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Observations of a Nassau grouper, *Epinephelus striatus*, spawning aggregation site in Little Cayman, Cayman Islands, including multi-species spawning information

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Synopsis

Mass spawning aggregations of Caribbean grouper species are a conservation priority because of declines due to over-fishing. Previous studies have documented five historical aggregation sites in the Cayman Islands. Today, three of these sites are inactive or commercially extinct. In January 2002, the Reef Environmental Education Foundation led an expedition to Little Cayman Island to document a recently re-discovered spawning aggregation of Nassau grouper, *Epinephelus striatus*. A team of divers estimated the abundance, color phase composition, and courtship and spawning behavior of the aggregating grouper. The color phase composition of the aggregation shifted both during the course of each evening and throughout the 10-day project. Divers documented atypical coloration and courtship behavior in 10 additional fish species, of which five were seen spawning. Artisanal fishing occurred daily on the aggregation. The Cayman Islands Department of the Environment collected landings data and sampled catches to obtain length and sex ratios. The Cayman fishing fleet, while small, had a significant impact on the aggregation with a harvest of almost 2 000 Nassau grouper during the 10-day project. The study site supports the largest known Nassau grouper aggregation in the Cayman Islands. The relatively large size of fish and the high proportion of males indicate that this site supports a relatively healthy aggregation compared to other Nassau grouper aggregation sites throughout the Caribbean.

Introduction

Reproductive aggregations in mobile marine species are common, yet poorly understood. Possible benefits of aggregating to reproduce include reduction of egg predation, increased genetic exchange, and higher fertilization rates (Domeier & Colin 1997, Bolden 2000, Sala et al. 2001). Adequately characterizing the biology of animals that aggregate to reproduce requires documenting the location and spatial and temporal dynamics of aggregations, as well as the behavior of aggregating individuals. This is particularly true for species deemed 'at risk' from a conservation standpoint, as aggregations tend to increase the vulnerability of individuals to harvest. Additionally, because animals that exhibit this type of life history rely on behavioral interactions that may be mediated by density, declines in the number of individuals may result in disproportionate declines in the reproductive potential of the population (Allee 1931). In the Caribbean approximately 110 spawning aggregations of 16 different species have been documented (Luckhurst 2001). Once discovered, aggregation sites are typically heavily fished.

Nassau grouper, *Epinephelus striatus* (Bloch 1792), migrate to specific sites during the winter full moons to reproduce in aggregations (Domeier & Colin 1997, Bolden 2000, Sala et al. 2001). Nassau grouper have an average life span of 16 years (Sadovy & Eklund 1999), can reach a total length of 91 cm, and weigh up to 25 kg (Olsen & LaPlace 1979, Domeier & Colin 1997). The species appears to be gonochoristic with the capacity to change sex (Sadovy & Colin 1995, Sadovy & Eklund 1999). Sexual maturation is reached at ~1.87 kg (Sadovy et al. 1994b) or 40–45 cm, which is between 4 and 7 years old (Sadovy & Eklund 1999). The environmental and social triggers that cause Nassau grouper to aggregate are not well understood, though changing lunar light conditions, water temperature, currents, learned behavior, or a combination of multiple factors may be the basis for aggregation formation (Colin et al. 1987, Carter 1989, Tucker et al. 1993, Domeier & Colin 1997, Sadovy & Eklund 1999, Paz & Grimshaw 2001). Aggregations are typically located near significant geomorphological features, such as near the ends of islands or projections of the reef seaward from the general reef contour (Colin et al. 1987).

Between 60 and 80 Nassau grouper spawning aggregations have been identified. Of these, between one-quarter to one-half have been fished to exhaustion and most others are declining (Sadovy & Eklund 1999). Historical aggregations had up to tens of thousands of individuals (Smith 1972); however, all currently known active aggregations have a few thousand to less than 100 fish (Sadovy & Eklund 1999, Paz & Grimshaw 2001).

Courtship coloration in Nassau grouper falls into four phases: barred pattern (typical non-courtship coloration), white belly, bicolor, and dark (Colin 1992). Both sexes exhibit bicolor and white belly phases (Colin 1992, Carter et al. 1994, Aguilar-Perera & Aguilar-Davila 1996). Colin (1992) postulated that the bicolor phase signals submissive behavior, and is thus important for large schools of aggregating, typically territorial individuals. Paz & Grimshaw (2001) suggested that the bicolor and white belly phases were forms of cryptic coloration specific to the unique habitats of the aggregation site. There has been conflicting speculation as to whether dark color phase fish are either male (Paz & Grimshaw 2001) or female (Colin 1992).

Nassau grouper are heavily fished in the Cayman Islands (Colin et al. 1987). Of the total Nassau grouper currently harvested each year in the Cayman Islands, fishermen take 90% or more from aggregations (P. Bush, pers. observ.). Tucker et al. (1993) described five historical Nassau grouper aggregation sites in the Cayman Islands: one each on the southeast corners of Little Cayman and Cayman Brac and three on Grand Cayman. Intense harvest has resulted in the commercial extinction or complete disappearance of three of the aggregation sites (Colin et al. 1987, Carter 1989, Tucker et al. 1993, Domeier & Colin 1997, Sadovy & Eklund 1999, Paz & Grimshaw 2001). In 2001, fishermen re-discovered an aggregation site on the west end of Little Cayman Island that had been previously fished as recently as the 1960s. In 2001, fishermen harvested 2 000 Nassau grouper from the site. In the winter of 2002, the Reef Environmental Education Foundation (REEF) coordinated an expedition to study the aggregation site. In this paper we document the characteristics of the aggregation, describe courtship and spawning behavior, and document the use of the site by other species of spawning fishes. We also report shifts in the location, behavior, and color patterns of Nassau grouper at the site over the course of the lunar cycle and the sex ratio and sex–length relationship of Nassau grouper in the aggregation based on measurements taken from harvested fish.

Methods

Study area

The Cayman Islands, consisting of Grand Cayman, Little Cayman, and Cayman Brac, lie between 19°15′ and 19°45′ N latitude and between 79°44′ and 81°27′ W longitude. In this study we documented an aggregation located at the terminus of the southwestern end of Little Cayman's shelf (Figure 1). This reef promontory features a sloping drop-off extending 0.6 km from shore that includes a 15 m terrace followed by a deeper terrace at 24–33 m depth that slopes to the shelf edge. Benthic habitat of this deeper terrace features low relief (3–5 m) broad ridges with hard and soft corals and sponges, interspersed with wide (30 m) valleys of sand. The shelf edge drops off at 33 m to a near vertical wall. The area's currents are complex and range from slack to estimated speeds of 3 kn.

Field observations

A team of seven divers conducted fieldwork from 27 January to 5 February 2002 on Little Cayman Island. The team documented activity at the west end aggregation site each sunset period, beginning the evening of the full moon (28 January). In addition,

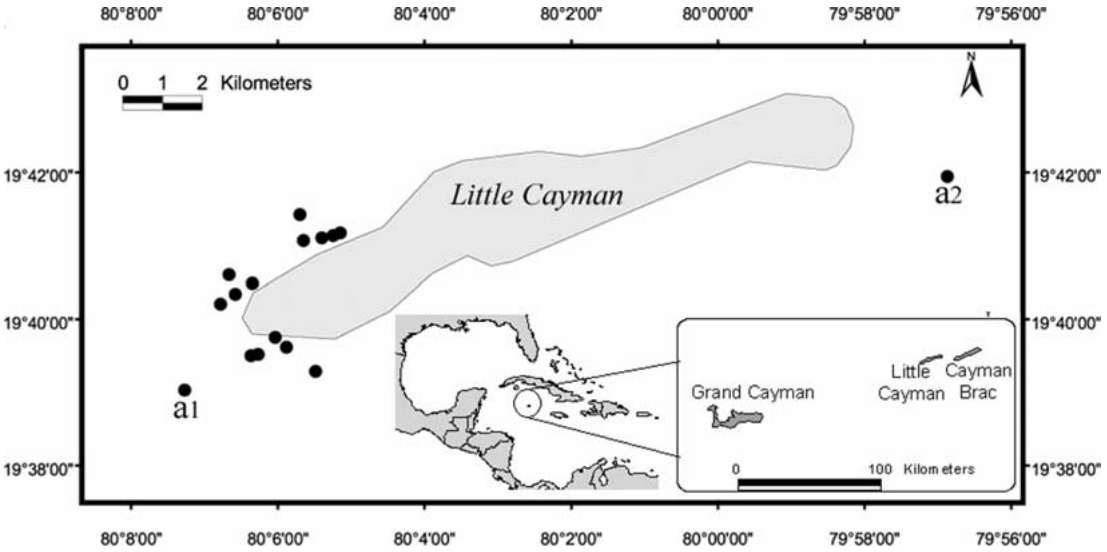

Figure 1. Map of the study area, indicating locations of the west end aggregation site (a1), the historical east end aggregation site visited on February 4 (a2), and the 14 reef sites surveyed during the day (indicated by dots).

staff from the Cayman Islands Department of the Environment (CIDOE) and local dive operators accompanied the team of observers on several evenings. The team entered the water 10–72 min before sunset (mbs) each night and remained in the water approximately 40 min each evening. Dives averaged 25 m in depth. Five members of the team estimated the number of individual Nassau grouper present, the color phase composition of the aggregation, the presence of fish with distended abdomens (an indication of readiness to spawn seen in both males and females), and recorded courting/spawning behavior.

On the evenings when spawning was observed, divers reported the time of each gamete release. Because at least some of the team members observed and recorded the same spawning events, we used the maximum number of spawning events recorded by any one team member to compare spawning activity between nights. Observations on the presence and activity of other fish species were also recorded. Two additional divers took underwater video footage using digital video cameras without lights.

Each evening, the team estimated the dimensions of the aggregation using topographic reference points. Team members then counted Nassau grouper within visually estimated 3.3 m^3 cubes and extrapolated those values to generate an estimate of the total number present on the aggregation. We generated nightly estimates of the abundance of grouper in the aggregation by averaging the divers' abundance estimates.

In addition to the observations made on the aggregation site each evening, five members of the team conducted daytime visual, non-point roving surveys on reefs around Little Cayman. Divers recorded information on the size, depth, color phase, presence of a distended abdomen, group size (if traveling with others), and direction of movement for all Nassau grouper.

Fishermen were present on the aggregation site each day of the project but rarely fished on the aggregation after sunset. The total number of fishing boats at any given time ranged from 1 to 13 and each boat carried two fishermen. All fishing was hook and line. Though no special license is needed, Cayman Island law permits only Caymanians to fish aggregation sites during grouper spawning season. CIDOE collected data on daily landings and sampled catches throughout the aggregation period to obtain length and sex of aggregated Nassau grouper.

Results

Aggregation characteristics

Estimates of the average number of Nassau grouper present at the aggregation site ranged from 5 200 individuals 2 days after the full moon (dafm) to 400 on the 8th dafm, the last evening the aggregation was documented. During the aggregation cycle, fishermen harvested a total of 1 934 Nassau grouper from the

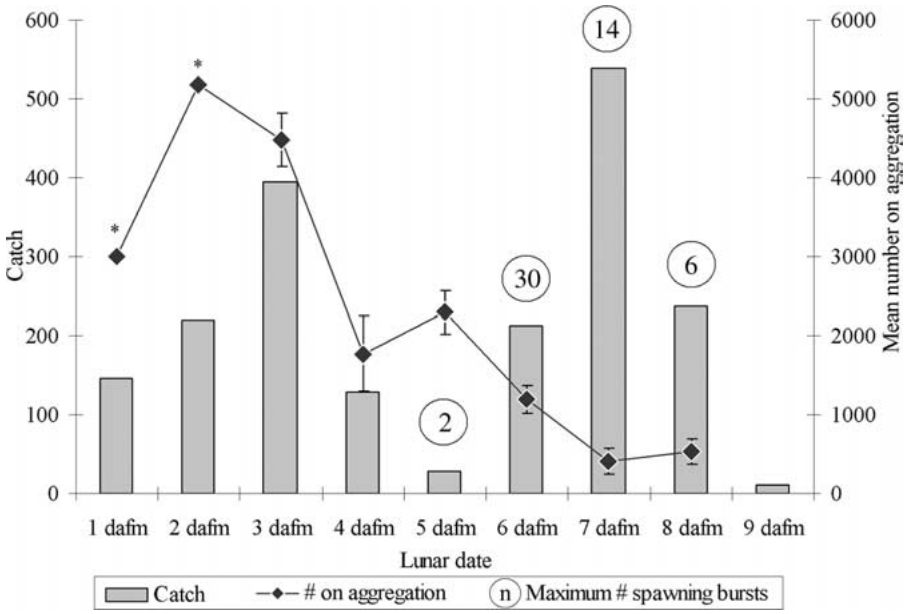

Figure 2. Daily catch of Nassau grouper from the aggregation site and mean number of Nassau grouper in the aggregation visually estimated by divers. Error bars represent one standard deviation. The circles show the maximum number of spawning bursts reported each evening, if any. $*$ = error bars are not shown because less than three divers found aggregating fish.

aggregation site. Figure 2 depicts the mean estimated number of Nassau grouper present at the aggregation site each evening and the total catch reported by fishermen each day.

Staff from the CIDOE recorded total length of 319 Nassau grouper, representing 17% of fish landed. Based on the individuals sampled, the harvested fish averaged 62.8 cm total length (range 47–86 cm, SD = 9.0), which equates to an 8+ year old fish (Sadovy & Eklund 1999). CIDOE staff determined the sex of 22% of the catch (431 fish). The female to male sex ratio of harvested fish varied through time; males dominated the catch early and late in the aggregation cycle while females dominated just prior to the peak of spawning activity (Figure 3). The average female to male sex ratio across all days was approximately 1 : 1.6 (166 females and 265 males). CIDOE staff also measured the length of a subset of all sexed fish; male grouper caught on the aggregation site were significantly larger than females (67.5 and 72.3 cm mean total length in females and males, respectively; t-test $p = 0.033$).

Characteristics and behavior on reef sites

Team members conducted a total of 67 visual roving surveys on 14 reefs around the island (Figure 1) during daytime hours, representing 60 h of survey time. Divers reported information on 261 Nassau grouper. Early in the aggregation cycle (1 day before full moon (dbfm) to 4 dafm), approximately half of the Nassau grouper encountered during the daytime dives displayed white belly and dark body colorations and had distended abdomens. The majority (65%) of all individuals seen during this time traveled in a directed manner along the shelf edge between 19 and 38 m. Of those in transit, most traveled in groups of 2–8 individuals. Divers recorded the largest number of Nassau grouper 2 dafm, with 27 fish observed during one dive. Mean total length for all Nassau grouper observed during daytime dives was 42 cm, ranging from 26 to 60 cm. On two occasions, divers observed individual grouper changing color while in transit; one barred phase changed to bicolor phase and one dark phase changed to barred phase.

Coloration shifts and behavior on the aggregation site

During the initial days of observation (full moon to 4 dafm) at the aggregation site, divers observed a consistent pattern of crepuscular movement and shift in dominant color phases. Each evening during this time,

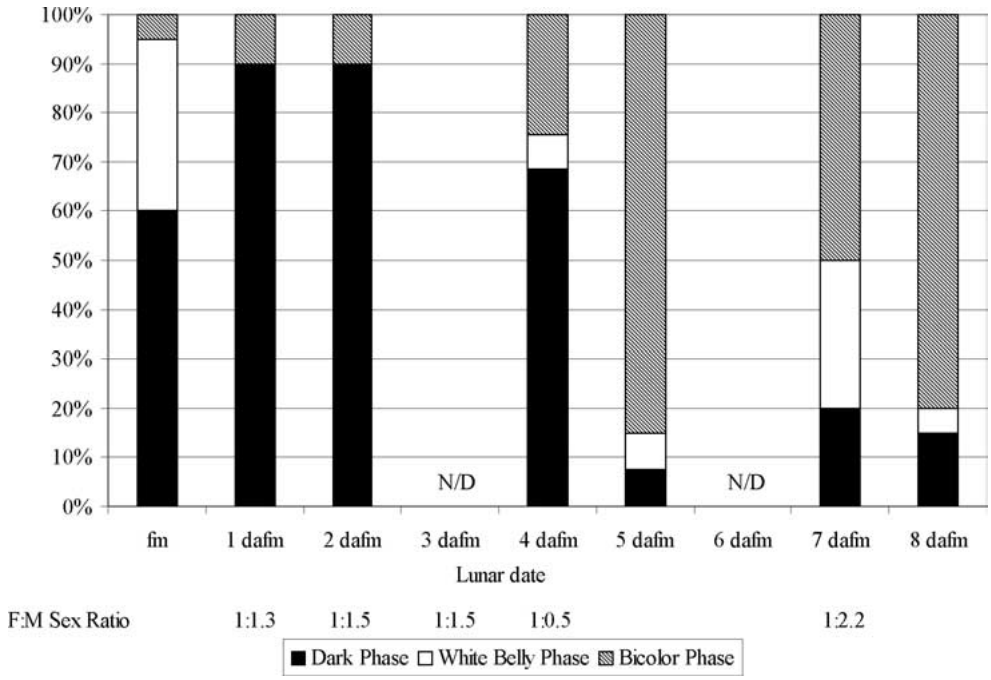

Figure 3. The shift in color phases during the aggregation cycle and the sex ratios based on catch data. Bars indicate the proportional color phase composition at the aggregation site.

most Nassau grouper took on the dark phase as sunset approached and the entire aggregation moved from hovering 1–6 m above the plateau to hovering at and beyond the shelf edge (Figure 4a,b). A small portion of the individuals exhibited the barred or white belly color patterns, and these individuals were distributed toward the bottom of the aggregation along the perimeter and interior. The aggregation contained few bicolor phase fish. Individual fishes rarely interacted during this time.

As the lunar phase approached 5 dafm, 'herding' activity, where several grouper (often in bicolor phase) closely followed and partially surrounded a dark phase fish, became common and the grouper moved more rapidly. In addition, bicolor phase fish would nudge white belly phase fish from the bottom up into the water column. During this time, bicolor phase fish dominated (85% of fish present vs. 10% earlier in the aggregation cycle) and the aggregation concentrated over the shelf edge (Figures 3 and 4c).

Courtship and spawning behavior

Team members documented Nassau grouper spawning on 4 nights (2–5 February 2002) beginning 5 dafm. On each of those evenings, surveys began 28–30 mbs and lasted until between 7 and 15 min after sunset (mas). Spawning occurred as early as 26 mbs and as late as 15 mas. Figure 2 shows the maximum number of gamete releases reported each night. The highest level of spawning activity occurred 6 dafm, when a single diver observed at least 30 gamete releases. Team members also documented a large amount of spawning activity 7 dafm.

On each of the evenings that team members observed spawning, the Nassau grouper formed a cone between 33 and 18 m. The grouper exhibited several types of pre-spawning behavior on these nights, including (1) vertical spirals, (2) vertical movement without spiraling, (3) rapid horizontal runs near the substratum, and (4) rapidly coming together after a short vertical movement and then radiating outward (Colin 1992). Gamete release only occurred during the radiating outward behavior (hereafter called spawning bursts). Each spawning burst started with 1–7 bicolor fish chasing one dark phase fish. The group, led by the dark phase individual, would swim vertically for 3–6 m, resulting in gamete release before radiating outward. Additional bicolor fish often joined in during the ascent and the resulting spawning burst typically involved

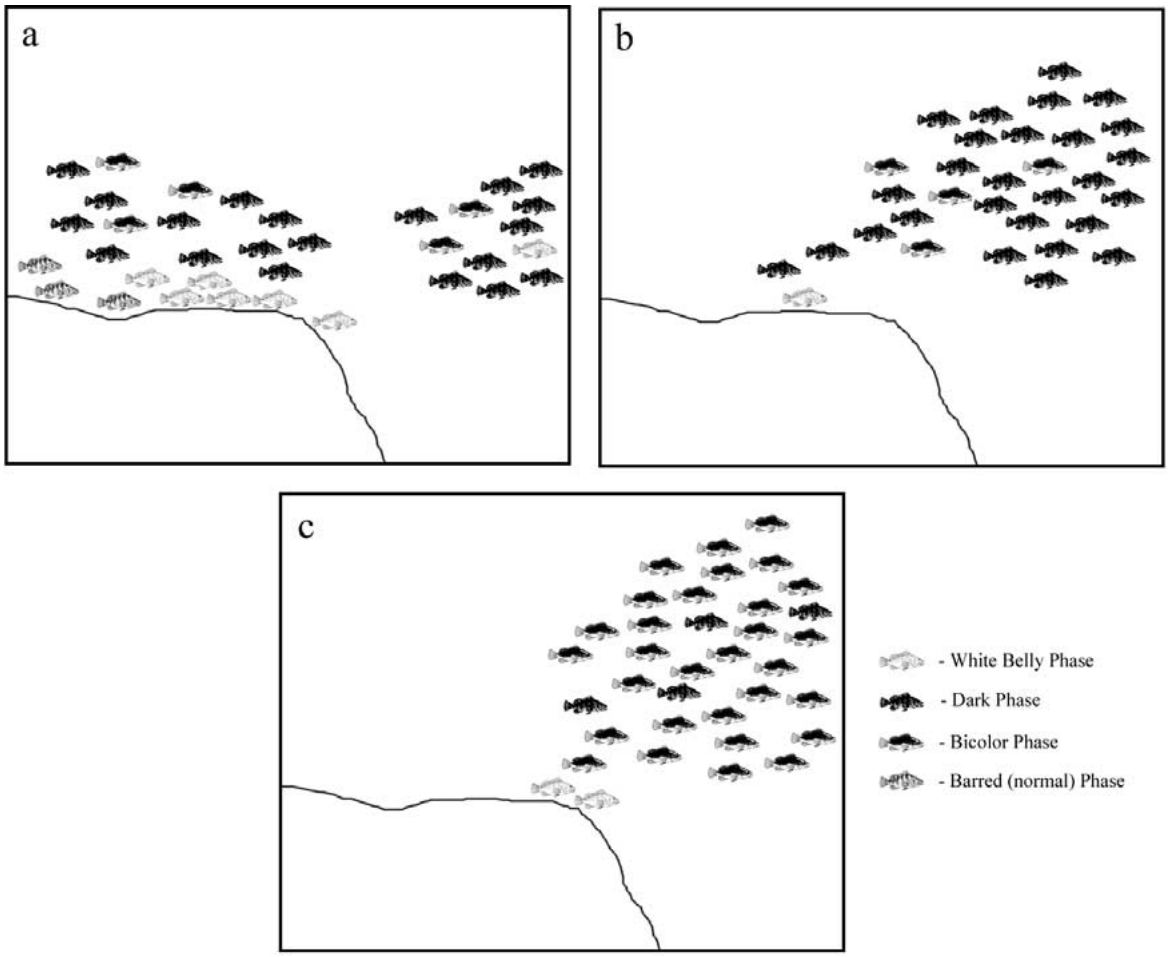

Figure 4. Crepuscular and lunar phase shifts in color phase composition and location of the aggregation. (a and b) Crepuscular shifts seen early in the aggregation cycle (full moon to 4 dafm); (a) prior to sunset, (b) as sunset approached and passed. (c) Later in the aggregation cycle (5–8 dafm), there was no nightly shift in color phase or location. In each figure, the top of the box represents the surface and the top of the reef is 33 m.

6–25 individuals, although divers observed spawning groups of up to 50 individuals. Spawning bursts often appeared to initiate additional nearby spawning bursts so that in some instances divers saw as many as four in 1 min. Divers also witnessed many false starts or failed spawning bursts.

Multiple species observations

Divers documented several other primarily large predatory fish species at the aggregation site. Small, site-attached reef fish were scarce. Divers witnessed atypical color patterns, courtship behavior, and/or spawning in ten additional species – tiger grouper *Mycteroperca tigris* (Valenciennes 1833), yellowfin grouper *Mycteroperca venenosa* (Linnaeus 1758), black grouper *Mycteroperca bonaci* (Poey 1860), horse-eye jack *Caranx latus* (Agassiz 1831), bar jack *Caranx ruber* (Bloch 1793), black jack *Caranx lugubris* (Poey 1860), mackerel scad *Decapterus macarellus* (Cuvier 1833), yellow jack *Caranx bartholomaei* (Cuvier 1833), dog snapper *Lutjanus jocu* (Bloch & Schneider 1801), and ocean triggerfish *Canthidermis sufflamen* (Mitchill 1815). Of these, divers documented gamete release in five species (Table 1).

Between 4 and 8 dafm, tiger grouper at the aggregation site exhibited the tricolor coloration that occurs

Table 1. Summary of spawning seen in other species by date (dafm).

Lunar date (dafm)	Tiger grouper	Horse-eye jack	Bar jack	Black jack	Mackerel scad
2		Spawning		Spawning	
3		Spawning			
4		Spawning			
5	Spawning	Spawning	Spawning	Spawning	Spawning
6		Spawning	Spawning	Spawning	
7			Spawning		
8	Spawning		Spawning		Spawning

Colorations and other courting behavior are noted in the text.

during courting and spawning (Sadovy et al. 1994a). Tiger grouper spawned 5 and 8 dafm, with as many as 150 tricolor individuals present and spawning bursts containing 5–12 individuals. Divers also saw small groups (2–4 individuals) of yellowfin and black grouper with distended abdomens on several nights. Large schools of horse-eye, black, and bar jacks spawned on most nights and all displayed atypical color patterns. Horse-eye jacks assumed a bicolor coloration with dark dorsal and tail fins and a white ventral pattern, black jacks displayed brilliant white tips on their tails, and bar jacks displayed a yellow tail and flashed dark bars on their body during the gamete releases. Mackerel scad spawned 5 and 8 dafm. Schools of several hundred yellow jack, which are typically found solitary or in small groups, visited the aggregation site on two evenings. A small group of dog snapper exhibited spawning behavior and flashed white bars on their sides as they courted. Ocean triggerfish displayed a coloration that featured a dark bar on each cheek that extended from below the eye to the jaw.

Seven dafm, the team conducted a daytime dive on an area historically known as a Nassau grouper aggregation site (Figure 1). This site on the east end of Little Cayman had been fished since 1903, was heavily harvested in the mid-1980s, and no longer contained an aggregation by 1995. The divers documented small groups (2–5 individuals) of Nassau, black, and yellowfin grouper, along with a large aggregation (250 individuals) of tiger grouper.

Discussion

The Little Cayman west end aggregation site supports the largest known Nassau grouper aggregation in the Cayman Islands. Additionally, the mean size of aggregating Nassau grouper is larger than any other aggregation documented in the Cayman Islands or elsewhere (Sadovy & Eklund 1999). While use of aggregation sites by multiple species is common (Carter 1989, Aguilar-Perera 1994, Carter et al. 1994, Luckhurst 2001, Paz & Grimshaw 2001), the diversity of species documented spawning at the aggregation site is unique among Caribbean sites described in the literature. Clearly this area has properties of great reproductive benefit for many species of marine fish.

We believe that both sexes of aggregating Nassau grouper exhibit dark phase coloration at least some of the time. The sex ratios of daily fish catches were inconsistent with the evening proportions of fishes exhibiting dark phase coloration (Figure 3). For instance, the first night after the full moon fishermen caught 56% males, while 90% of the fishes observed on that evening were dark phase.

The observed nightly shift in color phase to mostly dark individuals during the early days of the aggregation cycle corroborated findings by Colin (1992). This shift may occur due to a trade off between predation risk and reproductive success. Early in the aggregation cycle when spawning does not occur, both sexes assume dark phase as a cryptic coloration. Later in the aggregation cycle when spawning occurs, individuals maintain bicolor phase throughout the evening to distinguish and advertise preparedness among spawners despite increased vulnerability to predation.

The high proportion of males present throughout the aggregation period contrasts strongly with that reported from other Nassau grouper aggregation sites. If protogynous hermaphroditism plays a greater role in Nassau grouper's sexuality than gonochorism, the difference in sex ratios between the historical east end spawning aggregation *versus* the aggregation studied here could be explained by the differences in fishing pressures. For example, 4 dbfm in January 1978, Little Cayman's historical east end spawning aggregation had

a sex ratio of 1 : 0.5 female to male. This aggregation was fished intensively until exhausted in 1995. Carter et al. (1994) found that heavily fished Nassau grouper aggregations in Belize showed higher female to male sex ratios than did unexploited aggregations. In heavily fished aggregations in the Bahamas, female to male sex ratios varied from 1 : 0.2 to 1 : 0.3 (Colin 1992). In each of these examples there appears to be a link, perhaps causal, between heavy fishing pressure and a high proportion of females. In this scenario, the demography of a fished population would be skewed towards smaller/younger individuals, a high proportion of which would be females who have not matured enough to undergo sex change. However, the change in sex ratio seen through the spawning cycle can complicate comparisons of sex ratios across aggregations, as catch statistics are often not reported throughout the entire duration of the aggregation.

In late February 2002, the Cayman Island Marine Conservation Board defined a spawning season of from November 1 to March 31 and implemented 'no trapping' buffer zones of 1 nm around each designated spawning area, along with an alternate year fishing strategy. During fishing years (i.e. 2004 and 2006), only 12 Nassau grouper may be taken per boat per day. No Nassau grouper may be taken from aggregation sites during non-fishing years. While this legislation was recommended in 1995 with the goal of reducing fishing mortality by half, the delay in implementation and the continuation of heavy fishing in the interim may have compromised its intended effect. In December 2003, the Marine Conservation Board implemented an eight-year harvest ban for spawning areas.

Throughout the Cayman Islands, Nassau grouper populations are relatively large in comparison to many places in the Caribbean (Pattengill-Semmens & Semmens 2003). It appears that Nassau grouper stocks in the Cayman Islands have demonstrated some degree of resilience under fishing pressure, perhaps due to the cumulative effects of inclement weather during aggregations, possible recruitment from proximal offshore banks, possible shifting of aggregation sites, and the existence of minor satellite aggregation sites that remain unfished. However, over the last 16 years catches have steadily declined in the Nassau grouper fishery (P. Bush, pers. observ.). While small, the Cayman fishing fleet is potent in its effects on seasonal reproductive aggregations. At present, the west end Little Cayman site is the only known Nassau grouper aggregation in the Cayman Islands that could reasonably be considered healthy, given that males numerically dominated the aggregation and that the size of harvested fish were large in comparison to other aggregation studies. As such, this aggregation probably provides a high proportion of the total recruitment of Nassau grouper to the Cayman Islands. Maintaining the health of this aggregation is of paramount importance in order to protect Nassau grouper stocks and the viability of the fishery now and in the future.

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