

**Spawning of Black Grouper (*Mycteroperca bonaci*, Serranidae) in Belize**

GUILLERMO PAZ

*Greenreef Belize*

*100 Coconut Drive*

*San Pedro, Ambergris Caye*

*Belize*

GEORGE R. SEDBERRY\*

*Marine Resources Research Institute, SCDNR*

*PO Box 12559*

*Charleston SC 29412*

*USA*

*sedberryg@dnr.sc.gov*

\*Corresponding Author

ABSTRACT.--Black grouper (*Mycteroperca bonaci*) is a protogynous serranid that spawns in late winter (peak in February-March). In Belize, black grouper form many small aggregations as spawning approaches. Spawning occurs in pairs that rush upward in the water column at dusk, spawn, and then rejoin the aggregation. During spawning, male exhibit a white-head phase, and spawn with dark-phase females. Blotched and light phases are also exhibited at all times of the year. Spawning occurs from the full moon to a few days after the new moon, and occurs along a variety of reef formations, including elbows, promontories and linear shelf-edge reef. The behavior of black grouper has made it less vulnerable to fisheries in Belize, but it has been overfished in other parts of its range, and additional protection of spawners and habitats of juveniles is needed.

KEYWORDS.--spawning aggregation, behavior, Epinephelinae, western Caribbean

## INTRODUCTION

It has been well-documented that many coral reef fishes spawn in aggregations of different types (Domeier and Colin 1997), and that groupers (Serranidae, Epinephelinae) are noted aggregations spawners. Some grouper spawning aggregations are composed of large numbers of fish (>1000), and are very time- and site-specific. Often, spawning occurs during very narrow temporal windows, and represents all of the annual reproductive output for those species. Often, these spawning events are cued by, or associated with, particular lunar, tidal or seasonal phenomena that are easily observed by fishers. They may also occur at reef features, such as promontories (Carter et al. 1994; Heyman et al. 2001; Graham and Castellanos 2005), that historically have been easy to locate using even crude bathymetric maps, and which are very

easy to locate now with newer technology. Because they are so predictable in time and space, this type of aggregation has historically been targeted by fisherman; many species that spawn in this manner (e.g., Nassau grouper, *Epinephelus striatus*, and red hind, *E. guttatus*) are overfished and in decline (Carter et al. 1994; Beets and Friedlander 1999; Coleman et al. 2000). Other modes of aggregation spawning (Domeier and Colin 1997) may not make the fish as vulnerable, particularly if spawning is spread out temporally and spatially (Morris et al. 2000) or is cued by, or associated with, factors that are not easily observed or predicted by fishers. Knowledge regarding the reproductive mode of exploited fishes is therefore, quite important for determining management of aggregations and other life history phases, as fishing on aggregations can alter sex ratios, reproductive behavior and population size, and result in spawning failure.

Some groupers and other reef fishes spawn in small sub-groups or in male-female pairs within a large spawning aggregation; alternatively, spawning may occur simultaneously among many individuals in a spawning rush. Pair or harem spawning within larger groups subjects the individual pairs or harems to the fishing vulnerability of the large group, if the timing and location of the larger aggregation can be predicted. However, groupers and other reef fishes that spawn in smaller scattered groups or pairs, or which spawn throughout the year, may be less subject to fishing pressure. Grouper species that are broadly distributed are at lower risk of extinction (Morris et al. 2000); likewise, species that have numerous widely-scattered spawning sites may be less vulnerable than those with narrow spawning ranges, when spawning sites are targeted by fishers. In managing reef fishes that are targeted during spawning, we need to first understand their spawning behavior and locations (Morris et al. 2000), in addition to determining season, size and age at spawning, and fecundity.

The black grouper like many other epinephelines, is protogynous and has a fairly restricted spawning season (Crabtree and Bullock 1998). By an average age of 5.2 years and 826 mm TL, 50% of female black grouper are mature; by age 15.5 and 1214 mm TL, 50% of females have transformed into males. Black grouper can be found in a state of sexual maturity year-round, but spawning peaks from December to March on Campeche Bank off the northern Yucatan (Brulé et al. 2003) and in Florida (Crabtree and Bullock 1998). Spawning season and location for black grouper in Belize have not been documented.

Crabtree and Bullock (1998) could not determine if black grouper formed spawning aggregations in Florida, and Eklund et al. (2000) observed an aggregation that formed in the Florida Keys during peak spawning months, but they did not report spawning activity or courtship coloration and behavior. It has been thought that black grouper form transient spawning aggregations, drawing individuals from a large area to spawn during a few weeks, representing the total annual reproductive output for the year, but this has not been documented (Domeier and Colin 1997). It has also not been determined if black grouper select particular reef features, such as promontories, as has been demonstrated for some other reef fishes (Carter et al. 1994; Carter and Perrine 1994; Graham and Castellanos 2005).

Black grouper is an important fishery species throughout its range. In the United States, black grouper are considered overfished and undergoing overfishing in the Atlantic, but not in Gulf of Mexico and U.S. Caribbean (NMFS 2006). In Belize, black grouper is targeted by spear and handline fishermen, but ranks behind red hind, Nassau grouper and tiger grouper (*M. tigris*) in the landings, and is reported only among “mixed groupers” or “scalefish” (Belize Fishery Statistics 1994). Black grouper have historically been fished during their peak spawning season in Belize, by fishermen who target spawning aggregations of Nassau grouper in December and

January. Some fishermen remain on the grouper spawning banks after the peak season for Nassau grouper, and catch black grouper that use the same sites, and perhaps others, appearing in moderate numbers in February and March.

Although the status of black grouper in Belize has not been determined, the species is listed as Vulnerable by IUCN, and is considered to be in decline throughout its range due to loss of mangrove and reef habitat. This loss and continued overfishing (e.g. NMFS 2006) is predicted to result in additional decline (Morris et al. 2000)

The purpose of this paper is to document spawning locations, spawning habitat features, and spawning seasons for black grouper in Belize; to describe the observed spawning behavior and aggregation; and to evaluate management measures for black grouper in light of its spawning behavior, in order to sustain fisheries for this species in Belize. Because of the historical fishing efforts on reef fish spawning aggregations in Belize, and recent efforts to manage the fishery and restore grouper stocks by closure of known spawning sites for Nassau grouper (Gibson et al. 2004), this documentation is needed to determine the value of existing spawning closures, and to determine the need for additional management. Large predictable aggregations can be easily managed by time/area closures, but species that form smaller, scattered aggregations present additional management difficulties.

## MATERIALS AND METHODS

Our objective was to document spawning locations and behavior for black grouper in Belize, by observing black grouper at as many reported aggregation sites as possible, primarily during the months of peak spawning. We did not randomly choose sites or times to sample, and chose times and locations based on reports from fishermen and divers. We used reports from

commercial fishermen, dive shop operators, data archived by the Belize Fisheries Department and our own diving and fishing experience to determine reported and potential aggregation or spawning sites for black grouper. Each site was visited during the peak spawning months (December to March) and at other times of the year from 2001-2003 and 2005-2006, to confirm the presence of black grouper. At each reported site where we observed black grouper, we used survey teams with underwater cameras and logbooks to record location, depth, water temperature, a visual estimate of number of individuals (for most sites), observations of color phase, and behavior. Color phases included blotched, light, dark and white head (see Results for explanation).

To estimate abundance, divers descended to the site and looked for black groupers. Unlike some *Epinephelus* species, black grouper are not strictly substrate-oriented, but are very mobile and often move off the reef into the water column, or out into open water at reef dropoffs at the edge of insular or continental shelves. In Belize as in other places (Eklund et al. 2000), they are also wary of divers and will swim away if approached. For this reason, standard visual count methods such as transects and point counts that provide quantitative estimates of areal abundance do not work. In order to enumerate black groupers, divers had to estimate abundance as the observers approached the bottom, or as the fish swam away from the divers. Black grouper swam away from the divers as a group, and could be more easily counted as they hovered in the water column off the edge of the dropoff, or above reef formations. Divers also estimated relative abundance of different color phases in aggregations where spawning was observed. Sex was determined by estimated size, the occurrence of fish with swollen abdomens (ripe females) and associated color phases. The sex of observed color phases was confirmed by

spearing selected fish for dissection and macroscopic examination of the gonads. Water temperature, depth, time of day, lunar phase and habitat features were also recorded.

## RESULTS AND DISCUSSION

We compiled a list of 28 potential sites where black grouper had been caught or observed (Table 1). In addition, we observed black grouper at two additional sites (Rugged Caye and Phillips Long Caye). Black grouper were observed at eight sites along the barrier reef and on all three atolls (16 sites) of Belize (Fig. 1, Table1). All sites where black grouper were observed were on the outer forereef in high-relief deep spur-and-groove or buttress formations, or along the outer reef ridge at the dropoff [see Burke (1982) and Rützler and Macintyre (1982) for detailed descriptions of these habitats]. Reef sites consisted of high-relief (10 m) coral and coral-rock spurs, with deep-cut sand channels, or low-relief coral rock with dense gorgonian growth. Bottom temperatures ranged from 24 to 27°C where black grouper were observed; depths ranged from 12 to 52 m.

Most black grouper were observed during the months of spawning (December to March), especially in January and February (Fig. 2), and were most densely aggregated in late afternoon, just before dusk. Observations were made around all moon phases (except for the day of new moon), and black grouper were more abundant between the full and last quarter moon (Fig. 2). Black groupers were generally solitary during most months of the year, but they were more aggregated during the known spawning months (December to March). As far as we know, all reproductive activity occurs in these aggregations. Aggregations were made up of small groups ranging in size from 25 individuals to about 200 (a few larger), and have been observed and

fished at some of these well-known locations for 50 years or more. These aggregations (observations with more than one black grouper) formed at depths between 20 and 45 m.

Color phases that were observed all months of the year in both sexes included blotched, which was a mottled dark-on-light pattern of blotches with imbedded coppery spots (Fig. 3B). At least two of the large blotches are shaped like lipstick kisses. The blotched pattern could be dark brown to reddish brown on a much lighter background. A light phase also occurred during all months in both sexes and was characterized by lighter blotches that were faded, on a background color that was very light (Fig. 3B). Dark-phase fish of both sexes were also found at all times of the year; the fish was uniformly dark, or very dark with the blotched pattern barely visible (Fig. 3C). A white-head phase was seen only in males during the months of peak spawning (Fig. 3D). The white-head phase also had a white bar on the caudal fin that contrasted sharply with the dark edge of the fin. A dark area in the membranous portions of all paired and vertical fins contrasted with an adjacent light area, but this was particularly obvious on the caudal fin.

Examination of gonad samples taken from examples of each color phase indicated that blotched, light and dark phases could be either male or female. Light and dark phases were observed only in larger fish, but fish of this same size could also be blotched. The white-head phase was observed only in mature males with ripe gonads, during the peak spawning months of February and March. White-head phase males were often observed hovering vertically in the water column, and flashing their white heads and tails by exaggerated but slow undulations of the body.

Crabtree and Bullock (1998) examined gonad condition and color variation in port-sampled black grouper from Florida, which had been dead and on ice for several hours to days.



They also noted the jet-black fin pigmentation in male black grouper as we observed, and they found this character to be the only useful color indication of male sex in dead black grouper.

In Belize, black groupers have historically aggregated around the full moons in November through April, although spawning comes after the last quarter moon. During spawning, we often observed color changes and courting behavior from the full moon up through the 2-3 days following the last quarter moon. Color patterns associated with actual spawning (see below) intensified during this period. Individual fish exhibited one or more of the four different color phases during courtship and spawning. There were intergradations of the four patterns and swift changes between patterns were observed in individual fish; however as spawning approached following the last quarter of the moon, the color patterns were intense and well-defined, with few intergradations.

The blotch color phase was seen among aggregating fish on the morning of the spawning event. The white-head phase occurred only in males and was found mainly in the late afternoon, with most males (i.e. the largest fish in the aggregation) becoming white-head by sunset, when spawning took place. In this phase, the head and the posterior region of the body became white. In the light phase, seen among presumed females with bulging abdomens (which were most likely full of eggs), the normal blotched color pattern changed such that the head and body were noticeably white, while the caudal, pectoral, anal and dorsal fins remained dark brown to black. The final pattern, the dark phase, was found in courting and spawning fish. Both males and females exhibited the dark color phase. The body and fins became dark brown with the blotch pattern totally invisible. The males were the larger fish and would change from the dark phase to the white-head phase and back. White-head males pursued females, but changed to dark phase if

ignored by females. The females were the smaller fish and were mostly in the dark phase; however some of the females were in the light phase or blotched phase.

Courtship behavior was often observed between the full and last quarter moon, from December to March. The head of a male would turn white while the rest of the body would be dark brown, and the male in white-head phase would slowly approach a dark-phase female from the rear and inspect or nudge her vent area at the posterior of the abdomen. If the female was not receptive or ready to spawn, the male sometimes swam away. Most of the time, however, the male was persistent and would continue to follow the female in close proximity, apparently trying to spawn with her. Closer to the last quarter of the moon, another type of courtship behavior was observed. At these later phases of the lunar cycle, a male in white-head phase would approach a female who was either hovering off the bottom or slowly rising in the water column. The male would position himself next to her, and the couple would then swim up in the water column together for 3-5 m before the female swam off. Both courtship behaviors were observed primarily in the late afternoon.

Spawning occurred at dusk. Towards the late afternoon aggregated males (15-20 individuals) moved off the dropoff at the shelf edge into the water column, and an increasing number exhibited the white-head phase in the aggregation. The females were usually at the edge of the dropoff in late afternoon. Shortly before spawning they moved into deeper water off the edge as a group (about 45-60) and joined the males off the edge of the dropoff. At this time all individuals in the aggregation were either dark (both sexes) or white-head (all males). A male in white-head phase would approach a female and position himself parallel to her. The couple would then do a quick vertical swim for 3-7 m in the water column, followed by a rapid shaking of their bodies and the release of eggs and sperm. This was followed by a quick return of the

couple to the rest of the fish milling in a loose aggregation below in the water column. The overall sex ratio observed in the spawning aggregation was one male for every 3-4 females. These aggregations could be as large as 200 total fish, occasionally to 375.

Spawning sites ranged in overall morphology from acute angular reef elbows (e.g., Caye Bokel at Turneffe Islands atoll), to obtuse angular promontories (e.g., Caye Glory on the barrier reef) extending out from the main reef axis, to rounded bulges in the reef (e.g., Dog Flea Caye at Turneffe Islands atoll), to nearly straight stretches of shelf-edge reef such as Sandbar at Hol Chan and Robinson at Ambergris Caye (Fig. 1). Black grouper were observed spawning off the shelf edge just to the north of angular ( $120^\circ$ ; e.g., Rope Walk Caye at Turneffe Islands atoll) or blunt (rounded) promontories (such as Rocky Point on the barrier reef). The promontories faced seaward (eastward on the barrier reef and east face of atolls; westward on the west face of atolls). Black grouper were also observed spawning at elbows, sharp ( $<90^\circ$ ) bends in the reef around the southern margin of the atolls (e.g., Caye Bokel at Turneffe Islands atoll, Half Moon Caye at Lighthouse Reef atoll). From our observations, there was no particular reef morphology that was favored by black grouper for spawning. Although promontories have been noted as being particularly important spawning sites for other groupers (Carter et al. 1994; Carter and Perrine; Graham and Castellanos 2005), black grouper are apparently less selective in their spawning locations.

The spawning strategy of black grouper appears to be to spawn in small aggregations ( $<200$  fish) at many sites along the coast of Belize and on the offshore atolls. Compared to other groupers, black grouper are less vulnerable to fishing, in that they do not form huge (e.g., tens of thousands of individuals for Nassau grouper) aggregations that are few in number and at very specific times and places (Morris et al. 2000). Black grouper spawn at all nine known Nassau

grouper spawning sites in Belize, although Nassau grouper no longer spawn at some of these sites. For these nine sites, six are still active Nassau grouper spawning sites. Three have disappeared and only two had more than 150 fish in a recent census (Carter and Morrow 1991; Sadovy and Eklund 1999; Sala et al. 2001). Black grouper spawn at many additional sites. Black grouper do not seem to be as tied to the northeast facing promontories on the reefs of Belize that are preferred by Nassau grouper (Carter et al. 1994).

Black grouper have historically been caught by spear and handline fisherman who target Nassau grouper aggregations in December and January, but the aggregations of black grouper appear to peak in abundance in February and March at Nassau grouper sites and other black grouper spawning locations. Most Nassau grouper fishermen today and historically leave the Nassau grouper spawning banks after January, but a few fishermen remain on to catch smaller numbers (much fewer than Nassau grouper) of black grouper. This apparently has afforded some protection to black grouper, whose populations in Belize appear to be in much better condition than those of Nassau grouper. Black grouper have also received some protection as a result of the seasonal (e.g., Glovers Reef) and year-round (Lighthouse Reef) fishery closure of the Nassau grouper spawning banks.

Unlike the Nassau grouper, however, the black grouper is protogynous as a normal reproductive mode. Protogynous groupers of the genus *Mycteroperca* face additional vulnerability in fisheries, because the largest individuals, which are all males, are selectively targeted because they are easier to spear, take a baited hook more aggressively than smaller individuals, or are more highly desired in recreational or commercial fisheries (Gilmore and Jones 1992; Coleman et al. 1996; McGovern et al. 1998). This size-selection makes protogynous groupers particularly vulnerable to fishing, and in species such as black grouper, with relatively

small aggregation size (relative to Nassau grouper), selective fishing on males can make the population particularly susceptible to sperm limitation (Alonzo and Mangel 2004). Alonzo and Mangel (2004) modeled three cases to determine the effects of spawning aggregation size on stock dynamics of protogynous fish, using the following simulations: 1) the entire population mates at one site (one mating site with up to 1000 individuals); 2) a few large mating groups exist (10 sites with a maximum of 100 individuals per site); and 3) many small mating aggregations exist (20 mating sites with a maximum of 50 individuals per site). Spawning black grouper in Belize represent the third option, which may result in increased effect of sperm limitation, if fishing effort remains constant or increases (Alonzo and Mangel 2004).

Black grouper form aggregations that are relatively small, which afford them some additional protection, although not as much as those groupers whose aggregations consist of fewer than 50 individuals (Morris et al. 2000). Because Belize has populations of other species of grouper, some of which (Nassau grouper, red hind) form larger aggregations than does black grouper, the black grouper population in Belize is in better condition than the population in, for example, the Florida Keys, where few species form large aggregations. Black grouper are not as severely overfished in Belize as are some other groupers that form more predictable, larger and fewer aggregations. Morris et al. (2000), based on their revised IUCN criteria, considered black grouper to be Vulnerable and in decline due to loss of habitat (mangrove for juveniles; coral reef for adults) throughout its range. Morris et al. (2000) also predicted additional future decline because of fishing and loss of habitat. Given the rate of coastal development that is occurring in Belize, we can expect additional loss of mangrove habitat that is important for juvenile black grouper.

About one-third of Nassau grouper spawning aggregations disappeared in Belize and the rest of the Caribbean due to overfishing, prior to 2001 (Sadovy and Eklund 1999; Sala et al. 2001); this pattern has been seen in other groupers as well, where fishing of aggregations results in local extirpation (Coleman et al. 1996). Most of these fished-out aggregations have not returned, even after fishing ceased as it became economically unfeasible and fishing on the spawning banks was abandoned (Sadovy and Eklund 1999; Sala et al. 2001). It is possible that some traditional black grouper spawning sites have also been fished to local extirpation, and that there may be some historically active sites that we missed because they have been fished out. It is also possible that some spawning sites for black grouper have not yet been discovered. Sala et al. (2001) determined that fishing of spawning aggregations of Nassau grouper became economically unfeasible and would be abandoned, if abundance in the aggregation fell below 48 fish. Black grouper are larger on average than Nassau grouper, so a slightly smaller number could support a fishery; however the fishery would need to catch almost every fish in most black grouper aggregations, or be supplemented with other groupers, as is the usual case.

IUCN minimally weights spawning behavior when determining the status of grouper species, because spawning behavior for many species is poorly known (Morris et al. 2000). From what we have observed in Belize, black grouper spawn in numerous medium-sized aggregations, and are thus less vulnerable than species like Nassau grouper and goliath grouper (*E. itajara*) that form far fewer, but far larger, aggregations. Aggregation sizes are greater than those considered small (<50 individuals) by Morris et al. (2000), but are not nearly as large as those of the Endangered Nassau grouper. Even wide-ranging groupers like black grouper are vulnerable to threats as ranges are reduced by fishing, and because they reach large size, mature late, and are highly-desired fishery species (Morris et al. 2000).

Marine Protected Areas (MPAs) that include fishing restrictions have the potential to mitigate or reverse the effects of fishing, particularly on protogynous groupers that are especially susceptible to fishing, and which continue to be caught as bycatch when traditional size/bag limits and temporal closures are utilized (Morris et al. 2000; Alonzo and Mangel 2004). However, if MPAs re-distribute fishing effort to unprotected areas, the benefit of no-take MPAs to protogynous species decreases (Alonzo and Mangel 2004). The network of no-take marine reserves that exists in Belize serves to protect black grouper during their spawning aggregations, as many of the sites where we observed courtship and spawning are within existing marine reserves. Of the 22 sites where black grouper were observed courting and/or spawning, 16 are now in MPAs legislated as no-take spawning aggregation sites year round and three (Hol Chan on the barrier reef, Half Moon Caye at Lighthouse Reef atoll and Middle Caye at Glovers Reef atoll) are in Marine Reserves, Natural Monuments or other types of no-take MPAs. No-take MPAs are important in conserving stocks of protogynous fishes like black grouper, because they ensure that some males are not subject to fishing mortality. Black grouper do not form huge, well-known aggregations and, in Belize, they are wary of divers and avoid spear fishermen. However, near a sanctuary area in Florida, black grouper appear to be unwary of divers (Eklund et al. 2000), and sanctuary designation may effect diver-avoidance behavior in black grouper within and along the edges of sanctuaries. Black grouper are not as easily hooked or trapped as *Epinephelus* groupers. Because they are less easily speared and caught than some other groupers, black grouper populations in Belize are in good condition. Continued monitoring of catch and effort, visual census of population size and conservation of juvenile and adult habitats are needed to ensure the health of the stock. It is likely that additional unmapped spawning locations occur in Belize. Future work should include characterizing spawning locations with

rapid methods (such as multibeam or side scan sonar) that can be applied to survey the entire reef system of Belize, so that additional spawning sites might be located and incorporated into management plans.

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TABLE 1. Sites where black grouper were observed during surveys of potential spawning sites. Fish observed from December through April at all sites were exhibiting courtship behavior or spawning. At some sites (\*), no spawning or courting fish were observed, but no observations were made during spawning season. Numbers of observations (N), mean number of individuals ( $\pm$  one standard deviation), range of number of individuals and months observed are listed. Atoll sites include those at Turneffe Islands, Lighthouse Reef and Glovers Reef; all others are barrier reef sites.

SITE	N	MEAN	RANGE	MONTHS
<b>Protected Areas</b>				
<i>Barrier Reef Sites</i>				
Rocky Point, Bacalar Chico	12	54.4 ( $\pm$ 87.9)	1-200	Jan 01; Jan 02; Mar 03; Jan 06
Sandbar, Hol Chan	5	14.0 ( $\pm$ 4.0)	8-20	Jan 06
Cay Glory	5	36.2 ( $\pm$ 31.8)	8-60	Jan 01
Gladden Spit	77	15.9 ( $\pm$ 25.2)	1-155	Jan, Apr 01; Jan, Jul 02; Jan, Feb, Mar, Apr May 03;
Nicholas Caye, Sapodilla Cayes	2	7.0 ( $\pm$ 4.2)	4-10	Jan 02; May 03
Rise and Fall Bank, Sapodilla	4	2.8 ( $\pm$ 1.7)	1-5	Jan 01; Jan 02; May 03
*Rugged Cay, Sapodilla	2	3.0 ( $\pm$ 2.8)	1-5	May 03
Seal Caye, Sapodilla	0			
<i>Atoll Sites</i>				
Dog Flea Caye, Turneffe	16	6.4 ( $\pm$ 13.0)	1-50	Jan 01; Jan 02; Jan 03
Caye Bokel Elbow, Turneffe	19	107.2 ( $\pm$ 71.3)	1-200	Jan 02; Jan 03; Feb, Mar 06
Sandbore, Lighthouse	29	21.5 ( $\pm$ 21.4)	1-100	Jan 01; Jan-Feb 02; Apr 02; Jun-Jul 02; Dec 02; Jan-Mar 03; Jun 03
Halfmoon Caye, Lighthouse	51	32.6 ( $\pm$ 71.9)	1-375	Jan 01; Jan-Jul 02; Oct 02; Dec 02; Jan-Mar 03
South Point, Lighthouse	29	31 ( $\pm$ 57.1)	2-250	Jan-Feb 02; Apr-Jun 02; Dec 02; Jan-Mar 03; Jun 03
East Reef, Lighthouse	2	20.5 ( $\pm$ 26.7)	1-40	Jan 03
Phillips Long Caye, Lighthouse	3	3.0 ( $\pm$ 1.7)	1-4	Mar 02; Jan 03
*Northern Point, Glovers	1	3.0	3	Aug 02
Middle Caye, Glovers	1	250.0	250	Jan 02

TABLE 1. Continued.

<b>SITE</b>	<b>N</b>	<b>MEAN</b>	<b>RANGE</b>	<b>MONTHS</b>
<b>Non-Protected Areas</b>				
<i>Barrier Reef Sites</i>				
Robinson, Ambergris Caye	6	45.8 ( $\pm$ 8.6)	35-60	Nov-Dec 05
Caye Caulker	0			
Goff's Caye	0			
Tobacco Caye	0			
<i>Atoll Sites</i>				
Mauger Caye (Crown), Turneffe	0			
Mauger Caye (East), Turneffe	0			
Soldier Cay, Turneffe	4	60.5 ( $\pm$ 36.5)	12-100	Jan 02, Jan 03
Rendezvous Point, Turneffe	1	3.0	3	Jan 03
Calabash Caye, Turneffe	2	11.0 ( $\pm$ 12.7)	2-22	Jan 02; Jan 03
Crawl Caye, Turneffe	1	12.0	12-12	Jan 03
Ropewalk Caye, Turneffe	1	10.0	10	Jan 03
Deadman's Caye, Turneffe	1	15.0	15	Jan 03
Southwestern End, Glovers	1	50.0	50	Jan 02

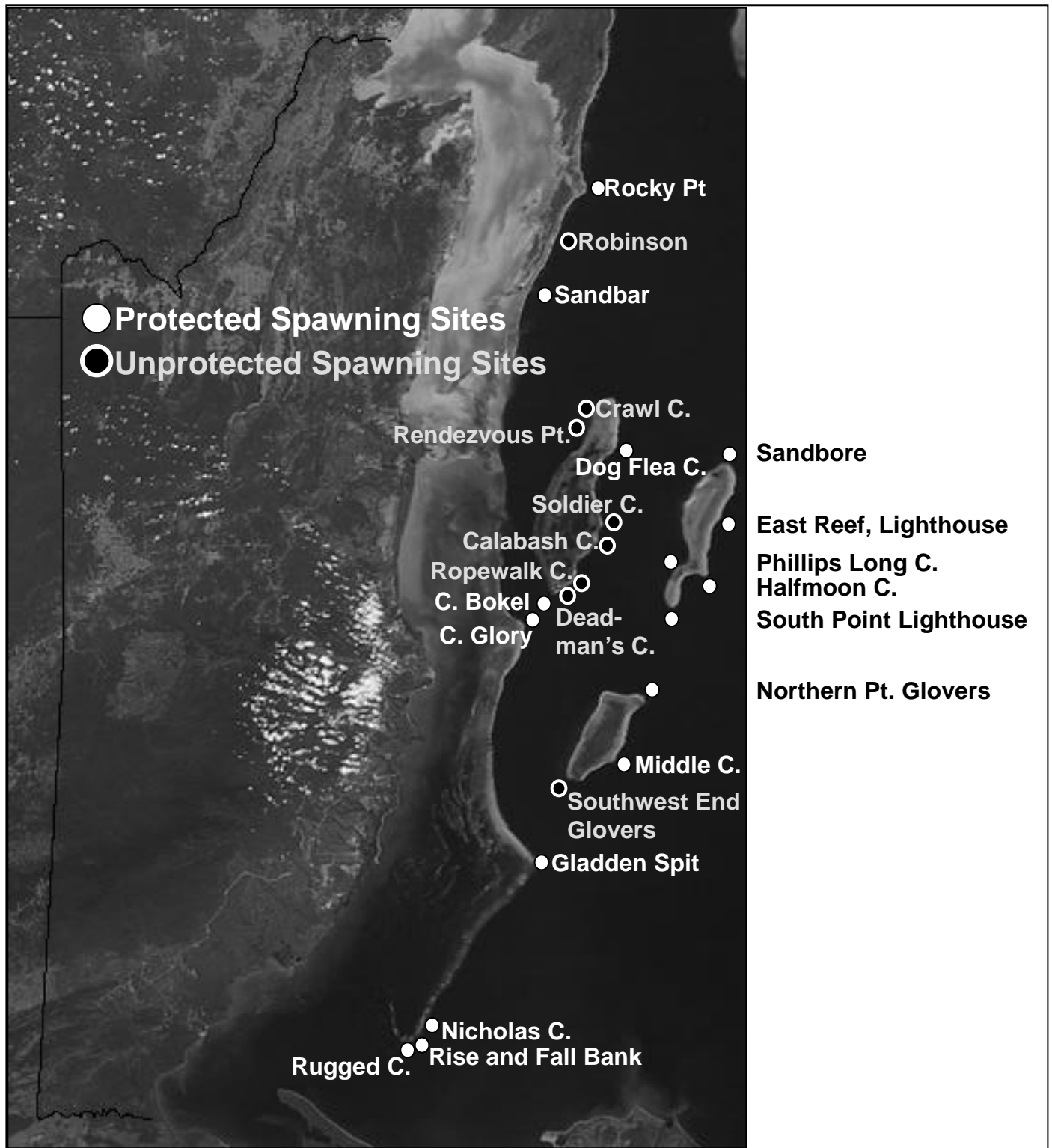


FIG. 1. Locations in Belize where we observed black grouper courtship and/or spawning.

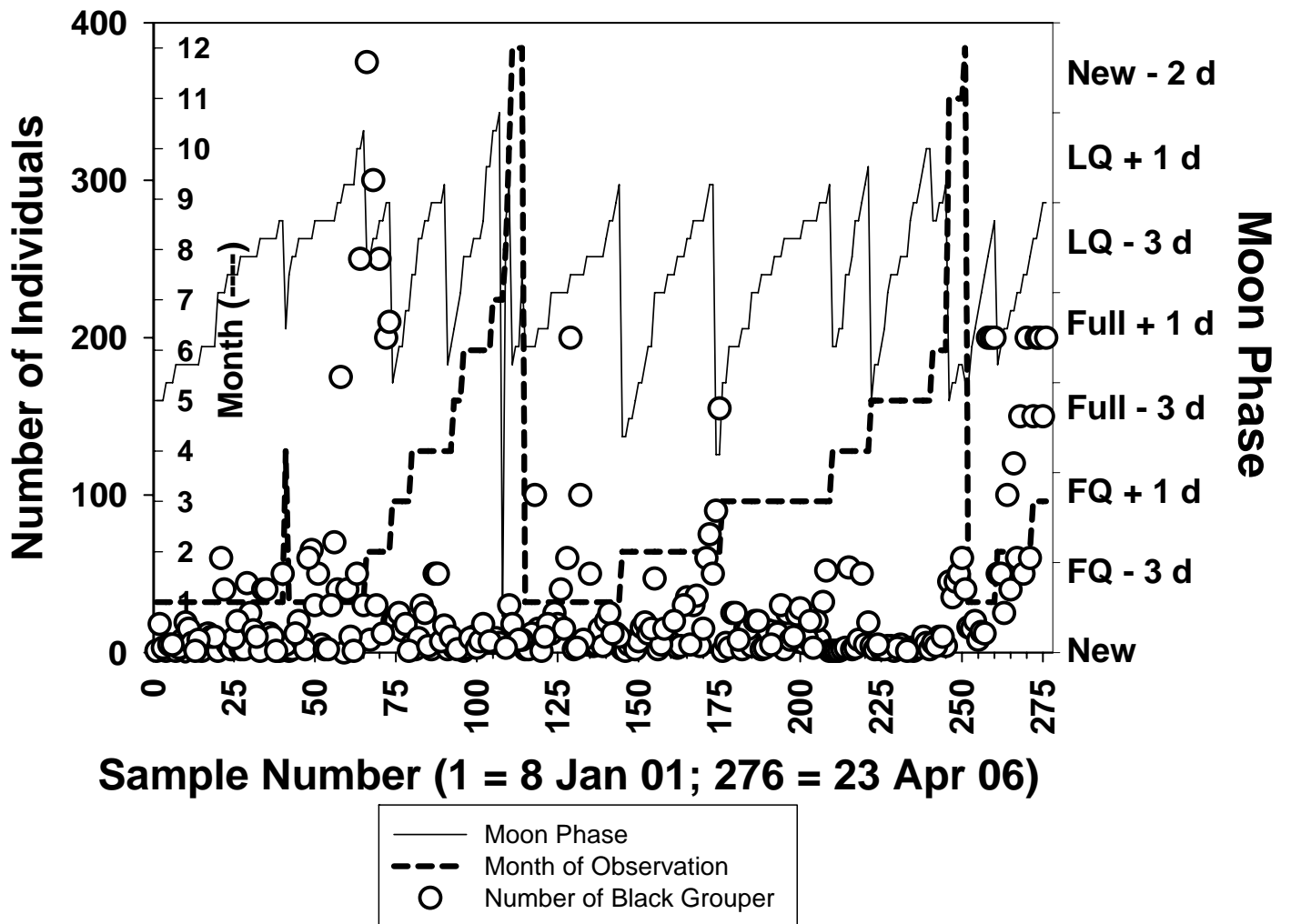


FIG. 2. Number of individuals, month of observation, and lunar phase for each observation of black grouper in Belize.

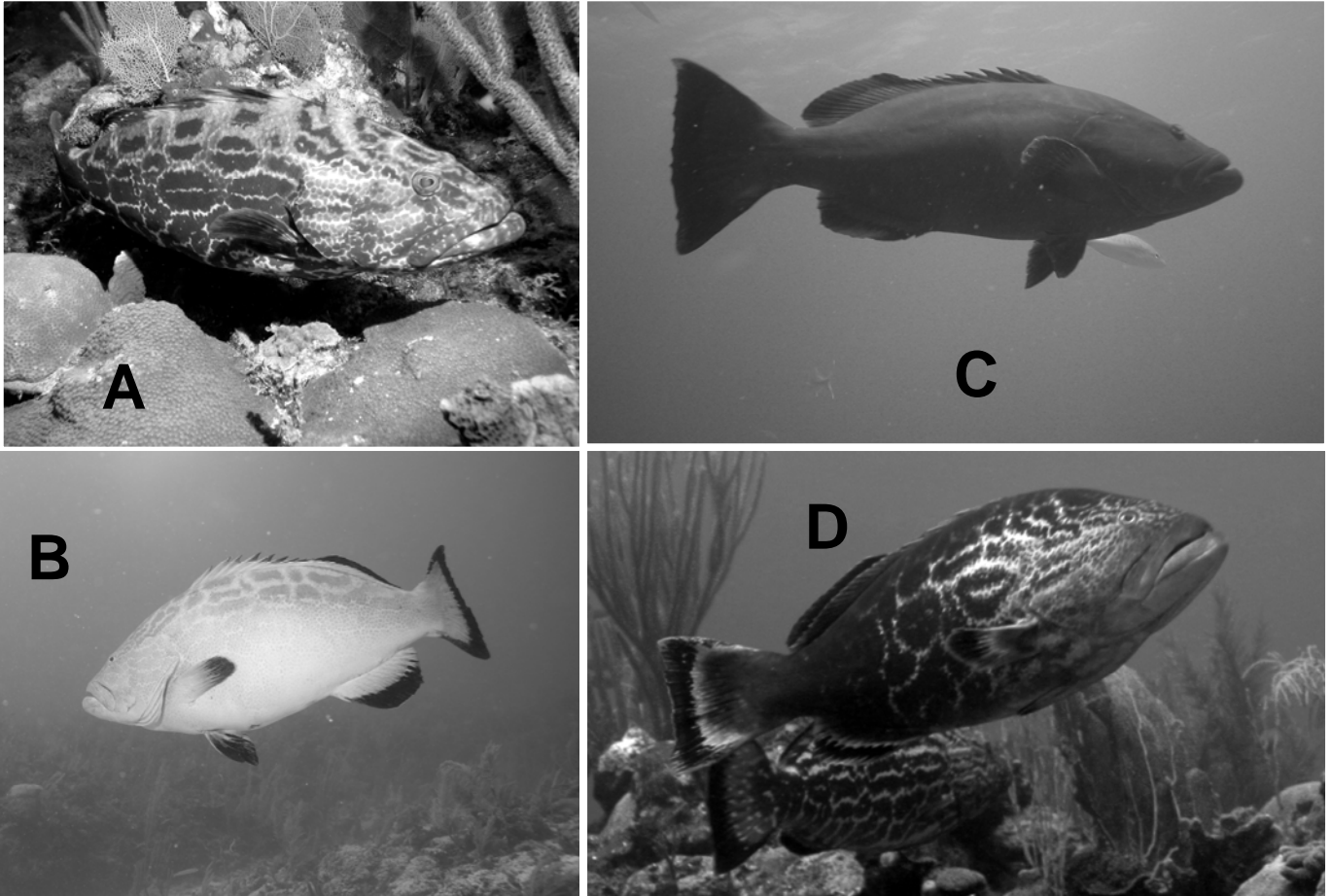


FIG 3. Color phases of black grouper observed in Belize, including blotched (A), light (B), dark © and white-head (D) phases. See text for details.