Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection

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ABSTRACT: Many species of groupers form spawning aggregations, dramatic events where 100s to 1000s of individuals gather annually at specific locations for reproduction. Spawning aggregations are often targeted by local fishermen, making them extremely vulnerable to over fishing. The Red Hind Bank Marine Conservation District located in St. Thomas, United States Virgin Islands, was closed seasonally in 1990 and closed permanently in 1999 to protect an important red hind *Epinephelus guttatus* spawning site. This study provides some of the first information on the population response of a spawning aggregation located within a marine protected area. Tag-and-release fishing and fish transects were used to evaluate population characteristics and habitat utilization patterns of a red hind spawning aggregation between 1999 and 2004. Compared with studies conducted before the permanent closure, the average size of red hind increased mostly during the seasonal closure period (10 cm over 12 yr), but the maximum total length of male red hind increased by nearly 7 cm following permanent closure. Average density and biomass of spawning red hind increased by over 60 % following permanent closure whereas maximum spawning density more than doubled. Information from tag returns indicated that red hind departed the protected area following spawning and migrated 6 to 33 km to a ca. 500 km^2 area. Protection of the spawning aggregation site may have also contributed to an overall increase in the size of red hind caught in the commercial fishery, thus increasing the value of the grouper fishery for local fishermen.

KEY WORDS: Marine protected areas · Fishery management · Serranidae · Caribbean · Habitat use · Fish migration · Tag-and-release · Size frequency

INTRODUCTION

Over the past 20 yr, many island nations throughout the Caribbean, including the United States Virgin Islands (USVI), have witnessed steady declines in catches of commercially important marine fishes (Council 1985, Roberts 1997). Sustained fishing pressure in multi-species tropical fisheries can cause progressive changes in fish communities as well as shifts in the size structure of targeted populations (Munro 1996). These effects are accelerated when fishers target the large, annual spawning aggregations formed at predictable locations by many species of tropical reef fishes, especially snappers and groupers (Johannes 1978, 1989, Olsen & LaPlace 1978, Colin et al. 1987,

Beets & Friedlander 1992, Sadovy et al. 1994a,b, Beets & Friedlander 1997, 1999). Since spawning aggregations are the primary source of larval production and may replenish the local fishery through larval retention and recruitment (Roberts 1996, Sadovy 1996), overfishing of spawning aggregations may dramatically reduce the local abundance of these species causing population-level impacts (Claro & Lindeman 2003). Where once snappers and groupers made up the bulk of the catch of the commercial fishery, landings throughout the Caribbean are now dominated by herbivorous species such as parrot fishes and surgeon fishes (Tobias 1997).

Marine protected areas (MPAs), which prohibit all fishing activity, are beginning to be recognized as

alternative marine conservation management tools implemented to attain sustainable fish populations by maintaining ecosystem biodiversity, conserving genetic diversity, enhancing spawning stock, increasing productivity and reproductive output and protecting habitat structure (reviews by Allison et al. 1998, Bohnsack 1998, Appeldoorn & Lindeman 2003). Most MPAs, regardless of size, seem to have a relatively rapid (1 to 3 yr) and positive effect on the density, biomass, size and diversity of organisms within the closed area compared to outside or after reserve formation versus before (Halpern & Warner 2002, review). Although these reviews showed the positive effects of MPA's on various biological measures inside reserves, most existing reserves may be too small to benefit regional fisheries (i.e. beyond the area immediately adjacent to reserve boundaries) and have a limited ability to permanently protect populations such as groupers and snappers that engage in long-distance migrations (McClanahan & Kaunda-Arara 1996, Bohnsack 1998, McClanahan & Mangi 2000, Roberts et al. 2001). However, well-placed MPAs can protect particularly vulnerable periods during a species life history such as temporary residence in nursery, feeding and spawning habitats (Kramer & Chapman 1999).

The life-history characteristics of groupers forming spawning aggregations render them particularly vulnerable to even moderate fishing mortality. For example, most species of Caribbean groupers are protogynous hermaphrodites that form size-structured spawning aggregations comprised of small females and large terminal-phase males (Domeier & Colin 1997). Intensive fishing pressure on grouper spawning aggregations can severely reduce overall biomass (Alcala 1988, Roberts 1995), decrease size and age at sexual maturity due to selective removal of the large reproductive males (PDT 1990), and drastically alter the sex ratio and disrupt the social structure necessary for successful reproduction (Colin et al. 1987, Shapiro et al. 1994, Beets & Friedlander 1999). Seasonal and permanent closures have been enacted to protect the biological integrity of single-species fish spawning aggregations (Sadovy 1994, Bohnsack 1996, Domeier & Colin 1997). Unfortunately, area closures can take years to establish and, when finally implemented, overfishing has usually caused serious damage to the spawning populations and either collapse of the aggregation has already occurred or recovery is very slow (Olsen & LaPlace 1978, Claro et al. 2001).

Negative impacts of fishing on grouper and snapper spawning aggregations have been documented throughout the Caribbean, e.g. Belize (Heyman et al. 2001, Sala et al. 2001), Bermuda (Luckhurst 1996), Cuba (Claro & Lindeman 2003), Florida Keys (Lindeman et al. 2000), Mexico (Aguilar-Perera & Aguilar-

Davila 1996), Puerto Rico (Shapiro et al. 1993, Sadovy et al. 1994a,b), and the US Virgin Islands (Olsen & LaPlace 1978). Few empirical examples exist, however, of a permanent marine protected area facilitating the recovery of a spawning aggregation. The primary objective of this paper was to report on the population response of a red hind spawning aggregation following establishment of a MPA.

In the United States Virgin Islands, intensive fishing throughout the 1970s and early 1980s eliminated several Nassau *Epinephelus striatus* and yellow-fin *Mycteroperca venenosa* grouper spawning aggregations (Olsen & LaPlace 1978). After the population collapse of these 2 species, commercial fishermen began targeting the red hind *E. guttatus*, a smaller serranid that also forms spawning aggregations (Beets & Friedlander 1999). Red hind contributed 70 to 99 % of the total catch of fin fish landed in the Virgin Islands between 1987 and 1992 (Cummings et al. 1997). By the late 1980s an evaluation of the red hind stock around St. Thomas showed dramatic decreases in average length and an extremely skewed female-to-male sex ratio (15:1) of the spawning population (Beets & Friedlander 1992), suggesting a disproportional harvest of large males (Sadovy & Figuerola 1992). In an effort to avert another fishery collapse, a 3 mo seasonal closure, which encompassed the December through February spawning season, was implemented in November 1990 on the island of St. Thomas to protect the annual spawning aggregation of red hind. This spawning aggregation site, known locally as the Red Hind Bank, is located along the shelf edge 12 km south of St. Thomas and includes the site of an extirpated Nassau grouper spawning aggregation (Beets & Friedlander 1999).

After several years of seasonal protection the red hind spawning population on St. Thomas began to show signs of recovery. By 1997 the average size of spawning adults had increased by 7 cm in length and the sex ratio had shifted to 4 females per male (Beets & Friedlander 1999). The potential value of this site to the local fishery led the Caribbean Fisheries Management Council, with the support of local fishermen, to recommend the Red Hind Bank as a permanent 'Marine Conservation District' (MCD). In December 1999 the Red Hind Bank MCD was established as the first no-take fishery reserve in the USVI, and protected 41 km^2 of deep coral reefs (33 to 45 m) along the southern shelf of the insular platform. The creation of the MCD, which represents approximately 1.5 % of the fishing grounds within the Virgin Islands (Bohnsack 2000), reflected a shift in management from a single-species approach (seasonal closure) to an ecosystem-level approach that protected not only key species of commercial importance but also provided protection of a large area of critical fish habitat (Allison et al. 1998).

However, because red hind migrate to their spawning aggregation sites on an annual basis, it was unclear if the permanent closure and protection of critical fish spawning habitat would have additional positive effects on the spawning population (as described by Beets & Friedlander 1999) or if it would enhance the local fishery. The primary objectives of the research presented in this paper were to (1) characterize the red hind spawning aggregation and document changes in size structure, density and biomass of the spawning population following establishment of the MCD, (2) compare these parameters with published data on the spawning population during seasonal closure, (3) characterize habitat use and movement patterns of the spawning population and (4) identify the source population of the St. Thomas spawning aggregation and determine if fish leaving the spawning aggregation contributed to the local fishery. Research by Shapiro (1987) and Sadovy et al. (1994b) indicated that, following spawning, females migrate to shallower inshore areas while the larger males remain on the deeper offshore reefs. Based on these gender-specific migratory patterns, it was hypothesized that the permanent closure would have additional positive effects, relative to the seasonal closure, on the size structure

and density of the red hind spawning population since a proportion of the spawning population, including larger males, would remain within the MCD and not be caught by the commercial fishery. Moreover, since red hind are known to disperse 10 to 18 km from the spawning aggregation (Colin et al. 1987, Sadovy et al. 1992), it was predicted that some of the red hind from the St. Thomas spawning aggregation would migrate beyond the boundaries of the MCD to be caught by the local fishery. This paper reports on the conservation management implications of protecting a red hind spawning aggregation site and evaluates the benefits to the local fishery.

MATERIALS AND METHODS

Study site and species. The MCD is 12 km south of St. Thomas, USVI, encompasses 41 km^2 of shelf-edge reef, and contains at least 1 primary red hind spawning aggregation site (Beets & Friedlander 1999). The primary spawning aggregation site extends from 18° 12.20′ N, 65° 0.10′ W to 18° 12.20 N, 65° 0.40 W and is located within the MCD (Fig. 1). Depth at the spawning aggregation site ranged from 33 to 45 m. Large
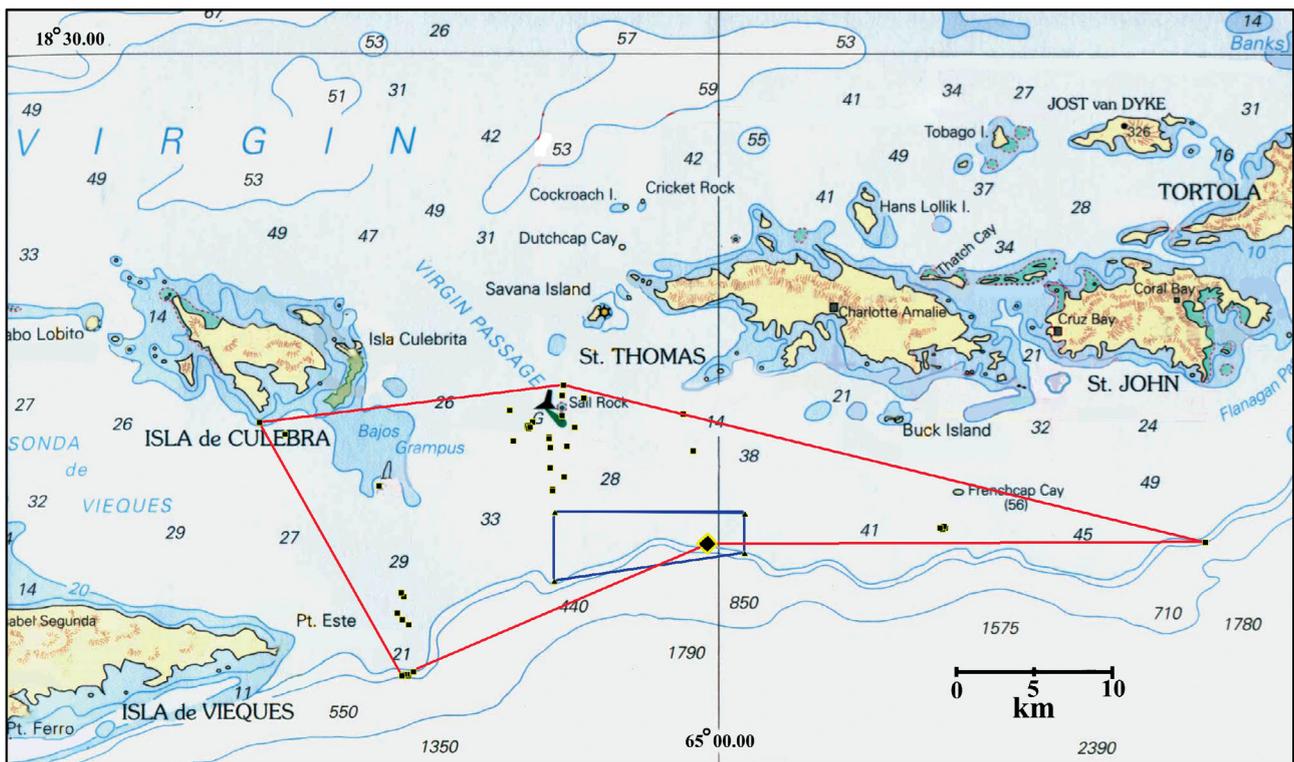

Fig. 1. Chart of northern Virgin Islands and eastern Puerto Rico showing boundaries of the Red Hind Marine Conservation District (small blue trapezoid), minimum boundary of red hind spawning population migration (large red polygon = 500 km^2), recapture locations of tagged red hind (■), and location of red hind spawning aggregation (◆). Depths in meters

areas within the MCD including the spawning aggregation site are composed of well developed and diverse coral reefs dominated by *Montastraea franksi* corals which form 1 to 2 m-wide mushroom-shaped colonies.

Red hind *Epinephelus guttatus* are long-lived reef fish (11 to 22 yr, Luckhurst et al. 1992, Sadovy et al. 1992, Potts & Manooch 1995) that form annual spawning aggregations. They migrate to spawning sites several weeks before the onset of the spawning season and begin to aggregate 5 to 7 d before the full moon between December and February. The aggregation usually peaks in January and spawning can occur from 0 to 4 d before the full moon (Shapiro et al. 1993, Beets & Friedlander 1999). In January 2000, 2001 and 2003, the area of the red hind spawning aggregation was estimated by drift-fishing, setting fish traps and diving around the aggregation area and recording GPS coordinates when visual counts and catch rates declined rapidly. The GPS coordinates were downloaded into OziExplorer shareware and the resulting polygon marked the outer boundaries of the aggregation. The primary aggregation site was marked with several semi-permanent moorings to assist in relocation and to avoid anchor damage on the coral reef.

Population characterization and assessment. SCUBA diver assessments of *Epinephelus guttatus* size structure and spawning aggregation density were conducted from December to February during 5 consecutive spawning seasons: 1999–2000, 2000–2001, 2001–2002, 2002–2003, 2003–2004. Since January was the primary spawning month, each spawning season will be referred to by a single calendar year (e.g. the period December 2002 to February 2003 as the 2003 spawning season). Due to rough sea conditions in 2002 and 2004, tag-and-release fishing and gender determination were only conducted during the 2000, 2001 and 2003 spawning seasons (i.e. only diver surveys were conducted in 2002 and 2004). Statistical tests analyzed density, length and biomass of the annual red hind spawning aggregation to determine if significant changes occurred among years following permanent closure of the St. Thomas red hind spawning site and between seasonal closure and permanent closure periods.

Changes in population density among years were assessed using visual SCUBA surveys (no. 100 m^{-2}) and trap catches (catch per unit effort, i.e. per trap haul, CPUE). SCUBA surveys consisted of a diver swimming at a constant speed with the tape unreeling behind and recording red hind in the following size classes: <10 cm, 11–20, 21–30, 31–40 and >41 cm. Each diver held a 1 m wide T-shaped bar constructed of 1.27 cm PVC pipe and marked with 5 cm increments that was used to estimate transect width and fish size.

Due to the depth of the spawning aggregation site, each diver was able to complete 3 to 4 belt transects of 30×2 m each per dive, and a minimum of 6 transects were conducted each day. Most visual surveys were conducted around the full moon period and encompassed the spawning peaks which could occur up to 4 d before the full moon (Beets & Friedlander 1999, R. S. Nemeth pers. obs.). Visual surveys were used to measure both the average and peak spawning densities. Average spawning density data included counts of red hind throughout the aggregation area 4 d before and up to 2 d after the full moon in December, January and February. Peak spawning density data included the maximum density seen on any one day during the spawning period at the approximate center of the primary spawning aggregation site. Beets & Friedlander (1999) also estimated red hind density by counting fish along 4 transects of 50×8 m each conducted at the center of the primary spawning aggregation on January 22, 1997, 1 d before the full moon. Based on my knowledge of this spawning aggregation and the fact that this day corresponded to the highest trap-catch rates in their study, the 1997 data most probably represented high average or maximum red hind densities. Since these data approximated maximum density, they were compared to annual peak spawning densities recorded each spawning season. However, as a conservative approach, the 1997 density data were also compared to average densities of red hind when testing for the effect of the MCD closure on spawning aggregation density. To standardize density estimates between years and allow comparison with published literature, only visual counts conducted during the month of January were included in the analysis. Biomass was calculated from fish transect data using the Bohnsack & Harper (1988) length–weight relationship: $W = aL^b$ where W = weight (g), a = 0.0111, b = 3.1124, and L = length (cm). Then $B = WD/1000$ where B = biomass (kg 100 m^{-2}) and D = fish density (no. 100 m^{-2}). Data for maximum spawning density met the assumptions of normality (Kolmogorov-Smirnov test, p > 0.05) and homogeneity of variances (Levene median test, p = 0.834) and were tested with 1-way ANOVA; Tukey′s test was used for multiple comparisons. Average density and biomass data did not conform to parametric testing, so the nonparametric Kruskall-Wallis analysis of variance on ranks and Dunn′s multiple-comparison tests were used.

Catch-and-release fishing was conducted during 3 of the 5 spawning seasons (Table 1) during the week preceding the full moon and a few days after. Extremely poor weather and rough sea conditions prevented fishing during the 2002 and 2004 seasons. Fishing gear included hand lines with 2 or 3 hooks baited with squid and single-funnel Antillean fish traps with 5.1 cm

Table 1. *Epinephelus guttatus*. Summary catch information for 1999–2000, 2000–2001, 2001–2002, 2002–2003 and 2003–2004 spawning seasons. Date: date of full moon; No. fish trans: no. of fish transects; CPUE: catch per unit effort; –: no trap fishing

Month	Date	No. fish trans	No. days fished	Total catch (n)	Hand line catch (%)	Trap catch (no. trap sets)	Trap CPUE	No. tagged
Dec 1999 [a]	22	5	2	156	146 (93.6)	10 (7)	1.43	124
Jan 2000 [a]	20	15	5	623	469 (75.3)	154 (54)	2.65	511
Feb 2000	19	2	4	13	7 (53.8)	6 (18)	0.33	5
Year 1 total		**22**	**11**	**792**	**622 (78.5)**	**170 (79)**	**2.14** [b]	**640**
Dec 2000	13	23	4	87	22 (25.3)	65 (48)	1.35	36
Jan 2001 [a]	9	75	14	936	609 (65.1)	327 (62)	5.27	788
Feb 2001 [a]	8	30	9	380	228 (60.0)	152 (54)	2.81	322
Year 2 total		**128**	**27**	**1403**	**859 (61.2)**	**544 (164)**	**4.04** [b]	**1146**
Dec 2001 [a]	29	24	0	0	0 (0)	-	-	0
Jan 2002 [a]	28	41	2	5	5 (100)	-	-	5
Feb 2002	26	7	0	0	0 (0)	-	-	0
Year 3 total		**72**	**2**	**5**	**5 (100)**	**-**	**-**	**5**
Dec 2002	19	28	3	73	48 (65.8)	25 (25)	1.00	57
Jan 2003 [a]	18	42	6	1114	92 (8.3)	1022 (109)	9.38	986
Feb 2003 [a]	16	29	4	211	20 (9.5)	191 (49)	3.90	162
Year 4 total		**99**	**13**	**1398**	**160 (11.5)**	**1238 (183)**	**6.64** [b]	**1205**
Dec 2003	8	9	0	0	0 (0)	-	-	0
Jan 2004 [a]	7	12	1	9	9 (100)	-	-	9
Feb 2004 [a]	6	12	0	0	0 (0)	-	-	0
Year 5 total		**33**	**1**	**9**	**9 (100)**	**-**	**-**	**9**
Total		**354**	**54**	**3607**	**1656 (45.9)**	**1952 (426)**	**4.27** [b]	**3004**

[a]Primary spawning months each year
[b]Mean CPUE calculated from primary spawning months

(2 inch) square coated-wire mesh baited with local baitfish (*Jenkinsia* sp. and *Anchoa* sp.). In 2000 6 traps were fished, with 10 in 2001 and 12 in 2003. Fishing effort for traps typically consisted of traps being set and hauled twice each day, once in the morning following an overnight set (mean soak time = 21.8 h, SD = 5.867, range = 17 to 45 h) and again in the afternoon (mean soak time = 3.8 h, SD = 1.195, range = 2 to 8 h). Short daytime trap sets (n = 227), which represented 53% of the trap effort, were fished between 7:30 and 12:30 h (mean = 10:30 h ± 0.047 SD) and caught nearly twice as many red hind than long overnight trap sets (n = 201), which were usually fished between 14:00 and 10:30 h (mean = 14:00 ± 0.070), (χ^2 = 21.83, p < 0.001; mean red hind per trap haul: short soak = 5.8 ± 6.56 SD, long soak = 3.1 ± 4.22 SD). Trap catch data were compared to Beets & Friedlander's (1999) study conducted in January 1997. They fished 12 traps constructed with 3.8 cm^2 (1.5 inch^2) mesh baited with local baitfish and used hand lines baited with squid. Beets & Friedlander (1999) pulled all traps only once a day, usually in the morning, followed by hand-line fishing. Since their 24 h soak time encompassed that of the 2 trap sets, data from my study were standardized as CPUE and long and short soak data were averaged for statistical comparison. Trap catch data did not conform to parametric testing, so nonparametric Kruskall-Wallis and Dunn's multiple-comparison tests were used.

Effort in hand-line fishing varied throughout the day and was difficult to quantify. For example, hand-line catch rates increased with slack tide and decreased as predatory fishes became more abundant. The number of persons fishing was also inversely related to catch rates. As catch rates increased, at least 2 persons stopped fishing in order to process the red hind and to record data (see below). Moreover, using hand lines as a method of catching fish became relatively less important as more traps were fished and catch rates from fish traps increased. For example, between the 2000 and 2003 spawning seasons, hand-line catch rates decreased from 78.5 to 11.5%, relative to trap catches (Table 1). Since hand-line fishing was difficult to standardize, no attempt was made to calculate its CPUE.

Red hind caught with hand lines and traps had over-inflated air bladders, which were vented using a 14 gauge hypodermic needle in 100 l tubs of seawater. Once fish regained buoyancy they were measured to the nearest 1 mm total length, tagged with numerically coded Floy T-bar anchor tags (Model FD-68B), and released overboard. Tags were inserted with a tagging gun into the dorsal musculature and through the pterigiophores of the second dorsal fin. Prior to release the abdomen of each fish was squeezed lightly, and if eggs or milt emerged, the gender was noted. In Year 4, gender was determined using ultrasound imaging (Whiteman et al. 2005).

Efforts were made to decrease mortality associated with catch-and-release fishing by reducing the amount of time that fish spent aboard the fishing vessel and increasing the supply of fresh seawater. Moreover, during the 2003 spawning season a specialized release cage was constructed that allowed fish to be lowered to the seafloor and remotely released, thus minimizing predation in the water column. These efforts were partly successful in that mortality associated with capture declined from 18 % (n = 141 fish) in the first year, to 14.4 % (n = 193 fish) in the second year to 11.5 % (n = 156 fish) in the last year of fishing (i.e. 2003 spawning season). Mortality, when it occurred, resulted from excessive bleeding from hook injury, air embolism from gas bladder expansion during ascent to the surface, or predation during retrieval or release of fish. The primary predators that attacked red hind near the boat were barracuda *Sphyraena barracuda* and occasionally king mackerel *Scomberomorous cavalla* and lemon sharks *Negaprion brevirostris*. Potential predators near the reef, in addition to those mentioned above, included large snappers *Lutjanus cyanopterus* and *L. joco*, green moray eels *Gymnothorax funebris*, nurse sharks *Ginglymostoma cirratum* and reef sharks *Carcharhinus perezii*. Green morays also contributed to pre-tagging mortality when they entered fish traps at night and swallowed several adult red hind.

Fish that did not survive capture were returned to the laboratory, measured, weighed to the nearest 0.1 g, and sexed by visual and microscopic inspection of their reproductive structures (Shapiro et al. 1993). A subsample of these fish was measured for total length (TL) and standard length (SL) which established the following relationship: TL = 1.6415 + 1.1174 SL (r^2 = 0.98, n = 23). Data on fish weight conformed to assumptions of ANOVA (Kolmogorov-Smirnov test for normality p > 0.05 and Levene test for homogeneity of variances p = 0.433). Analysis of covariance was used to test for differences in weight of males and females between years after homogeneity of regression slopes were confirmed (males: $F_{(1,81)}$ = 0.48, p = 0.49, female: $F_{(1,27)}$ = 0.13, p = 0.72). Weights for red hind are reported as adjusted least-square means.

Movement patterns and habitat usage. During the primary spawning week in January of 2000, 2001 and 2003, exploratory fishing with hand lines and traps was used to determine the boundary, and calculate the area of the spawning aggregation. Within this boundary occasional fish transects were conducted to verify the presence of red hind and calculate densities. Average densities of red hind throughout the aggregation area were used to estimate total number of fish within the spawning population.

Between January 4 and February 15, 2001, additional fish transects were conducted to record changes in red hind density and evaluate coral habitat usage patterns between monthly spawning peaks. Catch-and-release fishing was also continued every couple of days during this same period to determine the size structure of the spawning population between spawning peaks.

The tag-and-release program was designed to gather information on the source area of spawning population, migratory distance, time spent on the MCD spawning site and growth rates. The writing on each Floy tag included: a unique fish identification code, a local telephone number and a '$20 reward'. Press releases, fishermen workshops, and the distribution of reward posters at fishing ports and fish markets in St. Thomas, St. John, St. Croix, Culebra, Vieques, eastern Puerto Rico and the British Virgin Islands informed commercial and recreational fishermen of the tag reward program. Fishermen who returned a tag could receive the reward in exchange for information on date and location of capture. Fishermen who returned tagged red hind were paid market value for the fish in order to measure growth rates.

To document migratory pathways, Sonotronics acoustic tags (Model CT-82-2) were surgically implanted in the body cavity of 2 fish in January 2000 and 8 fish in January 2001. Prior to incision the area was sterilized with iodine then sutured following insertion of tag. Once the fish had recovered in a tub of flowing seawater it was carried in a mesh bag to the reef by divers, released by hand, and monitored for 10 to 15 min. Such fish were followed daily using a Sonotronics narrow-band tracking receiver (Model USR-96) and directional hydrophone (Model DH-4) until their signals were lost.

Statistical analysis of historical data. Results on population characteristics of the St. Thomas red hind spawning aggregation from this study were compared to data collected in 1997 during the seasonal closure period by Beets & Friedlander (1999). Statistical tests were conducted on fish length and weight, density, and biomass of the annual red hind spawning aggregation to determine if significant changes occurred following permanent closure of the St. Thomas Marine Conservation District, which included the red hind spawning aggregation site. This study was started in December 1999 (i.e. the Year 2000 spawning season), the same month that the MCD was established. Thus, the Year 2000 spawning season was considered part of the seasonal closure period because the characteristics of the red hind spawning population during this time period would still represent the effect of the seasonal closure and not that of the MCD. Any changes to the red hind spawning population that could be attributed to the MCD would not be evident until the following spawning season (i.e. December 2000 to February 2001), since the effective start date of the MCD was really March 1, 2000, the date the seasonal

closure would have ended. Thus, data from the 1997 and 2000 spawning seasons were considered part of the seasonal closure period, whereas the spawning seasons 2001, 2002, 2003 and 2004 were considered part of the permanent closure period. Density and biomass data were available for all years, whereas fish length, weight and catch data were available for only 1997 (Beets & Friedlander 1999) and 2000, 2001 and 2003 (this study). The null hypothesis that no difference in fish length, weight, density, biomass and CPUE of red hind existed before and after the establishment of MCD was tested using a 1-way ANOVA when data conformed to assumptions of parametric testing or a Kruskall-Wallis ranks test when data did not (see second subsection of 'Materials and methods').

To examine the impact of the MCD closure on the length of red hind caught in the fishery, size-frequency data from the beginning of the seasonal closure (1990) were extracted from published literature and reports, the National Marine Fisheries Service (NMFS) bio-statistical database, and the Virgin Islands Division of Fish and Wildlife sea map and port surveys (VIDFW). This included 1992 to 1996 and 2002 (NMFS), and 1999, 2000, 2002 and 2003 (VIDFW). When appropriate, these historical fish length data, often reported as SL, were converted to TL using the equation TL = 1.6415 + 1.1174 SL (see second subsection of 'Materials and methods'). Statistical tests on these data considered 1991 through 1999 as seasonal closure and 2000 through 2003 as permanent closure. In this case, Year 2000 is included as part of the permanent closure period since port surveys in this year were conducted after the establishment of the MCD (i.e. after February 2000). The null hypothesis was tested using a nonparametric Kruskall-Wallis ranks test, which revealed no difference in fish length before and after establishment of the MCD.

RESULTS

Spawning population abundance

The average density of red hind, estimated from fish transects (n = 354), varied among months and years. Red hind aggregated to spawn in December and January of the first (1999 to 2000) and third (2001 to 2002) years of the study, in January and February of the second (2000 to 2001) and fifth (2003 to 2004) years of the study, and primarily in January of the fourth year of the study (2002 to 2003) (Fig. 2). The spawning peak typically occurred within 2 d of the January full moon of each year. Only in February 2001 did the density of red hind exceed the January spawning density (Fig. 2), but this difference was not significant: $F_{(1,68)} = 0.85$, p =
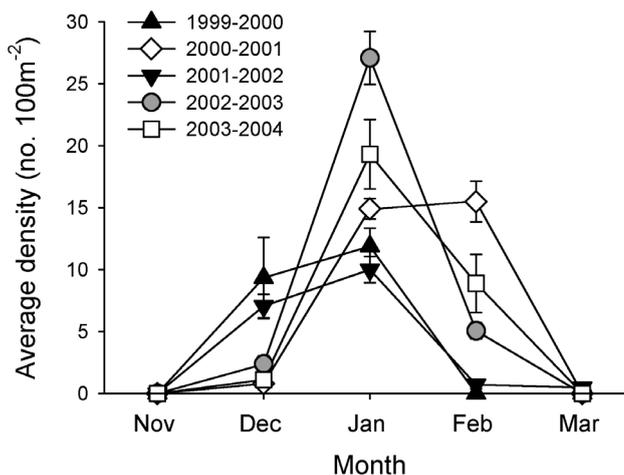

Fig. 2. *Epinephelus guttatus* Average (±SE) density in primary spawning aggregation site in St. Thomas, US Virgin Islands (USVI), from November to March. Symbols indicate primary months of spawning in the relevant years

0.36. Beets & Friedlander (1999) recorded 4.7 red hind 100 m^{-2} (±1.0 SD) on January 22, 1997 1 d before full moon. On this same day, trap catch rates peaked (Beets & Friedlander 1999), suggesting that the 1997 density estimate most probably represented the maximum density of spawning red hind, or at least a high average density. Since this value was a good approximation of maximum density, these data were compared with annual peak spawning densities found in this study. However, as a conservative approach, the 1997 density data were also used to compare average densities of red hind before and after MCD closure. Maximum spawning density of red hind was significantly greater in 2003 than in all other years (Fig. 3, $F_{(4,34)} =$
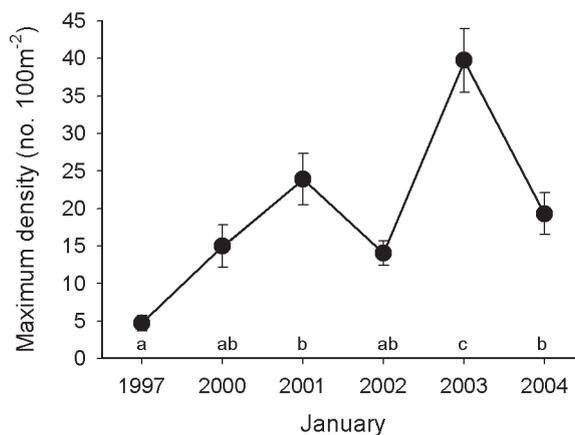

Fig. 3. *Epinephelus guttatus.* Maximum (±SE) spawning density (no. fish 100 m^{-2}) recorded during the January spawning peak for 6 spawning seasons at St. Thomas, USVI, red hind bank: 1997 (n = 4 transects), 2000 (n = 6), 2001 (n = 6), 2002 (n = 9), 2003 (n = 6), and 2004 (n = 12). Letters above *x*-axis indicate significant differences from Tukey's multiple-comparison test at p < 0.05

10.253, n = 43, p < 0.001). The maximum density of red hind more than doubled after the MCD took effect (before MCD = 10.39 red hind 100 m^{-2} ± 3.92 SD vs. after MCD = 24.25 red hind 100 m^{-2} ± 8.32 SD). The average density of red hind changed significantly between the seasonal closure period (data from 1997 and 2000 spawning seasons) and after the MCD was established (Fig. 4A, average density before MCD = 10.4 red hind 100 m^{-2} ± 5.81 SD, after MCD = 16.7 red hind 100 m^{-2} ± 11.49; Mann-Whitney U-test = 113.5, n = 43, p < 0.002).

A total of 3607 red hind were captured and measured during 3 yr of sampling with hand lines and fish traps (Table 1). Trap catches for the entire study period averaged 3.0 red hind trap^{-1} (± 4.27 SD, n = 426 trap sets) and ranged from 0 to 31 red hind trap^{-1}. CPUE for the 2 primary spawning months of each year (see Table 1) increased significantly between 2000 and 2003 (Kruskal-Wallis H = 44.38, n = 355, p < 0.001). The MCD had a significant effect on January trap catches (Fig. 4B, Mann-Whitney U-test = 6092, n =294, p < 0.001).

The mean biomass of spawning red hind increased by over 60% between the seasonal closure period (1997 and 2000) and after the establishment of the

Fig. 4. *Epinephelus guttatus.* Mean (±SE) change in (A) average density, (B) catch per trap haul and (C) biomass during seasonal closure and after the Red Hind Bank Marine Conservation District (MCD) was established at St. Thomas, USVI. p < 0.05 indicates significant change between level of protection

MCD (2001 and 2003) (Fig. 4C, Mann-Whitney U-test = 1222, n = 116, p < 0.025). Biomass estimates from SCUBA surveys for January of each year were 2000: 11.2 kg 100 m^{-2} (±6.48 SD); 2001: 9.2 kg 100 m^{-2} (±5.64 SD); 2002: 10.1 kg 100 m^{-2} (±4.10 SD); 2003: 25 kg 100 m^{-2} (±13.10 SD); 2004: 18.7 kg 100 m^{-2} (±10.30 SD). Biomass of red hind in 1997 was estimated from Beets & Friedlander (1999) to be 3.8 kg 100 m^{-2}. The maximum rate of change in biomass from 1997 to 2003 represented a 550% increase in a 6 yr period.

The area of the red hind aggregation within the MCD was calculated to be 0.24 km^2 in both 2000 and 2001 and 0.35 km^2 in 2003. This increase resulted from red hind occupying a larger area of contiguous coral reef to the west of the primary spawning aggregation. The average density of spawning red hind throughout the entire aggregation area (averaged from transects done from 4 d before to 1 d after full moon) for January 2000, 2001 and 2003 were 11.2, 16.4 and 24.0 red hind 100 m^{-2}, respectively. By multiplying the area of the aggregation by the average density of spawning red hind throughout this area, the total number of fish within the red hind spawning population was estimated to be 26 229 in 2000, 38 143 in 2001 and 84 000 in 2003. The dramatic increase of the spawning population between January 2000 and 2003 resulted from a combination of the westward expansion of the spawning aggregation and the higher densities of red hind within this area. The continuity of the spawning aggregation from the primary site to the western boundary was verified using fishing and diver surveys and was supported by concurrent increases in trap CPUE and biomass during this same time period (Table 1, Fig. 4B,C).
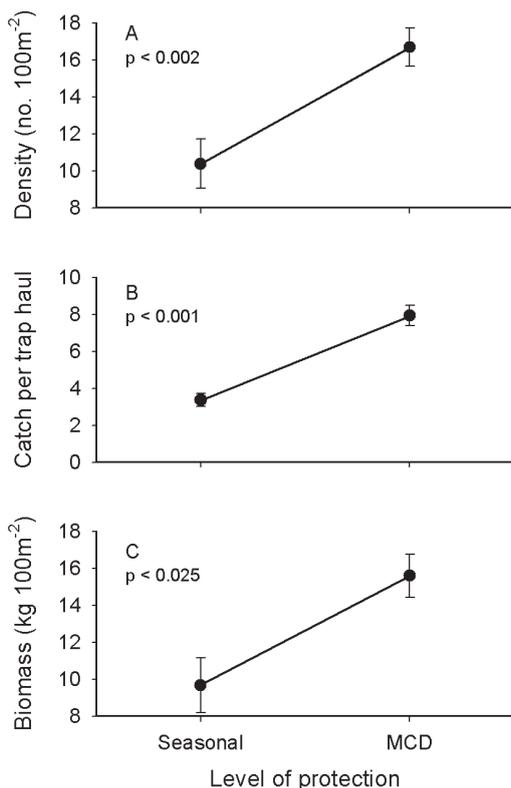
Spawning population size structure

The length of red hind in the spawning aggregation increased significantly toward the end of the seasonal closure (Fig. 5, Kruskal-Wallis H = 72.89, n = 3902, p < 0.001). Following the MCD closure, the size of fish in the spawning aggregation reached a plateau and even declined slightly from 38.8 cm in 2000 to 37.9 cm in 2003 (Fig. 5). This resulted in no significant change in fish length between the seasonal closure and MCD periods (Kruskal-Wallis H = 0.14, n = 3902, p > 0.05). However, analysis of port sampling data indicated that the length of red hind caught by the commercial fishery increased significantly after the MCD was established (Fig. 5; total length before MCD = 32.4 cm ± 6.06 SD, after MCD = 34.4 cm ± 5.10 SD, Mann-Whitney U-test = 60149, n = 637, p < 0.001).

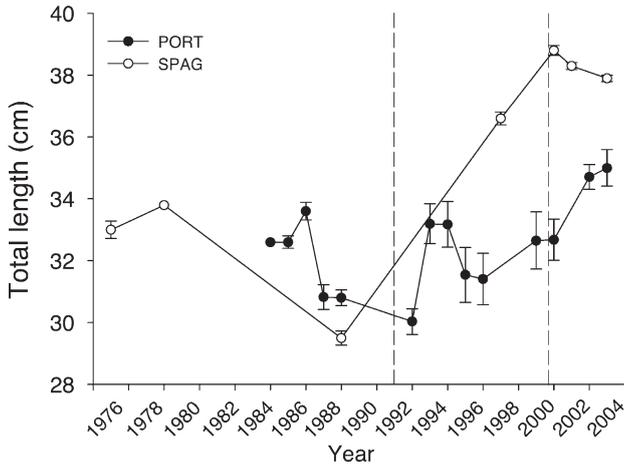Within each spawning season, the average size of fish differed significantly between months. Red hind

Fig. 5. *Epinephelus guttatus*. Mean (±SE) total length (cm) of St. Thomas red hind population over past 30 yr collected from port surveys (PORT) and red hind spawning aggregations (SPAG). Dashed vertical lines indicate start of seasonal closure in November 1990 and establishment of MCD in December 1999. Data recalculated from Olsen & LaPlace (1978), Sylvester et al. (1978), Morales-Santana (1984), Clavijo & Tobias (1985), Bohnsack et al. (1986), Clavijo et al. (1986), Beets & Friedlander (1992), Sadovy & Figuerola (1992), Sadovy et al. (1992), Cummings et al. (1997), Beets & Friedlander (1999), and National Marine Fisheries Service biostatistical data, Virgin Islands Division of Fish and Wildlife. Measurements in standard lengths (SL) were converted to total lengths (TL) using equation TL = 1.6415 + 1.1174 SL (r^2 = 0.98, n = 23: see second subsection of 'Materials and methods').

were consistently larger in December of each spawning season whether or not it was a primary spawning month (Fig. 6, Kruskal-Wallis, 1999 to 2000: H = 55.07, n = 783, p < 0.001; 2000 to 2001: H = 13.70, n = 1321, p < 0.001; and 2002 to 2003: H = 90.60, n=1383, p < 0.001). Between the years 2000, 2001 and 2003, the

size of fish remained largely unchanged during successive Decembers (p = 0.898), decreased each January (Kruskal-Wallis H = 19.48, n = 2658, p < 0.001) and increased each February (Kruskal-Wallis H = 17.35, n = 604, p < 0.001). The data for February 2000 should be interpreted with caution since this was not a primary spawning month and the sample size was small (Fig. 6). Since January was the primary spawning month each season it had the largest sample size of any month and had a strong influence on the overall fish size among years. The decrease in fish length from 2000 to 2003 during this month (Fig. 6) most probably contributed to the overall decline in average fish length between years (Fig. 5).

The total length of fish collected by hand line was 0.8 cm larger than fish caught in traps in 2001 (hand line = 38.6 cm ± 4.32 SD, trap = 37.8 cm ± 3.92 SD, Kruskal-Wallis H = 8.72, n = 1310, p < 0.003) and 2003 (hand line = 38.6 cm ± 4.81 SD, trap = 37.9 cm ± 3.72 SD, Kruskal-Wallis H = 4.69, n = 1224, p < 0.03). The proportion of red hind caught with hand line declined from 78.5% in 2000 to 11.5% in 2003 (Table 1). This slight gear bias may have also contributed to the 0.9 cm decline in average fish length during this period (Fig. 5).

The dominant size class of red hind calculated from SCUBA transects was 31 to 40 cm during all 5 yr (Fig. 7). There was an annual trend of increasing dominance of the larger size classes (i.e. 31 to 40 and >41 cm) and a subsequent decrease of smaller size classes from 2000 to 2004. Red hind <10 cm in length were also observed by divers and were found in the regurgitated gut contents of 2 adult red hind, indicating that recruitment of juvenile red hind may actually be occurring on these deeper reefs.

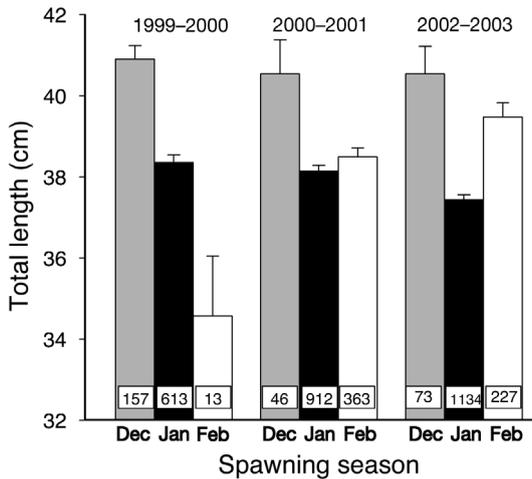Fig. 6. *Epinephelus guttatus*. Mean (±SE) total length (cm) of aggregating fish during each 3 mo spawning season in St. Thomas, USVI. Sample sizes are shown at base of bars; primary spawning months indicated in bold
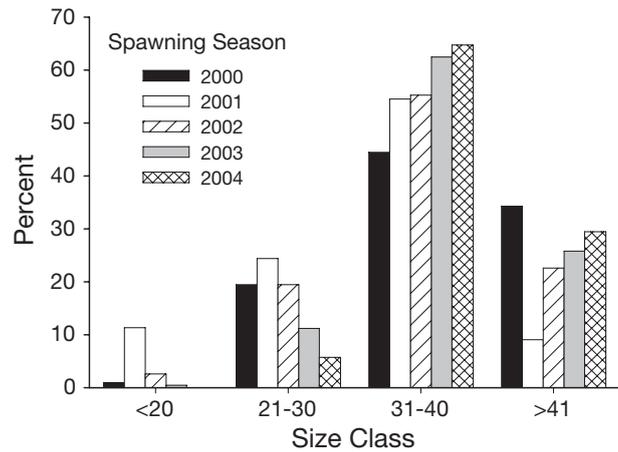

Fig. 7. *Epinephelus guttatus*. Percent size distribution of fish estimated from diver transects conducted at the red hind bank, St. Thomas, USVI, during January spawning aggregations of each year (n = no. transects): 2000 (n = 15), 2001 (n = 21), 2002 (n = 28), 2003 (n = 36), 2004 (n =12)

Table 2. *Epinephelus guttatus*. Mean ± SD. Total length and weight of male and female red hind from St. Thomas spawning aggregation. Individual letters in multiple comparisons indicate significant differences among years (p < 0.05). 1997 data from Beets & Friedlander (1999). n = number of fish

Year	n	Length (cm)	p	n	Weight (g)	p
Male						
1997	91	40.7 ± 2.66	A	91	1008 ± 221.7	A
2000	106	41.8 ± 3.90	B	76	1168 ± 309.3	AB
2001	39	41.4 ± 1.71	AB	9	1174 ± 182.4	AB
2003	49	42.3 ± 3.15	B	48	1199 ± 286.6	B
Female						
1997	264	35.3 ± 3.36	A	264	666 ± 215.8	A
2000	51	39.4 ± 3.31	B	10	865 ± 248.0	B
2001	37	34.6 ± 3.11	A	21	721 ± 205.5	AC
2003	139	36.4 ± 3.42	A	118	821 ± 253.6	C

The greatest period of change observed in the average length of males and females occurred between 1997 and 2000 (Table 2). Although this time period represented the end of the seasonal closure, the establishment of the MCD also had a positive effect on the total length and weight of females (length before MCD = 35.4 cm ± 3.45 SD, after MCD = 36.2 cm ± 3.43 SD, Mann-Whitney U-test = 21757, n = 413, p < 0.018; weight before MCD = 672 g ± 219.7 SD, after MCD = 806 g ± 248.9 SD, Mann-Whitney U-test = 24916, n = 413, p < 0.001). The maximum length of females increased from 43.9 cm to 44.5 cm over the study period (Fig. 8). Although the MCD had no effect on the average length or weight of males, their maximum size range increased dramatically from 48 cm in 1999–2000 to 54.6 cm in 2002–2003 (Fig. 8). An increase in the percentage of the youngest size classes of females in the 2002 to 2003 spawning season may be indicative of recruitment of young females into the spawning population. There was also a shift in the dominant size class of females from 36 cm in 1999–2000, to 36–38 cm in 2000–2001 to 38–40 in 2002–2003 (Fig. 8). Most interesting, was a decrease in the 42 cm size class of females in 2000 to 2001 and a subsequent increase in the 42 cm size class of males in 2002 to 2003 (Fig. 8), suggesting that a cohort of females may have changed sex during the previous 2 years to accommodate the recruitment of young females into the spawning population.

Growth rates, calculated from recaptured red hind, were greatest during the first 1 to 3 mo postspawning (0.18 mm d^{-1} ± 0.38 SD, n = 74, mean days at liberty = 33.2 d, range = 1 to 77 d). Fish that were recaptured 6 to 36 mo after release had average growth rates of only 0.043 mm d^{-1} ± 0.065 or 15.7 mm yr^{-1} (n = 31, mean days at liberty = 488 d, range = 138 to 1138 d).
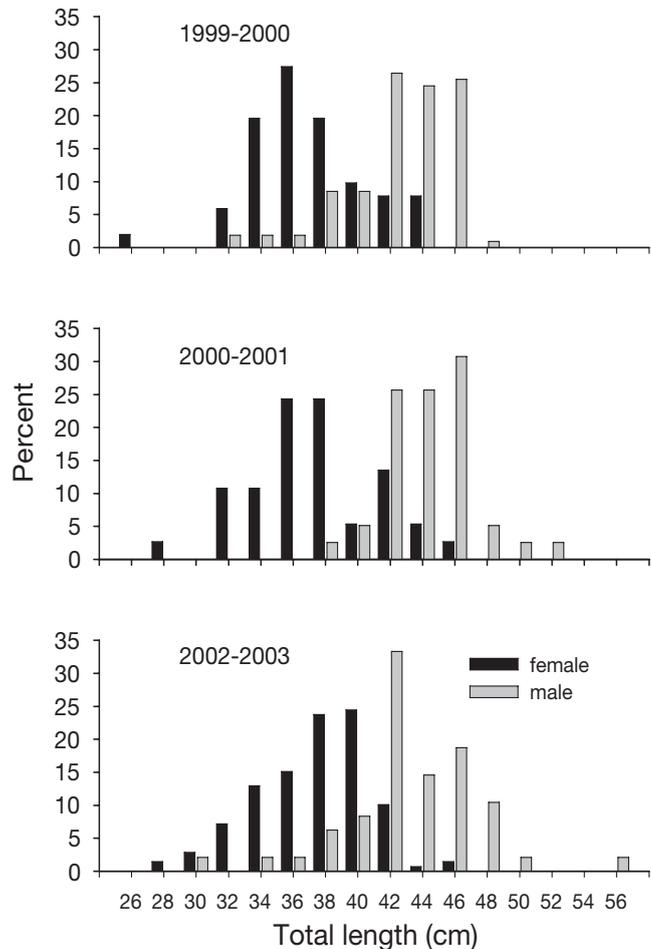

Fig. 8. *Epinephelus guttatus*. Size-frequency distribution of St. Thomas, USVI, fish spawning aggregation by gender in 1999 and 2000 (mean size: female 36.2 cm ± 3.56, n = 51; male 41.8 cm ± 3.28, n = 106), 2000 and 2001 (mean size: female 36.4 cm ± 3.82, n = 37; male 43.5 cm ± 2.44, n = 39) and 2002 and 2003 (mean size: female 36.5 cm ± 3.47, n = 139; male 42.3 cm ± 4.12, n = 49). *X*-axis labels show upper end of size range (i.e. 26 = 24.1 to 26 cm)

Movement patterns and habitat usage

Small-scale movement, habitat usage and population characteristics between full moon spawning periods were evaluated with 105 fish transects and 23 d of catch-and-release fishing completed between January 4 and February 10, 2001. The emerging pattern showed that red hind aggregated at high densities during the week preceding the full moon, reached peak densities on the full moon, and that 50 to 80% of the population then dispersed for about 3 wk before reforming the aggregation (Fig. 9A). In late January 2001 large numbers of red hind were observed 50 to 100 m (or more) off the primary coral reef in areas composed of sand, rubble and patch-reef habitat. A census of this area on January 31, 2001, verified this observation (Fig. 9A). Red hind that re-
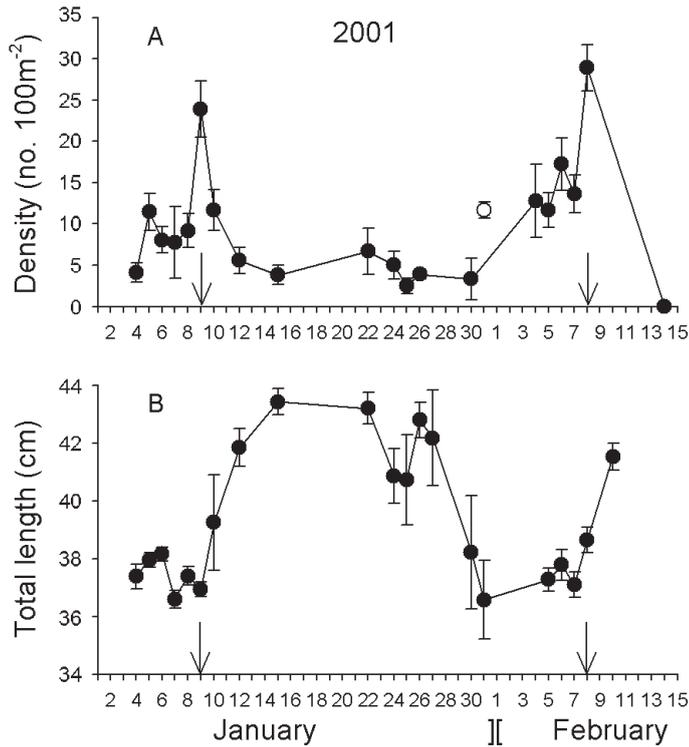
Fig. 9. *Epinephelus guttatus*. Results of intensive sampling of (A) mean (±SE) fish density from transects and (B) mean (±SE) total length measured during catch-and-release fishing between spawning peaks in January and February 2001 at St. Thomas USVI red hind bank spawning aggregation site. Arrows show dates of full moon. (○) sampling date that fish transects were made 100 m off the primary spawning coral habitat in an area of small patch reefs, sand and rubble

During the first 2 spawning seasons, 3004 fish were successfully tagged and released. Of these, 130 fish (4.3%) were recaptured either on the spawning grounds during subsequent sampling (n = 84) or were recaptured by fishermen outside the MCD (n = 46) and returned to the University of the Virgin Islands for reward; 8 tags were returned by commercial fisherman in Vieques, 1 from a commercial fisherman in St. Thomas, and the remaining tags by recreational fisherman. Although many St. Thomas commercial fishermen insisted that no tagged hind had been caught in traps, it leaves one skeptical of the actual participation from this sector of the fishery. Nearly 50% of red hind recaptured outside the MCD were caught within 4 mo of release (Fig. 10). The majority of red hind caught outside the MCD had migrated an average of 15.6 km (± 5.17 SD, range = 6 to 33 km) north and westward of the spawning site to their home territory (Fig. 1). Telemetry data confirmed this pattern. Of the 10 red hind that were tracked using acoustic tags, all moved westward following the coral reef ridges before the signal was lost. The maximum distance a fish was tracked was about 3 km. Based on the tag–recapture data, it was calculated that the red hind spawning aggregation south of St. Thomas draws fish from an area of at least 500 km².

DISCUSSION

The St. Thomas Red Hind Bank Marine Conservation District was closed seasonally in November 1990 and permanently in December 1999 to protect an important red hind *Epinephelus guttatus*
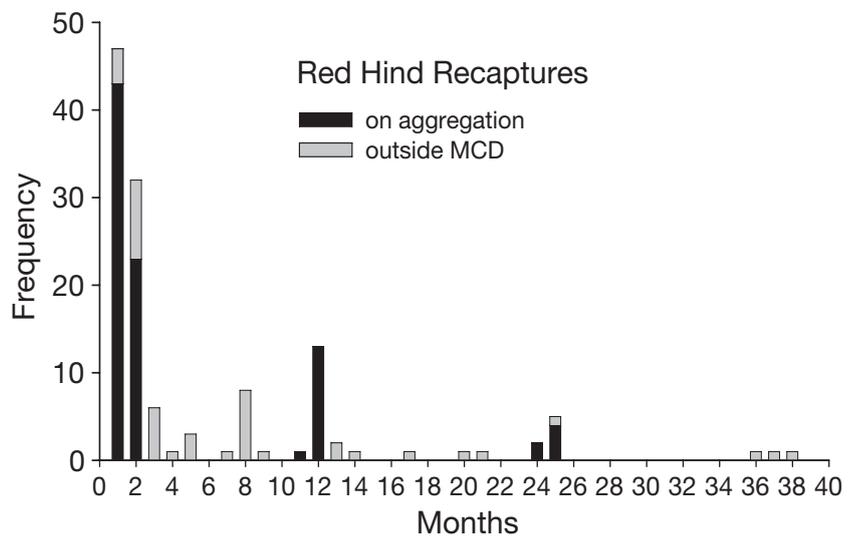
mained on the spawning aggregation site averaged 42.1 cm (±1.02 SD). Fish that were collected and measured between January 12 and 27 and on February 10 were significantly larger than the mean population size during spawning (repeated-measures ANOVA $F_{(20,176)}$ = 13.686, p < 0.001, Fig. 9B). Based on size estimates of males and females (Table 2), these data suggest that females depart the spawning site while males remain until the next spawning period. Red hind had reformed the spawning aggregation on the primary coral reef spawning habitat 1 wk prior to the February full moon. Within 1 wk following the February full moon, the spawning population rapidly and completely departed from the spawning aggregation site (Figs. 2 & 9).

Fig. 10. *Epinephelus guttatus*. Number of tagged red hind recaptured in spawning aggregation within (n = 84) and outside (n = 46) St. Thomas MCD between December 1999 and March 2004

spawning aggregation, to improve the declining red hind population and protect critical fisheries habitat. The seasonal closure resulted in impressive improvements in fish length and sex ratios of the spawning aggregation (Beets & Friedlander 1999). The establishment of the MCD following the seasonal closure provided a unique opportunity to examine the population response of a red hind spawning aggregation to this new management action and evaluate the effectiveness of a relatively large reserve (Halpern 2003) on the red hind fishery.

Since these management measures were implemented, the red hind spawning aggregation has shown positive trends in several population characteristics. Beets & Friedlander (1999) first collected density data on this red hind spawning aggregation in 1997, 7 yr after seasonal closure. During the last 3 yr of the seasonal closure, from 1997 to 2000, the density of the spawning population increased by over 200% (4.7 to 15.0 fish 100 m^{-2}) or about 66% yr^{-1}. Following the establishment of the MCD, density and biomass of red hind increased 60% on average, whereas peak spawning densities more than doubled during a 3 yr period (Years 2000 to 2003). These values were supported by the fish trap catch rates which more than doubled after the MCD was established. Annual fluctuations in density were also apparent. The density of red hind peaked in both 2001 and 2003 but declined in the intervening years 2002 and 2004 (Fig. 3). Olsen & LaPlace (1978) and Sylvester et al. (1978) recorded a similar phenomenon, whereby the St. Thomas red hind spawning aggregation showed high abundances based on catch rates in both 1975 and 1977 spawning seasons, extremely low abundance during the 1976 spawning season and moderate abundance in the 1978 season. Olsen & LaPlace (1978) suggested that these changes in abundance were the result of both fishing mortality and the relocation of the spawning aggregation due to heavy fishing pressure and possibly subsequent predation pressure by sharks. The drop in density in 2002 and 2004 also followed increased catch-and-release fishing activity from my research in 2001 and 2003, but diver surveys and catch rates verified that the primary site of the spawning aggregation still had the highest densities and did not shift to a different location. Alternatively, this pattern may suggest a biannual difference in spawning cohort strength (odd years being the strong cohort), a phenomenon that is well-documented for some species of Pacific salmon (Bond 1996). The density of red hind during these peak spawning seasons in 2001 (January = 23.8 fish 100 m^{-2} and February = 28.9 fish 100 m^{-2}) and 2003 (January = 39.72 fish 100 m^{-2}) were the highest densities ever documented for a red hind spawning aggregation in the Caribbean. The average density of

spawning red hind over the entire spawning area was 11.88, 14.91, 10.00, 27.08 and 19.31 red hind 100 m^{-2} for January 2000, 2001, 2002, 2003 and 2004, respectively. In 1984, Shapiro et al. (1993) recorded a peak density of 7.6 fish 100 m^{-2} with a mean of 3.8 fish 100 m^{-2} from a small red hind aggregation in SW Puerto Rico. The mean value for the Puerto Rico site is similar to the 4.7 fish 100 m^{-2} reported from the St. Thomas MCD in 1997 (Beets & Friedlander 1999). However, the average density from the unprotected spawning aggregation in Puerto Rico dropped to 0.88 fish 100 m^{-2} 2 yr later (Shapiro et al. 1993), whereas the average density of the St. Thomas MCD had increased to 11.88 fish 100 m^{-2} 3 yr later. This suggests that the heavily overfished St. Thomas spawning population was still in a state of recovery in 1997 and that continued protection from fishing mortality had been extremely beneficial to the population.

During the last 3 yr of seasonal closure, from 1997 (Beets & Friedlander 1999) to 2000, the average length of the spawning population showed a significant increase from 36.6 to 38.8 cm, or about 0.73 cm yr^{-1}. Although Beets & Friedlander (1999) used traps with smaller mesh (3.8 cm^2 vs. 5.1 cm^2), it probably did not influence the results, since red hind caught in both studies were all greater than 25 cm in total length. Most red hind smaller than 25 cm are not yet reproductively active (Sadovy et al. 1992) and would not have entered the spawning aggregation. In the years following the MCD closure, the average size of red hind actually decreased by 0.9 cm (from 38.8 to 37.9 cm) relative to the first year of sampling (Fig. 5). The decrease in average fish length may have been an artifact of sampling or a real change in the spawning population. Fish collected by hand line were 0.8 cm larger than fish caught with traps. Since the proportion of red hind caught by hand line decreased from 78.5% in 2000 to 11.5% in 2003 (Table 1) this size-related gear bias may have contributed to the 0.9 cm decline in average fish length during this period (Fig. 5). Alternatively, the decrease in fish length could have been effected by recruitment of small young females into the spawning population in 2003 (Fig. 8). A final alternative is that both gear bias and recruitment could have contributed to the slight decline in fish size from 2000 to 2003.

Beets & Friedlander (1999) calculated that the area utilized by the red hind aggregation in 1997 was between 0.1 to 0.24 km^2, the latter being comparable to the area calculated by the surveys in January 2000 and 2001 (0.24 km^2). Based on these calculations, total spawning population size ranged between 4700 to 11 280 fish in 1997 compared to 26 229 red hind in 2000, 38 143 in 2001 and an astonishing 84 000 in 2003. The dramatic increase in the estimated population size

of the red hind aggregation in 2003 resulted from both a westward expansion of the spawning aggregation and an increase in red hind density throughout this area. Prior to this study, most red hind spawning aggregations were thought to be small, ranging in size from 750 to 3000 fish (Shapiro 1987, Shapiro et al. 1993, Levin & Grimes 2002) and occupying a spawning area of 0.01 km². These early estimates were based on heavily fished aggregations in Puerto Rico. The population size estimates documented for the marine protected area in St. Thomas far exceed these values and begin to rival species such as Nassau grouper, for which up to 30 000 individuals have been reported in a single aggregation (Smith 1972).

One explanation for the dramatic increase in red hind density after establishment of the MCD is that the efficiency of the fishery to catch red hind had been substantially decreased. Prior to the year-round closure in December 1999, fishermen could begin fishing within the MCD immediately following the closed spawning season which lasted from December through February. Based on the telemetry data, fish departing the spawning site most probably follow the relatively narrow (<200 m) coral reef ridges to the west and east, which afford groupers shelter from predation, before dispersing to their home sites. Strategic placement of traps along these migratory pathways may have had a significant impact on the spawning population as they departed the spawning site (Johannes 1981). Once fish dispersed from the spawning aggregation, the efficiency of fishing gear to capture large numbers of red hind was reduced, resulting in greater escapement from the commercial fishery. The year-round closure and the relatively large size of the MCD eliminated a potential fishing mortality bottleneck by allowing red hind to depart the aggregation in relative safety before dispersing to areas outside the reserve boundaries. Based on the tag-recapture data, the majority of red hind traveled about 15 km northwest to a rocky reef area around Sail Rock, St. Thomas (Fig. 1). Other fish were recaptured from 6 km to at least 33 km from the aggregation site, creating a source population area of at least 500 km². These migration distances are comparable, if slightly higher, than those reported for red hind in SW Puerto Rico which dispersed 10 to 18 km from the spawning aggregation (Colin et al. 1987, Sadovy et al. 1992).

Another alternative is that the spawning aggregation may be composed largely of fish resident in the closed area, which now offers continued protection of red hind that remain on the shelf-edge reefs. Several studies in Puerto Rico found that red hind females migrate to shallower inshore areas, while males remain on the deeper offshore reefs (Shapiro 1987, Sadovy et al. 1994b). Commercial fishing on the deep

offshore reefs after the seasonal closure ended may have had a proportionally greater impact on male red hind relative to females, which dispersed over wider areas. However, Nemeth & Quandt (2004) found that, between the months of March and September, red hind densities on coral reef sites within the MCD (n = 8) were lower than at non-MCD (n = 8) sites (0.24 vs. 0.42 red hind 100 m², respectively). At this time it is unknown what proportion of the spawning population remains in non-coral reef habitats within the boundaries of the MCD. However, it is interesting that many tagged red hind were caught in a coral reef area within 6 km of the northwestern edge of the MCD. Of these fish, 3 were recaptured only 1.5 km outside the northwest corner of the MCD. This coral reef area extends into the MCD and may provide suitable habitat for red hind departing the spawning aggregation.

A final alternative to explain the significant increase in density, especially in 2003, is that a large cohort of young females recruited into the spawning population (Fig. 8). Sadovy et al. (1992) estimated that red hind from the St. Thomas region can grow to nearly 20 cm within 12 to 15 mo post-settlement and that up to 50% of red hind females within a population can reach sexual maturity within 3 yr. Growth rates in this study (1.2 to 4.8 cm yr⁻¹) were similar to rates for red hind in Puerto Rico (1.2 to 9.6 cm yr⁻¹, Sadovy et al. 1992). A cohort of young females could theoretically have been the result of increased reproductive output of the St. Thomas red hind aggregation during the Year 2000 spawning season. The larger size and number of red hind within this spawning population represents a substantial increase in fecundity over previous years. The estimated egg production for red hind females at 36 cm (i.e. mean size of females in St. Thomas) could produce over 500 000 eggs female⁻¹, and older, larger females that reach 40 cm in length can produce over 1 000 000 eggs (Olsen & LaPlace 1978, Thompson & Munro 1978, Sadovy et al. 1992, Whiteman et al. 2005). With the greatly increased reproductive output of females, subsequent larval recruitment and rapid growth rates of juveniles, one could expect larger cohorts of young females to enter the St. Thomas spawning aggregation in future years if self-recruiting occurs. Substantial increases in reproductive output is a major benefit of protected spawning populations of fish and invertebrates (Bohnsack 1992, Palsson & Pacunski 1995, Kelly et al. 2000, Roberts et al. 2001, Gell & Roberts 2003, Willis et al. 2003).

Protection of the St. Thomas red hind spawning aggregation seems to have had positive effects on the red hind population around St. Thomas. Based on a review of the literature and biostatistical data from port landings, the average length of red hind from the commercial catch has steadily increased and tracked the

average length of the spawning population (Fig. 5). The lengths of red hind from commercial landings were typically smaller than catches from the spawning aggregation, since the commercial catch includes subadult fish from inshore waters which tend to be smaller (Olsen & LaPlace 1978, Shapiro et al. 1993). The predominant factor affecting the size and abundance of groupers among diverse areas in the Caribbean is fishing pressure (Sluka et al. 1997, Chiappone et al. 2000). Thompson & Munro (1978) reported that the mean size of red hind in intensely fished nearshore areas of Jamaica versus offshore oceanic banks was 26 and 33 cm TL, respectively. With a reduction in fishing pressure of the red hind spawning aggregation in St. Thomas, the average size of red hind at the spawning aggregation steadily increased from a low of 29.5 cm in 1988 (Beets & Friedlander 1999) to nearly 39 cm 12 yr later (this study, Fig. 5). A concurrent increase in length of the red hind population outside the aggregation was clearly evident and increased significantly after the MCD was established (Fig. 5). Interviews with commercial and recreational fishermen around St. Thomas by the author during the past several years highlighted a general perception that the red hind being caught now are larger than before the MCD was established.

The results reported in this paper indicate that seasonal protection of the red hind spawning aggregation allowed the spawning population to rebound relatively rapidly from overfishing in terms of size, density and sex ratios. Permanent protection of large areas surrounding the spawning habitat provided additional benefits toward increasing spawning stock density and biomass as well as maintaining sex ratios between 3 and 5 females per male (Whiteman et al. 2005). Other factors which may have contributed to these changes include change in fishing effort or gear and the implementation of other fishery regulations. The number of licensed commercial fishermen in the Virgin Islands has been stable for over 15 yr (Tobias 1997, B. Kojis pers. comm.), whereas effort in trap-fishing doubled in St. Thomas from 1985 to 1996 (unpubl. data from NMFS biostatistical database). This increase in effort has apparently not influenced the red hind population. Between 1997 and 1999 fish traps with 3.8 cm^2 (1.5 inch^2) square mesh were phased-out in St. Thomas (but not St. Croix) and replaced by traps with 5.1 cm^2 (2.0 inch^2) square mesh. This change may have increased escapement of smaller red hind, but the effect on the larger sized fish comprising the spawning population was probably minor, as evidenced by the lack of difference in minimum-sized fish caught by traps used in Beets & Friedlander (1999) and this study. St. Croix also has a red hind spawning aggregation that has been seasonally protected since 1995. The

sizes of red hind in the spawning aggregation and in the commercial catch have been declining and are considerably smaller (32.3 and 27.6 cm, respectively) than red hind in the St. Thomas region (Nemeth unpubl. data). These factors suggest that the establishment of the MCD has been the primary stimulant for maintaining and improving the St. Thomas red hind spawning population, a finding which corroborates many studies on the benefits of using marine fishery reserves (MFR) as a management strategy (Pauly 1979, Roberts & Polunin 1991, 1993, Russ 1991, Roberts 1995, Bohnsack 1996, Gell & Roberts 2003).

Because red hind spawn in smaller social groups (3 to 5 fish^{-1} group) than the large social groups of 1000s to 10 000s of fish formed by other species like Nassau groupers *Epinephelus striatus* (Smith 1972, Olsen & LaPlace 1978), it is likely that red hind spawning populations are impacted less by short-term fishing pressure (Colin et al. 1987) and may show more rapid recovery once fishing is reduced. After the collapse of the Nassau grouper fishery in Virgin Islands (Olsen & LaPlace 1978) the red hind became the dominant grouper in the local fishery (Cummings et al. 1997). The change in catch composition from larger to smaller individuals and/or larger species being replaced by smaller species is well-documented (Luckhurst 1996, Chiappone et al. 2000). While Nassau grouper reach 850 to 950 mm (Olsen & LaPlace 1978, Colin et al. 1987, Colin 1992), red hind reach maximum lengths around 500 to 550 mm (Olsen & LaPlace 1978, Thompson & Munro 1978, Colin et al. 1987, Sadovy et al. 1992), although specimens from 620 to 720 mm have been recorded (Smith 1971, Randall 1983, Luckhurst et al. 1992). Whether the Nassau grouper will be able to reclaim its historical spawning site within the MCD (Olsen & LaPlace 1978) will require long-term monitoring efforts.

Other behavioral aspects of fish within spawning aggregations may also influence effects of differential fishing mortality. For example, males of many grouper species, including red hind, remain higher in the water column defending spawning territories or displaying to potential mates (Colin et al. 1987, Gillmore & Jones 1992). Sex and/or size-selective fishing mortality in spawning aggregations will occur when these more behaviorally dominant males take baited hooks more frequently than females (Gillmore & Jones 1992, Levin & Grimes 2002). Moreover, Levin & Grimes (2002) suggested that sex-changing female groupers of exploited populations may adopt stereotypical male behavior during the spawning season, making them more vulnerable to fishing and further disrupting reproduction.

Another example of the influence of behavior includes gender-biased small-scale movement patterns of aggregating groupers during the spawning season.

My data suggest that male red hind arrive early at the spawning aggregation site (i.e. December) and stay on-site between spawning peaks. Thus, short-term seasonal closures, from 1 to 2 mo, that protect only the primary spawning month may make a large portion of the spawning population, especially males, vulnerable to fishing mortality. Between spawning peaks, a substantial portion (50 to 80 %) of red hind disperses short distances (at least 100 m) into adjacent habitats (see Fig. 9). Size-frequency analysis suggests that most of these fish are probably females (fish < 40 cm TL). However, it is unknown what proportion of these fish seen in adjacent habitats were from the same group of spawning individuals that dispersed temporarily between full moon spawning events versus new arrivals waiting for the next full moon spawning event. If red hind and other larger grouper species disperse considerable distances between spawning peaks, then the size and placement of MPA boundaries may not provide sufficient protection from fishing if fish disperse beyond MPA boundaries during the spawning season. These findings suggest that the design of marine fishery reserves must take into account not only critical fish habitats but also the important life-history attributes that may exacerbate fishing mortality effects on protogynous species.

In the light of my findings, the potential economic and conservation benefits of establishing the Red Hind Bank Marine Conservation District to the Virgin Islands are becoming evident. Continued protection of the red hind spawning aggregation will mean greater reproductive output for this species and better catches in the near future for commercial fishermen of the Virgin Islands and eastern Puerto Rico. Most importantly, interviews with commercial and recreational fishermen indicate that a noticeable increase in the size and abundance of red hind has occurred over the past few years. The perception that the MCD is enhancing the local fishery may facilitate a positive change in social attitude and behavior toward the acceptance of marine fisheries reserves (Roberts 2001) and highlight the regional fishery benefits associated with protecting spawning aggregations.

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