Contributed Paper

A Global Baseline for Spawning Aggregations of Reef Fishes

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Abstract: *Species that periodically and predictably congregate on land or in the sea can be extremely vulnerable to overexploitation. Many coral reef fishes form spawning aggregations that are increasingly the target of fishing. Although serious declines are well known for a few species, the extent of this behavior among fishes and the impacts of aggregation fishing are not appreciated widely. To profile aggregating species globally, establish a baseline for future work, and strengthen the case for protection, we (as members of the Society for the Conservation of Reef Fish Aggregations) developed a global database on the occurrence, history, and management of spawning aggregations. We complemented the database with information from interviews with over 300 fishers in Asia and the western Pacific. Sixty-seven species, mainly commercial, in 9 families aggregate to spawn in the 29 countries or territories considered in the database. Ninety percent of aggregation records were from reef pass channels, promontories, and outer reef-slope drop-offs. Multispecies aggregation sites were common, and spawning seasons of most species typically lasted <3 months. The best-documented species in the database, the Nassau grouper (*Epinephelus striatus*), has undergone substantial declines in aggregations throughout its range and is now considered threatened. Our findings have important conservation and management implications for aggregating species given that exploitation pressures on them are increasing, there is little effective management, and 79% of those aggregations sufficiently well documented were reported to be in decline. Nonetheless, a few success stories demonstrate the benefits of aggregation management. A major shift in perspective on spawning aggregations of reef fish, from being seen as opportunities for exploitation to acknowledging them as important life-history phenomena in need of management, is urgently needed.*

Keywords: aggregation fishing, fish conservation, fisheries, fishery management, grouper, overexploitation, reef fishes, spawning aggregation

Una Referencia Global para Agregaciones de Desove de Peces de Arrecifes

Resumen: *Las especies que periódica y previsiblemente se congregan en tierra o en el mar pueden ser extremadamente vulnerables a la sobrexplotación. Muchos peces de arrecifes de coral forman agregaciones de desove que cada vez más son objeto de pesca. Aunque son bien conocidas las declinaciones severas de unas cuantas especies, la extensión de este comportamiento en los peces y los impactos de la pesca en agregaciones no son ampliamente conocidas. Para perfilar globalmente a las especies que forman agregaciones, establecer una referencia para trabajo futuro y reforzar el caso para protección, nosotros (como miembros de la Sociedad para la Conservación de Agregaciones de Peces de Arrecifes de Coral) desarrollamos una base de datos global*

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sobre la ocurrencia, historia y manejo de agregaciones de desove. Complementamos la base de datos con información de entrevistas con más de 300 pescadores en Asia y el Pacífico occidental. Sesenta y siete especies, casi todas comerciales, en nueve familias se agregan para desovar en los 29 países o territorios considerados en la base de datos. Noventa y nueve porciento de los registros de agregación fueron de canales de paso en arrecifes, promontorios y pendientes afuera de los arrecifes. Los sitios de agregación de numerosas especies fueron comunes y las temporadas de desove de la mayoría de las especies típicamente duraron <3 meses. La especie mejor documentada en la base de datos, Epinephelus striatus*, ha experimentado declinaciones sustanciales en agregaciones en todo su rango de distribución y actualmente es considerada amenazada. Nuestros hallazgos tienen importantes implicaciones de conservación y manejo para especies que forman agregaciones dado que las presiones de explotación están incrementando, casi no hay manejo efectivo y se reportó que 79% de las especies suficientemente documentadas están declinando. Sin embargo, algunas historias de éxito demuestran los beneficios del manejo de agregaciones. Se requiere urgentemente un cambio de fondo en la perspectiva de las agregaciones de desove de peces de arrecifes, en el que dejen de ser vistas como oportunidades de explotación y sean reconocidas como un fenómeno importante de la historia de vida que necesita ser manejado.*

Palabras Clave: base de datos de agregaciones de desove, conservación de peces, manejo de pesquerías, peces de arrecife, pesca en agregaciones, pesquerías, sobrexplotación

Introduction

Commercially exploited animals are particularly vulnerable to overexploitation if they form mass gatherings, especially if these are predictable in time and space and can be readily targeted. Such aggregations occur for a variety of reasons, including the need to find a mate, release offspring, feed, hibernate, or roost. Once an aggregation is discovered, uncontrolled exploitation can have devastating effects on the targeted population. Numerous examples of population crashes on land exist: the Short-tailed Albatross (*Diomedea albatrus*) in Japan (Austin & Kuroda 1953; Hasegawa & DeGange 1982); green turtles of Bermuda (Lehrer 1990); the Passenger Pigeon (*Ectopistes migratorius*) (Weidensaul 1994); and the entire genus *Pteropus*, which comprises the flying foxes (Baillie & Groombridge 1996). Considerably less is known about mass gatherings of animals in the sea, yet as researchers further study marine taxa, it is clear that many marine animals also form large, potentially vulnerable groupings for feeding, spawning, birthing, or schooling. One type of gathering highly at risk from human exploitation is spawning aggregations of coral reef fishes. A spawning aggregation is defined as "a group of conspecific fish gathered for the purposes of spawning with fish densities or numbers significantly higher than those found in the area of aggregation during the non-reproductive periods" (Domeier & Colin 1997).

One of the best-known examples of the demise of fish spawning aggregations due to over fishing is that of the Nassau grouper (*Epinephelus striatus*), which is classified as endangered primarily due to aggregation fishing. This was the first reef fish, and one of the only fully marine commercial species, to be listed as a species of concern under the U.S. Endangered Species Act. The species may travel more than 100 km from its resident reef to an aggregation site, where all reproduction occurs over just a few days in a couple of months each year. Many of its aggregations no longer form or do so with much reduced numbers. They are not recovering despite various management measures. Poor or no enforcement appears to be largely to blame (Colin 1992; Sadovy & Eklund 1999; Sala et al. 2001; Claro & Lindeman 2003). In the Pacific, aggregation declines are also implicated for squaretailed coral grouper (*Plectropomus areolatus*) and camouflage grouper (*E. polyphekadion*) (e.g., Hamilton et al. 2005).

Although species differ in the temporal and spatial predictability of aggregation behavior, there is a clear trend that strongly suggests there is a relationship between declines and the degree of formation of concentrated aggregations. In U.S. grouper fisheries, for example, the Nassau grouper lies at one extreme, with few aggregations, large numbers of fish per aggregation, and greatest declines. The closely related red grouper, *E. morio*, a species not known to aggregate, occurs at the other extreme (Coleman et al. 1996). Almost all groupers proposed for listing as threatened on the World Conservation Union (IUCN) Red List form spawning aggregations (www.iucnredlist.org).

Despite indications that rapid and marked declines in a few coral reef fishes are directly associated with aggregation fisheries, these have received little effective management or conservation attention, and pressure to exploit them grows. There are several likely reasons for inaction; one of the most important is a lack of information. In many tropical regions, most fisheries are not monitored at the species level; long-term data sets are few; there is little documented history of declines from which to draw lessons; and there are virtually no long-term data sets on aggregating species. A review of marine reserves in the Caribbean shows that only 10% of marine reserves explicitly consider spawning-aggregation management

(Appeldoorn & Lindeman 2003). Indeed, rather than natural events in need of management, aggregations are most typically viewed as opportunities for efficiently catching large numbers of fish. Moreover, technological advances make aggregations increasingly easy to locate and reach, and demand for reef fish is growing due to market forces and growing exports (Sadovy & Domeier 2005). Although many commercially valuable species aggregate, few are effectively protected. Indeed, even when reserves are put in place for aggregation management, inefficient enforcement can undermine the benefits (J. Gibson, personal communication), and very few are monitored regularly to determine the performance of management.

A major and rapid shift in perspective is needed to achieve effective protection for vulnerable spawning aggregations, but this cannot happen without information. Lack of information seriously compromises the ability to make a strong scientific and political case for the management of aggregating species. To address this situation, we developed a novel database to systematically document the history of these fisheries and their current condition. We developed a standardized approach that integrates global traditional knowledge, semistructured interviews of Southeast Asian and the western Pacific fishers, published literature on research and management, and anecdotal and unpublished accounts. Traditional knowledge can provide an invaluable baseline against which to compare subsequent changes where no formal data exist (e.g., Johannes et al. 2000; Saenz-Arroyo et al. 2005). Indeed, this is sometimes the only approach available to highlight recent or earlier baseline conditions against which changes can be evaluated where records are unavailable (e.g., Pauly 1995; Neis et al. 1999; Jackson et al. 2001).

We examined the database with 3 objectives in mind: (1) to determine the taxonomic and geographic incidence of aggregating reef fishes and spawning aggregation sites with a focus on commercially important species, (2) to summarize the fishing history and current status of species as a baseline for future work, and (3) to strengthen the case for management and identify management priorities and options.

Methods

From a global perspective, we assessed species composition, current status and exploitation history of aggregations of spawning coral reef fishes from published literature, unpublished information, and on the basis of outcomes from over 300 interviews conducted in 10 countries in the western Pacific and Southeast Asia between 2002 and 2006 by the Society for the Conservation of Reef Fish Aggregations (SCRFA). We entered the information into a Web-accessible database. To ensure standardization of database entries, we applied a predefined set of parameters for each record collected from the various sources of information (see Supporting Information): lunar phase (4 phases); geomorphological type (12 types); habitat; aggregation type (resident or transient—see later); months of spawning (number of months); direct or indirect sign/evidence of spawning (see later); current status (stable, increasing, decreasing numbers, catches, or catch per unit effort, gone); management or protection in place; source of information. Each record in the database represents a single fish species at a single aggregation site.

We used a semistructured interview format in interviews of full-time patriarch fishers in southern and eastern Indonesia, central and southern Philippines, eastern Malaysia, Palau, Micronesia (Pohnpei, Chuuk, Kosrae), Fiji, Solomon Islands, and Papua New Guinea (http://www.scrfa.org/server/studying/reports.htm [country reports]). Experienced interviewers, in collaboration with local field staff and sometimes translators, sought to conduct at least 5 interviews per community. Interviews were mostly one on one and were conducted in homes or community halls. Interviews typically lasted about 1 h. Interviewers were familiar with the local fishery and the biology of the species, used photographs of species and maps, and referred to fish and fishing gears by local names. We directly inspected fresh catches, if available, for species confirmation and recorded global positioning system (GPS) positions of reported aggregation sites, when these could be visited. As an indication of trends in catch data over time at specific aggregation sites, we recorded catches in effort units that were locally relevant and consistent, such as catch per boat, per day, or per fisher per day. We documented historic aggregation catches as maximum catch per unit of effort, during the aggregation season and for major target species, because extreme catches are more memorable than average catches. In the Pacific and Southeast Asia, we conducted interviews in neighboring communities and nearby markets and with local traders, which allowed for cross-checking for consistency between communities or trade sectors in an area.

Although spawning aggregations may appear easy to identify, this is not always the case, and we applied clear definitions of both *aggregation* and *spawning* to ensure consistency according to Domeier and Colin (1997). We considered any temporary increase in density or catch rates (nominally 3 times or more of the nonspawning density or catch rates) that likely occurred for the sole purpose of spawning evidence of aggregation behavior. Some species assemble regularly for many months of the year close to areas of residence (resident), whereas others group for just a few hours in the year at one of just a few known aggregation sites (transient). In either case, the number of fish involved may range from tens to tens of thousands. For a record to be considered a spawning event, it had to include at least one of several predetermined parameters that represented direct or indirect indicators of spawning (on-line database; Colin et al. 2003). Direct indicators included observations of spawning or presence of hydrated eggs or postovulatory follicles; the latter 2 features are signs of imminent or recent spawning, respectively. Indirect indicators of spawning included courtship, coloration changes exclusively associated with spawning, seasonal increase in GSI (see later), or seasonally high catches of gravid fish. Several different indicators of spawning were necessary in some species to distinguish spawning aggregations from feeding or migratory groupings that form temporarily and because the spawning act is often difficult to witness directly.

We used 377 records from a total of 558 records for the present analysis. To select these data, we removed records with no clear direct or indirect evidence of spawning; little-known species that spawn in small groups in or close to their normal territories (e.g., small wrasses and parrotfishes); species only marginally associated with reefs (e.g., Sparidae); and unique species records or other records for which information on the formation of spawning aggregations (as defined by Domeier & Colin [1997]) was insufficient or incomplete.

We considered some of the data sensitive, particularly those gathered from interviews, because many aggregations are still fished, are not protected, and are not widely known outside of the immediate community reporting them. Therefore, we did not publicize the exact location of individual aggregation sites at a resolution of $>1^\circ$ latitude by 1° longitude, so as to protect aggregations from additional exploitation and to respect local knowledge. Full details of each site are retained in the database and represent a valuable baseline for future work.

Results

Fishes That Aggregate to Spawn

The data subset we analyzed involved 9 families and 67 species from 29 countries (Table 1; http://www.scrfa.org/server/database/dbaccess.htm) and revealed the widespread nature of the aggregating habit in reef fishes of the Indo-Pacific region, largely undocumented prior to this study (57% of records were from the Indo-Pacific). The study also provided evidence of previously unreported aggregations in the tropical western Atlantic. The data were inevitably biased toward certain commercial species and transient spawners because of the extensive use of fisher interviews as sources of data. Most records were for groupers (Serranidae) and snappers (Lutjanidae), especially *E. striatus* (12%), *P. areolatus* (18%), and brown-marbled grouper (*E. fuscoguttatus*), *E. polyphekadion*, and leopard spotted coral grouper (*P. leopardus*) (20%, combined). *Lutjanus* species accounted for another 20%, especially mutton snapper (*Lutjanus analis*) and lane snapper (*L. synagris*). Fisher interviews provided the main source of information for the Indo-Pacific, where little fishery-related research is conducted and many aggregation sites have been documented or exploited only recently. Considerably more scientific research on aggregations and aggregating species was available for the tropical western Atlantic. Fishing gears were mainly hook and line, spear, and occasionally traps (particularly in the tropical western Atlantic). The use of gill nets and cyanide were reported in Indonesia and the Philippines.

Evidence that fish gatherings were indeed spawning aggregations was mainly obtained through indirect evidence of spawning (77%), especially high seasonal landings of multiple gravid females (75% of records), although often more than one spawning sign was indicated. Spawning was directly observed in 25% of records, reflecting the difficulty of observing spawning in the field for many species. Twelve percent of records reported hydrated eggs or postovulatory follicles. Despite ease of use, the gonado-somatic index (ratio of gonad to body weight) was used only as sole evidence of spawning in 2 records.

Temporal and Spatial Patterns

Of the 9 geomorphological types, 90% of records were of 3 types: reef passes, channels, promontories, and outer reef-slope drop-offs. Because most records in the database were for grouper and snapper aggregations, geomorphological type reflected bias toward these 2 families.

Multispecies spawning sites appeared common. In the Indo-Pacific, species often recorded to aggregate together were *P. areolatus*, *E. polyphekadion*, and *E. fuscoguttatus*. Although the location and timing of the aggregations of the 3 species generally overlapped, there were often clear differences between species sharing the sites with respect to habitat, depth, and seasonality of spawning. In the northern hemisphere of the tropical western Atlantic, *E. striatus*, black grouper (*Mycteroperca bonaci*), tiger grouper (*M. tigris*), and yellowfin grouper (*M. venenosa*) often shared the same sites with several lutjanids, although the timing of spawning varied somewhat among the species.

Most aggregating species spawned over 3 months or less each year (75% of our records) (Fig. 1), and about 50% spawned during the full moon. The timing of aggregations varied among species. About 8% of records for which spawning duration was given indicate monthly spawning throughout the year, including for several species of rabbitfish, snapper, several mullets (Mugilidae), surgeonfishes (Acanthuridae), and the Napoleon wrasse *Cheilinus undulatus* (Labridae). The groupers—green grouper (*E. coioides*), *P. leopardus*, and

Table 1. Species reported in interviews and in published and gray literature that spawn in aggregations as determined on the basis of direct or indirect criteria for spawning (see text for definitions), including number of records and countries noted for each species.*

Family and genus and species	*Records*	*Countries*	*Family and genus and species*	*Records*	*Countries*
Acanthuridae			*Hipposcarus longiceps*	2	1
Acanthurus bahianus	1	1	*Scarus iserti*	2	2
A. coeruleus	2	2	*S. prasignathos*	1	1
A. guttatus	3	1	*Sparisoma rubripinne*	1	1
A. triostegus	1	1	Serranidae		
A. lineatus	2	2	*Epinephelus adscensionis*	1	1
Ctenochaetus striatus	2	2	*E. coioides*	1	1
Caesionidae			*E. corallicola*	2	2
Caesio teres	1	1	*E. cyanopodus*	1	1
Labridae			*E. fuscoguttatus*	22	8
Cheilinus undulatus	5	2	*E. guttatus*	4	3
Chlorurus microrhinos	1	1	*E. itajara*	3	1
C. sordidus	3	2	*E. multinotatus*	1	1
Lethrinidae			*E. ongus*	10	2
Lethrinus atkinsoni	1	1	*E. polyphekadion*	30	7
L. erythropterus	3	2	*E. spilotoceps*	3	1
L. nebulosus	2	2	*E. striatus*	47	8
Lutjanidae			*E. trimaculatus*	3	1
Lutjanus analis	18	4	*Mycteroperca bonaci*	12	5
Lut. apodus	1	1	*M. jordani*	1	1
Lut. argentimaculatus	1	1	*M. microlepis*	1	1
Lut. argentiventris	1	1	*M. phenax*	2	1
Lut. bohar	2	2	*M. prionura*	2	1
Lut. campechanus	2	1	*M. rosacea*	1	1
Lut. cyanopterus	13	2	*M. tigris*	5	5
Lut. gibbus	2	2	*M. venenosa*	12	5
Lut. griseus	10	2	*Plectropomus areolatus*	49	8
Lut. jocu	6	3	*P. laevis*	1	1
Lut. novemfasciatus	1	1	*P. leopardus*	26	5
Lut. rivulatus	1	1	*P. maculatus*	6	2
Lut. synagris	15	2	*P. oligacanthus*	7	2
Lut. vitta	1	1	Siganidae		
Ocyurus chrysurus	1	1	*Siganus canaliculatus*	1	1
Mugilidae			*S. guttatus*	1	1
Crenimugil crenilabris	2	2	*S. puellus*	1	1
Mugil cephalus	1	1	*S. randalli*	2	1
Scaridae			*S. spinus*	2	2
Bolbometopon muricatum	2	2	*S. vermiculatus*	4	2

**Countries included in the analyzed subset of data are American Samoa, Australia, Bahamas, Belize, Bermuda, British Indian Ocean Territory, Cayman Islands, Cuba, Egypt, Fiji, Indonesia, Jamaica, Japan, Kiribati, Malaysia, Maldives, Marshall Islands, Mexico, Micronesia (Kosrae, Pohnpei, Chuuk), New Caledonia, Palau, Papua New Guinea, Puerto Rico, Seychelles, Solomon Islands, Turks and Caicos Islands, and United States including Virgin Islands.*

P. areolatus—and the snappers—humpback red snapper (*L. gibbus*) and red snapper (*L. bohar*)—varied in the number of months they spawned, whereas some mullet, rabbitfish (Siganidae), bonefish (Albulidae), and milkfish (Channidae) were highly consistent in their seasonality of spawning.

Spawning Aggregation Discovery, Current Status, and Management

Many aggregations of commercially important species have a long history of exploitation and, according to interviews, continued to produce good landings until intense exploitation began in recent decades. The data suggested a progressive increase in aggregation discovery rate, although the history of exploitation of many aggregations was unknown (Fig. 2). Some sites were fished for subsistence for over a generation (i.e., 70 years), possibly much longer, and there were marked declines over several decades. In Palau catch rates determined from interviews exceeded 1 t of groupers per boat trip in the 1960s. By the 1980s and 1990s, catch rates had dropped to approximately 200 kg per boat trip with even lower catches more recently (Fig. 3). The change in catch over time was significant (Kruskall–Wallis $H = 10.843$; $n = 36$; $df = 4$; $p < 0.05$). It was notable that despite a substantial number of interviews in the Philippines and Indonesia, few aggregations were reported compared with the western Pacific.

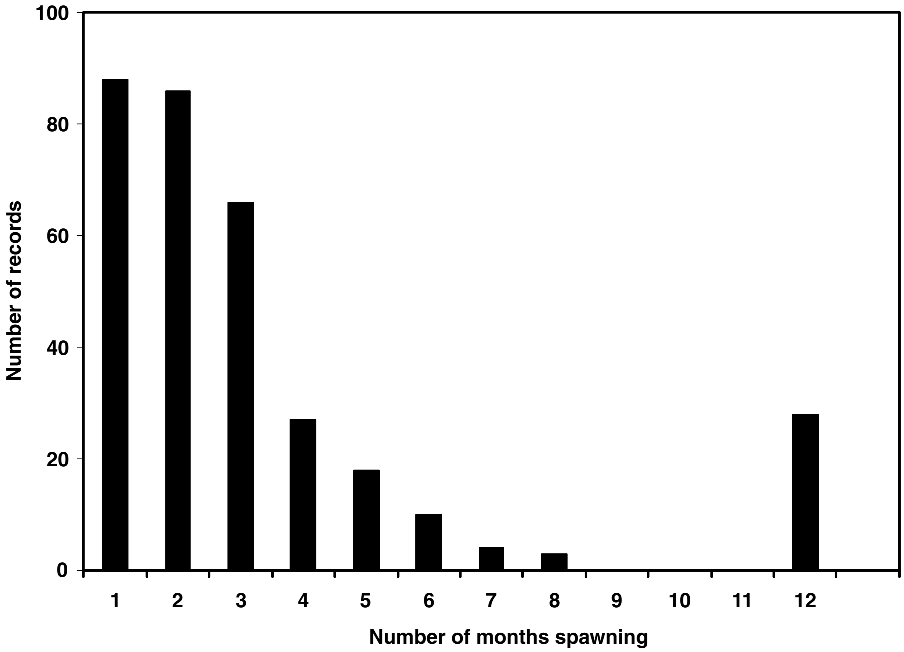

Figure 1. Number of records in the Society for the Conservation of Reef Fish Aggregations database used to determine the number of months aggregation and spawning occur each year for all species and locations. Each record represents one species at one site. Individual species can be included in multiple records if reported from more than one aggregation site, and a site can have more than one species. Some bias is introduced by larger numbers of records for commercial species derived from fisher interviews.

Of the 60% of aggregation records for which information on current status was available, 79% suggested declining landings, and few aggregations were protected. Our analysis was the first to demonstrate this pattern systematically from multiple locations in the Indo-Pacific. Of all the Indo-Pacific aggregations, 44% were either in decline or eliminated (possible extirpation or ecological extinction). For the tropical western Atlantic, 54% of aggregations had declined or had been eliminated. At a few sites aggregations were stable or increasing, and there was no information for many sites (Fig. 4). Reports of increasing numbers were few and occurred where management was in place (2 sites with no-take marine protected areas, U.S. Virgin Islands, and Pohnpei, the latter also had seasonal sales bans), where aggregations were recently discovered (Papua New Guinea, 4 aggregations), or where management measures such as fishing-gear controls for the species were in place (Cuba, 2 sites). Techniques used to record the increases included fishing and visual surveys. For the 55 aggregations with spatial protection, 19 were declining, 4 were considered extirpated, 5 were unchanged, and 2 (as indicated earlier) were increasing. No historical perspective was available for the remaining 25 aggregations. Where present, fishery management and conservation initiatives most commonly involved spawning-season sales bans and seasonal or spatial closures, often in combination. Quotas, limited entry, or fishing-gear controls were recorded infrequently ($n = 6$) (Fig. 5).

The best-known species threatened by aggregation fishing is the Nassau grouper, which made up 12% of our records. In major fishing areas for this species, Cuba

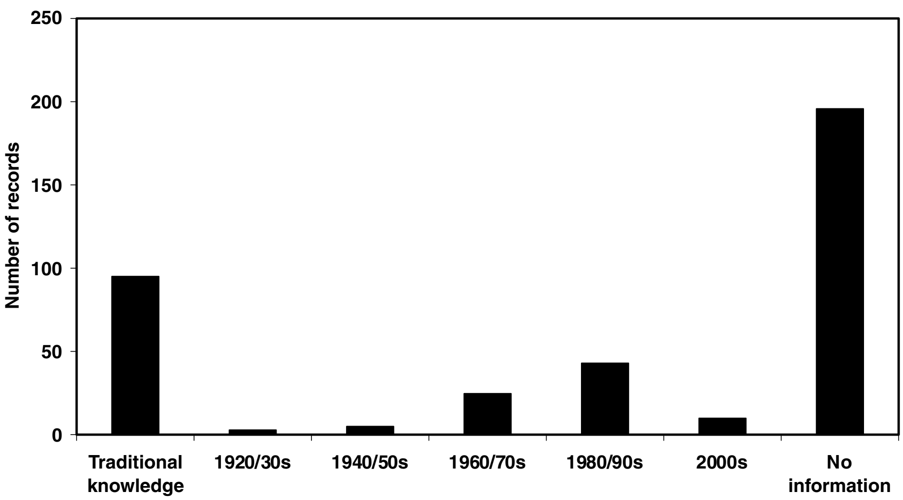

Figure 2. Number of records in the Society for the Conservation of Reef Fish Aggregations database used to determine the earliest time at which an aggregation was fished on the basis of fisher interviews and published work. For definition of record, *see Fig. 1. Traditional knowledge indicates the aggregation site had been known for over one generation.*

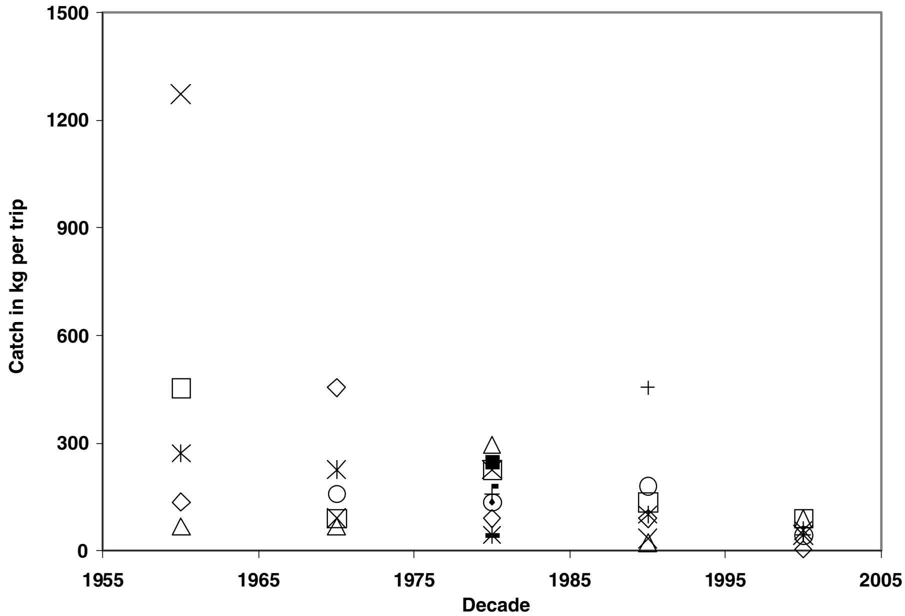

*Figure 3. Peak catches taken at spawning aggregations of groupers (*E. polyphekadion, E. fuscoguttatus, *and* P. areolatus*) at multispecies aggregation sites as reported from fisher interviews conducted in July 2003 in Palau. For each decade different symbols represent independent estimates by different fishers, although the same symbol in different decades may not represent estimates from the same fisher (http://www.scrfa.org/server/studying/reports.htm-Palau).*

and the Bahamas, much of the annual landings came from aggregations. Of at least 50 aggregation sites once known, <20 probably remain. Moreover, where recent estimates of aggregation size were made, fish numbers ranged from 100 to 3000, a major decrease from the tens of thousands of fish recorded just a few decades ago at many sites (Figs. 6a & 6b).

Discussion

The outcomes of this assessment highlighted the large number of commercially important reef fishes that aggregate to spawn and the high proportion of known aggregations in decline. Although the database afforded many analysis opportunities beyond those we present here, the key outcomes of the current assessment focused on the need for managing aggregations, provided a framework for collecting the necessary information to achieve better protection, and identified management options.

Management and Conservation of Spawning Aggregations

A wide taxonomic range of fishes aggregated to spawn, and many of them are exploited. Collectively, aggregating species exhibited large differences in the number of animals assembling, distances moved to the aggregation sites, proportion of an aggregation removed by fishing, and percentage of annual landings taken from

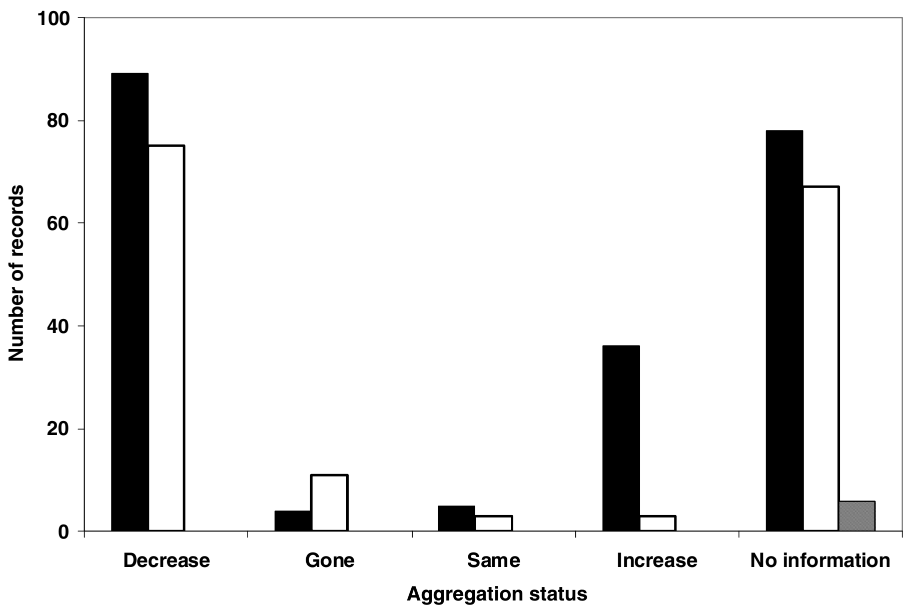

*Figure 4. Number of records in the Society for the Conservation of Reef Fish Aggregations database that indicate aggregation status (*record *defined in Fig. 1).* Gone *(eliminated) indicates the aggregation has not been found in recent years or that catches have not occurred in appreciable numbers in recent years, and* same, decrease, *or* increase *suggests that estimated numbers are unchanged relative to past reference points. Bar color key: Indo-Pacific, black; tropical western Atlantic, white; eastern Pacific, gray.*

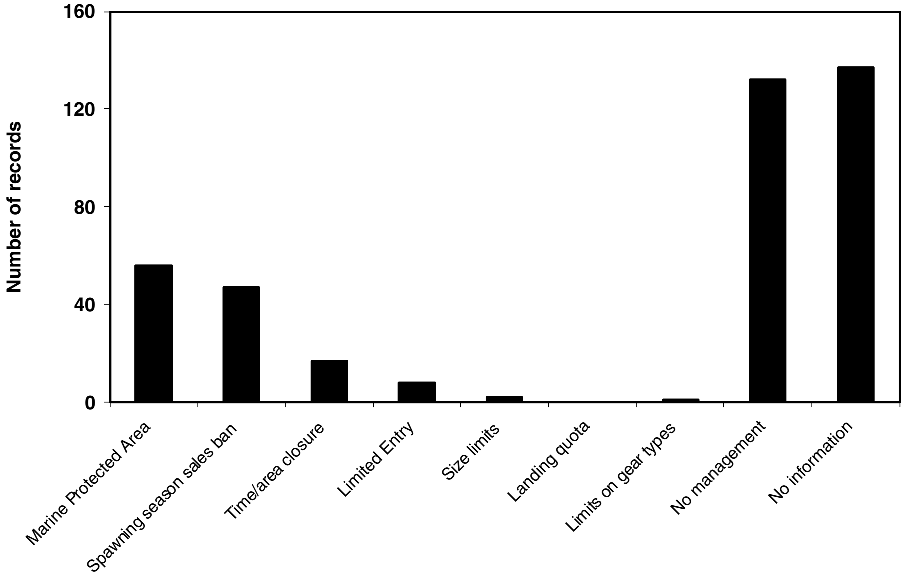

*Figure 5. Number of records in the Society for the Conservation of Reef Fish Aggregations database that show different management measures in areas that include spawning aggregation sites or aggregating species; a single site can have multiple management measures (*record *defined in Fig. 1). The majority of sites have no management and most of the no-information sites are evidently unmanaged.* Time/area closures *refers to the spawning season and* limited entry *can refer to numbers or types of fishers or fishing gear.*

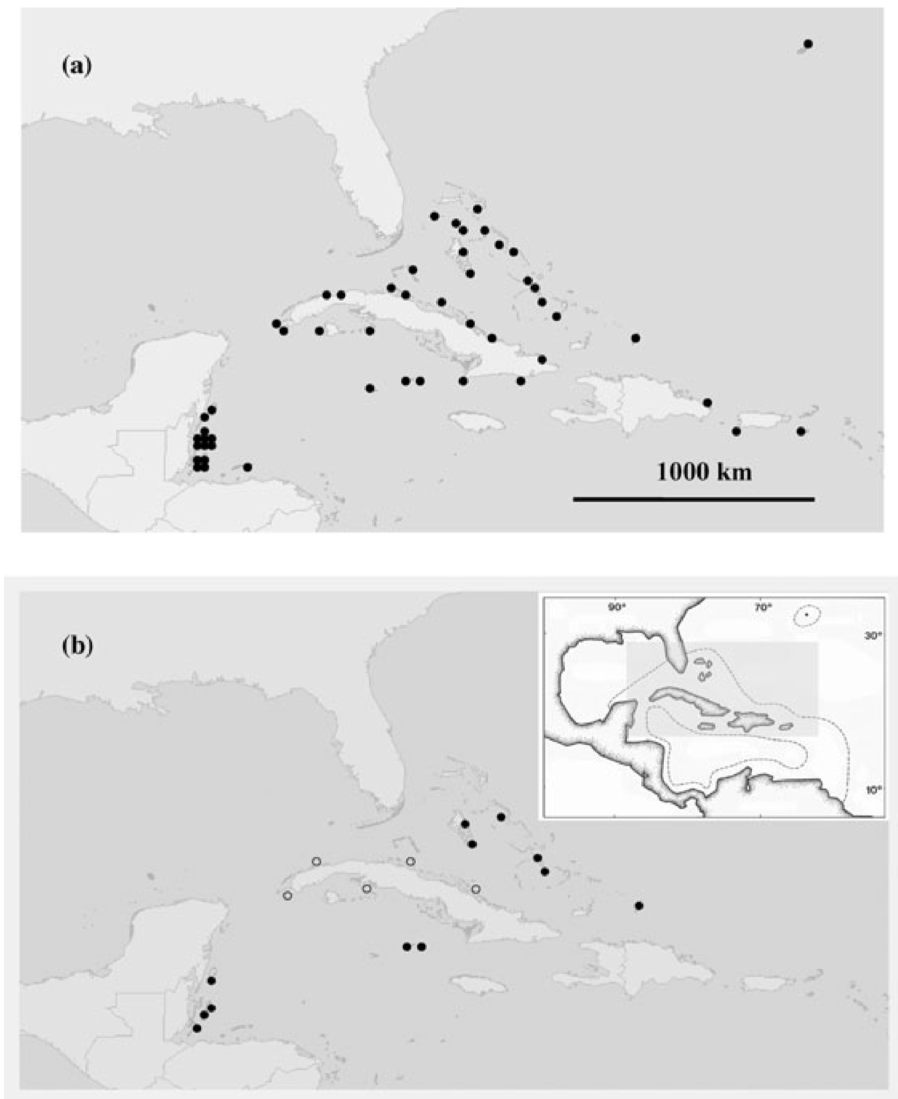

Figure 6. Known spawning aggregations of Nassau grouper. Inset shows full geographic range. (a) All known aggregations reported since 1884. Each closed circle represents 1, or occasionally 2, reported site. In the few cases where aggregation numbers were estimated, these ranged from approximately 10,000 to somewhere between 30,000 and 100,000 fish. (b) Closed circles represent sites believed to exist today with fish numbers estimated at between 100 and 3000 (estimates from fishing and direct observations). Open circles represent sites in Cuba still believed to produce small catches of Nassau grouper but sites have not been assessed directly. (Sources: Smith 1972; Sadovy & Eklund 1999; Sala et al. 2001; Whaylen et al. 2004; Belize Spawning Aggregation Working Group, unpublished data; R. Claro, unpublished data; E. Sala, unpublished data).

aggregations. Species also varied greatly in spatial and temporal predictability of aggregation formation. In some cases, such as groupers, *E. polyphekadion*, *E. fuscoguttatus*, *P. areolatus*, milkfish, bonefish, and certain rabbitfishes and mullets, most annual landings occurred at aggregation times when whole fishing communities targeted on them. Indeed, species such as *E. polyphekadion*, *E. striatus*, and *P. areolatus* were often not taken in substantial numbers at other times of the year.

Results of interviews with Pacific fishers showed that fishing pressure on aggregations of valuable species was increasing. Nevertheless, little consideration was being given to the capacity of the aggregations to support increased pressures (Sadovy & Domeier 2005). Mechanization of vessels and technological advances, including use of GPS, provided greater offshore access. The unplanned introduction of fish-processing facilities in remote areas, such as ice plants in Fiji (Y.S., personal observation), further enhance market access.

Given the diversity of aggregating species and fishery and market conditions, effective solutions may require multiple and novel approaches. Many commercially significant aggregation sites are located in outer reef channels or drop-offs, areas rarely specifically managed or incorporated into marine protected areas. Yet, these habitats may be the only remaining refuge for species that are heavily targeted inshore. Effective aggregation management is also severely hampered by a lack of understanding of connectivity, whether during adult, juvenile, or egg or larval phases. For example, because little is known about catchment areas (i.e., how far adults travel to spawn or larvae disperse from aggregation sites), it is difficult to determine the appropriate scale of spatial protection or appropriate network of protected areas for aggregating species. Paris et al. (2005) modeled larval-transport scenarios from multispecies spawning sites in Cuba and found that dispersal patterns vary around the island. Domeier (2004) noted that dispersal patterns from an aggregation within a marine protected area in Florida can vary between years, suggesting that design of marine protected areas can anticipate considerable out-of-area advection and some retention of spawning products.

Different approaches to managing transient and resident aggregations may be needed (Domeier & Colin 1997). Transient aggregations should at least receive seasonal protection, and resident aggregations or multispecies spawning sites should receive protection year-round. In the southeastern United States managers are increasingly applying regionwide seasonal spawning closures for transient grouper and snapper aggregations (e.g., recent management plan amendments by the South Atlantic Fishery Management Council) and no-take reserves for multispecies spawning sites (Lindeman et al. 2000). There are many important fishery-specific biological and socioeconomic variables, and we recommend aggregation-specific approaches that focus on maximizing compliance and enforcement. Information in the database that identifies spawning season by area could be a good starting point for seasonal protection regionally. Identification of typical spawning habitats, such as outer-reef channels and promontories, offer clear options for protection without the need for detailed studies in every area. In Australia, for example, management of the reef fish fishery on the Great Barrier Reef includes spawning season closures, and about 30% of the reef and shoal habitat, inclusive of outer-reef and deepwater habitats, is protected in a marine protected area. Moreover, to forestall possible impacts from human disturbance, tourist diving platforms cannot be sited within 200 m of a spawning site.

The database contains too few examples of aggregations that were recovering to make general conclusions about the effectiveness of different types of management, but permanently stopping fishing at aggregation sites clearly showed benefits. Creation of a large permanent no-take marine protected area on an aggregation site in the U.S. Virgin Islands, which was seasonally closed for 9 years prior, resulted in a dramatic increase in red hind (*E. guttatus*), with the estimated spawning population increasing 3-fold (from 26,200 to 84,000) in 3 years (Nemeth 2005).

There are other considerations relative to the protection of aggregating species, both during and outside the spawning season. In some areas increased protection is needed during the months before the fishes spawn or between spawning periods. Heavy fishery activity that targeted prespawning migrations in outer reef channels in Cuba significantly affected a major fishery for *L. synagris* (Claro et al. 2001). Fishing pressure increased on nonspawning *M. microlepis* after aggregation protection was introduced (Coleman et al. 2004). In other cases, even more complex threats arise that require solutions at the broader scale of coastal planning. For example, once-remote federal marine protected areas in the Mexican Caribbean are now compromised by the impact of major new tourism and coastal development pressures associated with the rapid increase in large cruise ships seeking new and unspoiled destinations (e.g., Arias et al., unpublished data). Inshore spawning aggregations, already highly affected or ecologically extinct (e.g., Aguilar-Perera 2006), face growing pressures from increased fishing activity and habitat modification. Coastal construction can seriously disrupt near-shore spawning runs. For example, 6 of 7 important spawning runs of bonefish (*Albula* spp.) in Kiribati, in the Pacific, have ceased to form. Causeway construction is believed to be a major factor in their decline (Johannes & Yeeting 2001).

Although it is not possible, without an appropriate comparative data set or controlled fishery experiment, to definitively point to aggregation fishing as the major cause of declines in a range of exploited aggregating versus nonaggregating species, the wealth of indications is compelling. Moreover, aggregating fish could be particularly susceptible to aggregation fishing if their reproductive behavior is temporarily disrupted by fishing (e.g., Atlantic cod [*Gadus morhua*]); Morgan et al. 1997), they show reduced courtship in depleted aggregations (e.g., Nassau grouper; Colin 1992), or cues for sex change are transmitted during aggregation in otherwise solitary fish (e.g., red hind; Shapiro et al. 1993). Although speculative, such possible behavioral responses merit examination.

Database compilation and analyses have increased awareness of the nature of aggregation fisheries and of the implications of failure to manage them, and form the basis for calls for action from NGOs and intergovernmental organizations. The Food and Agriculture Organisation (FAO) Code of Conduct for Responsible Fisheries (1995) states that, "Particular effort should be made to protect . . . *spawning and nursery areas* . . . from destruction, degradation, pollution and other significant impacts resulting from human activities that threaten the health and viability of the fishery resources" (emphasis added). Nevertheless, there are few examples of well-protected spawning areas.

Reconciliation of Traditional and Scientific Knowledge

With few exceptions (e.g., Colin 1978; Colin & Clavijo 1988), most of the original information identifying spawning aggregation sites, particularly for prominent exploited species, such as groupers and snappers, was achieved through interviews or discussions with commercial or subsistence fishers (e.g., Johannes 1981). This is because the chances of encountering a spatially and temporally limited gathering by chance are extremely low. Fishery-dependent data in the tropics, if collected at all, tend to be coarse in scale—data are yearly summaries and species and fishing areas are pooled—which obscures brief events that occur at fine spatial scales for particular species. Nevertheless, fishing communities often develop knowledge over generations about the locations and timing of fish aggregations. This was particularly apparent in the Pacific, where coastal communities depend heavily on the sea for food.

The value of fisher interviews for collecting otherwise unobtainable fishery information has been discussed and widely supported in a range of fisheries, including those for aggregating species (e.g., Drew 2005; Hamilton et al. 2005). Validation or cross-referencing of independent information with the outcomes of interviews conducted during this study also supports the validity of interview-sourced information. For example, in Fiji, a preliminary validation at 4 outer-reef channel sites found information from interviews with independent communities and traders along the coast, who source fish from the same sites, consistent in terms of major target species identified, spawning-site location, declines in catch rates over time since the 1970s, and general timing of spawning for a key fishery species (*E. polyphekadion*) (Sadovy 2006). Dive surveys revealed that interview outcomes were less reliable for detecting aggregating species of minor economic importance, or volume, at the same aggregation site and did not detect all aggregating species because not all gear types were surveyed. In all cases of cross-referencing and validation conducted, interview results were supported for major commercial species noted.

The relatively low number of aggregations recorded from the Philippines and Indonesia, and low awareness of aggregations among fishers, is intriguing. These 2 countries alone encompass around 27% of the world's coral reefs (Spalding et al. 2001), and species in the database that form spawning aggregations elsewhere in the Indo-Pacific also occur there. We cannot provide a definitive answer as to why aggregations are either scarce or little known, but there are several possible explanations. First, estimating numbers of marine fishers in each nation per square kilometer of coral reef, as a crude indicator of fishing pressure, revealed that fishing pressure was orders of magnitude greater in the Philippines and Indonesia than in any of the other nations in the database. Maybe past fishing pressure has long extirpated aggregations in many parts of these countries. Another possibility is that geomorphological or other large-scale environmental conditions yet to be revealed support, or otherwise, the formation of spawning aggregations in certain species of reef fishes in different countries. It is noteworthy, for example, that the relatively well-known Nassau grouper has never been reported to aggregate anywhere on the extensive coastal platform of northern South America where it is known to occur (Sadovy & Eklund 1999) (Fig. 6).

Recommendations and Conclusions

Despite significant advances in the general understanding and awareness of the problems faced by reef-associated fisheries and the need to manage them, significant challenges remain to achieving sustainable management of aggregating species.

1. Conventional management approaches, whether spatial or through input–output fishery controls, do not typically include aggregation management. Where measures do exist, enforcement is often inefficient.
2. Large aggregations may continue to form even though a fish population is being fished, giving an impression of abundance (e.g., hyperstability; Sadovy & Domeier 2005). This means that, if exploited, aggregations should always be identified for management consideration and monitoring protocols.
3. Declines in aggregations are not widely recognized or perceived as a problem, especially in areas where commercial exploitation of reef fishes is relatively recent. There is a need for a better understanding of aggregations in relevant socioeconomic sectors.

4. Multiple management measures, including nonaggregation management for targeted aggregating species, are often needed. Particular attention should be paid to those species that aggregate for very short periods and occupy few known spawning sites or are also taken at nonaggregation times.

5. A lack of understanding of adult and larval connectivity among aggregating species makes it difficult to effectively apply spatial protection measures, and additional measures should be considered.

6. Outer-reef areas where many aggregations occur, including reef channels and promontories, are typically not subject to protection or management, including marine protected area designation. These areas are increasingly a focus for fishing activity.

7. The possible impacts on reproduction and other behavioral interactions among assembled fishes due to removals or disturbance by fishing or diving activities is unknown and requires research.

8. Variability in timing of aggregations, even within small areas, can make temporal protection measures difficult to apply at the regional level if data on the timing of spawning are insufficient. Relevant temporal information can be readily collected through interviews or market sampling, whereas enforcement can be aided by seasonal regulations on the sale of target species.

9. Aggregations typically are viewed as important fishing opportunities for high and efficient catch rates, rather than recognized as vulnerable life-history events that need priority protection.

10. Every effort should be made to validate reports of spawning aggregations when only indirect evidence is available by directly sampling catches for gonad inspection or by observing spawning.

11. A precautionary approach is needed when a fishery targets or may target aggregating species.

Unchecked exploitation of aggregations will lead to negative consequences for the fish populations in question and the fisheries and livelihoods they support. Healthy aggregations indicate healthy fisheries, and aggregation loss is an important early indicator of a poorly managed fishery. In extreme cases aggregation fishing may become a major threat to the conservation status of targeted species, as in the case of the Nassau grouper. Nevertheless, if managed properly, aggregations can be the source of important sustainable production. Bristol Bay, Alaska, is the site of the largest aggregation of sockeye salmon (*Oncorhynchus nerka*) in the world. Strict management of this resource has led to a relatively stable fishery that has produced a 20-year average of over 35 million fish harvested per year (Westing et al. 2005). Similarly, the annual spawning aggregation of Togiak, Alaska, herring (*Clupea pallasii*) has produced a 20-year annual harvest of over 18,000 t (Westing et al. 2005). Although these successes involve fisheries and species that differ from those associated with coral reefs, they highlight the potential benefits of long-term, effective management. Protection of spawning aggregations of coral reef fishes in the Cayman Islands and the U. S. Virgin Islands is yielding encouraging results (Whaylen et al. 2004; Nemeth 2005).

The economic value of managing spawning aggregations of reef fishes is evident from both food and livelihood perspectives in much of the tropics, and aggregations may also yield important revenue for tourism. An economic analysis of income generated from divers visiting an aggregation in Belize suggests the aggregation could be worth 20 times the value of extracted fish per year if it was used for tourism (Sala et al. 2001). Such wildlife spectacles, like those on land, need to be conserved for biological and economic reasons: a better understanding of these phenomena greatly strengthens the case to do so.

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Supporting Information

Details of the parameters used to identify spawning aggregations are available as part of the on-line article (Appendix S1). The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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