Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation

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Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation

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Running title: Management of fish spawning aggregations

Abstract

Marine ecosystem management has traditionally been divided between fisheries management and biodiversity conservation approaches, and the merging of these disparate agendas has proven difficult. Here we offer a pathway that can unite fishers, scientists, resource managers, and conservationists towards a single vision for some areas of the ocean where small investments in management can offer disproportionately large benefits to fisheries and biodiversity conservation. Specifically, this provides a series of evidenced-based arguments that support an urgent need to recognize fish spawning aggregations (FSAs) as a focal point for fisheries management and conservation on a global scale, with a particular emphasis placed on the protection of multi-species FSA sites. We illustrate that these sites serve as productivity hotspots – small areas of the ocean that are dictated by the interactions between physical forces and geomorphology, attract multiple species to reproduce in large numbers, and support food web dynamics, ecosystem health, and robust fisheries. FSAs are comparable in vulnerability, importance, and magnificence to breeding aggregations of seabirds, sea turtles, and whales yet they receive insufficient attention and are declining worldwide. Numerous case studies confirm that protected aggregations do recover to benefit fisheries through increases in fish biomass, catch rates, and larval recruitment at fished sites. The small size and spatio-temporal predictability of FSAs allow monitoring, assessment, and enforcement to be scaled down while benefits of protection scale up to entire populations. Fishers intuitively understand the linkages between protecting FSAs and healthy fisheries and thus tend to support their protection.

Key words: fish spawning aggregations, fisheries management, marine conservation, marine productivity hotspots, physical-biological coupling, fisheries co-management

Introduction: Mammals, birds and reptiles; why not fishes?

Many animals in both the terrestrial and marine environment undergo large migrations to aggregate en mass at specific locations and during discrete, predictable times (Bauer and Hoye 2014). Breeding migrations of wildebeests and other land megafauna in Africa, the gray whales in the Eastern Pacific, the penguins of Antarctica, and all species of sea turtles are globally iconic, such that protection of these critical life history processes are widely acknowledged as a high priority in species conservation and as focal points for coordinated multi-agency management actions (Martin *et al.* 2007; Wilcove and Wikelski 2008). In some cases, these are areas where multiple species gather to breed either simultaneously or at different times of the year. Such locations are often labeled as temporary "hotspots" or places of periodic high biodiversity, productivity, and vulnerability whose protection can yield disproportionately high benefits for conservation (Myers *et al*. 2000; Roberts *et al*. 2002).

This reproductive phenomenon is also critical to the resilience of many populations of marine fishes and the sustainability of many fisheries. Fish spawning aggregation (FSAs; Figure 1) are temporary gatherings of large numbers of conspecific fish that form for the sole purpose of reproduction (Domeier 2012). FSAs are critical life-cycle events to those species that engage in such behavior, often representing the only opportunities when fish within the population reproduce, and thus comprising the major source of reproductive output (Sadovy de Mitcheson and Colin 2012). FSAs are predictable in time and space with locations and cycles dictated by the adaptation of various species to interactions between geomorphology, habitat features, and ocean dynamics that generate complex, localized, and ephemeral linkages through ocean food webs and attract top predators and mega-planktivores (Heyman *et al.* 2001; Ezer *et al.* 2011; Pittman and McAlpine 2003; Petitgas *et al.* 2010). Large, predictable concentrations of fish are also attractive sites for fishing, which explains why FSAs support highly productive commercial (both industrial and small-scale), recreational, and subsistence fisheries all over the world, but overexploitation has contributed to rapid stock depletions and localized extirpations (Sadovy and Domeier 2005; Sadovy *et al.* 2008).

Fishes rank only below birds in terms of the amount of published scientific information available on breeding migrations and aggregations (Bauer *et al*. 2009), and many fish aggregations are equivalent in scale, spectacle, vulnerability and importance to the most well known wildlife aggregations. For these reasons, FSAs have been recognized in principle as focal points for fisheries and marine management in some regions (Green *et al.* 2014). With the exception of salmonids (Elison *et al.* 2014; ADF&G 2015), however, there has been little directed management of spawning aggregations (Sadovy de Mitcheson *et al.* 2008). Many sites have not been documented and of those that have, few are managed or protected (Russell *et al.* 2014). Management focus on FSAs has been hindered in part by the belief that conventional management (e.g. size or catch limits) obviates the need for specific attention to aggregation sites (Tobin *et al.* 2013).

In a crowded world with declining financial and natural resources, investments in marine conservation and fisheries management must be efficient and enforceable and provide large measurable benefits to both resources and stakeholders. Here we argue that focusing protection on these predictable, productive and critical life-cycle events can provide large, rapid, and measurable benefits for both biodiversity conservation and sustainable fisheries management in a manner that is logistically feasible, economically practical, and garners broad consensus support. The high reproductive potential of FSA sites, particularly those where multiple species aggregate, means that effective protection from exploitation can help rebuild depleted local populations and the fisheries they support (Nemeth 2005; Pondella and Allen 2008; Luckhurst and Trott 2009; Aburto-Oropeza *et al*. 2011). Numerous case studies exist that demonstrate the effectiveness and enormous value to local communities of small investments in FSA protection (Hamilton *et al.* 2011; Aburto-Oropeza *et al.* 2011; Heyman and Granados-Dieseldorff 2012). While FSA protection is not a panacea for all the challenges facing the worlds' oceans or the shortcomings of traditional fisheries management, nor does it promise to solve all the challenges facing marine protected areas and marine conservation, it provides a clear pathway to integrate biodiversity conservation and fisheries management with the potential for strong support by fishers and other stakeholders.

Hotspots of marine productivity that support ecosystem health

FSAs are most studied on coral reefs, but they have been identified within nearly every marine eco-region and habitat type, ranging from shallow tropical coral reefs, subtropical estuaries, and temperate offshore banks to seamounts in the deep ocean. In the most comprehensive compilation of spawning aggregation records to date, 906 reports of FSAs have been documented across all 5 oceans, 53 countries, 44 families, and more than 300 species of fishes (Russell *et al.* 2014; SCRFA 2014) (Figure 2). Since the database is largely focused on tropical reef fishes, it likely omits the majority of known aggregations throughout the globe, particularly those in non-reef and non-tropical habitats. For example, a number of triggerfish species (Balistidae) form nesting aggregations over sandy bottoms adjacent to reefs (Erisman *et al.* 2010), and pelagic billfishes (e.g. Black Marlin: *Istiompax indica*, Istiophoridae) and mackerels (e.g. Monterey Spanish Mackerel: *Scomberomorus concolor*, Scombridae) also aggregate to spawn in a highly predictable manner (Domeier and Speare 2012; Erisman *et al.*

2015). Therefore, FSAs are broadly meaningful across taxa and global geography despite being under-documented.

Many FSA sites harbor aggregations of several or even tens of species (Sedberry *et al.* 2006; Heyman and Kjerfve 2008; Sadovy de Mitcheson *et al.* 2008; Kobara *et al.* 2013; Claydon *et al.* 2014) that gather in the same location at different times of the year according to specific seasonal, lunar, tidal, and diel cycles. As one notable example, Kobara and Heyman (2010) showed that all fourteen known Nassau Grouper (*Epinephelus striatus*, Epinephelidae) spawning sites in Belize harbor multi-species FSAs. A recent review of 108 transient FSA sites (Kobara *et al.* 2013) in the wider Caribbean illustrated that most sites in that region harbor aggregations of multiple species. Individual sites harbor as many as 24 species from 9 different families of fishes during different specific lunar phases within certain months. The majority of Caribbean multispecies FSA sites listed above occur at seaward projections of undersea shelf edges or reef promontories, while in other tropical regions such as the Indo-Pacific they are often associated with promontories and reef channels (Nemeth 2009, 2012; Colin 2012; Kobara et al., 2013). Synchronization of spawning with environmental cues has been documented elsewhere for aggregations that occur in lagoons and estuaries, temperate and coral reefs, and offshore habitats, although the temporal and spatial scales vary by location and species (Pankhurst 1988; Domeier and Speare 2012; Erisman *et al*. 2012; Russell *et al.* 2014; Zemeckis *et al*. 2014).

The spatio-temporal predictability and persistence of FSAs is a product of the life history strategies of fishes evolving in response to the geomorphological characteristics and the physical processes that occur at these locations only during certain periods (Choat 2012; Colin 2012) in order to maximize reproductive fitness (Molloy *et al.* 2012). Ocean currents interact with distinct habitat features (e.g., promontories, seamounts, channels) to generate intermittent upwellings and localized gyres, which retain massive volumes of nutrients and spawned eggs (Shcherbina *et al.* 2008; Karnauskas *et al.* 2011; Ezer *et al.* 2011). This scenario creates concentrated hotspots of primary and secondary productivity that cascade into diverse coastal and pelagic food webs (Morato *et al.* 2010; Wingfield *et al.* 2010). FSAs create "egg boons", immense but temporary concentrations of highly nutritious fatty acids, molecules that are especially important for the health of nearly all marine animals and the health of whole marine ecosystems. Egg boons represent a major trophic pathway that creates linkages and feedbacks between organisms and environments across all trophic levels and among the few pathways that recycle essential nutrients from apex predators to the lower trophic levels (Fuiman *et al.* 2014) (Figure 3). These events are comparable to the synchronized mass spawning of corals shown to create pulses of nutrients that are rapidly assimilated into local food webs (Guest 2008). The fatty acids and other nutrients produced en masse by spawning aggregations represent a cross-ecosystem spatial subsidy that can be advected to various microhabitats (e.g. intertidal and subtidal) and utilized by a variety of organisms (Hamner *et al.* 2007; Fox *et al.* 2014). Similarly, aggregations of spawning fish create biogeochemical "hot moments" that supply up to an order of magnitude more nitrogen and phosphorus than baseline levels on coral reefs, and overfishing of aggregations may reduce nutrient supplies by aggregating fish by up to 87% (Archer *et al*. 2014). Fish also forage and are preyed upon throughout their migrations to, from, and at aggregation sites thereby establishing transport and trophic interactions with resident communities, mediating the diversity and stability of ecological communities, and fostering ecosystem connectivity (Nemeth 2009; McCauley *et al.* 2012; Bauer and Hoye 2014).

The ephemeral concentration of food resources at FSA sites are also associated with timed migrations by a wide diversity of large, migratory predators (e.g. sharks, billfishes, dolphins, and tunas) that feed on aggregating fishes (Nemeth *et al*. 2010; Graham and Castellanos 2012) and mega-planktivores (e.g. Whale Sharks: *Rhincodon typus*, Rhincodontidae; and Manta Rays: *Manta birostris*, Myliobatidae) that aggregate to feed on the spawned eggs (Heyman *et al.* 2001; Hoffmayer *et al.* 2007; Nemeth 2009; Hartup *et al*. 2013; Kobara *et al.* 2013). Ecological benefits result from enhanced retention and survivorship of larvae (Ezer *et al.* 2011; Karnauskas *et al.* 2011), the dispersal of nutritious eggs, and the potential spillover of these rich sources of productivity into adjacent areas (Morato *et al.* 2010; Cherubin *et al.* 2011; Harrison *et al.* 2012; Almany *et al.* 2013; Kobara *et al.* 2013).

Protecting multi-species FSAs can have umbrella effects that support complex food webs and populations of apex predators necessary for maintaining healthy ecosystem function and structure (Pauly *et al.* 1998; Heithaus *et al.* 2008). The loss of aggregations, which in many tropical and temperate reefs is equated with the loss of apex predators such as groupers (Epinephelidae), snappers (Lutjanidae), and other piscivores (Pondella and Allen 2008; Choat 2012), has contributed to global declines in ecosystem health (Jackson *et al.* 2001; Burke and Maidens 2004; Estes *et al*. 2011). Similarly, the loss of forage fishes (e.g. herrings and menhaden) that migrate and aggregate to spawn in temperate regions may impact many kinds of predators, including fishes, seabirds, marine mammals, and squid (Pikitch *et al.* 2014). Protected FSA sites, particularly those involving apex predators or forage fishes, can therefore be used as indicators of healthy marine ecosystems that serve as baselines to assess the status of other areas (Sadovy and Domeier 2005). Likewise, these sites create lucrative opportunities for eco-tourism in the tropics and subtropics, in which aggregations of reef fishes, sharks, dolphins, and manta rays help generate hundreds of millions of dollars annually for the recreational diving industry from divers who prefer large animals and healthy reefs (Williams and Polunin 2000; Rudd and

Tupper 2002; Heyman *et al.* 2010; Vianna *et al.* 2012).

Globally important and threatened

FSAs currently support or once supported some of the most important and productive commercial, recreational, and subsistence fisheries across the globe, and multi-species FSAs sites often represent the most important regional fishing grounds (Sadovy de Mitcheson and Erisman 2012). Notable examples from commercial fisheries include Atlantic Cod (*Gadus morhua*, Gadidae), groupers and snappers from the Live Reef Fish Food Trade in Southeast Asia, Orange Roughy (*Hoplostethus atlanticus*, Trachichthyidae) fisheries at seamounts off New Zealand and Namibia, and salmon fisheries in the U.S. Pacific Northwest. Other commercially important species that migrate and aggregate to spawn include the Alaska Pollock (*Theragra chalcogramma*, Gadidae) and the Atlantic Herring (*Clupea harengus*, Clupeidae), which both contribute several million tons and tens of billions of dollars annually to global fisheries production (Dragesund *et al.* 1997; FAO 2014; Shida *et al.* 2014). The high abundance of fish present at aggregations during predictable periods and at known locations, which can range from tens to even millions of individuals confined to small areas, generates the ideal scenario for fishers; large catches and sizeable earnings with minimal effort (Sadovy and Domeier 2005; Erisman *et al.* 2012). Yet these same characteristics that can significantly elevate catchability render aggregations particularly vulnerable to overfishing, as targeted harvesting of fish from an aggregation may remove a large proportion of an entire population (Sadovy *et al.* 2008; Sadovy de Mitcheson and Erisman 2012). Since FSAs may attract the majority of breeding fish from a radius of 10s to 100s of kilometers, the extirpation of fish from the spawning site effectively removes the species from a much larger surrounding area (Nemeth 2009; Erisman *et al.* 2012).

For most species that form FSAs, it is the only time and place that they reproduce, so harvesting fish from these sites can rapidly and dramatically reduce the reproductive capacity of a stock by removing future egg production (Sadovy de Mitcheson and Erisman 2012; Dean *et al.* 2012; Erisman *et al.* 2014).

Exploitation of aggregated fish may directly or indirectly compromise reproductive function, reproductive output, and fertilization rates by interfering with the mating process (Petersen *et al.* 2001; Rowe and Hutchings 2003; Alonzo and Mangel 2004; Rowe *et al.* 2008; Erisman *et al.* 2007; Rose et al. 2008). This occurs via disruptions of complex courtship rituals and mate encounter rates, impairment of visual or auditory communication, alterations of operational sex ratios and social structure during mating (Rowe and Hutchings 2003; Rowe *et al.* 2004; Muñoz *et al.* 2010; Slabbekoorn *et al.* 2010); damage to critical spawning habitat by destructive fishing gear (Koslow *et al*. 2001; Coleman *et al.* 2000; Koenig *et al.* 2000; Kaiser *et al.* 2002); and stress-caused changes in hormone levels, fecundity, egg size and development, and egg survival (Morgan *et al.* 1999).

This type of vulnerability to fishing is an important characteristic of FSAs that can lead to loss of the functional integrity of marine ecosystems as a result of the mass removal of key carnivores (Choat 2012) and essential nutrients (e.g. fatty acids via eggs) from the food web (Heithaus *et al.* 2008; Fuiman *et al.* 2014). Collectively, these factors explain why the overfishing of aggregations has often been associated with rapid declines in fish stocks, fishery collapses, ecosystem imbalances, the complete extirpation of aggregations from specific areas or regions, and in the most extreme cases, the near extinction of entire species (Cisneros-Mata *et al.* 1995; Hutchings 1996; Sala *et al.* 2001; Erisman *et al.* 2011).

Numerous families of fishes (e.g. Epinephelidae, Lutjanidae, Sciaenidae, Siganidae, Scombridae, Channidae, Polyprionidae, Gadidae) include species that form spawning aggregations that have undergone severe declines (Sadovy de Mitcheson and Erisman 2012; Russell *et al.* 2012) in response to overfishing, and many are classified as threatened or endangered by the International Union for the Conservation of Nature (IUCN), the Convention on the International Trade in Endangered Species (CITES), or the Food and Agriculture Organization of the United Nations (FAO). Possibly the most well known example of a remarkable species and fishery collapse related to FSAs is the Nassau Grouper. Once the most important Caribbean finfish fishery, it is now considered endangered by IUCN and being considered for listing as Threatened under the U.S. Endangered Species Act (ESA) after decades of overfishing resulted in the disappearance of the majority of FSAs throughout its geographic range (Sadovy and Eklund 1999; Sadovy de Mitcheson *et al*. 2013). Twenty of 163 species (12%) of groupers risk extinction if current fishing trends continue (Sadovy de Mitcheson *et al.* 2013), and a comparative analysis among grouper species of known reproductive strategy demonstrated that spawning aggregation formation is associated with higher extinction risk (Sadovy de Mitcheson and Erisman 2012).

Many large-bodied sciaenid (Sciaenidae) fishes have experienced similar declines due to the overfishing of their spawning aggregations. In the Gulf of California, Mexico, the annual harvest of thousands of tons of Totoaba (*Totoaba macdonaldi,* Sciaenidae), the world's largest croaker, at its only spawning site from the 1920s to the 1950s resulted in its near extinction and the dubious distinction as the first marine fish listed on CITES as critically endangered (Cisneros Mata *et al.* 1995). The fishery for Totoaba has been replaced in recent years in the same region by a massive aggregation fishery for the Gulf Corvina (*Cynoscion othonopterus,* Sciaenidae), which may collapse if measures to reduce fishing pressure are not enacted soon (Erisman *et al.*

2012; Erisman *et al.* 2014). Severe declines and regional extirpations of spawning aggregations in other large sciaenids include the Giant Yellow Croaker (*Bahaba taipingensis,* Sciaenidae) in China (Cheung and Sadovy 2003), the White Seabass (*Atractoscion nobilis*, Sciaenidae) in California USA (Pondella and Allen 2008), and the Blackspotted Croaker (*Protonibea diacanthus*, Sciaenidae) in Australia (Phelan 2008).

Conservation and management status

The most recent and comprehensive report on the global status of marine fish aggregations revealed that 52% of the documented aggregations have not been assessed, less than 35% of FSAs are protected by any form of management (e.g. inclusion within marine protected areas, seasonal protection, harvest controls, total moratoria), and only about 25% have some form of monitoring in place (Russell *et al.* 2014). Among those FSAs in the database that have been evaluated, 53% are in decline and 10% have disappeared altogether. In congruence with much of the scientific literature on FSAs, the report is biased towards species that inhabit coral reefs (e.g. groupers and snappers). Greater representation by species and aggregations from higher latitudes and other ecosystems are needed to provide a more balanced understanding of FSAs and their fisheries (Russell *et al.* 2014).

While few FSAs are managed or protected, they are frequently recognized directly or indirectly within the language of national and multi-national management strategies. It is common practice that FSAs, or at least important spawning grounds of fishes, are mentioned in the language of marine spatial planning documents of states, federal fisheries agencies, and NGOs when setting criteria and designing marine reserves (Sale *et al.* 2004; Green *et al.* 2014). For example, in 1996, the US Magnuson–Stevens Act mandated the identification of essential fish habitat (EFH) for specific target fishery species and defined EFH as ‘those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity (DOC 1997). The purpose of the Act was to create a national program for the conservation and management of US fishery resources to prevent overfishing, to rebuild fish stocks, insure conservation and facilitate long-term protection of essential fish habitats that would realize the full potential of the Nation's fishery resources. Fishery management councils were tasked with identifying Habitat Areas of Particular Concern and minimizing adverse effects of fishing on EFH. The Caribbean Fishery Management Council and the South Atlantic Fisheries Management Council are pursuing networks of reserves that protect multi-species spawning aggregations as an important strategy for managing data-poor reef species (Parma *et al.* 2014; SAFMC 2015).

A recent reform of the European Union’s Common Fisheries Policy in line with the Marine Strategy Framework Directive considers a healthy population size structure and retention of full reproductive capacity to be indicative of Good Environmental Status. An ambitious target of ending overfishing by 2020 achieved through regulations that result in fishing at levels that do not endanger the reproduction of stocks while providing high long-term yields. A renewed focus on the protection of the functional role played by FSAs should be a step toward meeting the goal of sustainable fishing through maintenance of fish population size at maximum productivity. In the United Kingdom, the Marine Management Organization is evaluating sector-based marine spatial planning including a ‘core fishing grounds’ approach in which fishing might be given priority consideration over other activities (MMO 2014).

FSAs match well with the criteria set by several international conservation agendas and calls to action. For example, FSAs are prime candidates for designation as Ecologically and Biologically Significant Areas (EBSAs) under the Convention on Biological Diversity, because they fulfill all essential criteria: uniqueness or rarity, importance for life history stages, importance for declining species or habitats, biological productivity, biological diversity, and naturalness. Likewise, FSAs are mentioned in Article 6.8 of the General Principles of the FAO Code of Conduct for Responsible Fisheries that calls for "all critical fisheries habitats…such as spawning areas, should be protected and rehabilitated as far as possible and where necessary" (FAO 1995). At the 2004 IUCN World Conservation Congress, (Rec 3.100, p. 115) governments were urged to "establish sustainable management programmes for sustaining and protecting reef fish and their spawning aggregations…", and international and fisheries management organizations and non-governmental organizations were requested "to take action to promote and facilitate the conservation and management of fish spawning aggregations…". The International Coral Reef Initiative (ICRI) provided similar recommendations in 2006 and has since encouraged ICRI Operational Networks and Members, as well as inter-governmental, governmental and non-governmental organizations and the private sector, to contribute, as appropriate, to the implementation of these recommendations through appropriate projects, initiatives and campaigns that promote the conservation and sustainable management of reef fish spawning aggregations. In 2014, ICRI formally endorsed the latest global status report of fish aggregations produced by Science and Conservation of Fish Aggregations (Russell *et al.* 2014). Despite the fact that some species of aggregating fishes do migrate large distances that span international borders (e.g. Nassau and goliath groupers), none are currently recognized by the Convention on the Conservation of Migratory Species (CMS), which currently only lists a few species of sharks, rays, sawfishes (Pristidae), sturgeons (Acipenseridae) and related species, and the European Eel (*Anguilla Anguilla*, Anguillidae). In a recent statement that illustrates the growing recognition of FSA monitoring and protection, the FAO Western Central Atlantic

Fisheries Commission (FAO WCAFC 2014) adopted recommendations for grouper and snapper spawning aggregation protection throughout region.

Protection can be practical, generate measurable benefits, and build consensus support

The tendency of FSAs to form at spatially discrete locations at predictable times means that monitoring, enforcement, and research can all be scaled down and streamlined accordingly (Heyman 2014). A large proportion of the reproductive population for many wide-ranging species become concentrated at FSAs, providing a unique opportunity to rapidly and efficiently evaluate many aspects of fish stocks that would otherwise be dispersed over a much larger geographic area (Molloy *et al.* 2010; Heppell *et al.* 2012). Surveys and monitoring of the demographics, spawning activity and reproductive output of aggregations can be done more efficiently and quickly combined with other biological and life history parameters to assess stock size and condition (Jennings *et al.* 1996). Such efforts are facilitated by decades of research and protocols that are available on how to survey, assess, and manage FSAs and their fisheries (Colin *et al*. 2003; Heyman *et al.* 2004). Moreover, the rise of advanced, cost-effective technologies such as bioacoustics, biotelemetry, sonar, and remote and autonomous underwater vehicles now allow us to effectively monitor aggregations more accurately and remotely than in the past (Kobara and Heyman 2010; Dean *et al*. 2012; Heppell *et al.* 2012; Rowell *et al.* 2012; Parsons *et al*. 2013).

A focus on spawning aggregation sites and periods for conservation and management purposes epitomizes the original “hotspots” concept, which describes small areas that hold an abundance of rare or endemic organisms and are threatened by human activities, but also places importance on productivity for the benefit of fisheries. Assigning these events and sites, particularly those associated with multi-species aggregations, as priorities for investment will help protect the maximum diversity at minimum cost (Myers *et al.* 2000; Reid *et al.* 1998). The small area of spawning grounds compared to the area over which fish migrate and establish home ranges, creates the most “bang for the buck”, in that successful protection of spawning can scale up to the level of the entire population (Nemeth 2009; Nemeth 2012). Therefore, the management of small FSAs can help replenish fish populations at much larger scales that benefit stakeholders and are congruent with successful conservation practice. The high degree of geomorphological similarity among FSAs within regions also facilitates the designation of locations for seasonal or permanent marine reserves that have the potential to support a high diversity and biomass of fishes (Boomhower *et al.* 2010; Kobara and Heyman 2010; Kobara *et al.* 2013). In fact, scientists, fishers, and managers in Quintana Roo, Mexico and the U.S. South Atlantic are recognizing the geomorphic verisimilitude among multi-species spawning sites and their value for fisheries productivity and biodiversity conservation. Based on this recognition, collaborative efforts are underway to use this information to design and designate new marine managed areas in these regions (Heyman *et al.* 2014; Fulton *et al.* 2014; SAFMC 2015).

FSAs can show signs of recovery soon after protection due to the naturally high productivity of the sites where they form. Species that have been depleted can show marked increases in recruitment, biomass and size within a few years of protection and some that had been extirpated return and form aggregations once again (Beets and Freidlander 1999; Burton *et al*. 2005; Nemeth 2005; Luckhurst and Trott 2009; Aburto-Oropeza *et al.* 2011; Heppell *et al.* 2012). These hotspots of primary and secondary productivity serve as sources of regional ecosystem enhancement and resilience that seed replenishment and recovery (Adger *et al.* 2005).

Protected FSAs provide direct ecological benefits to conservation through the buildup of fish biomass at the protected site (Aburto-Oropeza *et al.* 2011). This translates to direct economic benefits to fisheries through the measurable spillover of adults (via movement) or the settlement of larvae into exploited areas (Harrison *et al*. 2012; Almany *et al.* 2013), increases in catch rate and the size of harvested fish (Nemeth *et al.* 2012). Prominent examples of recovery include White Seabass and Giant Sea Bass (*Stereolepis gigas*, Polyprionidae) in California (Pondella and Allen 2008), groupers and snappers in the Caribbean (Beets and Friedlander 1999; Heyman 2011; Kadison *et al.* 2009; Nemeth 2009; Burton *et al.* 2005; Heppell *et al.* 2012), Indo-Pacific (Hamilton *et al.* 2011), and several species of aggregating reef fishes in the Gulf of California, Mexico (Aburto-Oropeza *et al.* 2011).

Synergy between conservationists and fishers is rare but greatly enhances compliance and self-enforcement, and thus overcomes a prime barrier to successful fisheries management and conservation efforts (Hilborn *et al.* 2005). Fishers have known for centuries where and when aggregations form (Johannes 1978), as they have been critical sources of food security and their economic livelihoods. In fact, most of the biological and fisheries information that scientists and managers have acquired on FSAs has been acquired from fishers (Johannes *et al*. 1999; Hamilton *et al.* 2011). Fishers intuitively recognize spawning aggregations as critical to the perpetuity of their resource, which often increases their willingness to focus management on them in order to sustain their fishery (Heyman and Granados-Dieseldorff 2012; Hamilton *et al.* 2012). The small size of FSAs in relation to the entire population range also means limited restrictions for fishers, which reduces conflict since they minimize reductions in open fishing grounds or time closures for fishing (Heppell *et al*. 2012).

Some of the most successful population and fishery recoveries have occurred in areas with strong community support and participation in the monitoring and management of aggregations (Hamilton *et al.* 2011; Aburto Oropeza *et al.* 2011; Granados-Dieseldorff *et al.* 2013). Several of these have involved the inclusion of spawning aggregations within marine protected areas, providing examples in which some of the largest obstacle to successful marine reserves (e.g. opposition and noncompliance by fishers) were overcome through community participation (Berkes 2007; Karras and Agar 2009; Aburto-Oropeza *et al.* 2011; Hamilton *et al.* 2012; Edgar *et al.* 2014). In other regions, fishers have supported temporary fishing or area closures that protected spawning but still allowed them to harvest other species during those periods or at those sites. For example, the Coastal Conservation Association (CCA), a national association representing recreational anglers in the United States, recognized the need to protect spawning aggregations of Speckled Hind (*Epinephelus drummondhayi*, Epinephelidae) and Warsaw Grouper (*Hyporthodus nigritus*, Epinephelidae) in the South Atlantic. CCA supported seasonal fishing closures during the spawning seasons and seasonal area closures for those species at known aggregation sites that would allow them to harvest other species at those sites (SAFMC 2015). Similarly, commercial and subsistence fishers in the Upper Gulf of California, Mexico, are opposed to the total area closure of the estuaries of the Colorado River Delta due to its historical importance to regional fisheries and food security. However, they support daily closures during the peak spawning periods for the Gulf Corvina to allow fish to spawn undisturbed, enhance reproductive output, and maintain economically sustainable yields (MacCall *et al.* 2011). After the collapse of the Nassau Grouper fishery in the United States Virgin Islands (Olsen and LaPlace 1978), fishers supported the establishment of a seasonal spawning closure of Red Hind (*Epinephelus guttatus*, Epinephelidae) to protect this species and its fishery from a similar fate (Beets and Friedlander 1992).

Conclusions

Breeding aggregations are widespread among animals and are the focal points for conservation and management of many terrestrial and marine species. While an appreciation of the importance of fish breeding habitat within the language of fisheries management and marine conservation agendas has grown in recent years, implementation of measures specifically tasked with protecting FSAs have not followed at a similar pace. We contend that FSAs should be a focal point for marine conservation and fisheries management on a global scale, with a particular emphasis placed on the protection of FSA sites that house aggregations of multiple species. These sites are geographically and taxonomically widespread, are crucial to the reproductive success and perpetuity of stocks and species that engage in this behavior, support ecosystem food web dynamics and other aspects of ecosystem health, and represent important components of commercial, recreational, and subsistence fisheries wherever they occur. The numerous, extensive declines in FSAs and aggregating species from many areas of the world suggest that protection is urgently needed, and there is strong empirical evidence that FSAs can recover to provide measurable ecological and fisheries benefits. Most importantly, the concept is intuitive to fishers, managers, conservations, and the general public and the measures necessary for effective monitoring, assessment, and management are often relatively practical in scope and scale. Therefore, protection of FSAs offers the rare opportunity to merge agendas and support of fisheries and conservation sectors.

The primary purpose of this article was to present a series of arguments as to why FSAs must be protected and not to review or assess the specific management options to achieve this goal as this has been done elsewhere (see Sadovy and Domeier 2005; Russell *et al.* 2012; Grüss *et al.* 2014). However, a brief discussion of this topic is warranted as a means for stimulating debate on how to move forward in implementing the wider protection of FSAs. The reproductive biology of an exploited species plays an important role in the main concepts underlying the assessment and management of any fishery (Lowerre-Barbieri 2009). Similar to other fisheries and marine conservation issues, effective management of FSAs requires an understanding of the dynamics of the aggregations themselves (e.g. timing, duration, spatial distribution, mating behavior and life history of fished species) and how they interact with fishing activities in time and space (e.g., exploitation level on aggregations, catchability) to set the proper regulations (Coleman *et al.* 2004; Russell *et al*. 2012; Sadovy de Mitcheson and Erisman 2012; Grüss and Robinson 2014). When fishing pressure is focused primarily at aggregation sites or during the peak spawning, spawning reserves may offer meaningful protection that helps protect stocks or rebuild declining stocks through increased reproductive output and subsequent enhancement in recruitment, and which ideally offsets any increased mortality outside marine reserves due to displaced fishing effort (Pelc *et al.* 2010; Harrison *et al.* 2012). Reproductive activity and output are enhanced via the direct protection of the aggregation from disturbances by fishing and other human activities that allows for the persistence and stability of the mating process and the social structure associated with reproduction (Rowe and Hutchings 2003; Slabbekoorn *et al.* 2010; Dean *et al.* 2012). Notably, the direct and indirect (both lethal and non-lethal) effects of fishing activities on FSAs and how they may reduce reproductive activity and output continue to be largely ignored in assessments and theoretical studies related to the management of aggregation fisheries, such that reproductive output and potential fisheries yield are still estimated using traditional metrics such as fishing mortality and fecundity (Heppell et al. 2006; Grüss and Robinson 2014; Grüss *et al.* 2014). Field, experimental, and modeling studies that evaluate and incorporate aspects of reproductive success related to interactions between fishing activities and spawning behavior are likely to produce more realistic assessments of the benefits of spawning reserves to fisheries.

The success of spawning reserves hinges on the same factors as other reserves, including proper design, enforcement and compliance, and clearly defined management objectives (Edgar *et al.* 2014). Spawning reserves may not be effective in maintaining or rebuilding stocks if placed in the wrong location or if fishing activity is high outside the spawning season at different locations and no additional regulations are in place to limit fishing mortality (Eklund *et al.* 2000; Heppell *et al.* 2006; Ellis and Powers 2012; Chan *et al.* 2012). Unfortunately, the inclusion of spawning reserves within larger marine protected areas theoretical plans often lack rigor and full consideration of the dynamics of aggregations. As a result, reserves that have failed to meet their general objectives have also failed to protect aggregations (Rife *et al*. 2012; Grüss *et al*. 2014). Under those circumstances, greater fisheries and conservation benefits may result from the implementation of other measures that protect spawning activity and reproductive output such as seasonal closures, harvest restrictions during the spawning season, sales bans, or gear restrictions to aid in the protection of spawning fish (Rhodes and Rhodes 2005; Heppell *et al.* 2006; Russell *et al.* 2012).

Even if FSAs are effectively protected, a combination of measures is often necessary (e.g. seasonal closures, harvest limits, gear restrictions, moratoria) to ensure the maintenance of stable, healthy fish populations and sustainable, productive fisheries (Pondella and Allen 2008; Russell *et al.* 2012; Grüss and Robinson 2014; Grüss *et al.* 2014). However, a large proportion of the world's fisheries that target FSAs are considered "data poor" and lack the necessary fisheries or biological information to conduct robust stock assessments or effectively design and implement a suite of management strategies (Erisman *et al*. 2014). In these situations, we contend that focusing management first on spawning and later on other components will provide the highest benefit to cost ratio for both fisheries and conservation outcomes. Finally, and perhaps the biggest challenge facing FSAs, the effective management of FSAs must overcome the strong social and economic appeal for (over) fishing aggregations and incorporate market-based solutions that will create incentives for fishing at sustainable levels that also support viable fisheries for the economic livelihoods and food security of coastal communities (Sadovy de Mitcheson and Erisman 2012).

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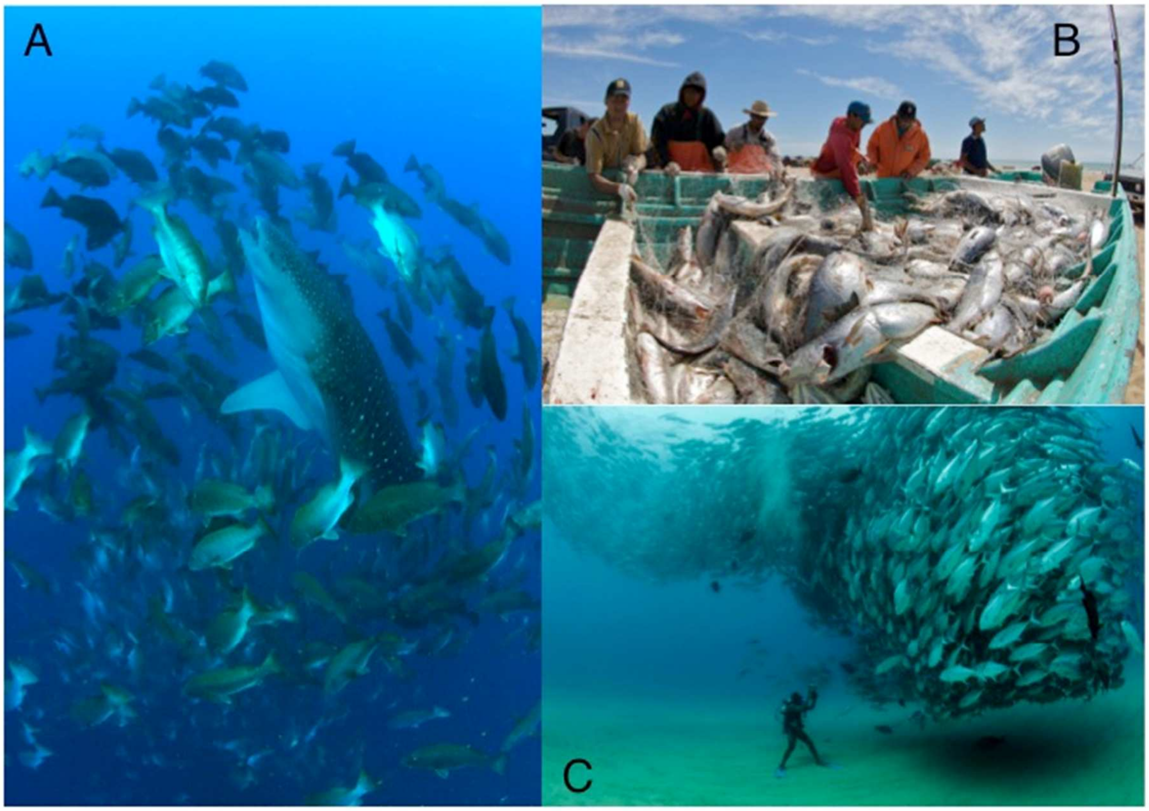
Figure Legends

Figure 1. Fish spawning aggregations are hotspots of biodiversity and productivity. (A) Whale sharks (*Rhincodon typus*) time their migrations to feed on the dense patches of nutrient-rich eggs released from Cubera snapper (*Lutjanus cyanopterus*) spawning aggregations (photo by D. Seifert). (B) Small-scale fishermen harvest more than 2 million individuals (5,000 tons) of Gulf corvina (*Cynoscion othonopterus*) in less than 30 days of fishing at a single spawning site in Mexico (photo by O. Aburto). (C) The spawning aggregation of thousands of Bigeye Trevally (*Caranx sexfasciatus*, Carangidae) that form each year inside Cabo Pulmo National Park in Mexico have become an icon of the well-documented recovery of this marine protected area that

attracts thousands of divers and generates millions of dollars for the surrounding community each year (photo by O. Aburto).

Figure 2. Global map showing areas of documented FSAs organized by region or country. Data (n=906 verified records) provided by Science and Conservation of Fish Aggregations Global Spawning Aggregations Database (http://www.scrfa.org/database/).

Figure 3. Benefits of FSAs to food webs. Counter-gradient redistribution of trophic resources to lower trophic levels through “egg boons” created by the spawning aggregation of a meso-carnivorous grouper. Broken black arrows show traditional trophic pathways and solid white arrows show flow through egg boons. Organisms are arranged vertically by trophic level. Length axis is logarithmic. Figure from Fuiman et al. 2015. Used with permission.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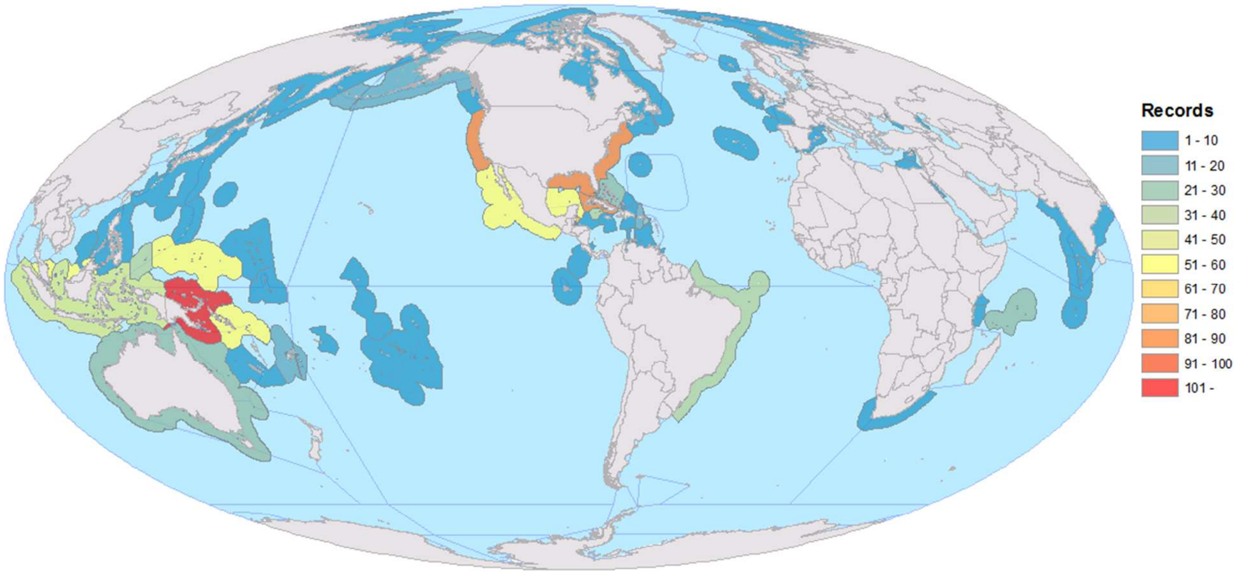
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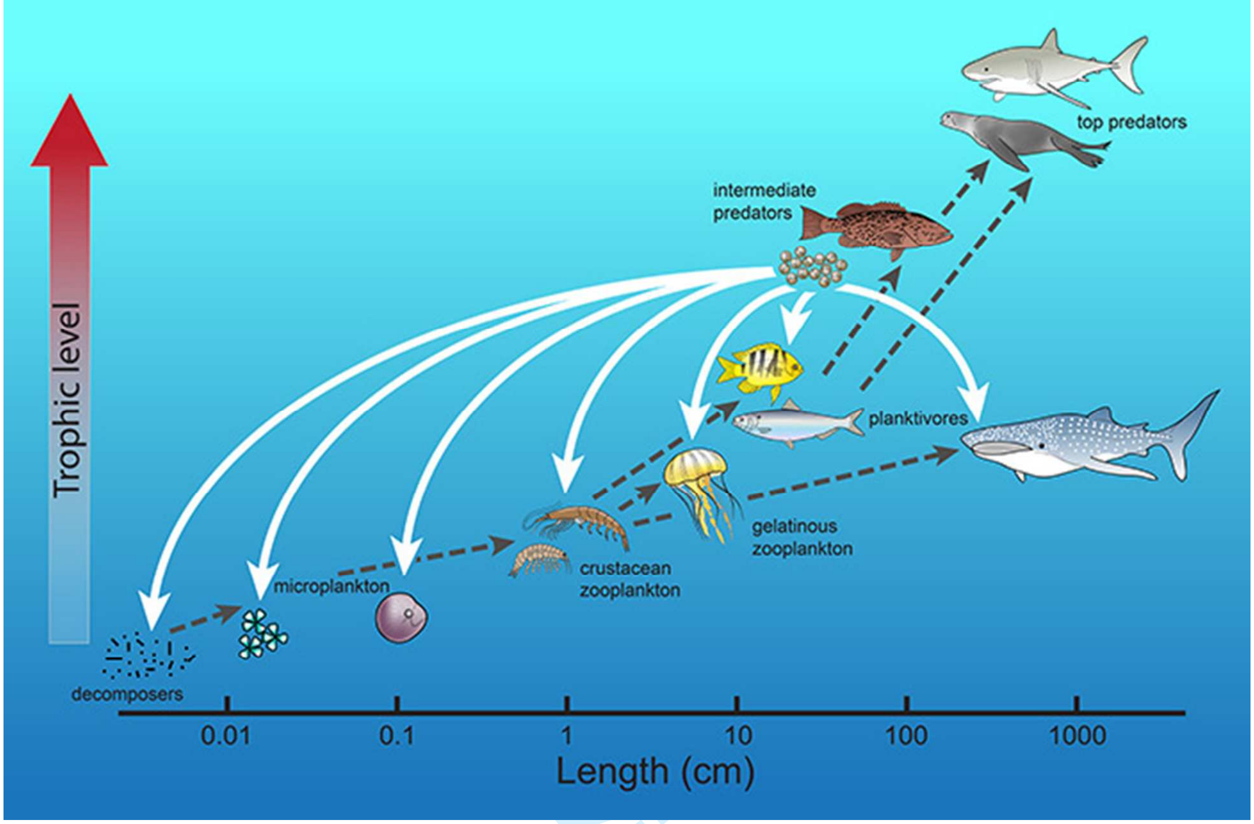
949 
Trophic level
top predators
intermediate predators
planktivores
gelatinous zooplankton
crustacean zooplankton
microplankton
decomposers
0.01
0.1
1
10
100
1000
Length (cm)