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Vulnerability to Fishing in Reef Fishes that Aggregate

Thesis submitted by

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ABSTRACT

Many species of coral reef fish form aggregations at predictable times and locations for the purpose of spawning. Targeted fishing of spawning aggregations can result in loss of aggregations, rapid population depletion and fishery collapses. However, there are also examples of spawning aggregation fisheries that have persisted for decades, including some that lack robust conservation or management measures. That spawning aggregation fisheries vary in their vulnerability to overfishing is often overlooked and can result in narrow recommendations for protection of spawning sites using marine reserves. To enable a broader range of societal objectives and management interventions to be considered, improved understanding of the risks posed by spawning aggregation fishing is therefore required.

This thesis integrated the roles of biology, fish and fisher behaviour, and the socioeconomic and cultural context of fisheries to disentangle causes of vulnerability to overfishing in coral reef spawning aggregation fisheries. I aimed to develop a bivariate, indicator-based risk assessment of spawning aggregations that could be applied in the data-poor management context of most of these fisheries. A bivariate approach is required since the risks posed by fishing of spawning aggregations depend on intrinsic and extrinsic components of the system. Life history traits and spawning behaviour determine the productivity of fish populations and their inherent (i.e. intrinsic) capacity to recover from depletion. Predictable increases in population density that are associated with spawning aggregation behaviour influence the potential for development of a targeted fishery. However, the exposure of populations to spawning aggregation fishing will be determined by extrinsic (i.e. fishery) factors that influence catchability and fishing effort at spawning sites. These factors include aspects of fisher knowledge, accessibility, technology, markets and management. Through four data chapters (Chapters 2 to 5), I explore mechanisms by which many of these intrinsic and extrinsic factors influence vulnerability to overfishing in these fisheries. The findings of these data chapters are used to develop robust indicators for a risk assessment framework, which is applied to a global selection of spawning aggregation fisheries and its predictive ability examined (Chapter 6).

Spawning aggregations are ephemeral events and fishers must first acquire knowledge on their location and timing for a targeted fishery to develop. In my first data chapter, interviewbased surveys were employed to examine how socioeconomic and cultural context leads to variation in knowledge and targeting at two case study locations (Ahus, Karkar islands) in Papua New Guinea (Chapter 2). While variable access rights among fishers and genders to reef habitats were sources of wide heterogeneity in knowledge at Ahus, knowledge was more homogenous at Karkar and influenced solely by gears used by fishers. However, the exposure of aggregations to fishing depended primarily on socioeconomic drivers of fishing effort (dependency on fishing, markets, management). While knowledge was equivalent for a few species (e.g. *Lutjanus gibbus*) across locations, highly efficient fishing techniques have emerged to exploit aggregating behaviour at Ahus. This finding demonstrates that, while knowledge clearly acts as a precursor, socioeconomic drivers determine how and to what extent aggregations are targeted.

Once fishers have acquired knowledge on reproductive behaviour, the development of a targeted fishery will depend on the level of population density changes associated with spawning aggregation formation and whether or not those changes translate into increases in catchability (i.e. exhibit density-dependence). Chapter 3 tests assumptions regarding density-dependent catchability in a trap fishery for rabbitfish (*Siganus sutor*) in Seychelles and models their management implications in terms of marine reserve outcomes for spawning stock biomass-per-recruit and yield-per-recruit. Though spawning aggregation formation involves nine to thirteen fold increases in population density, catch rates (a proxy for

catchability) exhibited weak density-dependence, being only fourfold greater in spawning habitat than catch rates in non-spawning habitat. Catch rates in spawning habitat were also highly variable across the spawning season and generally only peaked when currents were strong. Since spawning behaviour incurs lower than expected increases in catchability, marine reserves implemented in non-spawning areas would be more beneficial than those protecting spawning sites in terms of maintaining yield-per-recruit while rebuilding spawning stock biomass-per-recruit. These findings have implications for both fisheries management and ecological resilience, since *Siganus sutor* is a key macroalgal browser in Seychelles where a high proportion of reefs have transited to macroalgal-dominated states in the wake of mass coral bleaching.

Fish and fisher behaviour at multispecies spawning sites are highly dynamic and are likely to cause vulnerability to overfishing to vary across aggregations or between species. Chapter 4 examines these dynamics at a multi-species grouper spawning site in Papua New Guinea. Despite similar aggregation sizes, *Epinephelus polyphekadion* was 8-fold more vulnerable to capture than *E. fuscoguttatus*. Catch rates of both species were unrelated to the size of their respective aggregations. However, *E. polyphekadion* catch rates declined as the density of fishing effort increased at the site, with gear saturation identified as the likely mechanism for this effect. *E. fuscoguttatus* catch rates were negatively related to the size of aggregations formed by its congener, stemming from the superior competitiveness and therefore higher selectivity of the gear for *E. polyphekadion*. The findings have implications for gear-based management, which must be based on understanding of gear selectivity for aggregating species, and fishing effort controls, which must consider the potential for effort-dependent patterns in catchability.

Critically, changes in catchability that typically occur with spawning aggregation formation also offer an opportunity for rebuilding populations and sustaining fisheries. In Chapter 5, a per-recruit model was used to compare the long-term effects of marine reserves protecting either spawning or normal residence areas for *S. sutor* and *E. fuscoguttatus* populations in Seychelles, allowing for contrasts between catchability, life history traits and sexual modes. Normal residence reserves were more effective at improving both the spawning stock biomass-per-recruit and yield-per-recruit of *S. sutor*. By contrast, the protection of spawning sites is preferable for maintaining spawning stock biomass-per-recruit and normalising the sex ratio in the protogynous grouper *E. fuscoguttatus*. Neither spawning reserves nor normal residence reserves improved *E. fuscoguttatus* yield-per-recruit. Analyses revealed that relative reserve effects are more sensitive to changes in catchability than to life history traits. Because changes in catchability occurring with *S. sutor* aggregation formation are small, compared to many other aggregation-forming populations, this species suffered higher fishing mortality in normal residence areas than at spawning sites. Consequently, normal residence reserves will be more beneficial than spawning reserves. Marine reserves protecting spawning sites are not always the most effective tool for balancing conservation and exploitation objectives and should be weighed against other management options.

A major challenge for management stems from the data-poor context of many spawning aggregation fisheries, which typically lack information on productivity, catch and exploitation status. To address this gap, the thesis culminated in the design of an indicatorbased tool for assessing risks of overfishing in these fisheries, using the findings of earlier chapters to inform indicator development (Chapter 6). A bivariate risk assessment tool was selected, composed of an axis of intrinsic vulnerability comprising indicators of species life history and spawning behaviour, and an axis of extrinsic vulnerability comprising indicators of fisher knowledge, technology, accessibility, markets and management. Using interviews with fishery experts to score indicators, the tool was examined for a global selection of spawning aggregation fisheries and its predictive ability tested. The tool performed moderately in predicting fishery status. The risk of overfishing varied extensively, though many assessed fisheries scored as high risk in terms of intrinsic vulnerability and low risk for extrinsic vulnerability. Key intrinsic risk factors were species productivity and the type of spawning aggregation formed. A key driver of extrinsic vulnerability was management context, while the status of many fisheries was stable or improving due to management intervention. Successful management interventions included gear, fishing effort and catch controls, as well as measures that restrict access to spawning aggregations (e.g. marine reserves). The findings highlight the importance of considering fisheries management objectives in addition to conservation, which requires that these socio-ecologically complex fisheries are better integrated in fisheries management planning.

The discourse surrounding spawning aggregation fisheries has typically focused on the challenges they pose for population persistence, rarely recognising that not all fisheries will be at high risk of overfishing and that aggregating behaviour also presents opportunities for rebuilding populations and sustaining fisheries. This thesis provides insights for a broader approach to addressing these fisheries, identifying important causes of vulnerability and demonstrating their implications for assessment and management. Aggregating behaviour typically predisposes populations to density-dependent catchability, but fishing pressure will ultimately be determined by catchability and the socioeconomic drivers of fishing effort, which constitute levers for management intervention. Though management targets or limits for spawning aggregation fisheries must be precautionary and adaptive given the largely unknown indirect (i.e. non-lethal) impacts of fishing, fisheries management objectives should not be discounted in favour of conservation in all cases.

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Chapter 1: Introduction

Wild capture marine fisheries production has stagnated at around 80 million tonnes in recent decades as limits to exploitation have been reached or exceeded (Swartz et al. 2010; FAO 2014). A major divergence is now emerging in terms of the current state of fisheries, whereby considerable success in rebuilding stock biomass in parts of the developed world contrasts with worsening levels of overfishing and stock depletion in developing countries (Worm et al. 2009; Worm & Branch 2012; McClanahan et al. 2013). The prognosis for coral reef fisheries in the tropics is a particular concern since many are threatened by habitat degradation caused by climate change, pollution and coastal development in addition to overfishing (Graham et al. 2007; Newton et al. 2007; Maina et al. 2013). Rebuilding coral reef fisheries, which ultimately requires a reduction in fishing mortality rates (Beddington et al. 2007), is further challenged by a high level of dependency among coastal societies on these systems for economic and livelihood benefits (Cinner 2014), weaknesses or absence of governance (McClanahan et al. 2013; Cinner & McClanahan 2014), and high local and global demand for reef resources (Brewer et al. 2012; Sadovy de Mitcheson et al. 2013). Moreover, coral reef fisheries are typically data-limited and frequently lack basic information on fishing pressure and catch composition (Johannes 1998; Houk et al. 2012). As custodians of datalimited yet biologically and socioeconomically complex systems, coral reef managers and user communities would therefore benefit from innovative approaches for assessing and rebuilding fisheries.

Coral reef fisheries are typically unselective for species, leading to broad taxonomic catch compositions (Jennings & Polunin 1995; McClanahan & Cinner 2008). However, the impacts of exploitation will vary widely among species due to differences in life history, reproductive biology and the behaviour of fish and fishers (Jennings et al. 1999; Sadovy 2005). Traits such

as longevity and age at maturity directly relate to the productivity of a population and its potential to recover once depleted (Musick 1999; Dulvy et al. 2004). Fish and fisher behaviour largely determines the exposure, or susceptibility, of a population to a fishery (Arreguín-Sánchez 1996; Stoner 2004; Hobday et al. 2011). Thus, coral reef fishes that exhibit the fastest rates of decline and slowest rates of recovery are typically long-lived, late maturing, highly catchable and prized by fishers by virtue of their price or cultural preference (Dulvy et al. 2003). Many species of the families Epinephelidae (groupers) and Lutjanidae (snappers) exhibit these characteristics and are typically the first to be overfished on reefs (Coleman et al. 1999; Sadovy de Mitcheson et al. 2013).

Over the last two decades, coral reef fisheries research and management have increasingly focused on how types of spawning behaviour render certain species vulnerable to fishing (Domeier & Colin 1997; Sadovy & Domeier 2005). Many reef fishes aggregate at specific sites during certain periods for the purpose of spawning (Sadovy de Mitcheson et al. 2008). Constituting spatially and temporally predictable increases in population density, spawning aggregations are highly attractive targets for fishers, yielding high catch rates and economic returns in the short-term but often leading to rapid overfishing where management is lacking or ineffective (Coleman et al. 2000; Sadovy & Domeier 2005; Claro et al. 2009). On a global scale, there is increasing evidence of declines in the productivity of spawning aggregation fisheries, the extirpation of spawning aggregations, and the collapse of populations from which they form (Table 1.1). However, of equal importance to our understanding of the vulnerability caused by this behaviour is the fact that certain spawning aggregation fisheries appear relatively sustainable (Table 1.1). This dichotomy highlights key research areas, such as the relative roles of life history, aggregation dynamics and catchability in the response of reef species to aggregation fishing. A limited numbers of reviews addressing these research areas are available (Sadovy & Domeier 2005; Sadovy de Mitcheson & Erisman 2012), and

have identified the need for empirical investigations to disentangle sources of variation in

vulnerability to fishing among aggregative spawners.

Table 1.1 Case studies contrasting development trajectories for spawning aggregation fisheries. Studies were selected to highlight probable factors (in bold) important to sustainability in these fisheries

<u>Unsustainable.</u> A highly targeted spawning aggregation fishery for Nassau grouper (*Epinephelus striatus*) in Cuba collapsed after a few decades (Claro et al. 2009). The collapse was attributed to slow **life history**, lack of **management** and intense fishing pressure on spawning aggregations. The latter was promoted by large **catchability changes** in the spawning season - common in solitary species that form a few very large spawning aggregations in a narrow season.

<u>Unsustainable.</u> A large aggregation of *Epinephelus ongus* (named locally after the month of April when the aggregation formed) disappeared in Seychelles due to intense fishing pressure. Collapse was primarily attributed to **accessibility** to the spawning site, which was located at the entrance to the largest fishing port in the country (Robinson et al. 2004).

<u>Unsustainable.</u> The introduction of **technology** (underwater flashlights to enable night spearfishing) increased catchability, particularly for *Plectropomus areolatus*, in a multispecies spawning aggregation fishery in the Solomon Islands (Hamilton et al. 2012a). Unsustainable aggregation fishing for this species has also resulted from **market** pressures associated with the spread of the live reef food fish trade (Hamilton et al. 2011).

<u>Sustainable.</u> Robinson et al. (2011) found little evidence of overfishing in a rabbitfish (*Siganus sutor*) fishery in Seychelles. Concluded that the species is relatively resilient to spawning aggregation fishing due to its fast **life history** and because **catchability changes** are relatively minor (spawning period catches <15% of annual catch). This unmanaged fishery has been sustained for nearly a century (Hornell 1927).

<u>Sustainable.</u> Tobin et al. (2013) found little evidence that spawning behaviour results in increased vulnerability of coral trout (*Plectropomus leopardus*) to the fishery. Since aggregations that form for non-reproductive purposes are also **targeted** by fishers, **catchability changes** associated with spawning are minor. However, the study noted the indirect effects of fishing aggregations on reproductive potential in hermaphrodites.

<u>Sustainable.</u> In a study of the silver seabream (*Chrysophrys auratus*) in Western Australia, Jackson (2012) found that fishing effort, fisher knowledge and technology led to overfishing of stocks. However, effective **management** of spawning aggregation fishing, through a combination of measures including TAC/quotas and seasonal closures, has since been successful in recovering stocks.













The extent to which the exploitation of aggregations predisposes populations to overfishing will largely depend on catchability, notably whether or not catchability is density-dependent and increases with aggregation formation. Catchability (q) is defined as the constant of proportionality between fishing mortality (catch, C) and fishing effort (E) for a population of given size (N), giving C = qEN (Hilborn & Walters 1992; Wilberg et al. 2010). However, catchability is rarely constant. Critically, catchability is commonly density-dependent such that, where population density is distributed unevenly across habitat and fishing is nonrandom, catch rates relate more to density where fishing is occurring rather than to overall population size (Wilberg et al. 2010). Though increases in catchability should therefore accompany the formation of dense spawning aggregations, catchability is also influenced by other aspects, including fish behaviour and biology, fisher knowledge, behaviour or technology, and environmental factors (Arreguín-Sánchez 1996; Wilberg et al. 2010). For example, catchability increases may not occur with spawning aggregation formation, or may be limited, if other species forming aggregations at multispecies spawning sites are more competitive for baited gear (Mangubhai et al. 2011), or if spawning aggregations form at depths that limit gear efficiency (Hamilton et al. 2012a). Conversely, the introduction of new technologies or fishing practises can lead to marked increases in fishing efficiency and therefore catchability (Coleman et al. 1999; Claro & Lindeman 2003). Since 'aggregation' spawning is defined by density change (Domeier & Colin 1997), in examining vulnerability to fishing it is necessary to critically examine the potential for density-dependence relative to other factors known to influence catchability.

Life history and predictability of density change can be considered as intrinsic components of vulnerability in that they are inherent to population biology and behaviour but expose aggregation spawners to overfishing. However, spawning aggregations are, by nature, ephemeral events and for a targeted (as opposed to incidental) fishery to develop, fishers

must first gain knowledge on their location and timing. Fisher knowledge of spawning aggregations is highly variable among fishing communities, which has been attributed to factors such as dependency on fishing, gear use, resource status and customary tenure arrangements (Johannes 1981; Robinson et al. 2004; Hamilton et al. 2004, 2005; Samoilys et al. 2006). However, the socioeconomic and cultural context that leads to both variation in knowledge and the use of that knowledge in targeting spawning aggregations is poorly understood (Hamilton et al. 2012b), and would benefit from systematic or quantitative investigation. Given the multitude of factors that influence catchability (Wilberg et al. 2010), and that populations may also be accessible to fishing in non-reproductive periods, a spawning aggregation fishery may not develop or be limited in scale even though sites are known (Robinson et al. 2011; Tobin et al. 2013). Where knowledge is present, fishers must be able to access both spawning sites and the technology to exploit aggregations. Subsequently, markets, management, socioeconomic and cultural context will dictate the fishing effort directed at aggregations. The development of a targeted fishery can therefore be considered as the extrinsic component of vulnerability in spawning aggregation fisheries. Critically, catchability as a parameter provides for much of the interaction between intrinsic and extrinsic components of vulnerability, capturing the behaviour of both fish and fishers (Wilberg et al. 2010). However, many studies in the field focus on fish biology and behavioural ecology of spawning aggregations, while studies of aggregation fishery development and dynamics are relatively limited in spite of their importance for conservation and management (Sadovy de Mitcheson & Erisman 2012).

Spawning aggregation behaviour also provides opportunities for conservation and management. Some solitary species are rare in catches and only become accessible to a fishery when aggregated for spawning (e.g. Matos-Caraballo et al. 2006; Claro et al. 2009). Consequently, management measures that prevent access by fishers to spawning sites can

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potentially be effective in rebuilding populations in support of fisheries or ecological objectives (Grüss et al. 2014a). By contrast, in species that are accessible to a fishery throughout the year (e.g. species that also school or aggregate for non-reproductive functions (Sala et al. 2003), or for which spawning behaviour is less predictable (Claro et al. 2009; Sadovy de Mitcheson & Erisman 2012), catches taken at spawning aggregations may constitute only a minor portion of the annual fishing mortality incurred by the population (Robinson et al. 2011; Tobin et al. 2013). If management is aimed at controlling fishing mortality in such fisheries, then measures that focus solely on the spawning aggregation component of the fishery are unlikely to be effective (Grüss et al. 2014a).

In addition to management, information on how fishers exploit aggregating behaviour is essential for monitoring and assessment. Since spawning aggregation densities may decline at a slower rate than population abundance (Nemeth 2012), density-dependent catchability can cause catch rates (i.e. catch-per-unit-effort, CPUE) to remain relatively stable, in a process known as CPUE hyperstability (Hilborn & Waters 1992; Nemeth 2012; Sadovy de Mitcheson & Erisman 2012). If catch rates are assumed to be proportional to abundance, this process can result in perceptions of an 'illusion of plenty', whereby status is considered healthy in spite of overfishing (Erisman et al. 2011). A failure to detect CPUE hyperstability has resulted in the collapse of some notable fisheries and is likely to be common among aggregation spawning reef fishes (MacCall 1990; Rose & Kulka 1999; Sadovy & Domeier 2005). Regardless of the availability of catch rate data and their use in monitoring (Johannes 1998; Sadovy de Mitcheson et al. 2008), an understanding that spawning aggregation fisheries are susceptible to hyperstability should inform assessment and management since fisher perceptions of resource status are also informed by their experiences of catch rates, leading to decisions regarding fishing effort (Cinner et al. 2008, 2011).

A variety of indicator-based tools have been developed to assess vulnerability to overfishing in data-poor contexts, where estimates of productivity and catch are unavailable or highly uncertain. Life history parameters (e.g. age at maturity) can serve as indicators of productivity and identify risks of local extinction due to fishing (Musick 1999). Cheung et al. (2005) extended this approach to examine extinction vulnerability in marine fishes, firstly by adopting a fuzzy logic system to account for uncertainty in eight life history parameter attributes. Secondly, and of relevance to this thesis, Cheung et al. (2005) recognised that species with strong spatial behaviour, such as those that school or form spawning aggregations, are particularly vulnerable. The incorporation of this behaviour significantly improved the predictive ability of the fishing vulnerability index derived from the fuzzy logic system, which is now widely used in the field (Froese & Pauly 2013; Abesamis et al. 2014). However, the index of Cheung et al. (2005) relates to species-specific responses to (or recovery from) fishing and does not serve as an indicator of the exposure of populations to specific fisheries (i.e. catch).

As a proxy for catch, aggregating behaviour can be used in combination with basic fishery information to determine the potential exposure, or susceptibility, of populations to aggregation fishing. Therefore, productivity-susceptibility analysis (PSA; Hobday et al. 2007) may serve as an appropriate model for assessing data-poor spawning aggregation fisheries. Tools such as PSA enable indicators to be tailored to the specific fisheries being assessed, especially allowing for novel combinations of indicators relating to catchability and socioeconomic drivers of fishing effort (Patrick et al. 2010). Since governance operates through levers that regulate susceptibility, as opposed to productivity, PSA-based approaches assist in identifying key drivers of vulnerability and developing management advice for fisheries. An understanding of the dynamic interaction between aggregating behaviour and a fishery, much of which is encompassed in the concept of catchability, would therefore benefit

both the development of data-poor assessment tools and the identification of effective management approaches.

1.1. Thesis aim and outline

The aim of this thesis was to improve our understanding of the key factors that confer vulnerability to fishing among coral reef species. Since the risks to fish populations posed by aggregation fishing depend on biology, behaviour and the socioeconomic context of fisheries, a conceptual framework was employed to study multiple causes of vulnerability to overfishing in spawning aggregation fisheries. Study findings were used to inform the development of indicators to populate a risk assessment tool for data-poor fisheries (Chapter 6). The assessment tool comprised a bivariate approach that enabled vulnerability to overfishing to be assessed in terms of intrinsic and extrinsic fishery components (Fig. 1.1). In terms of intrinsic vulnerability, the primary study focus was on fish aggregating behaviour because the mechanisms by which life history parameters (e.g. longevity) influence productivity and response to fishing are generally well understood (Jennings et al. 1999; Dulvy et al. 2004; Cheung et al. 2005). Aggregating behaviour influences two important mechanisms in spawning aggregation fisheries and was a major focus of the thesis. Firstly, aggregating behaviour has a major influence on the exposure to the fishery through densitydependence in catchability (Sadovy & Domeier 2005; Wilberg et al. 2010; Grüss et al. 2014a). By definition, fisheries that exploit spawning aggregations are defined by large density changes occurring over a range of scales (Robinson et al. 2008; Erisman et al. 2011; Nemeth 2012). However, catchability also incorporates many concepts central to fisheries (e.g. gear selectivity and efficiency; Wilberg et al. 2010) and the thesis focused on addressing research gaps and testing critical assumptions relating to this key parameter. Secondly, aggregation behaviour influences productivity through its role in shaping the stockrecruitment relationship (Maunder & Deriso 2013). This second mechanism was addressed as an indicator in Chapter 6. The extrinsic component considered indictors that influence catchability and fishing effort (i.e. susceptibility), including fisher knowledge, technology, accessibility, markets and management (Fig. 1.1).



Figure 1.1 Thesis conceptual framework and basis for the development of an indicator-based risk assessment tool for spawning aggregation fisheries (Chapter 6). Vulnerability to overfishing is determined by intrinsic and extrinsic fishery components, for which indices are derived from indicators. Data chapters that empirically examine indicators are given in parentheses.

Five separate studies were undertaken to meet the thesis aim, each corresponding to a thesis chapter. **Chapter 2** explores how fisher knowledge on spawning aggregations varies in relation to socioeconomic and cultural factors, examining empirical evidence for earlier,

qualitative observations made in Papua New Guinea (Hamilton et al. 2004, 2005). Furthermore, it addresses a research gap in terms of the lack of quantitative evidence on the role fisher knowledge plays in the development of an aggregation fishery. Chapter 3 quantifies changes in vulnerability to fishing (catch rates) caused by spawning aggregation behaviour in Seychelles' trap fishery for rabbitfish (Siganus sutor), testing assumptions regarding density-dependence and exploring the influence of environmental, technological and behavioural factors on catchability. The management implications of changes to catchability caused by spawning aggregation fishing are also demonstrated using a marine reserve model (see Chapter 5). Chapter 4 builds on the previous chapter by examining how vulnerability to fishing (catchability) differs between co-aggregating grouper species (Epinephelus fuscoguttatus, E. polyphekadion) at a multispecies spawning site in Papua New Guinea. The assumption of a proportional relationship between catch rate and abundance is tested, and alternative factors explaining patterns in catch rates are identified. Chapter 5 develops a marine reserve model to explore the relative conservation (spawning stock biomass-per-recruit) and fisheries (yield-per-recruit) benefits of protecting either spawning or non-spawning habitat for S. sutor and E. fuscoguttatus fisheries in Seychelles. Sensitivity analyses were performed to demonstrate the relative importance of catchability and life history traits on marine reserve outcomes. In Chapter 6, an indicator-based risk assessment tool for examining spawning aggregation fisheries in data-poor contexts is developed, informed by the findings of previous chapters, and tested on a global set of fisheries for which indicators were scored by experts. Finally, in Chapter 7, the key findings of the thesis are discussed and future research directions are identified.

Chapter 2: The influence of fisher knowledge on the susceptibility of reef fish aggregations to fishing

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2.1. Introduction

The depletion of reef fish biomass is often attributed to overfishing driven by socioeconomic drivers such as local human population density and distance from reefs to markets (Mora et al. 2011; Cinner et al. 2013). As changes to these key socioeconomic drivers increase demand for resources, reef fishes with slow life histories, such as groupers (Epinephelidae), are typically the first to be depleted (Sadovy de Mitcheson et al. 2013). However, the rate of depletion will also be influenced by the ability of fishers to locate and exploit fish populations when they are most vulnerable to fishing. Vulnerability to fishing increases when fish aggregate or school and the history of fishing is marked by developments based on exploiting this aspect of fish behaviour (Parrish 1999; Pitcher 2001). In the context of coral reefs, the development of aggregation-based fisheries depends on many factors including local knowledge relating to fishers (Claro et al. 2009; Hamilton et al. 2011) and access to aggregation sites (Matos-Caraballo et al. 2006; Robinson et al. 2008). It is important to understand the key ecological and socioeconomic drivers controlling the evolution of fisheries for aggregating species if they are to be effectively managed.

The exploitation of reef fish spawning aggregations is an obvious example of fishers utilising knowledge on fish behaviour to target populations when their density has increased. A large number of important food fishes on coral reefs aggregate periodically at high density to spawn (Domeier & Colin 1997; Sadovy de Mitcheson et al. 2008). Spawning aggregations

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represent attractive fishing opportunities since increases in density typically lead to greater catch-per-unit-effort (CPUE) (Wilberg et al. 2010) and because they are highly predictable in time and space, as evidenced by acoustic telemetry techniques that reveal spawner fidelity to specific sites and lunar periods (Rhodes et al. 2012; Bijoux et al. 2013a). Predictable aggregating behaviour is not, however, confined to reproduction since reef fishes also aggregate at specific times and locations for other functions, such as foraging, resting and shelter (Meyer & Holland 2005; Hitt et al. 2011). Fishers regularly target non-reproductive aggregations (Parrish 1999; Johannes & Hviding 2000), though their vulnerability to fishing has received much less research attention than spawning aggregations.

Regardless of their biological predictability, fisher knowledge of aggregations is heterogeneous and will influence the extent to which aggregations are perceived as predictable and exploited by fishers. Fisher knowledge maybe stratified by factors such as gender, age, location and cultural background (Christie & White 1997; Hamilton et al. 2004; Sadovy de Mitcheson et al. 2008). For example, Hamilton et al. (2004) documented how fisher knowledge of spawning aggregations varied by clan both within and between locations in Manus Province, Papua New Guinea. Even if aggregations are predictable and their timing and location are known to fishers, accessibility to sites may be low due to factors such as prevailing weather and remoteness (Matos-Caraballo et al. 2006; Robinson et al. 2008), while inefficient gear use may constrain exploitation rates (Aguilar-Perera 2006). Gender preferences and customary marine tenure that specifies ownership rights among kinship groups may also influence fisher access to fish resources (Cinner 2007; Aswani & Vaccaro 2008). Furthermore, fishing effort on aggregations may be constrained by limited market access or fish preservation capacity (Matos-Caraballo et al. 2006). Consequently, the vulnerability to fishing conferred by aggregation formation will depend on both fisher

knowledge of aggregating behaviour and socioeconomic drivers influencing aggregation exploitation.

Fisher knowledge of fish aggregating behaviour will be influenced by cognitive processes (such as recall) and the formation of heuristic models (Daw et al. 2011). To understand how such knowledge develops, it is informative to deconstruct the biological attributes of this behaviour and consider their effects on fisher memory. The biological attributes of aggregation behaviour can be categorised by their temporal, spatial and physical manifestations. Firstly, aggregation formation aligning with diurnal, lunar and seasonal periods is likely to promote recall since coral reef fishers often allocate effort according to such schedules (Aswani 1998). Secondly, reef fishers often have detailed knowledge on the broad-scale (i.e. seascape) distribution of resources (Aswani & Vaccaro 2008), which coincides with the fact that aggregations often form at prominent reef features (Connell & Kingsford 1998; Choat 2012). However, some species are more mobile and therefore less predictable in space than others when aggregated for spawning (e.g. Carangidae) (Heyman & Kjerfve 2008). Lastly, the size of aggregations formed is expected to influence recall since memory varies according to how pleasurable, unusual or emotive an experience is (Matlin 2005), while the presence of eggs or milt (i.e. spawning) are physical manifestations of behaviour that enable fishers to reconcile aggregation formation with biological function. In combination, these attributes are expected to influence the extent to which fishers develop knowledge on aggregations and perceive them as predictable.

Assessing the status of aggregating reef fish populations is problematic due to the data-poor context of their fisheries (Sadovy & Domeier 2005). Vulnerability assessment frameworks developed for data-poor contexts, which combine measures of a species productivity and susceptibility to a fishery (e.g. Patrick et al. 2010; Hobday et al. 2011), are therefore worth examining for such species. Productivity defines the capacity of a stock to recover rapidly

following depletion, while susceptibility is the potential for the stock to be impacted by the fishery (Patrick et al. 2010). Measures of productivity are generally available for reef fishes through empirical tools based on life history invariants (Froese & Pauly 2013), whereas indicators of susceptibility can be tailored to the specific fisheries being assessed in terms of patterns in catchability and socioeconomic drivers (Patrick et al. 2010). Thus, a population's susceptibility to aggregation fishing will be governed by catchability that, among other factors, relates to the accessibility of the aggregation site and the selectivity or efficiency of gears used at the site (Arreguín-Sánchez 1996). Catchability will in turn be driven by socioeconomic drivers, such as market access and dependency on fishing, that influence technological development and fishing effort (Cinner et al. 2009; Cinner et al. 2013). However, aggregations are often transient phenomena, particularly in the case of spawning aggregations (Domeier & Colin 1997), and fisher knowledge of their dynamics should be considered a critical component of an aggregation-based fishery, the trajectory of which is subsequently affected by catchability attributes and socioeconomic drivers.

Studies documenting fisher knowledge of reef fish aggregations have primarily gathered information in order to identify research, conservation and management priorities (Samoilys et al. 2006). Attempts to quantify the influence of fisher knowledge in the susceptibility of populations to aggregation fishing are lacking, as is the use of indicator-based vulnerability frameworks for these fisheries. In this study, we aimed to examine how fisher knowledge of reproductive and non-reproductive aggregations influences the susceptibility of populations to fishing at two case study sites in Papua New Guinea. The specific research questions were: (1) to what extent are fishers knowledgeable of aggregations and do they perceive them as predictable?; (2) how does variation in fisher knowledge of aggregations relate to local

socioeconomic indicators?, and (3), what is the influence of fisher knowledge in conferring susceptibility to fishing relative to catchability and socioeconomic drivers of fishing pressure.

2.2. Materials and Methods

2.2.1. Study locations and communities

We studied reef fisheries at two locations in Papua New Guinea, representing two extremes of fishing pressure and comprising gear and fishing practices common to the region (Cinner 2007). Studies focused on the communities of Ahus Island (Manus Province) and Muluk and Wadau villages, Karkar Island (Madang Province) (Fig. 2.1).



Figure 2.1 Study locations. Papua New Guinea with details (insets) of Ahus Island, Manus Province, and Karkar Island, Madang Province.

Karkar is a large, elevated (1,839 m) volcanic island and fishing is a secondary occupation to agriculture. By contrast, fishing is the primary occupation for the community on the small (28 ha), low-lying Ahus Island where terrestrial resources are limited (Cinner 2007). The two locations also differ in coastal geomorphology and habitats. Fishers from Karkar have access to a narrow (<1 km) fringing reef system of less than 150 ha with a narrow lagoon (Cinner 2007; Feary et al. 2010), whereas fishers at Ahus Island are surrounded by a wide (>4 km in the west), extensive lagoon system of approximately 550 ha (Cinner 2007).

Fishers at the study sites use a combination of gear types including line, net and spears. Fishing effort at Ahus primarily comprises use of lines and spearguns (97%, of total fishing effort), whereas effort at Karkar comprises both of these gears (72%) in combination with hand spearing (24%). By comparison, a small proportion (<4%) of fishing effort at both study sites involves use of nets (Cinner 2007). Resource use is governed by a system of customary marine tenure (CMT) that recognises local ownership of inshore marine resources. Tenure in Karkar is a relatively centralised approach where governance is controlled by a council of chiefs. There is relatively high mobility, with fishers having the ability to switch between gears and fishing grounds (Cinner 2007). By contrast, tenure at Ahus is highly decentralized and access to fishing grounds and gears (particularly nets) is controlled by kinship group (individuals, families, clans). Both study communities have traditionally used customary taboos (*tambu*) to restrict fishing in certain areas in an effort to influence catchability (i.e. make fish less wary of spear fishers) or rebuild biomass for feasts (Cinner et al. 2005; Feary et al. 2010).

2.2.2. Quantifying fisher knowledge of aggregating behaviour and predictability

Interviews were conducted with fishers at Ahus (n=16) and Karkar (Muluk: n=7; Wadau: n=9) in October 2012 to quantify fisher knowledge on aggregating behaviour and to develop

an index of knowledge pertaining to fisher perceptions of aggregation predictability. At Karkar, interviews were conducted with all fishers for whom fishing was a regular livelihood activity. In Ahus, where the proportion of residents engaged in fishing was high by comparison, a sample of fishers, representative of fisher gender, clan membership and gear use, was taken. After pilot studies (n=4) with Karkar fishers, a semi-structured questionnaire was designed to investigate fisher knowledge of the form, function and predictability of aggregating behaviour for six species of reef fish common to fisheries in both locations. The six species comprised two groupers (*Epinephelus fuscoguttatus, Plectropomus areolatus*), two emperors (Lethrinidae; *Lethrinus harak, L. lentjan*) and two snappers (Lutjanidae; *Lutjanus fulviflamma, L. gibbus*). All species are high trophic level predators (trophic levels 3.6-4.5) and were selected to contrast forms and functions of aggregating behaviour (Table 2.1).

Species	Aggregating behaviour
Epinephelus fuscoguttatus	Primarily solitary and territorial; form large aggregations for spawning ^{a, b, c, d}
Plectropomus areolatus	Primarily solitary and territorial; form large aggregations for spawning ^{a, b, c, e}
Lutjanus gibbus	Primarily schooling; forms large aggregations for spawning ^{a, b, c}
Lutjanus fulviflamma	Primarily schooling; spawning aggregation formation not verified ^{a, c, f}
Lethrinus lentjan	Primarily solitary as adults; spawning aggregation formation suspected but not verified ^{a, b, c, g}
Lethrinus harak	Primarily solitary or forms small groups (<10 fish); spawning aggregation formation suspected but not verified ^{g, h}

 Table 2.1 Evidence of aggregating behaviour for study species

^a Sadovy de Mitcheson et al. (2008); ^b Claydon (2004); ^c Froese & Pauly (2013); ^d Robinson et al. (2008); ^eRhodes & Tupper (2008); ^f Grandcourt et al. (2006). ^gEbisawa (2006); ^hNanami & Yamada (2009)
Firstly, species recognition by fishers was established using a combination of pictures (landed specimens) and local names specific to location. Secondly, we asked fishers whether they caught each species frequently, infrequently or not at all and, if they encountered the species, to estimate the 'poor', 'normal' and 'good' catch rates (fish.trip⁻¹) that they typically obtain for each species when using their primary gear. Thirdly, fishers were questioned on their knowledge of aggregating behaviour, initially focusing on whether they observe a species to display solitary, shoaling (groups of three or more fish displaying unsynchronised swimming) and schooling (groups of three or more fish displaying synchronised swimming) behaviour (Pitcher 2001). Fishers could assign multiple behavioural types to each species, giving eight potential categories including a 'don't know' response. For example, a species could be identified as solitary and shoaling, or as displaying all three behaviour types. Unless specified, 'aggregation' refers to all forms (i.e. shoaling, schooling) and functions (e.g. resting) of social group behaviour.

Seven attributes of the spatial, temporal and physical manifestations of aggregating behaviour were employed to quantify fisher knowledge of aggregations and their perceived predictability (Table 2.2). Aggregation attributes were discussed for each species and scored according to fisher responses. For some statistical tests and analyses (*see below*), an index of fisher knowledge of aggregating behaviour was calculated for each fisher and species by summing the scores for the seven aggregation attributes (maximum score=17; Table 2.2). Thus, the fisher knowledge index essentially aims to measure the predictability of aggregations as perceived by fishers. For example, to obtain a maximum score, a fisher would need to recognise that aggregations form consistently at specific locations within a small home range, that formation aligns with diel, lunar and seasonal schedules, that aggregations are large (>500 fish), and that they form for spawning (Table 2.2). Aggregation

were assumed to promote recall and therefore perceived predictability. Since some species were reported as constantly shoaling or schooling, questions on periodicities of aggregation formation were obviously irrelevant. Therefore, fishers were asked as to whether aggregation size in frequently shoaling or schooling species (e.g. *L. gibbus*) increased with spawning.

Attribute	Scoring ^a			
Aggregation size	1 = solitary or pairing			
	2 = aggregations of 3-10 fish			
	3 = aggregations of 10-100 fish			
	4 = aggregations of 100-500 fish			
	5 = aggregations larger than 500 fish			
Aggregation location	1 = aggregation location is unknown or variable			
	2 = aggregations form in specific areas of the reef			
Home range	1 = species of high mobility and occupying large home range			
	2 = species of low mobility and occupying small home range			
Spawning	1 = aggregation formation not associated with spawning (eggs/milt absent)			
	2 = aggregation formation associated with spawning (eggs/milt present)			
Diel	1 = aggregation formation not aligned with time of day			
	2 = aggregation formation aligned with particular time of day			
Lunar	1 = aggregation formation not aligned with lunar phase			
	2 = aggregation formation aligned with particular lunar phase			
Seasonal	1 = aggregation formation not aligned with month or season			
	2 = aggregation formation aligned with particular month or season			

 Table 2.2 Scoring of aggregation attributes based on fisher knowledge of aggregating behaviour

^a If fishers had no knowledge of an attribute, a zero score was given.

2.2.3. Socioeconomic indicators related to heterogeneity in fisher knowledge within study locations

To investigate sources of variation in fisher knowledge within case study locations, data relating to socioeconomic indicators were collected during interviews. Indicators were

selected based on literature pertaining to sources of variation in knowledge among coral reef fishers and included gender, dependency on fishing as a livelihood, and access rights to major reef habitats and gear types (Table 2.3). Gender and the main reef habitats for which fishers hold access rights often structure fisher knowledge of fish behaviour (Christie & White 1997; Hamilton et al. 2004; Aswani & Vaccaro 2008). Fishing gears vary in species selectivity and the habitats where they can be deployed, influencing the potential for fishers to capture and develop knowledge of species behaviour (Crona 2006). Finally, dependency on fishing influences levels of fisher knowledge (Davis & Wagner 2003) and was derived from fisher rankings of importance of fishing as a livelihood (primary, secondary, tertiary) (Table 2.3).

Table 2.3 Socioeconomic indicators used in redundancy analysis (RDA) to identify sources
of variation in fisher knowledge of aggregating behaviour. Data are the number of fishers
scored at each factor level or category for case study locations

Factor	Measurement level or category	Ahus	Karkar	
Fisher gender	Male	12	15	
	Female	4	1	
Fisher access to habitat	Lagoon only	5	0	
	Outer reefs only	4	0	
	All habitats	7	16	
Primary gear type	Line	9	13	
	Speargun	6	2	
	Net	1	1	
Dependency on fishing	Primary	13	2	
	Secondary	2	7	
	Tertiary	1	7	

Category	Attribute	Scoring
Productivity	Average age at maturity	1: <2 years; 2: 2-4 years; 3: >4 years
	Average maximum age	1: <10 years; 2: 10-30 years; 3: >30 years
	Average size at maturity	1: <30 cm; 2: 30-50 cm; 3: >50 cm
	Average maximum size	1: <60 cm; 2: 60-150 cm; 3: >150 cm
	Reproductive strategy	1: broadcast spawner; 2: demersal egg layer; 3: live bearer
	Trophic level	1: <2.5; 2: 2.5-3.5; 3: >3.5
Catchability	Fisher knowledge index	1: index scores 1-6; 2 :index scores 7-12; 3: index scores 13-17
	Availability	Proportion of fisher's effort allocated in aggregation habitat, 1: none; 2: some; 3: all
	Encounterability	Species occurrence in fisher's catch, 1: never; 2:infrequently; 3: frequently
	Selectivity	1: gears unselective; 2: uses one of the two most selective gears; 3: uses both of the two most selective gears
Socio-	Habitat impact of gear	1: fisher uses spear guns and/or hook-and-line; 2: fisher uses gill nets; 3: fisher uses scare lines
economics	Fishing effort	1: 10-50 hrs/month; 2: 75-120 hrs/month; 3: 145-265 hrs/month
	Preference	1: low and medium preference spp.; 2: high preference spp.; 3: very high preference spp.
	Dependency on fishing	Importance of fishing as an occupation, 1: tertiary; 2: secondary; 3: primary
	Management strategy	Ownership rights, conservation measures (i.e. closures), 1: both exist; 2: one or the other exists; 3: none exist
	Access to markets*	1: Sell/barter in village; 2: sell/barter in neighbouring villages; 3: sell/barter in provincial capital markets

Table 2.4 Attributes and their scoring system employed for productivity-susceptibility analysis (PSA). Susceptibility attributes are subdivided into attributes associated with catchability and those associated with socioeconomic drivers of fishing pressure or habitat impacts

*: The provincial capital markets for Karkar and Ahus are Madang (Madang Province) and Lorengau (Manus Province), respectively.

2.2.4. Fisher knowledge and the susceptibility of aggregations to fishing

A productivity-susceptibility analysis (PSA) using the bivariate framework of Hobday et al. (2011) was employed to determine the relative importance of fisher knowledge in conferring susceptibility of aggregations to exploitation, and to assess the overall risk to populations posed by aggregation fishing. PSA reduces life history parameters associated with species productivity to a single x-axis index and susceptibility attributes to an index on the y-axis. In line with the approach of Hobday et al. (2011), we scored seven life history parameters (Table 2.4) for the six species, where productivity score categories are: 1=high, 2=moderate and 3=low productivity. Parameter estimates for each species were derived using the life-history tool of Fishbase.org (Froese & Pauly 2013). Cut-off points dictating membership of each productivity category were adopted from those used for fisheries of the United States, which include fisheries for reef fishes analogous to those of Papua New Guinea (Patrick et al. 2010). Fecundity was subsequently omitted from the index since data were lacking for the study species.

The four susceptibility attributes of Hobday et al. (2011) were adapted to address the susceptibility of populations to aggregation fishing. Firstly, the attribute of availability primarily concerns the overlap (spatial and depth) between fishing effort and species or population distribution, or in our case the access fishers have to habitats where aggregations or schools are perceived to occur (Table 2.4). Secondly, the attribute of encounterability concerns the likelihood that a specific gear will encounter aggregated fish if sites are available to fishers. Fisher responses to the question on whether they catch the species frequently, infrequently or not at all were used as a measure of encounterability, assuming that the gears used by that fisher would be as efficient in catching the fish while aggregated. Thirdly, to measure selectivity, i.e. the potential of the gear to capture and retain species, we used fisher reports of catch rates (fish.trip⁻¹). The mean 'good' catch rate across fisher

responses was taken on each gear used for a species, from which gear selectivity was ranked by order of catch rate. Fourthly, we replaced post-capture mortality (Hobday et al. 2011), which is less relevant to small-scale reef fisheries where discards are minimal (Jacquet & Pauly 2008), with our fisher knowledge index (described above). All susceptibility attributes were scored from 1 to 3, with 1 indicative of low susceptibility and 3 of high susceptibility (Table 2.4).

The attributes of Hobday et al. (2011) relate to potential for a fishery to access, encounter and select for a species, i.e. catchability. However, we also wanted to quantify fishing effort (e.g. days fished each month), which in combination with catchability will determine the fishing pressure (i.e. mortality rate) on resources, and explore the socioeconomic drivers of that fishing effort. Informed by known drivers of fishing pressure in reef fisheries (Newton et al. 2007; Cinner et al. 2009, 2013) and several of the 'management attributes' employed by Patrick et al. (2010), which also equate to socioeconomic drivers, we developed six additional susceptibility attributes. These were habitat impact of gear, fishing effort, preference for the species, dependency on fishing for a livelihood, management strategy and access to markets (Table 2.4). While catchability attributes were scored for each species and fisher, the socioeconomic attributes were not species-specific and combined fisher and location-level scoring (Table 2.4). A ranking of habitat impacts associated with gears used by fishers in our study was developed from Mangi and Roberts (2006) and Corpuz et al. (1985). Fishing effort was quantified for each fisher by questioning the hours and days they fish each day and week, respectively, which was converted to hours fished per month. Ranges associated with low, medium and high susceptibility was estimated by cluster analysis of individual effort reported by fishers. Preference, a location-level attribute used as a proxy for desirability or value of the species (Patrick et al. 2010), was derived for our six study species from a focus group held in each community. Dependency on fishing and access to markets are significant drivers

of fishing pressure in many reef fisheries (Newton et al. 2007; Cinner et al. 2013) and were derived from individual fisher rankings of the importance of fishing as a livelihood (*as detailed above*) and markets that they access, respectively. Management strategy was a location-level attribute adopted from Patrick et al. (2010) but modified for the local context (Table 2.4) (Cinner 2007).

2.2.5. Data analysis

The mean 'normal' catch rate estimated by fishers for each species was compared between locations using a *t*-test, assuming unequal variances. For each species, associations between fisher knowledge on aggregation form at Ahus and Karkar were analysed by constructing contingency tables of the frequency of observation for each of the eight categories (solitary, shoaling, schooling, combinations of the three forms, and the 'don't know' response). Cramér's V contingency coefficient was used as the measure of association; the coefficient ranges between 0 (no association) and 1 (perfect association). Since expected frequencies were less than five for a high proportion of cells in the contingency table, *p*-values were calculated using Monte Carlo simulation (10,000 sampled tables).

Several methods were employed to examine how fisher knowledge of aggregations varied by location and species. Firstly, for each species and aggregation attribute, fisher respondent scores were averaged in each location and the difference between the averages (Ahus minus Karkar) plotted. Secondly, Mann-Whitney U tests were used to compare fisher responses in each location, again for each species and attribute, with exact significance (2-sided) *p*-values reported rather than asymptotic values due to small sample sizes ($n \le 17$). Owing to the risk of type 1 errors arising from multiple comparisons, *p*-values were adjusted with a false discovery rate (FDR) correction for multiple testing using the Benjamini-Hochberg method (Benjamini & Hochberg 1995). To make comparisons between locations, the fisher

knowledge index was averaged across fishers for each location and the same statistical method as that applied to individual aggregation attributes was used. For statistical tests of variation in both individual aggregation attributes and in the fisher knowledge index, comparisons were restricted to those fishers knowledgeable on the species and its behaviour (i.e. excluding fishers that do not catch the species).

Redundancy analysis (RDA), which combines concepts of ordination and regression (Legendre & Legendre 1998), was used to examine the relationship between socioeconomic indicators (Table 2.3) and variance in fisher knowledge. RDA was conducted separately for each case study as the two locations differ significantly in their socioeconomic conditions and the aim was to examine local sources of variation in fisher knowledge. Here, all fisher respondents for a location were included in the analysis (n=16) since variation in knowledge was integral to the analysis. However, results for Ahus should be treated with caution since sample size relative to the number of indicator (factor) levels imposed limitations on the RDA. Access to habitat was not included in the RDA for Karkar since it did not vary among respondents.

Estimates of productivity attributes were averaged to give a single productivity score per species. To assess the relative importance of catchability and socioeconomic drivers of fishing pressure for the six species, each susceptibility attribute was first scored for each fisher respondent individually and then averaged across fishers to give a single attribute score for each location. Within location, the susceptibility attributes were combined by averaging across two sets of attributes; (1) the full set of 10 susceptibility attributes, and (2) the four catchability attributes (Table 2.4). Consequently, two bivariate PSA plots were produced for the 12 fish populations (six species per location), one for productivity and the full set of susceptibility attributes, and a second for productivity and using only the four catchability attributes (we only present the PSA plot for the full set of susceptibility attributes). From both

of these PSA plots, overall vulnerability (or risk) was derived for each population at Ahus and Karkar by taking the Euclidean distance between the origin and population location in the bivariate space (Hobday et al. 2011). Wilcoxon Signed Rank tests were used to determine if overall vulnerability (with species as paired samples and location as treatments) differed between Ahus and Karkar for the full susceptibility attribute set and for the catchability attributes. Exact significance (2-sided) p-values are reported due to the small number of paired-samples (n=6).

2.3. Results

A greater proportion of females engaged in fishing at Ahus and fishers were more dependent on fishing for a livelihood than their counterparts from Karkar (Table 2.3). Lines were the dominant gear type in both locations but a greater proportion of fishers from Ahus used spearguns as their primary gear. Contrasting with Karkar, some fishers from Ahus reported that they were limited to fishing in the lagoon or on the outer reefs (Table 2.3). Based on the median response among fishers, groupers were encountered infrequently in the catches at both study locations. The four species of snapper and emperor were encountered frequently in the catches of Karkar fishers, while at Ahus *L. gibbus* and *L. harak* were encountered frequently and *L. fulviflamma* and *L. lentjan* infrequently, again based on median fisher response. Reported catch rates of snappers tended to be greater than those of emperors and groupers (Fig. 2.2). Comparing between locations, the mean reported catch rates did not differ for most species. However, the mean catch rate for *E. fuscoguttatus* was greater at Karkar, while the opposite was true for *L. gibbus*.



Figure 2.2 Catch rates reported by fishers for the six study species. Data are the 'normal' catch rates fishers expect to obtain on a fishing trip, given as mean no. fish/trip⁻¹ with standard error bars. For each species, results of *t*-tests comparing mean catch rates between locations are shown, with significant differences indicated by bold font.

Fishers from Ahus and Karkar had different perceptions on the forms of aggregating behaviour exhibited by the two groupers (*E. fuscoguttatus*: V = 0.237, p = 0.584; *P. areolatus*: V = 0.393, p = 0.335). The groupers were primarily perceived as solitary by fishers from Karkar while a larger proportion of Ahus fishers recognised that they are generally solitary but also form spawning aggregations (Fig. 2.3a,b). By contrast, fishers from both Ahus and Karkar perceived snapper aggregating behaviour to be complex, alternating between solitary occurrence, loose shoal formation and synchronised schooling (Fig. 2.3c,d). In spite of this complexity, there were significant associations between locations in how fishers perceived the forms of aggregating behaviour (*L. gibbus*: V = 0.708, p = 0.009; *L. fulviflamma*: V = 0.674, p = 0.025). Emperor aggregating behaviour was also considered more complex than that of groupers, encompassing reports of schooling by two fishers, but also tended towards solitary and shoaling behaviour (Fig. 2.3e,f). Aggregation formation was considered a much more common behaviour by fishers on Ahus, especially for *L. harak*. As with the two groupers, the null hypothesis of no association between locations in perceived

behaviour was accepted for the lethrinids (*L. lentjan*: V = 0.732, p = 0.07; *L. harak*: V = 0.229, p = 1.0).



Figure 2.3 Fisher knowledge of the aggregating behaviour of study species. Stacked bars represent the proportion of fishers in Ahus and Karkar identifying the six study species as exhibiting solitary (SOL), shoaling (SHO) and schooling (SCH) behaviour, or any combinations thereof (SOL-SHO, SOL-SCH, SHO-SCH). DK denotes the proportion of fishers who didn't know the aggregating behaviour of the species



Difference in mean attribute score (Ahus minus Karkar)

Figure 2.4 Differences in fisher knowledge of aggregation attributes between study locations. For each species and location, attribute scores were averaged among fishers. The results of statistical tests (Wilcoxon Signed Rank tests) comparing the vulnerability of populations (species pooled) at Ahus and Karkar are given in the panel titles

Ahus fishers were generally more knowledgeable on the seasonal, lunar and diel periodicity of aggregations for *L. lentjan, L. harak* and *E. fuscoguttatus* (Fig. 2.4). By contrast, Ahus and Karkar fishers did not differ statistically in their knowledge of aggregation attributes for *L. gibbus* and *P. areolatus*, while significant differences for *L. fulviflamma* were limited to a greater knowledge of aggregation lunar timing among Ahus fishers. Fisher knowledge of

aggregation formation or increased catchability being associated with spawning was also more common on Ahus for *L. lentjan, L. harak* and *E. fuscoguttatus*. Moreover, aggregation locations for these three species were perceived as more predictable by Ahus fishers. There were no differences between Ahus and Karkar in the perceived home range sizes of the six species and the only species for which perceptions of aggregation size differed significantly was *L. harak*, with larger aggregations perceived on Ahus (Fig. 2.4).



Figure 2.5 Socioeconomic indicators associated with variation in fisher knowledge at Ahus Island. A redundancy analysis plot of fisher knowledge relating to aggregating behaviour of six study species. Indicators are fisher gender (black circles), fisher access to lagoon, outer reef or all habitats (white triangles), primary gear type (grey squares) and primary, secondary or tertiary dependency on fishing (inverted grey triangles)

For Ahus, ordination of species by fisher knowledge of their aggregating behaviour loosely clustered *L. lentjan*, *E. fuscoguttatus* and *P. areolatus*, separating them from the other species

along the first canonical axis that accounted for 44.9% of the variation (Fig. 2.5). Knowledge of the aggregating behaviour of these three species was primarily held by male fishers, whereas female and net fishers who fish in the lagoon were more knowledgeable of *L. harak* (Table 2.5). Knowledge of snapper (*L. gibbus* and *L. fulviflamma*) aggregating behaviour was largely shared among fishers, with the species orientated on the second canonical axis that only accounted for 6.1% of the variation. Therefore, with the exception of snappers, knowledge of species aggregating behaviour at Ahus was heterogeneous and explained by fisher gender and right of access to the major reef habitats (Table 2.5).

Table 2.5 Variation in fisher knowledge of aggregating behaviour explained by socioeconomic indicators. Redundancy analysis (RDA) results for Ahus and Karkar with significant p-values highlighted in bold. Access to habitat did not vary among Karkar fishers and was not included in the RDA

	Ahus		Karkar	
Factor: factor level	Explains (%)	Р	Explains (%)	Р
Fisher gender: male	31.4	0.004	4.8	0.582
Fisher gender: female	31.4	0.008	4.8	0.534
Access to habitat: lagoon only	43.1	0.002		
Access to habitat: outer reefs only	11.6	0.128		
Access to habitat: all habitats	13.8	0.084		
Primary gear type: line	8.9	0.266	10.2	0.124
Primary gear type: speargun	4.8	0.542	20.3	0.026
Primary gear type: net	6.7	0.472	5.2	0.494
Dependency on fishing: primary	3.3	0.662	4.4	0.644
Dependency on fishing: secondary	6.5	0.532	8.9	0.27
Dependency on fishing: tertiary	1.1	0.89	12.4	0.084



Figure 2.6 Socioeconomic indicators associated with variation in fisher knowledge at Karkar Island. A redundancy analysis plot of fisher knowledge relating to aggregating behaviour of six study species. Indicators are fisher gender (black circles), primary gear type (grey squares) and primary, secondary or tertiary dependency on fishing (inverted grey triangles)

The RDA explained less of the variation in fisher knowledge at Karkar compared to Ahus, with axes one and two accounting for 25.7% and 7.5%, respectively (Fig. 2.6). Knowledge of grouper (*E. fuscoguttatus* and *P. areolatus*) aggregating behaviour again clustered on the first canonical axis but was restricted to only two fishers primarily using spearguns. Use of this gear constituted the only factor that significantly explained variation in knowledge (Table 2.5). *Lutjanus fulviflamma* and *L. gibbus* orientated between the axes, again due to knowledge being largely shared among fishers, while the low level of knowledge pertaining to *L. lentjan* behaviour was not influential on the ordination. Line and net fishers with a tertiary level of dependence on fishing were knowledgeable of *L. harak*, but these factors were not statistically significant in explaining variation in knowledge (Table 2.5).

Productivity of the six species varied from less productive groupers to the more productive emperors and snappers. Three species (*L. harak*, *L. lentjan* and *L. gibbus*) were equal in their productivity scores (Fig. 2.7). All four grouper populations were in the medium risk category, while most of the other populations were low risk. However, *L. gibbus* aggregations at Ahus were assessed to be medium risk due to a high susceptibility score.



Figure 2.7 Productivity-susceptibility analysis (PSA) plot. The susceptibility axis in this plot combines all ten attributes associated with catchability and socioeconomic drivers of fishing pressure (see Table 2.4). Contour lines divide regions of equal vulnerability to fishing, and group species of similar risk levels: i.e. low, medium and high risk (after Hobday et al. 2011)



Figure 2.8 Influence of catchability and socioeconomic susceptibility attributes on the vulnerability of populations to aggregation fishing. Vulnerability, measured as the Euclidean distance of populations to the origin in the corresponding PSA plots, is compared for all susceptibility attributes (catchability and socioeconomic drivers; left panel) and catchability (right panel) attributes only. The results of statistical tests (Wilcoxon Signed Rank tests) comparing the vulnerability of populations (species pooled) at Ahus and Karkar are given in the panel titles

When all attributes were included in the measure of susceptibility, vulnerability to fishing was greater at Ahus than Karkar (Z = -2.2; p = 0.031) (Fig. 2.8). However, when only the four catchability attributes were included in the measure of susceptibility, vulnerability to aggregation fishing did not differ significantly between locations (Z = -1.6; p = 0.156) (Fig. 2.8). This occurs because differences in the four catchability attributes tend to cancel each other out, such that fisher knowledge and selectivity are higher at Ahus but the reverse is true for availability and encounterability (Fig. 2.9). With the exception of preference for the six species, the socioeconomic attributes used in the PSA scored more highly for Ahus than Karkar (Fig. 2.9). The score for fishing effort was higher at Ahus since fishers at that location averaged 93 hours of fishing each month compared to 58 hours at Karkar. Dependency on

fishing was also higher, with more than 80% of fishers reporting fishing as their primary livelihood compared to 12.5% at Karkar. The majority of fishers at Ahus also reported that they use scare lines for catching snappers, ensuring that habitat impacts were also comparatively high at that location. Moreover, fishers from Ahus regularly accessed markets of neighbouring villages (neighbouring islands and the northern coast of Manus) and the provincial capital, whereas fishers from Karkar generally traded locally or occasionally in neighbouring villages on Karkar. Ownership rights and customary reef closure measures still existed at Karkar, but at Ahus fishers reported during interviews that the customary closure was no longer being respected or complied with. Consequently, including attributes relating to socioeconomic drivers resulted in a greater susceptibility of aggregations to fishing at Ahus compared to Karkar.



Figure 2.9 Case study location scores for the ten susceptibility attributes. Clockwise from top, the first four attributes relate to catchability, while the remaining six are indicators of socioeconomic drivers. Attributes were scored from 1 (low susceptibility) to 3 (high susceptibility) for each fisher respondent or, in the case of preference and management strategy, at the level of location. For attributes scored at the respondent level, the mean score (N=16) is given.

2.4. Discussion

Supportive of previous research findings in Papua New Guinea (Hamilton et al. 2004), we found that fisher knowledge of aggregating behaviour varied between our two case study communities. While this finding is unsurprising in a country of such high cultural and socioeconomic diversity, our study makes a contribution by also highlighting the influence of local context in structuring knowledge within communities. Thus, the relatively high heterogeneity in knowledge at Ahus related to rights of access among fishers and genders to the main habitats of the relatively large reef system. By contrast, knowledge was more homogenous at Karkar and the sole source of variation was primary gear type. Though knowledge of aggregation location and timing are prerequisites for exploitation, factors that drive fishing effort will ultimately determine their susceptibility to fishing since knowledge, by itself, does not ensure that fishers will seek to maximize their extraction from the fishery (Johannes 1978; Colding & Folke 2001). Overfishing may be related to distance to markets (Cinner et al. 2013), while the overexploitation of spawning aggregations has been attributed to the emergence of commercial markets for aggregating species (Sadovy & Domeier 2005). Social norms operating outside customary tenure may also constrain fishing pressure (Carrier 1982; Colding & Folke 2001). However, our study objectives required a trade-off between the qualitative interviews that are required to explore social norms and quantitative approaches involving larger sample sizes that were needed for statistical inference of the factors relating to knowledge. Additional research exploring how knowledge is structured within communities will be important for assessing the role of social norms or customary management practices, such as *tambu* areas, in regulating fishing effort.

2.4.1. Factors associated with heterogeneity in fisher knowledge of aggregating behaviour

Fisher knowledge of aggregating behaviour was particularly heterogeneous at Ahus. Since variation at Ahus related to gender and access to reef habitats, it appears to stem from the decentralised tenure system that specifies ownership rights to space, species, gear and the techniques for using gears among kinship groups (Carrier 1982, 1987; Cinner 2007). An understanding of how knowledge is structured and maintained among kinship groups is important since the breakdown of customs and the spread of knowledge can lead to increased fishing pressure on aggregations (Hamilton et al. 2004). By contrast, marine tenure arrangements at Karkar allow for relatively higher mobility of fishers between gears and fishing grounds (Cinner 2007). With less specialisation in specific gears or habitats, knowledge was less structured at Karkar compared to Ahus, as indicated by the relatively low amount of variation explained by the redundancy analysis. Heterogeneity in knowledge was unrelated to dependency on fishing, which at Ahus resulted from the fact that fishing was the primary livelihood for 80% of fishers, encompassing both genders and fishers with differing right of access. Though our objective was to explore local sources of variation in knowledge, dependency on fishing may explain why fishing effort was higher and fishers used more efficient gears (i.e. scare lines) at Ahus.

Variation in fisher knowledge of aggregating behaviour differed among the three families of reef fish. Compared to emperors and groupers, knowledge of aggregations of the two snappers was greater and relatively homogenous. Snapper aggregation locations were perceived by fishers as spatially predictable and were associated with particular features of the reef, corresponding with empirical evidence for these species (Connell & Kingsford 1998; Newman & Williams 2001). Of our six study species, snappers generally had the highest reported catch rates, presumably since they are schooling species and are relatively abundant,

often forming an important component of reef fisheries catch in many parts of Papua New Guinea and other regions (Grandcourt et al. 2006; McClanahan & Cinner 2008).

Heterogeneity in fisher knowledge relating to grouper spawning aggregations was structured by access rights or gear type, depending on location. Grouper spawning aggregations mainly form on outer reef slopes and channels (Claydon 2004; Robinson et al. 2008; Hamilton et al. 2011). Since around one third of fisher respondents at Ahus, including all females and some male fishers, were limited to using nets or fishing in the large lagoon, they are therefore unlikely to have developed knowledge of this behaviour. Gear use also plays a role in knowledge acquisition (Crona 2006) and fishers using spearguns at Karkar held greater knowledge of grouper spawning aggregations, possibly benefitting from the direct observation of fish behaviour that this gear affords. However, few grouper spawning aggregations may exist at Karkar since the scales of migration (approximately 10-25 km; (Rhodes & Tupper 2008; Rhodes et al. 2012) that these species are known to undertake in attending spawning aggregations are larger than the linear extent (<5 km) of the reef fished (Feary et al. 2010).

As with groupers, heterogeneity in fisher knowledge of emperor behaviour also stemmed from variable rights of access among fishers. Thus, lagoon fishers at Ahus developed specialist knowledge of the behaviour of *L. harak*, a generally solitary species common to that habitat (Hamilton et al. 2004; Aswani & Vaccaro 2008), which forms spawning aggregations and small groups for non-reproductive functions (Ebisawa 2006; Nanami & Yamada 2009). Reports of *L. lentjan* spawning in aggregations were also limited to Ahus fishers, and are consistent with anecdotal reports of this behaviour from other countries (Johannes 1981). Contrasting with its congener, *L. lentjan* primarily feed in deeper water (Parrish 1987) and heterogeneity in knowledge emerged on Ahus as the species was mainly known to male fishers who can access the outer reefs. Fishers from both locations generally perceived emperors as being relatively mobile and of lower spatial predictability than groupers or snappers, which concurs with scientific evidence (Kaunda-Arara & Rose 2004).

Our study was a first step in quantitatively exploring the factors that influence local ecological knowledge of reef fish aggregating behaviour within communities, but was limited to a small number of socioeconomic indicators that reflect the contemporary context of the two communities. Consequently, we did not quantify important historical aspects of these communities and the role of oral histories in transferring knowledge, which may have influenced the patterns observed in our data. For example, though we pooled respondents from the two study villages of Karkar Island in our analyses, knowledge of grouper spawning aggregations was higher (by 52%, based on the sum fisher knowledge index for both grouper species) among Muluk fishers than neighbouring fishers from Wadau. Since fishers exhibit similar dependency on fishing, this finding may reflect the differing historical context of two communities, which may have settled on the coast at different times (Cinner 2007).

Comparing several locations in Melanesia, Hamilton et al. (2004) found that the Titan communities from southern Manus held the richest bodies of knowledge pertaining to grouper spawning aggregation sites, which had accumulated over generations. The knowledge base that supports the complex tenure systems of Ahus and neighbouring Ponam Island also extends over many generations and is likely reinforced through cultural mechanisms such as initiation rights for certain fishing practices (Carrier 1982; Cinner et al. 2005). Thus, knowledge of aggregating behaviour at Ahus has likely been retained through such mechanisms and is presumably limited to clans or kinship groups that can access those resources. While it would have been informative to stratify sampling of respondents by clans or kinship groups, this poses difficulties owing to the often complex relationships in communities such as Ahus (Cinner 2007). Adding further factors in the analysis would also have required more interviews to be conducted than our resources permitted, since RDA is a

constrained ordination analysis that is sensitive to the number of factors relative to sample size. Though our RDA results should be interpreted with caution, since the number of factor levels slightly exceeded the recommended number based on sample size, unconstrained analyses (i.e. principal components analysis) yielded similar relationships between fisher knowledge and socioeconomic indicators.

2.4.2. Susceptibility of reef fish populations to aggregation fishing

This study demonstrated the utility of PSA in examining how attributes relating to catchability and socioeconomic drivers of fishing effort influence the susceptibility of reef fish populations to aggregation fishing. Given that experts with access to scientific information have scored susceptibility indictors in previous applications of PSA (Patrick et al. 2010; Hobday et al. 2011), our study is also novel in that information to score indicators was sourced directly from resource users. Such an approach is more applicable to the many coral reef fisheries that lack fisheries and ecological information.

Knowledge of fish aggregating behaviour is commonly utilized by fishers to improve catchability and returns from a fishery (Parrish 1999). It is therefore appropriate to incorporate fisher knowledge as an indicator of susceptibility to fishing in risk analyses involving aggregating species, especially as it varies among communities (Hamilton et al. 2004). At Karkar, encounterability was higher and the main reef habitats were available for access by all fishers, including the outer reef slopes that are the typical aggregation habitat of at least three of our study species (*E. fuscoguttatus*, *L. gibbus* and *P. areolatus*) (Claydon 2004). However, knowledge of aggregating behaviour was less well developed than on Ahus. The selectivity of gears for many species was greater on Ahus, particularly in their use of a form of muro-ami to target snappers, whereby scare lines and nets are used to corral fish into an enclosed space where they are taken by speargun. This fishing technique is highly efficient

for shoaling and schooling fish such as *L. gibbus* (Corpuz et al. 1985), as evidenced by the higher catch rates at Ahus. Thus, after combining fisher knowledge with availability, encounterability and selectivity, study populations were assessed as equally susceptible to aggregation fishing at Ahus and Karkar using the catchability approach of Hobday et al. (2011).

An advantage of PSA is that the susceptibility attributes included can be adapted to local contexts or issues of importance. For example, Patrick et al. (2010) developed 22 susceptibility index indicators in a PSA, including attributes relating to socioeconomic drivers of fishing pressure (termed 'management' attributes). This proved important to our analysis since the use of catchability attributes alone did not separate study locations, whereas the inclusion of socioeconomic drivers identified a greater potential for overfishing of aggregating populations at Ahus. These drivers are known indicators of fishing pressure and resource depletion (Cinner et al. 2009, 2013). Moreover, conservation benefits provided by the *tambu* at Ahus will have been lost with the recent breakdown in this governance system (Cinner 2007). It is therefore beneficial to understand the socioeconomic factors that drive demand for marine resources and may lead to greater targeting of reef fish aggregations.

PSA and other semi-quantitative approaches are, however, sensitive to the assumptions made in developing indicators (Hobday et al. 2011). A number of assumptions had to be made in our application for aggregation-based fisheries. For example, our proxy for encounterability assumed that if a species appeared in a fisher's catch, then the gears used by that fisher were equally likely to encounter the species in aggregations if conditions of availability were met. This may be justified if aggregations did not form at depths beyond those typically fished by the gear, which would presumably affect fishers using gears that are generally constrained to shallower water (i.e. spearguns and nets) than fishers using lines. Our measure of availability was coarse but necessary in a data-poor context with limited time for observations on the spatial distribution of fishing effort. The use of CPUE to estimate selectivity was also subject to uncertainty, given the numerous factors that affect this parameter, and essentially constituted a measure of gear efficiency for a species rather than selectivity (Arreguín-Sánchez 1996). Further development of indicator-based frameworks for aggregation-based reef fisheries may improve on our methods for estimating susceptibility to fishing.

An additional caveat in the use of indicator-based approaches is that they can be overly reductionist in attempting to simplify complex socio-ecological systems. Consequently, PSA can be combined with more detailed social, economic or ecological research to better understand the management implications of more complex interactions that indicators fail to capture. It is ideally applied as a participatory risk assessment tool for supporting communication, promoting understanding, building consensus and prioritizing actions as part of community-based management planning. In our application of this tool, five populations were identified to be at medium risk from aggregation fishing. However, a participatory application of PSA in the two communities may have yielded different results. For example, resource users could develop their own indicators or choose to weight indicators according to their own priorities (Patrick et al. 2010). Though PSA has a strong basis in theoretical and empirical evidence (Arreguín-Sánchez 1996; Jennings et al. 1998), its validity as a predictive tool requires robust assessment (Patrick et al. 2010). We were unable to validate our application of this tool since biomass estimates for the study populations are absent. However, multispecies reef fish biomass was lower at Ahus than Karkar, both at the time of the interviews (D. Feary, pers. comm.) and in 2002 (Cinner et al. 2005, 2006), which is likely indicative of the higher fishing effort at Ahus (Cinner 2007) and may also reflect the status of our study populations. In addition to fisheries-independent estimates of biomass, preferably at the species level, other approaches to validation may involve fisher knowledge interviews to determine, for example, trends in catch rates over time (Daw et al. 2011).

To conclude, heterogeneity in fisher knowledge relating to reef fish aggregating behaviour will be influenced by social, economic and cultural factors that are specific to the local context. Understanding how knowledge is structured within a community will be important if customary practices for conservation, such as *tambu* areas, are to be supported by working with relevant kinship groups. While knowledge alone does not imply that fishers will maximize extraction from a fishery, shifts in socioeconomic drivers may serve to increase fishing pressure. For example, a breakdown in ownership rights and resulting spread of knowledge among kinship groups has been identified as a cause for concern in relation to pressure on spawning aggregations in PNG (Hamilton et al. 2004). At Ahus, the relatively high susceptibility of aggregations to fishing, caused by a combination of high dependency on fishing, access to larger markets and loss of the tambu areas, would be exacerbated if the system of ownership rights also weakened. However, aggregations forming for purposes other than reproduction are also predictable and may be highly susceptible to fishing if efficient gears are used (Claro et al. 2009). The findings of this study therefore call for a holistic approach to assessing the risks posed by fishing on reef fish aggregations, one that is grounded in the principals of fisheries science and emerging social-ecological thinking (Cinner et al. 2009).

Chapter 3: Managing critical habitats for herbivorous rabbitfish to benefit ecological processes and fisheries

In review for Coral Reefs

3.1. 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 (Graham et al. 2013; Ainsworth & Mumby 2015; Karr et al. 2015). Avoiding or reversing such regime shifts requires management interventions that influence key ecological processes on reefs, including the role played by herbivorous fish in depressing macroalgae (Edwards et al. 2014; Graham et al. 2015). However, the need to maintain or enhance herbivory rates for ecosystem resilience poses a challenge for managing small-scale reef fisheries if trade-offs emerge with socioeconomic fishery objectives. Herbivores are important food fishes and productive species may dominate catches in coral reef regions where socioeconomic dependence on small-scale fisheries is high, such as the Western Indian Ocean (Kamukuru 2009; Robinson et al. 2011; Hicks & McClanahan 2012). Management interventions that improve or maintain fisheries yields while rebuilding herbivore population biomass for ecological processes would avoid the need to trade-off objectives. However, such interventions are relatively rare in coral reef fisheries (McClanahan 2010; Johnson et al. 2013) and an understanding of the behaviour of species that are of ecological and socioeconomic importance is required if multiple objectives are to be met, in particular behavioural characteristics that render fish vulnerable to exploitation (Roberts & Sargant 2002; Grüss et al. 2014b).

Marine reserves, zones where fishing is prohibited, have emerged as a major conservation tool for coral reefs and are now ubiquitous on a global scale (Spalding et al. 2013). Relatively

small marine reserves can effectively protect mobile species if they are placed where populations occur at high densities and are particularly vulnerable to capture (i.e. catchable) (e.g., Roberts & Sargant 2002; Kerwath et al. 2008). Notably, many species of reef fish aggregate at specific times and locations for the purpose of spawning, though the change in population density involved in this behaviour varies widely (Domeier & Colin 1997). The redistribution of fishing effort to exploit spawning migrations and aggregations is typically associated with large changes to catchability (and catch-per-unit-effort, CPUE) (Pears et al. 2007; Hamilton et al. 2012a; Sadovy de Mitcheson & Erisman 2012). Consequently, management measures that protect spawning aggregations, including spawning site marine reserves, are often recommended as an approach to reduce fishing mortality and promote population recovery (Coleman et al. 2000; Rhodes & Warren-Rhodes 2005; Matos-Caraballo et al. 2006).

Critically, the magnitude of density change associated with spawning aggregation formation may or may not determine the extent to which catches from spawning sites contribute to annual fishing mortality (Robinson et al. 2011; Grüss et al. 2014a). For instance, several grouper species (Epinephelidae) are solitary, occur at low densities and are rare in catches outside of the spawning season, but they 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). By contrast, exploiting spawning aggregations may not contribute significantly to annual fishing mortality if changes to fish density are minor, or if other factors, such as targeting behaviour, reduce catchability and effort at spawning sites (Fulton et al. 1999; Robinson et al. 2011; Tobin et al. 2013). Regardless of whether catchability exhibits density-dependence or is influenced by other factors, the extent to which it increases when spawning aggregations are exploited largely dictates the benefits of spawning site reserves (Grüss et al. 2014a).

Assuming density-dependence requires caution since catchability 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, as well as environmental factors such as depth (Wilberg et al. 2010; Tobin et al. 2013). Consequently, direct measures of the change in catchability between spawning and non-spawning habitats appears to be more robust for assessing vulnerability to aggregation fishing than using density ratio (i.e., the ratio of density in spawning habitat to that in non-spawning habitat) as a proxy. Moreover, size- or age-based patterns of catchability emerge from changes to gear selectivity and the distribution of the fishery in relation to fish life stages, which has important implications for management (Quinn & Deriso 1999). Notably, if juveniles are selected for by gears, then implementing reserves in non-spawning habitat can increase the proportion of the population surviving to sexual maturity, offering greater benefits for spawning stock biomass and fisheries yields than spawning site reserves (Heppell et al. 2006; Grüss et al. 2011; Grüss & 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 a primary target species of Seychelles' trap fishery, constituting around 60% of an average annual fishery catch of 374 tonnes between 2003 and 2012 (Seychelles Fishing Authority, unpublished data). Adults of *S. sutor* are fished both at spawning aggregations and in non-spawning areas, whereas juveniles are fished in the latter habitat but are absent in the former (Robinson et al. 2011). The *S. sutor* population of the inner granitic islands is fully exploited but relatively resilient to fishing

pressure given that it is fast growing, short-lived and has a high natural mortality rate (Grandcourt 2002). A per-recruit model for this population predicted that protecting non-spawning habitat can increase spawning stock biomass-per-recruit and yield-per-recruit (exploitable biomass), offering potential benefits for both herbivory rates and fisher incomes (Grüss & Robinson 2015). However, the outcomes of the model are sensitive to assumptions regarding the extent to which catchability increases when fishers target spawning aggregations.

This study aimed to demonstrate the critical role of catchability in the management of a spawning aggregation fishery for the key herbivore *S. sutor* on Seychelles' reefs. Three research questions were addressed: Firstly, does CPUE differ between non-spawning and 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 spatially managing the *S. sutor* fishery to meet socioeconomic and ecological objectives?

3.2. Materials and Methods

3.2.1. Study area

The study area encompassed a *S. sutor* spawning aggregation site ('Dividi') and an adjacent carbonate fringing reef system located to the southwest of Praslin, Seychelles (Fig. 3.1). 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. Importantly, this reef system has shifted to a macroalgal-dominated state since the 1998 mass coral bleaching event (Graham et al. 2015). 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 the spawning site and form aggregations that last 2-3 d (Bijoux et al. 2013a). The spawning site 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 the spawning site (using trap sets and masks), to which they redistribute fishing effort when spawning aggregations have formed (Robinson et al. 2011). Recapture locations of *S. sutor* tagged at the spawning site indicate that the carbonate fringing reefs off Praslin constitute non-spawning habitat (Bijoux 2013a).



Figure 3.1 Map of the study location off the island of Praslin in the inner granitic islands of Seychelles. The map shows the extent of carbonate fringing reef (non-spawning habitat of *Siganus sutor*), the spawning habitat of *S. sutor* (Dividi) and the positions of non-spawning habitat trap sets. The inset shows the position of Praslin relative to the Exclusive Economic Zone of Seychelles.

3.2.2. 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 spawning site between November 2013 and June 2014. Both fishers are typical of experience and gear types used in the fishery. They were also selected on the basis that, among only four other fishers, they exploit spawning aggregations at the spawning site 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 (c. 15 yrs experience) used mainly metal, single entrance traps to fish both habitats, though was also experimenting with three double-entrance traps,. 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 the spawning site, and to new moon and early first quarter periods in non-spawning habitat (Table 3.1). Three fishing trips were observed in non-spawning habitat for each fisher. At the spawning site, four and five trips were observed for Fishers A and B, respectively. 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 due to higher catches in some periods and less time for processing samples between hauls. Since gear saturation or interference can influence catchability (Robinson et al. 2015), all boats and traps active at the study spawning and non-

spawning sites were recorded and fishing effort density estimated as the number of traps per km^2 (traps.km⁻²). Spawning aggregations are largely confined to two neighbouring granitic reefs (0.032km²; SFA unpublished data). Consequently, neither size nor location of the area fished differed greatly between trips in spawning habitat. By contrast, the area fished in non-spawning habitat by each fisher, approximated from constructing polygons in ArcGIS around GPS-derived set positions, differed substantially in location and size between days (range = 0.254 to 3.518 km²; mean = 1.298 km²).

Table 3.1 Summary of trips by habitat fished (S = spawning site; NS = non-spawning habitat), fisher (A or B), fishing effort (number of sets per trip), trip catch (no. caught per trip), mean catch-per-unit-effort (CPUE; fish.trap-hr⁻¹) and fish density metrics (presence and MaxN)

Trip	Date	Habitat	Fisher	Sets	Catch	CPUE	Presence	MaxN
1	16/11/13	S	В	9	0	0	18.3	48
2	17/11/13	S	В	10	87	2.3	26.7	101
3	19/11/13	S	А	4	0	0	27.1	93
4	17/12/13	S	В	14	1126	23.4	28.3	105
5	18/12/13	S	В	9	523	17.1	50.1	150
6	16/01/14	S	В	12	671	16.8	73.3	239
7	17/01/14	S	А	12	70	2.0	10.0	381
8	14/03/14	S	А	7	61	2.3	3.3	2
9	15/03/14	S	А	17	151	2.8	63.3	282
10	01/04/14	NS	В	21	109	2.4	0.8	2
11	02/04/14	NS	В	21	49	1.6	5.0	20
12	03/04/14	NS	В	14	44	1.3	5.8	24
13	30/04/14	NS	А	13	85	2.6	1.7	1
14	08/05/14	NS	А	14	30	0.7	8.3	12
15	09/05/14	NS	А	14	57	1.7	0.8	13

3.2.3. Fish surveys

During each fishing trip to spawning and non-spawning sites, metrics on the density of *S*. *sutor* 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. Surveys covered the entirety of the spawning 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.

3.2.4. 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 (MaxN) was recorded. 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 also 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 and was generally higher at the spawning site. Consequently, fish density metrics were only estimated when schools or individuals passed within a distance of 7 m from the cameras.

3.2.5. Data analysis

3.2.5.1. Comparison of CPUE and fish density across spawning and non-spawning habitats

To account for the zero-inflated and overdispersed distribution of the CPUE 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 that observed 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_eCPUE), assuming homogeneity in variances on the basis of a Levene's test. Differences in fish density metrics (presence and MaxN) between the spawning and non-spawning habitat were examined using Mann-Whitney U tests.

3.2.5.2. 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). Like any regression-based tool, BRT models perform better as sample sizes increase. Nevertheless, BRT settings can be adjusted for robust application to smaller data-sets (Elith et al. 2008; Wisz et al. 2008; Meffert et al. 2012). 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 1996; Stoner 2004; Wilberg et al. 2010; Table 3.2). Predictor variables were derived from data collected in this study, with the exception of current strength, which was estimated from satellite altimeter and scatterometer data (Appendix A). 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. Partial plots show the effect of a predictor variable on the response after accounting for the average effects of all other variables in the model (Elith et al. 2008). 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 the '*gbm*' package v2.1 and code written for BRT functions by Elith et al. (2008) in R (R Development Core Team).

Table 3.2 Predictor variables used in the boosted regression tree model, their units, their levels of measurement (trip or set), and the source of data (from the present study or secondary sources). *: bamboo, metal, double entrance metal; #: Appendix A.

Predictor variable	Units	Level	Data source
MaxN (density)	count	Trip	Video analysis
Presence (density)	%	Trip	Video analysis
Fisher	A, B	Set	Fishery observations
Fishing effort density	traps.km ²	Trip	Fishery observations
Soak time	mins	Set	Fishery observations
Trap type	*	Set	Fishery observations
Depth	m	Set	Fishery observations
Visibility	m	Trip	Video analysis
Current strength	m.s ⁻¹	Trip	Secondary source [#]

3.2.5.3. Management implications of catchability and size selection patterns

Mann-Whitney U and Hodges-Lehman tests were used to compare the size distributions and median sizes of spawning and non-spawning catches. Size distributions of catches by habitat were also compared to size at 50% maturity (L_{m50}), which is estimated at 23.75 cm FL for females (Robinson et al. 2011), and optimum length (L_{opt}), which is estimated at 26.98 cm FL using the empirical relationship of Froese and Binohlan (2000) with asymptotic length (L_{∞}) at 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 the per-recruit marine reserve model designed by Grüss & Robinson (2015). The model was developed for the same *S. sutor* population considered in this study and assesses the relative fisheries (yield-per-recruit) and conservation (spawning stock biomass-per-recruit) benefits of protecting spawning or non-spawning habitat. The model was structurally unchanged from Grüss & 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 (Appendix A). 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 Appendix A).

Point estimates of yield-per-recruit and spawning-stock biomass-per-recruit 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 yield-per-recruit and spawning stock biomass-per-recruit from protecting 30% of non-spawning habitat or spawning habitat 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 & Robinson 2015).

3.3. Results

3.3.1. Comparison of CPUE and fish density across spawning and non-spawning habitats

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 3.1). By contrast, daily catch was lower and less variable in non-spawning habitat, even though more sets were made in this habitat. Consequently, there was a greater range in CPUE at the spawning site (Fig. 3.2). The proportion of sets yielding zero catch (around one third) was equivalent between spawning and non-spawning sites ($\chi^2 = 1.27$; 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 (±1.24, SE) fish.trap-hr⁻¹. Density was higher at the spawning site than in non-spawning habitat, for both presence (Mann-Whitney U; Z = 2.83; P = 0.003) and MaxN (Mann-Whitney U; Z = 2.65; P = 0.005). On average, fish presence and MaxN increased at the spawning site by factors of 9 and 13, respectively.



Figure 3.2 Boxplots of CPUE pooled by fishing trips to spawning and non-spawning habitats

3.3.2. 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, based on the diver surveys, was marginally the most important predictor variable (Table 3.3). However, since the BRT model is stochastic, and since 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. 3.3). Nonetheless, the model fit did not account for trip 9, for which presence reached 63% but CPUE was low (Table 3.1). Depth was collinear to presence and MaxN (Appendix A), both of which peaked at the deeper spawning site. However, it is important to note that 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. 3.3). CPUE was predicted to increase at high levels of current strength (Fig. 3.3). 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).

Predictor variable	VI score
Presence	21.24
Depth	20.55
Current	20.30
MaxN	9.72
Fishing effort density	9.26
Soak time	8.44
Trap type	3.70
Fisher	3.53
Visibility	3.26

Table 3.3 Variable importance (VI) scores for predictive variables in the boosted regression tree model of logCPUE. VI scores sum to 100

Variable 1	Variable 2	Interaction size
Presence	Fisher	2.38
Presence	MaxN	0.86
Trap	Depth	0.4
Current	Effort density	0.29
Current	Soak time	0.25
Presence	Depth	0.17
MaxN	Depth	0.16
Fishing effort density	Soak	0.14
Soak	Depth	0.12

Table 3.4 Ranked interaction size of the nine most important two-way interactions (size>0.1)



Figure 3.3 Partial dependence plots of CPUE as a function of predictor variables (ordered left to right, top to bottom by high to low VI scores: Table 3.3). Abbreviated variables (Table 3.2): Current = current strength; EffortD = fishing effort density; Trap = trap type, Soak = soak time

Variables of moderate relative importance (8–10%; Table 3.3) indicated that CPUE declines with soak time and increases at moderate levels of MaxN and at high levels of fishing effort density (Fig. 3.3). 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 (Appendix A). 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 3.4). Four of the nine strongest interactions involved depth, while presence and soak time were involved in three.

3.3.3. Management implications of catchability and size selection patterns

Siganus sutor caught at the spawning site were significantly larger than fish caught in nonspawning 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. 3.4). 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 entails that less juvenile fish are caught in nonspawning habitat than previously estimated. Consequently, protecting non-spawning habitat results in lower benefits for spawning stock biomass-per-recruit if L_{c50} is the sole parameter updated in the marine reserve model (Table 3.5). Since the catchability ratio estimated in this study (q_s/q_{ns} = 4.31) is lower than that used in Grüss & Robinson (2015) (q_s/q_{ns} = 10), a larger proportion of the annual fishing mortality is directed to non-spawning habitat when q_s/q_{ns} is the sole parameter updated in the model. Consequently, when q_s/q_{ns} is decreased relative to the previous estimate, protecting 30% of the non-spawning habitat results in a much greater improvement in spawning stock biomass-per-recruit in addition to generating a strong, beneficial effect on yield-per-recruit. Moreover, given a lower value of q_s/q_{ns} , protecting spawning sites leads to a neutral effect on yield-per-recruit, rather than the negative effect obtained using previous estimates, though the benefits of spawning reserves for spawning stock biomass-per-recruit are halved. As an increase in L_{c50} combined with a decrease in q_s/q_{ns} have opposing effects on juvenile mortality rates, the benefits of reserves are diluted if both parameters are updated in the marine reserve model (Table 3.5). Nonetheless, in spite of the diluting effects, 72% of the annual fishing mortality incurred by the *S. sutor* population still occurs in non-spawning habitat (non-spawning fishing mortality = 2.73 year⁻¹, comprising adults and juveniles recruited to the fishery; spawning fishing mortality = 1.05 year⁻¹, comprising only adults).



Figure 3.4 Density plots of catch size composition in spawning and non-spawning habitats. Vertical lines indicate size at 50% maturity ($L_{m50} = 23.75$ cm FL) and optimum size ($L_{opt} = 26.98$ cm FL).

Table 3.5 Percentage change in yield-per-recruit (YPR) and spawning stock biomass-perrecruit (SSBR) resulting from the implementation of marine reserves protecting 30% of spawning or non-spawning habitat relative to a 'no reserve' scenario. Changes in YPR and SSBR based on previous parameter estimates are provided, as well as those derived in this study, comparing the model effects of either updating size at recruitment to the fishery (L_{c50}), the ratio of catchability for spawning (q_s) and non-spawning (q_{ns}) habitat, or both parameters in the per-recruit model

Habitat in reserves	Metric	This study ^a			Previous ^b
		L_{c50}	$q_{\rm s}/q_{\rm ns}$	Both	
Spawning habitat	YRP	-1.79	0.04	0.08	-1.56
	SSBR	9.24	4.01	4.01	9.24
Non-spawning habitat	YRP	-3.03	6.38	0.11	-2.84
	SSBR	16.88	306.73	98.75	27.67

^a: This study parameter estimates: $L_{c50} = 21.37$ cm FL, $q_s/q_{ns} = 4.305$ (Appendix A)

^b: Previous parameter estimates: $L_{c50} = 16.15$ cm FL, $q_s/q_{ns} = 10$ (Grüss & Robinson 2015)

3.4. Discussion

The increase in fish density associated with spawning aggregation formation is considered a key factor conferring vulnerability to overfishing (Sadovy de Mitcheson & Erisman 2012). Though density-dependent catchability is common to aggregation fisheries (Wilberg et al. 2010), and occurred in our study fishery, the environment and other aspects of fish and fisher behaviour may act in reducing vulnerability (Stoner 2004; Wilberg et al. 2010; Robinson et al. 2015). Possibly due to the effects of current strength on catchability, CPUE in the *S. sutor* spawning aggregation fishery studied here 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 increase in fish density (depending on the metric used, i.e. presence or MaxN). Due to weak density-dependence in catchability and gear selection for juveniles, most of the annual fishing mortality of the *S. sutor* population (72%) derives from the capture of fish at sub-optimal (92% of catches below optimum length) sizes in non-spawning habitat.

Therefore, marine reserves in that habitat were found to be more beneficial for *S. sutor* spawning stock biomass-per-recruit than spawning site reserves, by an even greater extent than previously estimated given the weak density dependence in catchability observed at the spawning site (Grüss & Robinson 2015). An increase in biomass of this key grazer is likely to improve herbivory rates in a carbonate reef system that has shifted to a macroalgal dominated state in the wake of the 1998 mass coral bleaching event (Chong-Seng et al. 2014; Graham et al. 2015).

3.4.1. 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 the spawning site with high catch rates confined to three of the nine fishing trips, 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 is weakly density dependent. 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.). Such sources of variation in catchability are ideally examined in the context of environmental factors, such as currents and visibility, which exert an important influence on fish physiology and behaviour (Stoner 2004). Moreover, aspects of fisher behaviour, stemming from experience and strategy decisions regarding gear design and deployment, also need to be considered due their effects on catchability (Arreguín-Sánchez 1996).

In addition to two fish density metrics, seven environmental and fishery variables were included in the BRT model. Spawning behaviour involves an offshore migration of S. sutor from a shallow (<15 m) fringing reef to a deeper (> 16 m), submerged granitic reef (Robinson et al. 2011). Though depth had a high variable importance score, intermediate depths (11-16 m) were not fished and the model fit to increases in CPUE at the deeper spawning site and at the shallow non-spawning habitat. Nonetheless, this confounding effect of depth does not detract from the interpretation of other variables using partial plots, for which effects are given at constant depth (Elith et al. 2008). 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.

Our analysis was limited in terms of sample size and explanatory variables relating to fish behaviour. Like any regression-based model, BRT performs better as sample sizes increase. Nevertheless, BRT settings can be adjusted to handle smaller data-sets and models have been used on sample sizes similar to that available in this study (Wisz et al. 2008; Meffert et al. 2012; Young et al. 2012). Sample size (n=191 sets) 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). Consequently, low complexity trees and a slow learning rate were required to grow enough trees (Elith et al. 2008). Future studies that could extend observations to two years and improve sample size would be beneficial, especially if additional predictor variables are to be explored. Fishers report that low catch rates occur when schooling behaviour dissipates and fish rise high in the water column. Attempts to record this behaviour during dives were often prevented by limited visibility so the function or frequency of this behaviour is unknown, though vertical distribution can relate to current strength (Michalsen et al. 1996). Nevertheless, adding more variables to the BRT model would further complicate interpretation (Elith et al. 2008; Soykan et al. 2014). Though BRT is robust to collinearity (Appendix A3), different scales of measurement (i.e. trip versus set-level variables) and nonindependence of samples (i.e. within-trip samples temporally-dependent), caution should be exercised in interpreting results (Elith et al. 2008).

Improved understanding of the relationship between CPUE and aggregating behaviour could also be achieved if sampling methods are extended to provide estimates of total spawning aggregation abundance in addition to our density metrics of school density (MaxN) and school size (presence). While information on density and total aggregation size is important if fish hyperaggregation and CPUE hyperstability operate in the fishery (Rose & Kulka 1999; Erisman et al. 2011; Nemeth 2012), estimating the latter using visual methods can be problematic when aggregations comprise multiple and highly dynamic schools with relatively rapid turnover of fish at the site (Bijoux et al. 2013a). Acoustic methods for estimating aggregation size could, however, be explored.

3.4.2. Management and ecological 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 are, however, highly dependent on this parameter (Grüss & Robinson 2015). Using CPUE and estimates of population abundance derived from visual-census (Erisman et al. 2011; Appendix A), 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 main consequence of a reduced catchability ratio was an increase in non-spawning fishing mortality rates relative to rates for spawning habitat, leading to much greater benefits for spawning stock biomass-per-recruit and a shift from a negative to positive effect on yield-per-recruit if reserves are established in non-spawning 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 (Appendix A). Even though a large proportion of catches from non-spawning habitat remained smaller than size at maturity and optimal size, increased size at recruitment to the fishery was sufficient to reduce the increase in spawning stock biomass-per-recruit, relative to previous estimates, when reserves are implemented in non-spawning habitat. Nonetheless, even when size at

recruitment to the fishery is increased, reserves in non-spawning habitat still increase spawning stock biomass-per-recruit over the no-reserve scenario. Coupled with increases in yield-per-recruit 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 stock and the ecosystem through increases in herbivory rates.

Herbivore biomass has been identified as a key factor for promoting recovery of coral cover on Seychelles' reefs impacted by the 1998 mass coral bleaching event (Graham et al. 2015) and S. sutor is key grazer of fleshy species of macroalgae (Chong-Seng et al. 2014). The findings highlighted in this study suggest that implementing marine reserves in the carbonate non-spawning habitat of S. sutor is likely to increase herbivory rates. Protecting nonspawning habitat increases the number of individuals surviving to sexual maturity, leading to an increase in the spawning stock (Grüss & Robinson 2015). This effect was magnified for the parameter estimates derived in this study, and would likely be of significant benefit to herbivory rates given that spawning stock biomass-per-recruit was essentially doubled over the no-reserve scenario (Table 3.5). Accounting for bite rate, bite size and numerical abundance, individuals of medium size in the population are expected to remove larger volumes of algal material than smaller or larger individuals (Fox & Bellwood 2007). A shift in the number of S. sutor surviving to size at sexual maturity, which approximates to medium size in the population (Fig. 3.4), would further enhance herbivory rates. Implementing marine reserves in non-spawning habitat therefore offers an opportunity to address regime shifts to macroalgal-dominated reefs, which has occurred at this and many other carbonate sites in Seychelles (Graham et al. 2015). While marine reserves are often identified as a tool to increase herbivory rates on coral reefs, the socioeconomic costs associated with such an intervention are also widely recognised in contexts where herbivores constitute important fishery target species (Chong-Seng et al. 2014; Edwards et al. 2014). A key finding of our

study is that marine reserves may not require a trade-off between socioeconomic and ecological objectives if reserve design takes into account spatial patterns in the vulnerability of populations to fishing.

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 & 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. 2013a). 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 (Rhodes & Warren-Rhodes 2005; Russell et al. 2012; Grüss et al. 2014b).

Chapter 4: Fish and fisher behaviour influence the vulnerability of groupers (Epinephelidae) to fishing at a multispecies spawning aggregation site

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4.1. Introduction

Many groupers common to coral reef fisheries (Epinephelidae) are highly prized and prone to overfishing, resulting in a high risk of extinction for numerous species (Sadovy de Mitcheson et al. 2013). The prognosis for groupers appears to be worsening given that exploitation rates are increasing in parts of the developing world (Worm & Branch 2012), where the majority of coral reefs are located. Consequently, there has been considerable emphasis on establishing marine reserves to rebuild populations, particularly through the protection of spawning aggregation sites where groupers are typically most at risk from overfishing (Grüss et al. 2014b). However, establishing effective marine reserves may be problematic due to a high dependency on reef fisheries for livelihoods, as well as a poor understanding of the nonmaterial benefits (e.g. lifestyle and prestige) derived from accessing traditional resources such as spawning sites (Cinner 2014). Management measures that allow access to spawning aggregations while limiting fishing pressure to levels that rebuild populations may, therefore, offer socially and culturally-preferable alternatives to no-take reserves. Compared to the effects of marine reserves, there is very little evidence regarding the effects of alternative management measures on spawning aggregations and their fisheries (Sadovy de Mitcheson & Erisman 2012; Grüss et al. 2014b).

Vulnerability to overfishing in groupers stems from life history characteristics such as longevity, late maturation and spawning aggregation behaviour (Sadovy de Mitcheson et al.

2013). The latter trait poses particular challenges for assessing and managing reef fisheries. Spawning aggregation formation at specific locations and times concentrates fish, and consequently fishers, changing the dynamics of the fishery and typically resulting in a much greater risk of overfishing (Claro et al. 2009; Rhodes et al. 2011). Due to the predictable and often large increase in adult fish density that occurs with aggregation formation, units of fishing effort (e.g. line-fishing hour) can be more efficient at spawning sites, removing a larger proportion of the population than is possible when fish are dispersed (Grüss et al. 2014a). Moreover, several species of grouper often aggregate at the same time and location (e.g. *Epinephelus fuscoguttatus, E. polyphekadion* and *Plectropomus areolatus*; Sadovy 2005), rendering a significant proportion of grouper biomass on reefs susceptible to overfishing when multi-species spawning sites are known to fishers (Heyman & Kjerfve 2008; Sadovy de Mitcheson et al. 2008).

The dynamics of spawning aggregation fisheries also pose challenges for assessment and management since population declines may go unnoticed by fishers and scientists (Sadovy de Mitcheson & Erisman 2012). Catch rate (i.e. catch-per-unit-effort, CPUE) is used extensively as an index of abundance in stock assessment (Quinn & Deriso 1999), and is one of the main signals that fishers perceive regarding the status of their resources, influencing commercial decisions regarding how much to fish and even whether they will exit or remain in a fishery (Cinner et al. 2011). However, CPUE is usually a poor indicator of fish abundance since catchability, defined quantitatively as the proportion of the population caught by a single unit of effort, is rarely constant (Wilberg et al. 2010). Catchability varies in response to numerous aspects of fish and fisher behaviour, including aggregation formation and the distribution of fishing effort (reviews by Arreguín-Sánchez 1996; Wilberg et al. 2010). As populations decline, densities at spawning aggregation sites often decline at a slower rate than those in the normal residence areas. Consequently, if aggregations are targeted by fishers, fishery-wide

and annual CPUE can remain relatively stable in spite of declines in the overall population (an effect known as hyperstability: Rose & Kulka 1999; Harley et al. 2001; Erisman et al. 2011). Moreover, CPUE may be insensitive to declines in the size of a single spawning aggregation over time, as the remaining fish contract into core areas of the site and maintain density (Nemeth 2012). Changes to fisher behaviour, technology and the spatial-temporal distribution and allocation of fishing effort can also cause catchability to vary (termed 'effort dependence'; Gillis & Peterman 1998; van Oostenbrugge et al. 2008; Wilberg et al. 2010). Therefore, by the time declines in CPUE are perceived, whether due to density or effortdependent catchability, populations may have declined to critical levels (Erisman et al. 2011).

Given that coral reef spawning aggregation fisheries are considered highly susceptible to time-varying catchability, which can cause hyperstability, it is surprising that few studies have assessed these effects and their management implications (Sadovy & Domeier 2005; Wilberg et al. 2010). Rather than the absence of such effects, this situation probably reflects the data-poor context of these fisheries, which often lack catch, effort and fisheries-independent biomass data (Sadovy & Domeier 2005). However, for a number of reasons, spawning aggregation fisheries provide a unique opportunity to collect empirical evidence on these effects and their underlying mechanisms. Fish and fishers are concentrated in a small area at predictable times, facilitating the scale and timing of data collection. Aggregations also vary naturally in size within and among spawning months, providing strong abundance gradients over which patterns in catchability can be assessed (Rhodes & Sadovy 2002; Hamilton et al. 2011). Finally, many species form spatially and temporally overlapping aggregations at multispecies spawning sites (Rhodes & Sadovy 2002; Sadovy 2005; Robinson et al. 2008), which enables the selectivity of gears for different species to be examined.

The aim of this study was to examine aspects of fish and fisher behaviour that influence the vulnerability of groupers to fishing (i.e. catchability) at multispecies spawning aggregation sites. To meet this aim, we posed three specific research questions. Firstly, are species of grouper equally vulnerable to fishing when aggregated at a multispecies spawning site? Secondly, are grouper catch rates proportional to the size of their spawning aggregations? Lastly, what aspects of fish or fisher behaviour influence grouper catch rates and their vulnerability to fishing?

4.2. Materials and Methods

4.2.1. Site description

The study site is located on an outer reef promontory near Dyual Island in New Ireland Province, Papua New Guinea (PNG), where *Epinephelus fuscoguttatus* and *E. polyphekadion* form overlapping spawning aggregations (Hamilton et al. 2011). The aggregation site extends over a linear distance of approximately 400 m in depths of between 4 and 40 m. From 4 m depth to a seaward reef edge occurring at between 7 and 10 m, the site comprises a relatively flat shelf area ('reef top'). Between the reef top and 40 m, aggregations extend over a precipitous reef slope ('reef wall'). Aggregations of both species are known to form in four to five consecutive months between March and July. Peak densities occur during the last quarter lunar phase and aggregations rapidly disperse after presumed spawning on or around the day of the new moon (Hamilton et al. 2011).

Spawning aggregations at the study site were exploited by local clans for subsistence purposes prior to the mid-1990s. In 1997, a more intensive fishery to supply the live reef food-fish trade was established that, according to local reports, caused major declines in

aggregation sizes over the six years that it operated (Hamilton et al. 2011). In 2004, clans holding ownership of the reef established a no-take marine reserve of 0.2 km² to protect the entire spawning aggregation site. The reserve is closed to fishing throughout the year and the level of compliance is reportedly high (Hamilton et al. 2011).

4.2.2. Fishery data

In May and June 2013, clan leaders opened the MPA and local communities were engaged to fish spawning aggregations of E. fuscoguttatus and E. polyphekadion for a tagging project (conventional and acoustic) being conducted in parallel to the present study. All fish caught were tagged and released at the site, with the exception of a small proportion (<3%) that did not survive the procedure. Catch and fishing effort data were collected from this fishery (Table 4.1). Fishers operated using baited hook-and-line gear from fibreglass boats that anchored or attached to mooring buoys at the site. Boats fished only the promontory of the site, where densities of E. fuscoguttatus and E. polyphekadion are highest (Hamilton et al. 2011). Fishing trips were conducted at day and night, sometimes overlapping dusk or dawn (Table 4.1). The timing of the trips and number of fishers were determined in collaboration with community leaders and depended on factors such as storm activity and sea state, and availability of fishers, boats and bait. The time that each fisher commenced and ceased fishing was recorded and adjusted for any periods of inactivity greater than one hour. In addition to recording fishing time and the number of boats and fishers on a trip (i.e. effort), information on hook size, bait and depth of capture was also collected. Hooks were supplied and the type (j-hooks 4/0-8/0) used by each fisher was recorded at the start of the trip. Bait was typically caught by fishers prior to starting a trip, or bycatch taken during a trip was used. On catching a fish, the depth (to the nearest 0.1 m) under the boat where the fisher was operating was measured using a hand-held depth sounder. Catch was recorded in number of fish.

Table 4.1 Fishing trip and underwater visual census (UVC) survey details and summary of estimated aggregation size and catch of *Epinephelus fuscoguttatus* and *Epinephelus polyphekadion*. DBNM = days before new moon. Start and end times of fishing trips are from when the first fishers arrived at the site to when the last fishers departed. UVC times represent the start of the dive.

Fishing	trip detail	S					UVC surve	y details	Aggreg	ation size a	nd catch		DBNM
Trip No.	Date start	Date end	Time start	Time end	No. of boats	No. of fishers	UVC date	UVC time	E. fusco Size	oguttatus Catch	<i>E. poly</i> Size	<i>phekadion</i> Catch	
1	03/05	04/05	16:30	06:00	3	11	03/05	13:15	32	7	24	62	7
2	05/05	06/05	20:00	05:00	4	21	05/05	16:00	70	12	76	52	5
3	07/05	07/05	00:20	05:00	4	19	07/05	15:20	153	8	106	32	3
							08/05	11:20	141		111		2
4	09/05	09/05	09:00	23:00	4	25	09/05	16:20	114	4	60	27	1
							10/05	16:00	52		29		0
5	31/05	31/05	17:15	22:45	2	5	31/05	10:30	76	2	119	32	9
							02/06	10:45	87		130		7
6	03/06	03/06	12:30	17:00	3	25	03/06	11:30	94	1	205	65	6
7	04/06	04/06	12:45	17:00	3	28	04/06	11:40	148	2	233	56	5
8	06/06	07/06	16:45	01:00	3	19	06/06	13:00	108	5	177	27	3

Catch and effort data were used to calculate CPUE, in terms of number of fish per fisher-trip (no.•fisher-trip⁻¹), standardised for trip duration of 10 hrs and rounded to the nearest integer, or in terms of number of fish per boat-hr (no.•boat-hr⁻¹) on a trip, with boat fishing time a cumulative function of the time fished by each fisher on the boat. Since the spatial concentration of fishing influences catchability (Wilberg et al. 2010), we also estimated effort density for each trip as a function of the number of fishers and time spent fishing per unit area of the aggregation site (standardised to 100 m^2). However, variation in effort density was driven only by changes in the number of fishers and fishing time since the area fished at the aggregation site did not differ in size among trips, due to boats using fixed moorings or anchoring on only the promontory.

4.2.3. Aggregation density surveys

Fish densities on the reef promontory were surveyed using underwater visual census (UVC) and used to estimate aggregation size. Six and five days were surveyed for the May and June spawning aggregations, respectively (Table 4.1). Surveys were undertaken between late morning and late afternoon. When fishing occurred in daylight hours, UVC surveys were undertaken during or immediately prior to a trip, with the exception of one survey that occurred approximately 4 hrs before fishing commenced. When fishing occurred at night, the time between surveys and commencement of fishing was longer, ranging from 3 to 12 hrs. As it was necessary to pair aggregation size estimates with CPUE from the nearest fishing trip for data analysis, night fishing was generally conducted every other day to prevent daytime UVC surveys falling intermediately to fishing trips on consecutive nights and presenting problems in pairing the data (Table 4.1).

UVC surveys followed a specific route through the aggregations of both species, beginning at 15 m depth on the reef wall to the west of the promontory (Hamilton et al. 2011). The 15 m depth contour was followed until the promontory had been rounded, after which divers ascended and surveyed the reef top in depths of 5-8 m. During each survey, fish were counted within 16 point count areas of 7 m radius (count area 154 m²) divided equally between the reef wall and top. Count areas were orientated on vertical and horizontal planes on the reef wall and reef top, respectively. Consequently, point counts on the reef wall were centred at 15 m but extended from 8 to 22 m in depth.

The aggregation size (*N*) for each species was estimated by extrapolating mean point count densities to the area of each stratum (wall: 4,200 m²; reef top: 4,800 m²), which were then summed. Strata survey areas were approximated from a bathymetry map of the site (R. Hamilton, unpublished data) and GPS coordinates of the survey start and end points in each strata. Since surveys were limited to a depth of 22 m and aggregations may extend to 40 m (Hamilton et al. 2011), estimates are considered a relative index of aggregation size over time rather than absolute aggregation abundance. The areas surveyed were representative of the fish available to the fishery as 96% of the catch was taken in the 5-22 m depth range.

4.2.4. Data analyses

The first research question, concerning the relative vulnerability of each species to hook-andline gear, was examined using two methods. Firstly, differences between species in aggregation sizes, both within and pooled across spawning months, were examined using a Wilcoxon Signed Rank test. Catches for each species were then compared qualitatively with the aggregation sizes available to fishers. Secondly, vulnerability to fishing was quantified by estimating the catchability parameter, q, for each species using:

$$q = \frac{Ut}{Nt}$$

where *U* is CPUE and *N* is aggregation size at time *t* (Ricker 1940). For individual boat trips (n = 26; Table 4.1), q was calculated for both species from mean boat CPUE (no.•boat-hr⁻¹) and aggregation size on that day, and a Wilcoxon Signed Rank test was used to examine the median of differences in this parameter. Boat CPUE was used for estimating *q*, rather than individual fisher catch rates, under the assumption that variation in fisher skill and targeting preference for particular species would be mitigated by aggregating data. Moreover, since there was less variation in depth and hook size between fishers on a boat than between boats, aggregating CPUE reduced the potential for confounding caused by these parameters.

Analysis of the association between CPUE and aggregation size required matching fishing trips to UVC surveys. Fishery data were collected for eight fishing trips that were split evenly between May and June, whereas eleven UVC surveys were conducted in those months. As three UVC surveys could not be matched to a corresponding fishing trip, eight matched pairs of fishery and UVC data were used for analysis (Table 4.1).

To answer the second research question, we tested the assumption that fisher CPUE of each species was proportional to their aggregation size using generalized linear models (GLM) . *E. polyphekadion* CPUE was analysed using a negative binomial GLM, from the Poisson regression family. A high percentage of zeros (close to 70%) in *E. fuscoguttatus* CPUE required binary transformation of CPUE data (0 = no catch, 1 = catch) and the fitting of a binomial GLM, which modelled the probability of catch. GLMs were fit using a logit-link, which outperformed other link functions (as determined by the corrected Akaike's Information Criterion, AIC_c).

Given an association, or lack thereof, between species CPUE and aggregation size, the influence of other explanatory variables on fisher CPUE was examined (research question 3). As per the second research question, negative binomial (*E. polyphekadion*) and binomial (*E.*

fuscoguttatus) GLMs with a logit-link function were used. Explanatory variables included in the model were effort density (ED), depth of capture (DE), and hook size (HK). Due to the potential effects of species interactions on catchability (i.e. competition among species for baited gear), we also considered the aggregation size (N) of the congener (*E. fuscoguttatus*: N_{Ef} ; E. polyphekadion: N_{Ep}) as an explanatory variable (i.e. N_{Ef} as an explanatory variable in the model of *E. polyphekadion* CPUE, and *vice-versa*). The aggregation size of a species was not included in the model of its CPUE due to collinearity with aggregation size of the congener (as determined from an analysis of variance inflation factor), and because the association was tested in the previous step (research question 2). Since depth data were only recorded on capture, data substitution was used to assign depth fished to fishers with zero CPUE. For E. polyphekadion, depth was missing for around 26.7% of fishers and data were substituted by the mean depth of capture by fishers on the respective boat. Given that E. fuscoguttatus was caught by a small percentage of fishers across trips (30%), the mean depth of capture of both species by the boat was used in substitution. Bait was not included in the model as boats utilised up to 6 types of bait per trip, making it problematic to assign any particular bait type to the 30.7% of missing data. Explanatory variables were continuous with the exception of hook size, which was categorical and grouped data into 3 levels due to small samples of hook sizes 4/0 and 8/0 (1 = size 4 and 5 hooks; 2 = size 6 hooks; 3: size 7 and 8 hooks).

GLMs were fit to all combinations of the four explanatory variables plus the intercept-only model. Two-way interactions were initially included, but were removed when found to be non-significant. In the case of the negative binomial GLM, model dispersion was checked using the theta parameter, which is assumed to 1.0. For the binomial GLM, model fit was checked using a Pearson's χ^2 test. Model selection was based on the smallest AIC_c value, and included all other models within two AIC_c units of the best model (Burnham & Anderson

2004). Model importance was assessed using AIC_c weights (wAIC_c), while the relative importance of explanatory variables was examined by summing wAIC_c values across subsets of models containing that variable (Burnham & Anderson 2004). We examined the effects of the most important explanatory variables using partial plots, holding others constant at mean levels and hook size at intermediate level.

If effects of effort density are associated with gear saturation, it was predicted that boat CPUE would decline with the number of fishers operating from a boat (i.e. crew size). Pooling data from all 8 fishing trips, the mean boat CPUE was derived for each level of crew size, which ranged from 2 to 11 fishers. Negative correlation between crew size and mean boat CPUE was then examined using a Kendall tau (τ) (1-tailed) test.

4.3. Results

4.3.1. Relative vulnerability of grouper spawning aggregations to fishing

Large gradients in relative aggregation size occurred for both species, with *E. fuscoguttatus* aggregations ranging from 32 to 153 fish, while those of *E. polyphekadion* ranged from 24 to 233 fish (Table 4.1). *E. fuscoguttatus* aggregation sizes (median = 92 fish) were significantly larger than those of *E. polyphekadion* (median = 68 fish) in May (Wilcoxon Signed Rank test: n = 5; p = 0.046; Fig. 4.1a). Conversely, *E. polyphekadion* aggregations (median = 177 fish) were larger than those of *E. fuscoguttatus* (median = 94 fish) in June (Wilcoxon Signed Rank test: n = 6; p = 0.043). There was no difference in aggregation size between species when data were pooled across months (Wilcoxon Signed Rank test; n = 11; p = 0.424; Fig. 4.1a).



Figure 4.1 Comparison of (a) mean \pm s.e. relative aggregation size (*N*) and (b) mean \pm s.e. CPUE (no.•boat-hr⁻¹) between *Epinephelus fuscoguttatus* and *Epinephelus polyphekadion*.

In spite of the larger *E. fuscoguttatus* aggregation size in May and equivalence in size between species when data were pooled across months, *E. polyphekadion* CPUE was greater than that of its congener in all periods (Fig. 4.1b). Consequently, the total catch of *E. polyphekadion* was more than 5-fold greater in May and more than 8-fold greater over both months (Table 4.1). The larger aggregation of *E. polyphekadion* that formed in June (2-fold

greater than *E. fuscoguttatus*) resulted in a catch of this species that was 18-fold greater than that of its congener.

Greater vulnerability of *E. polyphekadion* to fishing was confirmed by statistical comparison of the catchability parameter, *q* (Wilcoxon Signed Rank test: n = 26; *p* < 0.001). The median catchability of *E. polyphekadion* (*q* = 0.0027) was almost 8-fold greater than that of *E. fuscoguttatus* (*q* = 0.0004). This large difference in catchability results from differences in CPUE between the species being much greater than differences between sizes of their aggregations (Fig. 4.1a,b).

4.3.2. Association of CPUE with aggregation size

In the case of *E. fuscoguttatus*, fisher CPUE was significantly and negatively related to aggregation size (Table 4.2). However, only 3% of the variability in CPUE was explained by its relationship to aggregation size. For *E. polyphekadion*, there was no relationship between fisher CPUE and aggregation size. On the basis of these results, CPUE was largely disassociated from abundance and did not decline or increase across a large gradient in aggregation sizes.

Table 4.2 Results of binomial (*Epinephelus fuscoguttatus*) and negative binomial (*Epinephelus polyphekadion*) GLM models on the relationship between fisher CPUE and aggregation size (N). Results in bold are significant at $\alpha = 0.05$ level. Z is the Wald statistic for the slope parameter.

Species	Variables	Coefficient	Z	р
E. fuscoguttatus	Fisher CPUE/aggregation size (N_{Ef})	-0.012	-2.153	0.031
E. polyphekadion	Fisher CPUE/aggregation size (N_{Ep})	0.002	1.633	0.102

The aggregation size of *E. polyphekadion* (N_{Ep}) was common to both selected models of *E. fuscoguttatus* CPUE (Table 4.3) and was the strongest explanatory variable in terms of summed wAIC_c values (Table 4.4). Effort density (*ED*) was of secondary importance to models of *E. fuscoguttatus* CPUE (Table 4.4). Consequently, increases in the aggregation size of *E. polyphekadion* had slightly more of a depressing effect on the probability of *E. fuscoguttatus* CPUE (i.e. catch = 1) than did increases in effort density (Fig 4.2a,b). In terms of *E. polyphekadion* CPUE, five models were selected on the basis of AICc (Table 4.3). Though depth fished (*DE*) and hook size (*HK*) were present in selected models, the aggregation size of the congener (N_{Ef}) and effort density were again the most important predictors of CPUE (Table 4.4). However, contrasting with *E. fuscoguttatus*, effort density had a greater depressing effect on *E. polyphekadion* CPUE than aggregation size of the congener (Fig. 4.3a,b). Evidence for gear saturation as a mechanism for the effects of effort density was mixed, with mean boat CPUE negatively correlated with crew size for *E. fuscoguttatus* ($\tau = -0.597$; p = 0.01) but not for *E. polyphekadion* ($\tau = -0.244$; p = 0.16).

Table 4.3 GLM models examining the influence of explanatory variables on fisher CPUE. Explanatory variables are aggregation size of *Epinephelus polyphekadion* (N_{Ep}) and *Epinephelus fuscoguttatus* (N_{Ef}), effort density (*ED*), hook size (*HK*) and depth (*DE*). Best models are in bold and are based on (corrected) Akaike Information Criteria (AIC_c). Table limited to models with corrected Akaike Information Criterion weight (*w*AIC_c) > 0.01.

Species	Model	ΔAIC _c	wAICc
E. fuscoguttatus	N_{Ep} + ED	0	0.383
	N_{Ep}	1.89	0.149
	$N_{Ep}+ED+DE$	2.11	0.134
	$N_{Ep}+ED+HK$	2.56	0.106
	$N_{Ep}+HK$	2.99	0.086
	$N_{Ep} + DE$	3.96	0.053
	N_{Ep} + ED + HK + DE	4.73	0.036
	$N_{Ep}+DE+HK$	5.09	0.030
E. polyphekadion	N_{Ef} + ED	0	0.274
	N_{Ef} + ED + DE	0.09	0.262
	N _{Ef} +ED+DE+HK	1.39	0.137
	N _{Ef} +ED+HK	1.78	0.113
	ED	1.84	0.109
	ED+DE	3.37	0.051
	ED+HK	4.14	0.035
	ED+DE+HK	5.28	0.020

Table 4.4 Summed wAIC_c values that quantify the importance of independent variables in explaining CPUE for *Epinephelus fuscoguttatus* and *Epinephelus polyphekadion*.

	E. fuscoguttatus	E. polyphekadion
Abundance (N_{Ep}, N_{Ef})	0.98	0.79
Effort density (ED)	0.66	1.00
Hook size (HK)	0.26	0.31
Depth (DE)	0.25	0.47



Figure 4.2 Partial effect plots of predicted probability of *Epinephelus fuscoguttatus* catch by a fisher (i.e. catch = 1) against (a) the aggregation size of *Epinephelus polyphekadion* and (b) effort density. Line is predicted mean and grey polygon is standard error.



Figure 4.3 Partial effect plots of predicted *Epinephelus polyphekadion* CPUE (no.•fisher-trip⁻¹) against (a) effort density and (b) the aggregation size of *Epinephelus fuscoguttatus*. Line is predicted mean and grey polygon is standard error.

4.4. Discussion

Grouper fisheries pose difficulties for assessment and management unless critical aspects of their behaviour are accounted for in these processes. Combined with slow life histories in many species, the formation of spawning aggregations causes profound changes to the distribution and behaviour of fish and fishers. An understanding of these changes is critical for detecting the impacts of fishing on populations (Sadovy de Mitcheson & Erisman 2012). Contrasting with common assumptions regarding proportionality between CPUE and population size (Quinn & Deriso 1999), our study demonstrated that CPUE was disassociated from the size of spawning aggregations, in spite of strong gradients in abundance. CPUE is exhibiting an extreme form of hyperstability when unresponsive to declining abundances, which typically stems from changes in fish or fisher behaviour that cause catchability to increase (Arreguín-Sánchez 1996; Erisman et al. 2011). Exploring changes in fisher behaviour, we found that CPUE was not influenced by hook size and depth fished but, particularly in the case of E. polyphekadion, declined with increases in effort density. E. fuscoguttatus CPUE was negatively related to the size of aggregations formed by its congener, which clearly stems from the significantly higher vulnerability of E. polyphekadion to line fishing. Our findings point to the dynamic role of catchability in conferring vulnerability to hook-and-line fishing among groupers at multispecies spawning aggregation sites. Furthermore, the study highlights that the dynamic but highly concentrated fish and fisher behaviour involved in multispecies aggregation fisheries provides opportunities as well as challenges for assessment and management.

Dissimilarities in fish behaviour likely underlie the observed difference in catchability between the two species. Interspecific competition for bait is a key factor influencing catchability in multispecies line fisheries and can take the form of exploitative competition, when one species consumes baits more rapidly or efficiently than others, or interference competition, when a species actively prevents other species from accessing bait (Stoner 2004). Previous studies have recognised the links between the vulnerability of *E. polyphekadion* to a wide variety of gear types, its voracity as a predator and propensity to feed throughout the aggregation period (Rhodes et al. 2011). By contrast, *E. fuscoguttatus* is not considered particularly vulnerable to hook-and-line gear at multispecies spawning sites (Mangubhai et al. 2011). If interference competition for bait was occurring, then it would tend to favour the larger (i.e. *E. fuscoguttatus*) rather than the smaller (i.e. *E. polyphekadion*) species (Fernö et al. 1986; Godø et al. 1997). Therefore, exploitative competition is the most likely form of interaction between the species around baited lines, with *E. polyphekadion* exhibiting either an enhanced bait location ability or willingness to attack bait compared to its congener (Stoner 2004).

Competition for bait provides an explanation as to why *E. fuscoguttatus* CPUE declined with increasing aggregation size of its congener. By comparison, the influence of *E. fuscoguttatus* aggregation size on *E. polyphekadion* CPUE was weaker, though still demands an explanation as the effect was influential in the model. Males of both species establish and defend territorial space in aggregations. Given that inter-specific territorial disputes or disruption of territorial behaviour can increase with aggregation density (Rhodes and Sadovy 2002; Robinson et al. 2008), this may lead to a reduction in feeding rates and explain the depressing effect of *E. fuscoguttatus* aggregation size on *E. polyphekadion* CPUE.

Hyperstability is common to fisheries for aggregating species and is typically caused by fishers being able to target dense aggregations in spite of declines in overall population size (Wilberg et al. 2010). We demonstrated that CPUE can also be unresponsive to changes in the size of spawning aggregations, which is indicative of hyperstability at the scale of an aggregation fishery rather than in annual CPUE from a fishery that targets both spawning and

non-spawning periods (Erisman et al. 2011). While density-dependent catchability may be common in aggregation fisheries, other mechanisms influenced CPUE in our study fishery. Notably, the CPUE of E. polyphekadion was strongly depressed by increases in effort density. A plausible mechanism for this effect is gear saturation since, in the case of E. fuscoguttatus, boat CPUE tended to be lower in boats with larger numbers of fishers. However, the fact that crew size and boat CPUE for *E. polyphekadion* were not negatively correlated does not discount gear saturation as a mechanism. Gear saturation is manifested in time as well as space (Groeneveld et al. 2003), so may not be captured by crew size without also accounting for time fished, which was included in the measure of effort density. Effortdependent catchability has been observed in a few fisheries (review by Wilberg et al. 2010), but not, to the authors' knowledge, in a reef fish spawning aggregation fishery. Since grouper aggregations can attract high levels of concentrated effort (Graham et al. 2008), they are likely susceptible to this source of variation in catchability. There are clear management implications resulting from this result since a negative relationship with CPUE contributed to high levels of catch (i.e. fishing mortality) being observed at low levels of effort density. For example, comparing between trips of similar duration, the five fishers of Trip 5 produced more catch than the 19 fishers of Trip 8, while the 11 fishers of Trip 1 produced more than double the catch of the 25 fishers of Trip 4 (Table 4.1).

An important assumption of our study was that courtship and territorial behaviour, which change in intensity over the course of aggregation development (Robinson et al. 2008), did not influence feeding behaviour and, therefore, catchability. While Rhodes et al. (2011) report that *E. polyphekadion* feeds throughout the aggregation period, less is known regarding the feeding behaviour of aggregating *E. fuscoguttatus*. Any changes in feeding behaviour are unlikely to have confounded our finding of interspecific difference in catchability, since it occurred on all days, regardless of the state of aggregation development. However, any

reductions in feeding behaviour close to spawning, when aggregation sizes of these species are typically at their largest and intra- and inter-specific territorial interactions typically increase (Rhodes & Sadovy 2002; Robinson et al. 2008; Hamilton et al. 2011), may have affected the relationship of CPUE with abundance or other explanatory variables.

Compared to effort density and congener abundance, both hook size and depth were relatively unimportant predictors of CPUE. A lack of contrast in hook size, with over 95% of effort comprising 5/0-7/0 sizes, likely explains the absence of a strong effect and future studies could utilise a wider range of hooks to examine the importance of this parameter on catchability. Following protection in 2004, both *E. fuscoguttatus* and *E. polyphekadion* aggregations expanded to include deeper and shallower areas on the promontory (Hamilton et al. 2011). Without strong depth stratification in aggregation densities, depth of fishing was unlikely to be influential in the model. While these sources of variation in catchability were accounted for in the model, including bait posed difficulties. The absence of cold storage facilities in the communities meant that bait (species or size) could not be kept constant across the study. However, using a wide variety rather than a single type of bait rendered it less likely that selectivity would be biased towards one of our study species if their preference differs for any particular type.

A further assumption made in examining relative catchability was that UVC based on open circuit (OC) self-contained underwater breathing apparatus (SCUBA) sampled both species with equal efficiency. Possibly resulting from the disturbance caused by bubbles in OC systems, Rhodes et al. (2014) found that this method may considerably underestimate aggregation density of *E. polyphekadion*, by a factor of three, whereas *E. fuscoguttatus* densities were surveyed with similar efficiency on OC and closed circuit re-breather systems. However, if our *E. polyphekadion* aggregation abundance estimates are inflated by a factor of three to account for underestimation, catchability remained significantly higher than that

observed for its congener (by a factor of 3.25). Together with the fact that we estimated relative rather than absolute abundance, underestimation caused by diver disturbance likely contributed to the fact that Trip 1 catch was greater than aggregation size that day (Table 4.1).

Other sources of known error or bias in UVC surveys of grouper aggregations were mitigated by maintaining the same observer throughout (J.R), the consistently high visibility at the site (>20 m), avoiding peak tidal currents and dusk and dawn periods, and accounting for the flighty behaviour of *E. fuscoguttatus* by counting that species first (Colin et al. 2003; Robinson et al. 2008). However, in avoiding peak tidal currents, the time of day for surveys varied by up to 6 hours (10:30 am – 16:20 pm; Table 4.1). While variability in grouper spawning aggregation density during daylight hours may or may not occur, depending on factors such as the timing of arrivals and departures at the sites (Samoilys 1997; Robinson et al. 2008; Bijoux et al. 2013b; Rhodes et al. 2014), it clearly warrants further investigation at our study site in order to confirm our results and those of long-term monitoring programs (Hamilton et al. 2011). Coupled with the fact that relative rather than absolute aggregation size was estimated, diel variability in density at the study site, and night-time arrival of fish, may explain why catches were higher or close to aggregation abundance on some night fishing trips (Table 4.1).

Our findings have clear implications for the conservation and management of groupers that form spatially and temporally overlapping spawning aggregations (Sadovy 2005). Though rarely used compared to closures, gear controls offer potential for managing these fisheries (Sadovy de Mitcheson et al. 2008; Claro et al. 2009). Using these measures at multispecies spawning aggregation sites requires an understanding of gear selectivity and inter-specific differences in catchability. If a single gear is used, sequential fishing effects are likely, with higher rates of depletion initially occurring in species that are most vulnerable to the gear. Consequently, the decline in *E. fuscoguttatus* aggregations to a hook-and-line fishery may
involve a threshold, corresponding to the point at which the reduction in *E. polyphekadion* density overcomes the relative difference in catchability. However, *E. fuscoguttatus* is vulnerable to spears (Rhodes & Tupper 2007) and increasing the diversity of gear types at multispecies spawning sites will typically widen the species selectivity of the fishery and increase vulnerability for more co-aggregating species.

Fishing effort controls are also relatively rare in spawning aggregation fisheries (Sadovy de Mitcheson et al. 2008) and may, on the basis of our results, have unintended consequences. Assumptions of constant catchability and linearity in the relationship between fishing effort and mortality can undermine the effectiveness of effort restrictions (van Oostenbrugge et al. 2008). Though this may not preclude effort controls as a measure for managing these fisheries, the relationship of CPUE with a wider range of effort density levels than those observed in our study should be known, especially effort levels from zero to the point at which CPUE asymptotes and starts to decline. However, even if effort levels that yield a sustainable catch were identified, the use of this measure is not without risk since increases in catchability caused by other technological (e.g. bait, hook size) or biological (e.g. size of congener aggregations) factors could result in target catch levels being exceeded.

A range of tools are emerging for adaptive management of fisheries for aggregating groupers to meet both conservation and socioeconomic objectives. For example, no-take marine reserves protecting spawning aggregation can be effective in rebuilding populations and normalising sex ratio (Grüss et al. 2014a). Once recovered, management could shift to allowing a limited, sustainable catch of specific species taken annually or periodically, enabling communities to meet subsistence, cultural or other objectives. Specifying the catch (i.e. actual mortality rates) may be preferable to specifying allowable effort due to the dynamic nature of catchability, while specifying the gear would allow species selectivity to be controlled. Using our study site as a hypothetical example, if the goal is to rebuild the *E*.

fuscoguttatus population, a limited take of *E. polyphekadion* could be implemented by allowing hook-and-line gear to be used in months when the latter's aggregation numbers are at their peak, which should minimise catch of *E. fuscoguttatus*. Alternatively, if the goal is to rebuild the *E. polyphekadion* population, a spear fishery would be appropriate in obtaining a limited catch of *E. fuscoguttatus*, for which hook-and-line is less selective, while preventing catch of *E. polyphekadion*. Clearly, a combined approach of gear-based management and catch limits could also be used as an alternative to reserves in rebuilding populations of specific species of aggregating groupers at multispecies aggregation sites (Appendix B). Moreover, similar to the use of rotational closures, allowing controlled access to spawning aggregations may promote compliance with management since direct benefits are more easily perceived than those accruing from permanent no-take reserves.

A number of critical gaps or constraints are pertinent to adaptive management of spawning aggregations fisheries to meet multiple criteria. Firstly, catch levels will need to be estimated that consider both productivity of the populations and the non-lethal effects of fishing on spawning aggregations, such as disruption to mating systems and behavioural cues for sex change (Sadovy de Mitcheson & Erisman 2012). The non-lethal effects of fishing spawning aggregations remain poorly known (Dean et al. 2012), but it is clearly risky to set conventional economic objectives based on maximising yield in these fisheries. Consequently, catch limits should be highly conservative and aimed primarily at meeting social and cultural objectives. Monitoring is clearly critical to adaptive management and, due to the sensitivity of CPUE to changes in catchability, should ideally be based on a robust UVC sampling method that takes account of uncertainties and controls for biases in these data. However, conservation initiatives have clearly demonstrated that community-based monitoring programmes can be effective (Hamilton et al. 2012a), so the onus or lack of capacity for monitoring should not be construed as a barrier to adaptive management or to

advocate for data-less management approaches. Finally, selecting measures for the management of spawning aggregations will involve multiple objectives and trade-offs that are relevant to the local governance context, not least of which is the capacity for enforcement (Grüss et al. 2014b). However, enforcing catch limits in spawning aggregation fisheries, which occur over relatively small areas and narrow windows of time, poses less of a constraint than enforcement of limits for fisheries operating over much larger seascapes.

To conclude, fisheries that target spawning aggregations are complex socio-ecological systems involving shifts in the distribution and behaviour of fish and fishers on lunar, seasonal and annual scales. Consequently, catchability will vary during the build-up and dispersal of aggregations within a month, on the seasonal change in density between spawning and non-spawning habitats, and between years due to changes in aggregation size. Catchability at multispecies spawning sites will also be influenced by the behaviour and aggregation size of co-aggregating species. In addition to these density-dependent sources of variability, fisher behaviour in terms of gears used and effort density will influence catchability. Given the many sources of variation in catchability, it could be argued that permanently closing multispecies spawning aggregation sites to fishing is the most practical approach to management. However, our results highlights that adaptive management need not be overly complex or data-demanding. Should local communities prefer not to lose all opportunities that spawning aggregations provide, gear-based management and highly conservative catch limits could be used to rebuild and allow periodic access to sites, though care should be taken with effort controls due to the effects of effort-dependent catchability. Understanding patterns in catchability will enable a more robust assessment of the costs and benefits of marine reserves and alternative management measures, giving further options for managing complex spawning aggregation fisheries and conserving vulnerable groupers.

Chapter 5: Fish populations forming transient spawning aggregations: should spawners always be the targets of spatial protection efforts?

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5.1. Introduction

Numerous coral reef fishes form transient spawning aggregations at sites located a few to hundreds of kilometres from their normal residence areas (Domeier & Colin 1997). Most aggregation-forming species show strong fidelity to spawning sites, such that spawning aggregations represent bottlenecks in their life history (e.g. Domeier & Colin 1997; Sadovy & Eklund 1999; Nemeth et al. 2007). Slow life history, the spatial and temporal predictability of spawning aggregations and the substantial increase in catchability that usually occurs when fish aggregate act in concert to render aggregation-forming populations highly vulnerable to fishing (e.g. Coleman et al. 2000; Sadovy & Domeier 2005; Rhodes et al. 2011). Moreover, fishing often selects for larger, older individuals at spawning sites, which can lead to reduction in the reproductive output of aggregative populations (Sadovy 1996; Rhodes & Warren-Rhodes 2005). Further impacts of fishing are added in the case of protogynous populations (i.e. populations that mature first as female and then change into males), which can suffer declines in the relative number of males because males are generally larger than females and reside for longer periods at spawning sites (Coleman et al. 1996; Koenig et al. 1996). Significant bias in the female:male sex ratio of protogynous populations may lead to reduced egg fertilisation and reproductive failure (e.g. Coleman et al. 1996; Fitzhugh et al. 2006), and to the disruption of the sex change process (e.g. Koenig et al. 2000). Consequently, the protection of spawning aggregations using marine reserves, places where

fishing and other extractive activities are prohibited year-round, has been widely advocated (Johannes 1997; Koenig et al. 2000; Rhodes & Warren-Rhodes 2005; Sadovy de Mitcheson et al. 2013).

Spawning reserves protect adults, including the largest, most vulnerable individuals, and allow for the persistence and stability of the mating process (Bohnsack et al. 2004; Muñoz et al. 2010; Sadovy de Mitcheson et al. 2013). Therefore, they have the ability to maintain or recover spawning stock biomass (SSB) and mating to levels that ensure recruitment success (Bohnsack et al. 2004; Russell et al. 2012). Spawning reserves also reduce biases in female:male sex ratio in protogynous aggregative populations, potentially increasing egg fertilisation rates (Beets & Friedlander 1999; Koenig & Coleman 2013). Moreover, spawning reserves have been advocated to improve fisheries yields by enhancing yield-per-recruit (exploitable biomass) via an increase in the mean body size of the fish population; and via 'recruitment subsidy', i.e. by enhancing the supply of eggs and larvae to adjacent fished areas (Russ 2002; Roberts 2012; Sadovy de Mitcheson & Colin 2012). While the conservation benefits of spawning reserves are widely recognised, evidence is limited with respect to their fisheries benefits (Sale et al. 2005; Grüss et al. 2011).

To date, three models have explored the impacts of marine reserves for spawning aggregation-forming populations (Heppell et al. 2006; Ellis & Powers 2012; Grüss et al. 2014a). Heppell et al. (2006) and Ellis & Powers (2012) developed an age-structured, population model to evaluate marine reserve effectiveness for the gag grouper (*Mycteroperca microlepis*; Epinephelidae) population of the northeastern Gulf of Mexico, an overexploited fish population for which a large amount of data are available. Importantly, Heppell et al. (2006) found that protecting all spawning sites was less effective for population growth than other management measures, including the implementation of marine reserves in normal residence areas ('normal residence reserves') and fishing effort reduction. On the other hand,

spawning reserves helped female:male sex ratio normalisation, while normal residence reserves did not (Heppell et al. 2006). Grüss et al. (2014a) designed an age-structured, perrecruit model to assess the impacts of protecting a fraction or all spawning aggregation sites for two data-poor populations from Seychelles with contrasting life history traits and sexual modes: the shoemaker spinefoot rabbitfish (*Siganus sutor*; Siganidae) population of the main granitic islands, which has a fast life history and is gonochoristic; and the brown-marbled grouper (*Epinephelus fuscoguttatus*; Epinephelidae) population of Farquhar Atoll, which has a slow life history and is protogynous. For a wide range of fishing effort levels, spawning reserves for both populations generally improved female spawning stock biomass-per-recruit (SSBR), though benefits were often small, while increases in yield-per-recruit (YPR) were not achieved or were negligible.

Spawning aggregations of *S. sutor* in the main granitic islands of Seychelles support a smallscale and socioeconomically important trap fishery (Robinson et al. 2011), while the spawning aggregations of *E. fuscoguttatus* at Farquhar Atoll have historically contributed to the production of salted fish for local markets (J. Robinson, pers. obs.). Since these fisheries were first documented (Robinson et al. 2004, 2007), the opinion of stakeholders has diverged with regard to their management. Conservationists have often advocated for the use of spawning reserves, while fishers have argued that spawning aggregations of *S. sutor* and *E. fuscoguttatus* can be fished sustainably and that other management options are required for these fish populations. In the case of *S. sutor*, it has been argued by fishers that existing marine reserves, covering more than 30 km² of shallow reefs and lagoons around the main granitic islands, already provide protection to *S. sutor* in its normal residence areas. This debate therefore highlighted a critical question, namely: are normal residence reserves more beneficial for the long-term conservation and exploitation of *S. sutor* and *E. fuscoguttatus* than spawning reserves? A theoretical framework was used to inform the ongoing debate in Seychelles, based on modifying the model developed by Grüss et al. (2014a). We compared the long-term, equilibrium conservation (impacts on female SSBR and female:male sex ratio) and fisheries effects (impacts on YPR) of normal residence reserves to those of spawning reserves for the *S. sutor* population of the main granitic islands and the *E. fuscoguttatus* population of Farquhar Atoll. With regards to *S. sutor*, we aimed to determine the relative benefits of spawning and normal residence reserves in terms of both female SSBR and YPR. With regards to *E. fuscoguttatus*, the effectiveness of spawning reserves and normal residence reserves in reducing bias in female:male sex ratio normalisation is a prerequisite for long-term conservation and fisheries benefits (Coleman et al. 1996; Fitzhugh et al. 2006; Ellis & Powers 2012). In this paper, we: (1) describe the modifications introduced to the model designed by Grüss et al. (2014a); (2) apply the model to *S. sutor* and *E. fuscoguttatus* for a range of reserve scenarios; and (3) carry out sensitivity analyses to evaluate the influence of critical parameters (spawning-site catchability and life-history traits) on our results.

5.2. Materials and Methods

The model we used is based on that developed in Grüss et al. (2014a). Therefore, we provide only a short description of the model, since its structure, parameterisation and underlying assumptions are detailed in Grüss et al. (2014a).

Two life stages are represented in the model for gonochoristic populations (juveniles and adults), and three for protogynous populations (juveniles, adult females and males). The adult stage is decomposed into spawners and non-spawners. Adults are present at spawning sites only during the spawning period, whereas juveniles are absent from these sites. All larvae produced at spawning sites enter a common pool from which they settle uniformly over space

('mixed larval pool'; Hart 2006; Kaplan 2009). Fish are assumed to recruit into fisheries at or before the age of sexual maturity, with the rationale that reef fisheries traditionally select for a wide range of fish sizes and that many aggregation-forming species mature at a late age (Sadovy 1994; Sadovy & Eklund 1999; Rhodes & Tupper 2008). All life stages are subjected to the same natural mortality rate. Finally, for protogynous populations, sex change is assumed to take place at a fixed age.

5.2.1. Mortality rates

In the absence of marine reserves, the mortality rates given in Grüss et al. (2014a) also apply here. However, mortality rates in the presence of marine reserves are changed in this study by: (1) the consideration of normal residence reserves; and (2) the introduction of polymorphism in spawning behaviour in the model to account for the fact that only a fraction of adults is faithful to spawning aggregation sites in some aggregative populations, as was recently shown for *S. sutor* (Bijoux et al. 2013a).

Reserve scenario	Description
Scenario #1	A fraction of spawning sites is closed to fishing; the fishing effort previously in reserves disappears at the time of reserve creation
Scenario #2	A fraction of spawning sites is closed to fishing; the fishing effort previously in reserves is fully redistributed to spawning sites remaining open to fishing
Scenario #3	All spawning sites are closed to fishing; the fishing effort previously in reserves disappears at the time of reserve creation
Scenario #4	All spawning sites are closed to fishing; the fishing effort previously in reserves is fully redistributed to normal residence areas
Scenario #5	A fraction of normal residence areas is closed to fishing; the fishing effort previously in reserves disappears at the time of reserve creation
Scenario #6	A fraction of normal residence areas is closed to fishing; the fishing effort previously in reserves is fully redistributed to normal residence areas remaining open to fishing

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We considered the effects of protecting a fraction of normal residence areas relative to the effects of protecting a fraction or all spawning sites. Moreover, we made the following assumptions regarding fishing effort redistribution following reserve creation: (1) the fishing effort previously in reserves disappears; (2) when a fraction of spawning aggregation sites is protected, pre-reserve fishing effort is fully redistributed to non-protected spawning sites; (3) when all spawning sites are protected, the fishing effort previously in reserves is fully redistributed to normal residence areas are protected, pre-reserve fishing effort is fully redistributed to normal residence areas are protected, pre-reserve fishing effort is fully redistributed to normal residence areas. Thus, a total of six reserve scenarios were explored (Table 5.1).

5.2.1.1. Status quo

In the absence of marine reserves (under the 'status quo'), the total mortality rate of adults of a gonochoristic population (Z_{mat}) and of males of a protogynous population (Z_m) is:

$$Z_{mat} = Z_m = M + (1 - C_s)q_{ns}E + C_sq_sE$$
(1)

where *M* is the natural mortality rate (in year⁻¹); C_s the fraction of the annual fishing effort that is directed towards spawning aggregations; q_{ns} the catchability in normal residence areas; q_s the catchability at spawning sites; and *E* the total annual fishing effort (in year⁻¹).

Males of a protogynous population often spend more time at spawning sites than females (e.g., Rhodes & Sadovy 2002; Bijoux et al. 2013b; Rowell et al. 2012). Therefore, the total mortality rate of females of a protogynous population (Z_f) is given by:

$$Z_f = M + (1 - C_s)q_{ns}E + C_f C_s q_s E$$
⁽²⁾

where C_f is the fraction of the spawning period that females spend at spawning sites.

Finally, under the status quo, but also when a fraction of spawning sites is protected, or when all spawning sites are protected while pre-reserve fishing effort disappears, the total mortality rate of juveniles (Z_i) is:

$$Z_{j} = M + (1 - C_{s})q_{ns}E$$
⁽²⁾

5.2.1.2. Fraction of spawning aggregation sites in reserves

When only a fraction, C_r , of spawning sites is protected, given that we assume a mixed larval pool, the total mortality rate of adults must be split into two parts to distinguish between individuals that are faithful to spawning sites and individuals that are unfaithful to spawning sites. For example, for a gonochoristic population, the total mortality rate of adults becomes:

$$Z_{mat} = C_b Z_{mat}^b + (1 - C_b) Z_{mat}^{nb}$$
(4)

where C_b is the fraction of adults that is faithful to spawning sites; and Z_{mat}^b and Z_{mat}^{nb} are the total mortalities of the fraction of the adult population that is, respectively, faithful and unfaithful to spawning sites.

When pre-reserve fishing effort disappears, the adult subpopulation constituted of individuals faithful to spawning sites decomposes itself into two subpopulations, one that is fully protected while spawning, and one that remains fully exposed to fishing while spawning. Therefore, for gonochoristic populations:

$$Z_{mat}^{b} = C_r Z_{mat}^{br} + (1 - C_r) Z_{mat}^{bnr}$$
(5)

where Z_{mat}^{br} and Z_{mat}^{bnr} are the total mortalities of the fraction of the faithful adult subpopulation spawning at, respectively, protected and non-protected spawning sites; and C_r is the fraction of spawning sites protected. Z_{mat}^{br} is identical to the total mortality of juveniles under the status quo (Equation (3)), while Z_{mat}^{bnr} is the total mortality of adults given in Equation (1). As to the adult subpopulation constituted of individuals unfaithful to spawning sites, its spawning site fishing mortality is simply reduced by a factor (1- C_r), such that:

$$Z_{mat}^{nb} = M + (1 - C_s)q_{ns}E + (1 - C_r)C_sq_sE$$
(6)

When pre-reserve fishing effort is redistributed, fishing mortality at non-protected spawning sites is increased by a factor of $\frac{1}{(1-C_r)}$. Therefore, the total mortality of the fraction of the faithful adult population spawning at protected spawning sites (Z_{mat}^{br} for gonochoristic populations) remains the total mortality of juveniles under the status quo, whereas the total mortality of the fraction of the faithful adult population spawning at fished spawning sites (Z_{mat}^{bmr} for gonochoristic populations) is equal to the total mortality of adults under the status quo increased by a factor of $\frac{1}{(1-C_r)}$. As to the adult subpopulation constituted of individuals unfaithful to spawning sites, spawning aggregation fishing mortality is both decreased by a factor (1-C_r) and increased by a factor of $\frac{1}{(1-C_r)}$, so that its total mortality is that of adults under the status quo.

5.2.1.3. All spawning aggregation sites in reserves

If all spawning sites are protected and pre-reserve fishing effort disappears, the total mortality rate of adults becomes that of juveniles under the status quo. On the other hand, if pre-reserve fishing effort is redistributed to normal residence areas, fishing effort concentrates entirely in normal residence areas, and adults and juveniles are then subject to the same total mortality rate:

$$Z_{mat} = Z_m = Z_f = Z_j = M + q_{ns}E$$
⁽⁷⁾

5.2.1.4. Normal residence reserves

If a fraction, C_r , of normal residence areas is protected and the pre-reserve fishing effort disappears, the fishing mortality of adults and juveniles in normal residence areas ($(1-C_s)q_{ns}E$) is simply reduced by a factor $(1-C_r)$ compared to the status quo.

Conversely, if pre-reserve fishing effort is redistributed to non-protected normal residence areas, adult and juvenile populations must be divided into two subpopulations, one that experiences no fishing mortality in normal residence areas, and one that has the normal fishing mortality in these areas increased by a factor of $\frac{1}{(1-C_n)}$.

5.2.2. Metrics

To investigate the long-term impacts of spawning reserves and normal residence reserves, female SSBR and YPR are evaluated under the scenarios described above. Female SSBR (hereafter simply referred to as 'SSBR') and YPR are obtained by integrating the product of weight-at-age and survival-at-age over relevant age ranges. For protogynous populations, female:male sex ratio (SR) in the presence of marine reserves is also evaluated. SR is a proxy for the production of fertilised eggs (Coleman et al. 1996; Fitzhugh et al. 2006) and is given by the ratio of integrals of survival to age over the female and male age ranges. Equations for SSBR, YPR and SR are provided in Appendix C1.

For the reserve scenarios where the study population decomposes into several subpopulations, given that we assume a mixed larval pool, population-wide per-recruit quantities are weighted averages of the corresponding per-recruit quantities for the different

subpopulations. For example, when a fraction of spawning sites is protected and the fishing effort previously in reserves is redistributed to non-protected spawning sites, i.e., under Scenario #2, population-wide SSBR ($SSBR^{pop}$) is given by:

$$SSBR^{pop} = C_b \left[C_r SSBR^{br} + (1 - C_r) SSBR^{bnr} \right] + (1 - C_b) SSBR^{nb}$$
(8)

where C_b is the proportion of the population faithful to spawning sites; C_r is here the fraction of spawning sites in reserves; and $SSBR^{br}$ is the SSBR of the subpopulation faithful to protected spawning aggregation sites; $SSBR^{bnr}$ the SSBR of the subpopulation faithful to fished spawning sites; and $SSBR^{nb}$ the SSBR of the subpopulation unfaithful to spawning sites.

In the results and figures, SSBR is given relative to the natural (unfished) SSBR (i.e., the fraction of natural SSBR or FNSSBR), while YPR is given relative to the maximum YPR in the absence of marine reserves. Reduction in egg fertilisation rates due to biased SR occurs at a local level. Therefore, for protogynous populations, we report both population-wide average SR and the local SR at both protected and fished spawning aggregation sites. Local SRs are compared to a 'critical SR', above which local production of fertilised eggs and reproduction are assumed to fail (Coleman et al. 1996; Fitzhugh et al. 2006).

5.2.3. Analyses

We evaluated the six reserve scenarios described above for the *S. sutor* population of the main granitic islands of Seychelles and the *E. fuscoguttatus* population of Farquhar Atoll, Seychelles. Both *S. sutor* and *E. fuscoguttatus* populations are assumed to grow according to a von Bertalanffy growth function, and weight is an allometric function of growth. The parameterisation of our model for the two populations is detailed in Grüss et al. (2014a) and

parameter values are provided in Table 5.2. In addition, we made the assumption that 87% of the spawning individuals of the *S. sutor* population are faithful to FSA sites (Bijoux et al. 2013a) and that the adult population of *E. fuscoguttatus* is entirely faithful to spawning sites (Bijoux et al. 2013b). Finally, following Grüss et al. (2014a), we considered a critical SR of 50:1 for *E. fuscoguttatus*.

Under the status quo, the default total annual fishing effort of the *S. sutor* and *E. fuscoguttatus* populations, E_{base} , is the current annual fishing effort exerted on these populations in the main granitic islands and at Farquhar Atoll, respectively (95 000 trap sets per year for *S. sutor*; Robinson et al. 2011; 169 fishing days per year for *E. fuscoguttatus*; J. Robinson, pers. obs.). For *S. sutor*, the value of E_{base} is close to that of E_{max} , the annual fishing effort at which YPR reaches a maximum (Grüss et al. 2014a). By contrast, the value of E_{base} is around 13 times less than that of E_{max} for *E. fuscoguttatus* (Grüss et al. 2014a). All reserve scenarios were evaluated under annual fishing effort, *E*, levels ranging from 0 to 3 times E_{base} . For *E. fuscoguttatus*, all reserve scenarios were also evaluated under *E* levels ranging from 3 to 26 times E_{base} . *E* levels for *E. fuscoguttatus* ranging from 3 to 26 times E_{base} . Since *L* fuscoguttatus ranging from 3 to 26 times the set of the

Parameter	Definition	Siganus sutor	Epinephelus fuscoguttatus			
М	Natural mortality rate	0.63 year ^{-1 a}	0.1 year ^{-1 b}			
Ε	Total annual fishing effort	95×10^3 sets per year ^c	169 days per year ^d			
Cs	Fraction of annual fishing effort directed at spawning aggregations	0.0822 °	0.0329 ^d			
$C_{ m f}$	Fraction of the spawning period that females spend at spawning sites	-	0.45 °			
C_{b}	Fraction of the adults that is faithful to spawning sites	0.87 ^f	1 g			
$q_{ m s}$	Spawning site catchability	1.0758 × 10 ⁻⁴	6.5447 × 10 ⁻³			
<i>q</i> _{ns}	Catchability in normal residence areas	<i>q</i> _s /10 ^e	<i>q</i> _s /140 °			
a_{F}	Age of recruitment into the fishery	0.34 year °	9.2 year ^e			
<i>a</i> ₅₀	Age of sexual maturity	0.79 year ^d	9.2 year ^h			
<i>a</i> _{sx}	Age of sex change	-	25.5 year ^h			
K	Instantaneous growth rate at small size	0.65 year ^{-1 a}	0.16 year ^{-1 h}			
L_{∞}	Maximum size	43.3 cm ^a	80.7 cm ^h			
a_0	Theoretical age at zero length	-0.379 year ^a	-0.2 year ^h			
α	Constant of proportionality of the allometric length-weight relationship	$5.9 \times 10^{-3 i}$	6 × 10 ^{-6 j}			
β	Exponent of the allometric length- weight relationship	2.75 ⁱ	3.28 ^j			
SR	Female : male sex ratio	1:1°	Varies			
^a Grandcourt 2002; ^b Hoenig 1983; ^c Robinson et al. 2011; ^d J. Robinson pers. obs.; ^e Seychelles Fishing Authority, unpubl. data; Bijoux et al. 2013b; ^f Bijoux et al. 2013a; ^h Pears et al. 2006; ⁱ Samboo and Mauree 1988; ^j Grandcourt 2005						

Table 5.2 Parameter estimates for shoemaker spinefoot rabbitfish (*Siganus sutor*) and brown

 marbled grouper (*Epinephelus fuscoguttatus*)

S. sutor is a short-lived and fast-growing species (Grandcourt 2002), while E. fuscoguttatus is long-lived and slow-growing (Pears et al. 2006). To quantify the relative impacts of spawning-site catchability (q_s) and life-history traits on our results, we carried out sensitivity analyses consisting in evaluating the consequences of: (1) increasing q_s by a factor of 10 for S. sutor (yielding a ratio of q_s to catchability in normal residence areas (q_{ns}), $\frac{q_s}{q_{ns}}$, of the same magnitude as that of E. fuscoguttatus); (2) decreasing q_s by a factor of 10 for E. *fuscoguttatus* (yielding a_{ns}^{q}/q_{ns} of the same magnitude as that of *S. sutor*); (3) decreasing natural mortality rate, *M*, or instantaneous growth rate at small size, *k*, by a factor of 10 for *S. sutor*; and (4) increasing *M* or *k* by a factor of 10 for *E. fuscoguttatus*. All sensitivity analyses were conducted under *E* levels ranging from 0 to 3 times E_{base} .

5.3. Results

5.3.1. Conservation and fisheries effects of spawning reserves versus normal residence reserves for S. sutor

For *S. sutor*, conservation benefits in the form of increases in SSBR occur under all reserve scenarios, though these benefits are relatively minor when a fraction of spawning sites is protected and pre-reserve fishing effort is redistributed (Scenario #2) (Fig. 5.1a,b). Enhancement of SSBR is greater when normal residence areas are protected (Scenarios #5-6) than when a fraction of spawning sites is placed in reserves (Scenarios #1-2) under a wide range of fishing effort levels, even when pre-reserve fishing effort is redistributed (full and dashed black curves in Fig. 5.1a,b).

Increases in SSBR are greater when all spawning sites are protected (Scenarios #3-4) than when a moderate fraction of normal residence areas (30%) is set aside in reserves, except at high fishing effort levels (greater than ~1.75 times E_{base} ; full and dashed green vs. full and dashed violet curves in Fig. 5.1a). At high fishing effort levels, enhancement of SSBR is similar when all spawning sites or a moderate fraction of normal residence areas are in reserves. By contrast, protecting a large fraction of normal residence areas (60%) yields greater conservation benefits than protecting all spawning sites at fishing effort levels greater than E_{base} , even when pre-reserve fishing effort is redistributed (full and dashed violet vs. full and dashed green curves in Fig. 5.1b). Siganus sutor

Epinephelus fuscoguttatus



Figure 5.1 Fraction of natural spawning stock biomass-per-recruit (FNSSBR, i.e., SSBR over natural SSBR) as a function of multiplier of fishing effort (mE_{base}), for the status quo and the 6 reserve scenarios (Table 5.1). (a) and (b) are for *Siganus sutor*, whereas (c) and (d) are for *Epinephelus fuscoguttatus*. For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (a) and (c) and (b) and (d), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (a) and (c) and (c) and (b) and (d), respectively. For all panels, the vertical dashed-dotted black line indicates the default value of annual fishing effort exerted on the population, E_{base} . For *S. sutor*, the vertical dashed grey line indicates the value of annual fishing effort at which yield-per-recruit reaches a maximum for the population, E_{max} .



Epinephelus fuscoguttatus



Figure 5.2 Yield-per-recruit normalised by maximum yield-per-recruit in the absence of reserves (YPR/YPR_{max}) as a function of multiplier of fishing effort (mE_{base}) for the status quo and the 6 reserve scenarios (Table 5.1). (a) and (b) are for *Siganus sutor*, whereas (c) and (d) are for *Epinephelus fuscoguttatus*. For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (a) and (c) and (b) and (d), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (a) and 60% for (a) and (c) and (b) and (c) and (b) and (d), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line. For *S. sutor*, E_{max} is indicated by a vertical dashed grey line.

Fisheries benefits for *S. sutor* are primarily limited to protection of normal residence areas, while protecting spawning sites generally incurs costs for the trap fishery (Fig. 5.2a,b).

Protecting spawning sites has a negative effect on YPR at fishing effort levels lower than ~1.5 times E_{base} , whereas, at fishing effort levels greater than ~1.5 times E_{base} , spawning reserves have zero or negligible effect on YPR (full and dashed black and full and dashed green curves in Fig. 5.2a,b). By contrast, when pre-reserve fishing effort disappears, at fishing effort levels greater than E_{base} , normal residence reserves have a positive effect on YPR, which increases with both fishing effort and the fraction of normal residence areas in reserves (Scenario #5; full violet curve in Fig. 5.2a,b). Fishing effort redistribution reduces the fisheries benefits of normal residence reserves (Scenario #6; dashed violet curve in Fig. 5.2a,b). When a moderate fraction of normal residence areas ($C_r = 30\%$) is set aside as reserves, YPR increases only slightly with fishing effort at fishing effort levels greater than ~1.75 times E_{base} (dashed violet curve in Fig. 5.2a). With the protection of a large fraction of normal residence areas ($C_r = 60\%$), YPR increases with fishing effort at fishing effort at fishing effort levels greater than ~1.5 times E_{base} , and fisheries benefits are also greater than when a moderate fraction ($C_r = 30\%$) is protected (dashed violet curve in Fig. 5.2b).

5.3.2. Conservation and fisheries effects of spawning reserves versus normal residence reserves for E. fuscoguttatus

For *E. fuscoguttatus*, conservation benefits in the form of increases in SSBR occur under all reserve scenarios, though are limited when a fraction of normal residence areas is set aside as reserves and pre-reserve fishing effort is redistributed (Scenario #6) (Fig. 5.1c,d) (Appendix C: Fig. C2). Increases in SSBR are greater when spawning reserves are implemented than when a fraction of normal residence areas is protected. An exception to this general pattern occurs under fishing effort levels lower than ~2 times E_{base} , when 30% of the normal residence areas are protected and pre-reserve fishing effort disappears, which produces

similar increases in SSBR to protecting 30% of spawning sites when pre-reserve fishing effort is redistributed (Fig. 5.1c) (Appendix C: Fig. C2a). Decreases in YPR occur in all reserve scenarios (Fig. 5.2c,d) (Appendix C: Fig. C3). These decreases are substantial when all spawning sites are set aside as reserves (full and dashed green curves in Fig. 5.2c,d) (Appendix C: Fig. C3). YPR levels for *E. fuscoguttatus* are higher with normal residence reserves than with spawning reserves (Fig. 5.2c,d) (Appendix C: Fig. C3).

Reduction in population-wide average SR occurs under all reserve scenarios except when a fraction of spawning sites or of normal residence areas is in reserves while the fishing effort formerly in reserves is redistributed (Scenarios #2 and #6) (Fig. 5.3a,b) (Appendix C: Fig. C4a,b). When all spawning sites are set aside as reserves (Scenarios #3-4), decreases in population-wide average SR and in the SR of the fished subpopulation are substantial (full and dashed green curves in Fig. 5.3) (Appendix C: Fig. C4). Under these reserve scenarios, the SR of the fished subpopulation remains below the critical SR (i.e., 50 females for 1 male) under a very wide range of fishing effort levels (under fishing effort levels up to ~6.5 times *E*_{base}; full and dashed green curves; Appendix C: Fig. C4c,d). By contrast, when a fraction of spawning sites or of normal residence areas is protected while pre-reserve fishing effort disappears (Scenarios #1 and #5), reduction in population-wide average SR is more limited and reduction in the SR of the fished subpopulation does not occur (full black and full violet curves in Fig. 5.3) (Appendix C: Fig. C4). In these two reserve scenarios, like in the status quo, the SR of the fished subpopulation remains below the critical SR under fishing effort levels up to ~1.8 times E_{base} (full black and full violet curves in Fig. 5.3c,d). Moreover, the SR of protected subpopulation is significantly reduced with spawning reserves, while it remains close to the SR under the status quo with normal residence reserves (Appendix C: Fig. C5a). Therefore, it follows that closing a fraction of spawning sites or normal residence

areas while pre-reserve fishing effort disappears has, respectively, virtually no impact and limited positive impact on the overall production of fertilised eggs.



Figure 5.3 Female:male sex ratio of *Epinephelus fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}), for the status quo and the 6 reserve scenarios (Table 5.1). (a) and (b) give population-wide average female:male sex ratios, whereas (c) and (d) give female:male sex ratios for the fished subpopulation of *E. fuscoguttatus*. For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (a) and (c) and (b) and (d), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (a) and (c) and (c) and (b) and (d), respectively. For panels (c) and (d), the light grey area indicates when the sex ratio of the fished subpopulation is superior to the critical female:male sex ratio (i.e., 50:1). For all panels, E_{base} is indicated by a vertical dashed-dotted black line. Note that the full black and full violet curves overlap in panels (c) and (d).

When a fraction of spawning sites or of normal residence areas is protected while the fishing effort previously in reserves is redistributed (Scenarios #2 and #6), population-wide SR increases with marine reserves (dashed black and dashed violet curves in Fig. 5.3a,b) (Appendix C: Fig C4a,b), due to increases in the SR of the fished subpopulation (dashed black and dashed violet curves in Fig. 5.3c,d) (Appendix C: Fig C4c,d). Increases in the SR of the fished subpopulation are greater with spawning reserves than with normal residence reserves (dashed black vs. dashed violet curve in Fig. 5.3c,d) (Appendix C: Fig C4c,d). On the other hand, increases in the SR of the protected subpopulation with spawning reserves are substantial, whereas increases in the SR of the protected subpopulation with normal residence reserves are small (Appendix C: Fig. C5). Therefore, it follows that closing a fraction of normal residence areas while pre-reserve fishing effort is redistributed has a strong negative impact on the overall production of fertilised eggs. Moreover, the overall production of fertilised eggs may not be compromised with spawning reserves, if enough sites are protected, when pre-reserve fishing effort is redistributed.

5.3.3. Impacts of spawning-site catchability on reserve effects

For *S. sutor*, increasing spawning-site catchability, q_s , by a factor of 10 significantly reduces the positive effects of normal residence reserves (full and dashed violet curves in Fig. 5.4c,d vs. Fig. 5.4a,b). By contrast, when q_s is multiplied by a factor of 10, the positive effects of spawning reserves on SSBR are dramatically increased and become much greater than those of normal residence reserves (full and dashed black and full and dashed green curves in Fig. 5.4c,d). When q_s is multiplied by a factor of 10, spawning reserves have a positive effect on YPR only if fishing effort is much greater than E_{max} (full and dashed black and full and dashed green curves in Fig. 5.5c,d vs. Fig. 5.5a,b). Conversely, increasing q_s by a factor of 10 results in positive fisheries effects from protecting normal residence reserves under a wide range of fishing effort levels (full and dashed violet curves in Fig. 5.5c,d), though fisheries benefits are negligible or limited when pre-reserve fishing effort is redistributed (dashed violet curves in Fig. 5.5c,d).



Figure 5.4 Marine reserve effects on the fraction of natural spawning stock biomass-perrecruit (FNSSBR, i.e., SSBR over natural SSBR) of *Siganus sutor* for the status quo and the 6 reserve scenarios (Table 5.1) under alternate assumptions. Ratio of FNSSBR to FNSSBR in the status quo situation ((*FNSSBR*)/(*FNSSBR*)_{sq}) for *S. sutor* as a function of multiplier of fishing effort (mE_{base}) for the status quo and the 6 reserve scenarios, in the baseline situation (**a,b**); when spawning-site catchability (q_s) is increased by a factor of 10 (**c,d**); when natural mortality, *M*, is decreased by a factor of 10 (**e,f**); and when instantaneous growth rate at small size, *k*, is decreased by a factor of 10 (**g,h**). For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (**a,c,e,g**) and (**b,d,f,h**), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (**a,c,e,g**) and (**b,d,f,h**), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line, while E_{max} is indicated by a vertical dashed grey line.



Figure 5.5 Marine reserve effects on the yield per recruit normalised by maximum yield-perrecruit in the absence of reserves (YPR/YPR_{max}) of *Siganus sutor* for the status quo and the 6 reserve scenarios (Table 5.1), under alternate assumptions. Ratio of normalised YPR to normalised YPR in the status quo situation $((YPR/YPR_{max})/(YPR/YPR_{max})_{sq})$ for *S. sutor* as a function of multiplier of fishing effort (mE_{base}) for the status quo and the 6 reserve scenarios, in the baseline situation (\mathbf{a}, \mathbf{b}) ; when spawning-site catchability (q_s) is increased by a factor of 10 (\mathbf{c}, \mathbf{d}) ; when natural mortality, *M*, is decreased by a factor of 10 (\mathbf{e}, \mathbf{f}) ; and when instantaneous growth rate at small size, *k*, is decreased by a factor of 10 (\mathbf{g}, \mathbf{h}) . For Scenarios #1-2, the fraction of spawning sites in reserves, *C_r*, is 30% and 60% for $(\mathbf{a}, \mathbf{c}, \mathbf{e}, \mathbf{g})$ and $(\mathbf{b}, \mathbf{d}, \mathbf{f}, \mathbf{h})$, respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, *C_r*, is 30% and 60% for $(\mathbf{a}, \mathbf{c}, \mathbf{e}, \mathbf{g})$ and $(\mathbf{b}, \mathbf{d}, \mathbf{f}, \mathbf{h})$, respectively. For all panels, E_{base} is indicated by a vertical dasheddotted black line, while E_{max} is indicated by a vertical dashed grey line.

For *E. fuscoguttatus*, decreasing q_s by a factor of 10 dramatically reduces the positive effects of spawning reserves on SSBR, which become smaller than those of normal residence areas in the situation where pre-reserve fishing effort disappears (Scenario #5) (full and dashed black and full and dashed green curves vs. full violet curves in Fig. 5.6c,d). The positive effects of spawning reserves on SSBR are also smaller than those of protecting a large fraction of normal residence areas (60%) in the situation where pre-reserve fishing effort is redistributed (Scenario #6) (full and dashed black and full and dashed green curves vs. dashed violet curve in Fig. 5.6d). On the other hand, when q_s is reduced by a factor of 10, the negative effects of spawning reserves on YPR are decreased while those of normal residence reserves are increased (Fig. 5.7c,d vs. Fig. 5.7a,b). The negative effects of spawning reserves on YPR become smaller than those of normal residence reserves in the situation where pre-reserve fishing effort disappears (Fig. 5.7c,d), and smaller than those of closing a large fraction of normal residence reserves in the situation where pre-reserve fishing effort is redistributed (Fig. 5.7d).



Figure 5.6 Marine reserve effects on the fraction of natural spawning stock biomass-perrecruit (FNSSBR, i.e., SSBR over natural SSBR) of *Epinephelus fuscoguttatus* for the status quo and the 6 reserve scenarios (Table 5.1) under alternate assumptions. Ratio of FNSSBR to FNSSBR in the status quo situation (*(FNSSBR)/(FNSSBR)sq*) for *E. fuscoguttatus* for as a function of multiplier of fishing effort (mE_{base}) for the status quo and the 6 reserve scenarios, in the baseline situation (**a**,**b**); when spawning-site catchability (q_s) is decreased by a factor of 10 (**c**,**d**); when natural mortality, *M*, is increased by a factor of 10 (**e**,**f**); and when instantaneous growth rate at small size, *k*, is increased by a factor of 10 (**g**,**h**). For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (**a**,**c**,**e**,**g**) and (**b**,**d**,**f**,**h**), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (**a**,**c**,**e**,**g**) and (**b**,**d**,**f**,**h**), respectively. For all panels, E_{base} is indicated by a vertical dasheddotted black line.



Figure 5.7 Marine reserve effects on the yield per recruit normalised by maximum yield-perrecruit in the absence of reserves (YPR/YPR_{max}) of *Epinephelus fuscoguttatus* for the status quo and the 6 reserve scenarios (Table 5.1), under alternate assumptions. Ratio of normalised YPR to normalised YPR in the status quo situation $((YPR/YPR_{max})/(YPR/YPR_{max})_{sq})$ for *E. fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}) for the status quo and the 6 reserve scenarios, in the baseline situation (**a**,**b**); when spawning-site catchability (q_s) is decreased by a factor of 10 (**c**,**d**); when natural mortality, *M*, is increased by a factor of 10 (**e**,**f**); and when instantaneous growth rate at small size, *k*, is increased by a factor of 10 (**g**,**h**). For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (**a**,**c**,**e**,**g**) and (**b**,**d**,**f**,**h**), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (**a**,**c**,**e**,**g**) and (**b**,**d**,**f**,**h**), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line, while E_{max} is indicated by a vertical dashed grey line.

Decreasing q_s by a factor of 10 diminishes the positive effects of protecting all spawning sites on the SR of the fished subpopulation of *E. fuscoguttatus* (Scenarios #3-4; full and dashed green curves in Fig. 5.8c,d vs. Fig. 5.8a,b). By contrast, decreasing q_s by a factor of 10 does not impact the SR of the fished subpopulation when a fraction of spawning sites or normal residence areas is protected while pre-reserve fishing effort disappears (Scenarios #1 and #5; full black and full violet curves in Fig. 5.8c,d vs. Fig. 5.8a,b); and reduces the negative effects of protecting a fraction of spawning sites or normal residence areas in the fishing effort redistribution situation (Scenarios #2 and #6; dashed black and dashed violet curves in Fig. 5.8c,d vs. Fig. 5.8a,b). Moreover, when q_s is decreased by a factor of 10, the SR of the protected subpopulation of *E. fuscoguttatus* is closer to the SR under the status quo when a fraction of spawning sites is set aside as reserves than when a fraction of normal residence areas is protected (Appendix C: Fig. C5b). All these results suggest that both spawning reserves and normal residence reserves have limited effects on the overall production of fertilised eggs when q_s is reduced by a factor of 10.



Figure 5.8 Ratio of female:male sex ratio to female:male sex ratio in the status quo situation $(Sex \ ratio)/(Sex \ ratio)_{sq})$ for the fished subpopulation of *Epinephelus fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}) for the status quo and the 6 reserve scenarios, in the baseline situation (**a**,**b**); when spawning-site catchability (q_s) is decreased by a factor of 10 (**c**,**d**); when natural mortality, M, is increased by a factor of 10 (**e**,**f**); and when instantaneous growth rate at small size, k, is increased by a factor of 10 (**g**,**h**). For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (**a**,**c**,**e**,**g**) and (**b**,**d**,**f**,**h**), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (**a**,**c**,**e**,**g**) and (**b**,**d**,**f**,**h**), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line. Note that the full black and full violet curves overlap in all panels.

5.3.4. Impacts of life-history traits on reserve effects

For *S. sutor*, decreasing natural mortality rate, *M*, or instantaneous growth rate at small size, *k*, by a factor of 10 increases the positive effects of both spawning reserves and normal residence reserves on SSBR (Fig. 5.4e,h vs. Fig. 5.4a,b). Assuming a slower life history for *S. sutor* also enhances the fisheries benefits of normal residence areas and results in increases of YPR with spawning reserves at fishing effort levels much greater than E_{max} (Fig. 5.5e,h vs. Fig. 5.5a,b). Both the SSBR and YPR of *S. sutor* can increase with marine reserves when *M* or *k* is decreased by a factor by 10 because *S. sutor* is severely overexploited under the status quo in this situation, while the species is fully exploited under the status quo in the baseline situation (Fig. 5.5g,h vs. Fig. 5.5a,b). Therefore, implementing marine reserves reduce fishing mortality rates so that annual fishing mortality is moved to the left of the YPR curve and higher YPR levels can be obtained (results not shown here).

For *E. fuscoguttatus*, increasing *M* or *k* by a factor of 10 diminishes the positive effects of both spawning reserves and normal residence reserves on SSBR (Fig. 5.6e,h vs. Fig. 5.6a,b). Moreover, assuming a more rapid life history for *E. fuscoguttatus* increases the negative effects of spawning reserves on YPR, but has virtually no impact on the fisheries effects of normal residence reserves (Fig. 5.7e,h vs. Fig. 5.7a,b). Reductions of the positive effects of spawning reserves and normal residence reserves on SSBR and enhancement of the negative effects of spawning reserves on YPR are more pronounced when *M* is increased than when *k* is increased (Fig. 5.6e,f vs. Fig. 5.6g,h and Fig. 5.7e,f vs. Fig. 5.7g,h).

Increasing M or k by a factor of 10 does not impact on the effects of marine reserves on the SR of the fished subpopulation of E. *fuscoguttatus* (Fig. 5.8e,h vs. Fig. 5.8a,b). The SR of the protected subpopulation of E. *fuscoguttatus* remains closer to the SR under the status quo

when a fraction of normal residence areas is set aside as reserves than when a fraction of spawning sites is protected (Appendix C: Fig. C5c,d).

5.4. Discussion

This study applied a simple per-recruit model to determine whether spawning reserves or normal residence reserves achieve long-term conservation benefits (i.e. improve SSBR and reduce bias in female:male sex ratio) and fisheries benefits (i.e. enhance YPR) for two aggregation-forming populations from Seychelles. Selection of the two populations enabled contrasts of life history traits and sexual modes, as well as differing spawning-site catchability and current exploitation levels. Our results and recommendations differ markedly for these two populations.

5.4.1. Effectiveness of spawning reserves versus normal residence reserves for S. sutor

For the *S. sutor* population of the main granitic islands, our goal was to determine the relative benefits of spawning reserves and normal residence reserves in terms of both SSBR and YPR. Overall, our results suggest that normal residence reserves are more effective in providing both conservation and fisheries benefits for this species. In Seychelles and Kenya, many marine reserves are already established in normal residence areas of *S. sutor* (Graham et al. 2007; McClanahan et al. 2007), and may therefore contribute to the observed resilience of this species at high fishing effort (McClanahan & Hicks 2011; Robinson et al. 2011).

Nevertheless, the potential benefits of normal residence reserves for the *S. sutor* population need to be considered in light of total annual fishing effort, the potential for fishing effort displacement after reserve creation, and the fraction of habitat that can be protected without adverse socioeconomic impacts. Fishing effort evolution after reserve implementation is

difficult to predict (Fulton et al. 2010), yet increase in total annual fishing effort is likely given the growing pressure on coral reef resources (FAO 2014; Worm & Branch 2012). Consequently, assessing the effectiveness of normal residence reserves for *S. sutor* under the assumption of full fishing effort redistribution and/or increase in annual fishing effort is a conservative approach. Given that normal residence areas are much larger than spawning aggregation sites, protecting a large fraction of normal residence reserves would likely impose a significant socioeconomic burden (McClanahan et al. 2005). Moreover, contrary to spawning aggregations for *S. sutor*, the normal residence areas of the species typically support multispecies fisheries. Therefore, the benefits accruing to *S. sutor* from the implementation of normal residence reserves, even if a moderate fraction of normal residence areas (e.g., 30%) was protected, would need to be weighed against socioeconomic impacts resulting from loss of access to other resources in these areas.

As expected, the benefits of normal residence reserves are greater if *S. sutor* is overexploited (e.g. Polacheck 1990; Hart 2006; Le Quesne & Codling 2009). Stock assessments suggest that *S. sutor* is fully exploited in the main granitic islands at present (Robinson et al. 2011; Grüss et al. 2014a). If the current annual fishing effort of the *S. sutor* population remained unchanged, protecting 30% of normal residence areas would improve SSBR but slightly decrease YPR, assuming that the fishing effort formerly in reserves is fully redistributed to non-protected normal residence areas. By contrast, if the annual fishing effort currently exerted on *S. sutor* was doubled and the species became overexploited, protecting normal residence areas would be increased at this level of fishing effort. Under the more realistic scenario of protecting a moderate fraction (30%) of normal residence areas, increases of YPR would still occur but would be limited if the fishing effort previously in reserves is entirely redistributed to non-protected normal residence areas. If a larger fraction (60%) of normal residence areas

was protected, increases of YPR would be more pronounced, though still relatively moderate, even if pre-reserve fishing effort is redistributed to non-protected normal residence areas.

Our sensitivity analyses confirmed that *S. sutor*, which is a short-lived and fast-growing species, derives fewer conservation benefits and experiences greater decreases in YPR from spawning reserves than long-lived and slow-growing species (Gaylord et al. 2005; Chan et al. 2012; Grüss et al. 2014a). The same finding holds with normal residence reserves. However, the fact that normal residence reserves are more beneficial than spawning reserves for the conservation and exploitation of *S. sutor* essentially relates to the change in catchability occurring with spawning aggregation formation. If the change in catchability for spawning aggregations of *S. sutor* was much greater (e.g. 100-fold greater), spawning reserves would be more beneficial for the conservation of *S. sutor*, though still undesirable from a fisheries perspective. Given that the catchability of *S. sutor* at spawning sites is only 10 times greater than its catchability in normal residence areas, fishing mortality is higher in the latter areas in the absence of reserves ($0.83 \text{ year}^{-1} \text{ vs}$. 0.94 year^{-1}). Therefore, implementing normal residence reserves, which target juveniles and non-spawning adults, results in a significant increase in the number of individuals surviving to sexual maturity, leading to an increase in the SSB and exploitable biomass of *S. sutor*.

5.4.2. Effectiveness of spawning reserves versus normal residence reserves for E. fuscoguttatus

For the *E. fuscoguttatus* population of Farquhar Atoll, our primary goal was to determine the most effective spatial management strategy for normalising female:male sex ratio. Unsurprisingly, we found that spawning reserves are more effective than normal residence reserves in reducing bias in the female:male sex ratio of *E. fuscoguttatus* and, potentially,

improving the overall production of fertilised eggs of the species. For the same reasons as those highlighted for *S. sutor*, we argue for a conservative approach in assuming full fishing effort redistribution and/or increase in annual fishing effort in evaluating the effectiveness of spawning reserves for *E. fuscoguttatus*

The protection of all spawning aggregation sites is the most beneficial spatial management strategy for *E. fuscoguttatus* in terms of both female:male sex ratio and SSBR, but results in substantial decreases in YPR. Protecting only a fraction of spawning sites would lead to smaller declines in YPR at the expense of reduced conservation benefits. However, if trade-offs between conservation and exploitation were considered and only a fraction of spawning sites was set aside as reserves, this fraction would still have to be large to compensate for an increase in the sex ratio of the fished subpopulation due to fishing effort displacement.

E. fuscoguttatus is probably underexploited at Farquhar Atoll at present (Grüss et al. 2014a; J. Robinson, pers. obs). If the current annual fishing effort of the *E. fuscoguttatus* population remained unchanged, protecting a large fraction of spawning sites would produce limited conservation benefits but lead to a ~20% reduction in YPR over the status quo situation, assuming that the fishing effort formerly in reserves is fully redistributed to non-protected spawning sites. Protecting all spawning sites would produce significant conservation benefits at the expense of a ~55% reduction in YPR over the status quo situation, assuming that pre-reserve fishing effort is fully redistributed to normal residence areas. If spawning reserves were implemented, doubling the annual fishing effort currently exerted on *E. fuscoguttatus* would be better both for conservation and exploitation. In that case, the conservation benefits of protecting a fraction or all of spawning sites would be dramatically improved. Moreover, YPR would be reduced by, respectively, ~20% and ~43% over the status quo situation, assuming full fishing effort redistribution.

It is important to note that our per-recruit model, which was developed for the data-poor contexts of many reef fish spawning aggregation fisheries (Johannes 1998; Sadovy & Domeier 2005), is likely to underestimate the benefits of spawning reserves for fisheries yields. Since a stock-recruitment relationship is absent in per-recruit models, the effects of spawning area closures on recruitment cannot be quantified (Guénette & Pitcher 1999; Botsford et al. 2009). While increases in YPR for E. fuscoguttatus were not achieved though spawning reserves in our model, increases in fisheries yields may occur through recruitment subsidy if the study population was recruitment limited in the absence of reserves and increases in SSBR compensate for lost opportunities caused by the area closures (Guénette & Pitcher 1999; Hart 2006; Botsford et al. 2009). Future studies could consider combining hypothetical stock-recruitment relationships with the per-recruit quantities of our model to fully assess the potential fisheries effects of spawning reserves versus normal residence reserves for E. fuscoguttatus (Grüss et al. 2014b). Including hypothetical or empiricallyderived stock-recruitment relationships would also lead to different findings in the relative costs and benefits of reserves between species if the relationships differ substantially by taxa (Maunder & Deriso 2013). Our simple per-recruit model is also unable to fully capture the benefits of protecting spawning sites since, with the exception of sex ratio, the indirect effects of fishing on spawning behaviour and fertilisation success are not represented. Among other factors, model development would benefit from information on the levels or type of fishing effort that causes disruption to mating behaviour or aggregation dispersal (Dean et al. 2012).

While partly explained by the slow life history of the species, the positive effects of spawning reserves on the SSBR and female:male sex ratio of *E. fuscoguttatus* and their negative fisheries effects mainly relate to the change in catchability occurring with spawning aggregation formation. If the change in catchability associated with aggregation formation in *E. fuscoguttatus* was much lower (e.g. 14-fold greater, i.e., close to that for *S. sutor*), normal

residence reserves would be more effective than spawning reserves at improving SSBR. Assuming a 14-fold change in catchability, the fishing mortality of non-spawning females in the absence of reserves would become much greater than that of spawning individuals. This result concurs with Heppell et al. (2006), who found that protecting all of the spawning sites of gag grouper has a smaller effect on population growth than normal residence reserves, since the fishing mortality of gag grouper females is higher in normal residence areas than at spawning sites. A much lower catchability at spawning sites would also enhance the negative fisheries effects of normal residence reserves and diminish those of spawning aggregation formation was much lower, both spawning reserves and normal residence areas would have limited effects on female:male sex ratio and the overall production of fertilised eggs. However, in such a situation, normalising female:male sex ratio would be a lower priority since critical sex ratios are reached at much higher fishing effort levels (Appendix C: Fig. C5b) due to the reduced catchability of males at spawning sites.

Our per-recruit model, like any other model, is a simplified representation of a much more complex system. Simplifications that may impact on our results for *E. fuscoguttatus* include the representation of the sex change process and the relationship between sex ratio and egg fertilisation rates. While our model assumes that sex change occurs at a fixed age, sex change may in fact be controlled exogenously and triggered by cues such as local sex ratio, population density and individual fish body sizes in a social group (e.g. Shapiro 1989; Pears et al. 2006; Koenig & Coleman 2013). As discussed in Grüss et al. (2014a), the existence of exogenous factors controlling sex change may reduce the need for spawning reserves. However, assuming that sex change is mediated by age is a conservative approach and allowed our model to predict the maximum possible increases in female:male sex ratios. Moreover, the lack of a functional relationship between female:male sex ratio and egg

fertilisation rates in our model may have impacted on our findings. A few arbitrary relationships between sex ratio and egg fertilisation rates have been formulated in the modeling literature (e.g. Hunstman & Schaaf 1994; Alonzo & Mangel 2004; Heppell et al. 2006). To further evaluate the effectiveness of spawning reserves for *E. fuscoguttattus*, future studies could consider combining alternative forms of this relationship, as well as alternative relationships between the production of fertilised eggs and recruitment, with the per-recruit quantities of our model (Grüss et al. 2014b).

Our study confirmed that there is no 'one size fits all' for managing reef fish populations forming transient spawning aggregations (Sadovy & Domeier 2005). We demonstrated that, depending on life history, sexual mode, exploitation level and spawning-site catchability, spawning reserves may not always be the most appropriate tool for the conservation and exploitation of aggregation-forming populations, and that other management measures should be considered before deciding to implement these closures. Such measures include normal residence reserves and gear measures that increase selectivity for larger fish (Rhodes & Warren-Rhodes 2005; Russell et al. 2012). It is already established that populations possessing life history traits conferring low vulnerability to fishing, such as short life and rapid growth, are more resilient to spawning aggregation fishing and may derive few benefits from spawning reserves (Robinson et al. 2011; Chan et al. 2012). Our study also showed that benefits of spawning reserves essentially relate to the change in catchability occurring with aggregation formation. However, even where marine reserves offer greater benefits if used to protect normal residence areas, they are unlikely to be effective in isolation and must be complemented by other measures controlling fishing effort or fishing gear efficiency at spawning sites or in unprotected residence areas (Kaiser 2005; Nemeth 2005; Russell et al. 2012; Grüss et al. 2014b).

Chapter 6: Predicting vulnerability to overfishing in coral reef spawning aggregation fisheries

6.1. Introduction

The formation of spawning aggregations at specific times and locations is a common reproductive strategy among coral reef fishes (Domeier & Colin 1997). Fisheries have developed to exploit the predictable increases in fish density and catch rates that typically result from spawning aggregation behaviour (Hamilton et al. 2012a; Cheung et al. 2013). Unmanaged capture of fish at spawning aggregations increases the risk of overfishing and there are numerous examples of rapid population decline, aggregation extirpation and fishery collapse (Sadovy & Eklund 1999; Aguilar-Perera 2006; Graham et al. 2008; Table 1.1). Coral reef spawning aggregation fisheries are also notoriously data-deficient (Sadovy de Mitcheson et al. 2008), which in combination with the risk of overfishing has led to calls for precaution and marine reserves to protect spawning aggregations (Johannes 1998). However, some commercial and subsistence spawning aggregation fisheries have persisted for decades in the absence of data-led management (Sadovy & Domeier 2005; Robinson et al. 2011; Table 1.1), while management measures other than marine reserves can be effective in sustaining populations and fisheries in data-poor contexts (Jackson 2012; Erisman et al. 2014). Even basic information on aspects such as life history, size selectivity of gears or management context may clarify management objectives and identify levers for management (Robinson et al. 2014; Erisman et al. 2014; Grüss & Robinson 2015). Consequently, indicator-based approaches that identify vulnerability to fishing and key drivers of fishing pressure offer opportunities for improved management of spawning aggregation fisheries.
Intrinsic vulnerability to fishing is often assessed in data-poor contexts on the basis of indicators derived from life history or behavioural traits (Jennings et al. 1999; Cheung et al. 2005; Abesamis et al. 2014). Traits such as growth rate, longevity and age at maturity directly relate to the productivity of a population and its potential to recover from depletion (Musick 1999; Dulvy et al. 2004). Coral reef fishes are highly diverse in terms of life history and will subsequently exhibit a wide range of responses to depletion. For example, age at maturity, which is negatively related to productivity (Denney et al. 2002), ranges from less than a few months to more than 10 years among reef fishes (Froese & Pauly 2015; http://www.fishbase.org). Behavioural traits, which can relate to spatial attributes, such as schooling and aggregating behaviour, are often included in assessments since they influence susceptibility to fishing gear (Stoner 2004; Cheung et al. 2005; Abesamis et al. 2014). However, aggregation behaviour associated with spawning also links to productivity through the stock-recruitment relationship, since the distribution of spawning in space and time determines the levels of depletion at which recruitment is affected (Maunder & Deriso 2013).

Though distinctions between aggregation and non-aggregation spawners can better explain depletion due to fishing (Cheung et al. 2005), spawning aggregation behaviour is complex and will result in a range of responses to exploitation. Certain species migrate to form a few large spawning aggregations within narrow reproductive seasons (transient spawning aggregations), while others aggregate for spawning at many sites within or close to home ranges and across extended periods of the year (resident spawning aggregations) (Domeier & Colin 1997). Due to their predictability and concentration of spawning in time and space, transient aggregation types are considered to be most vulnerable to fishing (Sadovy & Domeier 2005; Sadovy de Mitcheson & Erisman 2012), which is consistent with emerging knowledge of stock-recruitment dynamics in aggregating spawners (Maunder & Deriso 2013). Nonetheless, there are numerous variations (both inter- and intra-specific) among

transient spawners in terms of the spatial and temporal dynamics of spawning, concentration of aggregations and density changes (Shapiro et al. 1993; Robinson et al. 2011; Bijoux et al. 2013a; Rhodes et al. 2014). Moreover, resident aggregation spawning and non-reproductive aggregating behaviour can also confer high vulnerability to fishing (Sadovy de Mitcheson & Colin 2012; Robinson et al. 2014). More accurate representation of variation in vulnerability to fishing among population and species could therefore be achieved by defining indicators for key aspects of spawning aggregation behaviour.

Indicator-based assessments based on intrinsic traits are useful in identifying species of concern for conservation policy and agenda (e.g. Graham et al. 2011), but they provide an incomplete understanding of the risk of overfishing for specific fisheries. Consequently, extrinsic, fishery-related factors that influence the potential for aggregations to be impacted by a fishery (i.e. susceptibility) must also be considered in order to support management of spawning aggregation fisheries. This is particularly important for these fisheries since they are based on migratory and ephemeral events and knowledge of their location and timing can be variable among fisher communities (Hamilton et al. 2005; Samoilys et al. 2006). High levels of variability in both fisher knowledge and status among fisheries are therefore likely a reflection of the highly localised and complex socioeconomic and cultural contexts in which spawning aggregation fisheries develop (Hamilton et al. 2004; Robinson et al. 2004; Sadovy de Mitcheson et al. 2008). Where the acquisition of knowledge by fishers does lead to the development of targeted fishery (Robinson et al. 2014), susceptibility to fishing will be determined by catchability and fishing effort directed at aggregations.

Catchability, which quantifies the proportion of the stock (or aggregations) removed by a single unit of effort, is highly dynamic and relates to gear efficiency, selectivity, availability and accessibility of the stock, and environmental factors (Arreguín-Sánchez 1996; Stoner 2004; Wilberg et al. 2010). Catchability plays a key role in these fisheries since spawning

aggregations, by definition, involve an increase in density (Domeier & Colin 1997) and catchability typically exhibits density-dependence (Wilberg et al. 2010). Assuming densitydependence can, however, overestimate vulnerability to fishing due to the multiple factors that affect catchability in spawning aggregation fisheries, including fisher targeting behaviour (Hamilton et al. 2004; Tobin et al. 2013), the selectivity and efficiency of gears used (Coleman et al. 1999; Claro et al. 2009; Erisman et al. 2014; Robinson et al. 2015), and environmental factors such as currents and depth (Mangubhai et al. 2011; Hamilton et al. 2012a). Though catchability is a critical parameter, fishing mortality incurred by the population while aggregated for spawning will be a function of catchability and fishing effort. Information on fishing effort is often absent for coral reef spawning aggregation fisheries but is influenced by distance to spawning sites (Aguilar-Perera 2006), weather (Matos-Caraballo et al. 2006), dependency on fishing (Robinson et al. 2014), markets (Pet et al. 2005) and management context (Graham et al. 2008). Indicators based on extrinsic fishery components of catchability and effort will therefore be informative for assessing the risks poses by spawning aggregation fishing in data-poor contexts. This highlights the need for improved fisheries and socioeconomic information to complement the fisheries-independent aggregation monitoring and behavioural ecology that have dominated previous research efforts (Sadovy de Mitcheson & Erisman 2012).

Spawning aggregation fisheries can rapidly deteriorate (Pet et al. 2005; Graham et al. 2008) or disappear entirely (Aguilar-Perera 2006) if fishing pressure is high. Risk assessments can therefore support a precautionary approach to these fisheries, allowing for rapid identification of management or conservation interventions (Hobday et al. 2011). Bivariate frameworks are particularly useful for examination of intrinsic (i.e. capacity of the system to respond) and extrinsic (i.e. pressures on the system) components of vulnerability in complex socio-ecological systems such as fisheries. For instance, productivity-susceptibility analysis (PSA)

is a flexible bivariate indicator-based tool that has been adapted to a range of fisheries contexts and is now widely used as a predictive tool in fisheries management where data on status are absent (Stobutzki et al. 2002; Hobday et al. 2011; Williams et al. 2011). Indicators related to extrinsic risk (i.e. susceptibility) also offer opportunities for monitoring the evolution of fishing pressure and catchability, which can change rapidly with, for example, the introduction of new technologies or the redistribution of effort from another fishery. In the context of spawning aggregation fisheries, indicator development can be informed by intrinsic or extrinsic risk factors that have been identified as specific to those fisheries (Sadovy & Domeier 2005; Sadovy de Mitcheson & Colin 2012) and combined with more generic indicators developed for PSA (e.g. Patrick et al. 2010) or other risk assessments (e.g. Cheung et al. 2005). Since the mechanisms by which life history traits confer vulnerability are well known (Jennings et al. 1999; Dulvy et al. 2004), of particular interest is the development of indicators that specifically address how fisheries interact with spawning aggregation behaviour.

The aim of this study was to develop a predictive framework to assess the vulnerability of spawning fisheries to overfishing in data-limited contexts. Specifically, the study (1) identified a framework structure and indicators of population productivity and susceptibility to fishing, (2) applied the framework to a global set of fisheries and tested its predictive ability, and (3) used the framework to explore key drivers of vulnerability to overfishing in spawning aggregation fisheries.

6.2. Materials and methods

6.2.1. A predictive risk assessment framework for spawning aggregation fisheries

A predictive bivariate framework was developed to assess the vulnerability of spawning aggregation fisheries to overfishing. The unit of assessment addressed by the framework is a fishery that targets spawning aggregations, incorporating the productivity of the species, or its capacity to recover from fishing, on one axis, and the potential exposure or susceptibility of the population to aggregation fishing on the other axis (Fig. 6.1). Spawning aggregation behaviour could conceivably be located on either axis (or could even warrant its own axis) as it influences both productivity, through its role in shaping the stock-recruitment relationship (Pitcher 2001; Maunder and Deriso 2013), and susceptibility to fishing, through density-dependence in catchability. For simplicity, we located spawning behaviour on the y-axis since like productivity it is an inherent behaviour of the species, acted on by the fishery (Cheung et al. 2005). However, in recognition that it relates not only to productivity, the axes were relabelled intrinsic (inherent behaviours of species) and extrinsic (behaviour of the fishery) components of vulnerability and indices were derived for each.

Overall vulnerability to overfishing is a composite of intrinsic and extrinsic components, and can therefore be derived from the position of a fishery in the bivariate space (i.e. Euclidean distance from zero on both axes) (Fig. 6.1a). Alternatively, a quadrant approach recognising three levels of vulnerability can be applied to the framework (Fig. 6.1b), based on the fact that Fisheries exploiting slow life histories or vulnerable spawning behaviour (i.e. high intrinsic index score) will be prone to overfishing at lower levels of fishing pressure and depletion (i.e. low extrinsic index score) than species with opposing intrinsic traits (Myers et al. 1999).



Figure 6.1 A predictive risk assessment framework for spawning aggregation fisheries. The intrinsic and extrinsic indices are expert-weighted composite indices of life history and spawning behaviour, and exposure of the population to aggregation fishing, respectively. Overall vulnerability to overfishing in a fishery (e.g. fisheries A, B, C), can either be derived from (a) the position of a fishery in the bivariate space in terms of Euclidean distance, or from (b) the position of a fishery in relation to quadrants.

6.2.2. Indicator development

Life history parameters included in the intrinsic index were the von Bertalanffy growth parameter (*K*), longevity (t_{max}), age at maturity (t_m), asymptotic length (L_∞) and natural mortality (*M*) (Table 6.1). Parameter estimates for each species assessed were derived using the life history tool of FishBase (Froese and Pauly 2015, <u>http://www.fishbase.org</u>). Due to its low influence on vulnerability to fishing relative to other life history traits (Cheung et al. 2005), fecundity was not included in the index. Estimates for the remaining indicators included in the intrinsic and extrinsic indices are sourced from expert knowledge and are specific to the population and fishery being assessed. Three indicators of spawning aggregation behaviour were developed for the intrinsic index (Table 6.1). Firstly, aggregation type relates to the number, frequency and migration patterns of aggregations formed, which influence predictability and vulnerability to overfishing (Sadovy de Mitcheson & Erisman 2012). Secondly, the magnitude of population density change between non-spawning and

spawning periods provides the basis for density-dependent catchability and for aggregation fishing to drive annual fishing mortality rates (Sadovy & Domeier 2005; Claro et al. 2009). Thirdly, the duration of individual spawning aggregations from formation to dispersal determines the exposure of aggregations to fishing, with longer duration typically allowing for rapid rates of depletion (Aguilar-Perera 2006; Matos-Caraballo et al. 2006). Both density change and duration also influence predictability. Expert knowledge on the length of the spawning season was considered foremost as a productivity indicator since reproductive output that is concentrated in time (and space) can limit recruitment at relatively low levels of population depletion (Maunder & Deriso 2013). Consequently, species with short spawning seasons are particularly prone to depletion (Sadovy de Mitcheson & Erisman 2012).

The extrinsic index was developed around five, first-order indicators (Table 6.2). First-order indicators were selected on the premise that the development of a spawning aggregation fishery initially involves fishers acquiring knowledge on spawning behaviour, and then being able to access both the spawning sites and the technology to exploit aggregations within a management and market context that allows for, and influences the levels of, exploitation. With the exception of fisher knowledge, the first-order indicators were disaggregated into more specific, second-order indicators that are scored by expert knowledge. In terms of accessibility, distance to and depth of spawning sites can influence fishing pressure, while exposure of sites to unfavourable sea states or weather conditions can also constrain exploitation (Johannes et al. 1999; Matos-Caraballo et al. 2006; Mangubhai et al. 2011). Technology was considered in terms of the capacity, selectivity and efficiency of fishing gear, as well as the habitat impacts of gears (Patrick et al. 2010; Micheli et al. 2014). Management considered six measures that have been applied in the context of spawning aggregation fisheries (Sadovy de Mitcheson et al. 2008; Russell et al. 2012). In addition to addressing highly variable supply in spawning aggregation fisheries, preservation capacity is

important for market access and demand (Sadovy de Mitcheson & Erisman 2012). Finally, we developed an indicator relating to potential size and distance of markets accessed by the fishery, with highest vulnerability for fisheries integrated in the live reef food fish trade (Sadovy & Domeier 2005; Aumeeruddy & Robinson 2006; Hamilton & Matawai 2006). In case respondents felt unable to score an indicator, a 'don't know' option was included. In line with a precautionary approach, 'don't know' responses were reassigned with the most vulnerable score for analysis (Hobday et al. 2007).

Table 6.1 Productivity and spawning behaviour indicators included in the intrinsic index. With the exception of life history parameters, indicators are scored by experts for each assessed fishery, according to predefined scoring scales with criteria. Life history indicator values were obtained from FishBase. Indicator weights derived from Analytic Hierarchy Process.

Indicator	Scoring	Indicator description	Weight
Productivity indicators	-	Life history parameters. Longevity (t_{max}) , age at maturity (t_m) and asymptotic length (L_{∞}) : positive relationship with vulnerability. Growth parameter (K) and natural mortality (M) : negative relationship with vulnerability [#]	0.293
	1-4	Spawning season. Scales the duration of the spawning season ranging from 1-3 months to 9-12 months, with shorter spawning seasons conferring higher vulnerability to aggregation fishing	
Aggregation type	1-4	Distinguishes between resident (levels 1 and 2) and transient (levels 3 and 4) spawning aggregation types. Resident types distinguished by migration range, spatial concentration, distinctiveness of spawning sites. Transient types distinguished by spatial concentration and distinctiveness of spawning sites.	0.261
Density change	1-6	Based on order of magnitude comparisons between peak spawning aggregation densities and population densities during non-spawning period. Scale distinguishes between species that are solitary, grouping or schooling for non- reproductive functions. Larger density changes confer higher vulnerability to aggregation fishing	
Aggregation duration	1-4	Scales the duration of spawning aggregations ranging from less than one day to more than two weeks, with longer durations conferring higher vulnerability to aggregation fishing	0.215

[#]: Reciprocal of *K* and *M* taken to reverse direction of relationship with vulnerability and harmonise with other life history parameters

Indicators	Scoring	Indicator description	Weight
Fisher knowledge			0.1725
Fisher knowledge	1-4	Incidental catch but knowledge absent or low (1) scaling to precise knowledge used in targeting (2)	0.1725
Technology			0.1369
Vessel capacity	1-7	Fishers without a vessel (1) scaling to inboard-powered vessels greater than 12 m in length (7)	0.0252
Species selectivity	1-4	Little probability of gear selecting for species (1) scaling to very high probability of retention (4)	0.0211
Size selectivity	1-4	Balanced selectivity for size (1) scaling to unbalanced selectivity for size (4)	0.0134
Efficiency	1-4	Gears inefficient (1) scaling to highly efficient (4) in proportion of biomass removed by unit of effort	0.0364
Habitat impacts (of gear)	1-4	Minimal impact of gears on habitat (1) scaling to highly destructive gears (4)	0.0133
Secondary gears	1-4	Single gear used in fishery (1) scaling to 3 or more selective (for species) gears used (4)	
Accessibility			0.1428
Distance	1-6	Aggregation site more than 500 km from main user group (1) scaling to less than 10 km (6)	0.0608
Depth	1-4	Aggregation depth inhibits efficient gear use (1) scaling to depth not limiting to exploitation (4)	0.0298
Exposure	1-4	Currents, sea states or weather frequently prevent aggregation access (1) scaling to not limiting (4)	
Management			0.3191
Access to fishery	1-4	High compliance with limited access secured by rights (1) scaling to open access fishery (4)	
Effort limits	1-4	4 High compliance with fine-scale (e.g. days, trips) effort limits (1) scaling to no effort controls (4)	
Catch limits	1-4	High compliance with precautionary catch limits (1) scaling to no catch limits (4)	
Gear measures	1-4	High compliance with gear restrictions (1) scaling to no limits on gear use (4)	
Seasonal restrictions	1-4	High compliance with spawning season prohibition of take or trade (1) scaling to no restrictions (4)	
Site closures	1-4	High compliance spatial closure of spawning site (1) scaling to no spatial closures (4)	0.0836
Markets			0.2288
Market type	1-4	Markets small and local (1) scaling to market integration in live reef food fish trade (4)	0.1342
Preservation capacity	1-4	No fish preservation capacity (1) scaling to capacity for cold storage (<18°C) and live fish holding (4)	0.0946

Table 6.2 Indicators included in the extrinsic index. Weights for first- (in bold) and second-order indicators from Analytic Hierarchy Process. Case study fisheries were scored on second-order indicators.

Indicators were weighted by their importance in conferring vulnerability to overfishing using Analytic Hierarchy Process (AHP), an expert ranked weighting scheme (Saaty 1980). The lead author (JR) and seven scientists with expertise on spawning aggregation fisheries (see acknowledgements) performed pair-wise comparisons of indicators in terms of their relative importance (1 = equal; 2 = one indicator slightly more important; 3 = one indicator much more)important). Pair-wise comparisons by each expert were used to create a matrix of weights and indicator weight was assigned from the average weight taken across expert matrices (Saaty 1980). For the intrinsic index, parameters relating to productivity, including life history (K, t_{max} , t_{m} , L_{∞} , M) and spawning season, were grouped as one indicator ('productivity') for weighting as the main focus of study was the relative importance of spawning behaviour indicators (Table 6.1). For the extrinsic index, comparisons were made within each hierarchical level, i.e. between first-order indicators, and then between second-order indicators within each of the first-order indicators (Table 6.2). The final weight of secondorder indicators was then derived following the methods of Pascoe et al. (2009). A Bray-Curtis similarity matrix derived from expert weightings indicated moderate to high consensus on indicator importance, ranging in similarity from 58% to 95% on intrinsic indicators, 61% to 90% on first-order extrinsic indicators and 76% to 91% on second-order extrinsic indicators. Prior to applying weights, the scores assigned to indicators assessed by fishery experts or parameter estimates for life history indicators were scaled 0-1. The final intrinsic and extrinsic indices for each fishery were derived by summing across the weighted indicators and re-scaling 0-1.

Region	Country	Species	Multispecies	Gear	Sector
TWA	Belize	Lutjanus analis		L	С
	Bermuda	Epinephelus guttatus		T, L	С
		Mycteroperca bonaci		L	С
	Cuba	L. analis		L, N, S, TL	С
		Lutjanus griseus		T, N, TL	С
		Lutjanus synagris		T, N, TL	С
	Mexico	Epinephelus striatus		L	С
	Puerto Rico	Epinephelus guttatus		L, S	C, R
	US Virgin Isles	E. guttatus		L, S	С
		L. analis		L	С
WIO	Kenya	Epinephelus fuscoguttatus		L	С
		Siganus sutor		T, L	С
	Maldives	E. fuscoguttatus	Yes	L	LF
		Plectropomus areolatus	Yes	L	LF
		Plectropomus laevis	Yes	L	LF
	Seychelles	E. fuscoguttatus	Yes	L	С
		Epinephelus polyphekadion	Yes	L	С
		S. sutor		Т	С
	Tanzania	Epinephelus lanceolatus		L	С
EIO	Australia	Chrysophrys auratus		L	R
		C. auratus		L	С
	Indonesia	E fuscoguttatus	Yes	L	LF
		P. areolatus	Yes	L	LF
WPO	Australia	E. fuscoguttatus		L	С
		Scomberomorus commerson		L	С
	Micronesia	E. fuscoguttatus	Yes	L	С
		E. polyphekadion	Yes	L	С
		P. areolatus	Yes	L	С
	Palau	E. fuscoguttatus	Yes	L	С
		E. polyphekadion	Yes	L	С
		P. areolatus	Yes	L	С
		Siganus fuscescens		Ν	С
	Solomon Islands	Lethrinus erythropterus		S	С
EPO	Mexico	Cynoscion othonopterus		Ν	С
		Paralabrax nebulifer		Т	С
	USA	P. nebulifer		L	R

Table 6.3 Fisheries assessed in the study. 'Multispecies' refers to fisheries that target multispecies spawning aggregation sites and for which co-aggregating species were also assessed in the country.

Regions: TWA = tropical western Atlantic; WIO = western Indian Ocean; EIO = eastern Indian Ocean; WPO = western Pacific Ocean. Gears: L = hook-and-line; T = trap; N = net; S = spear; TL = trawl. Sector: C = commercial; LF = live reef food fish trade; R = recreational

6.2.3. Applying the framework and examining predictive ability

The framework was applied to a global set of tropical spawning aggregation fisheries, spanning the Indo-Pacific and tropical western Atlantic (Table 6.3). Candidate fisheries for assessment were selected on the basis of a Google Scholar search using the search terms 'spawning', 'aggregation' and 'fishery'. The results were sorted for studies that demonstrated observations of fisheries as opposed to those focusing solely on behavioural ecology or reproductive biology. Though most fisheries assessed were tropical, coral reef-associated, a few sub-tropical reefal (Cynoscion othonopterus, Paralabrax nebulifer) and non-reefal (Cynoscion othonopterus, Scomberomorus commerson) fisheries were also included for contrast. From the final list, fishery experts were approached by email to participate in the study by conducting an interview remotely. Fishery experts were typically lead authors on the published studies resulting from the search. Interviews were conducted using a structured questionnaire that was sent to participants in advance. The questionnaire comprised a suite of indicators considered important components of intrinsic and extrinsic vulnerability in spawning aggregation fisheries, and corresponding, descriptive scales for scoring fisheries. While second-order extrinsic indicators were scored in terms of their current conditions (e.g. current market type accessed), experts were also asked to anticipate and score future directions of the fishery in terms of first-order extrinsic indicators (e.g. is market demand likely to change?).

Predictive ability of the framework was examined using two approaches. Firstly, the relationships between status and three metrics of vulnerability derived from the framework (Euclidean distance, intrinsic and extrinsic index scores) were explored using regression models. Estimates of status from quantitative stock assessment were unavailable for the

majority of fisheries. Therefore, a data-poor approach was employed with fishery experts assigning declining, stable or increasing trends to several indicators, depending on availability of information from their research, the research of others on the fishery or anecdotal data. Indicators assessed were biomass/abundance, fish size, sex ratio, catch-per-unit-effort, catch, fishing effort and mortality rates, derived for either the aggregation component or overall fishery. Insufficient data precluded multinomial regression with three levels of status (declining, stable and increasing trends) as the dependent variable. Status was therefore reclassified as 'no overfishing' (stable or increasing trends) or 'overfishing' (declining trend) and logistic regression performed. Model fit was examined by the Hosmer-Lemeshow statistic and Nagelkerke's R^2 used as an approximation of variance explained by the model.

Secondly, predictive ability was examined by testing the relationships between our three metrics of vulnerability (intrinsic and extrinsic indices, and overall vulnerability, i.e. Euclidean distance) and the fishing vulnerability index developed by Cheung et al. (2005). The fishing vulnerability index of Cheung et al. (2005) has good predictive power and is widely used (Graham et al. 2011; Abesamis et al. 2014). Importantly, in the context of coral reef fish populations, the predictive power of the index was improved by incorporating information on spawning aggregation behaviour (Cheung et al. 2005). Therefore, we postulated that our intrinsic vulnerability index, which includes many of the same life history parameters and more detailed information on spawning, should relate positively to the fishing vulnerability index, while the extrinsic index should not as it is derived from fishery rather than species-specific information. In combining intrinsic and extrinsic indices, Euclidean distance may or may not be related to the index of Cheung et al. (2005). These postulations were tested by fitting linear regression models of the three metrics of vulnerability derived from the framework to the fishing vulnerability index for each species (Froese and Pauly

2015; <u>http://www.fishbase.org</u>). The intrinsic index and Euclidean vulnerability were square transformed to centralise data distributions.

6.2.4. Identifying key risk factors and drivers of vulnerability to overfishing

In the first instance, AHP provides an expert-elicited assessment of indicator importance and weighting provided for qualitative interpretation of the role of indicators as drivers of vulnerability to overfishing. Secondly, a Venn diagram was produced to explore the relative importance of extrinsic drivers. The diagram was constructed on the five first-order extrinsic indicators, but with membership based on fisheries attaining the maximum, most vulnerable score for the second-order indicator of highest weight (i.e. fisher knowledge, efficiency, distance, seasonal restrictions, market type) within each first-order category (Table 6.2).

Secondly, the role of extrinsic indicators as drivers of fishery status was examined using a generalised linear model (GLM). Since status information was limited to two categories ('no overfishing', 'overfishing'), a binomial GLM was employed. Predictor variables comprised first-order indicators, namely fisher knowledge, technology, accessibility, management and markets (Table 6.2). Scaled and weighted second-order indicator scores were summed (hierarchically) to provide first-order indicator scores. GLMs were fit to all combinations of predictor variables and model goodness-of-fit examined using a Pearson's χ^2 test and deviance of the residuals. The relative importance of predictor variables was examined by summing wAIC_c values across subsets of models containing that variable (Burnham & Anderson 2004). Interactions were not included.

6.3. Results

6.3.1. Application and predictability of the framework

Eight of the nine fisheries most vulnerable to overfishing were for groupers (Fig. 6.2a), with five of those integrated in the live reef food fish trade (Table 6.1). The majority of fisheries, for a wide range of fish families, scored in the upper panels, reflecting the fact that there were few studies of aggregation fisheries for species of low intrinsic vulnerability, i.e. fast life histories or resident type spawning aggregations. Very high vulnerability to overfishing occurred mainly for fisheries in the Indian Ocean, while fisheries from other regions mainly scored less than 0.5 in terms of extrinsic vulnerability (Fig 6.2b). Risk of overfishing appeared consistent with status indicators at the highest risk level, with six of the nine fisheries in the (top right) very high risk panel reported to be declining (Fig. 6.2c). However, six fisheries of declining status also occurred in low and high risk panels. Status of fisheries in the top left panel was highly variable, potentially including recovering, stable or declining fisheries. Of concern for the most vulnerable fisheries is that conditions were considered to be worsening (Fig. 6.2d). Fisheries scoring less than 0.5 on extrinsic vulnerability were variable in terms of perceived future direction, with equivalent numbers of fisheries in each of the three direction categories. With the exception of the top right panel, there was little concordance between status, which reflects past fishery conditions, and future direction, which reflects status quo, improvement or worsening in the fishery depending on perceived changes to extrinsic drivers.



Figure 6.2 Weighted data for 36 spawning aggregation fisheries. Fishery scores, which are identical across panels, are shown in terms of (a) family, (b) geographic region, (c) fishery status, and (d) perceived future fishery direction. EIO: Eastern Indian Ocean; EPO: Eastern Pacific Ocean; TWA: Tropical Western Atlantic; WIO: Western Indian Ocean; WPO: Western Pacific Ocean. Symbol size in panel d specifies strength of perceived fishery direction.

Firstly, the predictive ability of the framework was assessed by examining the relationships between fishery status ('overfishing', 'no overfishing') and our three metrics of vulnerability. Status was unrelated to Euclidean distance (Hosmer-Lemeshow: $\chi 2 = 8.0$, p = 0.333; Nagelkerke's $R^2 = 0.08$; β : p = 0.05) or intrinsic score ($\chi 2 = 8.4$, p = 0.213; $R^2 = 0.02$; β : p = 0.2). The model of extrinsic index score as a predictor of status was adequate in terms of fit ($\chi 2 = 12.53$; p = 0.051) and variance explained (Nagelkerke's $R^2 = 0.255$), though the coefficient was not quite significant (β : p = 0.06). Insignificance of the model stemmed from problems in correctly classifying overfishing status, with the model only correct in 53.8% of cases, whereas predictions of no overfishing status were correct in 84.6% of cases (69.2% predictions correct overall). This discrepancy in assigning the two levels of status correctly is apparent from the framework plot (Fig. 6.2c), with most fisheries of 'no overfishing' status (stable or increasing trends) predominately confined to the left panels (i.e. extrinsic index scores < 0.5), whereas those of 'overfishing' status (declining trends) are spread more equally across the range of extrinsic index scores.

Secondly, the predictive ability of the framework was assessed by examining the relationships between the fishing vulnerability index of Cheung et al. (2005) and our three metrics of vulnerability. The intrinsic (vulnerability) index (β : 95% CI = 17.5-47.9; R² = 0.36, *p* < 0.001; Fig. 6.3a) and Euclidean distance (β : 95% CI = 13.5-36.3; R² =0.37, *p* < 0.001; Fig. 6.3c) were positively related to fishing vulnerability index of Cheung et al. (2005), while the extrinsic index was not (β : 95% CI = -8.2-29.8; R² = 0.04, *p* = 0.257; Fig. 6.3b).



Figure 6.3 Relationships (with 95% CI intervals) between the fishing vulnerability index of Cheung et al. (2005) and (a) the intrinsic vulnerability index, (b) the extrinsic vulnerability index, and (c) Euclidean distance. Intrinsic and Euclidean vulnerability square transformed.

6.3.2. Key risk factors and drivers of vulnerability to overfishing

The elicitation of expert knowledge to weight indicators identified productivity (combining life history and spawning season indicators) as more important than any of three individual indicators relating to spawning behaviour (i.e. aggregation type, density change or aggregation duration) (Table 6.1). In terms of spawning behaviour, the type of spawning aggregation formed was estimated as the most important indicator. For the extrinsic component of vulnerability, management and, to a lesser extent markets, were weighted as the key drivers of vulnerability to overfishing (Table 6.2). Within management, seasonal restrictions that limit the take, possession or trade in species during their spawning season, or

spawning site closures to fishing, were considered to offer the greatest protection and reductions in risks of overfishing. Measures that limit entry to fishing, fishing effort or gearuse were considered to offer relatively low protection. Markets were identified as key drivers primarily through the type of markets accessed, in terms of their potential size (Table 6.2).



Figure 6.4 Venn diagram of membership among 36 assessed spawning aggregation fisheries to five first-order extrinsic indicators of vulnerability to overfishing. Membership based on fisheries attaining the maximum vulnerability score for the second-order indicator of highest weight (i.e. widespread, detailed fisher knowledge and targeting of multiple spawning sites, very high gear efficiency, distance to spawning sites minor (<10 km), absence of seasonal restrictions, fishery integrated in LRFFT) within each first-order category (Table 6.2).

Membership was highest in terms of fisher knowledge as most fisheries were characterised by precise and widespread knowledge on aggregation location and timing, leading to targeting of one or many sites (Fig. 6.4). Therefore, fisher knowledge was not particularly limiting. By comparison, membership of technology was low as the use of highly efficient gears to exploit

spawning aggregations was limited to eight of the 36 fisheries assessed. In most (63%) of the assessed fisheries, spawning sites were located less than 10 km from the main user community, so distance was not a constraint on fishing effort. Seasonal restrictions that limit the take, possession or trade in species during their spawning season were present in 14 fisheries. Though this excluded these fisheries from membership of management in the Venn diagram, seasonal restrictions were not considered to be adequately designed or enforced in eight of these fisheries and still allowed for some mortality to aggregating fish (i.e. fisheries that scored two or three rather than one on the scale for this indicator). Membership was lowest in terms of markets with only five fisheries involving the LRFFT, which conferred the highest score in terms of market type (Fig. 6.4).

Secondly, a GLM was used to examine the relative importance of extrinsic indicators as drivers of fishery status. Neither Pearson's χ^2 nor deviance indicated a lack of fit and the model explained 41% of the deviance. Management and fisher knowledge were the only significant predictors in model (p < 0.05) and wAICc values highlight their relative importance as predictors of status (Table 6.4). Fisheries with overfishing status had an average management score 24% greater (i.e. more vulnerable due to lack of management) than those with no overfishing. In terms of fisher knowledge, fisheries with overfishing status have average indicator scores 8% larger (i.e. knowledge more detailed and widespread) than those of no overfishing status. While the primary importance of management as a driver was consistent across the two methods, fisher knowledge increased slightly in relative importance on the basis of GLM results while markets declined (Table. 6.4).

Table 6.4 The relative importance of extrinsic first-order predictors as drivers of fishery status. Indicators are ordered high to low importance on the basis of $wAIC_c$ (derived from a generalised linear model) and are compared with the rank of indicator importance determined by expert weighting (Table 6.2).

First-order extrinsic indicator	wAIC _c	Expert weighting rank
Management	1.00	1 st
Fisher knowledge	0.94	3 rd
Accessibility	0.52	4 th
Technology	0.30	5 th
Markets	0.29	2 nd

6.4. Discussion

Information on exploitation status and key drivers of fishing pressure is critical for management but typically lacking in the data-poor context of coral reef fisheries (Johannes 1998; Grüss et al. 2014a; van Overzee & Rijnsdorp 2015). Spawning aggregation fisheries are no exception, yet advice is often urgently required as depletion can be rapid and irreversible (Sadovy & Domeier 2005; Russell et al. 2012). In response, this study developed a bivariate framework to assess risk of overfishing in these fisheries. Combining intrinsic and extrinsic vulnerability indices, the tool was applied to a global selection of data-poor spawning aggregation fisheries. Fisheries varied extensively in their vulnerability to overfishing with the highest risk observed for grouper spawning aggregation fisheries, especially a subset of Indian Ocean fisheries that supply the live reef food fish trade. By comparison, the risk of overfishing was lower in most fisheries and experts were optimistic that conditions were improving in certain fisheries as a result of management interventions or changes to other drivers. The findings highlight that management, considered the most influential extrinsic indicator of vulnerability to overfishing, can be effective in rebuilding populations and avoiding fisheries collapses. However, in addition to commonly applied measures that protect spawning sites (e.g. marine reserves) or periods (e.g. seasonal bans on take), a range of other

levers appear successful in reducing the risk of overfishing, including controls on gear, fishing effort and catch. Importantly, the bivariate approach adopted here allows for spawning aggregation fisheries to be assessed as complex socio-ecological systems, which recognises that risk of overfishing is also fishery-specific rather than predetermined entirely by species biology and behaviour.

Based on intrinsic indicators derived from life history and behavioural traits, univariate approaches for assessing extinction risk in coral reef fishes have influenced conservation policy and agenda (Jennings et al. 1999; Cheung et al. 2005; Graham et al. 2011; Abesamis et al. 2014). However, the lack of fisheries-specific information can limit their practical application. Incorporating catchability and socioeconomic drivers of fishing pressure focuses attention on how fisheries act on these intrinsic traits and can assist communities, conservation practitioners and fisheries managers in identifying levers for intervention. Nonetheless, for risk assessment tools to support management, robust examination of their predictive ability is required (Patrick et al. 2010). This can be problematic for the same reason that underpins their development, namely the lack of independent, fishery-specific data on status or trends with which to compare vulnerability scores derived from the tools. If tools are for general fisheries applications, then predictive ability can initially be examined in data-rich contexts (e.g. PSA; Patrick et al. 2010). This avenue was not available in the notoriously data-poor context of coral reef spawning aggregation fisheries.

6.4.1. Predictive ability

As expected, the intrinsic vulnerability index was positively related to the fishing vulnerability index of Cheung et al. (2005). Since that index was improved for coral reef fishes when information on spawning aggregation behaviour was included (Cheung et al. 2005), this finding bodes well for the predictive power of the intrinsic vulnerability

component of our tool given that it refined spawning behaviour in terms of aggregation type, density changes and duration. Unexpected was the finding that the fishing vulnerability index, which is species-specific, also related to Euclidean distance (i.e. overall vulnerability to fishing). This is likely due to the influence of the relationship between the intrinsic index and fishing vulnerability index, and is a spurious result in that the latter should not relate to specific fisheries.

In terms of the extrinsic index an ability to predict 'no overfishing' status contrasted with an inability to predict 'overfishing' status. This may stem from the fact that extrinsic indicators were scored in terms of the current context of fisheries, yet historic effects of fishing were also exhibited in the status indicators used for most of the assessed fisheries, notably abundance, biomass and size-related trends. Especially where recruitment overfishing has occurred (Hilborn & Walters 1992), biomass, abundance (or CPUE) or fish size may still be declining even though current fishing pressure, for which the extrinsic index serves as a proxy, is low. By contrast, fisheries for which status indicators suggest stable or increasing trends (i.e. 'no overfishing') are less likely to be currently subjected to high fishing pressure, unless interventions or socioeconomic changes that led to stability or rebuilding have only recently reversed and depletion has not yet been detected. This highlights the importance of a dynamic approach to risk assessment tools, considering current conditions in the fishery but also asking experts to anticipate future directions of fishing pressure based on emerging changes in, for example, management or markets. Thus, in our study, many of the fisheries for which fishing pressure is currently low warrant enhanced monitoring and improved management since experts perceived a worsening of fishing pressure.

6.4.2. Key risk factors and drivers of vulnerability to overfishing

Expert weighting identified spawning aggregation type as a key risk factor. This finding supports widely held concerns regarding the high risk of overfishing in species that form highly predictable aggregations at few spawning sites per population (Sadovy de Mitcheson & Erisman 2012). Density and duration of spawning aggregations, the other spawning behaviour risk factors assessed, typically correlate with aggregation type and predictability (Domeier & Colin 1997). Consequently, they play an important role in the potential for density-dependent catchability once predictability has allowed for the acquisition of knowledge and development of a targeted fishery. Productivity indicators were weighted even more highly than those relating to spawning behaviour. Experts therefore converged on the fact that, regardless of spawning behaviour, the capacity of populations to recover from depletion is a critical risk factor (Jennings et al. 1999; Dulvy et al. 2004; Hobday et al. 2011). However, spawning aggregation type also correlates with productivity since the spatial and temporal extent of spawning, which varies widely among resident and transient aggregation spawners, influences the stock-recruitment relationship (Maunder & Deriso 2013). Indeed, the lack of recovery of many extirpated spawning aggregations (Sadovy de Mitcheson & Erisman 2012) may result from the strong interrelationship between the stock-recruitment relationship and the distribution of spawning.

In serving to clarify management objectives and interventions, the identification of risk factors and key drivers of fishing pressure is an important outcome of risk assessment frameworks. For example, the rabbitfish *S. sutor* is a relatively productive species (Robinson et al. 2011) and a high risk of overfishing typically stemmed from a lack of fisheries management rather than other extrinsic factors. By contrast, conservation objectives and protection of spawning site come to the fore in species of very low productivity and for which spawning is spatially and temporally limited (Myers et al. 1999; Maunder & Deriso 2013),

especially if most fishing mortality is derived from aggregation fishing (Sadovy & Domeier 2005; Grüss et al. 2014a). Opening grouper fisheries to the live reef food fish trade should also be carefully monitored and controlled given the risks of overfishing observed in this study and by other authors (Sadovy 2005; Aumeeruddy & Robinson 2006). Most assessed fisheries remain small-scale and the use of highly efficient gears, the key technology risk factor identified by expert weighting, was uncommon. In some countries, measures to prohibit highly efficient and destructive gears, such as trawls and nets, were made only after their negative impacts were obvious (Koenig et al. 2000; Aguilar-Perera 2004; Claro et al. 2009), whereas policies to prevent their introduction are clearly preferable.

Other extrinsic indicators provide less immediate levers for intervention, such as accessibility to spawning sites in terms of distance, depth or environmental conditions. However, technology gains can overcome certain environmental constraints and should be monitored (Coleman et al. 1999). For example, strong currents that limit the efficiency of current gears for *E. guttatus* and *S. sutor* spawning aggregations in the US Virgin Islands and Seychelles, respectively, would be less likely to limit effective use of gill nets or towed gears. Likewise, fisher knowledge was an important driver of spawning aggregation status but is beyond the remit of management, though efforts aimed at maintaining rights-based structures such as customary tenure may prevent the spread of knowledge (Hamilton et al. 2004).

In terms of results from both the AHP and GLM, the management context of fisheries was the key extrinsic (first-order) indicator of vulnerability to overfishing. Expert weighting unsurprisingly recognised that protection of spawning aggregations using marine reserves or seasonal bans conferred the lowest risk of overfishing. Constituting conservation interventions that aim to close spawning aggregation fisheries, their design or compliance were inadequate in many locations and populations remained exposed to a degree of aggregation fishing. Community-based or co-management of conservation measures for spawning aggregations

may promote compliance (Almany et al. 2010; Hamilton et al. 2011), but communities should be aware that losses in yield following closures may not be recovered (Grüss et al. 2014b). Moreover, management measures limiting gears, fishing effort and catches at spawning aggregations are also being applied to prevent overfishing and rebuild fisheries (e.g. snapper fisheries in Cuba, the *Pagrus auratus* fishery in Western Australia and the *Paralabrax nebulifer* fishery in California). While the improving status or perceived fishery direction for many assessed fisheries hints at an effective toolbox for managing spawning aggregation fisheries, externalities such as increases in fuel prices were considered important by experts in some cases (e.g. US Virgin Islands and Belize).

6.4.3. Caveats and further refinement of the risk assessment tool

Reviews of spawning aggregation fisheries generally converge on the finding that anything other than limited subsistence fishing or occasional harvest is unlikely to be sustainable, primarily due to uncertainties regarding risks of overfishing and indirect (i.e. non-lethal) effects of fishing (Sadovy & Domeier 2005; Russell et al. 2012). The fisheries examined in this study were recreational and commercial rather than for subsistence and tended towards species with high intrinsic vulnerability, yet there was a large variation in terms of risk of overfishing. However, risk of overfishing does not equate to sustainability. Very few of the assessed spawning aggregations fisheries were considered by experts to be adequately managed while fishing pressure is increasing in many developing country regions (Worm & Branch 2012). A greater emphasis on integrating spawning aggregations in fisheries management planning is necessary, especially for fisheries less intrinsically at risk from overfishing.

The framework and indicators would benefit from wider examination across a broad range of fisheries contexts. Since tests of predictive ability relied on status indicators that varied in

their robustness or relevance (e.g. CPUE: Harley et al. 2001; catch: Branch et al. 2011), it would be useful to test the framework on temperate spawning aggregation fisheries for which exploitation status is less uncertain. Once better understood, more factors that relate to the indirect effects of fishing could also be developed as indicators, for example, the impacts of gears on mating behaviour.

6.4.4. Concluding comments

The discourse concerning spawning aggregation fisheries has generally focused on the challenges they pose for fish population persistence. Perceptions of sustainability have undoubtedly been influenced by the collapse of spawning aggregation fisheries for species that are highly vulnerable to overfishing in terms of both intrinsic traits (e.g. low productivity) and extrinsic pressures (e.g. high value) (e.g. groupers: Sadovy de Mitcheson et al. 2013). Further support for a conservation imperative stems from the data-poor context of coral reef fisheries, which has justified calls for data-less approaches such as marine reserves (Johannes 1998). However, spawning aggregation fisheries vary in their risk of overfishing (Robinson et al. 2011; Tobin et al. 2013) and a wide range of levers can be applied to control fishing pressure (Russell et al. 2012; Grüss et al. 2014b; Robinson et al. 2015). Thus, while aggregating behaviour usually predisposes populations to density-dependent catchability, fishing pressure will be determined by factors that influence catchability and the socioeconomic drivers of fishing effort. A greater emphasis on developing management plans for aggregation fisheries is therefore warranted, comprising measures such as gear, fishing effort or catch controls in combination with spatial or seasonal restrictions. In allowing for vulnerability to overfishing to be assessed in terms in multiple intrinsic risk factors and drivers of fishing pressure, the framework presented here can support both conservation and management planning in the data-poor context of coral reef spawning aggregation fisheries.

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Chapter 7: General discussion

Human societies have long exploited animal aggregating behaviour related to reproduction, feeding and migration as well as to other functions such as predator evasion (Parrish 1999; Wilcove & Wikelski 2008). From the interception of migrating aggregations of large mammals (Harris et al. 2008; Wilcove & Wikelski 2008) and birds (Stanton 2014) in terrestrial systems to the targeting of nesting aggregations of turtles (Frazier 1980) and seabirds (Hasegawa & DeGange 1982) in marine systems, high rates of exploitation were predicated by accessibility to concentrations of animal populations that were typically predictable in time and space. Throughout history, fishing gears and practises have developed to exploit schooling and aggregating behaviour of fishes (Parrish 1999) and the dramatic industrialisation of fisheries in the past century was founded upon gears such as trawls and purse seines that could efficiently exploit concentrations of resources (Pauly et al. 2002). While many of these once abundant populations have collapsed or been extirpated, others have not. This highlights the need to identify key factors that predispose aggregating populations to overexploitation. For instance, among aggregating marine fishes, value is an important factor contributing to a risk of overexploitation (Collette et al. 2011; Sadovy de Mitcheson et al. 2013) and it has proven particularly difficult to modify economic incentives when resource value rises with levels of scarcity (Hall et al. 2008). The identification of management solutions for fisheries that exploit aggregating behaviour must, therefore, be grounded on a broad range of biological and socioeconomic disciplines.

Given the historical context, it is not surprising that an increasing body of evidence highlights that targeted fishing of coral reef fish spawning aggregations can result in decline and loss of aggregations, rapid population depletion and fishery collapses (Aguilar-Perera 2006; Matos-Caraballo et al. 2006; Table 1.1). Yet, there are also examples of spawning aggregation

fisheries that are managed sustainably or have persisted for decades in spite of an absence of regulatory control or conservation measures (Sadovy & Domeier 2005; Claro et al. 2009; Robinson et al. 2011; Jackson 2012; Table 1.1). The fact that spawning aggregation fisheries vary widely in their vulnerability to overfishing is often overlooked, which can lead to a very narrow set of management tools being applied. For example, recommendations for full protection of spawning sites using no-take reserves are sometimes made when the fishery is not at risk of overfishing, which ignores a wider range of tools that could be applied to meet community, conservation or management objectives. This thesis aimed at improving our understanding of the causes of vulnerability to overfishing in these fisheries, framed by a conceptual approach that integrated the roles of biology, fish and fisher behaviour, and the socioeconomic and cultural context in which the fisheries operate. An understanding of the causes of vulnerability to overfishing is required if a broader range of societal objectives and management interventions for spawning aggregation fisheries are to be considered.

The findings of this thesis suggest that both dependency on fishing and customary tenure influence how knowledge of spawning behaviour is distributed and used among fisher communities to develop targeted spawning aggregation fisheries (Chapter 2). If a fishery develops, then the contribution of spawning aggregation exploitation to annual fishing mortality rates will depend on the extent to which fish population density changes with aggregation formation, and the relationship between these density changes and vulnerability to capture (i.e. whether or not density-dependent catchability operates) (Chapters 2 and 3). However, the findings from this thesis demonstrate that catchability is also influenced by environmental conditions (e.g. currents, Chapter 3), the targeting behaviour of fishers (Chapter 2), concentration of fishing effort and gear saturation (Chapter 4), and species selectivity of the gears at multispecies spawning aggregation sites (Chapter 4). These findings have clear implications for conservation and management. For instance, the efficacy of

seasonal restrictions or closures that limit access to aggregations for part of the spawning season will depend on whether their timing aligns with environmental conditions favourable or unfavourable to catchability (Chapters 3 and 5). Moreover, the effects of marine reserves on fisheries yields and population biomass were also found to be highly dependent on changes to catchability between spawning and non-spawning periods, to a greater degree than differences between species in terms of life history or sexual pattern (Chapter 5). Spawning aggregation fisheries vary in their vulnerability to overfishing, with species productivity and type of spawning aggregation identified as key intrinsic risk factors, while fisher knowledge, markets and particularly management context were key drivers of fishing pressure. In addition to marine reserves, fisheries management interventions such as gear, fishing effort and catch controls can also stabilise or rebuild spawning aggregation fisheries (Chapter 6). To enable a broader approach that considers both socioeconomic and biological objectives, spawning aggregation behaviour should therefore be fully integrated in management planning.

This chapter aims to (1) frame the findings of the thesis within the wider literature in order to identify the key causes of vulnerability to overfishing and their implications for managing spawning aggregation fisheries, and to (2) propose research gaps and future directions for studying these complex fisheries.

7.1. Key causes of vulnerability to overfishing in spawning aggregation fisheries

To address the goal of this thesis and identify causes of vulnerability to overfishing, it is first necessary to address a popular misconception concerning the risks that fishing on spawning aggregations pose for sustainability. It is often asserted that spawning aggregations must not be exploited since fish are usually caught prior to gamete release (Johannes 1998; Rhodes & Warren-Rhodes 2005). However, many aggregating reef fishes are relatively long-lived and

highly fecund and it matters little to an individual's lifetime egg production whether it is caught prior to, during or after spawning in a particular month. Of primary importance for population persistence is that fishing mortality rates are sustainable and do not overly truncate population age structure (Berkeley et al. 2004a; Botsford et al. 2004). Consequently, a more important issue is the extent to which aggregating behaviour associated with spawning exposes populations to higher rates of fishing mortality. This depends on changes to catchability associated with aggregation formation and the fishing effort directed at aggregations (Robinson et al. 2011; Sadovy de Mitcheson & Erisman 2012; Tobin et al. 2013). This thesis focused on these critical factors and their implications for management.

Relating to important fisheries concepts such as selectivity, efficiency, behaviour and vulnerability, catchability is an elusive but critical parameter for fisheries assessment and management (Arreguín-Sánchez 1996). Given that catchability often exhibits density-dependence (Wilberg et al. 2010), it is surprising that assumptions and implications of this parameter are rarely examined explicitly in the context of coral reef spawning aggregation fisheries, which by definition are based on large (at least 3-4 fold) changes to population density (Domeier & Colin 1997). The few studies that have addressed catchability demonstrate its importance for both assessment (Erisman et al. 2011) and management (Grüss et al. 2014b; Grüss & Robinson 2015). The findings of this thesis further highlight the importance of understanding the effects of catchability in spawning aggregation fisheries.

In the first instance, spawning aggregations are migratory and ephemeral events, requiring acquisition or sharing of knowledge on their location and timing as a precursor to fisheries development. While socioeconomic and cultural context influence how fishers acquire or share knowledge, factors such as dependency on fishing influence fishing strategies and the amount of effort in the fishery (Chapter 2). High levels of variability in both fisher knowledge and status among fisheries are therefore likely a reflection of the highly localised and complex

socioeconomic and cultural contexts in which spawning aggregation fisheries develop (Hamilton et al. 2004; Robinson et al. 2004; Samoilys et al. 2006; Sadovy de Mitcheson et al. 2008). However, where knowledge and demand for aggregating species exist, the status of spawning aggregation fisheries will also depend on aggregating behaviour and the extent to which catchability exhibits density-dependence (Chapter 3). With the exception of some extreme cases where the population is primarily accessible to the fishery during the spawning season (e.g. Nassau grouper fisheries; Claro et al. 2009), annual catches may not be dominated by fish taken from spawning aggregations, particularly if environmental factors (Chapter 3), multispecies competition and gear selectivity (Chapter 4) depress catchability at spawning sites. Weather and strong currents may inhibit the efficiency of fishing at spawning sites and constrain fishing effort, offering a degree of protection if they prevent access to the sites (Chapter 6; Hamilton 2003; Matos-Caraballo et al. 2006). Given that spawning sites are often located in exposed and high current environments (Pet et al. 2005; Heyman & Kjerfve 2008; Sadovy de Mitcheson & Colin 2012), overlooking the impacts of environmental conditions on fishing may overestimate risks. Catchability may also exhibit effort-dependence and vary with fisher behaviour in terms of density of fishing effort (Chapter 4). In addition to density-dependence and the many other factors that cause catchability to vary, it is perhaps unsurprising that the relationship of CPUE to population abundance is likely to be weak or absent, potentially giving rise to hyperstability (Chapter 4; Hilborn & Walters 1992; Erisman et al. 2011). Catchability is clearly highly dynamic in spawning aggregation fisheries, with sources of variation observed in the thesis common to many fisheries (Stoner 2004; Wilberg et al. 2010). It is therefore necessary to consider multiple factors that influence catchability when assessing the risks of overfishing in spawning aggregation fisheries. This thesis makes a novel contribution by developing a marine reserve model (Chapters 3 and 5) and an indicatorbased risk assessment framework for spawning aggregation fisheries (Chapter 6), both of which incorporate key factors that can cause catchability to vary.

Our understanding of the importance of catchability-related processes, such as effortdependence, would benefit from examination of this parameter across a wider selection of spawning aggregation fisheries than those examined here. For example, the relationship between catch rates and abundance is ideally examined where large gradients in the latter exist. By broadening the geographical and fisheries scope, it will eventually be possible to rank species in terms of their vulnerability to a range of gears and fishing practises. An additional constraint stemmed from the fact that large sample sizes were difficult to achieve for spawning aggregation fisheries in the time-span of a doctoral thesis. Having identified their importance, the measurement of key fisheries parameters in long-term monitoring programmes is therefore warranted to address this constraint. The relative costs and benefits of marine reserves identified in this thesis are also sensitive to assumptions of the theoretical per-recruit model applied. Consequently, my findings on the relative importance of catchability may shift in relation to other parameters if a stock-recruitment relationship were included in further applications of the model, or if assumptions regarding sex change processes are challenged. The application of the indicator-based assessment framework to other fisheries would also help validate key drivers and risk factors in spawning aggregation fisheries. Moreover, my thesis primarily provided evidence for the development of indicators relating to catchability (i.e. fisher knowledge, technology, accessibility) and further empirical studies on how markets and governance context influence fishing effort are a priority.

Critically, the application of indicator-based risk assessments focuses attention on questions regarding the sustainability of spawning aggregation fisheries. Are coral reef fish spawning aggregation fisheries sustainable? This question has been posed for a number of reviews, which generally converge on the finding that anything other than limited subsistence fishing

or occasional harvest is unlikely to be sustainable, primarily due to uncertainties regarding risks of overfishing and indirect (i.e. non-lethal) effects of fishing (Sadovy & Domeier 2005). Perceptions of sustainability have undoubtedly been influenced by the decline and collapse of spawning aggregation fisheries for groupers and snappers characterised by slow life histories (Aguilar-Perera 2006; Matos-Caraballo et al. 2006; Claro et al. 2009; Table 1.1). However, since reviews indicate that a limited degree of fishing mortality has allowed for the persistence of spawning aggregation fisheries, fisheries management objectives should not necessarily be discounted in favour of spawning site closures. For example, findings of this thesis show that closing spawning sites to fishing may be less efficient for securing population persistence and fisheries yield than closing other habitats (Chapters 3 and 5). Moreover, fisheries management and changes to other socioeconomic drivers can reverse the trajectory of spawning aggregation fisheries to more sustainable levels of exploitation (Chapter 6). Thus, the fundamental issue is not whether spawning aggregation fisheries are sustainable, but how to limit fishing mortality to levels that do not lead to recruitment overfishing and aggregation loss given the poor prognosis for recovery following collapses in these fisheries (Sadovy de Mitcheson & Erisman 2012; Maunder & Deriso 2013).

It is important to recognise that an emphasis on fisheries management rather than conservation does not preclude protection of spawning sites using marine reserves or other measures. If recruitment overfishing and aggregation extirpation have not occurred, then closing spawning sites can be effective in rebuilding aggregations and biomass (Chapter 5; Nemeth 2005; Heppell et al. 2006; Grüss et al. 2014a). Once rebuilt, sustained or periodic harvest may be managed using catch limits (Chapter 4; Jackson 2012). Although our understanding of target and limit reference points by which to set effort or catch limits remains a major challenge given uncertainties regarding the indirect impacts of fishing (Dean et al. 2012), adaptive management involving periodic rebuilding and revision of reference

points can mitigate for this constraint (Chapter 4). Moreover, while lack of compliance and information requirements are frequently cited as barriers to fisheries management (Johannes 1998; Sadovy de Mitcheson and Erisman 2012), these are also challenges to the efficacy of conservation tools such as marine reserves (Botsford et al. 2009; Le Quesne 2009; Mangubhai et al. 2011; Grüss et al. 2014b). A more nuanced and broader approach to conservation and management is therefore required, especially since the benefits of spawning site reserves, the dominant conservation tool, are also dependent on exploitation status (Grüss et al. 2014a; van Overzee & Rijnsdorp 2015).

Knowledge of exploitation status is typically absent for spawning aggregation fisheries and highlights the importance of indicator-based approaches for assessing risks posed by aggregation fishing (Chapter 6). While extinction risk in coral reef fishes has been assessed on the basis of intrinsic indicators derived from life history or behavioural traits (Jennings et al. 1999; Cheung et al. 2005; Abesamis et al. 2014), the adopted bivariate approach offers advantages for local management interventions. The addition of the extrinsic component, which is increasingly common to risk assessment approaches in fisheries (Patrick et al. 2010; Williams et al. 2011), explicitly addresses how fishing (i.e. extrinsic indicators) acts on intrinsic traits and incorporates the socioeconomic context of fisheries, which can help identify levers for management interventions. The fisheries examined in Chapter 6 were recreational and commercial rather than exclusively for subsistence. Nonetheless, there was large variation among them in terms of the risk posed by aggregation fishing, which probably reflects recent documentation of sustainability in some spawning aggregation fisheries (Robinson et al. 2011; Jackson 2012; Tobin et al. 2013; Table 1.1). Fishery scores derived from the indicator-based tool that indicate low or high risk of overfishing do not, however, equate to sustainability. Further management intervention is likely required in all cases, but a wide range of objectives and interventions are available depending on key risk factors and drivers of fishing pressure. For example, in the case of the *S. sutor* trap fishery of Seychelles, vulnerability to overfishing stems from unmanaged fishing effort rather than life history or spawning behaviour (Chapter 6). At the other extreme, the very high risk of overfishing in the *Epinephelus lanceolatus* fishery of Zanzibar derives from both intrinsic and extrinsic factors (Chapter 6). Species of such low productivity cannot sustain heavy exploitation (Myers et al. 1999) and many require a management focus on spawning aggregations since they are rare in catches outside of the spawning season (Robinson et al. 2011; Grüss et al. 2014a). Conservation objectives come to the fore in such fisheries, especially where spawning aggregations have been extirpated and fisheries have collapsed.

7.2. Research gaps and future directions

Spawning aggregation fisheries as socio-ecological systems. Coral reef spawning aggregation fisheries have developed in most regions of the tropics and encompass a broad spectrum of life history traits, aggregation types, sexual patterns and trophic ecologies (Sadovy de Mitcheson et al. 2008). Ranging from small-scale subsistence to highly commercial fisheries with integration in global seafood trades (Almany et al. 2010; Sadovy de Mitcheson et al. 2013; Tobin et al. 2013; Bejarano Chavarro et al. 2014), it is unsurprising that spawning aggregation fisheries are complex socio-ecological systems requiring a case-by-case approach to address issues of sustainability. An emphasis on behavioural ecology (e.g. site fidelity) and monitoring of aggregation indicators (e.g. density, fish size) has defined much of the early research effort, with less focus on studying fisheries and in particular the social, economic and cultural drivers of fishing pressure. Unmanaged commercialisation of fisheries through improved market integration is a primary driver of reef fish biomass in general (Cinner et al. 2013) and has led to overexploitation in spawning aggregation fisheries (Claro et al. 2009;
Granados-Dieseldorff et al. 2013). Increases in catchability ensure that spawning aggregation fisheries can result in gluts of fish supply, leading to seasonal decreases in unit price or increases in wastage. While this may limit spawning aggregation fisheries, market integration and expansion of infrastructure such as cold storage capacity or ports, many of which are linked to development aid interventions, can overcome these commercial constraints and increase fishing effort (Sadovy de Mitcheson & Erisman 2012). However, even if fisheries persist for subsistence, fishing effort can also reach unsustainable levels (Olsen & LaPlace 1979; Rhodes & Sadovy 2002; Phelan et al. 2008; Claro et al. 2009) and may go unmonitored if fisheries data collection is primarily for the commercial sector (Rhodes & Tupper 2008; Russell et al. 2012). Consequently, the management of spawning aggregation fisheries would benefit from more holistic approach, embedded within a socio-ecological systems framework to address drivers of fishing effort (Cinner et al. 2009).

The role of catchability. Basic knowledge on how catchability varies in spawning aggregation fisheries can be informative for assessment and monitoring. The thesis has demonstrated a complex relationship between catchability, CPUE and spawning aggregation behaviour. For example, in Chapter 4, CPUE was relatively insensitive to gradients in aggregation abundance, which highlights the need for caution in using catch rates to monitor aggregation status. CPUE hyperstability may occur at the level of a single spawning site by a similar mechanism that underpins the basin model of MacCall (1990), where population range collapses into preferred habitat as population abundance diminishes. Likewise, when abundances are depleted by fishing, spawning aggregations (and their fisheries) may contract and only occupy the core spawning or courtship zones, reducing the areal extent of aggregations but maintaining core densities (Robinson et al. 2008; Nemeth 2012). Fine-scale processes of spawning aggregation collapse and CPUE hyperstability are an area requiring

further investigation, especially in locations where larger gradients in aggregation abundance are present (e.g. Pohnpei; Rhodes et al. 2014)'.

Understanding patterns in catchability also offers numerous insights regarding potential management solutions for spawning aggregation fisheries. Changes in catchability are particularly important for comparing the costs and benefits of implementing marine reserves (Chapter 5; Fulton et al. 1999; Grüss et al. 2014a), but also inform decisions regarding the efficacy of alternative measures (Chapters 4 and 5; Erisman et al. 2014). Technological change such as the introduction of larger boats, GPS and efficient gears can increase both fishing effort and catchability at spawning sites (Coleman et al. 1999; Claro & Lindeman 2003; Aguilar-Perera 2006), highlighting the importance of addressing capacity and technology creep in management. Since catchability is gear-specific (Arreguín-Sánchez 1996) it may constitute an effective lever for reducing fishing mortality using gear-based controls (e.g. bans on highly efficient gears; Claro et al. 2009) where effort reduction or catch limits are impractical (Chapter 4). In small-scale fisheries where dependency on fishing for livelihoods and food security is high, gear-based controls are often preferable to other measures (McClanahan et al. 2013). Nonetheless, the application of measures other than spawning season sales bans and spatial closures remains rare in spawning aggregation fisheries (Sadovy de Mitcheson et al. 2008). This situation probably reflects the strong support for spatial closures in coral reef systems generally (Mora et al. 2006), while deficiencies in fisheries management and the data-poor context of spawning aggregations fisheries have been used to justify marine reserves as a data-less management solution (Johannes 1998). Given their potential socio-economic impacts, reserves should not be viewed as a data-less solution. Local communities need to be informed on the costs and benefits of marine reserves relative to other measures (Chapter 3 and 5; Grüss et al. 2014a, b) and empowered to participate in the identification and implementation of management

solutions for their context. Further empirical and theoretical research on the costs and benefits of managing spawning aggregations fisheries using a wide range of measures is therefore required.

Indirect effects of fishing. This thesis has argued that the assessment and management of spawning aggregation fisheries must, in the first instance, account for how patterns catchability and the distribution of effort determine the direct impacts of aggregation fishing (i.e. fishing mortality). However, the sustainability of spawning aggregation fisheries remains an important research topic due to uncertainties regarding the indirect effects of fishing on fertilisation success and recruitment processes. These effects are potentially numerous, as identified by other authors (Sadovy de Mitcheson & Colin 2012). Theoretical studies on marine reserves have attempted to incorporate the potential for female-bias in sex ratio to impact fertilisation success in protogynous species (Heppell et al. 2006; Ellis & Powers 2012), yet empirical evidence for sperm limitation is lacking and thresholds remain unknown (Grüss et al. 2014a,b). Moreover, the same impacts can also emerge from size-selective fishing in the absence of a spawning aggregation fishery, while gonochoristic species are also vulnerable to overfishing given maternal age effects (Berkeley et al. 2004b). Fishing gear impacts to mating behaviour have been shown in cod (Dean et al. 2012) but are yet to be studied in coral reef contexts, where gears are often diverse and will vary in their impacts. The indirect effect of habitat degradation on fertilisation success is also uncertain, including impacts caused by gears (Koenig et al. 2000) or natural disasters such as cyclones (Robinson & Samoilys 2013). What is certain is that the validity of stock assessments and management advice can be challenged if they do not compensate for the indirect effects of fishing aggregations as well as fishing mortality.

Distribution of spawning and recruitment. Understanding the role of the spatial and temporal extent of spawning for recruitment is a critical research gap (Berkeley et al. 2004a; Maunder

& Deriso 2013). Indeed, the lack of recovery of many extirpated spawning aggregations (Sadovy de Mitcheson & Erisman 2012) may result from the strong interrelationship between the stock-recruitment relationship and the distribution of spawning (Maunder & Deriso 2013). Both direct (e.g. decline and extirpation of spawning sites) and indirect (e.g. disruption of spawning) impacts of fishing can influence fertilisation rates and recruitment processes. However, further examination of stock-recruitment relationships is critical for aggregating spawners in coral reef contexts since the concentration of spawning in space and time is far greater than assumptions modelled to date (Maunder & Deriso 2013). Subsequently, the findings of such research may require that we revise our management or conservation approach to these fisheries. For example, the implications of Maunder & Deriso (2013) suggest that it is better to harvest all spawning aggregation sites sustainably rather than to fully protect a few and allow the remaining sites to be lost due to unmanaged exploitation.

Assessment in data-poor contexts. An increasing number of data-poor tools have been applied to spawning aggregation fisheries (Erisman et al. 2014; Grüss et al. 2014a). The approach taken in this thesis was to apply modified versions of existing tools (PSA: Chapter 2; per recruit model: Chapters 3 and 5), but also to develop a novel framework for data-poor assessment (Chapters 6). Indicators developed in Chapter 6 would, however, benefit from wider testing and examination across a broad range of fisheries contexts. Once better understood, more factors that relate to the indirect effects of fishing could also be developed as indicators. For example, while size selectivity and habitat impacts were incorporated in Chapter 6, the indirect impacts of fishing on mating behaviour was not and could potentially be investigated for a range of gear types. Indicator-based tools also require validation of their ability to predict status (Cheung et al. 2005), which is undermined for the very reason that underpins their development, namely the absence of independent information on status. This is particularly problematic if an extrinsic component is considered since status information for testing must be specific to the fishery. Independent estimates of exploitation status were only known for four (of the 36) fisheries assessed by the indicator-based tool, and also varied in the stock assessment method applied. Testing predictive ability therefore relied on employing status indicators that vary in their robustness or relevance, such as trends in catch or catch rates that can be affected by changes to catchability and targeting behaviour (Harley et al. 2001; Branch et al. 2011). A greater emphasis on developing and testing data-poor tools for spawning aggregation fisheries is therefore needed (Erisman et al. 2014).

7.3. Concluding comments

This thesis has provided an interdisciplinary perspective on the causes of vulnerability to fishing in coral reef fish spawning aggregation fisheries. The diversity of life history traits and spawning behaviour exhibited by aggregative spawners ensure that biological responses to aggregation exploitation will vary extensively among populations. Catchability and socioeconomic drivers of fishing pressure, which also vary in time and among fisheries, serve as the critical factors and lever points for conservation and management. However, the dynamics of fisheries and their socioeconomic context are often overlooked in spawning aggregation research, which can result in narrow recommendations for protection using reserves or spawning season fishery closures. A growing evidence base, including findings presented in this thesis, indicates that commercial spawning aggregation fisheries can be rebuilt and sustained to meet biological and socioeconomic objectives using alternative approaches. This is not to suggest that conservation approaches aimed at preventing exploitation of spawning aggregations are redundant. Rather, a more holistic approach that considers both biological and socioeconomic objectives is required, informed by cost and benefit analysis of a broad range of management options. Given that fishing mortality

experienced by fish populations is rarely exclusive to exploitation of their spawning aggregations, efforts to manage these fisheries should be embedded within wider fisheries management planning. This thesis identifies important parameters, drivers and mechanisms that influence how humans interact with these biological phenomena, and develops novel assessment tools for examining vulnerability to fishing and the effects of marine reserves. Therefore, my thesis contributes to our understanding of how spawning aggregation fisheries can be managed to protect critical biological function while offering opportunities for sustaining the significant socioeconomic benefits that these fisheries can provide.

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Appendix A: Supplementary Information for Chapter 3

A1. Estimating current strength

Current strength was derived from OSCAR (Ocean Surface Current Analyses – Real time; <u>www.oscar.noaa.gov</u>), which generates 5-day mean estimates of near-real time ocean surface current strength from satellite altimeter and scatterometer data, validated by mooring buoys and drifters. Data resolution was 1/3 degree, approximating to the scale of Praslin and surrounding areas of plateau on which the spawning site resides. Current speed data were extracted for the period 1st January 2013 to 31st December 2014, and standardised to an index of 0-1. Indexed current strength for 5-days periods corresponding to our survey dates were obtained from this data. Previous studies measured currents at the spawning site using an *insitu* current meter deployed on the seabed, finding that tidal forcing was a strong determinant of current speed at the site (C. Gerry, unpublished report).

A2. Management implications: estimating catchability and size at capture

Management implications of findings of the present study were examined in terms of the relative effects of spawning site reserves or non-spawning habitat marine reserves on yield-per-recruit (exploitable biomass) and spawning stock biomass-per-recruit. Specifically, we updated the marine reserve model of Grüss and Robinson (2015) with estimates of catchability and size at recruitment to the fishery derived from the present study.

Estimating catchability

The change in catchability between spawning and non-spawning habitat is a key parameter in the marine reserve model of Grüss and Robinson (2015). Catchability (q) is defined as the proportion of the stock or population abundance caught by a single unit of fishing effort:

$$q = \frac{Ut}{Nt}$$

where *Ut* is CPUE at time *t* and *N* is population abundance at time *t* (Ricker 1940; Arreguín-Sánchez 1996).

Estimating absolute abundance (*N*) for *Siganus sutor* spawning aggregations from visual census is problematic, due to the size, mobility and number of schools that form at the spawning site, which is further confounded by the turnover of aggregations, as fish constantly arrive, spawn, and depart the site (Bijoux et al. 2013). Therefore, we used mean CPUE (*U*) and the abundance of the population from non-spawning habitat to derive an absolute value of *q* in non-spawning habitat (q_{ns}). The ratio of mean spawning CPUE (7.421 fish.trap-hr⁻¹) to non-spawning CPUE (1.724 fish.trap-hr⁻¹) was then used as a multiplier of non-spawning *q* to obtain an estimate of *q* in spawning habitat (q_{s}).

Population abundance (N) in the non-spawning habitat was estimated by raising a mean density estimate, derived from underwater visual census (UVC) at 12 sites, to the total area of the SW Praslin fringing carbonate reef. For each of the 20-minute timed swims in non-spawning habitat that were used to estimate MaxN (see the Methods section), the distance swam was also measured. Using a video transect width of 7 m, the survey area was then calculated for each site. School size and densities were amenable to absolute counts (rather than MaxN) in non-spawning habitat, and the potential for double counting was mitigated by much lower fish mobility compared to the spawning site. Counts of *S. sutor* were obtained from the video footage and averaged across sites to obtain mean density (no. of fish.m²). The area of the SW Praslin fringing reef was estimated in ArcGIS from a carbonate reef layer for the inner islands of Seychelles.

Two important assumptions were required in adopting this approach. Firstly, we assumed that aggregations at the spawning site primarily comprise the population from the non-spawning habitat of the SW Praslin fringing reef, where fishing and visual census surveys were conducted. Secondly, it was assumed that the population was at equilibrium throughout since spawning CPUE (November 2013-March 2014) and non-spawning CPUE (April and May 2014) did not overlap in time. Evidence for the first assumption stems from a number of sources, including conventional tagging results and observations of pre-spawning aggregations at, and migration from, the SW Praslin reef (Wheeler 1946; Robinson et al. 2011; Bijoux 2013). Moreover, *S. sutor* are uncommon on submerged granitic reefs when not spawning and most non-spawning catch is obtained from lagoons and carbonate platforms (Grandcourt 1999). Finally, in spite of smaller fringing reef and non-spawning habitat in the area (e.g. around the small island of Cousin), the SW Praslin reef is by far the largest known habitat in the area. In terms of the second assumption, there is high stability in fishing effort

on monthly and inter-annual scales, and *S. sutor* spawns across a protracted spawning season (Robinson et al. 2011; Bijoux et al. 2013). Consequently, mortality and recruitment rates may not fluctuate greatly within a spawning season.

Metric	Estimate
SW Praslin reef area (m ²)	14,841,414.69
Mean fish density (fish.m ⁻²)	0.003823
Population abundance (N)	56,743.04
Mean non-spawning <i>CPUE</i> (fish.trap-hr ⁻¹)	1.724
Mean spawning CPUE (fish.trap-hr ⁻¹)	7.421
Ratio spawning/non-spawning CPUE	4.305
Non-spawning catchability (q_{ns})	0.0000304
Spawning site catchability (q_s)	0.0001308

Table A1 Summary of metric estimates used to derive non-spawning population abundance (N) and catchability (q).

Estimating size at recruitment to the fishery

Previous applications of the marine reserve model (Grüss et al. 2014; Grüss and Robinson 2015) were based on an estimate of size at recruitment to the fishery (L_{c50}) from Robinson et al. (2011), who employed length data collected in 2007. Using the same method as that of Robinson et al. (2011), the present study derived catch curves and probability of capture from length samples of *S. sutor* (N=141) caught in non-spawning habitat in 2014.

A selectivity curve was generated from a length-converted catch curve (Sparre and Venema 1998), based on backwards extrapolation of the curve to add fish to the curve that 'ought' to have been caught, had it not been for the effect of incomplete selection and recruitment. The ratio of expected numbers to those actually caught was then used to estimate probabilities of capture by size. To derive the catch curve, estimates of the von Bertalanffy growth parameters

for *S. sutor* (K = 0.648; $L_{\infty} = 43.3$ cm FL) were obtained from Grandcourt (2002) (using estimates derived for both males and females).

In 2007, L_{c50} in the fishery was 16.15 cm FL (Robinson et al. 2011). L_{c50} had increased to 21.37 cm FL in 2014.

A3. Collinearity between continuous predictor variables in the boosted regression tree model

			Effort				
	Depth	Soak	density	MaxN	Presence	Visibility	Current
Depth		0.46	0.81	0.67	0.68	0.70	0.27
Soak	0.46		0.45	0.33	0.42	0.29	0.01
Effort density	0.81	0.45		0.69	0.69	0.64	0.30
MaxN	0.67	0.33	0.69		0.85	0.67	0.17
Presence	0.68	0.42	0.69	0.85		0.70	0.98
Visibility	0.71	0.30	0.64	0.67	0.70		0.11
Current	0.27	0.01	0.30	0.17	0.98	0.11	

Table A2 Spearman's rank correlation coefficients between pairs of continuous predictor variables

Literature cited (not in main thesis list)

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- Grandcourt EM. 1999. *The population biology of a selection of exploited reef fish from the Seychelles and Great Barrier Reef.* MSc Thesis, James Cook University, Australia.
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Appendix B: Supplementary Information for Chapter 4

Conceptual scheme highlighting management implications of study findings

Options for implementing adaptive management of spawning aggregation fisheries for the coaggregating groupers *Epinephelus fuscoguttatus* and *Epinephelus polyphekadion*. No-take reserves (i.e. protecting both species) or prohibiting the relevant gear (i.e. spear fishing that selects for *E. fuscoguttatus*, line fishing that selects for *E. polyphekadion*) can be used to meet the objective of rebuilding aggregation populations. Alternatively, allowing either spear or line fishing in combination with conservative catch limits can meet the objective of a sustainable harvest for the relevant species, reverting to a rebuilding objective if population depletion is detected. Adaptive management is underpinned by monitoring and evaluation of population status and compliance with the measures.



Appendix C: Supplementary Information for Chapter 5

Appendix C1 Equations for female spawning stock biomass-per-recruit (female SSBR), yield-per-recruit (YPR) and female:male sex ratio (SR).

Female spawning stock biomass-per-recruit (female SSBR) and yield-per-recruit (YPR) are obtained by integrating the product of survival to age and weight-at-age over the relevant age ranges. For instance, in the absence of marine reserves, female SSBR for a gonochoristic population is given by:

$$SSBR = \frac{SR}{1+SR} \int_{a_{s_0}}^{\infty} e^{-[M+(1-C_s)q_{ns}E](a_{s_0}-a_F)} e^{-[M+((1-C_s)q_{ns}+C_sq_s)E](a-a_{s_0})} w(a) da$$
(C1.3)

where SR is the female:male sex ratio; *M* the natural mortality rate (in year⁻¹); *C_s* the fraction of annual fishing effort that is directed towards FSAs; q_{ns} the catchability in normal residence areas; q_s is the catchability at FSA sites; *E* the total annual fishing effort (year⁻¹); a_{50} the age at 50% fecundity equated here to the age of sexual maturity; a_F the age of recruitment to the fishery; and w(a) the biomass per adult female at a certain age *a*. For a protogynous population, female SSBR is given by:

$$SSBR = \int_{a_{50}}^{a_{5x}} e^{-[M+(1-C_s)q_{ns}E](a_{50}-a_F)} e^{-[M+((1-C_s)q_{ns}+C_fC_sq_s)E](a_{5x}-a_{50})} w(a) da$$
(C1.4)

where C_f is the fraction of the spawning period that females spend at FSA sites; and a_{sx} the age of sex change. Still in the absence of marine reserves, YPR for a gonochoristic population is given by:

$$YPR = (1 - C_{s})q_{ns}E\int_{a_{F}}^{a_{50}}e^{-[M + (1 - C_{s})q_{ns}E](a - a_{F})}w(a)da$$

$$+ [((1 - C_{s})q_{ns} + C_{s}q_{s})E]\int_{a_{50}}^{\infty}e^{-[M + (1 - C_{s})q_{ns}E](a_{50} - a_{F})}e^{-[M + ((1 - C_{s})q_{ns} + C_{s}q_{s})E](a - a_{50})}w(a)da$$
(C1.5)

and for a protogynous population by:

$$YPR = (1 - C_{s})q_{ns}E\int_{a_{F}}^{a_{50}} e^{-[M + (1 - C_{s})q_{ns}E](a - a_{F})}w(a)da$$

+ $[((1 - C_{s})q_{ns} + C_{f}C_{s}q_{s})E]\int_{a_{50}}^{a_{5x}} e^{-[M + (1 - C_{s})q_{ns}E](a_{50} - a_{F})}e^{-[M + ((1 - C_{s})q_{ns} + C_{f}C_{s}q_{s})E](a - a_{50})}w(a)da$
+ $[((1 - C_{s})q_{ns} + C_{s}q_{s})]E$
 $\int_{a_{5x}}^{\infty} e^{-[M + (1 - C_{s})q_{ns}E](a_{50} - a_{F})}e^{-[M + ((1 - C_{s})q_{ns} + C_{f}C_{s}q_{s})E](a - a_{5x})}w(a)da$ (C1.6)

In the absence of marine reserves, the SR of the protogynous populations is given by:

$$SR = \frac{\int_{a_{50}}^{a_{sx}} e^{-[M + ((1-C_s)q_{ns} + C_f C_s q_s)E](a-a_{50})} da}{\int_{a_{sx}}^{\infty} e^{-[M + ((1-C_s)q_{ns} + C_f C_s q_s)E](a_{sx} - a_{50})} e^{-[M + ((1-C_s)q_{ns} + C_s q_s)E](a-a_{sx})} da}$$
(C1.7)

Eq. A.1.5 can be simplified and then solved:

$$SR = \frac{\int_{a_{sx}}^{a_{sx}} e^{-[M + ((1-C_s)q_{ns} + C_f C_s q_s)E](a - a_{sx})} da}{\int_{a_{sx}}^{\infty} e^{-[M + ((1-C_s)q_{ns} + C_s q_s)E](a - a_{sx})} da}$$

$$= \frac{M + ((1-C_s)q_{ns} + C_s q_s)E}{M + ((1-C_s)q_{ns} + C_f C_s q_s)E} \left[e^{[M + ((1-C_s)q_{ns} + C_f C_s q_s)E](a_{sx} - a_{50})} - 1 \right]$$
(C1.8)



Figure C2. Fraction of natural spawning stock biomass-per-recruit (FNSSBR, i.e., SSBR over natural SSBR) of *Epinephelus fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}), for the status quo and the 6 reserve scenarios (Table 5.1). For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (**a**) and (**b**), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (**a**) and (**b**), respectively. For all panels, the vertical dashed-dotted black line indicates the default value of annual fishing effort exerted on the population, E_{base} , whereas the vertical dashed grey line indicates the value of annual fishing effort at which yield-per-recruit reaches a maximum for the population, E_{max} .


Figure C3. Yield-per-recruit of *Epinephelus fuscoguttatus* normalised by maximum yieldper-recruit of the species in the absence of reserves (YPR/YPR_{max}) as a function of multiplier of fishing effort (mE_{base}) for the status quo and the 6 reserve scenarios (Table 5.1). The fraction of spawning sites in reserves, C_r , is 30% and 60% for Scenarios #1-2 for (**a**) and (**b**), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. The fraction of normal residence areas in reserves, C_r , is 30% and 60% for reserve scenarios #5-6 for (**a**) and (**b**), respectively. For all panels, E_{base} is indicated by a vertical dashed-dotted black line, whereas E_{max} is indicated by a vertical dashed grey line.



Figure C4. Female:male sex ratio of *Epinephelus fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}), for the status quo and the 6 reserve scenarios (Table 5.1). (a) and (b) give population-wide average female:male sex ratios, whereas (c) and (d) give female:male sex ratios for the fished subpopulation of *E. fuscoguttatus*. For Scenarios #1-2, the fraction of spawning sites in reserves, C_r , is 30% and 60% for (a) and (c) and (b) and (d), respectively. All spawning sites are set aside as reserves for Scenarios #3-4. For Scenarios #5-6, the fraction of normal residence areas in reserves, C_r , is 30% and 60% for (a) and (c) and (b) and (d) and (d), respectively. For panels (c) and (d), the light grey area indicates when the sex ratio of the fished subpopulation is superior to the critical female:male sex ratio (i.e., 50:1). For all panels, E_{base} is indicated by a vertical dashed-dotted black line, whereas E_{max} is indicated by a vertical dashed full violet curves overlap in panels (c) and (d).



Figure C5. Female:male sex ratio for the protected subpopulation of *Epinephelus fuscoguttatus* as a function of multiplier of fishing effort (mE_{base}) for the status quo and Scenarios #2 and #6, in the baseline situation (**a**); when spawning-site catchability (q_s) is decreased by a factor of 10 (**b**); when natural mortality, M, is increased by a factor of 10 (**c**); and when instantaneous growth rate at small size, k, is increased by a factor of 10 (**d**). For Scenario #2, a fraction of spawning sites is protected and the fishing effort previously in reserves is fully redistributed to non-protected spawning sites. For Scenario #6, a fraction of normal residence areas is protected and the fishing effort previously in reserves is redistributed to non-protected and the fishing effort previously in reserves is is protected normal residence areas. Female:male sex ratio for the protected subpopulation of *E. fuscoguttatus* as a function of mE_{base} for Scenarios #1 and #5 (Table 5.1) is identical to that for Scenarios #2 and #6, respectively. E_{base} is indicated by a vertical dashed-dotted black line.

Appendix D: Publications arising from thesis

- Robinson J, Cinner JE, Graham NAJ. 2014. The influence of fisher knowledge on the susceptibility of reef fish aggregations to fishing. *PLoS ONE* **9**:e91296
- Grüss A, Robinson J. 2015. Fish populations forming transient spawning aggregations: should spawners always be the targets of spatial protection efforts? *ICES Journal of Marine Science* 72: 480–497
- Robinson J, Graham NAJ, Cinner JE, Almany GR, Waldie P. 2015. Fish and fisher behaviour influence the vulnerability of groupers (Epinephelidae) to fishing at a multispecies spawning aggregation site. *Coral Reefs* **34**: 371-382
- Robinson J, Graham NAJ, Grüss A, Gerry C, Bijoux J (in review with *Coral Reefs*) Managing critical habitats for herbivorous rabbitfish to benefit ecological processes and fisheries.

Publications in preparation

Robinson J, Cinner JE, Graham NAJ, Samoilys MA. A predictive framework for assessing the vulnerability to overfishing in spawning aggregation fisheries

Appendix E: Other peer-reviewed articles published during my candidature

Publications specific to reef fish spawning aggregations

- Bijoux JP, Dagorn L, Berke G, Cowley PD, Soria M, Gaertner J-C, Robinson J. 2013. Temporal dynamics, residency and site fidelity of spawning aggregations of a herbivorous tropical reef fish, *Siganus sutor*. *Marine Ecology Progress Series* 475: 233–247.
- Bijoux J, Dagorn L, Cowley PD, Simier M, Adam P-A, Robinson J. 2013. Spawning aggregation dynamics of brown-marbled *Epinephelus fuscoguttatus* and camouflage grouper *Epinephelus polyphekadion* at a remote Indian Ocean atoll. *Endangered Species Research* 22: 145–157.
- Bijoux J, Dagorn L, Gaertner J-C, Cowley PD, Robinson J. 2013. The influence of natural cycles on coral reef fish movement: implication for underwater visual census (UVC) surveys. *Coral Reefs* 32: 1135–1140.
- Grüss A, Kaplan DM, Robinson J. 2014. Evaluation of the effectiveness of marine reserves for transient spawning aggregations in data-limited situations. *ICES Journal of Marine Science* 71: 435–449
- Grüss A, Robinson J, Heppell SS, Heppell SA, Semmens BX. 2014. Conservation and fisheries effects of spawning aggregation marine protected areas: what we know, where we should go, and what we need to get there. *ICES Journal of Marine Science* 71: 1515–1534.

Publications not specific to reef fish spawning aggregations

Cariglia N, Wilson SK, Graham NAJ, Fisher R, Robinson J, Aumeeruddy R, Quatre R, Polunin NVC. 2012. Sea cucumbers in the Seychelles: effects of marine protected areas on high-value species. *Aquatic Conservation: Marine and Freshwater Ecosystems* 23: 418–428.

- Guillotreau P, Campling L, Robinson, J. 2012. Vulnerability of small island fishery economies to climate and institutional changes. *Current Opinion in Environmental Sustainability* **4**: 287–291.
- Hicks CC, Stoeckl N, Cinner J, Robinson J. 2014. Fishery benefits and stakeholder priorities associated with a coral reef fishery and their implications for management. *Environmental Science and Policy* 44: 258–270.
- Nash KL, Bijoux J, Robinson J, Wilson SK, Graham NAJ. In press. Harnessing fisheryindependent indicators to aid management of data-poor fisheries: weighting habitat and fishing effects. *Ecosphere*.
- Waldie PA, Almany GR, Sinclair-Taylor TH, Hamilton RJ, Potuku T, Priest MA, Rhodes KL, Robinson J, Berumen ML. In press. Restricted grouper movements support community-based management. Royal Society Open Science.
- Wilson SK, Graham NAJ, Fisher R, Robinson J, Nash K, Chong-Seng K, Polunin NVC, Aumeeruddy R, Quatre R. 2012. Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. *Conservation Biology* 26: 995–1004.