

Spawning aggregation dynamics of brown-marbled grouper and camouflage grouper at a remote Indian Ocean atoll

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ABSTRACT: The protection of grouper spawning aggregations is a global conservation issue: populations of many grouper species are threatened with collapse due to exploitation of this critical life history behaviour by fisheries. Effective protection of spawning aggregations requires information on spawning site fidelity, residence time and timing of arrivals at, and departures from, the site. To estimate these parameters at a spawning aggregation site at Farquhar Atoll, southern Seychelles, 12 brown-marbled groupers *Epinephelus fuscoguttatus* and 20 camouflage groupers *E. polyphkadion* were tagged with acoustic transmitters, and their presence and absence was monitored by an array of acoustic receivers positioned at the site over 2 spawning seasons (2010/2011 and 2011/2012). Spawning aggregations formed during 3 consecutive spawning months each season and overlapped spatially and temporally in the 2 species. Intra- and inter-season site fidelity was high, with 91.7% of tagged *E. fuscoguttatus* and 89.5% of tagged *E. polyphkadion* detected at the site 1 yr after tagging. The majority (2010/2011: 82.4%, 2011/2012: 80.0%) of fish detected in a spawning season visited the site during at least 2 spawning months. Residence time at the fish spawning aggregation site was influenced by sex (*E. fuscoguttatus* only) and spawning month (both species). Distinct periodicity in lunar timing of arrivals and departures was observed in both species. This study highlights the spatio-temporal scales involved during spawning aggregations of 2 long-lived, slow-growing coral reef fishes, which need to be considered for their effective management.

KEY WORDS: Spawning aggregation dynamics · Lunar and diel periodicity · Residence time · Site fidelity · Groupers · *Epinephelus* · Seychelles

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INTRODUCTION

The annual global catch of wild groupers (Epinephelinae) is close to 200 000 tons (Tupper & Sheriff

2008) with market demand continuing to increase, especially within the Southeast Asian-based Live Reef Food Fish Trade. Many species of groupers spawn as part of transient fish spawning aggrega-

tions (FSAs) comprising several hundred to several thousand individuals (Rhodes & Sadovy 2002b, Pet et al. 2005, Nemeth 2012). These FSAs are often spatially and temporally predictable (Rhodes & Sadovy 2002b, Nemeth et al. 2007, Robinson et al. 2008) and at many locations, fisheries have developed to specifically target them (Olsen & LaPlace 1979, Sala et al. 2001, Erisman et al. 2012, Sadovy de Mitcheson & Erisman 2012). Targeted fishing of FSAs has led to demographic changes (Beets & Friedlander 1999, Rhodes et al. 2011), stock decline (Aguilar-Perera 2006) and, in extreme cases, the disappearance or effective reproductive failure of aggregating populations (Johannes et al. 1999, Mangubhai et al. 2011).

Camouflage grouper *Epinephelus polyphkadion* and brown-marbled grouper *E. fuscoguttatus* are 2 species that form spawning aggregations. Both species are economically important and are targeted by coral reef fisheries throughout the Indo-Pacific (Pears 2012, Rhodes 2012). Similar to other tropical groupers, *E. fuscoguttatus* and *E. polyphkadion* are slow-growing, late-maturing and occur at low densities throughout much of their range (Russell et al. 2006, Pears 2012), except when they form spawning aggregations (Rhodes & Sadovy 2002b, Robinson et al. 2008). They are both listed as Near Threatened on the 2012 IUCN Red List of Threatened Species due to their susceptibility to overfishing.

At Farquhar Atoll, in the southern Seychelles, mixed *Epinephelus fuscoguttatus* and *E. polyphkadion* spawning aggregations occur on the edge of the main channel leading into the lagoon (Robinson et al. 2008). The aggregations form over 3 consecutive months between November and February, with the actual months of the aggregation showing a certain degree of inter-annual variability (Robinson et al. 2008). The number of months over which *E. polyphkadion* form spawning aggregations at Farquhar is consistent with observations made in a number of other locales throughout their range (Johannes et al. 1999, Rhodes & Sadovy 2002b, Hamilton et al. 2012), but there appears to be more variability in the duration of the reproductive season among locations for *E. fuscoguttatus* (Pet et al. 2005, Hamilton et al. 2012, Rhodes 2012, Rhodes et al. 2012). Recaptures and underwater observations of tagged *E. polyphkadion* at the Farquhar FSA site suggest a certain degree of inter- and intra-seasonal FSA site fidelity (Robinson et al. 2008). FSA site fidelity appears to be a common trait among some aggregation-forming groupers, including these 2 species (Johannes et al. 1999, Rhodes et al. 2012). Observa-

tions of gonads in fish caught directly from the aggregations in the weeks preceding spawning suggests that males begin aggregating before females (Robinson et al. 2008), which agrees with observations from Pohnpei, Micronesia (Rhodes & Sadovy 2002b, Rhodes et al. 2012). There is evidence that spawning takes place around the new moon at Farquhar (Robinson et al. 2008), similar to Palau and Australia (Johannes et al. 1999, Pears et al. 2007), but different to at least 1 other location in Micronesia and Komodo, Indonesia, where spawning occurs around the full moon (Mangubhai et al. 2011, Rhodes et al. 2012).

Many studies that have contributed to our understanding of spawning aggregation dynamics of *Epinephelus fuscoguttatus* and *E. polyphkadion* have used fishing-based mark-recapture methods (Rhodes & Sadovy 2002b, Robinson et al. 2008). As a result of the extractive nature of fishing-based studies and the difficulty in identifying tagged individuals underwater, little information is available on the dynamics of individuals across multiple spawning months or seasons. Acoustic receivers can be used to monitor the presence and absence of acoustically tagged fish at FSA sites and make it possible to study the same individuals over multiple spawning months and seasons. There is an urgent need to improve knowledge of the spawning aggregation dynamics of these 2 species among spawning months and spawning aggregation seasons to guide potential management and conservation measures. For example, information is required regarding the frequency of individual visits per season, residence time, and the influence of rhythmic natural cycles on the timing of arrivals and departures of aggregating fish at FSA sites.

We used acoustic telemetry to study the spawning aggregation dynamics of *Epinephelus fuscoguttatus* and *E. polyphkadion* over 2 complete spawning seasons and 6 spawning months at the Farquhar FSA site verified by Robinson et al. (2008). The aim of the study was to provide fundamental data on the spawning aggregation characteristics of the 2 species. Where relevant, knowledge of spawning aggregation characteristics is used to propose management actions. The specific objectives were to (1) determine fidelity and frequency of visitations of acoustically tagged fish to the FSA site, (2) calculate residence times of acoustically tagged fish at the FSA site, and (3) describe rhythmic cycles in the form of lunar and diel patterns in the timing of arrivals and departures of tagged fish at the FSA site.

MATERIALS AND METHODS

Study site

The study was undertaken at an *Epinephelus fuscoguttatus* and *E. polyphemus* spawning aggregation site at Farquhar Atoll, southern Seychelles (Fig. 1) between January 2010 and May 2012. The FSA site is a carbonate patch reef with a horizontal area of 7700 m² and an average depth of 10 m.

Fish tagging

Tagging took place at the study site between 11 and 15 January 2010. All fish were caught using hook and line (baited with bonito *Euthynnus affinis*) from a small boat (ca. 7 m overall length) anchored at the site. The smallest size *Epinephelus fuscoguttatus* and *E. polyphemus* tagged were 70 and 56 cm (total length [TL]) respectively, well above the size of 50% maturity for females (*E. fuscoguttatus*: 408 mm, *E. polyphemus*: 352 mm) from other populations (Pears et al. 2006, Rhodes et al. 2011). Once hooked, each fish was brought slowly to the surface to reduce the risk of

barotrauma that is common in groupers caught below 16 m and rapidly brought to the surface (Alós 2008). Fish were placed dorso-ventrally in a stretcher and a wet towel was placed over the head to reduce stress. Total length was measured to the nearest cm and fish were tagged externally using individually numbered T-bar tags (Floy) inserted at the 4th dorsal pterygiophore. Whenever possible, fish were sexed based on the appearance of the gonopore and by stripping for the presence of milt or eggs (Robinson et al. 2008). In the event that no milt or eggs were observed, the sex of the fish was recorded as unidentified. A Vemco V13-1L-S256 acoustic transmitter (69 kHz, 90 s delay, 879 d battery life) (Amirix Systems), disinfected in absolute ethanol, was inserted in the body cavity through a small incision made 2 cm anterior of the anus. The incision was closed using 2 non-absorbable polynylon sutures. Tagged fish were released at the point of capture within 5 min of being captured.

Acoustic array

To characterise residence time, site fidelity, diel and lunar timing of arrivals and departures, an array

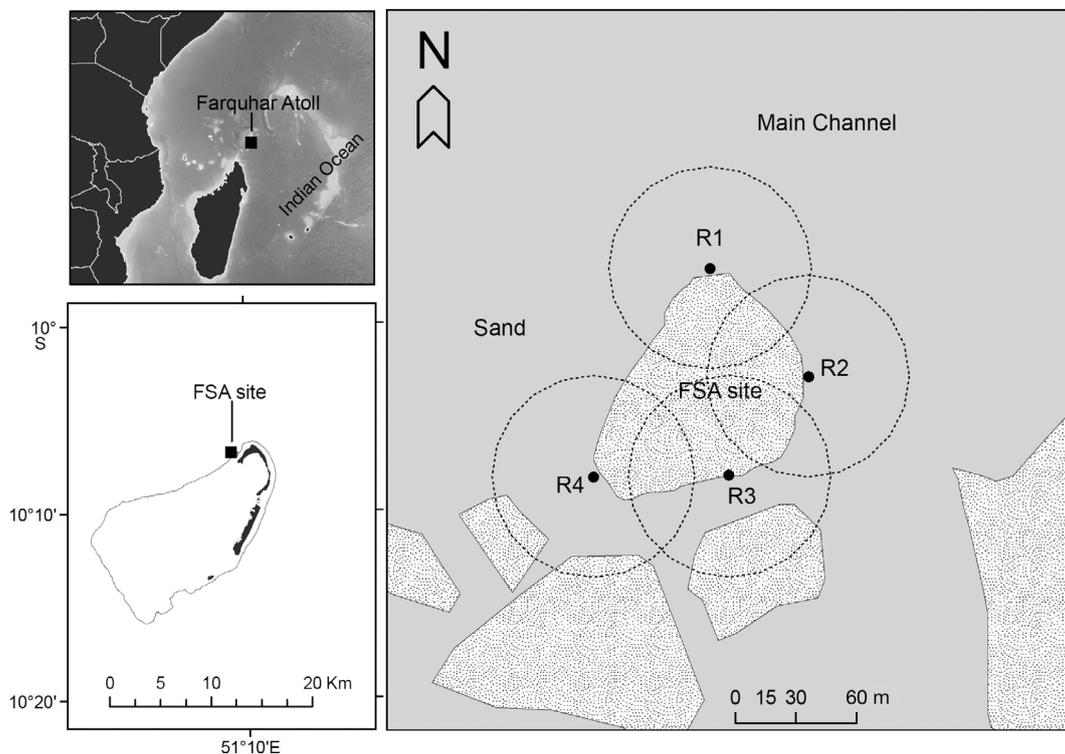


Fig. 1. Location of the study fish spawning aggregation (FSA) site in the main channel of Farquhar Atoll, southern Seychelles, showing the location of acoustic receivers that (●, R1 to R4) formed part of the acoustic array. The dashed lines around each receiver represent the 50 m detection range; dotted areas represent reefs; grey represents sandy areas. Contours around the islands and continent on the large scale map (upper left) indicate differences in water depths, with deeper greys representing greater depths

of 4 VR2 and VR2W acoustic receivers (R1, R2, R3, R4) (Amirix Systems) was deployed around the study site on 15 January 2010; these were removed on 11 May 2012. The receivers were secured to the reef bottom on concrete blocks that had been strategically placed around the study area to maximise detections of acoustically tagged fish. Receivers were replaced every 6 to 12 mo for servicing and download of stored data. For unknown reasons, receiver R3 did not make any detection after it was serviced in May 2011. Acoustic tag range testing undertaken during the day recorded 32% of transmitted signals at 50 m and 0% at 100 m distance from the receiver. Given an estimated acoustic tag range of 50 m, the array design covered approximately 95% of the study site up to May 2011 and 79% thereafter.

Data analyses

Our definition of a spawning season is based on observations of spawning aggregations made at the same FSA site by Robinson et al. (2008) and encompasses the months of November to February. We excluded all acoustic detections that were made during the 2009/2010 spawning season, as data for this season was incomplete as fish were tagged in the middle of the spawning season (January 2010). Additionally, we excluded all detections that were made outside the spawning seasons and all detections of (1) fish ID 59061, which appeared to reside at the FSA site for most of the study period, and (2) fish ID 59051 for the 2011/2012 spawning season, as it remained at the FSA site over multiple spawning months. We defined a spawning month as the period within a spawning season during which a spawning event is believed to have taken place. The arrival of an acoustically tagged fish at the FSA site marked the start of the spawning month, while the departure of the last acoustically tagged fish from the site, with no further acoustic detections for a 7 d period, marked the end of the spawning month. Acoustic data indicated that there were 3 distinct but consecutive spawning months in both the 2010/2011 (Year 1) and 2011/2012 (Year 2) spawning seasons.

Fidelity to the FSA site, for each species, was calculated as the proportion of acoustically tagged fish detected during a spawning season relative to the total number of fish tagged. Frequency of visitation was calculated as the number of spawning months that an acoustically tagged fish was detected at the FSA site during a spawning season. Residence time of a tagged fish at the FSA site was calculated as the

time between its first and last detection by the acoustic array using a maximum blanking period (MBP) (Capello et al. 2012) of 7 d. The MBP is the maximum time during which a tagged fish was not detected by the acoustic receiver array at the FSA site but was still considered to be at the site (Capello et al. 2012). A residence time based on a 7 d MBP was justified in our study as we were interested in large-scale (between spawning months) as opposed to small-scale (within spawning months) temporal dynamics. In order to consider repeated measures of residence time for the same individuals, a linear mixed-effects (LME) model (Laird & Ware 1982), using maximum likelihood estimation, was used to model the residence time of acoustically tagged fish at the FSA site. Year (1, 2), species (*Epinephelus fuscoguttatus*, *E. polyphekadion*), sex (male, female, unidentified) and spawning month (1, 2, 3) were used as fixed effects, while fish ID was used as a random effect. After the first run of the model, non-significant effects (species and year) were removed and the model was run again for each species, using sex and spawning month as fixed effects and fish ID as a random effect, to come up with the best prediction of residence time for each species, based on sex and spawning month. Linear regression was used to test for the influence of fish size (TL) on the number of spawning months tagged fish were detected at the FSA site by species, with data pooled for the 2010/2011 and 2011/2012 spawning seasons. Fish recaptured or known to have died ($n = 2$) during the study were omitted from the analysis.

To determine periodicity in the lunar timing of arrivals and departures of tagged fish at the FSA site, the lunar day in relation to the new moon ($-1 = 1$ d before new moon, $+1 = 1$ d after new moon, etc.) was calculated for each arrival at, and departure from, the site. To meet the assumption of independence, a mean lunar timing of arrival and departure was calculated for each fish (Childs et al. 2008). The mean lunar timing of arrival and departure of each fish was then converted into angles with $\pm 12.2^\circ$ representing 1 d either side of the new moon (using a 29.5 d lunar cycle). The angles representing mean lunar timing of arrivals and departures of tagged fish detected at the FSA site in relation to the new moon were then analysed by means of Rayleigh's uniformity test with $\alpha = 0.5$ (Batschelet 1981) using the Oriana 4 software package (Kovach Computing Services). Rayleigh's Uniformity test determines whether the angles representing the mean lunar timing of arrivals and departures from the FSA site exhibited non-randomness towards a particular lunar day. The effects of

species and sex on individual observations of lunar timing of arrivals and departures of tagged fish at the FSA site were analysed using LME models. Species effect was tested using species as a fixed effect and fish ID as a random effect, whereas the influence of sex was tested for each species using sex as a fixed effect and fish ID as a random effect.

Analysis of periodicity in diel timing of arrivals and departures of tagged fish at the FSA site was undertaken using a protocol similar to that for the analysis of periodicity in lunar timing of arrivals and departures. The hour at which a tagged fish arrived and left the FSA site was calculated in relation to midnight ($-1 = 1$ h before midnight, $+1 = 1$ h after midnight etc.). The mean diel timing of arrival and departure at the FSA site in relation to midnight was converted into angles, with $\pm 15^\circ$ representing 1 h either side of midnight, etc. The mean arrival and departure angles were then analysed using Rayleigh's uniformity test with $\alpha = 0.5$ to determine whether mean diel timing of arrivals and departures at the FSA site exhibited non-randomness towards a particular time of the day. An LME model with species as a fixed effect and fish ID as a random effect was applied on individual observations of diel timing of arrival and departure hour in relation to midnight to test for the influence of species on diel timing of arrivals and departures of tagged fish at the FSA site. The effect of sex on diel timing of arrival and departure hour relative to midnight was tested individually for each species using other LME models, with sex as a fixed effect and fish ID as a random effect.

RESULTS

Number of fish tagged and recaptured

Twelve *Epinephelus fuscoguttatus* (70 to 93 cm TL) and 20 *E. polyphkadion* (56 to 67 cm TL) were tagged at the FSA site. Tagged *E. fuscoguttatus* included 4 females, 5 males and 3 individuals of unidentified sex, whereas tagged *E. polyphkadion* included 7 females, 9 males and 4 individuals of unidentified sex. One tagged *E. polyphkadion* (ID 59052) was recaptured by fishermen in the lagoon of the atoll in April 2011 (exact date not known), 6 km away from the FSA site after a minimum of 444 d at liberty. In January 2012, a tag that was inserted in a 56 cm *E. polyphkadion* (ID 59041) was found inside the gut of a *Plectropomus punctatus* of about 45 cm caught outside the lagoon of the atoll about 10 km from the FSA site.

Site fidelity and frequency of visitations

Fidelity to the FSA site was high, as 91.7% of tagged *Epinephelus fuscoguttatus* and 89.5% of tagged *E. polyphkadion* were detected by the receiver array during the 2010/2011 spawning season, approximately 1 yr after tagging (Fig. 2). However, the percentage of tagged *E. fuscoguttatus* and *E. polyphkadion* detected during the 2011/2012 spawning season reduced to 66.7 and 47.4%, respectively. Tagged *E. polyphkadion* were detected in up to 2 spawning months per season, while tagged *E. fuscoguttatus* were detected in up to 3 spawning months (Fig. 2). During the 2010/2011 and 2011/2012 spawning season, 80.0 and 82.4%, respectively, of the fish detected at the FSA site were present in more than 1 spawning month. Two thirds (66.7%) of the tagged females of both species were detected at the FSA site in at least 2 spawning months during a spawning season. In both species, fish size (TL) had no influence on the number of spawning months in which a tagged fish was detected at the FSA site.

Residence time

Residence time of tagged *Epinephelus fuscoguttatus* and *E. polyphkadion* at the FSA site ranged between 0.1 and 60.3 d and between 4.0 and 37.1 d, respectively, and was variable between species, among spawning months and among sexes (Table 1). Predicted residence time did not differ significantly between species and between years but it did differ among sexes (*E. fuscoguttatus* only; LME: $F_{2,23} = 7.2$, $p = 0.004$; Fig. 3a, Table 2) and spawning months (LME: *E. fuscoguttatus*:

Table 1. *Epinephelus fuscoguttatus* and *E. polyphkadion*. Observed residence time in days (mean \pm SD), according to spawning month and sex, of tagged fish at the fish spawning aggregation site during the 2010/2011 (Year 1) and 2011/2012 (Year 2) spawning seasons combined

	Residence time	
	<i>E. fuscoguttatus</i>	<i>E. polyphkadion</i>
Spawning month		
Month 1	23.02 \pm 15.71	14.43 \pm 6.60
Month 2	9.84 \pm 5.58	10.05 \pm 4.21
Month 3	6.15 \pm 4.60	7.85 \pm 1.29
Sex		
Females	7.37 \pm 5.10	8.68 \pm 4.06
Males	22.41 \pm 12.92	12.86 \pm 6.24
Unidentified	3.97 \pm 3.08	11.90 \pm 4.21

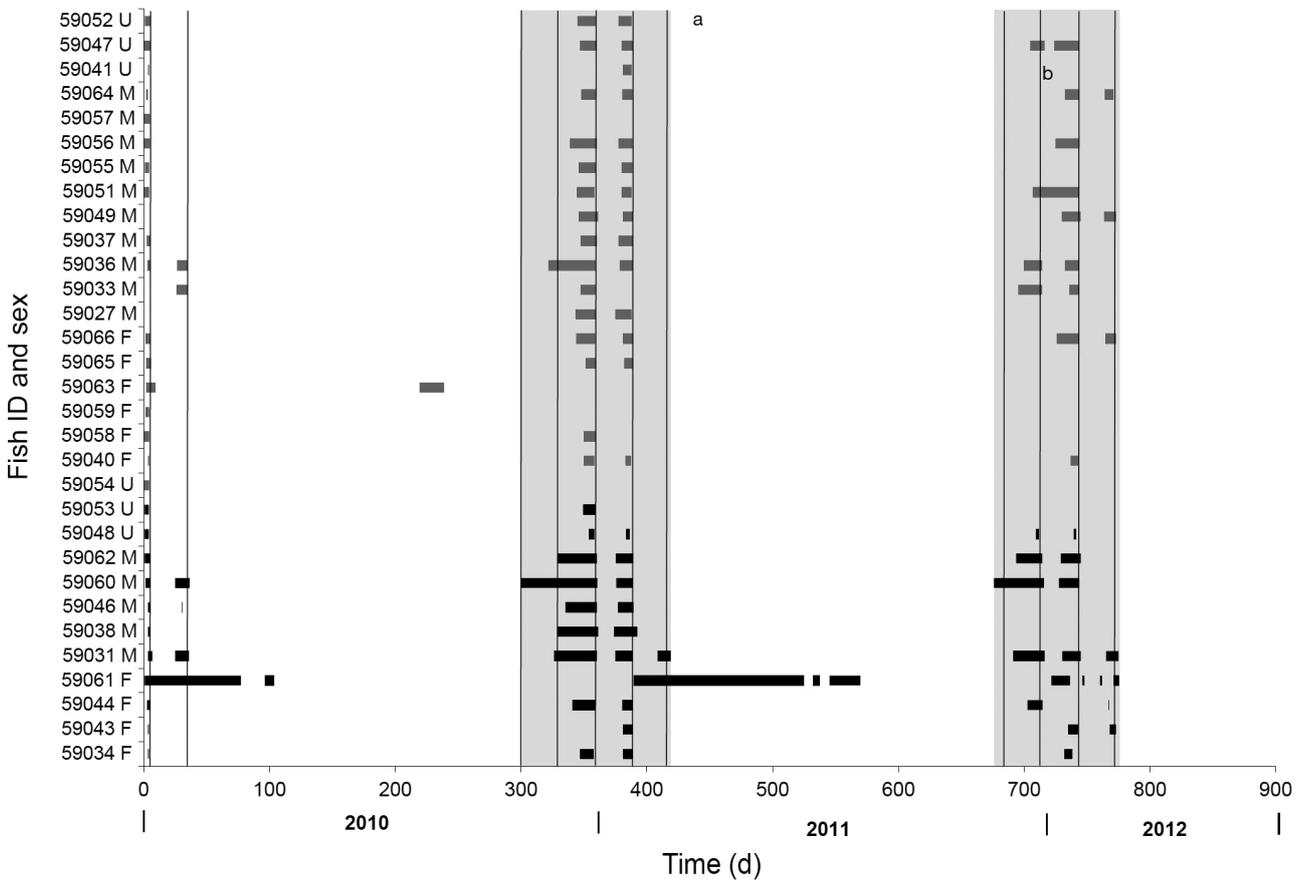


Fig. 2. *Epinephelus fuscoguttatus* and *E. polyphkadion*. The presence and absence of acoustically tagged fish at the fish spawning aggregation (FSA) site between January 2010 and May 2012. The horizontal bars indicate residence time of tagged *E. fuscoguttatus* (black) and *E. polyphkadion* (dark grey). The letters after the fish tag ID code indicate the sex of the fish (F = female, M = male, U = unidentified sex). The areas shaded light grey represent the 2010/2011 (Year 1) and 2011/2012 (Year 2) spawning seasons. Black vertical lines represent the day of the new moon within the spawning seasons. ^aFish recaptured in April 2011. ^bTag was found in the gut of a *Plectropomus punctatus* caught in January 2012

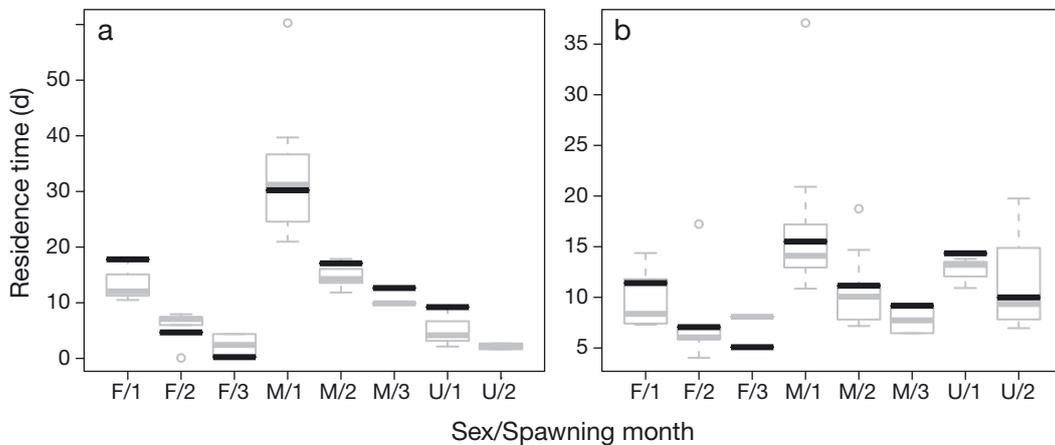


Fig. 3. *Epinephelus fuscoguttatus* and *E. polyphkadion*. Boxplots (in grey) showing observed residence time of acoustically tagged (a) *E. fuscoguttatus* and (b) *E. polyphkadion* at the fish spawning aggregation site during the spawning seasons of the entire study period in relation to sex and spawning month. Boxes show the 25th to 75th percentiles; the black line represents the predicted value from fixed effects of the linear mixed-effects (LME) models; the grey line is the median; and the whiskers the lowest and highest observation. F = female, M = male, U = unidentified sex, 1 = first spawning month, 2 = second spawning month, 3 = third spawning month

$F_{2,22} = 15.58$, $p = 0.001$; *E. polyphkadion*: $F_{2,25} = 4.48$, $p = 0.022$; Fig. 3, Table 2). The LME model showed that *E. fuscoguttatus* males spent significantly more time at the FSA site than females and individuals of unidentified sex, and that there was no significant difference in residence time between females and individuals of unidentified sex (Table 2). The predicted residence time was significantly higher during the first than the second and third spawning month of the seasons for *E. fuscoguttatus* but not significantly different between the second and third spawning month (Table 2). Conversely, the predicted residence time for *E. polyphkadion* was significantly higher during the first than the second spawning month of the seasons but there was no significant difference between the first and third spawning month and between the second and third spawning month of the seasons (Table 2).

Lunar timing of arrivals and departures

Distinct periodicity in the mean lunar timing of arrivals and departures of tagged *Epinephelus fuscoguttatus* and *E. polyphkadion* at the FSA site were observed (Fig. 4). In *E. fuscoguttatus*, mean lunar timing of arrivals occurred from around the third quarter to the new moon, while in *E. polyphkadion*, it occurred throughout the period between the full and new moon. Although there was considerable variability in the average lunar timing of arrivals and departures between species and among sexes (Table 3), the LME models showed that mean lunar timing of arrivals did not significantly differ among sexes in both species. All mean departures from the FSA site occurred within a period of 5 d after the new moon (Table 3). While

there was no significant difference among sexes in the mean lunar timing of departures of *E. polyphkadion* from the FSA site, male *E. fuscoguttatus* left the site later than females ($t_7 = 4.37$, $p = 0.003$) and individuals of unidentified sex ($t_7 = 3.75$, $p = 0.007$). However, there was no difference in the lunar timing of departures between *E. fuscoguttatus* females and individuals of unidentified sex.

Diel timing of arrivals and departures

Periodicity was observed in the average diel timing of arrivals (*Epinephelus polyphkadion* only) and departures (both species) at the FSA site (Fig. 5). The percentage of mean diel arrivals was divided equally between day and night in *E. fuscoguttatus* but was mostly (87.5%) concentrated at night in *E. polyphkadion*. On average, both male and female *E. fuscoguttatus* arrived at the FSA site approximately 4 h after midnight, whereas male and female *E. polyphkadion* arrived approximately 1 and 2 h after midnight, respectively (Table 4). However, the LME models found that the average diel timing of arrivals did not differ significantly among sexes in both study species. All average diel departures from the FSA site occurred at night in both *E. fuscoguttatus* and *E. polyphkadion* (Fig. 5). There were significant differences among sexes in the diel timing of departures in *E. polyphkadion* (LME: $F_{2,13} = 4.7$, $p = 0.03$) but not in *E. fuscoguttatus*. Mean time of departure was close to midnight for male and female *E. fuscoguttatus*, whereas it was 3.4 h after midnight for individuals of unidentified sex (Table 4). Female *E. polyphkadion* left the FSA site on average 3.1 h after midnight, after males ($t_{13} = -2.99$, $p = 0.01$) and individuals of unidentified sex ($t_{13} = -2.25$, $p = 0.04$), which left the site on average 4 h earlier (Table 4). There was no significant difference in the time that *E. polyphkadion* males and individuals of unidentified sex left the site, with both groups leaving on average 1 h before midnight (Table 4).

Table 2. *Epinephelus fuscoguttatus* and *E. polyphkadion*. Comparison of residence times of acoustically tagged fish at the fish spawning aggregation site among sex and spawning months using linear mixed-effect models. **Bold** p-values are significant ($p < 0.05$)

	<i>E. fuscoguttatus</i>			<i>E. polyphkadion</i>		
	Estimate	t	p	Estimate	t	p
Comparison between sex						
Males vs. females	-12.42	-3.99	0.005	-4.09	-2.08	0.06
Males vs. unidentified sex	-21.00	-5.20	0.001	-1.56	-0.51	0.62
Females vs. unidentified sex	-8.58	-1.95	0.09	2.93	1.12	0.28
Comparison between spawning months						
Month 1 vs. Month 2	-13.13	-4.98	0.001	-4.35	-2.71	0.01
Month 1 vs. Month 3	-17.57	-4.18	0.004	-6.33	-1.98	0.06
Month 2 vs. Month 3	-4.44	-1.09	0.29	-1.98	-0.62	0.54

DISCUSSION

The use of acoustic telemetry to study the spawning aggregation dynamics of *Epinephelus fuscoguttatus* and *E. polyphkadion* showed that

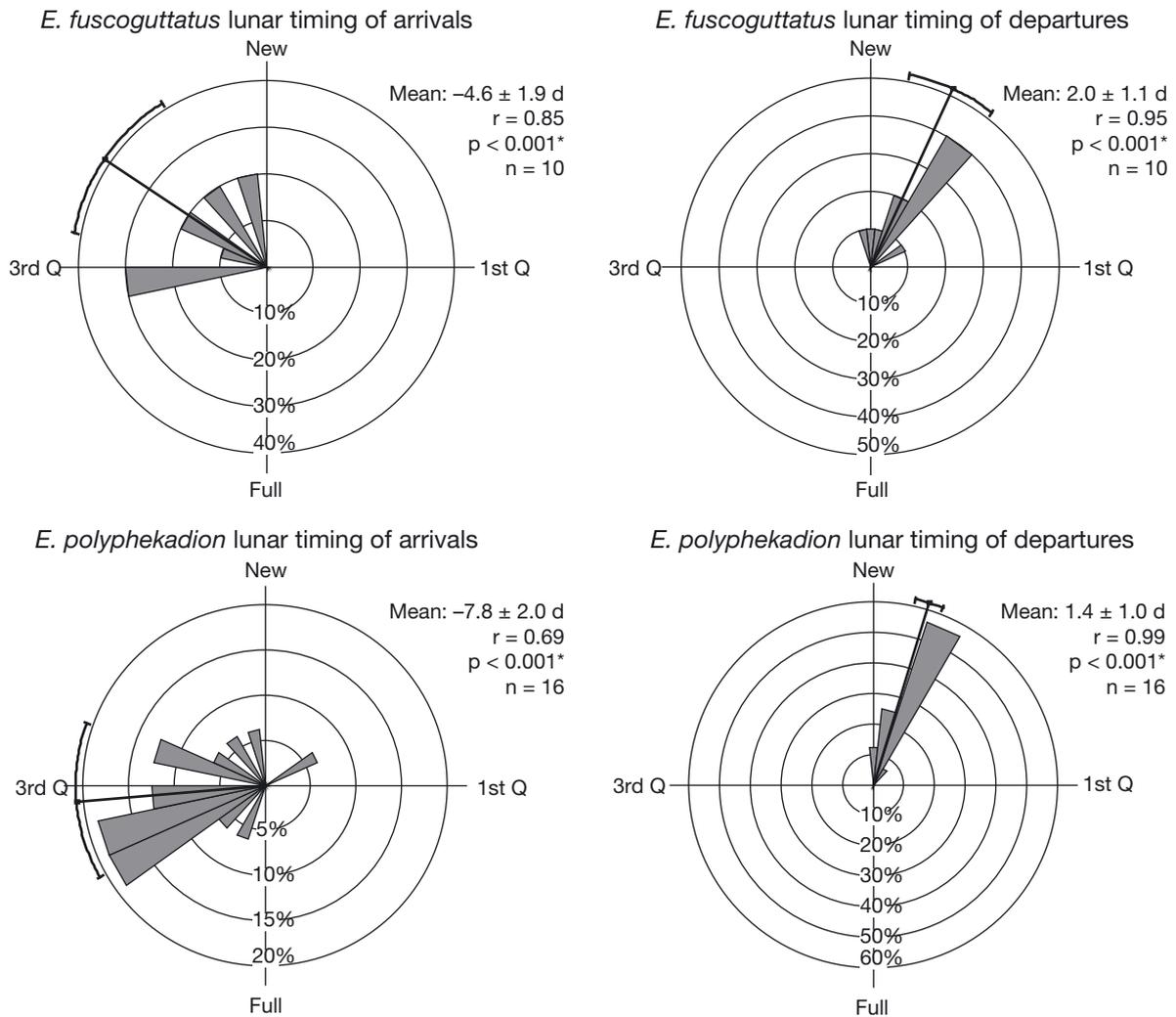


Fig. 4. *Epinephelus fuscoguttatus* and *E. polyphkadion*. Percentage lunar timing of arrivals and departures of acoustically tagged fish at the fish spawning aggregation (FSA) site. Mean arrival and departure day are superimposed. Q = quarter, mean = mean arrival or departure day in relation to the new moon \pm 95% CI, r = length of mean vector, n = number of samples, p = probability of data being randomly distributed (Rayleigh test of randomness: $\alpha = 0.05$), and * indicates significant difference. Note that mean timing of arrivals and departures was calculated for each fish, as the majority of individuals recorded more than one residence time at the site

Table 3. *Epinephelus fuscoguttatus* and *E. polyphkadion*. Observed day of arrival and departure (mean \pm SD) relative to the day of the new moon of tagged fish at the fish spawning aggregation site according to sex for the 2010/2011 (Year 1) and 2011/2012 (Year 2) spawning seasons combined

Species	Day of arrival (mean \pm SD)			Day of departure (mean \pm SD)		
	Females	Males	Unidentified sex	Females	Males	Unidentified sex
<i>E. fuscoguttatus</i>	-3.90 ± 6.61	-4.56 ± 8.38	-3.80 ± 2.49	0.73 ± 2.00	3.17 ± 1.10	0.40 ± 1.14
<i>E. polyphkadion</i>	-7.40 ± 3.72	-6.58 ± 7.59	-5.57 ± 8.54	1.30 ± 0.95	1.62 ± 0.90	1.43 ± 1.40

arrival at, and departure from, the FSA site were influenced by diel and lunar cycles. Tagged fish of both species also showed high site fidelity, with most fish being detected at the spawning site in at least 2

spawning months each season. Mean residence time at the FSA site differed among spawning months and sexes (*E. fuscoguttatus* only), but was not influenced by species or fish length.

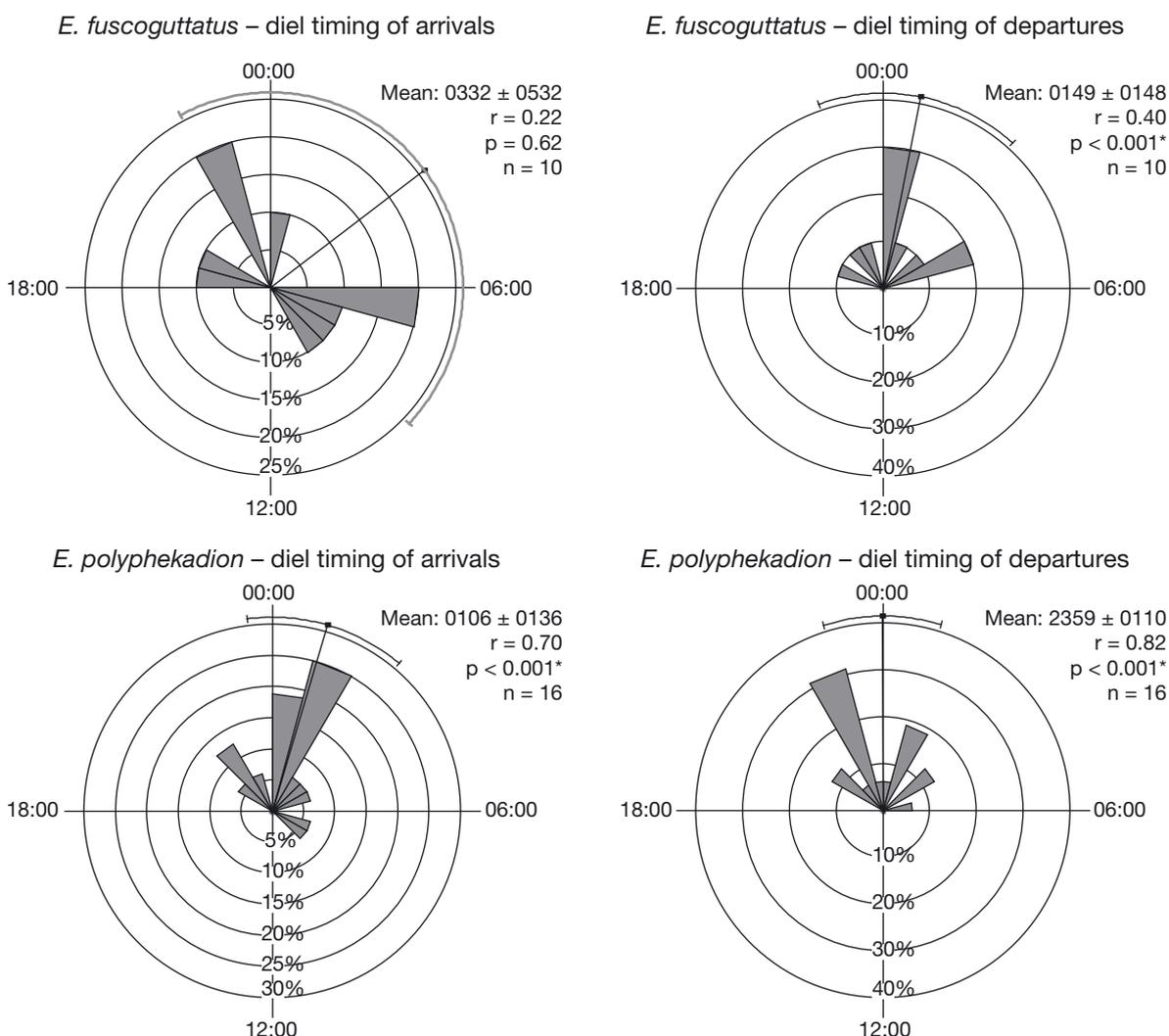


Fig. 5. *Epinephelus fuscoguttatus* and *E. polyphekadion*. Percentage diel timing of arrivals and departures of acoustically tagged fish at the fish spawning aggregation (FSA) site. Mean arrival and departure time are superimposed. Mean = mean arrival or departure time \pm 95% CI, r = length of mean vector, n = number of samples, p = probability of data being randomly distributed (Rayleigh test of randomness: $\alpha = 0.05$), and * indicates significant difference. Note that mean timing of arrivals and departures was calculated for each fish, as the majority of individuals recorded more than one residence time at the site

Table 4. *Epinephelus fuscoguttatus* and *E. polyphekadion*. Observed time (h) of arrivals and departures (mean \pm SD) relative to midnight of tagged fish at the fish spawning aggregation site according to sex for the 2010/2011 (Year 1) and 2011/2012 (Year 2) spawning seasons combined

Species	Time of arrival (mean \pm SD)			Time of departure (mean \pm SD)		
	Females	Males	Unidentified sex	Females	Males	Unidentified sex
<i>E. fuscoguttatus</i>	3.73 \pm 7.04	3.50 \pm 6.76	-5.40 \pm 4.83	-0.36 \pm 6.74	0.11 \pm 4.78	3.40 \pm 7.67
<i>E. polyphekadion</i>	1.10 \pm 3.54	1.54 \pm 5.00	1.29 \pm 4.15	3.10 \pm 4.38	-1.00 \pm 3.86	-1.00 \pm 0.00

Site fidelity, frequency of visitations and residence time

The majority of tagged individuals exhibited high FSA site fidelity within and among spawning sea-

sons. Equivalent levels of fidelity to spawning sites have been documented in *Epinephelus fuscoguttatus* (Rhodes et al. 2012) and other species of groupers (Zeller 1998, Nemeth 2005, Starr et al. 2007), and may be indicative of a general pattern for aggregat-

ing groupers. The presence of high percentages of tagged individuals at the FSA site over multiple spawning months within a spawning season provides some evidence of multiple spawning in the majority of individuals and supports previous hypotheses based on histological analysis (Rhodes & Sadovy 2002a, Pears et al. 2007).

The difference in the maximum number of spawning months within a spawning season in which individuals of the 2 species participate could be related to species size, with the generally larger *Epinephelus fuscoguttatus* presumably being able to mature greater batches of gametes and participate in more spawning months than the smaller *E. polyphkadion*. Variation in the number of spawning months in which tagged individuals of the same species were observed at the spawning site could indicate 2 things: (1) physiological differences among individuals in ability to mature and spawn batches of gametes over a spawning season; or (2) the use of different FSA sites by the same individual within a spawning season. While there is no empirical evidence to support the use of multiple spawning sites in groupers, the use of more than 1 spawning site by some siganids has been reported (Bijoux et al. 2013). One other mixed *E. fuscoguttatus* and *E. polyphkadion* spawning aggregation site is known at the atoll (Robinson et al. 2008) but there is no data to show whether some individuals spawn at both sites. Simultaneous acoustic monitoring of the 2 FSA sites would determine whether there are exchanges of spawning fish between sites.

Our results show that the frequency of visits to the FSA sites is not influenced by sex in either species. The maximum number of spawning months within a spawning season in which female *Epinephelus fuscoguttatus* were detected at the FSA site in our study contrasts with that from a similar study in Pohnpei, where females were observed to participate in only 1 spawning aggregation each season (Rhodes et al. 2012) and could indicate regional differences in the reproductive biology of this species and/or differences in environmental conditions. No information on the behavioural dynamics of individual *E. polyphkadion* during a spawning season has been published. However, *E. polyphkadion* tagged at a spawning site in Palau were recaptured at the same site in over 2 consecutive spawning months (Johannes et al. 1999), but sex of the captured fish was not reported.

The reduction in the number of tagged fish detected at the spawning site by the second season of monitoring can be attributable to a combination of

factors. While it is possible that not all fish spawn or attend the same aggregation each season, some individuals may have died as a result of the tagging, or suffered fishing or natural mortality. Alternatively, tag failure may also have occurred. The surgical implantation of acoustic tags was not considered to be an important source of mortality, as 88 % of tagged fish were detected at the FSA a year after tagging. Similarly, fishing mortality is relatively minor at Faguhar, and only 1 fish was recaptured during the course of the study. Natural mortality in large species of grouper is also low (Grandcourt 2005) but may have accounted for a few losses of tagged fish, as evident from the tag that was found inside the gut of the *Plectropomus punctatus*.

Our finding of longer mean residence times of males at the spawning site compared to females is consistent with studies of the same species in Pohnpei (Rhodes & Sadovy 2002b, Rhodes et al. 2012) and of other groupers (Zeller 1998, Nemeth et al. 2007, Starr et al. 2007, Rhodes & Tupper 2008). Longer residence times of males at the FSA site could be a strategy to ensure spawning with more females, thereby maximising their reproductive success. The longer residence time of males renders them more vulnerable to fishing at the spawning aggregation, whereby the selective removal of males from the spawning stock can result in sperm limitation (Koenig et al. 1996). As *Epinephelus fuscoguttatus* is a protogynous hermaphrodite with most of the larger individuals presumably being males (Pears et al. 2006), and as fishing tends to select for larger individuals (Friedlander & DeMartini 2002), the problem of sperm limitation is a greater cause for concern for this species compared to the functionally gonochoristic *E. polyphkadion* (Rhodes et al. 2011). Reduction in aggregation residence time as the spawning season progresses has also been documented elsewhere in groupers (Rhodes et al. 2012) and other species (Bijoux et al. 2013), and could be linked to reduced energy allocation to reproduction after the first spawning month of a season. As we tagged in only 1 month of the spawning season, it is possible that the patterns in site fidelity, frequency of site visitation and residence time that were observed could be different to those that we would have been seen if fish were tagged in several spawning months of a spawning season (Rhodes et al. 2012). Future acoustic studies of species that spawn over multiple spawning months should attempt to tag in several months to investigate whether the month of tagging has any influence on the observed behavioural patterns.

Lunar and diel timing of arrivals and departures

Both species arrived at the FSA site at approximately the same time in relation to the date of the new moon, with no significant difference in mean lunar timing of arrivals among individuals of known sex in either species. These results agree with observations made in a similar study, using similar methodology, of *Epinephelus fuscoguttatus* in Pohnpei (Rhodes et al. 2012). In Pohnpei, *E. fuscoguttatus* aggregate and spawn around the full moon, as opposed to our study site, where they aggregate and spawn around the new moon, suggesting that the contrasting moon phases elicit the same cues at these 2 locations. An earlier study at the same FSA site reported that males of both species appear earlier than females in samples taken from aggregation catches (Robinson et al. 2008). Likewise, in Pohnpei, male *E. polyphekadion* started to aggregate 10 to 12 d prior to the full moon, and females started to appear in the catch 4 d before the full moon (Rhodes & Sadovy 2002b). Differences in the lunar timing of arrivals at the FSA site between males and females of the 2 study species is not supported by our data and could be the result of differences in spawning aggregation dynamics among locations or among years at the same site.

Acoustic detections indicate that there is a gradual build-up of aggregating fish at the FSA site during the fortnight preceding a new moon within a spawning month and that this is followed by a sudden decrease just after the new moon. In Pohnpei, *Epinephelus polyphekadion* spawned 1 to 2 d prior to the full moon and dispersed from the site within 48 to 72 h (Rhodes & Sadovy 2002b), while *E. fuscoguttatus* spawned around the full moon and dispersed within 4 d after (Rhodes et al. 2012). Few studies have compared the diel timing of spawning fish arrival at and departure from FSA sites. We showed distinct periodicity in mean diel timing of departure of both species from the FSA site, with mean departure time occurring exclusively during the night in both species. It has been shown that diel patterns in detection frequency without correction for environmental effects can lead to wrong interpretation of animal behaviour (Payne et al. 2010). As we used the time of first and last detection as a proxy for the time that a fish arrived and left the FSA site we do not think that environmental effects would have greatly affected the diel patterns we observed. Periodicity in diel timing of arrivals and departures of fish at the FSA site has limited use in fisheries management but is an interesting result from a behavioural perspective.

Management considerations and orientation of future FSA research

Though fishing pressure at this remote atoll has remained comparatively low due to its isolation from population centres in the main Seychelles islands, large catches of *Epinephelus fuscoguttatus* and *E. polyphekadion* were periodically taken from the aggregation site until 2005, which resulted in recommendations for the site to be managed (Robinson et al. 2008). The results of the present study can be used to design more effective management measures for the aggregations than previous information allowed. If a seasonal fishing closure were to be imposed at the site, we recommend that it should cover the period from November to March to account for inter-annual variation in aggregation formation (Robinson et al. 2008). Fishery closure linked to the lunar cycle will not be appropriate at this site as a small percentage of aggregating groupers stay at the spawning site between some spawning months. The role of monitoring in the management of spawning aggregations has been stressed by several authors (Sadovy & Domeier 2005, Mangubhai et al. 2011, Sadovy de Mitcheson & Colin 2012). As it is important to determine changes in the aggregations if formal management is introduced at our study site, we recommend the establishment of a long-term monitoring programme. Future research into grouper spawning aggregations in the Seychelles should focus on identifying other FSA sites (Robinson et al. 2004), while expanding studies of the spawning dynamics at known sites, particularly with regards to potential inter-annual variations in the duration of spawning seasons, the use of migratory pathways and the identification of the functional migration area to FSA sites. Findings from these investigations will inform managers and allow the development of effective, biologically meaningful, temporal and spatial management measures. Aggregations of groupers often form on channel aprons or the outer reef areas, although not exclusively (Claydon 2004, Colin 2012). In particular, channels of other atolls in the southern Seychelles should be investigated for potential signs of FSAs. High operational costs and the inability to preserve and store fish for long periods of time have reduced the amount of fishing that occurs in the Seychelles' southern islands. However, it is expected that the growing demand for high-valued fish, such as groupers, may increase pressure in the future. While the known FSAs of *E. fuscoguttatus* and *E. polyphekadion* occur around the new moon and around the same month in the Seychelles, it would be

informative to study variation in spawning aggregation dynamics of the 2 species among aggregation sites. As many of the Seychelles outer islands are isolated and as groupers have larval durations of just over 10 to more than 50 d (Colin et al. 1997, Macpherson & Raventos 2006), genetic analysis would provide important data on the dispersal and connectivity of populations from different island groups. Research integrating grouper spawning aggregation dynamics and larval dispersal could assist in the design and implementation of a region-wide management plan for these species (Almany et al. 2013).

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LITERATURE CITED

- Aguilar-Perera A (2006) Disappearance of a Nassau grouper spawning aggregation off the southern Mexican Caribbean coast. *Mar Ecol Prog Ser* 327:289–296
- Almany GR, Hamilton RJ, Bode M, Matawai M and others (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Curr Biol* 23: 626–630
- Alós J (2008) Influence of anatomical hooking depth, capture depth, and venting on mortality of painted comber (*Serranus scriba*) released by recreational anglers. *ICES J Mar Sci* 65:1620–1625
- Batschelet E (1981) Circular statistics in biology. Academic Press, London
- Beets J, Friedlander A (1999) Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. *Environ Biol Fishes* 55:91–98
- Bijoux JP, Dagorn L, Berke G, Cowley PD, Soria M, Gaertner JC, Robinson J (2013) Temporal dynamics, residency and site fidelity of spawning aggregations of a herbivorous tropical reef fish *Siganus sutor*. *Mar Ecol Prog Ser* 475: 233–247
- Capello M, Soria M, Cotel P, Potin G, Dagorn L, Fréon P (2012) The heterogeneous spatial and temporal patterns of behavior of small pelagic fish in an array of Fish Aggregating Devices (FADs). *J Exp Mar Biol Ecol* 430-431:56–62
- Childs AR, Cowley PD, Næsje TF, Booth AJ, Potts WM, Thorstad EB, Økland F (2008) Estuarine use by spotted grunter *Pomadasys commersonnii* in a South African estuary, as determined by acoustic telemetry. *Afr J Mar Sci* 30:123–132
- Claydon J (2004) Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. *Oceanogr Mar Biol Annu Rev* 42:265–302
- Colin PL (2012) Timing and location of aggregation and spawning in reef fishes. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Fish & Fisheries Ser, Vol 35. Springer, Heidelberg, p 117–158
- Colin PL, Laroche WA, Brothers EB (1997) Ingress and settlement in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. *Bull Mar Sci* 60:656–667
- Erisman B, Aburto-Oropeza O, Gonzalez-Abraham C, Mascarenas-Osorio I, Moreno-Baez M, Hastings PA (2012) Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. *Sci Rep* 2:284
- Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar Ecol Prog Ser* 230:253–264
- Grandcourt E (2005) Demographic characteristics of selected epinepheline groupers (Family: Serranidae; Subfamily: Epinephelinae) from Aldabra atoll, Seychelles. *Atoll Res Bull* 539:199–216
- Hamilton RJ, Giningele M, Aswani S, Ecochard JL (2012) Fishing in the dark—local knowledge, night spearfishing and spawning aggregations in the western Solomon Islands. *Biol Conserv* 145:246–257
- Johannes RE, Squire L, Graham T, Sadovy Y, Renguul H (1999) Spawning aggregations of groupers (Serranidae) in Palau. *Mar Conserv Res Ser Publ* 1. The Nature Conservancy, Arlington, VA
- Koenig CC, Coleman FC, Collins LA, Sadovy Y, Colin P (1996) Reproduction in gag (*Mycteroperca microlepis*) (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fish spawning aggregations. In: Arreguin-Sanchez F, Munro JL, Balgos MC, Pauly D (eds) Biology, fisheries and culture of tropical groups and snappers. ICLARM Conf Proc 48:307–323
- Laird NM, Ware JH (1982) Random-effects models for longitudinal data. *Biometrics* 38:963–974
- Macpherson E, Raventos N (2006) Relationship between pelagic larval duration and geographic distribution of Mediterranean littoral fishes. *Mar Ecol Prog Ser* 327: 257–265
- Mangubhai S, Saleh M, Suprayitno, Muljadi A, Purwanto, Rhodes KL, Tjandra K (2011) Do not stop: The importance of seamless monitoring and enforcement in an Indonesian marine protected area. *J Mar Biol* 2011 Article ID 501465
- Nemeth RS (2005) Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Mar Ecol Prog Ser* 286:81–97
- Nemeth RS (2012) Ecosystem aspects of species that aggregate to spawn. In: Sadovy de Mitcheson Y, Colin PL (eds)

- Reef fish spawning aggregations: biology, research and management. Fish & Fisheries Ser, Vol 35. Springer, Heidelberg, p 21–55
- Nemeth RS, Blondeau J, Herzlie S, Kadison E (2007) Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. Environ Biol Fishes 78: 365–381
- Olsen DA, LaPlace JA (1979) A study of a Virgin Islands grouper fishery based on a breeding aggregation. Proc Gulf Caribb Fish Inst 31:130–144
- Payne NL, Gillanders BM, Webber DM, Semmens JM (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. Mar Ecol Prog Ser 419:295–301
- Pears RJ (2012) Brown-marbled grouper—*Epinephelus fuscoguttatus*. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Fish & Fisheries Ser, Vol 35. Springer, Heidelberg, p 406–412
- Pears RJ, Choat JH, Mapstone BD, Begg GA (2006) Demography of a large grouper, *Epinephelus fuscoguttatus*, from Australia's Great Barrier Reef: implications for fishery management. Mar Ecol Prog Ser 307:259–272
- Pears RJ, Choat JH, Mapstone BD, Begg GA (2007) Reproductive biology of a large, aggregation-spawning serranid, *Epinephelus fuscoguttatus* (Forsskål): management implications. J Fish Biol 71:795–817
- Pet JS, Mous PJ, Muljadi AH, Sadovy YJ, Squire L (2005) Aggregations of *Plectropomus areolatus* and *Epinephelus fuscoguttatus* (groupers, Serranidae) in the Komodo National Park, Indonesia: monitoring and implications for management. Environ Biol Fishes 74:209–218
- Rhodes KL (2012) Camouflage grouper—*Epinephelus polyphkadion*. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Fish & Fisheries Ser, Vol 35. Springer, Heidelberg, p 422–428
- Rhodes KL, Sadovy Y (2002a) Reproduction in the camouflage grouper, *Epinephelus polyphkadion* (Pisces: Serranidae), in Pohnpei, Federated States of Micronesia. Bull Mar Sci 70:851–869
- Rhodes KL, Sadovy Y (2002b) Temporal and spatial trends in spawning aggregations of camouflage grouper, *Epinephelus polyphkadion*, in Pohnpei, Micronesia. Environ Biol Fishes 63:27–39
- Rhodes KL, Tupper MH (2008) The vulnerability of reproductively active squaretail coral grouper (*Plectropomus areolatus*) to fishing, based on acoustic and conventional tagging surveys in Pohnpei, Micronesia. Fish Bull 106: 194–203
- Rhodes KL, Taylor BM, McIlwain JL (2011) Detailed demographic analysis of an *Epinephelus polyphkadion* spawning aggregation and fishery. Mar Ecol Prog Ser 421:183–198
- Rhodes KL, McIlwain J, Joseph E, Nemeth RS (2012) Reproductive movement, residency and fisheries vulnerability of brown-marbled grouper, *Epinephelus fuscoguttatus* (Forsskål, 1775). Coral Reefs 31:443–453
- Robinson J, Isidore M, Marguerite MA, Öhman MC, Payet RJ (2004) Spatial and temporal distribution of reef fish spawning aggregations in the Seychelles—an interview-based survey of artisanal fishers. West Indian Ocean J Mar Sci 3:63–69
- Robinson J, Aumeeruddy R, Jörgensen TL, Öhman MC (2008) Dynamics of camouflage (*Epinephelus polyphkadion*) and brown marbled grouper (*Epinephelus fuscoguttatus*) spawning aggregations at a remote reef site, Seychelles. Bull Mar Sci 83:415–431
- Russell B, Situ A, Cornish A, Grouper & Wrasse Specialist Group (2006) *Epinephelus polyphkadion*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. IUCN, Gland, www.iucnredlist.org/details/61339/0 (accessed 23 October 2013)
- Sadovy Y, Domeier M (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs 24:254–262
- Sadovy de Mitcheson Y, Colin PL (2012) Conclusion. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Fish & Fisheries Ser, Vol 35. Springer, Heidelberg, p 567–584
- Sadovy de Mitcheson Y, Erisman B (2012) Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. In: Sadovy de Mitcheson Y, Colin PL (eds) Reef fish spawning aggregations: biology, research and management. Fish & Fisheries Ser, Vol 35. Springer, Heidelberg, p 225–284
- Sala E, Ballesteros E, Starr RM (2001) Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. Fish Bull 26:23–30
- Starr RM, Sala E, Ballesteros E, Zabala M (2007) Spatial dynamics of the Nassau grouper *Epinephelus striatus* in a Caribbean atoll. Mar Ecol Prog Ser 343:239–249
- Tupper M, Sheriff N (2008) Capture-based aquaculture of groupers. In: Lovatelli A, Holthuis PF (eds) Capture-based aquaculture. Global overview. FAO Fisheries Tech Pap 508. FAO, Rome
- Zeller DC (1998) Spawning aggregations: patterns of movement of the coral trout *Plectropomus leopardus* (Serranidae) as determined by ultrasonic telemetry. Mar Ecol Prog Ser 162:253–263

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