Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands

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ORIGINAL PAPER

Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands

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Abstract This study compared the spatial and temporal patterns of red hind, *Epinephelus guttatus*, movement and migration from annual spawning aggregations on St Thomas (STT) and St Croix (STX), United States Virgin Islands. Around STT *E. guttatus* migrated 6–33 km from a functional spawning migration area of 500 km^2 and around STX *E. guttatus* migrated 5–18 km from an area of 90 km^2. Similarities between sites were found in regards to timing of movement, temporal and spatial changes in sex ratios, annual and lunar predictability and were synchronized with environmental cues. *E. guttatus* spawning aggregations in the Virgin Islands occur between the winter solstice (i.e., after December 20) and about February 20 of any year and show a distinctive peak 20–40 days after the winter solstice. Spawning typically occurred during periods of declining seawater temperature and slacking currents within a temperature range of 26–27.5°C and current speed of 2.5–3.5 cm s^{-1}. Males arrived early to spawning sites and stayed longer than females. These gender-based behavioral patterns are important to *E. guttatus* reproductive dynamics and must be factored into future studies and the design of fisheries regulations to ensure sustainability of spawning aggregation sites. The predictability of *E. guttatus* spawning aggregations relative to the winter solstice will be extremely beneficial for defining the temporal and spatial aspects of area closures. The consistency and synchrony of movement and migration will improve both the efficiency of planning research and monitoring programs and directing enforcement activities during critical time periods. Applying this knowledge strategically will maximize the limited resources available for research and enforcement and lead to greater protection of spawning aggregations.

Keywords Marine protected areas · Serranidae · Fish tagging · Behavior · Fisheries management · Caribbean

Introduction

Coral reef fishes employ a wide spectrum of reproductive strategies (Thresher 1984). One common strategy is to form spawning aggregations where hundreds to thousands of fish migrate to specific sites to spawn in pairs, harems or large groups (Thresher 1984; Domeier and Colin 1997). Some species such as wrasses, surgeon fishes and parrotfishes undergo daily or monthly spawning

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migrations over relatively short distances (Randall and Randall 1963; Robertson and Hoffman 1977; Colin and Clavijo 1978, 1988; Robertson 1983; Warner 1988, 1990). Larger species, such as snappers and groupers undergo seasonal migrations covering tens to hundreds of kilometers (Colin et al. 1987; Colin 1992; Shapiro et al. 1993; Zeller 1998; Heyman et al. 2005; Nemeth 2005). Annual spawning migrations are important life history events that function to connect individuals from large areas of an insular or continental shelf to specific sites. They also represent the reproductive potential of the regional population and the primary source of larvae for future generations. Strong site fidelity allows spawning aggregation sites to persist for many years (Olsen and LaPlace 1978; Shapiro et al. 1993; Colin 1996; Luckhurst 1998; Nemeth 2005), but their predictability makes them very vulnerable to over-exploitation once the location is known by fishermen.

Hinds and groupers (Serranidae) form a valuable component of reef fisheries throughout the Caribbean (Thompson and Munro 1978). The red hind, *Epinephelus guttatus*, in particular, contributed 67–99% of the total fin fish catch in the United States Virgin Islands (USVI) between 1987 and 1991 (Cummings et al. 1997) and over 30% of the grouper catch in Bermuda (Luckhurst 1996). *E. guttatus* life history and demographics are relatively well known. Their spawning aggregations have been studied in the USVI (Olsen and LaPlace 1978; Beets and Friedlander 1999; Nemeth 2005; Whiteman et al. 2005; Nemeth et al. 2006), Puerto Rico (Colin et al. 1987; Sadovy et al. 1992, 1994b; Shapiro et al. 1993) and Bermuda (Burnett-Herkes 1975 in Colin et al. 1987; Luckhurst 1998) and have been reported from the British Virgin Islands (Munro and Blok 2003; Eristhee et al., in press) and Jamaica (Munro et al. 1973). *E. guttatus* is a protogynous hermaphrodite, changes sex from female to male at 32–38 cm total length (Sadovy et al. 1992; Nemeth 2005; Whiteman et al. 2005), and reaches maximum length and age at 50–55 cm and 11–22 years (Smith 1971; Olsen and LaPlace 1978; Thompson and Munro 1978; Randall 1983; Colin et al. 1987; Luckhurst et al. 1992; Sadovy et al. 1992). Information on the spatial structure of *E. guttatus* aggregations indicates that they consist of small haremic groups with one male defending three to five females and spawning occurs in pairs 1–2 m above the reef (Shapiro et al. 1993). Sadovy et al. (1994b) found that *E. guttatus* females are determinate spawners and spawn more than once during the course of the annual spawning season. The spawning aggregation can occupy an area from 0.015 to 0.35 km^2 (Shapiro 1987b; Shapiro et al. 1993; Levin and Grimes 2002; Nemeth 2005) and typically occurs on the top of deep coral reef ridges which are located on or near the shelf edge (Colin et al. 1987; Beets and Friedlander 1999; Nemeth 2005). In the USVI *E. guttatus* aggregations form the week before the full moon from December to February. Spawning typically peaks in January and aggregations completely disperse following the January or February full moon (Shapiro et al. 1993; Beets and Friedlander 1999; Nemeth 2005).

Fishing of spawning aggregations can have a wide range of effects on target species and local fisheries. Most severe is the documented collapse of many spawning aggregations (Olsen and LaPlace 1978; Beets and Friedlander 1992; Colin 1992) and the resulting commercial extinction of several important species of groupers throughout the Caribbean (Luckhurst 1996; Huntsman et al. 1999; NMFS 1999). Unregulated fishing on aggregations may have contributed to a 65–95% decline of commercial grouper landings in Puerto Rico and Bermuda, respectively (Sadovy and Figuerola 1992; Sadovy et al. 1992; Luckhurst 1996). Less dramatic, but equally important to reproductive output, are the subtle effects of fishing on spawning aggregations of protogynous species such as decreased average fish size, smaller size at sexual transformation and altered male:female sex ratio (Coleman et al. 1996).

Different management measures have been used to protect spawning aggregations, including seasonal restrictions on catch of spawning species, seasonal area closures and permanent marine fishery reserves. In the Caribbean closures have been implemented to protect spawning aggregations of various groupers and snappers (Sala et al. 2001; Heyman et al. 2005;

Nemeth 2005), but insufficient information on spawning aggregations may actually fail to encompass a spawning site (Eklund et al. 2000) or a protected area may not have the desired effect on the spawning population. For example, a comparative study of two spawning aggregations in the USVI found that 10 years of seasonal protection resulted in significant increases in length and biomass of *E. guttatus* on St Thomas (STT) but little change on St Croix (STX; Nemeth et al. 2006). Although a variety of factors may have influenced these differences, it was found that the STX spawning site was only 600 m from the closure boundary while on STT the closure boundary was over 3 km distant (Nemeth et al. 2006). The close proximity of the spawning aggregation to the closure boundary may not have been sufficient to protect the aggregation from fishing activity on the boundary edge during daily or monthly movements of spawning *E. guttatus*. Lack of important information such as identification of specific spawning location, habitat utilization patterns, migration routes, species- or gender-specific behaviors, or temporal patterns of movement before, during or after spawning are critical to the integrity of a spawning aggregation and its management.

A variety of techniques have been used to study the dynamics and structure of spawning aggregations including ultrasonic telemetry (Zeller 1998, 1999), external tags (Colin 1992; Sadovy et al. 1994b; Nemeth 2005), stereo-videography (Rand et al. 2005) and direct observations (Colin et al. 1987; Shapiro et al. 1993; Sadovy et al. 1994a; Heyman et al. 2005; Nemeth 2005). Understanding the factors influencing timing of migration, functional spawning migration area (i.e., the area from which fish migrate to an aggregation site), and the similarities and differences in residence time and movement patterns among males and females may provide predictable patterns that can be used in the management of this species throughout the Caribbean region. The purpose of this study was to compare and contrast the spatial and temporal patterns of migration and gender-specific movement of two *E. guttatus* spawning aggregations located in STT and STX, USVI.

Materials and methods

Study area and species

The STT and STX *E. guttatus* spawning aggregation sites are separated by 80 km and the 4,000 m deep Virgin Islands trough. The Red Hind Bank spawning aggregation is located along the shelf edge 12 km south of STT (18°12N, 65°00W). The well-developed linear reef is 35–45 m in depth and of high topographic complexity created primarily by large (1–2 m) colonies of *Montastraea franksi*, *Montastraea faveolata* and *Montastraea cavernosa* (Armstrong et al. 2006; Herzlieb et al. 2006). Two deep-water coral ridges 50–100 m wide and 5–20 km long are separated by a deeper 5–100 m wide channel (50 m) composed of sand, patch reef and rubble habitat. The two coral ridges run parallel to the southern edge of the insular platform with the outer ridge immediately adjacent to the drop-off and the inner ridge about 300 m from the drop-off. The northern edge of the inner reef gives way to patch reef habitat which may extend for several kilometers northward. The Red Hind Bank was closed seasonally in December 1990 and established as the permanently closed Red Hind Bank Marine Conservation District (MCD) in December 1999 [Federal Registers 55(213), November 2, 1990 and 64(213), November 4, 1999, respectively].

The Lang Bank spawning aggregation site is located 16 km east of STX (17°49N, 64°27W) on a 30–35-m deep spur and groove reef located several kilometers from the shelf edge. This reef has smaller coral colonies and lower relief than the Red Hind Bank but has a similar composition of coral species (R.S. Nemeth, unpublished data). The spawning aggregation site is located on the tip of a coral spur that projects into a deep-water basin (50–60 m deep) which separates the inner and the outer coral ridges (Nemeth et al. 2006). The Lang Bank seasonal closure was implemented December 1993 [Federal Register, 58(197), October 14, 1993].

Timing of spawning and habitat utilization

The STT site was surveyed December, January and February from 1999 to 2006 and intensively sampled during the 2000, 2001 and 2003 spawning seasons. The STX site was intensively sampled January and February 2004 and January 2005 and surveyed December 2005 to February 2006. The arrival to and departure from the spawning aggregation sites and the area occupied by *E. guttatus* during spawning were determined using scuba surveys, drift fishing and setting fish traps around the aggregation area. Once the approximate center of the spawning aggregation was determined, focused density estimates were conducted at each aggregation site using 30 m× 2 m belt transects. Because of the large size of the STT aggregation three separate diver survey stations were established approximately 200 m apart to measure differences in *E. guttatus* density and size distribution within the spawning aggregation. Fish transects were conducted at all three stations in 2001 and 2003 and thus provided site-specific information. In other years surveys were focused on the eastern end of the reef which had the highest density of *E. guttatus* and was identified as the primary spawning aggregation site. Based on 7 years of underwater visual counts a lunar-based model was developed to predict the arrival and departure and approximate density of *E. guttatus* to spawning aggregations.

A tag-reward program was established using Floy T-bar anchor tags (model # FD–68B) as described in Nemeth (2005). *E. guttatus* on STT and STX were tagged and released at their respective spawning aggregation sites. *E. guttatus* recaptured on the spawning aggregation sites during subsequent sampling provided information on timing and frequency of spawning whereas recaptures by fishermen off the spawning site provided information on distance traveled, potential home sites and functional spawning migration area.

Up to February 2001, gender of *E. guttatus* was determined by squeezing the abdomen of each fish lightly and if eggs or milt emerged the gender was noted before being released. About 5–10% of the fish were successfully sexed using this method. Starting in December 2002 gender of nearly all *E. guttatus* on both islands was determined with ultrasound imaging (Whiteman et al. 2005). In STX the coordinates (latitude and longitude) of trap hauls were recorded on a Garmin 12X GPS and trap catches were separated in tubs of seawater until all fish had been processed. These data provided detailed spatial–temporal patterns of distribution of male and female *E. guttatus* during the week of spawning. Fish which died while sampling in STT were retained to measure body and ovary weight and used to calculate gonado-somatic index (GSI = gonad weight/body weight × 100).

From April 2003 to September 2005 water temperature, current speed and current direction were recorded every 20 min with an Aanderaa data logger (model RCM9) deployed on the STT Red Hind Bank. Temperature gauges on electronic dive computers supplemented temperature data when loggers were not deployed.

Statistical analyses included *t*-test (t), ANOVA (F) and linear and non-linear regression on data which met statistical assumptions (e.g., equal variances and normal distribution). Data which were not normally distributed or had unequal variances were either transformed to meet assumptions of normality or analyzed with non-parametric Mann–Whitney rank sum test (U) or Kruskall–Wallace test (H).

Results

Migration

A total of 2,911 and 934 *E. guttatus* were tagged and released on the spawning aggregations of STT and STX, with 132 (4.5%) and 49 (5.2%) recaptured, respectively (Table 1). About two thirds of tagged *E. guttatus* in both STT and STX were recaptured during spawning on the aggregation site with the remaining being caught by fishermen after spawning and outside the spawning grounds (Table 1). Tag returns by fisherman showed *E. guttatus* migrated from distinct areas of the insular shelf and spread over a functional spawning migration area of ca. 500 km^2 on STT and 90 km^2 on STX (Fig. 1). In both cases the majority of *E. guttatus* were recaptured west of the spawning aggregation sites. *E. guttatus* migrated significantly shorter distances on the STX shelf than *E. guttatus* on STT ($U = 285$, $p < 0.001$, STX: 9.4 km ± 4.25 SD vs. STT: 16.6 km ± 5.74 SD). Migration distances

Table 1 Tagging, survey information and recapture rates for *E. guttatus* from two spawning aggregation sites located at the Marine Conservation District, St Thomas and Lang Bank, St Croix

Field dates	Full moon date	Sampling days (*n*)	Fish transects (*n*)	Number tagged	Recap on spawning sites (%)[b]	Recap off spawning sites (%)[b]	Total recaps *n* (%)
St Thomas							
December 21–22, 1999[a]	22	2	5	109	5 (4.6)	5 (4.6)	10 (9.2)
January 17–21, 2000[a]	20	5	15	510	15 (2.9)	9 (1.8)	24 (4.7)
February 15–19, 2000	19	5	2	5	0	0	0 (0)
Subtotal		12	22	624	20 (3.2)	14 (2.2)	34 (5.4)
December 8–13, 2000	13	5	23	35	13 (37.1)	0	13 (37.1)
January 4–30, 2001[a]	9	14	75	756	28 (3.7)	9 (1.2)	37 (4.9)
February 5–15, 2001[a]	8	9	30	288	3 (1.0)	2 (0.7)	5 (1.7)
Subtotal		28	128	1079	44 (4.1)	11 (1.0)	55 (5.1)
December 9–19, 2002	19	4	28	61	6 (9.8)	5 (8.2)	11 (18.0)
January 13–18, 2003[a]	18	6	42	984	15 (1.5)	15 (1.5)	30 (3.0)
February 11–14, 2003[a]	16	4	29	163	0	2 (1.2)	2 (1.2)
Subtotal		14	99	1208	21 (1.8)	22 (1.8)	43 (3.6)
Total		54	159	2911	85 (2.9)	47 (1.5)	132 (4.5)
St Croix							
January 9–11, 2004[a]	7	3	25	99	13	3	16 (16.2)
February 2–5, 2004[a]	6	4	44	285	5	6	11 (3.9)
Subtotal		7	69	384	18	9	27 (7.0)
January 21–27, 2005[a]	25	7	72	550	13	9	22 (4.0)
Subtotal		7	72	550	13	9	22 (4.0)
Total		14	141	934	31 (3.3)	18 (1.9)	49 (5.2)

[a] Primary spawning months

[b] Recaps on spawning aggregations were caught during subsequent sampling on spawning site whereas recaps off spawning aggregation represent data from tags returned by recreational and commercial fishermen

ranged from 1.8 to 16.1 km on STX to 6.3 to 32.3 km on STT (Fig. 2). No significant differences in migration distance were found between male and female *E. guttatus* on either island (STX: $p > 0.235$; STT: $p > 0.808$). In STX, however, a strong negative relationship was found between migration distance and size of male *E. guttatus* ($r^2 = 0.91$, migration distance = 37.814 - 0.812 × length, $F_{1,3} = 31.3$, $p < 0.01$) but not for females ($r^2 = 0.03$) nor for either sex ($r^2 = 0.04$) on STT (Fig. 3). The relationship between gender and migration distance on STT, however, must be viewed with caution since the MCD is closed to fishing year round and therefore excluded those fish that migrated short distances but remained resident within the MCD boundaries.

Visitation rates and residence times on the spawning aggregation sites were estimated from recapture frequency. In STT 110 (91%) were recaptured once, 8 (7.2%) were recaptured twice and 2 (1.8%) were recaptured three times. Sixteen percent of the recaptured fish on STT were females, 10% were males and, unfortunately, the remaining 74% were of unknown gender. The high percentage of unknown gender resulted because most recaptured fish were tagged prior to the use of ultrasound. The gender of all fish was known on STX at time of tagging due to the use of ultrasound imaging for both spawning seasons. In STX, 47 (96%) were captured once and 1 (4%) was captured twice and 55% were female and 45% were male. Of the tagged *E. guttatus* on STX nine females (64.4%) and seven males (41.2%) were recaptured within 1 week, five females (35.7%) and eight males (47.1%) were recaptured the next month and zero female and two males (11.7%) were recaptured 1 year later. In STT 67% of tagged fish were recaptured on the spawning aggregation site 1 or 2 months after tagging

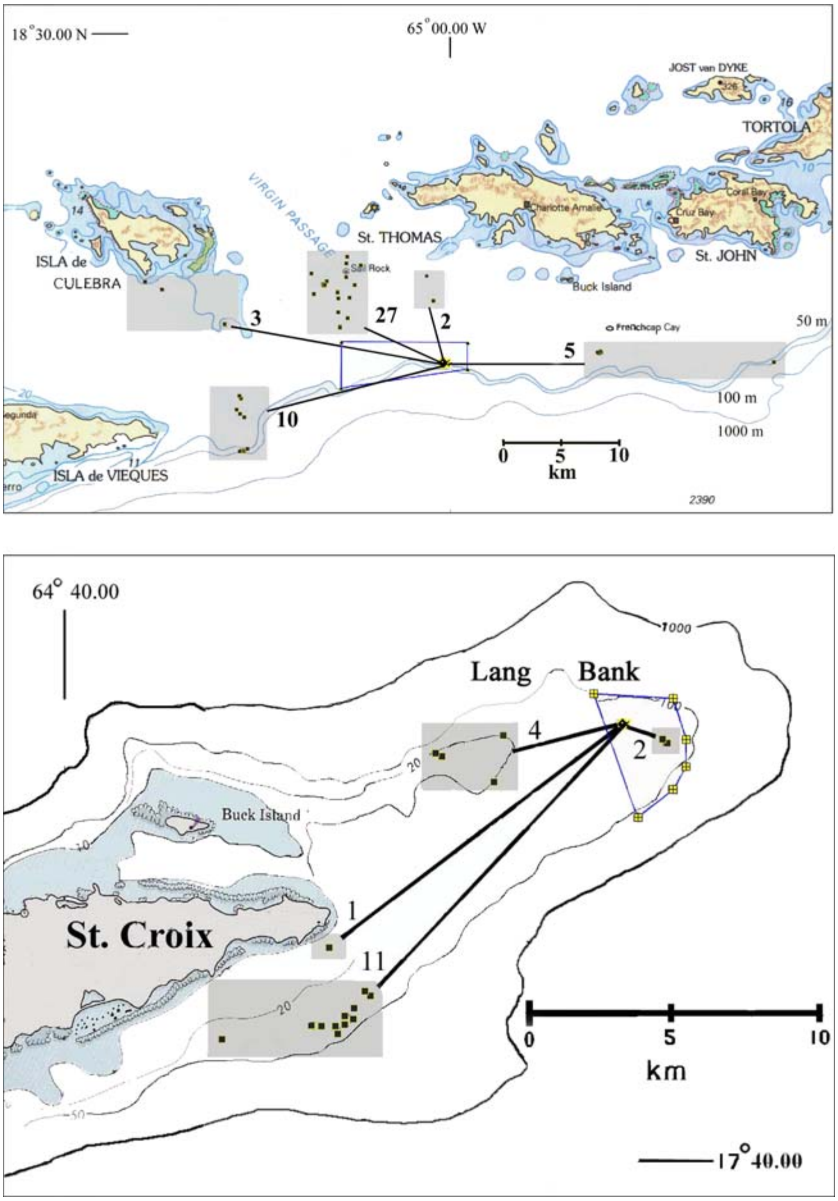

Fig. 1 Recapture locations (*dots* within *shaded areas*) of *E. guttatus* tagged at spawning aggregation sites on St Thomas and St Croix and recaptured by fishermen. Spawning aggregations are located with the two protected areas shown as *polygons* and *numbers* along *radiating lines* indicate total recaptured fish within each *shaded area*

(Fig. 4). In contrast, 94% of tagged fish on STX were recaptured within 1 month with half of the fish recaptured during the same week of tagging (Fig. 4). Average recapture rates for 3 years of sampling in STT varied among the three spawning months. These data (Table 1, last column) were transformed (sqrt $x + 1$) to meet assumptions of normality and analyzed using one-way ANOVA. Overall recapture rates of *E. guttatus* tagged in December (16.6%) were significantly higher ($F_{(2,\,6)} = 10.125$, $p = 0.012$) than fish tagged in either January (4.0%) or February (1.5%) even though the number of fish tagged in December, January and February represented 7.0, 77.3 and 15.7% of total fish tagged, respectively. Recapture rates of *E. guttatus* on the spawning aggregation (Table 1, column 6) were also significantly higher for fish tagged in December of any year ($H = 7.026$, $p = 0.027$).

Habitat use

A total of 493 and 177 fish transects were conducted on the spawning aggregation sites in STT and STX,

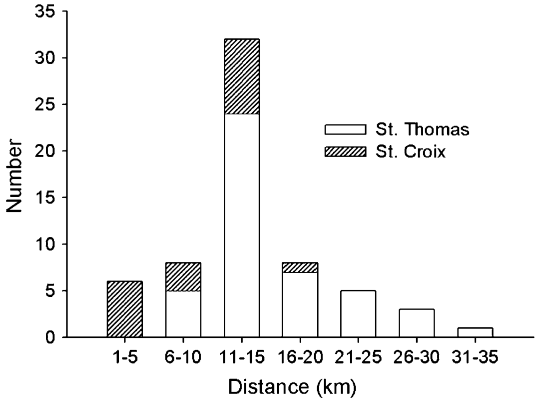

Fig. 2 Migration distance of *E. guttatus* from spawning aggregation sites to recapture location on St Croix and St Thomas, United States Virgin Islands

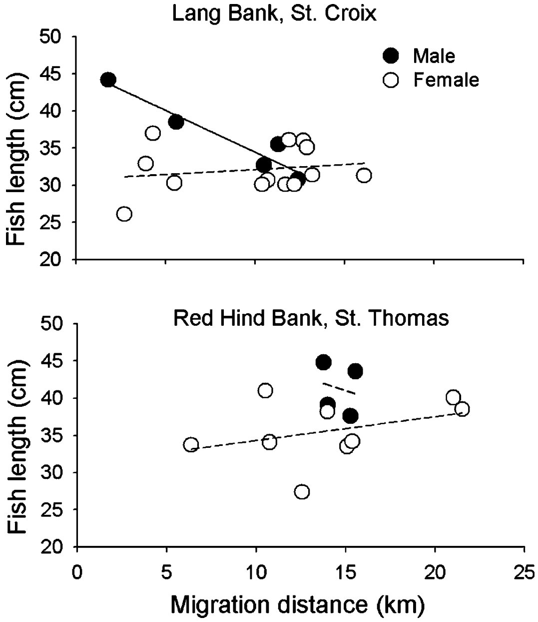

Fig. 3 Relationship between male and female *E. guttatus* length and spawning migration distance on St Croix and St Thomas. Regression of male *E. guttatus* in St Croix was significant ($r^2 = 0.91$, $p < 0.01$)

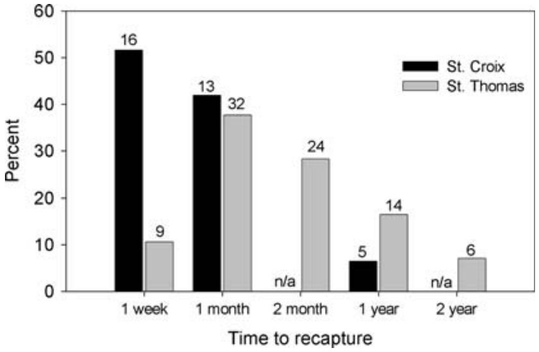

Fig. 4 Time between tagging of *E. guttatus* and recapture on St Thomas and St Croix (STX) spawning aggregations. *Numbers* denote how many fish were recaptured during each time interval. Two-month and two-year time intervals for STX were not applicable (n/a) due to limited sampling

respectively. SCUBA transects from three separate areas of the STT spawning aggregation (eastern and western ends and central section) provided data on small-scale movement (<1 km) patterns of *E. guttatus*. The highest densities occurred in the eastern, upcurrent end of the spawning aggregation ($H = 7.226, p = 0.027$). However, distribution patterns varied among months. *E. guttatus* densities were highest around the western end of the spawning site in December ($H = 29.77, p < 0.001$), early in the spawning season. In January, *E. guttatus* densities were highest in the east ($H = 25.91$, $p < 0.001$) whereas in February, late in the spawning season, fish were evenly distributed among sites ($H = 3.12, p = 0.21$, Fig. 5). No difference in fish size was detected among sites within the STT spawning aggregation ($H = 4.678, p = 0.096$). Fish transects from STX showed *E. guttatus* densities were also significantly higher at the upcurrent end of the reef in January 2005 ($F_{6,\,47} = 5.39$, $p < 0.001$). *E. guttatus* on STT showed a dramatic influx to the primary spawning aggregation site just before the full moon and a rapid exodus immediately following spawning (Fig. 6A). The spawning aggregation on STX showed a similar pattern in 2004 where fish densities were very low right after the January full moon then increased rapidly in the days leading up to the February full moon. In January 2005 the STX spawning aggregation persisted several days after the full moon (Fig. 6A) but during this year the aggregation did not reform in February 2005.

Approximately 5–20% of the fish remained on the aggregation site between the January and February spawning peak. These fish were significantly larger (Fig. 6B) than the mean size of the spawning population on both islands (STT: between spawning peaks: 42.1 cm ± 1.02 SD vs. during spawning: 38.3 cm ± 3.90 SD, $t = 11.2$, $p < 0.001$; STX: between spawning peaks:

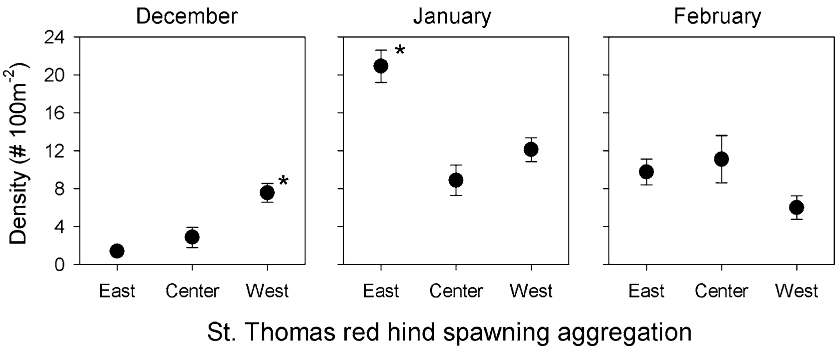

Fig. 5 *E. guttatus* density from visual fish transects at three locations within St Thomas spawning aggregation site during the 2002–2003 spawning season. *Asterisk* indicates significant differences among locations

35.4 cm ± 1.09 SD vs. during spawning: 31.9 cm ± 0.81 SD, $t = 5.5$, $p < 0.001$). While gender information was not available for STT during this period, in STX female to male sex ratios for January 2004 were 0.87:1.0, 3 and 4 days after the full moon. This indicates that, at least on STX, the largest males and females of the spawning population remained on site between full moon spawning peaks. Daily variation in sex ratios also showed a consistent pattern between the two spawning aggregation sites and between years and months. Four to five days before the full moon females were more abundant than males at the spawning aggregation site and surrounding reef

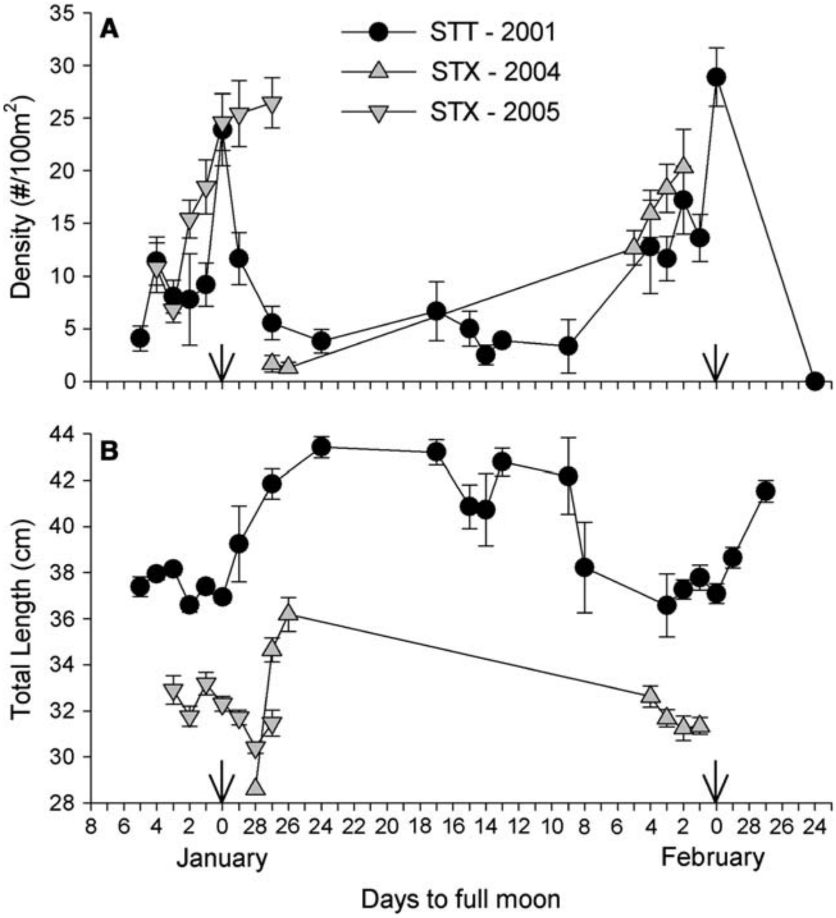

Fig. 6 Variation in density (**A**) and total length (**B**) over time of *E. guttatus* on St Thomas and St Croix spawning aggregations during full moon periods (*arrows*) in January and February

areas (Fig. 7). Two to three days before the full moon and up to the day of apparent spawning the sex ratio tended toward unity or became dominated by males (Fig. 7). Following spawning the female to male ratio increased again over 2 days before declining after the full moon. In STT a significant decline in the GSI of females ($T = 6.03$, $df = 77$, $p \leq 0.001$) and males ($T = 15.8$, $df = 7$, $p \leq 0.001$) corresponded to a rapid decline in female to male sex ratios, both of which occurred January 15, 2003, 3 days before the full moon (Fig. 7).

In January 2005, 10–20 traps were hauled each day for seven consecutive days around the Lang Bank STX spawning aggregations site. Catches averaged 4.7 ± 4.27 SD *E. guttatus* per trap ($n = 140$ trap sets). Catch data were analyzed spatially for most of the traps which were set across 3 km of reef. During the course of trap fishing, catch rates of *E. guttatus* from outlying traps declined to zero so these traps were moved closer to the spawning aggregation site where catch rates were increasing. Four days before the January 2005 full moon, trap catches of *E. guttatus* declined slightly from 3.3 to 2.5 fish per trap even though outlying traps were moved closer to the spawning aggregation. *E. guttatus* catch rates reached a maximum of 7.1 per trap on the full moon then declined to 2.7 per trap 2 days later (Fig. 8).

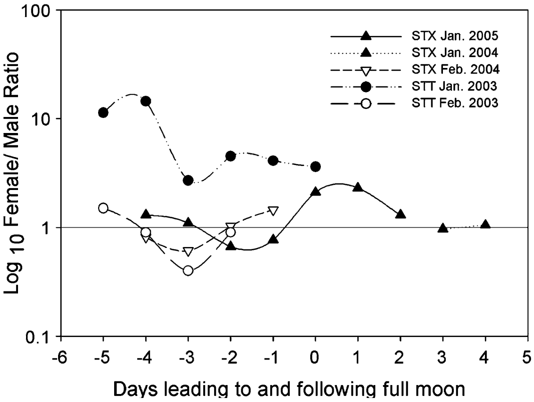

Fig. 7 Change in *E. guttatus* sex ratios ($\log_{10}$) on the St Thomas and St Croix spawning aggregations before and after the January and February full moon. *Horizontal line* indicates unity of sex

Epinephelus guttatus on STX showed distinct spatial distribution patterns around the spawning aggregation site and fluctuations in sex ratio were influenced by gender-specific movements. On January 21 and 22, 2005 (i.e., 4 and 3 days before the full moon) trap catches were dominated by males in an area of reef 50–200 m west of the spawning site (Fig. 8). One hundred and fifty meters east and west of this male-dominated area, trap catches were mostly females, while in between, catches were composed of equal proportions of males and females. On January 23, 2 days before the full moon distinct groups of males were caught at the primary spawning site and east and west along the reef edge. Over the next 3 days trap catch rates more than doubled and many traps around the spawning site contained mostly female *E. guttatus*, particularly on January 25, the day of the full moon (Fig. 8). The increase in female catch rate also corresponded to an increase in density of *E. guttatus* at the spawning aggregations site (Fig. 6A). These data suggest that female *E. guttatus* converge rapidly on the spawning site which helps to explain the fluctuating sex ratios observed at the STX and STT spawning aggregations (Fig. 7).

Timing of spawning aggregations

Diver surveys showed the timing of *E. guttatus* spawning aggregations formed either in December and January, January and February or occasionally only in January. By examining the timing of the January full moon relative to the beginning of the new year or the number of days from the winter solstice, which usually occurs on December 21 or 22, the timing of future *E. guttatus* spawning aggregations in the USVI were predicted (Table 2). When the full moon occurs from January 1 to 11 (10–20 days after the winter solstice) then the primary spawning months are January and February. When the full moon occurs between January 21 and 31 (30–40 days after the winter solstice) the primary spawning aggregation months are December and January. When the full moon occurs mid January (ca. 20–30 days after the winter solstice) *E. guttatus* spawning aggregations form primarily

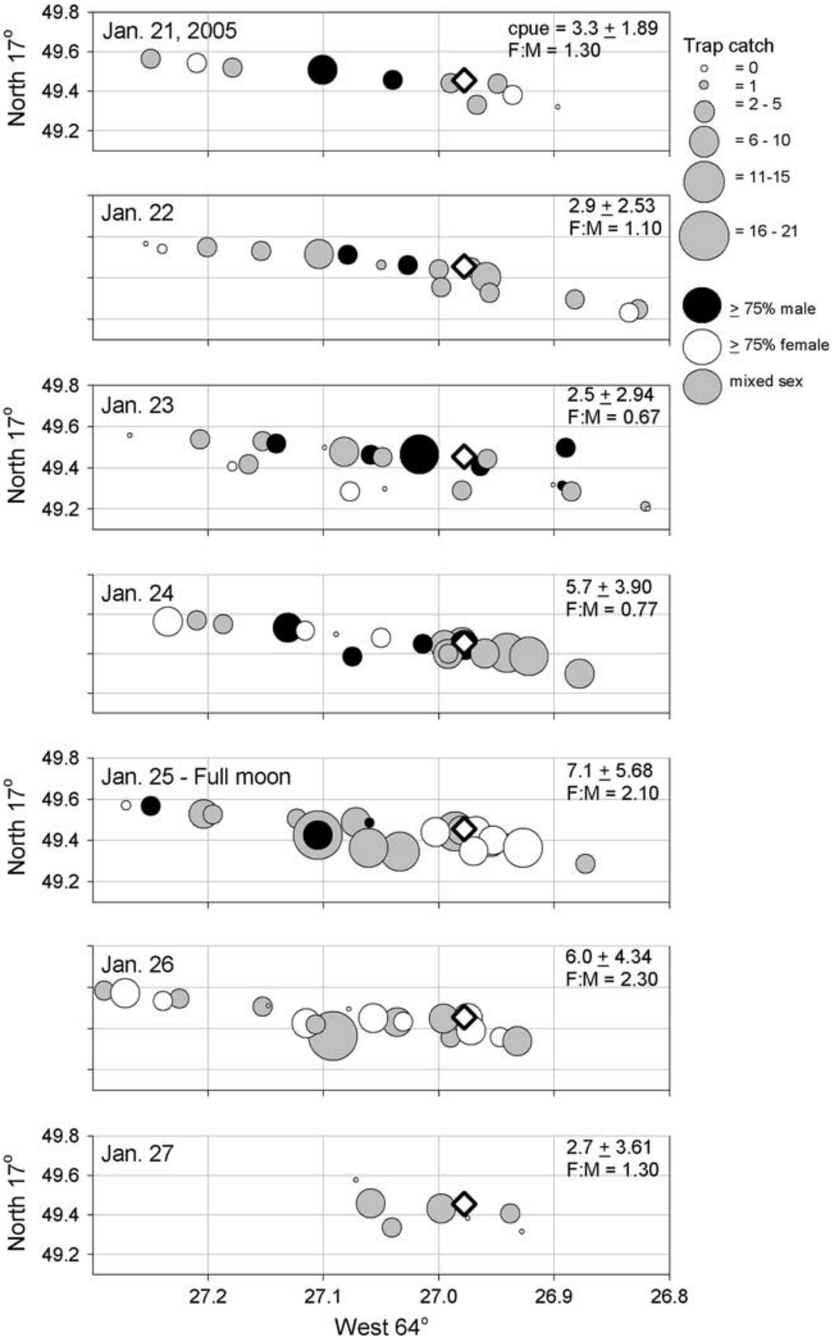

Fig. 8 *E. guttatus* trap catches and ratio of male (*M*, *black*) and female (*F*, *white*) or mixed gender (*gray*) on St Croix in 2005 relative to location of primary spawning site (*diamond*) and North latitude and West longitude coordinates. cpue = no. *E. guttatus* per trap ± SD

in January but this may vary among sites. For instance, during the 2005–2006 spawning season the full moon occurred January 13, 24 days after winter solstice. *E. guttatus* departed the STX aggregation after January whereas some fish remained on the STT spawning aggregation site during the February full moon (Fig. 9). Non-linear regression was used develop a Gaussian three parameter equation to model the average density of *E. guttatus* during the spawning season using data from STT and STX from 1999 to 2006. The number of days from each winter solstice to the December, January and February full moons accounted for 92% of the variation in

Table 2 Dates of December, January and February full moons and actual and predicted (shaded italics) timing of spawning aggregations from 1999 to 2010 in the Virgin Islands

Year	December full moon	January full moon	February full moon	Days from winter solstice to Jan full moon	Actual and *predicted* peak spawning months
1999–2000	22	21	20	30	December–January
2000–2001	11	9	8	19	January–February
2001–2002	30	28	27	38	December–January
2002–2003	19	18	17	27	January
2003–2004	8	7	6	16	January–February
2004–2005	26	25	24	35	December–January
2005–2006	15	13	13	24	January*
2006–2007	5	3	2	12	*January–February*
2007–2008	24	22	21	31	*December–January*
2008–2009	12	11	10	21	*January–February*
2009–2010	31	30	29	40	*December–January*

* Varied among sites

density of *E. guttatus* spawning aggregations (Fig. 9). The optimum spawning period for *E. guttatus* during any year was 20–40 days after the winter solstice.

Oceanographic parameters

Temperature profiles during two spawning seasons on STT showed that mean monthly temperatures decreased rapidly from October through February before beginning to warm again from March through August (Fig. 10). Spawning in STT occurred during periods of declining water temperature and slacking currents between the winter solstice (i.e., after December 20) and about February 20. At 40 m depth seawater temperature and current speed during spawning typically averaged 26–27.5°C and 2.5–3.5 cm s^{-1} (Figs. 10, 11). The full moon was associated with decreased water temperature and current speed relative to other lunar periods (e.g., quarter moons). Current speeds during the week of spawning in January and February 2004 ranged from 2.6 to 3.8 and 2.2 to 3.3 cm s^{-1}, respectively (Fig. 11). Current direction at 40 m depth was southerly (mean = 181°, range = 156°–230°) during the spawning season. Significant changes in water temperature, current speed and direction over the spawning season resulted from the strong interaction between month and lunar cycle (two-way ANOVA for water temperature: $F_{12,\,129} = 20.05$, $p < 0.001$, current speed: $F_{12,\,129} = 4.22$, $p < 0.001$, current direction: $F_{12,\,129} = 2.59$, $p < 0.004$).

Discussion

Patterns of migration, movement and timing of the STT and STX *E. guttatus* spawning aggregations showed remarkable similarities at various spatial and temporal scales despite differences in population structure (Nemeth et al. 2006). At the largest spatial and temporal scales *E. guttatus* generally migrated eastward and spawning aggregations formed on the upcurrent edge of shelf-edge reefs, a pattern consistent with *E. guttatus* in Bermuda (Luckhurst 1998) and Nassau grouper, *Epinephelus striatus*, in the Cayman Islands (Colin et al. 1987). The timing of migration and arrival of *E. guttatus* to the spawning aggregation sites were synchronized with changes in the lunar and solar cycles and seasonal declines in seawater temperatures and current speeds. Spawning of *E. guttatus* in the USVI was restricted to brief periods between the winter solstice in December when the photoperiod begins to increase and the end of February when annual seawater temperature and current speed reach their minimum. Reproductive activity around the full moon corresponded to rapid declines in seawater temperature and current speed relative to other lunar phases (e.g., quarter moons) within each month. Spawning of *E. guttatus* in STT typically occurred during a relatively narrow range of temperature (26–27.5°C) and current speed (2.5–3.5 cm s^{-1}), although Shapiro et al. (1993) found current velocities during spawning fluctuated from 6.0 to 13.6 cm s^{-1} in Puerto Rico. At higher latitudes (e.g., Bermuda) *E. guttatus* aggregate from May

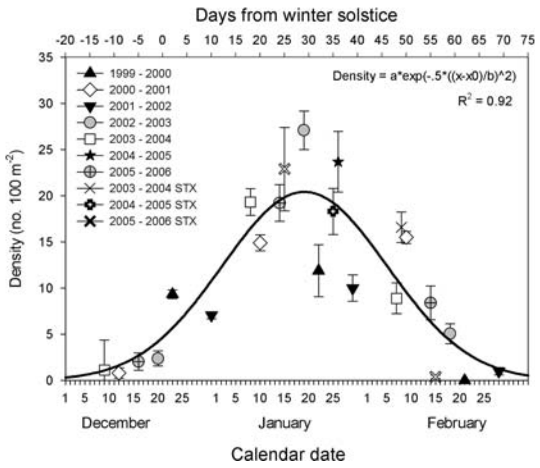

Fig. 9 *E. guttatus* density (± SE) on St Thomas and St Croix spawning aggregations during seven and three consecutive spawning seasons, respectively. Line fitted with Gaussian equation to estimate density of *E. guttatus* on spawning aggregation where x = number of days from winter solstice to January full moon, a = 20.42, b = 16.95 and x_0 = 29.13. $p < 0.001$

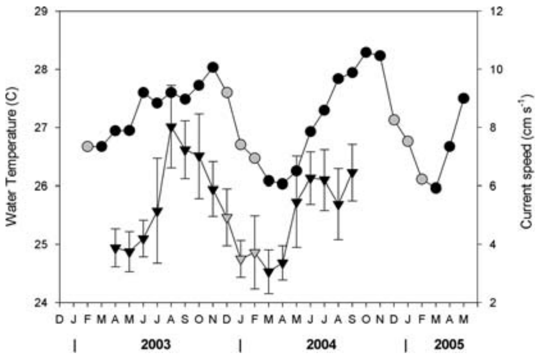

Fig. 10 Monthly seawater temperature (*filled circle*) and current speed (*filled downward triangle*) for the St Thomas *E. guttatus* spawning site from December 2003 to May 2005. *Gray* symbols highlight the primary spawning months of December, January and February

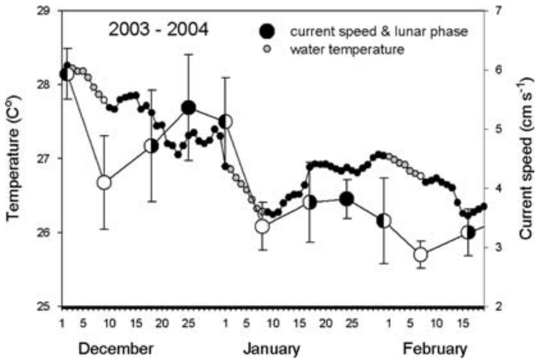

Fig. 11 Daily seawater temperature (*small filled circle* with potential spawning periods shown in *gray* and date of full moon in *white*), and average current speed ± SD (*large open circle*) for 7-day periods of lunar cycle (full moon = *open circle*, new moon = *filled*, quarter moons = *half filled*). Average current speed is calculated from the 7 days preceding each lunar symbol

to July with peak spawning in June (Munro et al. 1973; Burnett-Herkes 1975; Colin et al. 1987; Luckhurst 1998). In Bermuda *E. guttatus* formed spawning aggregations when water temperature warmed up to approximately 25°C (Luckhurst 1998). In the Bahamas and Belize *E. striatus* spawn between 25 and 26°C during periods of gradually decreasing water temperatures (Carter 1987; Colin 1992). This suggests the appropriate seawater temperature range for reproduction of Caribbean epinephelid groupers is between 25 and 27°C. Further study is needed to determine whether these physical oceanographic features synchronize the behavior, movement and timing of migration of the adult spawning population (e.g., hormonal changes and gonad development), synchronize timing of spawning to enhance fertilization success, increase egg and larval growth and survival and/or optimize retention or dispersal of larvae.

In both STT and STX *E. guttatus* synchronized spawning activity with the full moon which is consistent with earlier studies in STT (Beets and Freidlander 1999) and western Puerto Rico (Colin et al. 1987; Shapiro et al. 1993) and is similar to half-moon grouper, *Epinephelus rivulatus*, of western Australia (Mackie 2000), camouflage grouper, *Epinephelus polyphekadion*, of Micronesia (Rhodes and Sadovy 2002) and other epinepheline fishes in the Indo-Pacific (Randall and Brock 1960). The magnitude of spawning activity during each full moon period, measured as average density of *E. guttatus*, was largely determined by the timing of the full moon relative to the winter solstice. Spawning density of *E. guttatus* over seven seasons provided a broad temporal view of aggregation formation and allowed us to predict future timing. The optimum spawning period was about 20–40 days after the winter solstice (i.e., from about January 10 to 30) when *E. guttatus* densities reached their maximum. If the January full moon occurred before or after this period then January fish densities declined while February and December densities increased, respectively. The consistency in timing of arrival and departure of *E. guttatus* to its spawning aggregation sites allowed us to test our prediction at several sites during the 2005–2006 spawning season. Since the January 2006 full moon occurred on the 13th of the month (24 days after the winter solstice), we predicted that *E. guttatus* would depart the STX and STT spawning sites after the January 2006 full moon. This prediction held true for STX as well as another *E. guttatus* spawning site on Saba, Netherlands Antilles (R.S. Nemeth, unpublished data). However, some *E. guttatus* remained on the STT spawning aggregation site during the February 2006 full moon. Deviation from the predicted pattern could have resulted from the large spawning population in STT which was estimated to contain ca. 80,000 fish (Nemeth 2005) whereas STX and Saba spawning populations were estimated to contain ca. 3,000 and 10,000 *E. guttatus*, respectively. The large spawning population on STT may necessitate some fish to remain at the spawning aggregation during suboptimal months due to increased competition for spawning sites during the January spawning period. Synchronized timing with the full moon and day-length cycles suggest that cues for initiating and terminating reproduction for *E. guttatus* are operating at spatial scales of at least 100 km.

At spatial scales of 1–20 km, differences and similarities between the STT and STX spawning aggregations were found. *E. guttatus* in STX had a smaller functional spawning migration area and traveled shorter distances to the spawning site than on STT. Swim speeds of 3 km day^{-1} over 20 km by *E. guttatus* in Burmuda (Luckhurst 1998) showed that they can cover relatively large distances in short periods of time to reach spawning aggregation sites. The smaller area of the STX shelf (ca. 650 km^2) relative to shelf around Puerto Rico and STT (ca. 18,000 km^2) and the smaller size of *E. guttatus* in STX vs. STT (mean: 32.5 cm vs. 38.5 cm total length, Nemeth et al. 2006), most likely account for differences in functional spawning migration area and migration distance. Other tagging studies have shown considerable variation in migration distance among species relative to fish length and shelf area. *E. guttatus* migration ranged from 5 to 20 km (mean: 8.9 km) in Bermuda which has a shelf area of ca. 1,000 km^2 and average fish length of 42.9 cm (Luckhurst 1998) to 18 km in southern Puerto Rico where fish averaged 27 cm in length (Sadovy et al. 1994b). Red grouper, *Epinephelus morio*, have been tracked from 29 to 72 km and Nassau, *E. striatus*, 60 cm mean length, from 100 to 240 km (Colin 1992; Carter et al. 1994 and Moe 1969 in Sadovy 1994; Bolden 2000). Using ultrasonic telemetry, Zeller (1998) tracked 44–58 cm *Plectropomus leopardus* from 1 to 11 km from home ranges to spawning sites and calculated a functional spawning migration area of ca. 80 km^2.

At spatial scales of less than 1 km *E. guttatus* showed daily fluctuations of sex ratios around the full moon most likely associated with reproductive activity of females and males during the course of an aggregation (Olsen and LaPlace 1978; Sadovy et al. 1994b; Beets and Friedlander 1999). Trap catch data from STX showed that females occupied outlying areas while males preceded to the aggregation site apparently to establish territories (Colin et al. 1987). This is typical of males of haremic spawners such as *Plectropomus areolatus* in the Indo-Pacific (Johannes 1988), *P. leopardus* on the Great Barrier Reef (Samoilys 1997) and *E. polyphekadion* whose males arrive to the spawning site 7–10 days prior to females (Rhodes and Sadovy 2002). In STT, a large influx of males 3 days before the full moon in January 2003 corresponded to a decline in female and male GSI and was indicative of spawning (Sadovy et al. 1994b; Beets and Friedlander 1999).

Rapid changes in sex ratios may also reflect the short-term small-scale movements of females for brief spawning episodes (Sadovy et al. 1994b; Rhodes and Sadovy 2002) during the course of the annual spawning season. Recapture rates of tagged *E. guttatus* indicate turnover rates were higher for females than males since only 22% of the recaptured females returned for a second month in one season whereas 50% of recaptured males returned for the second month. Acoustic tracking of *P. leopardus* at spawning aggregation sites showed residence times averaged 13 days for males while females undertook only one trip over the 2-month spawning period and stayed 1.5 days (Zeller 1998). These gender-based movement patterns most likely play an important role in grouper reproductive dynamics and should be factored into future studies as well as management decisions.

After spawning, the majority of *E. guttatus* dispersed quickly, but 5–20% of *E. guttatus* remained on STT and STX spawning aggregation sites between monthly spawning peaks. These fish were significantly larger and, at least on STX, were composed of equal numbers of large males and females. Why do only the largest females remain while smaller females depart the aggregation site? Perhaps only the largest females possess enough eggs to spawn two consecutive months. Alternatively these inter-spawning periods may allow the largest females an opportunity to assess the relative proportion of dominant males within the population or these large females may already be initiating sex change and are starting to express male behavioral traits (Levin and Grimes 2002). Little is known about what initiates sex change in serranids or if females can evaluate the advantages of changing sex at any particular point in time. It has been suggested that spawning aggregations may be the only opportunity for female *E. guttatus* to evaluate the number or size of males in the population since males and females may be segregated after the spawning season (Shapiro 1987b; Sadovy et al. 1994b; Coleman et al. 1996). If sex change in *E. guttatus* is size dependent and behaviorally mediated as in some scarids and labrids (Shapiro 1980, 1987a; Warner and Swearer 1991), then the rate of female sex change should increase when the proportion of large males is low and their ability to exert sufficient aggressive control of large females is minimal (Vincent and Sadovy 1998).

Summary/conclusion

The similarities in timing, movement and migration of the two *E. guttatus* spawning populations of STT and STX were striking despite large differences in the size and sex structure (Nemeth et al. 2006). Predictability of grouper spawning aggregations and behavior has been exploited by fisherman for centuries (Colin 1992) and has intensified during the past 30 years due to advances in fishing technology. While many fisherman acknowledge the short-term gains and the devastating effects of intensive aggregation fishing, some suggest that a limited harvest would be acceptable (Pickert et al. 2006). Recent evidence, however, shows that spawning aggregations may exhibit hyperstability, a situation where catch per unit effort of the aggregation is relatively stable over many years while abundance of fish within the aggregation declines to critical levels and possible collapse (Sadovy and Domeier 2005). If fishing is allowed on spawning aggregations, even on a limited basis, there are also subtle negative effects such as size and sex-selective fishing (Gilmore and Jones 1992; Zeller 1998; Nemeth 2005). Behaviorally dominant males may experience higher fishing mortality rates which alters sex ratios of the spawning population (Coleman et al. 1996) and disrupts the socially mediated system of sex change such that reproductive success of protogynous species declines (Bannerot et al. 1987; Nemeth 2005). The inability of groupers to rapidly compensate for skewed protogynous sex ratios could result in reduced fertilization rates or sperm limitation (Sadovy et al. 1994b) or disruption of the complex social organization required for courtship resulting in some females going unspawned (Coleman et al. 1996, 1999; Vincent and Sadovy 1998; Levin and Grimes 2002). This study showed *E. guttatus* departed spawning aggregation sites for several weeks before returning for a second month. Conservation of *E. guttatus* spawning aggregations requires closure boundaries sufficiently large for the duration of the spawning season to protect the spawning population. Since fishermen often concentrate their effort along these boundaries, insufficient buffer zones around a spawning aggregation may actually intensify fishing mortality as fish cross over boundaries during the spawning season. Predictability of grouper spawning behavior has important implications for their management and this knowledge must be utilized by fisheries managers. The timing of spawning migrations, site fidelity of spawning aggregations, and gender-based distribution and movement patterns observed during and after spawning may be used to guide the timing and boundaries of area closures (either seasonal or permanent) where fishing is prohibited within a designated area, or market closures which prohibit the capture, possession or sale of a protected species during its spawning season. The predictability of *E. guttatus* spawning aggregations can also benefit the allocation of limited resources for directing enforcement activities during critical time periods and improving the efficiency of research and monitoring programs. From a management perspective maintaining as many spawning aggregations as possible will maximize the reproductive output and subsequent recruitment of a species (Levin and Grimes 2002) and will increase the likelihood of sustaining regional fish populations and improving local fisheries.

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