



## Conservation and fisheries effects of spawning aggregation marine protected areas: What we know, where we should go, and what we need to get there

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There is a global trend in the depletion of transient reef fish spawning aggregations (“FSAs”), making them a primary target for management with marine protected areas (MPAs). Here, we review the observed and likely effectiveness of FSA MPAs, discuss how future studies could fill knowledge gaps, and provide recommendations for MPA design based on species’ life history and behaviour, enforcement potential, and management goals. Modelling studies indicate that FSA MPAs can increase spawning-stock biomass and normalize sex ratio in protogynous fish populations, unless fishing mortality remains high outside protected FSA sites and spawning times. In the field, observations of no change or continued decline in spawning biomass are more common than population recovery. When empirical studies suggest that FSA MPAs may not benefit fish productivity or recovery, extenuating factors such as insufficient time since MPA creation, poor or lack of enforcement, inadequate design, and poorly defined management objectives are generally blamed rather than failure of the MPA concept. Results from both the empirical and modelling literature indicate that FSA MPAs may not improve exploitable biomass and fisheries yields; however, investigations are currently too limited to draw conclusions on this point. To implement effective FSA MPAs, additional modelling work, long-term monitoring programmes at FSA sites, and collections of fisheries-dependent data are required, with greater attention paid to the design and enforcement of area closures. We recommend a harmonized, adaptive approach that combines FSA MPA design with additional management measures to achieve explicitly stated objectives. Conservation objectives and, therefore, an overall reduction in mortality rates should be targeted first. Fisheries objectives build on conservation objectives, in that they require an overall reduction in mortality rates while maintaining sufficient access to exploitable biomass. Communication among researchers, regulatory agencies, park authorities, and fishers will be paramount for effective action, along with significant funds for implementation and enforcement.

**Keywords:** design implications, fisheries management, knowledge gaps, marine conservation, marine protected areas (MPAs), modelling, monitoring, reef fish spawning aggregations (FSAs), transient spawning aggregations.

### Introduction

Many coral reef fish form short-term spawning aggregations each year that are highly predictable in space and time. Transient reef fish spawning aggregations (“transient FSAs”, hereafter usually

simply referred to as “FSAs”; see Glossary) are common among socio-economically important species of the Epinephelidae, Lutjanidae, and Siganidae families. These aggregations last from days to weeks at specific sites during 1 to a few months each year

(Domeier and Colin, 1997; Domeier, 2012). FSAs are composed of fish that have migrated from a few to hundreds of kilometres from their normal residence areas, and they represent most, if not all, of the total annual reproductive effort for the populations forming them (Sadovy and Eklund, 1999; Bolden, 2000; Domeier, 2012). FSAs have received growing attention during the last 20 years as a result of their vulnerability to fishing (Sadovy and Domeier, 2005; Sadovy de Mitcheson and Colin, 2012a). Worldwide, many FSAs are depleted, while others have collapsed and no longer form (e.g. Sadovy and Eklund, 1999; Hamilton and Matawai, 2006; Aguilar-Perera, 2007). Therefore, effective management measures are urgently needed to protect exploited transient reef FSAs (Sadovy and Domeier, 2005; Sadovy de Mitcheson et al., 2008; Sadovy de Mitcheson and Colin, 2012a).

Spawning aggregation marine protected areas (MPAs), i.e. the partial or total prohibition of fishing and other extractive activities at FSA sites, is one of the management tools identified to enable the persistence and recovery of FSAs, the fish populations from which they form and the long-term viability of the fisheries depending on them (Sadovy and Domeier, 2005; Russell et al., 2012; Sadovy de Mitcheson et al., 2013). Though the number of studies devoted to spawning aggregation MPAs (hereafter also referred to as “FSA MPAs” or “spawning area closures”) has increased over recent years, knowledge gaps and uncertainties remain regarding their effectiveness. Essentially, it is not yet clear whether FSA MPAs alone are sufficient to ensure for the long-term sustainability of aggregation-forming species (Sale et al., 2005; Sadovy de Mitcheson et al., 2008; Grüss et al., 2011).

Transient FSAs are complex phenomena that often involve multiple species with sex-specific spatio-temporal patterns of behaviour and movement related to reproduction, sometimes associated with regional variability. Migration patterns and behaviours are often sex-specific, particularly in protogynous species (i.e. species that mature first as females and then change sex to males). Spawning migrations are generally synchronized to a specific lunar phase within a spawning season and relate to seasonal changes in seawater temperatures and current speeds (e.g. Bolden, 2000; Heyman et al., 2005; Nemeth et al., 2007; Bijoux et al., 2013). Males often spend more time than females at FSA sites (e.g. many Epinephelidae; Rhodes and Sadovy, 2002; Nemeth et al., 2007; Robinson et al., 2008; Rowell et al., 2012), and in a few species stay year-round in these areas (e.g. several Epinephelidae such as gag grouper, *Mycteroperca microlepis*; Shapiro, 1987; Sadovy et al., 1994; Coleman et al., 1996). Many FSA-forming species show strong aggregation site fidelity within and between spawning seasons, such that FSAs represent bottlenecks in the life history of the species (e.g. Domeier and Colin, 1997; Luckhurst, 1998; Sadovy and Eklund, 1999; Nemeth et al., 2007). Some FSA sites are used by multiple species, either sequentially or simultaneously, while others are only used by one species (Whaylen et al., 2006; Heyman and Kjerfve, 2008; Sadovy de Mitcheson et al., 2008; Colin, 2012a). The complexity of spawning aggregations is further highlighted by regional differences in FSA timing (seasonal and lunar) and spawning behaviour that exist among populations of the same species (e.g. Rhodes and Sadovy, 2002; Claro and Lindeman, 2003; Rowell et al., 2012).

There are a number of factors that conspire to make FSAs highly vulnerable to overfishing, including the predictability of FSA formation, the substantial increase in catchability that usually occurs when fish aggregate, the life histories of most aggregative species (including long life, late sexual maturation, and protogynous hermaphroditism), the general relationship in fish between

body size, fecundity and egg quality, and the high economic value of most aggregation-forming species. The fact that fish are generally caught at FSA sites before reproducing, preventing the populations from maximizing reproductive output and compensating for off-FSA mortality (Sadovy and Vincent, 2001; Rhodes et al., 2011) leads to a rapid decline in FSA fish once they become targeted. Because fishers often only have ready access to larger, older individuals during FSA times (because they are deeper or dispersed during the rest of the year), their removals can contribute disproportionately to decreased reproductive output both directly through reduced egg output (Koenig et al., 1996; Sadovy, 1996) and potentially indirectly because of a positive relationship between egg quality and body size as reported in some fish species (Berkeley et al., 2004). For protogynous species, because males are usually larger than females and often spend more time at FSA sites, FSA fishing can also significantly bias female:male sex ratios towards females (e.g. >20:1 currently vs. 5:1 in natural conditions for gag grouper; SEDAR 10, 2006), possibly leading to reduced egg fertilization through sperm limitation (e.g. Coleman et al., 1996; Koenig et al., 1996). Sperm limitation has the potential to trigger reproductive failure if thresholds in sex ratio exist, although empirical evidence for this is lacking and thresholds remain unknown (Koenig et al., 1996; Armsworth, 2001; Fitzhugh et al., 2006). Finally, FSA fishing may disrupt mating behaviours (e.g. Dean et al., 2012; Sadovy de Mitcheson and Erisman, 2012), and may also hinder sex change by affecting the cues thought to trigger sexual transition, such as population density, local sex ratio, and the body size of an individual fish relative to the other members of its social group (e.g. Shapiro, 1989; Coleman et al., 2000). Commercial fishing activities and the live reef food fish trade (in the Indo-Pacific) are responsible for many of the depletions of FSAs (Sadovy, 2005a, b; Sadovy de Mitcheson and Colin, 2012a; Sadovy de Mitcheson et al., 2013). In some regions, subsistence and recreational fishing also have a highly negative impact on FSAs (Sadovy and Eklund, 1999; Coleman et al., 2004a; Aguilar-Perera, 2007).

MPAs are increasingly considered and applied for reef fish conservation and fisheries management, although their effectiveness in these respects is not well understood. FSA MPAs limit access to a fraction or all the spawning individuals of a fish population, and they are promoted mainly as a precautionary approach in data-less situations, and for their simplicity of enforcement relative to traditional fisheries measures such as fishing effort controls, particularly when the most fisheries impacts stem from highly distributed artisanal/small-scale fisheries (Johannes, 1998; Sadovy and Domeier, 2005; Russell et al., 2012). Both seasonal and permanent FSA MPAs can potentially allow for the persistence and stability of mating structures and to maintain or recover SSB and sex ratio to levels that ensure recruitment success (Bohnsack et al., 2004; Russell et al., 2012). If permanent rather than seasonal, FSA MPAs are also expected to benefit reef habitat and other species using that habitat (Bohnsack et al., 2004; Sadovy de Mitcheson et al., 2013) and may generate alternative livelihoods to fishing, such as the case of ecotourism (Ruitenbeek, 2001; Sala et al., 2001; Heyman et al., 2010). It has been proposed that spawning area closures could enhance fisheries yields in the long term through “recruitment subsidy”, i.e. by delivering significantly more eggs and larvae to surrounding fished areas than before MPA creation; and by improving exploitable biomass through an increase in the mean fish body size (Gell and Roberts, 2003; Roberts, 2012; Sadovy de Mitcheson and Erisman, 2012), but evidence that

MPAs produce fisheries benefits is not strong, particularly for mobile fish populations (Hilborn *et al.*, 2004; Sale *et al.*, 2005; Grüss *et al.*, 2011). Rather, FSA MPAs are likely to reduce fisheries catches and profitability, both in the short and long term (Sale *et al.*, 2005; Sadovy de Mitcheson and Erisman, 2012). Seasonal fisheries closures during reproductive periods are often recommended as a viable alternative to FSA MPAs, particularly when it is unclear whether all the FSA sites of the study population have been identified and/or when site-based enforcement is difficult (Russell *et al.*, 2012). However, seasonal fisheries closures also have pros and cons depending on management objectives, and can lead to significant economic loss [see Russell *et al.* (2012) for a review].

Given that many FSA-forming species are highly vulnerable to fishing, that FSA behaviour is common to a wide range of socio-economically important reef fish families, and that there is conflicting evidence and opinion whether FSA protections either increase or decrease long-term fisheries opportunities, there is a need to understand the costs and benefits of different management approaches for FSAs, the populations from which they form, and the fisheries depending on them. Here, we focus on FSA MPAs and (i) review both the empirical and modelling literature on the conservation and fisheries effects of this management tool and identify critical knowledge gaps for the conservation and sustainable exploitation of aggregation-forming populations; (ii) recommend modelling and empirical research directions to assist the design, evaluation, and implementation of effective FSA MPAs; and (iii) highlight the need for a strong enforcement of FSA MPAs, increased interactions between empiricists and modellers and all other stakeholders, and the implementation of complementary management measures, with a focus on seasonal fisheries closures. Here, “conservation effects” pertain to impacts on the abundance, body size, spawning-stock biomass (SSB), recruitment levels, and sex ratio of the populations targeted by protection efforts (direct conservation effects), and to impacts on habitat and the conservation of species not targeted by protection efforts (indirect conservation effects). “Fisheries effects” refer to impacts on exploitable biomass, yields, and fisheries catch per unit effort (cpue).

## Review of the effects of FSA MPAs

Existing empirical and modelling studies provide different insights into the conservation and fisheries outcomes of FSA MPAs. The most empirical studies report local and short- to medium-term direct and indirect impacts of spawning area closures, while modelling studies have explored longer-term direct consequences of protecting transient FSAs at the population level.

## Insights from empirical studies

### Direct effects

We compiled insights from the empirical literature by searching relevant peer-reviewed publications, US governmental reports, and readily available proceedings using *Web of Science* and *Google Scholar* in early 2013. The search string was “spawning aggregation(s)” and (“marine protected areas” or “marine reserves” or “closures”). We identified 17 spatial management case studies directed at transient FSAs that focus on 14 different species in the Epinephelidae and Lutjanidae families (Table 1). In all 30 peer-reviewed publications, US governmental reports and proceedings on the effects of FSA MPAs have been produced based on research at these 17 locations (Table 2 and Supplementary Table S1). The outcomes of FSA MPAs have been more widely documented in the

Caribbean and Atlantic ( $n = 21$  studies) than in the Indo-Pacific ( $n = 9$ ). Fisheries-independent data collected at FSA sites were used in nearly all studies [except in Graham *et al.* (2008) and in the “Cuban case study”, i.e. in Claro and Lindeman (2003) and Claro *et al.* (2009)], while fisheries-dependent data were used in about half (55%; Supplementary Table S1).

In our evaluation of FSA MPA effects, we differentiated between positive and non-positive effects of FSA MPAs. Spawning area closures were deemed to have positive direct conservation effects when they lead to increases in abundance, body size, recruitment levels or SSB, or to sex ratio normalization. When the aforementioned benefits do not occur consistently over the period of a study, FSA MPAs were considered to have non-positive direct conservation effects. Spawning area closures were deemed to have positive direct fisheries effects when their implementation is accompanied by increases in exploitable biomass, fisheries yields, or fisheries cpue. Following these definitions, we found more documentation of non-positive than positive effects of FSA MPAs in the empirical literature. Positive direct conservation and fisheries benefits were demonstrated in only 43% ( $n = 13$ ) and 17% ( $n = 5$ ) of the studies, respectively (Table 2), although the fisheries outcomes of FSA MPAs were not evaluated in most studies ( $n = 17$ ).

The main positive direct conservation effects of FSA MPAs reported in the empirical literature included, in the following sequence, increased abundance, density and biomass of target species at FSA sites (e.g. Chiappone and Sealey, 2000; Burton *et al.*, 2005; Nemeth, 2005), increased mean body size (e.g. Beets and Friedlander, 1999; Luckhurst and Trott, 2008; Kadison *et al.*, 2010), and a shift of sex ratio towards more natural levels at FSA sites (Beets and Friedlander, 1999; Whaylen *et al.*, 2004; Kadison *et al.*, 2010). Using a novel laser video method, Heppell *et al.* (2012) found that the mean body size of aggregating Nassau grouper (*Epinephelus striatus*) decreased in Little Cayman following FSA MPA creation, a result of an increase in the number of smaller adult Nassau grouper at the FSA site indicating a rapid MPA-mediated demographic recovery of the population through recruitment of new spawning adults. Only five empirical studies have presented empirical evidence, or used their findings to hypothesize, that spawning area closures have positive fisheries effects. Matos-Caraballo (2002) and Matos-Caraballo *et al.* (2006) reported increases in landings of red hind (*Epinephelus guttatus*) and in the cpue of the red hind fishery shortly after the implementation of three seasonal FSA MPAs in Puerto Rico. However, this trend was not observed in a more recent study of the fishery (Marshak and Appeldoorn, 2007). From data analyses and fishers’ interviews, Nemeth (2005) found that the closure of a red hind FSA site off St Thomas Island (US Virgin Islands) may have contributed to an overall increase in the size of red hind caught in the local commercial fishery. Finally, the positive fisheries effects of FSA MPAs reported in Chiappone and Sealey (2000) and Whaylen *et al.* (2004) are hypothetical. These two studies discuss that, because the MPAs studied are important sources of eggs and larvae to adjacent fished areas, they may over time improve the fisheries yields of the fish populations targeted by protection efforts through recruitment subsidy.

In contrast, a relatively large number of studies in our review found that FSA MPAs were inadequate for conserving aggregations, the populations from which they form, or benefiting their respective fisheries. The non-positive direct conservation effects of FSA MPAs have mostly been attributed to four factors: (i) poor or non-existent enforcement (e.g. Nemeth *et al.*, 2006a; Graham *et al.*, 2008;

**Table 1.** Spatial management case studies directed at transient reef FSAs identified in the peer-reviewed empirical literature and among US government reports and readily available proceedings.

Geographical area	MPA type and history	Species targeted by protection efforts	Studies
Red Hind Bank Marine Conservation District, St Thomas, US Virgin Islands	Seasonal no-take MPA (1990–1999), then year-round no-take MPA (1999–); designed to protect an FSA	Red hind ( <i>E. guttatus</i> )	Beets and Friedlander (1999), Nemeth (2005)
Tourmaline Bank, Abrir la Sierra Bank, and Bajo de Sica Bank, Puerto Rico	Tourmaline Bank: seasonal no-take MPA (1993–). Abrir la Sierra Bank and Bajo de Sica Bank: seasonal no-take MPAs (1996–); all fishing prohibited at three red hind FSA sites	Red hind ( <i>E. guttatus</i> )	Matos-Caraballo (2002), Matos-Caraballo et al. (2006), Marshak and Appeldoorn (2007)
Lang Bank, St Croix, US Virgin Islands	Seasonal no-take MPA (1993–)	Red hind ( <i>E. guttatus</i> )	Nemeth et al. (2006a), Karras and Agar (2009)
Bermuda Reef Platform, Bermuda	Seasonal (May–August) no-take MPAs (1975–); all fishing prohibited at three red hind FSA sites	Red hind ( <i>E. guttatus</i> )	Luckhurst and Trott (2008)
Kehpara Marine Sanctuary, Pohnpei, Micronesia	Year-round no-take MPA (1995–); expanded in 1999, again in 2010 (migration routes, adjacent home ranges)	Brown-marbled grouper ( <i>E. fuscoguttatus</i> ), camouflage grouper ( <i>Epinephelus polyphkadion</i> ), squaretail coralgrouper ( <i>P. areolatus</i> )	Rhodes and Sadovy (2002), Rhodes and Tupper (2007, 2008), Rhodes et al. (2011)
Komodo National Park, Indonesia	Year-round partial-take MPA (2001–); hookah, blast, and cyanide fishing prohibited	Brown-marbled grouper ( <i>E. fuscoguttatus</i> ), squaretail coralgrouper ( <i>P. areolatus</i> )	Pet et al. (2005), Mangubhai et al. (2011)
Ebiil Channel and Ngerumekaol Channel, Palau	Ebiil Channel: year-round no-take MPA (2000–). Ngerumekaol Channel: Seasonal (April–July) no-take MPA (1976–1999), then year-round no-take MPA (1999–)	Brown-marbled grouper ( <i>E. fuscoguttatus</i> ), camouflage grouper ( <i>E. polyphkadion</i> ), squaretail coralgrouper ( <i>P. areolatus</i> )	Golbuu and Friedlander (2011)
Northern New Ireland, Papua New Guinea	Year-round no-take MPAs (2004–); established by community consensus	Brown-marbled grouper ( <i>E. fuscoguttatus</i> ), camouflage grouper ( <i>E. polyphkadion</i> ), squaretail coralgrouper ( <i>P. areolatus</i> )	Hamilton et al. (2011)
Western Roviana Lagoon, Solomon Islands	Year-round no-take MPAs (2006–); established by community consensus	Brown-marbled grouper ( <i>E. fuscoguttatus</i> ), camouflage grouper ( <i>E. polyphkadion</i> ), squaretail coralgrouper ( <i>P. areolatus</i> )	Hamilton et al. (2012a)
Exuma Cays Land and Sea Park, Bahamas	Year-round partial-take MPA (1958–1986), then year-round no-take MPA (1986–)	Nassau grouper ( <i>E. striatus</i> )	Chiappone and Sealey (2000), Chiappone et al. (2000)
West End Little Cayman, Cayman Islands	Seasonal no-take MPA (November–March 2002–2003), then year-round no-take MPA (2003–); “1 km no trapping” zones also included	Nassau grouper ( <i>E. striatus</i> )	Whaylen et al. (2004), Heppell et al. (2012)
Grammanik Bank, St Thomas Island, US Virgin Islands	Seasonal (February–April) partial-take MPA (2005–); no bottom fishing allowed	Nassau grouper ( <i>E. striatus</i> )	Kadison et al. (2010)
Marine Reserve Caleta de Avalo, Marine Reserve Pta. Francés, Marine Reserve Cabo Cruz, Marine Reserve Cayo la Leña, Marine Reserve Norte de Matanzas, and nine other MPAs established at spawning aggregation sites	Multiple year-round partial take MPAs (1996–), designed to protect spawning aggregations of snappers and groupers	Nassau grouper ( <i>E. striatus</i> ), cubera snapper ( <i>Lutjanus cyanopterus</i> ), grey snapper ( <i>Lutjanus griseus</i> ), lane snapper ( <i>Lutjanus synagris</i> ), mutton snapper ( <i>Lutjanus analis</i> ), yellowtail snapper ( <i>Ocyurus chrysurus</i> )	Claro and Lindeman (2003), Claro et al. (2009)
Gladden Spit and Caye Glory, Belize	Year-round partial-take MPAs (Gladden Spit: 2000–; Caye Glory: 2003–)	Nassau grouper ( <i>E. striatus</i> ), cubera snapper ( <i>L. cyanopterus</i> ), mutton snapper ( <i>Lutjanus campechanus</i> )	Heyman and Wade (2007), Graham et al. (2008)
Florida Keys National Marine Sanctuary, Florida, USA	Year-round partial-take MPA (1990–)	Black grouper ( <i>Mycteroperca bonaci</i> )	Eklund et al. (2000)
Madison Swanson Marine Reserve, Florida, USA	Partial-take year-round MPAs (2000–); recreational pelagic trolling fishery operating inside the MPA from May to October	Gag grouper ( <i>M. microlepis</i> ), scamp ( <i>Mycteroperca phenax</i> ), red snapper ( <i>Lutjanus campechanus</i> )	Koenig and Coleman (2013)
Tortugas South Ecological Reserve, Florida, USA	No-take year-round MPA (2001)	Mutton snapper ( <i>Lutjanus analis</i> )	Coleman et al. (2004b), Burton et al. (2005)



**Table 2.** Conservation and fisheries effects of spawning aggregation MPAs (FSA MPAs) reported in the empirical literature.

Geographical area	Study	Duration between MPA creation and last data collected	Conservation effects	Fisheries effects
Red Hind Bank Marine Conservation District, St Thomas, US Virgin Islands	Beets and Friedlander (1999)	7 years	Increases in the number of fish aggregating to spawn, mean individual fish body size, and biomass and density at the FSA site; sex ratio normalization	NI
Red Hind Bank Marine Conservation District, St Thomas, US Virgin Islands	Nemeth (2005)	14 years	Increases in the body size of males, average density and biomass of spawning individuals, and maximum spawning density	Data analyses and fishers' interviews indicate an increase in the body size of red hind caught in the commercial fishery
Tourmaline Bank, Abrir la Sierra Bank and Bajo de Sica Bank, Puerto Rico	Matos-Caraballo (2002)	4 years	Increase in fish body size	Increase in landings
Tourmaline Bank, Abrir la Sierra Bank, and Bajo de Sica Bank, Puerto Rico	Matos-Caraballo et al. (2006)	6 years	No sign of population recovery	Increase in cpue of red hind
Tourmaline Bank, Abrir la Sierra Bank, and Bajo de Sica Bank, Puerto Rico	Marshak and Appeldoorn (2007)	10 years	Increase in mean fish body size short after MPA creation; decreases in abundance, and the proportion of large individuals and males in the red hind population in more recent years	No sign of improved landings and cpue
Lang Bank, St Croix, US Virgin Islands	Nemeth et al. (2006a)	9 years	Estimates of density suggest that the FSA is not in an healthy state; average body size of fish in the FSA MPA considerably smaller than in an adjacent red hind FSA MPA (St. Thomas)	NI
Lang Bank, St Croix, US Virgin Islands	Karras and Agar (2009)	15 years	The FSA MPA may have increased fish abundance within the closure	MPA implementation and gear restrictions curtailed access to productive lobster and conch fishing grounds and made fishers become more reliant on fishing grounds with lower quality
Bermuda Reef Platform, Bermuda	Luckhurst and Trott (2008)	32 years	Increase in mean fish body size	Decline in landings
Kehpara Marine Sanctuary, Pohnpei, Micronesia	Rhodes and Sadovy (2002)	4 years	Decrease in abundance of camouflage grouper	NI
Kehpara Marine Sanctuary, Pohnpei, Micronesia	Rhodes and Tupper (2007)	11 years	Displacement of fishing pressure on vulnerable life stages, i.e. juveniles and small adults	NI
Kehpara Marine Sanctuary, Pohnpei, Micronesia	Rhodes and Tupper (2008)	10 years	Signs of decline of the squaretail coral grouper FSA	NI
Kehpara Marine Sanctuary, Pohnpei, Micronesia	Rhodes et al. (2011)	11 years	Decline in FSA abundance; truncation in age and body size structure	NI
Komodo National Park, Indonesia	Pet et al. (2005)	2 years	Declines in mean body size of squaretail coral grouper and in the numbers of aggregating brown-marbled groupers; decreases in mean body size and abundance of another commercially important grouper that does not form transient FSAs, <i>Plectropomus leopardus</i> , in the same area	NI
Komodo National Park, Indonesia	Mangubhai et al. (2011)	7 years	Declines in the abundance of squaretail coral grouper and brown-marbled grouper; decrease in abundance of a non-aggregating species, humphead wrasse ( <i>Cheilinus undulates</i> ), at FSA sites	NI

Continued

Table 2. Continued

Geographical area	Study	Duration between MPA creation and last data collected	Conservation effects	Fisheries effects
Ebiil Channel and Ngerumekaol Channel, Palau	<a href="#">Golbuu and Friedlander (2011)</a>	5 years (Ebiil Channel)/29 years (Ngerumekaol Channel)	Declines in the proportional abundance of brown-marbled and camouflage grouper at Ebiil Channel; increase in the proportional abundance of squaretail coralgrouper at Ebiil Channel; numerical abundance and biomass of the three grouper species higher at Ngerumekaol Channel; declines in the proportional abundance of camouflage grouper at Ngerumekaol Channel; increases in the proportional abundance of brown-marbled and squaretail coralgrouper at Ngerumekaol Channel	NI
Northern New Ireland, Papua New Guinea	<a href="#">Hamilton et al. (2011)</a>	5 years	Increases in the densities of brown-marbled and camouflage groupers; squaretail coralgrouper densities unchanged	NI
Western Roviana Lagoon, Solomon Islands	<a href="#">Hamilton et al. (2012a)</a>	4 years	No changes in the abundance of camouflage and brown-marbled groupers; slight reduction in the abundance of squaretail coralgrouper	No changes in landings and cpue of squaretail coralgrouper
Exuma Cays Land and Sea Park, Bahamas	<a href="#">Chiappone and Sealey (2000)</a>	37 years	Nassau grouper density, body size, biomass, and potential egg production significantly higher in the FSA MPA than in adjacent non-protected areas; <i>queen conch and spiny lobster reported to benefit from FSA MPA protection (density, biomass, and potential egg production significantly greater than in adjacent non-protected areas)</i>	Recruitment subsidy effects expected
Exuma Cays Land and Sea Park, Bahamas	<a href="#">Chiappone et al. (2000)</a>	38 years	Nassau grouper density, body size, and biomass significantly higher in the FSA MPA than in adjacent non-protected areas	NI
West End Little Cayman, Cayman Islands	<a href="#">Whaylen et al. (2004)</a>	1 year	FSA site considered healthy, given that males dominate numerically the FSA; body size of fish large compared with other sites	Recruitment subsidy effects expected
West End Little Cayman, Cayman Islands	<a href="#">Heppell et al. (2012)</a>	7 years	Increase in smaller adult Nassau grouper in the population, a sign of recruitment; increase in the body size diversity of the population	NI
Grammanik Bank, St Thomas Island, US Virgin Islands	<a href="#">Kadison et al. (2010)</a>	4 years	Increases in numbers and mean fish body size; sex ratio normalization; presence of younger cohorts on the FSA site in recent years suggesting the possibility of continuity and perhaps the rebounding of the healthy Nassau grouper FSA	NI
Marine Reserve Caleta de Avalo, Marine Reserve Pta. Francés, Marine Reserve Cabo Cruz, Marine Reserve Cayo la Leña, Marine Reserve Norte de Matanzas, and nine other MPAs established at spawning aggregation sites	<a href="#">Claro and Lindeman (2003)</a>	5 years	Nassau grouper FSAs not recovering in substantial manners	No changes in catches of lane snapper

Marine Reserve Caleta de Avalo, Marine Reserve Pta. Francés, Marine Reserve Cabo Cruz, Marine Reserve Cayo la Leña, Marine Reserve Norte de Matanzas, and nine other MPAs established at spawning aggregation sites	<a href="#">Claro et al. (2009)</a>	9 years	Analyses of fisheries-dependent data suggest further decline or no recovery for all the studied species; <i>marked declines also reported for mullets that do not form transient FSAs but are often targeted by fishers on or moving to spawning aggregations</i>	Declines in catches of Nassau grouper and lane snapper; declines in catches of mutton snapper
Gladden Spit and Caye Glory, Belize	<a href="#">Heyman and Wade (2007)</a>	6 years	Increase in abundance of cubera snapper at Gladden Spit; increases in Nassau grouper abundance insufficient to ensure species recovery	NI
Gladden Spit, Belize	<a href="#">Graham et al. (2008)</a>	6 years	Analyses of fisheries-dependent data suggest decline for mutton snapper	Decrease in fisheries cpue
Florida Keys National Marine Sanctuary, Florida, USA	<a href="#">Eklund et al. (2000)</a>	8 years	Black grouper FSA highly vulnerable to exploitation because fishing was often concentrated along MPA edges, and the aggregation actually occurred outside the MPA and within 100 m of its boundaries at the time of the study	NI
Madison Swanson Marine Reserve, Florida, USA	<a href="#">Koenig and Coleman (2013)</a>	11 years	The mean body size and age of gag grouper and the percentage of gag grouper males within the MPA increased between 2007 and 2010. However, the MPA has been closed to fishing for a decade, and body size/age differences for gag grouper would be expected to be greater than observed in the study. Moreover, even if the percentage of males within the MPA has increased, gag grouper sex ratio is still at an alarming low level; <i>abundance of several non-aggregating species (red grouper, vermilion snapper, greater amberjack, almaco jack) is significantly higher inside than outside the MPA; the MPA also ensures the protection of threatened and endangered non-aggregating species, including Warsaw grouper, speckled hind and snowy grouper</i>	NI
Tortugas South Ecological Reserve, Florida, USA	<a href="#">Coleman et al. (2004a)</a>	3 years	NI	Landings considered stable at the time the MPA went into effect have declined since
Tortugas South Ecological Reserve, Florida, USA	<a href="#">Burton et al. (2005)</a>	3 years	Increase in abundance	NI

Indirect effects of FSA MPAs (i.e. effects for, or related to, species not targeted by protection efforts) are indicated in italics. Positive effects of FSA MPAs are highlighted in grey. NI, not investigated.

Golbuu and Friedlander, 2011; Mangubhai *et al.*, 2011); (ii) the absence or ineffective use of additional measures to control fishing mortality on the populations during non-aggregating times (e.g. Rhodes and Sadovy, 2002; Heyman and Wade, 2007; Hamilton *et al.*, 2011); (iii) the MPAs being too small to completely enclose the FSA (Eklund *et al.*, 2000; Nemeth *et al.*, 2006a; Hutchinson and Rhodes, 2010); and (iv) the exploitation of migration routes used by fish attending FSAs and, for seasonal FSA MPAs, the exploitation of the portion of the population that resides at the FSA sites outside the spawning period (e.g. Heyman and Wade, 2007; Marshak and Appeldoorn, 2007; Claro *et al.*, 2009; Rhodes *et al.*, 2011). Seven studies reported that FSA MPAs had non-positive direct fisheries effects. Claro and Lindeman (2003), Marshak and Appeldoorn (2007), and Hamilton *et al.* (2012a) found no change in fisheries cpue and/or landings following implementation of spawning area closures, while Coleman *et al.* (2004a), Luckhurst and Trott (2008), and Claro *et al.* (2009) reported declines in landings, and Graham *et al.* (2008) decreases in cpue.

Based on available empirical evidence, the direct conservation and fisheries effects of FSA MPAs remain uncertain, given the lack of consistent findings, the small number of studies, and the widely differing experimental objectives and designs. Moreover, the time frames over which the effects of this management tool have been measured are relatively short in relation to biological processes such as population growth, especially in the long-lived species that are often the focus of research and management (Supplementary Table S1). Long-lived populations may only show clear signs of recovery after decades of effective protection (Russ and Alcalá, 2010; Sadovy de Mitcheson and Colin, 2012a), and recruitment subsidy will not occur until biomass (or sex ratio) has improved (Palumbi, 2004). In some studies, authors also found difficult to disentangle the impacts of FSA MPAs from those of other management measures, especially if a baseline before implementation was lacking (e.g. Heyman and Wade, 2007; Luckhurst and Trott, 2008; Claro *et al.*, 2009).

A robust experimental design is required to clearly identify impacts of FSA MPAs. None of the studies analysing fisheries-independent data in our review (Supplementary Table S1) adopted the before–after–control–impact (BACI) experimental design that is recommended for a rigorous evaluation of MPA effectiveness (Sale *et al.*, 2005; Osenberg *et al.*, 2011). In most of the studies, after-only designs with one impact (protected FSA) site ( $n = 7$ ), before–after designs with one impact site ( $n = 4$ ), or before–after designs with two impact sites ( $n = 3$ ) were used. Monitoring design was more robust in two studies (Golbuu and Friedlander, 2011; Hamilton *et al.*, 2011). Golbuu and Friedlander (2011) used an after-only, control–impact design with multiple impact (protected FSA sites) and control sites (non-protected FSA sites), though the validity of the control sites has been questioned (Colin *et al.*, 2013); while Hamilton *et al.* (2011) used an after-only, control–impact design with one impact site and multiple control sites. The lack of BACI designs in assessing the effectiveness of FSA MPAs probably relates to cost and personnel constraints, and because spawning area closures have rarely been established with enough forethought and temporal lags to properly collect “before” data. The monitoring design used in the most existing studies was likely the best possible, given local logistical, monetary, and political circumstances.

#### Indirect effects

All the results reported in the previous subsection pertain to “direct” effects of FSA MPAs, i.e. effects on the fish populations targeted by

protection efforts. “Indirect” effects of FSA MPAs, i.e. effects on habitat and fish populations not targeted by protection efforts, were reported in 21% of the empirical studies that we identified ( $n = 6$ ; indirect conservation effects:  $n = 5$ ; indirect fisheries effects:  $n = 1$ ) (Table 2).

When indirect conservation effects of FSA MPAs were reported, trends evaluated for fish populations that are not targeted by protection efforts were similar to those evaluated for populations targeted by protection efforts (Chiappone and Sealey, 2000; Pet *et al.*, 2005; Claro *et al.*, 2009; Mangubhai *et al.*, 2011; Koenig and Coleman, 2013). For example, Mangubhai *et al.* (2011) showed that hump-head wrasse (*Cheilinus undulatus*) declined in abundance at FSA sites where an MPA had been created for the protection of brown-marbled grouper (*Epinephelus fuscoguttatus*) and squaretail coral-grouper (*Plectropomus areolatus*) transient FSAs. Ten years after the establishment of a reserve designed to protect a gag grouper FSA site, both gag grouper and many non-aggregating species, including red grouper (*Epinephelus morio*) and greater amberjack (*Scomberomorus cavalla*), were found to be significantly more abundant in the MPA than at adjacent non-protected gag grouper FSA sites (Koenig and Coleman, 2013). In this latter example, species recoveries are tied to multiple management measures, including minimum size limits and seasonal fisheries closures (Supplementary Table S1).

Karras and Agar (2009) produced the only study in our search that assessed indirect fisheries effects of FSA MPAs. The authors note that the closure of a red hind FSA site off St Croix Island (US Virgin Islands) incurred economic costs because fishers lost access to productive lobster and conch fishing grounds and become more reliant on areas with lower habitat quality.

#### Insights from modelling studies

The practical limitations of field research and the time needed for a biological and fishery response to protection make it difficult to empirically assess the effects of area closures (e.g. Eklund *et al.*, 2000; Luckhurst *et al.*, 2009; Rhodes *et al.*, 2011). MPAs are often implemented as a reaction to declining fish populations (or catches) and consistent evaluation of the outcomes of protection may not always be possible. Moreover, some FSA sites are particularly deep, difficult, or dangerous to study, or it may be difficult to obtain funding for regular surveys (e.g. Eklund *et al.*, 2000; Koenig and Coleman, 2013). In such contexts, modelling approaches are valuable for providing rapid, detailed, and relatively cheap assessment and forecasting of the exploitation status of the populations targeted by protection efforts, and of the potential effects of MPAs, under a wide range of biological, ecological, and management scenarios. Over the last 15 years, models have been increasingly used in MPA research (Gerber *et al.*, 2003; Botsford *et al.*, 2009a, b; Grüss *et al.*, 2011); however, modelling efforts specifically to evaluate FSA MPAs have received less attention. To our knowledge, only three non-spatially explicit models have been developed to explore the long-term conservation and fisheries effects of MPAs used to protect transient reef FSAs (Heppell *et al.*, 2006; Ellis and Powers, 2012; Grüss *et al.*, 2013; Table 3). These three models focused on the direct effects of FSA MPAs, i.e. the impacts of FSA MPAs on the populations targeted by protection efforts and their fisheries.

Heppell *et al.* (2006) designed an age-structured, population model to evaluate the conservation effects of different management measures for gag grouper of the Gulf of Mexico, an overexploited population for which significant data were available. Gag grouper



**Table 3.** Main features of the models exploring the impacts of spawning aggregation MPAs.

Authors	Heppell <i>et al.</i> (2006)	Ellis and Powers (2012)	Grüss <i>et al.</i> (2013), Robinson <i>et al.</i> (2012a)
Species	Gag grouper ( <i>M. microlepis</i> )	Gag grouper ( <i>M. microlepis</i> )	Brown-marbled grouper ( <i>E. fuscoguttatus</i> ), shoemaker spinefoot rabbitfish ( <i>Siganus sutor</i> )
Geographical area	Gulf of Mexico, USA	Gulf of Mexico, USA	Farquhar atoll, Seychelles ( <i>E. fuscoguttatus</i> )/main granitic islands, Seychelles ( <i>S. sutor</i> )
Model type	Spatially non-explicit, population model	Spatially non-explicit, population model	Spatially non-explicit, per recruit model
Age structure	Larvae and young of the year, juveniles, females, males	Larvae and young of the year, juveniles, females, males	Larvae and juveniles, females, males ( <i>E. fuscoguttatus</i> )/larvae and juveniles, adults ( <i>S. sutor</i> )
Spawning site fidelity	Yes	Yes	Yes or no
Recruitment function	Hockey-stick	Hockey-stick	None
Sex change	Age-mediated	Size-mediated or density-dependent	Age-mediated ( <i>E. fuscoguttatus</i> )/none ( <i>S. sutor</i> )
Possibility of sperm limitation considered?	Yes	Yes	No
MPA types	Year-round or seasonal no-take MPAs	Year-round no-take MPAs	Year-round no-take MPAs
Catchability	Implicitly differs between the spawning and non-spawning seasons	Implicitly differs between the spawning and non-spawning seasons	Explicitly differs between spawning and non-spawning individuals
Fishing effort adjusted? <sup>a</sup>	Yes	Yes	Yes
Total fishing effort increased?	No	Yes	No
Additional and/or alternative management measures	No-take nearshore MPAs, fishing effort control, size limits	Fishing effort control	Fishing effort control, no-take MPAs implemented in normal residence areas
Positive conservation effects of spawning aggregation MPAs?	Yes	Yes/no	Yes/no
Positive fisheries effects of spawning aggregation MPAs?	NI	No	No

<sup>a</sup>Assume redistribution of fishing effort in the non-protected areas after MPA creation.

NI, not investigated.

is protogynous, and relatively unique in that male gag groupers stay year-round at FSA sites, whereas mature females undertake migrations to these sites in winter and stay the rest of the year in nearshore areas that they share with juveniles (Coleman *et al.*, 1996). Sex change occurs over a fixed range of age classes in the model. Heppell *et al.* (2006) found that a seasonal closure of all FSA sites to all fishing activities resulted in increased SSB and moderate population growth but did not reduce sex ratio bias. On the other hand, year-round closure of all FSA sites to all fishing activities helped sex ratio normalization, but not population recovery compared with other management measures (nearshore no-take MPAs or fishing effort reduction), especially when the fishing effort previously in FSAs is redistributed to nearshore areas at the time of MPA creation.

Ellis and Powers (2012) built a model based on Heppell *et al.* (2006)'s model to investigate the impacts of no-take, year-round spawning area closures of different sizes on the sex ratio of the gag grouper population of the Gulf of Mexico and on fisheries yields. Ellis and Powers (2012)'s model allows for changes in fishing effort after MPA implementation, both in terms of total fishing effort and effort redistribution at the time of MPA creation. The authors showed that FSA MPAs can maintain and even reduce female: male gag grouper sex ratio, yet predicted benefits are highly sensitive to changes in fishing effort that lead to higher fishing mortality on non-protected individuals. Moreover, when

sex change is density-dependent and not age- or size-mediated (a more likely scenario according to what is currently known on sex change patterns; Koenig and Coleman, 2013), the gag grouper population is more resilient to high fishing pressure and FSA MPAs do not significantly reduce gag grouper sex ratio bias.

The gag grouper population studied in the Gulf of Mexico is relatively data-rich; there is a need for models for data-poor contexts, which applies to the most FSA-forming populations (Johannes, 1998; Sadovy and Domeier, 2005; Zeller *et al.*, 2005). Grüss *et al.* (2013) developed an age-structured, per recruit model to explore the conservation and fisheries effects of closing a fraction or all FSA sites to all fishing activities in data-poor situations. Being a per-recruit model, it avoids the need for specifying a relationship linking egg fertilization success to sex ratio and a stock–recruitment relationship, both of which are highly uncertain or unknown (Armstrong, 2001; Alonzo and Mangel, 2004; Sadovy and Domeier, 2005). The model was applied to two aggregation-forming populations from Seychelles with contrasting life history traits: the brown-marbled grouper population of Farquhar Atoll, which is protogynous and long-lived; and the shoemaker spinefoot rabbitfish (*Siganus sutor*) population of the main granitic islands, which is gonochoristic and short-lived. Alternative possible scenarios for fish spawning-site fidelity (entirely faithful or entirely unfaithful) and the fate of the fishing effort formerly at FSA sites (disappears or is fully redistributed

to non-protected FSA sites) were explored. For a wide range of levels of total annual fishing effort, the authors found that spawning area closures are generally effective at improving SSB-per-recruit and normalizing sex ratio, though these benefits were often small. However, if brown-marbled grouper individuals are faithful to specific FSA sites and fishing effort is redistributed, the sex ratio of its fished subpopulation may become considerably biased towards females, thereby potentially impairing population-wide egg fertilization rates unless a substantial fraction of FSA sites is placed in MPAs.

Grüss *et al.* (2013) also reported that increases in yield-per-recruit (exploitable biomass) with FSA MPAs did not occur or were negligible, for either species, regardless of the degree of fish spawning-site fidelity and the fate of fishing effort previously in MPAs. However, the authors suggested that increases in yields with FSA MPAs may occur through recruitment subsidy, if the populations targeted by protection efforts are recruitment limited before MPA creation and that increases in SSB-per-recruit counterbalances lost fishing opportunities due to closing areas. This idea finds support in other MPA modelling studies (Guénette and Pitcher, 1999; Hart, 2006; Botsford *et al.*, 2009a). A further application of Grüss *et al.* (2013)'s model examined the impacts of closing a fraction of shoemaker spinefoot rabbitfish normal residence areas to fishing rather than FSA sites (Robinson *et al.*, 2012a). The authors found that protecting non-spawning areas led to a slight increase in yield-per-recruit when the population is overexploited and that this approach is more effective at improving fish SSB-per-recruit than FSA MPAs (Robinson *et al.*, 2012a).

### Where we should go and what we need to get there

Though existing studies provide a degree of insights into the impacts of FSA MPAs, the effectiveness of this management tool remains uncertain. Existing modelling studies concur that spawning area closures can improve SSB and normalize sex ratio in the long term, unless fishing mortality remains high outside protected FSA sites and spawning times. In contrast, in the field, observations of no change or continued decline in SSB are more common than population recovery. In the former case, several factors, such as insufficient time since MPA creation, poor or non-existent enforcement, inadequate design, and poorly defined management objectives are generally blamed rather than failure of the MPA concept itself. These factors are among those listed as keys to conservation success in a recent large-scale review of MPA effectiveness (Edgar *et al.*, 2014). Furthermore, results from both modelling and empirical studies suggest that spawning area closures may not produce fisheries benefits, yet at present investigations are too limited for any certainty on this point.

Additional modelling work, long-term monitoring programmes at FSA sites, and collections of fisheries-dependent data are needed to ascertain the true effects of FSA MPAs. The many apparent “failures” of spawning area closures in the empirical literature also highlight the necessity to (i) clarify management objectives, (ii) improve research for the design of FSA MPAs, (iii) improve the enforcement of FSA MPAs, (iv) consider the implementation of supplemental management measures, and (v) enhance interactions between empiricists, modellers, and other stakeholders.

### Clarifying management objectives

An explicit statement of FSA MPA objectives should be clearly articulated, with individual management objectives listed and ranked, before any modelling and fieldwork. Direct conservation objectives (protection/recovery of FSA-forming populations, i.e.

sex ratio normalization, increase in SSB, stability, or increase in recruitment), indirect conservation objectives (biodiversity protection/recovery, i.e. habitat enhancement, protection/recovery of other species), and fisheries objectives (i.e. stability or increase in exploitable biomass, stability or improvement of fisheries cpue or yields) must be defined for both the short/medium and the long term. For example, it may be relevant to target stability in recruitment and increases in SSB for the medium term and stability or improvement of yields for the long term. Clarifying management objectives for the short, medium, and the long term will preclude stakeholders, mainly fishers, from having unrealistic expectations and, therefore, will improve the reliability and enforcement of management measures.

In fact, fisheries objectives should build on conservation objectives. MPA modelling studies have demonstrated that stability or improvement in fisheries yields may occur in the long term, once the reproductive capacity of populations targeted for protection has dramatically built up. Population build-up allows for an increase in recruitment, which can offset lost fishing opportunities due to closing areas (Hart, 2006; Botsford *et al.*, 2009a). Put another way, conservation objectives, which generally target an overall reduction in mortality rates, should be a primary goal. Fisheries objectives build on conservation objectives, in that they require an overall reduction in mortality rates while maintaining sufficient access to exploitable biomass.

### Making more use of models

More effort should be made to use models to assess the exploitation status of FSA-forming populations and the potential effectiveness of spawning aggregation MPAs on a case-by-case basis, especially before the implementation of new area closures. To the extent that one understands a study system, models are valuable for teasing apart how MPAs and conventional management measures such as fishing effort control may address trade-offs between conservation and fisheries objectives in particular contexts.

Regardless of the objectives, models may help to identify relevant management strategies that combine measures (i.e. percentage of FSA sites protected, no-take or partial protection, seasonal or year-round protection, specific additional management measures) to obtain specific fishing mortality targets for the population. Importantly, models will be useful in highlighting when spawning area closures are unlikely to generate the desired outcomes.

The complexity and scope of the models used will depend on available data. Simple non-spatial per-recruit models can be used in “data-poor contexts”, while more complex, spatially explicit population models may be developed in “data-rich contexts” (Box 1). Per-recruit models are relatively easy to construct and use with limited data but have the disadvantage of ignoring the effects of MPAs on recruitment. This constrain is important since models combining per-recruit quantities and a stock–recruitment relationship found that MPAs have the potential to generate fisheries benefits over a greater range of conditions than those that lacked this relationship (Guénette and Pitcher, 1999; Botsford *et al.*, 2009a). The major disadvantages of spatially explicit population models are their large data demands and their need for representation of connectivity (Box 1).

All models must consider alternative scenarios of the fate of fishing effort after MPA implementation, both in terms of total fishing effort and effort redistribution at the time of MPA creation. The fishing effort previously in protected FSA sites is unlikely to disappear, unless fishing effort is also controlled, and models must

**Box 1.** Developing models to explore the potential effects of spawning aggregation MPAs (FSA MPAs)

The minimum fisheries information needed for parameterizing spatially non-explicit and spatially explicit models is the fraction of annual fishing effort or fishing mortality specific to FSAs (related to total fishing effort and the proportion of spawning adults protected by the FSA MPA), and an idea of the difference in catchability between spawning and non-spawning individuals. If data are available, migration routes can be considered in these models, by specifying catchability during migration and the fraction of annual fishing effort or fishing mortality specific to migration routes and period. This is desirable given that fishing pressure is often high on migration routes, and that the fishing effort formerly in protected FSA sites may be partially or totally redistributed to migration routes at the time of MPA creation (Claro *et al.*, 2009; Rhodes *et al.*, 2011; Sadovy de Mitcheson and Erisman, 2012). Per-recruit and spatially non-explicit population models may also formulate assumptions on the degree of fidelity of fish to FSA sites, especially when tagging studies have revealed a degree of aggregation site infidelity (e.g. shoemaker spinefoot rabbitfish; Bijoux *et al.*, 2013; Grüss *et al.*, 2013).

Per-recruit models ignore the potential direct effects of MPAs on recruitment and, therefore, on fisheries yield. To provide a better picture of the potential fisheries effects of FSA MPAs, when the stock–recruitment relationship and relationship between sex ratio and egg fertilization rate are unknown for the populations being studied, different alternative functional forms may be represented in models. Potential MPA effects should then be discussed in the light of the functional forms used. Several arbitrary relationships between sex ratio and egg fertilization rate have already been proposed in the modelling literature (e.g. Hunstman and Schaaf, 1994; Armsworth, 2001; Alonzo and Mangel, 2004; Heppell *et al.*, 2006).

Eventually, spatially explicit population models may be developed for aggregation-forming populations of high conservation concern and/or high socio-economic importance (e.g. some populations of Nassau grouper and gag grouper) for which reliable data are available. The scale of the spatial units of these models will depend on the spatial distribution and extent of migrations of the fish populations considered and on the accuracy of data available (especially the fisheries data). Their temporal resolution should be tuned according to the timing of spawning aggregations. The primary benefit of spatially explicit population models is that they can thoroughly evaluate the effectiveness of MPA networks, including MPAs protecting normal residence areas and/or migration routes and/or nursery areas. Such an integrated approach is critical, given that the establishment of spawning area closures in isolation could do more harm than good by redirecting high levels of fishing effort to other areas where the population is highly vulnerable (e.g. Heppell *et al.*, 2006; Rhodes and Tupper, 2007; Claro *et al.*, 2009; Rhodes *et al.*, 2011).

The major challenge for building spatially explicit models is the representation of connectivity. For species spawning pelagic eggs or larvae (i.e. the great most FSA-forming species; Colin, 2012a), larval connectivity matrices may be built from the simulations of a biophysical transport model, using information collected by satellite-tracked current-following drifter buoys (Paris *et al.*, 2005; Heyman *et al.*, 2006; Heppell *et al.*, 2008; Karnauskas *et al.*, 2011), or through a cheaper alternative, the use of ballasted laboratory scintillation vials (Domeier, 2004). Capture of larvae with light traps, moored larval traps, and plankton tows, as well as rearing of eggs in culture could provide information on larval behaviour for biophysical transport models (Colin, 2012c), as well as egg fertilization rates. Adult movement may be parameterized from the results of tagging studies. Acoustic telemetry is an increasingly utilized tool quantifying the range size of juveniles, non-spawning and spawning mature individuals (e.g. Semmens *et al.*, 2006; Taylor *et al.*, 2006; Hutchinson and Rhodes, 2010) and both conventional mark-recapture and acoustic tagging can be used to measure distances of migration between normal residence sites and FSA sites, determine migration routes and estimate residence times and the degree of fidelity of fish to spawning aggregation sites (e.g. Nemeth *et al.*, 2007; Starr *et al.*, 2007; Rhodes *et al.*, 2012). Estimation of total spatial movement and migration patterns should be conducted independently for males and females (e.g. Nemeth *et al.*, 2007; Robinson *et al.*, 2008; Hutchinson and Rhodes, 2010).

In the long term, when consistent monospecific models have been built, more complex multispecies and ecosystem models may eventually be developed. Given the multispecies nature of nearly all transient FSA sites (Heyman and Kjerfve, 2008; Sadovy de Mitcheson *et al.*, 2008; Colin, 2012a), the possible ecosystem-level impacts of depleting or eliminating FSAs (Sadovy and Domeier, 2005; Rhodes and Tupper, 2007; Nemeth, 2012), and the potential redistribution of fishing effort to other species (Rhodes and Tupper, 2008; Karras and Agar, 2009; Golbuu and Friedlander, 2011), these models will be useful to better integrate FSA MPAs into ecosystem-based management. Future ecosystem models could eventually be coupled with hydrodynamic models to take into account the impacts of environmental and climate changes (e.g. changes in seawater temperature and current speeds, timing, and direction) on the dynamics of FSAs and their long-term persistence (Colin, 2012a).

inform decision-makers of the consequences of redistributing this effort partially or totally to non-protected FSA sites or non-reproductive areas. Models can also show whether overall effort has to be reduced or explore the impacts of increasing total fishing effort after MPA implementation (Ellis and Powers, 2012). Such scenarios are highly relevant given the growing pressure on coral reef resources (Sadovy, 2005a, b; Robinson *et al.*, 2008, 2011). Existing modelling studies have only examined the effects of no-take FSA MPAs, but in some contexts, it may be of interest to evaluate the effects of partial-take MPAs, and consider the

consequences of banning exports in favour of subsistence fishing and local food security (Sadovy de Mitcheson and Erisman, 2012).

**Improving research for designing FSA MPAs**

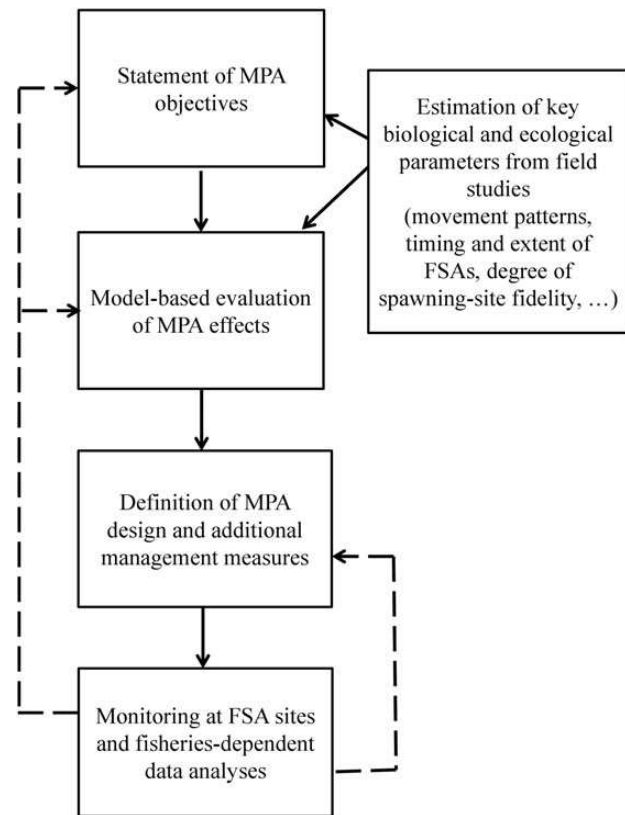
Ideally, the design of FSA MPAs should be guided and adapted from the results of both modelling and field studies (Figure 1). Before creating a new spawning area closure, field studies are required to gather data on the timing of aggregations, residency time of males and females at the sites, and their degree of fidelity to aggregation sites (e.g. using tagging and underwater visual census; Colin *et al.*,

2003; Colin, 2012b; Bijoux *et al.*, 2013). The timing of the FSAs must be precisely determined if the spawning aggregation MPAs are only to be implemented in seasonal or lunar periods, especially when area closures are not combined with spawning-season bans on sales, catch, possession, or export (e.g. Rhodes *et al.*, 2011; Russell *et al.*, 2012). If males or a large portion of the population stay at aggregation sites year-round, then FSA MPAs should be permanent as opposed to seasonal. This is particularly desirable for protogynous species (e.g. gag grouper), to ensure that males are not exposed to high levels of fishing effort outside of the spawning season and that sex ratio is not significantly biased towards females in the population (Heppell *et al.*, 2006; Koenig and Coleman, 2012, 2013). The degree of fidelity of fish to FSA sites is also important for MPA effectiveness. Fidelity not only involves the degree to which individuals consistently use the same site for spawning, but also the proportion of aggregations that an individual participates in during a season. More FSAs will need to be protected if fidelity to a specific site is low. This is especially relevant for protogynous species if MPA creation creates a redistribution of fishing effort, a situation that models predict will lead to a strong female bias in sex ratio at unprotected FSA sites and, possibly, to population-wide egg fertilization rate impairment (Grüss *et al.*, 2013). In contrast, if individuals do not attend every aggregation within a season (e.g. brown-marbled grouper in Pohnpei, Micronesia; Rhodes *et al.*, 2012), then FSA MPAs will offer less protection than anticipated and redistribution of effort to the areas where those individuals remain will influence fishing mortality rates.

The overall spatial extent of an FSA site should be precisely determined before the establishment of a spawning area closure (see, e.g. Eklund *et al.*, 2000; Rhodes and Sadovy, 2002; Nemeth *et al.*, 2007), ideally using acoustic telemetry (e.g. Semmens *et al.*, 2006; Hutchinson and Rhodes, 2010). In particular, staging areas, where fish congregate in groups to rest, feed or occupy cleaning stations before and after spawning, should be properly identified (Nemeth, 2012). Typically, FSA sites are stable in location over decades (Sadovy de Mitcheson *et al.*, 2008; Colin, 2012a); however, changes in location of 10 s to a few 100 m may occur from 1 year to the next due to environmental events, such as changes in current direction or cyclones (e.g. Colin, 1992; Whaylen *et al.*, 2006; Heyman and Kjerfve, 2008; Robinson *et al.*, 2012b). Therefore, the boundaries of a spawning area closure may need to be either large enough to cover this interannual repositioning or require revision over time to ensure that the FSA remains protected from fishing. The potential for revisions based on occasional shift in the FSA location provides a strong argument for creating FSA MPAs that encompass both current and potential aggregation locations in a particular area, i.e. for creating “buffer areas” (Robinson *et al.*, 2012b; Russell *et al.*, 2012). Larger MPAs are also likely to better protect migration routes close to FSA sites and, therefore, may significantly improve the value of FSA MPAs (Nemeth, 2005; Hutchinson and Rhodes, 2010; Rhodes *et al.*, 2012). Larger MPAs are also justified for depleted FSAs since recovery in aggregation abundance over time may increase the area over which fish aggregate due to increased competition for habitat (Nemeth, 2012).

### Improving the evaluation of FSA MPAs

Significant improvements in the evaluation of FSA MPA effectiveness are required if spawning aggregation MPAs are to be accepted as a viable tool for conservation and fisheries management. Central to effective evaluation is the establishment of specific objectives and reference points for parameters such as a target



**Figure 1.** Diagrammatic representation of the different steps required for the design and implementation of effective spawning aggregation MPAs (FSA MPAs).

fishing mortality rate reduction. Long-term well-designed studies are required to evaluate whether objectives are being met and to attribute the outcomes of spawning area closures to the closures themselves (Colin *et al.*, 2003; Sadovy de Mitcheson and Colin, 2012a).

As discussed earlier, follow-up monitoring would ideally be based on a BACI design. The BACI design allows for a rigorous assessment of the impacts of FSA MPAs on fish body size, abundance, density, biomass, and sex ratio, and could also be used to better understand and quantify the impacts of aggregation fishing (Colin *et al.*, 2003; Colin, 2012b; Molloy *et al.*, 2012). Passive acoustics can be utilized to estimate densities of soniferous fish at FSA sites while studying their behaviour and habitat use, relatively easily and over a long period (Rowell *et al.*, 2012; Schärer *et al.*, 2012). The study of Heppell *et al.* (2012) demonstrated that evaluating only mean body size provides an incomplete picture of the conservation effects of FSA MPAs. The novel and non-harmful laser video method the authors developed is useful to track fish body size distribution trends at FSA sites over time and, hence, detect MPA-mediated increases in recruitment. Comparing FSA dynamics at control (unprotected FSA sites) and impact (protected) sites in the same region may help to estimate the relationships between protection and aggregation size, density, and reproductive activity, as well as threshold densities below which reproduction may be compromised (Colin *et al.*, 2003; Sadovy de Mitcheson and Erisman, 2012). Studies at both impact and control sites may also be useful for protogynous species to quantify how fishing may disturb the sex change process when it is under exogenous control, and the



relationship between sex ratio and the chances of egg fertilization (Alonzo and Mangel, 2005; Koenig and Coleman, 2012; Sadovy de Mitcheson and Erisman, 2012). Threshold densities and the relationships between sex ratio and egg fertilization rate estimated from field observations may then be used to improve the parameterization of models (Ellis and Powers, 2012).

To date, the fisheries effects of FSA MPAs have been poorly evaluated. In parallel with fisheries-independent monitoring of abundance and other aggregation parameters, traditional fisheries data, including catch and effort time-series should be collected (Marshak and Appeldoorn, 2007; Hamilton *et al.*, 2012a; Sadovy de Mitcheson and Erisman, 2012). These data can be integrated with fishers' knowledge and perceptions of changes in aggregation fisheries (Karras and Agar, 2009; Hamilton *et al.*, 2012b) to discuss the impacts of spawning area closures on fisheries. Importantly, data on annual fishing effort and mortality should be disaggregated by the spawning and non-spawning seasons (or areas) to evaluate and manage fishing effort redistribution and, therefore, population-wide fishing mortality rates (Marshak and Appeldoorn, 2007; Rhodes *et al.*, 2011; Robinson *et al.*, 2011; Sadovy de Mitcheson and Erisman, 2012).

Indirect effects of FSA MPAs have also received little attention. A reason for this is that monitoring other species or habitat would add further burden to what is already a costly and logistically difficult task (Colin, 2012b; Colin *et al.*, 2013). However, spawning area closures may have unintended and profound impacts on fish communities due to the complexity of trophic interactions and the multispecies nature of reef fisheries (e.g. Rhodes and Tupper, 2007; Nemeth, 2012). FSA sites are often used sequentially or simultaneously by multiple species, many of which may also benefit from protection (e.g. Nemeth *et al.*, 2006b; Kadison *et al.*, 2010; Heyman, 2011). Non-aggregating species residing at spawning sites may also benefit (e.g. Chiappone and Sealey, 2000; Koenig and Coleman, 2013), as would the reef habitat at that location if destructive gears were excluded from the MPA (e.g. Beets and Friedlander, 1999). Maintaining or improving biodiversity is a classical objective of MPAs (Bohnsack *et al.*, 2004; Claudet, 2011). If biodiversity is an additionally stated goal of the spawning area closure, then metrics for other species (e.g. abundance, biomass) and communities (e.g. Shannon's index) should be evaluated in parallel with metrics for the specific populations targeted by protection efforts. On the other hand, the creation of an FSA MPA to protect a given fish population may place increased fishing pressure on other species, particularly when the FSA MPA is seasonal (Rhodes and Tupper, 2008; Karras and Agar, 2009; Golbuu and Friedlander, 2011). Ideally, catch and the FSA and non-FSA components of annual fishing effort and mortality should also be monitored for the exploited species that use protected FSA sites but are not targeted by protection efforts.

### Improving the enforcement of FSA MPAs

One major advantage of FSA MPAs is simplicity of enforcement when compared with traditional fisheries actions such as bag limits or length-based rules. Despite this, poor or non-existent enforcement is identified as one of the major causes of perceived failure at many FSA MPAs (e.g. Nemeth *et al.*, 2006a; Graham *et al.*, 2008; Golbuu and Friedlander, 2011; Hamilton *et al.*, 2011; Mangubhai *et al.*, 2011). Without strong enforcement, FSA MPAs will not provide all the benefits they are capable of delivering (Russell *et al.*, 2012). Both in developing and developed countries, FSA MPAs often are not patrolled properly (e.g. Rhodes and

Sadovy, 2002; Marshak and Appeldoorn, 2007; Mangubhai *et al.*, 2011) or not patrolled at all (e.g. Nemeth *et al.*, 2006a), primarily because of a lack of personnel. For example, in the Cayman Islands, which is a relatively rich territory, there is only one enforcement officer per island to patrol their FSA MPAs, but this officer is already overwhelmed by all the other island-wide management measures he/she also has to enforce, such as bag limits, for a multitude of species (B. Semmens, pers. obs.). In a few developed regions, at-sea enforcement patrols are supplemented or replaced by the installation of Vessel Monitoring Systems (VMS) on licensed boats (Koenig and Coleman, 2013) and aerial surveillance (Russell *et al.*, 2012). Even when enforcement and surveillance of spawning area closures are effective, some poaching occurs inside protected areas (e.g. Chiappone and Sealey, 2000; Nemeth, 2005; Koenig and Coleman, 2013).

Means of enforcement and surveillance of FSA MPAs must be carefully considered, ideally long before the implementation of the area closures. In developing regions, where resources and funding are limited, the best way to ensure that FSA MPAs will be effectively enforced is to empower fishing communities that support such management measures. Community-based co-management or customary marine tenure agreements resulting in shared costs and efforts are likely to be more beneficial to FSAs and fishers than top-down management measures and at-sea enforcement patrols by official personnel (e.g. Heyman, 2011; Hamilton *et al.*, 2012a; Heppell *et al.*, 2012). In developed regions (but also in a few developing countries such as the Seychelles), the VMS method works well and should continue to be used, but it is imperfect in that it is usually not applied to all the vessels targeting FSAs (Coleman *et al.*, 2004b; Koenig and Coleman, 2013; J. Robinson, pers. obs.). It has recently been argued that VMS on licensed boats could be substituted by simple acoustic receivers at FSA sites, so as to monitor boat traffic in and around spawning area closures with reduced effort and cost (Koenig and Coleman, 2013). The quality of recordings of basic acoustic receivers is sufficient to identify individual fishing boats, and such receivers can incorporate radar for real-time surveillance (Sorensen *et al.*, 2010; Koenig and Coleman, 2013). Acoustic receivers equipped with radars are not excessively expensive, such that their use could be envisioned in both developed and developing regions for the surveillance of protected FSA sites that are relatively close to the shore.

### Implementing other management measures

FSA MPAs, like any form of MPA, are not likely to be effective at reaching their conservation and fisheries objectives in isolation (Russell *et al.*, 2012; Grüss *et al.*, 2013; Sadovy de Mitcheson *et al.*, 2013). Management measures complementary to spawning area closures include seasonal fisheries closures, seasonal sales or export bans, quotas and bag limits, size limits, gear restrictions, and licensing [see Russell *et al.* (2012) for a review]. Moreover, the above-cited rabbitfish example from the Seychelles highlights that FSA MPAs may not always be the most appropriate management tool (Robinson *et al.*, 2012a).

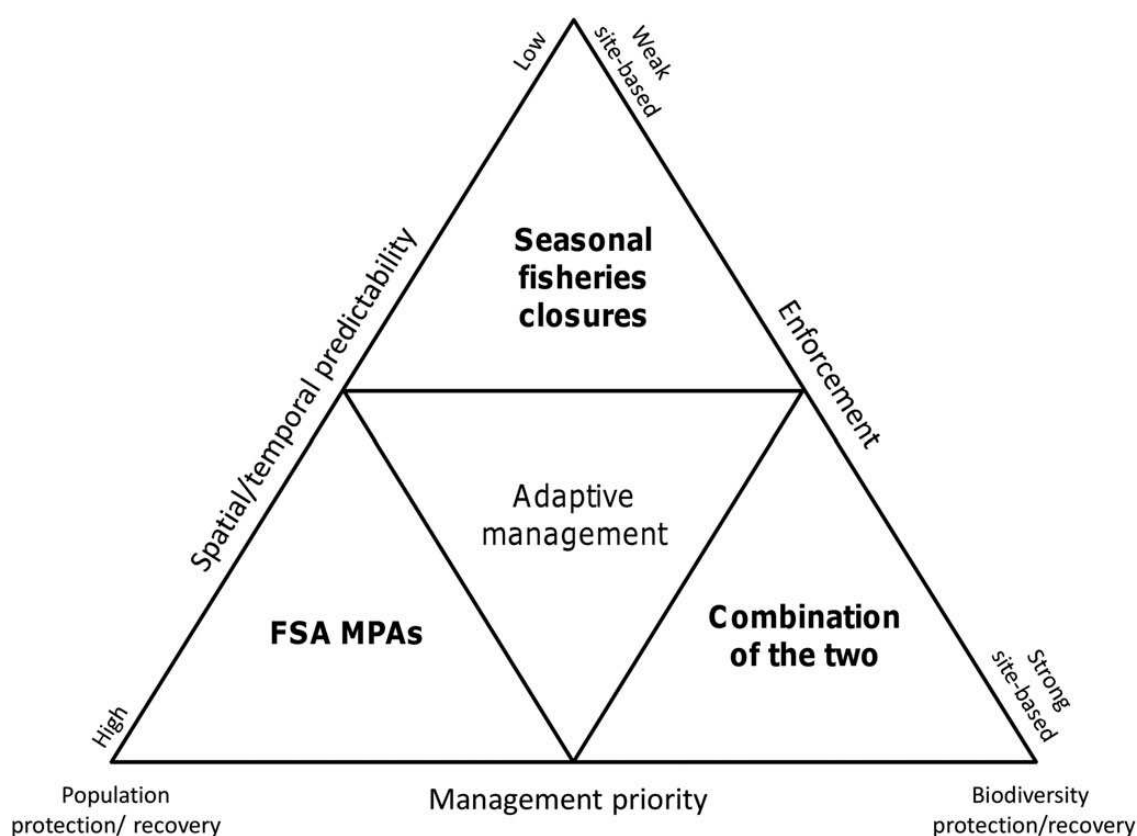
Seasonal fisheries closures are very often advocated to complement or replace FSA MPAs (e.g. Heyman and Wade, 2007; Kadison *et al.*, 2010). The use of seasonal fisheries closure in combination or replacement of FSA MPAs primarily depends on management objectives, the spatial and temporal predictability of FSAs, and the probable strength of enforcement (Table 4 and Figure 2). When the recovery of aggregation-forming populations is the primary goal of management, FSA MPAs should be preferred over seasonal fisheries closures when FSAs are highly predictable in



**Table 4.** Relative impacts of spawning aggregation MPAs (FSA MPAs), seasonal fisheries closures, and a combination of the two measures, and needs for their enforcement.

	<b>Protection/recovery of FSA-forming populations</b>	<b>Biodiversity protection/recovery</b>	<b>Fisheries impacts</b>	<b>Needs for enforcement</b>
FSA MPAs	Good if FSAs are highly predictable in space and time, when no increase in total annual fishing mortality occurs, and when on-water enforcement is effective	Effective, especially if FSA sites are used by many species	Depends primarily on the size of MPAs and area productivity	Requires at-sea enforcement patrols, aerial surveillance <sup>a</sup> , radars <sup>a</sup> , or VMS year-round <sup>a</sup> , or acoustic receivers at FSA sites equipped with radars
Seasonal fisheries closures	Good for FSAs without predictable locations or with potential for substantial movement across closure boundaries (such as defined migration corridors), or when on-water enforcement is poor	Much less effective, only indirect result of target species protection	Worse for fisheries that depend primarily on FSA fishing, possibly less impact for fisheries targeting multiple species	Requires some enforcement patrols, possession controls in points of catch or sale (e.g. restaurants, markets and docks)
Combination of the two	Good for FSAs with a mix of substantial target species movement, spatial enforcement issues, where poaching may be very likely, and where overall fishing mortality is not a concern	More effective	Less impact if the MPA is small and/or implemented over a short period every year	Requires at-sea enforcement patrols, aerial surveillance <sup>a</sup> , radar <sup>a</sup> , or VMS during closure <sup>a</sup> , or acoustic receivers at FSA sites equipped with radars

<sup>a</sup>Applicable in developed regions mainly.

**Figure 2.** Conceptual scheme for deciding whether spawning aggregation MPAs (FSA MPAs), seasonal fisheries closures, or a combination of the two, may be a more effective strategy, based on spawning aggregation predictability, probable strength of enforcement, and conservation objectives.

space and time, no increase in total annual fishing mortality occurs (e.g. due to fishing effort displacement), and on-water enforcement is effective. On the other hand, seasonal fisheries closures will be preferred when FSA sites remain unknown, fish have the potential for

substantial movement across closure boundaries, and on-water enforcement is poor. Finally, a combination of FSA MPAs and seasonal fisheries closures may be adopted primarily when poaching potential is high and overall fishing mortality is not a concern. FSA MPAs

are very attractive for biodiversity protection when many species use spawning aggregation sites, and even more when the FSA MPAs are complemented by fisheries closures. Seasonal fisheries closures are more constraining to fisheries than FSA MPAs when fisheries strongly depend on aggregation fishing, but less constraining when fisheries target a wide diversity of species. Enforcement of seasonal fisheries closures is generally less costly than that of MPAs, but involves some patrolling at sea and possession controls in points of catch or sale (e.g. docks and markets).

### Fostering collaborative, adaptive, and communicative research projects

Clearly, for FSA MPAs to be effective, a collaborative approach involving both empirical and modelling techniques is essential (Botsford *et al.*, 2009b; White *et al.*, 2011; Nemeth, 2012), and management must be adaptive (Colin *et al.*, 2003; Russell *et al.*, 2012) (Figure 1). Ideally, a harmonized approach should be used that combines MPA design with additional management measures, informed from the results of models and field studies. A rigorous monitoring programme at FSA sites, and collection of fisheries-dependent data, should be implemented at least 1–2 years before MPA establishment to provide the “before” data critical to evaluation using the BACI design. Often, the BACI design is logistically not possible due to money and personnel constraints, and monitoring design should then be the best possible, given the logistical and monetary context. Following closure of FSA sites to fishing, model revision and reparameterization based on the results of empirical studies should be done. Systematic, objective evaluation of each FSA MPA, with a strategy directed towards explicitly stated MPA objectives and fishing mortality targets, is crucial to developing, updating, and improving general MPA design and management strategies.

Many governments and research institutions do not have the expertise necessary to implement modelling studies and sophisticated MPA evaluations. Therefore, capacity building will be needed in many regions where transient FSAs occur to make sure that the approaches recommended here are adopted. Moreover, it is critical that people involved in research projects ensure a wider public and stakeholder awareness of the state of FSAs and of the need for management measures, enforcement, and community buy-in. The success of FSA MPAs will be strongly dependent on a higher level of communication between empiricists and modellers, but also between researchers, regulatory agencies, park authorities, fishers, and other stakeholders and the public (Heyman, 2011; Sadovy de Mitcheson *et al.*, 2013).

### Discussion

Fish that reproduce at transient spawning aggregations are notoriously vulnerable to overexploitation, and multiple aggregation-forming species are now listed as threatened or endangered by various governments and organizations (Sadovy de Mitcheson *et al.*, 2008, 2013; Sadovy de Mitcheson and Erisman, 2012). The predictability in location and timing of FSAs, particularly in the absence of enforceable (or enforced) regulations, creates a situation where a fish population can be rapidly depleted to the point that the FSAs fail to form. If remaining FSA species and sites are to be protected, then urgent and decisive management is required to prevent further decline of FSAs and rebuild the populations from which they form. Part of this management should include consideration of spatial protection (Sadovy and Domeier, 2005; Sadovy de Mitcheson *et al.*, 2008, 2013).

The conservation and fisheries effects of FSA MPAs have to date only been partially evaluated, especially for the Indo-Pacific. Current evidence does not well document whether establishment of spawning area closures by themselves are successful for protecting or recovering species, or for stabilizing or increasing fishery yields, leading us to call for additional theoretical and empirical work to more rigorously assess the potential of FSA MPAs. Models should be used to explore the potential effectiveness of spawning area closures on a case-by-case basis, particularly before the implementation of new MPAs, so as to inform the MPA planning process. Simple per-recruit models are advocated in data-poor contexts, while spatially non-explicit, or even spatially explicit population models may be developed in data-rich contexts. Furthermore, MPA evaluation should be improved through (i) the identification of specific objectives for the MPAs and fishing mortality reduction targets; (ii) long-term, rigorous monitoring programmes at FSA sites that are directed at evaluating the stated objectives of the MPAs; and (iii) the collection of fisheries-dependent data for the fish populations targeted by protection efforts to track the influence of MPA establishment on population-wide fishing mortality rates and fisheries yields. We emphasize that conservation objectives and, therefore, an overall reduction in mortality rates should be targeted first. Fisheries objectives build on conservation objectives, in that they require an overall reduction in mortality rates while maintaining sufficient access to the exploitable biomass of aggregative fish populations.

All the aforementioned modelling and empirical efforts must be complemented by improved research for the design of FSA MPAs, the consideration of other management measures to complement or replace spawning areas closures, such as fisheries seasonal closures, and enhanced interactions between empiricists, modellers, and all other stakeholders. Last but not least, these efforts will not provide all the benefits they are capable of delivering if protection measures are implemented without strong enforcement (Sadovy de Mitcheson *et al.*, 2008; Mangubhai *et al.*, 2011; Russell *et al.*, 2012). In fact, the design of spatial measures should explicitly account for the logistical constraints of enforcement.

In the present study, we chose to focus on the use and effectiveness of spawning area closures in tropical regions. However, many temperate species also migrate seasonally to specific spawning areas and may very well also need spatial protection to reduce their probability of overexploitation (e.g. haddock, *Melanogrammus aeglefinus*; Murawski *et al.*, 2000; Atlantic cod, *Gadus morhua*; Windle and Rose, 2007; Armstrong *et al.*, 2012; Dean *et al.*, 2012). Tropical and temperate ecosystems are relatively different in terms of fish ecology, fisheries, socio-economics, and management. In particular, fish spawning areas are generally much more extensive in temperate than in tropical areas, though recent studies suggest that spawning events of some temperate fish populations may be concentrated in smaller areas than previously thought (e.g. Atlantic cod; Bradbury *et al.*, 2008; Skjæraasen *et al.*, 2011). Moreover, conflicting views have been expressed as to the spatial protection of spawners of temperate fish populations over that of their juveniles (e.g. Edwards and Plaganyi, 2011; Grüss *et al.*, 2011). Future empirical, modelling, and review studies should clarify the value and impacts of spawning area closures for temperate fish populations, and conduct extensive comparisons of the effects of spawning MPAs in temperate regions and in tropical regions.

Our aim with the present review was to discuss issues that we hope will provide guidance for the establishment and evaluation

of effective FSA MPAs, and encourage the development of collaborative, adaptive, and communicative research programmes to identify management strategies that satisfy both conservationists and those whose livelihoods depend on fishing. Clearly, significant money and energy will have to be invested to ensure the design and enforcement of effective MPAs and complementary management measures for transient reef FSAs, but given the ecological and economic role that FSAs play in the marine environment, efforts to ensure the persistence and recovery of these spectacular phenomena are undoubtedly worth it.

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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## Glossary

**Reef fish spawning aggregations (FSAs):** Gatherings of large numbers of coral reef fish at predictable times and places for the sole purpose of reproduction. Two main types of FSAs have been identified. Some species form spawning aggregations lasting days to weeks at a limited number of sites located some to hundreds of kilometres from non-reproductive areas during a few months each year (“transient FSAs”; e.g. many Epinephelidae, Lutjanidae, and Siganidae), whereas others form daily aggregations during a lengthyspawning season (sometimes year-round) within or in proximity to their home ranges (“resident FSAs”; e.g. many Scaridae, Labridae, and Acanthuridae) (Domeier and Colin, 1997; Domeier, 2012). A few species do not conform to these two types and form many small spawning aggregations at many sites over a wide area (e.g. leopard coral grouper, *Plectropomus leopardus*; Samoilys, 1997; Zeller, 1998). In the present study, we focus only on transient FSAs and the term “FSAs” refers to “transient FSAs”.

**Marine protected areas (MPAs):** Zones where fishing and other human extractive activities are partially (“partial-take MPAs”) or

totally disallowed (“no-take MPAs”), year-round or seasonally, except when these activities are conducted for scientific purposes.

**Direct and indirect effects of MPAs:** “Direct” effects of MPAs refer here to effects on fish populations targeted by protection efforts and their fisheries. “Indirect” effects of MPAs pertain to effects on habitat and species not targeted by protection efforts.

**Fisheries-independent and fisheries-dependent data:** Fisheries independent data are fisheries information collected by scientists using a variety of sampling techniques including trapping, netting, and underwater visual census. Fisheries-dependent data rely on fishing activities and are collated with the help of fishers.

**Catch per unit effort (cpue):** The amount of fish caught by a fixed amount of fishing, e.g. the weight of fish caught per hour or per day. cpue is an indicator of the economic efficiency of fisheries.

**Before–after-control–impact (BACI) design:** Sampling design for evaluating the effectiveness of MPAs that includes temporal replication before and after MPA creation and spatial replication inside and outside protected areas. Sites selected inside and outside protected areas must be relatively similar (e.g. have similar habitat features, house the same biological processes).

**Shannon’s index:** Popular diversity index that accounts for both abundance and evenness of the species present in a given ecosystem.

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