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ASSESSMENT OF AN UNPROTECTED RED HIND (*EPINEPHELUS GUTTATUS*) SPAWNING AGGREGATION ON SABA BANK IN THE NETHERLANDS ANTILLES

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ABSTRACT

Although little fisheries data exist for red hind, *Epinephelus guttatus* (Linnaeus, 1758) on the Saba Bank, Netherlands Antilles, spawning aggregation characteristics from other populations can be used to assess the health of a red hind spawning population previously undocumented there. In December 2005, a spawning aggregation site for red hind was surveyed on Saba Bank at 17°33.6´N, 63°17.7´W. Red hind aggregated on the northeast edge of the bank, in an area of 0.053 km^2. Spawning occurred in January 2006 during the week prior to and possibly after the full moon. Reproductively developed males and females were collected from December through February, however, in January average fish density increased from 1.46 ± 0.26 fish 100 m^{-2} to 34.27 ± 2.20 fish 100 m^{-2} and the M:F sex ratio shifted from 4:1 to unity. Fish were observed exhibiting little territorial or haremic behavior. Gonadosomatic indices in females reached high daily averages in January and February of 15.86 ± 5.4 and 6.93 ± 2.40 respectively, one day prior to the full moon. Average daily water temperature dropped throughout the study period, and during the week prior to the full moon in January, ranged from 26.7 °C to 26.5 °C. Current direction was dominated by tidal fluctuations but during the spawning period was predominantly directed to the southwest. Comparison of spawning population characteristics across red hind aggregation sites in the eastern Caribbean under varying degrees of protection suggests that the Saba Bank aggregation is moderately exploited and should be monitored and more closely managed.

In the Caribbean and tropical Atlantic, hinds and groupers (Serranidae) comprise one of the most valuable components of the commercial fishery. After years of overfishing and extirpation of several of the larger species, red hind [*Epinephelus guttatus* (Linnaeus, 1758)] has become the dominant fish in many of the grouper fisheries. Red hind comprises one fifth of the total commercial finfish landed in the US Virgin Islands (USVI; Cummings et al., 1997), nearly 20% by weight of commercial landings in the British Virgin Islands (Eristhee et al., 2004), and over one third of the grouper sold in both Bermuda and Puerto Rico (Appledorn and Meyers, 1993; Luckhurst, 1996; Matos-Caraballo, 2000).

Like many commercially important groupers and snappers, red hind return to specific locations each year to form large spawning aggregations (Shapiro et al., 1993; Sadovy et al., 1994; Beets and Friedlander, 1999, review by Nemeth, in press). Due to this high degree of site and temporal fidelity, as well as to the sheer concentration of fish in relatively small areas, spawning aggregations are especially vulnerable to exploitation by fishers. Because spawning aggregations may be the primary if not sole source of larval production for a fish population, over-exploitation of spawning aggregations may not only jeopardize the sustainability of regional stocks, but may also cause dramatic short and long term local fisheries declines.

In the USVI, long term monitoring of two red hind spawning aggregations showed that the density, biomass, and length of spawning adults can increase significantly when a spawning aggregation is adequately protected from fishing and can result in an overall increase in the size of red hind caught in the commercial fishery (Nemeth, 2005). Nemeth (2005) reported that after 10 yrs of well enforced seasonal protection and 3 yrs of year-round protection of a red hind spawning aggregation off St. Thomas, spawning adults at the aggregation increased 60% in average density and biomass and 10 cm in average total length (TL). A corresponding 3 cm increase in TL in commercial landings was documented (Nemeth, 2005). Alternatively, red hind spawning aggregation populations and the associated commercial catch can decline if protection is insufficient, as documented on a poorly enforced seasonally closed spawning aggregation site off St. Croix (Nemeth et al., 2006a).

Because red hind are relatively long-lived (max. age = 22 yrs) and are protogynous hermaphrodites (Luckhurst et al., 1992; Sadovy et al., 1994), they are a useful model for evaluating population characteristics of a spawning population. Red hind mature at about 25 cm TL, change sex from female to male at 32–38 cm, and reach a maximum TL of 55 cm or longer (Luckhurst et al., 1992; Sadovy et al., 1994; Nemeth, 2005; Whiteman et al., 2005). In well protected spawning aggregations, the average size of adults in the spawning population may reach 40 cm after 15 yrs (Nemeth, 2005) or nearly 50 cm after 30 yrs (B. Luckhurst, Bermuda Department of Environmental Protection, unpubl. data). In poorly protected aggregations, the average size of spawning adults may be as small as 32 cm (Nemeth et al., 2006a,b). Sex-change results in a strong bimodal size distribution and can also be used as an indicator of fishing pressure. For example, Nemeth et al. (2006a) showed that the length frequencies of male and female red hind collected at spawning aggregations off St. Thomas (mean length: male = 41.8 cm, female = 36.2 cm) showed a stronger bimodal distribution than red hind collected off St. Croix (mean length: male = 33.4 cm, female = 31.7 cm). Moreover, as an aggregation is fished, the larger individuals, usually males, experience higher fishing mortality that can decrease the size and age at sexual maturity and result in a highly skewed sex ratio (Colin et al., 1987; Shapiro et al., 1994; Beets and Friedlander, 1999). These population characteristics may be useful metrics to assess the "health" of other unstudied red hind spawning aggregations.

Another important characteristic of red hind spawning behavior that can be used to facilitate their management is the consistency in timing of spawning aggregation formation. A comparison of red hind spawning aggregations in the USVI, British Virgin Islands and Puerto Rico, illustrates that timing of spawning is relatively consistent along the Puerto Rican plateau and neighboring islands (e.g., St. Croix) and occurs the week before the full moon in December, January or February (Sadovy et al., 1994b; Nemeth, 2005; Whiteman et al., 2005; Eristhee et al., 2006; Nemeth et al., 2006a). Spawning appears to occur when average seawater temperatures range between 25° and 26.5 °C (Nemeth et al., 2008). In the eastern Caribbean red hind spawn as temperatures drop to the appropriate range where as in Bermuda, 1550 km to the north, they spawn between May and July when seawater temperatures warm to above 25 °C. At all sites, hundreds to thousands of red hind migrate up to 33 km from their home range to form aggregations approximately 1 wk before spawning (Shapiro et al., 1993; Nemeth, 2005). Although spawning has rarely been observed, gonosomatic indices (GSIs) in females increase steadily in the days prior to spawning and drop rapidly afterwards (Sadovy et al., 1994). This index can therefore be used to identify the timing of spawning. The majority of the aggregation disperses soon after spawning but some fish may return the following month on the same moon phase to spawn again (Sadovy et al., 1994; Nemeth et al., 2006b). This synchronized timing of spawning is most likely dictated by changes in the lunar and solar cycle, seasonal changes in seawater temperature and possibly ocean currents (Nemeth et al., in press).

The Saba Bank, one of the few isolated submarine banks in the Caribbean Sea (Macintyre et al., 1975) and one of the largest atolls in the world (Van der Land, 1977), is located 5 km southwest of the small volcanic island of Saba and 40 km east of the USVI. Saba Bank is enclosed entirely in the Exclusive Economic Zone (EEZ) of the Netherlands Antilles (NA) and economic benefits of the bank are derived solely from fisheries, dominated by spiny lobster [Palinuridae: *Panulirus argus* (Latreille, 1804)], silk snapper [Lutjanidae: *Lutjanus vivanus* (Cuvier, 1828)], and blackfin snapper [*Lutjanus buccanella* (Cuvier, 1828)]. In 1999, an estimated US$1.1 million of the gross domestic product of the island economy of Saba came directly from these fisheries (Dilrosun, 2000). Fishers on the neighboring Caribbean islands of St. Maarten and St. Eustatius also fish the bank heavily, targeting primarily reef and bottom fish with hook and line. There are currently no marine reserves on the bank, no reporting system for St. Maarten catches, and no current estimates on annual yield.

There are anecdotal reports of several spawning aggregations on Saba Bank, primarily those of queen triggerfish [Balistidae: *Balistes vetula* (Linnaeus, 1758)] and squirrelfish [Holocentridae; *Holocentrus adscensionis* (Osbeck, 1765)]. The primary queen triggerfish aggregation, fished from December through February, occurs on a site called locally Moonfish Bank. Munro and Blok (2005) reported a red hind aggregation formed annually on Moonfish Bank during the same period; however, their report was based on the traditional knowledge of local fishers and had never been documented scientifically.

The aim of this work was to investigate and document the reported but unprotected red hind spawning aggregation, to assess spawning stock health based on fish density, biomass, size and sex ratio, and to compare red hind spawning seasonality and behavior, along with the corresponding oceanographic processes at Saba Bank with two other sites in the Eastern Caribbean.

Methods

Locating and Characterizing the Aggregation Site.—Rising from the sea floor at 1000 m, Saba Bank is a completely submerged platform 20–30 m below sea level (Fig. 1). With a length of 60–65 km and width of 30–40 km, the total surface area < 50 m in depth is approximately 1600 km^2 (Macintyre et al., 1975). The origin of the bank remains controversial, and until as recently as the mid-1970s minimal reef development was believed to exist there (Macintyre et al., 1975). Large areas (> 150 km^2) of actively growing stony coral reef on the windward (southeast) edge of the bank, discovered unexpectedly in 1974 by a Dutch expedition (Van der Land, 1977), are in sharp contrast to the center and leeward regions of the Saba Bank, that are dominated by sand, rubble, seagrass, and algal plains.

Informal interviews were conducted with fishermen on the island of Saba in September 2005 to locate red hind spawning aggregation sites on the bank. Beginning in December 2005, baited Antillean fish traps were set in and around areas indicated by fishermen and trap locations and catches were recorded using a Global Positioning System (GPS) receiver. In addition, exploratory roving dives using SCUBA were made in the same area. Subsequent fishing and diving was conducted in January and February 2006 in areas with high trap CPUE (catch per unit effort = catch per trap haul) and high densities of observed red hind. Due to the patchiness of red hind densities across the bank, two underwater stations were established in areas with the highest fish abundance, representing the primary aggregation sites.

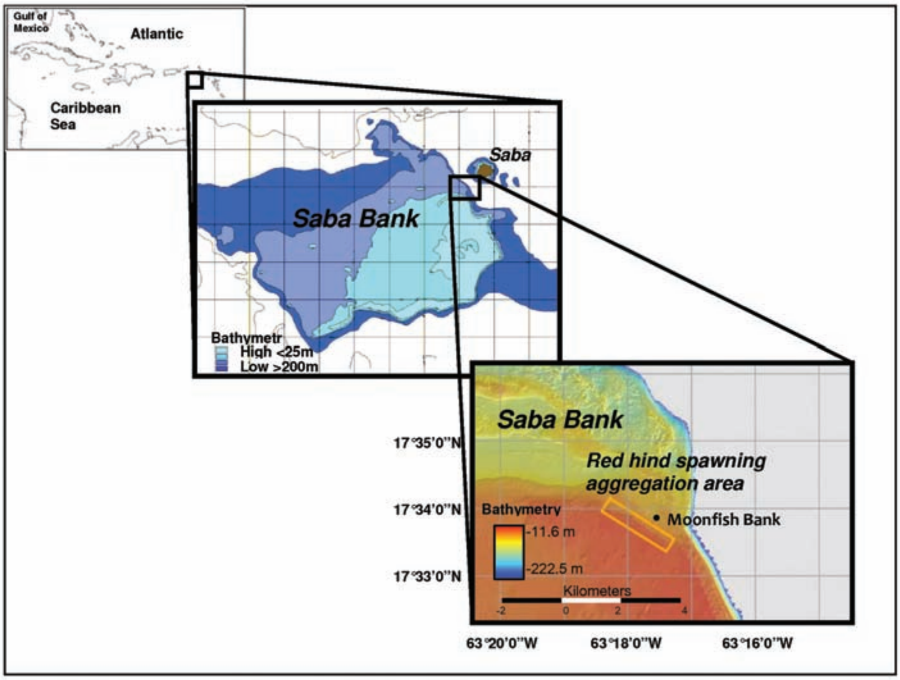

Figure 1. Bathymetric chart of Saba Bank in the Netherlands Antilles showing the red hind spawning aggregation study area (rectangle).

These stations were both located 635 m apart, on the leading edge of a low relief reef that ran northeast to southwest. They were marked with submerged 20 cm polystyrene trap floats attached to the bottom on 3 m long polypropylene lines. The benthic habitat of these primary aggregation sites was characterized by analyzing video transects captured by a diver-operated Sony TR950 digital video camera in a Light in Motion Stingray 2 underwater housing. Three transects were conducted on each site, using the protocol established by Aronson et al. (1994). Divers swam at a slow and uniform speed in a randomly chosen direction across the reef, videotaping a 10 m transect with the camera perpendicular to and approximately 40 cm above the substratum. Digital transects were processed and analyzed using the random dot methodology developed by Rogers et al. (2001).

Determining Spawning Density, Fish Size, Movement, and Fecundity.—Spawning population density was assessed using visual surveys (number of red hind per 100 m^2) and trap catches (CPUE). Fish transects were conducted by divers on 30%–32% Nitrox at the two stations and at randomly selected sites between and outside of these stations. Random survey sites were chosen by swimming along the bank in either direction from a primary site for a randomly determined time period. Divers then attached the end of a 30 m transect tape to the bottom and swam in a random compass direction at a constant speed unreeling the transect tape as they swam. During surveys each diver held a 1 m wide t-bar constructed of 1.27 cm PVC pipe marked with 5 cm increments which was used to estimate transect width and fish TL in the following size classes: < 20 cm, 20–29 cm, 30–39 cm, 40–49 cm, and > 50 cm. A minimum of eight 30 × 2 m belt transects were conducted per day over 3–6 d around the full moon in December 2005, and January and February 2006.

Fish were collected using standard hexagonal, single funnel, 3.8 cm mesh Antillian fish traps baited with commercially sold baitfish (*Decapterus* sp.) and squid. Traps were initially set around the anecdotal historic site in all directions; however, when the primary aggregation sites were determined, sets were made on these primary sites and along the top of the bank in both directions. Generally two sets of traps were deployed and hauled each day (12–

15 traps per set), once in the morning between 0900 and 1100 after an overnight soak (mean soak time = 20.3 hrs, SD = 1.63, range = 16–24 hrs), and again in the afternoon between 1300 and 1600 (mean soak time = 3.2 hrs, SD = 0.98, range = 1–6 hrs). Short daytime trap sets are generally more successful in catching red hind than longer overnight sets (Nemeth, 2005), thus CPUE in this study was defined as the average number of fish caught per trap for the long and short trap sets combined.

Red hind collected in traps were measured for TL (to the nearest mm) and tagged through the dorsal fin pterygiophores with a numerically coded Floy T-bar anchor tag (model 3 FD-68B). Tags contained the following information: identification number, reward $20, Saba National Marine Park, and a contact telephone number. Prior to release, the gender of each red hind was determined using ultrasound imaging (Whiteman et al., 2005) or by gently squeezing the body cavity above the vent to extract milt or eggs. Fish were released close to the collection site using a release cage that could be opened remotely when the cage reached the sea floor, thereby minimizing predation (Nemeth, 2005). Between 1 and 16 female red hind were sacrificed daily in order to collect weight and fecundity data. Ovaries of sacrificed fish were examined macroscopically, and total body weight and gonad weight were recorded to determine the fish's gonadosomatic index (GSI, gonad weight/somatic weight * 100).

Statistical analyses included t-test (t) and two way ANOVA (F) on data that met statistical assumptions (e.g., equal variances and normal distribution). Raw length data were used and month and sex were treated as fixed factors. Data that were not normally distributed or had unequal variances were analyzed with nonparametric Kruskal-Wallace test by ranks (H) and Dunn's multiple–comparison post hoc test (Q).

Characterization of Temperature and Current Strength and Direction.—An acoustic doppler current profiler (ADCP, Nortek 600 kH) was deployed on Moonfish Bank (17°34.00´N, 63°17.45´W) on 11 December 2005. This site was 27 m deep and within 750 m of the two primary spawning sites in the red hind aggregation area (Fig. 1). The ADCP was programmed to record temperature at the bottom, and current speed and direction at 1 m intervals from the bottom to the surface, every 30 min. Here we present bottom temperature (at 27 m) and current speed and direction data from the 23 m depth bin or about 4 m off the bottom which corresponded to the maximum depth at the spawning aggregation site. The profiler was retrieved on 12 February 2006 and data were downloaded and analyzed (Storm Ver. 1.04, Nortek AS, Norway).

Results

Spawning Aggregation Area.—The red hind aggregation site was located on the northeast side of Saba Bank, on the outer edge of a shallow reef that ran in a northwest to southeast direction (Fig. 1). The reef top was 16–18 m deep, dropping at the leading, eastern edge to sand at 21–23 m. The reef appeared to be the remains of a very old spur and groove zone, now an eroded limestone foundation colonized sparsely by sponge, gorgonians, and scleractinian corals. Bare limestone pavement with little sand or rubble made up 69% of the bottom, with an additional 19% covered by macroalgae, primarily *Dictyota* spp. Scleractinian corals, sponges, and gorgonians combined comprised < 9% of the benthic habitat. Stony coral species present included *Diplora strigosa* (Dana, 1846), *Montastrea cavernosa* (Linnaeus, 1767), and *Colpophyllia natans* (Houttuyn, 1772), but all colonies were small (< 50 cm).

Along the leading edge of the reef, a series of small caves and undercut ledges were formed that provided fish habitat and shelter. Red hind density, which was very patchy across the top of the reef, was relatively high under and immediately surrounding these ledges. The two permanent sampling stations established in Decem-

Table 1. Survey and catch information for a red hind spawning aggregation, located on the Saba Bank, Netherlands Antilles, from December 2005 through February 2006, CPUE is catch per unit effort = red hind trap^{-1}.

Field dates	Full moon date	Sampling days (n)	Fish transects (n)	Average red hind density ± SE (fish 100 m^{-2})	Traps set (n)	Avg CPUE ± SE	Red hind collected
Dec. 11–17	15	7	70	1.46 ± 0.26	129	0.98 ± 0.14	126
Jan. 10–17	14	6	98	34.27 ± 2.20	121	5.79 ± 0.52	886
Feb. 10–13	13	4	62	1.54 ± 0.39	111	0.77 ± 0.07	86

ber 2005 were located on the reef edge where ledges were most developed, rising 1.0–1.5 m above the sand, with 0.5–2.0 m undercuts.

The spawning aggregation area terminated to the northwest at 17°34.0´N, 63°18.4´W, where the reef edge flattened. The southeast extent of the spawning aggregation area was never conclusively determined. In January 2006, dives were conducted and traps were set in a southeast direction along the reef to 17°33.3´N, 63°17.1´W, where red hind were found patchily distributed around undercuts and ledges along the reef edge. Although time did not allow the study to be extended farther southeast, commercial trap catches were reported to decline within 200 m of the study site in that direction (Pieterson, commercial fisherman, pers. comm.). The distance from the northwest end of the aggregation area to the southeast extent of our study was 2.1 km. The width of the area averaged 25 m providing an aggregation area of 0.053 km^2.

Abundance, Sex Ratio, and Size Frequency of Red Hind.—From December 2005 to February 2006, 361 traps were deployed on the Saba Bank in the red hind aggregation area and 230 fish transects were conducted. A total of 1094 red hind were collected in traps (Table 1), most of which were tagged (584) and, or released (965). The monthly average CPUE ranged from a low of 0.77 ± 1.39 in February to a high of 5.79 ± 5.67 in January (Fig. 2). Average CPUE was significantly higher in January than in December and February (Dunn's Method, $Q = 0.314$, $P > 0.05$). The CPUE increased four-fold with the waxing moon in January and remained high the day following the full moon, whereas CPUE remained relatively stable throughout the sampling period in December and February (Fig. 2). Higher trap catches occurred at the two primary spawning sites in January relative to other sets across the aggregation area, ranging from 0 to 21 fish trap^{-1} and reflecting the patchy distribution of red hind in the aggregation area (Table 2).

Average densities of red hind on visual transects ranged from 1.46 ± 0.26 fish 100 m^{-2} in December to 34.27 ± 2.20 fish 100 m^{-2} in January, and were significantly higher in January than the other 2 mo. (Dunn's Method, $Q = 0.773$, $P > 0.05$). At the primary aggregation sites, average density of red hind in January 2006 exceeded 40 fish 100 m^{-2} whereas average density recorded at random sites in the aggregation area was < 27 fish 100 m^{-2} (Table 2). Densities observed in fish transects peaked slightly the day before the full moon in January and remained high the following 2 d (Fig. 3). The spawning population size on Saba Bank, estimated based on the site area (0.053 km^2) and average density of red hind across the entire aggregation site at peak reproductive season in January 2006 (34.3 fish 100 m^{-2}), was approximately 18,000 fish. The daily sex ratio of red hind was significantly different in January relative to December and February (Dunn's Method, $Q = 0.629$, $P > 0.05$): male fish dominated the catch, in December and February when the sex ratio for all fish collected was

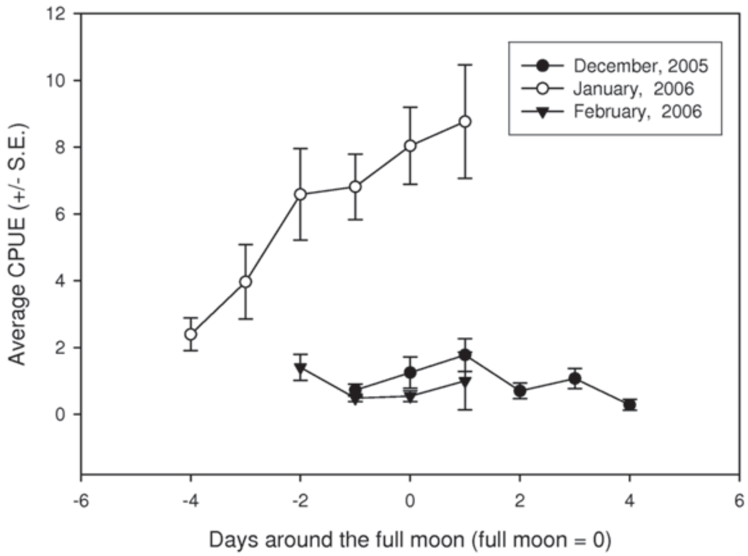

Figure 2. Daily catch per unit effort (CPUE) in the Saba Bank spawning aggregation area on days before, on and after the full moon in December 2005 and January and February 2006.

4.7:1 and 3.7:1 (M:F), respectively, and never fell below 1.7:1 (Fig. 4), however, the sex ratio of the total catch in January was 1.14:1. On the day of and the day after the full moon in January the sex ratio was 0.8:1, in favor of females.

Across the entire reproductive period, male red hind were significantly longer than females (mean ± SD: males 35.4 ± 2.8 cm TL, and females 31.8 ± 2.5 cm TL; Table 3). Mean (± SD) body weight of males was 712.1 ± 168.8 g and females 561.2 ± 161.9 g. The sex-specific size distribution (Fig. 5) reflects the protogynous hermaphroditic life history characteristic of red hind. Although the mean length of all red hind in the sampling population during the 2005–2006 spawning season was not significantly different between months (mean ± SD = 33.9 ± 3.3 cm TL), the interaction between sex and month was significant ($P = 0.008$, Table 3). This was because the length of males arriving in December were, on average, 1 cm larger than males at the spawning site in January and February (December, 36.5 ± 3.6 cm TL; January, 35.2 ± 2.6 cm TL; $t = 4.23$, $P < 0.001$; February, 35.5 ± 3.3 cm; $t = 2.42$, $P < 0.016$). Size of females was not significantly different between months although the average size of females tended to be largest in January (31.9 ± 2.5 cm TL) and smallest in February (30.8 ± 2.6 cm TL).

In December, the majority of red hind observed on fish transects (51.4%) were in the 30–40 cm size class (Fig. 6) and an additional 22.9% were large fish, > 40 cm TL.

Table 2. Red hind densities based on belt transects, and CPUE (catch per unit effort = red hind per trap) on established stations and outside of stations within the Saba Bank red hind spawning aggregation area in January 2006.

	Location	Number of transects	Avg density (fish 100 m^{-2}) ± SD	Traps set	Avg CPUE ± SD
Station 1	17°33.6′N, 63°17.6′W	34	44.2 ± 16.5	21	11.9 ± 5.7
Station 2	17°33.8′N, 63°17.9′W	18	41.3 ± 21.3	13	10.2 ± 4.8
Off station	N/A	38	26.9 ± 9.3	101	4.5 ± 4.7

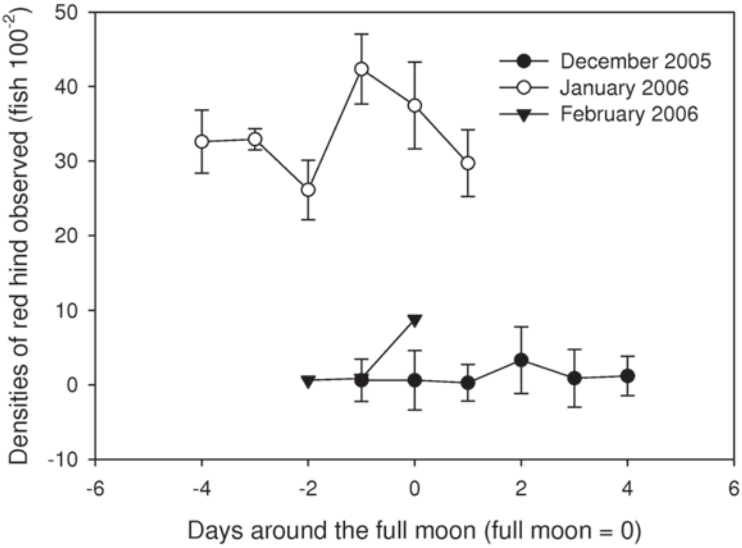

Figure 3. Daily average density of red hind (± SE) observed over the entire spawning aggregation area on days before, on or after the full moon in December 2005 and January and February 2006.

In January 88% of fish recorded in transects were between 30 and 40 cm TL and few small or very large fish were recorded. In February, red hind were more normally distributed between four size classes.

Time of Spawning.—Females with developing ovaries were collected in both January and February, and milt was released by males during all three months. Gonadosomatic indices of females tended to be higher in January than in February (mean ± SD: January, 12.6 ± 4.3 and February, 6.5 ± 3.0; Fig. 7). Large decreases were not seen as would be expected just after a spawning event, however sampling extended

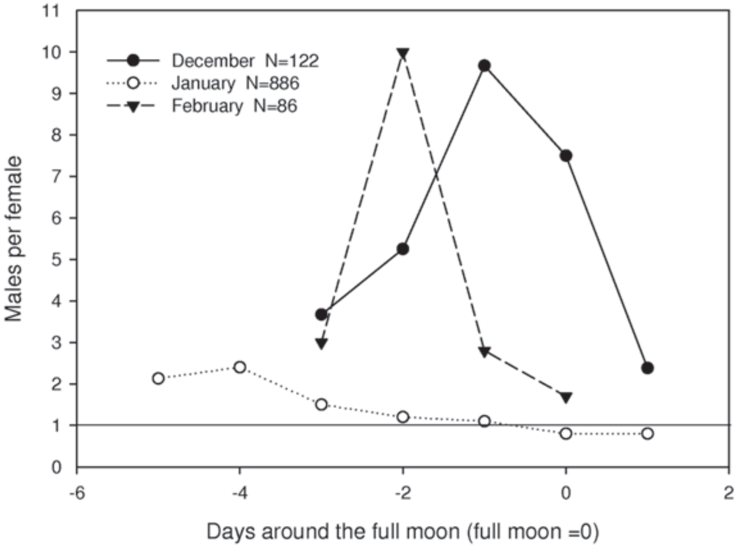

Figure 4. Male to female ratio of red hind collected in fish traps on days before, on and after the full moon in December 2005 and January and February 2006.

Table 3. Results of two way analysis of variance comparing total length of red hind among 3 mo of spawning season (December, January, and February) and between sex (males vs females).

Source of variation	d.f.	SS	MS	F	P
Month	2	19.6	9.8	1.33	0.265
Sex	1	1,264.9	1,264.9	171.77	< 0.001
Month × sex	2	71.8	35.9	4.88	0.008
Residual	1,080	7,953.2	7.4		

only 1 d past the full moon. None of the females sampled from January 9 to 12 contained hydrated ovaries. On January 13, 1 d before full moon (1 dbfm), 14 (fm), and 15 (1 dafm) the percent of female ovaries containing hydrated oocytes was 17%, 7%, and 31% respectively. The following month, the percent of sampled females with hydrated oocytes was 0%, 20%, and 33% on February 11 (2 dbfm), 12 (1 dbfm), and 13 (fm). Female ovaries comprised about 10% of body weight (n = 101). Male testes were an order of magnitude smaller than female gonads, and averaged 0.97% (n = 14) of somatic weight in the week prior to the January full moon.

Behavioral indicators of spawning readiness, such as aggression or physical contact between fish, were not observed at any time on the bank. The haremic distribution pattern seen on other red hind spawning aggregation sites appeared to be absent and fish exhibited little obvious territoriality. Fish were observed either evenly dispersed and well camouflaged among dense patches of brown *Dictyota* sp. algae or aggregated in groups of 50–200 fish along the shelf edge close to undercut ledges. Predators [*Sphyraena barracuda* (Walbaum, 1792) and *Ginglymostoma cirratum* (Bonnaterre, 1788)] were commonly seen swimming along the reef.

Temperature and Current.—Water temperature measured at 27 m depth dropped continually through the spawning season (Fig. 8). The maximum average daily temperature recorded on the bank during the study period was 27.5 °C (20 December) and minimum was 26.1 °C (1 February). The average sea temperature during

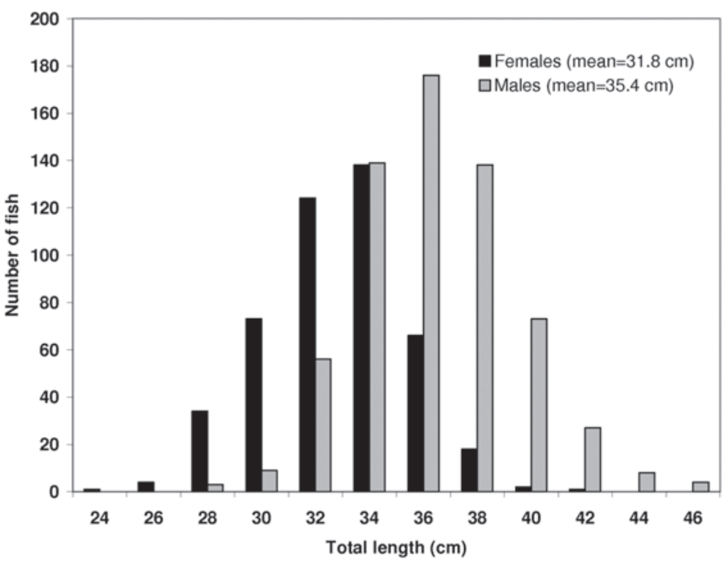

Figure 5. Size frequencies of male (n = 634) and female (n = 454) red hind collected in fish traps from the Saba Bank spawning aggregation site.

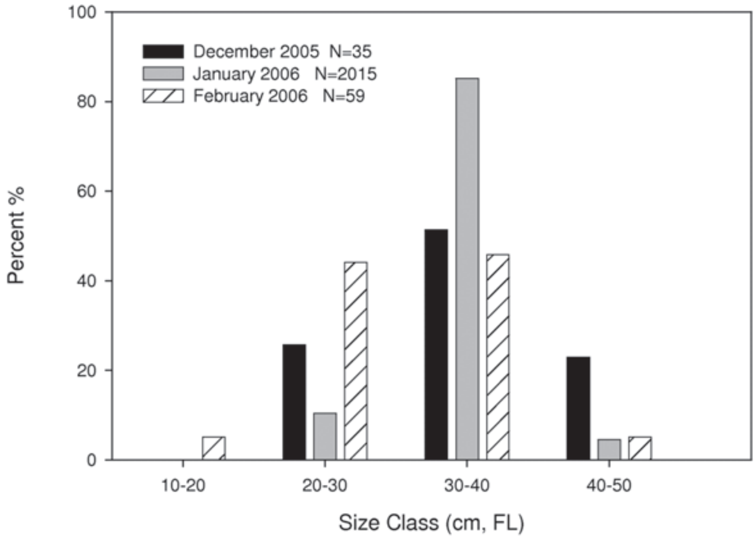

Figure 6. Size frequencies of red hind observed in visual fish transects in December 2005, and January and February 2006 on Saba Bank.

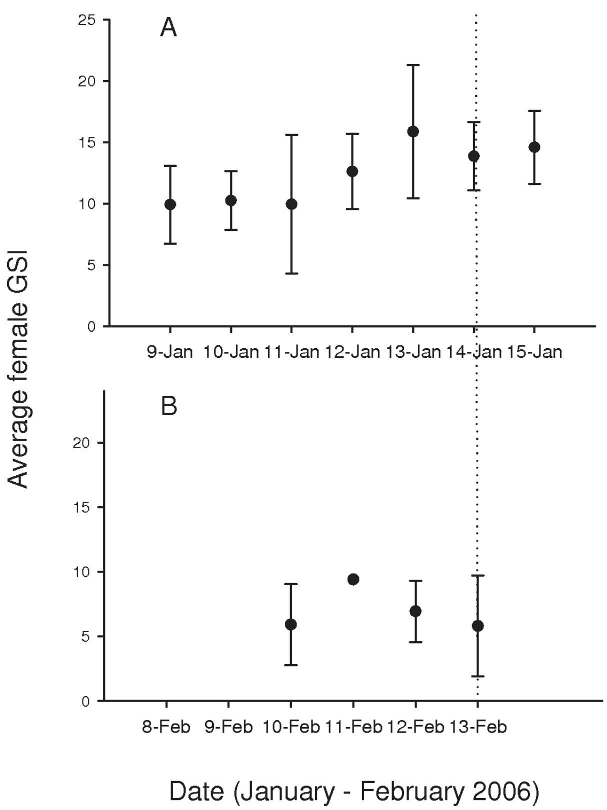

Figure 7. Daily average gonadosomatic indices (GSI ± SD) for female red hind sacrificed in (A) January (n = 84) and (B) February 2006 (n = 17) on Saba Bank. Full moon indicated by dashed line.

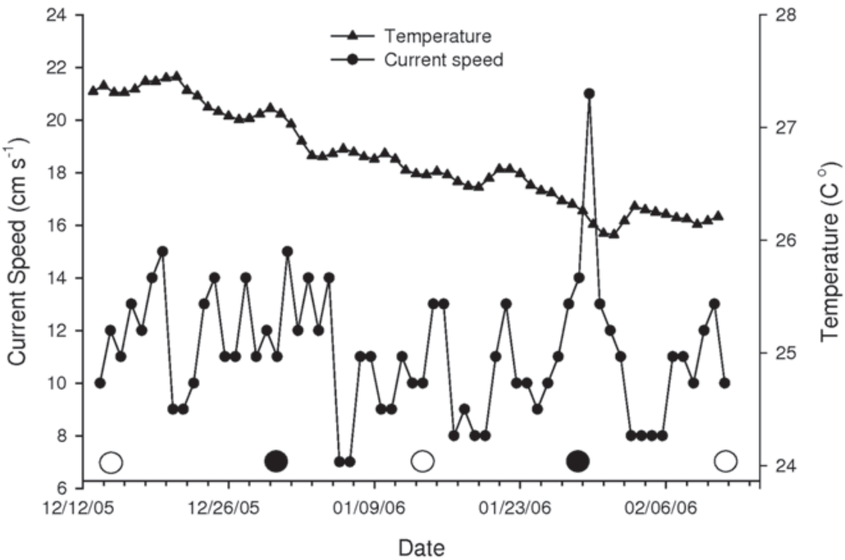

Figure 8. Average daily temperature at 27 m depth and current velocity at 23 m depth (4 m above the bottom) near the Saba Bank red hind spawning aggregation site from 12 December 2005 through 11 February 2006. Full moon = ○, new moon = ●.

the week preceding the full moon in December, January, and February was 27.5 °C, 26.6 °C, and 26.2 °C, respectively.

Water movement across Saba Bank during the study period was dominated by tidal cycles in which current direction alternated from north-northwest to south-southeast at regular 12 hr intervals. These tidal cycles corresponded to barometric pressure changes. The winter tidal cycle of 2005–2006 resulted in a bulk flow of water to the southwest (Fig. 9). A few days before and after the January full moon, when red hind were thought to spawn, stronger northwest currents associated with the prevailing southeasterly tradewinds slackened and tidal flow to the south increased (Fig. 9). These temporary shifts in current speed and direction led to a net flow of water in a southerly direction across the spawning area on Saba Bank during the January and February 2006 full moons.

Recaptures and Tag Returns.—The total number of red hind tagged on Saba Bank was 584, eight of which were recaptured while sampling the aggregation site. Two tagged fish were caught by St. Maarten fishers approximately 3 km due west of the aggregation site at 17°33.81´N, 63°20.86´W on 11 February 2006. These fish had been tagged sequentially on 14 December 2005 and were caught together on the same hand line. The fishers reported catching approximately 100 kg of red hind in the same location that day.

Discussion

Change in catch composition from larger to smaller individuals in an exploited population has been well-documented (e.g., Luckhurst, 1996; Chiappone et al., 2000) and the length of spawning adults can be used as a measure of fishing pressure (Sluka et al., 1967; Nemeth, 2005). Historically, red hind in the eastern Caribbean reach sizes of 50–55 cm TL (Olsen and La Place, 1978; Thompson and Munro, 1978; Colin

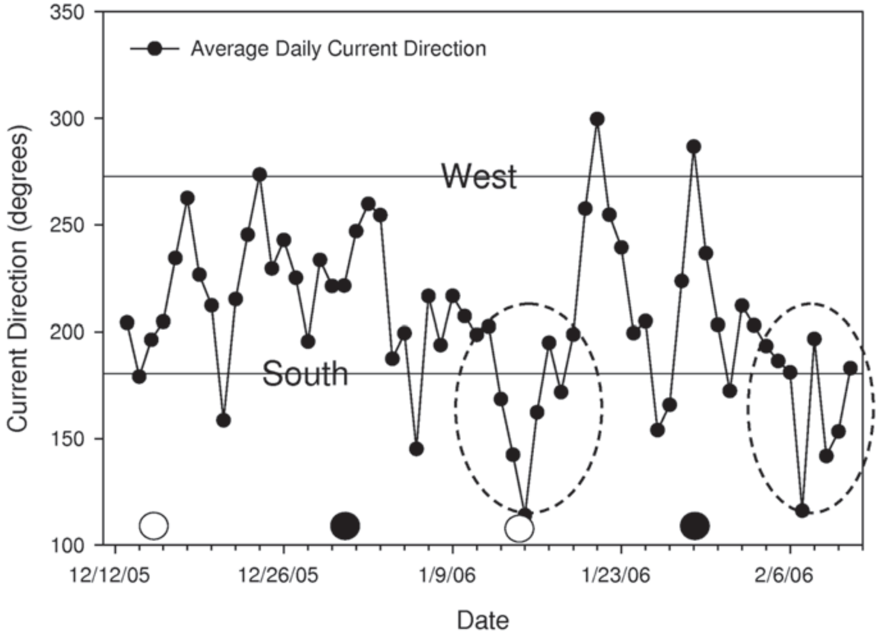

Figure 9. Direction of average daily currents 1 m below the surface on the Saba Bank red hind spawning aggregation site from 12 December 2005 through 11 February 2006. Solid horizontal lines indicate the compass directions of due west and due south. Dashed lines indicate time period when red hind aggregated and may have spawned. Full moon = ○, new moon = ●.

et al., 1987; Sadovy et al., 1992) and specimens in Bermuda have been reported at 62–72 cm TL (Luckhurst et al., 1992). The mean size of reproductive adults on Saba Bank was about 1.5 cm larger than the mean size reported for the seasonally closed spawning site off St. Croix, but 4 cm smaller than that reported for an aggregation site in the St. Thomas marine reserve (Table 4; Nemeth, 2005; Nemeth et al., 2006a). In addition, males were on average 3.6 cm larger than females on Saba Bank (Table 4), creating a gender-specific size distribution similar to that found off St. Thomas but not St. Croix. (Nemeth, 2005; Nemeth et al., 2006a). Based on the relative average length of spawning adults and size distribution, it appears that the aggregation is over-exploited on the Saba Bank, but only moderately so.

Comparison of commercial catch statistics of fish TL suggests that the red hind population is sustainable at currently fished levels but close monitoring of the aggregation is strongly recommended. After the St. Thomas red hind aggregation was protected, average length of red hind caught in the commercial fishery increased from 30 to 35 cm TL over 12 yrs (Nemeth, 2005). In contrast, red hind in St. Croix, whose aggregation was seasonally protected during spawning, decreased from 33 cm to under 28 cm TL over the same time period (Nemeth et al., 2006a). These declines were probably due to poaching, and differences in fishing regulations and gear types (R. Nemeth, pers. obs.). When we examined limited catch records for the Saba Bank commercial fishery, we found that the average size of red hind caught outside the spawning season has not changed significantly between 1999 (32.9 cm TL, n = 100) and 2007 (33.2 cm TL, n = 107; Dilrosun, 2000; W. Toller, Netherlands Antilles Department of Environment and Nature, unpubl. data).

Table 4. Comparison of red hind spawning aggregation characteristics (mean ± SD) at three sites in the eastern Caribbean: Saba Bank, St. Thomas, and St. Croix.

Parameter	Saba Bank	St. Thomas	St. Croix
Management	None	Seasonal closure (9 yrs) Year-round closure (3 yrs)	Seasonal closure (9 yrs)
Est. spawning population size	18,000	84,000	3,000
Peak aggregation density (fish 100 m^{-2})	34.27 ± 2.20	14.4 ± 5.9	20.3 ± 11.4
Length (cm, TL)			
all	33.6 ± 3.0	38.0 ± 5.8	32.5 ± 5.6
male	35.4 ± 2.8	41.8 ± 3.9	33.4 ± 4.8
female	31.8 ± 2.5	36.2 ± 3.6	31.7 ± 6.3
Spawning sex ratio	1:1	5:1	1:1
Site area (km^2)	0.053	0.24	0.015
Commercial catch mean size	33.2 cm	34.5 cm	27.7 cm
Reference	Present study	Nemeth, 2005	Nemeth et al., 2006

Recent studies have shown significant daily variability of sex ratios of red hind in spawning aggregations (Whiteman et al., 2005; Nemeth et al., 2006a). In general, a haremic-type spawning strategy, in which one male spawns with a group of two or more females, is facilitated with female-dominated sex ratios (Colin et al., 1987; Sadovy et al., 1992; Shapiro et al., 1993; Nemeth, 2005; Whiteman et al., 2005; Nemeth et al., 2006a). On Saba Bank, the sex ratio was highly skewed toward males 1–3 d before the full moon, especially in December and February. This temporary bias towards males has been reported elsewhere and may be related to the greater residence times of males at the spawning site (Whiteman et al., 2005; Nemeth et al., 2006b). In December, the size of males was significantly larger than in January and February, suggesting that the large males arrived first to the spawning site. Tag-recapture studies of red hind off St. Croix and St. Thomas have indicated that the migration distance of males may be negatively correlated with fish size (i.e., large males have home ranges that are closer to the spawning aggregation site; Nemeth, 2006b). Cues that trigger movement to spawning sites may occur simultaneously across the region, with the larger, more aggressive fish able to maximize spawning potential by arriving and preparing (setting up territories and finding mates) earlier than their smaller conspecifics. During January, the sex ratio changed to near unity just prior to the full moon. This shift corresponded to an increase in fish density and CPUE which indicated that a proportionally large number of females moved onto the site from 1 d before to 1 d after the full moon, a pattern also found by Nemeth et al. (2006b) at the sites off St. Thomas and St. Croix, USVI. In February, sex ratios and fish densities returned to levels similar to those recorded in December, suggesting that the majority of females spawned in January and had departed the aggregation site for the year.

While many studies report a typical territorial defense and courtship behavior of red hind in spawning aggregations, spawning of red hind has rarely been observed and therefore reproduction is believed to occur well after sunset (Shapiro et al., 1993; Nemeth et al., 2006b). In our study, we did not observe the characteristic haremic structure (i.e., male-defended multi-female clusters) that typically forms over the reef at a red hind spawning aggregation site, nor any courtship or aggression usually associated with spawning (Shapiro et al., 1993). This difference in reproductive behavior on Saba Bank may be due to the lack of suitable habitat. The narrow strip of old spur and groove reef is similar to the spawning habitat found off St. Croix

(Nemeth et al., 2006a,b) but is much lower in live coral cover and benthic structure, and appears to offer little refuge for spawning adults. This lack of refuge may explain the large groups of red hind associated with the small caves and ledges near the reef edge. The male-skewed sex ratio and the fact that we did not observe males establishing territories during the spawning season suggests that this population of red hind may use a different spawning strategy (i.e., group spawning) and that sperm competition may occur. However, male testes were similar in size to those found on female-dominated aggregation sites off Puerto Rico (Sadovy et al., 1994), suggesting that sperm competition was probably not occurring. The sex ratio near unity around the full moon suggests that this spawning population may simply pair spawn instead of forming the typical territories associated with harems. More research is needed to determine if the Saba Bank red hind spawning population uses a different reproductive strategy or whether other factors are contributing to the observed differences.

The Saba Bank red hind spawning aggregation area that we investigated is located on the northeast side of the extensive submerged plateau, in a relatively shallow area with little living coral. Although site selection for spawning aggregations in terms of bathymetry, physical orientation, and benthic habitat composition is variable for red hind in the region, spawning aggregation sites off Puerto Rico, the British Virgin Islands, and the USVI are generally reported to be in deeper water, closer to the shelf edge, and on more complex reef communities (Olsen and LaPlace, 1978; Beets and Friedlander, 1992; Sadovy et al., 1994; Eristhee et al., 2006; Nemeth et al., 2006a). Although extensive deep coral reef more proximal to the shelf edge exists on Saba Bank, red hind aggregations have developed and persisted in sparsely colonized benthic habitats along the northeast corner of the platform. This might be explained by the local current regimes that could be important for larval retention and local recruitment in an area isolated and separated by deep water from other islands and major land masses (Nemeth et al., 2008). On Saba Bank, the current direction during our study period was primarily influenced by tidal flow fluctuating from northwest to southeast twice daily. The predominant current direction from December 2005 through February 2006 was to the south-southwest, potentially pushing and retaining larvae and other plankton from the northeast region of the plateau onto the shallow central section of the bank (Nemeth et al., 2008). While this might be consistent with the specific spawning location contributing to local population maintenance, we collected data for one season during one year, and there exists no previous local current information or regional oceanographic models for Saba Bank. Making inferences is therefore premature given the certain variability of the system, which would include storms, seasonal change and variations in mesoscale current patterns.

Although spawning was never observed on Saba Bank, high densities of ripe males and gravid females with hydrated ovaries indicated that spawning was imminent and occurred in January as well as to a very limited extent in February. Spawning coincided with decreasing water temperature, which during the week leading to the full moon in January ranged from 26.8° to 26.6 °C. This range is within temperature limits delineated as potential red hind spawning cues by Nemeth et al. (in press) in studies conducted in the USVI. During the week prior to the full moon in January 2006, water temperature also decreased on the Puerto Rican and Crucian shelf edges, ranging from 26.7° to 26.6 °C and 26.9° to 26.8 °C on aggregation sites off St. Thomas and St. Croix, respectively (Nemeth, in press). Using a model developed by Nemeth et al. (2006b) to predict the month of spawning between December and February based on the number of days from winter solstice to the January full moon, we predicted that January would be the only month spawning aggregations would form in the eastern Caribbean during the 2005–2006 red hind season. Dramatic declines in density and a reversion to a very highly skewed male sex ratio in the aggregation area indicated that most spawning ceased before the full moon in February 2006 on Saba Bank. Densities of red hind also peaked in the aggregations off St. Thomas and St. Croix in January 2006, and declined to pre-aggregating levels in February (R. Nemeth, unpubl. data), indicating that spawning aggregations of red hind are synchronized over regional spatial scales of at least 100s of km.

Red hind spawning aggregations display strong lunar periodicity and their formation is typically associated with the full moon (Colin et al., 1987; Shapiro et al., 1993; Nemeth, 2005). Red hind density on Saba Bank, based on CPUE and transect data, increased the week prior to the full moon in January. Sampling continued only one day past the January full moon, however, fishermen reported high catches for two weeks following. Gonadosomatic indices and the number of females with hydrated oocytes increased steadily the week prior to and the day after the full moon. Our data indicate that spawning may have occurred immediately after the full moon but might possibly have continued longer. Although in both the St. Thomas and St. Croix aggregations, red hind spawning generally occurs 1–2 d prior to the full moon with fish dispersing soon after (Nemeth, 2005; Nemeth et al., 2006a), red hind have been reported to continue spawning up until the new moon in Puerto Rico (Sadovy et al., 1994). Extended spawning could not be confirmed in the present study.

As an aside, there was indirect evidence of queen triggerfish spawning in the vicinity of the reef on Saba Bank after the full moon during December through February. A total of 181 queen triggers were collected, 85 (47%) of which were ripe males and 64 (35%) gravid females. Trap catches and fish transects detected relatively high numbers of queen triggerfish on the ADCP site (Moon Bank), approximately 750 m from the primary red hind aggregation sites. Some individuals showed intraspecific aggression (vigorous chasing) but no spawning or nesting behavior was observed.

The level of exploitation on the Saba Bank red hind spawning aggregation is not well known. Fishermen from the island of Saba generally concentrate on lobster and deep water snappers and have little interest in the harvest or sale of red hind. Boats from St. Maarten regularly fish the red hind aggregation, but these catches are not documented or controlled (D. Kooistra, Saba Marine Park, pers. comm.). The different fishery preference of people on neighbor islands is probably due to historical, economic, and cultural differences. Two boats from St. Maarten were observed fishing the site with hook and line during January and February 2006, with estimates of around 273 kg (ca. 300–350 red hind) per 2 d fishing trip reported by each boat (L. Pieterson, commercial fisherman, pers. comm.). The distribution of spawning adults across the Saba Bank aggregation site is characterized by very high densities of fish scattered along a narrow margin of relatively shallow reef. The multi-satellite structure of this and other red hind spawning aggregations may be more robust to over-fishing than larger grouper species which form mass spawning aggregations at a single location (Sadovy and Domeier, 2005). However, based on very limited recapture data, these localized satellite aggregations may represent red hind which migrate as a reproductive unit from a locality elsewhere on Saba Bank. Concentrated fishing effort in one location may therefore deplete not only the satellite aggregation but also the majority of adult red hind from their home reef. As the aggregation continues to be fished, smaller satellite aggregations may be eliminated, reducing the area over which the aggregation occurs. This situation can be illustrated by comparing fishing effort and habitat use of the red hind spawning aggregations located in St. Croix, USVI. The St. Croix aggregation was fished heavily for many years before being seasonally closed to fishing in 1995. This spawning aggregation was composed of about 3,000 fish which occupied 0.015 km^2 of linear reef (Nemeth et al., 2006a). Historically, the St. Croix spawning aggregation was fished over a much larger section of linear reef (T. Daly, commercial fisherman, pers. comm.) than was found by Nemeth et al. (2006a) from 2004 to 2005. Continuous fishing pressure over many decades probably depleted or eliminated satellite aggregations and only one or two primary aggregation sites remain today. The spawning population size on Saba Bank, estimated to be approximately 18,000 fish over 0.053 km^2 of linear reef, is currently much larger than the spawning population in St. Croix (Table 4). It is also larger than an aggregation in Puerto Rico which was studied in the 1980s but subsequently eliminated by fishing (Shapiro et al., 1993; Levin and Grimes, 2002). Red hind spawning aggregation sites that have been well protected for many years may cover an area of over 0.24 km^2 and encompass up to 84,000 spawning adults (Nemeth, 2005).

Currently the level of harvest of red hind on Saba Bank and adults on the spawning aggregation is presumed to be relatively moderate. This is consistent with our data that, based on comparison with protected and semi-protected sites in the USVI, indicate some exploitation but currently at a sustainable level. However, increased interest in fishing the spawning aggregation may rapidly decimate the spawning population due to their concentration along the narrow linear reef. Applying the cautionary principal, a 3-mo seasonal closure (December–February) of the red hind spawning aggregation site on Saba Bank would be an important management step to prevent the over-exploitation or potential collapse of this spawning aggregation.

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