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Perspective

Should we protect extirpated fish spawning aggregation sites?

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ABSTRACT

Some locations have extraordinary ecological and conservation significance and subsequently need protection to guarantee the persistence of species that depend on them. Fish Spawning Aggregation (FSA) sites, where fish congregate to breed, are examples of such places, but are being extirpated worldwide through overfishing. Although transient FSA sites figure prominently as priority areas for conservation, extirpated aggregations, that due to current low abundance at spawning times are no longer recognizable as FSAs, represent a dilemma for managers. Given the limited resources available for conservation actions, should we protect extirpated FSAs or omit them from spatial management plans? Here we present two contrasting points of view, look into the mechanisms associated with the emergence and maintenance of aggregation sites, and review available evidence of recovery in the field. Of the 53 extirpated FSA sites examined, 9 (17%) reported recovery, always after strict management was implemented. All recovered sites were located in the wider Caribbean and western Atlantic. We make the case that extirpated FSAs seem to have the potential to recover and their protection may provide a cost effective way to help rebuild fisheries. It is unclear, however, if a remnant population is needed to allow recovery. Current methods used to monitor and assess FSA status and extirpation are not consistent, hindering site trend analysis, between-site comparisons and meta-analysis. We suggest that monitoring and management should be made more consistent and strengthened to boost FSA recovery.

1. Fish spawning aggregation sites

Certain places are critical for species to complete their life cycle. Many animals gather in specific places to breed, nest or rear their young, and return to these sites repeatedly for generations. Salmon return to their natal rivers for spawning (Ueda, 2013), turtles use the same beaches for nesting (Broderick et al., 2007) and some penguin species undertake long migrations to find the right place to breed and rear their young (Ancel et al., 2013). These sites are crucial to guarantee the persistence of animal populations. Fish Spawning Aggregation (FSA) sites, where conspecific fishes gather predictably and repeatedly for the purpose of reproduction, are examples of those special places (definition by Claydon, 2004; Domeier, 2012; see example of gathering in Fig. 1). Gatherings for spawning are common across a large diversity of marine fishes, from the tropics to temperate areas, including many species of commercial importance (Munro et al., 1990; Sadovy de Mitcheson and Colin, 2012).

There are two recognized types of FSAs, resident and transient. Resident spawners spawn frequently within their home range. For example, the western Atlantic wrasse (*Thalassoma bifasciatum*) spawns daily, year-round at the same locations with site fidelity that can last four generations (Warner, 1988). Transient spawners, generally with 'slow' life history traits (slow growth, large size, long lifespan, late maturity), migrate relatively large distances (over 100 km for Nassau grouper: *Epinephelus striatus*, Bolden, 2000) to spawn in aggregations during only a limited portion of the year (Choat, 2012; Claydon, 2004; Nemeth, 2012). In many FSAs multiple species gather to breed either simultaneously or sequentially (Kobara et al., 2013), constituting hotspots of high biodiversity, productivity and reproductive potential as well as sustaining complex food webs (Erisman et al., 2017b; Sadovy de Mitcheson and Colin, 2012).

2. The value of fish spawning aggregation sites

FSA sites are critical both in an ecological and conservation context. Because many fishes depend on these sites to produce the next generation, FSA sites are crucial for the persistence of fish populations and have a disproportionately large ecological and conservation value

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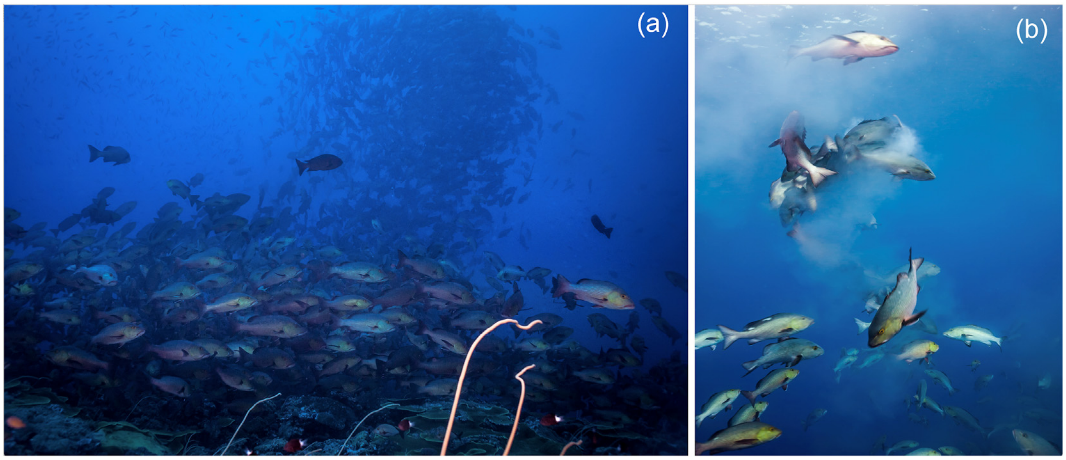

Fig. 1. Spawning aggregation of *Lutjanus bohar* at Shark City, Palau, during the spawning season of July 2016 (photos: Mark Priest). (a) High density of individuals at the staging area; (b) release of gametes during a spawning rush.

(Erisman et al., 2017b).

Due to their spatial and temporal predictability and the high catch rates at spawning sites, transient FSAs (the focus of this article) are the target of both commercial and small-scale fishers, who can complement their seasonal catch or focus their activity entirely on these brief events (Johannes, 1978; Sadovy de Mitcheson and Erisman, 2012). Aggregations are not only targeted for fish flesh, but also for ripe gonads, swim bladders, and live fish for capture-based aquaculture (Sadovy de Mitcheson and Erisman, 2012).

While most individuals of transient aggregating species live within relatively small home ranges during most of the year, they migrate long distances to spawn in dense FSAs. Therefore fishing FSAs removes breeding adults from large catchment areas from which the spawning individuals are drawn, amplifying impacts of FSA site depletion to regional stocks (Nemeth, 2012, 2009). Species that form transient FSAs and with 'slow' life history traits (larger adult body size and longer generation times) and stochastic recruitment, are particularly susceptible to overfishing (Nemeth, 2012). Once discovered by fishers, FSAs can be rapidly overfished (Sadovy de Mitcheson et al., 2008); particularly with increasing technical capacity that allows quicker transit to and from FSAs, increased catch efficiency, greater frozen storage volume, and access to export markets which can absorb the surge in catch (Russell et al., 2012).

As a result of fishing, many FSAs are now extirpated. An extirpated FSA is an aggregation that because of its current low abundance at spawning times is no longer recognizable as a FSA. A review of FSA status according to the Science and Conservation of Fish Aggregations database (SCRFA, March 2018) indicates that of the 423 sites with known status, 233 (55%) are in decline, and 37 (9%) are "gone" or extirpated (Fig. 2). Extirpated aggregations have been reported worldwide, from the Caribbean to the East China Sea, in tropical and temperate areas, evidencing the vulnerability of such sites and the paucity of management actions focused on this important phenomenon.

3. Managing FSAs

Effective management measures are urgently needed to protect exploited FSAs, halt their decline, and support fish populations (Erisman et al., 2017b; Johannes et al., 1999). FSAs can be managed using combinations of standard catch and effort controls and seasonal or spatial closures. The appropriate approach depends on intrinsic (biological) and extrinsic (fisheries and socio economic) factors of the specific species and its fishery (Grüss and Robinson, 2015; Sadovy de Mitcheson, 2016). Effort and catch limits have been suggested effective for species with 'fast' life history traits (fast growth, small size, short life, early maturity: Grüss and Robinson, 2015), when species have low vulnerability to fishing (i.e. catchability) and catch rates at FSA sites do not increase considerably (Grüss and Robinson, 2015; Robinson et al., 2015), or when socio-economic factors constrain the demand or the access to a particular fish species (Erisman et al., 2017b; Robinson et al., 2014).

Seasonal bans can be useful to prevent fishing during critical times (i.e. spawning seasons), particularly when the capacity to spatially protect FSAs is limited or their locations are uncertain. However, seasonal closures require tight enforcement to be effective (Sadovy de Mitcheson, 2016) and can be impractical in multi-species fisheries with unselective gear types, where the banned species can be caught as bycatch.

Spatial closures where fishing is not allowed are increasingly being adopted as a cost effective management measure to protect transient spawners and offer disproportionately large benefits to fisheries management and conservation compared to other forms of management (Erisman et al., 2017a). Spatial closures are particularly relevant for FSA management in small-scale fisheries where managers have limited capacity to monitor a large number of landing sites that are typical of these fisheries (Russell et al., 2012). Spawning site closures have also been adopted within large scale fisheries to support recovery of FSA-forming species in areas where catch and effort limits have proven insufficient such as the U.S. South Atlantic (Farmer et al., 2017). Small spatial closures to protect spawning are often supported by fishing communities that understand the benefits to their fisheries. Community support increases compliance, reduces enforcement costs and thus makes spatial closures a cost-effective measure (Fulton et al., 2018; Heyman, 2011; Waldie et al., 2016). Additionally, because FSA sites are commonly used by many species (either simultaneously or sequentially: Kobara et al., 2013) spatial protection benefits multiple species and thus makes an attractive tool for ecosystem management (Erisman et al., 2017b; Sadovy de Mitcheson, 2016).

To meet Aichi biodiversity targets and protect 10% of the marine environment by 2020, the declaration of marine protected areas has escalated during the last decade (Thomas et al., 2014). There has been a general call to increase focus on the protection of areas that prevent extraction (Costello and Ballantine, 2015), including FSA sites (Erisman et al., 2017b; Green et al., 2014; Johannes, 1998; Russell et al., 2012). For example, the Food and Agriculture Organization's Western Central Atlantic Fisheries Commission (FAO WECAFC) recently held the second meeting of the Spawning Aggregations Working Group (Western Central Atlantic Fishery Commission, 2019), which echoed an urgent, earlier call for FSA protection and management in the region (Western Central Atlantic Fishery Commission, 2014, 2019). Nonetheless, of a

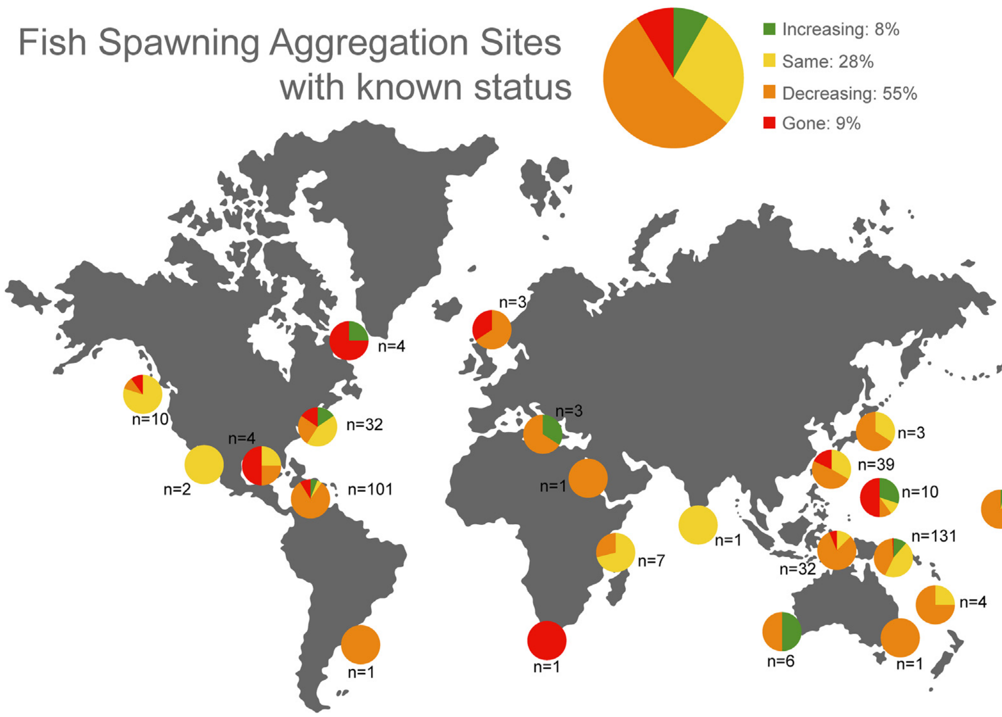

Fig. 2. Location of reported FSAs with known status (increasing, same, decreasing, gone) by region, n indicates number of reports. Pie chart on top right corner shows the overall frequency by status category. Data from SCRFA's database (http:scrfa.org) March 2018.

total of 864 recorded FSAs globally, only 154 (18%) are presently under some sort of spatial management and only 322 (37%) are under any form of management (SCRFA database, accessed March 2018).

A few countries have taken bold measures to protect FSA sites. Belize fully protects 11 multispecies spawning aggregations (Statutory Instrument No. 161 of 2003; Heyman, 2011) and Cayman Islands eight (Whaylen et al., 2007). The Bahamas, the United States, Bermuda, Palau and Pohnpei have also protected some of their FSAs as a fisheries management measure. Mexico and the US South Atlantic Fishery Management Council are the most recent to enact networks of protected areas that protect multi-species FSAs (Farmer et al., 2017; Fulton et al., 2018; SAFMC, 2016). Much of the success of these measures is based on strong governance structures, backed by consistent enforcement (Brownscombe et al., 2019; Symes, 2006).

4. Extirpated FSAs, a conservation dilemma

Given the limited budget available for conservation actions, the inclusion of extirpated FSA sites in spatial management plans represents a dilemma. Should these sites be included? Although recent FSA literature advocates for the protection of existing aggregation sites (Erisman et al., 2017b) and raised awareness of their alarming decline (Sadovy de Mitcheson et al., 2008), there is currently no guidance on how to proceed when these two issues meet.

While drafting a spatial management plan one of the authors faced this dilemma. After consulting experts in the area two diametrically opposite viewpoints emerged, which are commonplace in the FSA literature. Recent, mostly Caribbean-centric, literature presents an optimistic viewpoint "*FSAs can recover to provide measurable ecological and fisheries benefits*" (Erisman et al., 2017b). By contrast, the world's most well-recognized FSA conservation group, Science and Conservation of Fish Aggregations, is pessimistic in its prognosis "*What we do know is that once an aggregation has been so overfished that it ceases to form, there is no evidence that it will recover*" (SCRFA: http:scrfa.org accessed May 2019).

Here we present two alternative views and the rationale behind each. We offer analysis of these positions based on documented evidence of recovery in the field. We intend for this review to stimulate discussion and help managers to make informed decisions when facing this question during the drafting of spatial management plans in the future, and to support the strengthening of research, monitoring and management of FSA sites worldwide.

5. The case for protecting extirpated FSAs: predictable unique sites

Intrinsic environmental characteristics make FSA sites ideal locations to maximize reproductive success. Because of their predictability, such sites should be protected even if aggregations have ceased to form there. As the location of FSAs is temporally stable, with many spanning several decades and others nearly 100 years (Claro and Lindeman, 2003; Colin, 2012a; Craig, 1969), it is therefore likely that extirpated FSA sites will be "found again" or "reform" and become functional if surrounding fish populations are allowed to recover and extirpated sites are protected from fishing. Although it was originally thought spawning occurred at sites that maximize propagule dispersal away from shallow, predator-rich habitats (Choat, 2012), it is increasingly recognized that aggregation location and time of spawning can promote the retention of eggs and larvae close to the source (Donahue et al., 2015; Hamner and Largier, 2012; Karnauskas et al., 2011). Indeed, empirical measurements of grouper dispersal revealed 50% of larvae settled within 14 km of the source aggregation (Almany et al., 2013). Retention could increase survival rates of larvae by decreasing planktonic mortality due to long times expend in the plankton and transport to unsuitable areas (Burgess et al., 2015), increasing recruitment and reproductive success and potentially providing an evolutionary advantage (Domeier, 2012; Karnauskas et al., 2011).

In the western Atlantic, a large body of research indicates FSAs occur at predictable locations with particular geomorphology and oceanography that maximize retention (Karnauskas et al., 2011; Kobara and Heyman, 2010). Geomorphological characteristics of a site are the main variables predicting its suitability as a FSA in the region (Kobara et al., 2013; Kobara and Heyman, 2010). FSAs typically occur at distinctive bathymetric features. Fishes in the snapper grouper complex in the wider Caribbean tend to form multi-species aggregations in 20–60 m depth close to the inflection point (often promontories) along the edges of convex, steep shelf edge dropoffs adjacent to relatively deep water (Kobara et al., 2013; Kobara and Heyman, 2010). These patterns hold true for the Cayman Islands (Kobara and Heyman, 2008); Cuba (Claro and Lindeman, 2003); Florida (Gleason et al., 2011); Mexico (Heyman et al., 2014) and Belize (Kobara and Heyman, 2010). Further research on oceanographic modelling indicates reef promontories hosting FSAs produce eddies and upwelling fronts that retain larvae (Ezer et al., 2011; Karnauskas et al., 2011), supporting other modelling research that highlights the relevance of retention around FSA sites (Cherubin et al., 2011; Ezer et al., 2011; Kough et al., 2016) and observations of slow currents at the time of spawning (Colin, 1992; Nemeth et al., 2007). Currently the literature in this research area focuses in the wider Caribbean, making the pattern seem region specific. However, some studies in the Pacific have also illustrated geographic predictability of multi-species FSA formation, particularly at reef channels and passes with relatively strong tidal currents (Colin, 2012a; Hamner et al., 2007; Russell et al., 2014).

Given the temporal stability of FSAs, the predictability of sites based on their geomorphology and oceanographic patterns, and their potential evolutionary advantage, it is possible that sites were chosen due to these features. Initial selection of FSA sites could be guided by instinctual or genetically determined detection of local conditions or environmental cues (Domeier, 2012). If that is the case, there is a strong argument to suggest extirpated FSAs could recover at these sites, and they should be protected, as it has been suggested by some (Erisman et al., 2017b; Karnauskas et al., 2011; Russell et al., 2012).

6. The case against investing limited resources to protect extirpated FSAs: critical thresholds and loss of recovery potential

Extirpated FSAs might never re-form. Species with characteristic social behavior such as group mating may be at increased risk of extirpation under heavy exploitation due to Allee effects and depensatory dynamics (Sadovy de Mitcheson and Erisman, 2012). Under low densities critical mass that triggers normal courtship rituals and spawning may not be reached (Carolsfeld et al., 1997; Sadovy de Mitcheson, 2016). For example, in the Caribbean, Nassau grouper has not been reported to spawn in aggregations where they are found, but where their density is low such as eastern Florida and the Southern Caribbean (Colin, 2012a), and courtship behavior is less intense in regions where densities have been diminished (Colin, 1992).

If aggregations stop occurring temporarily, they might stop altogether because fish may no longer have the ability of finding the sites again. There are social aspects associated with FSA formation and persistence. Many fishes are observed arriving or leaving FSA sites in groups using consistent migratory corridors (Claro and Lindeman, 2003; Rhodes et al., 2012). Younger fish may learn migration routes, timing, and FSA locations from older individuals, perhaps aided by hormonal signaling (Mazeroll and Montgomery, 1998; Rose, 1993; Warner, 1990, 1988) or sound production by older migrators to guide new spawners to spawning aggregation sites (Rowell et al., 2015; Schärer et al., 2012, but see Bernard et al., 2016). Population reductions of older spawners may compromise group knowledge of migration routes and sites (Dodson, 1988) and ultimately if population levels fall below critical mass a population might cease migratory behavior entirely (Fagan et al., 2012; Foss-Grant et al., 2018). This could subsequently compromise recovery of extirpated FSAs, even if the regional population starts to recover (Sadovy de Mitcheson and Erisman, 2012).

Furthermore, the detrimental effects of fishing can be exacerbated by hyper-stability (Erisman et al., 2011; Hamilton et al., 2016), when catch rate is decoupled from fish abundance and remains stable, masking the decline of populations until collapse occurs (Hilborn and Walters, 2013). Unexpected, sudden population crashes are common for many species showing transient spawning behavior (Sadovy de Mitcheson, 2016), compromising decision making and complicating reactive fisheries management (Russell et al., 2012).

7. Evidence from field studies

Evidence of recovery of extirpated FSAs is scarce and it has never been summarized in the literature. Although a recent review indicates there is strong evidence of recovery of extirpated aggregations (Erisman et al., 2017b), most of the literature cited reported increases in abundances after protection, rather than recovery after extirpation has occurred, i.e., in Erisman's study, only three examples of recovery after true extirpation are presented (Beets and Friedlander, 1999; Burton et al., 2005; Kadison et al., 2009).

We gathered information on the location of extirpated FSAs and any subsequent recovery through literature review and personal communication with researchers (see full review table in Supplementary material). Here we define an extirpated FSA as one in which the abundance of individuals at spawning times is depressed to the point where no signs of spawning (sensu Colin et al., 2003) have been recorded in underwater surveys or no fish aggregations have been observed above water by fishers. Signs of spawning include both direct evidence (e.g. observations of gamete release) and indirect indications of spawning (e.g. courtship behavior, or color changes associated with spawning, Colin et al., 2003). This definition includes both extant sites that are severely depleted and sites where aggregations have completely disappeared and no longer form (Nemeth, 2009). These are mixed together in the literature and are difficult to pull apart in the field without exhaustive surveys. We define recovery as re-forming of the aggregation and an increasing trend over time in numbers of aggregating individuals, as in most cases there are no historical population estimates (baselines) from which to quantify recovery. Therefore our reports of recovery only include observations at aggregation sites during aggregation times, although in many regions lack of recovery of the aggregation is assumed when regional stock densities are low (e.g. Kadison et al., 2017). Our review collates 53 extirpated FSA sites of which 9 (17%) have demonstrated recovery (Fig. 3). However, none of the recovery examples reported returns to pre-harvest levels.

There is an obvious geographic bias in recovery, with all sites reported as recovered in the wider Caribbean or the northwest Atlantic (Fig. 3a). Recovery has been documented for a wide range of species and life history characteristics. Recovery has been reported for species with relatively 'fast' life history traits such as Red Hind (*Epinephelus guttatus*, Epinephelinae, with maximum length 76 cm and length at maturity 25 cm). Recovery has also been documented for larger bodied, 'slow' growing and presumably more vulnerable species such as the critically endangered Goliath grouper (*Epinephelus itajara*, Epinephelinae, with maximum length 250 cm and length at maturity 128 cm, Fig. 3b).

All extirpated FSAs that recovered were located in areas with stringent management: either effective spatial closures or moratoria (Fig. 3c). Strict management, however, does not ensure recovery. We found 13 (59%) of FSA sites under protection were still extirpated (Fig. 3c). This heterogeneity in response is exhibited even among sites under identical management regime for the same species. Cayman Islands, for example, introduced spatial closures in FSAs in 2003 and additional management restrictions in 2016. Recovery of extirpated FSAs for Nassau grouper has been reported in two sites (Cayman Brac and the east end of Grand Cayman) but is lacking in three sites (the east end of Little Cayman, the NE corner 12 Mile Bank and SW Grand Cayman; Grouper Moon Project, March 2018, Supplementary material).

Most (77%, $n = 41$) reports of extirpation were based on fishers' knowledge (Fig. 3d), while all reports of recovery were based on direct scientific observations (Fig. 3d). Direct observations of extirpation indicated lack of aggregation formation and either entire lack of

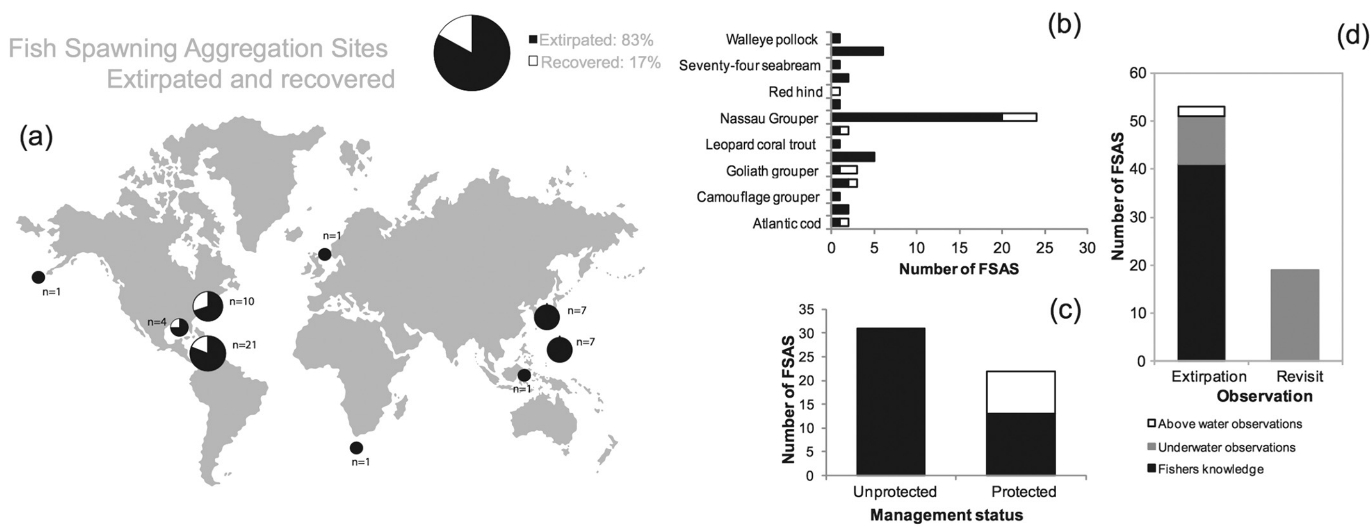

Fig. 3. (a) Location of extirpated and recovered FSAs by region. The pie charts are scaled to the number of sites per region (n). Pie chart on top right corner indicates overall frequency by category. (b) Status category by fish species; (c) Status category by management status: only sites with enforced spatial closures or moratoria were identified as protected; (d) Type of observation used to identify extirpation and recovery.

individuals (e.g. Paz and Grimshaw, 2001) or very low abundances (e.g. Burton et al., 2005). Reports from fishers were generally presented without much elaboration. For example, "disappeared" or "aggregation no longer forms" were common descriptions for extirpated sites (e.g. Sadovy, 1999; Sadovy and Eklund, 1999).

8. Discussion

The collected evidence suggests extirpated FSAs do have the potential to recover after spatial closures have been implemented, supporting the continued protection of these sites after extirpation, and their inclusion in future spatial management plans. Although recovery of extirpated sites was overwhelmingly related to the presence of strong management actions, not all protected aggregations exhibited recovery. Lack of recovery in protected FSAs could be associated with several factors, including uncertainty about the status of the FSA; low initial population levels; regional fishery collapse; insufficient recovery time; or inadequate monitoring.

The lack of consistency in the definition of extirpation and the evidence used to make that determination have made this analysis challenging. Fisher reported "extirpation" could imply that the aggregation has been depleted to the point where fishing the aggregation site is no longer profitable. It is also possible that some FSAs reported as extirpated may be severely depleted but not necessarily extirpated according to the strict definition of the term (i.e. spawning activity ceased). Underwater surveys can also provide equivocal information. In many species spawning is restricted to a short period of time, can vary from year to year, and may involve subtle shifts in location (Colin et al., 2003). As a result, in situ underwater monitoring might miss the formation of a depleted remnant aggregation. Several years of monitoring data conducted over several months, during the appropriate, lunar period may be needed to truly and accurately assess the status of a FSA. The use of a common methodology and terminology could permit better insight into this issue and produce a more accurate assessment of extirpation and recovery of sites in the future. Given this uncertainty, we cannot conclusively state that all the extirpated aggregations reported here had ceased to form, but we can state that recovery has been documented from depletion so severe that sites were thought, to all intents and purposes, to be extirpated by researchers in the field. It is possible that critical thresholds do play a role and recovery is only possible at sites with a remnant aggregation. More research in the area needs to be carried out to unequivocally answer this question. On a similar note, the magnitude of resource depletion likely differed among sites, which could delay recovery in locations where populations have been strongly reduced.

Species may adapt and change behaviors to overcome some of the limitations to successful spawning imposed by low densities. While Nassau grouper is well-known for group courtship and spawning, under low densities and at the edges of their distribution where FSAs are lacking Nassau are capable of pair spawning (Domeier, 2012; Sadovy and Eklund, 1999). Additionally, some fish populations can use alternative mechanisms to artificially boost their numbers. After extirpation of a Nassau grouper aggregation in St. Thomas, US Virgin Islands, Kadison et al. (2013) reported the recovery of the FSA through shifts in seasonality and location that allow the Nassau grouper to form mixed aggregations with Yellowfin grouper (*Mycteroperca venenosa*) possibly using them as surrogate aggregation members to trigger reproduction.

The wider population status of the aggregating species is also likely to influence recovery as rarely does a single aggregation represent an isolated fish stock. If the regional stock is unable to contribute aggregating adults, recovery will not happen. Some species stop aggregating for spawning at low regional densities (e.g. Domeier, 2012). It is also possible that under low regional densities the catchment areas of active FSAs expand to encompass the catchment areas of extirpated sites. Engaging all reproductive adults would ensure high enough densities to trigger courtship and spawning, at the expense of the recovery of additional FSAs. This could explain why sometimes fish seem to bypass a known extirpated aggregation en route to an active site (Stump et al., 2017, M Priest, pers. comm.). When the resource is overfished and regional densities are low, additional regulations to limit fishing mortality outside spatial closures are key to rebuild stocks (Erisman et al., 2017b). Considering the population abundance constraints of successful FSA formation and reproduction, knowledge of times and biomass outside of FSA locations can also provide insight into the likelihood of recovery of extirpated FSAs.

FSAs could continue being inactive because the time elapsed since protection has been insufficient to allow recovery. Empirical data suggest that large predators with 'slow' life history traits such as groupers and snappers can take a long time to recover to pre-harvested levels after full protection (Russ and Alcala, 2010; 20–40 years, Stockwell et al., 2009, but see Hamilton et al., 2011). Besides life history traits, population recovery will also depend on the size of, and connectivity to, the regional population, the degree of compensation or depensation (higher or lower than expected recruitment as adult abundance decreases) and environmental variability that influences recruitment success (Abesamis et al., 2014). This highlights the need of ensuring management is in place for the long term (Russell et al., 2012).

Finally, apparent lack of recovery could be merely associated to the absence of monitoring, and to the fact that the FSA site has not been visited again. A large amount of research has been done to develop methodologies to study and monitor spawning aggregations, including novel methods to track the movement of the adults using acoustic telemetry and identify migration routes residence times and fidelity to a FSA site (Colin, 2012b; Colin et al., 2003). However, monitoring FSAs is expensive and time consuming, and lacking in many regions (Colin, 2012b). Cooperative research and monitoring, involving fishers and other stakeholders can maximize FSA monitoring and management efficiency may facilitate detection of changes in FSA status over time (Heyman et al., 2019). Once a FSA is reported as gone, few efforts are devoted to assessing any change in status. Within our review, only seven sites that have failed to recover were visited again and made it into the literature, and three other sites were reported as still extirpated by personal communication (Supplementary material). It is possible that recovery has occurred in other sites but remains unrecorded and/or unreported. As fishers are routinely on the water, they can be trained to use simple yet standardized techniques (e.g. biological sampling and underwater video cameras) to document FSA status (Heyman et al., 2019). Advanced technologies can also be used to document and monitor FSAs, e.g. acoustic telemetry to document migration and site fidelity (Feeley et al., 2018; Biggs and Nemeth, 2016), and passive acoustics to monitor courtship and spawning sounds (e.g. Rowell et al., 2015; Schärer et al., 2012). Recording the status of FSAs and making that information widely available would advance the science of fish spawning aggregations. In this regard, contributing to the existing SCRFA database would be the easiest way of aiding progress in the field. Modifying SCRFA's database structure to include changes in FSA status along time would prove to be beneficial to acknowledge and track the dynamic nature of these sites and the processes of extirpation and recovery.

Recovery of extirpated FSAs has only been recorded in the wider Caribbean and northwest Atlantic. This geographic bias is likely associated to more abundant management and research in the region, as well as the presence of cooperative regional efforts for research, monitoring, conservation, management and communication in these areas (e.g. the FAO Western Central Atlantic Fisheries Commission). While management actions can trigger recovery, continuous monitoring allows the discovery of reactivated FSAs. Increased robust monitoring and management is needed to provide more positive management outcomes across the globe.

Our literature search revealed extirpated FSAs that demonstrated recovery were all subject to stringent management actions, and in many cases spatial protection. Spatial closures are often opposed by fishers because of their negative short-term economic impact as access to fishing grounds are reduced (Ovando et al., 2016). However, as extirpated FSA sites have little value to fishers, their protection should be met with minimal social conflict, at low cost, and compliance should be high, simplifying their inclusion into spatial management plans and reducing enforcement costs (Ban and Klein, 2009). Moreover, in some cases only a small spatial closure is needed to protect a large proportion of an aggregation's abundance (Waldie et al., 2016). While the objective of extirpated FSA protection is to promote FSA recovery, spatial closures will also provide the added benefit of protection to a number of other species that also inhabit the FSA site (Friedlander et al., 2017). To aid in the recovery of FSAs, it has also been recommended to intensify the study on the status of FSA sites, develop regional fisheries management plans that recognize the high mobility of the fisheries resources and engage fishers more directly in FSA conservation and management (Western Central Atlantic Fishery Commission, 2019).

The historical exploitation and current rate of decline of FSAs highlights our inability to effectively manage and conserve these ecologically crucial events. While extirpated FSAs have been reported worldwide, little attention has been paid to their recovery potential after extirpation as in many cases they have been thought of as 'gone for good'. Our literature review reveals a number of examples of extirpated FSAs that demonstrate recovery after strict management implementation, providing a promising opportunity for cost effective safeguarding and rebuilding fisheries stocks. However, 59% protected FSAs did not exhibit recovery and our understanding of the behavioral and social mechanisms involved in the processes of aggregating and spawning is currently limited. Although some work indicates these processes can be modulated by density-dependent factors (e.g. Kadison et al., 2013; Sadovy and Eklund, 1999), greater research in this area is needed, and might be the key to understanding recovery rates and setting realistic expectations after protection of extirpated sites is implemented.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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