Mainstreaming Fish Spawning Aggregations into Fishery Management Calls for a Precautionary Approach

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Many marine fishes mate in massive and spectacular gatherings at predictable times and places. These spawning aggregations are often attractive targets of fisheries. Many commercially important fish species exhibit aggregation spawning, and many have undergone serious declines from overfishing. It is timely to explore whether the exploitation of spawning aggregations makes species particularly susceptible to overfishing; if so, why and how we can better manage these species. I present evidence that aggregate fish spawners are especially vulnerable because of both increased catchability (lethal effects) and biological factors (nonlethal effects). For these species to continue contributing to food security and livelihoods while retaining their ecosystem function, a truly precautionary approach is essential to reduce the risk of declines, particularly in the case of small-scale commercial fisheries of low-productivity species and where management and monitoring are lacking. There is a pressing need to mainstream spawning aggregations into marine resource management.

Keywords: food security, sustainable fishing, reproduction

Marine fishes are the last remaining animal resources that we still take in huge quantities from the wild. They provide about one-fifth of our global protein supply and are massively important for food security and livelihoods (FAO 2014). However, roughly 60% of capture fisheries today—for which there is sufficient information (a small proportion of global fisheries)—are either collapsed or overfished and need management for rebuilding (e.g., Worm et al. 2009, Pitcher and Cheung 2013). Millions of people will continue to depend on ready access to wild populations of fishes, which must be adequately safeguarded.

Many exploited marine fishes have as their sole means of reproduction the formation of large temporary gatherings (variously referred to as "spawning aggregations," "fishing grounds," "fishing seasons," "spawning runs," etc.), representing some of our oceans' most spectacular, fascinating and biologically productive phenomena. Many of these species face growing threats to their populations from increasing harvest and lack of effective management, which can be particularly challenging to implement when species become more accessible to fishing during temporary periods of high abundance (Sadovy de Mitcheson and Erisman 2012). The history of the prolific passenger pigeon (*Ectopistes migratorius*) of North America, estimated to formerly number billions of animals and once a major protein supply, is a cautionary tale with parallels to many marine species today. The bird was driven to extinction by 1914, following just a few decades of heavy hunting of its massive flocks as they migrated across the country. As numbers plummeted, its economic value rose. It turns out that the group-breeding habit of this nomadic and highly gregarious species became increasingly compromised as populations declined, further exacerbated by the loss of nesting habitat (Conrad 2005, Stanton 2014).

Nobody could have imagined the extinction of the once-super-abundant passenger pigeon from hunting, but stories similar to that of the pigeon are unfolding across our oceans for species once considered to be so abundant and prolific they could never be threatened with extinction. In the western Pacific, the numbers of the spectacular Atlantic bluefin tuna (ABT; *Thunnus thynnus*), an economically valuable and once highly abundant species, have plunged since the 1970s. Its biology, brief reproductive season, and spatially restricted spawning areas make it naturally vulnerable to overexploitation in the absence of sufficient management (Collette et al. 2011). As their numbers dropped from billions of animals

BioScience 66: 295–306.
doi:10.1093/biosci/biw013 Advance Access publication XX XXXX, XXXX

to a few million and a tiny fraction of its natural spawning biomass, prices soared for the sushi–sashimi market, further stimulating fishing and leading to a downward spiral toward extinction; it is now endangered (Fromentin and Powers 2005, Collette et al. 2011). Despite various management measures, including protection from directed fishing while reproducing, there is concern that spawners are still incidentally caught (and large proportions subsequently die) by longlines targeting yellowfin tuna and swordfish in their aggregation areas (Armsworth et al. 2010, Collette et al. 2011). The transnational distribution of this fishery presents further challenges to management. But even at the national level, once-abundant species have been extirpated. In East Asia, seasonal spawning aggregations are formed by the large yellow croaker (*Larimichthyes crocea*), once a major coastal fishery of China (Liu and Sadovy de Mitcheson 2008). This fishery collapsed after peaking at about 200,000 tonnes in the mid-1970s, after which catches declined by over 90% in 20 years. Fishing was mainly on spawning aggregations and overwintering grounds, with loss of important inshore nursery habitat to development also implicated. The species has never recovered despite massive restocking programs and management measures. Wild fish are now uncommon and fetch high market value when encountered (e.g., Liu and Sadovy de Mitcheson 2008). What is little understood for these—and many other—species that aggregate to spawn and that have declined markedly over the last few decades (see below) is the specific role that fishing on their spawning aggregations has had in their declines. Understanding this is crucially important for successfully managing species exploited on their spawning aggregations.

The aggregation mode has emerged as the reproductive strategy for a large and diverse range of marine taxa across temperate, tropical, deep-sea, and pelagic realms, including among many species of commercial importance. The habit presumably confers considerable reproductive advantage—and ultimately greater fitness—compared with the nonaggregating reproductive habit, all else being equal (e.g., Molloy et al. 2012), because there are costs to migration and assembly. These range from heightened risk of disease and parasites and increased exposure to predation to energetically demanding migrations to and from spawning sites (Molloy et al. 2012). On the evolutionary factors driving broadcast spawning fishes to aggregate where and when they do we can only speculate. Whether the time and location of spawning evolved for the benefit of eggs and larvae to disperse or retain them close to natal areas or for larvae to have access to abundant food is not known. Large concentrated pulses of eggs may reduce *per capita* egg predation rates. Aggregate spawning may have evolved predominantly for the benefit of adults that must live dispersed at other times to survive, enabling them to meet, undergo sexual selection, and maximize fertilization rates.

Whatever the ultimate evolutionary driver(s) of aggregation spawning, the immediate benefits of aggregation fishing are obvious, with large numbers of fish becoming predictably and efficiently available and catchability (fishing effectiveness) increasing markedly for many species when they assemble. Monitoring and management of such fisheries, whereby both fish and fisher behavior temporarily change, can be particularly challenging. Conventional management theory focuses on addressing the "lethal" effects of removals and the maintenance of sufficient spawning biomass (Hilborn and Walters 1992). It does not distinguish an aggregated from a nonaggregated fish or typically consider nonlethal effects (such as depensation).

In this article, I explore the thesis that fishes exploited on their spawning aggregations are particularly susceptible to overfishing and, in extreme cases, threat of extinction (conservation status is assigned according to IUCN categories and criteria; IUCN 2015) because of a combination of both the lethal and nonlethal impacts of aggregation fisheries (i.e., fisheries that target spawning aggregations). Specifically, I consider (a) the extent of the aggregating habit among exploited fishes as a reproductive mode, (b) the possible role of aggregation fishing in declines of exploited species, (c) the possible ways that fishing affects spawning aggregations, (d) the challenges of and opportunities for managing fisheries that target spawning aggregations, and (e) the role of spawning aggregations in marine ecosystems and future food security.

Spawning aggregations in global fisheries

Congregatory reproduction in pelagic egg producing marine fishes is characterized by intense bouts of multiple gamete release, constituting brief, passive, and often massive sources of sperms and eggs within groups of temporarily gathered males and females (figure 1a). Some aggregations last just a few hours a year, some form monthly or even daily, some are synchronized to the lunar cycle, some to tidal patterns or to narrow temperature regimes, some are highly defined spatially, and some form over extensive areas (Sadovy and Colin 2012). Irrespective of spatial or temporal scales, all involve events with tens, hundreds, thousands, or tens of thousands of conspecifics gathering predictably and solely for the purpose of spawning (Domeier 2012). Aggregating demersal egg layers, such as capelin, flying fish, herring, or triggerfish, head for the substrate they need to deposit their eggs. Many pelagic spawning reef fishes migrate seasonally to outer reef slopes, channels, and promontories. Seamounts, estuaries, and other coastal habitats are the destinations of deep water and tropical and temperate coastal species, from croakers to orange roughy, from cod to haddock, from rabbitfish to mullet. A handful of large ocean patches are the preferred spawning grounds for highly mobile pelagic fishes, such as certain tunas, marlin, and small pelagics, from sardines to herring.

The numbers of fish that gather seasonally to spawn in any one location can be, or once were, considerable. Prior to large-scale fishing, enormous shoals of gravid Atlantic herring (*Clupea harengus*) "became absolutely a nuisance" in the Chesapeake Bay area (Buffon 1793), the implication being

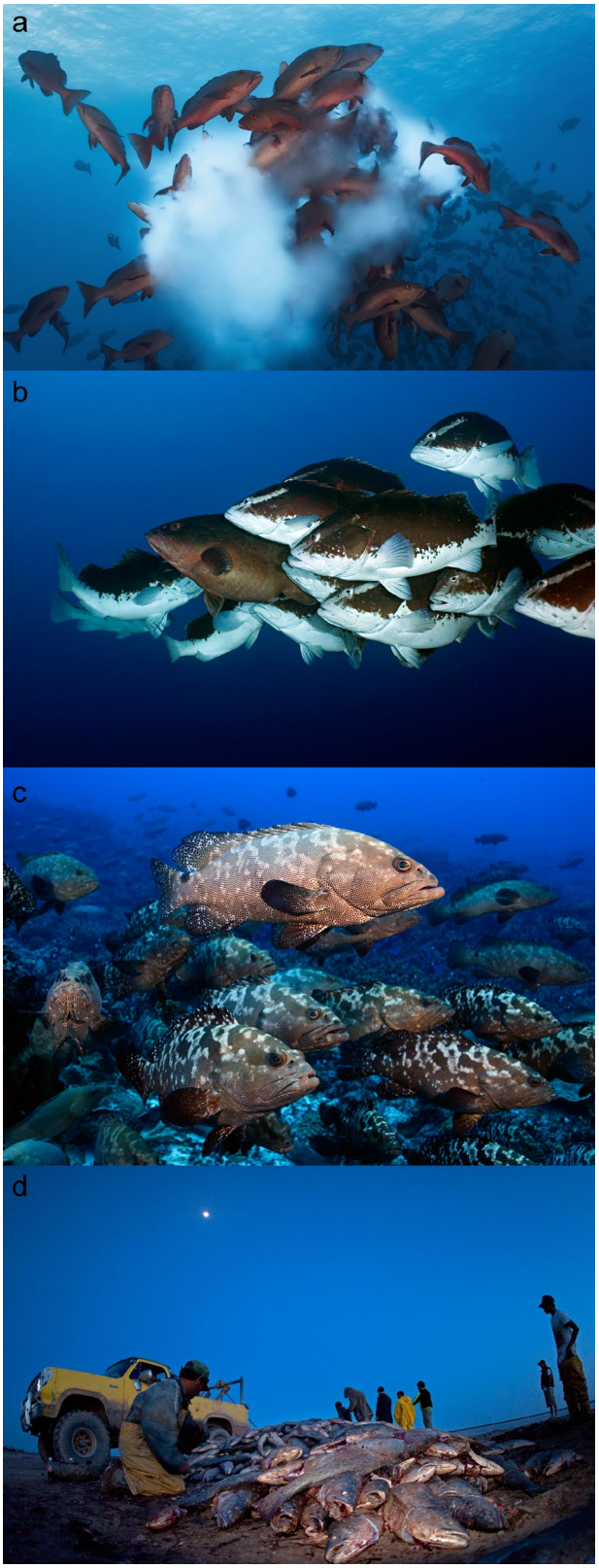

*Figure 1. (a) Spawning in twinspot snapper (***Lutjanus bohar***) in Palau, showing massive and highly concentrated release of eggs which occurs predictably over just a few hours each year. Photograph: Tony Wu (***www.tonywublog.com***). (b) A spawning group of endangered Nassau grouper (***Epinephelus striatus***) has formed within a much larger spawning aggregation. Spawning seems to be structured; this group consists of a leading female (dark color) and multiple males (bicolored). Photograph: Doug Perrine (***SeaPics.com***). (c) The camouflage grouper (***Epinephelus polyphekadion***) spawns in subgroups in large aggregations, but when numbers are depleted, intraspecific interactions are few. Photo: Yvonne Sadovy de Mitcheson (d) The short spawning season of the corvina (***Cynoscion othonopterus***) in Mexico produces high landings to meet Easter demand, but once demand drops, the glut results in falling prices and much wastage. Photograph: Octavio Aburto / iLCP.*

that fish far exceeded fishing effort. Aggregate-spawning species, from subsistence to small-scale/artisanal to industrial-scale fisheries, are of great economic and food security value, so it is of utmost importance to understand the impact of aggregation-fishing on such species and how this can best be managed. Of the top 20 fishes by weight supplying global fisheries (FAO 2014), many undergo regular spawning migrations, aggregate to spawn, and are exploited at these times. Examples range from Alaska (walleye) pollock (*Theragra chalcogramma*), Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus)*, and Atlantic mackerel (*Scomber scombrus*) to largehead hairtail (*Trichiurus lepturus*), European pilchard (*Sardina pilchardus*), and herring.

Among coral reef fishes, more than 100 species exhibit this reproductive habit, and for many of these species aggregation times mark the fishing season. Although the catches and natural productivities of these reef fishes are orders of magnitude less than those of major temperate species, producing tens of tonnes rather than tens of thousands or even millions of tonnes annually, they are nonetheless crucially important for the hundreds of thousands of communities that depend on them. Their low productivity makes them particularly susceptible to overfishing (Sadovy de Mitcheson and Colin 2012). Some of these species are taken mainly or only while spawning or migrating to spawning areas, from groupers and snappers to rabbitfish, mullet, and bonefish (e.g., Johannes 2002, Fox et al. 2012). In these small-scale fisheries, just a few boats have the capacity to remove a large proportion of a single aggregation in a single season.

The implications of aggregation fishing

Fishing on spawning aggregations is heavily implicated in the declines of many species, although it is challenging to distinguish such impacts from those attributable to the sum of fishing activities on all life-history stages of target species. The distinction is important, however, for applying appropriate management and can best be understood, perhaps, by comparative analyses. Using fuzzy logic, Cheung and colleagues (2005) concluded that high intrinsic vulnerability to overfishing and extinction in fishes is associated with large body size and long life and that factoring in spatial aggregation factors increased the goodness of fit between estimated vulnerabilities and empirical population trends.

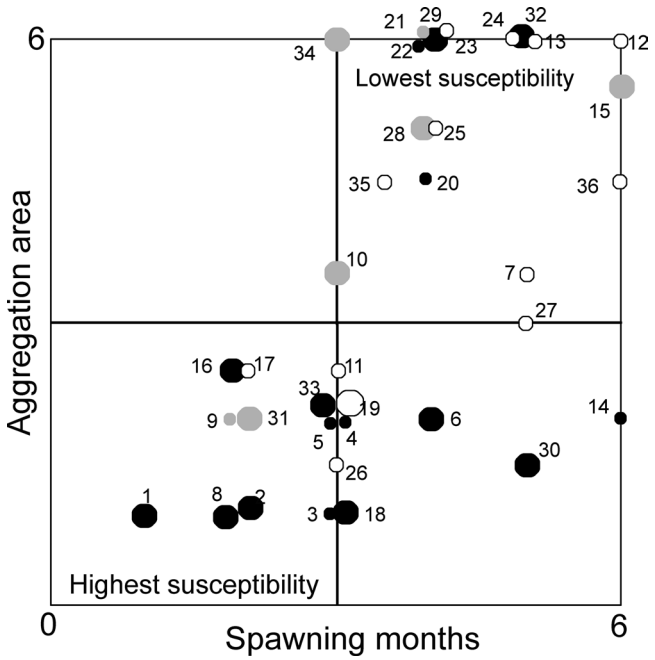

Figure 2. Thirty-six species of exploited aggregating and nonaggregating species of varying size (from 21 to 458 millimeters total length, TL; FishBase 2015) and conservation status (IUCN 2015) plotted according to a qualitative indicator of catchability. The indicator combines length of spawning season (1–6 months) and spatial concentration from 1 (highly concentrated when aggregated to spawn and easy to target) to 6 (no aggregate spawning and therefore no change in susceptibility to catch) using available biological information (IUCN 2015). Each dot is one fish: small dots are less than 100 centimeters (cm) TL and large ones more than 100 cm TL. The darkness of the circles refers to IUCN Red List status: threatened (critically endangered + endangered + vulnerable) is represented in black; near-threatened is represented in grey; least concern is represented in white with black margin; IUCN 2015). Dot numbers: (sciaenids 1–4, lutjanids 5–7, epinephelids 8–15, gadid 16, clupeid 17, sparids 18–25, serranids 26–27, scombrids 28–34, acanthurid 35, siganid 36).

Although a detailed quantitative analysis to explore this further is beyond the scope of this article, a semiquantitative treatment of 36 species of aggregating and nonaggregating species across a range of taxa, life-history types, maximum body size (FishBase 2015), and conservation status (IUCN 2015) suggests that threat is negatively associated with a qualitative measure of catchability, independent of body size (figure 2). Robinson and Samoilys (2013) developed a framework for examining extrinsic (fishery-specific) and intrinsic (population-specific) factors in relation to catchability. They identified clusters of low and high levels of relative vulnerability to fishing linked to life-history characters, such as longevity and type of aggregating behavior, and fishery factors, such as management and accessibility. These various analyses suggest that, all else being equal, species that aggregate to spawn and are targeted on their aggregations are more likely to be threatened than nonaggregators, especially when catchability is elevated.

Detailed monthly data from fisheries in Cuba and California allow the examination of differences among similar species that vary in their catchabilities within two very different fisheries. In Cuba, decades of monthly data show that groupers (Epinephelidae) and snappers (Lutjanidae) that aggregate most predictably at a small number of spawning sites underwent more marked and sudden declines compared with species in the same commercial fishery that have longer reproductive seasons and less predictable spawning aggregation patterns (and therefore lower catchability; Sadovy de Mitcheson and Erisman 2012). Off southern California, among the most important recreational fisheries are those for barred sandbass (*Paralabrax nebulifer*) and kelp bass (*P. clathratus*). These two species combined once peaked at over 3000 tonnes annually. Commercial fishing ceased in the early 1950s, and the species were subsequently managed by recreational bag limits and minimum sizes. Then, in the early 2000s, after many decades of steady catch per unit effort (CPUE) and increasing catches, the barred sandbass underwent an abrupt decline (figure 2). This species forms highly predictable spawning aggregations of up to thousands of fish at just six areas during 2 months of each year, otherwise dispersing widely along inshore habitats (Erisman et al. 2012). By contrast, kelp bass spawning aggregations are less concentrated in both time and location, comprise a few hundred individuals each, and its catchability is therefore lower than that of the sandbass. Declines in the kelp bass species were considerably less marked. Although there have been overall declines in recreational fisheries in southern California and in commercial fisheries in Cuba and environmental effects could also be involved, the differential responses of the various species in these two fisheries are almost certainly partly attributable to their different spatial and temporal aggregating patterns and resultant differential catchabilities.

Of all 163 groupers and 134 seabreams (Sparidae) globally, many of those that aggregate to spawn are the most threatened species within their taxa, although other life-history characters, such as longevity and late sexual maturation, are also relevant to level of extinction risk under exploitation (e.g., Sadovy de Mitcheson et al. 2013). The closely related, similar-sized, tropical western Atlantic Nassau (*Epinephelus striatus*) and red (*E. morio*) groupers make for an interesting comparison. The Nassau grouper forms relatively few, brief, and large aggregations that are heavily fished and little managed or only managed after they become severely reduced; the species is now endangered, and most of its aggregations have disappeared or became severely reduced (Sadovy de Mitcheson et al. 2008). Although its congenor does not form spawning aggregations and its catchability increases only slightly during the reproductive season, the fishery

remains viable, and it is near threatened (IUCN 2015). Of all 134 seabreams (Sparidae), the few that are threatened and for which their mode of reproduction is known, are aggregate-spawners. The red Steenbras (*Petris rupestris*), the "seventy-four" (*Polysteganus undulosus*), and the red stumpnose seabream (*Chrysoblephus gibbiceps*) are endangered or critically endangered (IUCN 2015). Although these South African species are endemics, a characteristic that could itself be a vulnerability factor, the great majority of South Africa's nonaggregating endemic sparids are not similarly threatened.

Of all 150 croakers (Sciaenidae) for which information is available on the IUCN Red List, those that are globally threatened are aggregate spawners that are also overfished (IUCN 2015). Both of the world's largest croakers, Chinese bahaba (*Bahaba taipingensis*) and totoaba (*Totoaba macdonaldi*), spawn (or once spawned) at a few estuarine aggregation sites where their fisheries were heavily focused; both species are critically endangered (Sadovy and Cheung 2003). Although limited geographic distributions, high prices for their swim bladders, and environmental factors—such as the degradation of estuarine habitats where they spawn combined with lack of management—have no doubt contributed to their devastating declines, the fact that they were targeted on their aggregations is likely a major contributing factor. Other threatened croakers aggregate to spawn, including Japanese meagre (*Argyrosomus japonicus*; Labbish Chao, National Museum of Marine Biology and Aquarium, Taiwan, personal communication, 18 May 2014) and the large yellow croaker, whereas nonthreatened species are not known to spawn in aggregations (Sadovy and Cheung 2003, IUCN 2015).

Catchability is clearly an important factor in susceptibility of aggregating species, but are other factors involved? I now consider in more detail lethal (fishing mortality and catchability) and possible nonlethal (selectivity, disruption of spawning, etc.) effects in relation to the exploitation of spawning aggregations and the associated challenges of monitoring and managing aggregation fisheries.

How does fishing affect spawning aggregations

A major question is whether the declines in fisheries that heavily target spawning aggregations are just a matter of overfishing (i.e., lethal effects) and failure of management systems to adequately account for increased catchability or whether there are other nonlethal effects involved. Possible nonlethal impacts could result from reduced reproductive output at lowered animal densities, impacts on the numbers and quality of eggs produced, selective removals, or physical disruption of the act of spawning itself. Does conventional fishery management based on the "stock" concept and focus on effort and biomass adequately accommodate the important spatial, temporal, and biocomplexity elements (see below) associated with aggregate spawners? Put another way, is removing a fish from a spawning aggregation the same, in terms of its effect on reproductive output, as taking the same fish in the nonreproductive season, as is assumed by conventional stock assessments? If not, what are the implications for management?

Selectivity. Fisheries management is primarily concerned with populations (or "stocks"), biomasses and numbers, and rarely with inter- and intra-individual differences despite the fact that many longer-lived fishes have complex reproductive lives associated with which mature individuals contribute differentially to reproduction. Is there evidence that selective removals of particular size classes, genotypes, or sex can affect reproductive output in the short or long term or that the act of removal itself negatively affects reproduction or other population components? Possible effects range from the physical disturbance of spawning and the reduction of egg output to the disruption of reproductive processes, such as mate selection, sex-change schedules, or spawning mode, or possible genetic impacts. In the Patagonian hake (*Merluccius hubbsi*) and brown-marbled (*E. fuscoguttatus*) groupers, for example, males arrive at spawning grounds prior to females, and in the hake, they stay longer, leaving one sex exposed to fishing for longer (Pajaro et al. 2005, Robinson and Samoilys 2013). In a range of marine fishes, offspring size and/or quality increase with female age and/or size, whereas in some species, larger females spawn for longer periods and more frequently than smaller females (e.g., Hixon et al. 2014). In such cases, size-selective fishing on gathered ripe adults could have implications for reproduction through sex ratio shifts or egg production. Significant and differential exposure to fishing by size or sex could have genetic consequences (Hutchings and Fraser 2008) or influence sex-change schedules in species with social control of sex change (Sadovy de Mitcheson and Erisman 2012).

A fascinating but little-understood aspect of aggregation spawning is how migrating young fish know where spawning sites are located, their degree of site fidelity, and what happens if migrations are disrupted. Many aggregation sites are highly consistent in location over long time periods, with indications of a strong degree of aggregation-site fidelity by individuals across tropical and temperate species (e.g., Warner 1990, Colin 1996, Lowerre-Barbieri et al. 2013). Studies suggest that aggregation sites, or migration routes to them, are learned by young fish following older, more experienced, conspecifics, as in brown surgeonfish (*Acanthurus nigrofuscus*; Mazeroll and Montgomery 1998), or are otherwise culturally transmitted, as in bluehead wrasse (*Thalassoma bifasciatum*), plaice (*Pleuronectes platessa*), and Atlantic cod (Warner 1990, Arnold and Metcalfe 1995, Petitgas et al. 2010). Learning in fishes can be important in species composed of multiple age groups that provide the opportunity for social transmission and could therefore be important for many longer-lived aggregating species. Petitgas and colleagues (2010) determined for nine marine fish stocks that stock collapses and poor recovery involved the loss of biomass from fishing and structural biological elements related to life-cycle diversity

in long-lived stocks with complex life cycles (e.g., North Sea herring, California sardine, capelin).

Depensation. For a phenomenon of abundance, such as congregatory spawning, whereby benefits are somehow derived from coming together to spawn in large and concentrated numbers, it is reasonable to predict that thresholds of animal numbers or density might exist below which reproduction may be negatively affected or recovery impeded (e.g., Hutchings and Reynolds 2004). Positive relationships between population size or density and various indicators of fitness are referred to as *Allee effects*, and negative rates of population growth that occur below a critical population level are termed *depensation* (Berec et al. 2006). Allee effects have two forms: Component effects are positive relationships between surrogates of individual fitness and population density, such as mate finding, fertilization success or probability, or predator avoidance; demographic effects, which are harder to demonstrate, are positive relationships between *per capita* population growth rate and population size or density that could substantially reduce fitness (and therefore recovery potential) at low population densities (Courchamp et al. 2006). Both are indicated in aggregation fisheries.

Although evidence for depensation at anything other than low population levels is weak and sufficient information for the majority of species is scant, quantitative assessments across a taxonomic range of exploited marine fish taxa show that depensation cannot be ignored. Hilborn and colleagues (2014) examined over 100 stocks that were depleted to less than 20% of their maximum observed stock size. Their hierarchical meta-analysis showed little evidence for depensation. However, they could not rule out depensation at low stock sizes because they had examined few populations at very low levels (i.e., 1% of unfished biomass). Myers and colleagues (1995) came to similar conclusions but did detect some evidence of depensation in several stocks of salmon and a herring. Using meta-analyses, Keith and Hutchings (2012) found considerable variability among 104 exploited marine fish species in standardized *per capita* population growth changes with abundance. Evidence for an Allee effect was found in Atlantic cod and pollock, both aggregate spawners. Gascoigne and Lipcius (2004) found indications of Allee effects in 59 marine species mainly invertebrates (sedentary and mobile) and particularly among broadcast spawners and in exploited populations. The vast majority of fished populations globally, however, are not assessed, and the growing number of threatened listings in marine fishes and declines in many fisheries attest to serious reductions among many; clearly, the jury is still out on depensation.

As we learn more about the biocomplexities of fish reproductive processes from field observations and experimental work, signs of Allee-like effects are emerging with indications of possible underlying causation (e.g., Liermann and Hilborn 2001). In Atlantic cod and halibut (*Hippoglossus hippoglossus*), for example, stress or physical disruption exhibited by aggregated animals subjected to fishing gear can influence complex mating behaviors and sexual selection (mate choice, mate competition) and could ultimately affect reproductive success and population growth (e.g., Rowe and Hutchings 2004, Dean et al. 2012). The physical disturbance of aggregations by fishing was one of two likely reasons for the rapid collapse, within a few years of initiation, of the Namibian orange roughy (*Hoplostethus atlanticus*) fishery (Oelofson and Staby 2005). In Pacific herring (*Clupea harengus pallasi*), pheromone concentrations from milt that trigger spawning in sexually mature fish drop below critical thresholds at reduced male numbers (Carolsfeld and colleagues 1997).

Within large and highly concentrated spawning aggregations, severely reduced fish numbers could affect fertilization success or the outcomes of predation, including from fishing. The Nassau and camouflage groupers form small mating groups of a single female and multiple males within larger aggregations, a mode of reproduction referred to as *group spawning* (figure 1b). In Nassau grouper, direct observations suggest lower rates of courtship and color changes in these mating subgroups that could feasibly result in lower overall *per capita* reproductive or fertilization rates (Brice Semmens, Scripps Institute of Oceanography, UCSD, personal communication, November 2005). In camouflage grouper, adults in severely reduced aggregations were rarely seen to interact, unlike in unfished ones (pers. obs.) (figure 1c). Although this hypothesis has yet to be tested, studies do indicate that in aggregating Atlantic cod, fertilization rates are sensitive to sperm concentration, and in bluehead wrasse, sperm numbers and fertilization rates are higher in multi- as opposed to single-male spawnings (Marconato et al. 1997, Rowe et al. 2004, Butts et al. 2009). Moreover, for several snappers, as the number of aggregating adults in a spawning group become reduced, egg predation by specialist egg feeders such as the black snapper (*Macolor niger*), or opportunistic predators such as whale sharks (*Rhincodon typus*) and mantas, may become more problematic (Sadovy de Mitcheson and Colin 2012). Similarly, in the ABT, reduced spawning groups could lead to "predator pits," resulting in reduced larval survival (Bakun 2013).

In summary, although firm evidence for functionally significant depensation in exploited fish populations at anything other than very low abundance may be uncommon in fishes, few reduced populations have been studied, and there are clear indications that depensation does or could occur in aggregate spawners. If it does, there are important management implications. Liermann and Hilborn (2001) concluded that very low population abundances should be avoided for many reasons and that the range of abundance where depensation cannot be ruled out is likely to be well below commonly adopted limit reference points for fisheries. Nonetheless, many fisheries are dropping to very low abundances or are not recovering at rates predicted by fishery science (e.g., Hutchings and Reynolds 2004). For aggregate spawners, it is reasonable to predict that reproduction could

be negatively affected when the functional reproductive units, or behaviors that depend on high numbers and densities, break down at low fish densities or abundance.

Population structure. Largely for practical reasons, fisheries management was long (and largely still is) based on the concept of "stocks," with management units and monitoring typically treating localized demographic effects and local overfishing as unimportant (e.g., Stephenson 2002). A *stock* describes characteristics of semidiscrete groups of fish with some definable attributes of interest to fishery managers. Such groups may or may not be biologically discrete reproductive units (populations), but this reality was largely ignored until relatively recently, mainly because early genetic work on most marine species involving electrophoresis showed little intraspecific variation (Cadrin and Secor 2009). Genetic methods have since advanced to distinguish population structure in marine fishes at a much finer scale than assumed previously. However, population modeling has yet to broadly incorporate this new knowledge into most fish stock assessments, partly because genetic studies are available for relatively few highly valuable commercial, mostly temperate, species and partly because metapopulations were previously not considered to apply to wide-ranging broadcast spawners (Kritzer and Sale 2006, Cadrin and Secor 2009).

As we are learning, combining fishery data across subpopulations or, conversely, ignoring spatial population structures and reproductive units can obscure localized declines, deplete genetic resources, and lead to collapses even if a stock is managed at apparently sustainable levels (numbers/biomass) of exploitation (e.g., Stephenson 2002, Ying et al. 2011). Such considerations are particularly relevant for mobile species that home to spawning areas, have complicated or spatially restricted population structures, and/or exhibit localized responses to fishing, such as Atlantic cod, herring, and pollock (Ruzzante et al. 2006, Bailey 2011, Armstrong et al. 2013). Fishing on spawning and prespawning fish was implicated as one of several factors in the spectacular crash of the Aleutian Basin Donut Hole stock of pollock; the stock has still not recovered 20 years after a moratorium was introduced in the early 1990s suggesting a local breeding stock which was not considered in management (Bailey 2011).

In tropical aggregate spawners, molecular, fishery, and field research have revealed spatial scales from extremely localized to regional patterns of population distribution—of much relevance for determining units for management. For example, localized (subnational) measures are important when there is high larval retention and limited adult movement. Considering larval dispersal kernels from a single managed spawning aggregation of squaretail coral grouper (*Plectropomus areolatus)*, Almany and colleagues (2013) predicted that 50% of larvae settled within 14 kilometers of the study site in Papua New Guinea. A combination of local and regional approaches to management within several genetically isolated regions in the Caribbean is clearly called for in the case of the Nassau grouper (Jackson et al. 2014). For wide-ranging species, although time–area protection can be beneficial, international measures to reduce overfishing may be the most crucial measure for recovery, as in ABT (Armsworth et al. 2010), which return to just a few spawning areas (Fromentin and Powers 2005).

Challenges and opportunities in the management of spawning aggregation fisheries

There is nothing inherently wrong with fishing on spawning aggregations—if it is done right. At subsistence levels, this was done for centuries, and if properly managed, commercial targeting of spawning fish can be sustained (e.g., Bering sea Pollock stock; Morell 2009). For some species, it is the only time that fish are readily accessible for fishing, whereas others, such as capelin and herring, are sought specifically for roe. However, such fisheries are particularly challenging to monitor and manage and evidently need a more precautionary approach than nonaggregating species do. There would appear to be excellent opportunities for efficient management if enforcement effort can be concentrated on small areas for brief periods each year on well-understood spawning aggregations. What does history and experience tell us about the challenges and opportunities for the management of large- and small-scale spawning aggregation fisheries?

For many fisheries, closed reproductive seasons and areas were among the earliest of all management measures. In the 1660s, for example, for groundfish in North America, according to the Massachusetts legislature, "no man shall henceforth kill any codfish, hake, haddock, or pollock to dry for sale in the month of December or January because of their spawning tyme" (Armstrong et al. 2013). Native Hawaiians prohibited the take of ocean bonito and mackerel during the spawning season (Titcomb 1972). In Palau, a traditional management tool was used to restrict the harvest of migrating rabbitfish and groupers in the early 1990s after declines in landings were noted. And although spawning aggregations or associated migrations were often a focus of subsistence fisheries in many tropical countries, where traditional knowledge of their timing and locations was often detailed, their protection was among the first measures to be considered by communities if fish numbers declined, as in Palau, Kiribati, and Papua New Guinea (e.g., Johannes 2002, Hamilton et al. 2005). However, with the breakdown of traditional practices and following the growing commercialization (including export) of inshore fisheries, fishing intensified, and management and enforcement did not keep pace. In temperate regions, although many fisheries are managed for fishing effort and biomass, the science largely ignores nonlethal effects, and data can be sparse for species with spatially varying catch histories (Cope and Punt 2011).

For multiple reasons already discussed, aggregations are attractive targets to fish, but there are also compelling biological and economic reasons not to fish them if they are not managed. High catchability, reduced cost per unit of catch

and high temporal and spatial predictability can readily lead to waste and overexploitation (Sadovy de Mitcheson and Erisman 2012). For the Gulf corvina (*Cynoscion othonopterus*), in Mexico, high demand during the Easter period was met by fishing during its brief aggregation period and good prices gained (figure 1d). Approximately 1.5–1.8 million fish are harvested annually from spawning aggregations of Gulf corvina during 21–25 days of fishing (Erisman et al. 2012); however, a post-Easter slump in demand produced a market glut and prices plummeted, leading to wastage. Similarly, seasonal variations in the first sale price of adult plaice and turbot (*Scophthalmus maximus*) were considerably lower when a large number of ripe fish became available (van Overzee and Rijnsdorp 2014). Even the physical condition (and therefore the economic value and mortality) of fish can differ between seasons. In the live fish trade, for example, gravid grouper females experience higher rates of mortality than at other times (Patrick Chan, commercial live fish trader, Hong Kong, personal communication, February 2003), whereas the flesh of Atlantic cod and other species may be softer or less acceptable (and therefore cheaper) because of energy transfer from the soma to the gonads during the reproductive season (Love 2001).

Economically, a further consideration has emerged. Exploited fishes were once safeguarded because as their numbers declined they became increasingly expensive to exploit, reaching economic before biological lower limits of fishery viability. However, this "safety valve" vanishes for particularly desirable species when consumers can afford to pay almost any price, and price increases with rarity. In such cases, ecological extinction can precede economic extinction—the so-called anthropogenic-Allee effect (Courchamp et al. 2006). The Chinese bahaba, initially fished mainly on its aggregations, is highly prized for its swim bladder in Chinese markets; as the species approaches extinction, the price of a single large swim bladder rocketed to over US$600,000 in 2015 in China, stimulating interest and sales despite its protected status in China (Sadovy and Cheung 2003, Apple 2015). Such economic shifts make enforcement particularly challenging.

Monitoring and hyperstability. Good monitoring is essential for effective management and for aggregate spawners is often done only using CPUE on aggregated fish or by underwater visual census for some species. Exploited species, or the fishers who exploit them, that change their behavior over time face a breakdown in the assumed proportional relationship between CPUE and abundance (CPUE is considered a proxy for abundance in stock assessments; its measurement is an important input to fishery models). As populations decline from overfishing, adults continue to concentrate to spawn maintaining CPUE and masking population decline until close to collapse. This condition is termed *hyperstability* (Hilborn and Walters 1992). Unrecognized by fishers able to maintain their catches from aggregations and undetected by managers seeing stable aggregation catches or CPUE if monitoring focuses only on aggregations, populations can dwindle undetected, becoming so severely reduced that recovery may become compromised, especially if depensation is also acting (Hutchings 2000, Mullon et al. 2005). In exploring different patterns of fishery collapse (i.e., to less than 10%), Mullon and colleagues (2005) attributed "plateau-shaped" trajectories preceding collapses to surreptitiously increasing exploitation combined with a depensatory mechanism at low population levels. These collapses are difficult to predict, happen relatively suddenly, and typify those of many aggregate-spawning species exploited on their aggregations (figure 3).

For aggregations accessible enough to be surveyed by underwater visual census (UVC), as for many reef fishes, several factors make their meaningful assessment challenging. During short spawning seasons or periods, fish numbers can change daily as fish enter and leave the aggregation site, current conditions can influence whether fish are more or less visible, the day of peak spawning numbers can vary from month to month, large sites may need to be subsampled, and core aggregation areas can shift from year to year (Sadovy de Mitcheson and Colin 2012). Such spatial and temporal variability require careful and well-designed monitoring and can be expensive and challenging to do regularly. Although technology greatly assists these studies (acoustic telemetry, video, etc.), UVC remains a challenging assessment method for fish spawning aggregations.

Management. There is no one-size-fits-all for managing fisheries of aggregate spawners, whether small- or industrial-scale, but to manage them effectively requires considerable information at the appropriate temporal and spatial scales, appropriate management, and effective enforcement. Catchability increases when fish aggregate to spawn, but whether exploited aggregations themselves need management or the fishery as a whole depends on both intrinsic (biological) and extrinsic (fishery) factors (e.g., Grüss and Robinson 2014, van Overzee and Rijnsdorp 2014). Assessing the condition of such fisheries can be very difficult, whether by fishery-dependent or -independent means, whereas catch data compiled across multiple reproductive units, as is typical, are likely to be insensitive to localized population declines. And although both hyperstability and catchability are risk factors for fisheries management that can be addressed (e.g., cod, orange roughy) and ignoring them can result in sudden and serious collapses, at a global level, very few fisheries address these factors (Hutchings and Reynolds 2004, Oelofson and Staby 2005). Standard fishery monitoring (CPUE, annual catches, etc.) and conventional management tools of effort controls (total fishers, bag limits, etc.) and catch limits (total allowable catches, quotas, etc.) can work for fisheries that focus on spawning aggregations—but only if applied at the appropriate biological (fish population) scale. Standard fishery models involve assumptions that may not be valid for aggregate spawners. For example, per-recruit models assume

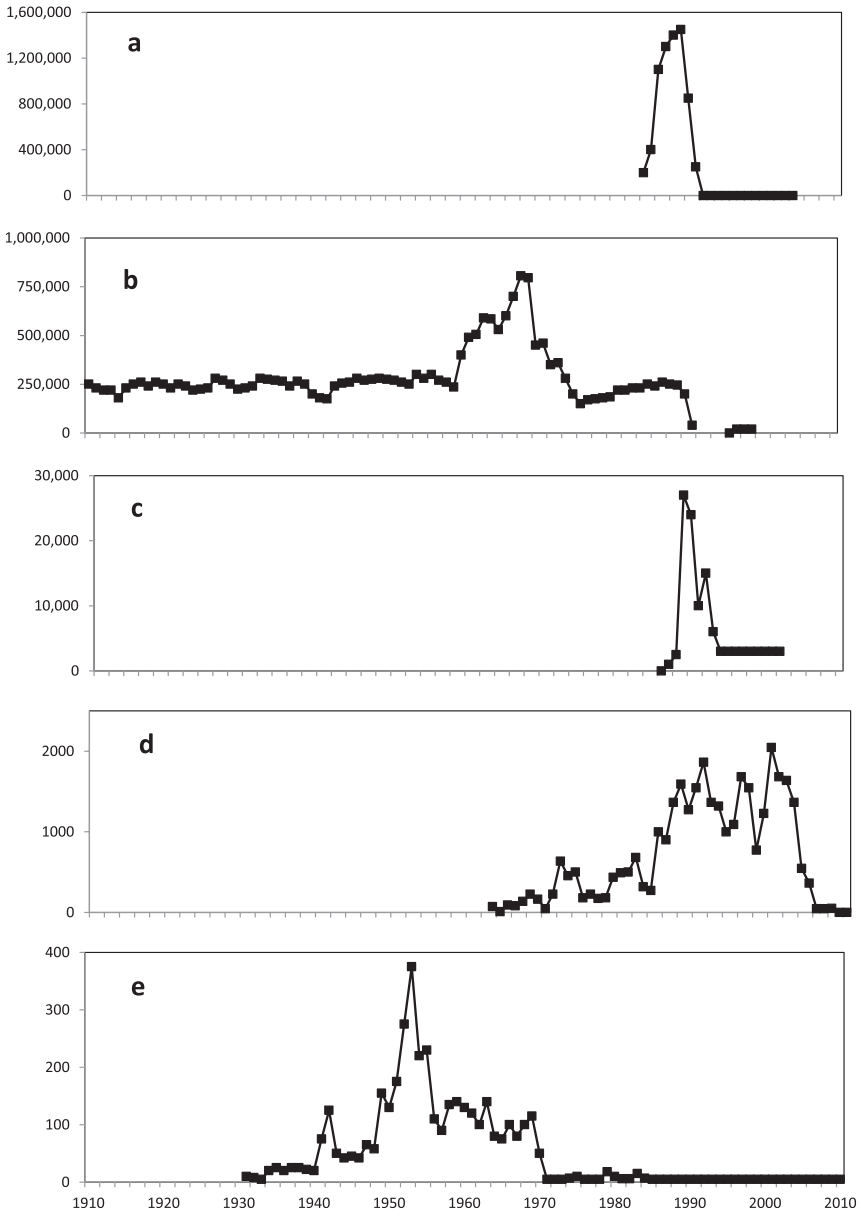

Figure 3. Catch in tonnes from five fisheries of species with very different natural productivities that target spawning aggregations. All illustrated fisheries underwent sudden collapses for reasons not fully understood and for which depensation cannot be ruled out as a possible reason for lack of recovery: (a) commercial Alaska (walleye) pollock (*Theragra chalcogramma*) at the Donut Hole ground (Bailey 2011); (b) commercial Atlantic cod (*Gadus morhua*; Millenium Ecosystem Assessment); (c) commercial orange roughy (*Hoplostethus atlanticus*; Oelofson and Staby 2005); (d) barred sandbass (*Paralabrax nebulifer*; Erisman et al. 2012) recreational; the original data, given in numbers of fish, were converted to weight at 0.9 kilograms (kg) per fish (B. Erisman, Department of Marine Science, University of Texas at Austin, personal communication, 5 May 2015); (e) commercial Gulf and broomtail groupers (*Mycteroperca jordani *and* M. xenarcha*; www.nmfs.noaa.gov/pr/species/Status%20Reviews/gulf_grouper_sr_2015.pdf).

reproductive output to be proportional to spawning stock biomass and usually ignore possible nonlethal effects.

Spatial and temporal management measures merit greater attention and can be very effective if implemented with other measures and adequately scaled for reproductive units and connectivity. Indeed, relatively small investments in spatial management of spawning aggregations can potentially offer disproportionately large benefits to fisheries and biodiversity conservation (Erisman et al. 2015a). For some species, spatial protection must account for migration pathways to and from aggregations and be adequately buffered for within- and between-year shifts in core aggregation areas (Nemeth 2012, Robinson and Samoilys 2013). Seasonal measures such as sales bans or catch shares during the reproductive season can address gluts due to market flooding and may be particularly appropriate where capacity is limited to protect spawning sites or there is limited knowledge of their locations. Indeed, the best-protected aggregations are those not yet discovered! Seasonal protection is likely to become increasingly important as we become better able to predict where spawning sites might be and relocate them once found but remain hard-pressed to manage them.

In small-scale tropical coastal fisheries where local communities have a history of taking fish from spawning aggregations in seasonally defined fisheries but little enforcement capacity or biological knowledge, there are both challenges and opportunities for sustaining exploited aggregate spawners. Management is particularly problematic for species of low productivity, particularly when export markets are introduced (which increases demand further). Over 60% of exploited reef fish aggregations of known status have declined or disappeared (*www.SCRFA.org*). Although there is considerable opportunity for management at the local community level in many places, much depends on community perceptions regarding the condition of the resource, the cultural significance of the species involved, and the governance system. For example, in Bua Province, Fiji, communities banned grouper catch during its main spawning month of August but were reluctant to protect a well-known mullet aggregation site because of the cultural practice of holding an annual feast associated with the congregation of two mullet runs. Declines had been noted in both species, but groupers were not a species of choice for local consumption, and the community did not associate their own fishing with the declines, blaming it on

outsiders (Fox et al. 2012). In many communities, greater awareness of the significance of spawning aggregations, better understanding of the implications of their extirpation for local catches, and greater capacity for stewardship could substantially influence local decisionmaking and resource-use practices (e.g., Hamilton et al. 2005, Robinson and Samoilys 2013, Erisman et al. 2015b).

At the national level, better stewardship and supporting policies can come from an improved understanding of the cultural and economic importance of small-scale fisheries and the implications of exports. A recent web-based pledge campaign for the protection of spawning groupers in Fiji, for example, gained much public support (8500 pledges currently) on the basis of the concept that protecting these fish is also part of protecting a traditional way of life (4FJ 2015). Value-chain analyses can help to raise awareness of winners and losers in these fisheries and of the implications of exporting aggregation-caught fish (Sadovy de Mitcheson and Yin 2015). The globalization of small-scale fisheries of low productivity and lack of management, in particular, poses a very real risk in many developing countries, but smaller economies can exercise control over their exports (e.g., Fiji and Palau banned the export of live groupers because of concerns about overfishing; Sadovy de Mitcheson and Yin 2015).

The bigger picture

Wilcove and Wikelski (2008) have stated, "If migration is seen as a phenomenon of abundance, then its protection will require decisionmakers to adopt a much more pro-active approach to conservation—in effect, to protect species while they are still abundant"—much the same can be said for aggregation-spawning species when fisheries are heavily focused on their reproductive aggregations. At stake are not just enormously important sources of fishery production and spectacular natural phenomena but also important components of marine ecosystems and their biodiversity. For example, the collapse of capelin stocks affected other species in the ecosystem at higher levels in the food web (Hopkins and Nilssen 1991). The brief annual cubera snapper (*Lutjanus cyanopterus*) and dog snapper (*L. jocu*) aggregations in Belize are stopping places for migrating whale sharks that time their movements to gorge on the billions of nutritious eggs produced (Heyman et al. 2001). Spawning Bering Sea pollock are a staple for marine mammals, seabirds and fishes, and its management should be considered within this ecosystem context (Morell 2009). The egg "boons" produced by high numbers of predictably concentrated adults are an exceptionally nutrient-rich trophic injection into the marine food web (figure 1; Archer et al. 2015, Fuiman et al. 2015), whereas large biomass fluxes accompany seasonal movements of reef fishes (Nemeth 2012).

The good news is that the management of aggregating marine species can and does work with sufficient knowledge and commitment to enforcement. The annual spawning aggregation of Togiak, Alaska, herring under management has produced a 20-year annual harvest of over 18,000 tonnes. The careful management of the largest aggregation of sockeye salmon (*Oncorhynchus nerka*) in the world, in Bristol Bay, Alaska, led to a relatively stable fishery that produced a 20-year average of over 35 million fish harvested per year (Westing et al. 2005). Positive outcomes came from the management of plaice spawning aggregations in the North Sea (Rijnsdorp et al. 2012). Several grouper aggregations show increases in mean size and/or catches and numbers following effective protection based on good science (Nemeth 2005, Hamilton et al. 2011). Genetic, fishery, and biological information on the reproduction of the red seabream (*Chrysophrys/Pagrus auratus*) enabled the determination of the appropriate temporal and spatial scales to successfully safeguard their spawning aggregations in a recreational fishery in western Australia (Wakefield 2010).

The bottom line is that evidence strongly suggests that we should fish spawning aggregations at commercial levels cautiously—and only with adequate management and monitoring. In reality, however, for the great majority of commercial and recreational fisheries globally (i.e., nonsubsistence), such conditions are unlikely to be met, and a precautionary approach is urgently called for to manage risk (Hilborn et al. 2001, Pitcher and Cheung 2013). For aggregating species, that risk appears to be particularly acute because of both lethal and nonlethal factors—especially in the case of low-productivity species. Therefore, where there is insufficient management and enforcement, it is proposed that no fishing of spawning aggregations should occur until appropriate measures are implemented to ensure their sustainable use. There is also a need to conduct further research to ensure that fishery models, certifications, standards, and guidelines adequately accommodate the risk factors. In other words, the sustainable exploitation of fish spawning aggregations needs to be mainstreamed into fishery management.

Spawning aggregations are the foundation of many of our major large- and small-scale fisheries and are integral components of marine ecosystems. As we learn more about the biocomplexities of aggregating marine fishes and mainstream that understanding into standard fishery-management practices and trade, we can ensure that fish spawning aggregations persist as beautiful, natural, and highly productive phenomena that play an essential and unique role on our planet. Managing fisheries that target spawning aggregations, as we must do while they are still abundant, will seriously test our ability to apply truly precautionary management.

Acknowledgments

I am most grateful to Michael Domeier, William Cheung, and George Mitcheson for their helpful comments during the preparation of this manuscript. Rachel Wong provided technical support. Science and Conservation of Fish Aggregations (*www.SCRFA.org*) is largely supported with funds from the David and Lucile Packard Foundation. The comments and insights of Howard Choat and Keith Sainsbury and the anonymous reviewers significantly improved the article.

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