertilization rates through poor mate choice or high predation at low population levels) or 2) behavioral (e.g., lack of behavioral cues leading to spawning) (Semmens *et al.* 2008a, Sadovy de Mitcheson and Erisman 2011). Colin (1992) and Semmens (pers. comm.) have described variance in behavior of small groups of spawning Nassau grouper. They tend to stay at the spawning aggregation sites longer, they show spawning coloration and behavior to lesser degrees than spawners in larger numbers. In the US Virgin Islands (Nemeth *et al.* 2006), although small numbers of Nassau groupers showed up at a presumed spawning aggregation site south of St. Thomas, they showed only minimal color change and they did not spawn.

Because of the size and apparent behavioral complexity (Whaylen *et al.* 2004) of Nassau grouper spawning migrations and aggregations, behavioral depensation could be the most widely accepted mechanism for the lack of aggregation formations and recovery (Bolden 2000, Sadovy 2001). Bolden (2000) and Nemeth and coworkers (2006) have suggested that the “*ecological knowledge*” of spawning site locations, timing, and behavior may be lost to grouper populations when intense fishing on aggregation sites removes the old individuals with such knowledge. If true, this could have important implications for any future spawning aggregation formations.

Semmens *et al.* (2006) hypothesize: *Alternatively, it may be that the grouper are migrating to spawning site locations, but due to low densities, individuals are choosing to leave and explore alternative shelf edges and reef promontories in expectation of finding higher densities elsewhere. Thus, fish spend the spawning season in search of spawning sites, and never spawn. Finally, it may be that fish are able to find the spawning site, and stay at the spawning site during spawning season, but due to perceived poor mate choice and low densities, fish forgo spawning.*

Given that many of the spawning aggregations have become severely depleted and between 25- 50% no longer form, it is probable that reproductive output and potential for some populations have been seriously compromised (Smith 1972; Sadovy and Eklund 1999; Sala *et al.* 2001; Whaylen *et al.* 2004; Belize Spawning Aggregation Working Group, unpublished data; R. Claro, unpublished data; E. Sala, unpublished data, as presented in Sadovy de Mitcheson *et al.* 2008). Two of the most well-known sites, one off Bimini, Bahamas (Smith 1972) and one at Mahahual, Mexico (Aguilar-Perera, pers. obs. 2013) appear to have disappeared ([www.SCRFA.org-blog](http://www.SCRFA.org-blog) 2013). Moreover, observations of reproductive activity, duration of aggregations, and intensity of color changes suggest that spawning becomes abbreviated or ceases when fish numbers are low (Colin 1992, Aguilar-Perera and Aguilar-Davila 1996). In extreme cases, such as Bermuda, or Puerto Rico, where aggregations no longer form, Nassau grouper are now rarely taken or observed.

### **2.e. Disease, parasites, and abnormalities**

Parasites occur in both wild-caught and cultivated Nassau grouper, predominantly in the viscera and gonads. Encysted larval tapeworms are common in the viscera and a reddish brown nematode occurs in the gonads (Thompson and Munro 1978). Parasitic isopods are found in nostrils (Thompson and Munro 1978). The digenetic trematode *Helicometra torta* (pyloric caeca), *Lecithochirum parvum* and *L. microstomum* (stomach), and *Sterrhurus musculus* (stomach) were identified in Florida-caught fish (Manter 1947, Overstreet 1969).

Diseases and abnormalities are not described. Although several species of western Atlantic groupers are known to be ciguatoxic (especially when large), Nassau groupers have been thought to be uniformly non-toxic throughout their range (Halstead 1967, Jory and Iverson 1989) with the interesting exception of one small toxic Nassau grouper in the Virgin Islands (Brownell and Rainey 1971). Excrescences were noted on otoliths and one fish had a completely malformed sagittal pair with the whole of the concave surface overgrown with a large excrescence (Thompson and Munro, 1978).

### **2.f. Aquaculture – successes, failures, potential threats**

The Nassau grouper is considered a prime species for aquaculture (Tucker 1992a, 1992b). In the late 1980s and into the 1990s, considerable progress was made in hatchery spawning and rearing of groupers under aquarium conditions (Tucker 1992a, Watanabe et al. 1995a, 1995b, Tucker et al. 1996).

Female Nassau groupers were induced to ovulate using human chorionic gonadotropin (HCG) injections, luteinizing hormone-releasing hormone analog (LHRHa) and carp pituitary homogenate (CPH), or combinations thereof (Tucker 1992b, Kelley et al. 1994, Watanabe et al. 1995b). Females with mean oocyte diameters ranging from 482-561 micrometers ( $\mu\text{m}$ ) were suitable for hormone-induced spawning (Watanabe et al. 1995b). Tucker et al. (1996) described four methods for achieving fertilized eggs, including combinations of induced or natural ovulation and artificial fertilization with fresh milt or natural spawning in tanks.

Fertilization rates in artificially induced spawns ranged from 18-100% and hatching success ranged from 68-100% (Head et al. 1996, Tucker et al. 1996). Multiple spawns occurred on consecutive days and hatchery reared juvenile Nassau groupers grew to 1.5- 2.0 kg in 2 years (Tucker and Woodward 1993).

Following hormone injections, Nassau grouper females produced clutches of between 23,000 and 600,000 mature eggs per kg of body weight, with large females capable of yielding almost 5,000,000 eggs. Kelley et al. (1994) reported one to two clutches produced during the natural reproductive season, with each clutch totaling 50,000-600,000 eggs per kilogram body weight. Head et al. (1996) found that females could spawn two to three times at intervals of 28 to 75 days, producing 200,000- 2,000,000 eggs per female (54,000 and 340,000 eggs/kg body

weight) with females ranging in size from 3.5-6.8 kg. Tucker *et al.* (1991) noted clutches of 500,000 to 700,000 for females ranging from 3-5 kg (166,666 to 140,000 eggs/kg), while Watanabe *et al.* (1995b) reported stripped females of 4.2-12 kg releasing between 95,000 and 4,750,000 eggs (22,619-395,833 eggs/kg), with a significant relationship between body weight and eggs stripped ( $y=0.385x-0.5589$ ;  $r^2=0.40$ ,  $n=41$ ,  $p<0.001$ ;  $y$  is eggs stripped and  $x$  is body weight in kg).

Larval survival to first feeding was generally high, with declines thereafter depending on feeding regime. Survival of larvae to first feeding in one set of experiments was 65% (Tucker 1992b) but was found to decline to about 1% by day 62 post-hatching in another (Watanabe *et al.* 1994, 1996); larval survival declined once the yolk sac was absorbed. Feeding with oyster trochophores and sieved rotifers, combined, achieved higher larval survival rates than feeding with unsieved rotifers alone (Watanabe *et al.* 1994) and small prey size was important (Watanabe *et al.* 1996). Results of feeding experiments indicated that cultured juveniles require a dietary protein level above 55% and an energy-to-protein ratio of below 28.9 kJ/g for optimum growth (Ellis *et al.* 1996). Control of turbulence, salinity, and light intensity improves survival to the first-feeding stage (Ellis *et al.* 1997b). Increased growth and feeding rates occurred with increased water temperatures (Ellis *et al.* 1997a).

Experiments to determine the success rate of larval Nassau grouper culture (Watanabe *et al.* 1995a, 1995b) and survival of released hatchery-reared juveniles (Roberts *et al.* 1994) have been conducted. Although temperature manipulation might be used to condition Nassau grouper to spawn any month of the year (Tucker *et al.* 1996), hatching success was higher between 26-28°C compared to hatching at 30°C (Watanabe *et al.* 1995b). Nassau grouper juveniles (309-367 mm TL) reared from eggs ( $n=27$ ) at Harbor Branch were used to test the feasibility of restocking reefs (Roberts *et al.* 1994) in St. Thomas. Despite some mortality and dispersal, a few tagged fish were observed up to nine months after release. The potential of Nassau grouper stock enhancement, as with any other grouper species, has yet to be determined (Roberts *et al.* 1994). Serious concerns about the genetic consequences of introductions and about possible problems of juvenile habitat availability, introduction of maladapted individuals, or inability to locate traditional spawning aggregations, continue to be raised.

### **3. DESCRIPTION OF FISHERIES AND FISHERIES MANAGEMENT AND CONSERVATION**

Data on recruitment into the fishery indicate that age and size first susceptible to capture are 4-7 years and 275+ mm TL, respectively. In some areas, most of the catch is, or has been, composed of juveniles (e.g. Puerto Rico and Cuba) (Puerto Rico Fisheries Research Laboratory 1991, Claro *et al.* 1990). Olsen and LaPlace (1979) calculated age of first capture at 4-5 years, although immature fish of 2 years (< 300 mm TL) were also recruited. Mean size of recruitment into the fishery in Jamaica was estimated at 570 mm TL (about 5 years old) on oceanic banks for

handline and fish trap fisheries; the minimum length captured was 275 mm TL and the full retention length was 625 mm TL (Thompson and Munro 1978). Modal ages reported for a Cayman Islands aggregation and a stock in Cuba were 6-8 years (Claro *et al.* 1990, Bush *et al.* 2006), suggesting that individuals were not fully recruited until this age range.

### **3.a. Abundance indices and trends over time**

*Stock assessments.* Despite long-acknowledged problems with conservation of this species very little formal stock assessment has been carried out, partly because of the lack of appropriate data collection. The most recently published assessment, conducted in the Bahamas, clearly indicates, even with a conservative approach, a need to reduce fishing pressure to levels of a decade ago (Cheung *et al.* 2013). Population dynamic modeling indicates that if fishing effort for the Bahamas' Nassau grouper has not been reduced from the 1998 to 2001 level, the stocks are likely to be overexploited. (Cheung *et al.* 2013). Cheung *et al.*'s (2013) population dynamic modeling found: "assuming that the closure of the spawning aggregation season is perfectly implemented and enforced, the median value of  $FSPR=35\%$  on non-spawning fish would be 50% of the fishing mortality of the 1998 to 2001 level. The 5 and 95% confidence limits are estimated to be less than 20% and more than 100% of the fishing mortality at the 1998 to 2001 level, respectively. In other words, if (1) fishing mortality rates of non-spawning fish are maintained at the 1998 to 2001 level and (2) fishing on spawning aggregations is negligible, the median spawning potential (spawner biomass relative to the unexploited level) is expected to be around 25% (5 and 95% CI of 20 and 30%, respectively). This is significantly below the reference limit of 35% of spawning potential, meaning that there is a high chance of recruitment overfishing because of the low spawning stock biomass."

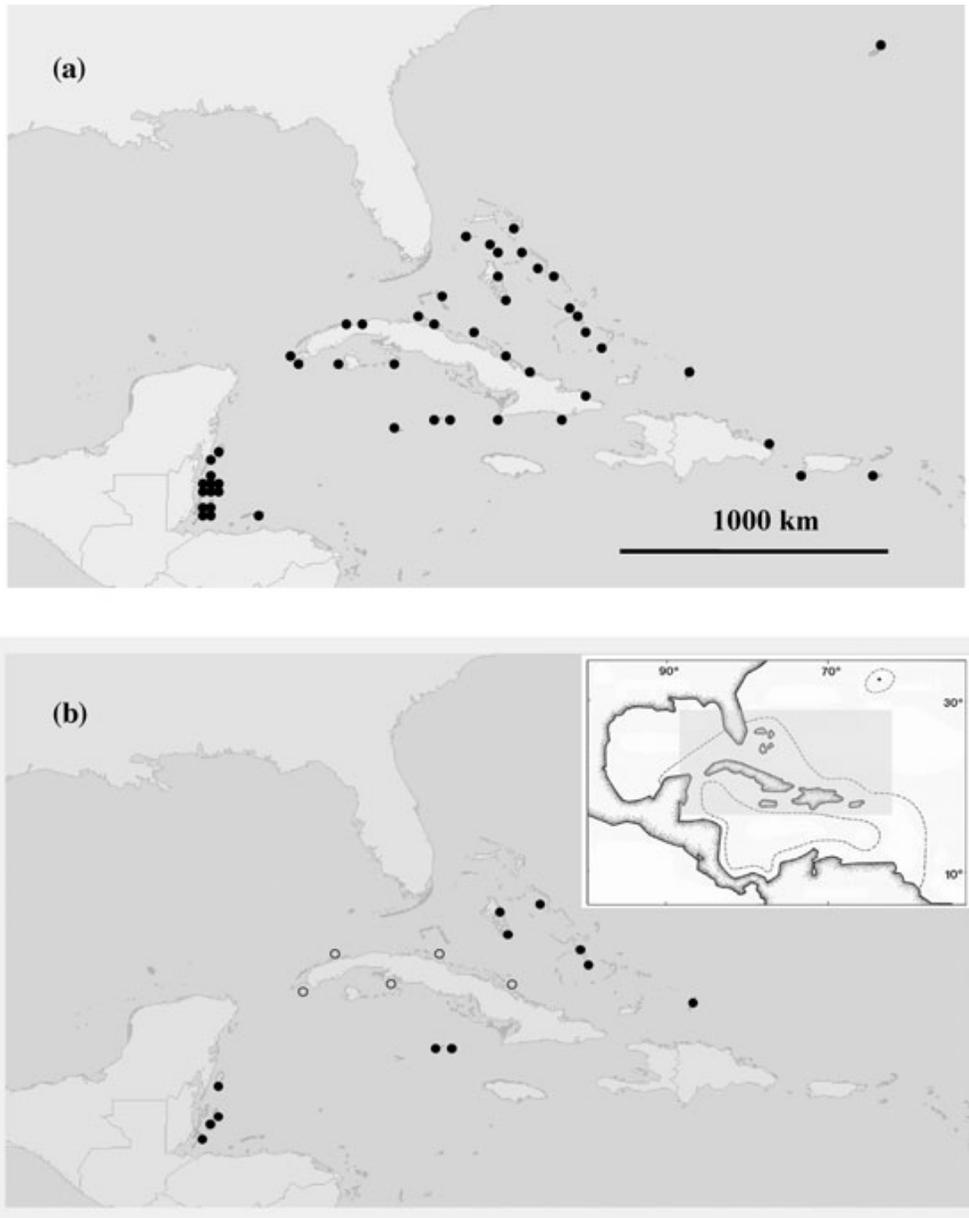
During the first U.S. survey of the fishery resources of Puerto Rico, the Nassau grouper was noted as a common and very important food fish, reaching a weight of 50 lbs. (22.7 kg) or more (Evermann 1900). By 1970, Nassau grouper was still the fourth most common shallow-water species landed in Puerto Rico (Thompson 1978), and it was common in the reef fish fishery of the Virgin Islands, where an aggregation in the 1970s contained an estimated 2,000-3,000 individuals (Olsen and LaPlace 1979). During the 1980's, port sampling in the USVI showed that Nassau grouper accounted for 22 percent of grouper landings with 85 percent of the Nassau grouper catch coming from spawning aggregations (Olsen, pers. comm.). By 1981 "the Nassau grouper ha(d) practically disappeared from the local catches and the ones that d(id) appear (were)-small compared with previous years" (CFMC 1985) and by 1986 was considered commercially extinct in the U.S. Virgin Islands/Puerto Rico region (Bohnsack *et al.* 1986). About 1,000 kg were landed from the Reef Fish fishery during the latter half of the 1980s in Puerto Rico, most of them were less than 500 mm, indicating they were likely sexually immature (Sadovy 1997).

Little is known about the dynamics of unexploited stocks of Nassau grouper although some of the data from the 1980s give us some insight (Carter *et al.* 1994). Spawning stock biomass per recruit has not been quantified for the species but landings data clearly show a chronological trend from abundance to rarity in many areas (e.g. Sadovy 1997). Of particular concern has been the rapid and extreme decline in numbers taken from traditional aggregation sites (Sala *et al.* 2001). In general, slow-growing, long-lived species (such as snappers and groupers) with limited spawning periods and, possibly, with only a narrow recruitment window

are susceptible to overexploitation (Bannerot *et al.* 1987, Polovina and Ralston 1987). Hodgson and Liebler (2002) noted that Nassau grouper were absent from 82% of shallow Caribbean reefs (3 – 10m) during a 5-year period (1997-2001) of underwater surveys for the ReefCheck project. This is derived from underwater surveys in most countries in the range of the species.

Known spawning aggregations of Nassau grouper are displayed in Figure 10 as available in published and gray literature and interviews (Sadovy de Mitcheson *et al.* 2008). Data have been archived in the scrfa.org website database. The map shows all known aggregations reported to exist since 1884 (a). In the few cases where aggregation numbers were estimated, abundances ranged from approximately 10,000 to somewhere between 30,000 and 100,000 fish (Smith 1972, Olsen and LaPlace 1979, Colin *et al.* 1987, Fine 1990, 1992, Carter *et al.* 1994, Sadovy 1997). For comparison, it also shows those aggregation sites reported to exist as of about 2007 (b). The closed circles represent sites believed to exist, with fish numbers estimated at between 100 and 3000 (estimates from fishing and direct observations). The open circles represent sites in Cuba still believed to produce small catches of Nassau grouper but sites have not been assessed directly. The data suggest that over half of all known aggregations no longer form.

While it appears (Fig. 10) that heavy fishing on spawning aggregations was a primary driver of population declines (Sadovy de Mitcheson and Erisman 2012), other factors may affect populations at a national level. Heavy fishing of adults away from or during spawning runs, the intensive capture of juveniles, either through direct targeting (e.g., spearfishing) or using small mesh traps or nets, will compromise population stability and spawning potential, and loss or degradation of habitat could affect populations because reef associated habitats are used as shelter at all life history phases may all have detrimental effects (e.g. Semmens *et al.* 2007a).



**Figure 11.** Maps showing locations of known Nassau grouper spawning aggregations both historically (a) and as of about 2007 (b) according to available information-not all sites have been validated. Inset shows full geographic range, main concentrations (shaded) and extended areas (dashed lines). Each closed circle represents 1, or occasionally 2, reported site(s). Open circles are “probable” sites. [(Sources: Smith 1972; Sadovy & Eklund 1999; Sala et al. 2001; Whaylen et al. 2004; Belize Spawning Aggregation Working Group, unpublished data; R. Claro, unpublished data; E. Sala, unpublished data, as presented in Sadovy de Mitcheson et al. 2008)]

*Ecological assessments.* The Nassau grouper was formerly one of the most common and important commercial groupers in the insular tropical western Atlantic and Caribbean (Smith 1978, Randall 1983, Appeldoorn *et al.* 1987, Sadovy 1997). Declines in landings, catch per unit

of effort (CPUE), and, by implication, abundance, have been reported throughout its range, and it is now considered to be commercially extinct in a number of areas. Information on past and present abundance and density, in both aggregation and non-aggregation habitat, is based on a combination of anecdotal accounts, visual census surveys and fisheries data. The lack of species-level fisheries data severely limits fishery dependent analysis of the species throughout its range. Fishery independent surveys provide the only broad scale data with which to assess current population condition. Such studies are referenced in the following sections, as available. Unfortunately time series data are generally lacking and comparisons between reefs or between countries are the only possible ways to compare as a measure of relative abundance.

A number of organizations or agencies have undertaken surveys to elucidate the status of coral reefs and reef fish populations throughout the western Atlantic, as well as other parts of the world. Results from these monitoring studies (Kellison *et al.* 2009) offer some indication of relative abundance in various locations for Nassau grouper (Table 10) although generally different methods are employed and results cannot be directly compared. Sighting frequency and density may offer information. Results from Atlantic and Gulf Rapid Reef Assessment Program (AGRRA) show few Nassau groupers throughout their surveys. The sighting frequency (proportion of all surveys with at least one Nassau present) ranged from less than 1% to less than 10%. Densities would scale up to range from 1 to 15 fish/hectare with a mean of 5.6 fish/hectare across all areas surveyed. NOAA's Coral Reef Ecosystem Monitoring Program (CREMP) has conducted studies in Puerto Rico and the US Virgin Islands since 2000 and sighting frequency has ranged from 0 to 0.5% and density has ranged from 0 to 0.5 fish/hectare. Data from University of the Virgin Islands (UVI Vis. Sur.) sampling as part of their jurisdictional coral reef monitoring (funded by the NOAA Coral Reef Conservation Program), was not readily available to compute sighting frequency but densities were 4 fish/hectare. NOAA's (NMFS FRVC) and Florida's Fish and Wildlife Conservation Commission (FFWCC Vis. Sur.) studies that focus on the Florida Keys indicate sighting frequencies ranged between 2-10%; densities from both studies were 1 fish/hectare (Table 10). Beyond these monitoring surveys, the Reef Environmental Education Foundation (REEF) sponsors and supports volunteer dive-based surveys across the region. Observers rank species abundance as Single=1, Few=2-10, Many=11-100, and Abundant=over 100 rather than recording precise numbers. The data are then calculated as a Density Index (Den), which is a measure of relative abundance when the species is seen but does not give an indication of lack of occurrence and as a Sighting Frequency (%SF), which is a measure of how often the species was observed. The Den and %SF scores could be multiplied to provide a measure of species abundance, which accounts for zero observations. Where REEF survey information is available, it is included in the following Country Accounts. The data are not necessarily as easy to interpret as desired without additional spatial context (e.g., management regime).

**Table 8. Fishery Independent Surveys from various sources. Sighting Frequency is the number of surveys in which at least one Nassau grouper was encountered; Density is the total number counted per unit area, standardized by area of each survey type. AGRRA info: Kramer 2003.**

Survey	Location/Extent	Year	Num. E. Stri. Observed	Num. Surveys w/ E. Stri.	Total Num. of Surveys	Sighting Frequency	Density (Num/m <sup>2</sup> )
AGRRA	Andros Island, Bahamas	1998	23	23	295	0.078	0.0013
AGRRA	Abaco Islands, Bahamas	1999	4	4	130	0.031	0.0005
AGRRA	Lighthouse Atoll, Belize	1999	1	1	110	0.009	0.0002
AGRRA	Glovers, Turnette, Barrier Reefs, Belize	2000	6	6	349	0.017	0.0003
AGRRA	Little and Grand Cayman	1999	23	20	341	0.059	0.0011
AGRRA	Batabano, Cuba	2001	29	27	686	0.039	0.0007
AGRRA	Sabana and Camaguey, Cuba	2001	6	6	368	0.016	0.0003
AGRRA	Jardines de la Reina, Cuba	2001	7	7	535	0.013	0.0002
AGRRA	Boca del Toro and Comarca de Kuna, Panama	2002	4	4	451	0.009	0.0001
AGRRA	Caicos, Turks, and Mouchair Banks, Turks and Caicos	1999	25	25	279	0.09	0.0015
AGRRA	Culebra, Vieques, and Cayos de la Cordillera, PR	2003	2	2	174	0.011	0.0002
CREMP	La Parguera, PR	Average 2000-2007	2	2	1010	0.002	0.000025
CREMP**	Vieques, PR	2007	0	0	75	0	0
AGRRA	Biscayne National Park and Keys NMS, Florida	2003	8	7	381	0.018	0.0003
FFWCC Vis. Sur.	Keys NMS (Key Largo to Key West)	Average 1999-2007	79	76	7396	0.01	0.0001
NMFS FRVC	Keys NMS (Key Largo to Dry Tortugas)	Average 2000-2007	210	198	8563	0.0208	0.0001
AGRRA	St Croix, St Thomas, USVI and Guana, BVI	1999	1	1	144	0.007	0.0001
AGRRA	St Thomas, St John, USVI and Aneгада, Virgin Gorda, BVI	2000	6	6	100	0.06	0.001
UVI Vis. Sur.	St. Thomas, USVI	Average 2003-2007	8	N/A*	290	N/A*	0.0004
CREMP USVI	St. John and St. Croix, USVI	Average 2001-2008	14	13	2638	0.005	0.00005

\* Lack of raw dataset prevented computation of surveys in which Nassau grouper were sighted, and hence, sighting frequency as well

\*\*This data not included in computation of density and sighting frequency trends for CREMP visual surveys in Puerto Rico

### 3.b. COUNTRY ACCOUNTS

Few population analyses or stock assessments have been conducted on the Nassau grouper such that our understanding of population status and condition is largely dependent on fishery trends (catches or catch per unit of effort) over time, fishery-independent underwater reef fish surveys, sizes landed, and a narrow range of biological studies. Genetic work to date suggests a single panmictic population connected throughout its range although the amount of gene flow between separate areas has yet to be quantified and there is suggestion of sub-structuring by work currently in progress (Jackson PhD research in progress). Results of on-going studies should help to inform on the degree of self-recruitment versus long distance replenishment of subpopulations. Studies of circulation patterns at spawning aggregation sites generally have indicated the presence of eddies and local retention mechanisms that result in self-recruitment in most areas although a mix of local and long distance egg and larval transport appears most likely and somewhat unpredictable.

Nassau grouper are no longer common on reefs. For example, Hodgson and Liebeler (2002) noted that Nassau grouper were absent from 82% of shallow Caribbean reefs during a 5-year period of underwater surveys for the ReefCheck project. Of 162 reefs surveyed for Nassau grouper, only eight reefs had more than one fish. Of the 106 total fish counted during five years of monitoring, 76 were found on two reefs in the World Heritage Site in San Andrés Archipelago in Colombia, where spearfishing is prohibited on both reefs. In the Atlantic region, grouper abundance (including Nassau grouper) declined from 1999 (1.13 grouper  $\pm$  3.2 per 100 m<sup>2</sup>) to 2000 (0.25  $\pm$  0.54 per 100 m<sup>2</sup>) although this is not statistically significant. This trend is consistent with underwater surveys in most countries across the range of the species.

Many of the countries where Nassau grouper have been reported have mechanisms to report fishery landings, either as a means of understanding local management status and needs or as a participant in broader regional or international management or conservation efforts (i.e., FAO). Unfortunately many do not collect data at the species level but rather collect data, landings or effort, for instance, only at some functional group or family level. While this may be mildly informative it is rarely useful in understanding fishery impacts to particular species. Most of what is known of the current status of Nassau grouper stocks must be derived from research or monitoring efforts or as interpretation of the scarce data.

In addition to the country accounts that follow, IUCN lists the following as islands/countries where Nassau grouper is considered to be native. To date, little ecological or fisheries data, information or anecdotal evidence is available to provide insight into the status of Nassau grouper in the following jurisdictions: Antigua and Barbuda; Aruba; Costa Rica; Curaçao; Dominica; French Guiana; Grenada; Guadeloupe; Guatemala; Guyana; Haiti; Montserrat; Netherlands Antilles (Curaçao); Nicaragua; Panama; Saint Kitts and Nevis; Saint Lucia; Saint Vincent and the Grenadines; Suriname; Trinidad and Tobago; United States Minor Outlying Islands (i.e., Navassa); and Venezuela. Some of these locations are combined into the section entitled “Lesser Antilles, Central, and South America.”



## **ANGUILLA<sup>17</sup>**

### **Anguilla – Populations**

Little information is available from published sources on the status of Nassau grouper in Anguilla's waters. According to the Fisheries Department in 2012: "With regards to the Nassau grouper it is not very abundant in Anguilla. Officers at the Department have reported only seeing one or two juveniles on their dives and other in-water work. We do not have the historical data in Anguilla to determine their former abundance, however it is believed that they were more abundant than they are now, judging from past fish catch observations."

### **Anguilla – Fisheries**

No data are available from published sources on the fisheries that take or have taken Nassau grouper. According to the Fisheries Department in 2012: "The Nassau grouper is a species that was observed in fish catches in the 80s and prior to that (not any great amounts) but now they are not a part of the current fish catches (fish traps and lines). A fish catch data collection programme [has only been] implemented at the department in the past four years and so an analysis of historical trends is not possible. However, like I have said this species is not present in current fish catches."

### **Anguilla – Conservation and Management**

"There are no known spawning aggregation sites and there are no special conservation or management regulations in place."

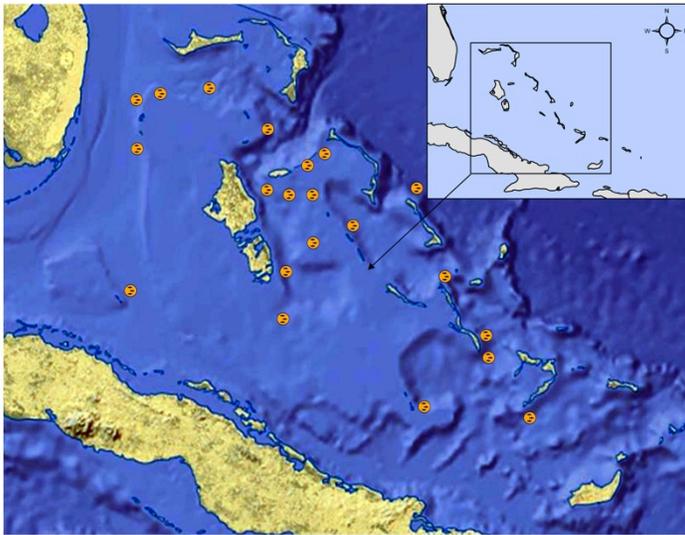
---

<sup>17</sup> James C. Gumbs, Director of Fisheries and Marine Resources, Ministry of Home Affairs, Government of Anguilla. Pers. Commun.

## BAHAMAS

### Bahamas – Populations

The Bahamas with its many islands and extensive shallow reef areas very possibly holds or held one of the largest populations of Nassau grouper throughout its range. The species has long been the major landed finfish for the country and the first and largest ever reported spawning aggregation (with an estimated 30,000 to 100,000 fish) was documented from the



**Figure 12. Approximate locations of Nassau grouper spawning aggregation sites in the Bahamas.**

and marine protected areas (Cheung *et al.* 2013). There is no indication that these declines are due to reduced fishing effort or to changes in fishing practices; overfishing is most likely the cause. Reductions in numbers of fish observed in reef surveys, also suggest that populations are declining. One major concern is with poaching, especially by non-Bahamians: Bahamian fishermen largely abide by the seasonal closures for Nassau grouper (Michael Braynen pers. comm.).

More than 20 aggregations have been reported from the Bahamas but very few have been studied in any detail and the current status of the great majority is unknown. Counts of fishes in aggregations provide one indication of possible changes in population status. Underwater visual census (UVC) surveys, outside of aggregations, provide an alternative indication of abundance and further suggest that the species is now an uncommon member of the reef assemblage. While some data are available from research organizations such as REEF, in a country like the Bahamas, the results are difficult to interpret without knowing more about the spatial

Bahamas in Bimini (Smith 1972). By the late 1990s/early 2000s, the Nassau grouper population(s) in the Bahamas was likely fully exploited to over-exploited (Ehrhardt and Deleveaux 2007, Cheung *et al.* 2013). Both fisheries landings and mean body size in catches have declined since the 1990s, despite a minimum size regulation, protection during the spawning aggregation season, establishment of several protected aggregation sites,

distributions of samples, e.g., locations inside versus outside of marine protected areas or reef zones. Cumulative data from REEF (2003-2013) show high numbers of sightings of 402 Nassau grouper in 1471 surveys (density index 1.5, sighting frequency 27.3%) in the north Bahamas, 3729 Nassau grouper in 6527 surveys (density index 1.6, sighting frequency 57.1%) in the central Bahamas, and 49 Nassau grouper in 75 surveys (density index 1.6, sighting frequency 65.3%) in the south Bahamas across the 10-year period. Examinations of time periods of 1990-95 vs. 2008-13 do not show great differences in sighting frequency or density index but spatial/management zone data are lacking so comparability of sites is not known (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>). Atlantic and Gulf Rapid Reef Assessment (AGRRA) surveys in Andros Island (1998) and Abaco Islands (1999) found relatively low numbers of encounters (sighting frequencies of 7.8% and 3.1%, respectively; densities of 13 fish/hectare and 5 fish/hectare, respectively) (AGRRA data, from T. Kellison,). These are between 37.5 and 14.4% of the densities cited by Bardach in a relatively lightly impacted Bermuda in the 1950. Again, we do not have spatial or management zoning information with which to interpret these data.

A novel assessment of the number of fish in a single spawning aggregation using a hydroacoustic surveys was undertaken (Ehrhardt and Deleveaux 2007), however no in-water observations validated the data so the outcomes of the study remain uncertain. This study reported many thousands of fish in the sampled aggregation but, given that no other aggregation in recent times has contained such numbers according to direct visual censuses, these data need to be treated with caution. Counts of fish in aggregations in the Bahamas in recent years have rarely exceeded a few hundred (Sadovy de Mitcheson *et al.* 2012). This contrasts strikingly with the many tens of thousands (30,000-100,000) estimated by Smith (1972) in the first scientific report of an aggregation in the country, and, indeed, of the species. Hydroacoustic surveys are promising research tools and are being applied in spawning aggregation work in Florida and Puerto Rico, among others, but must be validated until reliable techniques are defined (e.g. Taylor *et al.* 2006).

In January 2013, over the full moon period, SCRFA organized a resurvey of the famous Bimini aggregation site reported by Smith in 1972. The site and extensive surrounding areas along the reef were surveyed multiple times and interviews with fishers and businesses conducted. It was clear that this aggregation had long since ceased to form and appears to have disappeared – see blog on [www.SCRFA.org](http://www.SCRFA.org) and SCRFA Newsletter 17 for accounts of the survey. Also during this aggregation period, during which there is a national ban on Nassau grouper catches, large numbers of fish were being taken according to fisher accounts with photo-documentation and confirming reports of poaching of the species during the aggregation season (BREEF unpub. data).

## Bahamas - Fisheries

The Bahamas is one of the most important countries in the distribution of the species. There has been a long-established and financially important Nassau grouper fishery for many decades. In terms of weight and value, Nassau grouper is the fourth most important commercial fishery resource in the Bahamas Exclusive Economic Zone (behind spiny lobster, snappers and queen conch). In 2007, the most recent summary available, Nassau grouper comprised 2% by both weight and value of the recorded commercial landings of all commercially exploited species in the Bahamas (FAO 2009); spiny lobster makes up the great majority of the country's commercial landings. Nassau grouper in 2007 accounted for 73% of all commercial grouper landings in the country; recreational and subsistence use data of the species are not available (FAO 2009). Buchan (2000) indicated that the shallow banks throughout Great and Little Bahamas Banks, the Cay Sal Bank, and the Crooked Island and Acklins Island Banks were the major fishing grounds for Nassau grouper. In the Bahamas, fishermen use handlines, traps, and spearguns (including compressors/compressed air) to take Nassau grouper (Sadovy 1997).

Much of the annual landings historically came from spawning aggregations with as many as 31 different sites (Table 11) (Sadovy de Mitcheson 2012). A BREEF report (1998) indicated between 13 and 31 aggregations in the country but only a handful of the sites have actually been confirmed to exist by direct observation or catch monitoring (Sadovy and Eklund 1999). Those assessed recently are far smaller than previously indicated (Table 11). Sullivan-Sealy *et al.* (2002) indicated that New Providence Island is within 1-day's range of fishing for 5 reported Nassau grouper spawning aggregation sites, the two largest being reported off High Cay, Andros Island and in the northern Berry Islands. Landings data from 1995-2006 showed that most landings are taken from December to February although regulations have now restricted fishing during most of the spawning season.

Spearfishing (often with the use of compressed air), fish traps, hook and line and gillnet are commonly used to take fish from aggregations (Cushion and Sullivan-Sealey 2008). Spearfishing and fish-trapping, in particular, result in significantly higher CPUE than other fishing methods (Cheung *et al.* 2013). Compressor-based spear and gillnet fishing were the primary methods used by the Montagu Ramp fishermen (Cushion and Sullivan-Sealey 2007). The use of speargun is illegal, but spear with a sling is legal.

Research (2000-2002) on spawning aggregations reported in Gascoigne (2002, as cited in Sadovy de Mitcheson 2012) in Long Island shows that some aggregations have already disappeared and others are disappearing very rapidly, with only a few tens of fish aggregating where there were formerly thousands or tens of thousands. In one aggregation studied in the winter of 2000-2001 (scientists from North Carolina State University), every single aggregating fish was caught by trapping; this aggregation did not form in the winter of 2001-2002 (Gascoigne 2002, as reported in Sadovy 2012). The most recent survey (January 2002) covered four historic aggregation sites, and found two completely gone (no fish, although lots of traps in

the water) and two very reduced with aggregations of 14 and 28 fish, respectively. The aggregation at High Cay is probably also an order of magnitude smaller than its historical size (hundreds of fish rather than thousands or tens of thousands). Estimates by divers are of the order of 100-1,000 fish for 1999-2000 (Ehrhardt and Deleveaux 2007, Ray *et al.* 2000). In 2000-2001, divers could not locate the aggregation and believe that it may not have formed at all (G. Carleton Ray, University of Virginia, pers. comm.). There is no survey data available for 2002, but fishing was allowed on the aggregation for the first time in three years, and catches were low (J. Birch, Small Hope Bay, Andros, pers. comm. to J. Gascoigne). The High Cay aggregation is evidently undergoing decline relative to historic estimates (Ray *et al.* 2000).

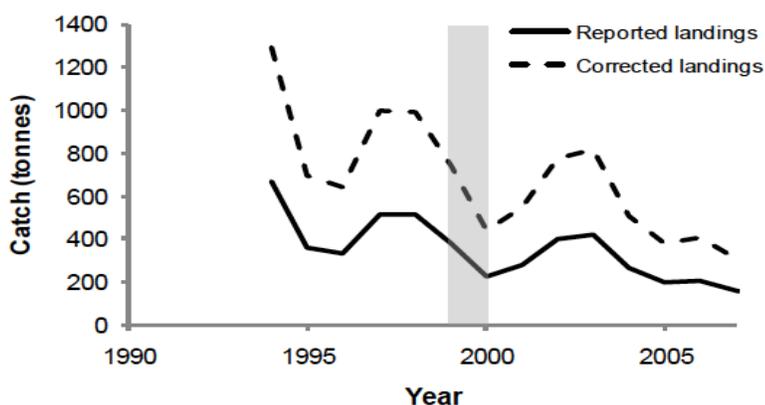
**Table 9. Aggregation sites in the Bahamas in 1998. Bahamas aggregations - modified from BREEF (1998): DoF=Department of Fisheries**

Location	Number	Discussion/Source
Cat Cay	1	100,000 individuals observed 1970 <sup>(1)</sup> . 2013 survey at January full moon and local interviews indicate that the aggregation has long ceased to form (SCRFA Newsletter 17).
Great Issac Light	1	May have disappeared due to fishing pressure from Florida <sup>(2)</sup>
Andros	2	Locations High Cay and Tinker Rock <sup>(3)</sup>
<i>Andros</i>	<i>3 more</i>	<i>Locations and source of report not known<sup>(4)</sup>. Not apparently known by local fishermen so probably not true.</i>
Long Island	1	Decline in catches from several thousand to less than 100 fish <sup>(5)</sup> . However 1997 catches on the aggregation reported to be good by Long Island fishermen. One aggregation site in Long Island reported by fishermen in San Salvador as their nearest aggregation
<i>Long Island</i>	<i>2 more</i>	<i>Locations and source not given<sup>(6)</sup>. DoF believe that there are two aggregation sites in Long Island.</i>
Exuma Cays	1	From work by Pat Colin <sup>(7)</sup>
Cat Island	1	Locations and source of report not given <sup>(8)</sup>
Berry Islands	4	Locations and source of report not given
New Providence	1	Locations and source of report not given. Not reported by New Providence fishermen so unlikely to be true.
Ragged Island	1	Locations and source of report not given. If exists may be threatened by fishing pressure from other countries
Cay Sal	1	Locations and source of report not given. If exists may be threatened by fishing pressure from other countries
Eleuthera	4	Locations and sources of report not given
Acklins	1	Locations and source of report not given. If exists may be threatened by fishing pressure from other countries
Abaco	3	Discussions with Hopetown and Marsh Harbour fishermen
Grand Bahamas	4	Reported to be known and fished by a Grand Bahama based fishing company <sup>(9)</sup>
<b>Minimum total</b>	4	Aggregations confirmed in recent scientific literature
<b>Approximation</b>	13	Aggregations confirmed by local reports and literature
<b>Maximum total</b>	31	All reports above, some of which are fairly unlikely

**Sources:** (1) Smith, 1972; (2) Reported by CL Smith in the early 1970s; (3) From discussions with fishermen- Dr. Tim Turnbull (4) 5 spawning aggregations in Andros reported in Sadovy (1997) (5) Colin 1992; (6) Sadovy (1997); (7) Dr. Tim

Turnbull, Sadovy (1997); (8) Sadovy (1997)-also source for Berry Islands, New Providence, Ragged Island, Cal Say, Eleuthera and Acklins; (9) Vallierre Deleveaux, Bahamas Dept. of Fisheries

In a recent detailed analysis, catches from 1994 to 2009 were assessed using fishery-modeling approaches (Cheung *et al.* 2013). The study showed that total landings of Nassau grouper in the Bahamas declined gradually from 1994 to 2009. Compensating for unreported catch (Cheung *et al.* 2013), the Bahamas' Nassau grouper catches were estimated to have declined about 70%, from around 1,300 t in 1994 to 400 t in 2009. Moreover, the proportion of Nassau grouper in the total fishery landings (all species) in the Bahamas also declined from 10%



**Figure 13.** Reported landings (in t) of Nassau grouper in the Bahamas from 1994 to 2009 as compiled by the Bahamas Department of Marine Resources (solid line) and corrected for under reporting of fisheries landings by a factor of 94% (broken line, sensu Ehrhardt and Deleveaux, 2007). The grey area indicates the year fishing of spawning aggregations fishing ban started, although there was little evidence of enforcement (as of 2003) except for one site where voluntary enforcement was implemented (Cornish and Eklund, 2003) (from Cheung *et al.* 2013).

to 4% during this period, suggesting that the decline in landings was not mirrored in other exploited taxa which might indicate a change in fishing effort or market conditions. This strongly suggests a differentially high decline in the Nassau grouper compared to other species taken in the multi-species fishery. Various reasons may explain the decline in Nassau grouper's landings, including decline in stock abundance, reduction in fishing effort (unlikely for reason given above), and an increase in level of under-reporting of fishery landings. It is noteworthy that unit price appears to be increasing as commercial landings decline, consistent with declining availability (Cheung *et al.* 2013).

The results of the Cheung *et al.* (2013) study suggest that the population may now be fully- to over-exploited and undergoing decline, although this needs to be validated when more fishery and population data are collected. Results of the study suggest that the fishing mortality during non-aggregation fishing is sufficient to drive populations below a target Spawning Potential Ratio (SPR) of 35% to SPR of 20% without fishing aggregations, although poaching during the aggregation season continues to be a concern. A decade ago, Sullivan-Sealy *et al.*

(2002) found that the majority of Nassau grouper landed in New Providence, a major landing area, from 24 November 1999 to 15 February 2000 were not in spawning condition; almost one third were likely immature or reproductively inactive, being within the size range of late juveniles and early adults (528 +/- 61 mm TL.). They were either caught during spawning migrations or were sexually immature. Fishers reported that ‘aggregations’ of migrating fish, which were not ripe, were quite common, but this behavior is not widely reported.

Information on trade is largely limited to within-country sales except for grouper imports from the Bahamas into the United States. Market surveys reveal different aspects of the fishery. According to monthly fishermen interviews and landing abundance surveys conducted at Montagu ramp (Nassau), a key market outlet, from May 2007 to October 2007, the cost for a 4-4.5 kg Nassau grouper averaged US\$35.00. Of a total of 54,000 fish landed during the 6-month survey period, Nassau groupers made up an average of 10% (by number) monthly (i.e. about 5,400 individual fish) with June being the lowest (4%) and October being the highest (13%) (Cushion and Sullivan-Sealey 2007). This study also noted that a sizeable proportion of Nassau grouper were marketed by sellers who purchased them from large-scale commercial fisheries in New Providence. Thus, the total abundance noted in the study did not solely represent the effort of Montagu-based fishermen.

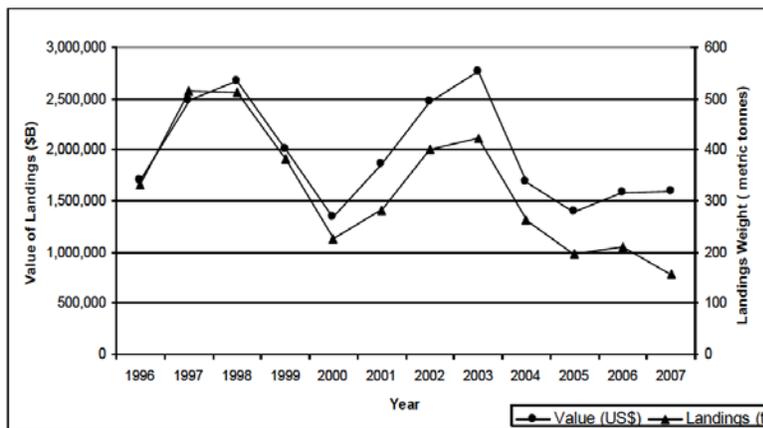


Figure 14. Landings and Value.

There has been significant international trade of grouper to the United States from the Bahamas since at least 1993. Data suggest that over an 18-year period the proportion of total Bahamas commercial production exported to the United States annually is consistently about 10% (by weight). This is calculated based on NOAA statistics of imports of ‘Grouper’ into the United States

(<http://www.st.nmfs.noaa.gov/st1/trade/index.html>) corrected by a factor of 73% which represents the proportion of all grouper commercially landed in the Bahamas (according to Bahamas national statistics), which are comprised of Nassau grouper (FAO 2009). The impact of possible Nassau grouper importation into the US is unknown at this time.

### The Bahamas – Conservation and Management

Several measures are in place for the management of the Nassau grouper. In the 1980s a minimum size of 3 lbs. (1.36 kg) was introduced, a no-take marine reserve was established in the

mid-1980s in the Exuma Cays (and others subsequently), seasonal closures of several spawning aggregation sites were first implemented in 1998, and an annual “two-month” (variable according to full moon) fishery closure was first implemented in December 2003. This closure was extended in 2005 to last from December through February. This is applied on a yearly basis and unlike seasonal protection for other key marine resources, aggregation protection legislation is not solidly in place. It may be shortened or otherwise influenced by such factors as the economy (Sadovy and Eklund 1999). For example, following the economic downturn of 2008 the closure was lifted to lessen the economic burden of a closed fishery to fishermen.

In the Bahamas both spatial and seasonal protective measures are in force. The Exuma Cays Land and Sea Park, first established in 1959, has been closed to fishing since 1986, thus protecting both development and adult habitat for Nassau grouper and other depleted marine species, such as queen conch, spiny lobster and marine turtles. Evidence from the Exuma Cays Land and Sea Park shows a clear difference in the number and size of all large grouper species between fished and non-fished areas. The biomass of Nassau grouper was shown to be statistically greater inside and within 5 km of the Park boundaries and reproductive output (egg production) was calculated as six times higher than outside the park (Sluka *et al.* 1997). Recent studies by Dahlgren and co-workers (unpub. data) have seen additional increases in biomass from less than 300 g/100 m<sup>2</sup> in 2000-2004 to near 1100 g/100 m<sup>2</sup> in the 2005-2009 period and more than 1100 g/m<sup>2</sup> from 2010 -2013. The current level is about twice that seen by Sluka *et al.* (1997) in the mid-1990s. Other sites, including the South Berry Islands Marine Reserve (SBIMR) (declared on December 29, 2008), Southwest New Providence National Park site, and north Exumas study site also have shown some increases in biomass in recent surveys but none is even half of that seen in the Exuma Cays Land and Sea Park.

During Nassau grouper spawning seasons between 1998 and 2006, the aggregation at High Cay, Andros, and those found on the eastern coasts of North and South Long Island were protected from fishing activities five days before and after the full moon during the months of December, January and February. On 16 December 2003, the Bahamas Director of Fisheries announced the first-ever closed season for the species, thus prohibiting throughout the country the “taking, landing, processing, selling and offering for sale of fresh Nassau grouper” during spawning periods. The closure was subsequently replaced by an annually renewable nationwide closure of fishing for the Nassau grouper during the winter months (December to February) (Department of Marine Resources 2007, Cheung *et al.* 2013). Local NGOs are working to have this changed to a permanent rather than an annually renewable measure (BREEF.org). There is no available information on the current status of all spawning aggregations.

Several gear controls in place are relevant for, but not specific to, the Nassau grouper. Fishing with SCUBA and the use of explosives, poisons, and spearguns is prohibited, although sling spears are allowed. The use of bleach or other noxious or poisonous substances for fishing, or possession of such substances on board a fishing vessel, without written approval of the Minister, is prohibited. Government policy restricts commercial fishing to the native population

and, as a consequence, all vessels fishing within the Bahamas Exclusive Fishery Zone must be fully owned by a Bahamian citizen residing in the Bahamas.

Spear fishing within one mile of the coast of New Providence and Freeport and 200 yards of the coast of all other Family Islands is prohibited, as is the use of firearms or explosives. For nets, a minimum mesh size of 2 in. is necessary, except when fishing goggle-eye (big-eye scad) or pilchard. Fish traps are required to have self-destruct panels and minimum mesh sizes of 1 by 2 in. for rectangular wire mesh traps and 1.5 in. (greatest length of mesh) for hexagonal wire mesh traps. Those wishing to sell fish catches in New Providence must possess a permit. A permit is required to use air compressors for fishing purposes and the use of compressors is restricted to the period 1 August-31 March and to depths of 10-20 m. The capture of grouper and rock fish weighing less than 3 lbs. is prohibited. Dalhgren (pers. comm.) has pointed out that a 3 lb. Nassau grouper is only about 45 cm long, roughly 3 cm shorter than the minimum size of maturity for females. A 10 cm increase to 57 cm would ensure that at least 75% of fish could spawn before legal fishery removals.

Other means to improve Nassau grouper sustainability include suggestions that poaching must be more carefully controlled and that fishing effort during the non-spawning periods should be reduced from the 1998-2001 level (Cheung *et al.* 2013). Such measures would address the main concerns expressed by fishers about the Nassau grouper fishery; poaching and enforcement of fishery management measures were mentioned by almost half of the fishermen interviewed. Although a reduction in fishing mortality through reduction of fishing effort, may affect the short-term economic benefits, the fishery would perform better economically and as a food source over the long-term (Cheung *et al.* 2013).

There is no mechanism in the Bahamas for declaring a species “endangered,” “threatened,” or “protected.” To advise the public and develop support for, and understanding of, the need for protective measures, outreach campaigns were conducted on the closures and to discourage the purchase of Nassau grouper during the protected season. The invasive lionfish was suggested, with some success, as an alternative fishing target and food choice.

## BELIZE

### Belize -- Populations

Belize, with its extensive reef system and coastline, was once a major habitat for the Nassau grouper and by all accounts the species was historically extremely abundant. Grouper aggregations have been severely reduced in Belize, at sites such as Mexico Rocks, Rise and Fall Bank, and Caye Glory, as indicated by Green Reef's national Grouper Spawning Aggregation Assessment (2001). Estimated numbers of fish taken from spawning aggregations was the main indicator available of population size with these once exceeding an estimated 30 thousand fish during just one spawning season at just one aggregation site (Caye Glory) and reports of tens of thousands of fish were once the norm (Craig 1966). At Caye Glory, once Belize's most productive grouper bank, where catches reached 2 tons per day in the late 1960's, the January 2001 assessment found a maximum of 21 fish underwater. Fishermen at the site caught only 9 fish during four days of intense fishing (Heyman and Wade 2005).

In Belize, there are at least 15 known spawning aggregation sites (Fig. 15) that occur along the barrier reef and on outer atolls. All sites occur within 120 m of (satellite-image visible) shelf edge lines, with the average distance to the shelf edge being about 80 m. Most sites are near inflection points of convex-shaped seaward-extending reefs (within 360 m of reef promontories) (Kobara and Heyman 2007, Kobara 2009). These features have been used to try to identify unknown spawning aggregations in Belize and other parts of the Nassau groupers range.

Species-specific annual landings data at the national level are not available. However, starting in 2003, an effort was undertaken to monitor numbers of spawners at priority spawning sites. Recent monitoring yielded counts of a few hundred fish in most remaining aggregations surveyed (Table 12), with a few thousand in a couple (Belize Spawning Aggregation working group: (<http://collaborations.wcs.org/Default.aspx?alias=collaborations.wcs.org/spag&>)). Dog Flea Caye was highlighted as a site where illegal fishing has continued and the numbers of spawners have greatly decreased compared to sites with good enforcement (e.g., NE Point in Glovers Reef and Sandbore Cay in Lighthouse).

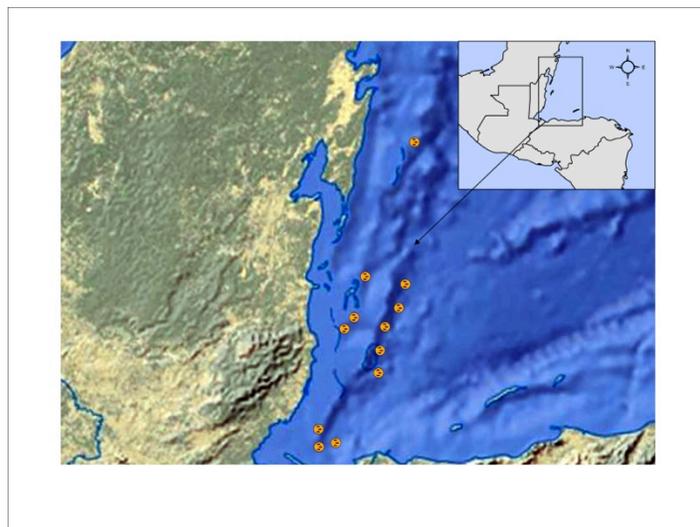


Figure 15. Belize spawning aggregation sites.

**Table 10. Fish count results for 10 years of monitoring priority spawning aggregation sites in Belize. (Belize Spawning Aggregation Working Group Information Circular 10, November 2012)**

<b>Maximum Nassau Grouper Counts for 2003 – 2012</b>										
<b>Site</b>	<b>2003</b>	<b>2004</b>	<b>2005</b>	<b>2006</b>	<b>2007</b>	<b>2008</b>	<b>2009</b>	<b>2010</b>	<b>2011</b>	<b>2012</b>
Rocky Point	0	200	200	0 <sup>1</sup>	N/A	0	N/A	N/A	0	2
Dog Flea Caye, Turneffe	1,500	100 <sup>3</sup>	-	2 <sup>2</sup>	N/A	N/A	N/A	N/A	4	4
Sandbore, Lighthouse	1,800	2,500	1,800	1,205 <sup>4</sup>	1,495	1,250	2,050	2,000	1,300	1,350
Caye Glory	1,000	1,000	350	7 <sup>5</sup>	69	405	3,000	N/A	400	120
NE Pt., Glover's	2,400	1,700	2,240	3,000	800	1190	1,100	3,328	1,800	1,050
Gladden Spit <sup>5</sup>	250	450	360	700	500	1106	260	238	375	164
Nicholas Caye	52	~50	80	48	80	100	25	30	45	85

<sup>1</sup> Only one dive; <sup>2</sup> Site only monitored in February; <sup>3</sup> Site only monitored in January; <sup>4</sup> Probably missed peak spawning due to bad weather, <sup>5</sup> Numbers for Gladden Spit revised by SEA in 2011)

Specific examples of declines in the species are inferred from spawning aggregation counts. Most of the declines occurred prior to the initiation of spawning aggregation monitoring (Table 12). At Glovers Reef a decline of 80% was recorded over the last 25 years (15,000 down to 1000-3,000 fish). Only 2 of the 9 aggregation sites known at that time remained by 2001; reduced from 30,000 to 1000-5,000 fish. All known aggregation sites have undergone dramatic declines in the abundance of spawning fish over the last 2 decades. Current aggregation protection does not appear to be restoring this species although almost certainly the efforts have stemmed decline. Minimum and maximum capture sizes were introduced a decade ago (Sala *et al.* 2001, Carter *et al.* 1994, Heyman and Requena 2002, Janet Gibson pers. comm., Sadovy de Mitcheson *et al.* 2008).

All known aggregation sites underwent dramatic declines in the abundance of spawning fish over the decades of the 1970-90s (Sala *et al.* 2001, Carter *et al.* 1994, Heyman and Requena 2002, Janet Gibson pers. comm.). Only a few of the 15 known aggregation sites remained by 2001 with maximum estimated numbers declining from 30,000 to 1-5,000 fish in single aggregations (Paz and Grimshaw 2001a, 2001b). Caye Glory, also known as Emily, was exploited for over 80 years with declines attributed to lack of management and a lucrative fishing industry that attracted many fishers (Paz and Truly 2007). At Glover's Reef, the spawning aggregation which harbored 15,000 Nassau groupers in 1975 had declined by 80% to less than 3,000 groupers in 1999 (Sala *et al.* 2001) and to about a thousand in 2011 and 2012 (Sadovy pers. obs).

Aggregation numbers assessed during the period 2003-2007 ranged from a high of 3,000 fish at Glover's Reef to lows of less than 10 fish at three other sites, although it was noted that surveys were not always as complete as desired. The 2012 data showed 2 sites with fewer than 5 fish, 3 sites with less than 200 fish and 2 sites with between 1000-1500 fish. Apparent declines resumed after the 2009-2010 surveys.

Several studies have examined movements of tagged fish. Along the barrier coastal reef, migrations in excess of 200 km have been recorded (Carter *et al.* 1994), while at Glover's Reef (an atoll) Nassau grouper showed strong fidelity to non-reproductive and spawning areas on the atoll and may not migrate off it (Starr *et al.* 2007). These studies suggest that Nassau grouper

might require contiguous reef tracts to migrate long distances, with population replenishment solely from larval recruitment in the case of atolls. Based on the findings of acoustic telemetry, Nassau grouper exhibited greatly synchronous migration to spawning sites during full moons from December through March despite their otherwise solitary habits. Groups of 50-100 fish have been seen migrating to aggregation sites. Reproductive adults leave their individual territories in shallow waters near the winter full moons, and migrate to the same spawning site up to four times per year staying an average of 11.6 days at the site during the winter full moons (Starr *et al.* 2007). Using tagging with VEMCO V16 acoustic tags at 7 locations, including spawning aggregation sites off the coast of Belize from April 2000 to January 2003, Heyman and Carr (2007) demonstrated that individuals stayed near spawning aggregations during their spawning season. Following spawning a remarkable population-wide depth change has been reported within an hour as individuals in a group dive to a maximum depth of 255 meters (Starr *et al.* 2007).

## **Belize - Fishing**

Historically, the Nassau grouper was the basis of a very important finfish fishery in Belize, which included export trade, using handline, speargun, and fish traps. Spearguns and handlines were used to fish grouper aggregations at least as early as the 1940s (Thompson 1945, Perkins 1983), and fish traps increased after 1986 (Auil<sup>18</sup>). Handlines are often rigged with 3 to 15 hooks per line (Munro 1983a). The fishing boats of Belize are typically 5-7 m vessels equipped with outboard engines or larger sail-powered boats (Perkins 1983). Along with Cuba and the Bahamas, Belize reefs were among the most important locales for this reef-associated species, an assumption based on documentation of spawning sites and the large reef areas (i.e., suitable habitat for the species) available. Although there are no official annual national landings statistics for the species (finfish are lumped in landings data) accounts of the reef fishery over the years are clear testimony to its one-time importance to the country (Craig 1968, Carter *et al.* 1994, Paz and Truly 2007).

Apparent reductions in Belize population(s) of Nassau grouper are most strongly indicated by a trend of reduced catches from spawning aggregations, once the major source of annual landings of the species, and historic accounts, Craig 1966: "*On the seaward side of the reef (Caye Glory), grouper (Epinephelus striatus) congregate in astonishing numbers in waters fifteen to twenty fathoms deep where they can be seen moving slowly over the rocky bottom. These fish are believed to be spawning...*" Craig's account talks about up to 300 boats at the site with a single experienced crew catching from 1200 to 1800 fish during a single reproductive season. Craig (1968) estimated catches from this site at as much as 90,000 kg per season. Overfishing was already apparent by the 1960s as indicated by reduced aggregation catches.

Despite the declines, the fishery still has value. Large volumes were once exported

---

<sup>18</sup> Auil, Stephanie. 1991. University of the West Indies, P.O. Box 863, Belize City, Belize. Pers. Comm.

internationally although most sales today are evidently made within the country (Paz and Truly 2007). Shortly before fishing on spawning aggregations was banned countrywide, the economic value of the 2000-2001 Nassau grouper catch in Belize, largely derived from the domestic market and although negligible relative to prior years, was estimated at approximately US\$210 per fisherman, or US \$40 per fisherman-day, for a small number of fishers in the study. This is approximately four times the minimum wage in Belize (Paz and Grimshaw 2001b). Fishermen continue to have an economic incentive to catch Nassau grouper in Belize, even though its reduced population cannot support a large number of fishermen (Paz and Truly 2007).

Non-aggregation catches of Nassau grouper have also become important in more recent decades. Beginning in the 1970s, Nassau grouper were taken throughout the year and not just from aggregations (Paz and Truly 2007); Sala and colleagues (2001), for example, noted that 14% of the adult population is removed annually by year-round spear fishing. Information on fish sizes caught in the non-aggregation season is suggestive of the start of a recovery. At Glover's reef, surveys of fisher catches from 2004 to 2010 suggest an increase in average length from a mean of 371 mm (total length) and 493 in 2007 to 563 in 2010 (Janet Gibson pers. comm.). Since Glover's Reef may well be largely self-recruiting and its aggregation is protected this may suggest the start of a recovery.

## **Belize – Conservation and Management**

Management of the Nassau grouper has a long history in Belize although there are still no annual national landings figures for the species. Its status is determined by numbers of fish at spawning aggregations and also by fishermen experiences and sporadic reports. The Fisheries Department is responsible for the monitoring, control, and surveillance of the fishing industry (Carcamo 2008). The first measure to protect Nassau grouper was a seasonal closure within the Glover's Reef Marine Reserve in 1993; the area was closed from Dec 1 to March 1 of the following year. In 1996, the new marine reserve, Bacalar Chico, also included a seasonal closure zone for the protection of the Nassau grouper spawning aggregation (Paz and Truly 2007).

Given growing interest and concern for the species, in 2001 the Belize National Spawning Aggregation Working Group was established. During 2002, a coalition of seven NGOs, government, fishers, and other stakeholders worked successfully to establish protective legislation for 11 of the known Nassau grouper spawning sites, and to introduce a four-month closed reproductive season in 2003 (O'Connor 2002, Gibson 2008). Seven sites (Table 12) are monitored as regularly as possible and include: Rocky Pt. (Bacalar Chico Marine Reserve), Dogflea Caye (Turneffe Islands), Sandbore (Lighthouse Reef), Emily/Caye Glory, Gladden Spit (Gladden Spit and Silk Cayes Marine Reserve), Northeast Point (Glover's Reef Marine Reserve) and Nicholas Caye (Sapodilla Cayes Marine Reserve). The Working Group meets regularly to share data and develop management strategies ([www.spagbelize.org](http://www.spagbelize.org); retrieved on 15 April 2012) and monitoring continues at several sites.

In 2003 two Statutory Instruments were enacted. The first declared 11 sites, including “Emily” (= Caye Glory) as marine reserves closed to fishing all year round. Those sites that were wholly or partially located in marine reserves, but not included in any seasonal closure or conservation zone, could be used only by traditional fishermen recommended by the respective co-managers of the reserve and with special license granted by the Fisheries Administrator. The second Statutory Instrument established a four-month closed season for Nassau grouper, extending from December to March. Fishermen at Mauge Caye and Northern Two Cayes, however, were allowed to fish during the spawning season, but only under special license granted by the Fisheries Administrator, a condition of which was that all catch would be verified by a Fisheries Officer (Paz and Truly 2007). These exceptions made the national protection difficult to enforce and hence starting in the 2010-2011 season, special licenses to fish for Nassau grouper at these two sites during the closed season were no longer issued. These final two sites, however, are not yet designated as fully protected areas closed to fishing. Therefore 13 aggregation sites are now protected out of the 15 known. Of the remaining two sites, Mauge Caye should be protected when the Turneffe Islands marine reserve is declared. North Two Caye's protection is still being worked on.

In early April 2009 the Minister of Fisheries signed into law additional measures to help manage and protect the Nassau grouper. These include minimum and maximum size limits of 510 mm (20 inches) and 760 mm (30 inches), respectively, and a planned ban on spear fishing within all marine reserves (yet to be implemented). Furthermore, as a large proportion of fin fish catches are landed as fillets, the new regulations require that all Nassau grouper be landed whole, and if filleted must have a 1-2 inch (25-50 mm) skin patch (The Belize Spawning Aggregation Working Group 2009). Other gear restrictions are in place for reef fishes generally to aid in their management, such as no spearfishing on compressed air.

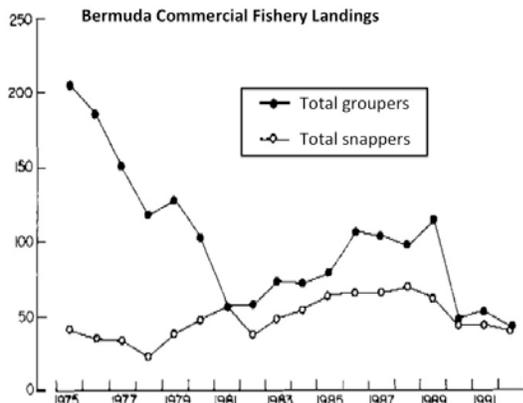
Gibson *et al.* (2007) indicated that the provision of assistance for management and enforcement, and sustaining the political will at the highest levels would be necessary to enforce the laws to enhance the protection of spawning aggregations. There has been extensive public outreach in the country to inform the public of the management measures and the need to protect the Nassau grouper, including film, TV, radio, etc. Although marked recoveries have not yet been noted following implementation of management it is almost certain that this has prevented further declines and more time will be needed for recovery to be evident. The multi-sector national working group model in Belize appears to have been very effective in gathering support for management measures and may serve as a useful model.

## BERMUDA

### Bermuda – Populations

The understanding of population change and status of Nassau grouper in Bermuda must be derived from a combination of ecological studies and fishery dependent data reports. In a historical context, groupers have dominated Bermuda's fisheries. Bardach *et al.* (1958) discussed the abundance and importance of groupers to the island while providing information on aspects of their biology. Density of Nassau grouper on surveyed shallow reefs in Bermuda in the 1950s was estimated at 12 fish per acre (34.6/hectare), with the fish weighing an average of 1.1 kg (2.42 lbs.) (Bardach and Menzel 1957). Bardach *et al.* (1958) estimated that groupers comprised approximately 70% of total food-fish landings during the period of their study (middle 1950s), with snappers contributing 20% to the total. Cumulative data from REEF (2003-2013) show sightings of only 9 Nassau grouper in 1594 surveys (density index 1.1, sighting frequency 0.3%) across the 10-year period (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>). This means that primarily surveys only detected a single Nassau grouper when seen on a dive and only 0.3% of the dives actually had Nassau grouper. While the surveys do not have a way to convert to areal comparisons, the frequency of occurrence is quite low

compared to earlier conditions.



**Figure 16. Proportions of Groupers and Snappers in Commercial Landings - Bermuda.**

In 1975, a fisheries statistics program became fully operational providing catch and effort data from the industry on a compulsory basis. In the first year of the program (Fig. 16), groupers comprised 47.6% of the total landed weight of food-fish (total 431 mt) while snappers contributed 9.8% (Luckhurst and Ward 1996). Density and landings declined drastically between 1975 and 1981 (Luckhurst 1996). By 1989, total food-fish catch had increased to 623 mt but the species composition of the catch had changed significantly with the grouper landings being reduced to 18.7%

of the total, while snappers were largely unchanged at 10.1 %.

The overall pattern in landings of groupers declined sharply from about 231 mt in 1975 to approximately 58 mt in 1981 (Fig. 17), followed by an increasing trend until 1989. However, the species composition of the grouper catch changed markedly during the 1980s with two smaller species comprising almost 50% of total landings in 1989 (Luckhurst and Ward 1996). A fish pot ban was put into effect in April 1990 in an effort to allow the recovery of coral reef fish stocks, which had been subjected to heavy fishing pressure with fish pots (traps).

Following the fish pot ban, the total grouper landings level declined by 58% and remained stable through 1992. An analysis of the trends in individual grouper species indicates the relative contribution of each species to this general pattern. Nassau grouper underwent a sharp decline from over 33 mt in 1975 to less than 2 mt in 1981, a drop of 95.0% in landings. Despite over 10-years of no-take protection of the Nassau grouper in Bermuda, Nassau grouper had made no appreciable recovery and numbers remained extremely low as of 1999 into the early 2000s (Sadovy and Eklund 1999, Semmens *et al.* 2008a). The species had not shown any evidence of a subsequent recovery by 2005 (Luckhurst 2005). Although they are still considered rare, there are some anecdotal reports by divers of more Nassau grouper in the past 10-15 years (Brian Luckhurst pers. comm., Sept. 2012). As far as anyone knows, Nassau grouper spawning aggregations no longer form in Bermuda.

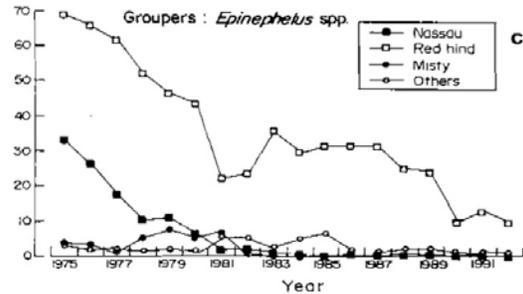


Figure 17. Proportion of grouper species in landing from Bermuda commercial catch.

## Bermuda – Fishing

In the 1950s, the annual food-fish harvest totaled approximately 450,000 kg (450 mt) and consisted of an estimated 70% grouper (grouper and rockfish); 20% snapper; 9% jack, mackerel and tuna and 1% other species (e.g., hogfish) (Bardach *et al.* 1958). According to fishery records available since 1975, commercial grouper landings declined in Bermuda despite an increase in effort over the period (Bannerot *et al.* 1987). By 1989, the total catch of food-fish had increased to about 621,000 kg (621 mt) per year. The composition of the catch in 1989 showed significant changes, 18.7% of the catch consisted of grouper; 10.1% snapper; 15% jacks; 25% tunas and related species and 31% was comprised of miscellaneous reef fish, such as parrotfish, porgy, grunt, triggerfish, hogfish and Bermuda chub. The shift from a catch dominated by grouper and snapper to one dominated by herbivorous reef fish, such as parrotfish and surgeonfish, resulted from the severe decline in the preferred target species (groupers) (Burnett-Herkes and Barnes 1996). While all groupers were affected, among those most severely reduced was the Nassau grouper. Landings of *E. striatus* declined from 16% of total grouper (all species) catch, by weight, in 1975 to <1% in 1989 (Bannerot *et al.* 1987, Report of the Commission of Inquiry, Bermuda 1991).

Nassau grouper were fished primarily during aggregation periods using handlines, traps, and spearguns; commercial fishermen exploited concentrations of *E. striatus* in Bermuda for generations (Burnett-Herkes 1975). Aggregations were known from the Challenger and Argus

(=Plantagenet) banks. Three sites were fished until the mid-1970s (Burnett-Herkes 1975). The four known historical aggregation sites no longer form and had probably crashed by 1981 according to fisher accounts (Bannerot *et al.* 1987, Luckhurst 1996). By the early 1990s, no aggregations were known to have formed for at least a decade (Jack Ward pers comm). Despite subsequent protection, the fishery for this species is considered commercially extinct (Bannerot *et al.* 1987, Luckhurst 1996; Brian Luckhurst, pers. comm. Sept. 2012). It appears that the spawning stock biomass was reduced below a critical but unknown level so that the population has apparently been unable to recover (see Sadovy 1996). Mean size and frequency of sighting has reflected these changes. Mean size sampled at offshore banks in the mid-1950s was approximately 620 mm FL (Bardach *et al.*, 1958) with considerably smaller individuals inshore. Following the collapse of the aggregations, only juvenile Nassau grouper were seen but only rarely inshore (Jack Ward. pers. comm.). There have been anecdotal accounts of catches of Nassau grouper, involving good-sized fish, however, since Nassau groupers are protected fishermen are reluctant to report catching or possessing them. Fish are often filleted to avoid detection so the extent of any perceived increase is unknown (Brian Luckhurst, pers. comm. Sept. 2012).

### **Bermuda – Conservation and Management**

The earliest fisheries management measure to conserve spawning aggregations was in Bermuda in 1974. This involved the seasonal closure (4 months) of two red hind aggregation sites. This management action was called for by commercial fishermen and the regulation was enacted by the Fisheries Department. Following this measure, catches continued to decline but then stabilized in the longer term. Compliance or enforcement is not well documented. Nassau grouper aggregations seaward of these red hind sites were not protected under the regulations and were heavily fished. As a result, Nassau grouper landings declined 95% from 1975-1981 and all known aggregations disappeared. Bag limits (2 fish) and minimum size restrictions (356 mm FL) were in effect for the Nassau grouper prior to 1990 (Luckhurst 1990).

There has been no demonstrable recovery to date. The seasonal closure of the red hind aggregation sites is still in effect 31 years later although there have been some modifications of boundaries and the size of the protected areas.

Nassau grouper in Bermuda have been managed since 1996 with no-take and no-possession regulations but in spite of those conservation measures, Nassau grouper has made no appreciable recovery. The species is completely protected through prohibition on take and possession and possibly benefits from numerous no-take marine reserves (Brian Luckhurst pers. comm., Sept. 2012).

## **BRITISH VIRGIN ISLANDS**

### **British Virgin Islands – Populations**

Little information is available on Nassau grouper in the British Virgin Islands (BVI) although anecdotal accounts suggest that considerable landings still occur although not from aggregations. Cumulative data from REEF (2003-2013) show sightings of only 107 Nassau grouper in 2003 surveys (density index 1.2, sighting frequency 5.3%) across the 10-year period (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>). Requests for updated information through the fisheries department have received no response.

### **British Virgin Islands – Fishing**

Little information is available on Nassau grouper landings or aggregations in the BVI although anecdotal accounts suggest that landings still occur. In the mid-1990s, large Nassau grouper were still being caught east of Pajaros Point, Virgin Gorda, but these were evidently incidental catches (Munro and Blok 2005). More recently, fishers report that medium-sized Nassau grouper are still quite common but that aggregations are no longer actively targeted. Only a few Nassau grouper were landed at the BVI Fisheries Complex during the winter months of 2003 (Munro and Blok 2005). Based on the findings of a survey conducted in January to February 2003, Munro and Blok (2005) found no evidence of any spawning aggregation from a previously reported site on the Saba shelf. Fishers interviewed claimed that they could catch 20-40 Nassau groupers per day at the site 15-20 years ago.

### **British Virgin Islands – Conservation and Management**

Nassau grouper can be seen for sale in the BVI Fisheries Complex and in supermarkets. There is reportedly a closed season for landing Nassau grouper between March 1 and May 31, *subject to confirmation* (Munro and Blok 2005).

## CAYMAN ISLANDS

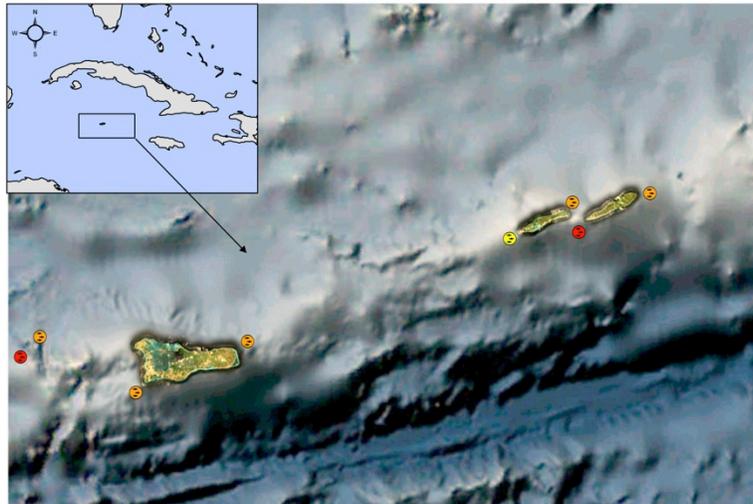
### Cayman Islands – Populations

The Nassau grouper may still be relatively abundant in the Cayman Islands compared to many other locations (Patengill-Semmens and Semmens 2003) according to visual surveys and the status of several spawning aggregations. Cumulative data from REEF (2003-2013) show sightings of 1857 Nassau grouper in 3746 surveys (density index 1.7, sighting frequency 49.6%) across the 10-year period (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>). In the Cayman Islands, the Nassau grouper fishery was once considered to be on the brink of collapse even though fishing was managed. Spawning aggregations are now protected to allow recovery; a second of two 8-year protected periods was recently approved and, indeed, numbers of fish are showing promising signs of increase in at least one aggregation site (Semmens *et al.*

2007a; Department of Environment 2011, Heppell *et al.* 2012).

The Nassau grouper stocks in the Cayman Islands appear to have shown some degree of resilience under fishing pressure, due to the cumulative effects of inclement weather during the aggregation seasons (i.e., limiting fishing opportunities), some protection from poaching with the

regular presence of researchers at the site during the spawning season, possible recruitment from nearby offshore banks, and a possible shifting of aggregation sites that remain unfished or unknown (Whaylen *et al.* 2007). Researchers observed shifting of the aggregated spawners on the scale of several hundred meters (Whaylen *et al.* 2007) and there are some reports of similar shifts at other sites (Aguilar 2006) that make this a possibility. It is possible there are other minor satellite aggregation sites that remain unfished but it is unlikely and over the last 16 years catches have steadily declined in the Nassau grouper fishery (P. Bush, pers. observ.).



**Figure 18. Cayman Islands (islands west to east Grand Cayman, Little Cayman and Cayman Brac).**

Historically, fishing on the sites produced thousands of fish annually and in the 1970s even included the sale of catch to Jamaican vessels (Whaylen *et al.* 2004).

There are 5 traditional aggregation sites confirmed in the Cayman Islands, one of which, off Little Cayman's west end, is likely the largest aggregation (in terms of fish numbers) known in recent times anywhere within the geographic range of the species. The Little Cayman site is located on a reef promontory on the western edge of Little Cayman Island (Rand *et al.* 2005). Whaylen *et al.* (2004) recorded (from underwater observations) that the average estimated number of Nassau grouper present at the aggregation site off Little Cayman in 2002 was 5,200 individuals two days after full moon. The mean size of aggregating grouper was 620 mm TL and the overall female to male sex ratio was 1:1.6. Whaylen *et al.* (2004) from this 2002 study and others report that females exhibit dark phase and males exhibit bicolor phase at the point of gamete release although in the lead-up to spawning both sexes might display both colors at other times (Archer *et al.* 2012). A hydroacoustic study of the aggregation suggested the presence of more fish than counted by divers due to the fact that the aggregation appeared to be spread patchily over a wider area than that covered by divers; on the other hand, fish close to the substrate were noted by divers but not hydroacoustically; a combination of divers and hydroacoustics is suggested for such studies (Taylor *et al.* 2006).

In the Cayman Islands, all spawning aggregation sites are located within 50 m of the shelf edge (30 or 40 m depth) and adjacent to deep water (> 200 m). Heppell *et al.* (2008) proposed that spawning might be timed to allow larvae to return on local gyres to Cayman Island waters suggesting that the condition of local populations may be critical to their long-term sustainability. Kobara (2009) revealed that all 5 best-known Cayman Islands spawning aggregation sites are located at convex-shaped seaward extending reefs (reef promontories) jutting into deep water, within 1 km of reef promontory tips.

### **Cayman Islands – Fishing**

The Cayman Islands once had a small local traditional fishery for Nassau grouper with 90% or more of the landings coming from the 5 then-known annual spawning aggregations (Whaylen *et al.* 2004b). The traditional fishing culture evolved into one economically dependent on marine tourism and finance over the past 30 years (Bush *et al.* 2006). Tucker *et al.* (1993) reported five Nassau grouper spawning aggregation sites historically in the country: one at the southeast corners of each of the three islands, one at the southwestern corner of Grand Cayman, and another at the southeast corner of the Twelve Mile Banks west of Grand Cayman. The aggregations at the eastern ends of the islands were the most well-known, and traditionally exploited since the early 1900s with the use of small open boats and hand lines (Bush *et al.* 2006). K. P. Tibbets of Cayman Brac (pers. comm. in Colin 1987) reported having fished these aggregating locations since 1925-1926, and his father had fished them since about 1903.

In 2001, fishermen found aggregated Nassau grouper on the west end of Little Cayman

Island (Whaylen *et al.* 2004, Bush *et al.* 2006), although based on more recent discussions with elders in the fishing community, it appears that the west end spawning site was fished earlier in the century (late 1960s) but perhaps fished out. Two more sites have been noted as potential spawning aggregations bringing the likely total to eight (Bush *et al.* 2006).

Of the sites monitored between 1987 and 2001, (Bush *et al.* 2006: “*three of the country’s sites were considered fished out, catch from Grand Cayman and Little Cayman during the early years of the monitoring period was in the low hundreds and has since dwindled. In Cayman Brac, while catch was in the low thousands during the initial years following the re-discovery of the spawning aggregation, it too has declined drastically in the last six years. Little Cayman east end site was abandoned in 1993 when the aggregation ceased to form, three sites were in serious decline (Catch, CPUE, and size all declined), and one, the rediscovered site off the western end of Little Cayman, though affected by two years of heavy fishing, is still relatively healthy. Catch-per-unit effort and size for all three islands show similar marked trends.*” During 20 days of fishing at the aggregation site off the western end of Little Cayman approximately 4,000 fish were taken during the 2001 and 2002 spawning season (Whaylen *et al.* 2004). Pre-fishing abundance for this aggregation was estimated at over 7,000 fish so a large proportion of estimated fish were removed in a very short time period (Bush *et al.* 2006).

The sharp decline in catches of Nassau grouper in the Cayman Islands since 1996 (Whaylen *et al.* 2004, Bush *et al.* 2006) is presumably due both to aggregation and non-aggregation catches. Based on a mark-recapture study from Cayman Brac, fishermen are capturing 15-20% of the spawning population outside the spawning season, implying the Nassau grouper population may continue to decline even with a full spawning season closure (B. Semmens pers. comm.)

According to the estimated spawning aggregation fish numbers in Grand Cayman, and a detailed report of poaching, it is believed that about 30% of all adult Nassau grouper were caught while spawning (Dept. of Environment 2011). Semmens *et al.* (2007b) suggested that older, larger fish are more susceptible to harvest on unprotected spawning sites due to the amount of time they spend aggregating compared to smaller individuals. Also, smaller aggregations tend to stay longer on site possibly exposing them to more fishing (Brice Semmens pers. comm.).

## **Cayman Islands – Conservation and Management**

Nassau grouper have long been a target of local traditional fishermen. In about 1978 (Phil Bush pers. comm. 2001), the three main (“traditional”) grouper “holes” were officially recognized as such and only residents were allowed to fish at the designated grouper holes during spawning season. Only line fishing was permitted. In 1986 increasing complaints from fishermen of a decline in both numbers and size of Nassau grouper taken from the fishery

prompted the implementation of a monitoring program by the Department of the Environment (Bush *et al.* 2006).

In the 1990s several management measures were tried. In 1995, an “Alternate Year Fishing” strategy was recommended but was not implemented due to lack of political support (Bush *et al.* 2006). In 1998, the three main spawning areas at the eastern ends of the islands were formally designated as “Restricted Marine Areas” for which access required licensing by the Marine Conservation Board (the statutory authority responsible for the administration of the Marine Conservation Law) (Bush *et al.* 2006). In the 1990s legislation prohibited spearfishing at spawning aggregation sites. In February 2002, protective legislation defined a spawning season as November 1 to March 31, and the “Alternate Year Fishing” rule was passed. This law allowed fishing every other year with the first non-fishing year starting with 2003, and also set a catch limit of 12 Nassau grouper per boat per day during fishing years. The law defined the one nautical mile “no trapping” zones around each spawning site, and set a minimum size limit of 12 inches for Nassau grouper in 2002 in response to juveniles being taken by fish traps inside the sounds (Whaylen *et al.* 2004, Bush *et al.* 2006). In 2003 spearguns were restricted from use within 1 nautical mile of any designated grouper spawning area (DGSA) November through March.

Effective 29 December 2003, fishing was closed at all designated Nassau grouper spawning sites for a period of 8 years. In adopting this decision, the Marine Conservation Board noted that two of the six areas were “fished out and three in serious decline.” According to research results from surveys on the Little Cayman west end spawning site, the number of spawners increased from approximately 2,500 fish to 4,000 fish over the eight year protection period. The conservation measure was renewed for a further 8 years in 2011. In 2008 it was prohibited to take any Nassau grouper by speargun anywhere in Cayman waters with no trapping within 1 nm of a protected aggregation during the spawning season (Nov. 1 – Mar. 31). Seasonal and spatial measures state that no Nassau grouper is to be taken from any DGSA from November to March until 2019. Total area of the current 8 DGSA’s is 17.56 km<sup>2</sup>. From the results of a mark-recapture study on Cayman Brac, Cayman Island fishermen appear to be skilled enough to catch sufficient adult grouper outside the spawning season to seriously impact populations (Semmens *et al.* 2012).

The indications of recovery (as determined by increased abundance of fish) are encouraging in Little Cayman and on Cayman Brac, but the aggregation there has not been assessed in several years. Grand Cayman, however, still has very few grouper, and the high fishing pressure surrounding the small no-take area aggregation site, as well as poaching, appear to keep the population depressed. The importance to the Cayman Islands of larvae originating outside the country is not known but ongoing genetics studies should contribute to that knowledge.

## **COLOMBIA**

### **Colombia – Populations**

Little information on the species in Colombia is available, with fish evidently mainly on offshore banks. Cumulative data from REEF (2003-2013) show sightings of only 11 Nassau grouper in 401 surveys (density index 1, sighting frequency 2.7%) across the 10-year period from the populated islands of the San Andrés Archipelago (San Andrés Island, Providencia, and Santa Catalina (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>)). In a report by Prada et al. (2004) artisanal fishermen indicated that in the San Andrés, Providencia, and Santa Catalina Archipelago (Old Providence) on the northeast and south banks, local people once fished Nassau grouper during spawning aggregations from around five different sites. Occasionally, a few Nassau grouper are still caught, but past abundances had not been seen in a decade. In the study, ten sites were identified as potential spawning aggregation sites, including five for Nassau grouper, fished for many years, although nowadays only a few individuals are ever seen.

### **Colombia – Fishing**

Colombia reported to FAO a maximum of 120 mt of Nassau grouper landed in the early 1990s. However, by the early 2000s the fishery may have collapsed with no landings reported thereafter. No large spawning aggregations have been reported for this species from Colombia. In a study of information collected from commercial fishing companies for 2006-2007, Nassau grouper represented 12% of longline catches of large serranids in San Andrés; aggregations of 50 or so Nassau grouper have been reported (Hooker 2012, pers. comm.).

### **Colombia – Conservation and Management**

In the San Andrés Archipelago of Colombia, there are a number of areas that are designated as no-take fishing zones; in 2000, the archipelago was declared by UNESCO as the Seaflower Biosphere Reserve. In 2004, large portions of the archipelago were declared as a system of marine protected areas with varying zones of fisheries management however enforcement is largely lacking. Right-to-fish laws also require that fishermen, particularly elder fishermen, be allowed to fish at a subsistence level even within the no-take zones (Prada pers. comm.). No other regulations could be identified that might benefit Nassau grouper within Colombian waters.

## CUBA

### Cuba – Populations

Biological studies on the Nassau grouper have not been undertaken in recent years but biological and fishery details may be found in Claro et al. (1990, 2009). Claro et al. (2001) and Claro and Lindeman 2003



Figure 19. Confirmed Nassau grouper spawning aggregation sites of Cuba.

documented known spawning aggregation sites of snapper and grouper, most of them multi-species; information was primarily fishery-dependent rather than from underwater surveys. The earliest documentation of Nassau grouper aggregations and seasonal migrations anywhere was in the 1800s in Cuba indicating a substantial fishery at that time (Vilaro Diaz 1884). Little information on the current status of the species is available (Fabian Pina pers. comm.).

Cumulative data from REEF (2003-2013) show sightings of 38 Nassau grouper in 120 surveys (density index 1.6, sighting frequency 31.7%) across the 10-year period. The bulk of these samples (n=105, 33 Nassau grouper/ density index: 1.6, sighting frequency: 31.4) were taken on the west side of Cuba (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>).

### Cuba – Fishing

Off Cuba, Jamaica, and Hispaniola, trap fishing has been the primary method for catching grouper (Munro and Thompson 1983). Boats are typically non-mechanized and less than 6 m long (Claro et al. 1990, Baisre 1993). The Antillean (arrowhead) fish traps are wooden-framed with galvanized wire mesh and one or two entrance funnels (Munro 1983a). The single funnel “chevron traps” are commonly used in the eastern Caribbean, and the “S” or “Z” shaped traps, with dual entrance funnels, are found in Cuba and Jamaica. Most traps had mesh sizes between 25- 50 mm (Munro 1983a).

Historically, the Nassau grouper was among the most important finfish species landed in Cuban fisheries, yielding some of the highest catches for the species anywhere within its geographic range. Given the very high quality of landings data for key commercial species in the country, which extends from the 1960s and, for some species was recorded monthly, there is an excellent and unmatched record of landings for this species over almost 5 decades (Claro et al. 2002, 2009). Fishing pressure on the Nassau grouper increased notably after 1959, reaching 1,700 mt in 1963, after which time landings declined (Fig. 20). The detailed dataset from the 1960s shows that the great majority of landings was taken from spawning aggregation sites and times, 50% of the annual catch from December to February (Fig. 21). Most catches of Nassau grouper (35–50% of the national capture of the species) were historically taken in the Archipelago Sabana-Camagüey (north-central area), although up until 1969 an important proportion of this catch was obtained from the Bahamas shelf. A somewhat sudden collapse, suggesting a *hyperstability* condition (in which concentrations of fish, e.g., aggregating for spawning, mask a general population decline), occurred in the late 1970s, despite some protective management. The data also show that, despite a gradual increase in finfish landings (Fig. 20) between 1962 and 1998 (Claro et al. 2001), probably due to increasing fishing effort, Nassau grouper showed a precipitous decline, strongly suggesting that it is more vulnerable to fishing, or more heavily targeted, than other reef fish species (Claro et al. 2009, Sadovy de Mitcheson et al. 2008).

Most landings were reportedly taken by fish traps and, of the 20 or so historically reported aggregation sites, none have been confirmed to still form in significant numbers in recent years although about 9 have been reported in the most recently available fisher accounts. Claro et al. 2009: “*Due to declining fish yields over time and the resulting reduction in profitability of fishing on aggregations, fishing effort on the spawning aggregations declined. The peak catches noted after 1980 occurred mainly*

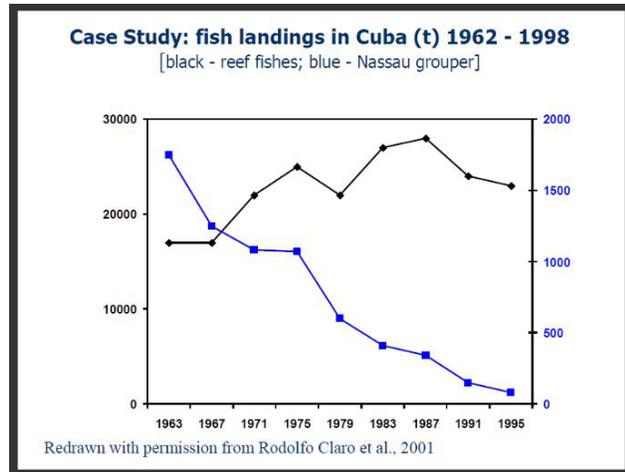


Figure 21. Fishery landings in Cuba (1962-1998)

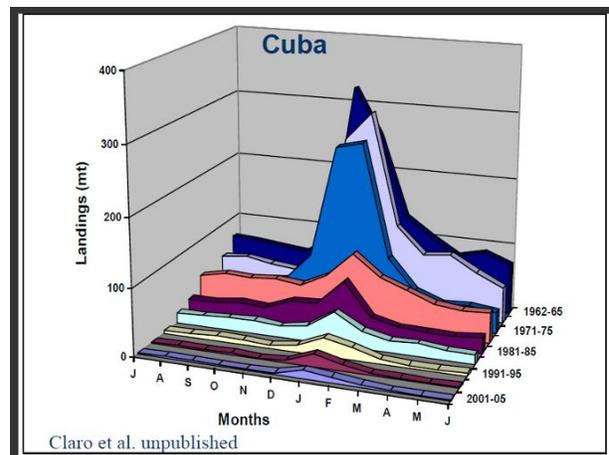


Figure 20. Seasonal landings from Cuba, noting decrease of catches of Nassau grouper during spawning season.

*during spawning migrations when the vulnerability of fishes to fishing gears such as set nets was high. Nevertheless, there persisted an important recreational fishery, using both hook and line and spear-gun, on the spawning aggregation sites in the northern Cuban Archipelago. The size of this fishery is unknown due to lack of statistical information and divers have not surveyed spawning aggregation sites to assess the numbers of fish assembling to spawn. The main aggregation sites in southern Cuba (Puntalón de C. Guano and Banco de Jagua) are no longer regularly fished due to the difficult accessibility of these sites. Overall, relatively few viable spawning aggregations are thought to persist in Cuba today.”*

## **Cuba – Conservation and Management**

Cuba has a long and well-documented history of exploitation and management of the Nassau grouper, which was once an important commercial species landed in the country. Cuban fleets also fished extensively for the species outside of Cuban waters, particularly in the Bahamas. The fishery was largely based on catches taken during the spawning aggregation season (Fig. 21). In the 1970s, aggregation catches suddenly dropped, indicating a severe reduction in the fishery which was not attributable to change in effort or other factors as far as could be determined (Claro et al. 2009). Data on current status of the fishery are unavailable. There are reported to persist a possible 9 out of 20/21 previously known aggregation sites although these have not been validated recently.

Since the 1980s, many regulations have been introduced to address particular species, issues, such as declines in catches, or regions, e.g. seasonal spawning closures, gear bans, fishing effort control, etc. These were often introduced for short periods of time and by particular Fishing Associations. For Nassau grouper, there was an almost complete absence of species-specific protective management, with the exception of a minimum legal size (32cm TL=570g) that is too small for the species based on size at maturity. Of some benefit to the Nassau grouper were bag limits for recreational fishing, regulations to increase selectivity of several fishing gears (mesh size) to avoid the catch of juveniles, control of set net use and limits during spawning aggregation time, and controls of speargun use both commercially and recreationally. Marine protected areas have been introduced. In 2002, the total number of recreational licenses was limited to 3,500 for the whole country hoping to reduce directed fishing pressure. Enforcement of these regulations has been variously effective (Claro et al. 2009) but recovery of the species is not recorded.

## **DOMINICAN REPUBLIC**

### **Dominican Republic - Populations**

The current status of Nassau grouper is largely unknown although indications are that the species has been largely depleted from local reefs. Reports suggest that large fish can still be seen in the fish markets on the north coast (J. Mateo pers. comm.) although the locations from which those catches derive are unknown (but see Bahamas, above). Cumulative data from REEF (2003-2013) show sightings of only 4 Nassau grouper in 116 surveys (density index 1.3, sighting frequency 3.4%) across the 10-year period. All sighting in these samples (n=84, 4 Nassau grouper/ density index: 1.3, sighting frequency: 4.8%) were from Manzanillo Bay to Cabo Engano on the north coast (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>). Data from Sadovy (1997) indicated one known spawning aggregation from Punta Rusia although status was listed at the time, as “probably disappeared.” Underwater visual censuses in the Dominican Republic, (1994) produced no records of Nassau grouper (Schmitt and Sullivan 1994).

### **Dominican Republic – Fishing**

Off Cuba, Jamaica, and Hispaniola, trap fishing has been the primary method for catching grouper (Munro and Thompson 1983). No landings have been reported from the Dominican Republic for many years and the species appears to have been severely depleted in local waters. Poaching by Dominican vessels in Bahamian waters for this species has been reported.

### **Dominican Republic – Conservation and Management**

In the Dominican Republic little information could be obtained about specific fishing regulations however it is reported that since the mid-1980s no catch or sale of ripe females in spawning season is allowed (Bohnsack 1989, Sadovy and Eklund 1999, Box and Bonilla Mejia 2008). At least one marine park has been established with fishing regulations however no information is available on Nassau grouper presence in the Park.

## HONDURAS

### Honduras – Populations

Despite the economic importance of the Nassau grouper in Honduras there are few data on the species or its fishery, either artisanal or commercial. Much of the ecological studies have appeared in reports that are not readily available (see citations in Fonseca et al 2004).

Cumulative data from REEF (2003-2013) show sightings of 809 Nassau grouper in 3047 surveys (density index 1.3, sighting frequency 26.6%) across the 10-year period. Most of the sighting in these samples came from Roatan (n=1884, 585 Nassau grouper-density index: 1.4, sighting frequency: 31.1%) and Utila (n=1071, 202 Nassau grouper-density index: 1.2, sighting frequency: 18.9%) (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>). No government unit or institution collects data on the species. To provide an overview of the species, a review was commissioned (Box and Bonilla Mejia 2008). The only other published studies located are those by Fine (1990, 1992) documenting the rapid demise of one aggregation site.

The Box and Bonilla Mejia (2008) report found that Nassau grouper landings increased up until the end of the 1980s and early 1990s and then declined, losing commercial importance in 2003. In the early 1990s there was evidence of uncontrolled fishing of Nassau grouper spawning aggregations. For example, at one site close to Guanaja, local and foreign vessels reduced the aggregations from approximately 10,000 fish to less than 500 in 2 years; fishers removed 13.64 t (30,000 lbs.) per season (Fine 1990, 1992). Other aggregations probably

occurred in the area historically but since declined, according to anecdotal fisher accounts (Box and Bonilla Mejia 2008).

Further evidence of declines of this species is reflected in reduced exports of Nassau and red groupers in the last few decades (Box and Bonilla Mejia 2008). Peak exports occurred during the Nassau grouper spawning season but declined severely overall between 1995 and 2004. Anecdotal reports from fishing communities suggest that the ‘Grouper’s Joy’ site and

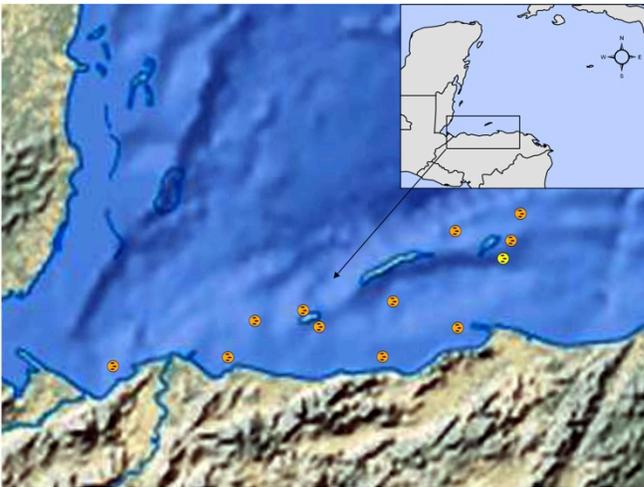


Figure 22. Confirmed and suspected (yellow circle) spawning sites in Honduras.

migration routes into spawning areas have been intensively fished since the late 1990s and that the fish is now uncommon. The 2008 report concludes that the species is now a much smaller proportion of reef fish taken in the country, representing <5% of income from the fishery. Nassau grouper declined from 7% by weight of exports to the USA in 1996 to 0.7% in 2007. Fishing communities report that Nassau grouper are being replaced by *Mycteroperca venenosa*, yellowfin grouper. Catch of Nassau grouper tends to be incidental to that of snappers and lobster fisheries, which are conducted largely by spear.

## **Honduras – Fishing**

Local fishermen and commercial boats in the Bay Islands have exploited Nassau grouper; Roatan, La Ceiba and Guanaja are the main commercial fishery centers for the country, including for catches of Nassau grouper. Spawning aggregations were fished with traps and spears. Most Nassau grouper landed were exported to the USA (about 95%); there has never been an important market for the species within Honduras (Box and Bonilla Mejia 2008). The one documented spawning in Honduras, Caldera del Diablo, outside Guanaja appears to have been eradicated in the early 1990s (Fine 1990, 1992) although there are no supporting biological data on its current condition. Fishers have reported many other locations that are likely to be spawning sites although their current condition is likewise unknown. It is thought that only the more inaccessible sites, such as Banco Campiche, are still likely to have aggregations (Box and Bonilla Mejia 2008).

One instance of poaching/enforcement was documented in February 2009. Four Honduran fishermen from Puerto Cortez were arrested while actively night fishing in Belize waters at the closed Nassau grouper site in Gladden Spit and Silk Cayes Marine Reserve (GSSCMR). Their catch, including 19 Nassau groupers was inventoried and they were fined approximately \$19,200. Two fishermen, unable to pay their fines, were remanded to jail (Belize Spawning Aggregation Working Group Information Circular No. 7, June 2009).

## **Honduras – Conservation And Management**

There is no legislation that controls fishing in the snapper/grouper fishery in the country although traps and spear are illegal in the Bahia Islands. A black market evidently continues particularly in the illegal sale of fish by lobster fishermen but its extent and impact are unknown. Some fish leave the country illegally on vessels and some are taken illegally on local boats not licensed to take fish. Confidential interviews indicated that during the spawning season of up to 1,000 lbs. of grouper per boat were once landed causing local saturation and reducing sale prices (Box and Bonilla Mejia 2008).

## **JAMAICA**

### **Jamaica – Populations**

Jamaica's coral reefs are among the best studied in the world beginning with research by T.F. Goreau and co-workers in the 1950s (Goreau 1992). Observations by researchers at the Discovery Bay Marine Laboratory of the University of West Indies and other scientists have added to the information base (M. Vierros, [www.agrra.org/reports/jamaica2.html](http://www.agrra.org/reports/jamaica2.html)). Jamaica is located at the center of coral diversity in the Atlantic Ocean (Wells and Lang 1973), with over 60 species of reef building corals, and with fringing reefs occurring on a narrow, 1-2 km shelf along most of the north coast of Jamaica. Reefs also grow sporadically on the south coast on a broad shelf over 20 km wide (Hughes 1994). In addition, reefs and corals can be found on the neighboring banks of the Pedro Cays, 70 km to the south, and the Morant Cays, 50 km to the southwest (Woodley et al. 1998).

Jamaica's coral reefs reflect changes over the past 4-5 decades from the combined effects of human and natural disturbances reinforcing one another (Woodley 1995). The natural impacts, most notably the die-off of *Diadema antillarum*, the spiny sea urchin, in the 1980s and hurricane damage, pushed the deterioration in Jamaica's coral reefs. Recovery after the natural disturbance was prevented by chronic human disturbance, notably over-fishing and increased sediment and pollution runoff (Woodley et al. 1998). Depletion of reef fish populations in Jamaica has been well documented. Extensive studies in Jamaica by Munro (1993) showed that in the decades leading up to the 1960s fish biomass had been reduced up to 80% on the extensive fringing reefs of the north coast, mainly a result of intensive artisanal trap fishing. By 1973, the number of fishing canoes deploying traps on the north coast was approximately 1800 (or 3.5 canoes per square kilometer of coastal shelf), which was two to three times the sustainable levels (Munro 1983). The taxonomic composition of fish had changed markedly and large predatory species, including groupers had virtually disappeared (Hughes 1994) and a marked decline in the equilibrium productivity of the fishery (Koslow et al. 1994).

When asked about present conditions, K. Aiken (2012, per. comm.) stated that while Nassau grouper were occasional in the 1970s, they are now rare. "I haven't seen one since 2011 and only at one location at the extreme east of Jamaica."

### **Jamaica – Fishing**

The fisheries of Jamaica, as reported by Aiken and Street (1993) were largely made up of artisanal fishermen operating from open canoe type boats powered by either outboard motors or oars. Approximately 12,000 registered fishermen using approximately 400 boats (reduced from earlier reports) worked from 168 fishing beaches scattered around Jamaica's coastline. The fisheries may be further subdivided into the inshore fishery and the offshore fishery. The offshore fishery began operating primarily from the south coast following a government program to mechanize more than half of the fishing boats. The offshore fishery harvests from offshore cays, as well as remote deepwater areas. The fisheries of Jamaica are multispecies, targeting all coral reef fish resources.

The Fisheries Division collects catch and effort data under the LRS (Licensing and Registration System). Jamaica also enters the data collected under a statistical sampling frame into the TIP (Trip Interview Program database developed by CFRAMP (CARICOM Fisheries Resource Assessment and Management Programme). A query to the CARICOMP data manager failed to uncover any data pertinent to Nassau grouper (Hill, pers. comm., Dec. 2012).

Off Jamaica trap fishing has been the primary method for catching grouper (Munro and Thompson 1983). The Antillean (arrowhead) fish traps are wooden-framed with galvanized wire mesh and one or two entrance funnels (Munro 1983a). The single funnel "chevron traps" are commonly used in the eastern Caribbean, and the "S" or "Z" shaped traps, with dual entrance funnels, are found in Cuba and Jamaica. Most traps have mesh sizes between 25-50 mm (Munro 1983a).

In Jamaica, fishing surveys conducted in the early 1970s resulted in Nassau grouper CPUE of 1.4 kg per line hour in 20-30 m of water and 1.7 kg per line hour in 30- 45 m (Munro, 1983b). With the advent of motorized boats and mechanized gears, intense exploitation led to lower catch rates of all reef fish and the disappearance of some species from multispecies catches (Stevenson 1981). A survey of reef fishes in Jamaica in 1986 revealed no groupers (Koslow et al. 1988) and by 1989 Nassau grouper were rarely caught (Sadovy 1997).

### **Jamaica – Conservation And Management**

No special regulations exist for Nassau grouper specifically. There are some MPAs but they are only 2 years old so not a lot of changes are expected yet (K. Aiken, pers. comm.).

## **LESSER ANTILLES, CENTRAL AMERICA, AND SOUTH AMERICA**

### **Lesser Antilles, Central America, and South America – Populations**

Nassau grouper are known to occur on the northern coast of South America, but aggregations have never been recorded from the continental shelf even where substantial fisheries have existed such as in Colombia (Sadovy and Eklund 1999). Little abundance information could be found from Venezuela although they were reported at least from Los Roques (Cervigón 1994, Boomhower et al. 2010). Cumulative data from REEF (2003-2013) show sightings of 2 Nassau grouper in 32 surveys (density index 1, sighting frequency 6.3%) across the 10-year period. Additional surveys are listed for Venezuela (n=148) but locations are not given and no additional Nassau grouper were recorded (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>).

In the Lesser Antilles, Nassau grouper was reported to be very scarce in St. Eustatius (Munro and Blok 2005). On the Antigua-Barbuda bank, according to findings of a survey conducted in January and February 2003, Munro and Blok (2005) reported a spawning aggregation site at Knolls in the central area of the shelf of Antigua-Barbuda Bank. Cumulative data from REEF (2003-2013) show sightings in the Leeward Islands (i.e., Anguilla, St. Martin/St. Maarten, St. Bartholomy, Saba, St. Eustatius, St. Kitts, Nevis, Antigua, Guadeloupe, and Dominica) of 123 Nassau grouper in 1815 surveys (density index 1.3, sighting frequency 6.8%) across the 10-year period. Sightings in the Windward Islands (i.e., Martinique, St. Lucia, St. Vincent, Barbados, The Grenadines, Grenada) for the same period (n=3004, 12 Nassau grouper/ density index: 1.8, sighting frequency: 0.4%) suggest that Nassau grouper are much more scarce (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>). H. Oxenford (2012 pers. comm.) stated that she has not seen a Nassau grouper in 30 years of diving for reef research in Barbados.

In Trinidad and Tobago, Nassau grouper are considered to be locally extinct (Bouchon et al. 2008). Contacts to the fisheries department elicited the response that Nassau grouper are quite rare and never show up in the fish market (J. Alemu 2012 pers. comm.).

### **Lesser Antilles, Central America, and South America – Fishing**

In the Lesser Antilles, larger groupers are fished with handlines and with traps from 4-8 m long boats equipped with 8 to 48-horsepower outboard engines (Mahon 1990); since the shelf is so narrow off the Lesser Antillean Islands, there has been no great need for larger boats. Groupers are sometimes caught off the deeper slopes using electric reels or mechanized winches for hauling traps (Mahon 1990). Little information is available regarding other fisheries from the area that target Nassau grouper.

## **Lesser Antilles, Central America, and South America – Conservation and Management**

In Antigua-Barbuda the *Fisheries Act, No.14 of 1983* and the *Fisheries Regulations, No.10 of 1990*, are the primary legislative basis for fisheries management and development of all fisheries including the (Nassau) grouper fishery. The Act and Regulations make provision for 1) fisheries management elements, such as fishing licensing, enhanced fisheries research and enforcement, the registration of fishing vessels and the establishment of a fisheries advisory committee and 2) conservation measures, such as prohibiting the use of certain fishing methods and gear, setting species size restrictions, establishing closed seasons, and creating marine reserves. With the assistance from the FAO of the UN, initiated in 2003, the Fisheries Act, No. 22 of 2006 was passed and enacted (Horsford, 2009) to bring local regulations more in line with current international fisheries laws including the European seafood provisions, primarily benefiting exports. It also gave the Minister improved management capabilities, such as moving most fisheries from open access to licensed or permitted fishing. Nassau grouper is not specifically managed or protected but in 2008 there was consideration of closed seasons for both it and red hind, the more dominant species in the local grouper fishery.

In Guadeloupe and Martinique, there are plans to protect the species (Franck Gourdin, pers. comm.) although no details are available at this time.

Other locations seem to have a few spatial closures (e.g., St. Lucia) that would benefit Nassau grouper but they were not designed for the species or their aggregations.

## MEXICO

### Mexico – Populations

A total of 28 aggregation sites have been reported in Mexico (Aguilar et al. 2008) but, only four (Fig. 23) have been verified (Aguilar-Perera et al. 2008). The two best studied sites (Aguilar-Perera 2006) include Mahahual, which apparently no longer forms; recent checks from Dr. A. Aguilar-Perera found no fish spawning in 2013 (pers. comm.), and Xcalak, the largest known aggregation in Mexico. Historically, aggregations of up to 15,000 fish formed each year at Mahahual, but due to increased fishing pressure in the 1990s aggregations have not formed since 1996. Despite conservation concerns, the Nassau grouper is little managed (but see below),

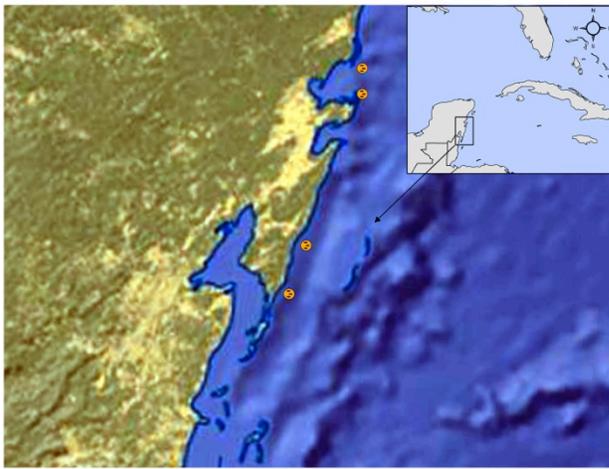


Figure 23. Nassau grouper spawning aggregation sites confirmed off Quintana Roo, Mexico.

with the limited exception of the Xcalak site, which is in a national park. In addition to these two aggregations, two other sites have been confirmed by diving (Nichehabin and San Juan Chenchomac) the biggest of which had 800 groupers; this was identified for the first time by fisher accounts in 2005 (Aguilar-Perera et al. 2008). A further 24 sites, reported from fisher interviews along the coast and on Chinchorro Bank, have not yet been verified to have Nassau grouper and many are likely to be located on migration routes rather than traditional

spawning sites (Sosa-Cordero et al. 2002, Aguilar-Perera et al. 2008, Aguilar-Perera pers. comm.).

Detailed studies have only been conducted at two of the four confirmed sites, Xcalak and Mahahual, the latter, highly accessible to fishing. According to the results of UVC conducted in Mahahual during the reproductive seasons of December and January from 1991 to 1997, migrating aggregations (about 50 to 800 groupers) were found moving along the forereef border 1 km south of the traditional aggregation site from December 1991 to January 1993. In December 1993, only 15 groupers were observed at the site while no aggregation was found during the 1996 and 1997 seasons (Aguilar-Perera 2006) suggesting that the aggregation had either ceased to form or formed elsewhere. Extensive searches of the area by divers failed to locate any Nassau grouper within kilometers of the spawning site (Aguilar-Perera pers. comm.). Aguilar-Perera (2006) suggested that decline and apparent disappearance of individuals from the

traditional aggregation site off Mahahual was due to overfishing over the last 50 years.

The aggregation site at Xcalak was the largest known in Mexico with 4,100 fish reported in 2004-5, up from 203 fish in 2001-2 (Medina-Quej et al. 2004, Aguilar-Perera 2006, Bolio-Moguel 2007). The other studied aggregations occur at “El Blanquizal” on the south coast of Quintana Roo and Punta Gavilan (Medina-Quej et al. 2004). Fisher interviews suggested the presence of several extant spawning aggregations on the offshore Chinchorro Bank but these have not been validated (Aguilar-Perera et al. 2008). There is little indication of overall population status of the Nassau grouper in Mexico but concern exists about the overfishing of any remaining spawning aggregations.

Cumulative data from REEF (2003-2013) show sightings of 314 Nassau grouper in 5916 surveys in the Mexican Caribbean (density index 1.2, sighting frequency 5.3%) across the 10-year period. The largest number of these surveys were conducted at Isla Cozumel (n=5218) with sightings of 279 Nassau grouper (s.f.=5.3%, d.i.=1.2). The coastline including Veracruz also lists 11 Nassau grouper from 625 surveys with sighting frequency of 1.2% (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>).

## **Mexico – Fishing**

The Nassau grouper has long been an important food and commercial fish in Mexico, exploited for over 70 years. In the Mexican Caribbean, while secondary as a fishing target to the Caribbean spiny lobster (*Panulirus argus*) and the queen conch (*Strombus gigas*), the Nassau grouper has been seasonally important and generally taken at its spawning aggregations in December, January and February. There has been concern by fishers, biologists, and fisheries authorities over declines in catches although there are no species-specific landings data collected (Aguilar-Perera, pers comm.).

At Mahahual, Mexico, fishermen used 3 types of fishing gears (i.e. hook-and-line, speargun and gillnets) for exploiting the aggregation (Aguilar-Perera 1994). From the early 1950s to the 1970s, hook-and-line was used; spear guns were used in the late 1960s through the early 1990s. The efficiency of spearguns led to a decline in annual landings (Aguilar-Perera 1994). Gillnets were used from 1989 and after spearguns were banned (1993) at spawning aggregations, gillnets (15-20.3 cm mesh) use increased as barrier nets around aggregation sites and blocking migration routes. Mean size for gillnetted fish caught at two aggregations sites was about 600 mm TL (Sosa-Cordero and Cardenas-Vidal 1997). In Quintana Roo, Mexican fishermen are known to capture grouper by tying a live female to a line, pulling her up rapidly, and netting the males that follow her to the surface (Aguilar-Perera, pers. comm.).

At Mahahual in Quintana Roo, fishermen’s accounts (as early as the 1950s) indicate catches of up to 24 t of groupers per reproductive season directly from the spawning aggregation off Mahahual. This catch represents only 4 to 5 days of fishing during December and January using only hook-and-line gear (Aguilar 2006). These landings contrast sharply

with data gathered from the commercial catch (using gillnets with 15 cm mesh size) during the reproductive seasons each December and January from 1991-1997. By the early to mid-1990s landings from December aggregations had dropped to 3 mt and landings from January aggregations dropped to 1 mt (Aguilar-Perera 2006).

## **Mexico – Conservation and Management**

In the Mexican Caribbean Sea, there were no traditional fishery regulations (e.g. size, quotas, and fishing gear restrictions) from fishery authorities governing the exploitation of Nassau grouper aggregations. However, regulations were established following scientific documentation of declines at Mahahual (Aguilar-Perera 1994). In 1993, spear-fishing was banned at any spawning aggregation sites in southern Quintana Roo and in 1997 the fishing of any grouper species was banned during December and January (Aguilar-Perera 2006). However, these measures were temporary and were evidently not respected by fishermen. As is common in so many areas, lack of enforcement has been a persistent problem.

For all grouper species, a closed season from 15 February to 15 March was established for the first time in February 2003; it applies to all waters of the Mexican EEZ from Campeche and Yucatán (Gulf of Mexico) and Quintana Roo (Caribbean) states, as well as from Rio San Pedro, between Tabasco and Campeche states to the Belize border. While mainly offering protection to the related red grouper, *E. morio*, the Nassau grouper receives general protections (Aguilar-Perera et al. 2008), particularly during late spawning seasons. This law prohibits the removal of other grouper species (including *Mycteroperca venenosa*) during the reproductive season. The lack of continuous population monitoring from the start of the ban prevents assessment of rates of recovery of the Nassau grouper aggregations.

By the end of 2012, a management plan was to go into effect in the southern Gulf of Mexico and Caribbean for all commercially exploited groupers (about 17 species). This management plan is an initiative of the federal government through its office INAPESCA supported by scientists based on the best scientific knowledge available. For the first time, the Nassau grouper will have its own ban period in Mexico from December 1st to January 31 each year, mainly for the Mexican Caribbean where this species is more abundant. Another ban for all groupers in the Gulf of Mexico will extend from January 15 to March 14 each year. In the case of the Mexican Caribbean, the ban will also cover other aggregating groupers, such as black grouper, *Mycteroperca bonaci*. Status at this time is uncertain.

## **TURKS AND CAICOS ISLANDS**

### **Turks and Caicos Islands – Populations**

Nassau grouper in the Turks and Caicos Islands (TCI) is not subjected to significant commercial fishing pressure, one of the few countries where this appears to be the case, and is considered to still be in healthy condition with relatively high densities in some areas. Tupper (2002) and Tupper and Rudd (2002) reported densities in the range of 0.45 to 0.9 individuals per 100 square meters (45-90/hectare), with densities higher on deeper reefs and no difference in fish length by depth (Tupper 2002, Tupper and Rudd 2002, Rudd 2003a, Rudd, 2004). Chiappone et al. (2000) reported a density of 0.35-0.62 Nassau grouper per 100 square meters at South Caicos sites. These figures compare favorably with 0.01 per 100 square meters in the depleted Florida area and 0.16-0.20 per 100 square meters in the Bahamas in non-spawning times. Cumulative data from REEF (2003-2013) show sightings of 885 Nassau grouper in 1345 surveys (density index 1.7, sighting frequency 65.8%) across the 10-year period. With the exception of Salt Cay (s.f.=18.3%), all other survey sites have sighting frequencies ranging from 59.3 to 100% (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>).

Since the species is relatively unfished, field studies can provide valuable insights into its ecology and biology. Rudd (2003a) showed that Nassau grouper abundance did not vary with habitat type (channel reefs, fringing reefs, patch reefs and shelf edge reefs) and determined that while density was higher on deeper than shallower reefs, body length did not differ by depth.

Nassau grouper from South Caicos travel approximately 40 km to a large spawning aggregation at Philips Reef, off the island of East Caicos around the full moon in January. The aggregation is rarely fished due its remote location and rough seas (Rudd 2003a). Little else is known about this aggregation which is the only one reported in the country. Studies on juveniles show settlement in inshore areas (Claydon and Kroetz 2007). In an underwater survey conducted from 20 May to 23 August 2007 south of South Caicos, 209 Nassau grouper juveniles (< 12 cm TL) were observed within or close to (20 m) seagrass beds. Solitary conch shells were occupied by early juvenile Nassau grouper but these were largely absent from seagrass areas to the north of Dove Cay possibly because these habitats are threatened by their close proximity to land and the activities of large vessels, especially being on the route of container ships heading to and leaving the nearby dock.

### **Turks And Caicos Islands – Fishing**

The Nassau grouper has not been heavily exploited according to accounts although it is highly valued for the local tourism and restaurant markets and is also important in the diver tourism sector. Local populations are assumed to be in good health. Main target species in the

country are queen conch and lobster although in the past few years, fishers have increased their catch of scale fish, including Nassau grouper, for the local markets (unpublished Dept. of Environment and Coastal Resources, Turks and Caicos Islands National Report, 2008). The TCI are moving to diversify fisheries including for scale fish, which are evidently underutilized.

Larger boats with electric reels have now established a local market for their catch and increased harvest. With a growth in tourism, the local market has increased for the Nassau grouper. Many local fishers have found additional income from targeting reef fish in general. The problem with tracking scale fish is that all of the catch is not landed at licensed processors. Rudd and Tupper (2002) reported that the landing prices for the Nassau grouper at dockside reached US\$3.50 per kg while fishermen might sell Nassau grouper directly to restaurants for up to US\$15.00 per kg. There is a “back door” for the sale of scale fish to the local economy and little information available to assess stock condition. Some South Caicos fishers have begun to target grouper more recently as the value of the catch is often worth the expense of travelling 60 km to land the catch in Providenciales where their catch exceeds about 100 kg (Rudd, 2003b). Nassau grouper are an important component of restaurant consumption.

The Nassau grouper is a popular grouper because some other grouper species (e.g. tiger grouper, *Mycteroperca tigris*) contain ciguatoxin which limits their sales in restaurants. Rudd (2004) found that the introduction of an import tariff on fish significantly increased demand for local Nassau grouper. Many Nassau grouper caught on the South Caicos fishing grounds are taken by lobster divers who opportunistically spear fish (Rudd 2003b).

Few data are available on total catch of Nassau grouper but limited CPUE data suggest relatively low catch rates compared to other reef fishes. Tupper and Rudd (2002) found CPUE for Nassau grouper to be 0.7 kg per hour compared with 3.2 kg per hour for all reef fish. Fish abundance, as indicated by CPUE, is lower by 50% or more in fished rather than lightly fished or unfished (i.e. protected) areas but differed little between the latter two zones (Tupper and Rudd 2002). Tupper and Rudd (2002) found no differences in size, abundance or biomass between zones of different fishing intensity and suggested that fishing intensity was unlikely to explain the greater abundance and biomass on deeper reefs.

In addition to food, Nassau groupers provide non-extractive economic value (e.g. non-lethal catch-and-release fishing and wildlife viewing) to divers for tourism. An increase in Nassau grouper abundance and/or mean size adds value to the dive experience because most divers have preferences for viewing more fish and many divers express preferences for viewing larger fish (Rudd 2003a). Rudd and Tupper (2002) also reported that snorkelers as well as divers prefer viewing larger and/or more abundant Nassau grouper.

## **Turks And Caicos Islands – Conservation and Management**

One spawning aggregation site is protected from fishing in Northwest Point Marine National Park, Providenciales (DECR 2004; National Parks Ordinance and Subsidiary

Legislation CAP. 80 of 1988). In the Turks and Caicos Islands, the main aggregation site is remote and rough weather during the spawning season has generally restricted fishing activity. Seasonal closures may play a role in fisheries management planning in the future but in the short-term are not significant factors for Nassau grouper conservation in the Turks and Caicos Islands (Rudd, 2003b). Full protection of essential Nassau grouper habitat and spawning migration corridors on the very narrow fringe of Caicos Bank would impose economic hardship on local fishers who depend on those areas for commercial species (spiny lobsters) and subsistence fishing (Rudd 2004). Tupper and Rudd (2002) suggested that seasonal spawning closures in the Turks and Caicos Islands might have to be several months in length (e.g. November through March) to be effective. Despite relatively little fishery focus on the Nassau grouper, there is consumer interest in the species (a strong local tourism sector) and a significant proportion of fish in one recent study was taken below the size-at-maturation so pressure is expected to grow in the absence of management (Landsman et al. 2009).

## UNITED STATES (FLORIDA)

### United States (Florida) – Populations

Although there are few data on historic abundance of Nassau grouper off the U.S. mainland, it appears that abundance was once high in southern Florida (Springer and McErlean, 1962). Anecdotal reports from spearfishers noted large daily catches in the 1950s (Bohnsack 1990). Interviews of Florida Keys' residents suggested that Nassau grouper were once caught in much greater numbers from the upper Florida Keys and the Bahamas (Sadovy and Eklund 1999). Starck (1968) reported Nassau grouper frequently at Alligator Reef in the Florida Keys.

Historically there was a fishery for Nassau grouper in Florida suggesting once healthy (sub)population(s) in southeastern US mainland waters (Sadovy and Eklund 1999). However, now the species is rarely encountered. In the Dry Tortugas, where Nassau grouper were once abundant, only one individual was recorded in 1994 out of 183 point censuses and none in 37 predator censuses. On Elbow Reef, Florida Keys, mean Nassau grouper densities were 0.01-0.04 fish per 100 m<sup>2</sup> in 1993-94 (Sluka et al. 1998), with few seen on census dives through the Florida Keys. Censuses comparing areas protected and unprotected from fishing indicated that Nassau grouper, where protected, had a higher density and were one of the dominant grouper species observed (Sluka et al. 1994). Despite 10-20 years of no-take protection of the Nassau grouper in the Florida Keys, Nassau grouper has made no appreciable recovery and numbers remain extremely low (Semmens et al., 2007a, Don DeMaria pers. comm. 2012).

Reef fish surveys by the NMFS Southeast Fisheries Science Center's (SEFSC) Reef Team revealed low and declining densities from 1979-94 in southern Florida (Fig. 24); of 3,518 visual point counts Nassau grouper were recorded 29 times, the number declining to zero in

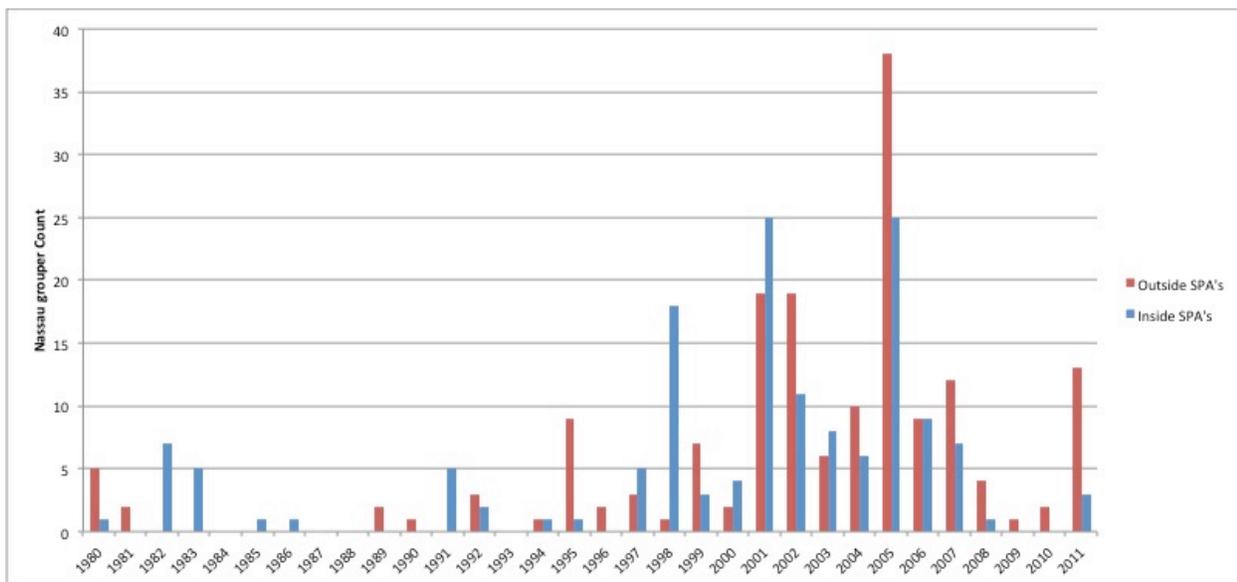


Figure 24. Counts of Nassau grouper observed in SEFSC reef fish visual census in the Florida Keys from 1980-2011.

1993. Numbers of Nassau grouper increased up to 2005, although so did the numbers of surveys (Fig. 25.). From 1980 to 1996, Looe Key and Molasses were the only protected (marine reserve)

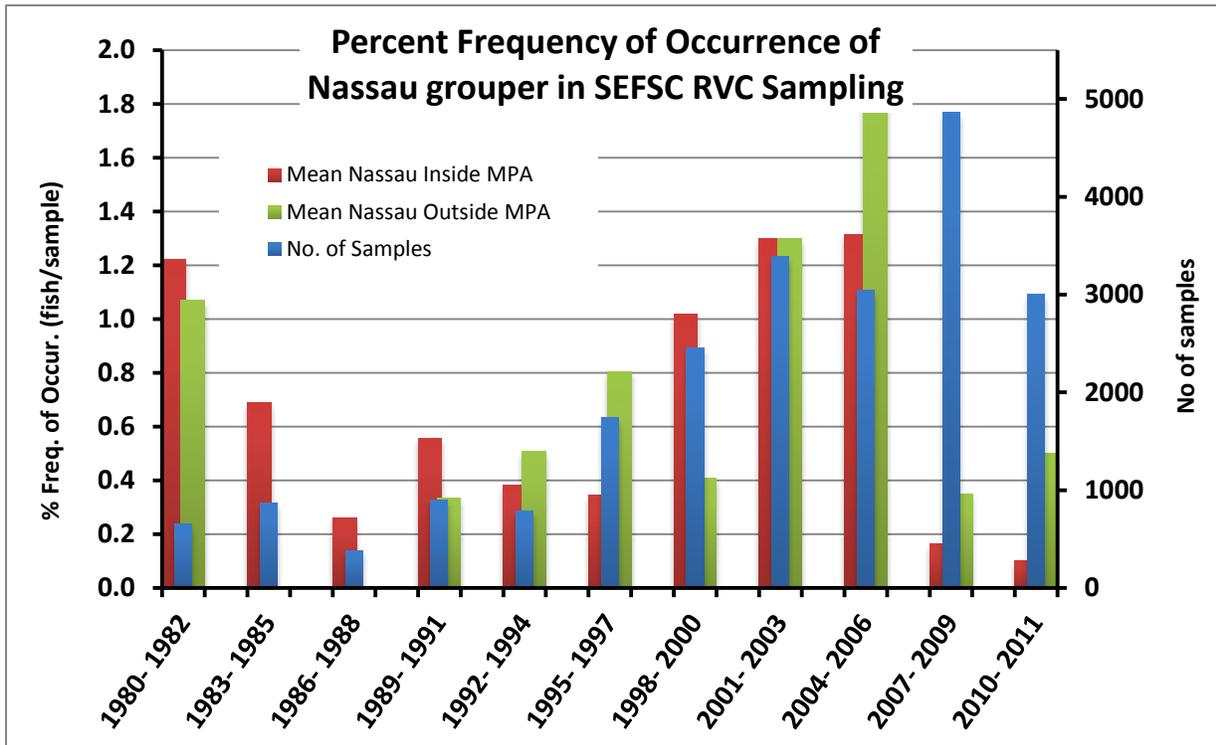


Figure 25. Mean Percent Frequency of Occurrence of Nassau grouper in 3-year Intervals (except for 2010-2011), data from SEFSC.

sites. In 1997, the marine reserve zones for the Florida Keys National Marine Sanctuary were established, including SPAs (Sanctuary Preservation Areas), and the Keys wide sampling design was developed to monitor reef ecosystem conditions. Throughout the range of surveys frequency of occurrence for Nassau grouper was low and comparable both inside and outside of marine reserves: 0 to 1.9% of samples included Nassau grouper (NMFS SEFSC data, supplied by J. Blondeau, 2012). A map of the distribution of positive encounters suggests they are distributed throughout Monroe County and does not suggest any clear pattern. In additional data, covering 2000-2007 (Key Largo to Dry Tortugas), in 8563 surveys 210 Nassau grouper were observed on 198 of the surveys

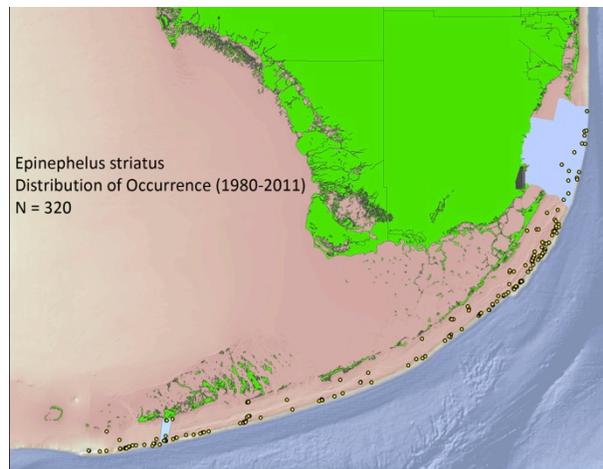


Figure 26. Distribution of samples with positive counts of Nassau grouper (SEFSC data, map by J. Blondeau).

(density: 0.0001/m<sup>2</sup> and 2.1% sighting frequency) (SEFSC data, supplied by T. Kellison 2012).

A large number and diversity of additional fishery-independent surveys over the last decade have resulted in records of only a few hundred fish overall (Alejandro Acosta, FWCC, pers. comm.). Florida Fish and Wildlife Commission underwater visual census has been conducted from 1999-2007 using two sampling approaches: Linear transects (a total of 10 individual Nassau grouper were recorded from 1127 transects (30m by 10m wide) and point counts (a total of 69 individual Nassau grouper were recorded from 7398 (5 m radius) surveys). During eight years of surveys only 79 Nassau groupers (out of 3927 total groupers) were observed. 92% of these fish were between 35 and 70 cm in length (J. McCawley, Director, Div. of Marine Fisheries Management letter to SERO).

Cumulative data from REEF (2003-2013) show sightings of 1322 Nassau grouper in 9706 surveys (density index 1.2, sighting frequency 13.6%) across the 10-year period. Surveys up the east coast to Jupiter Inlet report 83 Nassau grouper in 6763 surveys (density index 1.2, sighting frequency 1.2%) and on the west coast of Florida from Cape Sable to Tampa Bay 12 Nassau grouper in 590 surveys (density index 2, sighting frequency 2%) (<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>).

No Nassau grouper spawning aggregation sites have been identified in Florida waters.

### **United States (Florida) – Fishing**

Off Florida's Atlantic coast, Nassau grouper were caught primarily by handlines, although catches from spearfishing took more than one quarter of the commercial landings in 1989, 1991, and 1992 (cited in Sadovy and Eklund 1999). Commercial fisheries data prior to 1986 did not distinguish landings to species (e.g., grouper) so detailed data are unavailable prior to that year. Most recreational catch in the U.S. Atlantic came from private/rental boats.

In the eastern Gulf of Mexico, handlines and longlines accounted for 80-100% of Nassau grouper commercially landed, by weight, from 1986-92 (Sadovy and Eklund 1999). Incidental catch of Nassau grouper also occurred in fish traps, with the number of trap-caught groupers increasing since 1984 (GMFMC 1989). In the 1990s, most catch from the recreational fishery was from private/rental boats (detailed in Sadovy and Eklund 1999). An analysis of the headboat sector of the fishery showed a peak in headboat catches in 1981-1982 around 1.4 mt with a steep decline to about 0.35 mt by 1989 (Bohnsack 2003). By matching trends with Cuban fisheries, it is not unreasonable to conclude that headboat catches in the Florida Keys in the 1960s would have been 3 to 4 times higher than existing and temporally limited landings data.

There is currently no fishery for Nassau grouper in the United States (for additional details of the history see Sadovy and Eklund 1999). It is possible that fishing may still be a concern; Nassau grouper may show up as bycatch in various fisheries around south Florida. Barotrauma from rapid decompression, increased time in warm surface waters, and increased

exposure to predation threats may continue to result in species mortality even in the absence of a directed fishery (Bartholomew and Bohnsack 2005). Hook-and-line, longline, and trap fisheries, in which the target species are not seen may all result in unintended mortality for Nassau grouper.

### **United States (Florida) – Conservation and Management**

The species was once part of the multi-species commercial fishery in Southeastern USA but is now uncommon. Take and possession of Nassau grouper have been prohibited in federal waters since 1990. This includes federal waters around Puerto Rico and the U.S. Virgin Islands. A ban on fishing/possessing Nassau grouper has been in effect in the state of Florida since 1993 and has been enacted in all US state waters. The species is protected in Dry Tortugas Marine Reserve and Florida Keys National Marine Sanctuary. Information on import of the species into the US is needed to understand implications of international trade on regional Nassau grouper populations.

## UNITED STATES (PUERTO RICO)

### United States (Puerto Rico) – Populations

Puerto Rico once had significant landings and, hence, (sub)population(s) of Nassau grouper and at least one substantial aggregation in its southwest corner, according to anecdotal reports (Sadovy 1993). This aggregation appears to have long since disappeared and landings of the species, according to regular port surveys conducted by the government's 'Laboratorio de Investigaciones Pesqueras' (Fishery Research Laboratory) over several decades, dropped to negligible levels before the species was fully protected (in commonwealth and federal waters) in 2004. Although only a single (perhaps reforming) spawning aggregation has recently been found (Schärer et al. 2012), there were occasional reports of juvenile settlement in local waters suggesting either spawning aggregations at unknown sites in the region, and/or that mating in smaller groups (e.g., paired individuals) occurs. It is also possible that larvae are coming on currents from distant islands in the region (Aguilar-Perera et al. 2006).

Several studies have been conducted around the islands of Puerto Rico but in recent years the numbers of Nassau grouper are very small. Based on the findings of visual surveys for reef fishes at Mona and Monito, small islands to the west of Puerto Rico, in 2000 and 2005, 7 Nassau grouper juveniles were found in shallow seagrass and rubble habitats within the reef lagoon. In winter 2004, 2 adult Nassau grouper were found in coral reefs off southern Mona during surveys for grouper spawning aggregations (Aguilar-Perera et al. 2006). According to underwater visual surveys from 2004 to 2007 at Mona Island, Puerto Rico, the abundance of Nassau grouper is extremely low and its distribution is limited to specific depths and habitat types according to fish size class (Schärer et al. 2007). No spawning aggregations of Nassau grouper were encountered (Appeldoorn pers. obs.) even though reports from fishermen described abundant aggregations dating back decades (Schärer et al. 2007). Early juveniles (< 10 cm TL) are occasionally observed, suggesting successful reproduction somewhere at or near Mona (Schärer et al. 2007) although the larval life of about 40 days (Colin et al. 1997) would provide time for larvae to reach Mona from more distant locations where aggregations are still present.

Currently research is underway at three grouper spawning sites off the western coast of Puerto Rico. This work is using passive acoustic monitoring and divers to quantify spatial extent, spawner abundance, and spawning timing. At one of the three sites, the researchers have identified a small number of Nassau grouper associated with other spawners (Schärer et al. 2012). Additional work is being undertaken to measure and characterize the spawning of Nassau grouper at this site (R. Appeldoorn and M. Schärer pers. comm.). One of the peculiarities of the possibly "reconstituted" spawning aggregation is that the timing seems to differ from the traditional winter months and evidence suggests it may be occurring months later than expected.

Cumulative data from REEF (2003-2013) show sightings of 32 Nassau grouper in 1239 surveys (density index 1.1, sighting frequency 2.6%) across the 10-year period. Of the Nassau

grouper included in these surveys almost one-third of them are from the island of Culebra where the Luis Peña no-take marine reserve is located.

(<http://www.reef.org/db/reports/dist/species/TWA/0097/2003-01-01/2013-04-07>).

### **United States (Puerto Rico) – Fishing**

In the U.S. Virgin Islands and Puerto Rico, reef fish are caught by fish trap with some spearfishing and handlining. The boats used are small, ranging from 14 to 40 ft. in the trap fishery - less than 7.9 m long (Appeldoorn and Myers 1993, Agar et al. 2005, CFMC). Fishers have targeted Nassau grouper spawning aggregations since the 1950s. According to fisher interviews Nassau grouper landings from Mona Island ranged from 227 kg (500 pounds) to 681 kg (1,500 pounds) per 5-7 day trip before the 1980s but subsequently declined so that fishing trips to Mona Island were no longer feasible (Schärer et al. 2007).

Puerto Rico has long collected some landings data at the species level from its fishing communities. It is thus well-documented that the Nassau grouper, dominant in the 1950s to 1970s, has since vanished from the commercial fishery. The species was evidently heavily fished, including during its spawning periods, with smaller (immature sized) fish taken in fish traps (Sadovy 1993, Sadovy and Eklund 1999, Sadovy pers. obs.). During the early 1980s, landings declined and, by 1988-89, Nassau grouper, the dominant commercial grouper since the 1950s, was rare and represented only 2% of all grouper landings and 0.2% of all demersal fish species. It was considered extinct commercially before 1990 (Matos-Caraballo 2008); although the species still appears in landings reports where it has averaged approximately 11,000 pounds a year from 1994 - 2006.

Similar long-term declines were seen in Puerto Rico and the U.S. Virgin Islands. Commercial landings of Nassau grouper in Puerto Rico represented a major component of the fishery in the late 1800s (Wilcox 1899, Nichols 1929) but declined to an insignificant component by the 1990s. *Appeldoorn et al. (1992) reported that Nassau grouper accounted for 141 out of 26,294 total fishes sampled in 1985 and only 38 out of 26,054 fish sampled in 1990* (Bohnsack 2003).

### **United States (Puerto Rico) – Conservation and Management**

The management of fishery resources, including Nassau grouper, is shared between the local jurisdictional fishery managers of Puerto Rico and the Caribbean Fisheries Management Council with some authorities split between commonwealth/territorial waters and federal waters. A minimum size was introduced in 1985 and, effective November 1990, take and possession of the species were prohibited in US federal waters (CFMC 1996). In Puerto Rico, the species was fully protected in both state and federal waters by 2004. Since most of the capture of Nassau grouper in the US Caribbean was in territorial waters (Puerto Rico and the US Virgin Islands),

where federal fisheries restrictions do not apply, the introduction of protection in Puerto Rico jurisdictional waters in 2004 was particularly important (Table 13).

**Table 11. Summary of Nassau grouper regulations in the US Caribbean (García-Moliner and Sadovy 2008); PR = Puerto Rico, St. Thomas and St. Croix. USVI**

<b>Year</b>	<b>Reef Fish FMP Regulations</b>
1985	Min Size 12” to 24” (increasing 1 in/yr); Seasonal closure (prohibition on take) from January 1 to March 31 each year in Federal waters
1990	No harvest or possession in US federal waters (9-200 nm); Seasonal closure at Red Hind Bank St. Thomas (Dec-Feb) [1999 no-take]
1993	Seasonal closure for red hind at Tourmaline (PR) and Lang Bank (St. Croix)
1996	Seasonal closure for red hind Bajo de Sico, Abrir La Sierra (PR)
2004	No harvest or possession in Puerto Rico state waters (to 9 nm); no filleting at sea
2005	All seasonal area closures: prohibit bottom tending gear; no filleting fish at sea
2006	No harvest or possession in USVI; no filleting at sea

## UNITED STATES (VIRGIN ISLANDS)

### United States (Virgin Islands) – Populations

Some of the earliest examples of ecological studies examined fish assemblages on reefs and these provide the chance to examine declines in Nassau grouper from St. John in the U.S. Virgin Islands. Between 1959 and 1961, a total of 124 adult Nassau grouper were tagged at Lameshur Bay, St. John (Randall 1962, 1963) and about 255 Nassau grouper, ranging in size from 170 to 686 mm SL, were speared for stomach content analyses prior to 1965 (Randall 1967). By the 1990s, only 37 Nassau grouper were seen over five years of intensive field sampling in 32 sample plots of 5000 m<sup>2</sup> each around St. John (Beets and Rogers 2000). During the same time frame, using *in situ* fish trap observations for sampling off Yawzi Point reef, Lameshur Bay, researchers marked a severe decline. Among the 22 numerically dominant fish species observed in the fish traps, Nassau grouper declined from 30 of 1164 fish (2.58%) observed in 1982-83 to 4 of 934 fish (0.43%) observed in 1993–1994 (Beets 1996).

One of the longest running data sets in the USVI is that maintained by Beets and Friedlander from surveys associated with the National Parks in St. John and St. Croix. From the St. John work, surveys have been conducted annually at the same sites (since 1989, average number of sites=7.9). These data show a small number of Nassau grouper were observed each

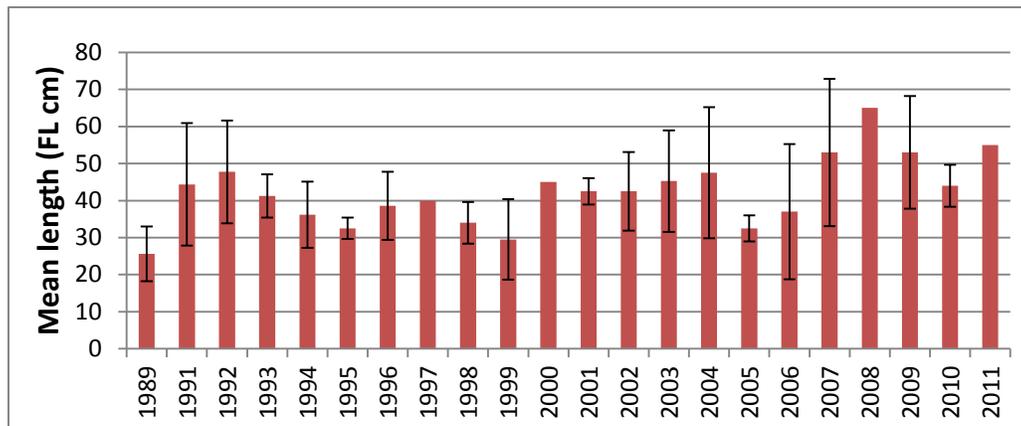


Figure 27. Mean Length of Nassau grouper from St. John surveys (A. Friedlander, unpub. data)

year and all were near or below the size at first maturity (Fig. 25). In the years from 1989-1994, a mean number of 10 fish were seen during each year's sampling. From 1995-2011, an average of 2.8 fish were encountered in sampling sites. Across the 2 decades of monitoring, only 97 Nassau grouper were recorded (A. Friedlander, 2012, unpub. data.). Estimates of biomass, while low, seem to show that recent surveys are equivalent to surveys early in the series, although those samples were also taken at a time after the extirpation of known spawning aggregations in the northern USVI.

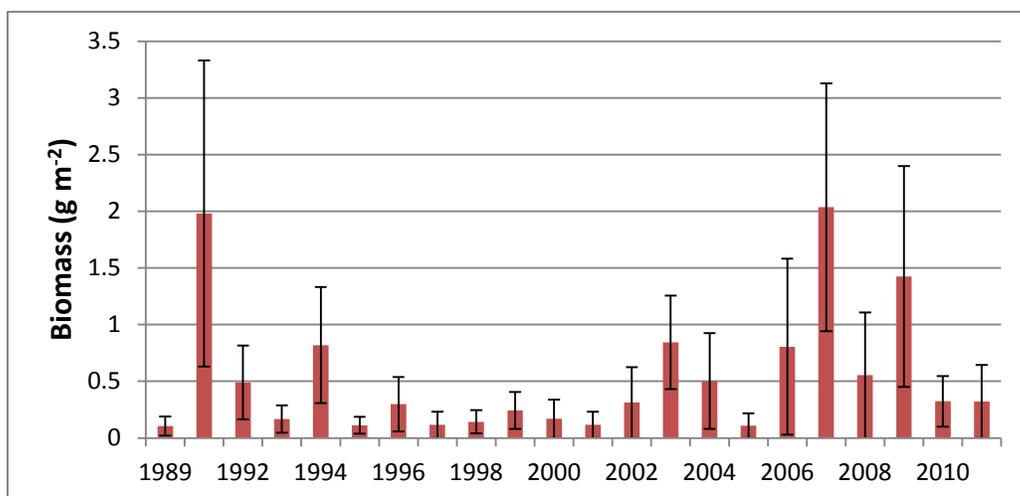


Figure 28. Mean biomass of Nassau grouper from St. John surveys (A. Friedlander, unpub. data).

In other UVC surveys conducted at random sites during daylight hours along 25-meter long by 4-meter wide belt-transects between 2001 and 2006, only three Nassau grouper were observed in the study region over the course of the six years of monitoring, giving mean abundance, frequency, and mean biomass of 0.2, <0.01 and 69.9 gram, respectively (Pittman et al. 2008).

Following the collapse of the Nassau grouper fishery in the USVI in the late 1970s (Olsen and LaPlace 1979), there was no significant spawning aggregation for this species on the shelf south of St. Thomas or St. John. However, fishermen are reporting a possible recurrence south of St. John (D. Olsen pers. comm. 2011) and Kadison et al. (2010) and Nemeth et al. (2006) suggest that there might be an aggregation re-forming at one of the sites south of St. Thomas. According to diver surveys conducted in 2001-2004, a small Nassau grouper aggregation has been observed at the Grammanik Bank, a deep reef (30-40 m) located on the shelf edge south of St. Thomas. In 2002, small clusters of Nassau grouper, possibly representing the earliest stages in the recovery of a spawning aggregation, were noted at Grammanik Bank, while in March 2003, a single cluster of Nassau grouper, not previously recorded in either December or January, was observed at the same site (Nemeth et al. 2006). There was, however, no clear evidence (*e.g.*, behavior, coloration) that Nassau grouper successfully spawned in 2002 or 2003 at Grammanik Bank. In April 2004, about 60 Nassau groupers aggregated on the Grammanik Bank; 4 out of 60 fish were seen in bicolor phase but no courtship or spawning was observed (Nemeth et al. 2006). It is possible that although an aggregation may be re-forming, there may not yet be spawning. Recent work by Nemeth and coworkers (pers. comm.) has documented some increased settlement/recruitment (2004-6) in nearshore habitats in both St. Thomas and St. John, and they have demonstrated success tracking Nassau grouper to the Grammanik Bank spawning site. It is possible that a year or two of strong recruitment occurred with resulting small increases in local

abundance (Nemeth et al. in prep).

According to Kadison et al. (2010): “*On St. Croix, where no Nassau grouper aggregation is believed to exist, fishermen and dive operators agree that grouper are almost completely absent from their isolated shelf (Gerson Martinez, fisherman pers. comm., Michele Pugh, dive business owner and operator pers. comm.). Only one has been observed in six years of fish surveys conducted annually on 14 sites around St. Croix (Nemeth Unpub. data).*”

### **United States (Virgin Islands) – Fishing**

In the U.S. Virgin Islands and Puerto Rico, reef fish are caught by fish trap with some spearfishing and handlining. In the USVI, the St. Croix fishery tends to be a diver-dominated fishery, whereas in St. Thomas the fishery tends to be trap-dominated (Olsen, pers. comm.). Traps are designed with biodegradable panels and mesh sizes have been adjusted repeatedly to reduce the bycatch of small fish. Juvenile Nassau grouper, prior to reaching maturity, would be readily retained in traps.

As reported by Munro and Blok (2005): “*Grouper aggregations in USVI waters were heavily exploited from the 1960s through the 1980s with the greatest effort having started north of the Puerto Rican island of Culebra. Aggregations on the Barracouta Bank, north of St. Thomas, were fished to extinction by the late 1970s, producing as much as 2.3 mt (metric tons)(5000 lbs.) of grouper per day at its peak*” (K. Turbe, pers comm).

### **United States (Virgin Islands) – Conservation and Management**

In the 1970s, the commercial harvest of the Nassau grouper reached its highest recorded point and it was also in this decade that well-documented declines occurred at one important aggregation site (Olsen and LaPlace 1979). Local fishermen were so concerned with catch levels that in 1976, St. Thomas fishermen requested (to the local government) that the grouper bank be closed for 5 years. Their only condition was that the closure should be accompanied by enforcement. This request was ignored entirely (Olsen, pers. comm.). In 1990, the Caribbean Fishery Management Council (CFMC) enacted a prohibition on “fishing for or possession of Nassau grouper in or from the US Caribbean Exclusive Economic Zone” through its Shallow-water Reef Fish Management Plan. In addition, the CFMC, with support of local fishermen, established a no-take marine protected area off the southwest coast of St. Thomas, Hind Bank Marine Conservation District (Brown 2007) intended to protect red hind and red hind spawning aggregations. The Hind Bank Marine Conservation District was first subject to a seasonal closure, beginning in 1990 (Beets and Friedlander 1999, Nemeth 2005, Nemeth et al. 2006) to protect spawning aggregations of red hind, followed by year-round closure to fishing in 1998 (DPNR 2005). The closed area has been effective at restoring red hind even though compliance has, at times, been questionable (J. Rivera, SERO, pers. comm./unpub. data), although a St.

Thomas fisherman was arrested and prosecuted in 2008 by NOAA Law Enforcement (Olsen, pers. comm.).

In US Virgin Islands territorial waters the species, prior to 2006, benefited from general fisheries restrictions, such as gear restrictions and rules on the marketing of fish, and those applying to specifically protected sites, such as the Virgin Islands Coral Reef National Monument (no-take), Virgin Islands National Park (no commercial fishing), Buck Island Reef National Monument (no-take) and several USVI marine reserves. In 2006, the USVI instituted regulations to prohibit harvest or possession of Nassau grouper in USVI water and to prohibit fileting at sea (García-Moliner and Sadovy 2007). In 2010, as part of a SeaGrant project to bring attention to the Nassau grouper, the St. Thomas Fisherman's Association distributed needles to vent swim bladders on captured Nassau grouper and recorded all Nassau grouper caught from April to July. Nassau grouper were regularly caught although not as abundantly as in the past (Olsen, pers. comm).

Following research for many years documenting grouper spawning and migration, Nemeth et al. (2006) suggested that the seasonal closure of the Grammanik Bank from February 1 to April 30 could provide protection (via management measures in a multi-species spawning aggregation site) for the potentially reforming Nassau grouper spawning aggregation. The Grammanik Bank spawning aggregation site has been seasonally protected from February through April since 2006 but recent evidence from acoustic tagging and hydrophone vocalizations suggests that Nassau aggregate to spawn at the Grammanik Bank from January through May which may warrant an extension of the Grammanik Bank closed season to five months. The Hind Bank Marine Conservation District, St. Thomas, remains closed to fishing year-round, protecting a red hind spawning aggregation and a former Nassau grouper spawning site.

## LITERATURE CITED

- Acero, A.P., and J. Garzon-Ferreira. 1991. Meros, chernas y cabrillas del Caribe Colombiano (Pisces: Serranidae: epinephelinae: epinephelini). *Caldasia* 16 (78):355-376.
- Agar, J.J., M. Shivlani, J.R. Waters, M. Valdés-Pizzini, T. Murray, J. Kirkley, and D. Suman. 2005. *U.S. Caribbean Fish Trap Fishery Costs and Earnings Study*. NOAA Technical Memorandum NMFS-SEFSC- 534, 127 p.
- Aguilar-Perera, A. 1994. Preliminary observations of the spawning aggregation of Nassau grouper, *Epinephelus striatus*, at Majahual, Quintana Roo, Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **43**:112-122.
- Aguilar-Perera, A. 2004. Detection of fishing effects on a Nassau grouper spawning aggregation from southern Quintana Roo, Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **55**:544-556.
- Aguilar-Perera, A. 2006. Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast. *Marine Ecology Progress Series*, **327**:289-296.
- Aguilar-Perera, J.A. 2000. Stock analysis for an aggregating reef fish, the Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) from the Mexican Caribbean. MS Thesis, UPR-Mayagüez, 85 pp.
- Aguilar-Perera A., and Aguilar-Davila W. 1996. A spawning aggregation of Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environmental Biology of Fishes*, **45**:351-361.
- Aguilar-Perera, A., M. Schärer, and M. Nemeth. 2006. Occurrence of juvenile Nassau grouper, *Epinephelus striatus* (Teleostei: Serranidae), off Mona Island, Puerto Rico: considerations of recruitment potential. *Caribbean Journal of Science*, **42(2)**: 261-265.
- Aguilar-Perera, A., C. González-Salas, and H. Villegas-Hernández. 2008. Fishing, management, and conservation of the Nassau grouper, *Epinephelus striatus*, in the Mexican Caribbean. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **61**:313-319.
- Aiken, K.A., and T. Street. 1993. Jamaica. Part III. In: *Marine Fishery Resources of the Antilles: Lesser Antilles, Puerto Rico and Hispaniola, Jamaica, Cuba*, p. 159-180. FAO Fisheries Technical Paper. 326, 235 pp.
- Albins M.A., and M.A. Hixon. 2008. Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series*, **367**:233-238.
- Albins and Hixon. 2011. Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes*, Online First. DOI: 10.1007/s10641-011-9795-1.
- Albins, M.A., M.A. Hixon, and Y. Sadovy. 2009. Threatened fishes of the world: *Epinephelus striatus* (Bloch, 1792) (Serranidae). *Environmental Biology of Fishes*, **86**:309-310.
- Alvarez-Filip L., N.K. Dulvy, J.A. Gill, I.M. Cote, and A.R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B*. **276**:3019–3025.
- Amargós, F.P., G.G. Sansón, A.J. del Castillo, A.Z. Fernández, F.M. Blanco, and W.A. de la Red. 2010. An experiment of fish spillover from a marine reserve in Cuba. *Environmental Biology of Fishes*, **87**:363–372.
- Appeldoorn, R., and S. Meyers. 1993. Puerto Rico and Hispaniola. Part II. In: *Marine Fishery Resources of the Antilles: Lesser Antilles, Puerto Rico and Hispaniola, Jamaica, Cuba*, p. 99-158. FAO Fisheries Technical Paper. 326, 235 pp.

- Appeldoorn, R. S., G.D. Dennis, and O. Monterrosa Lopez. 1987. Review of shared demersal resources of Puerto Rico and the Lesser Antilles region, p. 36-106, in: Report and proceedings of the expert consultation on shared fishery resources of the Lesser Antilles region, Mayaguez, Puerto Rico, 8-12 September 1986. FAO Fisheries Report 383, 278 pp.
- Appeldoorn, R.S, J. Beets, J. Bohnsack, S. Bolden, D. Matos, S. Meyers, A. Rosario, Y. Sadovy, and W. Tobias. 1992. *Shallow water reef fish stock assessment for the U.S. Caribbean*. NOAA Technical Memorandum NMFS-SEFSC-304, 70 pp.
- Archer, S.K., S.A. Heppell, B.X. Semmens, C.V. Pattengell-Semmens, P.G. Bush, C. McCoy, and B.C. Johnson. 2012. Patterns of color phase indicate spawn timing at a Nassau grouper *Epinephelus striatus* spawning aggregation. *Current Zoology* 58 (1): 73–83.
- Baisre, J.A. 1993. Cuba. Part IV. In, *Marine Fishery Resources of the Antilles: Lesser Antilles, Puerto Rico and Hispaniola, Jamaica, Cuba*, p. 181- 235. FAO Fisheries Technical Paper 326, 235 p.
- Baisre, J.A., and J. Paez. 1981. Los recursos pesqueros del archipelago Cubano. WECAF Stud. 8, 79 pp.
- Baldwin, C.C., G.D. Johnson, and P.L. Colin. 1991. Larvae of *Diplorion bifasciatum*, *Belonoperca chabanaudi* and *Grammistes sellineatus* (Serranidae: Epinephelinae) with a comparison of known larvae of other epinephelines. *Bulletin of Marine Science*, **48(1)**:67-93.
- Bannerot S.P., W.W. Fox, Jr, and J.E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean, p. 561-603, in: J.J. Polovina and S. Ralston (eds). *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder, CO.
- Bardach, J.E. 1958. On the movements of certain Bermuda reef fishes. *Ecology* 39(1):139-146.
- Bardach, J.E., and D.W. Menzel. 1957. Field and laboratory observations on the growth of some Bermuda reef fishes. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **9**:106-112.
- Bardach, J.E., C.L. Smith, and D.W. Menzel. 1958. Bermuda fisheries research program final report. Bermuda Trade Development Board, Hamilton, 59 p.
- Bartholomew, A., and J.A. Bohnsack. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries*, **15**:129–154
- Beaumariage, D.S., and L.H. Bullock. 1976. Biological research on snappers and groupers as related to fishery management requirements, p. 86- 94, in: H.R. Bullis, Jr. and A.C. Jones (eds.), *Proceedings of the Colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean*, Fla. Sea Grant Coll. Rep. 17. 333 pp.
- Beets, J. 1996. The effects of fishing and fish traps on fish assemblages within Virgin Islands National Park and Buck Island Reef National Monument. A technical report for the U.S. Department of Interior, National Park Service. Technical Report VINP 5/96. 21 p.
- Beets J., and A. Friedlander. 1999. Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. *Environmental Biology of Fishes*, **55**:91-98.
- Beets, J., and M.A. Hixon. 1994. Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. *Bulletin of Marine Science*, **55**:470- 483.

- Beets, J. and C. Rogers. 2000. Decline of fishery resources in marine protected areas in the U.S. Virgin Islands: The need for marine reserves. *Proceedings of the International Coral Reef Symposium*. **9(1)**:449-454.
- The Belize Spawning Aggregation Working Group. 2009. Information Circular No 7. June 2009, 2pp. from <http://www.spagbelize.org/LinkClick.aspx?fileticket=7doBoeM1PRk%3d&tabid=2807&language=en-US> retrieved on 15 December 2011.
- The Belize Spawning Aggregation Working Group. 2012. Information Circular No 10. November 2012, 2pp. from [http://www.spagbelize.org/Portals/3/PDFs/SpAg\\_Newsletter\\_10\\_final.pdf](http://www.spagbelize.org/Portals/3/PDFs/SpAg_Newsletter_10_final.pdf) retrieved on 15 April 2013.
- Böhlke, J.E., and C.G. Chaplin. 1968. *Fishes of the Bahamas and Adjacent Tropical Waters*. Livingston Publ. Co., Wynnewood, PA, 771 pp.
- Bohnsack, J.A. 1989. Protection of grouper spawning aggregations. Coastal Resources Division Contr. No. 88-89-06, 8 p.
- Bohnsack, J.A. 1990. Black and Nassau grouper fishery trends. Appendix in South Atlantic Reef Fish Plan Development Team Report of the Snapper-Grouper Assessment of the South Atlantic Fishery Management Council, 18 p.
- Bohnsack, J.A. 2003. Shifting baselines, marine reserves, and Leopold's biotic ethic. *Gulf and Caribbean Research* **14(2)**:1-7.
- Bohnsack, J.A., and S.P. Bannerot. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Tech. Rep. NMFS 41. 15 p.
- Bohnsack, J.A., and D.E. Harper. 1988. *Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean*. NOAA Tech. Memo. NMFS-SEFC-215. 31 pp.
- Bohnsack, J.A., D.L. Sutherland, A. Brown, D.E. Harper, and D.B. McClellan. 1986. An analysis of the Caribbean biostatistical database for 1985. Coast. Res. Dev. Rep. CFMC Contr. No. CRD-86/87-10, 35 p.
- Bolden, S.K. 1994. A summary of biological and fishery data on red hind (*Epinephelus guttatus*) and coney (*Cephalopholis fulva*) stocks in the U.S. Virgin Islands. NOAA/NMFS Miami Laboratory Contrib. No. 93/94-32, 33 p.
- Bolden, S.K. 2000. Long-distance movement of a Nassau grouper (*Epinephelus striatus*) to spawning aggregation in the central Bahamas. *Fishery Bulletin*, **98(3)**:642-645.
- Bolden, S.K. 2001. Using Ultrasonic Telemetry to Determine Home Range of a Coral-Reef Fish. *in*: J.R. Sibert and J.L. Nielsen (eds.), *Proceedings of the Symposium on Tagging and Tracking Marine Fish with Electronic Devices*, February 2000, Hawaii, (Springer Publishing). *Reviews: Methods and Technologies in Fish Biology and Fisheries* 1:167-188.
- Bolio-Moguel, K.M. 2007. Caracterización y descripción pesquera del sitio de agrupación de peces "El blanquizal – Santa Julia", Quintana Roo, México: Invierno 2004-Primavera 2005. Tesis Maestría. ECOSUR, 90 pp.
- Boomhower, J., M. Romero, J. Posada, S. Kobara, and W. Heyman. 2008. Identification of reef fish spawning aggregation sites in Los Roques Archipelago National Park, Venezuela. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**:559-565.
- Boomhower, J., M. Romero, J. Posada, S. Kobara, and W. Heyman. 2010. Prediction and verification of possible reef-fish spawning aggregation sites in Los Roques Archipelago National Park, Venezuela. *Journal of Fish Biology* **77**:822-840.

- Bouchon, C., P. Portillo, Y. Bouchon-Navaro, M. Loius, P. Hoetjes, K. De Meyer, D. Macrae, H. Armstrong, V. Datadin, S. Harding, J. Mallela, R. Parkinson, J-W. Van Bochove, D. Lirman, J. Herlan, A. Baker, L. Collado and S.C. Isaac. 2008. Status of Coral Reef Resources of the Lesser Antilles: The French West Indies, The Netherlands Antilles, Anguilla, Antigua, Grenada, Trinidad and Tobago . In: Wilkinson, C. (ed.). Status of Coral Reefs of the World: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, Townsville, Australia. p265-280.
- Box, S., and Bonilla Mejía. 2008. El estado de la conservación y explotación del Mero Nassau en la Costa Atlántica de Honduras June 2008, TNC Report, pp. 51
- BREEF (Bahamas Reef Environment Educational Foundation). 1998. Fisheries Management Action Plan for the Bahamas. Report to the Bahamas Department of Fisheries. The Bahamas Reef Environment Educational Foundation and MacAlister Elliott and Partners Ltd.
- Brown, V. 2007 The policymaking process and the politics of managing the Nassau grouper and other marine resources. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**:605-606.
- Brownell, W.N., and W.E. Rainey. 1971. Research and development of deep water commercial and sport fisheries around the Virgin Islands plateau. Virgin Islands Ecological Research Station Contrib. No. 3, 88 pp.
- Bryant, D., L. Burke, J.W. McManus, and M. Spalding. 1998. Reefs at Risk: a Map-based Indicator of Potential Threats to the World's Coral Reefs. World Resources Institute, Washington, D.C. 56 pp.
- Buchan, K. 2000. The Bahamas. *Marine Pollution Bulletin*, **41(1-6)**:94-111.
- Buesa, R.J. 1987. Growth rate of tropical demersal fishes. *Marine Ecology Progress Series* **36**:191- 199.
- Burnett-Herkes, J. 1975. Contribution to the biology of the red hind, *Epinephelus guttatus*, a commercially important serranid fish from the tropical western Atlantic. PhD dissertation, U. Miami, Coral Gables, 154 p.
- Burnett-Herkes, James, and John A. Barnes. 1996. Banning the use of pots and other management introduced in Bermuda to protect declining reef fish stocks. *Proceedings of the Gulf and Caribbean Fisheries Institute*. **44**: 239-256.
- Bush, P.G., Ebanks, G.C. and Lane, E.D. 1996. Validation of the ageing technique for the Nassau grouper (*Epinephelus striatus*) in the Cayman Islands, p. 150-158, in: F. Arreguin-Sanchez, J.L. Munro, M.C. Balgos, and D. Pauly (eds.) *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM Conf. Proc. 48, 449pp.
- Bush, P.G., D.E. Lane, G.C. Ebanks-Petrie, K. Luke, B. Johnson, C. McCoy, J. Bothwell, and, E. Parsons. 2006. The Nassau grouper spawning aggregation fishery of the Cayman Islands – an historical and management perspective. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **57**:515-524.
- Carcamo, R., Jr. 2008. National Report of the Nassau Grouper (*Epinephelus striatus*), Fishery of Belize. Belize Fisheries Department, Ministry of Agriculture & Fisheries, October 2008.
- Carleton Ray G., M.G. McCormick-Ray, C.A. Layman, and B.R. Silliman. 2000. *Investigations of Nassau grouper breeding aggregations at High Cay, Andros: implication for a conservation strategy*. Final report. The Department of Fisheries, Ministry of Agriculture and Fisheries, Nassau, The Bahamas
- Carter, J. 1986. Moonlight mating of the multitudes. *Animal Kingdom Magazine* **89(6)**:63-71.
- Carter, J. 1988. Grouper mating ritual on a Caribbean reef. *Underwater Naturalist* **17**:8-11.

- Carter, J. 1989. Grouper sex in Belize. *Natural History*, Oct: 60- 69.
- Carter, J., G.J. Marrow, and V. Pryor. 1994. Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **43**:65–111.
- Cervigón, F. 1966. Los Peces Marinas de Venezuela. Vols. I and II. Fund. La Salle Cienc. Nat., 951 p.
- Cervigón, F. 1994. *Los peces marinas de Venezuela, Fundacion Cientifica Los Roques*, C. Fundación Cientifica las Roques (ed.), Caracas, Venezuela, 2nd edition Vol 3, 295 p.
- CFMC (Caribbean Fishery Management Council). 1985. Fishery Management Plan, Final Environmental Impact Statement, and Draft Regulatory Impact Review, for the Shallow-water Reef Fish Fishery of Puerto Rico and the U.S. Virgin Islands, 104 pp.
- CFMC (Caribbean Fishery Management Council). 1993. Amendment 2 to the Fishery Management Plan for the Shallow-water Reef Fish Fishery of Puerto Rico and the U.S. Virgin Islands. 29 pp.
- CFMC (Caribbean Fishery Management Council). 1996. Regulatory Amendment to the Fishery Management Plan for the Reef Fish Fishery of Puerto Rico and the United States Virgin Islands Concerning Red Hind Spawning Aggregation Closures including a Regulatory Impact Review and an Environmental Assessment. August. <http://www.caribbeanfmc.com/SCANNED%20FMPS/REEF-FISH%20FMP.htm>
- Cheung, W.W.L., Y. Sadovy, M.T. Braynen, and L.G. Gittens. 2013. Are the last remaining Nassau grouper (*Epinephelus striatus*) fisheries sustainable? The case in the Bahamas. *Endangered Species Research*, **20**:27-39.
- Chiappone, M., R. Sluka, and K. Sullivan Sealey. 2000. Groupers (Pisces: Serranidae) in fished and protected areas of the Florida Keys, Bahamas and northern Caribbean. *Marine Ecology Progress Series*, **198**:261-272.
- Clark, M.R., O.F. Anderson, R.I.C. Chris Francis, and D. M. Tracey. 2000. The effects of commercial exploitation on orange roughy (*Hoplostethus atlanticus*) from the continental slope of the Chatham Rise, New Zealand, from 1979 to 1997. *Fisheries Research*, **45**:217–238.
- Claro, R. and K.C. Lindeman. 2003. Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. *Gulf and Caribbean Research* **14(2)**:91-106.
- Claro, R., García-Cagide, A., Sierra, L.M., García-Arteaga, J.P. 1990. Características biológico-pesqueras de la cherna criolla *Epinephelus striatus* (Bloch) (Pisces: Serranidae) en la plataforma cubana. *Cienc. Biol.* **23**: 23–42.
- Claro, R., K.C. Lindeman, and L.R. Parenti. 2002. *Ecology of the Marine Fishes of Cuba*. Washington, DC: Smithsonian Institution Press.
- Claro R., J.A. Baisre, K.C. Lindeman, J.P. García-Arteaga. 2001. Cuban fisheries: historical trends and current status, p. 194-219, in: R. Claro, K.C. Lindeman, L.R. Parenti (eds.) *Ecology of the Marine Fishes of Cuba*. Smithsonian Institution Press, Washington, D.C. 253 pp.
- Claro, R., Y. Sadovy de Mitcheson, K.C. Lindeman, A.R. García-Cagide. 2009. Historical analysis of Cuban commercial fishing effort and the effects of management interventions on important reef fishes from 1960–2005. *Fisheries Research* **99(1)**:7-16
- Claydon, J. 2004. Spawning aggregations of coral reef fishes: characteristics, hypothesis, threats and management.

- Oceanography and Marine Biology: An annual review 2004: 42, 265-302.
- Claydon, J.A.B., and A.M. Kroetz. 2007. The distribution of early juvenile groupers around South Caicos, Turks and Caicos Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**:345-350.
- Claydon, J.A.B., M.C. Calosso, and S.E. Jacob. 2010. Large-scale deployment of discarded conch shells enhances juvenile habitat for spiny lobster, Nassau grouper and red hind. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **63**:457-461.
- Coleman, F.C., W.F. Figueira, J.S. Ueland, and L.B. Crowder. 2004. The impact of United States recreational fisheries on marine fish populations. *Science* **305**:1958-1960.
- Coleman, F.C., and C.C. Koenig. 2010. The effects of fishing, climate change, and other anthropogenic disturbances on red grouper and other reef fishes in the Gulf of Mexico. *Integrative and Comparative Biology* 50(2): 201-212.
- Colin P.L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Environmental Biology of Fishes*, **34**:357-377.
- Colin, P.L., W.A. Laroche, and E.B. Brothers. 1997. Ingress and settlement in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. *Bulletin of Marine Science*, **60**(3):656-667.
- Colin, P.L., D.Y. Shapiro, and D. Weiler. 1987. Preliminary investigations of reproduction of two species of groupers. *Epinephelus guttatus* and *E. striatus* in the West Indies. *Bulletin of Marine Science*, **40**:220-230.
- Collette, B. B., and F. H. Talbot. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover p. 98-124, in B. B. Collette and S. A. Earle (eds.), Results of the Tektite Program: ecology of coral reef fishes. *Bulletin of Natural History of the Museum of Los Angeles County* 14.
- Cooke, S.J., and I.G. Cowx. 2006. Contrasting recreational and commercial fishing: searching for common issues to promote unified conservation of fisheries resources and aquatic environments. *Biological Conservation*, **128**:93-108.
- Cornish, A., and A.-M. Eklund. 2003. *Epinephelus striatus*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. <[www.iucnredlist.org](http://www.iucnredlist.org)>. Downloaded on 09 January 2013.
- Craig, A.K. 1966. Geography of fishing in British Honduras and adjacent coastal areas. Technical Report no. 28 Coastal Studies Institute Louisiana State University, Louisiana. Cont. No. 66-2. 143 pp. available on-line: [ambergriscaje.com/pages/mayan/geographyoffishing.html](http://ambergriscaje.com/pages/mayan/geographyoffishing.html), accessed April 2013.
- Craig, A.K. 1968. The Grouper Fishery at Cay Glory, British Honduras. *Annals of the Association of American Geographers*, 59: 252-263.
- Craig, M.T., and P.A. Hastings. 2007. A molecular phylogeny of the groupers of the subfamily Epinephelinae (Serranidae) with a revised classification of the Epinephelini. *Ichthyological Research*, **54**(1): 1-17.
- Craig, M.T., Y.J. Sadovy de Mitcheson, and P.C. Heemstra. 2011. Groupers of the World: A Field and Market Guide. Grahamstown: NISC (Pty) Ltd. 424pp
- Craig, M.T., D. Pondella, II, J.P.C. Franckb, and J.C. Hafner. 2001. On the status of the serranid fish genus *Epinephelus*: evidence for paraphyly based upon 16S rDNA sequence. *Molecular Phylogenetics and Evolution*, **19**(1):121-130.

- Cushion, N.M. and K. Sullivan-Sealey. 2007. Landings, effort and socio-economics of a small scale commercial fishery in the Bahamas. *Proceedings of the Gulf and Caribbean Fisheries Institute* **60**:162-166.
- Dahlgren C.P. 1998. *Population dynamics of early juvenile Nassau grouper: an integrated modeling and field study*. Ph.D dissertation. North Carolina State University. Raleigh, NC USA. 145 pp.
- Dahlgren C.P., and D.B. Eggleston. 2000. Ecological Processes Underlying Ontogenetic Habitat Shifts in a Coral Reef Fish. *Ecology* **81**(8):2227-2240.
- Dahlgren C.P., and D.B. Eggleston. 2001. Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. *Marine Ecology Progress Series*, **217**:145-156.
- Dahlgren et al, [in prep]
- Department of Marine Resources. 2007. The Bahamas. April 2007. Briefing Documents, 55pp.
- DNER (Puerto Rico Department of Natural and Environmental Resources). 2004. Puerto Rico Fishing Regulations. N°6768. Supplementary Flier. <http://www.drna.gobierno.pr/>
- DPNR (Division of Planning and Natural Resources, US Virgin Islands). 2005. Commercial & Recreational Fisher's Information Booklet. Department of Planning and Natural Resources, Division of Fish & Wildlife and Division of Environmental Enforcement. July 2005. <http://www.vifishandwildlife.com>.
- Domeier, M.L., and P.L. Colin. 1997. Tropical reef fish spawning aggregations defined and reviewed. *Bulletin of Marine Science*, **60**(3):698-726.
- Eggleston D.B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features and ontogenetic habitat shifts. *Marine Ecology Progress Series*, **124**:9-22.
- Eggleston, D.B., J.J. Grover, and R.N. Lipcius. 1998. Ontogenetic diet shifts in Nassau grouper: trophic linkages and predatory impact. *Bulletin of Marine Science*, **63**(1):111-126.
- Ehrhardt, N.M., and V.K.W. Deleveaux. 2007. The Bahamas' Nassau grouper (*Epinephelus striatus*) fishery - two assessment methods applied to a data - deficient coastal population. *Fisheries Research*, **87**:17-27.
- Ellis, S., G. Viala, and W.O. Watanabe. 1996. Growth and feed utilization of hatchery-reared juvenile Nassau grouper fed four practical diets. *Progressive Fish-Culturist*, **58**(3):67-172.
- Ellis, S. C., W.O. Watanabe, and E.P. Ellis. 1997a. Temperature effects on feed utilization and growth of post-settlement stage Nassau grouper. *Transactions of the American Fisheries Society*, **126**(2):309- 315.
- Ellis, E. P., W.O. Watanabe, S.C. Ellis, J. Ginoza, and A. Moriwake. 1997b. Effects of turbulence, salinity, and light intensity on hatching rate and survival of larval Nassau grouper, *Epinephelus striatus*. *Journal of Applied Aquaculture*, **7**(3):33-43.
- Erdman, D.S. 1976. Spawning patterns of fishes from the northeastern Caribbean. *Contrib. Agric. Pesq., Dept. Agric. Commonwealth of Puerto Rico*, 8:1-37.
- Evermann, B.W. 1900. *Fishes and Fisheries of Porto Rico*. U.S. Commission on Fish and Fisheries, 350 p.
- FAO. 2009. National Fishery Sector Overview. The Commonwealth of the Bahamas. Fishery and Aquaculture Country Profiles, FAO, FID/CP/BHS May 2009; 8 pp.

- Fine, J.C. 1990. Groupers in Love: Spawning aggregations of Nassau groupers in Honduras. *Sea Frontiers*, p 42-45.
- Fine J.C. 1992. Greedy for Groupers. *Wildlife Conservation*. May/June 1992:1-5.
- Froese, R. and D. Pauly. 2010. Fishbase. [www.fishbase.org](http://www.fishbase.org).
- Garcia-Moliner, G., and Y. Sadovy. 2008. The case for regional management of the Nassau grouper, *Epinephelus striatus*. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**:576-602.
- Gardner, T.A., I.M. Côté, J.A. Gill, A. Grant, and A.R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. *Science*, **301**:958-960.
- Gascoigne, J. 2002. *Nassau Grouper and Queen Conch in the Bahamas. Status and Management Options*. MacAlister Elliott and Partners Lt. for The Bahamas Reef Environment Educational Foundation. BREEF. 44 pp.
- Gibson, J., R.F. Pott, G. Paz, I. Majil, N. Requena. 2007. Experiences of the Belize spawning aggregation working group. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **59**:455-462.
- Gibson, J. 2008. Managing a Nassau Grouper Fishery – A Case Study from Belize. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**:603-604.
- GMFMC (Gulf of Mexico Fishery Management Council). 1989. Amendment Number 1 to the Fishery Management Plan for the Reef Fish Fishery of the Gulf of Mexico. Tampa, Florida. 356 p.
- Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use, p. 67- 81, *in*: S.J. Smith, J.J. Hunt, and D. Rivard (eds.), Risk evaluation and biological reference points for fisheries management, Can. Spec. Publ. Fish. Aquat. Sci. 120.
- Goreau, T.J. 1992. Bleaching and reef community change in Jamaica: 1851-1991. *American Zoologist*, **32**:683-695.
- Greenwood, C.B. 1991. Distribution and feeding habits of larval Epinepheline groupers in Exuma Sound, Bahamas. MS thesis, Florida Institute of Technology, Melbourne, FL, 61 pp.
- Grover, J.J. 1993. Trophic ecology of pelagic early-juvenile Nassau grouper, *Epinephelus striatus*, during an early phase of recruitment into demersal habitats. *Bulletin of Marine Science*, **53**:1117-1125.
- Grover, J.J. 1994. Feeding habits of early-juvenile Nassau grouper. *Bahamas Journal of Science* **2**(1):22-26.
- Grover, J.J., D.B. Eggleston, and J.M. Shenker. 1998. Transition from pelagic to demersal phase in early-juvenile Nassau grouper, *Epinephelus striatus*: Pigmentation, squamation, and ontogeny of diet. *Bulletin of Marine Science*, **62**(1):97-113.
- Guitart-Manday, D., and F. Juárez-Fernandez. 1966. Desarrollo embrionario y primeros estudios larvales de la cherna criolla, *Epinephelus striatus* (Bloch) (Perciformes: Serranidae). Academia Ciencias de Cuba, Instituto de Oceanologica. La Habana **1**:35-45.
- Gunter, G., and L. Knapp. 1951. Fishes, new, rare or seldom recorded from the Texas coast. *Texas Journal of Science*, **3**(1): 134-138.
- Halstead, B.W. 1967. *Poisonous and Venomous Marine Animals of the World. Vol. 2- Vertebrates*. U.S. Govt. Printing Office, 1,070 pp.

- Harvell, C.D., C.E. Mitchell, J.R. Ward, S. Altizer, A.P. Dobson, R.S. Ostfeld, and M.D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* 296: 2158–2162.
- Hateley, J.G. 2005. Preliminary results of a protein electrophoretic analysis of genetic variation, population structure and gene flow in the Nassau grouper, *Epinephelus striatus*. *Proceedings of the Gulf and Caribbean Fisheries Institute*. **47**:888-905.
- Head, W. D., W.O. Watanabe, S.C. Ellis, and E.P. Ellis. 1996. Hormone-induced multiple spawning of captive Nassau grouper broodstock. *Progressive Fish-Culturist*, **58(1)**:65-69.
- Heemstra, P.C., and J.E. Randall. 1993. FAO species catalogue. Vol. 16. Groupers of the world (Family Serranidae, Subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. FAO Fisheries Synopsis. No. 125, Vol. 16. Rome, FAO.
- Heppell, S.A., B.X. Semmens, C.V. Pattengill-Semmens, P.G. Bush, B.C. Johnson, C.M. McCoy, J. Gibb, and S.S. Heppell. 2011. Oceanographic patterns associated with Nassau grouper aggregation spawn timing: shifts in surface currents on the nights of peak spawning. *Proceedings of the Gulf and Caribbean Fisheries Institute* 63: 152-154.
- Heppell, S.A., B.X. Semmens, S.K. Archer, C.V. Pattengill-Semmens, P.G. Bush, C.M. McCoy, S.S. Heppell, and B.C. Johnson. 2012. Documenting recovery of a spawning aggregation through size frequency analysis from underwater laser calipers measurements. *Biological Conservation*. **155**:119-127.
- Heyman, W., and L. Carr. 2007. Using acoustic tags to track fish movements at spawning aggregations in Belize. *Proceedings of the Gulf and Caribbean Fisheries Institute* **60**:651.
- Heyman W., and N. Requena. 2002. Status of multi-species spawning aggregations in Belize. The Nature Conservancy, Punta Gorda (report)
- Heyman, W., and B. Kjerfve. 2008. Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bulletin of Marine Science*, **83(3)**:531-551.
- Heyman, W.D., and B. Wade. 2007. Status of reef fish spawning aggregations in Belize. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **58**:286-291.
- Hildebrand, H.H., H. Chavez, and H. Compton. 1964. Aporte al conocimiento de los peces del arrecife Alacranes, Yucatan (Mexico). *Ciencia (Mex.)* 23 (3):107-134.
- Hinegardner, R., and D.E. Rosen. 1972. Cellular DNA content and the evolution of teleostean fishes. *American Naturalist*, **106**:621-644
- Hodgson, G. and J. Liebler. 2002. *The Global Coral Reef Crisis: Trends and Solutions*. Los Angeles: Reef Check Foundation.
- Hoese, H. D., and R. H. Moore. 1998. Fishes of the Gulf of Mexico: Texas, Louisiana, and adjacent waters. Texas A&M Univ. Press, College Station. 422 pp.
- Hooker, H.C.B. 2012. Los grandes serranidos de la Reserva de Biosfera Seaflower, Caribe Insular Colombiano: evaluacion de la pesca, abundancia relative y agregaciones reproductivas. Thesis Universidad Nacional de Colombia, CECIMAR, San Andrés, Colombia. Pages 152.
- Horsford, I. 2009. The Grouper Fishery of Antigua and Barbuda. Report on Regional Workshop of Nassau Grouper, Cartagena, Colombia, 20-21 October 2008, revised January 2009, 12 pp.

- Hughes, T.P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**:1547-1551.
- Humann, P., and N. DeLoach. 2002. *Reef Fish Identification -- Florida-Caribbean-Bahamas* (3<sup>rd</sup> Edition). New World Publications, Inc. Jacksonville, Florida.
- IUCN. 2003. 2003 IUCN Red List of Threatened Species. [www.iucnredlist.org](http://www.iucnredlist.org). Downloaded on 18 November 2003.
- Johnson, D.G., and Keener, P. 1984. Aid to identification of American grouper larvae. *Bulletin of Marine Science*, **34(1)**:106-134.
- Jones, G.P., S. Planes, S.R. Thorrold. 2005. Coral reef fish larvae settle close to home." *Current Biology* **15(14)**:1314-1318.
- Jory, D.E., and E.S. Iversen. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida) -- black, red, and Nassau groupers. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.110). U.S. Army Corps of Engineers, TR EL-82-4. 21 pp.
- Kadison, E., R.S. Nemeth, J. Blondeau, T. Smith, and J. Calnan. 2010. Nassau grouper (*Epinephelus striatus*) in St. Thomas, US Virgin Islands, with evidence for a spawning aggregation site recovery. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **62**:273-279.
- Kaufman, L., and E. Romero. 2011. Fisheries based on Belizean biodiversity: why they're so vulnerable to offshore oil, p. 135-141, in: M.L.D. Palomares and D. Pauly (eds.), *Too Precious to Drill: the Marine Biodiversity of Belize*. Fisheries Centre Research Reports 19(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].
- Kelley, C.D., A. Moriwake, G. Miyamoto, V. Nicol, and W. Watanabe. 1994. The use of LHRH-a for induced spawning of five different species of marine teleost fishes. Abstract for World Aquaculture '94. World Aquaculture Society. New Orleans. LA. January 14-18, 1994. 147 p.
- Kellison, T., S. Heppell, B. Semmens, N. Ehrhardt, I. Zink. 2009. Review of Databases Available and Trends in Abundance Relating to Nassau Grouper *Epinephelus striatus* in United States and U.S. Territorial Waters Including Recommendations for a Formal Status Review. Workgroup Report. 14 pp.
- Kendall, A.W., Jr. 1979. Morphological comparisons of North American sea bass larvae (Pisces: Serranidae) NOAA Tech. Rep. NMFS Circ. 428, 50 p.
- Kendall, A.W., Jr, and M.P. Fahay. 1979. Larva of the serranid fish *Gonioplectrus hispanus* with comments on its relationships. *Bulletin of Marine Science*, **29**:117-121.
- Kobara, S. 2009. Regional Analysis of Seafloor Characteristics at Reef Fish Spawning Aggregation Sites in the Caribbean. Ph.D. Dissertation, Texas A&M University (Geography).
- Kobara, S. and Heyman, W.D. 2007. Comparative geomorphic analysis of Nassau grouper spawning aggregation sites in Belize and the Cayman Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**:573-576.
- Kobara, S. and Heyman, W.D. 2010. Sea bottom geomorphology of multi-species spawning aggregation sites in Belize. *Marine Ecology Progress Series*, **405**:243-254.
- Koslow, J.A., F. Hanley, and R. Wicklund. 1988. Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. *Marine Ecology Progress Series* **43**:201-212.

- Koslow, J. A., K. Aiken, S. Auil, and A. Clementson. 1994. Catch and effort analysis of the reef fisheries of Jamaica and Belize. *Fishery Bulletin* **92**:737-747.
- Koslow, J. A., G.W. Boehlert, J.D.M. Gordon, R.L. Haedrich, P. Lorance, and N. Parin. 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science*, **57**:548–557.
- Kramer, P. 2003. Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA Programme (1997–2000). *Atoll Research Bulletin*, **496**:1–58.
- La Gorce, J. Oliver (ed.). 1939. *The Book of Fishes*. National Geographic Society, Washington, D.C., 367 p.
- Landsman, S.J., C. Jadot, M. Ashley, and J.A.B. Claydon. 2009. Investigation of the Nassau grouper (*Epinephelus striatus*) fishery in the Turks and Caicos Islands: implications for conservation and management. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **61**:82-89.
- Leis, J.M. 1986. Larval development in four species of Indo-Pacific coral trout *Plectropomus* (Pisces: Serranidae: Epinephelinae) with an analysis of the relationships of the genus. *Bulletin Marine Science*, **38**(3):525-552.
- Leis, J.M. 1987. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae), p. 189-238, in: J.J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press. Boulder.
- Longley, W.H. 1917. Studies upon the biological significance of animal coloration. I. The colors and color changes of West Indian reef fishes. *Journal of Experimental Zoology*, **23**(3):533-601.
- Luckhurst, B.E. 1996. Trends in commercial fishery landings of groupers and snappers in Bermuda from 1975 to 1992 and associated fishery management issues, p 286-297, in: F. Arregun-Sanchez, J.L. Munro, M.C. Balgos, and D. Pauly (eds.). *Biology, Fisheries and Culture of Tropical Groupers and Snappers*, ICLARM No. 48, 449 pp.
- Luckhurst, B.E. 2003. Development of a Caribbean regional conservation strategy for reef fish spawning aggregations. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **54**:668-678.
- Luckhurst, B.E. 2004. Current status of conservation and management of reef fish spawning aggregations in the Greater Caribbean. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **55**:530-542.
- Luckhurst, B.E. 2005. Evaluation of fisheries management and conservation measures taken to protect grouper spawning aggregations in the wider Caribbean: Case studies of Bermuda, Belize and Cayman Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **58**:268-269.
- Luckhurst, B.E., and J.A. Ward. 1996. Analysis of trends in Bermuda's Fishery Statistical Database from 1975 to 1990, with reference to fishery management measures implemented during this period. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **44**:306-324.
- Mahon, R. 1990. *Fishery Management Options for Lesser Antilles Countries (Antigua and Barbuda, Barbados, Dominica, Granada, St. Kitts and Nevis, St. Lucia, St. Vincent and the Grenadines)*. FAO Tech. Pap. 313. FAO, Rome.
- Mahon, R. 1993. Lesser Antilles. Part I, p. 1-98, in: *Marine Fishery Resources of the Antilles: Lesser Antilles, Puerto Rico and Hispaniola, Jamaica, Cuba*. FAO Tech. Pap. 326, 235 pp.
- Maljković, A., T.E. van Leeuwen, and S.N. Cove 2008. Reef Sites: Predation on the invasive red lionfish, *Pterois volitans* (Pisces: Scorpaenidae), by native groupers in the Bahamas. *Coral Reefs*, **27**:501

- Manter, H. W. 1947. The digenetic trematodes of marine fishes of Tortugas, Florida. *American Midland Naturalist*, **38(2)**:257-416.
- Marcogliese, DJ. 2001. Implications of climate change for parasitism of animals in the aquatic environment. *Canadian Journal of Zoology* 79(8): 1331-1352.
- Matos-Caraballo, D. 2008. Lessons learned from Puerto Rico's commercial fishery 1988-2008. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **61**:123-129.
- McClanahan, T., N. Polunin, and T. Done. 2002. Ecological states and the resilience of coral reefs. *Conservation Ecology* **6(2)**:18.
- Medina-Quej, A., A.R. Herrera-Pavon, G.Poot-Lopez, E. Sosa-Cordero, K. Bolio-Moguel, and W. Hadad. 2004. A preliminary survey of the Nassau grouper *Epinephelus striatus* spawning aggregation at "El Blanquizal" in the south coast of Quintana Roo, Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **55**:557-569.
- Mora, C., and P.F. Sale. 2002. Are populations of coral reef fish open or closed? *Trends in Ecology & Evolution* **17(9)**: 422-428.
- Morris, J.A., and J.L. Akins. 2009. Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes*, **86**:389-398.
- Moura, R.L. 2001. Serranidae. In: P.A. Buckup and N.A. Menezes (eds). Catálogo das Especies de Peixes Marinhos do Brasil. Museu de Zoologia Universidade de São Paulo
- Mumby, P.J., A.R. Harborne, and D.R. Brumbaugh. 2011. Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE* 6(6): e21510. doi:10.1371/journal.pone.0021510.
- Mumby, P.J., C.P. Dahlgren, A.R. Harborne, C.V. Kappel, F. Micheli, D.R. Brumbaugh, K.E. Holmes, J.M. Mendes, K. Broad, J.N. Sanchirico, K. Buch, S. Box, R.W. Stoffle and A.B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**:98-101
- Mumby, P.J., R.S. Steneck, A.J. Edwards, R. Ferrari, R. Coleman, A.R. Harborne, and J.P. Gibson. 2012. Fishing down a Caribbean food web relaxes trophic cascades. *Marine Ecology Progress Series* **445**:13-24.
- Munday, P.L., G.P.Jones, M.S. Pratchett, A.J. Williams. 2008 Climate change and the future for coral reef fishes. *Fish and Fisheries*, **9(3)**:261-285.
- Munro, J.L. 1983a. Chapter 1: Coral reef fish and fisheries of the Caribbean Sea, p. 1-9, in, J.L. Munro (ed.), Caribbean Coral Reef Fishery Resources: ICLARM Studies and Reviews, Vol. 7. International Center for Living and Aquatic Resources Management, Manilla, Philippines. Contrib. 125. 2nd ed., 276 p.
- Munro, J.L. 1983b. Chapter 4: The composition and magnitude of line catches in Jamaican waters, p. 26-32 in: J.L. Munro (ed.), Caribbean Coral Reef Fishery Resources: ICLARM Studies and Reviews, Vol. 7. International Center for Living and Aquatic Resources Management, Manilla, Philippines. Contrib. 125. 2nd ed., 276 p.
- Munro, J.L. 1983c. Chapter 5: The composition and magnitude of trap catches in Jamaican waters, p. 33-49, in: J.L. Munro (ed.), Caribbean Coral Reef Fishery Resources: ICLARM Studies and Reviews, Vol. 7. International Center for Living and Aquatic Resources Management, Manilla, Philippines. Contrib. 125. 2nd ed., 276 p.

- Munro, J.L., and L. Blok. 2005. The status of stocks of groupers and hinds in the northeastern Caribbean. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **56**: 283-294.
- Munro, J.L., and R. Thompson. 1983. Chapter 2: The Jamaican fishing industry, p. 10-14, *in*: J.L. Munro (ed.), Caribbean Coral Reef Fishery Resources: ICLARM Studies and Reviews, Vol. 7. International Center for Living and Aquatic Resources Management, Manilla, Philippines. Contrib. 125, 2nd ed., 276 p.
- Munro, J.L., V.C. Gaut, R. Thompson, and P.H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. *Journal of Fish Biology*, **5**:69-84.
- Musick, J.A., M.M. Harbin, S.A. Berkeley, G.H. Burgess, A.-M. Eklund, L. Findley, R.G. Gilmore, J.T. Golden, D.S. Ha, G.R. Huntsman, J.C. McGovern, S.J. Parker, S.G. Poss, E. Sala, T.W. Schmidt, G.R. Sedberry, H. Weeks, and S.G. Wright. 2000. Marine, estuarine and diadromous fish stocks at risk of extinction in North America (Exclusive of Pacific Salmonids). *Fisheries*, **25(11)**:6-30.
- Nadeau, D.A., and D.B. Eggleston. 1996. Determinants of Nassau grouper recruitment success in macroalgae versus seagrass (Abstract). 24<sup>th</sup> Annual Benthic Ecology Meeting, Colombia, SC (USA), 7- 10 Mar. 1996, p. 62.
- Nagelkerken, W.P. 1981. Distribution and ecology of the groupers (Serranidae) and snappers (Lutjanidae) of the Netherlands Antilles. Found. Scientif. Research Surinam and the Netherland Antilles, 107, 71 pp.
- Nagelkerken, W.P. 1982. Distribution of the groupers and snappers of the Netherlands Antilles. *Proceedings of the International Coral Reef Symposium*. Manila, 1981, **4(2)**:479-484.
- Nemeth, R.S. 2005. Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Marine Ecology Progress Series*, **286**:81-97.
- Nemeth, R.S. 2012. Chapter 2. Ecosystem aspects of species that aggregate to spawn, p. 21-55, *in*: Y. Sadovy de Mitcheson and P.L. Colin (eds.) *Reef Fish Spawning Aggregations: Biology, Research, and Management*, Fish & Fisheries Series 35. Springer Science, pp. 644.
- Nemeth, R.S., E. Kadison, and J. Blondeau. 2009. Defining marine protected areas for yellowfin and Nassau grouper spawning aggregation sites. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **61**:329-330.
- Nemeth, R.S., B. Legare, K. Maize, and S. Hitt. (in prep) Habitat preferences, home range, activity patterns and ontogenetic movements of juvenile Nassau grouper (*Epinephelus striatus*) in the United States Virgin Islands.
- Nemeth, R.S., E. Kadison, S. Herzlieb, J. Blondeau, and E.A. Whiteman. 2006. Status of a yellowfin (*Mycteroperca venenosa*) grouper spawning aggregation in the US Virgin Islands with notes on other species. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **57**:543-558.
- Nichols, J.T. 1929. Scientific survey of Puerto Rico, and the Virgin Islands: Vol. X, Part 2, Branchiostomidae to Sciaenidae. New York Academy of Sciences. N.Y., USA.
- O'Connor, A. 2002. New Help for Nassau Grouper, a Sitting Duck Facing Extinction. The New York Times, 3 December 2002.
- Olsen, D.A. and J.A. LaPlace. 1979. A study of the Virgin Island grouper fishery based on breeding aggregations. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **31**:130-144.
- Overstreet, R. M. 1969. Digenetic trematodes of marine teleost fishes from Biscayne Bay, Florida. *Tulane Studies in Zoology and Botany*, **15(4)**:119-175.

- Patengill-Semmens, C.V. and B.X. Semmens. 2003. The status of reef fishes in the Cayman Islands (BWI). Status of coral reefs in the Western Atlantic: Results of initial survey, Atlantic Gulf Rapid Reef Assessment (AGRRA) Program. *Atoll Research Bulletin*, **498**:226-247.
- Patterson, H.M., S.R. Thorrold, and J.M. Shenker. 1999. Analysis of otolith chemistry in Nassau grouper (*Epinephelus striatus*) from the Bahamas and Belize using solution-based ICP-MS. *Coral Reefs*, **18**:171-178.
- Paz, G. and Grimshaw, T. 2001a. Status report on Nassau groupers for Belize, central America. Scientific report of the Green Reef Environmental Institute. San Pedro Town, Ambergris Caye, Belize
- Paz, G. and Grimshaw, T. 2001b. Status Report on Nassau Grouper Aggregations in Belize, Central America. *Proceedings of the First National Workshop on the Status of Nassau Groupers in Belize: Working Towards Sustainable Management*, at Belize City, 30 July 2001, Green Reef Environmental Institute pp.27-36.
- Paz, G.E., and T. Grimshaw. 2001c. Life History Characteristics & Management Recommendations for the Nassau Grouper Population in Belize. Report by Green Reef Environmental Institute. (UNEP/GEF Grant No. BZE 98 G52-PRO 03)
- Paz, G., and E. Truly. 2007. The Nassau grouper spawning aggregation at Caye Glory, Belize: A brief history. A case study by The Nature Conservancy, Mesoamerican Reef Program. 64pp.
- PDT (Plan Development Team). 1990a. South Atlantic reef fish: Plan Development Team report to the South Atlantic Fishery Management Council, 527 p.
- PDT (Plan Development Team). 1990b. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. NOAA. NMFS, Coastal Resources Division, Contr. No. CRD/89-90/04. 41 pp.
- Perkins. J.S. 1983. The Belize Barrier Reef Ecosystem: An assessment of its resources, conservation status and management. New York Zoological Society Report, 148 p.
- Pittman, S.J., S.D. Hile, C.F.G. Jeffrey, C. Caldw, M.S. Kendall, M.E. Monaco, and Z. Hillis-Starr. 2008. Fish Assemblages and Benthic Habitats of Buck Island Reef National Monument (St. Croix, U.S. Virgin Islands) and the Surrounding Seascape: A Characterization of Spatial and Temporal Patterns. NOAA Technical Memorandum NOS NCCOS 71. Silver Spring, MD. 96pp.
- Polovina, J.J. and S. Ralston (eds). 1987. *Tropical Snappers and Groupers: Biology and Fisheries Management*. pp. 561-603. Westview Press, Boulder, CO.
- Polunin, N.V.C., and C.M. Roberts. 1993. Greater biomass and value of target coral reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series*, **100**:167-176.
- Powell, A.B., and J.W. Tucker Jr. 1992. Egg and larval development of laboratory-reared Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae). *Bulletin of Marine Science*, **50(1)**:171-185.
- Prada, M.C., G. Penalzoza, S. Posada, N. Howard, P. Herron, L. Salinas, E. Castro, F. Cabezas, and H. Robinson. 2004. Fish spawning aggregations in the San Andres Archipelago, a first approximation. Final Report. Coralina and The Ocean Conservancy, 50 pp.
- Radakov, D. V., A.D. Motchek, Y.N. Sbikin, R. Claro Madruga, and A. Silva Lee. 1975. Acerca de la longitud de los peces comerciales en capturas de la zona noroccidental de Cuba. Serie Oceanologica. No. 28. Academia de Ciencias de Cuba. Instituto de Oceanologia. Habana. Cuba, 9 pp.

- Rand, P., C. Taylor, and D. Eggleston. 2005. A video method for quantifying size distribution, density and three-dimensional spatial structure of reef fish spawning aggregations. *Emerging Technologies Abstracts. Proceedings of the Gulf and Caribbean Fisheries Institute*, **56**:429-430.
- Randall, J.E. 1962. Tagging reef fishes in the Virgin Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute* **14**:201–241.
- Randall, J.E. 1963. Additional recoveries of tagged reef fishes from the Virgin Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute* **15**:155-157.
- Randall, J.E. 1965. Food habits of the Nassau grouper (*Epinephelus striatus*). Assoc. Island Mar. Labs Carib. 6th Meeting. Jan. 1965:13- 16.
- Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography*, Miami **5**:665–847.
- Randall, J.E. 1983. *Caribbean Reef Fishes*. Second edition. T.F.H. Publications, Neptune City. NJ. 350 p.
- Randall, J.E., and V.E. Brock. 1960. Observations on the ecology of epinepheline and lutjanid fishes of the Society Islands with emphasis on food habits. *Transactions of the American Fisheries Society*, **89**(1):9-16.
- Ray G.C., M.G. McCormick-Ray, C.A. Layman, and B.R. Silliman. 2000. Investigations of Nassau Grouper Breeding Aggregations at High Cay, Andros: Implications for a Conservation Strategy. Report to the Department of Fisheries, Nassau, Bahamas.
- Reed, C.T. 1941. Marine life in Texas waters. *Texas Academy Sci. Publ. Nat. Hist.* Vol. 2. 88 pp.
- REEF. 2012. Reef Environmental Education Foundation Volunteer Survey Project Database. World Wide Web electronic publication. [www.reef.org](http://www.reef.org). date of download: December 2012.
- Report of the Commission of Inquiry. 1991. Report of the Commission of Inquiry to examine and make recommendations for the future of the fishing industry and for the future protection of the marine environment in Bermuda. Government of Bermuda. February, 1991.
- Richards, W.J., C.C. Baldwin, and A. Röpké. 2006. Chapter 119. Serranidae: Sea basses, p. 1225-1332 in: W.J. Richards (ed.), *Early Stages of Atlantic Fishes: An Identification Guide for the Western Central North Atlantic*, Vol. I. CRC Press, Boca Raton, FL, 1335 p.
- Roberts, C.M., and N.V.C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries* **1**:65-91.
- Roberts, C.M., N. Quinn, J.W. Tucker Jr., and P.N. Woodward. 1995. Introduction of hatchery-reared Nassau grouper to a coral reef environment. *North American Journal of Fisheries Management*, **15**(1):159-164.
- Rogers, C.S., and J. Beets. 2001. Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the US Virgin Islands. *Environmental Conservation*, **28**(4):312-322.
- Rudd, M.A. 2003a. Institutional analysis of marine reserves and fisheries governance policy experiments: a case study of Nassau grouper conservation in the Turks and Caicos Islands. Ph.D. thesis. Wageningen University, The Netherlands, 276pp.
- Rudd, M. A. 2003b. Fisheries Landings and Trade of the Turks and Caicos Islands. *Fisheries Centre Research Reports* (2003), **11**(6):149-161

- Rudd, M.A. 2004. The effects of seafood import tariffs on market demand of Nassau grouper in the Turks and Caicos Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **55**:179-190.
- Rudd, M.A. and M.H. Tupper. 2002. The impact of Nassau grouper size and abundance on scuba diver site selection and MPA economics. *Coastal Management*, **30**:133-151.
- Sadovy Y. 1993. The Nassau grouper, endangered or just unlucky? *Reef Encounters* June 10–12.
- Sadovy Y. 1994. Grouper stocks of the western central Atlantic: the need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **43**:43-64.
- Sadovy, Y. 1996. Reproduction in reef fishery species, pp. 15-59 in, N. V. C. Polunin & C.M. Roberts (eds.). *Reef Fisheries* London: Chapman & Hall. 477 pp.
- Sadovy, Y. 1997. The case of the disappearing grouper: *Epinephelus striatus*, the Nassau grouper in the Caribbean and western Atlantic. *Proceedings of the Gulf and Caribbean Fisheries Institute* **45**:5-22
- Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. *Journal of Fish Biology*, **59**:90-108.
- Sadovy Y, and P.L. Colin. 1995. Sexual development and sexuality in the Nassau grouper, *Epinephelus striatus* (Bloch) (Pisces: Serranidae). *Journal of Fish Biology* **46**:961–976
- Sadovy, Y., and M. Domeier. 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs*, **24**:254–262.
- Sadovy, Y. and Eklund, A.-M. 1999. *Synopsis of biological information on the Nassau Grouper, Epinephelus striatus* (Bloch, 1792), and the Jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Technical Report NMFS 146. Technical Report of the *Fishery Bulletin*. FAO Fisheries Synopsis 157. US Department of Commerce, Seattle, WA USA, 65 pp.
- Sadovy, Y., and M. Figuerola. 1992. The status of the red hind fishery in Puerto Rico and St. Thomas as determined by yield-per-recruit analysis. *Proceedings of the Gulf and Caribbean Fisheries Institute* **42**:23-38.
- Sadovy, Y., and D.Y. Shapiro. 1987. Criteria for the diagnosis of hermaphroditism in fishes. *Copeia* **1987**:136-156.
- Sadovy de Mitcheson, Y. 2009. Visit to the Bahamas regarding Nassau grouper, *Epinephelus striatus*, 18-28 January 2009. Summary report February 2009 on visit 18-28 January. 8pp.
- Sadovy de Mitcheson, Y. 2012. Status Update: The Nassau Grouper, *Epinephelus striatus*. Final Report to the Caribbean Fishery Management Council. 70 pp.
- Sadovy de Mitcheson, Y. and B. Erisman. 2012. Chapter 8. Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes, p. 225-284 in: Y. Sadovy de Mitcheson and P.L. Colin (eds.), *Reef Fish Spawning Aggregations: Biology, Research and Management*, Fish & Fisheries Series 35, Springer, 644 pp.
- Sadovy de Mitcheson, Y., S.A. Heppell, and P.L. Colin. 2012. Chapter 12.6, Nassau grouper – *Epinephelus striatus*, p. 429-445 in: Y. Sadovy de Mitcheson and P.L. Colin (eds.), *Reef Fish Spawning Aggregations: Biology, Research and Management*, Fish & Fisheries Series 35, Springer, 644 pp.
- Sadovy de Mitcheson, Y., A. Cornish, M. Domeier, P. Colin, M. Russell, and K. Lindeman. 2008. A Global Baseline for Spawning Aggregations of Reef Fishes. *Conservation Biology* **22**(5):1233-1244.

- SAFMC (South Atlantic Fishery Management Council). 1983. Fishery Management Plan, Regulatory Impact Review, and Final Environmental Impact Statement for the Snapper Grouper Fishery of the South Atlantic Region, 173 p.
- SAFMC (South Atlantic Fishery Management Council). 1990. Amendment Number 2, Regulatory Impact Review, Regulatory Flexibility Analysis and Environmental Assessment for Fishery Management Plan for the Snapper Grouper Fishery of the South Atlantic Region, 47 pp.
- Sala, E., and E. Ballesteros. 2000. *Conservation status and dynamics of the Glover's Reef, Belize, spawning aggregation. December 1999 - January 2000*. Scientific report to the Wildlife Conservation Society's Glover's Reef Marine Research Station, Belize, Central America.
- 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.
- Schärer, M., M. Nemeth, and R. Appeldoorn. 2007. Past exploitation and present distribution of Nassau grouper at Mona Island, Puerto Rico (poster and abstract). *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**: 675.
- Schärer, M.T., T.J. Rowell, M.I. Nemeth, R.S. Appeldoorn. 2012. Sound production associated with reproductive behavior of Nassau grouper *Epinephelus striatus* at spawning aggregations. *Endangered Species Research*, **19**:29-38.
- Schmitt, E.F., and K.M. Sullivan. 1994. Research applications of volunteer generated coral reef fish surveys. The Nature Conservancy and the University of Miami, Department of Biology Report. Coral Gables, Florida. 38 pp.
- SCRFA (2003) SCRFA Newsletter Number 4. December 2003. Society for the Conservation of Reef Fish Aggregations. [www.scrfa.org](http://www.scrfa.org)
- Sedberry, G.R., D.E. Stevenson, and R.W. Chapman. 1996. Stock identification in potentially threatened species of grouper (Teleostei: Serranidae: Epinephelinae) in Atlantic and Caribbean Waters. Final Rep. MARFIN Grant No. NA47FF0012. South Carolina Dept. of Natural Resources, Marine Resources Research Institute. 51 pp.
- Semmens, B.X., P. Bush, S. Heppell, B. Johnson, C. McCoy, C. Pattengill-Semmens. 2012. An *in situ* visual mark-recapture method to assess the abundance of spawners at an aggregation site. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **64**:224-226.
- Semmens, B.X., K.E. Luke, P.G. Bush, C. Pattengill-Semmens, B. Johnson, C. McCoy, and S. Heppell. 2007. Investigating the reproductive migration and spatial ecology of Nassau grouper (*Epinephelus striatus*) on Little Cayman Island using acoustic tags – an overview. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **58**:191-198.
- Semmens, B.X., P. Bush, S. Heppell, B. Johnson, C. McCoy, C. Pattengill-Semmens, and L. Whylen. 2008a. Charting a course for Nassau grouper recovery in the Caribbean: what we've learned and what we still need to know. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**:607-609.
- Semmens, B.X., S. Heppell, P. Bush, B. Johnson, C. McCoy, C. Pattengill-Semmens, and L. Whylen. 2008b. An intra- and inter-annual analysis of Nassau grouper size distributions from a recently protected spawning aggregation in the Cayman Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **60**:585-586.
- Shapiro, D.Y. 1987. Reproduction in groupers, p. 295-327, in J.J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press. Boulder, CO.

- Shenker, J.M., E.D. Maddox, E. Wishinski, A. Pearl, S.R. Thorrold, and N. Smith. 1993. Onshore transport of settlement-stage Nassau grouper (*Epinephelus striatus*) and other fishes in Exuma Sound, Bahamas. *Marine Ecology Progress Series*, **98**:31-43.
- Silva Lee, A.F. 1974. Hábitos alimentarios de la cherna criolla *Epinephelus striatus* Bloch y algunos datos sobre su biología. *Serie Oceanologica Academia de Ciencias de Cuba* **25**:3-14.
- Silva Lee, A.F. 1977. Nota sobre la coloración y la conducta de la cherna criolla (*Epinephelus striatus* Bloch). Academia de Ciencias de Cuba, Institute de Oceanologia, Informe Cientifico Tecnico No. 14, Cuba, 8 pp.
- Sluka, R., M. Chiappone, K.M. Sullivan, and R. Wright. 1996. Habitat and Life in the Exuma Cays, the Bahamas: the status of groupers and coral reefs in the Northern Cays. The Nature Conservancy.
- Sluka, R., M. Chiappone, K.M. Sullivan, T. Potts, J.M. Levy, E.F. Schmitt, and G. Meester. 1998. Density, species and size distribution of groupers (Serranidae) in three habitats at Elbow Reef, Florida Keys. *Bulletin Marine Science*, **62**:219-228.
- Smith, C.L. 1961. Synopsis of biological data on groupers (*Epinephelus* and allied genera) of the western North Atlantic. FAO Fish. Biol. Synop. No. 23, 61 pp.
- Smith, C.L. 1971. A revision of the American groupers: *Epinephelus* and allied genera. *Bulletin of the American Museum of Natural History*. **146**:69-241.
- Smith, C. L. 1972. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). *Transactions of the American Fisheries Society*, **101**:257-261
- Smith, C. L. 1978. Serranidae. in: W. Fischer (ed.), FAO Species Identification Sheets for Fishery Purposes, Western Central Atlantic, Fishing Area 31. Vols. IV, V. FAO, Rome. [Unpaginated].
- Smith-Vaniz, W.F., B.B. Collette, and B.E. Luckhurst. 1999. *Fishes Of Bermuda: History, Zoogeography, Annotated Checklist, and Identification Keys*. American Society of Ichthyologists and Herpetologist Special Publication No. 4. *Reviews in Fish Biology and Fisheries*.
- Sosa-Cordero E., A. Medina-Quej, R. Herrera, and W. Aguilar Dávila. 2002. Agregaciones reproductivas de peces en el Sistema Arrecifal Mesoamericano: Consultoría Nacional México. Informe preparado para el consultor internacional, Research Planning Inc. y Proyecto sam. Ecosur, Chetumal, Quintana Roo. 25 pp.
- Springer, V.G., and A.J. McErlean. 1962. A study of the behavior of some tagged Southern Florida coral reef fishes. *American Midland Naturalist*, **67**:386-397.
- Stallings, C.D. 2008. Indirect effects of an exploited predator on recruitment of coral-reef fishes. *Ecology*. 89(8).
- Starck, W.A., II. 1968. A list of fishes of Alligator Reef, Florida with comments on the nature of the Florida reef fish fauna. *Undersea Biology*, **1**:5-36.
- Starck, W.A., II, and W.P. Davis. 1966. Night habits of fishes at Alligator Reef, Florida. *Ichthyologica* **38(4)**:313-356.
- Starr, R.M., E. Sala, E. Ballesteros, and M. Zabala. 2007. Spatial dynamics of the Nassau grouper *Epinephelus striatus* in a Caribbean atoll. *Marine Ecology Progress Series*, **343**:239-249.
- Stevenson, D.K. 1981. *A review of the marine resources of the Western Central Atlantic Fisheries Commission (WECAFC) Region*. FAO Fish. Tech. Pap. 211. FAO, Rome, 132 p.

- Sullivan, K.M., and M. de Garine-Witchatitsky. 1994. Energetics of juvenile *Epinephelus* groupers: impact of summer temperatures and activity patterns on growth rates. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **43**:148-167.
- Sullivan-Sealey, K., T. Rahming, and M. Rolle. 2002. Size, sex ratio, and fecundity of Nassau grouper (*Epinephelus striatus*) landed during spawning season in the Central Bahamas. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **53**:472-481.
- Taylor, J. C., D.B. Eggleston, and P.S. Rand. 2006. Nassau grouper (*Epinephelus striatus*) spawning aggregations: hydroacoustic surveys and geostatistical analysis. In: Emerging Technologies For Reef Fisheries Research And Management. NOAA Professional Papers NMFS (5). NOAA, Seattle, WA, pp. 18-25
- Thompson, E.F. 1945. *The Fisheries of British Honduras*. Development and Welfare in the West Indies, Advocate Co., Bridgetown, Barbados. Bull. **21**:1-32.
- Thompson, R.W. 1978. Results of the UNDP /FAO Bahamas deep water fishery survey 1972-1975. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **30**:44-70.
- Thompson, R., and J.L. Munro. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). *Journal of Fish Biology*, **12**:115-146.
- Thompson, R., and J.L. Munro. 1983. Chapter 7: The biology, ecology and bionomics of the hinds and groupers, Serranidae, p. 59-81, in: J.L. Munro (ed.), *Caribbean Coral Reef Fishery Resources*. ICLARM Studies and Reviews, Vol. 7. International Center for Living and Aquatic Resources Management, Manilla, Philippines. Contrib. 125, 2nd ed., 276 p.
- Townsend, C.H. 1905. Report of the director of the aquarium. Ninth Annual Report of the New York Zoological Society, *Biology*. **9**:89-103.
- Tucker, J.W., Jr. 1992a. Spawning serranid fishes in captivity. In, *Aquaculture '92 -Growing towards the 21st Century*, p. 219.
- Tucker, J.W., Jr. 1992b. Grouper culture for the Caribbean. Progress report. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **41**:587.
- Tucker, J.W., Jr. 1994. Spawning by captive serranid fishes: a review. *Journal of the World Aquaculture Society*, **25**:345-359.
- Tucker, J.W., Jr., and P.N. Woodward. 1993. Nassau grouper aquaculture, p. 363-377, in: F. Arreguin-Sanchez, J. L. Munro, M.C. Balgos, and D. Pauly (eds.), *Biology, Fisheries, and Culture of Tropical Groupers and Snappers*, ICLARM Conf. Proc. 48, 449 p.
- Tucker, J.W., Jr., and P.N. Woodward. 1994. Growth and development of domestic juvenile Nassau groupers. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **43**:389-391.
- Tucker, J.W., P.G. Bush, and S.T. Slaybaugh. 1993. Reproductive patterns of Cayman Islands Nassau grouper (*Epinephelus striatus*) populations. *Bulletin of Marine Science*, **52**:961-969.
- Tucker, J.W., Jr., P.N. Woodward, and D.G. Sennet. 1996. Voluntary spawning of captive Nassau groupers *Epinephelus striatus* in a concrete raceway. *Journal of the World Aquaculture Society*, **27**(4):373-383.
- Tucker, J.W., Jr., J.E. Parsons, G.C. Ebanks, and P.G. Bush. 1991. Induced spawning of Nassau grouper *Epinephelus striatus*. *Journal of the World Aquaculture Society*, **22**:187-191.

- Tupper, M. 2002. Essential fish habitat and marine reserves for groupers in the Turks and Caicos Islands. *Proceedings of the Gulf Caribbean Fisheries Institute*, **53**:606-622.
- Tupper, M.H. and Rudd, M.A. 2002. Species-specific impacts of a small marine reserve on reef fish production and fishing productivity in the Turks and Caicos Islands. *Environmental Conservation*, **29**:484-492.
- L. Vásquez-Yeomans, U. Ordoñez-López and E. Sosa-Cordero. 1998. Fish larvae adjacent to a coral reef in the western Caribbean Sea off Mahahual, Mexico. *Bulletin of Marine Science*, **62(1)**:229-245.
- Vilaro Diaz, D.J. 1884. Corrida y arribazon de algunos peces cubanos. Manuel Gomez de la Maza, La Habana, Cuba
- Watanabe, W.O., C.S. Lee, S.C. Ellis, and E.P. Ellis. 1995a. Hatchery study of the effects of temperature on eggs and yolksac larvae of the Nassau grouper *Epinephelus striatus*. *Aquaculture*, **136**:141- 147.
- Watanabe, W.O., S.C. Ellis, E.P. Ellis, W.D. Head, C.D. Kelley, A. Moriwake, C-S Lee, and P.K. Bienfang. 1995b. Progress in controlled breeding of Nassau grouper (*Epinephelus striatus*) broodstock by hormone induction. *Aquaculture*, **138**:205-219.
- Watanabe, W.O., S.C. Ellis, E.P. Ellis, Y.G. Lopez, P. Bass, J. Ginoza, and A. Moriwake. 1996. Evaluation of first-feeding regimens for larval Nassau grouper *Epinephelus striatus* and preliminary, pilot-scale culture through metamorphosis. *Journal of the World Aquaculture Society*, **27(3)**:323-331.
- Watanabe, W.O., C.S. Lee, S.C. Ellis, E.P. Ellis, W.D. Head, C.D. Kelley, G. Miyamoto, K. Liu, and J. Ginoza. 1994. Experimental culture of larval Nassau grouper (*E. striatus*): the effects of temperature on egg and yolksac stages and of prey quality on survival at first feeding. Abstract for World Aquaculture '94, p. 287. World Aquaculture Society. New Orleans, LA, Jan. 14- 18, 1994.
- Wells, J.W. and J.C. Lang. 1973. Systematic list of Jamaican shallow-water scleractinia. *Bulletin of Marine Science*, **23**:55-58.
- Whaylen, L., C.V. Pattengill-Semmens, B.X. Semmens, P.G. Bush, and M.R. Boardman. 2004. Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information. *Environmental Biology of Fishes*, **70**:305-313.
- Whaylen, L., P. Bush, B. Johnson, K. Luke, C. McCroy, S. Heppell, B. Semmens, M.R. Boardman. 2007. Aggregation dynamics and lessons learned from five years of monitoring at a Nassau grouper (*Epinephelus striatus*) spawning aggregation in Little Cayman, Cayman Islands, BWI. *Proceedings of the Gulf and Caribbean Fisheries Institute*, **59**:413-421
- Wilcox, W.A. 1899. The fisheries and fish trade of Porto Rico, p. 27-48, *in*: Investigations of the aquatic resources and fisheries of Porto Rico. U.S. Commission of Fish and Fisheries,.
- Wing, E. S., and E.J. Reitz. 1982. Prehistoric fishing economies of the Caribbean. *Journal of New World Archaeology*, **5(2)**:13-32.
- Wing, E.S., C.A. Hoffman, Jr, and C.E. Ray. 1968. Vertebrate remains from Indian sites on Antigua, West Indies. *Caribbean Journal of Science*, **8(3&4)**:123-139.
- Woodley, J.D. 1995. *Tropical Americas Regional Report on the Issues and Activities Associated with Coral Reefs and Related Ecosystems*. Prepared for the 1995 International Coral Reef Initiative Workshop, Dumaguete City, Philippines.
- Woodley, J.D., K. De Meyer, P. Bush, G. Ebanks-Petrie, J. Garzon-Ferreira, E. Klein, L. Pors, and C. Wilson. 1998.

Status of coral reefs in the south-central Caribbean. In: *Status of Coral Reefs of the World: 1998*. C. Wilkinson (ed.) Australian Institute of Marine Science.