

Chapter 5. Dynamics of rabbitfish (*Siganus sutor*) spawning aggregations in southern Kenya

Melita Samoily, Nyaga Kanyange, Denis Macharia, George Waweru Maina and Jan Robinson

Introduction

Overfishing, destructive fishing methods and weak governance are widespread and re-occurring problems in eastern Africa's coastal fisheries (McClanahan and Mangi 2004; UNEP 2009; Burke et al. 2011; Samoily et al. 2011b), the effects of which are further exacerbated by climate change (Schubert et al. 2006; Graham et al. 2007). The Shoemaker spinefoot rabbitfish, *Siganus sutor*, is one of the most widely targeted and heavily fished species on the Kenyan coast (McClanahan and Mangi 2004; Maina et al. 2008; Samoily et al. 2011b) and therefore likely a significant species for food security in coastal communities (Foale et al. 2012). Studies have documented fisher knowledge of reef fish spawning aggregations in the western Indian Ocean, including those of *S. sutor*, since 2006 through the World Conservation Union (IUCN) and the Western Indian Ocean Marine Science Association (WIOMSA) funded programmes in Kenya and Seychelles (Samoily et al. 2006; Kimani 2007; Robinson et al. 2007; Samoily et al. 2007). Concerns regarding the sustainability of fisheries that target spawning aggregations (Sadovy and Domeier 2005; Robinson et al. 2011; Sadovy de Mitcheson and Colin 2012) highlight the need to determine the management implications of this fishing (Grüss et al. *in press*).

Major factors confound the study of spawning aggregations, notably their ephemeral nature, the remoteness of many sites and the cost and risks of diver-based studies on sufficiently replicated time and spatial scales (Johannes et al. 1999; Colin 2012). Previous studies on *S. sutor* in Kenya have not adequately verified fisher's knowledge, aggregation sites have not been confirmed and there is inadequate information on their spatial and temporal dynamics. We addressed these difficulties by employing four different methods: (1) acoustic telemetry at spawning aggregation sites; (2) underwater visual census (UVC) surveys and observations of fish behaviour, (3) *in situ* observations of the aggregation fishery; and (4) fishers' knowledge. This study was also part of a broader multi-disciplinary study on the *S. sutor* fishery in the same area (*see* Chapters 3 and 4). The aim of the acoustic telemetry component was to obtain information on the spatial and temporal dynamics of aggregations than cannot be achieved by UVC alone and to estimate remote parameters such as individual site fidelity and residency times which are critical to management development. While acoustic telemetry has been extensively used for studies of pelagic fish behaviour (e.g. Dagorn et al. 2007), the technology was under-utilised in the WIO in the context of reef fish resources prior to this WIOMSA-MASMA Programme (*see* Chapters 6 and 8).

To verify that fish aggregations are reproductive requires the application of strict criteria (Colin et al. 2003; Domeier 2012; SCFRA database: <http://www.scfra.org/database>). According to Domeier (2012), a spawning aggregation is defined as “*a repeated concentration of conspecific marine animals, gathered for the purpose of spawning, that is predictable in time and space. The density/number of individuals participating in a spawning aggregation is at least four times that found outside the aggregation. The spawning aggregation results in a masspoint source of offspring*”. Reproductive activity within spawning aggregations is defined by either direct or indirect indicators. Direct indicators include observation of spawning, such as release of gametes in a spawning rush, or presence of hydrated eggs and/or post-ovulatory follicles in the gonads. Indirect indicators include observations of spawning-related behaviour, such as courtship, colour changes only known to be associated with reproduction and high catches of gravid fishes confirmed, for example, through increases in gonadosomatic index (GSI).

This study was designed to verify *S. sutor* spawning aggregation sites and behaviour using Domeier's (2012) criteria. We also sought to determine periodicity and duration of aggregation formation, fish residency times at aggregation sites and spawning site fidelity to provide a basic understanding of the spatial and temporal dynamics of *S. sutor* spawning aggregations to aid in the development of conservation and fisheries management measures.

Methods

Study sites

Three putative *S. sutor* spawning aggregation sites (A, B, C), located a few kilometres off Msambweni in southern Kenya (Fig. 1) were selected for the study. These sites had been identified through fisher knowledge surveys in 2004 (Samoilys et al. 2006) and were also reported by fishers in 2009-2010 by a complimentary study (Chapter 3). With the assistance of patriarch fishers familiar with the sites, the three sites were re-located in 2009 and the general areas of the putative spawning aggregations marked by boat using a handheld Garmin GPS.

Finer details and descriptions of sites were subsequently made during diver surveys in 2009-2010 from which site maps were hand drawn to be used for UVC surveys. In addition, the distribution of fishing boats and trap sets at each site was recorded by GPS and combined readings mapped onto geo-referenced Landsat 7 (2003) imagery. Area estimates of aggregation sites were then derived using ArcGIS and measured 19,972 m² (site B), 20,008 m² (site C) and 24,200m² (site A).

All three sites were offshore (~ 3km) coral patch reefs around 8-12m in depth, running in a northeast-southwest direction and surrounded by a gently sloping soft substrate of sand, rubble and seagrass beds at depths ranging from 12-16m. The patch reefs comprised hard carbonate substrate with scattered hard corals and many soft corals, generally of low relief, but with occasional coral bommies. Site B that had many large bommies (>1-2m high) at its northern end that were scattered over a gentle slope of rock, sand and rubble.

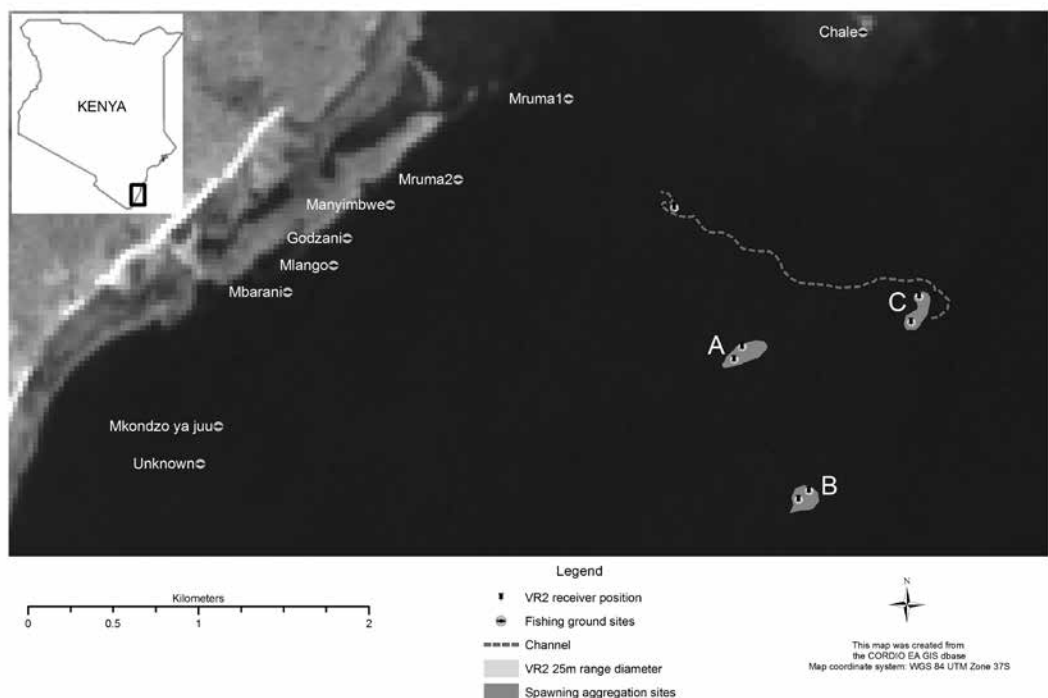


Fig.1. Spawning aggregation sites (A, B, C), fishing grounds, putative migratory corridor (channel) and acoustic telemetry array of 7 receivers (VR2) for *Siganus sutor* off the southern coast of Kenya.

In addition to offshore spawning sites, fishers also identified commonly fished nearshore sites that are putative non-spawning areas for *S. sutor* (Fig. 1). Fishers also identified a relatively deep channel running seaward from shore to the offshore putative spawning aggregation sites that they reported *S. sutor* use as a migratory corridor to the sites. Positions along the corridor were obtained by a diver on snorkel and subsequently mapped in ArcGIS as described above (Fig. 1).

*Verification and description of the *S. sutor* aggregation fishery*

Twenty-seven experienced spawning aggregation fishers from the Msambweni area were interviewed about the location and timing of *Siganus sutor* spawning aggregations (see also Chapter 3). Observations of fishing effort at Sites A, B and C, including the number of fishing boats and traps deployed, were made from November 2009 to March 2010 between lunar days (hereafter, LD) 13 and 20, the full moon and last quarter. These were constrained due to limited boat access and were done during UVC surveys (see below).

Underwater visual census and observations of fish behaviour

UVC surveys were conducted by a single diver (MS) at Sites A, B, C during the period of Nov 2009 to Mar 2010 (timing based on fisher knowledge surveys), the putative spawning season (see Chapter 4). Surveys aimed to verify aggregation formation and to determine aggregation duration and timing, however, they were constrained to LD 13-20 and four months because we did not have the diving resources to survey all lunar phases and throughout the year. Using the site maps the entire aggregation site was surveyed using a standardised swim of 25-30 minutes. Density estimates reported herein are considered approximate due to possible double counting of the highly mobile *S. sutor* and frequent poor visibility at aggregation sites (~ 10-12 m), both known to affect UVC accuracy (Samoilys 1997a). Following abundance counts, the observer remained on site for 10-20



Plate 1. VR2(W) acoustic receiver in position at an aggregation site.

min to record any reproductive behaviour including direct (spawning rushes and gamete release) and indirect (courtship behaviour, colour changes) signs of spawning (Colin et al. 2003).

Acoustic telemetry

A total of 29 Vemco acoustic transmitters (V7-2L, 69 kHz, 60-sec delay, 94-d battery life; Amirix Systems, Inc, Halifax Nova Scotia) and seven Vemco VR2(W) acoustic receivers were used to examine residency, movement and site fidelity by *S. sutor* at the three putative spawning aggregation sites. Receivers were moored to the bottom with aggregate cement blocks reinforced with weld mesh (Plate 1). Receivers were secured by cable ties to a T-bar embedded in the blocks. To further secure receivers, piano wire was attached to shackles cemented into the blocks. Receivers were positioned and their batteries activated just prior to tagging the fish.

Due to the less than optimal detection range (~ 50-100m) of tags in coral reef habitat (Bijoux, pers. comm.), two receivers were placed at each of Sites A, B and C, with efforts made to ensure good line of sight. A seventh receiver was installed at the edge of the channel to determine its potential as a migratory corridor (Fig. 1). The detection range of tags was tested by suspending a tag for ~ 20 minutes at 6 stations varying in distance from one receiver (Plate 2).

Fish were tagged during full moon in January 2010 to provide 3 months of potential tag detection during the spawning season (determined from concurrent studies in the same area, see Chapters 3 and 4) and while tags were operational. We worked with fishers who captured *S. sutor* using basket traps set the previous day on the aggregations sites. The trap was emptied into a bucket and fish >23 cm FL (size at 50% maturity) (Seychelles Fishing Authority, unpublished data; see Chapter 4)

were selected. Fish selected for tagging were retained in a perforated holding bucket strapped to the side of the boat (Plate 3). Prior to acoustic tagging, fish were measured (nearest mm, fork length, FL) and tagged with an external T-bar spaghetti-type tag (Floy Tag and Mfg, Inc, Seattle, WA), inserted between the dorsal pterygiophores, to enable fishers to identify acoustically tagged fish in their catches.

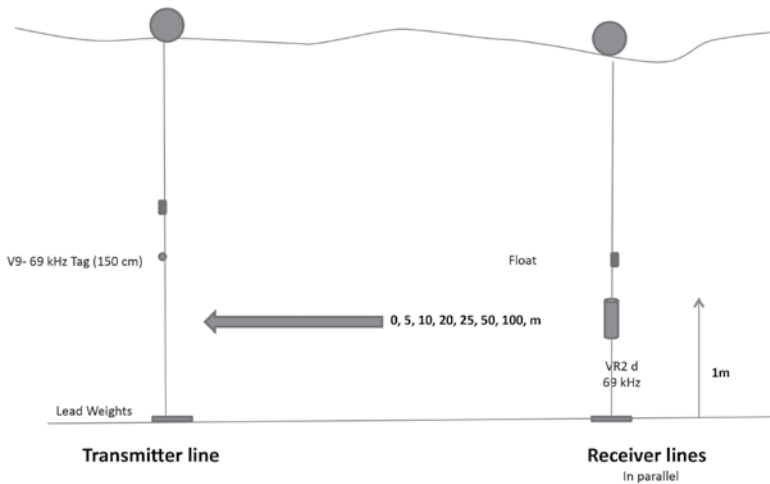


Plate 2. Schematic diagram showing the method used for range-testing transmitters.



Plate 3. a) Traditional basket traps used to capture *Siganus sutor*; b) perforated bucket strapped to side of boat for holding live fish. (See colour plates.)

Acoustic transmitters were inserted into the body cavity through through the ventral body wall. Using a surgical scalpel blade, incisions of ~ 2 cm in length were made, positioned slightly above the anus and about 2/3 distance below the lateral line. Surgeries were performed following 3 min anaesthesia using 45 mg/l clove oil dissolved in seawater, a concentration based on prior tests (see Appendix II). For surgery, anaesthetised fish were placed upside down in a canvas cradle suspended in an aerated aquarium cushioned with soft sponge on the walls (Plate 4). After tag insertion, the incision was sutured with two nylon-polyamide sutures and the fish was transferred to the holding bucket until normal movement had resumed. Untagged fish were retained and released in groups with tagged fish to help them orientate. Fish were released near acoustic receivers and observed on snorkel. All tagged fish swam rapidly to the bottom and disappeared into holes in the reef. To aid in tag recovery, an awareness-raising programme involving seminars and distribution of a tag return form was conducted in collaboration with a local conservation group in Msambweni.

Data Analysis

Residency time at a spawning aggregation site was defined as the time (hr) between the first acoustic detection and the last detection within a 24-hr period. If the fish was not detected for >24 hr it was assumed to have left the site or died. Continuous detections in 24-hr periods were summed to give total residency.

All data were assigned a lunar phase following Samoily (1997b) where the lunar cycle starts with the new moon (NM) on lunar day (LD) 1: NM = LD 28-3; First Quarter (FQ) = LD 6-10; full moon (FM) = LD 14-18; Last Quarter (LQ) = LD 21-25.



Plate 4. a) *S. sutor* anaesthetised with clove oil in 10 litres of aerated seawater; b) surgical incision prior to V7-2L tag insertion and suturing.

Results

Verification of spawning aggregation formation, sites and targeted fishing

UVC surveys provided evidence that *S. sutor* aggregations formed at the three sites, although a strong time-series of data was not obtained. Highest abundances at all three sites were observed in December and February (Fig. 2), with the largest aggregations occurring at Site B. At Site A, aggregations were only observed during December and no aggregations were observed in January at any of the sites. Maximum numbers were recorded on LD 14, 17 and 18 (~ full moon) at Sites B and C, and ranged from 62-257. Minimum numbers were in November and ranged from 0-8 fish (Fig. 2). Differences between minimum and maximum numbers at Sites B and C provide evidence of aggregation formation.

S. sutor school for purposes other than reproduction, making verification of aggregation for spawning imperative. Of the four behaviours typically used as indicators of reproductive activity (i.e. courtship, colour change, spawning rushes and gamete release) only changes in colouration were observed. The change was represented by a white and a black line appearing mid-laterally. At the sites, *S. sutor* swam at high speed close to the bottom in small groups of typically 2-15 fish and up to 25 fish per group. Individuals observed changing colour represented 6-23% of the fish in these schools. The schools swam in all directions and the majority (42% of fish) were recorded circling. Detailed behavioural patterns were hard to discern because the fish swam in and out of the diver's field of view.

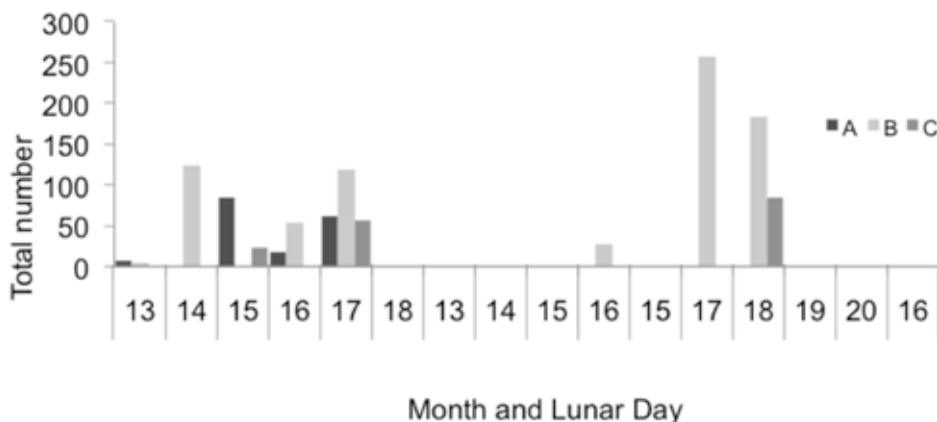
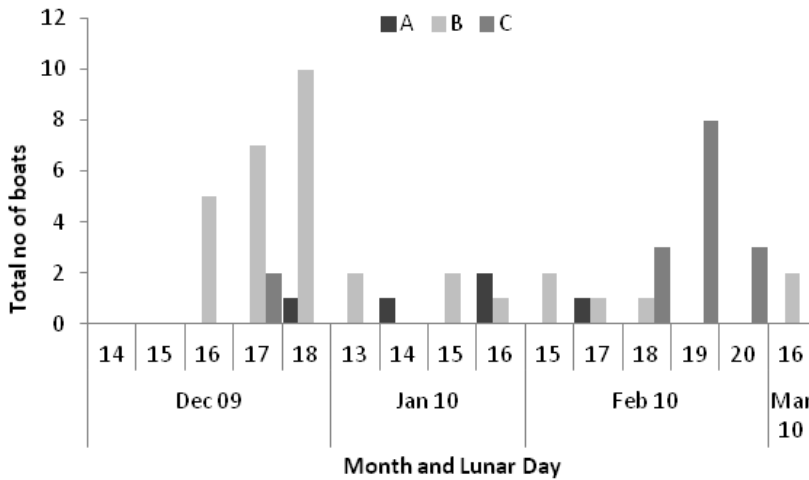


Fig. 2. Total numbers of *S. sutor* on Sites A, B and C during November 2009 to March 2010. Lunar day: 1= new moon, 15-16 = full moon.

The number of traps increased on the three sites from LD 15 to 17 in December, LD 15 and 16 in January, and LD 18 to 20 in February (Fig. 3). Daily increases in boat numbers were only observed in December and February. The sharp increase in boats and traps in December and February corresponded with the increase in *S. sutor* at the sites (Fig. 2). Although trap numbers increased in January, UVC did not record increases in fish densities. We were unable to monitor boats and traps throughout the spawning and non-spawning season, nor were we able to record catches at the sites.

During interviews with 27 experienced fishers Sites A, B and C were mentioned as *S. sutor* spawning sites by 12, 9, 8 of the fishers, respectively. Three other sites were mentioned as spawning aggregation sites, but only by two fishers. Fishers reported the peak spawning aggregation period for *S. sutor* was from October through January, with a protracted season that extends until April or May (Fig. 4a). Based on interviews, fishers reported spawning occurs during or just after full moon (LD 14-19) (Fig. 4b).

a) Number of boats



b) Number of traps

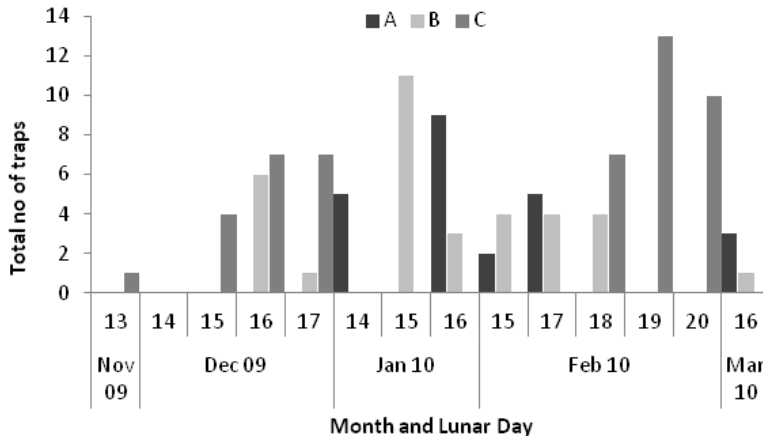
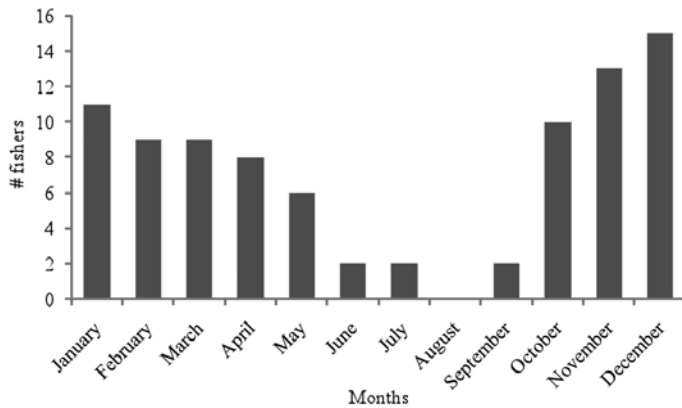


Fig. 3. Number of a) fishing boats and b) basket traps on Sites A, B and C) during monitoring days from November 2009 to March 2010.

a) seasonal



b) lunar

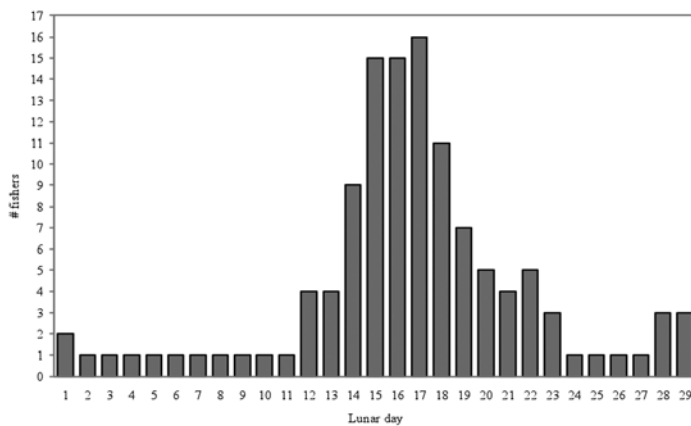


Fig. 4. Fishers' knowledge of a) seasonal and b) lunar spawning periodicity in *S. sutor* off Msambweni, Kenyan south coast. n=27 fishers.

Detections of tagged fish at aggregation sites, lunar and diel periodicity and residency

Surface and bottom mapping estimated that the three spawning aggregation sites ranged from 19,972 m² to 24,200m² (Table 1). Range testing of the acoustic transmitters estimated an average detection distance of only 25 m. Therefore the combination of two receivers at each site covered an average of only 3,928 m² (equivalent to 18.5% of the spawning site area; see Table 1). Therefore, coverage of sites was partial and a lack of detections may not indicate that tagged fish had left the site.

A total of 29 fish, ranging from 23 to 29 cm FL, were tagged with transmitters over a 4-day period (31 January-3 February 2010) and released at the site of capture (Table 1). In total, 12 (41%) of the tagged fish were subsequently detected by the array or recaptured by fishers (Table 1; Fig. 5). Nine were detected by receivers, including two that were subsequently recaptured at the tagging site. Three other acoustically tagged fish were recaptured by fishers at other sites and were never detected by the array. All the fish detected by receivers were detected at the same spawning aggregation sites at which they were tagged.

All six receivers at the three aggregation sites detected tagged fish and a total of 221 detections were obtained over the 3-month experiment (Fig. 5). No detections were obtained at the 7th receiver located in the putative migratory corridor (Fig. 1).

Of the 9 tagged fish detected by receivers, 3 were detected only on the day they were tagged (Table 1, Fig. 5). Thus 6 of the 9 individuals detected by the array provided data useful for understanding

reproductive behaviour. These included 3 fish tagged and detected at Site C and 3 fish tagged and detected at Site B.

Table 1. Summary of tagging, recaptures and detections of acoustically tagged *S. sutor* at Msambweni.

	Aggregation sites			Fishing sites	
	C	A	B	Mabarani	Chale
Site area (m ²)	20,008	24,200	19,972	N/A	N/A
No. of fish tagged	12	8	9	N/A	N/A
No. of fish detected acoustically	3	1	5	N/A	N/A
Number of fish only detected on day of tagging	0	1	2	N/A	N/A
Number recaptured by fishers (Floy tags)	0	1	1	2 (tagged at Sites A and B)	1 (tagged at Site B)
Days at liberty	1-96	9	3-58	29-35	46

Five fish were recaptured (Fig. 5), including two taken at the same aggregation sites where they were originally tagged (Nos. 14 and 15). Three fish (Nos. 08, 03, 02) were recaptured at other fishing grounds that appeared to be non-spawning areas (Table 1). Of the two fish recaptured at the Mabarani fishing ground, one was tagged at Site B (distance=3.3 km) and one at Site A (distance=2.6 km). The fish recaptured at Chale was tagged at Site B, a distance of 2.8 km away (Fig. 1). These three recaptures provide the first evidence of the scale of linear displacement between spawning sites and presumed areas of residence. The recaptures at Mabarani suggest that while fish may intermingle at non-spawning areas, they otherwise demonstrate site fidelity to individual spawning sites, and inversely, that aggregations are not comprised of fish that all came from the same non-spawning/ home range area.

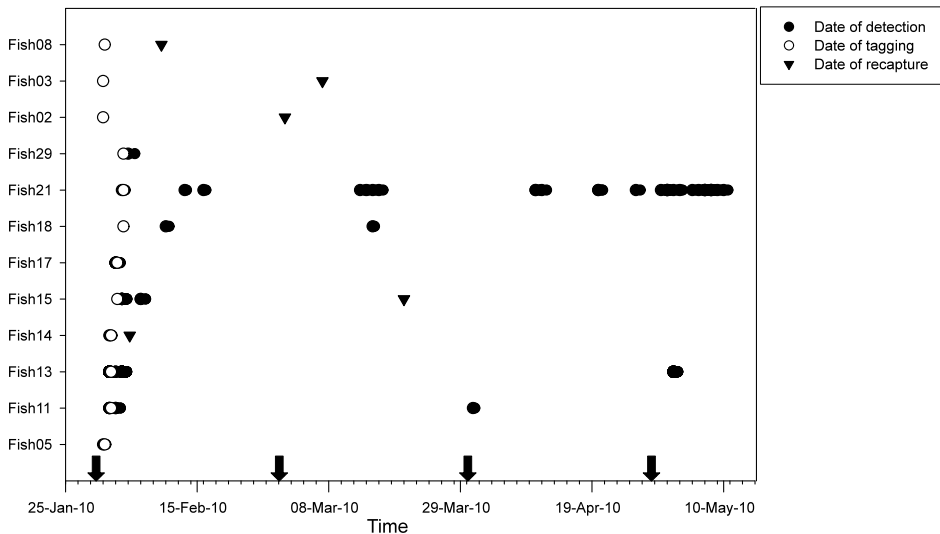


Fig. 5. Plot showing detections of 12 acoustically tagged fish, 31 January to 10 May 2010. Nine fish were detected acoustically at the three spawning aggregation sites, two of which were recaptured by fishers. Three were recaptured by fishers at non-tagging sites. Recaptured fish are represented by filled diamonds. The arrows represent full moon periods.

Eighty-six percent of detections occurred during LD 18-20 suggesting fish arrived on the aggregation site on the full moon and dispersed 2 days later, which concurs with fishers' reports (*see above*). However one individual (No. 21) remained at Site C throughout much of the study period, suggesting it was resident at this site (Fig. 6). Two other individuals were detected sporadically by receivers during other lunar cycles (LD 21 and 27), but did not appear to be resident. Assuming Fish No. 21 was a permanent resident at the site (*see below*), we removed it to examine diel timing in spawning activity. Pooling data from all three aggregation sites gave the time of detections as ranging from 06:13 hrs to 19:02 hrs, suggesting the species is most active during daytime at spawning sites (Fig. 7). However, no clear pattern to demonstrate actual reproduction was observed within this period. Some clustering in the evening was seen in fish Nos. 11 and 15, and fish No. 13 was detected all day; no fish were detected at night.

Two fish (Nos. 11 and 13) were detected at their respective aggregation sites two and three months, respectively, after tagging and just after the full moon, suggesting possible repeat spawning by these individuals within the reported spawning season (Fig. 5). The third fish (No. 18) was detected in each of two subsequent months at its tagging site, but the timing did not coincide with the full moon periods.

Because of the small area coverage of the receivers, establishing spawning site residency times was problematic. Only 3 fish (Nos. 11, 13 and 15) were considered resident (detected >1 within 24 hr; *see Methods*) on an aggregation site. Residency ranged from 6 to 57 hr with an average 25.2 hr. The residency periods of fish Nos. 11 and 13 corresponded to days just after full moon (LD 17-20). Fish No. 15 was only resident during the initial tagging period, early February (LD 20), and then again three days later (LD 23).

Spawning site fidelity

Tagged fish were only acoustically detected at the spawning site where they were tagged, demonstrating site fidelity. However, given the limited receiver coverage (19% of the total area of the spawning site), we cannot entirely exclude the possibility that fish attended other aggregation sites. Over 96 days, between 2 and 157 detections per individual were made of four fish at the aggregation sites (Fish No. 21 was excluded from this analysis). All acoustic detections were at Sites B and C. One fish (No. 08) from Site A also provided data on site fidelity: it was recaptured nine days after tagging at Site A suggesting that it had remained on, or returned to, the aggregation site.

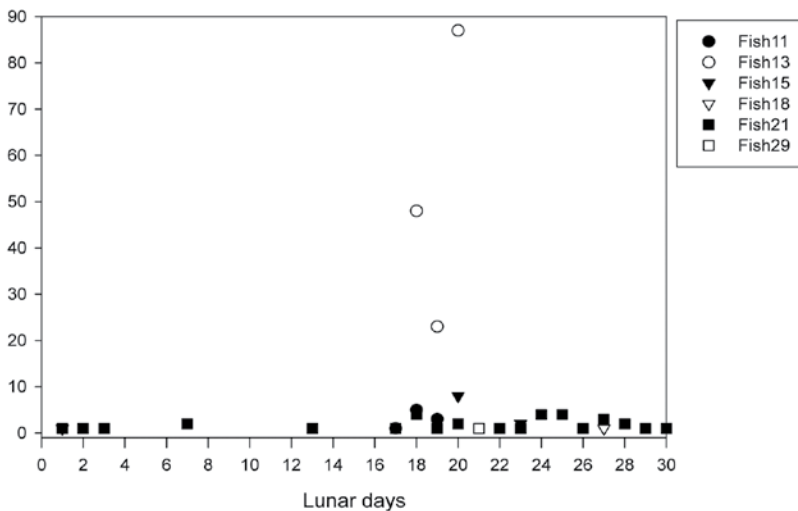


Fig. 6. Frequency of detections of tagged fish by lunar day.

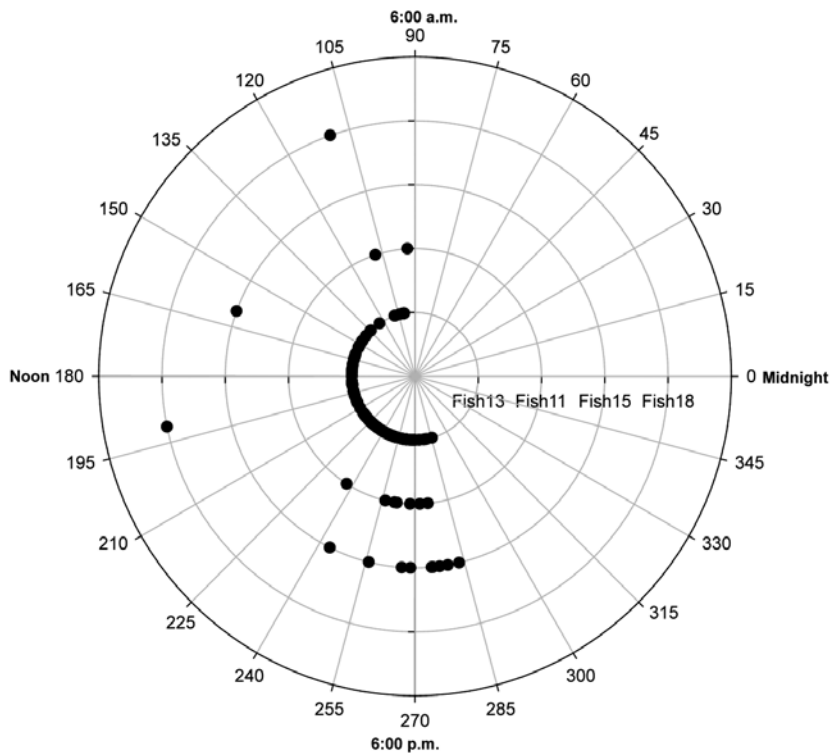


Fig. 7. Diel patterns of detection for four tagged fish at the three spawning aggregation sites. Each slot of 15 degrees represents 1 hr.

Discussion

We provide preliminary evidence that *S. sutor* migrates from inshore areas to nearby offshore submerged coral reef sites to aggregate and spawn between November and February, on the south coast of Kenya. Using a range of methods, three spawning aggregation sites were located, aggregation formation was verified and spatial and temporal patterns investigated. Combined with the results of companion studies (Chapters 3 and 4), there is evidence that the aggregations were for spawning but we were unable to verify this in situ. Colour changes displayed by *S. sutor* in small schools were indicative of males, based on findings from other studies (Johannes et al. 1999; Colin et al. 2003), however, since no other spawning related behaviour was observed, we cannot conclude this colour change was associated with spawning. Both fisher interviews and site-based surveys provided evidence that fishers are targeting *S. sutor* populations at these aggregation sites. Twenty-seven fishers provided reliable information on these spawning sites, with three helping us locate and measure parameters in the field. UVC surveys, though not conclusive (*see below*), suggested that *S. sutor* were not always present on the three sites and therefore may only move to these offshore patch reefs to spawn. Acoustic telemetry provided evidence for this behaviour with six fish tagged and subsequently detected at spawning sites at intervals of up to three months in the spawning season, suggesting that at least some fish leave and return to the sites during the season. Tag-recaptures provided estimates of distances of movement of 2-3.5 km from inshore (putative) residence areas to aggregation sites. We had originally intended to include non-spawning fishing grounds in the array to identify catchment reefs (Nemeth et al. 2007). However, with limited range of the transmitters and the low number of receivers available, this was not possible and remains an important research question for management.

Collectively, these results support the interpretation that *S. sutor* only move to offshore patch reefs to spawn, similar to other rabbitfish studied (Hasse et al. 1977; Robinson et al. 2011; Kitalong 2012; *see also* Chapter 6). In Palau, fishers target schools of the dusky rabbitfish, *Siganus fuscescens*, inshore prior to migration to offshore spawning sites (Kitalong 2012). Our observations of

increased fishing activity in the form of boats and traps on the three aggregation sites during the lunar spawning period, combined with observations of fully hydrated ovaries in these catches and increased landings during aggregation periods (*see* Chapters 3 and 4) provide reinforcing evidence of reproduction at aggregation sites that are subject to a targeted fishery.

Seasonal and lunar spawning periodicity

Seasonal and lunar periodicity in spawning aggregation formation were inferred from patterns in UVC data and fishing effort at the sites, though neither of these were replicated across all months or lunar phases. Visual census surveys recorded a 23-fold increase in numbers of fish at the aggregation sites during December and February during full moon and third quarter providing the first *in situ* suggestive evidence of the seasonal and lunar periodicity of this phenomenon in *S. sutor* in Kenya. However, without pre- and post- survey data it is difficult to draw conclusions from these numbers. Further, the peak densities recorded by UVC were very low, less than 300 fish per site, in strong contrast to reports of *Siganus* spp. aggregations elsewhere where numbers up to 1000 have been observed (Robinson et al. 2007; Kitalong 2012). Such low densities make detection of patterns in spawning aggregation formation in a schooling species difficult. While we were unable to regularly count numbers of boats and traps on the aggregation sites across different seasons and lunar phases, the movement of boats away from nearshore areas to Sites A, B and C, combined with the concentrated fishing effort at these sites in December, January and February provides evidence of targeted aggregation fishing and this is corroborated by elevated catch rates from these sites during the reproductive season (*see* Chapter 3). This concentrated effort was observed at the same time that UVC recorded elevated numbers of *S. sutor* at these sites. Future research should establish a regular and comprehensive UVC and *in situ* fishery monitoring protocol to confirm these preliminary results.

Fishers report that *S. sutor* abundance peaks at aggregations between October and January, with a protracted season that extends from October until April (*see* Chapter 3). Regardless, we observed detections of tagged fish as late as May. These data may suggest that the reproductive season is more protracted than fishers report though GSI data do not demonstrate reproductive activity beyond February (*see* Chapter 4). Recent work shows that fisher perception of spawning times may not concur with actual reproductive periods and demonstrate the need for independent *in situ* verification of reproductive times (Hamilton et al. 2012a, b). Gonadosomatic indices of reproductive activity in *S. sutor* indicate a bimodal spawning season, with peaks in activity from November to January and June to July, which may be common among siganids (Takemura et al. 2004).

UVC surveys and acoustic tagging provided evidence of aggregation formation on (LD 14-18) and just after (LD 19-20) the full moon, similar to *S. sutor* populations in Seychelles (Robinson et al. 2011; *see* Chapter 6). This lunar periodicity of aggregation formation was also understood by Kenyan fishers. However, UVC abundance estimates of *S. sutor* at the three aggregation sites during the full moon were high in December and February but not in January. We suggest this anomaly may reflect slight inter-monthly variation in timing of aggregation formation relative to the full moon which may have affected our ability to detect aggregations in January when our last survey date for that month was on LD 16. Measures of oocyte development partially support these results, though show a more protracted lunar period with hydrated oocytes (indicative of imminent spawning, West 1990) present from first quarter through full moon and into the last quarter periods (~ LD 9-24; *see* Chapter 4). Based on this combined information, we conclude that aggregation formation and spawning is variable and likely occurs between LD 14 and 20, though *S. sutor* also appears to spawn outside this period (*see* Chapter 4). Inter-monthly and annual variability in spawning and aggregation formation has been reported in other aggregative spawners (Samoilys 1997b).

Spawning aggregation site fidelity and residency

Information on site fidelity and residency time is only possible to obtain through detection of known individuals at the spawning aggregation sites. Acoustic telemetry can provide such data but is constrained by a number of factors related to the technology employed, the physical environment and the species' behaviour. Whereas the manufacturer stated that V7 tags had an optimal range of 300 m, range testing at our site found an effective detection range of only 25 m (*this study*; Chapter 6). Further, coral reef environments are 'noisy', which may interrupt detections of fish within range (*see* Chapter 6). Moreover, the complex topography of coral reefs makes it difficult to moor VR2 receivers on the bottom and position them with clear line-of-sight. Confounding these physical constraints was the high mobility of *S. sutor*, which may have resulted in fish moving out of receiver range before they could be detected. In retrospect, suspending the receivers high in the water column from a submerged buoy and chain would have increased the line of sight, although simultaneously increasing the potential for loss of equipment. This should be considered in follow up studies. Given the limited range, increasing the density of the array may improve results in future studies. Nevertheless, with two receivers on each of the aggregation sites, the tag detections did provide evidence of return movements of *S. sutor* to spawning sites, evidence of fidelity and estimates of residence times.

Fidelity to a single spawning aggregation site appears to be a common feature of groupers that migrate to spawn in transient aggregations (Bolden 2000; Samoilys 2000; Rhodes and Tupper 2008) and may be indicative of cultural transmission of information on traditional spawning sites between con-specifics (Warner 1988, 1990). The trends in acoustic data were consistent with the patterns in both aggregation (as determined from UVC) and fishing effort development, indicating that *S. sutor* are only present at a single aggregation site for 3 to 6 days (*this study*) or 4 to 7 days (Chapter 3) per month during the spawning season. Further, *S. sutor* were only detected at the aggregation site of tagging suggesting that the fish consistently use the same site for spawning, providing preliminary evidence for aggregation site fidelity. Moreover, the spawning aggregation sites are only 1 to 1.3 km apart, well within the mobility range of *S. sutor* as determined by the recapture of tagged fish on fishing grounds up to 3.3 km away from the spawning sites. This contrasts with Seychelles where fidelity was not absolute, with around 15% of detections occurring at spawning sites other than the site of tagging (*see* Chapter 6). Interestingly, the two recaptures at Mabarani fishing ground showed that fish from a single fishing ground (assumed to be a non-spawning, home range area) do not use the same aggregation site. Therefore, aggregations appear to be comprised of fish from different home range areas, suggesting complex factors are involved in cultural transmission of information on spawning sites among populations of *S. sutor*.

Residency time at an aggregation site and the diel periodicity of detections did not yield clear patterns in the use of aggregation sites by *S. sutor* due to the limited area coverage of the receivers. Moreover, termination in fish detections could be due to capture by fishers. Within the context of these constraints, the acoustic detections suggest individual *S. sutor* remained on the aggregation sites for at least 6 hours and up to just over 2 days. Detections between 06:00 hrs and 19:00 hrs were indicative of daytime activity at the sites. No detections at night may be because *S. sutor* rest inside the reef beyond the range of the receivers. Alternatively, *S. sutor* may forage at night beyond the patch reefs. The increase in detections for 2 fish at sunset may be indicative of spawning, however, more detailed histological work is required to determine finer-scale patterns in egg development and hence spawning times (e.g. Samoilys and Roelofs 2000).

In summary, the acoustic telemetry was limited by interrelated constraints of environment, technology and fish behaviour, but provided evidence of seasonal and lunar migration of *S. sutor* to offshore aggregation sites to spawn, as well as a high degree of site fidelity. Further evidence for this phenomenon was provided by fishers' knowledge on spawning behaviour, fishing activity on the aggregation sites and underwater visual observation. *S. sutor* returned to the same offshore coral patch reef aggregation site to spawn on subsequent full moons, migrating up to 3.3 km from

fishing grounds closer to shore. Since *S. sutor* is a major component (~40%) of artisanal catches in Kenya (McClanahan and Mangi 2004, Maina et al. 2008, Locham et al. 2010, Samoilys et al. 2011b; Chapter 3) the implications of its offshore spawning aggregations and the fishery that targets them must now be considered in management discussions involving fishers.