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REPORT

Temporal patterns and behavioral characteristics of aggregation formation and spawning in the Bermuda chub (*Kyphosus sectatrix*)

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Abstract Reef fish spawning aggregations are important life history events that occur at specific times and locations and represent the primary mode of reproduction for many species. This paper provides detailed descriptions of aggregation formation and mass spawning of the Bermuda chub (*Kyphosus sectatrix*). Spawning coloration and gamete release of *K. sectatrix* were observed and filmed at the Grammanik Bank, a deep spawning aggregation site used by many different species located on the southern edge of the Puerto Rican shelf 10 km south of St. Thomas, US Virgin Islands. Underwater visual surveys using technical Nitrox and closed circuit re-breathers were conducted from December 2002 to March 2013 and documented spatial and temporal patterns of movement and aggregation formation along 1.5 km of mesophotic reef. The largest aggregations of *K. sectatrix* (>200 fish) were observed on the Grammanik Bank January to March from 0 to 11 d after the full moon with peak abundance from 60 to 80 d after the winter solstice across all survey years. Aggregation formation of *K. sectatrix* coincided with the spawning season of Nassau (*Epinephelus striatus*) and yellowfin (*Mycteroperca venenosa*) groupers. These spatial and temporal patterns of aggregation formation and spawning suggest that *K. sectatrix*, an herbivore, may also be a transient aggregating species. On several occasions, chubs were observed both pair spawning and mass spawning. Color patterns and behaviors associated with aggregation and spawning are described and compared to spawning characteristics observed in other species, many of which are similar but others that appear unique to *K. sectatrix*. This represents the first report of a kyphosid species aggregating to spawn and illuminates a portion of the poorly understood life history of the Bermuda chub.

Keywords Reef fish spawning aggregation · Virgin Islands · Eastern Caribbean · Spawning site characteristics · Kyphosidae

Introduction

Approximately 85 species of reef fish are known to form spawning aggregations in tropical oceans of the world with another 82 species suspected of spawning in aggregations (see Appendix 1 in Sadovy de Mitcheson and Colin 2012). In total, these 167 species are represented in 20 fish families and include diverse species from all trophic groups including predators (e.g., Epinephelidae, Lutjanidae), herbivores (Acanthuridae, Scaridae), planktivores (Caesionidae), invertivores (Labridae, Sparidae, Haemulidae), spongivores (Pomacanthidae), corallivores (Chaetodontidae), and detritivores (Mullidae). Reef fish spawning aggregations are typically categorized as resident or transient. Resident spawning aggregations form when individuals move relatively short distances from feeding sites, often staying within their home range, and aggregate to spawn on a daily basis over a lengthy reproductive season (Nemeth 2009). Transient aggregations form when individuals migrate days to weeks over tens to hundreds of kilometers to a discrete site that is generally at the edge of an insular or continental shelf, or in or near a reef channel. Transient species typically aggregate from 1 to 3 months

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during very specific seasons and lunar periods, and these occasions often represent the total annual reproductive effort of the participants (Domeier and Colin 1997).

Many transient aggregation sites host multiple species of fish that may or may not be separated by time or microhabitat (Heyman and Kjerfve 2008). For example, predictable suites of species co-occur at spawning aggregations. Some of these species groups include yellowfin (*Mycteroperca venenosa*), Nassau (*Epinephelus striatus*), and tiger (*Mycteroperca tigris*) groupers in the Caribbean (Nemeth et al. 2006; Heyman and Kjerfve 2008) and camouflage (*Epinephelus polyphekadion*), brown-marbled (*Epinephelus fuscoguttatus*), and square-tailed (*Plectropomus areolatus*) groupers in the Pacific and Indian Oceans (Johannes et al. 1999; Rhodes and Sadovy 2002; Robinson et al. 2008). Whether physical or hydrological properties of the multi-species spawning sites are advantageous for successful reproduction (Colin 1992; Cherubin et al. 2011; Kobara and Heyman 2008; Nemeth et al. 2008) or the sites represent areas that are merely cues for synchrony, these multi-species fish aggregating areas are not uncommon and have been reported throughout tropical oceans of the world (Johannes et al. 1999; Heyman and Kjerfve 2008; Robinson et al. 2008).

Although published accounts of spawning aggregations have been increasing, there remains a lack of information on the reproductive biology and behavior of many fish species. One family of fishes for which the reproductive biology remains poorly described is Kyphosidae, and, in fact, little is known of the general life histories for most of the 12 species that comprise the genus *Kyphosus*. Rhodes (2003) reported yearlong spawning of *Kyphosus bigibbus*, *K. cinerascens*, and *K. vaigiensis* in the western Pacific on an outer reef slope off Pohnpei, Micronesia, and Yamaguchi et al. (2011) reported *K. bigibbus* were reproductively active only during June through October off the reefs of Kyushu, Japan. These reports were based on indirect methods (the collection of gravid females) but direct observations of spawning or spawning aggregations have not been published for any species in the family. Here, we present the first description of the temporal and behavioral patterns of reproduction of *Kyphosus sectatrix* in the western Atlantic and compare and contrast these data with other species known to form spawning aggregations.

Methods

Study site

The Grammanik Bank is a multi-species spawning aggregation site located on the Puerto Rican shelf edge, 15 km south of St. Thomas in the US Virgin Islands (Fig. 1). Nassau grouper (*E. striatus*), yellowfin grouper (*M. venenosa*), tiger grouper (*M. tigris*), yellowmouth grouper (*Mycteroperca interstitialis*), dog snapper (*Lutjanus jocu*), and cubera snapper (*Lutjanus cyanopterus*) have been documented aggregating to spawn on the site (Kadison et al. 2006; Nemeth et al. 2006). The top of the bank is approximately 29–42 m deep, with high coral cover that is predominantly *Montastraea* spp. (Herzlieb et al. 2006; Smith et al. 2008). The western end of the Grammanik Bank becomes slightly shallower and transitions to a hard-bottom benthic habitat sparsely colonized with *Montastraea* spp. corals. Groupers and snappers are observed in elevated numbers along the entire length of linear 1.2 km reef from morning through early afternoon during the spawning season. In the late afternoon, movement is to the west and formation of large aggregations and spawning of most species occur at a core spawning site, located on the southern edge of the west end of the bank (Nemeth et al. 2006). At this particular location, the reef bank forms a depression or saddle (40 m depth) that is 5–10 m deeper than the reef bank to the east and west (Fig. 1). This sparsely colonized hard-bottom saddle provides a corridor between the shelf edge to the south and well-developed reefs and deep sand channels to the north. Physical oceanographic data were collected with a Seabird CTD deployed on the seaward edge of the shelf drop-off at the core spawning site and with a Nortek Acoustic Doppler Current Profiler (ADCP) moored in 45 m of water at the core spawning site.

Species

Two species of Kyphosidae occur in the Caribbean: the Bermuda chub, *K. sectatrix* (Linnaeus), and the yellow chub, *Kyphosus incisor* (Cuvier). These species are indistinguishable in the field, but can be easily identified by dorsal and anal soft ray counts, and number of gill rakers. Two chubs (45.0 and 43.8 cm TL) that were part of a large aggregation were speared on the Grammanik Bank on March 15, 2012, and species identification to *K. sectatrix* was confirmed (Moore 1962). *K. sectatrix* is a relatively common species that occurs throughout the western Atlantic from Massachusetts south to Brazil, including the Gulf of Mexico and Caribbean Sea (Humann and DeLoach 2002). It is much less common in the eastern Atlantic south of Morocco to the Gulf of Guinea and Angola (Desoutter 1990) and though it does occur, is extremely rare in the Mediterranean (Tortonese 1986; Merella et al. 1998). Bermuda chubs are active diurnally and are typically seen swimming as individuals or small groups near rocky reefs from 5 to 25 m deep (Randall 1967; Humann and DeLoach 2002). Adults are primarily if not exclusively herbivores, with morphological and physiological adaptations for algae consumption such as fermentation in the gut (Clements and Choat 1997). Eristhee and Oxenford (2001) found adult *K. sectatrix* migrated daily across coral reef areas of Barbados during feeding episodes

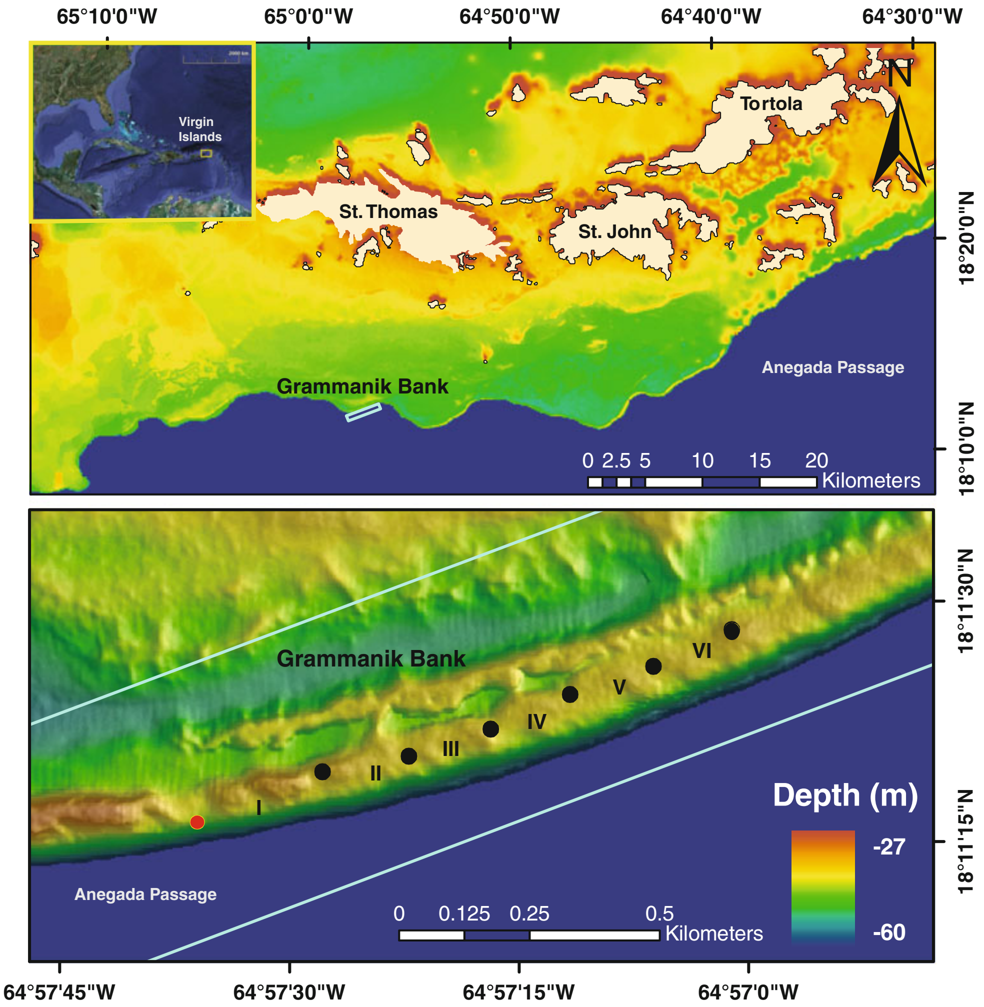

Fig. 1 Map of the Caribbean region (*inset*) and Grammanik Bank located along the southern edge of the Puerto Rican shelf south of St. Thomas, US Virgin Islands (*upper panel*). A color-coded bathymetric relief map of the western half of the Grammanik Bank protected area shows the location of six scooter segments (*I* to *VI*) and marker buoys (*black dots*) and location of Acoustic Doppler Current Profiler (ADCP) marking the beginning of segment I (*red dot*) and approximate location of the spawning aggregation site. Note the relatively deeper saddle at ADCP location

with home ranges from 1.5 to 5.2 km^2. They were commonly observed in foraging schools of up to 70 fish that split into very small schools or individuals at night. Due to their relative size, with adults commonly 50 cm TL or larger (Bauchot 1987), and abundance on Caribbean and Pacific reefs, herbivory by chubs plays an important role in the benthic dynamics of coral reef ecosystems (Downie et al. 2013; Michael et al. 2013).

Large numbers of juvenile sea chubs have been collected offshore in the Atlantic, drifting under floating mats of sargassum algae (Moore 1962; Bohlke and Chaplin 1968). Unlike juveniles of Pacific kyphosids, *K. incisor* collected off South America had a more omnivorous diet of zooplankton (mainly copepods) as well as phytoplankton, then switched to a strictly herbaceous diet at around 160 mm (Silvano and Güth 2006).

Aggregating and spawning

Data on the abundance of *K. sectatrix* at the Grammanik Bank were collected opportunistically from December 2002 to March 2013. Focused surveys for aggregating species were conducted on technical NITROX or Megalodon closed circuit re-breathers (Innerspace Corp.) from the full moon to 10 d after full moon (dafm) in February, March, and April each year from 2003 to 2012. These lunar dates corresponded to the arrival and departure of *E. striatus* and *M. venenosa* during their spawning season. Occasional dives were made before and after this 10 d lunar period (17 %) and in other months throughout the year (33 %).

Underwater visual surveys were conducted at all times of the day ranging from 09:15 to 18:25 hrs using a variety of techniques including underwater scooter surveys (2003–2008), fixed belt transects (2008–2012), roving dives and unrestricted point counts. For scooter surveys, the western half of the Grammanik Bank was divided into six 150 m segments marked with polystyrene floats tied 5 m above the bottom. The first segment (I) was on the western end of the Grammanik Bank and included the FSA site, and the last segment (VI) was 900 m to the east (Fig. 1). One diver would count all target species from the line of floats 30 m to the south, and the other diver conducted counts up to 30 m north of the floats. Therefore, the north and south halves of each segment represented a belt transect approximately 150 m long and 30 m wide. The coral cover to the south declined rapidly at the edge of the drop-off and the reef to the north ended abruptly at a deep water sand channel, thus providing natural boundaries for scooter surveys. Scooter surveys were terminated in 2008 when it was observed that noise from the scooter motor disrupted aggregation formation of *L. cyanopterus* and possibly other species (RSN pers obs). In 2008, fixed belt transects were established within the two western scooter survey segments (I and II) in an area where several species of groupers and snappers were observed aggregating and spawning. This portion of the Grammanik Bank was divided into twelve 30 m segments that were marked with a polystyrene float tied 3 m above the bottom. As with scooter surveys, each diver would swim and count all target species up to 20 m to the south or north of the line of floats (i.e., 30 m × 20 m belt transects). Roving dives would be used to count target species in areas outside the belt transects, and unrestricted point counts would be used to collect data on fish behavior and abundance at a specific site. Divers conducting unrestricted point counts would remain in a specific location and estimate total abundance of aggregating species and record behaviors within a 360° area defined by the limits of underwater visibility (Samoilys and Carlos 2000). During roving dives and unrestricted point counts, divers would also be equipped with underwater digital video recorders or cameras and data sheets to document frequency and timing of spawning behaviors (i.e., intraspecific aggression, courtship, and spawning) and associated coloration.

Data analysis

Kyphosus sectatrix typically occurred in schools so the total number of fish was counted or, if group size exceeded 100, numbers were estimated to the nearest five fish. Because schools of kyphosids would often split and join throughout the day, roving dives or point counts often encountered the same group of chubs repeatedly so the maximum number of chubs seen in any one group was recorded. Divers conducting scooter surveys or belt transects typically encountered chubs as isolated non-overlapping groups of varying sizes which were summed to get total number of chubs per survey. Here, we consider maximum group number and total number of chubs as equivalent estimates of chub abundance on any 1 d. Therefore, the maximum number of fish (or maximum group size) seen on any 1 d was used to analyze patterns of kyphosid abundance for each calendar month and during the solar cycle (days after the winter solstice) and the lunar cycle (days before or after full moon). For example, to analyze trends for calendar months, maximum group size was taken for each calendar month and averaged across years (i.e., maximum group size for each January from 2003 to 2013 was averaged). Data for the lunar cycle were treated the same way as described above but maximum daily group size was averaged for each lunar date (i.e., 1 dafm, 2 dafm, etc.) across all years. Because many solar cycle days were missing data, maximum daily group size was summed for each 20 d interval following the winter solstice across all years then converted to percentages.

Results

Abundance and distribution

Between 2002 and 2013, 866 fish surveys were conducted during 749 dives and included 223 scooter surveys, 330 belt transects, 189 roving dives, and 124 unrestricted point counts. The majority of dives occurred from February to June (Fig. 2) and corresponded to projects studying grouper spawning aggregations. Kyphosids were recorded on 96 fish surveys (11 %) and occupied the Grammanik Bank from January to April (Fig. 2). Due to the limited number of dives from July through December, there is a possibility that *K. sectatrix* aggregations may also occur during these months. When kyphosid abundance was examined relative to the northern winter solstice, peak abundance occurred from late February to mid-March (Fig. 3), when seawater temperatures are at their annual minimum. Water temperature ranged from 25.9 to 27 °C during this period and was 26.1 °C when spawning was observed on February 16, 2012. Salinity was 35.5–36.0 ‰ at 40 m depth and the thermocline occurred at 70 m in February 2012. Current at this time was moving north-northeast and averaged 0.07 m s^{-1} (range 0.02–0.16 m s^{-1}) between 30 and 40 m (bottom) depth. Between 10 and 20 m depth (i.e., mid-water), which is where gamete release was observed (see below), current speed shifted easterly and averaged 0.3 m s^{-1} (range 0.10–0.40 m s^{-1}).

During each month of the spawning season, chubs were most abundant from the day of the full moon to about 11 dafm (Fig. 4). *K. sectatrix* group size increased as fish moved westward throughout the day toward the core spawning site (Fig. 5). Average group size less than 150 m from the spawning site (segment I) was nearly double than that in other segments further away (Kruskal–Wallis rank test $H = 12.296$, 5 *df*, $p < 0.031$). Groups were seen in segment III to VI from 11:00 to 15:00 hrs, in segment II from 10:00 to 16:00 hrs, and in segment I from 10:00 to 18:00 hrs, suggesting that fish moved toward and aggregated at the spawning site during late afternoon. The

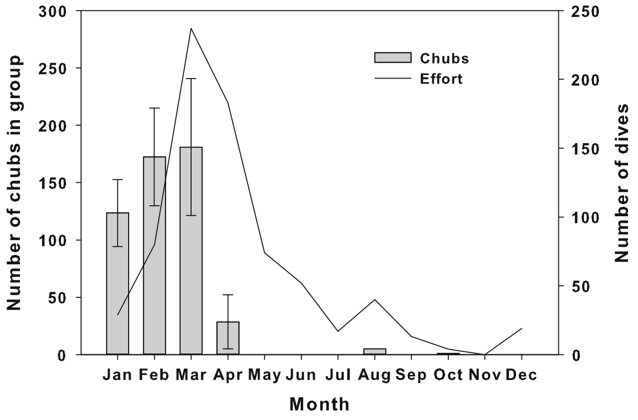

Fig. 2 Average group size (±S.E.) of *K. sectatrix* each month at the Grammanik Bank spawning aggregation site for all years 2002–2013 and survey effort (number of dives) by month

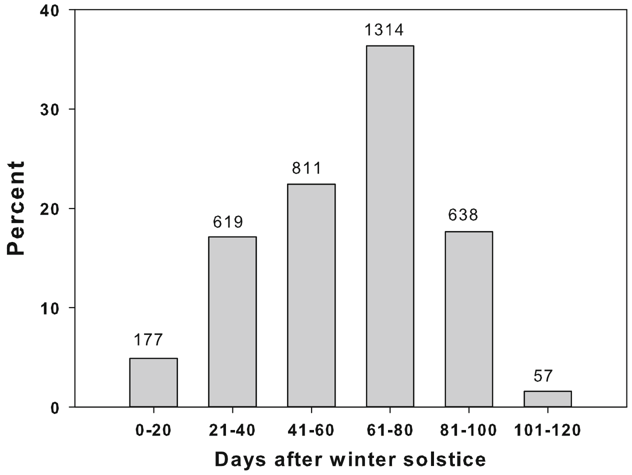

Fig. 3 Percent abundance of *K. sectatrix* at the Grammanik Bank spawning aggregation site relative to the northern winter solstice. *Numbers above bars* indicate the sum of all *K. sectatrix* groups within each 20 d time period summed across all survey years. Peak abundance occurred 61–80 d after winter solstice and corresponds to late February to mid-March

unique color patterns and behaviors associated with courtship and spawning, including gamete release, were only observed in segment I (see below).

Behavioral observations

Kyphosus sectatrix was commonly seen schooling in loose formations, milling throughout the water column, splitting into smaller groups and then reforming. The normal coloration of chubs appeared bronze to light gray with dull yellow horizontal stripes on the body and dusky colored fins. Small groups of chubs were occasionally seen descending to the reef to feed on benthic algae. *K. sectatrix* groups were largest around the core aggregation site, typically exceeding 150 individuals, and fish were more tightly clustered and synchronized in their movements than on other areas of the bank.

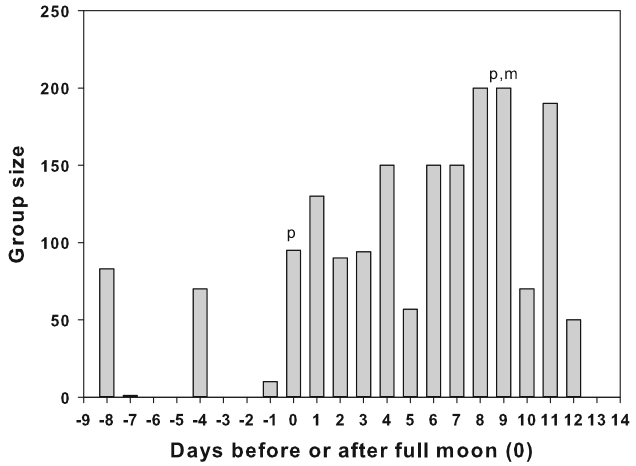

Fig. 4 *K. sectatrix* aggregation formation (average group size) relative to the full moon at the Grammanik Bank. *p* pair spawn, *m* mass spawn observed

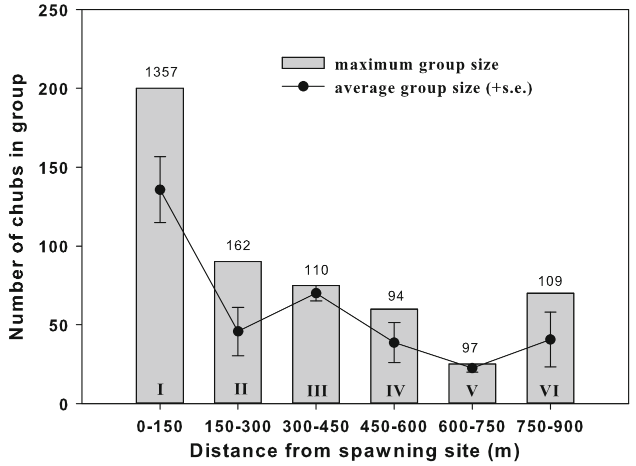

Fig. 5 Maximum (*bar*) and average (*line* ±S.E.) group size of *K. sectatrix* at the Grammanik Bank. *Numbers above bars* indicate the number of surveys within each segment. Each 150 m segment shown as Roman numeral. (see Fig. 1)

On February 16, 2012, nine dafm, *K. sectatrix* was observed spawning. *K. sectatrix* was first encountered at 15:33 hrs when a small group of 35 individuals swam around divers. During the next 10 min, distinct changes occurred within the school including more synchronized swimming and intensifying coloration. The normal coloration described above changed progressively with the body becoming silver in color and the dorsal and anal fins darkening (Fig. 6a, b). Next, the caudal fin transitioned from dusky to black and a bright white stripe appeared along the basal margin of the dorsal fin (Fig. 6c). On some individuals, the black pigment became more intense on the caudal fin and spread anteriorly over the caudal peduncle (Fig. 6d) and finally to the posterior margin

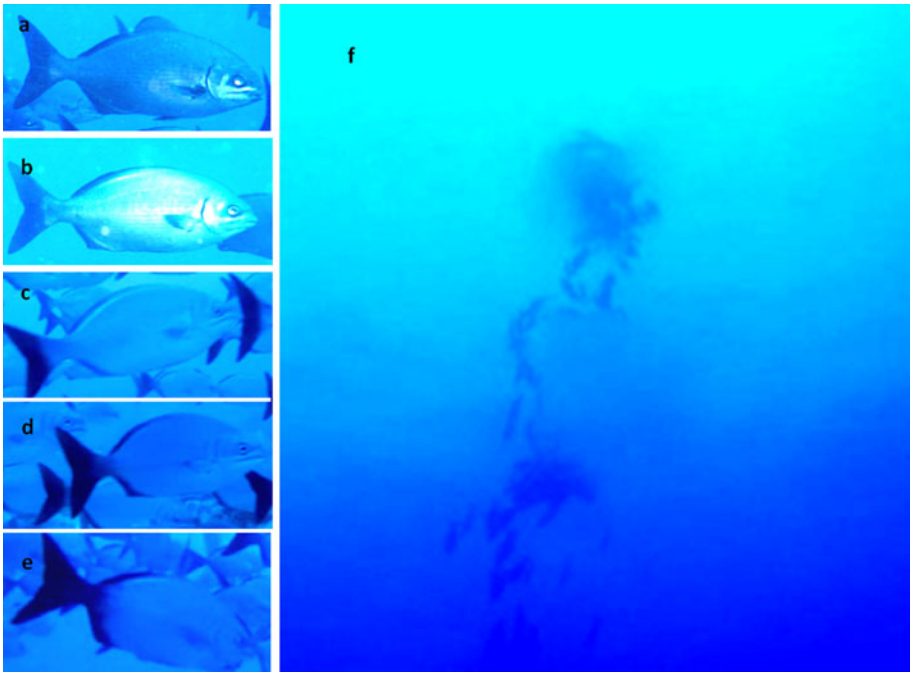

Fig. 6 *K. sectatrix* progressive color phases displayed during spawning aggregation at Grammanik Bank: **a** normal bronze or *gray*; **b** bright *silver*; **c** *black* caudal fin; **d** dusky peduncle; **e** *black* posterior margin; **f** group spawning rush of approximately 200 *K. sectatrix* at 17:42 hrs showing two gamete clouds. Note fish at *bottom* of image have already spawned and are descending to reef

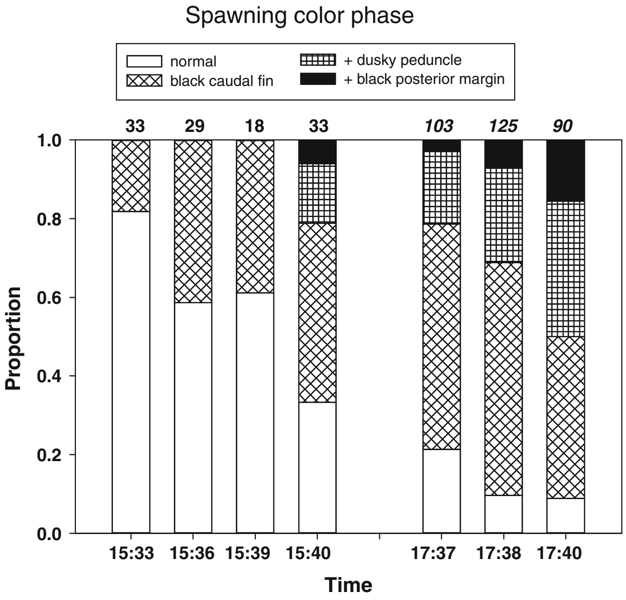

Fig. 7 Proportion of *K. sectatrix* at Grammanik Bank that displayed one of the four sequential color phases during their spawning aggregation on February 16, 2012. *Number above each bar* indicates the number of fish that was categorized into each color phase from video recordings during two dives between 15:30 and 17:45 hrs. Maximum group size on each dive was 35 and 200 fish, respectively. Spawning rushes and release of gametes occurred at 17:42 (Fig. 6f) and 17:44 hrs

of the body and dorsal and anal fins (Fig. 6e). Interestingly, most small groups of *K. sectatrix* were led by individuals who displayed black pigment on the caudal peduncle and posterior margins of body. The focal school approached and milled around divers over a period of 10 min. From 15:33 to 15:40 hrs, the percentage of individuals that displayed normal dusky fins decreased from 82 to 40 %, while fish with black caudal fins increased from 18 to 45 % (Fig. 7) and fish with black body margins increased from 0 to 12 % (first observed at 15:40 hrs). As divers ascended, the aggregation was about 30 m in depth swimming slowly to the east above coral bottom and about 40 m from the shelf edge. At this time, pair spawning of *K. sectatrix* was observed twice between 15:43 and 15:44 hrs before divers lost visual contact with the group. Pair spawning occurred as the aggregation swam approximately 10 m above the bottom in a loose elongated group. Two chubs (presumably a male and female) ascended rapidly approximately 5 m above the aggregation in a spawning rush, released gametes and descended back into the aggregation. This was repeated by a second pair of fish about a minute later. A third pair spawning was observed at 17:29 hrs on January 27, 2013 (full moon), when a pair of fish emerged from a group of 20 *K. sectatrix* in a rapid lateral spawning rush. Prior to pair spawning, courtship consisted of one fish (presumably a male) approaching a second fish (presumably female) from below and pressing its head against the vent of the presumed female while all remaining fish swam in a loose school around the pair. The presumed female would occasionally turn its body lateral to the approaching fish, so that its vent was facing away from the presumed male. The coloration between the two individuals was not distinguishable although the presumed male seemed to have a slightly darker caudal fin.

By 17:30 hrs on February 16, 2012, the kyphosid aggregation had increased to over 200 fish and spawning was observed and videotaped three times between 17:42 and 17:44 hrs (Fig. 6f). Sunset on this day occurred at

18:02 hrs. Two minutes prior to spawning, three color phases, black caudal fin, dusky peduncle and black posterior margin, were observed on 90 % of the fish (Fig. 7). The first spawning rush was initiated when the entire aggregation ascended to the middle of the water column (about 15–20 m depth or 20–25 m above the bottom), in a loosely formed oval school approximately 5 m × 3 m in diameter that elongated to approximately 5.5 m × 1.8 m. At this time, 40 fish returned rapidly to the bottom, while the remaining fish (ca. 160 fish) formed a tight ball 2 m in diameter at the apex of the ascent. Mass spawning followed for about 8 s producing a large gamete cloud, which obscured nearly all the spawning fish. About half of the aggregation rapidly descended, while the other half (ca. 75 fish) ascended approximately 2 m and spawned a second time for 3 s in a tight ball (1.5 m × 1 m in diameter) before also descending rapidly in a long column to join the other group of fish near the bottom (Fig. 6f). Two min later, the entire aggregation ascended again to mid-water. The size and shape of the aggregation was similar to the first large oval. This time, however, the spawning rush was initiated about 10 m below the apex of ascent. A sudden downward rush of fish at the ascending apex facilitated the formation of a tight ball 4 m diameter, and the resulting gamete cloud again obscured nearly all the spawning fish. All spawning rushes occurred directly over sparsely colonized hard-bottom habitat approximately 30 m from the edge of the drop-off. No predation attempts on spawning kyphosids or their gamete clouds were seen; however, pelagic planktivores including creole wrasse (*Clepticus parrae*), yellowtail snapper (*Ocyurus chrysurus*), black durgeon (*Melichthys niger*) and creole-fish (*Paranthias furcifer*) were all abundant in the water column.

Discussion

The temporal and behavioral characteristics of spawning in the Bermuda chub are reported here for the first time and confirm this species as an aggregative spawner (Sadovy de Mitcheson and Colin 2012). Although chubs are common inhabitants of shallow tropical reefs, little is known of their reproductive behavior, and direct observations of spawning or spawning aggregations have not been published for any species in the family Kyphosidae. The spawning of *K. sectatrix* showed a number of similarities as well as differences when compared to other fish families. During winter months, *K. sectatrix* was observed across the Grammanik Bank during the day but moved west to the core spawning aggregation site used by other species in the mid to late afternoon and only displayed behaviors and coloration associated with courtship and spawning at a specific location. This spatial pattern of habitat use seems to be consistent with the staging area, courtship arena, and spawning site described for transient aggregating species such as groupers (Nemeth 2012). Chubs moved around the reef in large schools sometimes splitting into smaller groups or joining to form larger aggregations and spawning occurred high in the water column, behaviors typical of snappers at FSA sites (Heyman et al. 2005). The formation of large aggregations, courtship, and spawning of *K. sectatrix* was most evident in the late afternoon and evening hours in the days following the winter full moons of January, February, and March. These daily, seasonal, and lunar patterns are very similar to most Caribbean groupers such as the red hind (*Epinephelus guttatus*), Nassau grouper (*E. striatus*), and yellowfin grouper (*M. venenosa*; Sadovy et al. 1994b; Whaylen et al. 2004; Nemeth 2005; Nemeth et al. 2006, 2007). In the Cayman Islands, Whaylen et al. (2007) reported *Kyphosus* sp. aggregated and displayed courtship behavior during the same months and lunar cycle as *E. striatus*. Spawning in these serranids, and *K. sectatrix* as well, is tightly coupled with the full moon cycle when seasonal water temperatures are at their annual lowest (Colin 1992; Nemeth 2009) although some variations do occur. For example, *K. sectatrix* was most abundant across all survey years from 60 to 80 d after the winter solstice, whereas *E. guttatus* was found to be most abundant 20–40 d after the winter solstice (Nemeth et al. 2007). In contrast, courtship and spawning in the Cortez chub (*Kyphosus elegans*) and rainbow chub (*Sectator ocyurus*) in the southern Sea of Cortez have been observed within groups of 20–100 fish in the late afternoon and early evening but occurred, instead, in the summer and fall months when annual water temperatures are relatively high (B. Erisman pers comm).

Kyphosus sectatrix displayed distinctive color patterns which intensified throughout the spawning population as spawning time approached (Fig. 6). The progressively greater contrast with black against a white or light colored background is also a common feature of several Caribbean groupers such as *E. striatus* (Colin 1992; Whaylen et al. 2004), *M. venenosa* (Nemeth et al. 2006), *M. tigris* (Sadovy et al. 1994b), and *M. interstitialis* (RSN pers obs). The bicolor phase in *E. striatus* (and also *M. interstitialis*) occurs when the dorsal half of the body becomes black and the ventral half becomes white (Archer et al. 2012). In *M. venenosa* and *M. tigris,* the males display a pale or white head (Sadovy et al. 1994a; Nemeth et al. 2006) and *M. tigris* males also display black spots on a white background around the vent (see Figure 4.1c in Nemeth 2009). Variations in contrasting coloration are also displayed in several Pacific groupers including *E. fuscoguttatus* (Pears 2012) and *Plectropomus laevis* (RSN pers obs) as well as the parrotfish *Bolbometopon muricatum* (Hamilton and Choat 2012). One notable aspect of *K. sectatrix* coloration was the progressively greater proportion of the spawning population which displayed the blackening of the caudal fin and posterior margin of the body just prior to mass spawning. This is also a unique feature of *E. striatus* spawning in which the bicolor phase becomes progressively more dominant during the lunar days leading up to spawning as well as the afternoon hours leading up to sunset (Whaylen et al. 2004). Archer et al. (2012) reported that the relative proportion of *E. striatus* displaying the bicolor phase increased to nearly 50 % on the day of spawning, suggesting that fish are behaviorally and physiologically prepared to spawn. Courtship coloration of *K. elegans* in the Sea of Cortez, in contrast to *K. sectatrix*, was light gray with black spots covering their bodies (B. Erisman pers comm). These reports and observations highlight the considerable variation in spawning coloration within and among families of fish that form spawning aggregations.

The reproductive mode of *K. sectatrix* consisted of pair spawning by a few individuals followed by mass spawning of the entire aggregation. Reported reproductive modes of most aggregating species include either individual pair spawning, pair spawning in harems (one male spawns individually with multiple females), group spawning (one female and several males ascend rapidly away from the aggregation and release gametes at same time), and mass spawning (large numbers of females and males release gametes simultaneously en masse). With the exception of pair spawning, the mass spawning of *K. sectatrix* is similar to that described for several *Lutjanus* species such as *L. jocu* and *L. cyanopterus* (Carter and Perrine 1994; Heyman et al. 2005). However, Krajewski and Bonaldo (2005) recorded pair spawning by *L. jocu* outside of an aggregation. Intra-specific variation in reproductive behaviors is common in surgeonfish, parrotfish, and wrasses and can range from localized group spawning where a female spawns with groups of males or pair spawning where large terminal-phase males defend spawning territories and pair spawns with nearby females (Choat 2012). Pair spawning by *K. sectatrix* within an aggregation that also mass spawns is unusual, but may serve to increase reproductive fitness of pair spawning individuals within an aggregation by restricting fertilization of gametes to specific spawning partners. However, pair spawning may mean reduced fertilization success for females, whereas males gain the benefit of reduced sperm competition (Malloy et al. 2012).

The aggregation and spawning of herbivorous fishes have been described in detail for many species, notably scarids and acanthurinids (Randall and Randall 1963; Robertson 1983; Colin and Clavijo 1988; Colin and Bell 1991; Craig 1998; Claydon 2004; Kuwamura et al. 2009). The formation of seasonal spawning aggregations of *K. sectatrix* on the deep shelf reef (transient spawners) differs from spawning behavior reported in Caribbean scarids and acanthurids (resident spawners), which spawn year round and migrate short distances from or within home ranges and territories (Colin and Clavijo 1988; Nemeth 2009; Domeier 2012). Chubs are rarely observed on the Grammanik Bank or other offshore reefs in the US Virgin Islands (RSN pers obs) except during the 3-month spawning season suggesting that they undergo migrations from nearshore reefs to offshore spawning sites. Migrating to shelf edge spawning sites may facilitate advection of larvae into nursery habitats consisting of floating sargassum mats (Moore 1962; Bohlke and Chaplin 1968) and would be advantageous for larval survival into the post larval phase which is not dependant on settlement into nearshore habitats.

Kyphosus sectatrix is unusual in that the occurrence of herbivorous transient spawners has not yet been reported (Nemeth 2009; Sadovy de Mitcheson and Colin 2012). Choat (2012) conducted an analysis of the ecological features associated with resident and transient spawning modes and showed that transient spawners were characterized by large bodied carnivorous species which occur at low densities. Moreover, body morphology (i.e., lateral compression) and long intestines typical of herbivorous fishes reduce the space available for development of large ovaries (Choat 1991) and storage of lipids for energy, key requirements for long migrations and capital breeding (Stephens et al. 2009; Choat 2012). Capital breeding relies on energy reserves accumulated over periods of time prior to spawning at infrequent intervals. In contrast, income breeding relies on continuous feeding to support daily reproduction (Warner 1995). Adult *kyphosids* are considered roving herbivores with a nearly complete diet of brown macroalgae, primarily of the genera *Dictyota* and *Sargassum* (Moore 1962; Randall 1967; Silvano and Güth 2006; Downie et al. 2013; Michael et al. 2013). The two individuals collected on the Grammanik Bank had full stomachs of *Lobophora variegata*, a food source which may have originated from deep reefs since groups of *K. sectatrix* were often observed descending to the reef to feed (RSN pers obs). Annual coral reef monitoring conducted on the Grammanik Bank from 2003 through 2011 recorded between 29 and 40 % macroalgae, which was dominated by *L. variegata* (Herzlieb et al. 2006; Smith et al. 2008). If not the preferred diet, the switch from *Dictyota* and *Sargassum* to *L. variegata* may provide a plentiful supply of nutrition while on the spawning aggregation site. Further analysis of these key physiological elements will be required to determine whether *K. sectatrix* and other members of the Kyphosidae fall within the ecological and morphological constraints of herbivorous species or more closely resemble grouper and snapper in terms of successful spawning characteristics and reproductive strategies.

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