Weak density-dependent catchability in a siganid spawning aggregation fishery:

implications for fishery management and coral reef resilience

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Abstract

Introduction

The ecosystem goods and services provided by many coral reefs are being eroded by the transition from coral dominated to less desirable, macroalgal dominated states (Hughes et al. 2010; Cinner et al. 2013). Avoiding or reversing such phase shifts requires management interventions that influence key ecological processes on reefs, including the role played by herbivorous fish in depressing macroalgae (Graham et al. 2015). Since herbivorous species often constitute important food fishes (Hicks and McClanahan 2012; Kitalong 2012; Edwards et al. 2014), the need to maintain or enhance herbivory rates for ecosystem resilience poses a challenge for fisheries management, which typically seeks to maximise yield. Where phase shifts have occurred, the fishery target levels for herbivore biomass may need to be more conservative than those at which maximum sustainable yield occurs. These should be informed by emerging data on thresholds at which ecosystem functions such as herbivory are compromised (McClanahan et al. 2011). However, achieving such targets can be problematic in coral reef fisheries where input (e.g. total allowable fishing effort) and output (e.g. quotas) management controls must overcome issues of multiple gears and species, limited capacity for science and management, and an often high socioeconomic dependency on fishing (McClanahan et al. 1997; Sadovy 2005; Houk et al. 2012).

Marine reserves have emerged as the major conservation and fisheries management tool for coral reefs, and are ubiquitous to this ecosystem on a global scale (Mora et al. 2006). Evidence for marine reserves resulting in net benefits for fisheries yield remains limited (Hilborn et al. 2004; Sale et al. 2005; Kerwath et al. 2013). Furthermore, an objective of ensuring population persistence is challenging for mobile species, given that reserves or their

networks must protect a large fraction of habitat (e.g., Le Quesne and Codling 2009; Grüss et al. 2011). Conservation benefits can, however be achieved for mobile species by establishing relatively small reserves in areas where the population occurs at high densities and is particularly vulnerable to capture (i.e. catchable) (Roberts and Sargant 2002). Notably, large changes in catchability (and catch-per-unit-effort, CPUE) often occur in fisheries that redistribute effort seasonally and spatially to exploit spawning migrations and aggregations (Pears et al. 2007; Hamilton et al. 2012; Sadovy de Mitcheson and Erisman 2012). Many species of reef fish aggregate at specific times and locations for the purpose of spawning, but the change in population density involved in this behaviour varies widely (Domeier and Colin 1997).

Critically, the magnitude of density change associated with spawning aggregation formation may determine the contribution of catches from spawning sites to annual fishing mortality, (Robinson et al. 2011; Grüss et al. 2014a). Thus, several groupers (Serranidae) occur in low densities and are rare in catches outside of the spawning season, but become highly vulnerable to capture when densely aggregated for spawning (Matos-Caraballo et al. 2006; Claro et al. 2009). In an extreme example, up to 90% of annual landings of Nassau grouper (*Epinephelus striatus*) were once taken at spawning aggregations in Cuba (Claro et al. 2009). At the other extreme, exploiting spawning aggregations may not contribute significantly to annual fishing mortality if changes in fish density are minor, for example in many schooling species that are vulnerable to gears throughout the year, or if other factors, such as targeting behaviour, minimise catchability at spawning sites (Fulton et al. 1999; Claro et al. 2009; Tobin et al. 2013). The extent to which density changes influences catchability will therefore dictate the effects of spawning site reserves on annual fishing mortality rates (Grüss et al. 2014a).

Assuming density-dependence in catchability requires caution since the parameter is dynamic and influenced by a wide range of other factors. Other factors include changes in fisher preferences and targeting behaviour, adoption of more efficient gears and fish-finding equipment, and environmental factors, including depth (Wilberg et al. 2010; Tobin et al. 2013). Consequently, direct measures of the change in catchability (or at least CPUE) between spawning and non-spawning habitats will be more robust for assessing vulnerability to aggregation fishing than using density ratio as a proxy. Moreover, catchability varies due to the selectivity pattern, influenced by gear and the distribution of the fishery in relation to life stages. In aggregation-forming species, juveniles may overlap with adults in non-spawning habitats or occupy specific areas but are typically absent at spawning sites (e.g. Heppell et al. 2006; Grüss et al. 2011). If gears select for juveniles, implementing reserves in juvenile habitat has the potential to increase the proportion of the population surviving to sexual maturity, offering greater benefits for spawning stock and exploitable biomass than spawning site reserves (Grüss and Robinson 2015).

Many coral reefs of Seychelles have shifted to macroalgal dominated states in the wake of the 1998 mass bleaching event (Graham et al. 2015). The shoemaker spinefoot rabbitfish, *Siganus sutor* (Siganidae), is a browsing herbivore that plays a key role in removing macroalgal biomass (Chong-Seng et al. 2014). It is also an important target species of the trap fishery and is fished both at spawning aggregations and in non-spawning habitats of Seychelles' inner granitic islands (Robinson et al. 2011; Bijoux et al. 2013). The *S. sutor* population of the inner granitic islands is fully exploited but relatively resilient to fishing pressure given that the species is fast growing, short-lived and has a high natural mortality rate (Grandcourt 2002). Modeling simulations indicated that greater fisheries (yield-per-recruit, YPR) and conservation (spawning stock biomass-per-recruit, SSBR) benefits may be derived from protecting non-spawning habitat of *S. sutor* than from implementing spawning

site reserves (Grüss and Robinson 2015). The trade-off between economic and ecological objectives could, therefore, be mitigated if non-spawning reserves are situated in reef areas critical for resilience and lead to increases in both yield and spawning stock biomass. However, reserve model outcomes are sensitive to assumptions regarding changes in catchability and selection patterns in space and time (Grüss and Robinson 2015).

This study aimed to demonstrate the critical role of catchability in the management of a spawning aggregation fishery for a key herbivore on Seychelles' reefs. Three research questions were addressed. Firstly, does CPUE differ between spawning and non-spawning habitats? Secondly, to what extent is CPUE dependent on changes in fish density (i.e., density-dependent catchability) relative to other aspects of fish and fisher behaviour or environmental factors? Finally, what are the implications of catchability and size selection patterns for management of the fishery using marine reserves?

Methods

Study area

The study area encompassed a *S. sutor* spawning aggregation site (local name 'Dividi') and an adjacent carbonate fringing reef system located to the southwest of Praslin, Seychelles (Fig. 1). The carbonate fringing reef comprises an extensive lagoon (maximum depth c. 10 m) and an outer slope that extends to a soft sediment shelf at between 10 and 15 m depth. In non-spawning periods, trap fishing effort for *S. sutor* typically occurs on or close to nearshore carbonate fringing reefs (Christophe 2006). Between October and April each year, around the full moon, *S. sutor* migrate to Dividi and form spawning aggregations that last 2-3 d (Bijoux et al. 2013). Dividi is a submerged granitic reef, ranging in depth from 16 to 25 m, situated

approximately 2 km from the Praslin fringing reef system. Close to full moon, trap fishers monitor the arrival of *S. sutor* at Dividi (using trap sets and masks), redistributing fishing effort to the site when spawning aggregations have formed (Robinson et al. 2011). Recapture locations of *S. sutor* tagged at Dividi indicate that the carbonate fringing reefs off Praslin and adjacent islands serve as non-spawning habitat (Bijoux 2013).

Fishery observations

Fishery data were collected from observations of two trap fishers targeting *S. sutor* on the SW Praslin fringing reef (hereafter referred to as 'non-spawning habitat') and at the Dividi spawning site between November 2013 and June 2014. Both fishers are representative of the gear types and experience in the trap fishery, but were also selected on the basis that they, among only four others, exploit spawning aggregations at Dividi during most months of the spawning season. Bait differed between fishers, but each fisher was consistent in their bait use across spawning and non-spawning habitats. Fisher A (>30 yrs experience) used single-entrance bamboo traps to fish both spawning and non-spawning habitats, while Fisher B (<10 yrs experience) used metal traps, including single and double-entrance designs, to fish both habitats. All traps conformed to the legal minimum mesh size of 40 mm. Fishers decided on the number of traps and sets during each trip, including set, haul and soak times, and selected fishing location, depth and trap orientation.

Observations were limited to a single fisher on each day and were timed to fishing trips on or around the full moon at Dividi and to new moon and early first quarter periods in non-spawning habitat (Table 1). Three fishing days were observed for each fisher in non-spawning habitat, while at Dividi four and five trips were observed for Fishers A and B, respectively. It was not possible to alternate or randomise the days of observation between

the two fishers since both were only present at the spawning site on four of the nine days of observation.

Depth, soak time and catch of *S. sutor* were recorded for each trap set by fishers. CPUE was derived as the number of fish caught per set, standardised to a set soak time of one hour (no.trap-hr^{-1}). Due to limited space for researchers in the boat of Fisher A, fish length measurements were limited to Fisher B. All fish caught at the non-spawning site were measured for fork length (FL, to the nearest mm), whereas spawning site catch was sub-sampled for fork length estimation. Since gear saturation or interference can influence catchability (Robinson et al. 2014), all boats and traps active at the sites were recorded and fishing effort density estimated as the number of traps per km^2 (traps.km^{-2}). Spawning aggregations at Dividi are largely confined to two neighbouring granitic reefs (0.032 km^2; SFA unpublished data). Consequently, neither size nor location of the area fished differed greatly between trips in spawning habitat. By contrast, area fished in non-spawning habitat, approximated from constructing polygons in ArcGIS around GPS-derived set positions for each day, differed substantially in location and size between days (range = 0.254 to 3.518 km^2; mean = 1.298 km^2).

Fish surveys

Metrics on the density of *S. sutor* at spawning and non-spawning sites were obtained using diver operated stereo-video (DOV) surveys. The DOV system comprised 2 SONY TRV900E video cameras mounted horizontally on a base bar 0.8 m apart and inwardly converged. During each survey, SCUBA divers conducted a 20 minute swim transect that followed a zigzag pattern across the site, with divers remaining 1-2 m above the substrate and maintaining a slow swim speed (1-2 m.s^{-1}). On encountering a *S. sutor* school, divers remained stationary with the DOV maintained in the swim direction until the school had

passed in front of camera, after which divers continued on the transect. At Dividi, surveys covered the entirety of the site in 20 minutes. Since fishing occurred over a larger area in non-spawning habitat, sampling effort was doubled and two sites were randomly selected and surveyed within the area fished each day.

Video analysis

The DOV system was calibrated prior to surveys (precision = 2.9 to 3.6 mm for objects at a distance of 4 m), and the software EventMeasure (www.seagis.com.au) was used to analyse survey video. Two metrics of fish density were derived from 60 frames drawn at random (assuming uniform distribution) from the 30,000 frames comprising each 20-min survey. Firstly, presence/absence of *S. sutor* in sampled frames was recorded (Watson et al. 2005). This metric was considered indicative of school size with larger schools taking longer to pass in front of the cameras. Secondly, the numerical abundance of *S. sutor* in each sampled frame was estimated and the maximum number observed per survey recorded (*MaxN*). *MaxN* is a conservative estimate of abundance in high-density locations and for species that form schools (Cappo et al. 2004). While typically employed as a metric to account for repeat observations of individual fish in remote video deployments (Watson et al. 2005), the high mobility of *S. sutor* schools at the spawning site meant that repeated observations could not be discounted in our diver-swum transects. In non-spawning habitat, density metrics were pooled across the two sites surveyed each day. In 10 frames randomly selected from the video at each spawning and non-spawning site, maximum visibility was estimated as the distance to the furthest visible benthic feature (e.g., coral head). Mean (maximum) visibility across sites ranged from 6.9 to 18.3 m. Consequently, fish density metrics were only estimated when schools or individuals passed within a distance of 7 m from the cameras.

Data analysis

Comparison of CPUE across spawning and non-spawning habitats

To account for the right-skewed, zero-inflated and overdispersed distribution of the data collected, a two-stage approach was used to test for differences in CPUE between spawning and non-spawning habitat (Lo et al. 1992). Firstly, a Chi-square goodness-of-fit test on binomial CPUE data was employed to examine whether the proportions of sets with (1) or without (0) catch in non-spawning habitat conformed to those in spawning habitat. Zero-truncated data (i.e., non-zero CPUE data) were then tested for habitat differences using an Independent-Samples T test on log-transformed data ($\log_e$CPUE), assuming homogeneity in variances on the basis of a Levene's test.

The influence of fish density and other factors on CPUE

A boosted regression tree (BRT) analysis was performed to determine the extent to which CPUE is density dependent relative to other factors. BRT is a machine-learning, statistical regression method that is robust to nonlinearities, collinearity among predictor variables, missing data, and complex interactions (Elith et al. 2008). To stabilise variance, CPUE data were transformed for the BRT analysis using: $\log_e$ (CPUE+C), where C is a constant equal to the lower 10th percentile of non-zero CPUE observations. The BRT model was built to include nine predictor variables known to influence catchability (Arreguín-Sánchez F 1996; Stoner 2004; Wilberg et al. 2010; Table 2). Predictor variables were derived from data collected in this study, with the exception of current strength, which was derived from satellite altimeter and scatterometer data (see Supplementary Material S1). Cross-validation was used to converge on optimal settings and number of trees, while allowing for growth of at least 1000 trees (Elith et al. 2008). Learning rate was set at 0.005 and bag fraction at 0.6, while tree complexity was limited to two-way interactions (tree complexity = 2) due to small sample size (n = 191). Model performance was assessed using (1) the cross-validated mean

percent deviance explained, and (2) the cross-validated mean correlation coefficient between model predictions and observed data (Soykan et al. 2014). Predictors were ranked by variable importance (VI) scores, based on their prevalence in building the BRT model, and their relationship to CPUE examined using partial dependence plots. Spearman's rank correlation was used to examine the association of important predictive variables with CPUE by habitat if partial plots indicated that effects differed. Though BRT predictions are robust to collinearity, a Spearman's rank correlation matrix was constructed for continuous predictor variables to facilitate the interpretation of dependence plots and VI scores (Soykan et al. 2014). Interaction strength was estimated for all two-way combinations of predictor variables. BRT Models were constructed using '*gbm*' package v2.1 and code written for BRT functions by Elith et al. (2008) in R (R Development Core Team).

Management implications of catchability and size selection patterns

Mann-Whitney *U* and Hodges-Lehman tests were used to compare the size distributions and medians of spawning and non-spawning catches. Size distributions of the spawning and non-spawning catches were also compared to size at 50% maturity (L_{m50}), estimated at 23.75 cm FL for females (Robinson et al. 2011), and optimum length (L_{opt}), estimated at 26.98 cm FL using the empirical relationship of Froese and Binohlan (2000) with an estimate of asymptotic length (L_∞) of 43.3 cm FL from Grandcourt (2002):

$$\log(L_{opt}) = 1.0421 * \log(L_\infty) - 0.2742$$

To quantify management implications, our findings were used to update key parameters in a marine reserve model. The model was developed for the same *S. sutor* population considered in this study and assesses the relative fisheries (YPR) and conservation (SSBR) benefits of protecting spawning or non-spawning habitat (Grüss and Robinson 2015). The model was structurally unchanged from Grüss and Robinson (2015), with all parameter estimates

retained except size at recruitment to the fishery and the catchability ratio (i.e., the ratio of catchability in spawning habitat, q_s, over catchability in non-spawning habitat, q_{ns}). Size at recruitment to the fishery (L_{c50}) was estimated from a length-based catch curve based on length data collected in non-spawning habitat (Supplementary Material S2). The catchability ratio (q_s/q_{ns}) was estimated using the *CPUE* ratio across habitats as a multiplier of an absolute value of catchability derived for non-spawning habitat (see Supplementary Material S2).

Point estimates of YPR and SSBR were derived for 2013 annual levels of fishing effort in the fishery (97,802 trap sets; Seychelles Fishing Authority, unpublished data). We examined the percentage change in YPR and SSBR from protecting 30% of non-spawning habitat or spawning sites relative to a scenario of no reserves, assuming full fishing effort redistribution to areas remaining open to fishing in the respective habitat. To test sensitivity to the parameter estimates generated in the present study, we performed three model runs updating either L_{c50}, the catchability ratio, or both parameters, comparing these results to those obtained using previous parameter estimates (Grüss and Robinson 2015).

Results

Comparison of CPUE across spawning and non-spawning habitats

Regardless of the metric and with the exception of a single day, fish densities were higher at the spawning site than in non-spawning habitat (Table 1). Daily *S. sutor* catch at the spawning site varied from zero to greater than 1,000 fish, with particularly high catches in December and January (Table 1). By contrast, daily catch was lower and less variable in non-spawning habitat, even though more sets were made in these areas. Consequently, there was a greater range in CPUE at the spawning site (Fig. 2). The proportion of sets yielding zero

catch (around one third) was equivalent across habitat ($\chi^2 = 1.27$; $p = 0.26$). However, in sets yielding non-zero catch, spawning site CPUE exceeded that observed in non-spawning habitat ($t = 6.95$; $p < 0.001$) by a mean difference of 4.67 ($\pm$ 1.24, SE) fish.trap-hr^{-1}.

The influence of fish density and other factors on CPUE

Using cross validation, the BRT model explained 37.8% of the deviance in the data with a mean correlation between predicted and observed data of 0.61. Fish presence was marginally the most important predictor variable (Table 3). However, since the model is stochastic and presence, depth and current strength had similar VI scores, the relative importance of the three predictors often shifted between runs. High catch rates were generally observed when presence exceeded 28%, corresponding to the strong step in fitted CPUE (Fig. 3). Nonetheless, the model fit did not account for trip 9, for which presence reached 63% but CPUE was low (Table 1). Depth was collinear to presence and MaxN (Supplementary Material S3), both of which peaked at the deeper spawning site. However, since traps were not set in the 12-16 m depth range, the model fitted increases in CPUE to both the shallow non-spawning (2-12 m) and deep spawning (16-24 m) habitat (Fig. 3). CPUE was predicted to increase at high levels of current strength (Fig. 3). Separating the dataset by habitat, CPUE was positively correlated with current strength at the spawning site ($\rho = 0.86$; p < 0.01), but not in non-spawning habitat ($\rho = 0.27$; p > 0.05). Variables of moderate relative importance (8-10%; Table 3) indicated that CPUE declines with soak time and increases at moderate levels of MaxN and at high levels of fishing effort density (Fig. 3). As expected, collinearity was strongest between the two fish density metrics, MaxN and presence, and also among these metrics and depth, visibility and fishing effort density (Supplementary Material S3). In spite of a low VI score, the fisher variable was involved in the largest interaction, relating to a multiplicative effect on CPUE when Fisher B targeted high presence spawning aggregations

(Table 4). Four of the nine strongest interactions involved depth, while presence and soak time were involved in three.

Management implications of catchability and size selection patterns

S. sutor caught at the spawning site were significantly larger than those caught in non-spawning habitat (Mann-Whitney U; $Z = -5.2$; $p < 0.001$), corresponding to a difference in median size of 2 cm FL (95% CI: 1.3-2.8). Size distributions were bimodal but modal strength contrasted between catches from the two habitats (Fig. 4). Consequently, 31% and 59% of spawning and non-spawning catches were below the size at maturity (23.75 cm FL), respectively, while 67% and 92% were below size at optimal length (26.98 cm FL).

A change in L_{c50} from 16.15 to 21.37 cm FL means that less juvenile fish are caught in non-spawning habitat than previously estimated. Consequently, protecting non-spawning habitat results in lower benefits for SSBR if L_{c50} is the sole parameter updated in the marine reserve model (Table 5). Since the catchability ratio estimated in this study ($q_s/q_{ns} = 4.31$) is lower than that used in Grüss and Robinson (2015) ($q_s/q_{ns} = 10$), fishing mortality increases in non-spawning habitat when this is the sole parameter updated in the model. Protecting 30% of the non-spawning habitat therefore results in a much greater improvement in SSBR than previously estimated, in addition to generating a strong, beneficial effect on YPR. Moreover, given a lower catchability ratio, protecting spawning sites leads to a neutral effect on YPR, rather than the negative effect obtained using previous estimates, though the benefits of spawning reserves for SSBR are halved. As increases in L_{c50} and decreases in the catchability ratio have opposing effects, the benefits of reserves in non-spawning habitat are diluted if both parameters are updated in the marine reserve model (Table 5).

Discussion

The increase in fish density associated with spawning aggregation formation is considered a key factor conferring vulnerability to overfishing (Sadovy de Mitcheson and Erisman 2012). Though density-dependent catchability is common to aggregation fisheries, and occurred in our study fishery, the environment and other aspects of fish and fisher behaviour may act in reducing vulnerability to the gear (Stoner 2004; Wilberg et al. 2010; Robinson et al. 2014). Possibly due to the effects of current strength on catchability, CPUE in a *S. sutor* spawning aggregation fishery in Seychelles was found to be highly variable. Consequently, CPUE only increased by a factor of four when fishers targeted spawning aggregations in spite of a nine to thirteen-fold (depending on the metric) increase in fish density. Given the short duration of *S. sutor* spawning aggregations (Bijoux et al. 2013), the weak density-dependence in catchability and selection pattern means that most of the annual fishing mortality of the population derives from the capture of smaller individuals in non-spawning habitat. Therefore, marine reserves in that habitat were found to be more beneficial for the *S. sutor* population of Southwest Praslin than spawning site reserves, by an even greater extent than previously estimated (Grüss and Robinson 2015) given the weak density-dependent catchability observed at the spawning site.

Factors influencing catchability and CPUE in the S. sutor fishery

Fishers from Praslin have targeted *S. sutor* spawning aggregations for at least a century, recognising the opportunity for higher catch rates and economic returns (Hornell 1927). Nonetheless, CPUE was highly variable at Dividi with high catch rates confined to three of the nine fishing trips to the site, even though spawning aggregations with densities in excess of those observed in non-spawning habitat were present on five other trips. Therefore, in spite of fish presence constituting the predictor variable most selected for tree splitting (Elith et al.

2008), the high variability in CPUE at the spawning site reduced the relative importance of fish density metrics in the BRT model and suggests that catchability exhibits weak density-dependence. This finding supports an assertion by contemporary fishers of dynamic catchability at the spawning sites, which is typically attributed to changes in feeding motivation or fish behaviour between days or months (Praslin Fishers Association, pers. comm.). Sources of variation in catchability in baited fisheries also include aspects of fisher behaviour and are ideally examined in the context of environmental factors, many of which correlate with fish physiology and behaviour (Stoner 2004; Wilberg et al. 2010).

In addition to two fish density metrics, seven environmental and fishery variables were included in the BRT model. However, as spawning behaviour involves migration of *S. sutor* from a fringing reef to an offshore and submerged granitic reef (Robinson et al. 2011), certain explanatory variables were prone to confounding or collinearity, the latter of which can affect the interpretation of model results (Soykan et al. 2014). Thus, in spite of its importance to the BRT model, the relationship between depth and CPUE was confounded by the absence of fishing in depths intermediate to spawning and non-spawning habitat. As depth was a continuous variable, this caused the model to erroneously fit increases in CPUE in the non-spawning habitat commensurate with those at the spawning site.

By contrast, current strength, the next most important variable in the BRT model, provides a plausible explanation for variable CPUE at the spawning site. The relative importance of visual and olfactory cues for feeding varies among fish species and has implications for the effects of visibility and currents on catchability (Stoner 2004). While visibility was collinear with depth, tending to be greater at the spawning site, the variable had little effect in the model. Therefore, olfactory cues may play a key role in *S. sutor* feeding behaviour, evidenced by the relative importance of current strength to the model. Stronger currents disperse bait plumes and increase the active space for baited gear (Eggers et al. 1982). Though insensitive

to a wide range of current strengths in non-spawning habitat, CPUE exhibited a positive relationship with this variable at the spawning site, potentially explaining why rates were decoupled from density in certain periods. Providing further evidence for the influence of current strength, CPUE was higher for double-entrance traps, which are designed to overcome incorrect orientation of traps in relation to current on setting or variable current during a soak. The effects of current on CPUE may differ between habitats due to numerous factors, including higher fishing effort density at the spawning site, leading to overlapping and indistinct bait plumes from traps at low current strength, and the need for stronger olfactory cues due to competing motivations for feeding and reproduction.

Other predictors had less influence on CPUE and none, in isolation, provided a strong explanation for variable catchability at the spawning site. Escapement through the trap mouth or mesh is often a function of soak time, especially if fish species are mobile in the traps and can squeeze through meshes smaller than body depth (Robichaud et al. 2000). However, soak time varied within as opposed to between trips. By contrast, CPUE was predicted to increase with fishing effort density. Though high densities of baited gear can stimulate cues, feeding motivation and catchability (Stoner 2004), fishing effort was observed to increase in response to high catchability, with more boats and traps being introduced if initial sets yielded positive results. However, fisher identity did have an influence on CPUE through an interaction with fish presence, stemming from observations of Fisher B coinciding with periods of highest catchability.

Our analysis was limited in terms of explanatory variables relating to fish behaviour and sample size. Fishers report that low catch rates occur when schooling behaviour dissipates and fish rise high in the water column. The function or frequency of this behaviour is unknown, though vertical distribution can relate to current strength (Michalsen et al. 1996). Attempts to record the behaviour during dives were often prevented by limited visibility.

Moreover, when observed, fish typically resumed schooling behaviour close to the substrate on the approach of divers. Monitoring catch rates and *in-situ* current strength in combination with passive acoustic telemetry, using depth sensor transmitters, would therefore be informative. Feeding motivation will also vary if the relative investment in somatic and reproductive growth changes over the spawning season (Bijoux et al. 2013), potentially explaining why our results, as well as reports from fishers, indicate that highest catch rates tend to occur early-mid season rather than at the end. Nevertheless, adding more variables to the BRT model would require larger sample sizes or further trade-offs in model complexity (Elith et al. 2008; Soykan et al. 2014). In the present study, small sample size (n=191 sets) was an important consideration in constructing the BRT model, requiring low complexity trees and a slow learning rate to grow enough trees (Elith et al. 2008). Sample size was constrained in spawning habitat with fishers not moving traps to the site if weather was unfavourable (e.g. February 2014), if aggregations were perceived to be small, or if catchability was low (e.g. October 2013, April 2014). Extending the study to two years would be beneficial, especially if additional predictor variables are to be explored.

Management implications

Catchability is a critical parameter for fishery assessment and management but is dynamic and difficult to estimate (Arreguín-Sánchez 1996; Wilberg et al. 2010). The effects of protecting fractions of spawning or non-spawning habitat on populations and fisheries yield are, however, highly dependent on this parameter (Grüss and Robinson 2015). Using CPUE and estimates of population abundance derived from visual-census (Erisman et al. 2011; Supplementary Material S2), this study improved on previous, indirect methods for estimating a catchability coefficient, while a more robust catchability ratio was provided by incorporating seasonal variation in spawning site CPUE (Grüss et al. 2014a). The consequences of a reduced catchability ratio were increases in fishing mortality in non-

spawning habitat, leading to much greater benefits for SSB and a shift from a negative to positive effect on YPR if reserves are established in this habitat.

The management implications of changes to the catchability ratio must also be considered in parallel to changing selectivity patterns. Assuming no change in compliance with a 40 mm mesh size regulation (Robinson et al. 2011), lower recruitment strength prior to our study may have served to increase the size at recruitment to the fishery (Supplementary Material S2). Even though a large proportion of catches from non-spawning habitat were smaller than size at maturity and optimal size, increased size at recruitment to the fishery was sufficient to reduce SSBR, relative to previous estimates, when marine reserves are implemented in non-spawning habitat. Nonetheless, when size at recruitment to the fishery is increased, reserves in non-spawning habitat still increase SSBR over the no-reserve scenario. Coupled with increases in YPR resulting from a lower catchability ratio, this result suggests that a spatial management strategy can provide both fishery and conservation benefits, the latter in terms of stocks and the ecosystem. Stock size was essentially doubled over the no-reserve scenario when both the size at recruitment to the fishery and the catchability ratio were updated and non-spawning habitat was protected, which would conceivably promote greater algal removal by *S. sutor* (Chong-Seng et al. 2014). Since the *S. sutor* fishery mainly operates on carbonate reefs during non-reproductive periods, focusing management on this habitat therefore offers an opportunity to address pervasive resilience issues in Seychelles, notably the phase shift to macroalgal-domination that has occurred at many carbonate sites (Graham et al. 2015).

Conclusions

Spawning aggregation behaviour that is predictable, typically evoked by the formation of a few high density aggregations during a narrow reproductive season, predisposes fish populations to overfishing (Sadovy de Mitcheson and Erisman 2012). *S. sutor* differs from

many transient aggregation spawners in that it forms spawning aggregations at many sites over a wide reproductive season, though fisher knowledge of location and timing is well developed (Bijoux et al. 2013). Catchability at a *S. sutor* spawning site proved to be highly dynamic, potentially due to the effects of current strength, which limited the ability of fishers to predict and maximise returns based on increases in fish density. Sources of variation in catchability therefore play a critical role in determining the extent to which changes in fish density confer vulnerability to overfishing. Nevertheless, catchability is gear-specific (Arreguín-Sánchez 1996) and its variability can be mitigated in fisheries that utilise a wide range of gears, fishing techniques or technologies (e.g. Cuba; Claro et al. 2009), enabling fishers to overcome unfavourable environmental conditions such as strong currents. Thus, while the protection of non-spawning habitat offers benefits for populations and ecosystems, gear and fishing effort controls are still required at spawning sites to regulate fishing pressure (Russell et al. 2012; Grüss et al. 2014b).

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