Reef Fish Spawning Aggregations in the Western Indian Ocean: Research for Management

Jan Robinson and Melita Samoilys (Co-editors)
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Foreword

This book is one of firsts. It is the first documentation of commercially important reef fishes that aggregate to spawn in the western Indian Ocean. It is the first to develop a framework for processing information in data- and management-poor situations where fisheries important to local communities must, somehow, nonetheless be managed. It is the first to explore in detail the outcomes of different management scenarios across very different species fished in very different ways within the same region. In taking this approach, the book also tackles head-on some of the critical questions that we must ask as we come to learn more about spawning aggregations and their fisheries. Questions about the ethics of using traditional knowledge for management; questions about the influence of conservation agendas, linked to scarce funding, that may not serve the best interests of communities or species.

Through the thirteen chapters we explore some very different aggregating species with very different responses to fishing. From rabbitfishes to massive groupers, from species resilient to those highly vulnerable to fishing, we are led to consider how important it is to consider the selectivity of fishing gear, the importance of when most fishing occurs relative to the aggregation season, and how catchability can change everything. Field and novel modelling approaches were used to develop a predictive vulnerability framework for the data-poor contexts typical of the region. The contrast of spatial protection, often the conservation measure of choice, with more conventional management was particularly interesting in highlighting the need to examine each fishery separately; protecting the aggregation itself is not necessarily the best way to protect the fishery. The devil is in the detail!

It is now widely accepted that spawning aggregations of reef fishes throughout the tropics are undergoing declines, and the western Indian Ocean is no exception. Although it is less than a decade since these were first described in the region, much progress has been made towards understanding their dynamics and how they interact with local fishing practices. This highly readable book is not only of much value for developing effective management plans that will benefit local communities in the long term, it is also relevant to a much wider audience. The studies remind us of the challenges of understanding these complex fisheries and that we must seek to think honestly and ‘outside of the box’ if real progress is to be made.

Yvonne Sadovy de Mitcheson
Director, Science and Conservation of Fish Aggregations (SCRFA)
University of Hong Kong
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Co-editors

Jan Robinson
Seychelles Fishing Authority, Fishing Port, Victoria, Mahé, Seychelles; and
ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia
janrobinson71@gmail.com

Melita Samoilys
CORDIO East Africa
PO Box 24562
Nairobi 00502, Kenya
www.cordioea.net
melita.samoilys@gmail.com

Contributing Authors and Institutes

Seychelles Fishing Authority, Fishing Port, Victoria, Mahé, Seychelles
Gregory Berke, Jude Bijoux, Calvin Gerry, Jan Robinson

CORDIO East Africa, P.O.BOX 10135, Mombasa 80101, Kenya
Hussein Alidina, Nyaga Kanyange, Denis Macharia, George Waweru Maina, Kennedy Osuka, Melita Samoilys

Institute of Marine Sciences, Mizingani Rd, P.O Box 668 Zanzibar Tanzania
Narriman Jiddawi

Kenya Marine and Fisheries Research Institute, P.O. Box 81651, Mombasa, 80100, Kenya
Simon Agembe

Institut de Recherche pour Développement (IRD), UMR 212, Victoria, Mahé, Seychelles
Laurent Dagorn

Institut de Recherche pour le Développement (IRD), UMR EME 212 (IRD/Ifremer/Université Montpellier 2), Centre de Recherche Halieutique Méditerranéenne et Tropicale, Avenue Jean Monnet, B.P. 171, 34203 Sete cedex, France
Arnaud Grüss, David Kaplan

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Chapter 1: Introduction
Jan Robinson, Melita Samoily and Kennedy Osuka

The vital role of small-scale fisheries for poverty alleviation and food security is beginning to receive much needed global attention, particularly in the face of climate change (Allison et al. 2009; FAO 2010, 2012). Numerous challenges must be overcome if this role is to be maintained, especially in much of the developing world where there is a high level of dependency on marine resources (Mangi et al. 2007; Béné et al. 2010). Coral reefs typically support small-scale fisheries that are highly complex in terms of species targeted, gears used, management systems applied, degree of societal dependency and markets supplied (Munro and Williams 1988; Polunin and Roberts 1996; McClanahan and Mangi 2004). Moreover, it is now recognised that sustaining such complex fisheries requires the adoption of an integrated socio-ecological systems approach that explicitly incorporates the numerous socio-economic drivers and pressures determining how societies interact with reef ecosystems (Bellwood et al. 2004; Cinner et al. 2009; Gutiérrez et al. 2011; Salomon et al. 2011).

The response of coral reef ecosystems to human interaction is dependent on an equally multifaceted system of ecological (e.g. interactions among species, such as competition) and biological processes (e.g. natural mortality, reproductive output) (Hughes 1994; Jennings and Lock 1996; Wilson et al. 2006). However, for many reef fishes, biological processes are not well understood or are often overlooked in conservation and management measures, such as no-take marine reserves (Sale et al. 2005; Kaplan 2009). While it is clearly impractical to design and implement management measures for all species in diverse coral reef ecosystems, an understanding of key biological processes for vulnerable, commercial or functionally important taxa can assist in designing more effective management interventions.

The wide-ranging life histories and behavioural traits of socio-economically important coral reef species create considerable complexity in the management of their fisheries. A critical aspect that influences the responses of reef fishes to human impacts, including management, is reproduction. In combination with other vital life cycle rates (i.e. growth and survival), reproductive output determines, to a large extent, the vulnerability of populations to exploitation (Dulvy et al. 2004; Patrick, et al. 2010). Reproduction has a profound influence on the productivity, behaviour and mobility of reef fishes. 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 commercially exploited reef fish species (Froese and Pauly 2003. http://www.fishbase.org). Behavioural

![Fig 1. Numbers of species that are known to form spawning aggregations in 9 commercially important coral reef fish families. Adapted from Table 1 of Sadovy de Mitcheson et al. 2008.](image-url)
traits associated with reproduction also differ markedly between species and often alter the spatial distribution and density of populations. For example, some species form large aggregations for the purpose of spawning (Johannes 1981; Shapiro 1987; Domeier and Colin 1997; Sadovy de Mitcheson and Colin 2012). Since spawning aggregations are highly predictable in time and space, they are often subjected to highly targeted fishing once discovered by fishers (Sadovy and Domeier 2005; Robinson et al. 2011).

The regional study that forms the basis for this book focused on the formation of spawning aggregations. A wide range of reef fishes aggregate in large numbers to spawn, including many species from highly valued food fish families such as the Lutjanidae and Serranidae (Domeier and Colin 1997; Domeier 2012) (Fig. 1). Reef fish species forming spawning aggregations are often highly mobile, with migrations to spawning sites ranging from a few to hundreds of kilometres (Sadovy 1996). Targeted fishing on fish migrating to and from aggregations also occurs, though is less well documented than fishing on aggregations (Fulton et al. 1999; Claro et al. 2009; Kitalong 2012). In the early stages of the exploitation of a spawning aggregation, very high catch rates and revenues may be achieved because aggregation formation elevates population density (often by an order or more of magnitude) and tends to increase catchability (Robinson et al. 2011). It is, therefore, not surprising that spawning aggregations are fished in all tropical regions (Domeier et al. 2002), including the western Indian Ocean (Robinson et al. 2004; Samoilys et al. 2006).

The effects of fishing spawning aggregations range in severity. Decreases in average fish size (Pet et al. 2005; Rhodes et al. 2011), altered male-to-female sex ratio in protogynous species (Beets and Friedlander 1998) and reduced aggregation size (Johannes et al. 1999) have been documented. More dramatic effects of fishing include the disappearance of spawning aggregations and collapse of associated fisheries (Olsen and LaPlace 1978; Claro and Lindeman 2003; Aguilar-Perera 2006). In extreme cases, aggregation fishing may endanger species survival (e.g. Epinephelus striatus; Sadovy and Eklund 1999). Many aggregating species such as grouper, are also characterised by additional life history traits that increase their vulnerability to exploitation, such as slow growth and late sexual maturation (Sadovy 1996; Coleman et al. 1999; Jennings et al. 1999; Dulvy et al. 2004).

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthuridae</td>
<td>Acanthurus guttatus</td>
<td>Mugidae</td>
<td>Mugil cephalus</td>
</tr>
<tr>
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<td>A. triostegus</td>
<td></td>
<td>Epinephelus coioides</td>
</tr>
<tr>
<td></td>
<td>A. lineatus</td>
<td>Serranidae</td>
<td>E. fuscoguttatus</td>
</tr>
<tr>
<td>Caesionidae</td>
<td>Caesio teres</td>
<td></td>
<td>E. multinotatus</td>
</tr>
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<td>Cheilinus undulatus</td>
<td></td>
<td>E. ongus</td>
</tr>
<tr>
<td></td>
<td>C. sordidus</td>
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<td>E. polypekadiom</td>
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<tr>
<td>Lethrinidae</td>
<td>Lethrinus erythrophorus</td>
<td>Scarinae</td>
<td>Bolbometopon muricatum</td>
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<td>L. nebulosus</td>
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<td>Scarus prasiognathus</td>
</tr>
<tr>
<td>Lutjanidae</td>
<td>Lutjanus argentimaculatus</td>
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<td>L. bohar</td>
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</tr>
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<td></td>
<td>L. rivulatus</td>
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</table>

Table 1. Indo-Pacific species which have been verified as aggregative spawners and are known to occur in the western Indian Ocean. Verification of aggregation formation from Table 1 of Sadovy de Mitcheson et al. (2008). Regional occurrence of species based on FishBase records (Froese and Pauly 2003), Catalogue of Fishes (Eschmeyer 2012) and unpublished regional visual survey data (MS). Note: Scarinae are a subfamily within the Labridae but for functional purposes are listed separately.
Two main types of spawning aggregations have been defined: transient and resident (Domeier and Colin 1997; Domeier 2012). Transient spawning aggregations persist for several days or weeks, usually form around specific lunar phases within certain months of the year, and may involve relatively long migrations for participating fish. Resident spawning aggregations form more regularly, often over a lengthy spawning season, last for shorter periods (minutes to hours), and occur close to or within the areas of residence for participating fish (Domeier and Colin 1997; Domeier 2012).

It has been suggested that transient spawners are more vulnerable to aggregation fishing than resident spawners (Domeier et al. 2002), not least because a significant proportion of the annual reproductive output of participating fish may be invested in a single aggregation (Shapiro et al. 1993). However, within these broad types of transient and resident spawners, vulnerability is expected to vary depending on the relative importance of any single aggregation to the annual reproductive output of the population, as well as on predictability and concentration of aggregations. For example, some transient spawners form relatively small aggregations at numerous sites and also spawn outside aggregations (e.g. Plectropomus leopardus; Samoilys 2000, 2012), while others form numerous, large aggregations across a protracted spawning season (e.g. Robinson et al. 2011). In both cases, the contribution of each aggregation to annual reproductive output is reduced compared to transient spawners that spawn in large aggregations at a few sites and within a narrow time period. Transient spawners forming aggregations that are patchily distributed or vary slightly in their location on inter-annual scales may be less vulnerable than transient spawners which form predictable, spatially discrete, highly concentrated aggregations such as Nassau grouper, Epinephelus striatus (Sadovy et al. 1994; Sadovy and Eklund 1999).

Based on a growing literature documenting the vulnerability of reef fish that spawn in aggregations, Sadovy and Domeier (2005) proposed that aggregation fishing may only be sustainable at

<table>
<thead>
<tr>
<th>Country</th>
<th>Site</th>
<th>Species</th>
<th>Spawning*</th>
<th>Abundance**</th>
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</thead>
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<tr>
<td></td>
<td></td>
<td></td>
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<td>Indirect</td>
</tr>
<tr>
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<td>S1</td>
<td>Epinephelus polyphekadion</td>
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<tr>
<td></td>
<td>S1</td>
<td>E. fuscoguttatus</td>
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<td>Yes</td>
</tr>
<tr>
<td></td>
<td>S1</td>
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</tr>
<tr>
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<td>S2</td>
<td>E. polyphekadion</td>
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<td>Yes</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>E. fuscoguttatus</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>P. punctatus</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td></td>
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<td>E. polyphekadion</td>
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<td>Yes</td>
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<td>S3</td>
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</tr>
<tr>
<td></td>
<td>S4</td>
<td>P. punctatus</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td>S5</td>
<td>E. polyphekadion</td>
<td>No</td>
<td>Yes</td>
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<tr>
<td></td>
<td>S6</td>
<td>Siganus sutor</td>
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</tr>
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<td></td>
<td>S7</td>
<td>S. sutor</td>
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<td>No</td>
</tr>
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<td>E. fuscoguttatus</td>
<td>No</td>
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</tr>
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<td>E. fuscoguttatus</td>
<td>No</td>
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<td>Mullolichthys vanicolensis</td>
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<tr>
<td></td>
<td>K5</td>
<td>M. vanicolensis</td>
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<td>Yes</td>
</tr>
</tbody>
</table>

*: Direct signs of spawning include observations of gamete release or hydrated ovaries. Indirect signs include patterns in gonado-somatic index, colour changes and territorial/courtship behaviour associated with spawning, and observations of gravid females. **: Increases in abundances determined quantitatively.
limited, subsistence levels of exploitation. Commercial exploitation of spawning aggregations in the Caribbean and tropical western Atlantic has resulted in the collapse of economically important fisheries (Sadovy and Eklund 1999; Claro and Lindeman 2003). Consequently, conservation and management organisations have increasingly adopted measures to protect these vulnerable life history occurrences (Beets and Friedlander 1998; Koenig et al. 2000; Lindeman et al. 2000; Nemeth 2005, Heyman and Kjerfve 2008). In the Indo-Pacific region, comparatively less is known about the occurrence and status of spawning aggregations and their fisheries, although recent programmes of the Society for the Conservation of Reef Fish Aggregations (SCRFA) and other organisations have begun to reverse this trend.

A recent review of global information on reef fish spawning aggregations, based on a database developed by SCRFA, identified 67 species that spawn in aggregations (Sadovy de Mitcheson et al. 2008). Some 26 of those species occur in the western Indian Ocean (WIO) and most are important to small-scale fisheries (Table 1). Species such as *Lutjanus bohar* and *Lethrinus nebulosus* are highly valuable target species in several countries of the region and are also targeted by more commercialised or industrialised fisheries (Everett et al. 2010; Samoilys et al. 2011a). One species of particular importance to small-scale fisheries across the WIO is *Siganus sutor* (Everett et al. 2010), a rabbitfish endemic to the region (Woodland 1990). It is now known that *S. sutor* forms large spawning aggregations that are often well known to fishers in Kenya (Samoilys et al. 2006) and Seychelles (Robinson et al. 2004; Robinson et al. 2011). Another regional endemic species that has been reported and verified as an aggregative spawner is the grouper *Plectropomus punctatus* (Samoilys et al. 2006; Robinson et al. 2008b). Given the degree of stability of this reproductive trait in some families, it is likely that additional species will be confirmed as research progresses.

In many tropical regions, spawning aggregation fisheries are being increasingly commercialised and their populations subjected to unsustainable levels of exploitation due to technological advances and increased market access (Sadovy de Mitcheson et al. 2008). In the WIO, the development of infrastructure important for markets and increased access to technologies, among other factors associated with socio-economic development, exert a strong influence on resource status (Cinner et al. 2009). While human population density acts as a driver of resource overexploitation on local scales (Newton et al. 2007; Mora 2008), export demand is also growing and exports of fisheries products from developing countries now exceed those of any other agricultural product (FAO 2012).

As it is likely that aggregative spawners are subject to increasing fishing pressure in the region, it is of concern that very little is known regarding their stock status and the health of their spawning aggregations. Previous studies in the WIO have documented fisher knowledge on spawning aggregations (Robinson et al. 2004; Samoilys et al. 2006), with 10 aggregation sites for 5 species having been verified (Robinson et al. 2007; Samoilys et al. 2007) (Table 2). Due to the absence of long-term monitoring, it is not known if these aggregations are stable, declining or increasing in size. The costs and logistical constraints involved in monitoring, particularly at remote sites, undermines efforts to determine aggregation status. Moreover, there are few fisheries data on trends in catch or effort for aggregative spawners in the region since catch assessment surveys are lacking, poorly developed or highly aggregated in terms of species resolution; and stock assessments are rarely conducted (Everett et al. 2010). However, if aggregations can be monitored on sufficient scales, they may also provide opportunities for stock assessment (Johannes 1980; Samoilys and Squire 1994), though there is a need for empirical research to determine relationships between aggregation abundance and spawning stock biomass.

As most spawning aggregation-based fisheries lack data on aggregation and population status, a precautionary approach is required whereby the data-poor context of such fisheries should not constitute a barrier to evaluating their management needs (Turnbull and Samoilys 1997; FAO 1995). The development of indicator frameworks to assess the intrinsic vulnerabilities of spawn-
ing aggregations and their exposure to extrinsic pressures and drivers can support a precautionary approach through their ability to estimate the risks posed by fishing. On demonstrating that a spawning aggregation and its fishery are at risk from unsustainable levels of fishing, a process to determine the management or conservation response would follow. However, data on spawning aggregations are highly sensitive and there is still debate on how such information should be treated. Commonly, spawning aggregations are initially ‘discovered’ and documented by scientists through surveys of fisher knowledge (Johannes 1981; Samoilys and Squire 1994; Colin et al. 2003; Sadovy de Mitcheson et al. 2008). Information on the location and timing of rare events, sometimes involving threatened and/or highly valuable fishes, can predispose vulnerable populations to higher levels of exploitation if made available in the public domain (Courchamp et al. 2006). Moreover, there are ethical concerns over the extraction, use and publication of fisher knowledge (Maurstad 2002). Daw (2008) highlights issues arising from the extraction of fisher knowledge on spawning aggregations and recommends participatory engagement with this knowledge for improved contextual understanding and fisher control over its use. These issues highlight the need for a co-management approach to governance of spawning aggregation fisheries, which is known to be effective provided certain conditions are met (Andrew and Evans 2011; Gutiérrez et al. 2011).

Globally, several types of management measures have been applied or recommended to protect spawning aggregations and aggregating species, including spawning season sales bans, time/area closures, marine protected areas, limited entry and size limits (Turnbull and Samoilys 1997; Rhodes and Warren-Rhodes 2005; Sadovy and Domeier 2005). However, the majority of spawning aggregations and their fisheries are unmanaged (Sadovy de Mitcheson et al. 2008). For those that are managed, measures introduced to protect aggregations are not always effective. Incomplete knowledge of important parameters may lead to ineffectual spatial management (Eklund et al. 2000; Rhodes and Sadovy 2002a; Rhodes et al. 2011) and can even predispose fish to higher levels of effort.

Explicit management of reef fish spawning aggregations is lacking in the WIO at present though informal agreements and social norms have emerged that influence their exploitation in Seychelles (Robinson et al. 2008a; Robinson et al. 2011). If progress is to be made, it will be necessary to align spawning aggregation protection in the wider context of marine resource management in the region. Conventional approaches to fisheries management involving input and output controls are largely absent in the WIO. Similar to other developing regions in the tropics, the WIO is constrained by limited capacity and the difficulties in implementing such measures, particularly in the context of small-scale and multispecies coral reef fisheries (Johannes 2002; Beddington et al. 2007; Sadovy de Mitcheson et al. 2008; Samoilys et al. 2011). Fisheries management in the region has largely proceeded through a combination of no-take reserves (NTRs), multi-use marine protected areas (MPAs) and gear-based measures (De Young 2006). In Kenya, the combination of closures and gear-based measures has resulted in successful outcomes for fisheries and biodiversity conservation (McClanahan and Mangi 2004; McClanahan et al. 2008; McClanahan 2010; Samoilys and Obura 2011). The lessons learned from these successes may be informative for finding management and conservation solutions to spawning aggregation fisheries. In some regions, gear-based measures may be particularly effective in controlling the exploitation of spawning and migrating fish (Koenig et al. 2000; Claro and Lindeman 2003; Aguilar-Perera 2006).

Permanent or temporary NTRs have been recommended and in cases applied for the protection of spawning aggregations (Bohnsack 1990; Johannes et al. 1999; Coleman et al. 2000; Lindeman et al. 2000; Domeier et al. 2002; Pet et al. 2005; Rhodes et al. 2011), to notable effect in some cases (Burton 2005; Nemeth 2005; Hamilton et al. 2011). While 55 spawning aggregations were found to be under some form of spatial protection in a recent review (Sadovy de Mitcheson et al. 2008), empirical evidence on the effects of these measures is limited to a few studies (e.g. Beets and Friedlander 1998; Burton et al. 2005; Nemeth 2005), partly due to a lack of monitoring (e.g. Samoilys 2012). In view of limited empirical data, researchers have begun exploring the effects of
NTRs for spawning aggregations using modelling approaches. While also limited to a handful of studies, interesting results are emerging. For example, in a model developed for gag (*Mycteroperca microlepis*), a protogynous grouper, Heppell et al. (2006) showed that spatial closures for spawning sites needed to be combined with effort limits on non-spawning fish to recover depleted populations and skewed sex ratios. A model by Fulton et al. (1999) found that protecting migration routes was important and should be complementary to protection of spawning sites. The effects of spawning site closures also differ between protogynous and gonochoristic aggregative spawners (Alonzo and Mangel 2004). However, many critical science gaps remain (Sale et al. 2005; Heppell et al. 2006). Moreover, NTRs can be burdensome and socially unacceptable for fishing communities (McClanahan et al. 2005; McClanahan et al. 2006). Thus, there is a need for careful consideration of NTRs and alternative approaches for managing spawning aggregation fisheries require wider attention (Sadovy and Domeier 2005).

The initial research documenting reef fish spawning aggregations in the WIO (Robinson et al. 2004; Samoilys et al. 2006; Robinson et al. 2007; Samoilys et al. 2007; Robinson et al. 2008a) raised significant research questions and issues for management. For example, we had verified several spawning aggregations but time-series data were insufficient to determine aggregation status. For most sites we lacked data to determine their spatial and temporal dynamics and were therefore unable to provide appropriate information for consideration of management measures. In Seychelles, many conservation non-governmental organisations and the Department of Environment were advocating for fisheries closures, or NTRs, for spawning aggregation sites, but models on the effects of such measures in terms of yields or protection of the aggregations and their populations were unavailable at the time. Given the high sensitivity and ethical concerns of data derived from fisher knowledge (Daw 2008), it was also recognised that any management process should proceed under participatory governance structures, and that such processes would need to be better informed in terms of comparing, selecting and designing effective management measures. The research programme documented here attempted to respond to some of these management needs.

The overall goal of the research programme was to address critical information gaps and develop robust scientific approaches for the management and conservation of commercially important species that aggregate to spawn in the western Indian Ocean. To address this goal, a conceptual framework was developed (Chapter Two) which linked hypotheses, methods and analyses within an overall approach for addressing the management needs of spawning aggregation-based fisheries. A spawning aggregation-based fishery is defined here as a fishery targeting a population of a particular species either entirely or partially when aggregated for spawning at single or at multiple spawning aggregation sites. Six spawning aggregation fisheries were selected in order to test the conceptual approach, with different methods and analyses applied at each depending on the level of prior information. The spawning aggregation fisheries were selected to encompass four commercially important species that varied in their demographics and vulnerability to fishing, namely *Epinephelus fuscoguttatus* (Seychelles and Kenya), *E. polyphekadion* (Seychelles), *E. lanceolatus* (Zanzibar) and *Siganus sutor* (Seychelles and Kenya).

The study was implemented through three work programmes. Firstly, we conducted site-based surveys and sampling programmes to determine key parameters and information for management, focusing on reproductive biology, the spatial and temporal dynamics of aggregations and key aspects of the fisheries for aggregating species (Chapters Three to Ten). Secondly, we developed novel approaches for assessing the management needs of spawning aggregations, including the development of a predictive vulnerability framework for data-poor contexts (Chapter Eleven) and models to examine the effects of no-take reserves for spawning aggregations (Chapter Twelve). The third broad objective was to develop policy advice for the management of spawning aggregation fisheries. This book provides the content for the policy advice but not the policy documents. Developing policy requires time, consultation and full participation of fishers and managers, which was beyond the scope of this research programme, but is currently in progress.
Chapter 2: Conceptual Framework

Jan Robinson and Melita Samoilys

“The overall goal of the research programme was to develop robust scientific approaches for the management and conservation of commercially important species that aggregate to spawn in the western Indian Ocean.”

Small-scale coral reef fisheries are recognized as problematic for the application of conventional fisheries assessment and management approaches (McClanahan and Mangi 2004; Clua et al. 2005; McClanahan et al. 2008; Mumby and Steneck 2008). Even in data-rich contexts, uncertainties in parameter estimates and model processes can weaken assessments and undermine management effectiveness (Hilborn and Walters 1992; Walters and Martell 2004). Consequently, perceived data-less management approaches such as marine protected areas (MPAs) are often advocated for reef fisheries as an alternative to conventional methods. MPAs that prohibit fishing, hereafter referred to as no-take reserves (NTRs), have been specifically recommended for the protection of aggregative spawners (Johannes 1998; Huntsman et al. 1999; Rhodes and Warren-Rhodes 2005). However, these perceived solutions for the management of reef fisheries are anything but data-less. Justifying, designing and monitoring the effects of NTRs require significant data, and their application may be undermined by similar levels of uncertainty that are associated with conventional approaches (Le Quesne 2009). Although conservation benefits can be attained with NTRs, the high socio-economic dependency on coral reef resources throughout much of the tropics dictates that NTRs should ideally attain fisheries benefits, an application for which critical science gaps remain (Sale et al. 2005).

The justification of a specific management response to a spawning aggregation-based fishery must be founded on two facts, namely that (1) the population aggregates for the purpose of spawning, and that (2) spawning aggregations are fished. Once these facts are established, a relatively data-less management response is to completely prohibit fishing on a population, a measure that does not require information on aggregation dynamics, such as the specific periods in which they form. This may only be justifiable in extreme cases, for example, if the practice of aggregation fishing places the population at risk of local extinction. However, the populations of less vulnerable aggregative spawners will require a combination of conservation and management measures that regulate the amount, type, location and timing of fishing on a population (Robinson et al. 2011), for which data on aggregation and fishery dynamics are a prerequisite. In the context of most aggregative spawners, it is therefore necessary to advocate data-poor as opposed to data-less management. Moreover, conventional stock assessment approaches are not redundant in data-poor contexts and parsimonious theoretical tools such as yield-per-recruit models can offer valuable insight into the costs and benefits of certain management measures (Grandcourt et al. 2004).

To meet our research goal, we developed a conceptual model that aimed at identifying the management and conservation implications of aggregation-based fisheries in data-poor contexts. The conceptual model was designed to provide timely information and parameter estimates that enable measures to be examined using novel analytical tools, also developed in this programme. Funding for research and management in the western Indian Ocean (WIO) is limited and the approach is intended to enable scientific management advice to be provided on the basis of 2-3 years of research.

Conceptual model

Spawning aggregations previously reported by fishers in Kenya and Zanzibar (Samoilsy et al. 2006; Kimani 2007) require verification, while aggregation formation had only been verified for one of the many *S. sutor* aggregation sites in SW Praslin prior to this study (Robinson et al. 2011). As with verification, information on other important spawning and aggregation parameters was absent or lacking for many sites (Table 1). Nevertheless, the conceptual model represents a holistic approach and, with the methods and tools validated, the model can be applied in full to individual fisheries.
Verification of fish spawning aggregations and aggregation-based fisheries

To justify any restrictions on spawning aggregation-based fisheries, it is necessary to verify that a population forms spawning aggregations and that those aggregations are fished. Spatial (e.g., MPAs) and temporal restrictions (e.g., seasonal sales bans), or a combination of both, are the most commonly applied management measures for aggregation-based fisheries (Rhodes and Warren-Rhodes 2005; Sadovy and Domeier 2005; Russell et al. 2012). Temporal measures (e.g., sale restrictions during the spawning season) require information on spawning periodicity, accounting for any inter-annual and site-specific variation in this parameter. Spatial management measures require verification of aggregation formation at specific sites, accounting for any intra- or inter-annual variation in their distribution. Therefore, as a minimal requirement, the project aimed at providing information for these key parameters. Aggregation formation required verification across all sites (Table 1), based on previous reports of aggregation fishing at the sites (i.e. Samoilys et al. 2006; Kimani 2007). Likewise, information on spawning and aggregation periodicity was required at those sites for which it was lacking (Table 1).

Spawning aggregation verification is achieved through confirmation of aggregation formation (change in abundance or density) and reproductive activity using established guidelines (Colin et
Verification may include direct (i.e. gamete release) or indirect (e.g. courtship, colour changes) observations of reproductive behaviour (Fig. 1). Verification of aggregation fishing is also required, which is achieved through a combination of fisher knowledge surveys and direct observations of fishing activity on spawning aggregations. Fishers may be directly targeting aggregations or may be taking fish incidentally while targeting other species. However, spawning aggregations that are reported during fisher knowledge surveys tend to be targeted rather than fished incidentally (e.g. Robinson et al. 2004; Samoilys et al. 2006).

Table 1. Site-specific summary of prior knowledge on critical biological and physical parameters for spawning aggregation-based fisheries studied in the project and the methods/tools applied for each fishery in the current programme. ‘Partial’ denotes that gaps remained in prior knowledge or that some information was collected in the current study though methods could not be fully implemented.

<table>
<thead>
<tr>
<th>Country</th>
<th>Kenya</th>
<th>Kenya</th>
<th>Zanzibar</th>
<th>Seychelles</th>
<th>Seychelles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Msambweni</td>
<td>Diani-Chale</td>
<td>Kizimkazi</td>
<td>SW Praslin</td>
<td>Farquhar</td>
</tr>
<tr>
<td>Species</td>
<td>Siganus sutor</td>
<td>Epinephelus fuscoguttatus</td>
<td>Epinephelus lanceolatus</td>
<td>Siganus sutor</td>
<td>Epinephelus spp #.</td>
</tr>
<tr>
<td>Verification</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Partial</td>
<td>Yes</td>
</tr>
<tr>
<td>Spawning: seasonality¹</td>
<td>Yes</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Spawning: lunar²</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Aggregation: timing³</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Partial</td>
<td>Yes</td>
</tr>
<tr>
<td>Aggregation: duration⁴</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Partial</td>
<td>Partial</td>
</tr>
<tr>
<td>Residency time⁵</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Partial</td>
</tr>
<tr>
<td>Site fidelity⁶</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Partial</td>
</tr>
<tr>
<td>Catchment area⁷</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
</tbody>
</table>

| Fisher knowledge survey | Yes | Yes | Yes | Yes | No | No |
| Catch assessment survey | Yes | Yes | Yes | Yes | No | No |
| Effort mapping | Yes | No | No | No | No | No |
| Reproductive studies | Yes | No | Partial | No | No | No |
| Underwater visual census | Yes | Yes | No* | Yes | Yes | Yes |
| Acoustic telemetry | Yes | No* | No | Yes | Yes | Yes |
| Indicator-based assessment | Yes | Yes | Yes | Yes | Yes | Yes |
| No-take reserves model | No | No | No | No | Yes | Yes |

#: *Epinephelus polyphekadion and Epinephelus fuscoguttatus*
1: Seasons/months of spawning derived from analysis of annual time-series of gonad samples
2: Lunar days/period of spawning derived from analysis of weekly/daily time-series of gonad samples
3: Timing of aggregation formation, including onset, peak and dispersal (months of year, weeks/lunar days of month)
4: The duration of spawning aggregations (hours, days, weeks)
5: Residency time: time individual fish reside at aggregations, including arrival/departure times; relates to aggregation turnover
6: Site fidelity is the fidelity fish show to individual spawning sites on seasonal (i.e. between months) and interannual scales
7: Catchment area is the source area or identification of source reefs for fish attending an aggregation
*# attempted but unsuccessful
Dynamics of spawning aggregations and aggregation fisheries

We identified a set of parameters that require estimation in order to effectively implement management measures that are commonly applied to spawning aggregation-based fisheries (e.g., measures identified in Rhodes and Warren-Rhodes 2005; Sadovy de Mitcheson et al. 2008; Russell et al. 2012). For example, for short-term temporal restrictions on catch, possession or trade to be applied to protect spawning aggregations, important parameters that need to be estimated include the lunar and seasonal periodicity of aggregation formation and duration (Fig. 2). By contrast, if specific spawning sites are to be closed to fishing, then spatial parameters need to be estimated, such as aggregation distribution. Justification for the selection of other parameters, particularly those that are less intuitive, is provided in subsequent paragraphs. The project then set out to identify and apply a range of methods and experimental techniques to estimate the selected parameters (Fig. 2). In designing site-specific studies, it was considered important to select methods that would enable parameters to be estimated within typical project timeframes (e.g. 2-3 years). This approach enabled parameter estimates derived by the project to be used in tools, developed herein, for evaluating management needs and measures (see next section).

In addition to typical methods applied in studies of spawning aggregation dynamics, such as underwater visual census and reproductive biology (e.g. Samoilys 1997b; Rhodes and Sadovy 2002a; Pears et al. 2007; Robinson et al. 2008), this study also employed acoustic telemetry. Acoustic telemetry was used to estimate fine-scale patterns in aggregation timing as well as parameters that can only be obtained from tagging studies, namely patterns in residency time and site fidelity (Fig. 2). Site fidelity is a critical but often misunderstood parameter that exerts a strong influence on the efficacy of spatial management measures (Nemeth et al. 2007). It is often assumed that individual fish use the same sites for spawning during each month of the spawning season. Though evidence for aggregation fidelity exists for several groupers (e.g. Luckhurst 1998; Zeller 1998; Starr et al. 2007), it may vary by sex. For example, females of some groupers do not attend every spawning aggregation event during the spawning season (Rhodes et al. 2012) and may therefore be exposed to fishing mortality for longer periods than males if management only involves protection of aggregation sites. Moreover, prior to the current study, levels of spawning aggregation fidelity in S. sutor were entirely unknown. Fidelity has implications for the consideration and design of spatial management measures, such as the fraction of spawning sites to protect. Clearly, individuals will be exposed to fishing mortality at unprotected spawning sites if fidelity is not absolute and only
a fraction of spawning sites are protected. As with MPAs for any mobile species, even relatively minor exposure to fishing mortality for nominally protected populations can undermine their persistence (Grüss et al. 2011a).

In order to examine the potential and need for gear-based management measures, the specificity of aggregation fishing practices was obtained from in-situ observations of aggregation fishing and landing site surveys. Aggregation-based fisheries are susceptible to overexploitation if highly efficient and habitat-destructive gears are introduced or effort is increased (Koenig et al. 2000; Aguilar-Perera 2006; Claro et al. 2009). The spatial and temporal distribution of effort among life history stages also influences fishing mortality. In most cases, a population will be fished while aggregating to spawn and also during the non-reproductive periods when it is distributed across home range areas. The proportion of annual catch or effort (i.e. fishing mortality) arising from the aggregation component of the fishery is a critical parameter for identifying vulnerability and the appropriate management response (Sadovy 2005; Robinson et al. 2011). This ratio of aggregation catch or effort to total annual catch estimates for the species is explicitly incorporated in the vulnerability indicator framework and NTRs model (see below). Moreover, it can be used as a proxy of the socio-economic importance of aggregation components of the fishery. For Kenyan studies, we conducted catch assessment, fisher knowledge surveys and mapping of fishing grounds to provide information on the ratio of aggregation catch to total annual catch, and also to provide information for other simple indicators on the socio-economic importance of spawning aggregation fisheries, including: (1) the importance of fishing for fisher and household income, (2) the importance of study species relative to the overall multispecies catch, (3) the relative importance of spawning sites relative to other fishing grounds, and (4) aggregation catch/effort relative to total annual catch/effort for the study species. Such assessments were conducted in Seychelles prior to the current project (Robinson et al. 2007; Robinson et al. 2011).

**Developing an indicator-based vulnerability framework**

Identifying the status of spawning aggregations and the populations that form them is a costly and scientifically rigorous exercise. For example, establishing a robust signal in trends of aggregation abundance through fisheries-independent methods, such as underwater visual census, typically requires several years of data collection. Sufficient time-series of data are also needed for fisheries-dependent indicators and assessment. However, existing fisheries data are often lacking or aggregated among multiple species, while some indicators, such as catch-per-unit-effort (CPUE), are complicated by hyperstability, whereby CPUE remains stable as abundance declines (Sadovy and Domeier 2005; Erisman et al. 2012; Robinson et al. 2011). We recognised the potential for an indicator-based framework to assess the vulnerability of aggregative spawners in data-poor contexts. Timely indication of vulnerability is important for prioritization of sites for intervention, consideration of precautionary management and justification of further research and monitoring.

To assess vulnerability of a fish population to aggregation fishing, we developed a framework that combines intrinsic and extrinsic indices. Intrinsic indices relate to the productivity and sensitivity of populations, in terms of their inherent capacity to respond to aggregation fishing. Extrinsic indices relate to the potential exposure (or susceptibility) of populations to the aggregation fishery. The intrinsic index is derived from published life history and reproductive parameters (www.fishbase.org) for a global list of verified aggregative spawners (Sadovy de Mitcheson et al. 2008). The extrinsic index is derived from fisheries information for the study fisheries, plus a group of other verified aggregation-based fisheries in the WIO. We identified relevant extrinsic indicators relating to the potential exposure of aggregations to a fishery. These indicators were scored on an ordinal scale by project team members with expertise in the study fisheries, with the scoring informed or quantified by data collected during field studies, either as part of this MASMA research programme or earlier studies (e.g. Aumeeruddy and Robinson 2006; Robinson et al. 2007).
Evaluation of management options: A per-recruit model to assess effects of spawning aggregation-based no-take reserves

A per-recruit model was designed to assess the effects of spawning aggregation-based NTRs in data-poor contexts. Per-recruit analysis models the fate of a cohort (i.e. population year class) following recruitment to the fishery, whereby estimates of yield in biomass from a given year class of recruits can be calculated based simply on knowledge of gains in biomass due to growth and the loss of biomass due to mortality. By varying levels of fishing mortality and selectivity characteristics of the fishery, these models can examine the effects of management measures in terms of fisheries and conservation objectives, measured as yield-per-recruit (YPR) and spawning stock biomass-per-recruit (SSBR), respectively.

While the model was designed to assess the effects of spawning aggregation-based NTRs, it is important to note that its utility enables other spawning aggregation management and conservation measures to be considered. The model is structured to control access by the fishery to spawning fish by varying the fraction of spawning sites protected. However, if all spawning sites are protected then the effects of NTRs (assuming they also protect migratory corridors and staging areas, Nemeth 2012) will be the same as prohibiting possession, catch and sale of fish during periods when aggregations form. Either way, fish would escape mortality during the spawning periods. In recognition of the fact that NTRs are already widely applied in the region (IUCN 2004), we also compare the effects of protecting fractions of spawning aggregation sites (direct spawning aggregation measures; Fig. 1) with the effects of protecting fractions of the non-reproductive residence area that includes juvenile habitat (here considered a fishery measure together with, for example, gear restrictions; Fig. 1). Gear-based measures are not explicit in the model. However, the effect of prohibiting specific gears, or gear-use practices, for migrating or aggregating fish (e.g. setting nets on migratory corridors or around aggregations) would be equivalent to protecting all spawning sites if these are the sole method used. Gear measures that protect juveniles will also be equivalent to protecting juvenile habitat with NTRs. Other measures commonly applied to spawning aggregation-based fisheries (Fig. 2) are, where applicable, considered qualitatively for our study fisheries.

Table 2. Key parameters included in the per-recruit model for which estimates can be derived from field studies (CAS: catch assessment survey; FK: fisher knowledge survey; AT: acoustic telemetry; UVC: underwater visual census; EM: effort mapping).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total annual fishing effort</td>
<td>CAS, FK</td>
</tr>
<tr>
<td>Spawning aggregation duration</td>
<td>AT, UVC</td>
</tr>
<tr>
<td>Sex-specific spawning aggregation residency</td>
<td>AT, UVC</td>
</tr>
<tr>
<td>Fraction of annual effort on spawning aggregations</td>
<td>CAS, EM</td>
</tr>
<tr>
<td>Spawning and non-spawning site catchability</td>
<td>CAS, UVC</td>
</tr>
<tr>
<td>Spawning site fidelity</td>
<td>AT</td>
</tr>
</tbody>
</table>

In line with the aim of developing a model that could be applied in data-poor contexts, we included parameters that can be estimated based on data typically collected in relatively short term studies of spawning aggregations and specifically addressed through our site-based field studies (Table 2). The information needed to run the model is relatively easy to obtain and includes the level of annual fishing effort exerted on fish populations and the fraction of this annual effort directed towards spawning aggregations. Estimates (by proxy) of catchability at spawning and non-spawning sites are required, as are a number of other biological parameters such as a length-weight relationship, age at maturity and age at sex-change for protogynous populations. While these parameters were not specifically addressed in our research programme, estimates from the same or other populations are often available. The indicator framework is explored in Chapter 11 and the application of the conceptual model in Seychelles is presented in Chapter 12.
Chapter 3: Targeted fishing of the shoemaker spinefoot rabbitfish, *Siganus sutor*, on potential spawning aggregations in southern Kenya
George Waweru Maina, Melita Samoilys, Hussein Alidina and Kennedy Osuka

Introduction
The importance of understanding the reproductive behaviour of reef fishes for formulating sound management practices is now globally recognised (Sadovy 1996, Sadovy de Mitcheson et al. 2008). Further, the occurrence of spawning aggregation formation as a reproductive strategy that renders fish potentially vulnerable to fishing is now recognised as a conservation and fisheries management concern (Russell et al. 2012). However, in the Western Indian Ocean (WIO), information on fish spawning aggregations is still scarce, with most reports coming from Seychelles and Kenya (Robinson et al. 2004; 2008a, b; 2011; Samoilys et al. 2006). These have identified that the shoemaker spinefoot rabbitfish, *Siganus sutor*, forms spawning aggregations and that they are targeted by fishers (Robinson et al. 2004; 2008a; 2011; Samoilys et al. 2006).

Weak fisheries management regimes in the WIO have left reef fisheries prone to overfishing and compound the ability of reef fishes to maintain their roles in ecosystem functioning and promoting reef resilience. As a herbivore, *S. sutor* potentially plays a role in conferring coral reef resilience to bleaching (Hughes et al. 2003; Bellwood et al. 2004). The identification and protection of reef fish spawning aggregations is also considered central to designing resilience based management practices and marine protected areas (TNC 2004; Obura and Grimsditch 2009). There is therefore an urgent need to identify and assess the management requirements of aggregation spawners, particularly those targeted by local fisheries.

The sustainability of a fishery that targets spawning aggregations is generally considered to be low (Sadovy de Mitcheson et al. 2008), though there are exceptions and these include a recent analysis of the targeted fishery on spawning aggregations of *S. sutor* in Seychelles (Robinson et. al. 2011). In Kenya *S. sutor* comprises a significant component of the artisanal fisheries and is taken mainly by basket traps, nets and hook and line (Ntiba and Jaccarini 1988; Kaunda-Arara and Rose 2004; McClanahan and Mangi 2004). While heavily fished, *S. sutor* is assumed to be resilient to fishing since studies from Mauritius and Seychelles show it is fast growing and short-lived, with a maximum age of 2-2.5 years (Jehangeer 1988; Grandcourt 2002). Although the species is among the most targeted in artisanal gear catches along the Kenyan coast (Samoilys et al. 2011a), sustainable harvest levels have not been determined. The relative contribution of catches taken from *S. sutor* spawning aggregations to fishers’ incomes remains unstudied and the impacts of targeted fishing of spawning aggregations of *S. sutor* in Kenya is unknown.

Local knowledge of fish and fisheries can compliment biological and ecological studies and is critical to formulating appropriate fisheries management. Fisher knowledge of reef fish spawning aggregations is increasingly recognised and incorporated in research and management (Johannes 1989; Johannes et al. 2000; Robinson et al. 2004; Hamilton 2005; Samoilys et al. 2006; Tamelander et al. 2008). Fisher knowledge surveys are generally a cost-effective and expeditious way to locate potential spawning aggregations when conducted under appropriate cultural and methodological guidelines (Hamilton et al. 2012). This study used fisher knowledge to compliment a broader multi-disciplinary study on the *S. sutor* fishery in southern Kenya, and worked with the fishery co-management institutions, the Beach Management Units (BMUs), which were established in Kenya through Fisheries Regulations in 2007 (GoK 2007).

This study aimed to quantify the *S. sutor* fishery, to identify potential spawning aggregation sites and how these are fished by fishers from Msambweni on the south coast of Kenya. We sought
to identify critical information gaps for management by: (i) documenting spatial and temporal patterns in catch rates to determine the extent to which spawning aggregations are fished; and (ii) determining the relative contribution and economic importance of *S. sutor* and its reported spawning aggregations to the local fishery and to fishers’ incomes.

**Methods**

The study was conducted in 2009-2010 in the Msambweni area on the south coast of Kenya. Two principal methods were used in this study: (1) questionnaire-based interviews with fishers to determine their knowledge of spawning aggregations and (2) fishery creel surveys to quantity landed catch, effort, species composition and to identify fishing grounds. During interviews and fishery creel surveys, a disparity in the names and locations of individual fishing sites among surveyed fishers was identified. As a result, four reliable senior (patriarch) fishers were invited to a 2010 mapping workshop to collectively standardise names and locations of fishing grounds.

**Fisher knowledge surveys**

A total of 32 experienced fishers were surveyed, including 25 that used basket traps and handlines, the principal gears for *S. sutor*, and 7 fishers that used other gears (Table 1). Fishers were chosen from prior interviews or with assistance from local government data collection personnel.

To document fisher knowledge of spawning aggregations and aspects of the value of the *S. sutor* fishery, a modified questionnaire (see Annex 1) was developed from previous regional surveys (Robinson et al. 2004; Samoilys et al. 2006). Interviews were conducted in Swahili between March 2009 and December 2010 at three fish landing sites (Table 1), and typically lasted 30–60 min. The questionnaire was designed to quantify catch, effort, location and usage of fishing grounds, spawning aggregation knowledge (time, location, targeted fishing), markets, income and revenue.

**Creel survey**

Creel surveys were conducted for three consecutive days over the new moon period every month for one year at the Mkunguni Beach Management Unit (BMU) landing site, in Msambweni. Surveys quantified the frequency of occurrence and quantity of *S. sutor* in artisanal catches, gear type used and fishing location. Gravid females were identified by swollen abdomens and the extrusion of eggs and were noted during catch monitoring, where possible. Individual catches were sorted to species, and weighed (to 0.1 kg), with unidentifiable species photographed for subsequent identification based on published sources (Smith and Heemstra 1998; Lieske and Myers 2001). Surveys also recorded gear type, trip time, fisher number and captain, and fishing location. Catches >20 kg were sub-sampled and weighed by species and extrapolated to provide total catch volume. The BMU leaders of Mkunguni and their records were used to verify fisher and gear numbers and fishing effort from this landing site.

**Data Analysis**

The questionnaire survey data were analysed to identify possible *S. sutor* spawning aggregations, following Robinson et al. (2004) and Samoilys et al. (2006). Spawning aggregation information was only considered reliable if independently corroborated by two or more fishers. To verify that the spawning aggregation information reported by fishers corresponded with defined criteria for
verifying spawning aggregations, we used the definitions recommended by the Society for the Conservation of Reef Fish Spawning Aggregations (SCRFA: www.scrfa.org) whereby an aggregation is defined as finding densities of four times or more at a site, temporarily, and spawning is defined by either direct or indirect indicators (Colin et al. 2003). Direct indicators include gamete release in the water and multiple gravid females. Indirect indicators include high seasonal landings, high GSI, courtship behaviour and colour changes associated with spawning (Domeier 2012; SCRFA database: http://www.scrfa.org/database/index.php).

The weight and value of the *S. sutor* fishery in Msambweni and the relative contribution of catches from possible spawning aggregations to fishers’ total catches and income from fishing were calculated for 2010 from estimations of annual catch from Msambweni. This was estimated as follows:

Annual *S. sutor* catch (kg per year) = CPUE (kg/fisher/day) x fishers/day x fishing days/yr

CPUE for *S. sutor* was estimated as a proportion of total catch (all species) by gear owing to an inability to separate catch by species prior to sale. The proportion of *S. sutor* contributing to catch was obtained from fishers’ recall. Total number of fishers per day was taken from BMU records, while the number of fishing days per year was estimated from fishers’ interviews. Error terms are standard error (SE) throughout.

**Results**

**Catch composition**

A total of 37 fish families were identified in the creel surveys at Msambweni landing site during the study period (Figure 1a). Lethrinidae and Siganidae dominated the catch, accounting for 39.2% and 39.1% of the total catch, respectively. *S. sutor* (38.2%), the Thumbprint emperor, *Lethrinus harak* (18.3%) and the Sky emperor, *Lethrinus mahsena* (9.3%), represented nearly two-thirds (65.8%) of the total catch by number (Figure 1b).

**Fishing gears, operation and catch rates**

Creel surveys determined that basket trap, gill nets and hook and line contributed 99% of the landed *S. sutor* by number, with 51% contributed exclusively by basket traps (Table 2). For combined species catch, gill nets produced the highest CPUE of 4.6 (±0.25) kg/fisher/trip. During interviews fishers reported that basket traps and hook and line were the primary gears they used to target the presumed spawning aggregations. They also said that these gears averaged 62.5% of all landed catch by weight (range=50-75%) and catch rates of 2.3 and 2.1 kg/fisher/trip, respectively (Table 2).

Fishers were asked to recall unusually high catches of *S. sutor* as a possible indication of spawning aggregation fishing. They reported declines in these high catches over a 20-year period (1989-2009) in both basket traps and hand lines (Figure 2): from 27.5 to 7.6 kg/fisher/year for basket traps and from 92.5 to 14.9 kg/fisher/trip for handlines. Lowest catch rates also followed a similar declining trend (Figure 2). However, recall estimates were greater than those from creel surveys (Table 2), suggesting fishers may exaggerate their catch rates.

Hook and line fishers reported in interviews that they used dried octopus ink sacs for catching *S. sutor* with handlines (Plate 1) on presumed spawning aggregations, though reported the *S. sutor* infrequently bite during spawning. Fishers also reported that spear fishers pass on information about large numbers of *S. sutor* on the presumed spawning aggregation sites to the basket trap and hook and line fishers in return for a portion of their catch. Some Msambweni fishers suggested that if not fished, fish would escape to areas inaccessible to them.
Spatio-temporal distribution of catches and fishing effort for S. sutor

Creel survey data, aggregated across the year, identified that fishers from Msambweni fished at 17 different fishing grounds, with 10 fishing grounds accounting for the majority of catches. Details of fishing ground name and location are not fully reported here for confidentiality reasons. Basket traps and hook and line catch rates showed similar spatial patterns with the highest catch rates

Fig. 1. Composition (by number) of fish catches by (a) family and (b) species at Msambweni landing site, March 2009 - March 2010 (n= 16,217 individual fish). Families and species whose catch composition was less than 1% were combined and categorised as “others”.

Spatio-temporal distribution of catches and fishing effort for S. sutor

Creel survey data, aggregated across the year, identified that fishers from Msambweni fished at 17 different fishing grounds, with 10 fishing grounds accounting for the majority of catches. Details of fishing ground name and location are not fully reported here for confidentiality reasons. Basket traps and hook and line catch rates showed similar spatial patterns with the highest catch rates
recorded from inshore close to the coastline of Msambweni just south of the Mkunguni landing site and around Chale Island (Figure 3a,b). Both these areas are dominated by seagrass beds with some patches of corals (MS pers. obs.). Catches were also recorded from site A, B and C, the presumed spawning aggregation sites (Figure 3), which comprised offshore coral patch reefs around 8-12 m in depth surrounded by a gently sloping soft substrate of sand, rubble and seagrass beds which are further described in Chapter 5. Siganidae comprised more than 40% of fish by number in catches from 5 fishing grounds: Msingini (91%), Site B (64%), Site C (60%), Chale (51%) and site A (47%) (Figure 3c), though relative differences in total catch between sites were large with low numbers of fish taken from site B.

Table 2. Msambweni fishery statistics showing fishing duration by gear; catch proportions (% by numbers of individual fish, n = 16,257) by gear for all species combined and for S. sutor alone (n = 6,200); and catch rates (mean ±SE CPUE) by gear. All data are from creel surveys except CPUE for S. sutor which was derived from fishers’ recall.

<table>
<thead>
<tr>
<th>Fishing gear</th>
<th>Fishing duration (hrs)</th>
<th>Catch proportions (%)</th>
<th>CPUE (kg/fisher/trip)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>All spp.</td>
<td>S. sutor</td>
</tr>
<tr>
<td>Basket trap</td>
<td>4.90 ± 0.05</td>
<td>29.2</td>
<td>51.0</td>
</tr>
<tr>
<td>Gillnet</td>
<td>6.85 ± 0.11</td>
<td>34.6</td>
<td>26.0</td>
</tr>
<tr>
<td>Hook &amp; line</td>
<td>6.83 ± 0.05</td>
<td>33.2</td>
<td>22.1</td>
</tr>
<tr>
<td>Speargun</td>
<td>5.65 ± 0.13</td>
<td>3.0</td>
<td>0.8</td>
</tr>
<tr>
<td>All gears</td>
<td>100</td>
<td>38.2</td>
<td></td>
</tr>
</tbody>
</table>

Seasonal changes in the location of fishing reflected in catch rates of siganids were evident with the highest CPUE recorded from offshore fishing sites during the presumed spawning season whereas during the non-spawning season the highest catch rates were recorded inshore (Figure 4).
This seasonal shift was seen in both fishing gears (Figure 4a,b,c,d). Spawning season months (November to February) are defined below and were verified through concurrent studies (Chapters 4, 5).

**Fishers’ knowledge of S. sutor spawning aggregations**

Interviewed fishers averaged 29.3±2.2 (SE) years of fishing experience, while those who reported knowledge of *S. sutor* aggregations averaged 48.6±2.0 years old. The descriptions of *S. sutor* spawning aggregations from fishers and the frequency of fishers citing these spawning signs indicated that awareness of *S. sutor* spawning aggregations was found in 27 out of the 32 fishers interviewed. The most frequently reported indicators of possible reproductive activity (indirect verification, Colin et al. 2003) were increased abundance of fish (71.9% of fishers) and courtship (40.6% of fishers). Note that basket trap fishers enter the water with masks to check and set their traps. Only 14% of fishers said they had observed cloudy/misty substance in water and gravid females with swollen abdomens. Direct observations of gamete release were reported by two fishers. Out of the 27 fishers knowledgeable about spawning aggregation activity, 15 fishers reported knowledge of sites of spawning aggregations, mentioning six *S. sutor* spawning aggregation sites. Twelve of these fishers mentioned the three presumed spawning aggregation sites, A, B, and C, which were cited by 12, 9 and 8 interviewees respectively, and they described indicators of spawning from these sites. The other 3 sites were mentioned by 2 fishers each. Fishers from Mvuleni (25 km north of Msambweni) reported that 10 years previously (prior to 2000) they used to target *S. sutor* spawning aggregations sites off Msambweni, indicating that these presumed spawning aggregation sites were well known regionally and have been fished for at least a decade (Mzee Hemedi and Mzee Chicho, pers. comm.).

**Spawning season**

Fishers reported that peak spawning aggregation activity occurred between November and February, though reports ranged from March through October (Figure 5). Only 2 fishers reported *S. sutor* aggregations during June, July or September with no reports of aggregation formation in August. Monthly catch rates varied through the year with the highest CPUE recorded in August (Figure 5). Catch rates during the full moon of December doubled that of new moon, but not in January (Figure 5). This information was used to define the purported spawning months of *S. sutor* as November to February, and non-spawning months as March to October.

Ninety percent of fishers reported that *S. sutor* aggregates to spawn during the full moon period between the 14th and 19th day of the lunar cycle (Figure 6). One fisher reported spawning throughout the year.

Observations of swollen abdomens and hydrated eggs (Plate 2) were observed during creel surveys of *S. sutor* catches between November and January but these were not quantified. A concurrent study on the reproductive biology of *S. sutor* from these same catches recorded the highest peak of gonadosomatic index and running ripe females in November and January (Chapter 4).
Fig. 3. Spatial patterns of catches in the Msambweni area: (a) kg/fisher/trip from basket traps; (b) kg/fisher/trip from hook and line; (c) Number of siganids/fisher/trip, all gears combined. Sites A, B and C are presumed spawning sites. (See colour plates.)

Targeted fishing of spawning aggregations
Using hook and line and basket traps, fishers reported targeting Sites A, B and C for 4 days per month, from November to February (Table 3, parameter iv). They also reported that the duration of aggregation formation, and therefore their fishing of them, had declined in recent years from
7 to 4 days which they said was due to fishing pressure and disturbance. Msambweni fishers reported conflicts with other fishers, particularly those from Gazi, who they said used nets to target aggregations at these three sites.

Fig. 4. Shifts in fishing effort reflected by catch rates (kg/fisher/day) of siganids in the Msambweni area during the presumed spawning season (November-February, a and c) and presumed non-spawning season (May-September, b and d). (See colour plates.)
Fishers reported that they increased their fishing effort during November to February on the presumed spawning aggregation sites by using additional traps, increasing the number of traps set per day from 1 to 2, and increasing the duration of fishing by 1.6 (±0.3) hr. per day, equivalent to an increased fishing duration of 32.7% for traps and 23.4% for hook and line (Table 2). Fishers also reported their catch rate increased during this period by 3.5 (±0.4) times relative to other months (Table 3, i and ii).

**Importance of S. sutor and their spawning aggregations to artisanal fishers**

BMU records showed there were 164 fishers, 50 fishing canoes and 158 basket traps in Msambweni. BMU reports indicated that 45% of fishers were full-time, while the remainder engaged in farming and business part-time when fishing income is poor. Of the 164 fishers, 75 used basket trap, 30 used hook and line and 18 used nets. Based on 45% being full time, we calculated 34 trap fishers, 14 hook and line fishers and 8 net fishers as full time fishers and estimated total catches of *S. sutor* from presumed spawning aggregations for this group only. Fishers (n=32) reported that they make 1.0 (±0.0) fishing trip per day, 5.7 (±1.5) fishing trips per week, and fish on average 3.2 (± 0.2) weeks per month.

The total catch of *S. sutor* harvested by full time fishers (Table 3, iii) in Msambweni during the 16 days of putative spawning aggregation formation (Table 3, iv) was estimated at 6,077kg/year (Table 3, v). This represented 25.8% (Table 3, viii) of the annual catch, 23,551kg/yr (Table 3, vii). The value of the *S. sutor* catch from presumed spawning aggregations in 2010 was USD ($) 6,685 (Table 3, v). These estimates were derived from all possible spawning aggregations in the total fishing area used by the 45 full time Msambweni fishers. Estimating the catch taken only from the three presumed spawning sites (A,B,C) was difficult because the spatial and temporal pattern in the fishers’ fishing activity was not measured. An approximate value was calculated from the proportion of fishers in the sample of interviewees that fished these three sites, 12 of the 27 knowledgeable fishers, and this value (44%) applied to the total catch of all 45 fishers to give a crude estimate of 2,701kg/yr (Table 3, xi) taken from the three putative spawning sites (Table 3, ix). Clearly this estimate is very approximate. An alternative yield per area method, based on total yield during the presumed spawning season, the total area of the fishing grounds and the

![Fig. 5. Monthly timing of *S. sutor* spawning aggregations from fishers interviews (bars, primary axis, n=27) and mean CPUE (kg/fisher/trip) during the new moon, for basket traps and hook and line combined (dark circles, secondary axis) from creel surveys (data not collected in November). Additional CPUE creel measures on the full moon were recorded in December and January (open circles).](image-url)
pooled sizes of the three spawning aggregation sites (0.064km², see Chapter 5) gave implausibly low estimates of total annual catch from the three sites and was therefore dismissed.

Income, revenue and dependence on fishing
Fishers reported that fish price varies depending on species, preference and fish availability, with fish value graded as “small” (low value) and “large” (high value). Large grade fish include *S. sutor* and range in price from KES. 114.2 (± 14.1) to 80.0 (± 22.1), with a mean of KES. 89.4 (± 26.9) (~$ 1.1 at an average 2011 exchange rate). Fish are marketed through middlemen who sell locally. *S. sutor* obtained during the presumed spawning season were sold both locally and in nearby towns (Ukunda, Likoni and Mombasa) when the local market in Msambweni was saturated. Fishers reported that they rarely got surplus catches that would require storage facilities or ice, since landed fish have a ready market.

For 90% (n=32) of the respondents, income from fishing accounted for >75% of their total household income, with fisher households having an average of 7.7 (±0.5) members. In terms of socio-economic dependence, 20 of the 32 fishers (63%) depended exclusively on fishing as their income activity. Note that these fishers were preferentially selected for this study based on their likely knowledge of fishing spawning aggregations and therefore these dependency values are not representative of all fishers on the Kenyan coast.
The input costs of fishing were minimal because non-motorised boats are used and bait is collected by hand on the shore. The cost of hiring a canoe for a day of fishing was reported as KES. 200 (~$ 2.4). None of the fishers stated a value for their time spent fishing as part of their input costs.

Discussion
Through interview-based fisher knowledge surveys and creel surveys over 12 months this study provides an in-depth view on a siganid fishery at an artisanal catch landing site in southern Kenya. It was part of a wider multi-disciplinary study on this species reported further in Chapters 4 and 5. The results show that *Siganus sutor* is a major contributor to the local artisanal catches in Msambweni and it is also subjected to targeted fishing of reported spawning aggregations.

Description of Siganus sutor fishery
*S. sutor* was the single species contributing the highest proportion by number of fish in catches pooled across four primary gears used in Msambweni, with basket traps catching the most, at 51.0% of the catch. Previous studies for different locations on the Kenyan coast also report *S. sutor* as a major component of artisanal catches (Kaunda-Arara and Rose 2004, McClanahan and Mangi 2004, Maina et al. 2008, Locham et al. 2010) and a recent coast wide analysis of all fishery data

### Table 3. Calculations of the proportion of *S. sutor* catches taken from presumed spawning aggregation sites and their economic importance in the *S. sutor* fishery in Msambweni. Parameters (i) – (ix) are referred to in main text

<table>
<thead>
<tr>
<th>Indicator</th>
<th>Calculations</th>
<th>Basket trap</th>
<th>Hook and line</th>
</tr>
</thead>
<tbody>
<tr>
<td>i. Mean (all months) <em>S. sutor</em> CPUE (kg/fisher/trip)</td>
<td>see Table 2</td>
<td>2.3</td>
<td>2.1</td>
</tr>
<tr>
<td>ii. Predicted <em>S. sutor</em> CPUE from presumed spawning aggregations (kg/fisher/trip)</td>
<td>3.53 * (i)</td>
<td>8.1</td>
<td>7.4</td>
</tr>
<tr>
<td>iii. Number of daily active fishers (fishers/day)</td>
<td>based on 45% of total</td>
<td>34</td>
<td>14</td>
</tr>
<tr>
<td>iv. Duration of targeted fishing on presumed spawning aggregations (days/year)</td>
<td>4 days/month x 4 months</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>v. Annual catch of <em>S. sutor</em> taken during times of presumed spawning aggregations (kg) and value (USD)</td>
<td>(ii) * (iii) * (iv) 1kg = 89.4KSh = $1.1</td>
<td>4,416.7</td>
<td>1,660.5</td>
</tr>
<tr>
<td>vi. Number of fishing days per year (^1)</td>
<td>5.7 * 3.2 * 12</td>
<td>219</td>
<td></td>
</tr>
<tr>
<td>vii. Annual <em>S. sutor</em> catch (kg/yr) (^3)</td>
<td>(i) * (iii) * (vi) 1kg = 89.4KSh = $1.1</td>
<td>17,116</td>
<td>6,435</td>
</tr>
<tr>
<td></td>
<td>total: 23,551</td>
<td>$ 25,906</td>
<td></td>
</tr>
<tr>
<td>viii. Proportion of annual <em>S. sutor</em> catch taken during presumed spawning times</td>
<td>(v / viii) * 100</td>
<td>18.75%</td>
<td>7.05%</td>
</tr>
<tr>
<td>ix. Proportion of <em>S. sutor</em> catches (kg &amp; %) taken annually from the three presumed spawning sites and value</td>
<td>44% * (v)</td>
<td>2,701kg/yr (11.5%) $2,971</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) Fishermen reported that they catch 3.53 ± 0.44 times more when they fish presumed spawning aggregations of *S. sutor* compared with non-spawning times.

\(^2\) Fishers reported that they make one fishing trip per day, 5.7 ± 1.45 fishing trips per week, and fish on average 3.2 ± 0.24 weeks per month.

\(^3\) Kg/fisher/trip x fishing days/yr x fishers/day
found *S. sutor* contributed up to 44.8% of the catch from five commonly used gears which include the same four gears in this study, plus beach seines (Samoilys et al. 2011b). Three fishing gears, basket trap, hook and line and gill net, dominated the *S. sutor* fishery in Msambweni but fishers reported that they only used basket traps and hand line to catch *S. sutor* on spawning aggregations which was supported by observations of fishing boats and traps on the three purported aggregation sites during December-March (GW, MS pers. obs; see also Chapter 5). This result is noteworthy as it indicates that gear based controls for these two gears could be considered in management options. Fishers also said that they used small gill nets on inshore fishing grounds to target *S. sutor* returning from aggregation sites, and that neighbouring fishers used small purse seines to target aggregations, but we were unable to verify these statements.

**Fishers’ knowledge of spawning aggregations and targeted fishing of spawning sites**

The majority of fishers (84%) reported that they were knowledgeable of spawning aggregations of *S. sutor* providing information on the movement of *S. sutor* to offshore spawning aggregation sites, the location of key spawning sites and the seasonal and lunar timing of their formation. The use of key informants, some recommended by other fishers, no doubt contributed to this extensive knowledge. This information does not provide direct verification of the existence of these spawning aggregations because none of the indicators of spawning aggregation occurrence (Colin et al. 2003, Domeier 2012) are fully met. In particular, high seasonal landings and multiple gravid females that could be attributed to these three sites were not measured. The fishers’ knowledge collected here was, however, corroborated by underwater visual census surveys and acoustic tagging of *S. sutor* around the same three spawning aggregation sites (Chapter 5). Further, the fishers’ information closely matched our observations of *S. sutor* with distended bellies and exuding hydrated (“running ripe”) eggs in artisanal catches during the November-February. We therefore conclude that these studies, together with measures of GSI (Chapter 4), collectively provide convincing evidence that the three sites were spawning aggregations sites. It is strongly recommended that a future study address this research gap by working with fishers targeting the three sites to measure their catches, document the total fishing effort and take samples to verify females are running ripe. Our study demonstrates the importance of using fishers’ knowledge in fisheries management and research (Johannes 1997, 1998, Seixas and Begossi, 2001, Sadovy and Cheung, 2003, Sadovy and Domeier 2005, Tamelander et al. 2008) which is also an inexpensive and relatively quick way of locating and understanding spawning aggregations.

Reproductive biology studies along the East African coast have reported two distinct spawning seasons for *S. sutor*: January/February and May/June off the Kenyan coast (Ntiba and Jaccarini 1990); and an extended December to May spawning season with a peak in March for *S. sutor* in Dar es Salaam marine reserve systems (Kamukuru 2006). Fishers reported spawning aggregations of *S. sutor* formed primarily during November to February during and just after the full moon period and they used the Islamic lunar calendar to precisely identify days of spawning, equivalent to the “lunar day” presented in this study. Many reef fishes spawn in time with the moon (Johannes, 1978, Robinson et al. 2004, Sadovy de Mitcheson 2008) including rabbitfish. For example Seagrass and Spiny rabbitfish spawn on or around new moon (Harahap et al. 2001; Rahman et al. 2003), whereas Golden rabbitfish and the Forktail rabbitfish synchronously spawn around the first and last quarters of the moon, respectively (Rahman et al. 2003; Takemura et al. 2004). Based on the present study and associated studies (Chapters 4 and 5) we suggest that *S. sutor* appears to have its peak spawning period between November and February which was corroborated by elevated gonadosomatic indices (GSI) which were highest during November-January (Chapter 4). This is very similar to that seen in the timing of *S. sutor* spawning aggregations on the Seychelles Banks which peak in November - December (Robinson et al. 2004). The full moon timing of the aggregations reported by fishers here was corroborated by elevated GSI values from females caught during the full moon period and UVC and acoustic tagging surveys in the same area (Chapters 4 and 5). Full moon timing of spawning aggregations was also detected by detailed acoustic tagging work on *S. sutor* in Seychelles (Chapter 6).
Spatial and temporal patterns in fishing and catch rates from the 12 months of creel survey data showed that the bulk of catches and hence fishing effort on *S. sutor* were from the inshore areas in the seagrass beds fringing the shore or within the lagoon inside the fringing reef, or within Gazi Bay. The shift in fishing effort during the spawning season to offshore, including the possible spawning aggregation sites, provides support for the existence of these temporal spawning aggregations and the interpretation that fishers target them. However, GSI values also showed a peak in June-July (Chapter 4). We were unable to verify this through fishers’ knowledge and rough weather confounds the fishing pattern: the fact that fishers do not fish offshore during the presumed non-spawning season may simply be a result of the strong seas during that south-easterly monsoon season. Nevertheless we maintain that fishing the three spawning aggregation sites during the full moon periods of Nov-Mar represents a targeted spawning aggregation fishery for *S. sutor* in the Msambweni area.

The results leave us with several questions: how common are offshore spawning aggregation sites for *S. sutor* along the Kenyan coast? Are the sites off Msambweni a feature of this broken up stretch of reef with no distinct fringing reef, or do *S. sutor* find offshore patch reefs outside the fringing reef further north? Do *S. sutor* spawn simply in pairs in their home ranges during June-July? Possibly, they do migrate to the offshore aggregation sites in June-July but fishers do not fish them at that time because the weather is very rough and the sites inaccessible to fishers in dug-out canoes. This was corroborated by very few landings from the three spawning sites during the south-east monsoon months of June-July.

Fishers reported a 3.5 fold increase in their catch rates when fishing spawning aggregations which gave them substantially higher catch rates. However, they also reported substantial declines (>70%) in catch rates of *S. sutor* over the last 20 years. This trend may reflect a rate of decline in the size of spawning aggregations or overall declines in the stock, or both. The maximum numbers of *S. sutor* observed underwater on the three aggregation sites was only 184 (Chapter 5), compared with several hundred observed in Seychelles (Robinson et al. 2004). Several fishers said that the sizes of *S. sutor* spawning aggregations today are far below the levels observed before the 1980s, and also last for a shorter period, and that knowledge of *S. sutor* spawning aggregations has become increasingly widely known, though, perhaps surprisingly, they did not attribute declines in catches to targeted fishing of aggregations. Negative impacts from targeted fishing of spawning aggregations are now well documented (e.g. Sadovy 1994, Claro and Lindeman, 2003, Sadovy and Domeier, 2005). The declines reported here by fishers, the possible changes in spawning behaviour of *S. sutor* and the low numbers in aggregations are all cause for concern over the sustainability of current fishing practices on *S. sutor* populations. However, the “r” strategy life history pattern seen in *S. sutor* of short life span of around 2 years (Jehangeer 1988; Grandcourt 2002), protracted spawning season and dual modes of spawning may make the species resilient to heavy fishing pressure.

**Value of spawning aggregation fishing of *S. sutor* to fishers**

This study established that fishers exploit three *S. sutor* likely spawning aggregation sites for home consumption and sale locally, a practise that they say has existed for generations. We calculated that catches of *S. sutor* landed from basket traps and hook and lines within the estimated total period of aggregation spawning (16 days), was valued at $6,685 and this represents 25.8% of the annual *S. sutor* catch (23,551 kg.yr⁻¹). However, this estimate is likely to be an over-estimate because it assumes that all active fishers would fish aggregations during the reproductive period. Therefore we proposed a more realistic, albeit approximate, estimate of the total annual catch from these three aggregations as 2,701 kg.yr⁻¹, valued at $2,971, representing 11.5% of the total annual *S. sutor* catch, based on a projected number of fishers potentially fishing these sites. A concurrent study measured the combined area of the three spawning aggregation sites at 0.064 km² (Chapter 5) which indicates the spawning aggregation harvest of 2,701 kg.yr⁻¹ is equivalent to a yield of 42.2 t.km⁻².yr⁻¹ of *S. sutor*, a yield that is 7 times more than the average productivity of Kenyan reefs (Samoilys et al. 2005).
However, observations of fishing boats on the aggregation sites during this study (see Chapter 5) suggest that fewer fishers engage in this targeted fishery and therefore our estimated catch of *S. sutor* from the spawning sites is likely still an over-estimate. Counts of fishing boats on the aggregation sites during December to February gave an average of 3.7 boats per day (Chapter 5). The average crew size of a basket trap fishing operation is 1.3 and that of a handline operation 1.5 (Samoilys et al. 2011a). Since observations did not distinguish gears, we take an average crew size of 1.4 to give an average of 5.2 fishers fishing per day on the three aggregations which gives a total number of 83 fishers for the 16 days of spawning. These calculations reduce the estimation of annual catch of the three aggregation sites from 2,701 kg yr\(^{-1}\) to 675.5 kg yr\(^{-1}\). In conclusion, aggregation fishing may yield somewhere between 2.9% and 11.5% of the total annual catch of *S. sutor* in this Msambweni area, with a corresponding value of between $743 and $2,971. These calculations further illustrate the difficulty in accurately measuring total catches from spawning aggregations. In addition, there are indications that *S. sutor* may spawn in aggregations for longer periods than estimated in this study and that the three aggregations studied are also exploited by fishers who land their catch at neighbouring fish landing sites. The wide disparity in values and the crude calculations clearly indicate further research is needed. However, as a first step, we recommend these values are fed back to the fishers in Msambweni to ask for their views on the most realistic values.

**Management implications**

A recent study has raised concerns of the increasing fishing pressure on *S. sutor* along the Kenyan coast (Samoilys et al. 2011b). Combined with the results of the present study, this finding led to the submission of a Policy Brief to the Kenyan government recommending that a species specific management plan for *S. sutor* be developed and that spawning aggregations be managed through protected areas (Samoilys et al. 2011c). This is in line with the government’s draft Fisheries Bill that advocates protection of spawning grounds (GoK 2012). It also built on global recommendations for protection of spawning aggregation sites through protected areas (Russell et al. 2012) which have been used successfully in local community fisheries in Papua New Guinea (Hamilton et al. 2011). Further, Locally Managed Marine Areas (LMMAs) are gaining momentum in Kenyan coastal communities with 14 established in the last five years (Abunge 2011; Maina et al. 2011) demonstrating protected areas as a viable management approach in Kenya. Although *S. sutor* is a fast growing species with low intrinsic vulnerability to fishing, a vulnerability assessment of the Msambweni *S. sutor* fishery found comparatively high extrinsic pressure on the aggregations due to use of nets and absence of management (Chapter 11). Protected areas have been demonstrated to be beneficial for a less heavily exploited *S. sutor* population in Seychelles and benefits are predicted to increase with level of fishing pressure (Chapter 12), lending further support for this approach for the Kenyan south coast.

Livelihood implications are critical to any discussions of management options. This study established that fishing is the main livelihood activity for the Msambweni community with 90% of fishers >75% reliant on fishing and therefore spawning closures would, initially at least, bring a loss in revenue to fishers. This loss or opportunity cost may range between $743 and $2,971 per year for all basket traps and handline fishers combined. A participatory process of engagement with fishers to discuss management of spawning aggregations is essential and is enshrined in Kenya’s co-management Fisheries Regulations, the BMUs (GoK 2007). Some of the fishers we interviewed have exploited these spawning aggregations for decades; they must therefore be fully involved in any management deliberations. The results of this study and associated studies (Chapter 5) have partially been fed back to the fishers of Msambweni and management options discussed. Fishers have expressed an interest in establishing protected areas for the spawning sites. Focused dialogue with fishers and relevant government agencies is now needed to discuss and present the results in detail and to evaluate protected areas together with other management options for the *S. sutor* aggregation fishery on the south coast of Kenya.
Chapter 4: Estimation of important reproductive parameters for management of the Shoemaker spinefoot rabbitfish (Siganus sutor) in Kenya

Simon Agembe

Introduction

The Shoemaker spinefoot, Siganus sutor (Figure 1), is a member of the family Siganidae, commonly known as rabbitfish. The family is widely distributed in the Indian Ocean region (Lam 1974; Randall, 1995) and 13 species occur in the western Indian Ocean (WIO), including the endemic S. sutor (Woodland 1990). Siganus sutor occurs in coastal waters to a depth of at least 40 m and is an important target species in many artisanal and commercial fisheries. The species is caught with a variety of gears (Woodland 1984).

Many demersal fish populations in the Kenyan waters are heavily exploited and fishing effort may be above optimum levels for some species (Kaunda-Arara et al. 2003, McClanahan and Omukoto 2011). While S. sutor constitutes one of the most commercially important demersal fish resources in the country (de Souza 1988), information on stock status is lacking and fisheries are not explicitly managed for this species. Knowledge of important reproductive parameters, such as the periodicity of spawning can support management efforts aimed at protecting critical life history stages, including spawning aggregations (Sadovy de Mitcheson et al. 2008). Similarly, estimates of size at maturity can be used to devise gear-based (e.g. mesh size regulations) or market-based (e.g. minimum size-at-sale) management measures aimed at reducing the potential for overfishing. Earlier studies in East Africa estimated a number of reproductive parameters for S. sutor, including seasonality of spawning, but information on lunar periodicity of spawning and size at maturity was lacking (Ntiba and Jacccarini 1988; de Souza 1988; Ntiba and Jaccarini 1990). Therefore, this study aimed at determining missing parameters on spawning periodicity and maturity of S. sutor in the Kenyan south coast area of Msambweni, complementing a suite of parallel studies on spawning aggregation fisheries for this species as part of the wider MASMA programme.

Fig. 1. Illustration of Siganus sutor (Source: Woodland 1984)
Methods

To identify seasonal and lunar spawning periodicity and size at sexual maturity for *S. sutor*, artisanal fishery catches were sampled during 11 of 13 months between March 2009 and March 2010, inclusive (catches were not sampled in May and December 2009), at a coastal landing site in Msambweni, southern Kenya. Sampling was stratified based on reported reproductive (November-March) and non-reproductive periods (Ntiba and Jaccarini 1988), with 5 days sampled each month during the spawning season and 3 days sampled each month for the remainder of the year. Sampling trips focused on new moon periods, but included other lunar phases during one cycle from November to December 2010 in order to estimate lunar periodicity in spawning. Females were preferentially sampled as ovarian development is more reliable for detailing spawning periodicity than testicular development (West 1990).

Fish were sampled for total length (TL, to the nearest mm; from snout to tip of longest lobe of caudal fin) and wet weight (nearest 0.1 g), and gonads were removed and weighed (nearest 0.01 g). To determine lunar periodicity in spawning, a sub-set of samples collected over one complete lunar cycle was evaluated microscopically and gonad maturity stage assessed using a developmental scale ranging from immature to spent (Table 1). To document lunar periodicity and confirm seasonal periodicity, gonadosomatic index (GSI) for females was estimated using the following formula:

\[
\text{GSI} = \frac{\text{weight of ovary (g)}}{\text{(weight of fish (g) - weight of ovary (g)) x 100}}
\]

For histological preparations, sampled gonads were preserved in a 10% formalin solution, buffered with acetic acid and calcium chloride (FAACC). Microscopic staging was based on standard techniques (Ntiba and Jaccarini 1990; West 1990; Samoilys and Roelofs 2000). An automatic tissue processor (Leica TP 1020, Wetzlar, Germany) was used to process haematoxylin/eosin-stained tissue samples which were then sectioned at 5-7 µm. Reading of slides was done by two observers using Table 1 criteria.

The size at sexual maturity (*L_{m50}*) was defined as the size at which 50% of females were reproductively active during the main spawning periods. This parameter was estimated by fitting a logistic curve, using the least square method, to the proportion of macroscopically mature individuals by size class (see Kolding and Skaalevik 2010). This method, termed *effective maturity*, recognises that, despite maturity, not all females are reproductively active in the spawning season (Pears et al. 2006) and also minimises errors in assigning immature fish as inactive females (Samoilys and Roelofs 2000). Gonads that were undetermined in terms of maturity stage were excluded from this assessment.
A total of 376 samples were collected over 12 months, including 85 that were collected over four lunar phases in November and December 2010. Excluded from the analysis were 177 individuals that were either immature or of undetermined sex. The highest GSI was observed in November while the lowest values occurred in April, August and September, based on the Mar 2009-Mar 2010 new moon dataset (Fig. 2a). Monthly GSI showed two distinct peaks, one in June and July and one in November and January, suggesting two distinct peak spawning periods within the year. These peaks, particularly the latter one, corresponded with high numbers of running ripe and spent ovaries in the samples (Figure 2b).

### Table 1. Macro-and microscopic criteria of female gonadal development (modified from de Souza 1988; Ntiba and Jaccarini 1990; Samoilys and Roelofs 2000; West 1990).

<table>
<thead>
<tr>
<th>Development stage</th>
<th>Microscopic oocyte stage</th>
<th>Microscopic: other criteria</th>
<th>Macro-stage description</th>
<th>Macro-stage no</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immature, IM</td>
<td>Pre-vitellogenic oocytes: Oogonia, chromatin nucleus, early perinucleolar stains darkly, late perinucleolar stains faintly, oocytes irregularly shaped with no defined cell membrane</td>
<td>No sign of prior spawning; Thin gonad wall, compact, lamellae well packed, no cytoplasmic vacuoles</td>
<td>Gonads thin and threadlike, running longitudinally along dorsal wall of the body cavity, sex indeterminate</td>
<td>I</td>
</tr>
<tr>
<td>Resting, RE</td>
<td>Pre-vitellogenic oocytes (as above): Residual atretic oocytes present, cytoplasmic vacuoles</td>
<td>Thick wall, lamellae not compact, often vacuolated, few rounded oocytes brown bodies</td>
<td>Ovaries are cylindrical and pinkish tapering gradually toward posterior end, and occupy half the body cavity</td>
<td>II</td>
</tr>
<tr>
<td>Mature, RI</td>
<td>Vitellogenic oocytes: Yolk vesicle, early and late yolk globule, migratory nucleus stage</td>
<td>May have atretic oocytes, may have post-ovulatory follicles (POFs) from previous spawning</td>
<td>Ovaries are opaque and yellowish with some large oocytes clearly visible; Ovaries fully swollen with oocytes clearly visible, heavy network of blood vessels appears on the surface of ovary wall</td>
<td>III</td>
</tr>
<tr>
<td></td>
<td>Hydrated oocyte, yolk granules in the cytoplasm, defined striated cell membrane</td>
<td>Final stage of oocyte development leading to egg release. Ovulation results in ruptured or empty POFs</td>
<td>Ovaries are very soft and swollen: translucent and full of water; slight pressure on abdomen produces eggs at the vent, yellowish in colour due to large yellow oocytes, blood vessels coalesce to form large ones on the external of ovary wall</td>
<td>IV</td>
</tr>
<tr>
<td>Running ripe, RR</td>
<td>Atretic vitellogenic oocytes, pre-vitellogenic oocytes, dense network of blood vessels</td>
<td>Lamellae disrupted and remnant late-stage oocytes and prominent muscle bundles present</td>
<td>Ovaries are small, flaccid, wrinkled and very red with loose follicular tissue</td>
<td>V</td>
</tr>
<tr>
<td>Spent, SP</td>
<td>Lamellae disrupted and remnant late-stage oocytes and prominent muscle bundles present</td>
<td>Sex indeterminate</td>
<td></td>
<td>VI</td>
</tr>
</tbody>
</table>
Resting (RE) ovaries predominated in the last quarter and spent (SP) ovaries were present in all phases except the full moon. Four ovaries had post-ovulatory follicles, which provide evidence of recent spawning, but these occurred in all lunar phases. While there were significant differences in GSI between moon phases (Kruskal-Wallis test: p<0.05; Fig 3), hydrated oocytes were present across several lunar phases suggesting spawning in this species is protracted on lunar scales as well as seasonally. An unclear lunar pattern in ovarian development was observed with the highest proportion of ripe ovaries (RI) observed in the full moon phase, whereas running ripe (RR) ovaries (i.e., hydrated ovaries indicating imminent spawning) dominated samples in the first quarter but were also observed in the full moon and last quarters (Fig. 4). The size at sexual maturity, $L_{50}$, was estimated to be 28.2 cm TL (Fig. 5).

**Discussion**

Trends in GSI indicated that reproductive seasonality in *S. sutor* is characterised by two peak periods of spawning (June to July and November to February) occurring within a protracted spawning season. These results concur with previous work on spawning seasonality of *S. sutor* by
Ntiba and Jaccarini (1990), who also found two distinct peak spawning seasons for this species in Kenyan waters (Table 2). By contrast, the current findings differ from those of de Souza (1988) that showed *S. sutor* spawning throughout the year in Kenyan inshore waters, though with an Oct-Jan seasonal peak. Tanzanian populations of *S. sutor* exhibit a less protracted spawning season than populations in Kenya (Table 2; Kamukuru 2006), though the methods differed between this and the present study. Environmental cues such as temperature or photoperiod are known to stimulate reproductive activity (Takemura et al. 2004) and bimodal spawning seasons may occur in monsoon driven systems (Nzioka 1979; Sadovy 1996). Such a pattern may therefore explain the observed seasonality of *S. sutor* in Kenya, where a protracted spawning season corresponds to the warmer NE monsoon.

A clear lunar pattern in ovarian development was not detected since hydrated ovaries were observed in the first quarter, full moon and last quarter lunar phases. This contrasted with the GSI that peaked on the full moon and also telemetry and visual survey results of related studies which show spawning was confined to a few days over the full moon (see Chapters 5 and 6). This discrepancy is surprising since in most transient aggregation spawners hydrated females are confined to a very short lunar period each spawning month (Smith 1972; Johannes 1978; Rhodes & Sadovy 2002). In summary, the results on lunar timing remain inconclusive. It is recommended that in future a more thorough sampling protocol and histological assessment is done to measure the presence of both hydrated oocytes and post-ovulatory follicles as clear determinants of imminent or recent spawning.

### Table 2. Seasonality and minimum size at maturity of *S. sutor* from previous studies and the present study.

<table>
<thead>
<tr>
<th>Source and year</th>
<th>Locale/site</th>
<th>Seasonal peaks – GSI</th>
<th>Min size at first maturity</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>24 cm TL – females</td>
</tr>
<tr>
<td>Ntiba and Jaccarini 1988</td>
<td>Mombasa</td>
<td>Jan/Feb and May/June</td>
<td>21.7 cm TL-males</td>
</tr>
<tr>
<td>Kamukuru 2006</td>
<td>Dar es Salaam</td>
<td>Dec – May</td>
<td>22.8 cm TL- females</td>
</tr>
<tr>
<td>This study</td>
<td>Msambweni</td>
<td>Nov and Jan (&gt;80%)</td>
<td>28.2 cm TL-females (Lm&lt;sub&gt;50&lt;/sub&gt;)</td>
</tr>
</tbody>
</table>
The estimate of size at maturity in this study was considerably higher than that reported by earlier studies in the region (Table 2). This partly relates to the parameter used by de Souza (1988), which was minimum size at maturity rather size at 50% maturity. In addition, prior studies did not use a logistic curve fit to the data. In view of these methodological differences, and since the size at 50% maturity (28 cm) of this study is also close to the empirical estimate (28.7 cm) using the method of Froese and Pauly (2003) and with a female $L_{\text{inf}}$ of 52 (Grandcourt 2002), we propose that 28.2 cm TL represents the best estimate of average size of first maturity in this species on Kenya’s south coast.

Despite limited sample size, this study contributes to the state of knowledge about the spawning patterns of $S. \text{sutor}$ in the Msambweni area, which can guide future management measures for a species that is subjected to spawning aggregation fishing.
Chapter 5. Dynamics of rabbitfish (*Siganus sutor*) spawning aggregations in southern Kenya

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

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

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

To verify that fish aggregations are reproductive requires the application of strict criteria (Colin et al. 2003; Domeier 2012; SCFRA database: http://www.scrfa.org/database). According to Domeier (2012), a spawning aggregation is defined as “a repeated concentration of conspecific marine animals, gathered for the purpose of spawning, that is predictable in time and space. The density/number of individuals participating in a spawning aggregation is at least four times that found outside the aggregation. The spawning aggregation results in a masspoint source of offspring”. Reproductive activity within spawning aggregations is defined by either direct or indirect indicators. Direct indicators include observation of spawning, such as release of gametes in a spawning rush, or presence of hydrated eggs and/or post-ovulatory follicles in the gonads. Indirect indicators include observations of spawning-related behaviour, such as courtship, colour changes only known to be associated with reproduction and high catches of gravid fishes confirmed, for example, through increases in gonadosomatic index (GSI).
This study was designed to verify *S. sutor* spawning aggregation sites and behaviour using Domeier’s (2012) criteria. We also sought to determine periodicity and duration of aggregation formation, fish residency times at aggregation sites and spawning site fidelity to provide a basic understanding of the spatial and temporal dynamics of *S. sutor* spawning aggregations to aid in the development of conservation and fisheries management measures.

**Methods**

**Study sites**

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

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

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

![Fig. 1. Spawning aggregation sites (A, B, C), fishing grounds, putative migratory corridor (channel) and acoustic telemetry array of 7 receivers (VR2) for *Siganus sutor* off the southern coast of Kenya.](image-url)
In addition to offshore spawning sites, fishers also identified commonly fished nearshore sites that are putative non-spawning areas for *S. sutor* (Fig. 1). Fishers also identified a relatively deep channel running seaward from shore to the offshore putative spawning aggregation sites that they reported *S. sutor* use as a migratory corridor to the sites. Positions along the corridor were obtained by a diver on snorkel and subsequently mapped in ArcGIS as described above (Fig. 1).

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

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

**Underwater visual census and observations of fish behaviour**

UVC surveys were conducted by a single diver (MS) at Sites A, B, C during the period of Nov 2009 to Mar 2010 (timing based on fisher knowledge surveys), the putative spawning season (see Chapter 4). Surveys aimed to verify aggregation formation and to determine aggregation duration and timing, however, they were constrained to LD 13-20 and four months because we did not have the diving resources to survey all lunar phases and throughout the year. Using the site maps the entire aggregation site was surveyed using a standardised swim of 25-30 minutes. Density estimates reported herein are considered approximate due to possible double counting of the highly mobile *S. sutor* and frequent poor visibility at aggregation sites (~ 10-12 m), both known to affect UVC accuracy (Samoilys 1997a). Following abundance counts, the observer remained on site for 10-20 min to record any reproductive behaviour including direct (spawning rushes and gamete release) and indirect (courtship behaviour, colour changes) signs of spawning (Colin et al. 2003).

**Acoustic telemetry**

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

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

Fish were tagged during full moon in January 2010 to provide 3 months of potential tag detection during the spawning season (determined from concurrent studies in the same area, see Chapters 3 and 4) and while tags were operational. We worked with fishers who captured *S. sutor* using basket traps set the previous day on the aggregations sites. The trap was emptied into a bucket and fish >23 cm FL (size at 50% maturity) (Seychelles Fishing Authority, unpublished data; see Chapter 4).
were selected. Fish selected for tagging were retained in a perforated holding bucket strapped to the side of the boat (Plate 3). Prior to acoustic tagging, fish were measured (nearest mm, fork length, FL) and tagged with an external T-bar spaghetti-type tag (Floy Tag and Mfg, Inc, Seattle, WA), inserted between the dorsal pterygiophores, to enable fishers to identify acoustically tagged fish in their catches.

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

Data Analysis
Residency time at a spawning aggregation site was defined as the time (hr) between the first acoustic detection and the last detection within a 24-hr period. If the fish was not detected for >24 hr it was assumed to have left the site or died. Continuous detections in 24-hr periods were summed to give total residency.
All data were assigned a lunar phase following Samoilys (1997b) where the lunar cycle starts with the new moon (NM) on lunar day (LD) 1: NM = LD 28-3; First Quarter (FQ) = LD 6-10; full moon (FM) = LD 14-18; Last Quarter (LQ) = LD 21-25.

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

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

![Plate 4](Plate4.jpg)

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

![Fig. 2](Fig2.jpg)

**Fig. 2.** Total numbers of *S. sutor* on Sites A, B and C during November 2009 to March 2010. Lunar day: 1= new moon, 15-16 = full moon.
The number of traps increased on the three sites from LD 15 to 17 in December, LD 15 and 16 in January, and LD 18 to 20 in February (Fig. 3). Daily increases in boat numbers were only observed in December and February. The sharp increase in boats and traps in December and February corresponded with the increase in *S. sutor* at the sites (Fig. 2). Although trap numbers increased in January, UVC did not record increases in fish densities. We were unable to monitor boats and traps throughout the spawning and non-spawning season, nor were we able to record catches at the sites.

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

**a) Number of boats**

![Number of boats](image)

**b) Number of traps**

![Number of traps](image)

*Fig. 3. Number of a) fishing boats and b) basket traps on Sites A, B and C during monitoring days from November 2009 to March 2010.*
Detections of tagged fish at aggregation sites, lunar and diel periodicity and residency

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

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

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

Of the 9 tagged fish detected by receivers, 3 were detected only on the day they were tagged (Table 1, Fig. 5). Thus 6 of the 9 individuals detected by the array provided data useful for understanding
reproductive behaviour. These included 3 fish tagged and detected at Site C and 3 fish tagged and detected at Site B.

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

<table>
<thead>
<tr>
<th>Aggregation sites</th>
<th>Fishing sites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C</td>
</tr>
<tr>
<td>Site area (m²)</td>
<td>20,008</td>
</tr>
<tr>
<td>No. of fish tagged</td>
<td>12</td>
</tr>
<tr>
<td>No. of fish detected acoustically</td>
<td>3</td>
</tr>
<tr>
<td>Number of fish only detected on day of tagging</td>
<td>0</td>
</tr>
<tr>
<td>Number recaptured by fishers (Floy tags)</td>
<td>0</td>
</tr>
<tr>
<td>Days at liberty</td>
<td>1-96</td>
</tr>
</tbody>
</table>

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

Fig. 5. Plot showing detections of 12 acoustically tagged fish, 31 January to 10 May 2010. Nine fish were detected acoustically at the three spawning aggregation sites, two of which were recaptured by fishers. Three were recaptured by fishers at non-tagging sites. Recaptured fish are represented by filled diamonds. The arrows represent full moon periods.
Eighty-six percent of detections occurred during LD 18-20 suggesting fish arrived on the aggregation site on the full moon and dispersed 2 days later, which concurs with fishers’ reports (see above). However one individual (No. 21) remained at Site C throughout much of the study period, suggesting it was resident at this site (Fig. 6). Two other individuals were detected sporadically by receivers during other lunar cycles (LD 21 and 27), but did not appear to be resident. Assuming Fish No. 21 was a permanent resident at the site (see below), we removed it to examine diel timing in spawning activity. Pooling data from all three aggregation sites gave the time of detections as ranging from 06:13 hrs to 19:02 hrs, suggesting the species is most active during daytime at spawning sites (Fig. 7). However, no clear pattern to demonstrate actual reproduction was observed within this period. Some clustering in the evening was seen in fish Nos. 11 and 15, and fish No. 13 was detected all day; no fish were detected at night.

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

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

**Spawning site fidelity**

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

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

Collectively, these results support the interpretation that *S. sutor* only move to offshore patch reefs to spawn, similar to other rabbitfish studied (Hasse et al. 1977; Robinson et al. 2011; Kitalong 2012; see also Chapter 6). In Palau, fishers target schools of the dusky rabbitfish, *Siganus fuscescens*, inshore prior to migration to offshore spawning sites (Kitalong 2012). Our observations of
increased fishing activity in the form of boats and traps on the three aggregation sites during the lunar spawning period, combined with observations of fully hydrated ovaries in these catches and increased landings during aggregation periods (see Chapters 3 and 4) provide reinforcing evidence of reproduction at aggregation sites that are subject to a targeted fishery.

**Seasonal and lunar spawning periodicity**

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

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

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

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

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

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

In summary, the acoustic telemetry was limited by interrelated constraints of environment, technology and fish behaviour, but provided evidence of seasonal and lunar migration of S. sutor to offshore aggregation sites to spawn, as well as a high degree of site fidelity. Further evidence for this phenomenon was provided by fishers’ knowledge on spawning behaviour, fishing activity on the aggregation sites and underwater visual observation. S. sutor returned to the same offshore coral patch reef aggregation site to spawn on subsequent full moons, migrating up to 3.3 km from
fishing grounds closer to shore. Since *S. sutor* is a major component (~40%) of artisanal catches in Kenya (McClanahan and Mangi 2004, Maina et al. 2008, Locham et al. 2010, Samoilys et al. 2011b; Chapter 3) the implications of its offshore spawning aggregations and the fishery that targets them must now be considered in management discussions involving fishers.
Chapter 6: Shoemaker spinefoot rabbitfish (*Siganus sutor*) spawning aggregations in Seychelles: temporal dynamics, residency times and site fidelity
Jude Bijoux, Jan Robinson, Laurent Dagorn and Gregory Berke

**Introduction**

The Shoemaker spinefoot rabbitfish (*Siganus sutor*) is endemic to the southwest Indian Ocean (Woodland 1990) and is a commercially important target species in much of the region (Grandcourt and Cesar 2002; Kaunda-Arara et al. 2003). *Siganus sutor* leave their home range during the spawning season and migrate to form transient spawning aggregations (Robinson et al. 2011). In Seychelles, the locations of several *S. sutor* spawning aggregation sites are known to fishers and have been targeted since the early 1900s (Hornell 1927; Robinson et al. 2004).

A small percentage (ca. 15%) of the annual catch of *S. sutor* in Seychelles is taken at spawning aggregations and current trends in yield indicate that siganid resources are being fished within sustainable limits (Robinson et al. 2011). However, a precautionary approach has been recommended as part of an ongoing co-management initiative for this fishery, including consideration of gear-based controls and capacity/effort limitations (Robinson et al. 2011). Co-management plans also need to incorporate the fact that fishers on Praslin Island exhibit informal resource partitioning in their exploitation of *S. sutor* aggregations, with fishers generally exploiting aggregations that form closest to their district of residence. In an emerging management context that may involve input controls and technical measures applied spatially and temporally, a basic understanding of spawning aggregation dynamics is required. Spawning aggregation parameters, such as residency time and site fidelity, are also important to the application of models that aim to examine the effects of no-take reserves and other management measures for spawning aggregation-based fisheries (Chapter 12). Spawning aggregation site fidelity is a critical parameter if resource partitioning is to serve as a basis for co-management arrangements.

In this study we applied passive acoustic telemetry to provide information on key spawning aggregation parameters. The technology enabled detection of tagged fish at spawning sites instrumented with acoustic receivers over a 3-month period. These data were used to determine the lunar and diel timing of arrivals and departures of individuals at spawning sites, spawning site residency times and site fidelity.

**Materials and Methods**

**Study area and receiver array**

An array of eighteen Vemco VR2 and VR2W acoustic receivers (Amirix Systems, Inc., Halifax Nova Scotia) was deployed at three known *S. sutor* spawning aggregation sites off the west coast of Praslin Island, Seychelles (Fig. 1). The acoustic receivers were installed between 15 and 19 October 2010 and retrieved between 16 and 20 April 2011, giving a 6 month deployment across a large portion of the known spawning season of September to June (Robinson et al. 2011). Six receivers were deployed at each of the three spawning aggregation sites of Paté Polite, Paté Désiré and Paté Dividi, hereafter called Polite Désiré and Dividi. The spawning sites had similar physical characteristics in that they were all fully submerged granite patch reefs surrounded by sandy areas at a base of about 20 m. The minimum depth was about 15 m. Receivers were secured to the bottom on concrete blocks (+40 kg), which had been strategically deployed on and around the patch reefs to provide maximum area coverage. Tag signal detection was 70% at 25 m but declined to nil at 50 m and beyond.
Tagging

Tagging took place in two periods at the spawning aggregation sites: 20-22 October 2010 and 19-21 January 2011. Since battery life was approximately 3 months and given that tagging was conducted in two periods at the start and middle of the spawning season, the study essentially comprised two acoustic monitoring periods (period 1: October 2010-January 2011; period 2: January-April 2011). During monitoring period 1, 10 fish were tagged and released at the Polite fish spawning aggregation (FSA) site and 9 at the Désiré FSA site. During monitoring period 2, 11 fish were tagged and released at the Polite FSA and 9 at the Dividi FSA. Tagged fish measured between 22.6 and 29.7 cm fork length and were considered sexually mature, based on the reported size at first maturity for this population (Robinson et al. 2011).

Fish were caught by local fishermen using traditional bamboo traps, following a 1-2 hour soak time. To reduce barotrauma, traps were hauled slowly to the surface, where fish were immediately transferred to a holding tank. Fish were then transported to an aerated holding tank on a larger ship, where they were allowed to acclimatize for at least 30 minutes prior to tagging. Fish were anaesthetized by placing them in a continuously aerated 30-l container filled with a 30 mg l⁻¹ seawater/benzocaine solution. Opercula and fin movements were monitored and recorded. After 5 minutes fish were removed, measured and double tagged using uniquely numbered T-bar tags (Floy Tag and Mfg, Inc., Seattle, WA) inserted at the 4th dorsal pterygiophore. Fish were then transferred to a small continuously aerated aquarium and placed dorso-ventrally to enable continual submergence of the gills. A V8-4H-S256 (69 kHz, 110-250 sec delay, 93 day battery life, 2 g in air, < 1% weight of smallest tagged fish) acoustic tag (Amirix Systems, Inc., Nova Scotia, Canada), sterilized in absolute ethanol, was then inserted in the body cavity through a small incision 2 cm
anterior of the anus and below the lateral line. The incision was then closed using 2 non-absorbable polynylon sutures. At the end of the surgical procedure, fish were transferred into a recovery tank and monitored until normal colour and behaviour returned. Fish were released in small groups at the point of capture within 3 hours after being fished.

Data analyses
All data files downloaded from the acoustic receivers were screened for false detections (foreign identification codes) caused by code collisions (Heupel et al. 2006). Fish that were only detected within the first 6 hours after tagging (n = 4) were excluded from analyses to increase the probability that monitored fish were actively participating in spawning aggregations and not simply transiting through the sites at the time of tagging. Residency time was calculated based on the methods of Ohta & Kakuma (2005) and was defined as the duration that an acoustically tagged fish was continuously detected by the acoustic array at one FSA site without day-scale (> 24 h) absences. If total residency time at a single FSA site represented more than 75% of the estimated tag battery life, the fish was considered to be resident at that site and was subsequently removed from all further analyses as it was not possible to distinguish between transient spawning and non-spawning related behaviour. FSA site residency times occurring in the month of tagging are termed truncated since time of arrival of the fish at the site was unknown. However, both truncated and non-truncated spawning residency times were used in the calculation of mean residency time at the FSA sites, as results from the plotting of survival curves (not shown) and the Wald statistic of the Cox proportional hazards regression model (Cox 1972) showed that the two types of residency times were not significantly different from each other (p = 0.29, df = 1). Spawning residency times are defined as those times that occur, at least partially, within the 7-day spawning aggregation period described by Robinson et al. (2011). This period comprises 3 days before the full moon, the day of the full moon and 3 days after the full moon, and accounts for inter-monthly variation in the timing of aggregation formation, duration and dispersal. Fidelity to a single FSA site or use of multiple FSA sites over the spawning aggregation season was based on the detections of tagged fish only within the 7-day spawning aggregation period. Due to the unavoidable constraint of using small tags with a maximum battery life less than the known duration of reproductive activity (approximately 10 months), fidelity to FSA sites could only be assessed for the active life of the tag (i.e. 93 days). The temporal dynamics of FSAs were assessed in relation to lunar and diel rhythmic cycles. The start and end of a residency time was taken as the time and day of arrival and departure. Lunar arrivals and departures were assessed in relation to the full moon with -1 and +1 being a day before and after the full moon, respectively. Diel arrivals and departures were assessed in relation to the 24 hour clock with time of arrivals and departures being grouped in 1 hour time bins.

Results
Lunar timing of arrivals and departures
Pooling data across sites, the 7-day reproductive period accounted for 86.5% of arrivals at the spawning sites (Fig. 2a). The number of arrivals peaked 1 day before the full moon and were also high 2 days before the full moon, on the full moon and 2 days after the full moon. Each of these days amounted to more than 10% of arrivals (Fig. 2a).
Between-site differences in the timing of arrivals (Fig. 1b–d) were apparent. The first 3 days of the reproductive period accounted for 73.9% of arrivals at Polite with peak arrival (39.1%) occurring 1 day before the full moon. At Dividi, arrivals were slightly later with 77.8% of arrivals occurring between the day of and 2 days after the full moon, with peak arrivals (38.9%) occurring 2 days after full moon. At both Polite and Dividi, no arrivals were detected outside the reproductive period. Conversely, only 36.4% of arrivals occurred within the reproductive period at Désiré with peak arrivals (18.2%) occurring on the day of the full moon. At Désiré, there were arrivals throughout the lunar month, which sets it apart from Polite and Dividi where tagged fish appeared to use the site only during the 7-day reproductive period.

Fig. 2. Arrival and departure day at the spawning sites in relation to the full moon at (a) all sites combined, (b) Polite, (c) Dividi and (d) Désiré.

Fig. 3. Arrival and departure time at the spawning sites at (a) all sites combined, (b) Polite, (c) Dividi and (d) Désiré.
A high percentage (80.8%) of departures from the spawning sites occurred during the 7-day reproductive period with the number of departures peaking at 1 and 2 days after the full moon (Fig. 1a). At Polite, peak departures occurred on and 1 day after the full moon with 30.4% of departures recorded on each day (Fig. 2b). As with arrivals, peak departures from Dividi were slightly later than Polite, occurring 2 (38.9% of departures) after the full moon (Fig. 2c). At Désiré, there were no discernible trends, with departures appearing haphazard (Fig. 2d).

Diel timing of arrivals and departures
Pooling data across sites, arrival time of fish at the spawning sites peaked in the morning with 42.3% of arrivals occurring between 0500 and 0700 (Fig. 3a). This was driven by patterns in peak hourly arrivals at Dividi (Fig. 3b) and Polite (Fig. 3c). The pattern differed at Désiré, with 2 small peaks of arrivals, one occurring between 0500 and 0600 and one between 1700 and 1900 (Fig. 3d). Peak period of departure occurred between 1700 and 1900 with 57.7% of all departures occurring within this period (Fig 3a). At other times of the day the number of departures remained low, with no hourly period accounting for more than 6% of departures. Most departures at Polite (78.3%) and Dividi (66.7%), occurred from 1700 to 1900 (Fig. 3b, c). At Désiré, there were 3 small peaks of departures, the largest occurring between 1800 and 1900 (27.3% of departures), whereas two smaller peaks, each accounting for 18.2% of departures, occurred between 0100 and 0200 and 0500 and 0600.

Residence time

![Residence time graph](image)

Fig. 4. Differences in the residency times of tagged between monitoring period 1 and 2 at all monitored spawning aggregation sites combined and at Polite.

Within each period residence time did not differ statistically between the FSA sites, i.e. between Polite and Désiré in Period 1, and between Polite and Dividi in Period 2. By contrast, significant differences in residence time (Wilcoxon Ranked Sum Test: $W = 1170$, $P < 0.001$) were observed from pooling data across site in each period and then comparing between periods, with residence time in Period 1 being on average ca. 4-fold greater than in Period 2 (Fig. 4). While period may be important for CRT, the difference may be an artefact of pooling data from different pairs of sites during each tagging periods. However, comparison of residence time between periods 1 and
2 for Polite, the only site where tagging was performed in both periods, was statistically significant (Wilcoxon Ranked Sum Test: \( W = 341, P < 0.001 \); Fig. 5) and provides evidence that period is important. There were important differences in residence time between months at Polite (\( H = 22.35, \text{ df} = 6, P = 0.001 \); Fig. 5). Post-hoc pair-wise comparisons revealed that the significant differences in residence time were present only between October and January and between October and February. There were no significant differences in residence time at Desire and Polite in Period 1 and at Dividi and Polite in Period 2.

![Fig. 5. Inter-monthly variation in residence time at Polite between October 2010 and April 2011. Grey bars are CRTs for fish that were tagged in Period 1, black bar is for fish that were tagged in both periods, and white bars are for fish that were tagged in Period 2.](image)

**Spawning site fidelity**

Fish showed high fidelity to spawning sites with 22 of the 35 tagged fish (62.9%) detected on more than one spawning month (Fig. 6). Fish that were detected on more than one spawning aggregation period exhibited a high but not absolute degree of site fidelity, with 19 of the 22 fish (86.4%) detected at only one monitored FSA site. Ten and 4 tagged fish visited the same FSA site on 3 and 4 consecutive spawning aggregation periods, respectively, whereas 5 others visited the same site twice. Two fish tagged in monitoring period 1 (ID 40182, 40189) and one fish (ID 41493) tagged in monitoring period 2 were detected at more than one FSA site (Fig. 6a, b). Fish ID 40182 was tagged at Polite in October 2010 and was subsequently detected at Dividi (more than 8 km away) over the next 3 spawning aggregation periods. Fish ID 40189 remained at the site of tagging (Désiré) for an extensive period (3 months), including 6 consecutive days of the 7-day spawning aggregation period in the last month (January 2011) of monitoring period 1. Further demonstrating the spatial and temporal scales of mobility, after departing Désiré at dusk on the 6th day of the spawning aggregation period (i.e. 2 days after the full moon), the same individual was detected the next morning at Dividi, where it stayed for 6 h and attended the spawning aggregation at that site with other tagged fish. An individual (Fish ID 41493) tagged at Dividi in January 2011 appeared at Désiré the day after tagging, where it stayed for 2.5 days, and returned to Dividi during the 2 subsequent spawning aggregation periods of February and March 2011.

**Discussion**

This study has provided new knowledge on the spawning aggregation dynamics of *S. sutor* at offshore spawning aggregation sites in the Seychelles. The findings of this study confirmed that *S. sutor* visit the Polite and Dividi aggregation sites mostly around the full moon, with the majority of
arrivals and departures at these two sites occurring within the 7-day spawning aggregation period defined by Robinson et al. (2011). Therefore, our findings provide further evidence that the use of these offshore sites by *S. sutor* is related to transient spawning aggregation formation. Site-specific observations that nearly all females caught at Dividi (Robinson et al. 2011) and at Polite (this study, unpublished data) in the 7-day period around the full moon comprise running ripe individuals confirm that these aggregations are being formed for spawning. Fishers have reported a full moon spawning periodicity for populations of this species elsewhere in the western Indian Ocean (Samoilys et al. 2006; see Chapters 3 & 5).

Peaks in arrivals at dawn and departures at dusk, for both Polite and Dividi, suggest that fish are mostly migrating to and from the spawning aggregation sites at night or during crepuscular periods. Home range reefs, migration routes and times are yet to be documented, though fishers appear to monitor the build up of small aggregations on near shore fringing reefs a day prior to shifting their fishing effort to the offshore aggregation sites (Robinson et al. 2011). However, at Polite, a few arrivals and departures also occurred in the middle of the day. A plausible explanation for differences in arrival and departures among sites stems from the acoustic coverage provided for the monitoring arrays. Acoustic coverage at Dividi and Désiré was high as the sites cover relatively small areas of 16,000 and 2,900 m², respectively. Conversely, acoustic coverage of Polite was low as the site is both comparatively large, covering an area of approximately 70,000 m², and complex, being comprised of many granite patch reefs (see Fig. 1). Consequently, exact timing of arrivals at and departures from Polite at dawn and dusk may not have been recorded. Alternatively, behavioural plasticity in preferred diel timing of migration from home reefs to FSA sites could exist in *S. sutor*. Plasticity of diel activity rhythm has been found in *Siganus lineatus* populations occurring in different habitats (Fox & Bellwood 2011). At Désiré the lunar and diel patterns of arrivals and departures were markedly different from those observed at the two other FSA sites. We believe that Désiré forms part of the home range of some of the fish that were tagged there and that most of the arrivals and departures that we recorded were related more to foraging than participation in spawning aggregations. This is supported by the fact that large number of detections of tagged

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**Fig. 6.** The number of tagged *Siganus sutor* detected (n = 35) at the monitored spawning aggregation sites against the number of spawning aggregation periods in which they were detected and the number of spawning aggregation sites at which detection of a tagged fish was made.
fish at Désiré were made outside the 7-day full moon spawning aggregation period, as opposed to Polite and Dividi where detections were mostly concentrated in that period. Siganids appear to utilise large home ranges (Fox and Bellwood 2011) and the Désiré, Dividi and Polite populations may display differential habitat use for foraging, depending on local geomorphology and habitat distribution. Crepuscular and night periods are generally associated with high rates of predation (Danilowicz and Sale 1999; Holbrook & Schmitt 2002, but see Sancho et al. 2000) and predation on spawning fish is known to be intense at some sites (Moyer 1987; Sancho et al. 2000). Therefore, the timing of arrivals and departures to crepuscular periods may be a strategy for reducing the encounter rate with predators at spawning aggregation sites.

_Siganus sutor_ exhibited high spawning site fidelity during the two monitoring periods, which when combined constituted almost the entire spawning season for the population (Robinson et al. 2011). Nonetheless, since fidelity was not absolute, a degree of behavioural polymorphism (Attwood and Bennett 1994) appears to occur in the population. For polymorphic individuals, selecting spawning sites is unlikely to be a random process as relatively high levels of inter-monthly fidelity to a single site (up to 3 consecutive months) were still observed after or prior to changing sites. Our interpretation of behavioural polymorphism could actually be a bet-hedging strategy against environmental variability (Lambert and Ware 1984) or a response to changes in mating opportunities (Draud and Itzkowitz 2004) at a particular FSA site.

Residency times of acoustically tagged fish at the three monitored FSA sites varied in time with higher mean residency time recorded in the first compared to the second monitoring period. A shortening of residency time with the progression of the spawning season may relate to changes in reproductive output if the energy budget tends towards increased somatic growth as the protracted spawning season progresses. Many species spawn multiple batches of eggs within a single spawning period (Hunter and Macewicz, 1980; Pears et al. 2007), including the closely related _Siganus canaliculatus_ (Hoque et al. 1999), and co-occurrence of post-ovulatory follicles and hydrated oocytes has been observed in ovaries of _S. sutor_ sampled from Praslin aggregations (Seychelles Fishing Authority, unpublished data). Detailed reproductive biology studies of batch size and the frequency of their release across the spawning season would offer insights on variation in residency times.

While several hypotheses have been postulated as to why fish select certain sites to spawn (Molloy et al. 2012), little in the way of consensus on underlying mechanisms has emerged from the existing empirical or theoretical evidence. In the case of the _S. sutor_ population at Praslin, coastal geomorphology and physical characteristics appear to be important in the selection of spawning sites. All spawning sites studied are located offshore at depths of between 15 and 20 m, with coral cover in excess of 60% and moderate current speed of between 0.1 – 0.3 m s⁻¹ (Seychelles Fishing Authority, unpublished data). Since siganids have negatively buoyant, demersal and adhesive eggs (Thresher 1991), they presumably require a clean surface for egg attachment (e.g. Gafny et al. (1992)), conditions that may be met on the offshore granite patch reefs selected by _Siganus sutor_ at Praslin, as opposed to inshore reefs that receive comparatively high levels of terrigenous sediment and run-off (Littler et al. 1991). Compared to emergent fringing reefs, submerged offshore sites may also prevent eggs from being dislodged by wave action. Similarly, in Kenya, _S. sutor_ are known to spawn on deeper offshore patch reefs (see Chapters 3 and 5), while spawning at similar depths has been documented in _Siganus lineatus_ from Micronesia (Johannes 1981).

This study provided information on the spatial and temporal spawning aggregation dynamics of a regionally important species of rabbitfish, a family for which reproductive behaviour is poorly documented compared to families such as the Serranidae. In the WIO, _S. sutor_ constitutes the most important target species in many coastal reef fisheries (Everett et al. 2010; Hicks & McClanahan 2012). Siganids are also key species for ecosystem resilience since they may be the dominant herbivores on coral reefs (Cheal et al. 2010). In addition to gear management, spatial measures
are typically applied for reef fisheries management in the region, increasingly in the context of co-management of locally managed marine areas that often include small-scale closures (Cinner et al. 2012). However, the efficacy of management and conservation for *S. sutor* will depend, to a large extent, on designing measures that address the many complex spatial and temporal dynamics demonstrated here, including the use of offshore sites for spawning, partial infidelity to spawning sites, and turnover within aggregations. It is imperative that behaviour of target species is understood and used to guide management (Semmens et al. 2010, Rhodes et al. 2012).
Chapter 2, Fig. 2 Schematic diagram outlining the methods and parameters required for management measures commonly applied in spawning aggregation-based fisheries.

Chapter 3, Plate 1: Octopus ink sac and viscera used by Msambweni hook and line fishers as bait for catching rabbitfish from spawning aggregations.

Chapter 3, Plate 2. *Siganus sutor* from artisanal catches with ovaries of hydrated eggs.

Chapter 5, Plate 3. a) Traditional basket traps used to capture *Siganus sutor*; b) perforated bucket strapped to side of boat for holding live fish.
Chapter 3, Figure 3. Spatial patterns of catches in the Msambweni area: (a) kg/fisher/trip from basket traps; (b) kg/fisher/trip from hook and line; (c) Number of siganids/fisher/trip, all gears combined. Sites A, B and C are presumed spawning sites.
Chapter 3, Figure 4. Shifts in fishing effort reflected by catch rates (kg/fisher/day) of siganids in the Msambweni area during the presumed spawning season (November-February, a and c) and presumed non-spawning season (May-September, b and d).
Chapter 7, Table 1. Spawning-related behaviour and colours observed in *E. fuscoguttatus* during the new moon period at aggregation sites. Each of the behaviours are described in Chapter 7. The normal colour (behaviour 1) is shown for comparison.
Chapter 9, Fig. 1 (a) Google Earth image (13 November 2006) of the site; (b) Polygons marking the perimeters of spawning site reefs A to F; (c) Areas constituting the core and boundary reef areas in 2003-2005; (d) reefs confirmed as core spawning reefs for both species in 2010, with loss of reef A due to burial in sand.

Chapter 10, Plate 1. Fisher holding heavy gauge monofilament fishing line, chain and hook used to catch *E. lanceolatus* off Zanzibar.
Chapter 12, Fig. 1 Fraction of female spawning stock biomass per recruit (FNSSBR, i.e., the ratio of female spawning stock biomass per recruit over natural female spawning stock biomass per recruit), as a function of the multiplier of fishing effort ($mE_{base}$), for NTR scenarios #2, #4, #7 and #8 (see Table 1 for a description of the different NTR scenarios). (a,b) rabbitfish; (c,d) grouper. The fraction of spawning sites or normal residence areas in NTRs, $C_r$, is 30% and 60% for (a,c) and (b,d). $E_{base}$ is the default level of annual fishing effort exerted on the population and is indicated by a dashed-dotted blue line. The level of annual effort at which yield-per-recruit in the absence of NTRs reaches a maximum is indicated by a dashed-dotted red line for rabbitfish.
Chapter 12, Fig. 2 Yield-per-recruit normalized by maximum yield-per-recruit in the absence of NTRs (YPR/YPR$_{\text{max}}$), as a function of multiplier of fishing effort ($mE_{\text{base}}$) for NTR scenarios #2, #4, #7 and #8 (see Table 1 for a description of the different NTR scenarios). (a,b) is for rabbitfish, while (c,d) is for grouper. The fraction of spawning sites or normal residence areas in NTRs, $C_r$, is 30% and 60% for (a,c) and (b,d), respectively. $E_{\text{base}}$ is the default level of annual fishing effort exerted on the population and is indicated by a dashed-dotted blue line. The level of annual effort at which yield-per-recruit reaches a maximum in the absence of NTRs is indicated by a dashed-dotted red line for rabbitfish.
Plates 8. Selected photographs from the research programme: Kenyan and Seychelles basket trap fishers; *Epinephelus polyphekadion* at the atoll spawning aggregation site in Seychelles; telemetry receiver in situ at spawning aggregation site and tagging *Siganus sutor* in Kenya; and running ripe gonads in *E. fuscogutattus* catches in Msambweni.
Chapter 7: Observations of spawning aggregations of the brown-marbled grouper, *Epinephelus fuscoguttatus*, in Kenya

Melita Samoilys, Denis Macharia, Jan Robinson, George Waweru Maina and Jude Bijoux

**Introduction**

The brown-marbled grouper, *Epinephelus fuscoguttatus* (Epinephelidae) (Forsskål 1775) is widely distributed throughout the Indo-Pacific region (Heemstra and Randall 1993) and is known to form spawning aggregations (Johannes et al. 1999; Pet et al. 2005; Robinson et al. 2008; Rhodes et al. 2012). In the western Indian Ocean, it has been reported by fishers to form spawning aggregations in Kenya and preliminary studies have verified the location of two aggregations (Samoilys et al. 2006, 2007), but little is known about their spatio-temporal formation. The reproductive biology of this species remains unstudied in eastern Africa, with the exception of reports of spawning in the northeast monsoon (October to March) period (Nzioka 1979).

*Epinephelus fuscoguttatus* is not considered an abundant grouper (Pears et al. 2006) and in Kenya it is rare in artisanal catches, with only 24 individuals recorded over a 6-month period in 2007 in southern Kenya (Agembe et al. 2010). Due to its large size, it is relatively important to the biomass of groupers caught. In Kenya, it is targeted by speargun and handline, however catches are so small that they are not reported separately (WIOFish database (www.wiofish.org); McClanahan and Mangi 2004).

Global concerns over the status of *Epinephelus fuscoguttatus* populations led to a Near Threatened Red List classification by the IUCN Groupers and Wrasses Specialist Group in 2007 (IUCN 2011). Concerns over the status of this species in Kenya have arisen from our awareness of two spawning aggregations within the Diani-Chale Reserve on the south coast of Kenya, which is not under active management and does not include no-take zones (Samoilys et al. 2007; Robinson et al. 2008a). Targeted fishing of these aggregations for the local tourism market is known and marketed catches of *E. fuscoguttatus* have been observed with running ripe gonads in 2007 (MS pers. obs.) suggesting aggregation fishing. *E. fuscoguttatus* inhabits depths of up to 60m (Heemstra and Randall 1993) and may therefore be partially protected through a depth refuge (Tyler et al. 2009; Mangubhai et al. 2011; Rhodes et al. 2012) since fishers in Kenya have less access to the seaward reef slopes where these fish are likely occur. Boats are still largely non-mechanised (Samoilys et al. 2011a) and the winds of the south-eastern monsoon (4-5 months) are prohibitively strong preventing easy access to these sites. However, with technological developments, notably the use of outboard engines, increasing effort by new fishers and an open access fishery (Samoilys et al. 2011a), the vulnerability of *E. fuscoguttatus* in Kenya is likely to be increasing.

There is strong evidence that targeted spawning aggregation fishing is rarely sustainable (Sadovy and Domeier 2005). This fact, combined with the life history characteristics of *E. fuscoguttatus* of slow growth, late maturity and long life (Pears et al. 2007) highlight the need to identify management needs for this species at and away from spawning sites vulnerable to fishing. This study was designed to verify the aggregation sites in the Diani-Chale Reserve on the south coast of Kenya, to describe the spawning behaviour of this species and to determine the seasonal and lunar periodicity of aggregation formation. We also intended to track the movements of *E. fuscoguttatus* to and from aggregations with acoustic tags, but were unsuccessful in capturing the fish. We document this separately (Appendix III) to aid in future research on tagging this species in Kenya.
**Methods**

**Study sites**

The study area was approximately 25 km south of Mombasa, and extended from Tiwi (4°12’36"S; 39°37.06"E) in the north to Chale island off Gazi Bay (04°27’807"S 39°32.158E) in the south, in Diani Sub-location encompassing the Diani Chale Marine Reserve (Fig. 1). A linear fringing reef characterises this coastline, broken by the Tiwi River in the north and Gazi Bay to the south. The fringing reef has a spur and groove structure accentuated in places to form promontories, and is broken by reef passes, all known and named by fishers.

Our study focused on two *E. fuscoguttatus* spawning aggregation sites in the Diani area, herein identified as KW and KM, both on the outer reef slope. These sites were originally reported by fishermen (no women were interviewed) during a questionnaire-based study in 2004 (Samoilys et al. 2006). These sites were subsequently located as potential spawning sites through observations on SCUBA and through further discussions with fishers (Samoilys et al. 2007). For confidentiality reasons aggregation site coordinates are not provided on the map.

Having found numbers of *E. fuscoguttatus* at the aggregation sites, the extent of the aggregation area, defined by the location of the groupers, was mapped by divers, including depth and habitat features. The map was used as the underwater datasheet for recording fish numbers and behaviour (Fig. 2). Positions marking the perimeter of the KM aggregation site were obtained using GPS. Due to the limitations of surveying two sites at the same time with only one dive team, detailed observations and mapping were only completed at KM. The KW site was surveyed twice and its area approximated by divers using underwater tape measures.
Underwater visual census surveys

Initial underwater visual census (UVC) counts of *E. fuscoguttatus* on the KM site were made during the new moon period (lunar days, LD, 25-3) of 11-18 November 2009. New moon was selected based on previous fishers’ reports of lunar periodicity of spawning in Kenya and verification of spawning in Seychelles (Samoilys et al. 2006; Robinson et al. 2008b). UVC counts and behavioural observations of *E. fuscoguttatus* were repeated each subsequent month to February 2010, covering the period reported as the spawning season by fishers (Samoilys et al. 2006). UVC counts were also performed during the purported non-spawning season in July - August 2010. In both seasons, counts were conducted during a 7-day period over the new moon (LD 27-3, where 1=new moon).

A single full moon period (LD 17-18) was also surveyed (31 Jan–1st Feb 2010). We calculated a non-spawning density from surveys conducted in July and August (winter), on the basis that fishers reported spawning aggregations occurred only in summer months and studies of this species from the Pacific show a strong seasonal reproductive pattern with peak aggregation abundance occurring over 3-4 months (Hamilton et al. 2012; Rhodes et al. 2012). To verify whether counts had detected a spawning aggregation, we used criteria detailed in Colin et al. (2003) and Domeier (2012), whereby an aggregation is defined by abundances at least 4 times that of non-reproductive periods and spawning is indicated by signs and behaviour (see below).

To estimate abundance, UVC counts were made by a single diver along a set path around the site during a 30-min swim on SCUBA. Counts started along the deeper ledges (max. 25m) and finished in shallower areas towards the reef crest (min. 10m). Swims consistently covered the same route and area, with either one of two trained observers (MS, DM) making all counts to minimise observer bias. Although fish were sometimes mobile and visibility was often poor (around 10 m), any biases caused by double counting were assumed to be consistent between counts. Fish locations and sizes (in 5-cm size classes) were recorded on the datasheet map.

Spawning-related behaviour and appearance of *E. fuscoguttatus* were recorded during all surveys, based on established criteria: distinct reproductive colouration of males, courtship, swollen abdomens in females, male-to-male aggression and fish suspended unusually high in the water column (Samoilys 1997b; Johannes et al. 1999; Colin et al. 2003; Robinson et al. 2008b), noting that verification of sexes underwater is not certain. Following abundance counts, fish behaviour was recorded over a 10-min period to estimate the frequency of occurrence of these events. Visual estimates of size of fish engaging in spawning-related behaviours were also recorded. Still digital photographs (using a Nikon Coolpix camera) of behaviours were recorded.

Fisher interviews

Thirty-two fishers were interviewed to provide knowledge of *E. fuscoguttatus* spawning aggregations on the south coast of Kenya, as part of a larger fisher knowledge survey of spawning aggregations in key fishery species (see Chapter 3 for full details and Appendix I for interview questionnaire). For the current survey, we focused on key informants and experienced fishers known to target *E. fuscoguttatus*. Questions included knowledge of spawning aggregation sites, behaviour and timing, based on established indicators defined by Colin et al. (2003). Fishers’ descriptions considered reliable were assessed against established indicators, such as increased fish abundances (at least 4-fold), courtship, territoriality, reproductive colouration, gravid females and gamete release. Information was only considered reliable if corroborated by more than two fishers.

Results

Spawning aggregation sites

Spawning aggregations of *E. fuscoguttatus* were verified at KW and KM in the Diani-Tiwi area, based on a combination of abundance increases and observations of spawning-related behaviour. These sites are approximately 23 km apart (Fig. 1). The area of site KM was estimated to be 2,744m². The site was characterised by abundant soft corals on the upper slope (ca. 10 m depth),
which shelved gently (ca. 25°) to the reef edge at (ca. 15-16 m) (Fig. 2), where it dropped steeply to over 30 m. The reef slope was high in relief with ledges, caves and overhangs. The site was bounded by a reef pass to the north and a continuous reef slope to the south. *E. fuscoguttatus* were observed aggregating along the upper reef edge near the overhangs and caves, and also on the upper, more open reef slope at depths of ca. 12-18 m. Exploratory surveys beyond the southern boundary on the Feb 2010 new moon located 2 males and 1 female (see Table 1 for visual identification of sexes).

The KW site ranged from 14-20 m in depth and had high reef rugosity with several large bommies and pinnacles. The top of the reef further inshore was ca. 11-12 m depth and sloped gently seaward to a sand-rubble bottom. The site was bordered to the north by a sand channel reef break that extended to shore. Strong currents characterised the channel. The core area where *E. fuscoguttatus* were concentrated was estimated to be around 500 m² and the total area of the site ca. 2000 m².
Verification and size of spawning aggregations

Relatively high numbers of *E. fuscoguttatus* were observed from November 2009 to February 2010 at KM, with maximum monthly estimates ranging from 16 to 32 (Fig. 3). Fewer data were available for KW with an estimated 14 and 8 *E. fuscoguttatus* observed during December and January, respectively (Fig. 3). Numbers of *E. fuscoguttatus* at KM in July and August, the winter months and putatively the non-spawning season, were lower, particularly in August when only 3 fish were observed. By contrast, a maximum of 13 fish was recorded in July (Fig. 3). We calculated a mean non-spawning density at KM of 6.0 fish (±2.5 SE) during these winter months, though sample size was limited (n= 4 counts). Based on published criteria (at least 4-fold, Domeier 2012), 24 fish would therefore constitute a spawning aggregation of *E. fuscoguttatus* at this site. Counts from November to February (LD 28-2) ranged from 10 to 32 (n=9, mean of 21.3 ±2.6 SE) and aggregation size exceeded the threshold in 3 consecutive months (Dec-Feb). Smaller numbers were present in November and through the reproductive season, characteristic of a build up in numbers at an aggregation site prior to spawning (Fig. 3).

Daily counts plotted against lunar day indicate that *E. fuscoguttatus* aggregations formed around the new moon (Fig. 4). A gradual increase in the numbers at KM was observed just prior to the new moon with peak numbers corresponding to LD 1. Aggregation number abruptly decreased on LD 2 and 3, suggesting fish were departing the site. Surveys were not conducted throughout a lunar cycle; however, lower numbers of fish were observed during the full moon period (Fig. 4). Insufficient data were collected from KW to determine seasonal or lunar patterns. Changes in aggregation abundance throughout the day were not apparent, though data were few (Fig. 5).
Verification of spawning behaviour

Fish behaviour indicative of spawning was observed at both sites, providing strong evidence for reproductive aggregations of *E. fuscoguttatus*. All five behavioural indicators were observed repeatedly at both sites during the new moon periods of December, January and February (Table 1; Table 2). Spawning rushes and gamete release were not observed.

Males did not appear to defend territories, rather moved within small areas that seemed to be either close to or overlapping with other males. For example, in December 2009 (LD 1) at KM we observed two males and two females together in a small area, approximately 5 x 5 m. Male-male aggression appeared in two forms (behaviour 4, Table 1), though chasing was the most frequent aggressive behaviour (Table 2).

Courtship behaviour was performed by the male with the female stationary on the reef bed (behaviour 5, Table 1). Observed courtship acts involved a male swimming slowly past a female, turning sideways to her and quivering its body. Males either engaged in multiple courtship acts with the same female, or with several females. Courtship behaviour ceased if divers approached too close. Females were observed either hidden within the reef or lying close to the substrate.

Fig. 4. Lunar periodicity in numbers of *E. fuscoguttatus* at the KM spawning aggregation site during the reported spawning season months (November-February).

Fig. 5. Diel patterns in numbers of *E. fuscoguttatus* at site KM during LD 28-2 from December through February.
Fish size and sex ratios of spawning aggregations

Twelve pairs of *E. fuscoguttatus* were observed courting and in all but one case the male was larger than the female. The modal size class of courting fish was 81-85 cm TL for males, and 71-75 cm TL for females. Since it is possible to sex males when they are in male colouration or showing male-male aggression (Table 1), an approximate value for the proportion of males in an aggregation was calculated. This ranged from 7 to 64% with a mean of 35% (±7.3% SE). Consistently higher proportions of males in aggregations (mean = 46%) were observed during the December new moon, when most spawning-related behaviours were recorded (Table 2). Size frequency plots of the aggregations show that the minimum sizes of aggregating fish were 56-60 cm TL (December) and the maximum size was 96-100 cm TL (November; Fig. 6). Size frequency by month shows that the largest fish were present only during the months of November, December and January.

Table 1. Spawning-related behaviour observed in *E. fuscoguttatus* during the new moon period at aggregation sites based on known criteria (Colin et al. 2003). Timing and frequency of these behaviours are given in Table 2. The normal colour is shown for comparison (behaviour 1). (See colour plates.)

<table>
<thead>
<tr>
<th>Behaviour and appearance</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Normal colour</td>
<td>Black splodges on pale brown background – normal colours of male and female <em>E. fuscoguttatus</em>.</td>
</tr>
<tr>
<td>2. Male colouration</td>
<td>The usual brown-and-black marbled colour pattern (see 1) disappears completely; fish displays white ventrally, on the opercula, and on dorsal, caudal and anal fins. Fin edges darken to black, and dorsal half of body blackens. When in this colour pattern, swims slowly around and above the coral. Also courts in this colour pattern (see 5). Assumed to be dominant males displaying to females within their territory. Possibly not all males display this colouration.</td>
</tr>
<tr>
<td>3. Female swollen with eggs</td>
<td>Female with clearly swollen abdomen, likely due to hydrating eggs expanding the gonad; normal colouration.</td>
</tr>
</tbody>
</table>
4. Male aggression

Assumed to be males, based on the behaviour, but they are not in male colouration. Two behaviours were observed:

i) One individual chases another away from its area, swimming rapidly and chasing for up to ca. 10 m. Assumed to be males fighting over territories.

ii) Two individuals circling tightly head to tail, moving very slowly; as one moves away (possibly a submissive response), the other uses its lips to hit (which is audible) the other fish on the caudal peduncle area. Some individuals were scarred with superficial wounds, while others were more severe. For example, one fish had a badly torn upper lip. These injuries were assumed to be from male-male aggression.

5. Courtship

Male in spawning colours (see 2) swims slowly close to a female (see 3), and turns sideways to the female and shakes its whole body, while swimming slowly past her. The action was sometimes repeated to the same female within 10 to 15 minutes of the first encounter.

6. Suspended in the water column

Stationary or moving slowly, well above substrate by at least 1 m. At KW, two individuals were seen hovering around 3 m above the bottom in the same area where other fish were aggregating. This behaviour continued for 5-10 minutes. The fish were assumed to be male, but were not displaying male courtship colours. This is assumed to be a pre-spawning action.

Table 2. Frequency of spawning related behaviour in spawning months (December-February) and non-spawning months (July-August). Data are the number of individuals observed exhibiting the behaviour within the set census (30 min count + 10 min. observations). * = numbers refer to a pair of fish. Numbers in parenthesis refer to behaviour described in Table 1. NM=new moon; FM=full moon.

<table>
<thead>
<tr>
<th>Month</th>
<th>Colour change (2)</th>
<th>Gravid female (3)</th>
<th>Male-male chase (4i)*</th>
<th>Male-male head to tail (4ii)*</th>
<th>Courting (5)*</th>
<th>Suspension in water column (6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dec NM</td>
<td>31</td>
<td>11</td>
<td>7</td>
<td>1</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Jan NM</td>
<td>7</td>
<td>5</td>
<td>2</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Feb NM</td>
<td>7</td>
<td>6</td>
<td>2</td>
<td>0</td>
<td>3</td>
<td>0</td>
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<tr>
<td>Jan-Feb FM</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Jul-Aug</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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</tr>
</tbody>
</table>
Fish size and sex ratios of spawning aggregations

Twelve pairs of *E. fuscoguttatus* were observed courting and in all but one case the male was larger than the female. The modal size class of courting fish was 81-85 cm TL for males, and 71-75 cm TL for females. Since it is possible to sex males when they are in male colouration or showing male-male aggression (Table 1), an approximate value for the proportion of males in an aggregation was calculated. This ranged from 7 to 64% with a mean of 35% (±7.3% SE). Consistently higher proportions of males in aggregations (mean = 46%) were observed during the December new moon, when most spawning-related behaviours were recorded (Table 2). Size frequency plots of the aggregations show that the minimum sizes of aggregating fish were 56-60 cm TL (December) and the maximum size was 96-100 cm TL (November) and that the largest fish (>85cm TL) were present only during the months of November, December and January (Fig. 6).

Fishers' information on spawning aggregations and their timing

Eight of the 32 fishers interviewed provided information on *E. fuscoguttatus* spawning aggregations that matched criteria for determining spawning aggregations (see Methods). More than one fisher
reported aggregations forming between January and April, while five and four fishers mentioned February and March, respectively (Fig. 7). Fishers were less knowledgeable on the lunar timing of spawning aggregations, with only two fishers reporting new moon spawning.

Discussion

Observations of spawning-related behaviour at aggregations sites, increased densities of fish and fishers’ knowledge combine to provide strong evidence for the occurrence of *E. fuscoguttatus* spawning aggregations at two sites on the south coast of Kenya.

The spawning behaviour observed for *E. fuscoguttatus* in Kenya is typical of many grouper that spawn in pairs within aggregations (Samoilys and Squire 1994; Samoilys 1997b; Johannes et al. 1999; Robinson et al. 2008). The distinct male colour changes and males swimming high up in the water column have also been described in Palau and Seychelles (Johannes et al. 1999; Robinson et al. 2008b). Strong territorial behaviour by males at aggregation sites, as seen in the smaller more mobile grouper, such as *Plectropomus leopardus* (Samoilys 1997b), was not apparent. Though aggressive encounters between males occurred, demarcation of territories was not observed, possibly as a reflection of the low densities that characterised the site. A lack of aggression between males during the development of a spawning aggregation in this species has been documented in Seychelles, where the level of aggression increased with aggregation density (Robinson et al. 2008b). Clear demarcation of territories occurred in the high density aggregations at Farquhar Atoll, with males regularly chasing other males out (Robinson et al. 2008b).

[Fig. 7. Number of fishers who positively described monthly periodicity of *E. fuscoguttatus* spawning aggregations (n=32, 8 fishers with knowledge of spawning aggregations)]

Spawning rushes and the release of gametes, direct evidence that aggregations have formed for the purpose of spawning, were not observed. This may be explained by SCUBA observations being limited to between 0900 and 1700 for boat safety reasons, since the sites were seaward of the fringing reef. However, courtship behaviour was observed as late as 1650 suggesting that spawning occurred after that, as has also been suggested for this species in Seychelles (Robinson et al. 2008b). Other grouper species are known to spawn during a narrow window before, during and after sunset (Colin et al. 1987; Samoilys 1997b; Domeier and Colin 1997; Heyman et al. 2005; Rhodes and Sadovy 2002a). The proportion of males in aggregations, 45% during December, is high for this protogynous grouper where overall population sex ratios are normally female-biased (Pears et al. 2007). This may be explained by females remaining hidden in the coral during survey periods. The observation of a male courting a female hidden deep within the coral supports this. Alternatively, sex ratios at aggregations may not mirror the overall population sex ratio, especially if females do not attend every aggregation (Rhodes et al. 2011).
Our UVC surveys did not provide conclusive evidence on reproductive seasonality or spawning because counts were not continued throughout the year or lunar month. However, the survey estimates of a three-month season (December–February) partially overlap with fisher reports of 4 months (January–April, Samoilys et al. 2006). Monitoring of acoustically tagged *E. fuscoguttatus* in Seychelles identified a 2-3 month aggregation period, with lower abundance in the final month. In Seychelles the spawning period started as early as November and finished as late as March (see Chapter 8). Pears et al. (2007) found that *E. fuscoguttatus* spawns for 3 months (November-January) on the Great Barrier Reef, while Hamilton et al. (2012b) report 4-5 months (between December and March) in Solomon Islands. Our winter count at the spawning site in July was relatively high. Possibly there is reproductive activity in winter, which is unknown to local fishers; however, this is not supported by studies in other regions. Collectively, these studies on *E. fuscoguttatus* in the Indo-Pacific indicate a 3-5 month spawning season for *E. fuscoguttatus* during the Austral summer.

In Kenya we found spawning aggregations occurred around the new moon (LD 28-2), which is also reported from Seychelles (Robinson et al. 2008b), Palau (Johannes et al. 1999), and Indonesia (Komodo, Pet et al. 2005; Mangubhai et al. 2011). In contrast, the species appears to spawn just after full moon in Pohnpei, Micronesia (Rhodes et al. 2012) and in Solomon Islands aggregations were found on both new and full moon (Hamilton et al. 2012b). Our observations of a gravid female during full moon requires further investigation but may suggest both lunar phases are used in Kenya. From studies elsewhere, *E. fuscoguttatus* aggregations gradually develop 1-3 weeks in advance of actual spawning. During these periods, females arrive later and stay for shorter periods than the males (Robinson et al. 2008b, Nemeth 2012; Rhodes et al. 2012).

The mean number of *E. fuscoguttatus* at the KM aggregation site was 21 fish, corresponding to a density of 7.6 fish/1000 m². This compared with a non-spawning number of 6 fish (2.2 fish/1000 m²). Spawning aggregations were confirmed (4-fold increase, Domeier 2012) in December-February at KM. Our estimate of non-spawning density (2.2 fish/1000 m²), though sample size was small, is comparable to estimates from UVC surveys elsewhere in the eastern African region, where densities ranged from 0.8 (Mozambique) to a maximum of 3.2 (Tanzania) fish/1000 m², with a mean of 1.8 (±0.73 SE) fish/1000 m² from three surveys sites. *E. fuscoguttatus* were not seen at a further 69 sites (Samoilys unpubl. data). *E. fuscoguttatus* aggregation sizes in Kenya appear small and most closely resemble those from Komodo, Indonesia, where high aggregation fishing pressure is reported (Pet. et al. 2005; Mangubhai et al. 2011). Densities at the KM site are 4 to 10-fold less than those from Solomon Islands, Palau, Micronesia and Seychelles (Johannes et al. 1999; Robinson et al. 2008b; Hamilton et al. 2012b; Rhodes et al. 2012). Possibly, fishing pressure is sufficiently intense that it has depleted numbers at this site. However, it is not strictly valid to assess the status of an aggregation through comparison with different sites as aggregation size may vary substantially within the same reef system (Johannes et al. 1999; Robinson et al. 2008b; Mangubhai et al. 2011). For example, at Farquhar Atoll in Seychelles, *E. fuscoguttatus* forms aggregations ranging in size from 10s to 100s of individuals at different sites and size is not obviously related to fishing pressure, since the larger aggregations (68 fish/1000 m²) occur at the most heavily exploited site (Robinson et al. 2008b; see Chapter 8). Recent studies of groupers have demonstrated complex dynamics within aggregation sites, with the actual spawning or core site being small and nested within a larger courtship area, which is further nested within a staging area (Nemeth 2012). This has been demonstrated in *E. polyphemus* and *E. fuscoguttatus* in Seychelles (Robinson et al. 2008b). Our surveys in Kenya were not sufficient to determine these zones but it is likely that the KM area of 2,744m² includes the core area and most of the courtship area, since courting individuals were observed 100m beyond the southern boundary. Densities will therefore depend on whether the core area alone is used or includes the staging area. We also cannot discount the possibility that Kenya is characterised by small aggregations of this species, or that larger aggregations of *E. fuscoguttatus* may form elsewhere in southern Kenya, particularly if located on deeper fringing or submerged reefs where fishing effort is generally constrained (Samoilys et al 2011b).
The sizes of *E. fuscoguttatus* aggregating in Kenya conform to those of reproductively active *E. fuscoguttatus* on the Great Barrier Reef (GBR), Australia. Pears et al. (2006) report that this species is a long-lived protogynous hermaphrodite with males ranging in size from 68.3 to 92.5 cm TL and mature females from 32.0 to 85.5 cm TL. No fish smaller than 56-60 cm TL was observed at the Kenyan aggregations. The change in size frequency distribution at the aggregation sites between the summer spawning and non-spawning winter period, with fish greater than 90 cm TL only observed during November-January suggests that the largest males migrate to the aggregation sites to spawn. These may be the males that dominate gaining access to females, as seen in other groupers (Samoilys and Squire 1994, Samoilys 1997b, Robinson et al. 2008b).

**Management implications**

*E. fuscoguttatus* demography of long life (40+ years), late onset of sexual maturity in females (at 9 years), increasing female fecundity with age over a reproductive lifespan of more than 30 yr (Pears et al. 2006) do not confer resilience to fishing. In fact, such life history traits are all closely correlated with vulnerability to extinction (Mace and Hudson 1999; Reynolds et al. 2003; Dulvy et al 2003). These demographic factors, coupled with heavy fishing pressure and the many unmanaged fisheries for this grouper, led to its Near Threatened classification on the Red List (IUCN 2011). The fact that *E. fuscoguttatus* also forms spawning aggregations that appear to be predictable in time and place increases the vulnerability of this species (Sadovy de Mitcheson et al. 2008). This is particularly so in Kenya where coastal fishing is not regulated by size class (both minimum and maximum size class fishery restrictions would be beneficial for this species). Additionally, the fully protected marine areas (the nationally gazetted Marine Parks) are small, protecting only 8.6% of the country’s coral reef area (Spalding 2001; Wells 2006) in contrast with global recommendations in the order of 30% (Fernandes et al. 2005). Recent reports of reproductive movement and estimates of catchment area for this species suggest large-scale marine parks are needed to protect populations of this species (Rhodes et al. 2012).

Local artisanal catches of *E. fuscoguttatus* have dwindled in recent years (see Chapter 3; Samoilys et al. 2011b) to the extent that we were unable to collect adequate gonads for reproductive assessment, or assess population abundance through catch rate analysis. Population abundance surveys (on SCUBA to 30 m) on eastern African reefs also show that this species is rare (Samoilys unpubls. data), possibly in response to historical targeted fishing of aggregations of this species. Our indicator-based vulnerability analysis of the spawning aggregations of this species also revealed that they have relatively high vulnerability (see Chapter 11).

Given the combined factors of life history, small aggregation size and low cover of protected areas at a national scale, there is a need to institute additional management if this species is to persist along the southern Kenyan coastline. The aggregation sites documented here are not managed or protected, despite one occurring within the nationally gazetted Diani-Chale Reserve. This Reserve is not enforced due to strong local opposition from fishers. Low aggregation sizes may be the result of past fishing at aggregation sites or on the population as a whole. Further, we know from studies in Australia (Pears et al. 2006, 2007) that *E. fuscoguttatus* females need to breed for 30+ years to reach their full reproductive potential and our results suggest that spawning aggregations are important sites for these females to spawn. We therefore recommend that management of these sites be discussed as a matter of priority with all stakeholders, including local fishing communities, the hotel/dive tourism industry and the government’s Kenya Wildlife Service (KWS) with authority over the Diani-Chale Reserve. Conflict between different users in this area has been ongoing for many years, but recent mitigation training and discussions have provided options for resolving these difficulties (Watson and Ater 2011). To protect this valuable and threatened grouper, it is important that management options, including permanent no-take zones, are discussed for the spawning aggregation sites within the Reserve.
Chapter 8: Spawning aggregation dynamics of brown-marbled, *Epinephelus fuscoguttatus* (Forsskål, 1775) and camouflage grouper, *E. polyphekadion* (Bleeker, 1849) at a mixed-species aggregation site

Jude Bijoux, Jan Robinson and Laurent Dagorn

**Introduction**

The global catch of wild groupers is close to 200,000 tons (Tupper and Sheriff 2008) and market demand continues to increase, especially within the Southeast Asia-based Live Reef Food Fish Trade (LRFFT). Camouflage (*Epinephelus polyphekadion*) and brown-marbled grouper (*E. fuscoguttatus*) are two important high value food fishes that are targeted by large-scale commercial (LRFFT) and small-scale reef fisheries throughout much of the Indo-Pacific (Sadovy 2005). Found in coral rich areas down to depths of 60 m, both species are voracious ambush predators that are slow growing, late maturing and occur at low densities throughout much of their range (Russell et al. 2006; Pears 2012) except during spawning aggregations (Sadovy 2005). *Epinephelus fuscoguttatus* has a sexual pattern corresponding to protogynous hermaphrodism (Pears et al. 2006; 2007) while *E. polyphekadion* is gonochoristic with the potential for sexual transition (Rhodes et al. 2011). Both species spawn in mixed-species transient spawning aggregations of 100s to 1000s of individuals that are ephemeral in nature and spatially and temporally predictable (Pears 2012; Rhodes et al. 2012). These life history traits make both species highly susceptible to even low levels of fishing. In many places, the location and timing of these aggregations are known by fishers and they have been heavily targeted, leading to stock decline (Sala et al. 2001), demographic changes (e.g. Beets and Friedlander 1998; Rhodes et al. 2011), and in extreme cases, the total disappearance or reproductive failure of aggregating populations (Johannes et al. 1999; Mangubhai et al. 2011).

Spawning aggregations of *E. polyphekadion* and *E. fuscoguttatus* have been verified at an atoll in the southern Seychelles. At one of the atoll aggregation sites, marbled coral grouper, *Plectropomus punctatus*, also forms spawning aggregations during the same period. Recent research has highlighted an urgent need to assess management requirements at spawning aggregation sites vulnerable to fishing in the WIO. At the study atoll in Seychelles, there is a basic understanding of the spatial and temporal dynamics of *E. fuscoguttatus* and *E. polyphekadion* aggregations at one of their known spawning sites (Robinson et al. 2008b). A stakeholder-driven process between 2003 and 2006 recommended the establishment of closed seasons or fishery reserves to protect the core aggregation sites at the atoll. Though formal management of the aggregation sites has yet to be adopted, stakeholders voluntarily ceased fishing the aggregation sites during the spawning period from 2005. This informal approach requires both spatial and temporal information on aggregation dynamics. Critical gaps in knowledge are known to undermine the current management and include fidelity to the sites, precise estimates of aggregation duration and periodicity, and the location of migration routes and catchment area (the area from which reproductive individuals are drawn). Major migration pathways in relation to the aggregation sites have not been identified, but are reported to exist in other locales for these species (Rhodes et al. 2012).

In this study, we applied passive acoustic telemetry to provide information on key spawning aggregation parameters. The technology enabled detection of tagged fish at spawning sites instrumented with acoustic receivers for periods of over one year. We make use of the detections to study the dynamics of camouflage and brown-marbled grouper over two spawning seasons and several spawning months. We specifically looked at the seasonal, lunar and diel timing of arrivals and departures at the fish spawning aggregation (FSA) site, spawning site residency times and fidelity, and the identification of catchment area for the sites.
**Materials and methods**

**Study area and receiver array**

The study was undertaken at an atoll in the southern Seychelles\(^1\) at a mixed species (*Epinephelus fuscoguttatus* and *Epinephelus polyphekadion*) spawning aggregation site (Fig. 1). An array of four Vemco VR2 and VR2W acoustic receivers (R1, R2, R3, R4) (Amirix Systems, Inc, Halifax, Nova Scotia) was deployed around the core aggregation area on 15 January 2010 and the last download was undertaken in May 2011. This time period partially covered the 2009-2010 spawning season and fully covered the 2010-2011 season. The receivers were secured to the reef bottom on concrete blocks (+100 kg) strategically placed within the core aggregation area (area of highest fish density). The array design provided maximum coverage of the sites, given tag range estimates of 50 m.

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\(^{1}\) The name and exact location of the study site cannot be disclosed due to sensitivity of the data.

![Fig.1. Location of Site A and B in two reef passes of an atoll in southern Seychelles and the location of the five acoustic listening stations deployed at the sites with their 50m detection range. The exact location of the study sites are not shown due to sensitivity of the data](image)

**Tagging**

Tagging took place between 11-15 January 2010 at Site A. All fish were caught using hook and line baited with bonito (*Euthynnus affinis*) from a small boat (c. 7 m overall length) anchored at the site. We aimed to target mature fish based on estimates of size at sexual maturity from other populations (Pears et al. 2006; Rhodes et al. 2011). As the site was generally less than 10 m in depth (max 12m), there were no incidences of barotrauma. Upon capture, fish were placed dorso-ventrally in a stretcher and a wet dark brown towel was placed over the head to reduce stress. Total length was measured to the nearest cm and fish were tagged externally using uniquely numbered T-bar tags (Floy Mfg, Inc., Seattle, Washington) inserted at the 4th dorsal pterygiophore. Fish were sexed based on the appearance of the gonopore and by stripping for the presence of milt or eggs. A Vemco V13-1L-S256 acoustic transmitter (69 kHz, 90 sec delay, 879 d battery life, Amirix
Systems, Inc, Halifax, Nova Scotia), sterilized in absolute ethanol, was then inserted in the body cavity through a small incision made 2 cm anterior of the anus. The incision was then closed using 2 non-absorbable polynylon sutures. Tagged fish were released at the point of capture within five minutes of being captured. In November 2011, an additional three *E. polyphekadion* were tagged using the same protocol in the vicinity of Site B.

**Spawning aggregation build-up and abundance**

Underwater visual census was used to estimate densities of *E. fuscoguttatus* and *E. polyphekadion* and verify the presence of spawning aggregations at Site A over three periods: 6-14 January 2010, 15-17 November 2010 and 9-13 May 2011 (Table 1). The number of the two species was estimated in 7m radius point count areas with the location of each point chosen haphazardly in the core area. Counts were conducted daily during each survey period by a single diver (JPB). Care was taken to search holes and crevices in the reef to record individuals that were hiding. All dives started one and a half hour before high tide when current speed in the pass was low and horizontal under water visibility was high (> 25 m). Peak aggregation abundance was estimated by multiplying the mean peak density of fish per m² by the total horizontal area of the core (7,700 m²). The horizontal area of the core was estimated by plotting its perimeter from a boat using a hand-held GPS (eTrex Legend HCx, Garmin, Kansas).

Table 1. Dates on which underwater visual census were undertaken at Site A to estimate densities of *Epinephelus fuscoguttatus* and *Epinephelus polyphekadion* along with the number of dives and total number of replicate counts made.

<table>
<thead>
<tr>
<th>Day/Month/Year</th>
<th>No. dives</th>
<th>Total No. replicates</th>
</tr>
</thead>
<tbody>
<tr>
<td>6, 7, 12, 13, 14 January 2010</td>
<td>5</td>
<td>27</td>
</tr>
<tr>
<td>9, 10, 11 November 2010</td>
<td>3</td>
<td>18</td>
</tr>
<tr>
<td>9, 10, 12, 13 May 2011</td>
<td>4</td>
<td>24</td>
</tr>
</tbody>
</table>

**Data analyses**

Diel patterns in detections of *E. fuscoguttatus* and *E. polyphekadion* at Site A were analysed by grouping detections in hourly time bins and by plotting mean hourly detection of each time bin. Residency time of a tagged fish at Site A was calculated as the time between its first and last detection at the site within a spawning month. Mean and standard deviation of residency time at the spawning aggregation site was calculated for each spawning month and each sex for both species.

For comparisons of residence time within species, data were square root transformed in the case of *E. fuscoguttatus* and log_{10} transformed in the case of *E. polyphekadion* to meet the assumption of normality. Comparisons of residency time between sex and spawning months within species were carried out using a two-way ANOVA with sex and spawning month as factors. All analyses excluded fish ID 59061 which appeared to reside at Site A for a large part of the study. They also excluded residency times made outside the spawning seasons by fish ID 59063, and all data from the month of tagging since residency times during this spawning month were truncated due to unknown time of arrival of fish at the site. Shapiro-Wilk’s and Levene’s test were used to test for normality of data and for equality of variance before undertaking all comparative analyses. Trends in diel and lunar timing of arrivals and departures of tagged fish at Site A were investigated by plotting percentage arrivals and departures in each hourly time bin.

**Results**

**Detections**

A total of 12 *E. fuscoguttatus* and 20 *E. polyphekadion* were tagged at Site A. Tagged *E. polyphekadion* ranged between 56 and 67 cm TL, whereas tagged *E. fuscoguttatus* ranged between 70 and 93 cm.
TL. All fish tagged were considered sexually mature given estimates of the size at first maturity for these species (Pears et al. 2006; Rhodes et al. 2011). A total of 417,121 detections were recorded at Site A, of which 237,154 were from *Epinephelus fuscoguttatus* and 179,967 from *E. polyphekadion* (Table 2). Apart from one *E. polyphekadion* (ID 59049), all tagged fish were detected at the FSA site. In both species, the number of detections was highest during the day with peak in detections observed in the early morning and early evening (Fig. 2). Daytime detections gradually decreased in both species from the early morning peak to its lowest daytime value at around noon, which was followed by a gradual increase until early evening.

![Graph](image)

**Fig. 2.** Variation in total hourly detection of *E. fuscoguttatus* and *E. polyphekadion* at Site A during the spawning aggregation periods between January 2010 and May 2011.

**Table 2.** Summary of acoustic detections by *Epinephelus fuscoguttatus* and *Epinephelus polyphekadion* recorded at Site A during the study period

<table>
<thead>
<tr>
<th></th>
<th><em>E. fuscoguttatus</em></th>
<th><em>E. polyphekadion</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of fish tagged</td>
<td>12</td>
<td>20</td>
</tr>
<tr>
<td>Number of fish detected</td>
<td>12</td>
<td>19</td>
</tr>
<tr>
<td>Total detections by all fish</td>
<td>319,989</td>
<td>264,222</td>
</tr>
<tr>
<td>Minimum detection by a detected individual</td>
<td>45</td>
<td>406</td>
</tr>
<tr>
<td>Maximum detection by a detected individual</td>
<td>121,870</td>
<td>62,711</td>
</tr>
<tr>
<td>Mean detection by an individual</td>
<td>26,666</td>
<td>13,901</td>
</tr>
<tr>
<td>Standard deviation of mean detection</td>
<td>38,254</td>
<td>17,599</td>
</tr>
</tbody>
</table>

**Spawning aggregation formation and abundance**

Underwater visual census undertaken at Site A during the January 2010 spawning month recorded an increase of 41.9% and 203.2% in the density of *E. fuscoguttatus* and *E. polyphekadion*, respectively, during the nine days preceding the new moon when spawning is known to occur (Fig. 3). Peak in mean density of *E. fuscoguttatus* and *E. polyphekadion* in January 2010 was 6.5 ± 4.1 (mean ± SD) and 18.7 ± 3.7 (mean ± SD) fish 100 m², respectively. The total number of *E. fuscoguttatus* and *E. polyphekadion* in the core area at peak mean density during the January 2010 spawning month was estimated at 470 and 1,440, respectively. Density at the site is associated with known
lunar and seasonal spawning periods for these species, since fish are absent or in much lower densities outside of these periods. At the start of the reproductive season (mid-November 2010), densities of *E. fuscoguttatus* up to $1.9 \pm 1.2$ (mean $\pm$ SD) fish 100 m$^2$ were recorded at Site A, while *E. polyphekadion* was totally absent. Censuses undertaken at Site A in May 2011 failed to record any individuals of either species.

Fig. 3. Trends in mean densities (± standard deviation) of *E. fuscoguttatus* and *E. polyphekadion* in relation to the days preceding the new moon at Site A in January 2010.

Fig. 4. Daily percentage arrivals and departures of a) *E. fuscoguttatus* and b) *E. polyphekadion* at Site A relative to the new moon (NM)
Lunar timing of arrivals and departures

Arrivals of *Epinephelus fuscoguttatus* at the FSA site occurred throughout most of the fortnight preceding the new moon, with this period accounting for 77.3% of arrivals. A small peak (18.2%) in arrivals occurred 8 days before the new moon (Fig. 4a). The arrival of *E. polyphekadion* at the FSA site mostly occurred in the same period with 96.8% of arrivals and peak in arrivals at 10 and 6 days before the new moon (Fig. 4b). Departures of *E. fuscoguttatus* from Site A occurred on 8 consecutive days, which stretched from 2 days before to 5 days after the new moon. However, most departures in *E. fuscoguttatus* occurred just after the new moon, with the first three days after the new moon accounting for 77.3% of departures. Departures of *E. polyphekadion* from the FSA site occurred on four consecutive days, which started on the day of the new moon. Peak departures of *E. polyphekadion* occurred one day after the new moon and accounted for 48.4% of departures from the site. On average the males arrive earlier than females in both species, but departure occurred at around the same time in both sexes of both species (Fig. 5).

**Fig. 5.** Mean arrivals (open circles) and departure (closed circles) times of males and females *E. fuscoguttatus* and *E. polyphekadion* at Site A calculated from the four spawning months after tagging. Information from the tagging month is excluded.

Hourly timing of arrivals and departures

There was no distinct diurnal pattern in arrivals of *E. fuscoguttatus* at the spawning aggregation site, which occurred throughout much of the night and day (Fig. 6a). Departures from the site occurred mostly in the evening and early morning with 86.4% of departures occurring between 2200 and 0700. In *E. polyphekadion*, 96.8% of arrivals and departures at the spawning site occurred between 1800 and 0800 with a peak in departures (48.4%) occurring between 2300 and 0100 (Fig. 6b).

Residence time

*Epinephelus fuscoguttatus* stayed on average (± SD) 15.7 ± 13.6 days at Site A, whereas *E. polyphekadion* stayed 11.1 ± 6.0 days. Male *E. fuscoguttatus* spent significantly longer time at the site than females, averaging twice the duration (Fig. 7; $F_{1,19} = 6.23$, $p = 0.027$). Longer residency times of males was also observed in *E. polyphekadion* (Fig. 7; $F_{1,26} = 9.55$, $p = 0.006$), with males exhibiting average stays 56.8% longer than those of females. Residence times were affected by spawning month in both *E. fuscoguttatus* ($F_{3,19} = 14.12$, $p < 0.001$) and *E. polyphekadion* ($F_{2,26} = 10.29$, $p < 0.001$). Tukey’s post-hoc tests showed that significantly longer residence times, for both species, occurred with Period 3, which was the first spawning month of the 2010/2011 spawning season. There were no significant sex-spawning month interactions. The average time (± SD) spent away from Site A between two consecutive spawning months within the same reproductive season was 19.2 ± 4.3 days for *E. fuscoguttatus* and 20.7 ± 2.4 days for *E. polyphekadion*.

80
Fig. 6. Percentage arrivals and departures of tagged a) *E. fuscoguttatus* and b) *E. polyphekadion* at the FSA in relation to hour of the day.

Fig. 7. Difference in residence time at Site A between males and females *E. fuscoguttatus* and *E. polyphekadion.*
Site fidelity and spawning frequency

None of the fish tagged at Site A were detected at Site B during the course of the study. Fidelity to Site A was high with 91.7 and 89.5% of tagged *E. fuscoguttatus* and *E. polyphekadion*, respectively, detected in the next spawning season, approximately one year after being tagged. Most *E. fuscoguttatus* that came back to the spawning site one year after tagging (spawning season 2) were detected on two spawning months, with smaller numbers being detected in only one or three of the spawning months of the second season (Fig. 8). The only *E. fuscoguttatus* that was detected on 3 consecutive spawning months in the second season was a male and the largest fish tagged, with a total length of 93 cm. Of the two *E. fuscoguttatus* that were detected in only one spawning month, one was a female and the other was of unidentified sex. *Epinephelus polyphekadion* were detected in only two months of the second monitored spawning season, with 13 of the 16 fish that came back being detected in both spawning months (Fig. 8). Out of the three *E. polyphekadion* that were detected on only one spawning month in the second season, one was a male, one a female and one was of unidentified sex. Our results suggest that the number of aggregations attended within a spawning season is not affected by sex and that most individuals of both species participate in aggregations over two consecutive months. No fish tagged at Site A were detected at Site B. The
three mature *E. polyphekadion* that were tagged inside the lagoon in the vicinity Site B in November 2010 were not detected at the two monitored FSA sites by May 2010, suggesting that there could be other spawning sites in addition to the two already known.

**Discussion**

**Detection**

Both *E. fuscoguttatus* and *E. polyphekadion* were detected less frequently at night than during the day. Reductions in night time detection of acoustic tags during range testing have been reported by some authors (e.g. Afonso et al. 2012) but not others (e.g. Welsh et al. 2012). We believe that the most plausible explanation for the observed diel pattern in detections is reduced signal detection caused by increased background noise at night in coral reef environments (Bijoux, J. unpubl data). Both *E. fuscoguttatus* and *E. polyphekadion* are known to be active at night (Johannes et al. 1999; Hamilton et al. 2005) but the level of activity between night and day has never been quantified. If distinct diel activity does occur, fewer night time detections could be attributed to signal blocking at times when individuals are resting within the reef structure (Zeller 1997; Pastor et al. 2009; Alós et al. 2011). During the day, both species are highly active, with the male *E. polyphekadion* being often involved in cheek to cheek posturing (Rhodes and Sadovy 2002b) and male *E. fuscoguttatus* chasing each other (Robinson et al. 2008b), thus increasing the probability of daytime detections. Alternatively, tagged fish may have moved from the FSA site during feeding forays at night and thereby reduced detections. Nocturnal active tracking of tagged fish would help elucidate the activity patterns.

**Lunar and hourly timing of arrivals and departures**

Sex-specific patterns of movement in the two species at Site A agree with observations made at other locations (Johannes et al. 1999; Rhodes and Sadovy 2002b; Rhodes et al. 2012). Earlier arrival of males has been documented for both study species (Rhodes and Sadovy 2002b; Robinson et al. 2008b; Rhodes et al. 2012) and numerous other serranids (Johannes 1989; Johannes et al. 1999; Nemeth et al. 2007), suggesting that this is a common trait among aggregating groupers. It has been suggested that the earlier arrivals of males at aggregations is for the purpose of establishing territories (Robinson et al. 2008b) and securing favourable spawning areas with increased probability of attracting females. Male arrival at spawning sites at least one month prior to reproduction has been reported for squaretail coral grouper, *Plectropomus areolatus* (Rhodes and Tupper 2008).

Departures from the spawning site were more abrupt than arrivals and occurred just after the new moon, with all tagged *E. fuscoguttatus* and *E. polyphekadion* having left aggregations within five and three days after the new moon, respectively. In Pohnpei, *E. polyphekadion* have been found to spawn one to two days prior to the full moon and to disperse from the site within 48 – 72 h (Rhodes and Sadovy 2002b), while *E. fuscoguttatus* have been found to spawn around the full moon and to disperse within 4 days (Rhodes et al. 2012). In both our study species departures mostly occurred at night, which contrasts with observations of *Plectropomus leopardus* from the Great Barrier Reef, Australia that departed the FSA during the day (Zeller 1998).

**Residency at the FSA**

The study accurately calculated aggregation site residence and absence times. The early arrival of males leads to longer residency time at the aggregation site than females, a pattern that has been documented for both species at other locations (Rhodes and Sadovy 2002b; Rhodes et al. 2012) and for other spawning aggregation forming serranids (Zeller 1998). Interestingly, male residency time was greater during the first spawning month of the season, and while this has been documented elsewhere in *E. fuscoguttatus* (Rhodes et al. 2012), an explanation has not been proposed. More research is needed to understand the biological mechanism of these longer residency times in the first month. Longer residency and shorter absence time at the spawning site by males also indicates that they are aggregated for longer and are therefore more vulnerable to
aggregation fishing. This critical dynamic of spawning aggregation behaviour will exacerbate sex and size selective fishing in *E. fuscoguttatus*. If fishing on the spawning aggregations is to be avoided in the informal management system currently applied, estimates of male arrival and residency time should be used to set periods when fishing should not occur at the site.

**Catchment area**

To determine catchment area, fish would ideally have been tagged at numerous home reef sites outside of the reproductive season and their attendance at spawning sites monitored. However, in order to achieve a high probability of detection, this method requires a good understanding of the number and location of spawning sites in the population area, where currently only two are known (Robinson et al. 2008b). The existence of unknown spawning sites at the atoll (or at least unknown to science) may explain why the 3 fish tagged near Site B outside of the spawning season were not detected at the two monitored spawning sites. The low number of receivers available to the project also prevented us from tagging at spawning sites but monitoring both those and large areas of the atoll assumed to be home range sites. Recaptures of tagged fish by fishing outside of the spawning season may also provide insights on catchment area, at least for setting the scale for dedicated research on this parameter. However, fishing effort at the atoll is extremely low and only one tagged *E. polyphekadion* was recaptured by fishers outside of the spawning season. The fish was caught in April 2011 in the atoll lagoon approximately 6 km away from Site A where it was tagged, suggesting that the catchment area constitutes a significant portion of the eastern part of the atoll. Based on reported maximum swimming speed for *E. fuscoguttatus* (1.8 ± 0.3 km h⁻¹) (Rhodes et al. 2012), it is plausible that individuals could move between home ranges and the aggregation site between spawning months.

**Inter and intra-spawning season fidelity to the spawning site**

The high number of tagged individuals of both species that visited Site A over the two monitored spawning seasons, and on more than one spawning month within a season, suggests that there is high inter- and intra-season fidelity (Rhodes and Sadovy 2002b). High fidelity to spawning sites has been documented in other groupers species (Zeller 1998; Nemeth 2005; Starr et al. 2007) and appears to be the norm rather than the exception. High fidelity to spawning sites known to fishers, together with long residency periods observed in these groupers, can lead to localised depletion of spawning populations if not adequately addressed in the management arrangements for such species (Zeller 1998).

Most females of both species participated in more than one spawning aggregations per season. Interestingly, the high fidelity of *E. fuscoguttatus* females to consecutive spawning aggregations within a season months at Site A contrasts with the findings from Pohnpei, were females participate in only one spawning aggregation per season (Rhodes et al. 2012). Though fidelity was comparatively high in our study, it was not absolute and some individuals did not attend every aggregation of the spawning season. Possible reasons for fidelity not being absolute in some individuals include: (1) individual differences in ability to mature and spawn several batches of gametes over a spawning season (i.e. variability in reproductive output); (2) some individuals may attend different aggregation sites; or (3) certain individuals may pair-spawn within their home range and away from aggregation sites, i.e. variable mating tactics. There is little or no empirical evidence in support of these possible explanations, and they are not mutually exclusive. Clearly, these findings highlight the plasticity of *E. fuscoguttatus* reproductive behaviour within and between populations. Since these complex individual dynamics of reproductive behaviour could play a major role in the reproductive output of populations, further research is warranted.

**Management**

Even though fishing pressure at this remote atoll has remained comparatively low due to its isolation from population centres in the main Seychelles islands, large catches of *E. fuscoguttatus*
and *E. polyphekadion* from spawning aggregations were made at the two study sites up until 2005 (Robinson et al. 2008b). The stakeholder process leading to the voluntarily decision by fishers and fishing entities to cease targeting the spawning aggregations has removed this fishing pressure, but the informal management approach is not without risks. Detailed information on spatial and temporal dynamics of spawning aggregations is required by fishers to enable them to avoid catching aggregating fish. This study has provided far more detailed estimates of key spawning parameters than previously available (Robinson et al. 2008b) and can be used in this informal management approach. However, the lack of formal management makes monitoring, control and surveillance problematic and there is no legal mechanism for dealing with breaches in the agreement should they occur. Should the management of these populations extend to reconsideration of the formal measures previously suggested as options (Robinson et al. 2008b), the findings presented here will also provide for their effective implementation.

The high site fidelity at Site A ensures that application of spatial management at this site would affect most of the population that uses this particular site during the spawning period, whereas the fine-scale information on temporal dynamics such as timing of arrivals and departures and residency times would enable fine-scale temporal measures (either spatial, such as temporary fishery reserves, or non-spatial, such as sales or possession restrictions) to be implemented. Though most fish disperse from Site A after spawning and return 20 days later, some fish remain at the spawning site between spawning months. Therefore, short-term lunar phase closures of the site, even if 3 weeks in duration, would potentially expose aggregated fish to fishing pressure, albeit at lower densities than in other periods. Lunar closures have been found to offer limited protection to aggregating groupers (Pears et al. 2007). If considered as a management option, seasonal restrictions would ideally cover the reproductive activity of most of the individuals, including the early arriving males at the start of the season and those individuals that return to the site for a third consecutive month in March.

The role of monitoring in the management of spawning aggregations has been stressed by several authors (Sadovy and Domeier 2005; Mangubhai et al. 2011). We recommend the establishment of a long-term monitoring program for groupers and their aggregations at the atoll to determine how the population is responding to the informal management currently employed. Future research on grouper spawning aggregations in the Seychelles should continue to focus on identifying other FSA sites (Robinson et al. 2004), while looking to expand studies on the spawning dynamics of aggregating fishes, particularly potential inter-annual variations in spawning season duration, the use of migratory pathways and identification of catchment areas.
Chapter 9: Persistence of grouper (Serranidae) spawning aggregations at high levels of habitat disturbance
Jan Robinson, Calvin Gerry and Jude Bijoux

Introduction
Targeted fishing constitutes the major threat to reef fish spawning aggregations (Sadovy and Domeier 2005; Sadovy de Mitcheson and Erisman 2012). As a consequence, the majority of studies conducted on these vulnerable life history stages have focused primarily on fishing impacts (Domeier and Colin 1997; Russell et al. 2012). In addition to fishing, the formation of spawning aggregations can also be compromised by degradation or loss of benthic reef habitat resulting from the use of destructive fishing gears, coastal development (e.g. reclamation), or natural disturbances, such as severe storms (Koenig et al. 2000; Sadovy and Domeier 2005; Robinson et al. 2007). However, few studies have explicitly documented the effects of habitat change, caused by natural or anthropogenic disturbances, on spawning aggregation formation and status.

The processes that determine why, where and when spawning aggregations form remain largely unknown, although several hypotheses have been proposed (Colin 2012). Predator evasion (Shapiro et al. 1988), egg predation (Johannes 1978; Löbel 1978) and dispersal (Barlow 1981; Doherty et al. 1985), and larval retention (Johannes 1978; Jones et al. 2005; Almany et al. 2007; Karnauskas et al. 2011) and survival (Robertson 1990) have all been identified as mechanisms conferring selective advantage of aggregative spawning at specific locations and times (Claydon 2004; Molloy et al. 2012). Specific timing and locations of spawning may also serve as simple cues to synchronise reproduction and confer no other selective advantage (Claydon 2004). Depending on the hypothesis, benthic habitat will act as a primary (e.g. in terms of predator evasion), lesser or even negligible factor in aggregation site selection. However, it is important to consider that different processes can operate on ecological and evolutionary time-scales (e.g. Colin 2012). The processes that confer selective advantage and lead to the establishment of stable spawning sites operate on evolutionary scales and are likely to differ from ecological processes that maintain persistence at established sites. Those ecological processes include social behaviour (e.g. learning: Warner 1988, 1990) that are thought to enable fish to migrate to and attend spawning events at established locations. Moreover, in certain species, benthic habitat complexity may play an important role in providing shelter (Beets and Friedlander 1992; Johannes et al. 1999) and substrate for territorial/courtship behaviour, influencing fine-scale spatial distribution, abundance and density of aggregations and, potentially, their persistence.

The existence of multi-species aggregation sites comprised of broad phylogenies highlights variation in the importance of benthic habitat among aggregative spawners. For example, at Gladden Spit on the Belize Barrier Reef, at least 17 species aggregate to spawn, including numerous species from the families Carangidae, Lutjanidae and Serranidae (Heyman and Kjerfve 2008). Though all aggregating species documented at Gladden Spit form aggregations associated with identical reef geomorphology, namely a pronounced reef promontory with strong currents, they vary in their association with benthic habitat, with some, such as the carangids, being semi-pelagic. Thus, while benthic habitat may provide aggregating serranids with shelter from predators (Beets and Friedlander 1992; Johannes et al. 1999), this is clearly not the case for many lutjanids and carangids that aggregate partially or fully well above the reef substrate.

Manipulative experiments and natural disturbances operating on ecological time-scales may offer useful insights on the mechanisms underlying spawning aggregation site selection and persistence. Controlled experiments are rare, but the widespread overfishing of spawning aggregations is unfortunately common (Sadovy de Mitcheson et al. 2008). Recovery from depletion or other non-destructive effects of fishing is clearly possible (Beets and Friedlander 1998; Nemeth 2005),

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but the potential for recovery at the same site following ‘complete’ eradication remains unknown (Sadovy and Domeier 2005) and may operate on time-scales not suited for study. By contrast, the mechanisms underlying the persistence of established spawning aggregations are more amenable to study. Here, we report on the impacts of a natural disturbance on the persistence of grouper spawning aggregation site at Farquhar atoll in Seychelles.

In December 2006, a cyclone passed directly over Farquhar atoll in the southwest corner of the Seychelles archipelago at which spawning aggregations are known to form in the months of December to February. Research conducted at a key spawning site at the atoll between 2003 and 2006 verified spawning aggregation by *Epinephelus polyphekadion* and *Epinephelus fuscoguttatus* (Robinson et al. 2008). The objectives of this study were to (1) assess the impacts of the 2006 cyclone on spawning aggregation habitat at the site and (2) determine whether spawning aggregations of *Epinephelus polyphekadion* and *Epinephelus fuscoguttatus* continue to form at the site following the disturbance.

**Methods**

Familiarisation dives conducted at the study site in January 2010 on lunar days (LD) 18 and 19 revealed that aggregation habitat had changed dramatically since the most recent site survey of November 2006 (Robinson et al. 2008). Using a November 2006 geo-referenced Google Earth image imported into ArcGIS, changes in spawning habitat and area usage between the 2003-2006 period and 2010 were examined. GPS positions that marked the perimeter of spawning aggregation areas during previous assessments (i.e. between 2003 and 2006; Robinson et al. 2008b) were reconciled with the outline of reefs in the 2006 imagery. Extrapolations were made where cloud cover obscured reefs. Over 2 days (LDs 28 and 29) in January 2010, a period close to the known spawning time for both species (Robinson et al. 2008b), the core spawning areas were reassessed by divers. As with earlier surveys (Robinson et al. 2008b), we considered the core of the aggregations to be areas where obvious signs of spawning behaviour were observed, as opposed to areas (‘boundary areas’; Robinson et al. 2008b) that had high densities of aggregating fish but no signs of spawning behaviour. Signs of spawning behaviour were primarily the presence of gravid females being guarded and courted by territorial males. The extent of boundary reef areas was not determined in 2010.

Fixed transects were used to survey aggregations between 2003 and 2006 (Robinson et al. 2008b). Following the disturbance, one of three fixed transects in the core was completely lost, while a second was partially lost. As a result, random point counts (7-m radius) were introduced in 2010 in order to confirm that aggregations of *E. fuscoguttatus* and *E. polyphekadion* still formed following the disturbance. Ten counts were conducted per census across reefs where signs of spawning behaviour were observed. In order to use this method for *E. fuscoguttatus*, censuses were only performed a few days (LD 27-29) before spawning, when gravid females were present and territorial males were generally tolerant of divers. Censuses of *E. polyphekadion*, which allow divers to approach closely, began earlier on LD 20. In 2010, bad weather prevented diving between LD 23 and 26, inclusive. Density estimates of *E. fuscoguttatus* and *E. polyphekadion* aggregations made in 2010 were compared qualitatively with density estimates from aggregations observed in January 2004, since formal statistical comparisons were invalidated by the change in sampling methodology (i.e. from fixed to random sampling units).

To determine if reproductive behaviour was affected by the habitat disturbance, the relative frequency of occurrence (RFOO) of spawning-related signs and behaviours, i.e. aggression, courtship, gravid females and gamete release, was assessed during the census. RFOO of behaviour (e.g. courtship) is the ratio of the number of fish showing that behaviour to the total number of fish observed in the point count (Pet et al. 2005).
**Results**

Between 2003 and 2006, the core (spawning) areas for both species comprised reef areas A and B (Fig. 1a, b, c). Areas C to F were defined as spawning aggregation boundary reefs where high densities of fish occurred, but spawning-related behaviours were absent (Fig. 1c). Boundary reefs are considered as staging areas for the spawning aggregations where fish spend time prior to spawning in the core reef area (Robinson et al. 2008). In 2010, reef area A (3624 m²; Table 1) had completely disappeared, buried under sand except for the tops of a few corals totalling less than 100 m² in area. Between November 2006 and January 2010, the overall area of the spawning site was reduced by at least 3,624 m² and the size of the initial core reefs (A and B) had declined by 38% (Table 1). Reef D, a small reef at the edge of the site, was not evaluated in 2010.

In response to this large-scale disturbance, the core area had shifted in 2010 and signs of spawning in both species extended across reefs that were previously defined as boundary areas (C to F), while reef B remained an important core reef. Mostly, this new distribution was overlapping for both species, except on reef C where partitioning occurred, with *E. fuscoguttatus* extending further into the pass (Fig. 1d). The redistribution of the aggregations led to increases in the size of core spawning areas, from 9332 m² prior to the disturbance for both species, to 11,131 m² for *E. polyphekadion* and 17,078 m² for *E. fuscoguttatus* in 2010; increases of 19 and 83%, respectively.

Table 1. Size, status and use of 7 reef areas (area is in m²) that constituted the spawning sites in 2003-2006 and 2010. Reef status in 2010 was defined as gone or present but degraded. Reef D was not assessed in 2010 (ND=no data). *Epinephelus fuscoguttatus* (Ef) and *E. polyphekadion* (Ep) used the same reefs for spawning (core reefs) and staging (boundary reefs) in the 2003-2006 period. By 2010, core areas changed for both species and continued to overlap at all reefs except C2, where only Ef showed evidence of spawning behaviour. In 2010, surveys to determine if staging areas had shifted to new boundary reefs were not performed.

<table>
<thead>
<tr>
<th>Reef</th>
<th>Area</th>
<th>Status 2010</th>
<th>Use: 2003-2006</th>
<th>Use: 2010</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>3624</td>
<td>Gone</td>
<td>Core</td>
<td>Not used</td>
</tr>
<tr>
<td>B</td>
<td>5708</td>
<td>Degraded</td>
<td>Core</td>
<td>Core: Ef, Ep</td>
</tr>
<tr>
<td>C1P</td>
<td>3533</td>
<td>Degraded</td>
<td>Boundary</td>
<td>Core: Ef, Ep</td>
</tr>
<tr>
<td>C2</td>
<td>5947</td>
<td>Degraded</td>
<td>Boundary</td>
<td>Core: Ef</td>
</tr>
<tr>
<td>D</td>
<td>861</td>
<td>ND</td>
<td>Boundary</td>
<td>ND</td>
</tr>
<tr>
<td>E</td>
<td>1365</td>
<td>Degraded</td>
<td>Boundary</td>
<td>Core: Ef, Ep</td>
</tr>
<tr>
<td>F</td>
<td>525</td>
<td>Degraded</td>
<td>Boundary</td>
<td>Core: Ef, Ep</td>
</tr>
</tbody>
</table>

Changes in habitat had no effect on *E. polyphekadion* aggregation formation in 2010. The 2010 aggregation developed as the new moon spawning period approached with densities on LD 29 significantly greater than those on LD 20 (Fig. 2) (Independent samples T-test: F=12.622; p=0.01). In January 2010, densities of *E. fuscoguttatus* were far greater than those observed during non-spawning periods at the site (e.g. zero fish were observed in November 2006; Robinson et al. 2008) and increased over the three days of surveys. Formal statistical comparisons were not made between 2004 and 2010 due to the aforementioned change in sampling method. However, any changes in density may have resulted from increases in the size of core spawning areas rather than from changes in aggregation size, with fish aggregating over larger areas in 2010.

Indirect spawning-related behaviours provided evidence that the loss and degradation of habitat had not disrupted reproductive activity. For both species, male-male aggression, typified by colour changes, posturing, chasing and biting, was the most commonly observed sign indicative of spawning (Fig. 3 a, b). Gravid females of both species became highly visible two days before NM and increased in number by the following day. In *E. polyphekadion*, aggression tended to decrease
Fig. 1(a). Google Earth image (13 November 2006) of the site; (b) Polygons marking the perimeters of spawning site reefs A to F; (c) Areas constituting the core and boundary reef areas in 2003-2005; (d) Reefs confirmed as core spawning reefs for both species in 2010, with loss of reef A due to burial in sand. (See colour plates.)
Fig. 3. Mean (± standard error, SE) relative frequency of occurrence (RFOO) of indirect and direct signs/behaviour associated with spawning in (a) E. polyphekadion and (b) E. fuscoguttatus on lunar days sampled in January 2010 (n=10). RFOO\textsubscript{a} = aggression; RFOO\textsubscript{c} = courtship; RFOO\textsubscript{g} = gravid females; RFOO\textsubscript{s} = spawning (gamete release).

Fig. 2. Mean (± standard error, SE) densities of E. polyphekadion (Poly) and E. fuscoguttatus (Fusco) on lunar days sampled in January 2010 (N=10) and January 2004 (N=5).
with the arrival of gravid females, whereas *E. fuscoguttatus* aggression remained relatively stable over the few days this species was surveyed. Courtship was rarely observed but occurrences increased on the last day of the surveys. Spawning rushes and gamete release were not observed.

**Discussion**

The most likely cause of the large-scale loss and degradation of spawning site habitat was Cyclone Bondo, which struck the atoll on 22 December 2006 (Chang-Seng 2007). Cyclones are infrequent (decadal-scale) and generally of low intensity in Seychelles’ southern atoll groups (Chang-Seng 2007). While reef degradation from sand inundation might be explained by changes in current or wave patterns, or increased rates of carbonate erosion, such processes typically operate on much longer time scales (Woodroffe 2003). Further visual evidence for a massive cyclone impact along the northern edge of the atoll included recent deposits of coral boulders on the reef crest and loss or accumulation of emergent sand banks. Moreover, fishers at the atoll report larger waves and more difficult navigation in the pass since the cyclone, possibly a result of sand accumulation.

Four years after the cyclone, large spawning aggregations of both species continue to form at the site. Based on known seasonality and lunar periodicity of aggregations at the study site (Robinson et al. 2008), spawning and dispersal of the December 2006 aggregations are likely to have occurred a few days prior to the impact of the storm. Fish departing the aggregation site were also unlikely to have suffered direct mortality as a result of the cyclone since large and mobile reef fishes are typically able to avoid such impacts (Lassig 1983). If immediate lethal effects of the cyclone on spawning and migrating adults are considered negligible, the potential for longer-term impacts may depend on the importance of habitat quality for aggregation formation and spawning success.

Aggregating *E. polyphekadion* and *E. fuscoguttatus* compensated for the considerable habitat disturbance through a redistribution of spawning areas, whereby the core of the aggregations shifted to the nearest available hard substrate habitat that bordered the reef pass. This suggests that specific features (e.g., individual coral heads) may not be critical for aggregation persistence in these species. Nonetheless, both species clearly require reef and a degree of coral structure for spawning aggregation formation, since fish redistributed themselves to coral areas rather than returning to the sand-inundated half of the core site. Consequently, spawning aggregation persistence is unlikely to be threatened by disturbances as long as reef areas remain available. However, we were unable to formally compare densities or abundances and it is possible that aggregation sizes may have changed following the disturbance. Moreover, the observed habitat changes may have affected reproductive output if, for example, female selection of male territories is based on specific hard substrate attributes, such as level of rugosity.

The mechanisms that enable persistence of aggregations at a site are of immediate concern for management of aggregation fisheries (Sadovy and Domeier 2005). Although they are not well understood, Warner (1988) identifies the potential role of tradition and social behaviour in spawning aggregation persistence, whereby young adult fish learn from older fish to identify established spawning sites. Since the aggregating populations at our study site appeared unperturbed by the cyclone, at least in the medium-term, any social behaviour enabling traditional use of the site seems to have remained intact. Also illustrated by the manipulative experiment of Warner (1988) is the fact that traditional use of a site appears to override specific habitat attributes, which is a pattern supported by our results. While traditional site use was maintained, many individuals arriving at the site after the cyclone compensated for a reduction in the traditional core (spawning) reef area by adopting different parts of the reef for spawning. Therefore, the exact location and distribution of aggregations within a spawning site may be dictated by the requirements for suitable habitat rather than specific features for territorial, courtship or predator avoidance behaviour, and will depend on habitat configuration. Location and distribution of aggregations also change with aggregation size since they develop from small regions of the core spawning area and then occupy increasing area of habitat as more fish arrive (JR, pers. observation).
A few species (e.g. *Epinephelus guttatus*) appear to form aggregations that vary naturally between years in terms of their distribution and density (Shapiro et al. 1993; Sadovy et al. 1994b). Our results indicate that the location and distribution of aggregations that are more localised, denser and discrete (Colin 1992; Eklund et al. 2000) may also change on longer time scales, which will require consideration in management design. If pre-cyclone area management had been applied only to core spawning areas A and B, the post-cyclone changes to distribution would have predisposed the aggregations to fishing. Thus, variability in aggregation distribution provides a strong argument for larger protected areas, or at least buffer areas (Nemeth 2012).

Such mechanisms identify the need for adaptive management in the use of spatial closures to protect spawning aggregations. At our study sites, fragmentation of the preferred spawning habitat results in the *E. fuscoguttatus* and *E. polyphekadion* aggregation cores splitting into relatively discrete units roughly defined by the boundaries of hard substrate (Fig. 1). In the absence of any further large-scale habitat modification, aggregation distribution may remain stable for these species at population carrying capacity. However, the application of spatial protection measures for many spawning aggregations will need to be adaptive, since protection is most often applied when populations are depleted. Following protection, subsequent recovery may lead to further changes in the distribution of aggregations, as the increased numbers of fish seek additional fragments of habitat. If the new distribution extends beyond boundaries, any benefits provided for by small, protected areas will be undermined.

The natural experiment afforded our study showed that the traditional use of spawning sites was maintained through habitat change. The fact that aggregating fish can adjust to a partial loss of spawning habitat reinforces the argument that the main threat to spawning aggregation persistence is fishing.
Chapter 10: A niche fishery targeting the Giant grouper (*Epinephelus lanceolatus*) in Zanzibar

Melita Samoilys, Narriman Jiddawi and Jan Robinson

**Introduction**

The brindle bass, or Giant grouper, *Epinephelus lanceolatus* (Epinephelidae, Bloch 1790) is the largest bony fish and the most widely distributed grouper in the world (Gomon et al. 1994; Heemstra and Randall 1993; Smith and Heemstra 2003; Craig and Hastings 2007). Records give a maximum weight of 400 kg, a maximum size of around 300 cm total length and male size at first maturity of approximately 129 cm (Heemstra and Randall 1993; Lau and Li 2000). It occurs from the Red Sea to Algoa Bay, South Africa, and eastward to the Hawaiian and Pitcairn islands, north to southern Japan and south to Australia. Little is know about its biology. The species appears to be rare across its range and is rarely reported in fisheries landings (Heemstra and Randall 1993, Pogonoski et al 2002; Daw 2004). It is a target of spearfishers and has naturally low population abundance though growth rates may be quite high (Myers 1991; IUCN 2011). Giant grouper is classified as Vulnerable on the IUCN Red List due to population declines attributed to extensive fishing pressure and species desirability in the Hong Kong live reef fish market combined with its natural low abundance (IUCN 2011, Sadovy de Mitcheson et al. 2012). Sattar and Adam (2005) listed this species as a commonly exported species in Maldives, particularly to Hong Kong.

Earlier investigations by the authors in 2005-2007 indicated that *E. lanceolatus* becomes temporarily important in catches in one location of Unguja Island in Zanzibar during certain months of the year and catch numbers were indicative of aggregation fishing (Jiddawi and Samoilys unpub.; Samoilys et al. 2006). This and other Red Listed species in general, are not specifically managed in Zanzibar Fisheries legislation (Zanzibar Fisheries Act 2010). Our study was designed to document this fishery and address the question: are fishers targeting a spawning aggregation(s) of the vulnerable Giant grouper in Zanzibar and what are the future research needs for the species and site(s)?

Many species of grouper aggregate to spawn at specific sites and times each year, which has made them highly vulnerable to fishing and over-exploitation (Domeier and Colin 1997; Sadovy and Domeier 2005; Sadovy de Mitcheson and Erisman 2012). Unusually elevated catches such as those reported for *E. lanceolatus* in Zanzibar are often indicative of aggregation formation and targeted aggregation fishing. No scientific research has been done on the spawning behaviour of *E. lanceolatus* and its demographics are poorly known, with only anecdotal reports from fishers available (Domeier et al. 2002). Interviews with fishermen in eastern Indonesia provided indirect evidence of spawning aggregations where seasonally, catches increased from an average of 1 to 6 fish/week/boat during the possible aggregation season. Multiple gravid females were observed during periods of high catch (Sadovy and Liu 2004).

The study is limited by the rarity of the species and its conservation status. Therefore, no extractive samples were taken for this research. The study was dependent on collaboration with fishers and in-water surveys to identify the potential aggregation site of this species in the Kizimkazi area where elevated catches had been reported.

**Methods**

**Study site**

The study was located at Kizimkazi which has two sub-villages, Mkunguni and Dimbani, on the southern end of Unguja Island, Zanzibar (Fig. 1) and an offshore reef to the south east of Kizimkazi whose location is being kept confidential due to the sensitivity of releasing information on the location of spawning aggregations.
Catch landings data
Landings of *E. lanceolatus* in Kizimkazi village were recorded on 36 different days between 13 November 2009 and 26 February 2010 during which 64 individual *E. lanceolatus* were sampled from 43 catches. Sample records included: vessel type, number of fishers, gear type and size, fishing location, fish total length and body depth (to 0.1 m), and gonad colour and weight (to 0.5 kg). Sampled fish were too large to be weighed at the landing site and therefore total fish weight was estimated approximately from fish lengths, based on a single 170 kg fish that was weighed in Zanzibar town. For reasons not clear, fishers were reluctant to sell us *E. lanceolatus* gonads, therefore, no samples were available for histological or macroscopic analysis. Instead gonads were only weighed and described by colour (red or white). Sampling effort was not stratified evenly across months or lunar phases, therefore, statistical differences should be interpreted with caution.

Fisher knowledge
Questionnaires (modified from the questionnaires used in Kenya, see Chapter 3) were used to interview 17 fishers in Kizimkazi to gain knowledge of their fishing patterns in relation to *E. lanceolatus* and their knowledge of spawning aggregations, including their occurrence, location, and timing. These fishers were selected based on information collected during an earlier study that identified them as the only fishers out of 150 fishers in Kizimkazi targeting *E. lanceolatus*. In addition, a focus group discussion (FGD) was held in February 2010 with 8 of the 17 fishers to further discuss their knowledge of the *E. lanceolatus* fishery and to cross check answers from prior interviews.

SCUBA observations
Two SCUBA dives were carried out on the full moon of February 2010 on the offshore reef fishing site where fishers reported catching *E. lanceolatus*. The dives were done to observe *E. lanceolatus*, to see if they were aggregating and whether they were exhibiting any recognisable spawning-related behaviour (Colin et al. 2003). The purpose of the dives was also to describe the reef topography of the presumed spawning site. Only two dives were done because the conditions were too dangerous with bottom depths in excess of 40 m and very strong currents.
Data Analysis
Data were assigned a lunar phase (LD) following Samoilys (1997b), where the lunar cycle starts with the new moon (NM, LD 1): NM = LD 28-3; first quarter (FQ) = LD 6-10; full moon (FM) = LD 14-18; last quarter (LQ) = LD 21-25. Samples from days in between these 4 phases (n=15) were not used in lunar comparisons.

A one-way ANOVA was used to compare GSI between months. February was excluded due to low sample size. Due to unequal monthly samples sizes, we selected the Scheffe post-hoc comparison following identification of significant differences between monthly GSI (Ruxton and Beauchamp 2008).

Results
Fishers interviewed at the Kizimkazi village landing site in July 2010 reported seasonal targeting of *E. lanceolatus* at an offshore reef located off the southern end of Unguja Island, the main island of Zanzibar. Fishers accessed the reef site using 4 fibreglass boats based in Kizimkazi, with an average of 4 crew using hook-and-line gear, set and hauled by hand.

Of the 17 fishers interviewed, 9 reported targeting *E. lanceolatus* from November to February, while 7 fishers reported October to February. These dates were confirmed in the FGD where fishers reported November to January or February. Surveys of landed catch at Kizimkazi between 13 November 2009 and 26 February 2010 confirmed that *E. lanceolatus* regularly appears in the catch during November – February, with the highest catches recorded in January (Fig. 1). A total of 64 *E. lanceolatus* were observed in landings during the 15 weeks of landings surveys, giving an average of more than 4 fish landed per week. Fish ranged in total length from 101 - 235 cm TL (mean 1.92 ± 0.33 cm SD, standard deviation). While landings surveys were not formally conducted in other months, fisheries data reports (Institute of Marine Studies (IMS), *unpubl. data*) indicated that this species was absent or rare in landed catches during other periods or locations.

A lunar pattern was apparent in the landings, with the highest catches corresponding to the full moon and the first quarter, although *E. lanceolatus* were caught throughout the lunar month (Fig. 2). All but one of the 17 fishers interviewed reported that they catch *E. lanceolatus* around the full moon. This was not supported by the FGD where fishers reported new moon and last quarter (LD 21 to 4) as the period in which they catch the most *E. lanceolatus*.

Gonads weighed between 1.0 and 9.0 kg with a mean of 4.9 kg (+ 2.1 SD). There were significant differences in mean GSI between months (*F* = 5.88; *P* = 0.02) (Fig. 3). Post-hoc comparisons indicate that GSI in November was greater than both December (*P* = 0.019) and January (*P* = 0.032), while other comparisons were insignificant. There were no significant differences in GSI between lunar phases (*F* < 1; *P* = 0.70) (Fig. 3).
Attempts to observe *E. lanceolatus* on SCUBA were limited by strong currents and depth constraints (> 40 m). We were taken by fishers to the seaward edge of the submerged reef where they fish for *E. lanceolatus*, approximately 2 km offshore. This reef extends for approximately 1.5 km NW-SE. Fishing is done by handline, drifting in the strong current, with the weight of the chain, hooks and bait carrying the tackle down so that the bait drifts near the bottom of > 30m depth. Fishers reported the strong current runs southeast for approximately 3 months from November to January. They also reported prime fishing times for *E. lanceolatus* are 0500-1000 and 1600-1800, claiming that the grouper disappear into their caves during the heat of the day.

We dived to 40 m depth (dive 1) and 35 m (dive 2) at 1200, with total dive times of 24 min and 28 min, respectively. Drift dives covered around 1 km, in total, on the two dives. We observed two *E. lanceolatus* together on the first dive at ca. 25 m depth on 27 February 2010, LD 14 (1 day before

![Fig. 2. Number of *E. lanceolatus* observed in landed catches at Kizimkazi by lunar day (LD), months pooled. Full moon period = LD 14-18. First quarter = LD 6-10.](image)

![Fig. 3. Mean (± SD) GSI of males and females (combined) sampled from landed catches at Kizimkazi by survey month (n=43) and lunar period (n=21): NM = new moon; FQ = first quarter; FM = full moon; LQ = Last quarter.](image)
full moon), estimated at around 125 cm TL and 290 cm TL. The smaller individual had yellow colouring on its caudal and dorsal fins, which is generally considered young adult colouration.

The reef slope profile of the fishing site where the two E. lanceolatus were observed was as follows: reef top at around 15 m depth; reef slopes at 30° to a small ledge at approximately 25-27 m; slope continued at around 45° to a reef edge at around 50 m, which then dropped vertically. The reef had very low rugosity with substrate dominated by algae with some sea fans, sponges, bare rock and sand. The E. lanceolatus were seen near the small ledge, behind which there must have been caves of sufficient size because the fish swam inside the reef and out of sight several times, seemingly unperturbed by our presence. We saw no indication of any spawning-type behaviour, such as courting. We experienced a cold upwelling on the second dive. Numerous planktivorous and pelagic fishes were seen along the reef slope including schools of Sleek unicornfish, Naso hexacanthus, Elongate surgeonfish, Acanthurus mata, Red-toothed triggerfish, Odontus niger and Rainbow runner, Elegatis bipinnulata, Carangoides spp., including Giant trevally, Caranx ignobilis and Yellowfin tuna, Thunnus albacares. Fishing line was commonly observed on the seabed.

Two years after this study we learnt that a local tourist diving company had dived on this same presumed aggregation site on November 9th 2012, which was the new moon (LD 29), at approximately 12:00 hrs and had seen >30 Giant grouper on the site which they recorded on video. This footage can be viewed at: www.extremebluewaterspearfishing.com: “giant grouper congregation” or on YouTube: http://www.youtube.com/watch?feature=player_embedded&v=jSR2Zvp1G-E#!

The 17 interviewees were relatively experienced fishers (21.5 ± 6.42 yrs fishing) and have been fishing E. lanceolatus for between 15 and 35 years. In the FGD, fishers said they had learnt the tradition of fishing E. lanceolatus from their fathers, some fishing E. lanceolatus since the 1970s, others entering the fishery in the last decade (Table 1). Fishers reported that a wide range of other species and fishing grounds are targeted when E. lanceolatus are not available, but 7 fishers reported only fishing E. lanceolatus. As evidence of a targeted fishery for E. lanceolatus, as opposed to incidental take when targeting other species, several fishers detailed the gear they specifically used for E. lanceolatus, which is usually sold for catching sharks: heavy monofilament line (300-400 lb and up to 600 lb), 100 m length, with generally two large hooks (size: 16 cm – 20 cm length x 6 cm gape) and ca. 1 m length of chain of ca. 4cm link size between hook and line (Plate 1). This gear is designed to catch fish that are significantly larger than the fishers’ other target species. Bait comprised a whole tuna or trevally, purchased and kept in freezers in the village fisher group, the Beach Management Unit’s, landing site building, prior to their fishing trip. The average cost for the gear (2 lines, 2 hooks) was reported as around 300,000/= Tz Sh (USD$180). Individuals fishing trips (fuel and bait) costs were around 30,000/= Tz Sh (USD$18).

For most interviewees (88%), fishing was their primary income source for themselves and their household, although most (94%) engaged in other economic activities, such as farming and dolphin tourism. Fishers reported that E. lanceolatus are sold individually to middlemen at an average price of 165,000 Tanzanian Shillings (Tz.Sh.; ca. USD$100), though in the FGD fishers reported prices ranging from 300,000 to 500,000 Tz. Sh. (USD$180-300, Table 1). The skin is sold separately (20,000/= Tz. Sh. for one fish) and so are the gonads (15,000-20,000/= Tz.Sh.). Fishers did not know what the skins were used for.

All fishers reported that catch rates (number of fish per trip) of this large grouper have declined over time with the highest catches reported in 1989, over double what they caught at the time of interviews (Table 2), and this response was repeated in the FGD (Table 1). However, all fishers also stated that there is no need to specifically manage the fishery for E. lanceolatus, although some identified the potential for non-extractive uses of the species, notably taking tourists to see the fish. This probably stems from the local dolphin tourism projects in which some fishers are involved. The fishers in the FGD did not suggest the grouper were aggregating to spawn or that their fishing...
was having any impact on the population. They did not associate the ripe gonads with spawning, possibly because it is the only time they catch this species and therefore only find it with ripe gonads.

Plate 1. Fisher holding heavy gauge monofilament fishing line, chain and hook used to catch *E. lanceolatus* off Zanzibar. (See colour plates).

Table 1. Focus group discussion held by MS and NJ with 8 *E. lanceolatus* fishers in Kizimkazi, February 2010. They represented a group of fishers using 4 boats with an average of 4 crew each, based in Kizimkazi. Questions and discussion synthesised. (1 Tanzania Shilling = USD$0.0006)

<table>
<thead>
<tr>
<th>Question</th>
<th>Answer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Why fish <em>E. lanceolatus</em>?</td>
<td>Because one fish brings a lot of money: between 300,000/= to 500,000/= Tz.Sh. per fish (USD$180-300)</td>
</tr>
<tr>
<td>Location and why</td>
<td>This is the reef we know we will find <em>E. lanceolatus</em>; we know it well and how to fish it; it is where the <em>E. lanceolatus</em> find food.</td>
</tr>
<tr>
<td>Other villages fishing this species at other sites</td>
<td>Have heard of 1 <em>E. lanceolatus</em> caught at a site in Chaka Bay. We believe we are the only fishers fishing this species in this way on the whole of Unguja Island. But there are 2 other boats that also try to fish them at the same site, with less success.</td>
</tr>
<tr>
<td>Year started fishing <em>E. lanceolatus</em></td>
<td>1 started in the 1970s, 1 in the 1980s, 5 in the 1990s, 1 in 2002.</td>
</tr>
<tr>
<td>How have catches changed over time</td>
<td>Declined from around 6-8 per day per vessel over 20 years ago to 1-2 day/vessel today.</td>
</tr>
<tr>
<td>Why have numbers in catches declined?</td>
<td>More vessels now take them as incidental catch. Much higher value now so more constant fishing of them when the fishery is operating.</td>
</tr>
</tbody>
</table>

Table 2. Fishers responses on maximum and minimum catch per fishing trip (number of fish per vessel) and typical average catches in a particular year (n = 17 fishers)

<table>
<thead>
<tr>
<th>Year / catch max and min</th>
<th>Mean no. fish per trip</th>
<th>Max and min. catch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>6.9</td>
<td>Highest catch ever</td>
</tr>
<tr>
<td>1999</td>
<td>5.7</td>
<td></td>
</tr>
<tr>
<td>2010</td>
<td>3.1</td>
<td></td>
</tr>
<tr>
<td>N/A</td>
<td>0.6</td>
<td>Lowest catch ever</td>
</tr>
</tbody>
</table>
Discussion

Through fisher interviews and catch surveys this study provides evidence of a specialised, targeted fishery on the Giant grouper in Zanzibar. We suggest that this fishery is relatively unique, comprising only four boats with a total of 17 fishers. The fishery is traditional, targeting *E. lanceolatus* for an average of four months each year, with knowledge of the site, season and methods apparently handed down from father to son. These fishers use specialised handline gear of heavy line and large hooks to fish exclusively for *E. lanceolatus*. About half of these fishers switch to other livelihoods at other times, while the other half switch to other fisheries of different species using different gears.

All fishers reported fishing for *E. lanceolatus* at one offshore submerged reef, along the outer reef slope, a distance of about 1.5 km. SCUBA dives to verify this information were thwarted by dangerous diving conditions of over 40 m depth and strong currents. Nevertheless, we observed two *E. lanceolatus* at the site in February 2010 around 1200 supporting fishers reports. The two fish disappeared into caves in the reef and re-emerged, which corroborated the fishers’ understanding that the fish disappear into the reef between ~1000 and 1600, which governed their fishing times outside this period. This may also reflect a diurnal pattern in the groupers’ feeding behaviour. More convincing was the video footage obtained two years later by a local diving company (www.extremebluewaterspearfishing.com) of over 30 *E. lanceolatus* aggregating on November 9th 2012, the new moon, at approximately 12:00 hrs. This footage provides evidence that the *E. lanceolatus* were aggregating to spawn since this species is not known otherwise to aggregate and is solitary or occurs occasionally in pairs (MS pers. obs.).

Several large grouper species are known to migrate several 10s or 100s of kilometers to fixed spawning sites (Sadovy 1996; Nemeth 2012), which are used year after year, termed transient spawning aggregations (Domeier 2012). Transient spawning aggregations are defined as: “spawning aggregations that draw individuals to a site well outside their typical adult home range. Transient spawning aggregations often (1) occur during a very specific portion of one or two months of the year; (2) persist for a period of days or at most a few weeks and (3) do not occur year round. A single transient spawning aggregation may represent the total reproductive effort for participating individuals.” One of the most documented transient aggregation spawners is the Nassau grouper, *Epinephelus striatus*, in the Caribbean, which migrates distances of up to to at least 240 km and can have catchment areas estimated at 7,500 km² (Smith 1971; Colin 1992; Carter et al. 1994; Aguilar-Perera 2006; Nemeth 2009). Transient spawning groupers remain on or near the site for the reproductive season, typically for 2-3 months. There they court and spawn in aggregations for short periods (Sadovy and Eklund 1999; Sala et al. 2001; Sadovy de Mitcheson et al. 2008). The short seasonal periodicity of fishing at one specific fishing site of the Zanzibar Giant grouper fishery is indicative of a transient spawning aggregation. Fishers did not fish at this reef site at other times of year. The information suggests that *E. lanceolatus* are migrating from surrounding areas to this one site to spawn. There are anecdotal reports from Vanuatu of two known individual *E. lanceolatus* that lived at two different sites (one in a river mouth, the other on a wreck) that would disappear every year around November within 1-2 days of each other and be gone from their resident site for three months (Jim Anderson pers. comm.). Possibly the reef site off the southern end of Unguja Island may draw *E. lanceolatus* from the whole island. We found no information on other sites or times for *E. lanceolatus* in fishery landings around Unguja Island, which lends support to this hypothesis. This would conform to studies elsewhere where larger grouper species typically have fewer spawning aggregation sites with larger catchment areas, depending upon species and location (Sadovy and Eklund 1999; Nemeth 2009, 2012). Due to its size and the likely large range of movements *E. lanceolatus*, we recommend that future research involve tagging to track movements of this species to spawning aggregations. Since the fishers in Kizimkazi are clearly able to catch these large fish tagging should be possible, however perhaps not straightforward since the depth may cause problems with barotrauma, with mooring receivers for internal tags, and external tags may be dislodged since these fish frequent caves. Nevertheless, opportunities are high for further research on this huge, intriguing and poorly understood grouper.
A spawning aggregation is said to occur when two criteria are satisfied: that an ‘aggregation’ has formed and that ‘spawning’ is occurring (Colin et al. 2003; SCFRA database: http://www.scrfa.org/database). An aggregation is defined as finding densities of at least 4 times that of non-reproductive periods (Domeier 2012), whereas confirmation of reproductive activity is by either direct or indirect indicators. Direct indicators are observations of spawning or the presence of hydrated eggs and/or post-ovulatory follicles (direct signs). Indirect indicators are spawning-related behaviours, such as courtship, colour changes, high catches of gravid fishes and seasonal increases in GSI. This study was unable to confirm that an aggregation had formed because of limited information on reproductive and non-reproductive fish densities, incomplete fisheries landings statistics and the lack of access to gonads. However, the seasonally limited and site-specific fishery for *E. lanceolatus* is most parsimoniously explained by the occurrence of a transient spawning aggregation and this is supported by the video footage obtained by the local diving company Extreme Bluewater Spearfishing. To further verify this, we would need to monitor handline catches at Kizimkazi and other Unguja Island landing sites year-round for at least two years. Remotely operated video (ROV) cameras could also be set on the site to monitor *in situ* fish behaviour and observe spawning.

Lunar periodicity in spawning of groupers is common, and is often synchronised with the full moon or new moon (Sadovy 1996; Sadovy de Mitcheson et al. 2008; Colin 2012). The fact that numbers of fish, albeit low, were caught throughout the lunar month would suggest that *E. lanceolatus* migrate to the site, potentially from all around Unguja Island, and remain on or near there for the duration of the season, where they are accessible to fishers. This is also seen in its con-specific the Goliath grouper in the Caribbean (Ferreira et al. 2012). However, egg maturation, spawning behaviour and gamete release may be restricted to a few days within the lunar month. This periodicity is typical of many groupers that migrate long distances to spawning aggregations (Nemeth 2012). Catch landings, fishers knowledge, the FGD and GSI gave conflicting results regarding full or new moon timing of aggregations. Catch landings suggest FM and first quarter spawning, however, GSI gave no indications of spawning periodicity relative to moon phase. For the current study, GSI proved an unreliable indicator of spawning seasonality, in part because gonads were not reliably sexed. Since ovaries are better indicators of spawning timing, knowing the sex of sampled fish would have enhanced our ability to determine seasonal and lunar reproductive patterns (Samoilys and Roelofs 2000). In contrast, the FGD stated new moon and last quarter spawning. The video footage of the aggregation was taken on the new moon (LD 29). Finally, higher catches during full moon may reflect changes in feeding behaviour rather than spawning. Although inconclusive, together these results suggest this species may aggregate on site throughout the spawning season, spawns around the new moon and is more readily caught by hook and line during the first quarter and full moon.

The fishery for Giant grouper in Zanzibar is unique in being highly targeted, with the use of specialised gear and highly constrained fishing, seasonally and spatially. We propose that the data presented here combined with known spawning behaviour of large groupers (e.g. *E. itajara*; Ferreira et al. 2012) strongly suggests that the Zanzibar fishery is targeting a single spawning aggregation of *E. lanceolatus*. If this aggregation represents the only spawning aggregation site for the Giant grouper population that resides on Unguja Island, then an indication of the possible catchment area of this site is 3,331 km², based on the total area of coastal waters to 50m depth around the island. Since this species is Vulnerable under IUCN Redlist criteria, is naturally rare, and may have a single transient spawning aggregation on Unguja Island, which may represent the total reproductive effort for participating individuals (Sadovy and Eklund 1999), we propose that this fishery is not sustainable. Comparison with the closely related Eastern Pacific/Atlantic Goliath grouper, *Epinephelus itajara*, which once formed aggregations of 100-150 individuals (Colin 1994) but recent estimates range from 0-12 (Ferreira et al. 2012), are useful. Assuming aggregations sizes and reproductive periodicity are similar, a seasonal catch of 64 *E. lanceolatus* in Zanzibar in...
2009-2010 would suggest that previous aggregations were sizable if this fishery has persisted for generations, but the low productivity of this species and improvements in fishing technology are depleting the aggregation. Recently, subsequent to the surveys and interviews, Kizimkazi fishers have reported to one of us (NJ) that the total catch in the 2011-2012 season has declined to ca. 45 individuals. We have also received anecdotal reports of increased incidental catch, which may reflect greater numbers of shark fishers operating with the same heavy hook and line gear used to catch *E. lanceolatus*. Using the vulnerability framework described later in Chapter 11, we assessed this species and its fishery as highly vulnerable because: a) fishers’ knowledge of the seasonal occurrence of the Giant grouper aggregation is good; b) fishers’ access to the site is high; c) aggregation fishing may be the main driver of potential population collapse, since fishers catch *E. lanceolatus* predominantly when aggregating, although year-round data are scant; d) there is no regulatory co-management framework for this species in Zanzibar; and e) the market demand is relatively high, since the fish are valuable in the Zanzibar town market. In conclusion we recommend that Zanzibar fisheries management agencies and institutes initiate discussions with fishers as a matter of urgency regarding this aggregation-based fishery before it disappears.
Chapter 11: Evaluation of an indicator-based framework for assessing the vulnerability of reef fish populations to spawning aggregation fisheries

Jan Robinson and Melita Samoilys

Introduction

Population and spawning aggregation status is often poorly known or lacking in the data-poor context of many coral reef fisheries (Johannes 1998; Sadovy de Mitcheson et al. 2008). Long-term catch, effort and size data may be absent or, if present, are rarely disaggregated by species or gear. Fisheries-independent assessment of populations and aggregation status is costly, time consuming and requires substantial monitoring to ascertain trends or status (Sadovy and Domeier 2005; Colin 2012). Research programmes in this field, especially those founded on local ecological knowledge, often document numerous spawning aggregation sites for multiple species. Consequently, there is usually a need to identify and prioritize management and conservation actions, usually before aggregation or fishery status is known. These constraints highlight the potential for development of indicator-based frameworks that allow timely and informed decision-making regarding the management response to emerging knowledge on spawning aggregations and their fisheries.

A ‘spawning aggregation-based fishery’ is defined here as a fishery targeting a population (i.e. stock) of a particular species either entirely or partially when aggregated for spawning at single or at multiple spawning aggregation sites. In the majority of cases, the catches made at spawning aggregations will constitute a proportion rather than the total of the annual catch derived from that population, meaning that the aggregation fishery is a component of a wider fishery (e.g. Claro et al. 2009). The vulnerability of a fish population to aggregation fishing can be considered in terms of the extent to which the practise predisposes both aggregations and the population to decline and potential collapse, undermining both the aggregation and non-aggregation components of the fishery for that population.

While there are many commonalities to vulnerability frameworks, their construction and interpretation should be adaptable to the particular system being assessed (Turner et al. 2003). Many frameworks developed for fish and fisheries employ measures of productivity, which determine capacity to respond (absorb and recover) to fishing, and susceptibility or exposure, which in turn determine the interaction of the population with the fishery (Jennings et al. 1998; Dulvy et al. 2004; Patrick et al. 2009). Thus, the vulnerability of reef fish populations to aggregation fisheries can be segregated into interacting intrinsic and extrinsic components, the former relating to the productivity and sensitivity of populations, in terms of their inherent capacity to respond to aggregation fishing and the latter relating to the potential exposure (or susceptibility) of aggregations to the aggregation fishery. This conceptual approach is common to models for productivity-susceptibility analysis which recognise that a population with low productivity is not vulnerable unless the population is susceptible to the fishery (Patrick et al. 2009).

Are all aggregative spawners equally vulnerable to fishing? Which socio-economic drivers and pressures predispose spawning aggregations to unsustainable levels of fishing? In spite of substantial evidence scattered across several reviews (e.g. Domeier and Colin 1997; Claydon 2004; Sadovy and Domeier 2005) and their source literature, a systematic approach for assessing the vulnerability of aggregative species is lacking. Systematic approaches typically include the identification of meaningful criteria and indicators for measuring vulnerability and the development of frameworks for assessment. Most frameworks have the common goal of enabling managers to assess and monitor the potential risks to species posed by fishing or other anthropogenic impacts. The objectives of this study were: (1) to identify measurable intrinsic and extrinsic indicators relevant
to aggregative spawners and fisheries from the literature; (2) to develop standardised indices for scoring aggregation fisheries based on groups of indicators; (3) to test the ability of the intrinsic index in predicting population declines in reef fishes, and (4) to conduct a preliminary evaluation of the vulnerability of aggregative spawners to targeted fisheries in the WIO.

**Methods**

**Framework and fisheries assessed**

A 4-quadrant framework developed by McClanahan et al. (2008b) for prioritizing conservation actions was modified to assess the vulnerability of 11 reef fish populations subject to targeted aggregation fisheries in the WIO (Fig. 1; Table 1). The framework is designed to determine the vulnerability of populations resulting from the intrinsic vulnerability of the species and the exposure, or susceptibility, of the populations to aggregation fishing.

The unit of assessment is an ‘aggregation fishery’, which is scored according to intrinsic (population-specific) and extrinsic (fishery-specific) indices of vulnerability. A bivariate plot is produced based on a quadrant framework that distributes fisheries by levels of relative vulnerability to aggregation fishing. The low vulnerability quadrant will comprise fisheries for relatively productive species forming resident and transient aggregations that are least susceptible to aggregation fishing. The moderate vulnerability quadrant will comprise fisheries for the same species but aggregation fishing may constitute a significant driver of population and fishery status, especially if species are transient spawners with a high targeting indicator value. The high vulnerability quadrant will comprise species of low productivity that tend to be transient spawners. Species with slow life histories are vulnerable at low levels of fishing pressure (e.g. Coleman et al. 1999), meaning that even a limited amount of aggregation fishing can significantly increase the risk of population collapse. For fisheries in the very high vulnerability quadrant, aggregation fishing would likely drive populations to local extirpation.

Both the intrinsic and extrinsic indices are derived from several indicators that are associated with vulnerability, based on empirical relationships and evidence from the literature. Due to the method by which the indices are constructed, the scores for a fishery and its position in the quadrant are relative, as opposed to fixed, and will depend on the number and vulnerability of other fisheries being assessed.

**Development of the intrinsic vulnerability index**

Intrinsic vulnerability was determined for the target species of the aggregation fisheries using a relative index that was derived from 7 life history and reproductive behaviour indicators known to influence the vulnerability of fishes to exploitation (Table 2). The basis for the relative index was the 67 species verified as aggregative spawners by the Society for the Conservation of Reef Fish
Aggregations (SCRFA: Sadovy de Mitcheson et al. 2008). Twenty species were subsequently removed from this provisional list since data on aggregation type (Table 2) were absent in the SCRFA Global Database (2010). Three species verified as aggregation spawners in the WIO, but not present in the SCRFA Global Database, namely *Epinephelus lanceolatus* (see Chapter 10), *Siganus sutor* (Robinson et al. 2011) and *Plectropomus punctatus* (Robinson et al. 2008b), were added to give a provisional list of 70 species.

Using the life history tool of FishBase (www.fishbase.org), estimates of the von Bertalanffy growth parameter (K), asymptotic length (L∞), natural mortality (M), longevity (tmax) and age at maturity (tm) were obtained for each of the 50 species. All 5 life history parameters are indicators of vulnerability (Cheung et al. 2005; Table 2) and are widely used in other frameworks for evaluating extinction risk and risk assessment (e.g. Jennings et al. 1999; Musick 1999; Stobutzki et al. 2001; Patrick et al. 2009). Reciprocals of the von Bertalanffy growth parameter and natural mortality were used so that all indicators exhibited a positive relationship with vulnerability. Indicators were scaled from 0 to 1 to normalise the unit of measurement. The scaled indicators were then examined for outliers and extreme cases. Three species (*Epinephelus lanceolatus*, *Siganus guttatus* and *S. vermiculatus*) were found to be extreme cases for 2 or more indicators, which tended to compress the values for the remaining species. Therefore, these were removed, leaving 47 species populating the index. Though the life history parameters of *E. lanceolatus* could not be used to construct the intrinsic index, this important study species was included in the vulnerability analysis but given the maximum intrinsic

<table>
<thead>
<tr>
<th>Aggregation fishery</th>
<th>Country</th>
<th>Sector</th>
<th>Gear</th>
<th>Period assessed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alphonse: <em>E. polyphekadion</em></td>
<td>Seychelles</td>
<td>Subsistence</td>
<td>Handline</td>
<td>2003-2005</td>
</tr>
<tr>
<td>Farquhar: <em>E. polyphekadion</em></td>
<td>Seychelles</td>
<td>Artisanal</td>
<td>Handline</td>
<td>2003-2005</td>
</tr>
<tr>
<td>Farquhar: <em>E. fuscoguttatus</em></td>
<td>Seychelles</td>
<td>Artisanal</td>
<td>Handline</td>
<td>2003-2005</td>
</tr>
<tr>
<td>Farquhar: <em>P. punctatus</em></td>
<td>Seychelles</td>
<td>Artisanal</td>
<td>Handline</td>
<td>2003-2005</td>
</tr>
<tr>
<td>Cosmoledo: <em>E. polyphekadion</em></td>
<td>Seychelles</td>
<td>LRFFT</td>
<td>Handline</td>
<td>1998-1999</td>
</tr>
<tr>
<td>Cosmoledo: <em>E. fuscoguttatus</em></td>
<td>Seychelles</td>
<td>LRFFT</td>
<td>Handline</td>
<td>1998-1999</td>
</tr>
<tr>
<td>Praslin: <em>S. sutor</em></td>
<td>Seychelles</td>
<td>Artisanal</td>
<td>Trap</td>
<td>2010</td>
</tr>
<tr>
<td>Mahé: <em>S. sutor</em></td>
<td>Seychelles</td>
<td>Artisanal</td>
<td>Trap, gillnet</td>
<td>2010</td>
</tr>
<tr>
<td>Msambweni: <em>S. sutor</em></td>
<td>Kenya</td>
<td>Artisanal</td>
<td>Trap, handline and spear</td>
<td>2010</td>
</tr>
<tr>
<td>Diani-Chale: <em>E. fuscoguttatus</em></td>
<td>Kenya</td>
<td>Artisanal</td>
<td>Spear, handline</td>
<td>2010</td>
</tr>
<tr>
<td>Kizimkazi: <em>E. lanceolatus</em></td>
<td>Zanzibar</td>
<td>Artisanal</td>
<td>Handline</td>
<td>2010</td>
</tr>
</tbody>
</table>

Aggregation fisheries assessed using the vulnerability framework with information on sector, gear types, management status and period of assessment. The assessment included the main study fisheries (in bold) plus additional fisheries documented elsewhere (Aumeeruddy and Robinson 2006; Robinson et al. 2007; Robinson et al. 2008b; Samoilys et al. 2011a)
index score of 1.0, corresponding to the value for *Myceteroperca phenax*. The mean value of the 5 scaled life history indicators was calculated for each species.

Table 2 Indicators included in the intrinsic vulnerability index with information on their attributes and key literature providing evidence for their selection.

<table>
<thead>
<tr>
<th>Indicator name</th>
<th>Attributes</th>
<th>Evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>K</td>
<td>von Bertalanffy growth parameter: negatively correlated with vulnerability</td>
<td>Jennings et al. 1999; Musick 1999; Hutchings 2001; Jennings 2001; Reynolds et al. 2001; Denney et al. 2002; Reynolds 2003; Hutchings and Reynolds 2004; Cheung et al. 2005</td>
</tr>
<tr>
<td>L&lt;sub&gt;∞&lt;/sub&gt;</td>
<td>Asymptotic length: positively correlated with vulnerability</td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>Natural mortality: negatively correlated with vulnerability</td>
<td></td>
</tr>
<tr>
<td>t&lt;sub&gt;max&lt;/sub&gt;</td>
<td>Longevity: positively correlated with vulnerability</td>
<td></td>
</tr>
<tr>
<td>t&lt;sub&gt;m&lt;/sub&gt;</td>
<td>Age at maturity: positively correlated with vulnerability</td>
<td>Banneor et al. 1987; Huntsman and Schaaf 1994; Armsworth 2001; Alonzo and Mangel 2004;</td>
</tr>
<tr>
<td>Sexual pattern</td>
<td>Non-sex changing: lower vulnerability Sex changing: higher vulnerability</td>
<td>Domeier and Colin 1997; Domeier et al. 2002; Sadovy and Domeier 2005</td>
</tr>
<tr>
<td>Aggregation type</td>
<td>Resident: lower vulnerability Transient: higher vulnerability</td>
<td></td>
</tr>
</tbody>
</table>

The two remaining indicators, sexual pattern and spawning aggregation type, were integrated in the index as multipliers. Sexual pattern based on information from FishBase was verified using recent published literature, while aggregation type was assigned to each species based on information extracted from the SCRFA Global Database (2010) in February 2010. For species with multiple records identifying both transient and resident aggregation types, we selected the most common aggregation type.

Many studies have shown that sex-changing populations are more vulnerable to fishing than gonochores (Bannerot et al. 1987; Huntsman and Schaaf 1994; Armsworth 2001). Though empirical evidence is lacking, theoretical models indicate that protogynous populations are sensitive to spawning aggregation size and sperm limitation caused by aggregation and size-selective fishing (Alonzo and Mangel 2004). Therefore, we considered that protogyny conferred higher vulnerability and used a multiplier of 1.2 for protogynous species and 1 for gonochores. Species forming transient aggregations are considered to be more vulnerable to aggregation fishing than species forming resident aggregations (Domeier and Colin 1997; Domeier et al. 2002; Sadovy and Domeier 2005) and a multiplier of 2 was applied to the former and 1 to the latter. After applying the multipliers of sexual pattern and aggregation type to the mean of the other indicators, the values were normalised from 0 to 1 to provide the final intrinsic vulnerability index. Finally, vulnerability groups were identified from cluster analysis based on a Bray-Curtis similarity matrix of untransformed intrinsic vulnerability.

Testing the intrinsic vulnerability index

To test the validity of the intrinsic vulnerability index, we examined its performance in predicting trends in population or status for two of the empirically derived sets of data tested by Cheung et al. (2005) for a fuzzy logic-based intrinsic vulnerability index.

Firstly, we extracted data on the population trends (slope) of aggregative spawning reef fish from Fiji (Jennings et al. 1999). Following the approach of Cheung et al. (2005), we selected only those species for which 15% or more of the variance in abundance was explained by fishing intensity. Only two aggregative spawners (*Epinephelus polyphekadion*, *Hipposcarus longiceps*) were common to
the lists of Jennings et al. (1999) and Sadovy de Mitcheson et al. (2008). Therefore, we extracted 5 additional species that were identified as aggregative spawners in the SCRFA Global Database (2010), and which had population trends explainable by fishing in the Fiji data, namely *Cephalopholis argus*, *Cephalopholis urodeta*, *Lutjanus bohar*, *Lutjanus gibbus* and *Plectropomus laevis*. While there is less evidence of spawning aggregation formation for these 5 species compared to species included in Sadovy de Mitcheson et al. (2008), they were considered putative aggregative spawners and were included in the index for the purpose of the test. After confirming that untransformed data met the assumptions of the tests (using Shapiro-Wilk and Levene tests), we examined the correlation (Pearson correlation coefficient) between the index and abundance trends and modelled their relationship using linear regression.

The second set of data examined were IUCN status categories for 28 aggregative spawners from our list of 47 species. Similar to Cheung et al. (2005), the intrinsic vulnerability index was tested in terms of its ability to predict IUCN status category using multinomial logistic regression. As many aggregative species were ‘Data Deficient’ we examined 4 IUCN categories, namely ‘Least Concern’, ‘Near Threatened’, ‘Vulnerable’ and ‘Endangered’, even though population trends were not known for all species in the first two categories.

**Quantifying extrinsic vulnerability**

For this framework it was necessary to identify and develop indicators that were specific to spawning aggregation fisheries. Numerous indicators predicting exposure or susceptibility to fishing have been developed (e.g. Patrick et al. 2009) and some indicators, or the underlying criteria, were adopted and modified for our index. Other indicators specific to aggregation fisheries were developed, based on evidence from the literature (Table 3).

Six fishery susceptibility indicators were selected that combine drivers, and to a lesser extent pressures, common to fisheries that exploit spawning aggregations (Table 3). The criteria for selection were: (1) ease of measurement and applicability to data-poor situations; (2) commonality, i.e. indicators applicable to all aggregation fisheries, and (3) complementary, i.e. indicators address different components of the fishery. The underlying premise of each indicator is well evidenced and the compliment of indicators is logical in that it forms a hierarchical structure that addresses the main components of an aggregation fishery. Thus, it is assumed that populations are most vulnerable to aggregation fishing if: (1) detailed knowledge of aggregation location and timing is widespread among fishers; (2) aggregations are easily accessible; (3) aggregations are heavily targeted; (4) a wide variety of gear-use combinations are involved in targeting aggregating or migrating fish; (5) there is an absence of regulatory or customary management for the fishery; and (6) the aggregation fisheries are highly commercialised with high demand. Weighting indicators was considered problematic as all represent different components of an aggregation fishery and the structure is hierarchical. For example, a targeted fishery cannot exist without knowledge on aggregation location and timing, whereas a fishery will not develop if accessibility is low, management is restrictive or there is little or no demand, regardless of knowledge.

Indicators were scored in a workshop in 2010 by 10 research team members with expertise in the study fisheries. To meet the criterion of applicability in data-poor contexts, ordinal scales of measurement were used (Table 3). After scoring, each indicator was scaled from 0 to 1 and combined (using mean) into a single index using the mean of the scaled indicator values for each fishery. Use of the mean values was considered more valid than re-scaling the means, which would have resulted in at least two fisheries being afforded minimum and maximum extrinsic vulnerability, i.e. scores of 0 and 1, respectively. Unlike the intrinsic index, the extrinsic index is specific to the case study fisheries and testing its validity requires independent data on those fisheries, relating for example to population trends, fishery status and socio-economic indicators.
Results

Intrinsic vulnerability index

Life history parameter estimates varied considerably among aggregative spawners and reflect a wide range of productivities and resilience to exploitation. For example, von Bertalanffy growth parameter ($K$) estimates vary from 0.09 in *Mycteroperca phenax* and *Epinephelus striatus* to greater than 1.6 in *Siganus guttatus* and *S. vermiculatus*. Likewise, size varied extensively, ranging from small acanthurids with asymptotic length ($L_{\infty}$) less than 30 cm TL to the large lutjanids and serranids with $L_{\infty}$ greater than 100 cm TL. Consequently, estimates of longevity, age at maturity and natural mortality exhibited order of magnitude differences among species.

The intrinsic vulnerability index was bracketed by *Acanthurus triostegus* and *Mycteroperca phenax* at the lowest and highest levels of relative vulnerability, respectively (Fig. 2). Cluster analysis separated 4 main species-groups on a within-group similarity greater than 88% and between-group dissimilarity greater than 19%. While *Acanthurus triostegus*, *Chlorurus sordidus* and *Ctenochaetus striatus* were of lower similarity as a group (82%), they were highly dissimilar to other groups (44%) and were assigned to a 5th group of very low vulnerability.

The cluster of very high vulnerability index values grouped mainly those serranids and a few lutjanids with the slowest life histories, i.e. slow growth, late maturity and high longevity (Fig. 2). Other serranids and most of the lutjanids were grouped in the high vulnerability cluster, together
with the more vulnerable labrids and scarids. The moderate cluster grouped scarids and siganids, while the low vulnerability clusters grouped the remaining scarids and most of the acanthurids.

Testing the intrinsic vulnerability index

The intrinsic vulnerability index was moderately correlated with population trends (slope of abundance) for seven aggregative species of reef fish from Fiji (Fig. 3; Pearson correlation coefficient $r = -0.678; p = 0.047$), though the regression model was only significant at the level of $p < 0.1$. The intrinsic vulnerability index was unable to predict IUCN category (Fig. 4; $\chi^2 = 2.59; p = 0.459$).

Fig. 2 Species ordered by intrinsic vulnerability and grouped by cluster (group-averaged Bray Curtis similarity): very high, high, moderate, low, very low vulnerability according to grey-scale.
Extrinsic vulnerability and the framework

Based on intrinsic vulnerability, the serranid and siganid aggregation fisheries were spread across the upper and lower quadrants of the framework, respectively (Fig. 5). The target species of the fisheries assessed included a moderately vulnerable siganid (\textit{S. sutor}), two serranid species of high vulnerability (\textit{E. fuscoguttatus}, \textit{E. polyphekadion}) and two serranid species of very high vulnerability (\textit{E. lanceolatus} (equivalent to \textit{M. phenax}), \textit{P. punctatus}; see Fig. 2).

The \textit{Epinephelus fuscoguttatus} and \textit{E. polyphekadion} populations at Cosmoledo Atoll were the most vulnerable to aggregation fishing (Fig. 5), mainly due to the fact that this was a highly targeted aggregation fishery for the Asian live reef fish food trade (LRFFT) and was characterised by high demand, value and storage capacity. Four other serranid populations were tending towards high extrinsic vulnerability, including the \textit{E. lanceolatus} population of Zanzibar. Fisheries targeted \textit{E. fuscoguttatus} and \textit{E. polyphekadion} at multispecies aggregation sites at Cosmoledo and Farquhar, gave rise to identical extrinsic index scores for both species at each location.
The remaining serranid populations were characterised by lower extrinsic vulnerability (Fig. 5). In the Alphonse Atoll group, the aggregation fishery for *E. polypheradion* is largely a subsistence fishery, whereas the Diani fishery for *E. fuscoguttatus* was marked by relatively low levels of fisher knowledge and accessibility. The extrinsic vulnerability of *Siganus sutor* populations, a species of moderate intrinsic vulnerability (see Fig. 2), varied mainly due to differences in gear use and management. The Praslin *S. sutor* aggregation-fishery employs traps as the sole fishing gear on aggregations, while the Mahé fishery also uses nets and the Msambweni fishery employs a total of four gears. A higher diversity of gears, and particularly the use of nets, considerably increases efficiency in aggregation-based fisheries. Moreover, the Praslin *S. sutor* aggregation-based fishery has historically been governed by community-based measures that have limited access to aggregation sites and have restricted gear use to traps, social norms that are lacking at the other sites.

**Discussion**

This preliminary evaluation highlights the potential for indicator-based frameworks to enable rapid assessment of the vulnerability of reef fish populations to aggregation fishing in data-poor contexts. However, several limitations and potential improvements to the framework were identified and are discussed here.

The intrinsic index is relatively easy to construct and based on readily available data (i.e. FishBase and the SCRFA Global Database, 2010) for populating the indicators. Many aggregative spawners are data deficient and it is necessary to use life history tools to provide parameter estimates for the indicators. While it is recognised that data derived from such tools are uncertain, the index is relative and the absolute values decrease in importance as more species of divergent life histories...
are added. Consequently, the life history indicators aligned the vulnerability of our 47 species with known variation in levels of vulnerability to fishing among reef fish species and families (Jennings et al. 1999; Hicks and McClanahan 2012). More accurate estimates of growth parameters may be obtained from published studies. However, this approach would not be without many of the problems that have prompted the development of life history tools for data deficient species. These include, among others, defining selection criteria or averaging methods when multiple estimates of parameters are available, and selecting empirical relationships or substitution procedures if certain parameter estimates were lacking.

The indicators for sexual pattern and aggregation type could be improved. Sexual pattern information on FishBase is outdated for many species and could be updated from recent reproductive studies (as was done for Epinephelus polyphekadion in Rhodes et al. 2011). Aggregation type was also unknown in the SCRFA Global Database (2010) for many species. These species can be reintroduced to the index as more information becomes available. Both these indicators were binomial in this preliminary evaluation of the framework. However, in the case of aggregation type, it may be possible to add additional levels of vulnerability, for example, based on the relative contribution of a single aggregation to the annual reproductive output of the population. There is evidence to suggest that transient spawners spreading their annual reproductive output over numerous but relatively small aggregations (e.g. Plectropomus leopardus; Samoilys 1997b; Sadovy and Domeier 2005), can be less vulnerable to fishing compared to species forming a few very large aggregations per population each year (e.g. E. striatus: Sadovy de Mitcheson et al. 2012; E. polyphekadion: Robinson et al. 2008b). Likewise, some siganids form numerous aggregations over protracted spawning seasons, thereby reducing the importance of any single aggregation to the annual reproductive output of the population (Robinson et al. 2011). However, there are many species in the index for which aggregation dynamics (e.g. number, size and periodicity) are less well known, which would complicate the use of a finer-scale indicator for aggregation type.

There is a need to identify further empirical datasets that can be used for testing the validity of the intrinsic index. While we found a strong correlation between the index and abundance trends for Fiji reef fish, the modelled linear relationship was only statistically significant at the 10% level. A low level of significance resulted from the low number of verified aggregative spawners (7 species) with trends explainable by fishing, and the high variation in intrinsic vulnerability for species exhibiting a moderate decline in abundance (i.e. L. gibbus, E. polyphekadion, C. argus, P. laevis). The test using the IUCN data was also inhibited by the high number (19 out of 47 species) of aggregative spawners lacking assessments, and most species with IUCN assessment were categorised as Least Concern. These constraints precluded a repeat of the test conducted by Cheung et al. (2005), wherein only categories of Vulnerable and above were used.

In constructing our intrinsic index, the indicators were not weighted, either in terms of their relative importance or their usefulness/ability in predicting vulnerability. Regarding the former approach, the empirical evidence for weighting among life history parameters is uncertain, a fact that may undermine weighting schemes based on expert opinion. For example, age at maturity is considered important (Musick 1999), but the relationships between several life history parameters are invariant and this parameter may be strongly correlated with the growth coefficient and with maximum age (Musick 1999; Dulvy et al. 2004). The perceived importance of certain parameters also varies between different schemes (e.g. fecundity: Musick 1999; Cheung et al. 2005). Moreover, weighting was inappropriate for sexual pattern and aggregation type as these were applied as multipliers. In terms of the second approach, the usefulness of indicators in constructing an index relates to properties of the data, such as contrast across samples (i.e. species) that can be examined using statistical analyses. However, initial attempts to weight intrinsic indicators using principal component analysis to derive factor scores for each parameter were invalidated since the life history invariants resulted in a strongly distorted ordination (‘horseshoe effect’).
Spawning aggregation behaviour is clearly an important determinant of the intrinsic vulnerability to fishing (Sadovy and Domeier 2005) and should be included in vulnerability frameworks for reef fish. While fish behaviour is increasingly incorporated in frameworks for temperate fisheries (Patrick et al. 2009), it has rarely been examined in the context of reef fisheries. Moreover, assumptions regarding the higher vulnerability conferred by schooling compared to aggregative behaviour (Cheung et al. 2005), which were largely derived for temperate fisheries (Pitcher 2001), may be less valid in coral reef fisheries where aggregative behaviour is often associated with spawning by protogynous species. Consequently, efforts at testing a vulnerability index based on life history and ecological traits by Cheung et al. (2005), which included a fish spatial social behaviour index derived from a temperate fisheries perspective, required the addition of supplementary information on spawning aggregation behaviour in order to predict reef fish population decline.

Socio-economic indicators have been developed and examined in several fisheries contexts, some of which were modified for our framework (e.g. Clua et al. 2005; Patrick et al. 2009). Our challenge was to identify indicators representing susceptibility to fishing and socio-economic drivers relevant to aggregation fisheries. However, much of the research on spawning aggregations is biological and there are few studies that focus on the fishery dynamics, including the socio-economic drivers of fishing though this is changing (see Sadovy de Mitcheson and Erisman 2012). It is important that the socio-economic context is assessed for improved monitoring and management of aggregation fisheries. Basic information can be obtained using rapid appraisal techniques and used to inform indicator-based approaches.

Although the aim of the framework is to evaluate fisheries in data-poor contexts, it will be necessary to test the extrinsic index and the framework in a data-rich context. Specifically, it would be informative to examine aggregation fisheries using this framework where independent assessment data on stock and aggregation status are available. For example, several tropical western Atlantic fisheries may meet these criteria and the extrinsic indicators could be scored by experts in those fisheries. Independent information on stock and aggregation status is available for only a few of the WIO fisheries assessed here. However, it is notable that LRFFT fishery at Cosmoledo, which was the most extrinsically vulnerable, was closed when aggregation fishing produced catches that exceeded limit reference points for the stocks in only two months of fishing (Aumeeruddy and Robinson 2006). By comparison, the Farquhar serranid populations had lower extrinsic vulnerability and their targeted fisheries do not appear to have severely depleted aggregations (Robinson et al. 2008b). Likewise, the Praslin S. sutor fishery scored in the bottom-left quadrant and is known to be a relatively sustainable fishery (Robinson et al. 2011).

A number of other improvements to the framework were identified in this preliminary evaluation. Even though the extrinsic indicators were hierarchical, it is recommended that indicators are weighted using expert opinion, as some were considered more important drivers or pressures. Additional indicators could include a technological index since navigation (GPS) and fish-finding equipment are known to increase susceptibility of spawning aggregations (Coleman et al. 1999; Koenig et al. 2000). In addition to improving the extrinsic indicators, both indices are relative measures of vulnerability and the strength of the framework depends of the number of fisheries assessed. As more aggregation-based fisheries in the WIO are documented they can be readily incorporated and evaluated by the framework. However, even with small numbers of fisheries, the framework can serve as a useful tool for fisheries monitoring in terms of tracking changes in extrinsic indicators over time and for prioritising management action.
Chapter 12: Conservation and fisheries effects of protecting species forming spawning aggregations using no-take marine reserves

Jan Robinson, Arnaud Grüss and David Kaplan

Introduction
The study of reef fish spawning aggregations and their fisheries typically raises concerns for conservation and management. This is due to the fact that many species forming aggregations for the purpose of spawning (hereafter referred to collectively as ‘aggregative spawners’) are vulnerable to exploitation and very few aggregation fisheries appear to be sustainable (Sadovy and Domeier 2005; Sadovy de Mitcheson and Erisman 2012). Given widespread decline and collapse of spawning aggregations and the unsustainable depletion of the populations from which they form, a conservation response is often imperative (Sadovy de Mitcheson et al. 2012). Consequently, no-take reserves (NTRs) combined with temporal catch and market restrictions are often recommended (Johannes 1998; Domeier et al. 2002; Rhodes and Warren-Rhodes 2005) and applied for the protection of spawning aggregations (Sadovy de Mitcheson et al. 2008; Russell et al. 2012). However, as is the case with the general application of NTRs for supporting fisheries management objectives, notably for enhancing yields (Hilborn et al. 2004), critical science and implementation constraints remain in the use of this tool for protecting aggregative spawners (Sale et al. 2005; Le Quesne 2009).

Spawning aggregation-based NTRs differ fundamentally from conventional NTRs models that aim to produce conservation and fisheries benefits. Conventional NTRs aim to confer both persistence of a proportion of population biomass within their boundaries and a net export of eggs and larvae (‘larval subsidy’) and adults (‘spillover’) to fished areas in order to enhance yield (Gell and Roberts 2003; Russ et al. 2004; McClanahan 2010). Small NTRs that only protect the area of reef where spawning aggregations form typically do not contain a significant resident biomass, since the vast majority of the population will reside in areas beyond the NTR for much of the year, only migrating into the protected area during spawning periods (e.g. Hutchinson and Rhodes 2010; Rhodes et al. 2012). Thus, spawning aggregation-based NTRs deviate from conventional models in that they do not create the conditions for spillover and larval subsidy and will only offer protection to most participating adult fish during a limited part of the year. This distinction may appear obvious, but the fundamental difference between movement leading to spillover and yield enhancement from a conventional reserve, and mobility associated with migrations to and from a spawning area, is often inexplicit in the discourse on NTR effects for highly mobile species (Gaines et al. 2010).

A few empirical (e.g. Beets and Friedlander 1998; Rhodes and Sadovy 2002b; Claro and Lindeman 2003; Burton et al. 2005; Rhodes and Warren-Rhodes 2005; Nemeth 2005; Rhodes and Tupper 2008; Mangubhai et al. 2011) and theoretical studies (Alonzo and Mangel 2004; Heppell et al. 2006) have addressed the effects of spawning aggregation-based NTRs. While empirical evidence of recovery remains scarce and is limited to a single site (e.g. Beets and Friedlander 1998; Nemeth 2005), the existing studies do generally concur that NTRs protecting spawning aggregation sites can lead to significant increases in population size, biomass and, in the case of protogynous populations, normalization of sex ratio (Beets and Friedlander 1998). The latter effect is thought to improve egg fertilization rates (Coleman et al. 1996; Rhodes and Warren-Rhodes 2005).

The caveat to this concurrence is that such benefits are undermined or lost if fish suffer high fishing mortality as juveniles or as adults when outside of the protected spawning sites. Due to generally low catchability outside of the spawning season, a few groupers are often fished almost exclusively while aggregating to spawn (e.g. Nassau grouper, Epinephelus striatus: Sadovy and Eklund 1999;
tiger grouper, *Mycteroperca tigris*: Matos-Caraballo et al. 2006). Coupled with the slow life histories of these species (Coleman et al. 1999), conservation objectives are paramount in these extreme cases and may be met by NTRs alone. However, since many aggregative spawners are also heavily fished as juveniles and as adults outside of the spawning season, and when migrating to and from spawning sites (e.g. Fulton et al. 1999; Claro et al. 2009; Robinson et al. 2011), conservation benefits are unlikely to be attained by NTRs alone. In those instances, additional fisheries management interventions are requisite. Benefits for fisheries are even less tangible, since any benefits of NTRs will take time to emerge for slow life histories, and large and immediate losses in yield usually result from closing areas of high fish density (Gaines et al. 2010). As with conventional application of NTRs for fisheries management, critical knowledge gaps remain regarding the effectiveness of NTRs for spawning aggregations in supporting socio-economic objectives, (Sale et al. 2005; Grüss et al. 2011a).

The impetus for this component of the project resulted from experiences of the lead author during an earlier MASMA-funded study on spawning aggregations in Seychelles (Robinson et al. 2007). That project identified and studied two important aggregation fisheries: a commercial trap fishery targeting aggregations of the Shoemaker spinefoot rabbitfish (*Siganus sutor*) and a subsistence and semi-commercial fishery targeting aggregations of camouflage (*Epinephelus polyphekadion*) and brown marbled (*E. fuscoguttatus*) groupers (Robinson et al. 2008b; Robinson et al. 2011). In discussing the findings of this research with key stakeholder groups, a divergence in opinion emerged in terms of the required management response. The environmental and conservation agencies and environmental non-governmental organisations argued that complete protection of spawning aggregations through the establishment of NTRs was required, whereas fishers and fishing companies argued that aggregations could be fished sustainably and that a conventional fisheries management approach was required. Attempts to inform the ensuing debate highlighted a critical science question, namely: would closing the spawning aggregations to fishing through the use of NTRs be beneficial for conservation (i.e. protection of high levels of spawning stock biomass, and normalization of the sex ratio of protogynous populations) and fisheries (i.e. by enhancing yield from the non-spawning areas and periods)?

The aim of this study was to develop and use a simple model to address concerns regarding the benefits of spawning aggregation-based NTRs. The specific objectives were to: (1) design a general model that can be applied to a variety of gonochoristic and protogynous fish populations forming transient spawning aggregations; (2) apply the model to two transient aggregation-forming reef fish populations from Seychelles and analyse NTR scenarios for these two populations; and (3) derive general observations on the conservation (spawning stock biomass-per recruit) and fisheries (yield-per-recruit) effects of spawning aggregation-based NTRs.

This chapter presents a simplified description of the model attributes and highlights the main findings from the study. The full model specifications and detailed results are reported in Grüss et al. (*in press*). That submission focuses exclusively on scenarios for NTRs sited on spawning aggregations, while in this chapter we also present the detailed results of an additional scenario that examined the effects of NTRs protecting the normal residence areas of both juveniles and non-spawning adults.

**Methods**

We developed a non-spatial, per-recruit model for evaluating the conservation and fisheries effects of spawning aggregation-based NTRs for gonochoristic populations and protogynous populations with age-mediated sex change. The model can be run with information that is relatively easy to obtain, namely:

- the level of annual fishing effort exerted on fish populations and the fraction of this annual fishing effort that is directed towards spawning aggregations;
• estimates (by proxy) of catchability at spawning and non-spawning sites, and
• estimates of a limited set of life history parameters.

The model is therefore highly flexible and can be widely applied for examining the effects of NTRs on spawning aggregations and their fisheries. In this study, we apply the model to populations of two species that form transient spawning aggregations in Seychelles: the protogynous brown-marbled grouper (*Epinephelus fuscoguttatus*) population of a remote atoll (Robinson et al. 2008b) and the gonochoristic shoemaker spinefoot rabbitfish (*Siganus sutor*) population of the main granitic islands (Robinson et al. 2011).

To evaluate the effectiveness of spawning aggregation-based NTRs, we use two metrics for gonochoristic populations: female spawning stock biomass-per-recruit (female SSBR) and yield-per-recruit (YPR). For protogynous populations, we use an additional metric: sex ratio (SR), defined here as the number of adult females over the number of adult males. Female SSBR is an indicator of reproductive capacity, SR is an indicator of the chances of egg fertilization for protogynous populations, and YPR is an indicator of fisheries benefits.

The model was run to examine the effects of setting aside either a fraction of or all spawning sites as NTRs. Fishing mortality with NTRs depends on spawning-site fidelity (faithful or not faithful) and on the fate of the fishing effort that was in reserves before they were closed. Several scenarios for the fate and redistribution of fishing effort after reserve creation were considered: effort previously in reserves disappears; pre-reserve effort is fully redistributed to spawning sites remaining open to fishing after some are protected, and pre-reserve effort is fully redistributed to non-spawning sites at the time of reserve creation for cases where all spawning sites are closed to fishing. Underlying these scenarios for fishing effort evolution is the assumption that fishers will preferentially move to other known spawning sites if not all spawning areas are closed to fishing. In this latter case, fishers will only resort to intensifying fishing in non-spawning areas if they have no other alternative. In total, six scenarios of spawning aggregation-based NTRs were assessed for both species (NTR Scenarios 1-6; Table 1). In parallel, two scenarios were evaluated where a fraction of normal residence areas is set aside as reserves (NTR Scenarios 7-8). Effort previously in reserves disappears for the first of these two scenarios, while pre-reserve effort is fully redistributed to normal residence areas remaining open to fishing at the time of reserve creation for the second (Table 1).

**Results**

In this section, the main findings from the model are highlighted. Firstly, we present the fisheries effects (i.e. effects on YPR) of protecting a fraction or all spawning aggregations. Secondly, the conservation effects (i.e. effects on SSBR and sex ratio) of protecting a fraction of spawning aggregations are provided, and thirdly the conservation effects of protecting all spawning aggregations. Finally, we compare the results of NTRs protecting spawning aggregations with those
of protecting the normal residence areas (i.e. juvenile and non-spawning adult habitats). All these results are summarized in Table 2.

1. Fisheries effects of spawning aggregation-based NTRs

Table 1 Description of the no-take reserve (NTR) scenarios simulated in the study

<table>
<thead>
<tr>
<th>NTR Scenario</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>#1</td>
<td>Some spawning sites are closed to fishing; the effort that was in reserves before they were closed disappears at the time of NTR creation; fish are not faithful to spawning sites</td>
</tr>
<tr>
<td>#2</td>
<td>Some spawning sites are closed to fishing; the effort that was in reserves before they were closed disappears at the time of NTR creation; fish are faithful to spawning sites</td>
</tr>
<tr>
<td>#3</td>
<td>Some spawning sites are closed to fishing; the effort that was in reserves before they were closed is fully redistributed to spawning sites remaining open to fishing at the time of NTR creation; fish are not faithful to spawning sites</td>
</tr>
<tr>
<td>#4</td>
<td>Some spawning sites are closed to fishing; the effort that was in reserves before they were closed is fully redistributed to spawning sites remaining open to fishing at the time of NTR creation; fish are faithful to spawning sites</td>
</tr>
<tr>
<td>#5</td>
<td>All spawning sites are closed to fishing; the effort that was in reserves before they were closed disappears on NTR creation</td>
</tr>
<tr>
<td>#6</td>
<td>All spawning sites are closed to fishing; the effort that was in reserves before they were closed is fully redistributed to non-spawning sites at the time of NTR creation</td>
</tr>
<tr>
<td>#7</td>
<td>Some normal residence areas are closed to fishing; the effort that was in reserves before they were closed disappears on NTR creation</td>
</tr>
<tr>
<td>#8</td>
<td>Some normal residence areas are closed to fishing; the effort that was in reserves before they were closed is fully redistributed to non-protected normal residence areas remaining open to fishing on NTR creation</td>
</tr>
</tbody>
</table>

Table 2 Summary of the main effects of NTRs on female spawning stock biomass-per-recruit (SSBR), sex ratio and yield-per-recruit (YPR) for *Epinephelus fuscoguttatus* and *Siganus sutor* for different scenarios of spawning site fidelity and the fate of effort formerly in NTRs. Colour scheme: light grey = positive effects; white = no effects; dark grey = negative effects.

<table>
<thead>
<tr>
<th>Closure type</th>
<th>Fate of the fishing effort formerly in reserves</th>
<th>Fidelity of fish to spawning sites</th>
<th>NTR Scenario No.</th>
<th>Female SSBR</th>
<th>Sex ratio (<em>E. fuscoguttatus only</em>)</th>
<th>YPR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Some spawning sites are closed to fishing</td>
<td>Effort disappears</td>
<td>Non-fidelity</td>
<td>1</td>
<td>1 = 2 (at low F)</td>
<td>1 = 2 (at low F)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Complete fidelity</td>
<td>2</td>
<td>1 = 2 (at low F)</td>
<td>1 = 2 (at low F)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Effort fully redistributed to non-protected spawning sites</td>
<td>Non-fidelity</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Complete fidelity</td>
<td>4</td>
<td>4 &lt; 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All spawning sites are closed to fishing</td>
<td>Effort disappears</td>
<td>NA</td>
<td>5</td>
<td>5 = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Effort fully redistributed to normal residence areas</td>
<td>NA</td>
<td>6</td>
<td>5 = 6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Some normal residence areas closed to fishing</td>
<td>Effort disappears</td>
<td>NA</td>
<td>7</td>
<td>7 &gt; 8</td>
<td>7 &gt; 8 (rabbitfish at high F)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Effort redistributed to non-protected normal residence areas</td>
<td>NA</td>
<td>8</td>
<td>8 &lt; 7</td>
<td>8 &lt; 7 (rabbitfish at high F)</td>
<td></td>
</tr>
</tbody>
</table>
Patterns of YPR in presence of NTRs were qualitatively similar for grouper and rabbitfish. For all scenarios examined, encompassing both the protection of a fraction or all spawning aggregations, there are no benefits for YPR and even negative effects under most scenarios. Only if effort is much higher than is currently applied in the trap fishery for rabbitfish, equating to an overexploited stock, can pre-reserve levels of YPR be maintained by protecting a fraction of spawning aggregations. For the grouper population, YPR decreases with the fraction of spawning areas protected and, the higher the value of effort, the more YPR decreases with the fraction of spawning sites in reserves. The greatest declines in YPR occur when all spawning aggregations are protected, since global fishing mortality is considerably reduced in this situation, both when effort disappears and when effort is redistributed. The negative effects on YPR are more pronounced for grouper than rabbitfish, since catchability increases to a larger extent with grouper aggregation formation.

2. Conservation effects of protecting a fraction of spawning aggregations using NTRs
Patterns of female SSBR in the presence of NTRs were qualitatively similar for grouper and rabbitfish. Unsurprisingly, the greatest conservation benefits (i.e. increases in SSBR and decreases in sex ratio) were obtained when effort previously expended on spawning aggregations simply disappeared when the NTRs were established. Interestingly, female SSBR and sex ratio were relatively unchanged between the site fidelity and non-site fidelity scenarios when effort disappears. However, at higher levels of annual effort than those observed in the fisheries, SSBR and sex ratio would benefit more from the site fidelity than the non-site fidelity situation, as the fraction of protected spawning sites increases. By contrast, site fidelity has important consequences for conservation benefits if effort at spawning sites is redistributed when NTRs are created. As we assumed that effort would be redistributed to the remaining unprotected spawning sites if only a fraction are protected using NTRs, SSBR is invariant with the fraction of spawning sites in reserves in the non-site fidelity scenario, as fish would suffer mortality when they attended non-protected spawning aggregations. Conversely, if fish are faithful to spawning sites, conservation benefits are attained on effort redistribution, but at lower levels than when effort disappears. However, the effects of effort redistribution on sex ratio for the protogynous grouper population were negative. At high effort levels and with a relatively large fraction of spawning sites protected by NTRs, sex ratio at fished spawning sites would be more heavily female-biased than if the same level of effort was applied in the fishery without any NTRs.

3. Conservation effects of protecting all spawning aggregations using NTRs
If all spawning aggregations are protected by NTRs, conservation benefits occur and do not differ much if effort disappears or is redistributed. This is because, under this assumption, all effort would be directed towards non-spawning periods and areas where catchability is much lower. Therefore, even the addition of redistributed effort on non-spawning fish does not affect SSBR to a large degree. There are greater conservation benefits for groupers than rabbitfish, since in the former, aggregation formation is associated with much larger increases in relative catchability. The benefits for male groupers are also higher than those for females – as males spend longer times aggregating, total closure of spawning sites increases SSB for males to a larger extent than for females.
• Since grouper males are afforded a greater reduction in mortality relative to females if all spawning aggregations are protected, again due to the longer time males spend aggregating, the greatest reduction in sex ratio bias occurs in these scenarios.

4. Conservation and fisheries effects of protecting normal residence areas using NTRs

• NTRs protecting normal residence areas have distinct impacts for rabbitfish and grouper.
• For rabbitfish, female SSBR increases with the fraction of normal residence areas in reserves, as well as YPR, when the stock is in an overexploited state, although increases in YPR are moderate (Figs. 1a-b and 2a-b). Increases in female SSBR and YPR are due to the release of fishing pressure on juveniles and non-spawning adults, shifting the demography of the population towards larger and older individuals.
• For grouper, female SSBR and YPR, respectively, increases and decreases with the fraction of normal residence areas in reserves. Yet, YPR decreases are less severe than when spawning aggregation-based NTRs are created and the effort that was in reserves disappears at the time of NTR creation (Figs. 1c-d and 2c-d). On the other hand, there are slightly more chances that grouper sex ratio will reach critical levels than when spawning aggregation-based NTRs are created in the effort disappearance situation (results not shown here).
• When the effort that was in reserves before they were closed is fully redistributed to the normal residence areas remaining open to fishing, NTR benefits are moderately reduced compared to when this effort disappears. In addition, at effort levels for which sex ratio was below some critical level in the absence of NTRs, grouper sex ratio is likely to exceed this level when a relatively high proportion of normal residence areas is protected.

Discussion

A parsimonious model was developed to examine the effects of spawning aggregation-based NTRs on three metrics, namely female spawning stock biomass-per-recruit (SSBR), sex ratio and yield-per-recruit (YPR), and was applied to two of the project study fisheries. Though parameterised for two populations in Seychelles, the model could readily be applied to our other study fisheries in Kenya and Zanzibar. Pending such an exercise, we offer hypotheses on the likely effects of NTRs for other study fisheries, facilitated by the fact that, in many cases, parameter estimates are quantitatively similar to those in Seychelles.

The model demonstrated that fisheries benefits (i.e. an increase in YPR) are unattainable for both study populations in Seychelles if spawning aggregations are protected by NTRs. Even if all spawning sites are protected, either through NTRs or prohibition on take or sale during spawning periods, this effect is unchanged. However, though not included in the model, Grüss et al. (in press) note that if a significant fraction of spawning sites is placed in NTRs, fisheries benefits may be achieved indirectly in the longer-term via enhanced recruitment from the increase in reproductive capacity resulting from protection. Of critical importance for the management of S. sutor fisheries is the finding that protecting non-spawning adults and juveniles, i.e. normal residence areas, can increase YPR as well as benefiting female SSBR. This effect only occurs if the population is heavily exploited, which is the case in both Seychelles (Robinson et al. 2011) and Kenya (Hicks and McClanahan 2012). This is achieved through shifting the demography of the population towards larger individuals, thereby enhancing harvestable biomass and compensating fisheries for the loss of fishing grounds. Many NTRs in both Kenya and Seychelles are already established in normal residence areas of S. sutor (Graham et al. 2007; McClanahan et al. 2007) and may already contribute to the resilience of this species at the high exploitation rates (Hicks and McClanahan 2012; Robinson et al. 2011). It is likely that gear measures that increase selectivity for adult and larger S. sutor will also achieve demographic shifts and attain equivalent conservation and fisheries benefits as protecting juveniles in normal residence areas.
Overall, the results indicate that spawning aggregation-based NTRs increase fish reproductive capacity (i.e. spawning stock biomass per recruit) regardless of the fate of the fishing effort that was in reserves before they were closed. An exception to this general pattern occurs if fish are not faithful to the fraction of spawning sites protected, which results in unchanged reproductive capacity if effort is redistributed to the remaining fraction of unprotected spawning sites. Since evidence from tagging studies indicates that many groupers are faithful to individual spawning sites (e.g. Zeller 1998; Bolden 2000; Nemeth 2005; Starr et al. 2007), including our brown-marbled grouper study populations (Chapter 8), this scenario is less likely to be relevant for aggregative spawners in this family. However, the same degree of spawning site fidelity may not occur in aggregative species from other families. For example, results from the acoustic monitoring of S. sutor at aggregation sites in Seychelles indicate that a degree of infidelity occurs with a small proportion of the population attending other aggregation sites during full moon spawning periods (Chapter 6). Infidelity will predispose individuals to mortality at unprotected spawning sites, which over time will erode the conservation benefits of NTRs, in a similar way to adult mobility weakening persistence in

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Fig. 1 Fraction of female spawning stock biomass per recruit (FNSSBR, i.e., the ratio of female spawning stock biomass per recruit over natural female spawning stock biomass per recruit), as a function of the multiplier of fishing effort ($mE_{base}$), for NTR scenarios #2, #4, #7 and #8 (see Table 1 for a description of the different NTR scenarios). (a,b) rabbitfish; (c,d) grouper. The fraction of spawning sites or normal residence areas in NTRs, $C_r$, is 30% and 60% for (a,c) and (b,d). $E_{base}$ is the default level of annual fishing effort exerted on the population and is indicated by a dashed-dotted blue line. The level of annual effort at which yield-per-recruit in the absence of NTRs reaches a maximum is indicated by a dashed-dotted red line for rabbitfish. (See colour plates.)
conventional NTRs (Grüss et al. 2011b). Moreover, from acoustic studies on grouper populations, evidence is emerging that a proportion of individuals may not attend the spawning aggregations that form at a particular site in all reproductive months (Starr et al. 2007; Rhodes et al. 2012). While there is no evidence to suggest that they attended other, unmonitored spawning aggregation sites in those ‘missed’ reproductive months, such behaviour also constitutes infidelity in so far as fidelity can be measured as the level of participation in all spawning aggregations that form at a particular site. Assuming adults that miss attending a spawning aggregation in any particular period remain in normal residence areas, infidelity of this type will not undermine spawning stock biomass through effort reallocation to unprotected spawning sites, although conservation benefits may be constrained as less of the population will be protected than expected. However, such a constraint is likely to be minor in groupers due to the much lower levels of catchability associated with normal residence areas. Clearly there is a degree of risk in extrapolating individual behaviour to the population-level, especially if tagging sample sizes are low and polymorphic spawning behaviour occurs (Grüss et al. 2011a). From a conservation perspective, it may be preferable to deconstruct fidelity into ‘site’ and ‘aggregation’ components to ensure that fidelity does not only invoke the use of a single site for spawning, but also the proportion of the population’s attendance at aggregations across spawning periods. Therefore, we recommend that fidelity assumptions be examined in models, especially for families other than groupers for which less is known regarding their spawning behaviour.
When the effort that was in reserves before they were closed disappears or is displaced to non-spawning sites, setting aside spawning sites as reserves reduces sex ratio bias for protogynous populations and therefore may increase the chances of egg fertilization (Coleman et al. 1996; Rhodes and Warren-Rhodes 2005). However, if only a small fraction of spawning aggregation sites is protected, fish are faithful to spawning sites and effort is displaced to non-protected spawning sites, the sex ratio of a part of the population is normalized, while that of the rest of the population becomes severely biased towards females. The finding that only partial protection of spawning sites can in fact worsen sex ratio has important practical implications in that fisher knowledge and targeted fishing often extends to aggregations at locations unknown to scientists and managers (Pears et al. 2007; Robinson et al. 2011). Effort displacement rather than disappearance is common upon creation of reserves (Valcic 2009) and, in the case of aggregation-based NTRs, effort can be readily displaced to unprotected spawning sites (Rhodes and Warren-Rhodes 2005) or equally vulnerable migratory routes (Claro and Lindeman 2003; Rhodes and Tupper 2008; Rhodes et al. 2012). Hence, seasonal prohibitions of take, possession or sale of groupers are expected to be more effective for conservation in cases where few spawning sites are known to managers.

The relative difference in catchability between spawning and non-spawning periods is a critical determinant of population vulnerability to targeted aggregation fishing (Robinson et al. 2011). In some species, non-spawning populations are of extremely low density, or are inaccessible, and catches outside the spawning season are rare. The formation of spawning aggregations greatly increases density and may result in large changes to catchability if aggregation sites are accessible. This is the case for the Nassau (Epinephelus striatus) and tiger (Mycteroperca tigris) groupers in the tropical western Atlantic (Sadovy and Eklund 1999; Matos-Caraballo et al. 2006). It also appears that Epinephelus lanceolatus in Unguja, Zanzibar, is subject to similar dramatic population and fishery changes, whereby catchability increases by orders of magnitude at spawning sites compared to negligible levels in non-spawning periods. For most other aggregative spawners, including our study populations of E. fuscoguttatus, E. polyphekadion and S. sutor, catchability does not differ to the same extent and annual catches comprise fish taken at spawning sites and fish taken from the normal areas of residence; i.e. there is less relative change in catchability between spawning and non-spawning periods. Catchability underlies the finding that female SSBR and sex ratio were relatively unchanged between the different fidelity scenarios. The creation of NTRs eliminates a portion of fishing mortality, but our study populations were still exposed to considerable fishing mortality outside of the spawning season, thereby reducing the negative impact of infidelity relative to populations that are only caught while aggregating to spawn (Grüss et al. in press).

As expected, the positive effects of spawning aggregation-based NTRs on fish reproductive capacity and their negative effects on yield-per-recruit are stronger for long-lived, slow-growing populations than for short-lived, fast-growing populations. This finding offers avenues for prioritising conservation and management objectives among species. In the case of protogynous groupers, which appear to show relatively high if not absolute fidelity, a precautionary approach would entail protecting spawning aggregations through spatial or non-spatial measures and aiming for moderate YPR targets. Since a significant proportion of spawning sites would require protection to achieve conservation benefits (i.e. maintain SSBR), non-spatial measures, such as seasonal sales bans, are likely to be more effective.

In the case of the more productive rabbitfish populations, maximum YPR can be targeted as a management objective. Since spawning aggregation-based NTRs will neither achieve this objective nor the conservation objective of maintaining stock biomass, especially given a degree of infidelity, control of fishing effort is the most viable management measure. Given that effort is difficult to regulate in small-scale multi-species and multi-gear fisheries (McClanahan et al. 2005a), an alternative approach would be to reduce juvenile mortality through gear measures that increase selectivity for larger fish or establishment of NTRs in juvenile habitats, though in the longer term, annual effort may increase in unprotected areas including spawning aggregations, potentially resulting in growth overfishing.
The approaches identified above are entirely precautionary and ultimately there will be a need to tackle pertinent issues that are common to many small-scale coastal fisheries. Our model was restricted to annual fishing effort that was either unchanged or decreased after NTR establishment. However, conservation benefits may be considerably reduced if annual effort was significantly increased and the efficiency of fishing gears was improved after adoption of NTRs, which are likely given the trajectory of demand for fish in the region and globally (FAO 2012) and the fact that fishing efficiency tends to increase over time (Hilborn and Walters 1992; Ruttan 2003; Grant and Berkes 2007). Thus, for spawning aggregation-based NTRs to be effective, the need for controls on fishing in non-protected areas cannot be ignored (Nemeth 2005; Rhodes & Warren-Rhodes 2005).
Chapter 13: Conclusions and management implications

Jan Robinson and Melita Samoilys

Data-poor approaches for the assessment and management of marine resources are especially important to regions such as the WIO where the potential for long-term data collection and research are limited. The research programme reported in this book demonstrated the feasibility of using basic information from spawning aggregation-based fisheries to systematically evaluate management needs in data-poor contexts. This was achieved through a conceptual approach (Chapter 2) that involved estimation of key aggregation and fishery parameters (Chapters 3 to 10), and the application of those parameters in a vulnerability assessment (Chapter 11) and a no-take reserve (NTR) model for spawning aggregations (Chapter 12). We are confident that the full application of this conceptual approach at any particular site, inclusive of the various methodologies and tools, can enable an informed management process to be initiated within a short time frame such as 2 years. As more information becomes available and if reserves are implemented, both the vulnerability assessment and model can be further refined and incorporated in an adaptive management cycle.

Considering management measures that focus specifically on a population’s spawning behaviour should be founded on knowledge that (i) the population aggregates for the purpose of spawning, and that (ii) the spawning aggregations are fished. This information was lacking at study sites in East Africa and therefore research on verifying spawning aggregations and their fisheries was required (Chapter 3, 5, 7, 10), highlighting how basic research on this phenomenon on the mainland lagged behind that of Seychelles. However, by electing to work on the same species in these two different areas of the WIO, we provided for valuable comparisons in the susceptibility of conspecific populations to aggregation fishing, which were addressed semi-quantitatively in the vulnerability analysis (Chapter 11) and are used qualitatively in this section to highlight management implications.

As in other tropical regions (Domeier and Colin 1997; Sadovy de Mitcheson et al. 2008), coastal fishers of the WIO exploit reef fish spawning aggregations, some on a commercial scale. Though this study was confined to six populations and their associated fisheries, the practice of aggregation fishing is undoubtedly more widespread, as indicated by this and earlier MASMA studies (Robinson et al. 2004; Samoilys et al. 2006; Robinson et al. 2007). For Siganus sutor, a shallow-water species of high fishery importance throughout the WIO (Everett et al. 2010; McClanahan and Mangi 2004), it is highly likely that spawning aggregations are commonly targeted at all known and accessible sites. While S. sutor is clearly more resilient to aggregation fishing (Robinson et al. 2011), extrinsic fishing pressures and drivers differ among fisheries in the region and highlight the need for a case-by-case approach.

This research programme confirmed regional similarities in aggregation dynamics among conspecific populations. For example, in southern Kenya, S. sutor migrates 2-4 kilometers to offshore reefs to form short-lived transient spawning aggregations around full moon within a protracted season (Chapters 3 and 5). Research results from multiple research approaches in Seychelles over the last decade (fisher knowledge surveys, reproductive biology, telemetry and UVC) show that S. sutor aggregate to spawn at specific sites a few days around the full moon during the north-easterly monsoon season, providing strong evidence that this represents their sole mode of reproduction (Robinson et al. 2011; Chapter 6). Results from Kenya do not contradict this pattern but were far less conclusive, a reflection of the more limited data obtained from the multiple approaches used in Kenya during this programme. Therefore, more detailed histological studies would be beneficial to confirm whether or not the total annual reproductive output comes from aggregations.
Siganus sutor showed high site fidelity to spawning aggregation sites in Kenya, though the more detailed telemetry data in Seychelles demonstrated that fidelity was not absolute. Moreover, results from Seychelles also revealed turnover of S. sutor aggregations, inferred from aggregation site residency times being much shorter than aggregation duration (Chapter 6).

Since this finding has implications for the estimation of aggregation size and therefore the impacts of fishing, further telemetry studies could be conducted on the Kenyan S. sutor aggregations to determine if it is an aggregating dynamic common to this species.

Rabbitfish (Siganidae) are schooling species with large home ranges (Fox and Bellwood 2011) both of which pose challenges to research of their aggregation fisheries. The UVC results from Kenya illustrated difficulties in distinguishing whether S. sutor were aggregating for spawning or were foraging at aggregation sites. However, telemetry results from Seychelles indicated that S. sutor were only present at spawning aggregation sites during known spawning periods (Robinson et al. 2007; 2011). Thus, a cautious interpretation of the Kenyan aggregations and study sites as being only for spawning is warranted.

Regional similarities were found in the aggregation dynamics of the grouper E. fuscoguttatus (Serranidae), further confirming that this species typically forms transient spawning aggregations on outer reef slopes in relation to the new moon for 2-4 months each year (Chapter 6, 7, 8, 9). However, acoustic telemetry studies and the existence of prior aggregation data in Seychelles yielded additional insights on aggregation dynamics in this species that should inform future research and management in Kenya. Notably, sex-specific differences in male and female arrival and residency times at aggregation sites in Seychelles highlight sex-specific variation in vulnerability to aggregation fishing, providing vital information for the design of fine-scale temporal management measures (e.g. temporary fishery reserves or sales/catch restrictions). In addition, variability in the spatial distribution of E. fuscoguttatus aggregations in Seychelles, due to habitat disturbance, provides a strong argument for larger protected areas that incorporate buffer zones.

Similarities also exist between study locations in the socio-economic importance of S. sutor aggregation fisheries. Although catch rates of S. sutor on spawning aggregations increased 4-fold in Kenya, aggregations were relatively short-lived and consequently yielded catches representing only around 12% of the total annual catch. Therefore management of this species in Kenya needs to consider the non-aggregation aspects of the fishery to control fishing mortality, a similar conclusion made in Seychelles (Robinson et al. 2011) and further demonstrated in the modeling results (Chapter 12). The importance of aggregation catch relative to the annual catch made on a population is partly dependent on density-dependent catchability, i.e. the increase in population density and vulnerability to fishing that occurs with aggregation formation, as well as on aggregation duration and seasonality. Density change is less extreme in rabbitfish than groupers, while aggregations are also much shorter in duration. Consequently, aggregation fishing is unlikely to be the primary source of annual fishing mortality rates in rabbitfish (Robinson et al. 2011).

Regional differences were seen in aggregation fisheries, such as in gear diversity. For example, while Praslin Island fishers only use traps to target S. sutor aggregations, fishers in southern Kenya also use hook-and-line and anecdotal reports indicate that ring-nets are used (Chapter 3). Kenyan fishers also use Gillnets and illegal beach seines on S. sutor populations inshore. Gear diversity is known to increase vulnerability in aggregation-based fisheries: the introduction of nets can result in a rapid depletion of aggregation abundance (Chapter 11; Claro et al. 2009). These regional differences further reinforce the need for a case-by-case approach to management.

A fundamental constraint in addressing the management needs of spawning aggregation-based fisheries is the difficulty in establishing aggregation status and its relationship to the population as a whole. Both parameters require years of continued monitoring. In Kenya, E. fuscoguttatus aggregations were at least an order of magnitude smaller than some of those observed in Seychelles.
and some other Indo-Pacific locations (Johannes et al. 1999; Robinson et al. 2008b; Rhodes et al. 2012). Peak abundances in Kenya were most similar to those reported in Komodo (Indonesia) (Pet et al. 2005; Mangubhai et al. 2011), the Solomon Islands (Hamilton et al. 2012b) and Papua New Guinea (Hamilton et al. 2011) where aggregation fishing has been prevalent, including by the live reef food fish trade. In Kenya, small aggregation sizes may not be exclusively a result of fishing, but also low natural abundances in association with limited reef habitat, or a combination of these factors. In Seychelles, this species also forms smaller, secondary aggregations in addition to large primary aggregations (Robinson et al. 2008b), a situation that may also exist in Kenya. It is clear that aggregation size varies naturally on a range of scales, both within and between sites, thereby precluding inter-site comparisons and highlighting the need to monitor individual sites at a sufficient resolution to account for intra-site variability (Johannes et al. 1999).

In the absence of status information for the majority of our study populations and spawning aggregations, the conceptual approach adopted by the research programme included the development of an indicator-based vulnerability framework that aims to identify fisheries of concern (Chapter 11). Based on our analyses, the vulnerability of our study populations to targeted aggregation fishing varied substantially. At one extreme, the targeting of a putative *Epinephelus lanceolatus* spawning aggregation off the southern tip of Unguja is likely to pose significant risk to the population from which it forms. At the other extreme, *S. sutor* is relatively productive and populations appear able to sustain high levels of fishing mortality, even when aggregations are targeted (Robinson et al. 2011; Grüss et al. in press). Regardless, fisheries management is still required to prevent biological limits from being exceeded, as demonstrated by the no-take reserves (NTR) effects model. In between these extremes are the fisheries for *Epinephelus fuscoguttatus* and *E. polyphekadion*.

There is considerable empirical and theoretical evidence (e.g. Jennings et al. 1998; Musick 1999; Dulvy et al. 2004) on the vulnerability to fishing conferred by the life history traits that we included in the intrinsic index of the vulnerability framework. However, knowledge of the socio-economic factors influencing exploitation rates is more limited for aggregation-based fisheries and has generally been confined to qualitative expert reviews. Reviewing aggregation-based fisheries globally, Sadovy and Domeier (2005) conclude that populations may be sustained if aggregations are subject to limited, subsistence levels of fishing. This implies that spawning aggregations can be lightly exploited. If so, reference points or thresholds can be derived and used to guide management actions, which is an important topic for future research. However, an understanding of the socio-economic drivers of fishing pressure and demand for aggregating species is critical if limits on aggregation fishing are to be effectively managed. The socio-economic drivers of fishing pressure that we included as indicators in our vulnerability framework (fishers’ knowledge, market demand, etc, see Chapter 11) were also based on a review of the literature pertaining to both aggregation fisheries and reef fisheries in general. Quantitative testing of these indicators and the overall extrinsic index is warranted to better understand their relationship with rates of exploitation and aggregation status.

The principal management measure we sought to evaluate was NTRs, given their widespread use in the WIO (IUCN 2004; McClanahan et al. 2009; Daw et al. 2011) and their potential use in promoting resilience to climate change and other human impacts, such as fishing (Hughes et al. 2003; McClanahan 2010). Our model for *S. sutor* and *E. fuscoguttatus* populations in Seychelles found that NTRs sited on spawning sites can improve reproductive capacity, and also help normalize sex ratio in the protogynous grouper (Chapter 12). However, these benefits were relatively minor, especially if fishing effort is redistributed to non-spawning sites on reserve creation, which is the most realistic scenario (Valcic 2009). Therefore, NTRs for spawning aggregations have a role to play in conserving populations but are only a part of the solution to overfishing. For example, reducing overall fishing effort on the population by even a small amount can produce a relatively large increase in reproductive capacity compared to NTR creation. Though not tested with the
model, many parameter estimates are equivalent for the Msambweni S. sutor aggregation-based fishery in Kenya and it is likely that similar NTR effects will occur.

The conservation benefits (i.e. recovery of spawning stock biomass and normalization of sex ratio) of spawning aggregation-based NTRs are stronger if populations are overfished and if all spawning sites are protected. The benefits were also stronger for the slow growing E. fuscoguttatus. Since it is likely that some fished grouper spawning sites remain unknown, temporal restrictions on possession or sale corresponding with spawning periods may therefore constitute a more effective measure to conserving grouper spawning stocks, as used for Plectropomus leopardus in Australia (Samoilys 2012). However, the telemetry results from Seychelles show that any restrictions associated with lunar spawning period would need to take into consideration the longer residency time at spawning sites by males. Thus, temporal restrictions should include a buffer period rather than be based only on the timing of actual spawning.

While NTRs have some benefits for fish populations, we show that they did not provide a benefit to fishers in terms of increases in yield-per-recruit (YPR). This effect was more marked for the grouper population and fishers may expect a loss in yield if spawning sites are closed to fishing, which has socio-economic implications that must be weighed against the conservation benefits. As an alternative measure to NTRs and to mitigate losses to fishers, the Kenyan S. sutor fishery may benefit from gear-based management measures that prohibit the use of certain gears on aggregations, especially nets (gillnets, beach-seines and ring-nets) since these increase efficiency that can result in rapid depletion (Claro et al. 2009). In spite of these results, NTRs on spawning aggregation sites may still benefit fisheries in the longer-term through improved yields. However, this would only occur if the recovery of biomass, and normalization of sex ratio in groupers, eventually provide a recruitment subsidy to fished areas that compensates for the losses caused by closing the spawning sites to fishing (Hart 2006). To mitigate the lost fishing opportunities caused by spawning site NTRs, the lag time between catch loss and future benefits may be valued for offset payments to fishers during their establishment (Samoilys 2011).

Protecting juvenile and non-spawning areas using NTRs can also provide conservation benefits, especially when the populations are overfished (Chapter 12). Moreover, this approach can moderately improve rabbitfish yields and reduce losses in grouper yield compared with NTRs sited on spawning aggregations. This is encouraging since the use of NTRs is widespread in the western Indian Ocean and many of these areas may incorporate rabbitfish and grouper juvenile and non-spawning habitats. Epinephelus lanceolatus constitutes an exception to the need for wider fisheries management, such as effort controls, or the protection of juvenile and non-spawning habitats, since it is rarely caught outside spawning periods. Urgent conservation action is recommended for this population in Zanzibar and should focus on protecting the spawning site. However, any use of NTRs for protecting spawning sites should include buffer zones. Support for buffer zones comes from observed shifts of aggregation core areas following habitat disturbances in Seychelles. In at least some species, spawners concentrate along common reproductive migratory corridors (Rhodes et al. 2012) and staging areas outside of core aggregation areas (Nemeth 2012). In those instances, buffer zones would provide additional protection to populations of reproductively active fish.

Operational fisheries management plans for demersal and reef fisheries are rare in the WIO (Everett et al. 2010). Efforts to promote their use (e.g. Van der Elst et al. 2009), increasingly advocated within the context of an Ecosystem Approach to Fisheries (EAF), should specifically address vulnerable aggregative species and life history stages. Selection of management measures to meet the objectives of plans must, however, be context-specific and recognise that the input (i.e. effort) and output (i.e. catch quotas) controls common to many temperate fisheries (Beddington et al. 2007) have been generally unsuccessful in the tropics and are not widely applicable to aggregation-based fisheries (Johannes 2002; Sadovy de Mitcheson et al. 2008). In the tropics, combinations of gear and closure-based measures have achieved a degree of success in fisheries management (Cinner 2007;
McClanahan et al. 2007; McClanahan 2010). While closures such as NTRs are widely applied in aggregation-based fisheries, gear-based approaches are rare (Sadovy de Mitcheson et al. 2008; Hamilton et al. 2011) yet may be particularly relevant for more resilient aggregative spawners such as *S. sutor* (Robertson et al. 2011). As demonstrated by our NTR model management plans must account for different life history stages, considering both the need for aggregation-specific measures and wider controls on the non-aggregation component of fishing mortality.

There is an ethical dilemma associated with research on fishing sites that are important to fishers, including spawning aggregations (Haggan and Neis 2007). Fishers clearly use their knowledge of spawning aggregation sites to maximize their catches and income (Hamilton et al. 2012a). Therefore using fisher knowledge to set conservation policies may result in ethical and validity issues (Maurstad 2002; Daw 2008). These issues are especially pertinent to research funded within predetermined conservation agenda. Consequently this study developed a conceptual approach to explicitly link the study of spawning aggregation-based fisheries to a more analytical evaluation of their management and conservation implications. Although this does not solve the ethical and validity concerns *per se*, it focuses attention on the fishery and its socio-economic drivers (i.e. the indicator-based framework), and promotes quantitative analysis of the fisheries and conservation costs and benefits (i.e. the NTR effects model). Both of these novel approaches enable a more balanced use of fisher knowledge and information sharing on the management and conservation implications of spawning aggregation fisheries.

Conservation initiatives will continue to provide much needed financial support to the WIO. Such initiatives would benefit from explicitly incorporating assessment and management of spawning aggregation-based fisheries. Moreover, conservation initiatives would benefit from avoiding the over-generalisation, lack of quantitative evaluation and ethical and validity issues that have sometimes emerged in other regions. Clearly, the conservation imperative is influenced by the fact that most research to date has focused on the more vulnerable aggregative spawners such as groupers. However, recognition that some aggregative spawners are relatively resilient to fishing is needed and the socio-economic aspects of the system must be understood. Upon verification of an aggregation-based fishery and when status information is lacking, it is necessary to consider taxa-specific vulnerability to fishing and the potential costs and benefits of both conservation and fisheries management approaches. The data-poor tools used in the studies described here can provide rapid information in such contexts.
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Appendix 1. Questionnaire

MASMA SPAWNING AGGREGATION PROJECT (2009-2010)
CORDIO: FISHER KNOWLEDGE & SOC-ECO QUESTIONNAIRE

NB. To be repeated with the same informant in the two seasons

Introduction
Recorder to describe the project and give a brief overview of reef fish spawning aggregations, using illustrations.

1. Informant

<table>
<thead>
<tr>
<th>Fisher ID</th>
<th>Name</th>
<th>Age</th>
<th>Years spent fishing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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</tbody>
</table>

2. Fishing Gear
2.1 What type of gear do you use at the moment?
2.2 Does your use of gears vary with season, and if so, how? (use calendar to record)

<table>
<thead>
<tr>
<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
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</tbody>
</table>

3. Fish Catch
3.1 Catch per gear
List species in typical catch per gear in current fishing trips, and as a % of total catch. Proportion defined as: 1= >75%, 2= 50-75%; 3= 25-50%; 4= ≤25%
(use extra page of this table if needed)

<table>
<thead>
<tr>
<th>Species caught</th>
<th>Gear</th>
<th>Proportion of catch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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</tbody>
</table>

3.2 Catch weight
What is your typical catch weight (kg) per fishing trip in this season (by gear)?
Gear: ___________________________________________________________________

<table>
<thead>
<tr>
<th>Gear</th>
<th>Kaskazi (kg)</th>
<th>Kusi (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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</table>

Gear: ___________________________________________________________________

<table>
<thead>
<tr>
<th>Gear</th>
<th>Kaskazi</th>
<th>Kusi</th>
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<tbody>
<tr>
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</tbody>
</table>
4. Fishing effort
4.1 How many fishing trips do you do a week at the moment? _______________________
4.2 Do you generally fish every week in a month? _________ / 4
4.3 How long are your fishing trips usually? ___________ hrs

5. Fishing grounds
Using the maps ask the fisher to mark where he fishes during this season (per gear):
5.1 Mark the grid squares where you fish this season.
5.2 Which grid squares do you fish the most? 1 = most; 2 = 50% of the time; 3 = least.
5.3 Mark where you get the highest total catches. i = highest; ii = medium; iii = lowest.
5.4 Mark where you catch E. fuscoguttatus. Fa = highest; Fb = medium; Fc = lowest.
5.5. Mark where you catch S. sutor. Sa = highest; Sb = medium; Sc = lowest.

6. Catch and effort trends
6.1 What is your highest total catch per trip now?
6.2 What is your lowest total catch per trip now?
6.3 What was your highest and lowest catch in the past? – see table:
(please historic events to help the fisher remember these years – e.g. political events)

<table>
<thead>
<tr>
<th>Total Catch</th>
<th>Now</th>
<th>2004</th>
<th>1999</th>
<th>1989</th>
</tr>
</thead>
<tbody>
<tr>
<td>Highest</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Lowest</td>
<td></td>
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</tbody>
</table>

6.4 What is your highest catch of E. fuscoguttatus per trip now?
6.5 What is your lowest catch of E. fuscoguttatus per trip now?
6.6 What was your highest and lowest catch E. fuscoguttatus in the past? – see table:
(please historic events to help the fisher remember these years – e.g. political events)

<table>
<thead>
<tr>
<th>E. fuscoguttatus Catch</th>
<th>Now</th>
<th>2004</th>
<th>1999</th>
<th>1989</th>
</tr>
</thead>
<tbody>
<tr>
<td>Highest</td>
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<td></td>
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<tr>
<td>Lowest</td>
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</tbody>
</table>

6.7 What is your highest catch of S. sutor per trip now?
6.8 What is your lowest catch of S. sutor per trip now?
6.9 What was your highest and lowest catch S. sutor in the past? – see table:
(please historic events to help the fisher remember these years – e.g. political events)

<table>
<thead>
<tr>
<th>S. sutor Catch</th>
<th>Now</th>
<th>2004</th>
<th>1999</th>
<th>1989</th>
</tr>
</thead>
<tbody>
<tr>
<td>Highest</td>
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<tr>
<td>Lowest</td>
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</table>

7. Fish size
7.1 What is your largest E. fuscoguttatus you catch these days?
7.2 Has this size changed over years and if so how? ________________
7.3 What is your largest S. sutor you catch these days?
7.4 Has this size changed over years and if so how? ________________

<table>
<thead>
<tr>
<th>Decreased</th>
<th>Remained stable</th>
<th>Increased</th>
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<tbody>
<tr>
<td>Previous size:</td>
<td></td>
<td>Previous size:</td>
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</table>
8. Spawning aggregation knowledge
Use resources/material (laminated fish id sheets and photographs of spawning aggregations and running ripe gonads to illustrate spawning fishes and aggregations.

8.1 Have you ever encountered a spawning aggregation?  Yes ☐  No ☐  
If answer is no stop here and go to question 9.

8.2 Can you give a description of what you encountered?

8.3 Can you remember the:

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>Moon phase</th>
<th>Year</th>
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8.4 In which months do you think *E. fuscoguttatus* spawns?

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</table>

8.5 In which months do you think *S. sutor* spawns?

<table>
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<th>Jan</th>
<th>Feb</th>
<th>Mar</th>
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8.6 Have you fished spawning aggregations?  Yes ☐  No ☐  
If answer is no stop here and go to question 10.

8.7 If yes, which species and when?

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>Year</th>
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8.8 For how many years have you been fishing groupers spawning aggregations?  _______ years OR since ________________

8.9 How much more do you typically catch when fishing on spawning aggregations?

<table>
<thead>
<tr>
<th>X 1.5</th>
<th>X 2.0</th>
<th>X 2.5</th>
<th>X 3.0</th>
<th>X 3.5</th>
</tr>
</thead>
</table>

8.10 Do you fish more on aggregations – e.g. more fishing trips per week or longer fishing trips?

No trips per week: ___________________  Length of fishing trip: ________________

8.11 What months do you target these spawning aggregations?

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8.12 Spawning aggregation sites
Can you name and locate the spawning sites that you fish on a map?
Mark sites on grids: FSP = _E. fuscoguttatus_ spawning site; SSP = _S. sutor_ spawning site.

NB: This is a sensitive question and should not be pushed if fisher reluctant to say.

Alternative question:
Would you be willing to work with us at your sites to tag and release fish to monitor their spawning behaviour?

9. Trends and Awareness of spawning aggregations
9.1 Do you think that there has been a general decline in the sizes of _E. fuscoguttatus_ and _S. sutor_ catches taken from spawning aggregation sites?
   Yes [ ] No [ ]

9.2 Do you think we need to manage fish spawning aggregations? [ ] If so, how? ___________________

9.3 Do you think that the spawning aggregations could disappear if too many fish are caught? ______

9.4 Which agency do you think should manage and monitor spawning aggregations?

10. Income and revenue

   Household Information

10.1 How many members are there in your family?

10.2 Are you the sole income earner in your family? Yes [ ] No [ ] Don’t Know [ ]

10.3 Is fishing your only source of income? Yes [ ] No [ ] Don’t Know [ ]

10.4 If No, what are your other sources of income?

   Fishery Related

   Non Fishery Related

10.5 During which months are your income from sources other than fishing?

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10.6 In your household how much does fishing contribute to the total income?

   ≥75% [ ] 75-50% [ ] 25-50% [ ] <25% [ ]

Vessel Ownership

10.7 Are you a full time or part time skipper? Full time [ ] Part Time [ ]

10.8 Are you the owner of the fishing vessel(s)? Yes [ ] No [ ]

10.9 If Yes, are you the sole owner? Yes [ ] No [ ] Don’t Know [ ]

10.10 If yes, How many crew members do you typically employ on a fishing trip? ______

10.11 If Yes, how many?

Input costs (all fishing)
Use maps already marked with fishing sites (Q. 5).

10.12 How much fuel does it cost for 1 fishing trip to your further fishing sites?

10.13 How much fuel does it cost for 1 fishing trip to your nearest fishing sites?

10.14 What other costs are there?
Example items | KSh | Furthest site | Closest site
---|---|---|---
Ice | | | |
Bait | | | |
Gear | | | |
Transport | | | |
Other - specify | | | |

**Revenue**

10.15 What is the highest kg sale price for the fish you catch at the moment? ____________
10.16 What is the lowest kg sale price for the fish you catch at the moment? ____________
10.17 Does this price change through the year/season?

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10.18 Is the price different for *E. fusco* or *S. sutor*? If so specify:
- *E. Fuscoguttatus*: ____________
- *S. sutor*: ____________
10.19 What costs are deducted before any sharing of revenue? ____________
10.20 What system do you use for sharing revenue? ____________

- Boat Share ______ %
- Crew Share ______ %

**Markets**

11.1 Where do you normally sell your catch at the moment?
- Middleman  □  Market  □  Hotel  □  Other(specify)  □  ____________
11.2 Does this change through the year?

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11.3 Where do you normally sell *E. fusco* at the moment?
- Middleman  □  Market  □  Hotel  □  Other(specify)  □  ____________
11.4 Does this change through the year?

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<th>Dec</th>
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</thead>
</table>

11.5 Where do you normally sell *S. sutor* at the moment?
- Middleman  □  Market  □  Hotel  □  Other(specify)  □  ____________
11.6 Does this change through the year?

<table>
<thead>
<tr>
<th>Jan</th>
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11.7 Do markets change when large catches are brought in, such as from spawning aggregations? ____________

11.8 Do middlemen influence targeting of spawning aggregations? ____________
- If so how? ____________
12. Conflicts and tenure

12.1 Do you experience any conflicts in your fishing, and if so what?
   a. other fishers
   b. other gears
   c. other users

12.2 What ownership rights do you believe you have over the fish you catch?

12.3 What role does/has Diani-Chale Reserve played in managing your fisheries?

12.4 Has the Reserve helped or improved, and if so how:
   Catches?
   Habitat?
   Conflict?

12.5 How would you improve the management of these issues and the Reserve?
Appendix II. Experimental testing of body cavity tagging and anaesthesia with clove oil in Siganus sutor

Introduction
As part of the MASMA research programme, we applied acoustic tags to study spawning movements and behaviour in the common rabbit fish, Siganus sutor. Application of internal acoustic tags in fish requires surgical procedures. In January 2010 in Msambweni, Kenya, we tested the use of clove oil as an anaesthetic and an internal tagging procedure for S. sutor. Clove oil, a natural anaesthetic, is recognised as GRAS (Generally Recognised as Safe) in many countries including the US. The objectives of our study were: i) to test desirable clove oil concentrations for anaesthetising S. sutor in order to minimise stress and facilitate ease of handling; and ii) to develop a standard procedure for body cavity tagging of S. sutor in the field.

Methods
The experiment involved six steps (see Chapter 5 for photographs):

Fishing
S. sutor were captured by traditional basket traps (malema) that were set by a local fisherman the previous day. The trap was emptied into a large bucket and 10 larger fish were selected for tagging and retained in a perforated holding bucket strapped to the side of the boat.

Anaesthetising
Clove oil was mixed with ethanol (96%) at a ratio of 1:10 to give a working solution of 100 mg eugenol (active ingredient of clove oil) per litre of stock solution. Soto & Burhanuddin (1995) recommended a concentration of 100 mg/l sea water of this stock solution for anesthetising rabbitfish (Siganus lineatus) with a maximum induction time of 2 mins and recovery time of 2.5 mins. At a concentration of 20 mg/l, we found fish continued to swim slowly in the bucket and did not become anesthetised for over 3 minutes. Since Marking and Meyer (1985) recommend an induction time (from placement in anesthesia solution to fully anesthetised) of 3 min we increased the clove oil solution concentration to 40 mg/l and tested this with the 10 fish. A 20 l bucket with the clove oil solution mixed in 10 l of sea water, aerated with a small battery operated aerator was used for the anesthetising procedure. A second experiment was conducted indoors with a further 5 fish obtained the following day. Fish were kept in an aerated holding plastic tank (80 litres) and the same anaesthetising bucket using 45 mg/l and 50 mg/l concentrations of clove oil, and induction times were recorded. Only one fish was anaesthetised at a time. Care was taken in handling the fish by wearing surgical gloves.

The four stages of going under anaesthesia in S. sutor were defined as follows based on our observations, and varied slightly from those defined in Seychelles. The time taken to reach each of these stages was recorded with a stop watch.

a) stopped swimming – no movement in caudal fin
b) no movement in pectoral fins
c) fish turned horizontal and floated on surface; opercula membrane continued to move
d) “retention time”: after stage c) fish were retained in the anaesthetic for increasing periods of time from 0 sec (3), to 30 sec (2), 60 sec (1), 90 sec (3) and 120 sec (1). Number in parentheses denotes the number of fish tested for different times. For the second experiment (n=5 fish) retention time was maintained at 1 min.
Induction time is defined by the total time taken from a) to d), i.e. from placement of fish into anesthesia solution to time removed from anesthesia for suturing.

Tagging
Prior to tagging the fork length (FL) of the anaesthetised fish was measured using a measuring board. The fish was then placed upside down in a soft canvas cradle suspended in an aerated shallow glass aquarium making sure the head was under water. Using a surgical scalpel a shallow incision was made through the ventral body wall slightly above the anus and about 2/3 distance below the lateral line (Plate 1a). A dummy acoustic transmitter tag was inserted gently at a steep angle in a posterior upward direction to avoid damage to the gonad (Plate 1b). The incision was sutured with two stitches, each with two knots using ½ cycle 3-0,2 metric nylon-polyamide sutures. Total incision time was recorded. The fish was returned to a bucket of fresh aerated sea-water to observe its recovery. It was then returned to the fish holding bucket strapped to the side of the boat with the other fish. Total time for holding the fish from capture in the basket trap was restricted to 1 hr. Additional untagged fish were retained as controls and also so that the tagged fish were kept in groups. This was important during release to enable them to swim together to the bottom and orient themselves easily. For the indoor experiment with 5 fish, fish were sacrificed after the experiment to dissect and examine the sutures.

Plate 1. a) Siganus sutor showing the position of the suture relative to lateral line; b) dissected fish showing good placement of dummy transmitter tag below ripe gonad.

Survival
Five fish tagged with dummy transmitter tags were returned to one trap by gently pouring them in a bucket of water down through the trap entry funnel, together with nine untagged fish. Five other fish put through the anaesthesia and suturing procedure, but with no dummy tags inserted, were returned to sea in a second basket trap. The traps were placed on the sea bed where the fish were captured and the entry funnel blocked with a stone so that they could not fish. Traps were left overnight, and fish survival was checked the following day.

Recovery and assessment of fish condition
Initial recovery from the anaesthesia was observed in an aerated bucket on the boat and then in the holding bucket beside the boat. In the indoor experiment this was restricted to the 80 l container. Recovery was defined as moving with caudal fin in normal vertical position. For the field experiment survival of tagged fish was assessed within 24 hrs at which point the traps were retrieved and the tagged fish brought to shore to assess the condition of the fish. This continued for 4 hrs in an aerated large plastic container indoors. Fish were then sacrificed to dissect them to inspect the placement of the tag in the body cavity, to measure the incision length and to examine the suture wound.

Results and Discussion
Retention time
Fish that were removed from the anaesthesia solution after 0 sec or 30 sec soon started to recover when in the tagging cradle, as seen in movement of caudal and pectoral fins. With retention times >1 min, 3 of the 5 fish did not start to recover from the anaesthesia while undergoing the suturing.
Clove oil concentration

At a concentration of 20 mg/l, *S. sutor* continued to swim slowly in the bucket and did not become anesthetised for over 3 minutes, therefore no trials were done with this concentration of clove oil solution. Increasing the concentration to 40 mg/l brought the induction time for anesthesia to 3:01 min. Increasing the concentration to 45 mg/l or 50 mg did not improve the induction time (Table 1). However, observations of fish beginning to recover while still undergoing the suturing, as seen in the caudal and/or pectoral fins starting to move, showed that there was a difference between 40-45mg and 50mg. At 50 mg/l, fish did not start recovering while still undergoing suturing whereas they did when anesthetised with 40 or 45mg/l.

Table 1. Induction and recovery time (mean ± standard deviation) for different clove oil concentrations.

<table>
<thead>
<tr>
<th>Clove oil concentration</th>
<th>40 mg/l (n=10)</th>
<th>45 mg/l (n=3)</th>
<th>50 mg/l (n=2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>induction time (mins)</td>
<td>3:01±0.461</td>
<td>3:15±0.034</td>
<td>3:00±0.053</td>
</tr>
<tr>
<td>recovery time (mins)</td>
<td>4:00±0.003</td>
<td>6:46±0.077</td>
<td>*12:01±0.296</td>
</tr>
</tbody>
</table>

* one fish took 7 min., the other took 17 min. and was very stressed.

Induction and recovery

Fish took a longer time to be anaesthetised and to fully recover as the concentration was increased from 40 to 50 mg/l (Table 1). This may be because the 45 mg/l and 50 mg/l were tested indoors where the chances of stress were higher due to handling fish in confinement.

Suturing and tag insertion

The time taken to complete the suturing ranged from 01:30 min to 04:30 min, improving with practice over time. A steady process completed within 2 minutes was considered the optimal time. Periods of 3-4 min, however, did not seem to have an adverse affect on the fish - all fish survived. Bruising was apparent around the suture wound immediately after surgery. However, by the next day this bruising had diminished and faded.

Average suture length for the field experiment was 2.0±0.271 cm (n=10) and 1.6±0.217 cm (n=5) for the indoor experiment. We strived to minimise the length of suture (relative to tag size and diameter) to improve the chances of the wound healing (Plate 2a). Sutures of greater than 2 cm appeared loose after 21 hours and therefore we recommend that they have more than two stitches. We recommend a suture length of <1.6 cm for *S. sutor*. A recaptured tagged fish after these experimental trials had a suture length of 1.5 cm. and the wound had almost completely healed after 72 hours (Plate 2b).

Plate 2. a) Recaptured fish ~22 hrs after tagging showing clean tight suture; b) Recaptured fish after ~72 hrs showing wound had healed well.
Dissection revealed the placement of the tag did not damage the ripe gonad (Plate 1b). Swimming of the tagged fish in the recovery tank and trap was observed to be normal. After 22 hours, normal swimming of tagged *S. sutor* in the traps was observed, with no discernible difference in behaviour between those with internal tags and those without, indicating no negative effects of the tagging procedure.

**Summary**
The experimental testing of clove oil as an anesthetic and the body cavity tagging described here provide a standard procedure for acoustic tagging of *S. sutor* in the field using V7-2 transmitter tags. The two variables that affected the anesthetising of *S. sutor* with clove oil solution were the concentration of the solution and the retention time in the solution. Based on observations of recovery during tagging the final combination recommended from the trials was 50mg/l and a retention time of 1 min. Although the stronger concentration was only tested on two fish, and this was indoors under less optimal conditions, and recovery time was longer, we recommended this because fish remained fully anesthetised during the suturing procedure. In the field recovery is likely to be improved because fish will be held in a holding tank beside the boat with sea water circulating freely through it. This latter is highly recommended for reducing stress and improving survival. We recommend that the suturing be completed within a period of around 2 min and that a suture length of <1.6 cm be used for *S. sutor*.

**References**
Appendix III. Application of acoustic tagging to *Epinephelus fuscoguttatus* in Diani, Kenya

**Introduction**
In Kenya there is preliminary verification and fisher knowledge of two spawning aggregations of the marbled grouper *Epinephelus fuscoguttatus* within the Diani-Chale Reserve (Samoilys et al. 2006, Robinson et al. 2008, see Chapter 7). This study was designed to build on this information and to determine the site fidelity and residence times of *E. fuscoguttatus* at aggregations within the Reserve as well as movement between the spawning sites along the linear fringing reef slope of the Reserve using acoustic telemetry. This appendix documents our unsuccessful attempts to capture and tag *E. fuscoguttatus*, to provide recommendations for future studies that need to capture this species alive for tagging.

**Methods**
Having first verified on SCUBA the presence of an aggregation of *E. fuscoguttatus* at one of the aggregation sites during the new moon period of November 2009, a variety of fishing methods were used to try and capture fish for acoustic tagging. These were:

i) Fishing with hook and line using 6 ‘O’ circular hooks, weighted, on 120 lb line, both anchored and drifting over the site, using a mix of gar fish and squid for bait. Three of us fished from the main boat on the aggregation site, supplemented with three local fishers in a local *ngalawa* boat (outrigger canoe with sail).

ii) Two local basket traps set over night on the site. The traps were those used by local fishers for mixed species, generally herbivorous fishes such as siganids and scarids, but also known to catch lethrinids, lutjanids and serranids. We enlarged the trap entrance to accommodate the size of the *E. fuscoguttatus* and baited them with up to six bait balls each of chopped octopus and/or garfish mixed with sand and semi-dried in the sun (Plate 2, 3 and 4a).

iii) An anaesthetic solution made from 30 ml clove oil shaken hard with sea-water in plastic “squeezy” bottles (Plate 4b). Divers squirted the clove oil solution into the caves where the fish were hiding as close to their heads as possible and then tried to pull them out into a canvas holding bag.

iv) A fine mesh 6 ft cast net deployed by two SCUBA divers around the caves where the *E. fuscoguttatus* were located on the aggregation site and using sticks to herd the fish into the net.

Plate 2. Enlarged entrance of basket trap for grouper using soft wire mesh attached to the original funnel cut in half.
Results and Discussion

Observations on SCUBA confirmed that the *E. fuscoguttatus* were aggregating to spawn during the November 2009 new moon period at the site, with between 7 and 16 fish seen at the site. However, despite five days of intense fishing using four different methods employed by up to 4 researchers and 4 local fishers, no grouper were captured for tagging. The hand-lining did not even elicit bites from the fish - it appeared the grouper were not interested in feeding. The method with the best potential was the clove oil: one grouper was temporarily stunned and the diver managed to get hold of it by the head but as soon as he moved the fish out of the cave it took off with tremendous force. Presumably the action of pulling the fish through the water flushed fresh water through the gills thereby enabling rapid recovery from the clove oil anaesthesia. On a second occasion the diver could feel and hold the fish but it had wedged itself in the cave with its operculae.

We believe that the use of clove could be adapted further to be successful for capturing this species. This would involve at least four divers with two squeezy bottles each, plus a further 2-3 divers with a cast or gill net placed over the cave entrances and the divers work as a team to first stun the fish and then ensure capture in the nets as they are pulled out of the caves. An alternative which requires further technology development would be an underwater dart gun to stun the fish with an intra-muscular anaesthetic. The fish can then be handled and brought to the surface for tagging. In conclusion, fishing gears such as handline with bait do not seem to be effective for capturing this species when it is aggregating to spawn. We believe alternative capture methods using anaesthetics such as clove oil or dart guns have potential but require further development.