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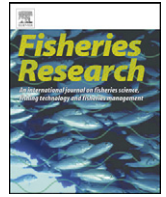
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The importance of targeted spawning aggregation fishing to the management of Seychelles' trap fishery

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ABSTRACT

The formation of spawning aggregations at predictable sites and times is known to confer vulnerability to overexploitation among reef fishes exhibiting this trait. The aim of this study was to determine the importance of targeted fishing on spawning aggregations for the status and management of the trap fishery for *Siganus sutor* (Rabbitfish: Siganidae) in Seychelles. *S. sutor* was verified as an aggregative spawner and, at two of the main spawning sites, aggregations were subject to a highly targeted trap fishery. Trends in catch-per-unit-effort and yield over time (1991–2006) were not indicative of an overfished siganid resource, and a yield curve signalled that fishing has been within sustainable limits. While a demographic assessment indicated that overfishing had occurred in 1998 and 2007, the reference points may have been overly conservative and the results reflect the size structure of only the exploited component of the population. Aggregation fishing was estimated to contribute 8% of annual effort and 15% of annual catch in the fishery, indicating that this practice does not exert a major influence on stock and fishery status. Given the conflicting results of yield and demographic assessments, precautionary management measures are warranted and should be informed by the distribution of effort among life history stages. Spatial or temporal measures to protect spawning aggregations will have limited effectiveness as the majority of effort is directed at non-spawning fish. We conclude that fisheries with aggregation components can be sustainable at commercial levels of use if based on relatively resilient transient spawners.

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1. Introduction

Many coral reef fish species are vulnerable to overexploitation due to aspects of their life history, such as slow growth, late maturation and the formation of spawning aggregations at predictable sites and times (Sadovy, 1996; Domeier and Colin, 1997; Claydon, 2004). It has been proposed that fisheries targeting spawning aggregations may only be sustainable at limited, subsistence levels of use (Sadovy and Domeier, 2005). Commercial fishing has resulted in the decline or extirpation of spawning aggregations, leading to economic collapse of fisheries (Claro and Lindeman, 2003) and, in a few cases, raising significant conservation concerns for the species (Cornish and Eklund, 2003). While conservation concerns are currently limited to a few species, the targeting of aggregations poses important questions for fisheries management, such as whether or

not spawning sites should be closed to fishing (Domeier et al., 2002; Sadovy and Domeier, 2005; Sale et al., 2005).

Aggregative spawning may confer particular vulnerability to overexploitation in species where populations form a few large and dense aggregations that are highly predictable in time and space (Sadovy de Mitcheson et al., 2008). The formation of spawning aggregations essentially involves a change in spatial behaviour that leads to increased population density. If accessibility is not reduced (e.g. aggregations form in deeper areas beyond the range of available gears), then increases in density may significantly elevate catchability (Fulton et al., 1999; Smith et al., 2008).

The strength of changes in spatial behaviour and catchability between spawning and non-spawning periods play an important role in determining the potential for aggregation fishing to act as a driver of stock and fishery status. In some species, for example the Nassau (*Epinephelus striatus*) and tiger (*Mycteroperca tigris*) groupers, the population densities of non-spawning individuals are low and catches are rarely taken except when the population is aggregating to spawn. Consequently, aggregation fishing was the primary driver of population declines for Nassau and tiger groupers (Sadovy and Eklund, 1999; Matos-Caraballo et al., 2006). However,

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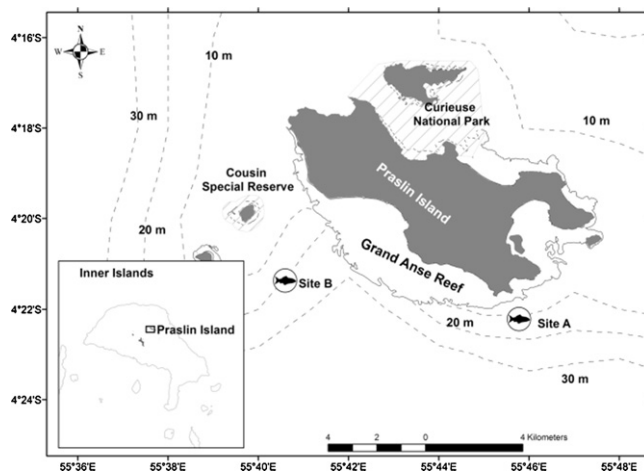


Fig. 1. Map of the study area close to Praslin. Spawning aggregation Sites A and B are denoted by the fish symbols. The location of Praslin within the inner granitic islands is shown in the inset.

such extreme changes in spatial behaviour and catchability are rare among aggregative spawners. For most aggregative spawners (for a recent list, see Sadovy de Mitcheson et al., 2008), annual catches usually comprise fish taken from spawning aggregation sites and fish taken from non-spawning areas of residence (home ranges), hereafter referred to as the aggregation and non-aggregation components of the fishery. Moreover, the non-aggregation components of these fisheries will often be further divided by adult and juvenile catches (Fulton et al., 1999). Therefore, fishing mortality will be apportioned between a number of fishery components and life history stages. Information on the apportioning of fishing mortality can be used to focus management on the component that acts as the primary driver of stock status.

The family Siganidae is one of many reef fish families for which aggregative spawning has been documented (Domeier and Colin, 1997). *Siganus canaliculatus*, *S. argenteus*, *S. lineatus*, *S. punctatus* and *S. spinus* aggregations have been described in Palau (Hasse et al., 1977; Johannes, 1981). In Seychelles, small-scale fishers have targeted 'breeding aggregations' of the shoemaker spinefoot rabbitfish (*Siganus sutor*; Valenciennes 1835) from early in the last century (Hornell, 1927). Early accounts of the fishery documented the onset of the spawning season (September), the lunar periodicity of aggregations (full moon), and the timing of migrations of fish from the shallow carbonate fringing reefs of Praslin Island to the deeper spawning sites (Wheeler, 1946). *S. sutor* spawning aggregations are also well known among contemporary Seychellois fishers and continue to be commercially exploited (Robinson et al., 2004). Fishers in Kenya and Tanzania have also reported fishing on *S. sutor* spawning aggregations (Samoilys et al., 2006).

S. sutor is endemic to the western Indian Ocean (Woodland, 1990) and of considerable socio-economic importance to small-scale fisheries in Kenya, Mauritius, Mozambique, Seychelles and Tanzania, where it is targeted by multi-species fisheries using a variety of gears (Jehangeer, 1988; Grandcourt, 2002; Kaunda-Arara et al., 2003) and often constitutes more than 30% of catches (McClanahan and Mangi, 2004). In Seychelles, siganids are fished inshore of the main granitic islands (Fig. 1) using bamboo fish traps mainly set from small (c. 6 m length) outboard-powered vessels. They are the most important fish family in the coastal trap fishery with an estimated catch of 190 metric tonnes (t) in 2008 (Seychelles Fishing Authority, 2009), and *S. sutor* is the main target species (Grandcourt and Cesar, 2002). Three types of traps are used in the fishery, of which two are sturdily constructed, fixed (static) traps with soak times of up to 3 days, while active traps are of lighter

construction and are soaked for several hours only (Daw et al., 2011). The fishery is subject to minimum mesh size requirements (40 mm) but otherwise is unmanaged.

The aim of this study was to determine the importance of targeted spawning aggregation fishing to the management of the *S. sutor* trap fishery. The specific objectives were: firstly, to verify spawning aggregations and their targeted fishery; secondly, to determine trends in the fishery and stock status using indicators and stock assessment; and thirdly, to quantify the extent to which the aggregation component of the fishery contributes to stock and fishery status. The implications of the findings for management are discussed in terms of selecting and designing effective measures.

2. Materials and methods

2.1. Study location

The Republic of Seychelles is an archipelago of 155 islands scattered over an exclusive economic zone of 1.37 million km² in the western Indian Ocean (WIO). Centrally located on the Mahé Plateau, a large mid-oceanic shelf, a group of 42 granitic islands contains the islands of Mahé, Praslin and La Digue where the vast majority of the population resides (NSB, 2007). Field studies to verify that *S. sutor* forms spawning aggregations, and to verify that they are subject to targeted fishing, were conducted at two reported sites situated close to Praslin (Fig. 1). While more spawning sites are known to fishers (Robinson et al., 2004), the selected sites were the only ones targeted by fishers during the period of field studies. Both sites are submerged granite outcrops ('pate') separated (by sandy substrate) from the base of the fringing carbonate reef slope of Grand Anse Reef on the southwest coast of Praslin (Fig. 1). The sites rise from the sandy substrate (at c. 20–25 m) and peak at approximately 14 m depth.

2.2. Verification of spawning aggregation formation and a targeted fishery

We adopted widely used criteria for verifying spawning and aggregation formation (Domeier and Colin, 1997; Colin et al., 2003), assessed on the basis of two trips to the study sites around the full moon in November 2003 (lunar days 13 and 14) and November 2004 (lunar days 11–17). Spawning within the aggregations was verified using direct (females with hydrated oocytes) and indirect (patterns in stages of maturation and gonado-somatic index, GSI) signs. A total of 137 fish were sub-sampled at random from trap catches taken directly by commercial fishers at Site A, and measured for length (fork length, L_F ; to 1 mm) and whole wet weight (W , to 10 g). Sex and maturation stage were determined macroscopically (Table 1) and gonads were removed, dried and weighed (gonad weight, W_G ; to 1 g) for analysis of GSI. To confirm the presence of hydrated oocytes (as a direct sign of spawning) and to examine the accuracy of macroscopic staging, a subset of ovaries was taken for histological analysis. A gonad portion (or whole gonad if <5 g) taken from the proximal end of one of the lobes was removed and preserved in 4% neutral buffered formalin. Gonad portions were dehydrated, embedded in paraffin and sectioned transversely at 7 μ m. Sections were mounted, stained in haematoxylin and eosin, and ovaries examined under a high-power light microscope. Accuracy of macroscopic staging was confirmed through microscopic evaluation (Table 1).

Aggregation formation was verified by diver observations of changes in abundance over the course of the aggregation, using a 3-fold change as a guideline (Colin et al., 2003). Aggregation size was estimated using underwater visual census and later checked from video footage. On the day of the largest aggregation (lunar day 13),

Table 1
Criteria for macroscopic and microscopic evaluation of maturation stages of ovaries of female *Siganus sutor* (modified from West, 1990; Samoilys and Roelofs, 2000). Maturity stage is defined by the most developed oocytes present, shown in bold.

Stage	Macroscopic	Microscopic
Immature	Small, rounded, strand-like structures, pink in colour	Small with thin gonad wall. Tightly packed with previtellogenic oocytes and gonidia
Undetermined inactive	Small, rounded, thickening gonad wall, pink-orange colour. Oocytes not visible. Unable to determine if female was resting following prior spawning (mature, inactive), or immature	Thicker gonad wall than immature females, no evidence of prior spawning (see below). Tightly packed previtellogenic oocytes throughout lamellae
Mature, inactive	Could not be determined (see above)	Thickened gonad wall, previtellogenic oocytes dominate, evidence of prior spawning in prominent intra-lamellae muscle bundles, yellow-brown bodies or atretic oocytes
Mature, active (Ripe)	Tightly packed oocytes visible when ovary cut. Ovary enlarged, grey colour with thinning wall.	Oocytes at various development stages but vitellogenic oocytes dominate, stretched and thin gonad wall, no atretic oocytes
Running Ripe	Close to spawning, ovary large with translucent wall, large, clear hydrated oocytes clearly visible. Exudes oocytes with pressure	Large and dominated by advanced vitellogenic and hydrated oocytes . Migratory nucleolus stage oocytes may be present, yolk fusion extensive
Spent	Ovary flaccid with pronounced capillaries. Purple red in colour	Large, disorganised with prominent muscle bundles and thick gonad wall. Post-ovulatory follicles and/or atretic oocytes present

school size was estimated to the nearest 250 fish, whereas more accurate estimates were possible on the other days (to the nearest 10 fish). SCUBA diving was limited to 3 dives at Site A (lunar days 11, 13 and 15) and one dive at Site B because fishers complained that divers modified *S. sutor* behaviour and caused reduced catches.

For identifying the management implications of the fishery, it was important to confirm that fishers actively target the spawning aggregations, as opposed to taking spawning fish incidentally. This was achieved through *in situ* observations of the development of the aggregation fishery in terms of spatial patterns in catch and effort in November 2004. As the observations were limited to a single month and only two sites, we interviewed 25 fishers to confirm that our observations were typical of spawning aggregation behaviour and of fishing practices.

2.3. Fishery status indicators and stock assessment

Two approaches to determining status were employed. Firstly, a time series of fisheries data were available for deriving long-term (16 year) indicators of the status of the fishery (yield, effort) and stocks (catch-per-unit-effort, CPUE). As these fisheries data were aggregated at the family level (Siganidae), demographic stock assessments using reference points were also conducted to determine status specific to *S. sutor*, based on samples of length data that were available for 1998 and 2007. The selectivity of the fishery was also examined to determine the management implications of juvenile retention.

Siganid trap fishery data from January 1991 to December 2006 were extracted from the Seychelles Fishing Authority's (SFA) Catch Assessment Survey (CAS) database. The CAS is a stratified catch, effort and species composition statistical system implemented since 1985 but modified in 1991 (Mees, 1990; Grandcourt and Cesar, 2002; Daw et al., 2011). Trap data are disaggregated into active and static trap-types. Siganids are aggregated to the family level but *S. sutor* comprises more than 70% of the total siganid catch (SFA, unpublished data).

Trends in siganid yield and fishing effort over the time-series were determined, and a yield curve was fitted to annual yield and effort (total annual trap effort) data to assess resource status. For these analyses, mean annual siganid yield per unit area (kg/km²) was calculated from monthly catch estimates, derived from the CAS, and estimates of the surface area of the trap fishing ground (4030 km²; Christophe, 2006). Total annual effort in the trap fishery was also derived from the CAS. As an indicator of relative abundance of the siganid resource, mean annual CPUE was calculated for the active (kg per trap-set) and static (kg per trap-day) gear type/fishing modes. All relationships were estimated using a

curve-fitting regression model procedure. Analysis-of-variance (ANOVA) was performed to test the statistical significance of regression models. Assumptions of normality and homogeneity of variances were tested using Shapiro–Wilk's and Levene's tests, respectively.

Two independent stock assessments of *S. sutor* were conducted based on weekly random sampling of length data from catches landed by the commercial fishery in the periods of June to August 1998 ($n = 607$) and April to June 2007 ($n = 625$). Fork length (L_F) data were pooled in 2 cm size class bins. The annual instantaneous rate of total mortality (Z) was determined using the length-converted catch curve method (Gaynilo and Pauly, 1997), where the natural logarithm of the number of fish in each size class, divided by the change in relative age, was plotted against the relative age, and Z ($\pm 95\%$ CI) estimated from the descending slope of the best-fit line using least-squares regression. The annual instantaneous rate of natural mortality (M) was estimated using the empirical equation derived by Hoenig (1983), using a maximum validated age estimate of 2.14 years for *S. sutor* (Jehangeer, 1988). The annual instantaneous rate of fishing mortality (F) was calculated ($F = Z - M$) for lower and upper bounds (95% CI) of Z to derive a range of estimates for F . The exploitation rate (E) was calculated ($E = F/Z$). Following the approach of Grandcourt et al. (2006) we assessed resource status by comparing estimates of F with the target (F_{opt}) and limit (F_{limit}) biological reference points of Patterson (1992), defined as: $F_{opt} = 0.5M$ and $F_{limit} = 2/3M$. These reference points are considered conservative and in line with a precautionary approach.

To examine if juvenile retention constitutes a management issue, the selectivity characteristics of the fishery were established and assessed relative to the length of maturity. The Gaynilo and Pauly (1997) method consists of extrapolating the right, descending side of a catch curve such that fish that 'ought' to have been caught (had it not been for the effect of incomplete selection and recruitment) are added to the curve, with the ratio of 'expected' numbers to those that are actually caught being used to estimate probabilities of capture. Selectivity curves were produced for 1998 and 2007 data by fitting a logistic function to the plot of probability of capture against size and used to derive the length at which fish were recruited to the fishery at a probability of 0.5 (L_{C50}). This was compared to a size at first maturity (L_{m50}) estimate of 23 cm (L_F) for females, derived from reproductive studies in Seychelles (SFA, unpublished information).

2.4. Estimation of the importance of spawning aggregation fishing

The extent to which the aggregation component of the fishery contributes to annual catch and effort was estimated in order

to examine different management approaches for the fishery. In the absence of fine-scale, spatially disaggregated fisheries data in the CAS, a time-structured approach was adopted to address this objective. Using the same dataset extracted from the CAS for derivation of CPUE, but with sample dates converted to lunar days, the percentage of annual siganid catches and effort made during spawning aggregation periods was obtained for the period 1991–2006. Spawning aggregation periods were defined from studies on the reproductive biology of *S. sutor* (Robinson et al., 2007; SFA, unpublished data). The spawning season lasts from September to June (10 months) and the lunar periodicity of spawning, as determined from the presence of hydrated oocytes, is a 5-day period centred on the full moon (SFA, unpublished data). The spawning aggregation period was extended to 7 days, also centred on the full moon, to account for aggregation duration (see results) and the fact that fishers reported that the exact timing of onset and termination varies slightly between months and years, sometimes forming a few days prior to full moon, on the full moon, or slightly after. Thus, the annual spawning aggregation period was estimated at 70 days (comprising a 7 day spawning aggregation period each month for 10 spawning months).

To account for the fact that not all effort in the fishery is directed at spawning sites when aggregations form, and that aggregations only form for around half the time of the 7 day lunar period (see results), a targeting ratio was calculated in order to estimate aggregation catch and effort. The proportion of catch and effort samples during the 70 day spawning aggregation period with catches that comprised 80% or more of siganids was assumed to be a conservative indicator of aggregation targeting, based on *in situ* observations of the species composition in aggregation catches (Robinson et al., 2007). These proportions, or targeting ratios, were used to adjust the percentage of annual catch and effort made during spawning aggregation periods to give an approximation of aggregation catch and effort. To determine the significance of any trends in aggregation targeting, the relationships of catch and effort targeting ratios with time were examined using the non-parametric Spearman rank correlation test since assumptions of normality were not met.

For this analysis, it was assumed that fish migrate to spawn at specific sites on the full moon in every month of the season. This assumption is supported by the fact that spawning in aggregations is generally a stable reproductive strategy (Domeier and Colin, 1997); very few aggregative spawners have been observed spawning outside aggregations, although exceptions may occur (Samoilys, 2000; Krajewski and Bonaldo, 2005). Moreover, initial experiments with acoustic telemetry at Sites A and B indicate that tagged fish show high fidelity and return to the granite spawning sites during each full moon across the season (J. Bijoux, pers. comm.).

3. Results

3.1. Verification of spawning aggregation formation and a targeted fishery

Aggregation formation was verified through diver observations of changes in fish abundance. In November 2004, between 60 and 100 *S. sutor* were observed at Site A on lunar day 11, comprised of loose schools of less than 20 individuals. By lunar day 13, *S. sutor* had formed a large aggregation at Site A that was comprised of several highly mobile schools, with abundances in excess of 1000 fish per school. By lunar day 15, the aggregation abundance had declined to less than 100 fish. Fishers reported that *S. sutor* is rarely caught or observed at the site outside of the full moon spawning period and that the patterns observed in November were typical of spawning aggregations throughout the season. Large schools (>500 fish) were also observed by divers at Site B on lunar day 13. There were

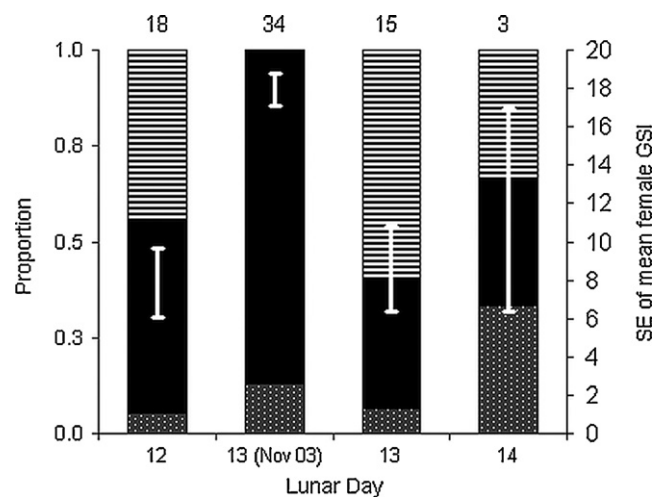


Fig. 2. Proportion of ovarian development stages (bars) and GSI (lines; standard error, SE, of mean) by lunar day (LD) in females sampled from aggregation catches in November 2003 (LD 13 only) and 2004 (LDs 12, 13, and 14). Daily sample sizes shown above bars. Grey/mottled = mature active; black = running ripe; white/horizontal black lines = spent.

no obvious colour changes, territorial interactions or courtship in aggregating fish and gamete release was not observed.

Observations of hydrated oocytes, and trends in maturation and GSI, verified that aggregations formed for the purpose of spawning. On each sampling day at Site A in November 2004, mature active, running ripe and spent individuals were observed, with values of GSI tracking changes in the relative abundance of the 3 stages (Fig. 2). Spent females were not observed in November 2003, meaning that GSI and the relative proportion of maturity stages differed markedly between years on lunar day 13 (Fig. 2). Histological diagnosis of sub-samples taken at Site A in 2003 ($n = 10$) and 2004 ($n = 12$) confirmed the accuracy (96%) of using macroscopically staged data to examine the rapid changes in maturation close to and during spawning. The smallest female sampled at Site A was 21 cm L_F ; and 22% of females were below 23 cm L_F , the size at first maturity. At Site B, verification of spawning was limited to observations of trap fishers hauling traps at the site on lunar day 13 in November 2003, when *S. sutor* released from the traps in fisher boats freely exuded hydrated oocytes and sperm.

The *in situ* observations of fishing practices and the spatial distribution of effort confirmed a highly targeted and cooperative active trap fishery for spawning fish. In November 2004, the aggregation component of the fishery lasted 3 days. Using masks, fishers monitored and communicated with each other on the timing of the event, including an apparent migration along the adjacent Grand Anse fringing reef, and 8 boats started to fish a developing aggregation at Site A on lunar day 12. Fishing effort peaked on lunar day 13, when more than 45 active traps were in operation. The peak in effort coincided with the highest GSI and largest proportion of running ripe individuals in the catch (Fig. 2). Observed trap hauls were dominated by *S. sutor*. Fishing pressure declined at the site during lunar day 14 and had completely ceased by the full moon (lunar day 15).

3.2. Fishery status indicators and stock assessment

Annual yields of *S. sutor* ranged from a low of 1.8 kg/km² in 2001 to a high of 9.7 kg/km² in 1992 (Fig. 3a). The best-fit curve (ANOVA: $F = 7.40$, $df = 2, 13$, $P = 0.0072$) describing the relationship between yield and time was a quadratic model. Yields declined from the early 1990s to reach a low in the period 1999–2001, followed by a period of recovery over the last 5 years. Effort was highest in the fishery

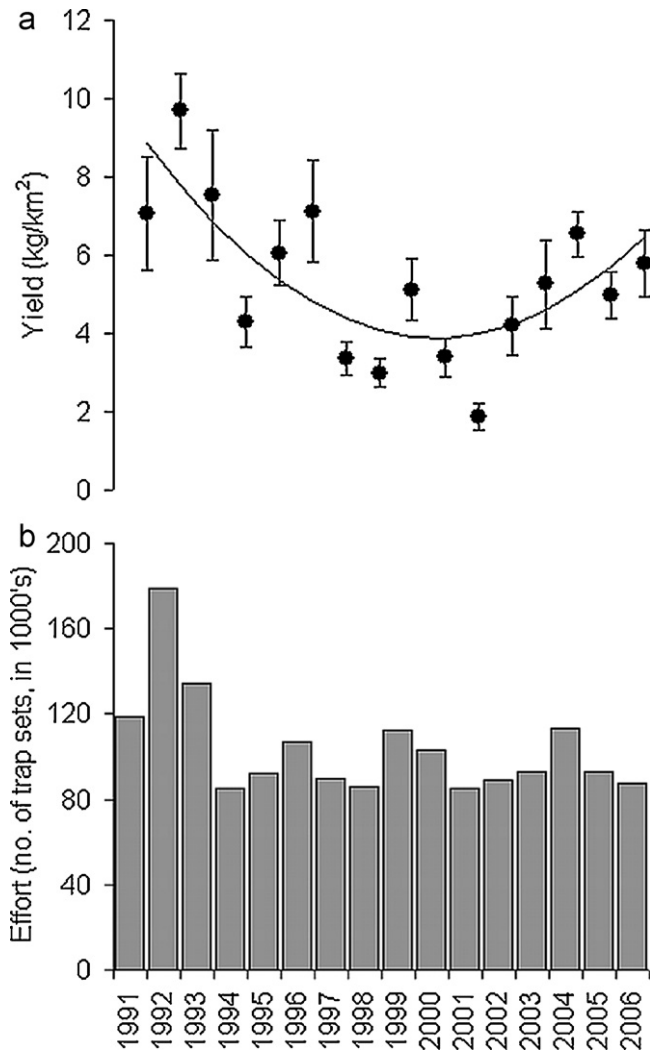


Fig. 3. Time-series trends in, (a) annual yield (kg/km²; mean ± SE) with best-fit curve ($R^2 = 0.53$; $y = 9.94 - 1.21x + 0.061x^2$), and (b) total annual fishing effort (no. of trap-sets, in 1000s).

during the first 3 years of the series, thereafter stabilising with slight peaks in some years (Fig. 3b). The best-fit curve for the relationship between yield and effort was a logarithm model (ANOVA: $F = 29.3$, $df = 1,14$, $P = 0.0001$). The yield curve did not reach an asymptote, with yields declining after 1993 as effort in the fishery reduced (Fig. 4). Only static trap CPUE showed a significant relationship with time, with the best-fit curve (ANOVA: $F = 4.30$, $df = 2,13$, $P = 0.037$) also a quadratic model, describing a decrease in CPUE towards the middle of the series followed by an increase (Fig. 5). Active traps were the most selective gear-type for siganids, averaging 3.7 kg per trap-set compared to 2.1 kg per trap-day for static traps. Although not strictly comparable due to the different measure of effort, sets of active traps achieve a much higher catch for a much more limited soak time.

The total mortality (Z), fishing mortality (F) and exploitation (E) rates were comparable for the two sampling periods (Table 2). With the exception of the lower fishing mortality confidence bound in 1998 being lower than the limit reference point, rates generally exceeded the target (F_{opt}) and limit (F_{limit}) reference points in both 1998 and 2007, indicating that overfishing occurred in those years. Depending on the proportionality between F and effort, overfishing may also have occurred in other years with the same or higher effort.

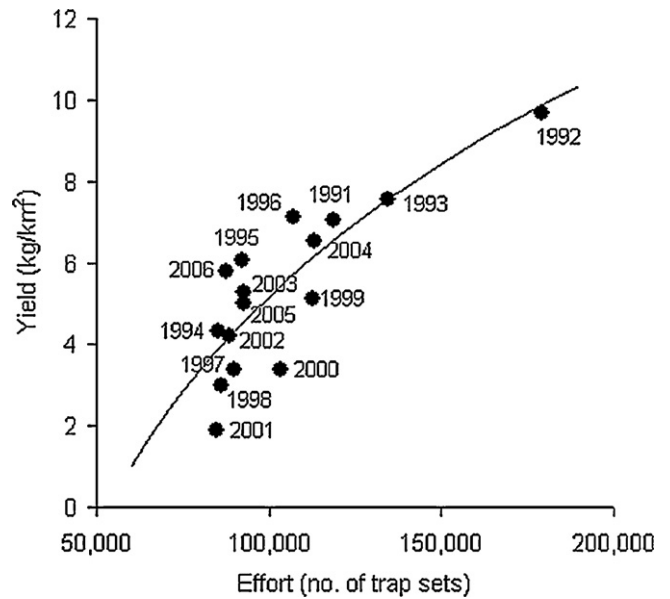


Fig. 4. The relationship between annual yield (kg/km²) and effort (total no. of trap sets in the fishery) for the period 1991–2006, with best-fit curve ($R^2 = 0.82$; $y = -87.78 + 9.07 \ln x$).

The size at which 50% of fish were vulnerable to capture in 1998 (L_{C50} : 23.4 cm L_F) approximated the size at first sexual maturity for females (L_{m50} : 23.0 cm L_F), whereas in 2007 it was considerably smaller (L_{C50} : 16.15 cm L_F). Juvenile retention rates for the fishery were 39% in 1998 and 45% in 2007.

3.3. Impacts of spawning aggregation fishing

The percentage of annual catch and effort achieved during the spawning aggregation periods varied from 16 to 24% (mean = 21.1%; Fig. 6a) and 16 to 25% (mean = 20.9%; Fig. 6b), respectively (Fig. 6). Spawning aggregation period catch and effort generally remained stable over the time series. The proportion of catches during the spawning period that comprised a siganid catch composition of 80% or more, i.e. aggregation catches, averaged 0.72. There was no trend in the aggregation catch targeting ratio over the period (Spearman rank correlation test: coefficient = 0.163, $P > 0.05$). With an average proportion of 0.41 of trap sets with catches comprising

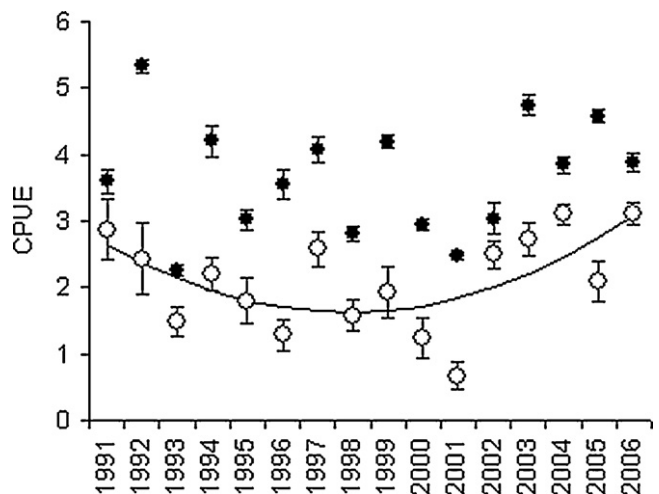


Fig. 5. Annual CPUE (mean ± SE) for static (kg per trap-day; open circles) and active traps (kg per trap-set; closed circles). Best-fit curve fitted to static trap data ($R^2 = 0.40$; $y = 2.98 - 0.35x + 0.022x^2$).

Table 2

Estimates of mortality (M , Z , F) and exploitation rate (E) compared to target (F_{opt}) and limit (F_{limit}) reference points (Patterson, 1992). All mortality rates are year⁻¹.

	M	F_{opt}	F_{limit}	Z (95% CI)	F (95% CI)	E
1998	2.0	1.0	1.3	4.27 (3.42–5.1)	2.27 (1.15–2.83)	0.53
2007	2.0	1.0	1.3	4.25 (3.87–4.63)	2.25 (1.87–2.63)	0.53

80% or more siganids, less than half of the effort applied during the spawning aggregation periods was directed at spawning aggregations. There was no trend in the aggregation effort targeting ratio over the period (Spearman rank correlation test: coefficient = 0.212, $P > 0.05$). Applying these targeting ratios to adjust the percentage of catch and effort during spawning aggregation periods, the effort directed at aggregations as a percentage of total annual effort in the fishery averaged 8.2% over the time series. This yielded an average aggregation catch of 15.2% of the total yearly catch of siganids, giving an approximate 2-fold relationship between aggregation catch and effort.

4. Discussion and conclusions

Our study verified that *S. sutor* forms spawning aggregations close to full moon at submerged granite reef sites near Praslin, Seychelles. Observations of running ripe females on 3 consecutive lunar days suggested that spawning occurred throughout the aggregation period, the duration of which was estimated at 3 days based on diver observations and patterns in fishing effort. Similarly, the congener *S. canaliculatus* forms short-lived spawning aggregations (Hasse et al., 1977). Although estimates of abundance were uncertain due to the highly mobile behaviour of fish at the site, aggregation formation was associated with an order of magnitude change in abundance, far in excess of the 3-fold difference often

used as a benchmark for spawning aggregation formation (Domeier and Colin, 1997).

This study also confirmed that *S. sutor* spawning aggregations are exploited by a highly targeted fishery and served to verify earlier reports of this practice (Hornell, 1927; Robinson et al., 2004). Targeting was enabled by detailed fisher knowledge on the dynamics of the spawning aggregations, as evidenced by patterns in effort that were highly synchronised with ovarian maturation and aggregation development. Such detailed fisher knowledge can be informative for placing our findings in a wider context. Although our observations were limited to two spawning sites and a single spawning month, fishers report that the observed spawning behaviour and targeted fishing practices occur consistently across the season (Robinson et al., 2004, 2007). Moreover, fisher knowledge extends to 8 additional spawning aggregation sites in the vicinity of Praslin that are also targeted (Robinson et al., 2004). As the names of these additional sites are prefixed with 'pate', meaning submerged granite reefs, the geomorphology at the sites observed in this study are considered representative of spawning habitat.

Trends in yield indicated that the siganid resource, of which *S. sutor* constitutes the dominant stock, has been fished within sustainable limits. The yield curve did not reach an asymptote at levels of effort applied in the fishery and, after the first 3 years (1991–1993), effort in the fishery dropped sharply and remained at lower levels throughout the remaining period of the time-series. The cause of this decline is not well understood but coincided with a 46% increase in fuel subsidies to the outboard fleet (Wakeford, 2000) that may have maintained profitability at lower levels of effort. Moreover, while an observed decline in annual siganid yields leading up to 2001 had previously been attributed to overfishing (Grandcourt and Cesar, 2002), yield showed a moderate recovery from 2001 to 2006. Notwithstanding these positive trends, it is recognised that aggregation of catch data at the family level causes a degree of uncertainty in the assessment. In addition, the yield estimates were limited to a point estimate of the size of fishing ground (Christophe, 2006) and any spatial expansion or contraction of effort over the period would influence the findings.

The marked decline in static trap CPUE at the turn of the last decade, particularly during 2001, can be attributed to factors other than overfishing. Decline in static trap CPUE coincided with major disturbances to inshore reef systems caused by severe bleaching-related coral mortality (Graham et al., 2006) and extensive land reclamation on reef flats around Mahé and Praslin (Jennings et al., 2000). The subsequent loss and degradation of reef habitat (Graham et al., 2006) may have reduced stock abundance and affected its distribution. Changes in catchability may also have occurred as fish and fishers adjusted to the disturbance. Notably, the trends in static trap CPUE and active trap CPUE diverged, with the latter not exhibiting significant decline during the period of disturbance. However, active traps are primarily used for targeting spawning aggregations and CPUE derived from this gear is potentially affected by hyperstability, a problem that can emerge in aggregation-based fisheries when the behaviour of fish and fishers act to stabilise catch rates as abundances decline (Sadovy and Domeier, 2005; Claro et al., 2009). Therefore, as a passive gear that is not used to the same extent in targeting aggregations, static trap CPUE is probably a more reliable indicator of siganid stock abundance.

The demographic stock assessment results indicated that overfishing had occurred, which therefore contrast with the results of

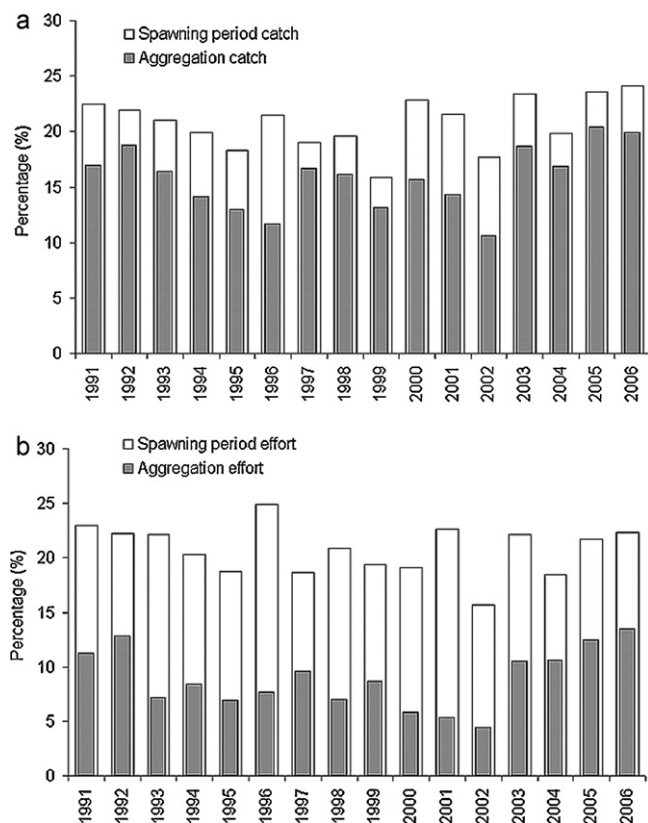


Fig. 6. Time-series patterns in the percentage of (a) annual siganid catch taken during spawning aggregation periods and on aggregations, and (b) annual trap fishing effort applied in the spawning periods and on aggregations.

the CPUE and yield analyses. Mortality rates of *S. sutor* were in excess of the target reference points in 1998 and 2007 and in excess of limit reference points in the latter year. Moreover, if it is assumed that fishing mortality rates are proportional to fishing effort, the stock is likely to have been overfished in several other years when effort was greater than that observed in 2007. There are two potential explanations for this divergence. Firstly, the reference points used are considered conservative as *S. sutor* has life history characteristics that confer resilience to overexploitation (Musick, 1999), such as short life span, rapid growth rate and a high population turnover rate (Grandcourt, 2002). Therefore, less conservative biological reference points could be considered for future assessments (e.g. $F=M$ or $E=0.5$). Secondly, the demographic assessments only reflect the size structure of the exploited component of the population. Since fishing effort is not uniform around the inner granitic islands and does not extend to the more distant shallow banks of the Mahé Plateau (Christophe, 2006), parts of the population remain unexploited. In addition, these spatial refugia potentially benefit productivity through recruitment subsidy (Caddy, 1999). Consequently, the overall resource, including components of the population not exposed to fishing effort, may be exploited within sustainable limits, as suggested by the yield curve.

Theoretical studies have demonstrated that the protection of juveniles may benefit populations and fisheries to a greater extent than management efforts concentrated on spawning adults (Pelletier and Magal, 1996; Heppell et al., 2006). Estimates of selectivity were limited to two time periods but the high retention rates observed in the non-aggregation component of the fishery dictates that juvenile protection constitutes an important issue for management. Moreover, any measures to protect aggregations may displace effort to juveniles and dissipate any conservation benefits resulting from the protection of spawning fish (Horwood et al., 1998). To identify management responses, it will therefore be necessary to determine the extent to which juvenile retention rate is influenced by biological processes (e.g. recruitment variability) and technical factors (e.g. illegal use of traps with smaller mesh sizes, targeting of nursery areas).

The approximate 2-fold relationship between aggregation effort and catch was less than expected given the size of spawning aggregations and is possibly explained by relative changes in spatial behaviour. While peak abundance was high, the aggregation often consisted of several schools. Since *S. sutor* also forms large feeding schools (Randall et al., 1997), the difference between non-aggregation and aggregation densities may not be large. Combined with other factors that can influence the catchability of aggregating fish, such as reduced interest in bait, current strength, visibility and gear saturation, catch rates may be less than expected based on the size of the aggregations. However, aggregation fishing still offers much improved catch rates (Robinson et al., 2007) and it is surprising that the effort directed at spawning aggregations has not increased given their high predictability and proximity to Praslin. The fishery is open access yet there was no evidence of any trend in the targeting ratio over the time series, suggesting that social or economic constraints to exploitation may exist. Market access and processing capacity can constrain effort in aggregation fisheries (Matos-Caraballo et al., 2006) and could conceivably occur on Praslin. Improved market access can commercialise fisheries that were previously for subsistence, or can drive expansion of commercial fisheries to unsustainable levels of exploitation (Sadovy and Domeier, 2005). However, this is one of many possible explanations and further research is needed to inform management on the drivers controlling the levels of effort.

Our findings are relevant to a recently initiated national programme aiming to establish co-management of the trap fishery. The apportioning of fishing effort among juvenile, non-spawning and spawning adult life history stages of *S. sutor* has important

implications for the selection of management measures. If a management objective was to control fishing in line with mortality-based reference points, then closing the spawning sites to fishing (e.g. using temporal or permanent no-take reserves) would have little effect since approximately 85% of the annual catch typically comprises fish that originate from the non-aggregation component of the fishery. Likewise, the introduction of restrictions on take or sales of *S. sutor* during a spawning aggregation period of 7 days each month would have minimal effect. Alternatively, management measures to control selectivity and fishing effort in the non-aggregation component of the fishery would be more effective. In considering management measures for this fishery, a precautionary approach should be adopted given uncertainties over biological reference points and the limitations of yield-based estimation methods.

Compared to many other aggregative spawners, aspects of *S. sutor* life history and aggregation dynamics are expected to confer relatively high resilience to aggregation fishing. Firstly, *S. sutor* is dioecious and therefore avoids many of the problems associated with fishing on protogynous aggregative spawners (Beets and Friedlander, 1998; Alonzo and Mangel, 2005). Secondly, the annual reproductive output of the stock is widely distributed, since *S. sutor* aggregations are spread across numerous sites and spawning occurs across a protracted season of 10 months (Robinson et al., 2007), a far longer season than most transient spawners (Sadovy de Mitcheson et al., 2008). However, due to the problems of hyperstability that can occur in these fisheries and the potential for Allee effects at low levels of spawning stock biomass (Sadovy and Domeier, 2005), a precautionary approach would involve monitoring of the aggregation component of the fishery to determine trends in exploitation rates and aggregation size.

In summary, levels of effort in the fishery have been within sustainable limits over the last few decades. Trends in yield and stock indicators (CPUE), and the relationship between yield and effort, are not indicative of an overfished resource. Moreover, there is no anecdotal evidence of past decline or collapse (Robinson et al., 2004) and the fishery appears to have been sustained over a significant historical timescale (Hornell, 1927). However, the fishery is open access and limits to sustainable exploitation may be reached or exceeded by increases in effort or use of high-take gears such as nets. While the targeting of spawning aggregations is not a principal driver of exploitation rates, this may change rapidly in an open access fishery due to increases in market demand and improved processing capacity to deal with high volumes of fish landed over short time periods. The management process for this fishery must also address the fact that the non-aggregation component of the trap fishery selects for a wide variety of reef fish families, most of which are more vulnerable to overexploitation than the Siganidae on which this study focused.

This study has demonstrated that aggregation fisheries can be sustainable at commercial levels of exploitation if based on relatively resilient transient spawners, which contrasts with the findings of Sadovy and Domeier (2005). It is widely recognised that transient spawners are more vulnerable to exploitation than resident spawners (Domeier and Colin, 1997; Domeier et al., 2002; Claydon, 2004; Sadovy de Mitcheson et al., 2008). Less widely recognised is the fact that vulnerability also varies substantially among transient spawners, due in part to relative changes in spatial behaviour and catchability between spawning and non-spawning fish, as well as in response to life history traits. While the more productive aggregative spawners such as *S. sutor* are unlikely to constitute a priority for conservation, their fisheries still require management to achieve sustainable yields. However, the spatial or temporal measures that are often advocated to protect spawning aggregations (Domeier et al., 2002) may have limited effectiveness if the majority of fishing mortality occurs in the non-aggregation

component of the fishery. Therefore, fisheries management should be informed on the distribution of effort among fisheries components and life history stages in order to select appropriate control or technical measures.

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