

**Ghoti****Ghoti papers**

Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.

**Etymology of Ghoti**

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

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

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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, we provide 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 multispecies 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

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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.

Keywords fish spawning aggregations, fisheries comanagement, fisheries management, marine conservation, marine productivity hotspots, physical–biological coupling

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

Many animals in both the terrestrial and marine environment undergo large migrations to aggregate en masse at specific locations and during discrete, predictable times (Bauer and Hoye 2014). Breeding migrations of wildebeests (*Connochaetes taurinus* Bovidae) and other land megafauna in Africa, the grey whales (*Eschrichtius robustus*, Eschrichtidae) 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 is 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 Wilkelski 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 labelled 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 aggregations (FSAs; Fig. 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 behaviour, 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 megaplanktivores (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 over-exploitation has contributed to rapid stock depletions and localized extirpations (Sadovy and Domeier 2005; Sadovy de Mitcheson *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

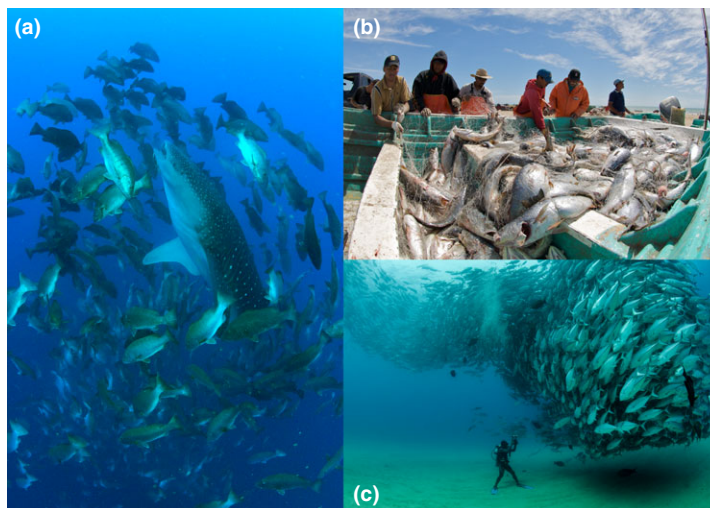


Figure 1 Fish spawning aggregations are hotspots of biodiversity and productivity. (a) Whale sharks (*Rhincodon typus*) time their migrations to feed on the dense patches of nutrient-rich eggs released from Cubera snapper (*Lutjanus cyanopterus*) spawning aggregations (photograph by D. Seifert). (b) Small-scale fishermen harvest more than 2 million individuals (5000 tons) of Gulf corvina (*Cynoscion othonopterus*) in < 30 days of fishing at a single spawning site in Mexico (photograph 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 (photograph by O. Aburto).

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 overexploitation 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 ecoregion 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 five oceans, 53 countries, 44 families and more than 300 species of fishes (Russell *et al.* 2014; SCRFA 2014) (Fig. 2). As the database is largely focused on tropical reef fishes, it likely omits many 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 bot-

toms 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 underdocumented.

Many FSA sites harbour 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 harbour multispecies FSAs. A recent review of 108 transient FSA sites (Kobara *et al.* 2013) in the wider Caribbean illustrated that most sites in that region harbour aggregations of multiple species. Individual sites harbour 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) to maximize reproductive fitness (Molloy *et al.* 2012). Ocean currents interact with distinct habitat features (e.g. promontories, seamounts and 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.* 2011). 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

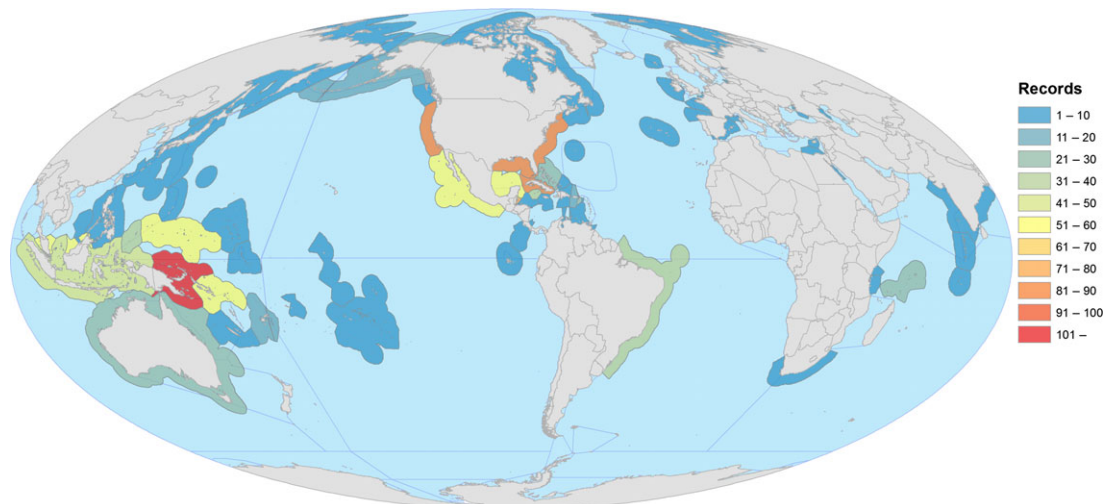


Figure 2 Global map showing areas of documented FSAs organized by region or country. Data ($n = 906$ verified records) provided by Science and Conservation of Fish Aggregations Global Spawning Aggregations Database (<http://www.scrga.org/database/>).

across all trophic levels and among the few pathways that recycle essential nutrients from apex predators to the lower trophic levels (Fuiman *et al.* 2015) (Fig. 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 megaplanktivores (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 multispecies 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 are 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

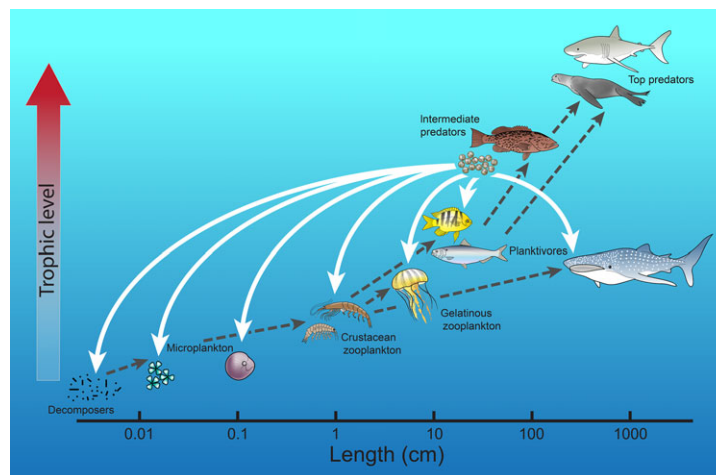


Figure 3 Benefits of FSAs to food webs. Counter-gradient redistribution of trophic resources to lower trophic levels through 'egg boons' created by the spawning aggregation of a mesocarnivorous grouper. Broken black arrows show traditional trophic pathways, and solid white arrows show flow through egg boons. Organisms are arranged vertically by trophic level. Length axis is logarithmic. Figure from Fuiman *et al.* 2015. Used with permission.

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 ecotourism 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 multispecies 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 South-East Asia, orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) fisheries at seamounts off New Zealand and Namibia, and salmon fisheries in the US 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 de Mitcheson *et al.* 2008; Sadovy de Mitcheson and Erisman 2012). As FSAs may attract the majority of breeding fish from a radius of 10–100 s of kilometres, 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.* 2015). 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, Scaenidae, 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 fin-fish fishery, it is now considered endangered by IUCN and being considered for listing as threatened under the US 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, 2014). Severe declines and regional extirpations of spawning aggregations in other large sciaenids include the giant yellow croaker (*Bahaba taipingensis*, Sciaenidae) in China (Sadovy and Cheung 2003), the white sea bass (*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, < 35% of FSAs are protected by any form of management (e.g. inclusion within

marine-protected areas, seasonal protection, harvest controls and 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 multinational 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.* 2005; 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 programme 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 multispecies 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 towards 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 fulfil 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 intergovernmental, 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 performed 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 multispecies aggregations, as priorities for investment will help protect the maximum diversity at minimum cost (Myers *et al.* 2000; Reid 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, 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 US South Atlantic are recognizing the geomorphic verisimilitude among multispecies 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 Friedlander 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 build-up 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 2012). Prominent examples of recovery include white sea bass 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.* 2000; 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 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 as 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 obstacles to successful marine reserves (e.g. opposition and non-compliance 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 (*Hypporthodus 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 has 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 behaviour, 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, conservators 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 performed 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 behaviour 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 modelling studies that evaluate and incorporate aspects of reproductive success related to interactions between fishing activities and spawning behaviour 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 often lack rigour 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 Warren-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 and 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, 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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References

- Aburto-Oropeza, O., Erisman, B.E., Galland, G.R., Mascareñas-Osorio, I., Sala, E. and Ezcurra, E. (2011) Large recovery of fish biomass in a no-take marine reserve. *PLoS One* **6**, e23601.
- ADF&G. (2015) *Alaska Department of Fish and Game*. Bristol Bay salmon districts. http://www.adfg.alaska.gov/index.cfm?adfg=CommercialByFisherySalmon.salmon-maps_districts_bristolbay (accessed 20 June 2015).
- Adger, W.N., Hughes, T.P., Folke, C., Carpenter, S.R. and Rockstrom, J. (2005) Social-ecological resilience to coastal disasters. *Science* **309**, 1036–1039.
- Almany, G.R., Hamilton, R.J., Bode, M. *et al.* (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Current Biology* **23**, 626–630.
- Alonzo, S.H. and Mangel, M. (2004) The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fishery Bulletin* **102**, 1–13.

- Archer, S.K., Allgeier, J.E., Semmens, B.X. *et al.* (2014) Hot moments in spawning aggregations: implications for ecosystem-scale nutrient cycling. *Coral Reefs*, **34**, 19–23.
- Bauer, S. and Hoyer, B.J. (2014) Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242–1245.
- Bauer, S., Barta, Z., Ens, B.J., Hays, G.C., McNamara, J.M. and Klaasen, M. (2009) Animal migration: linking models and data beyond taxonomic limits. *Biology Letters* **5**, 433–435.
- Beets, J. and Friedlander, A. (1992) Stock analysis and management strategies for red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute* **42**, 66–79.
- Beets, J. and Friedlander, A. (1999) Evaluation of a conservation strategy: a spawning aggregation closure for red hind, *Epinephelus guttatus*, in the U. S. Virgin Islands. *Environmental Biology of Fishes* **55**, 91–98.
- Berkes, F. (2007) Community-based conservation in a globalized world. *Proceedings of the National Academy of Sciences* **104**, 15188–15193.
- Boomhower, J., Romero, M., Posada, M., Kobara, S. and Heyman, W. (2010) Prediction and verification of possible reef-fish spawning aggregation sites in los Roques archipelago National Park, Venezuela. *Journal of Fish Biology* **77**, 822–840.
- Burke, L. and Maidens, J. (2004) *Reefs at Risk in the Caribbean*. World Resources Institute (WRI), Washington, DC. pp. 80.
- Burton, M.L., Brennan, K.J., Muñoz, R.C. and Parker, R.O. Jr (2005) Preliminary evidence of increased spawning aggregations of mutton snapper (*Lutjanus analis*) at Riley's Hump two years after establishment of the Tortugas South Ecological Reserve. *Fisheries Bulletin* **103**, 404–410.
- Chan, N.C.S., Connolly, S.R. and Mapstone, B.D. (2012) Effects of sex change on the implications of marine reserves for fisheries. *Ecological Applications* **22**, 778–791.
- Cherubin, L.M., Nemeth, R.S. and Idrisi, N. (2011) Flow and transport characteristics at an *Epinephelus guttatus* (red hind grouper) spawning aggregation site in St. Thomas (US Virgin Islands). *Ecological Modelling* **222**, 3132–3148.
- Choat, H. (2012) Spawning aggregations in reef fishes: ecological and evolutionary processes. In: *Reef Fish Spawning Aggregations: Biology, Research and Management*. (eds Y. Sadovy de Mitcheson and P.L. Colin). Springer, New York, pp. 85–116.
- Cisneros-Mata, M.A., Montemayor-Lopez, G. and Roman-Rodriguez, M.J. (1995) Life history and conservation of *Totoaba macdonaldi*. *Conservation Biology* **9**, 806–814.
- Claydon, J.A.B., McCormick, M.I. and Jones, G.P. (2014) Multispecies spawning sites for fishes on a low-latitude coral reef: spatial and temporal patterns. *Journal of Fish Biology* **84**, 1136–1163.
- Coleman, F.C., Koenig, C.C., Huntsman, G.R. *et al.* (2000) Long-lived reef fishes: the grouper-snapper complex. *Fisheries* **25**, 14–21.
- Coleman, F.C., Baker, P.B. and Koenig, C.C. (2004) A review of Gulf of Mexico marine protected areas: successes, failures, and lessons learned. *Fisheries* **29**, 10–21.
- Colin, P.L. (2012) Timing and location of aggregation and spawning in reef fishes. In: *Reef Fish Spawning Aggregations: Biology, Research and Management*. (eds Y. Sadovy de Mitcheson and P.L. Colin). Springer, New York, pp. 117–158.
- Colin, P.L., Sadovy, Y.J. and Domeier, M.L. (2003) *Manual for the Study and Conservation of Reef Fish Spawning Aggregations*. Society for the Conservation of Reef Fish Aggregations Special Publication No. 1 (Version 1.0), pp. 98.
- Dean, M.J., Hoffman, W.S. and Armstrong, M.P. (2012) Disruption of an Atlantic cod spawning aggregation resulting from the opening of a directed gill-net fishery. *North American Journal of Fisheries Management* **32**, 124–134.
- DOC (1997) Department of commerce. Magnuson-stevens act provisions: essential fish habitat (EFH). *Federal Register* **62**, 66531–66559.
- Domeier, M.L. (2012) Revisiting spawning aggregations: definitions and challenges. In: *Reef Fish Spawning Aggregations: Biology, Research and Management*. (eds Y. Sadovy de Mitcheson and P.L. Colin). Springer, New York, pp. 1–21.
- Domeier, M.L. and Speare, P. (2012) Dispersal of adult black marlin (*Istiompax indica*) from a Great Barrier Reef spawning aggregation. *PLoS One* **7**, e31629.
- Dragesund, O., Johannessen, A. and Ulltang, O. (1997) Variation in migration and abundance of Norwegian spring spawning herring (*Clupea harengus* L.). *Sarsia* **82**, 97–105.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J. *et al.* (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**, 216–220.
- Eklund, A.M., McClellan, D.B. and Harper, D.E. (2000) Black grouper aggregations in relation to protected areas within the Florida Keys National Marine Sanctuary. *Bulletin of Marine Science* **66**, 721–728.
- Elison, T., Salomone, P., Sands, T. *et al.* (2014) 2014 Bristol Bay area annual management report. *Alaska Department of Fish and Game Fishery Management Report* **15–24**, 1–126.
- Ellis, R.D. and Powers, J.E. (2012) Gag grouper, marine reserves, and density-dependent sex change in the Gulf of Mexico. *Fisheries Research* **115**, 89–98.
- Erisman, B.E., Buckhorn, M.L. and Hastings, P.A. (2007) Spawning patterns in the leopard grouper, *Mycteroperca rosacea*, in comparison with other aggregating groupers. *Marine Biology* **151**, 1849–1861.
- Erisman, B.E., Mascareñas, L., Paredes, G., Aburto-Oropeza, O. and Hastings, P.A. (2010) Seasonal, annual,

- and long-term trends for commercial fisheries of aggregating reef fishes in the Gulf of California, Mexico. *Fisheries Research* **106**, 279–288.
- Erisman, B.E., Allen, L.G., Pondella, D.J. II, Claisse, J., Miller, E. and Murray, J. (2011) Illusions of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 1705–1716.
- Erisman, B.E., Aburto-Oropeza, O., Gonzalez-Abraham, C., Mascareñas-Osorio, I., Moreno- Báez, M. and Hastings, P.A. (2012) Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the gulf of California. *Scientific Reports* **2**. doi:10.1038/srep00284.
- Erisman, B.E., Apel, A., MacCall, A., Román, M.J. and Fujita, R. (2014) The influence of gear selectivity and spawning behavior on a data-poor assessment of a spawning aggregation fishery. *Fisheries Research* **159**, 75–87.
- Erisman, B., Mascareñas, I., Lopez-Sagastegui, C., Moreno-Baez, M., Jimenez-Esquivel, V. and Aburto-Oropeza, O. (2015) A comparison of fishing activities between two coastal communities within a biosphere reserve in the Upper Gulf of California. *Fisheries Research* **164**, 254–265.
- Estes, J.A., Terborgh, J., Brashares, J.S. *et al.* (2011) Trophic downgrading of planet earth. *Science* **333**, 301–306.
- Ezer, T., Heyman, W.D., Houser, C. and Kjerfve, B. (2011) Modelling and observations of high-frequency flow variability and internal waves at a Caribbean reef spawning aggregation site. *Ocean Dynamics* **61**, 581–598.
- FAO (1995) *Code of Conduct for Responsible Fisheries*. FAO, Rome. pp. 41.
- FAO (2014) *The State of World Fisheries and Aquaculture*. FAO, Rome. pp. 223.
- FAO WCAFC. (2014) *FAO Western Central Atlantic Fishery Commission*. Report of the Western Central Atlantic Fisheries Commission, Fifteenth Session of the Commission. Port of Spain, Trinidad and Tobago, 26–28 March 2014. FAO Fisheries and Aquaculture Report No. 1069, pp. 133.
- Fox, C.H., El-Sabaawi, R.L., Paquet, P.C. and Reimchen, T.E. (2014) Pacific herring *Clupea pallasii* and wrack macrophytes subsidize semi-terrestrial detritivores. *Marine Ecology Progress Series* **495**, 49–64.
- Fuiman, L.A., Connelly, T.L., Lowerre-Barbieri, S.K. and McClelland, J.W. (2015) Egg boons: central components of marine fatty acid food webs. *Ecology* **96**, 362–372.
- Fulton, S., Bourillón, L., Ribot, C. *et al.* (2014) Fishermen investing in a network of fish refuges (No-Take Zones) in Quintana Roo, Mexico. In: *Enhancing Stewardship in Small-Scale Fisheries: Practices and Perspectives* (eds P. McConney, R.P. Medeiros and M. Pena). CERMES Technical Report No. 73, pp. 138–144.
- Graham, R.T. and Castellanos, D. (2012) Apex predators target mutton snapper spawning aggregation. *Coral Reefs* **31**, 1017.
- Granados-Dieseldorff, P., Heyman, W.D. and Azueta, J. (2013) History and co-management of the artisanal mutton snapper (*Lutjanus analis*) spawning aggregation fishery at Gladden Spit, Belize, 1950–2011. *Fisheries Research* **147**, 213–221.
- Green, A.L., Fernandes, L., Almany, G. *et al.* (2014) Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coastal Management* **42**, 143–159.
- Grüss, A. and Robinson, J. (2014) Fish populations forming transient spawning aggregations: should spawners always be the targets of spatial protection efforts? *ICES Journal of Marine Science* **72**, 480–497.
- Grüss, A., Robinson, J., Heppell, S.S., Heppell, S.A. and Semmens, B.X. (2014) Conservation and fisheries effects of spawning aggregation marine protected areas: what we know, where we should go and what we need to get there. *ICES Journal of Marine Science* **71**, 1515–1534.
- Guest, J. (2008) How reefs respond to mass coral spawning. *Science* **320**, 621–623.
- Hamilton, R.J., Potuku, T. and Montambault, J.R. (2011) Community-based conservation results in the recovery of reef fish spawning aggregations in the Coral Triangle. *Biological Conservation* **144**, 1850–1858.
- Hamilton, R.J., Sadovy de Mitcheson, Y. and Aguilar-Perera, A. (2012) The role of local ecological knowledge in the conservation and management of reef fish spawning aggregations. In: *Reef Fish Spawning Aggregations: Biology, Research and Management*. (eds Y. Sadovy de Mitcheson and P.L. Colin). Springer, New York, pp. 331–369.
- Hamner, W.M., Colin, P.L. and Hamner, P.P. (2007) Export-import dynamics of zooplankton on a coral reef in Palau. *Marine Ecology Progress Series* **334**, 83–92.
- Harrison, H.B., Williamson, D.H., Evans, R.D. *et al.* (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Current Biology* **22**, 1023–1028.
- Hartup, J.A., Marshall, A., Kottermair, M., Carlson, P. and Stevens, G. (2013) *Manta alfredi* target multi-species surgeonfish spawning aggregations. *Coral Reefs* **32**, 367.
- Heithaus, M.R., Frid, A., Wirsing, A.J. and Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* **23**, 202–210.
- Heppell, S.S., Heppell, S.A., Coleman, F.C. and Koenig, C.C. (2006) Models to compare management options for a protogynous fish. *Ecological Applications* **16**, 238–249.
- Heppell, S., Semmens, B.X., Archer, S.K. *et al.* (2012) Documenting recovery of a spawning aggregation through size frequency analysis from underwater laser

- calipers measurements. *Biological Conservation* **155**, 119–127.
- Heyman, W.D. (2011) Elements for building a participatory, ecosystem-based marine reserve network. *The Professional Geographer* **63**, 475–488.
- Heyman, W.D. (2014) Let them come to you: reinventing management of the snapper-grouper complex in the Western Atlantic: a contribution to the Data Poor Fisheries Management Symposium. *Proceedings of the Gulf and Caribbean Fisheries Institute* **66**, 104–109.
- Heyman, W.D. and Granados-Dieseldorff, P. (2012) The voice of the fishermen of the Gulf of Honduras: improving regional fisheries management through fisher participation. *Fisheries Research* **125–126**, 129–148.
- Heyman, W.D. and Kjerfve, B. (2008) Characterization of transient multi-species reef fish spawning aggregations at Gladden Spit, Belize. *Bulletin of Marine Science* **83**, 531–551.
- Heyman, W.D., Graham, R.T., Kjerfve, B. and Johannes, R.E. (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series* **215**, 275–282.
- Heyman, W., Azueta, J., Lara, O. et al. (2004) *Spawning Aggregation Monitoring Protocol for the Meso-American Reef and the Wider Caribbean. Version 2.0*. Meso-American Barrier Reef Systems Project, Belize City, Belize, pp. 55.
- Heyman, W.D., Carr, L.M. and Lobel, P.S. (2010) Diver ecotourism and disturbance to reef fish spawning aggregations: it is better to be disturbed than to be dead. *Marine Ecology Progress Series* **419**, 201–210.
- Heyman, W.D., Olivares, M., Fulton, S. et al. (2014) Prediction and verification of reef fish spawning aggregation sites in Quintana Roo Mexico. In: *Enhancing Stewardship in Small-Scale Fisheries: Practices and Perspectives* (eds P. McConney, R.P. Medeiros and M. Pena). CERMES Technical Report No. 73, pp. 73–81.
- Hilborn, R., Orensanz, J.M. and Parma, A.M. (2005) Institutions, incentives, and the future of fisheries. *Philosophical Transactions of the Royal Society of London Series B* **360**, 47–57.
- Hoffmayer, E.R., Franks, J.S., Driggers, W.B. III and Quattro, J.M. (2007) Observations of a feeding aggregation of whale sharks, *Rhincodon typus*, in the North Central Gulf of Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* **59**, 614.
- Hutchings, J.A. (1996) Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stocks' collapse. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 943–962.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H. et al. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–638.
- Jennings, S., Marshall, S.S. and Polunin, N.V.C. (1996) Seychelles' marine protected areas: comparative structure and status of reef fish communities. *Biological Conservation* **75**, 201–209.
- Johannes, R.E. (1978) Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* **3**, 65–84.
- Johannes, R.E., Freeman, M.M.R. and Hamilton, R.J. (2000) Ignore fishers' knowledge and miss the boat. *Fish and Fisheries* **1**, 257–271.
- Kadison, E., Nemeth, R.S., Herzlieb, S. and Blondeau, J. (2009) Temporal and spatial dynamics of *Lutjanus cyanopterus* (Pisces: Lutjanidae) and *L. jocu* spawning aggregations in the United States Virgin Islands. *Revista de Biología Tropical* **54**, 69–78.
- Kaiser, M., Collie, J., Hall, S., Jennings, S. and Poiner, I. (2002) Modification of marine habitats by trawling activities: prognosis and solutions. *Fish and Fisheries* **3**, 114–136.
- Karnauskas, M., Cherubin, L.M. and Paris, C.B. (2011) Adaptive significance of the formation of multi-species fish spawning aggregations near submerged capes. *PLoS One* **6**, e22067.
- Karras, C. and Agar, J. (2009) Cruzan fishermen's perspectives on the performance of the Buck Island Reef National Monument and the red hind seasonal closure. *Ocean and Coastal Management* **52**, 578–585.
- Kobara, S. and Heyman, W.D. (2010) Sea bottom geomorphology of multi-species spawning aggregation sites in Belize. *Marine Ecology Progress Series* **405**, 231–242.
- Kobara, S., Heyman, W.D., Pittman, S.J. and Nemeth, R.S. (2013) Biogeography of transient reef fish spawning aggregations in the Caribbean: a synthesis for future research and management. *Oceanography and Marine Biology: An Annual Review* **51**, 281–326.
- Koenig, C.C., Coleman, F.C., Grimes, C.B. et al. (2000) Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science* **66**, 593–616.
- Koslow, J.A., Gowlett-Holmes, K., Lowry, J.K., O'Hara, T., Poore, G.C.B. and Williams, A. (2001) Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Marine Ecology-Progress Series* **213**, 111–125.
- Lowerre-Barbieri, S.K. (2009) Reproduction in relation to conservation and exploitation of marine fishes. In: *Reproductive Biology and Phylogeny of Fishes (Agnathans and Bony Fishes)*. Vol. 8B, Part B (ed. B.G.M. Jamieson). CRC Press, London, pp. 371–394.
- Luckhurst, B.E. and Trott, T.M. (2009) Seasonally-closed spawning aggregation sites for red hind (*Epinephelus guttatus*): Bermuda's experience over 30 years (1974–2003). *Proceedings of the Gulf and Caribbean Fisheries Institute* **61**, 331–336.
- MacCall, A., Erisman, B.E., Apel, A. and Fujita, R. (2011) *Data-poor Models for Assessing the Fishery for the Gulf Curvina and Evaluating Management Alternatives*.

- Technical Report to the Grupo Technico Corvina. Available at: <https://swfsc.noaa.gov/publications/CR/2011/2011MacCall3.pdf> (accessed 25 June 2015).
- Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P. and Norris, D.R. (2007) Optimal conservation of migratory species. *PLoS One* **2**, e751.
- McCauley, D.J., Young, H.S., Dunbar, R.B., Estes, J.A., Semmens, B.X. and Micheli, F. (2012) Assessing the effects of large mobile predators on ecosystem connectivity. *Ecological Applications* **22**, 1711–1717.
- MMO. (2014) *Marine Management Organization*. Scoping the Opportunities and Challenges to Using a 'Core Fishing Grounds' Approach to Develop a Spatial Marine Plan Policy for Fishing. MMO Project No. 1074, 85 pp.
- Molloy, P.P., Anticamara, J.A., Rist, J.L. and Vincent, A.C.J. (2010) Frugal conservation: what does it take to detect changes in fish populations? *Biological Conservation* **143**, 2532–2542.
- Molloy, P.P., Cote, I.M. and Reynolds, J.D. (2012) Why spawn in aggregations? In: *Reef Fish Spawning Aggregations: Biology, Research and Management*. (eds Y. Sadovy de Mitcheson and P.L. Colin). Springer, New York, pp. 57–83.
- Morato, T., Hoyle, S.D., Allain, V. and Nicol, S.J. (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences* **107**, 9707–9711.
- Morgan, M.J., Wilson, C.E. and Crim, L.W. (1999) The effect of stress on reproduction in Atlantic cod. *Journal of Fish Biology* **54**, 477–488.
- Muñoz, R.C., Burton, M.L., Brennan, K.J. and Parker, R.O. Jr (2010) Reproduction, habitat utilization, and movements of hogfish (*Lachnolaimus maximus*) in the Florida Keys, U.S.A.: comparisons from fished versus unfished habitats. *Bulletin of Marine Science* **86**, 93–116.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- Nemeth, R.S. (2005) Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Marine Ecology Progress Series* **286**, 81–97.
- Nemeth, R.S. (2009) Dynamics of reef fish and decapod crustacean spawning aggregations: underlying mechanisms, habitat linkages, and trophic interactions. In: *Ecological Connectivity Among Tropical Coastal Ecosystems*. (ed I. Nagelkerken). Springer, New York, pp. 73–134.
- Nemeth, R.S. (2012) Ecosystem aspects of species that aggregate to spawn. In: *Reef Fish Spawning Aggregations: Biology, Research and Management*. (eds Y. Sadovy de Mitcheson and P.L. Colin). Springer, New York, pp. 21–55.
- Nemeth, R.S., Wetherbee, B., Shivji, M. *et al.* (2010) Interactions among three species of sharks and grouper spawning aggregations in the US Virgin Islands. *Proceedings of the Gulf and Caribbean Fisheries Institute*, November 1–5, San Juan, Puerto Rico, pp. 155–156.
- Olsen, D.A. and LaPlace, J.A. (1978) A study of Virgin Islands grouper fishery based on a breeding aggregation. *Proceedings of the Gulf and Caribbean Fisheries Institute* **31**, 130–144.
- Pankhurst, N.W. (1988) Spawning dynamics of orange roughy, *Hoplostethus atlanticus*, in mid-slope waters of New Zealand. *Environmental Biology of Fishes* **21**, 101–116.
- Parma, A.M., Sullivan, P.J., Collie, J. *et al.* (2014) *Evaluating the Effectiveness of Fish Stock Rebuilding Plans in the United States*. Ocean Studies Board, National Research Council. National Academies Press, Washington, DC, pp. 143.
- Parsons, M.J.G., Parnum, I.M. and McCauley, R.D. (2013) Visualizing samsonfish (*Seriola hippos*) with a Reson 7125 Seabat multibeam sonar. *ICES Journal of Marine Science* **70**, 665–674.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres, F.C. Jr (1998) Fishing down marine food webs. *Science* **279**, 860–863.
- Pelc, R.A., Warner, R.R., Gaines, S.D. and Paris, C.B. (2010) Detecting larval export from marine reserves. *Proceedings of the National Academy of Sciences* **107**, 18266–18271.
- Petersen, C.W., Warner, R.R., Shapiro, D.Y. and Marconato, A. (2001) Components of fertilization success in the bluehead wrasse, *Thalassoma bifasciatum*. *Behavioral Ecology* **12**, 237–245.
- Petitgas, P., Secor, D.H., McQuinn, I., Huse, G. and Lo, N. (2010) Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. *ICES Journal of Marine Science* **67**, 1841–1848.
- Phelan, M. (2008) *Assessment of the Implications of Target Fishing on Black Jewfish (Protonibea diacanthus) Aggregations in the Northern Territory*. Fishery report 91, Fisheries Research and Development Corporation project 2004/004, Northern Territory Department of Primary Industries, Fisheries and Mines, Darwin. pp. 115.
- Pikitch, E.K., Rountos, K.J., Essington, T.E. *et al.* (2014) The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* **15**, 43–64.
- Pittman, S.J. and McAlpine, C.A. (2003) Movements of marine fish and decapod crustaceans: process, theory and application. *Advances in Marine Biology* **44**, 205–294.
- Pondella, D.J. II and Allen, L.G. (2008) The decline and recovery of four predatory fishes from the Southern California Bight. *Marine Biology* **154**, 307–313.
- Reid, W.V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution* **13**, 275–280.

- Rhodes, K.L. and Warren-Rhodes, K. (2005) *Management Options for Fish Spawning Aggregations of Tropical Reef Fishes: A Perspective*. Report prepared for the Pacific Island Countries Coastal Marine Program, The Nature Conservancy. TNC Pacific Island Countries Report No. 7/05. 52 pp.
- Rife, A., Erisman, B., Sanchez, A. and Aburto-Oropeza, O. (2012) When good intentions aren't enough: insights on networks of "paper park" marine protected areas. *Conservation Letters* **6**, 200–212.
- Roberts, C.M., McClean, C.J., Veron, J.E.N. et al. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* **295**, 1280–1284.
- Rose, G.A., Bradbury, I.R., de Young, S.B. et al. (2008) Rebuilding Atlantic cod: lessons from a spawning ground in coastal Newfoundland. In: *Resiliency of Gadid Stocks to Fishing and Climate Change*. (eds G.H. Kruse, K. Drinkwater, J.N. Ianelli, J.S. Link, D.L. Stram, V. Weststad and D. Woodby). Alaska Sea Grant College Program, Fairbanks, Alaska, pp. 197–220.
- Rowe, S. and Hutchings, J.A. (2003) Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution* **18**, 567–572.
- Rowe, S., Hutchings, J.A., Bekkevold, D. and Rakitin, A. (2004) Depensation, probability of fertilization, and the mating system of Atlantic cod. *ICES Journal of Marine Science* **61**, 1144–1150.
- Rowe, S., Hutchings, J.A., Skjaeraasen, J.E. and Bezanson, L. (2008) Morphological and behavioral correlates of reproductive success in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* **354**, 257–265.
- Rowell, T.J., Schärer, M.T., Appeldoorn, R.S., Nemeth, M.I., Mann, D.A. and Rivera, J.A. (2012) Sound production as an indicator of red hind density at a spawning aggregation. *Marine Ecology Progress Series* **462**, 241–250.
- Rudd, M.A. and Tupper, M.H. (2002) The impact of Nassau grouper size and abundance on scuba diver site selection and MPA economics. *Coastal Management* **30**, 133–151.
- Russell, M.W., Luckhurst, B.E. and Lindeman, K.C. (2012) Management of spawning aggregations. In: *Reef Fish Spawning Aggregations: Biology, Research and Management*. (eds Y. Sadovy de Mitcheson and P.L. Colin). Springer, New York, pp. 371–404.
- Russell, M.W., deSadovy Mitcheson, Y., Erisman, B.E., Hamilton, R.J., Luckhurst, B.E. and Nemeth, R.S. (2014) *Status Report – World's Fish Aggregations 2014*. Science and Conservation of Fish Aggregations, California USA. International Coral Reef Initiative.
- Sadovy, Y. and Cheung, W.L. (2003) Near extinction of a highly fecund fish: the one that nearly got away. *Fish and Fisheries* **4**, 86–99.
- Sadovy de Mitcheson, Y. and Erisman, B.E. (2012) The social and economic importance of aggregating species and the biological implications of fishing on spawning aggregations. In: *Reef Fish Spawning Aggregations: Biology, Research and Management*. (eds Y. Sadovy de Mitcheson and P.L. Colin). Springer, New York, pp. 225–284.
- Sadovy de Mitcheson, Y., Cornish, A., Domeier, M., Colin, P.L., Russell, M. and Lindeman, K.C. (2008) A global baseline for spawning aggregations of reef fishes. *Conservation Biology* **22**, 1233–1244.
- Sadovy de Mitcheson, Y., Craig, M.T., Bertocini, A.A. et al. (2013) Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish and Fisheries* **14**, 119–136.
- Sadovy, Y. and Domeier, M. (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs* **24**, 254–262.
- Sadovy, Y. and Eklund, A.M. (1999) *Synopsis of biological data on the Nassau grouper, Epinephelus striatus (Bloch, 1792), and the jewfish, E. itajara (Lichtenstein, 1822)*. NOAA Technical Report NMFS No. 146. NOAA/National Marine Fisheries Service, Seattle, WA, pp. 65.
- Sadovy de Mitcheson, Y. and Colin, P.L. (eds.) (2012) *Reef Fish Spawning Aggregations: Biology, Research and Management*. Vol. 35. Fish and Fisheries Series. Springer, New York.
- SAFMC. (2015) *South Atlantic Fishery Management Council Decision Document - Amendment 36 to the Fishery Management Plan For the Snapper Grouper Fishery of the South Atlantic Region: Spawning SMZs off NC, SC, GA, and FL*. Available at: http://safmc.net/sites/default/files/meetings/pdf/Council/2015/03-2015/sg/2bb/A6_SGAm36DecisionDoc_022315.pdf (accessed 25 June 2015).
- Sala, E., Ballesteros, E. and Starr, R.M. (2001) Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* **26**, 23–30.
- Sale, P., Cowen, R., Danilowicz, B. et al. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution* **20**, 74–80.
- SCRFA. (2014) *Science and Conservation of Fish Aggregations*. Spawning aggregation database by Science and Conservation of Fish Aggregations. World Wide Web electronic publication. Available at: <http://www.scrfa.org/database/> (accessed 25 June 2015).
- Sedberry, G.R., Pashuk, O., Wyanski, D.M., Stephen, J.A. and Weinbach, P. (2006) Spawning locations for Atlantic reef fishes off the southeastern U.S. *Proceedings of the Gulf and Caribbean Fisheries Institute* **57**, 463–514.
- Shcherbina, A.Y., Gawarkiewicz, G.G., Linder, C.A. and Thorrold, S.R. (2008) Mapping bathymetric and hydrographic features of Glover's Reef, Belize, with a REMUS autonomous underwater vehicle. *Limnology and Oceanography* **53**, 2264–2272.
- Shida, O., Mihara, Y., Mutoh, T. and Miyashita, K. (2014) Interannual changes in the timing of walleye Pollock spawning migration and their impacts on the gillnet fishery in the southwestern Pacific coast of Hok-

- kaido, Donan area, Japan. *Fisheries Science* **80**, 173–179.
- Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C. and Popper, A.N. (2010) A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in Ecology and Evolution* **25**, 419–427.
- Tobin, A., Currey, L. and Simpfendorfer, C. (2013) Informing the vulnerability of species to spawning aggregation fishing using commercial catch data. *Fisheries Research* **143**, 47–56.
- Vianna, G., Meekan, M., Pannell, D., Marsh, S. and Meeuwig, J. (2012) Socio-economic value and community benefits from shark-diving tourism in Palau: a sustainable use of reef shark populations. *Biological Conservation* **145**, 267–277.
- Wilcove, D.S. and Wilkelski, M. (2008) Going, going, gone: is animal migration disappearing. *PLoS Biology* **6**, e188.
- Williams, I.D. and Polunin, N.V.C. (2000) Differences between protected and unprotected reefs of the western Caribbean in attributes preferred by dive tourists. *Environmental Conservation* **27**, 382–391.
- Wingfield, D.K., Peckham, S.H., Foley, D.G. et al. (2011) The making of a productivity hotspot in the coastal ocean. *PLoS One* **6**, e27874.
- Zemeckis, D.R., Dean, M.J. and Cadrin, S.X. (2014) Spawning dynamics and associated management implications for Atlantic cod. *North American Journal of Fisheries Management* **34**, 424–442.