Mainstreaming fish spawning aggregations into fishery management calls for truly precautionary approach[1]

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Abstract

Many marine fishes mate in massive and spectacular gatherings at predictable times and places. These spawning aggregations are often attractive targets of fishermen. 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, and, if so, why, and how we can better manage these species. I present evidence that aggregate fish spawners are especially vulnerable, due to both increased catchability (lethal effects) and to biological factors (non-lethal 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 and compromise the chance of recovery, 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.

Introduction

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). Yet 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. Pitcher and Cheung 2013; Worm et al. 2009). Many of the remaining and less-well documented fisheries are also likely to be fully or overfished. Despite the rapid growth in mariculture (or fish farming), which has helped to increase supply, this does not take pressure off wild populations on which millions of people will continue to depend and, hence, must be adequately safeguarded.

Many exploited marine fishes have as their sole means of reproduction the formation of large temporary gatherings and many face growing threats to their population when these become more accessible to fishing during temporary periods of high abundance (Sadovy de Mitcheson and Erisman 2012). Over 60% of reef fish aggregations of known status have declined or disappeared (Russell et al. 2014; www.SCRFA.org). In Cuba, for example, an unusually detailed dataset spanning decades of monthly landings show that groupers (Epinephelidae) and snappers (Lutjanidae) that aggregate most predictably at a small number of spawning sites underwent more marked and sudden declines than species in the same commercial fishery that have longer reproductive seasons and less predictable spawning aggregation patterns (hence lower catchability) (Sadovy de Mitcheson and Erisman 2012). 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 (according to the International Union for Conservation of Nature Red List) and being considered for listing under the United States Endangered Species Act; most of its aggregations have disappeared or became severely reduced (Sadovy de Mitcheson et al. 2008). Although its congener does not form spawning aggregations and its catchability increases only slightly during the reproductive season, its fisheries remain viable.

But the problem is by no means isolated to reef species. In east Asia, seasonal spawning aggregations are formed by the large yellow croaker, *Larimichthyes crocea*, once one of the four major coastal fisheries of China (Liu and Sadovy de Mitcheson 2008). This fishery collapsed after peaking at about 200,000 tonnes in the mid-1970s after which time catches declined by over 90% in 20 years.

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Fishing was mainly on spawning aggregations and over-wintering grounds, with loss of important inshore nursery habitat to development also implicated in declines. The species has never recovered despite massive and expensive restocking programmes 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 temperate, deepwater and tropical species that aggregate to spawn and that have declined markedly over the last few decades is the specific role that fishing on their spawning aggregations has had in their declines. Understanding this is critically important for successfully managing species exploited on their spawning aggregations.

Whatever the ultimate evolutionary driver(s) of aggregation-spawning (i.e. for the benefit of adults, for eggs and/or larvae, or for both), 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 behaviour 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) and does not distinguish an aggregated from a non-aggregated fish or typically consider "non-lethal" effects (such as depensation or behavioural effects).

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 massive sources of sperms and eggs within large groups of temporarily gathered males and females (Fig. 1). Irrespective of spatial or temporal scales, all involve events with tens, hundreds, thousands or tens of thousands of conspecifics gathering predictably and consistently and for the purpose of spawning (Colin 1996; 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, cod to haddock, 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 pelagic fish, from sardines to herring.

The numbers of fish that gather seasonally to spawn in any one location can be, or once were, massive. 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 that fish far exceeded fishing effort. Aggregate-spawning species, from subsistence to small-scale/artisanal to industrial scale fisheries, are of enormous economic and food security value so it is of utmost importance to understand the impact of aggregation-fishing on such species and how they can best be managed. Of the top 20 fish species, 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, 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 critically important for hundreds of thousands of communities that depend on them (Fig. 3). Their low productivity makes them very susceptible to overfishing and slow to recover (Sadovy de Mitcheson and Colin 2012). In small-scale fisheries, just a few boats have the capacity to remove a large proportion of a single aggregation in a single season (pers. obs.).

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. A semi-quantitative treatment of 36 species of aggregating and non-aggregating species across a range of taxa, life history types, maximum body size (FishBase 2015) and conservation status (IUCN 2015) suggest that threat is negatively associated with a qualitative measure of catchability, independent of body size (another threat factor) (Fig. 2). Robinson and Samoilys (2013) developed a framework 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, type of aggregating behaviour, and fishery factors such as management

Figure 1.

*a. Top. Twinspot snapper (*Lutjanus bohar*) spawning in Palau, showing the massive and highly concentrated release of eggs that occurs predictably over just a few hours each year. Image: Tony Wu (www. tonywublog. com).*

b. Second from top. 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 colour) and multiple males (bicoloured). Image: Doug Perrine/ SeaPics.com.*

c. Third from top. The camouflage grouper, Epinephelus polyphekadion, *spawns in sub-groups in large aggregations but when numbers are depleted, intraspecific interactions are few. Image: Yvonne Sadovy de Mitcheson*

d. Bottom. 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. Image: Octavio Aburto / iLCP.*

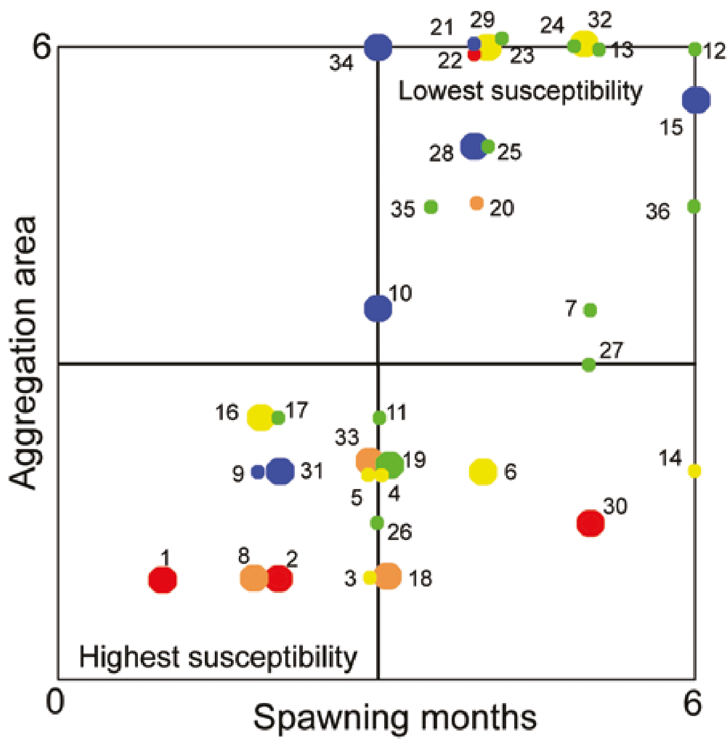

Figure 2. Thirty-six species of exploited aggregating and non-aggregating species of varying size (from 21 to 458 mm TL: FishBase 2015) and conservation status (IUCN 2015) plotted according to a qualitative indicator of catchability. The indicator combines length of spawning (1–6 months) and spatial concentration from 1 (highly concentrated when aggregated to spawn and easy to target) to 6 (no aggregate-spawning hence no change in susceptibility to catch) using available biological information (IUCN 2015). Each dot represents one fish: small dots are < 100 cm TL and large ones > 100 cm TL. Colours refer to IUCN Red List status: Red = critically endangered (CR); orange = endangered (EN); yellow = vulnerable (VU); blue = near threatened (NT); green = least concern (LT). 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).

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 non-aggregators, especially when their catchability is elevated. 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).

How does fishing impact on 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, non-lethal, effects involved. 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 non-reproductive 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 (weights) and numbers; rarely does it address 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 removal of reproducing fish of particular size classes, genotypes, or by 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 physical disturbance of spawning and reduction of egg output, to disruption of reproductive processes such as mate selection, sex change schedules or spawning mode, or there could be genetic impacts. In the Patagonian hake, *Merluccius hubbsi*, and brown-marbled grouper, *E. fuscoguttatus*, 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 increases with female age and/or size while 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 male to female, or female to male sex change (Sadovy de Mitcheson and Erisman 2012).

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).

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 et al. (2014) examined over 100 stocks depleted to less than 20% of their maximum observed stock size and could not rule out depensation at low stock sizes because they had examined so few populations at very low levels (i.e. 1% of unfished biomass). Myers et al. (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 of which are aggregate-spawners (e.g. Rowe and Hutchings 2004).

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 behaviours and sexual selection (mate choice, mate competition), and could ultimately affect reproductive success and population growth (e.g. Dean et al. 2012; Rowe and Hutchings 2004). Physical disturbance of aggregations by fishing was one of two likely reasons of the rapid collapse, within a few years of initiation, of the Namibian orange roughy, *Hoplostethus atlanticus*, fishery (Oelofsen 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 numbers (Carolsfeld et al. 1997).

Economically, a further consideration has emerged. Exploited fishes were once safeguarded because as their numbers declined they became increasingly expensive to exploit, reaching economic lower limits 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 USD 600,000 in 2015 in China, stimulating interest and sales despite its protected status in China (Apple 2015; Sadovy and Cheung 2003). Expensive tuna face the same situation (Collette et al. 2011). Such economic shifts make enforcement particularly challenging

Within large and highly concentrated spawning aggregations, severely reduced fish numbers could affect fertilisation success or the outcomes of predation, including fishing. The Nassau and camouflage groupers form small mating groups of a single female and multiple males within the larger aggregation, a mode of reproduction referred to as "group spawning" (Fig. 1b). In Nassau groupers, direct observations suggest lower rates of courtship and colour changes in these mating subgroups that could feasibly result in lower overall *per capita* reproductive or fertilisation rates (Brice Semmens, pers. comm.). In camouflage grouper, adults in severely reduced aggregations were rarely seen to interact, unlike in unfished ones (pers. obs.) (Fig. 1c). While this hypothesis has yet to be tested, studies do indicate that in aggregating Atlantic cod, fertilisation rates are sensitive to sperm concentration and in bluehead wrasse sperm numbers and fertilisation rates are higher in multi- as opposed to single-male spawnings (Butts et al. 2009; Marconato et al. 1997; Rowe et al. 2004). Moreover, for several snappers, as the numbers 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).

Population structure

Largely for practical reasons, fisheries management was long (and largely still is) based around the concept of "stocks", with management units and monitoring typically treating localised demographic effects, such as population structure and localised overfishing, as unimportant (e.g. Stephenson 2002). A stock describes characteristics of semi-discrete 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).

In tropical aggregate spawners, molecular, fishery and field research have revealed spatial scales from extremely localised to regional patterns of population distribution, of much relevance for determining units for management. For example, localised (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*, for example, Almany et al. (2013) predicted that 50% of larvae settled within 14 km of the study site in Papua New Guinea. On the other hand, a combination of local and regional approaches to management within several genetically isolated regions in the Caribbean for the Nassau grouper is clearly needed (Jackson et al. 2014).

Challenges and opportunities in managing 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 while 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 non-aggregating species. On the other hand, there are 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 amongst 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). 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 while 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. Hamilton et al. 2005; Johannes 2002). However, with the breakdown of traditional practices and following growing commercialisation (including export) of inshore fisheries, fishing continued 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 non-lethal 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. 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 (Fig. 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 variation in the first sale price of adult plaice and turbot, *Scophthalmus maximus*, were considerably lower when large numbers of ripe fish became available (van Overzee and Rijnsdorp 2014). Even the physical condition (and hence 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 pers. comm.), while the flesh of Atlantic cod and other species may be softer or less acceptable (hence cheaper) due to energy transfer from soma to gonads during the reproductive season (FAO no date).

Monitoring and hyperstability

Good monitoring is essential for effective management, and for aggregate-spawners can be done using catch per unit effort (CPUE) on aggregated fish and by underwater visual census for some. Exploited species, or the fishers who exploit them, that change their behaviour over time face a breakdown in the 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". Unrecognised 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 occurring (Erisman et al. 2015; Hutchings 2000; Mullon et al. 2005). 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 (Fig. 3). Underwater monitoring is well-suited for assessing accessible species in relatively discrete aggregations but the temporal and spatial dynamics of the target aggregation should be well-understood to avoid misleading outcomes (Colin et al. 2003).

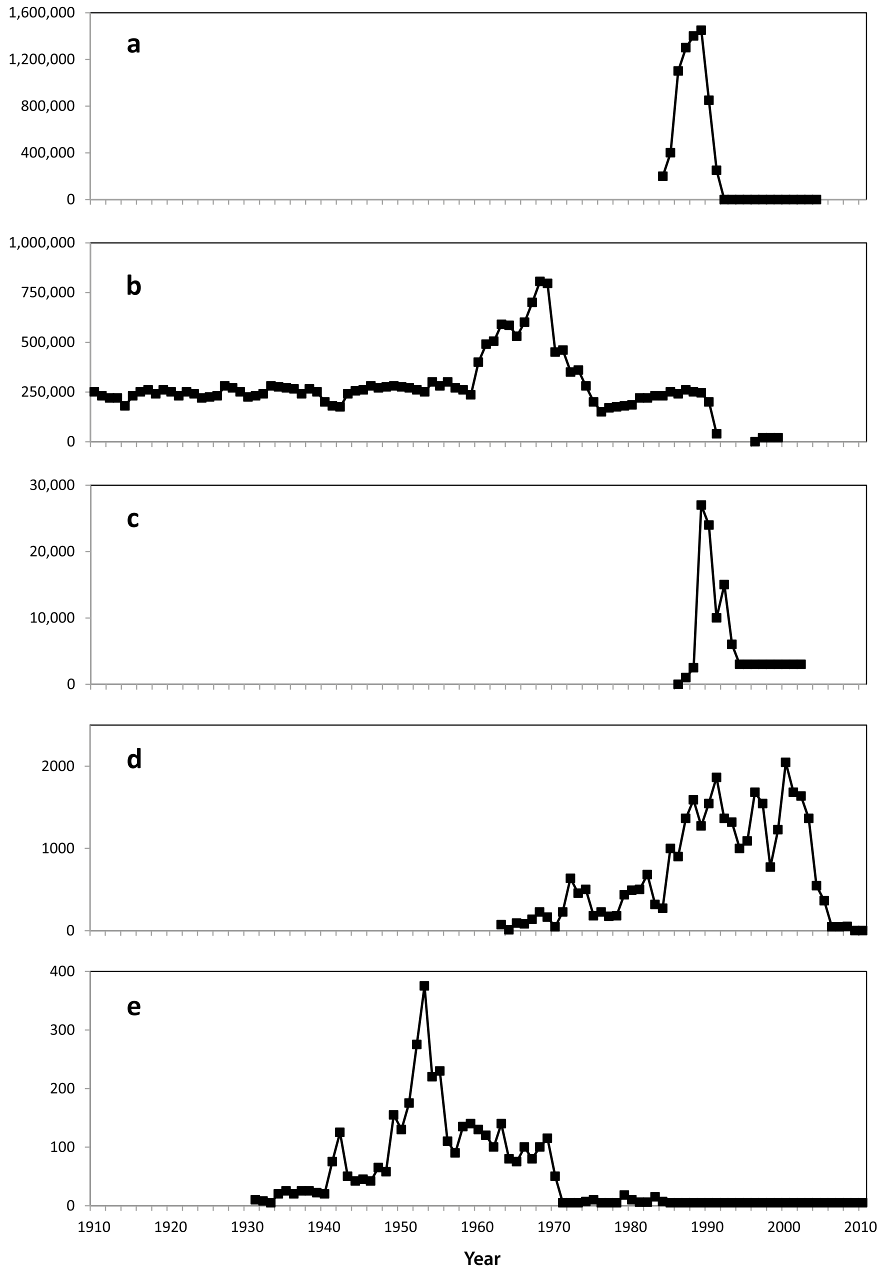

Figure 3. Catch in tonnes from five fisheries of species with very different natural productivities that target spawning aggregations. All illustrated fisheries underwent sudden collapses for reasons not fully understood and for which depensation cannot be ruled out as a possible reason for lack of recovery;

(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, *Oelofsen and Staby (2005);*
(d) *barred sandbass,* Paralabrax nebulifer, *Erisman et al. (2012) recreational; original data given in numbers of fish were converted to weight at 0.9 kg per fish (B. Erisman, pers. comm.)*
(e) *commercial Gulf and broomtail groupers* Mycteroperca jordani *and* M. xenarcha *(http://www.nmfs.noaa.gov/pr/species/Status%20Reviews/gulf_grouper_sr_2015.pdf).*

Management

There is no one-size-fits-all for managing fisheries of aggregate spawners (Russell et al. 2012). 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 fishery-independent means, while catch data compiled across multiple reproductive units, as is typical, are likely to be insensitive to localised 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 specifically 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 (e.g. total fishers, bag limits) and catch limits (e.g. total allowable catch, quotas) can work for fisheries that focus on spawning aggregations but only if applied at the appropriate biological (fish population) scale; moreover, they typically do not consider possible non-lethal effects, which should also be considered.

Spatial and temporal management measures far merit greater attention as management measures for aggregating species than they have received to date, and can be very effective and efficient 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. 2015). For some species, spatial protection must also account for migration pathways to and from aggregations and be adequately buffered for within-year 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 where there is limited knowledge of their locations. Indeed, the best-protected aggregations are those not yet discovered, but which should be seriously considered in the case of projects that seek only to locate aggregation sites without a spatial protection in place or soon to be introduced! Seasonal protection is likely to become increasingly important as we become better able to predict both where and when spawning occurs and better able to relocate spawning sites once found, but continue to be hard-pressed to manage them effectively.

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 further increases demand). While 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 the harvesting of groupers during their main spawning month of August but were reluctant to protect a well-known mullet aggregation site due to the cultural practice of holding an annual feast associated with the congregation of two mullet runs. Moreover, it is far from clear what benefits are gained by many source countries when vulnerable species, already limited in supply for domestic markets and exploited heavily from aggregations, are increasingly being exported; serious consideration should be given to ban exports of aggregation-caught fish to preserve local population, supply domestic markets and maximise economic benefits to source countries (e.g. Sadovy de Mitcheson and Ramoica 2015)

At the national level, greater stewardship and supporting policies can come from improved understanding of the cultural and economic importance of small-scale fisheries and implications of exports. A recent web-based pledge campaign for the protection of spawning groupers in Fij, for example, gained much public support (8,500 pledges currently) based on 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 for source countries of exporting (Sadovy de Mitcheson and Yin 2015). The globalisation of small-scale fisheries of low productivity and the lack of management, in particular, poses a very real risk in many developing countries but many smaller economies could effectively control their exports (e.g. Fiji banned the export of live groupers due to concerns about overfishing) (Sadovy de Mitcheson and Yin 2015). As examples, both Chuuk and Palau have bans on grouper exports, either seasonally (Chuuk) or all-year (Palau) (pers. obs.).

The bigger picture

"If migration is seen as a phenomenon of abundance, then its protection will require decision-makers to adopt a much more pro-active approach to conservation-in effect, to protect species while they are still abundant" (Wilcove and Wikelski 2008). 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, their biodiversity and other opportunities for income. 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, *Lutjanus cyanopterus*, and dog, *L. jocu*, snapper 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). The egg "boons" produced by high numbers of predictably concentrated adults are an exceptionally nutrient-rich trophic injection into the marine food web (Archer et al. 2015; Fuiman et al. 2015) (Fig. 1), while large biomass fluxes accompany seasonal movements of reef fishes (Nemeth 2012). An analysis of Nassau grouper aggregations in Belize showed that the net worth of not exploiting an aggregation could exceed by more than 20 times the value of landed fish (from ecotourism and fishery production) (Sala et al. 2001).

The good news is that managing 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. 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 managing 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 reproduction of the red seabream, *Chrysophrys* (=*Pagrus*) *auratus,* enabled the determination of 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 only cautiously, and only with adequate management and monitoring. In reality, however, for the great majority of commercial and recreational fisheries globally (i.e. non-subsistence) 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 non-lethal factors, and especially in the case of low productivity species (many reef and deepwater species in particular). 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 sufficiently accommodate the risk factors, and that other possible benefits (e.g. ecosystem, ecotourism) are considered. In other words, the sustainable exploitation of fish spawning aggregations needs to be mainstreamed into all aspects of fishery management and fish conservation.

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