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# BIOGEOGRAPHY OF TRANSIENT REEF-FISH SPAWNING AGGREGATIONS IN THE CARIBBEAN: A SYNTHESIS FOR FUTURE RESEARCH AND MANAGEMENT

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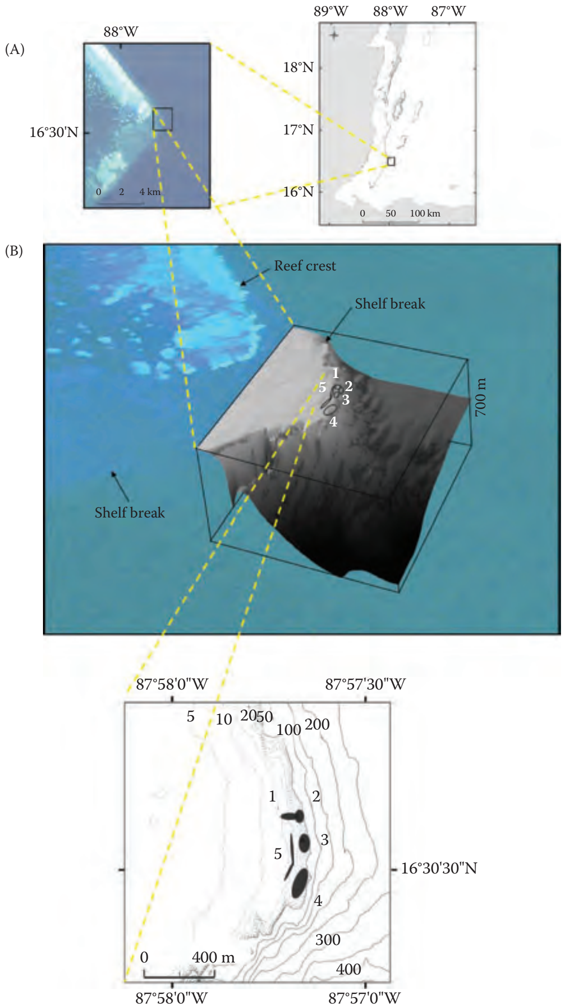
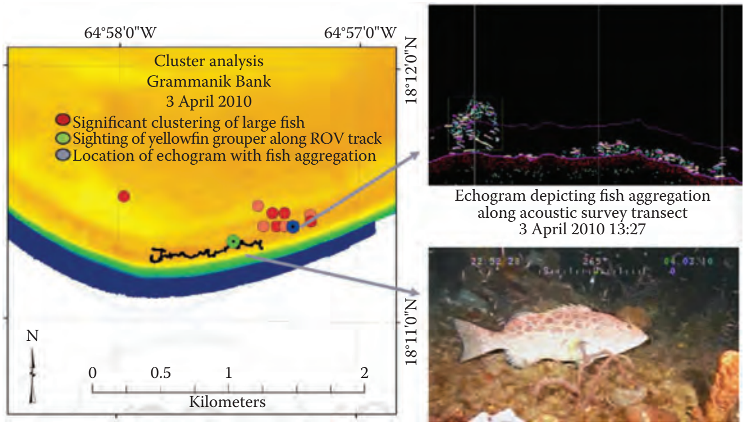
Transient fish spawning aggregations (tFSAs) are critical life-history phenomena where fish migrate to specific locations at predictable times of year to reproduce en masse. In the Wider Caribbean region, 37 species of fish from 10 families are now known to form tFSAs. Although tFSAs likely occur at times and in places that maximize reproductive success, little is known about the complex suite of interacting environmental patterns and ecological processes that dictate the timing and locations of tFSAs. This review synthesizes the latest advances in the study of tFSAs in the Wider Caribbean to (1) illustrate the current state of knowledge; (2) highlight gaps in our understanding of the geography and ecology of aggregation sites; and (3) suggest future research needs and conservation strategies. We have compiled multidisciplinary data on 108 tFSAs across 14 states and territories in the Wider Caribbean and reviewed the full range of approaches and technologies applied to study tFSAs. Existing research and associated hypotheses are grouped and examined by data type. We propose a multitier research framework that provides an incremental approach to information gathering at individual sites and suites of sites. We advocate applying the framework to facilitate consistent and coordinated data collection and monitoring across a Wider Caribbean network of tFSAs.

## Introduction

Spatial and temporal information on the reproductive ecology of marine species is vital to the development of effective strategies for marine resource management and biodiversity conservation (Vincent & Sadovy 1998, Pittman & McAlpine 2003). An estimated 164 species of fish globally have evolved a reproductive strategy that involves the mass aggregation (hundreds to thousands) of sexually mature males and females at specific geographical locations to spawn (Claydon 2004). Many fishes that are associated with coral reefs can travel relatively long distances over days and



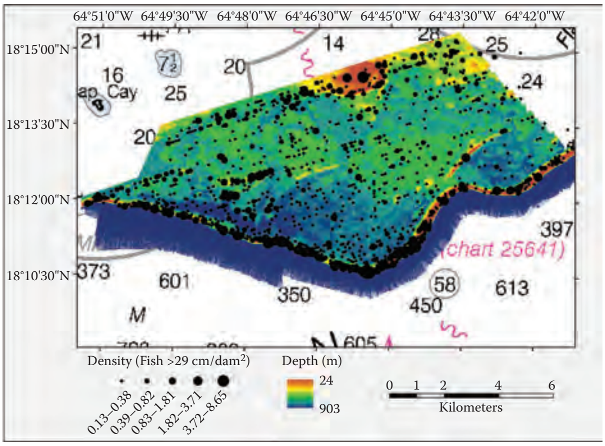
Colour Figure 8 (Kobara, Heyman, Pittman & Nemeth)



Echogram depicting fish aggregation along acoustic survey transect 3 April 2010 13:27

One of many yellowfin grouper *Mycteroperca venenosa* detected along ROV transect 3 April 2010 22:52

Colour Figure 9 (Kobara, Heyman, Pittman & Nemeth)



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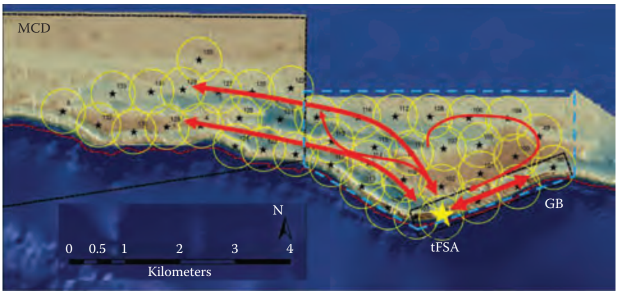

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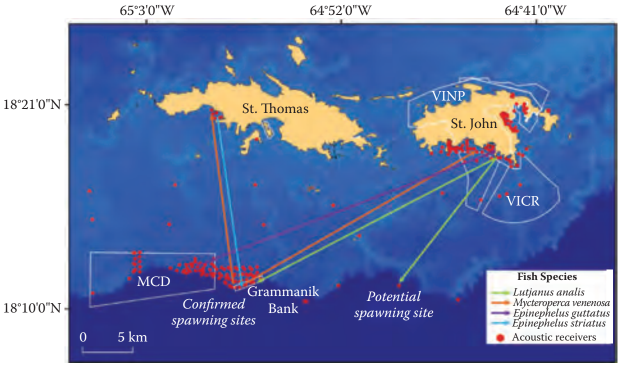

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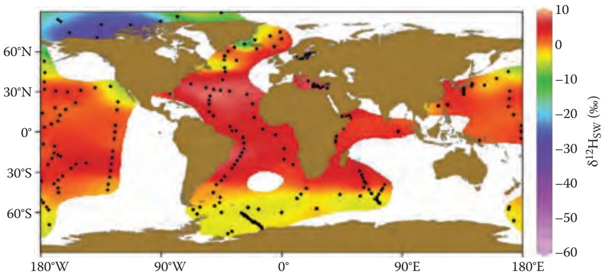

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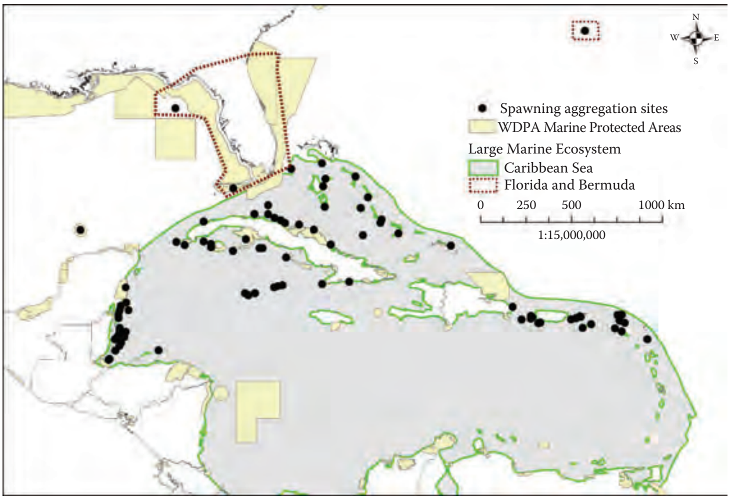

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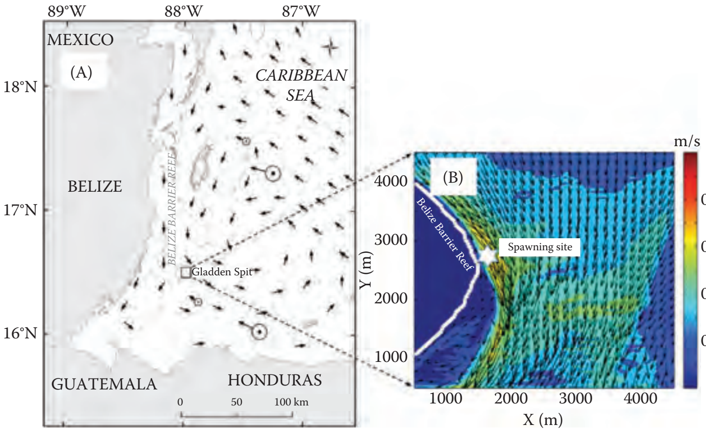
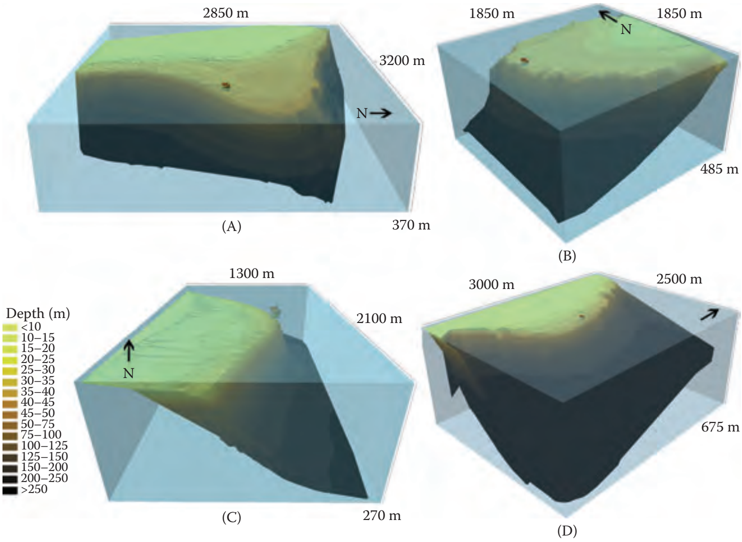


Colour Figure 5 (Kobara, Heyman, Pittman & Nemeth)



Colour Figure 7 (Kobara, Heyman, Pittman & Nemeth)

weeks to an aggregation site during a very specific portion of the day, month or year and then return to their routine home range area after spawning (Nemeth 2009). This life-history strategy creates a temporary or transient, yet critical, reproductive area in time and space (Johannes 1978, Domeier & Colin 1997) referred to here as a transient fish spawning aggregation (tFSA). Many of these species are key carnivores in tropical coral reef ecosystems and form a commercially and socially important component of reef fisheries (Hamilton et al. 2012, Sadovy de Mitcheson et al. 2012).

Species that form spawning aggregations can be grouped into two broad categories: (1) those that form transient aggregations (tFSA) and are typically large-bodied, slow-maturing, commercially valuable species, including several members of the snapper (Lutjanidae) and grouper (Serranidae) families, which can migrate tens to hundreds of kilometres to visit aggregation sites (Colin 1992, Bolden 2000); and (2) those that form resident spawning aggregations within or close to (<2 km) their routine home range. Fish families known to form resident aggregations include ecologically important species like some parrotfish (Scaridae), surgeonfish (Acanthuridae), goatfish (Mullidae), and wrasses (Labridae) among others (Sadovy de Mitcheson et al. 2008, Nemeth 2009). Resident spawners also tend to spawn more frequently than transient spawners, sometimes on a monthly, weekly or even daily basis (e.g., bluehead wrasse, *Thalassoma bifasciatum*; yellowtail parrotfish, *Sparisoma rubripinne*) (Randall & Randall 1963, Colin & Clavijo 1988, Warner 1995). The distinction between transient and resident spawning life-history strategies is based on not only interspecies similarities and differences in the frequency and longevity of aggregations and the relative distances travelled to the aggregation (Domeier & Colin 1997, Domeier 2012), but also how much reproductive effort is expended during a single aggregation event. Resident aggregating species invest only about 1–8% of their reproductive effort in a single spawning aggregation (Nemeth 2009). By contrast, transient aggregating species, which aggregate only a few times a year, invest from 33% to 100% of their reproductive effort per spawning episode (Domeier & Colin 1997, Nemeth 2009).

The tFSA sites are most often discovered first by fishers (Johannes 1978, Sadovy de Mitcheson et al., 2008). When fishers encounter these highly concentrated (in space and time) groups of large fish, they typically obtain high catch per unit of fishing effort. Most of the fish brought aboard fishing vessels have fully developed gonads and are often visibly reproductive, with eggs or sperm flowing from their vents. During these periods, local fish markets are flooded with large adult fish and roe.

Direct scientific evidence of a spawning site is gained through observations of spawning and the presence of hydrated oocytes within the gonads of females collected from the site (Heyman et al. 2004). Since tFSA species typically spawn in low ambient light at around sunset, scientists also consider indirect evidence of tFSA occurrence, including conspicuous and characteristic courtship behaviours, such as changes in colour (Archer et al. 2012, Heppell et al., 2012), nudging, shaking, or pair chasing; vocalization (Schärer et al. 2012a,b); biometric features, such as swollen abdomens; and an increase in the gonadosomatic index (Claro & Lindeman 2003, Heyman et al. 2004a,b); as well as elevated abundance, whereby the number of individuals at the site is at least three times greater than expected under non-spawning conditions (Domeier & Colin 1997). The indicative abundance has recently been redefined as a 4-fold increase at the site compared with other times of year (Domeier 2012).

The number of aggregating species and their co-occurrence in space and time vary among sites, but the majority of aggregation sites seem to have multispecies spawning aggregations. For instance, as many as 10 fish species are known to spawn at one particular spawning aggregation in Puerto Rico (Ojeda-Serrano et al. 2007), and as many as 17 fish species have been reported to spawn at different times of the year at a single site in Belize (Heyman & Kjerfve 2008). This suggests that some generality may exist across species in the physical suitability of a site for spawning. An understanding of exactly which physical characteristics make one area more suitable than another is just beginning to emerge, and the topic is reviewed here.

Aggregating behaviour, however, makes fish highly vulnerable to extraction by fisheries (Sadovy & Domeier 2005). The impact of fishing mortality on a local population is more acute for late-maturing species, and this is of particular concern to fisheries management when insufficient information exists about the species' population biology and tFSA site characteristics.

Unregulated fishing at tFSA sites is thought to have led to local extirpations and even the collapse of some fisheries (e.g., Nassau grouper, *Epinephelus striatus*) (Sadovy et al. 1994, Sadovy & Domeier 2005, Sadovy de Mitcheson et al. 2012). Nassau grouper was once the most valuable grouper species in the Caribbean fishery, but it is estimated that approximately 35% of all known Nassau grouper spawning aggregations have been extirpated, and population abundance and fishery landings of the species remain low (Claro et al. 2001), resulting in an 'endangered species' designation (International Union for Conservation of Nature and Natural Resources [IUCN] 2011). In Belize, catches from Nassau grouper spawning aggregation sites have declined by as much as 81% (Sala et al. 2001). Marked declines have also been reported for other aggregating species. For example, in Belize catch per unit effort from a mutton snapper (*Lutjanus analis*) spawning aggregation declined by nearly 60% (Graham et al. 2008). In Puerto Rico, declines in fish catch were reported by fishers at approximately 25% of all known spawning aggregation sites (Ojeda-Serrano et al. 2007). It appears that, in many areas, fishing spawning aggregations is an unsustainable practice that can, if unregulated, lead to the eventual loss of the resources (Sadovy & Domeier 2005). Conversely, enhanced protection of spawning aggregations can be a viable strategy for restoring the trophic structure of coral reef ecosystems and rebuilding fisheries and associated livelihoods. Nemeth (2005) reported a 60% increase in red hind (*Epinephelus guttatus*) density and biomass at a spawning site closed to fishing and increased catch rates outside the protected area just a few years after fishing was prohibited.

In the Caribbean region, one of the critical science gaps impeding the development of effective ecosystem-based fisheries management (EBFM) strategies is the lack of information on the specific geographical locations of spawning aggregations (Sale et al. 2005, Appeldoorn 2008, Crowder & Norse 2008) and on the environmental factors that may make some sites optimal for spawning. The identification and characterization of tFSAs can provide useful information to guide the strategic placement of marine reserves, seasonal closures for species or groups, redistribution of fishing effort, parameterization of connectivity models and community-based management initiatives.

The tFSAs occur at places and times that exhibit a complex suite of interacting environmental patterns and processes that are thought to maximize reproductive success. Yet, little is known about the key physical and biological factors and the interlinked ecological mechanisms that promote survival of spawning fish populations. The most actively studied explanatory factors are the geomorphological features of a site, seafloor habitat types and oceanography (Shcherbina et al. 2008, Kobara & Heyman 2010); yet, the interactions among these physical patterns and processes and the importance of coupling between benthic and pelagic realms remains largely unknown. In the Caribbean region and elsewhere, tFSAs typically occur at distinctive bathymetric features (slopes, promontories, channels, outer reef edges) in close proximity to deeper water (Johannes 1978, Heyman et al. 2007, Kobara & Heyman 2008, 2010, Wright & Heyman 2008). For example, geomorphological studies of Nassau grouper spawning aggregations in the Cayman Islands found that all five known sites were located within 1 km of the tips of reef promontories in water depths of 25 to 45 m and less than 50 m from the horizontal 'shelf edge' identified from bathymetric data (Kobara & Heyman 2008). We use the term 'shelf edge' (also 'shelf break') to refer to the seaward edge of a bank or reef, where there is a steep or vertical downward slope in the seabed.

Although existing studies suggest that geomorphological characteristics of the seabed may determine site suitability more than any other single variable (Harris & Baker 2011), studies are also emerging that suggest that other ecological patterns and processes, such as hydrodynamics, seawater temperature and proximity to suitable benthic habitats for settlement, could also be important

(Nemeth 2009). For example, several recent studies indicate that the structure and movement of the water mass, including the current speed and the prevailing direction of flow, are important in the effective dispersal of eggs and larvae from a spawning site (Heyman & Kjerfve 2008, Shcherbina et al. 2008), but may also provide a mechanism for retaining eggs and larvae near natal habitats (Nemeth et al. 2008, Cherubin et al. 2011, Ezer et al. 2011). Thus, conditions that result in optimal oceanographic connectivity between spawning sites and nursery areas could form an important evolutionary driver in the site selection process and consequently determine the regional distribution of the species, as has been postulated for other species of fish (Symonds & Rogers 1995).

Several theories have been proposed to explain the location and timing of spawning, including the hypothesis that spawning coincides with conditions that enhance the entrainment of larvae by ocean currents, which in turn increase their chances of finding food in patchy environments, avoiding predators, and finding suitable habitat for settlement (Johannes 1978, Lobel 1978, Barlow 1981). Others have proposed that tFSA sites might be correlated with optimal environmental parameters that confer some genetic or developmental advantages or that sites may be selected primarily to increase the likelihood that males and females will find one another when ready to reproduce (Zaiser & Moyer 1981, Shapiro et al. 1988).

Owing to the geographical remoteness of many tFSAs, their ephemeral nature and the fact that studies are generally disparate and uncoordinated, many gaps exist in our understanding of why fish select certain areas for spawning aggregations and exactly how these areas function to optimize reproductive success. Furthermore, a better understanding of the physical and biological characteristics of tFSAs will provide the information required to develop predictive models that can locate key sites, some of which may currently be unmanaged or even undiscovered. This dearth of information will limit the effectiveness of place-based management strategies such as marine spatial planning and could result in suboptimal marine protected area (MPA) performance and network design, specifically where productive fisheries and protection of essential fish habitat are goals (Friedlander et al. 2003, Sale et al. 2005, Crowder & Norse 2008). For example, lack of geographic information on grouper spawning aggregations in Florida resulted in the establishment of an MPA with a specific goal of protecting black grouper (*Mycteroperca bonaci*), yet unintentionally excluded an important black grouper spawning aggregation later discovered less than 100 m outside the MPA boundary (Eklund et al. 2000). Further compounding the error, the MPA was bounded by the 18-m depth contour, whereas the black grouper aggregation was found at depths of 18–28 m. Greater understanding of the physical characteristics of sites that support spawning aggregations will ensure that they can be easily and accurately identified and assessed during the MPA design phase. For population monitoring, tFSAs provide the best opportunity to collect data cost effectively on the status of adult fish populations that at other times are widely dispersed across tens to hundreds of square kilometres of ocean.

The Society for the Conservation of Reef Fish Aggregations (SCRFA) maintains a global database on FSAs based on data collected through fisher interviews and literature searches to document all known aggregation sites (Sadovy de Mitcheson et al. 2008). SCRFA compiled useful information on the biological characteristics of fish species, such as seasonality, photoperiod and lunar cycles of spawning, and spawning behaviours, but due to limited physical data for most sites, has limited information on site characteristics, such as bathymetry, geomorphology, oceanography and benthic communities. To date, no research has been conducted to synthesize the environmental characteristics of tFSAs across the Wider Caribbean region, including Florida, the Bahamas and Bermuda.

The overall goals of this review are to (1) synthesize the key biological and environmental characteristics of all currently known tFSA sites in the Wider Caribbean region; (2) provide a hierarchically ordered list of the data collection techniques commonly used to study individual tFSAs and suggest a minimum level of information needed for management action; (3) suggest future research directions for improving our understanding of tFSAs and their connectivity at the regional level; and (4) provide recommendations for a coherent network of MPAs designed strategically to monitor and protect multispecies tFSA sites across the Caribbean. A mutually replenishing network of well-managed and monitored tFSAs will support recovery of depleted predatory reef fish populations and thus contribute to restoring ecological integrity, sustainable coastal fisheries and community livelihoods at the regional scale.

## Methodology for compiling existing knowledge of Caribbean tFSA sites

### *Fish species that form tFSAs in the Wider Caribbean*

This review focuses on characterizing transient spawning aggregations in the Caribbean Large Marine Ecosystem (CLME) management unit, with some information from peripheral locations, such as Florida and Bermuda (Figure 1). We refer to this combined region as the Wider Caribbean, consistent with the area definition from the Regional Seas Programme of the United Nations Environment Programme. The Wider Caribbean region includes all island states and territories in the Caribbean Sea and the Caribbean coasts of Mexico, Central America and South America, as well as waters of the Atlantic Ocean adjacent to these states and territories (28 island and continental countries). Owing to similarities in fish communities associated with coral reefs of the Caribbean Sea and the presence of active spawning aggregations, we include Bermuda in our use of the term *Wider Caribbean*.

The SCRFA database served as the starting point for the analysis (Sadovy de Mitcheson et al. 2008, SCRFA 2011) and included 45 tFSAs for the Wider Caribbean region. No information was

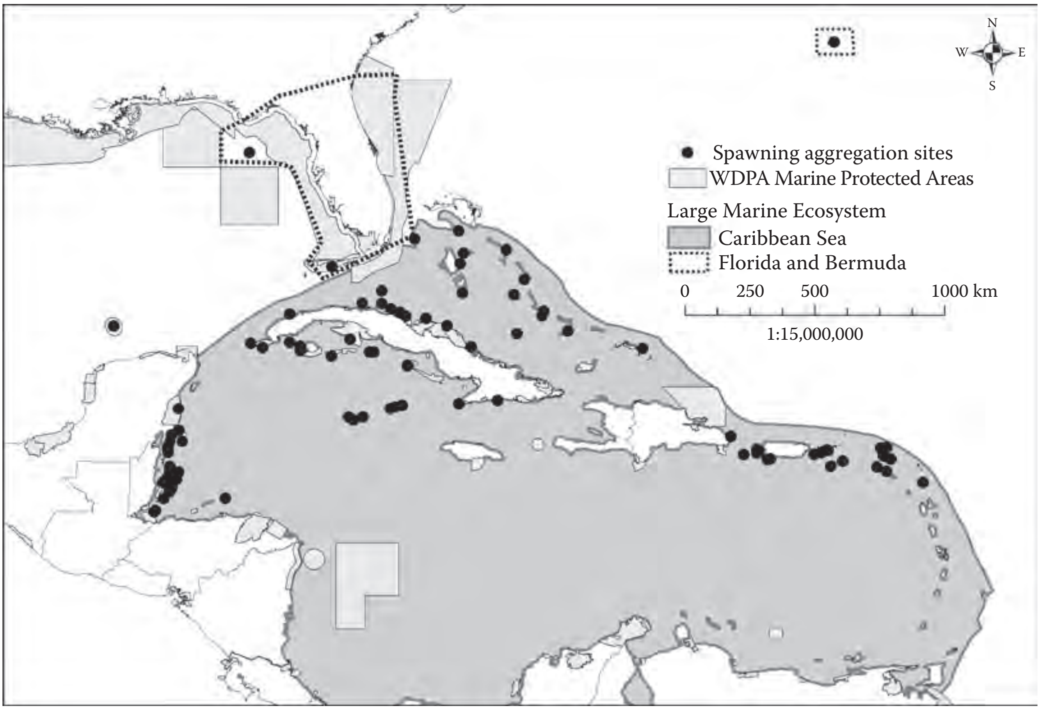


**Figure 1 (See also colour figure in the insert)** Historically known spawning aggregation sites of grouper and snapper with/without direct/indirect evidence since 1884. Filled circles represent the general area of FSA sites, not the exact location. The darker shaded area is the Caribbean Large Marine Ecosystem region. In addition, the study area includes Florida and Bermuda regions, shown by thick dotted lines. The lighter shading indicates marine protected areas listed in the World Database on Protected Areas (WDPA, www.wdpa.org).

available for the south-eastern and southern Caribbean, although species distribution records from FishBase (Froese & Pauly 2010) indicated that species known to form aggregations do inhabit these areas, suggesting a major geographic gap in the regional information on tFSAs. For some records, the type of spawning aggregation (resident vs. transient) was unspecified. For example, Nassau grouper (*Epinephelus striatus*) is well known as a transient aggregation spawner but was occasionally categorized as 'unspecified'. When these entries were corrected, 143 of 151 records were classified as transient spawning aggregations. Most records in the SCRFA database were for Nassau grouper (32 of 143, or 22%), mutton snapper (*Lutjanus analis*), cubera snapper (*L. cyanopterus*), gray snapper (*L. griseus*), red hind (*Epinephelus guttatus*), black grouper (*Mycteroperca bonaci*) and yellowfin grouper (*M. venenosa*). It is important to note, however, that the SCRFA database is biased towards the commercially important species, which make up the large majority of the database records, in large part because of the heavy reliance on fisher interviews (Sadovy de Mitcheson et al. 2008).

To address the data gap in the biogeography of tFSAs, we invited specialists to a regional workshop, "Characterization and Prediction of Transient Reef Fish Spawning Aggregations in the Gulf and Caribbean Region", held in Cumaná, Venezuela, as part of the 62nd Annual Gulf and Caribbean Fisheries Institute meeting on 5 November 2009. The workshop, sponsored by the National Science Foundation's Virgin Islands Experimental Program to Stimulate Competitive Research (VI-EPSCoR), included over 50 participants from 18 countries around the Caribbean. Participants compiled data on the location of multispecies tFSAs in their respective regions, the species-specific timing of spawning and conservation status, and reported on the types of information collected through scientific investigations and local knowledge. The results revealed an additional 13 tFSAs from six countries and territories that were not included in the SCRFA database at the time of review. To broaden our information gathering on the specific characteristics of individual tFSAs, we also conducted an online survey designed to collect metadata for each tFSA. Data requested included lists of fish species that aggregate to spawn, the timing and specific location of spawning and a wide range of ancillary information generated from fishery-dependent surveys at ports and landing sites, underwater visual censuses, visual and acoustic tag and recapture studies, bathymetric and habitat mapping exercises, *in situ* and remotely sensed oceanographic studies (chemical, biological and physical) and modelling.

In addition to the SCRFA database, this review included several additional records documented in the grey literature. For example, we included Nassau grouper tFSA sites that were documented in Honduras (Fine 1990, 1992), Dominican Republic (Sadovy 1997, Sadovy et al. 2008) and Antigua and Barbuda (Munro & Blok 2003). In addition, eight sites on Alacranes Reef, off northern Yucatan Peninsula, Mexico, were identified by local fishers' traditional ecological knowledge (Aguilar-Perera et al. 2008). Ojeda-Serrano et al. (2007) identified 94 potential spawning sites in Puerto Rico from interviews with fishers, although these sites have not been verified. We include five sites that Ojeda-Serrano et al. (2007) described as known spawning aggregations. Aguilar-Perera et al. (2009) provided 28 potential Nassau grouper tFSA sites at the Quintana Roo coasts and Banco de Chinchorro, Mexico, based on fisher interviews, of which four sites have been scientifically verified as active spawning sites and are included here.

In total, 37 species of fish from 10 families were documented to aggregate and spawn in tFSAs in the Wider Caribbean (Table 1). The major fish families included groupers (Serranidae), snappers (Lutjanidae) and jacks (Carangidae).

## *Geographical distribution of documented tFSAs*

A total of 108 geographically discrete spawning aggregations were identified from 14 states and territories throughout the Wider Caribbean (Figure 1, Table 2). Twenty-eight sites were identified in the western Atlantic Ocean, including the Bahamas and Bermuda; 47 in the northern Caribbean;

**Table 1** Species that form transient spawning aggregations in the Wider Caribbean, by country or geographic area

| Family | Species name | Common name | Countries |
|---|---|---|---|
| Serranidae | *Epinephelus striatus* | Nassau grouper | BM, BZ, CI, MX, STT, (BH), (CU), (DR), (HnD), (PR), (TCI) |
|  | *E. guttatus* | Red hind | BM, PR, STT, STX, MX, NA (AB), (AG), (BZ), (CU) |
|  | *E. adscensionis* | Rock hind | (BVI), (PR) |
|  | *E. itajara* | Goliath grouper | (FL), (MX) |
|  | *E. morio* | Red grouper | (FL), (CU), (MX) |
|  | *Mycteroperca bonaci* | Black grouper | BM, BZ, BH, (CI), (CU), (FL), (PR), (MX) |
|  | *M. venenosa* | Yellowfin grouper | BZ, PR, STT, (BH), (CI), (CU), (TCI), (MX), (FL) |
|  | *M. tigris* | Tiger grouper | CI, PR, STT, TCI, (BH), (BZ), (MX), (CU) |
|  | *M. interstitialis* | Yellowmouth grouper | (PR) |
|  | *M. phenax* | Scamp | (FL) |
|  | *M. microlepis* | Gag | (FL) |
| Lutjanidae | *Lutjanus analis* | Mutton snapper | BH, BZ, CU, STX, (FL), (TCI) |
|  | *L. jocu* | Dog snapper | BZ, STT, (CI), (CU), (FL), (PR), (MX) |
|  | *L. synagris* | Lane snapper | CU, STT, (FL) |
|  | *L. cyanopterus* | Cubera snapper | BZ, STT, (CU), (FL) |
|  | *L. griseus* | Gray snapper | STT, (CU), (FL), (MX) |
|  | *L. campechanus* | Red snapper | (FL) |
|  | *L. apodus* | Schoolmaster | (FL), (NA), (STT), (MX) |
|  | *Ocyurus chrysurus* | Yellowtail snapper | BZ, (FL) |
| Carangidae | *Caranx ruber* | Bar jack | CI, BZ |
|  | *C. bartholomaei* | Yellow jack | BZ |
|  | *C. lugubris* | Black jack | CI |
|  | *C. latus* | Horse-eye jack | CI, BZ, (PR) |
|  | *C. hippos* | Crevalle jack | BZ |
|  | *Seriola dumerili* | Greater amberjack | BZ |
|  | *Trachinotus falcatus* | Permit | BZ |
|  | *Decapterus macarellus* | Mackerel scad | CI |
| Ephippidae | *Chaetodipterus faber* | Atlantic spadefish | (BZ) |
| Scombridae | *Scomberomorus cavalla* | King mackerel | (BZ) |
| Labridae | *Lachnolaimus maximus* | Hogfish | BZ |
| Haemulidae | *Haemulon album* | White margate | BZ |
| Balistidae | *Canthidermis sufflamen* | Ocean triggerfish | BZ |
|  | *Xanthichthys ringens* | Sargassum triggerfish | BZ |
|  | *Balistes vetula* | Queen triggerfish | (NA), (STX), (PR) |
| Sparidae | *Calamus bajonado* | Jolthead porgy | BZ |
| Ostraciidae | *Lactophrys trigonus* | Buffalo trunkfish | BZ |
|  | *Rhinesomus triqueter* | Smooth trunkfish | BZ, (PR) |

*Notes:* Those countries for which there is direct evidence of spawning aggregation (i.e., observations of gamete release or the presence of hydrated eggs in mature females) are listed without parentheses. Abbreviated country names are given in brackets where only indirect evidence of aggregations exists for a species, for example, a 3-fold increase in abundance at the site over other times of year (Domeier & Colin 1997), courtship behaviours and colouration changes, abnormally high catch per unit effort with more than 70% mature individuals containing ripe gonads.

Antigua-Barbuda (AB), Anguilla (AG), the Bahamas (BH), Bermuda (BM), Belize (BZ), British Virgin Islands (BVI), the Cayman Islands (CI), Cuba (CU), Dominican Republic (DR), Florida (FL), Honduras (HnD), Mexico (MX), Netherlands Antilles (NA), Puerto Rico (PR), St. Thomas, VI (STT), St. Croix, VI (STX), and Turks and Caicos Islands (TCI).

**Table 2** Documented transient fish spawning aggregations (tFSAs) for reef fish at 108 sites in the Wider Caribbean based on both direct and indirect evidence

| Country | Total no. | Spawning sites/general area name | | Reference |
|---|---|---|---|---|
| Bermuda | 3 | Challenger and Argus Banks (3 sites): western, eastern hind ground, black grouper spawning site | | Sadovy 1997, Sadovy de Mitcheson et al. 2008, Luckhurst 2010 |
| Gulf of Mexico | 3 | Southern Florida Keys (Riley's Hump, Madison Swanson, Steamboat Lumps)<br>Eastern Gulf of Mexico (north-western coast of Florida) | | Coleman et al. 1996, 2011, Koenig et al. 1996, 2000, Sadovy 1997, Lindeman et al. 2000 |
| The Bahamas | 23 | Andros Island (5) | Ragged Island | Smith 1972, Colin 1992, Sadovy 1997, C. McKinney personal communication, November 2009 |
| | | Long Island (3) | Cay Sal | |
| | | Exuma | Cat Cay/Bimini (2) | |
| | | Berry Island (4) | Eleuthera (4) | |
| | | New Providence | Acklins | |
| Turks and Caicos Islands | 2 | Phillips Reef | Northwest Point | Sadovy 1997, Sadovy de Mitcheson et al. 2008 |
| Antigua-Barbuda | 2 | Green Island | Knolls between two islands | Munro & Blok 2003 |
| Netherlands Antilles | 4 | Saba Bank | St. Eustatius | Munro & Blok 2003, Kadison et al. 2009a |
| | | St. Maarten | St. Barthélemy Channel | |
| Anguilla | 3 | Seal Island | Scrub Island (2) | Munro & Blok 2003 |
| US Virgin Islands | 4 | St. Thomas: Hind Bank | Grammanik Bank | Sadovy 1997, Nemeth 2005, R.S. Nemeth et al. 2007, Sadovy de Mitcheson et al. 2008 |
| | | St. Croix: Lang Bank | Southwest area | Beets & Friedlander 1999 |
| Puerto Rico | 7 | El Seco, Vieques Island | | Sadovy et al. 1994, White et al. 2002, Matos-Caraballo et al. 2006, Ojeda-Serrano et al. 2007 |
| | | Multiple sites around main island (5): La Parguera, El Hoyo, Bajo de Sico, Abrir la Sierra, Tourmaline | | Colin et al. 1987, Colin & Clavijo 1988, Shapiro et al. 1993, Sadovy 1997, Sadovy de Mitcheson et al. 2008 |
| | | Mona Island | | Aguilar-Perera et al. 2006, Schärer et al. 2010 |
| Dominican Republic | 1 | Punta Rusia | | Sadovy 1997, Sadovy de Mitcheson et al. 2008 |
| Cuba | 21 | Bajo Mandinga | Cabo San Antonio | Sadovy 1997, Claro et al. 2001, 2009, Claro & Lindeman 2003, Sadovy de Mitcheson et al. 2008 |
| | | Cabo Cruz | Corona de San Carlos | |
| | | Cayo Bretón | Punta Hicacos-Cayo Mono | |
| | | Banco de Jagua | Cayo Megano de Nicolao | |
| | | Cay Guano | Boca de Sagua | |
| | | Cayo Diego Pérez | Cayo Lanzanillo | |
| | | Cayo Avalos | Cayo Fragoso | |
| | | Punta Francés | Cayo Calmán Grande | |
| | | Cayos Los Indios | Cayo Paredón | |
| | | Cayo San Felipe | Cayo Sabinal | |
| | | Cabo Corrientes | | |

**Table 2 (continued)** Documented transient fish spawning aggregations (tFSAs) for reef fish at 108 sites in the Wider Caribbean based on both direct and indirect evidence

| Country | Total no. | Spawning sites/general area name | | Reference |
|---|---|---|---|---|
| Cayman Islands | 6 | Grand Cayman | North-eastern end and Sand Caye | Colin et al. 1987, Tucker et al. 1993, Sadovy 1997, Whaylen et al. 2004, Sadovy de Mitcheson et al. 2008 |
| | | Twelve Mile Bank | | |
| | | Little Cayman | Eastern and western end | |
| | | Cayman Brac East | | |
| Mexico | 13 | Majahual | | Aguilar-Perera & Aguilar-Davila 1996, Sosa-Cordero & Cárdenas-Vidal 1996, Sadovy 1997, Aguilar-Perera 2006, Sadovy de Mitcheson et al. 2008 |
| | | Nichiehabin, San Juan-Chenchomac, Blanquizal-Sta Julia | | Aguilar-Perera et al. 2009 |
| | | Alacranes Reef (8) | | Aguilar-Perera et al. 2008 |
| | | Banco Chinchorro | | Aguilar-Perera & Aguilar-Davila 1996 |
| Belize | 14 | Rocky Point | Sandbore | Carter & Perrine 1994, Sadovy 1997, Paz & Grimshaw 2001, Sala et al. 2001, Heyman et al. 2005, Graham & Castellanos 2005, Heyman & Kjerfve 2008, Sadovy de Mitcheson et al. 2008, Kobara & Heyman 2010 |
| | | Dog Flea Caye | Halfmoon Caye | |
| | | Mauger Caye | South Point | |
| | | Soldier Caye | Northern Glovers | |
| | | Caye Bokel | Long Caye | |
| | | Caye Glory | Gladden Spit | |
| | | Nicholas Caye | Rise and Fall Bank | |
| Honduras | 2 | Guanaja | Cayos Cochinos | Fine 1990, 1992, Sadovy 1997, Sadovy de Mitcheson et al. 2008 |

29 in Central America and an additional 3 tFSAs sites in the Gulf of Mexico. Of these, 55 sites were Nassau grouper tFSAs, and at least 32 sites were shared with other species. No evidence of tFSAs was found for the southern Caribbean.

Distributions of tFSA sites vary geographically among species, but it is not clear if the distribution of tFSAs provides ecologically meaningful information, or if it simply represents the patchy availability of information about tFSA locations. For instance, some species records in our database shared the same sites, although the timing of spawning varied among species. Detailed observations of multispecies tFSAs were available from Belize (Heyman & Requena 2002, Heyman & Kjerfve 2008, Kobara & Heyman 2010), the Cayman Islands (Whaylen et al. 2004, 2006, Kobara & Heyman 2008), Cuba (Claro & Lindeman 2003), Puerto Rico (M.I. Nemeth et al. 2007, Schärer et al. 2010), US Virgin Islands (Nemeth 2005, Kadison et al. 2006, R.S. Nemeth et al. 2007, Nemeth 2009) and Florida (Coleman et al. 1996, 2011, Koenig et al. 1996, 2000).

The 108 documented sites are almost certainly a considerable underestimation of the true number of tFSAs in the Caribbean region and also supposedly represent only a small proportion of those known within the traditional knowledge of Caribbean fishing communities. Evidence for a geographical knowledge gap is highlighted in Figures 2–4, which reveals a large disparity between the spatial distributions of aggregating species and the spatial distribution of known tFSAs. For example, Nassau grouper, red hind and mutton snapper sightings have occurred across a much broader

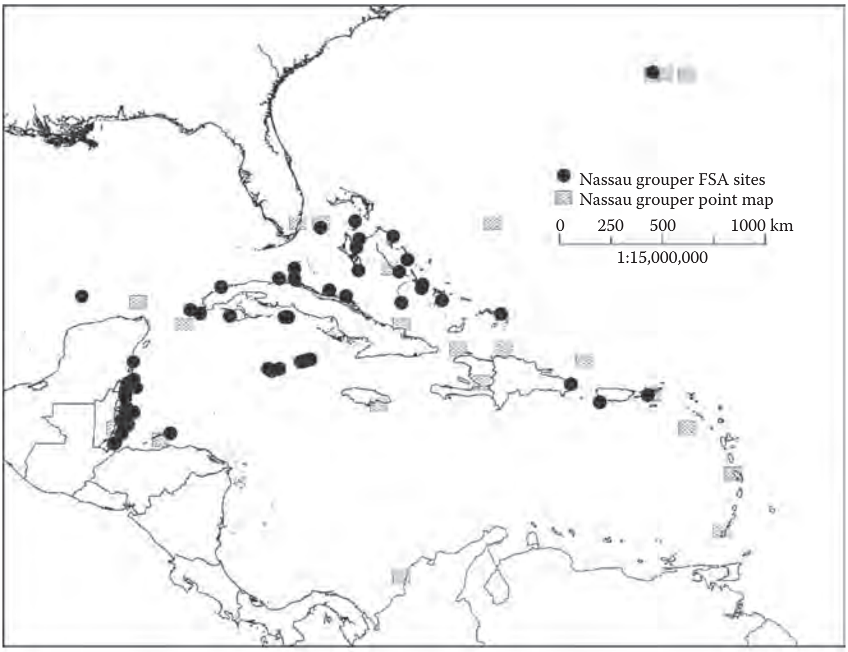


**Figure 2** Historically known spawning aggregation sites of Nassau grouper (*Epinephelus striatus*) with/without direct/indirect evidence (circles). Rectangles represent a computer-generated distribution point map for each species from FishBase (Froese & Pauly 2010).

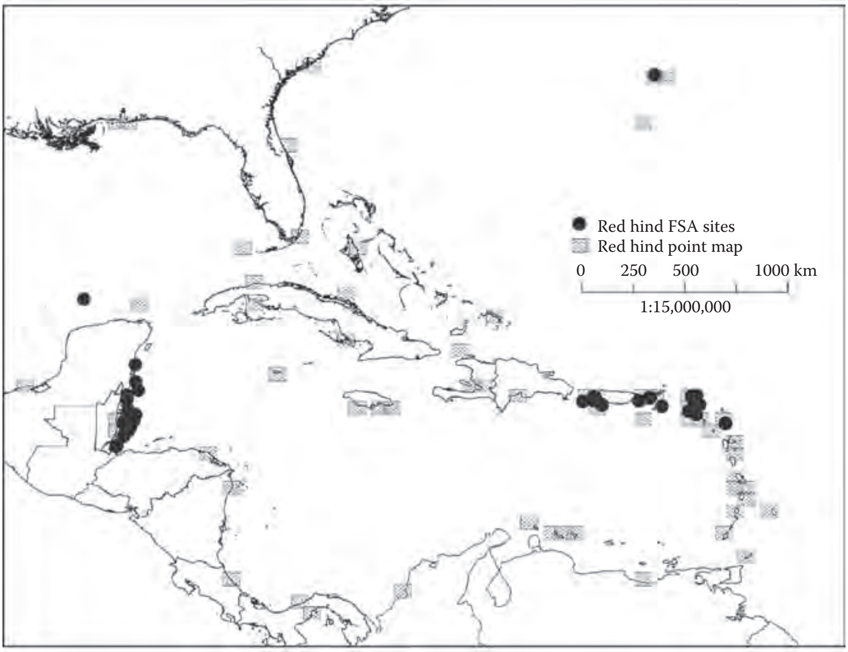


**Figure 3** Historically known spawning aggreation sites of red hind (*E. guttatus*) with/without direct/indirect evidence (circles). Rectangles represent a computer-generated distribution point map for each species from FishBase (Froese & Pauly 2010).

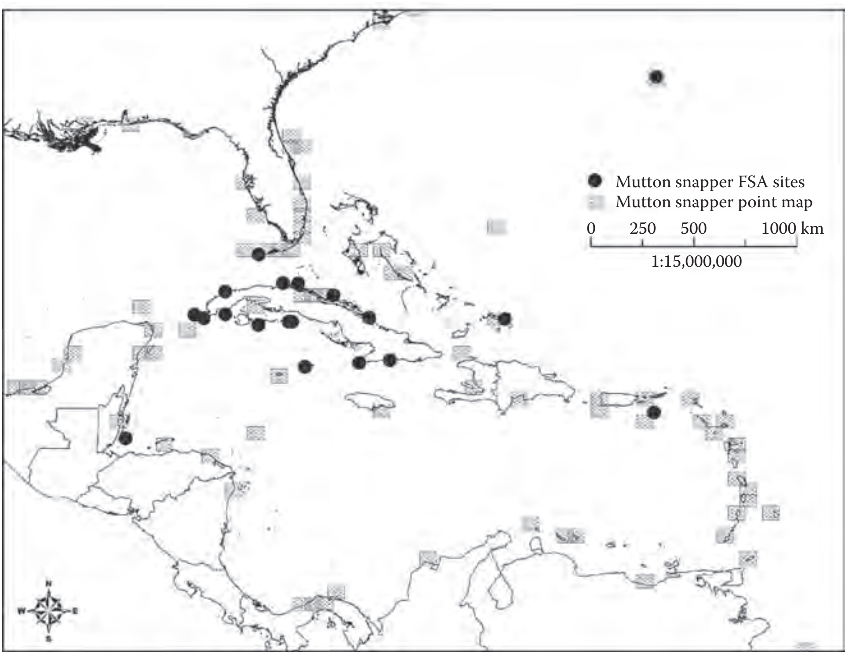


**Figure 4** Historically known spawning aggregation sites of mutton snapper (*Lutjanus analis*) with/without direct/indirect evidence (circles). Rectangles represent a computer-generated distribution point map for each species from FishBase (Froese & Pauly 2010).

spatial extent than would be feasible to sustain based only on known spawning aggregations. More specifically, documented red hind tFSAs are only reported for the eastern Caribbean, Bermuda and Mexico, while red hind are distributed throughout the Wider Caribbean. This knowledge gap is particularly evident in the southern Caribbean islands, where few aggregations are known, yet populations of spawning fish clearly exist and in some cases form an important component of the fisheries landings (e.g., red hind and mutton snapper in Grenada (Jeffrey 2000)). Islands most under-represented in the synthesis, but likely to support tFSAs, include Jamaica, Hispaniola, St. Vincent and the Grenadines, Netherlands Antilles, Barbados and Trinidad and Tobago. In addition, little has been reported on tFSAs off the Caribbean coast of South America or southern Central America (Panama, Costa Rica, Nicaragua, Honduras). A synthesis of local knowledge in fishing communities and tFSA-focussed research and surveys of bathymetric features are needed in these locations. Local fisher knowledge can also be used to determine if optimal sites exist that were once tFSAs with potential for recovery (e.g., Gleason et al. 2011).

## Biophysical characteristics of tFSA sites

### *Timing of tFSAs in the Wider Caribbean*

Since the 1970s, a number of papers have summarized the available information on the environmental and biological factors influencing the timing of reef FSAs, primarily from the Caribbean and the tropical western Pacific (Johannes 1978, Robertson 1991, Claydon 2004, Nemeth 2009, Colin 2012). Far fewer studies have examined the timing and location of tFSAs in the Gulf of Mexico (Heyman & Wright 2011). Synthesis of existing data on transient aggregating fish species suggests that the timing of migration, formation of aggregations and spawning are regulated by cues operating on at least three nested temporal scales: intraannual, lunar and diel (Nemeth 2009). Hierarchical cues for the scheduling of spawning-related activities have also been documented in other marine organisms. For example, spawning in some tropical corals is influenced by sea temperature (time of year), lunar or tidal cycles (time of month) and diel light cycles (time of day) (Mendes & Woodley 2002). Some evidence from long-term monitoring studies also suggests a fourth temporal scale, that of interannual periodicity; a portion of the adult population may only aggregate to spawn every other year (Nemeth 2005). Little is known about mechanisms and occurrence of biennial spawning, but this strategy could be an adaptive response to local environmental conditions or related to optimizing longer-term cost and benefits related to reproductive energetics. Studies of Atlantic salmon (*Salmo salar*) found that some fish spawn annually and some biennially, but that the proportion of biennial spawners increased with fish size, whereby the smallest repeat spawners (<60 cm) spawned annually and the largest (>90 cm) biennially (Jonsson et al. 1991). If such population dynamics characterize species that form tFSAs, then understanding population age structure could shed light on differential vulnerability to fishing and oscillations in fisheries catch and aid in forecasting recovery rates after protection from fishing.

The multiscale environmental and biological cues synchronizing behaviours leading to spawning may include photoperiod, water temperature, current speed and direction, lunar phase, tidal phase, ambient lighting (particularly times of sunset and sunrise), fish density, presence of mates displaying breeding colouration, intensity of courtship behaviour and production of specific pheromones and sounds (Colin 1992, Lobel 1992, Mann et al. 2009). Many of these cues are interrelated, thus confounding our ability to determine the relative importance of individual factors. For example, photoperiod and water temperature are both influenced by the amount of solar radiation reaching the earth. The depletion of gravid females and changes in these environmental and biological factors are also important for determining reproductive activity at daily, monthly and annual timescales (Thresher 1984, Domeier & Colin 1997, Heyman et al. 2005, R.S. Nemeth et al. 2007, Starr et al. 2007). These cues also operate across different spatial scales. Changing photoperiod and water temperature influence organisms at the broadest spatial scales (global to regional). Changes in water temperature, current speed, tidal cycle and ambient lighting operate at intermediate spatial scales (regional to local), and fish density and intraspecific sexual behaviours operate at the finest spatial scales (site-specific).

Determining the relative importance of these many complex interrelated spatial and temporal factors is an important challenge for applied research. Nevertheless, some generalities emerge for certain species and functional groups. At the broadest spatial scales, water temperature has a greater influence on timing of reproduction than photoperiod. For example, Nassau grouper and red hind in the Caribbean form spawning aggregations from December to March when water temperature cools to less than about 27°C (Colin et al. 1987, Carter 1989, Colin 1992, Carter et al. 1994, Sadovy & Eklund 1999, R.S. Nemeth et al. 2007). In contrast, spawning aggregations of Nassau grouper, red hind and black grouper farther north, in Bermuda, take place between May and August when water temperatures increase beyond 25°C (Smith 1971, Luckhurst 1998, 2010). In both regions, the ideal temperature range for spawning of these three species is between 25°C and 26.5°C (Tucker et al. 1993).

The importance of temperature to spawning may be related to the physiological limitations of vitellogenesis and egg development at higher water temperatures (Lam 1983). Watanabe et al. (1995b) examined the effects of temperature on eggs and yolk sac larvae of the Nassau grouper under controlled hatchery conditions. Development and survival of newly hatched larvae to first feeding was inversely related to temperatures of 26°C, 28°C and 30°C. A temperature of 26°C was deemed optimal for incubating Nassau grouper eggs and larvae, although even lower temperatures may provide additional benefits to survival (Watanabe et al. 1995a). Ellis et al. (1997) compared the feed utilization and growth of hatchery-reared, postsettlement-stage Nassau grouper juveniles at temperatures of 22°C, 25°C, 28°C and 31°C under controlled laboratory conditions. Final weights and growth rates were higher at 28°C and 31°C than at 22°C or 25°C; thus, a temperature range of 28–31°C was recommended for culture of early juveniles (Ellis et al. 1997). This experimental evidence suggests that Nassau grouper (and possibly red hind) may synchronize spawning to seasonal time periods when water temperature is not only optimal for egg development and larval survival but also sufficiently warm to maximize growth of postsettlement larvae. This may explain why Nassau grouper and red hind in Bermuda do not spawn in the autumn when temperatures for reproduction are optimal but conditions for juvenile growth and survival are poor due to cold water in the winter. Such thermal synchronization will likely have implications for the onset of migrations and the timing of spawning in a changing global climate, with as-yet-unknown consequences (Sims et al. 2005).

At regional and local spatial scales, the lunar cycle and its influence on tides is a widely recognized temporal cue for spawning. Although most aggregating fish species spawn during a distinct period of the lunar cycle (full moon, new moon, etc.), the tidal influence in the Caribbean may be relatively minor because of low tidal amplitude (40–55 cm daily) (Kjerfve 1981, Heyman et al. 2005). Indeed, tidal timing, as a trigger for formation of aggregations and spawning, is far more important in the Indo-western Pacific (Pet et al. 2005), where tidal amplitudes may range 1–3 m. However, many of the species that synchronize spawning activity to tidal patterns are resident aggregators that spawn during the day on outgoing tides within reef channels (Sancho et al. 2000b). Although no clear tidal cue has yet been detected, most transient aggregations in the Wider Caribbean, as well as in the Indo-Pacific, are formed in association with a time of day, usually with spawning at sunset or at night (Domeier & Colin 1997), and with a specific time of month around full moon or other phases of the lunar cycle (Claydon 2004, Nemeth 2009). In addition, field measurements and oceanographic models at Gladden Spit in Belize showed that spring tides can excite significant high-frequency flow variations near the reef, indicating that the preference for spawning in the days immediately following full moon may not be coincidental (Ezer et al. 2011). The strategies of spawning on an outgoing tide and when light levels are low are both advantageous to egg survival and dispersal. Low light enhances survival because egg predators are typically visual predators (Hamner et al. 2007).

### *Oceanographic characteristics of tFSAs in the Wider Caribbean*

Interacting site characteristics such as physical geomorphology, hydrodynamics and the composition of benthic biological communities, together with geographical factors, such as connectivity to suitable settlement sites, appear to combine to make some locations function as tFSA sites. The exact physical conditions remain unknown for most sites and may vary geographically, but it is likely that a subset of variables exists that explains much of why a spawning site persists at a single location over generations. Clearly, a diverse multidisciplinary approach is required to unravel the complexities of tFSA structure and function. The majority of research on site characteristics has focused on geographical location across the reef, seafloor geomorphology and oceanography.

The local geomorphology can have a very strong influence on oceanographic features that fish can use to their advantage when releasing eggs (Kingsford et al. 1991). For example, some hypotheses suggest that the location and timing of spawning aggregations coincide with preferable currents that increase larval dispersal to suitable places (Barlow 1981), enhancing connectivity within a patchy coral reef environment (Sale 2004). Ocean currents flowing towards and around reef promontories often result in the formation of gyres or eddies (Lobel & Lobel 2008). In contrast to the off-reef transport hypothesis, the presence of gyres during spawning seasons has generated alternative hypotheses that spawning is synchronized to exploit hydrographic features that entrain and retain developing eggs and larvae and return them to their natal seascapes (Johannes 1978, Lobel 1978, Lobel & Robinson 1988, Karnauskas et al. 2011). Levels of larval retention and the spatial extent of connectivity in fish are thought to be strongly influenced by physical setting (Jones et al. 2009). Local retention of fish larvae has been shown for several small-bodied reef fish species (Swearer et al. 1999, Planes et al. 2009, Hogan et al. 2012), but there have been very few ocean

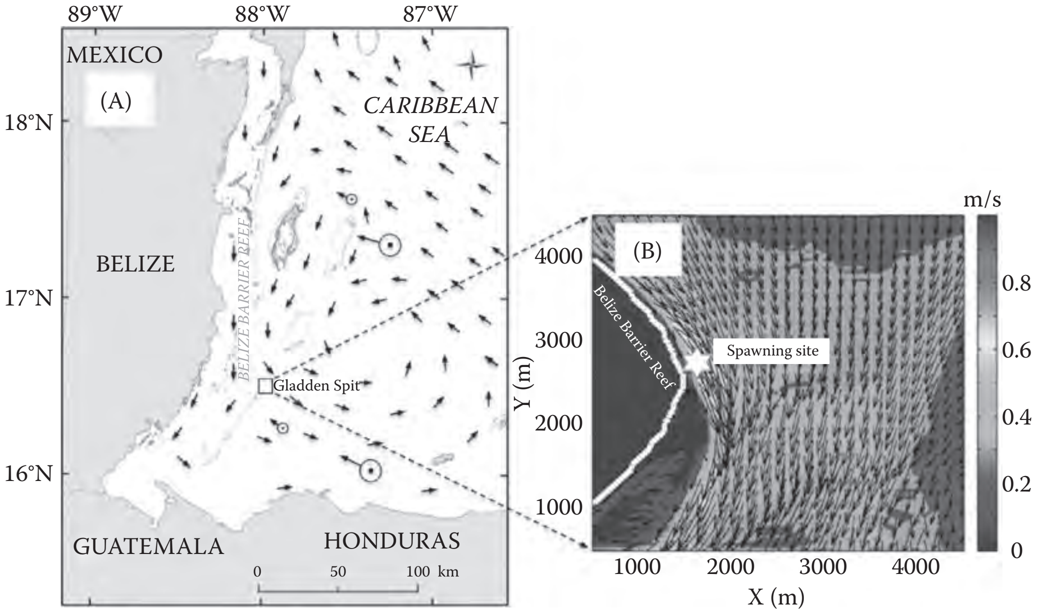


**Figure 5 (See also colour figure in the insert)** Currents at the Gladden Spit spawning aggregation site on the Belize Barrier Reef. (A) Mean currents (arrows) and winds (arrows with circles) as redrawn from Craig (1966) and Ezer et al. (2005). Note the recirculation eddy south of the reef promontory spawning site. (B) Detailed circulation at the Gladden Spit spawning aggregation site as modelled by Ezer et al. (2011, with permission from Springer).

current studies seeking to identify mechanisms of local retention and dispersal in relation to tFSA sites in the Caribbean. Studies of oceanic patterns (regional to local: >100-km distance) in the Bahamas (Colin 1995) and Belize (Figure 5) (Ezer et al. 2005, Heyman & Kjerfve 2008) suggest that currents around tFSA sites in those areas are oriented along the shelf edge. Ezer et al. (2005) illustrated that when westward-propagating cyclonic eddies approached the Mesoamerican Barrier Reef, the Caribbean Current shifted offshore, the cyclonic circulation in the Gulf of Honduras intensified, and a strong southwards flow resulted along the reefs (Figure 5). Conversely, when anti-cyclonic eddies approached the reef, the Caribbean Current moved shorewards, and the flow was predominantly northwards and westwards across the reefs. Local to small-scale studies (50 m x 50 m grid cells in a model domain of 5 km x 5 km) revealed potential mechanisms for larval transport and retention (Ezer et al. 2011). Ezer et al. (2012) further showed that the particular shape of the promontory amplified coastal currents at the spawning site, through non-linear interactions between flow and topography. Karnauskas et al. (2011) used a hydrodynamic model to explore the effects of topography on currents at the Gladden Spit reef promontory along the Mesoamerican Barrier Reef and predicted local retention of larvae.

In addition, internal waves play an important role in transport and concentration of plankton and other organisms across topographic features, such as shelf edges (Stevick et al. 2008). Ezer et al. (2011) demonstrated the occurrence of internal waves at a multispecies tFSA site in Belize (Figure 6). These high-frequency occurrences may affect larval transport and intermittent upwelling and are worthy of further study. Remote sensing (e.g., synthetic aperture radar [SAR] to map internal wave patterns) and *in situ* oceanographic sensors, such as acoustic current profilers, can be used to determine if the timing of spawning coincides with periods of high-frequency internal waves that may help transport the offspring to inshore settlement habitats. An alternative hypothesis

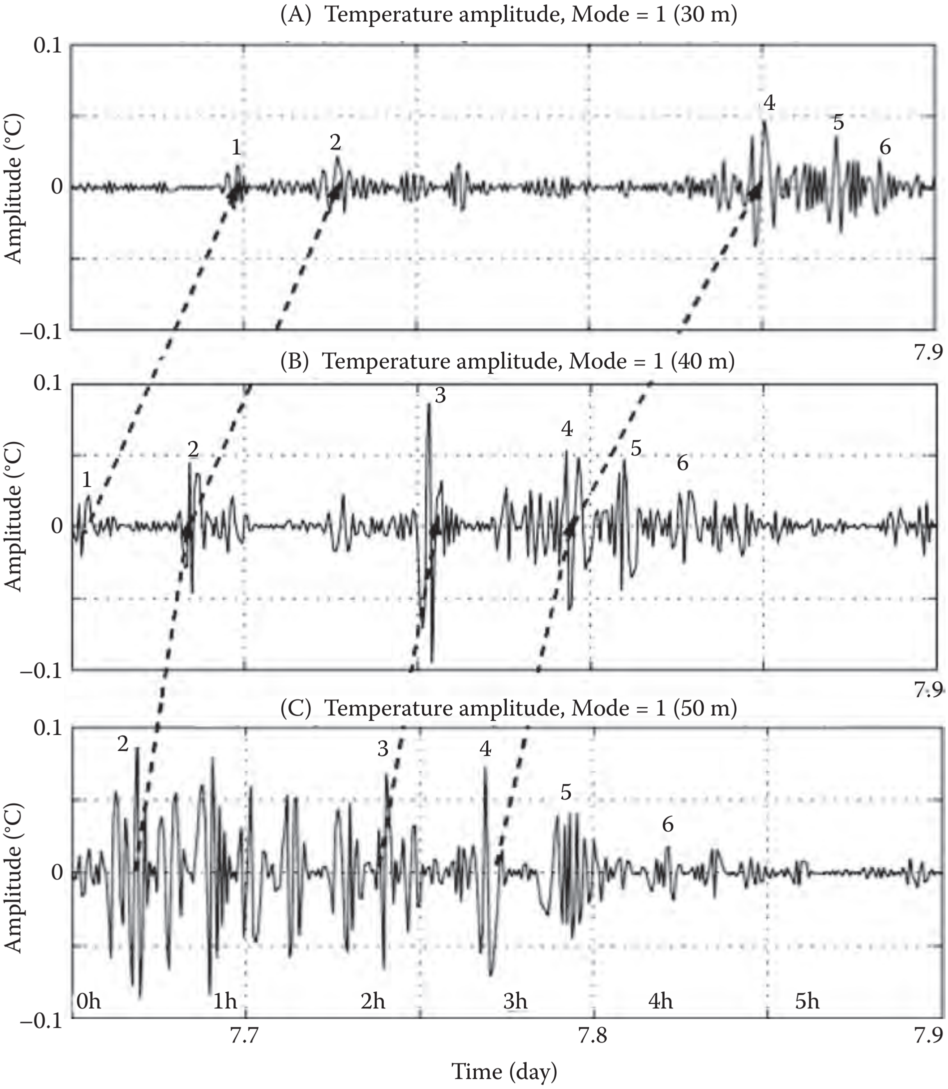


**Figure 6** An example of a 6-h period of the first mode (highest frequency) of the Hilbert-Huang transform (HHT). (A)–(C) The observed records at 30, 40 and 50 m depths, respectively. Dashed lines and numbers indicate examples of groups of waves that seem to propagate from deep to shallower water at about the speed of internal waves. (After Ezer et al. 2011 with permission from Springer.)

worthy of testing is that spawning is timed to avoid internal waves because they concentrate offspring at the surface where they are more susceptible to predators.

The interaction between these physical features likely explains why some sites host spawning aggregations by multiple species while other sites have little or no aggregation activity. Characterizations of existing sites will help identify the most relevant environmental predictors to input to models that predict locations of structurally suitable sites, some of which may be unfished and unknown. This then provides a cost-effective tool to address an information gap that will be important in developing comprehensive management strategies and understanding connectivity (Heyman & Kobara 2012). Here, we examine the structural characteristics hierarchically from broad-scale geological patterns and processes that shape continental shelves, to the finer-scale characteristics of benthic communities that provide food, refuge from predation and other resources for spawning fishes.

## *Seafloor geomorphology of tFSAs in the Wider Caribbean*

Seafloor geomorphology has emerged as a useful predictor of tFSA locations. Seafloor geomorphology is typically mapped from bathymetry, and derivative metrics (sometimes referred to as morphometrics) have been applied to quantify various physical characteristics (Prior & Hooper 1999, Pittman et al. 2009). The most useful metrics include water depth and surface geometry of the seafloor (slope, sinuosity, topographic complexity) and the orientation, or aspect, relative to waves and other water movements. A key characteristic of most multispecies tFSAs is their location in close proximity to sharp shelf edges and deeper water, typically where a steep (>20°) downward slope or abrupt change in depth occurs, commonly referred to as a drop-off. These structural edges in the seafloor terrain were formed as sea level rose and stabilized. Transgressive fringing and barrier reefs first grew upwards and then outwards between successive uplift events, forming wide reef crests bounded by relatively steep forereef slopes (Burbank & Anderson 2001). The environmental edge effect around tFSAs can occur at the shelf edge, along channels, along the slopes of fringing or barrier reefs, and at other distinctive bathymetric features such as promontories. A promontory was defined as a distinct turning point, or bend in the shelf edge, where the steep terrain protrudes prominently into deeper waters like a submerged headland (Figures 7 and 8; Kobara & Heyman 2008, 2010).

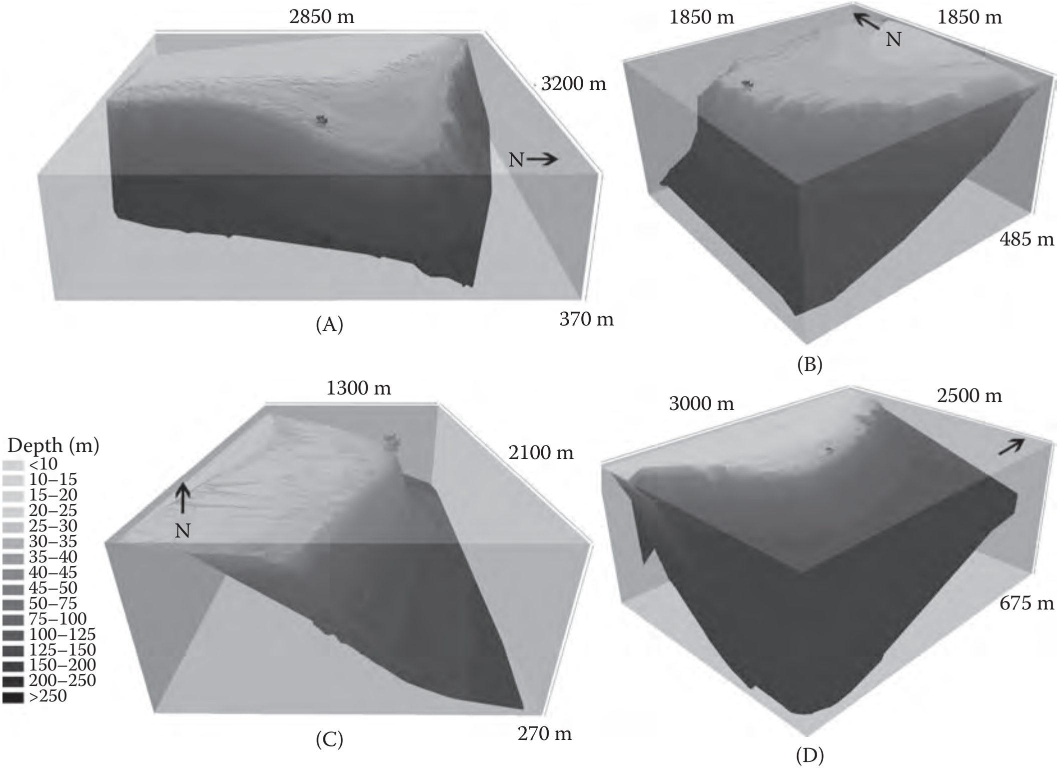


**Figure 7 (See also colour figure in the insert)** Three-dimensional bathymetry of two representative spawning sites in the Cayman Islands, (A) Grand Cayman East and (B) Little Cayman West, and two in Belize, (C) Emily (or Caye Glory) and (D) Gladden Spit. (Modified from Heyman & Kobara 2012.)

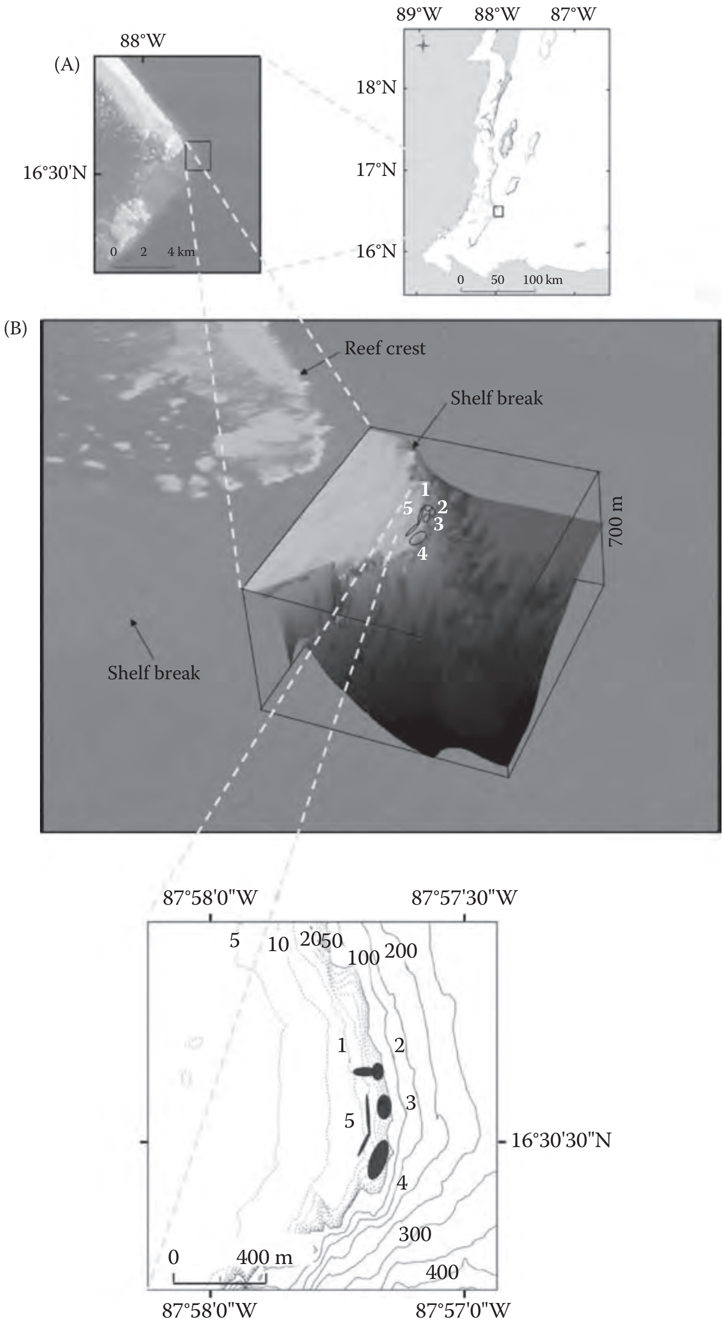


**Figure 8 (See also colour figure in the insert)** (A) Multispecies spawning aggregations at Gladden Spit in Belize. This oblique aerial view from the south-east was created in ARCGIS 10.1 and ARCScene and combines a Landsat™ satellite image with field-collected bathymetric and species-specific spawning aggregation location data. The primary spawning aggregation sites for various species are shown in relation to the shelf edge and labelled as follows: 1, *Epinephelus striatus*; 2, *Mycteroperca bonaci*, *M. venenosa*, *M. tigris*; 3, *Lutjanus jocu*; 4, *Lutjanus cyanopterus*; 5, *Lachnolaimus maximus*, *Lactophrys trigonus*, *Rhinesomus (=Lactophrys) triqueter.* (B) Detailed bathymetry of the site (depth contours in metres) showing the location of the same spawning aggregation sites as in Figure 8A.

**Table 3** Geomorphological type assigned to transient spawning aggregation sites in the Wider Caribbean based on site descriptions in the literature.

| Geographic region | tFSA site | Shelf edge | Reef promontory | Adjacent to drop-off | On reef crest | Near reef channel |
|---|---|---|---|---|---|---|
| Bahamas | Bimini | y | | | | |
| | Long Island East | y | | | | |
| | Long Island South | | | 250 m away | | |
| Turks and Caicos Islands | | y | y | y | | |
| US Virgin Islands | Grammanik Bank | y | y | y | | |
| | Red Hind Bank | y | n | 300 m away | | |
| | Lang Bank | n | y | y | | |
| Puerto Rico | El Hoyo | y | y | y | | |
| | El Seco | y | y | 250 m away | | |
| Cuba | Bajo Mandinga | y | y | y | | |
| | Cabo Cruz | y | | y | | |
| | Cayo Bretón | y | | y | | |
| | Banco de Jagua | y | | y | | |
| | Cayo Diego Pérez | | | y | | |
| | Cayo Avalos | y | | y | | |
| | Cayos Los Indios | y | | | | |
| | Cayo San Felipe | y | | | | |
| | Cabo Corrientes | y | | | | |
| | Cabo San Antonio | y | | | | |
| | Corona de San Carlos | y | | y | | |
| | Punta Hicacos-Cayo Mono | y | | | | |
| | Cayo Megano de Nicolao | y | | y | | |
| | Cayo Caimán Grande | | | | y | |
| | Cayo Paredón | | | | y | y |
| | Cayo Sabinal | | | | | y |
| Mexico | Mahahual | | | n | | |
| Honduras | Guanaja | y | | y | | |

*Notes:* y = yes, n = no, blank = no explicit description. These classifications are subjective, based on descriptions given in the original studies, since there is no consensus on how close a tFSA must be to a geomorphological feature to be considered ‘associated’ with it.

Our review revealed that most tFSAs were described as occurring close to shelf edges (80.6%) or drop-offs (63.9%) (Table 3). Two tFSAs (in Mexico and the Bahamas), however, were described as not located close to a drop-off (Colin 1992, Aguilar-Perera & Aguilar-Dávila 1996). It remains unclear if these exceptions are linked to species-specific preferences or unique site-specific characteristics, but possible causal mechanisms are being examined (S. Kobara et al. unpublished data). In most cases, however, the definition of ‘shelf edge’ and the actual distances from the shelf edge or drop-off were unspecified in the data. In addition, there are insufficient quantitative data to define ‘proximity’ accurately, i.e., the maximum distance that can be considered ‘close’ to a geomorphological feature. Kobara & Heyman (2008) observed that all Nassau grouper tFSA sites in the Cayman Islands were between 0 and 50 m from the shelf edge where (1) promontories occurred, and (2) water depth was between 25 and 45 m. These promontories also served as tFSA sites for at least two other fish species and in some cases up to 17 fish species aggregated to spawn. Distinct promontories supported tFSAs in Belize, Turks and Caicos Islands, Puerto Rico, Cuba and the Cayman Islands. In Belize, 12 multispecies tFSAs occurred in water deeper than 20 m, less than

100 m horizontally from shelf edges, less than 200 m from reef promontory tips and at a mean distance of 78 m from the 100-m isobath (Figures 7 and 8; Kobara & Heyman 2010). Each fish species appeared to maintain site fidelity to a specific spawning location within a distinct area of the greater promontory feature. At Gladden Spit, for example, geographically distinct spawning locations for 10 species have been observed and mapped within a 6-ha area at the tip of the reef promontory (Figure 8; Heyman & Kjerfve 2008).

The suitability for spawning of broad-scale and relatively easily detected geomorphological features provides a realistic, cost-effective and fisheries-independent method for locating not only existing tFSAs but also those that may have been extirpated or those remaining undiscovered. Using this fishery-independent method, Kobara & Heyman (2010) identified South Point in Belize as a multispecies tFSA site. Much of the geomorphological characterization was achieved using an acoustic depth sounder that recorded bathymetry with 30–50 m spatial resolution (Kobara & Heyman 2008, 2010), but it is also possible to detect promontories and other shelf-edge features through examination of the sinuosity and curvature of the shelf-edge contour or isobath (Kobara & Heyman 2006). Locations with shelf-edge curvature in a certain range (e.g., a reef promontory within a 1-km radius circle) were considered as potential tFSA sites. Some relatively large sites could be identified from smaller-scale bathymetry; however, it is likely that identification of many other biologically important sites would require higher resolution (<30 m) bathymetric data. Investigations of scale dependency in recognition of potential spawning sites from bathymetry alone are under way, and the results will determine the appropriate scale(s) for future bathymetric mapping missions aimed at characterizing tFSAs (J. Blondeau unpublished data, S. Kobara et al. unpublished data).

Not all tFSAs, however, occur at distinctive promontories. For example, red hind tFSA sites off western Puerto Rico, US Virgin Islands and Saba (Netherland Antilles) have been reported over relatively flat, non-promontory reef areas (Nemeth 2005, R.S. Nemeth et al. 2007, Kadison et al. 2009b). Boomhower et al. (2010) evaluated the predicted occurrence of tFSAs at reef promontories in Los Roques, Venezuela, based on a ‘reef promontory’ search image. Results did not show large tFSAs at predicted aggregation sites and were inconclusive. Closer examination revealed that while the sites were reef promontories, the shelf edges occurred in water less than 15 m deep, and although adjacent to a steep drop-off, the bottom levelled onto a shelf at 30–40 m, rather than dropping directly into deeper water (e.g., >70 m depth). Gag grouper (*Mycteroperca microlepis*) aggregate for spawning along the crests of ridges, adjacent to drop-offs in the eastern Gulf of Mexico (Coleman et al. 2011). These findings suggest that shelf-edge adjacency to deep water may be a critically important factor for the formation of tFSAs. In summary, although there are several geomorphological features that support spawning aggregations for a range of fish species, it is clear that bathymetry and its derivatives alone can be a valuable data type for identifying and studying the biogeography of tFSAs.

Use of a relatively static characteristic such as bathymetry, which is common to many multispecies tFSAs sites, provides an opportunity to conduct detailed comparative investigations to examine generalities in geomorphological structure. Sufficiently detailed bathymetric maps, however, are available from only a few countries in the region (Wright & Heyman 2008), thus limiting development of broad-scale pan-Caribbean predictive models. Relatively low-cost analytical options for mapping broad-scale shelf-edge geomorphology include modelled bathymetry or pseudobathymetry based on algorithms applied to reflected light in optical imagery, such as satellite data and aerial photography (Stumpf et al. 2003). Optical sensors, however, are limited by water clarity, turbidity and water roughness, which influence the light penetration/reflectivity through the water column (Jensen 2007). A better understanding of the relationship between tFSA occurrence and function and specific features of coastal geomorphology can be achieved through further comparative investigation with quantitative data. Establishing a clear definition of ‘shelf edge’, ‘deep water’ and other features, together with identifying ecologically meaningful spatial scale(s), are key challenges for future analyses.

**Table 4** Detailed descriptions of the benthic habitat found at each transient tFSA site in the Caribbean (from literature cited in Table 2)

| Country | tFSA sites | Benthic habitat |
|---|---|---|
| Bahamas | Bimini | A thin sand veneer over limestone base rock with abundant soft corals, sponges and occasional colonies of stony coral |
| | Long Island (eastern side) | Rocky shelf |
| | Long Island (southern point) | Rubble plain extended seawards to the actual rocky shelf edge, which dropped away vertically to great depth |
| Turks and Caicos | | Shallow fringing reefs dominated by *Montastraea annularis* and *Acropora palmata* |
| United States: Florida | Western Florida | High-relief, shelf-edge reefs of the south-eastern United States. A series of clustered limestone pinnacles 5–30 m in height, separated by a flat, soft-sediment bottom. The pinnacles were topped by the ivory tree coral, *Oculina varicosa*, which grows in spherical heads 1–2 m in diameter. Two 6-km long pronounced rocky ridges projecting up to 15 m off the seabed. |
| US Virgin Islands | St. Thomas | High topographic complexity and coral cover, primarily flat-surface colonies of *Montastraea annularis* species complex |
| | St. Croix | Low-relief spur-and-groove reef, low coral cover |
| Puerto Rico | El Hoyo | High coral cover and diversity |
| | El Seco | High topographically complex coral, predominantly *Montastraea annularis* species complex, extended over a relatively level area |
| Cuba | Bajo Mandinga | High coral cover |
| | Cabo Cruz | A rocky-sandy bottom until the drop-off at about 20–25 m depth |
| | Cayo Bretón | Reef slope: high coral cover |
| | Banco de Jagua | Oceanic bank: rocky bottom, moderate coral cover |
| | Puntalon de Cay Guano | Reef slope: high coral cover |
| | Cayo Diego Perez | Reef slope: high coral cover |
| | Cayo Avados | Reef slope: high coral cover |
| | Punta Francés | Reef slope: high coral cover |
| | Cayos Los Indios | Reef slope: high coral cover |
| | Cayo San Felipe | Reef slope: high coral cover |
| | Cabo Corrientes | Sandy, rocky, coral heads |
| | Cabo San Antonio | Reef slope: high coral cover |
| | Corona San Carios | Reef slope: sandy, rocky, coral heads |
| | Punta Hicacos-Cayo Mono | Reef slope: sandy, rocky, coral heads |
| | Cayo Megano de Nicolao | Reef slope: high coral cover |
| | Boca de Sagua | Reef slope: moderate coral cover |
| | Cayo Lanzanillo | Reef slope: moderate coral cover |
| | Cayo Fragoso | Reef slope: moderate coral cover |
| | Cayo Calmán Grande | Reef slope: high coral cover |
| | Cayo Paredón | Reef slope: high coral cover |
| | Cayo Sabinal | Reef slope: high coral cover |
| Cayman Islands | Little Cayman southeast | Sandy depression |
| | Little Cayman southwest | Low-relief broad ridges with hard and soft corals and sponges |
| Mexico | Mahahual | Low-relief, patchy, hard corals interspersed with plexaurids and gorgonians. Hard corals present were mountain coral, *Montastraea annularis,* and leaf coral, *Agaricia* spp., growing between sandy areas. |

**Table 4 (continued)** Detailed descriptions of the benthic habitat found at each transient tFSA site in the Caribbean (from literature cited in Table 2)

| Country | tFSA sites | Benthic habitat |
|---|---|---|
| Belize | Rocky Point | Hard substratum with sparse coral |
| | Dog Flea Caye | Low-relief spur-and-groove reef |
| | Caye Bokel | High-relief spur-and-groove reef |
| | Caye Glory | Low-relief spur-and-groove reef. The bottom consisted primarily of sand with scattered patches of hard and soft corals |
| | Sandbore | Low-relief spur-and-groove reef |
| | Half Moon Caye | High-relief spur-and-groove reef |
| | North Glover's | Coral ridges together with sandbars made up a spur-and-groove reef |
| | Gladden spit | Sand floor with low-profile mound |
| Honduras | Guanaja | Sandy plain began at about 135 ft (41 m) |
| Saba, NA | Saba Bank | Low-relief spur-and-groove reef with sparse coral cover |

### *Benthic habitat characteristics of tFSAs in the Wider Caribbean*

Well-developed deep coral reefs and areas with high topographic complexity characterized by ledges, undercuts and caves have been observed at most Caribbean tFSAs and are thought to offer refuge from predators during prespawning periods and during active mate selection by aggregating species (Carter et al. 1994, Sancho et al. 2000a, Nemeth 2005, Nemeth et al. 2006, Kadison et al. 2009b). Synthesis from site descriptions revealed that scleractinian corals were the dominant biogenic structural organisms at 87.5% of sites; however, sand or rock was also observed (Table 4). In the Turks and Caicos Islands, US Virgin Islands, Puerto Rico and Mexico, reef-building corals in the genus *Montastraea* dominate the coral community at tFSA sites. The *Montastraea* species complex is the most prevalent reef-building coral in the Caribbean, so its presence at tFSA sites may be coincidental. In the US Virgin Islands, extensive *Montastraea*-dominated mesophotic coral reefs occur on the shelf and along the shelf edge at tFSA and non-tFSA sites (Herzlieb et al. 2006, Armstrong et al. 2006, Smith et al. 2010). High coral cover at many sites was not always associated with high reef fish abundance (Nemeth & Quandt 2005). More research is needed to determine the importance of benthic communities at spawning sites (Rivera et al. 2006) and whether benthic components besides coral cover may be necessary to support the formation of tFSAs. For example, although red grouper (*Epinephelus morio*) in the Gulf of Mexico do not form large spawning aggregations like other groupers (Brule et al. 1999), they physically create suitable spawning habitat by excavating pits in soft sediments near the small-group aggregation sites (Coleman et al. 2011).

## Data types, availability and research needs for understanding and managing tFSAs

The overall aim of this section is to describe the data needed and methods to acquire those data to support effective information-based decision making and ecosystem-based management of individual sites and a network of sites. In the foregoing review, we identified two major information gaps that hinder the characterization and thus effective management of tFSAs. First is the insufficient fundamental baseline data for known, protected sites. Second is the lack of a synthesis of the available data for comparative purposes and for modelling. Though some specific data exist for many sites, there is high within-region variability in the amount, type and quality of information. This uneven data availability is a product of variability in research and management capacity, access to infrastructure and equipment and individual researchers' and managers' interests and priorities. Prior to this synthesis and review, regional studies of biogeography or comparative management status have been impossible. This section aims to (1) classify the data types and available methods to collect those data, (2) identify the minimum data requirement for management implementation and monitoring and (3) identify future research needs that will improve understanding and management of tFSAs across the Wider Caribbean region.

In this synthesis, a multitier research framework is suggested to classify existing methods and guide future research activities. We classify eight types of information most frequently collected at and around tFSA sites and organize them hierarchically with increasing technical complexity and cost. Examples for each information type are provided (Table 5). Although several sites have been intensively surveyed, much of our information about tFSAs across the Wider Caribbean has come from local fishers' knowledge and port surveys; these formed the base of our framework (Table 5, level 1).

The framework provides a consistent way of measuring and evaluating the information status of individual sites. When populated with information for each site across a network, it can be used to set strategic priorities, evaluate costs and select appropriate partners for the sharing of knowledge, data, expertise and equipment. We propose that for effective and appropriate decision making, and for comprehensive regional management, all known tFSA sites in the Wider Caribbean should eventually be documented using techniques from levels 1 to 4 inclusive. We consider these first four levels to include the minimum necessary information on which managers can confidently base management decisions. We advocate the establishment of a pan-Caribbean research and management network for tFSAs through scientist-community-manager partnerships that can share data up to level 4 in support of site and regional management and multinational research and hypothesis testing aimed at understanding tFSA phenomena and connectivity more broadly.

### *Research level 1: fisher interviews and port surveys*

We recognize the importance of local knowledge and the active participation of local fishing communities in studying and sustainably managing tFSAs. Detailed studies of fishers' knowledge of spawning aggregations were initiated by Johannes (1978). Numerous studies of fishers' knowledge of spawning aggregations have since been completed (Heyman & Hyatt 1996, Hamilton et al. 2005, 2011) and can often offer a baseline from which to begin field observations and measurements (Colin et al. 2003). Additional conversations with fishers can also provide auxiliary information on perceptions of historical trends and environmental change, geographical areas and specific habitat types preferentially targeted and other observations on the health and physical condition of fish.

In this case, however, our focus is primarily on physical and biological data collection methods. Surveys and macroscopic examination of landed catch can provide general biological information and conservation status for individual species at relatively low cost. Common direct measurements and information types include fish species, body length and weight, seasonality of reproduction, as well as landings per unit time and landings per unit effort where effort can be recorded accurately and fishing gear and area are consistent. Additional analyses of extracted body parts such as otoliths can provide information on age and growth rate, and tissue samples can provide information on trophic connectivity and habitat affinities via chemical signatures of accumulated radioisotopes (Elsdon et al. 2008). Proper assessments require knowledge of the size and age structure of fish populations in general. Fish that have been marked or tagged as part of mark-recapture studies can also be recorded during port surveys. Rates of growth, mortality and reproduction can only be calculated if changes in length at age can be monitored over time. Required equipment generally includes a measuring board and weighing scale (Table 5). Otolith age analysis requires more sophisticated and expensive equipment (diamond blade saw, microscopes, software), but otoliths can also be processed at national laboratories at a reasonable cost. Some examples of research questions are the following: Is there a seasonal pattern in landings of certain species? Are they gravid? What size ranges are being harvested and with what gear? Are there changes in species composition, size and age of individual species over time?

**Table 5** FSA data collection methods, equipment needs, expected outputs and examples studies

| Level | Data collection method | Equipment needs | Data and information generated | Expected output | References, examples and use of these techniques |
|---|---|---|---|---|---|
| 1 | Fisher interviews and port surveys | Access to and trust of fishers, survey instruments or interview forms | Approximate timing, species composition, location, historical exploitation and present status of tFSAs | Traditional ecological knowledge about tFSAs, observations from markets, unverified indications of tFSAs | Johannes 1978, Sadovy et al. 1994, Claro & Lindeman 2003, Hamilton et al. 2005, 2011, Ojeda-Serrano et al. 2007, Rhodes & Tupper 2007, Heyman 2011 |
| 2 | Fishery-dependent surveys | Access to landing sites, measuring boards, weighing scales, otolith-processing equipment and microscopes; access to historical catch data | Landings data, gear types, catch per unit effort (CPUE); length-weight frequencies, otolith analysis for age and growth, sex ratios, histological data, biometric information (e.g., gonadosomatic indices) | Detailed data on extraction from tFSA sites; valuable data for stock assessment; can provide verification of FSA | Beets & Friedlander 1999, Erisman & Allen 2006, Matos-Caraballo et al. 2006, R.S. Nemeth et al. 2007, Rhodes & Tupper 2007, Rhodes et al. 2011 |
| 3 | Underwater visual census (UVC) | Scuba gear, appropriate breathing mixtures, closed-circuit rebreathers (option: sound recorders); video cameras, video laser calipers, remotely operated vehicles (ROVs); video drop cameras, GPS (on boat to give approximate location) | Area; habitat use; depth; timing; density; length and abundance; behaviour (spawning, courtship, colouration, sound); temperature; qualitative description and benthic mapping of habitat and reef structures; site fidelity | Fish densities, timing of spawning and courtship behaviours; verification that aggregation is for spawning; valuable data for stock assessment; effects of divers on behaviour | Colin 1992, Sadovy et al. 1994, Samoilys 1997, Whaylen et al. 2004, 2006, Burton et al. 2005, Heyman et al. 2005, 2010, Pet et al. 2005, Erisman & Allen 2006, R.S. Nemeth et al. 2007, Heyman & Kjerfve 2008, Boomhower et al. 2010, Heppell et al. 2012 |

*continued*

**Table 5 (continued)** FSA data collection methods, equipment needs, expected outputs and examples studies

| Level | Data collection method | Equipment needs | Data and information generated | Expected output | References, examples and use of these techniques |
|---|---|---|---|---|---|
| 4 | Mapping bathymetry, benthic habitat, and fish utilization of tFSAs | Remotely sensed data (Landsat, IKONOS, Quickbird, lidar); existing nautical charts and bathymetric maps; GPS; sonar (single beam, dual beam, multibeam, or side scan); UVC data; seabed-mounted or drop video cameras; autonomous underwater vehicles (AUVs) | Bathymetric maps, benthic habitat maps showing substratum and biotic cover, rugosity, and slope | General site information can be valuable for MPA delineation; detailed map of spawning aggregation sites showing bathymetry, habitat types, and use by tFSAs | Stumpf et al. 2003, Armstrong et al. 2006, Taylor et al. 2006, Heyman et al. 2007, Kobara & Heyman 2008, 2010, Shcherbina et al. 2008, Coleman et al. 2011 |
| 5 | Mark and recapture studies using conventional and acoustic tagging and tracking | Standard identification tags, continuous and coded acoustic transmitters, acoustic receivers (e.g., VR2W), omni- and uni-directional hydrophones | Site utilization and site fidelity of fishes at FSA sites; time and date of arrival, residency time, and departure at tFSA site by species, sex, lunar period | Detailed information on temporal aspects of fish utilization of tFSA site, including site fidelity, movement patterns, migration pathways | Zeller 1998, Bolden 2000, Nemeth 2005, R.S. Nemeth et al. 2007, Starr et al. 2007, Mann et al. 2009, Rhodes et al. 2012 |
| 6 | Acoustic monitoring of courtship sounds of fishes | Digital sound recorders (both installed *in situ* as a monitoring station and mobile, attached to a video camera); rebreathers; baseline of spawning sounds for key species | Quantitative assessments of species' timing and level of participation in spawning based on acoustic monitoring | Monitoring of tFSA site use by various species | Lobel 1992, Mann & Lobel 1995, Holt 2008, Mann et al. 2009, Rowell et al. 2012, Schärer et al. 2012a,b |

**Table 5 (continued)** FSA data collection methods, equipment needs, expected outputs and examples studies

| Level | Data collection method | Equipment needs | Data and information generated | Expected output | References, examples and use of these techniques |
|---|---|---|---|---|---|
| 7 | Oceanographic and meteorological data collection from *in situ* measurements and remotely sensed data | Remotely sensed data (sea-surface temperature, sea-surface height, ocean colour from MODIS, others), weather stations, underwater temperature loggers, acoustic Doppler current profilers (ADCPs), electromagnetic current meters, conductivity temperature depth (CTD) meters, AUVs, surface drifters, underwater gliders, light meters | Weather patterns, including air temperature, wind speed and direction and rainfall; current speed and direction; hydrostatic pressure, which can offer tide and wave height information; temperature variability and profiles; light intensity; chlorophyll concentrations | Understanding of oceanographic variability and forcing factors at tFSA sites | Lobel 1978, Colin 1992, 1995, Ezer et al. 2005, 2011, Nemeth et al. 2008 |
| 8 | Modelling oceanographic and biophysical connectivity; predicting the location of tFSA sites based on geomorphology; predicting larval transport from known tFSA sites | Three-dimensional numerical simulation models (e.g., Regional Ocean Model [ROMS], Princeton Ocean Model [POM]); oceanographic and bathymetric data; spawning dates, times and locations; larval behaviour; otolith microchemistry; genetics | Predictions of larval connectivity to nursery habitats; local and regional hypothesis testing about connectivity | Models of larval transport and connectivity; models predicting timing and location of undiscovered tFSAs | Jones et al. 1999, 2005, Paris & Cowen 2004, Ezer et al. 2005, 2011, Paris et al. 2005, Kobara & Heyman 2006, Elsdon et al. 2008, Boomhower et al. 2010, Kobara & Heyman 2010, Cherubin et al. 2011, Karnauskas et al. 2011 |

### *Research level 2: fishery-dependent surveys*

Level 2 aims to obtain information on the spawning aggregation process. A common type of fishery data collection consists of formal observer programmes; personnel trained in scientific data collection work alongside fishers in their boats. Because not all fish that are caught are brought to market, this technique allows for a more accurate assessment of landings that include undersize, damaged or otherwise unmarketable fish, as well as by-catch that may be used as bait or discarded. Sampling on-board fishing vessels potentially provides data on the species composition and morphometrics by species (e.g., length and weight), age and growth, histology, fecundity, seasonality and lunar periodicity. While level 1 would provide a general idea of seasonal trends and the approximate location of fish aggregations, level 2 will determine more detailed biological information and approximate site fidelity. Species- and age-specific distribution patterns and catch per unit of effort (CPUE) can all be calculated and used to assess the fishery. Matos-Caraballo et al. (2006) provided an excellent example of a fishery-dependent characterization of a tiger grouper (*Mycteroperca tigris*) aggregation, and several others are also listed in Table 5. A spawning-aggregation study in the Gulf of California is another great example of cooperative research with fishers, who willingly put global positioning system (GPS) receivers on their boats and recorded aspects of the fishery, such as capture rates and volumes in space and time, as the aggregation developed and subsided (Erisman et al. 2012).

Fishery-independent surveys utilize either hired commercial fishing vessels or research vessels and use the same gear types as commercial or artisanal fishers. These surveys differ from fishery-dependent surveys in that the sampling is typically random or stratified-random, with strata being fishing areas or habitat types; the types and amounts of bait are standardized, and fishing effort (i.e., trap soak time) is carefully recorded. In addition to the equipment used as discussed previously, line fishing gear or baited fish traps, tags, tagging guns, and a GPS receiver are needed.

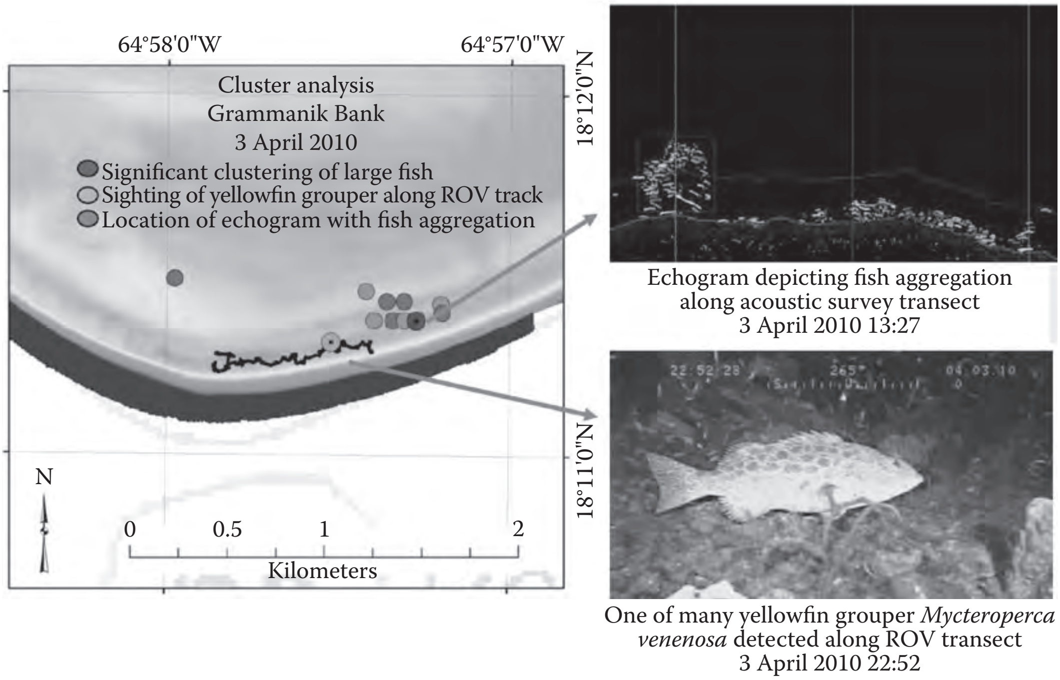
Fishery-dependent and -independent surveys can address questions such as the following: What is the distribution of effort and species among habitat types? How has CPUE or species composition changed over time? What is the percentage of by-catch relative to gear type and other factors? Can fishing gear be modified to reduce or eliminate by-catch (e.g., by incorporating escape vents in fish traps)?

### *Research level 3: underwater visual census and echo-sounding surveys*

Level 3 focuses on acquiring detailed *in situ* information on the spawning process to gain a greater understanding of when, where and how spawning aggregations of particular species occur. Underwater visual survey either by snorkelling (Mazeroll & Montgomery 1995) or using scuba gear (Nemeth 2005) is among the most common techniques used to verify the existence and status of tFSAs (e.g., Sala et al. 2001). Because many tFSA sites are located in depths of 30–70 m, they can be surveyed by divers, but in the deeper part of this range, advanced diving techniques using helium-based breathing mixtures and perhaps closed-circuit rebreathers are required to conduct underwater visual surveys safely and effectively. Underwater diver surveys are usually associated with disturbance to normal fish behaviour, yet observations suggest that small groups of experienced divers would not negatively affect some species of aggregating fishes (Heyman et al. 2010). Furthermore, the lack of bubbles from closed-circuit rebreathers is thought to reduce disturbance to fish and allow for a more realistic observation of spawning behaviours (Lobel 2005, R. Nemeth, personal observation).

Survey techniques will vary depending on species and habitat but may range from total counts of fish within an aggregation, stationary point counts or belt transects to estimate fish population density (Colin et al. 2003). Surveys can also utilize diver propulsion vehicles (underwater scooters) to count fish or search for aggregation sites over large areas, but the associated motor noise can influence fish behaviour and disrupt aggregation formation for certain species (Nemeth et al. 2006). The use of diver-operated video and still cameras has aided these efforts dramatically in recent years, and the increasing availability of low-cost drop cameras and remotely operated vehicles (ROVs) has facilitated observations of tFSAs in deep water. Stereo-cameras or laser measuring devices mounted on a video housing can also be used to estimate the size of fish within an aggregation (Rochet et al. 2006, Heppell et al. 2012). Since migration and spawning are often synchronized to seasonal and daily lunar, temperature and light cycles, underwater visual surveys are invaluable for detecting the arrival and departure of spawning fish from a tFSA site in relation to environmental conditions. In addition to observations of spawning behaviours (including courtship and colouration), underwater surveys can illustrate school density and abundance, spawning areas, timing and local habitat usage (Colin et al. 2003, Archer et al. 2012). Comparing data from this type of survey completed in various locations can address questions like the following: How has the abundance, size or behaviour of fish within the aggregation changed over time? How does lunar timing of spawning differ among sites? At what depth does spawning occur, and is this related to specific oceanographic conditions?

As an optional study, for deeper water and rapid surveys across large areas by day and night, echo-sounding technology provides a cost-effective solution for instantaneous mapping of fish size and abundance at tFSAs. An additional benefit from echo-sounding technology is that the vertical position of fish and other fauna, such as plankton, can be mapped and tracked over short distances. In the US Caribbean, a fisheries acoustic study of spawning aggregations was conducted through simultaneous application of a ship-mounted echo sounder (Simrad 120-kHz split-beam transducer) to detect fish swim bladders alongside a multibeam sonar (Reson 7125) to map seafloor bathymetry (Kracker et al. 2011). Researchers were able to collect large volumes of 3-dimensional data from known fish aggregations and to explore potential aggregations at shelf-edge promontories (Figure 9).



Echogram depicting fish aggregation along acoustic survey transect 3 April 2010 13:27

One of many yellowfin grouper *Mycteroperca venenosa* detected along ROV transect 3 April 2010 22:52

**Figure 9 (See also colour figure in the insert)** Locations with statistically significant clustering of large fish (>29 cm) from acoustic surveys. Top inset shows fish aggregations on echogram. Bright purple horizontal line denotes the contour of the seafloor, with thin purple line representing 5 m above seafloor. Bottom inset shows video still image providing direct evidence of yellowfin grouper (*Mycteroperca venenosa*) taken simultaneously by remotely operated vehicle (ROV) at locations with significant clustering of fish. (Adapted with permission from Kracker et al. 2011.)

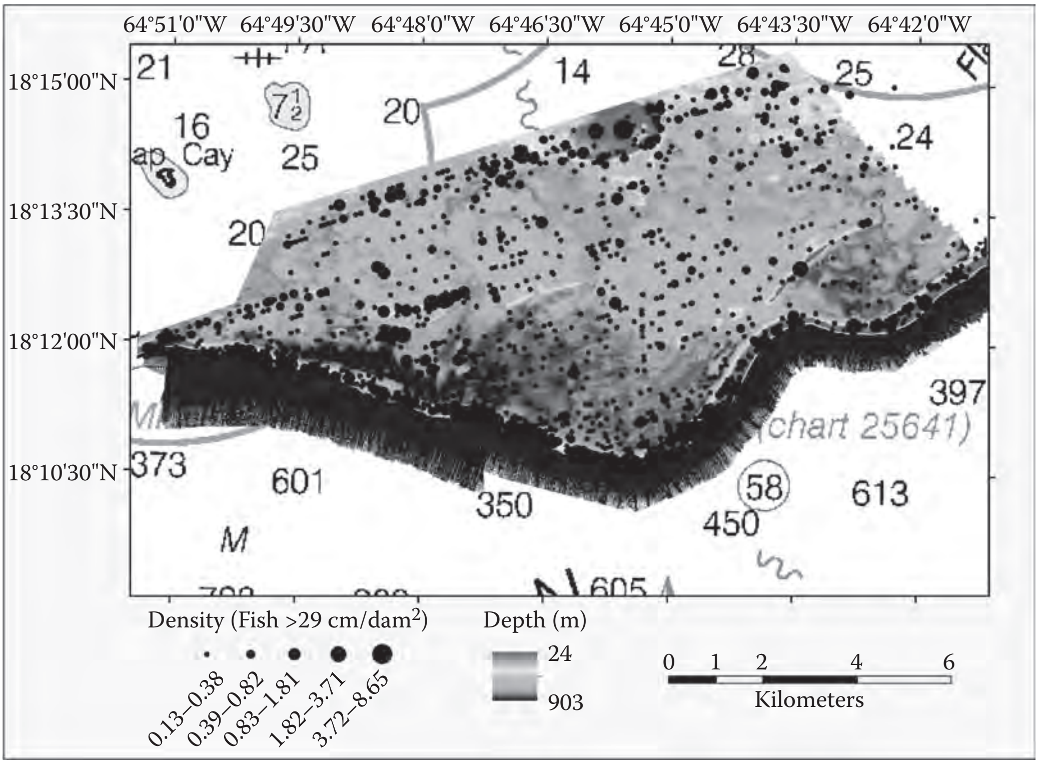


**Figure 10 (See also colour figure in the insert)** Population density of large-bodied (>30 cm) fish along the shelf edge south of St. John, US Virgin Islands. The target strength-length relationship of Love (1977) was used to estimate fish size. Fish density is expressed as number per square decametre ($dam^{-2}$). (Figure provided by C. Taylor, National Oceanic & Atmospheric Administration.)

These data allow for coupling of water column data with information on the heterogeneity of seafloor structure across an entire spawning site and neighbouring areas (Figure 10). Furthermore, repeat surveys at different times of the day can provide detailed information on the 3-dimensional spatial movements of fish at various stages of the spawning event.

### *Research level 4: mapping bathymetry, benthic habitat and fish utilization of tFSAs*

A comprehensive understanding of the seafloor characteristics associated with spawning aggregation sites is of great interest to environmental managers tasked with identifying priority areas for protecting and rebuilding sustainable fish populations and ecosystem resilience. In conservation prioritization and in ecosystem-based marine spatial planning, the locations of tFSAs are typically considered high-priority information to inform the decision-making process (Crowder & Norse 2008, Geselbracht et al. 2008). Within sites, bathymetric data provide an opportunity to study the influence of geomorphology on aggregating fish distributions, including species-specific distributions and movement patterns, if tracking data are also available. In addition, collecting geomorphological data at tFSA sites will contribute to the data necessary to understand and model the interacting effects of geomorphology and oceanography on biological aggregations (Hyrenbach et al. 2000, Heyman & Wright 2011). The 3-dimensional structure or bathymetry can be mapped with a wide range of sensors, both in the water and from aircraft and satellites. Several low-cost options for mapping the bathymetry of tFSAs range from the creation of pseudobathymetry from high-resolution satellite data (e.g., IKONOS; Stumpf et al. 2003) in optically suitable waters to directly collecting depth soundings using standard sonar from small boats (Heyman et al. 2007). Airborne lidar (light detection and ranging) can provide more detailed bathymetry over large areas to allow production of a highly accurate digital terrain model, but the cost would be prohibitive for many researchers. Lidar bathymetry has been used to map habitat suitability for fish associated with coral reefs, including grouper (Pittman & Brown 2011).

Geomorphology from multiple sites can be compared to evaluate the generality that multispecies tFSA sites occur at reef promontories and near shelf edges, adjacent to deep water. For example, can seafloor characteristics that are similar to the reef promontories described for Belize (Kobara & Heyman 2010) and the Cayman Islands (Kobara & Heyman 2008) serve as reliable proxies for the presence of tFSAs across the Caribbean?

Benthic habitat maps usually produced from interpretations of optical and acoustic mapping technologies provide useful spatial information on the types of benthic community that exist at and near tFSA sites. Benthic habitat maps of moderate-to-deep seabed (depths >35 m) can be rapidly and reliably classified from high-resolution bathymetry using semi-automated classification techniques (Costa & Battista 2008). Mapping benthic habitats also provides a baseline to evaluate future disturbances to coral reef ecosystems. Analysing seafloor habitat and seascape structure surrounding spawning sites will likely provide insights on the navigational routes and the structural features of the seascape that influence connectivity to suitable settlement habitats (Grober-Dunsmore et al. 2009). Few sites, however, have been mapped at sufficient resolution to provide useful ecological information for studying fish distributions at tFSA sites.

### *Research level 5: mark and recapture studies and ultrasonic tracking*

Individual and group movements by fish are intrinsically linked to the function of tFSAs. An understanding of space use by aggregating fish is essential to identifying habitat requirements at tFSAs and for assessing the amount of protection provided by place-based management strategies, such as no-take or seasonal MPAs. At finer temporal and spatial scales, movement information can provide insights into the behavioural mechanisms of individual fish at spawning sites. Little information is available on movement patterns during courtship and spawning or between spawning peaks (Nemeth 2009). At a few sites, acoustic tagging using a fixed acoustic array has provided detailed information on site fidelity, residence time, migration pathways, migration area, habitat use and fine-scale movement patterns during both night and day (Nemeth 2009, Rhodes et al. 2012). These types of study are helping better define spatial components of FSAs, including catchment area, staging area, courtship arena and the spawning aggregation site (Nemeth 2012). Mapping the migratory pathways to and from tFSAs provides valuable information on regional connectivity. Understanding of daily home range movements and seasonal migrations can be used at research level 5 to appropriately design the size, shape and placement of MPAs and to examine the efficacy of established MPAs.

Studies using acoustic transmitters and conventional tags show that movements of aggregating species are much more extensive than previously realized (Zeller 1998, Nemeth 2005, Starr et al. 2007, Rhodes & Tupper 2008). A mutton snapper moved 255 km from a tFSA site in 3 weeks (W.D. Heyman unpublished data); a Nassau grouper moved over 200 km to a tFSA site in the Bahamas (Bolden 2000). Nemeth (2009) produced direct evidence that yellowfin grouper (*Mycteroperca venenosa*) and Nassau grouper (*Epinephelus striatus*) swam distances of between 1 and 5 km during the day before returning to the spawning aggregation site by late afternoon. Some of the same individuals moved over 10 km per day between monthly spawning peaks (Figure 11). These species used deep linear coral reefs as pathways to and from their spawning aggregation site (R.S.

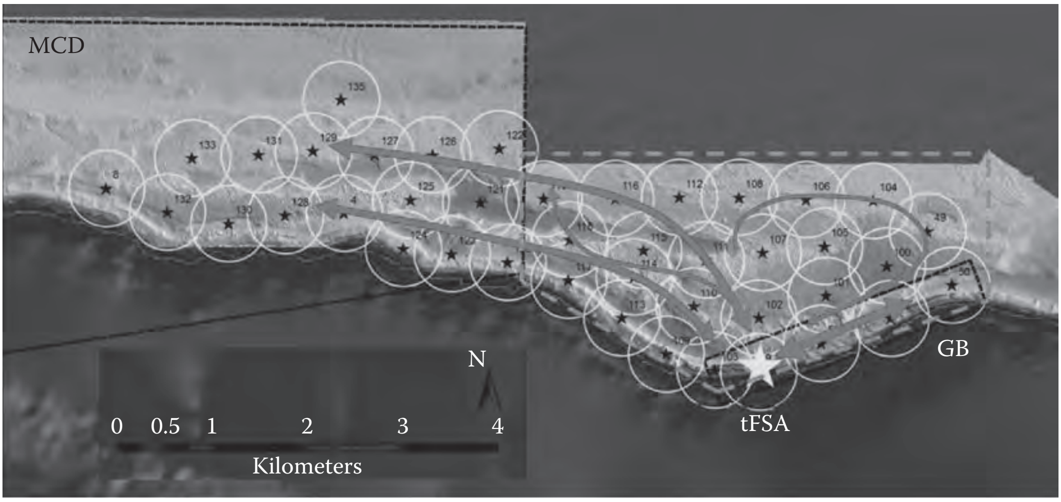


**Figure 11 (See also colour figure in the insert)** Daily movements and migration pathways of Nassau (*Epinephelus striatus*) and yellowfin (*Mycteroperca venenosa*) grouper. The red arrows in different thicknesses represent hourly (thickest), daily and weekly movements to and from the spawning aggregation site (large star). The Marine Conservation District (MCD; area within black dashed line on left) and the Grammanik Bank (GB; small rectangle on right) are two marine protected areas in the US Virgin Islands. Small stars and numbers indicate the positions of acoustic receivers. The thin red line along reefs is shelf edge. Migration pathways followed deep linear reefs, and the study indicated that an area of approximately 11 km$^2$ protected area boundary (blue dashed line) was required to fully protect both species during the spawning season. (After Nemeth 2009.)

Nemeth unpublished data). Tagging studies can also provide insights into the connectivity between MPAs and distant spawning sites. For example, several tagged grouper and snapper using shallow nearshore embayment within the US Virgin Islands National Park at St. John were also detected at acoustic receivers moored at shelf-edge spawning sites (S.J. Pittman & R.S. Nemeth unpublished data; Figure 12).

In addition to extensive horizontal migration, some fish at tFSAs exhibit vertical movements at different stages of the aggregation (pre- and postspawning and time of day). For example, Starr et al. (2007) observed Nassau grouper descending from an average depth of 20 m during the first month of spawning to over 50 m during the remaining 2 months of the spawning season. It is not clear what these fish were doing during these extensive periods of roaming or depth changes, but several hypotheses are emerging. Directed movements between spawning periods may represent foraging activity in particular habitats (i.e., staging areas), prespawning aggregations or regular visits to cleaning stations (Samoilys 1997, Rhodes & Sadovy 2002, Nemeth et al. 2006, Semmens et al. 2006, Coleman et al. 2011). Grouper movements may also be associated with attracting or leading conspecific adults to the spawning aggregation site, a behaviour that has been reported for resident aggregating species (Mazeroll & Montgomery 1998). Finally, dramatic changes in depth, as seen in Nassau grouper, may allow adult fish to enter cooler water, forage for preferred prey, avoid higher parasite or predation rates or release larvae in optimal currents or water strata (Starr et al. 2007). Studies that combine tracking and mapping of movement pathways with detailed benthic habitat maps and bathymetry over the entire staging area will likely offer new insights to our understanding of how fish use tFSAs (Hitt et al. 2011).

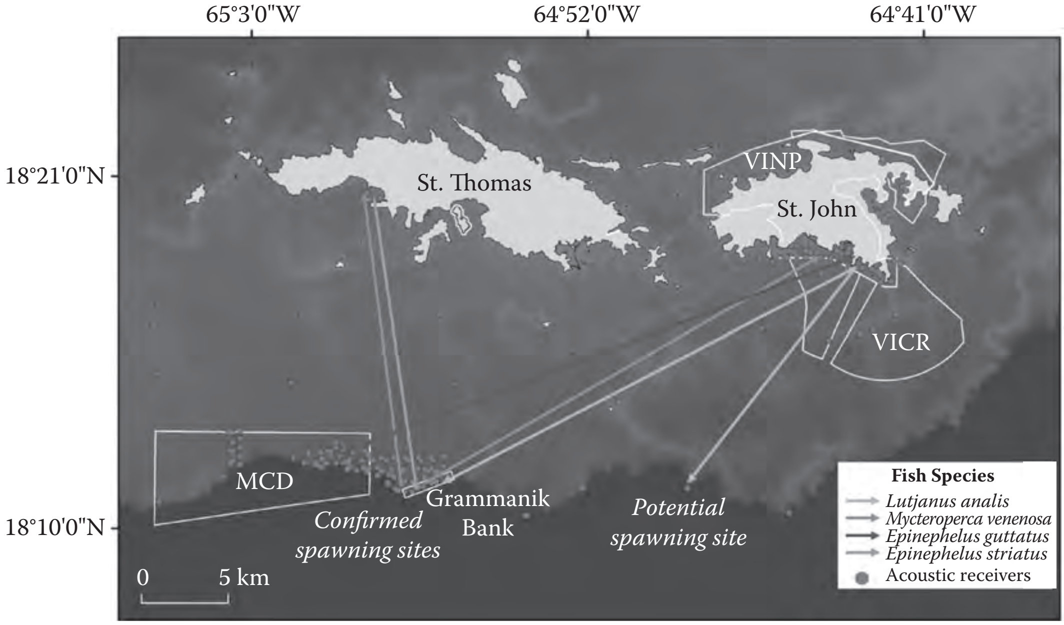


**Figure 12 (See also colour figure in the insert)** Acoustic array detections of tagged fishes providing direct evidence of connectivity between nearshore coral reef ecosystems and shelf-edge spawning aggregations for three species of grouper (*Mycteroperca venenosa*, *Epinephelus guttatus* and *E. striatus*) and a mutton snapper (*Lutjanus analis*) (Pittman & Legare 2010, CCMA 2011). Straight lines represent direct links between receiver locations rather than actual movement pathways. Marine Conservation District (MCD) and Grammanik Bank are sites of known spawning aggregations. Virgin Islands Coral Reef National Monument (VICR) and Virgin Islands National Park (VINP) are marine protected areas.

### *Research level 6: hydrophone monitoring of courtship sounds of fishes*

In addition to visual and echo-sounding surveys, the ability to detect fish vocalization and chemical cues can be useful in level 6 research. Hydroacoustic surveys of tFSAs have proven valuable in recent years because of species-specific courtship and spawning sounds emitted by some species (Lobel 1992, Mann & Lobel 1995, Locascio & Mann 2008, Mann et al. 2009, Nelson et al. 2011). Seafloor-mounted hydrophones at known or potential spawning sites (Rowell et al. 2012) provide utility as continuous listening stations regardless of sea conditions and visibility, although data storage capacity limits the duration of recordings, and interpretation of marine animal sounds at spawning sites is still in its infancy. In Puerto Rico, seafloor-mounted hydrophones have been used to record fish vocalization at a known spawning site for Nassau grouper (Schärer et al. 2012b), yellowfin grouper (Schärer et al. 2012a) and red hind (Mann et al. 2010, Rowell et al. 2012). Little is known about the sound production of snappers and other fish that aggregate to spawn. Boat-towed hydrophone arrays have been used to locate spawning aggregations and to estimate the abundance of fish across large spatial areas, such as for red drum (*Sciaenops ocellatus*) in the western Gulf of Mexico (Holt 2008), Nassau grouper in the Cayman Islands (Taylor et al. 2006) and red hind in Puerto Rico (Johnston et al. 2006). Autonomous underwater gliders have also been used successfully as mobile remote platforms to carry hydrophones over large distances for recording fish sounds (Wall et al. 2012). The technology offers great potential for exploratory deployments along shelf edges and promontories at known or suspected spawning times. Much can be learned from other more developed fields in animal vocalization and the broader field of acoustical engineering, and sophisticated algorithms can be developed for automated search and recognition of specific acoustic signatures of spawning fish (Mann et al. 2009).

Olfactory cues, such as pheromones, may be involved in attracting fish to spawning aggregations and synchronizing ovulation and milt production. Males could test the female for spawning readiness through an olfactory cue, which in turn elicits a behavioural response in the male (Pankhurst & Fitzgibbon 2006). In Pacific herring, olfactory detection of a pheromonal component of milt stimulates spawning behaviour in both sexes (Carolsfeld et al. 1997). However, little is known about the use of chemical signalling in Caribbean groupers and snappers. There have been no investigations of the possible role of species-specific pheromones in the formation of aggregations and initiation of spawning in Wider Caribbean fishes (Stacey et al. 2003, Ganias 2008).

### *Research level 7: oceanographic and meteorological measurements*

Research on oceanographic patterns and processes at tFSAs is required to understand the multiscale variables that influence the initial dispersal and destination of fertilized eggs. Techniques described in level 7 will collect *in situ* and satellite-derived information on the oceanography of a spawning site and the physical forcing factors that operate at spatial scales broader than the site. Suitable questions to address include testing the hypothesis that the interaction between far-field oceanic forces and localized physical-oceanographic conditions promote connectivity and contribute to making a location suitable for reproduction. Because recent findings indicate that many large, multispecies tFSAs occur at geomorphologically distinctive areas such as reef promontories, there may be specific advantages for spawning in these areas, indicating the wide applicability of research at this level. Ezer et al. (2011) developed a high-resolution 3-dimensional numerical circulation model using current data measured during spawning times, with a suite of *in situ* physical measurements from acoustic current profilers, electromagnetic current profilers, conductivity-temperature-depth instruments and tide gauges, complemented by remotely sensed sea-surface height anomaly and sea-surface temperature. Further studies are under way to calibrate and validate the numerical model under various conditions using Eulerian and Lagrangian field measurements of local currents, winds, tides, waves and temperature/salinity profiles at several locations surrounding the reef promontory.

Tracking the movement of fertilized eggs from spawning sites is difficult. Quantitative plankton tows or drifters can be used to analyse the track, an approach that typically assumes all larval movement is passive advection by currents. The transport fate of spawned material under various conditions can be predicted using particle-tracking algorithms within the numerical simulation model described in the next level (level 8).

To date, marine connectivity studies through movement of eggs and larvae largely rely on numerical simulation models. In situ and remotely sensed data to support these models are scarce. Although ocean current data could be used to evaluate the relative merits of several competing hypotheses, no extended data records or descriptions of local current patterns are yet available to test models at the resolution and scale at which biological activities occur (ca 100–1000 m). One study, however, simultaneously measured current profiles at three distant red hind (*Epinephelus guttatus*) spawning aggregation sites in the north-eastern Caribbean (St. Thomas, St. Croix, Saba Bank). In that study, Nemeth et al. (2008) found that the prevailing currents at each site tended to carry larvae to the shelf during the week of spawning, but not at other times of the lunar cycle.

### *Research level 8: modelling connectivity and ecosystem processes at FSA sites*

Mesoscale and nested numerical ocean circulation models are continually being refined, and resolution and predictive accuracy are being increased. Such models can be used to examine source-sink mechanisms and pathways to settlement sites and to estimate the importance of local retention versus broader dispersal. There are myriad ways to model biological and physical parameters that could be helpful for the management of tFSAs. This review, however, focuses primarily on data collection, analysis and use rather than modelling. Numerical and spatially explicit models can be applied at any stage of research, and although listed here as a final level, we acknowledge that if sufficient data are available, models can play a valuable exploratory role in understanding the environmental context of spawning sites, the potential connectivity across networks of sites and even processes at Caribbean basin-wide scales (Levin & Lubchenco 2008). Spawning at specific locations may increase the likelihood of successful recruitment by carrying fertilized eggs and developing larvae into favourable ocean currents that promote survival and growth while transporting settling larvae towards suitable nursery habitats. Although this idea is intuitive, evidence is insufficient to support any generalities on the oceanographic and larval transport processes that make one location more suitable than another for multispecies spawning aggregations.

Numerical ocean simulation models are based on mesoscale ocean currents (ca 10- to 100-km scales), although advances in higher-resolution hydrodynamic modelling, coupled with sophisticated biophysical individual-based simulations, provide increasingly reliable predictions of larval pathways (Paris et al. 2005, Werner et al. 2007, Cowen & Sponaugle 2009, Karnauskas et al. 2011). For example, in the Eastern Caribbean, Cherubin et al. (2011) found that virtual particles released in an oceanographic model of a spawning aggregation site were entrained in downwelling currents and returned to their release site within 8–10 days, suggesting a possible retention mechanism for red hind (*Epinephelus guttatus*).

From an ecosystem perspective, an understanding of the influence of large ephemeral spawning aggregations on energy transfer across coral reef environments and at aggregation sites will help to define the role that intact FSAs have on ecosystem integrity, trophic balance and marine ecosystem health. Larger populations of spawning fishes at tFSAs may influence food webs, both upwards to apex predators feeding on spawning fish (e.g., sharks and dolphins) and planktivores feeding on newly released eggs (e.g., whale sharks and manta rays) (Heyman et al. 2001), and downwards on the prey of spawning fish. Finally, larger spawning biomass will increase egg and larval production, which will sustain distant populations via dispersal and local populations via retention. Modelling these trophic interactions and the ecological ramifications of restoring populations of species from the snapper and grouper families represents an interesting avenue for further research. Scenario models that can show managers the ecosystem effects of various interventions might be particularly valuable.

## Existing status and management of Caribbean tFSAs

Many different strategies have been applied to better manage tFSAs, including fishery closures, species closures, seasonal closures, gear regulations and restrictions, size and weight restrictions, marketing restrictions, landing quotas, encouragement of alternative livelihoods and more (Sadovy de Mitcheson et al. 2008, Claro et al. 2009). Some of these restrictions are implemented through comanagement, voluntary compliance, taboo systems or national and international initiatives, with notable successes emerging from all levels of management. Suitability of a particular strategy or set of strategies will vary geographically depending on history, culture, prosperity, education and the local ecology. Regulatory strategies must be carefully considered as part of a more holistic, ecosystem-based fisheries and marine biodiversity management strategy.

MPAs, including no-take zones, are widely considered to protect habitat from destructive fishing practices; allow the recovery of overexploited fish populations and protected species during critical life-history stages, such as reproduction; and preserve biological and genetic diversity (Roberts 1995, 2000, Lauck et al. 1998, Agardy 2000, Roberts et al. 2001, McLeod et al. 2005, Grober-Dunsmore & Keller 2008) (Figure 1). There are examples of such closures in Belize, the

Cayman Islands, US Virgin Islands, and the Bahamas; seasonal and area closures have been used in Florida, Bermuda, and across the US Caribbean.

Importantly, some tFSA sites have shown remarkable recovery after their protection (Beets & Friedlander 1999, Whaylen et al. 2004, Burton et al. 2005, Nemeth 2005, Kadison et al. 2006, 2009b). Even sites in which certain species have been extirpated have seen recovery. The best example of this is provided from a well-studied, largely extirpated multispecies tFSA in the Virgin Islands. Kadison et al. (2009b) illustrated that once protected, aggregations of several species of groupers began to recover, and although Nassau grouper had been extirpated from the site long ago, this species had returned to the protected site. A similar example occurred at Caye Glory in Belize, where the Nassau grouper population dwindled to only 21 fish in 2001 (Sala et al. 2001) but has subsequently rebounded into the thousands (Belize Spawning Aggregations Working Committee unpublished data). These examples illustrate that protection of multispecies tFSA sites can provide protection for extant aggregations and recovery of extirpated species. Indeed, protection of defunct or extirpated sites may be an excellent strategy as the habitat is ideal for spawning in a variety of species at various times of year and may attract new reproductive adults. If sufficient numbers of regionally important tFSA sites can be protected, then evidence suggests that the spawning populations will recover rapidly and contribute to rebuilding of local fisheries and have positive impacts on the trophic integrity of Caribbean coral reef ecosystems through an increase in ecologically important carnivores.

## Future research to support management

To manage tFSA sites effectively, a minimum amount of information about their status and condition is required. A better ecological understanding of the environmental characteristics of tFSAs will enable scientists, resource managers and fishers to predict the consequences of environmental and management change on spawning behaviour and reproductive success at these ecologically and socioeconomically important locations. Clearly, monitoring population recovery after protection is required and forms a core component of adaptive management. Data gathered from multiple levels of organization and complexity can be synthesized into a compelling case for management and a baseline for future monitoring. We suggest that a minimum amount of information might include bathymetric maps, year-round characterizations of the numbers and species spawning using underwater visual assessments, baseline port surveys or fishery-dependent data, some amount of physical environmental data and supporting video and still imagery (levels 1–4 in Table 5). These data, coupled with data from other locations, can be used to illustrate the importance of any tFSA site and track the recovery rate of a wide range of ecologically and economically important species that aggregate to spawn, as well as those key species that visit aggregations to feed, such as sharks and manta rays.

Although beyond the scope of the present review, understanding life-cycle connectivity is important and may lead to enhanced recovery of aggregative fish stocks by allowing the correct identification and adequate protection of essential fish habitats of each life stage, especially for the areas in which tFSAs once existed. For example, Nassau grouper require a suite of habitat types to support changing requirements for food and refuge through the various stages of the life cycle (ontogenetic habitat shifts). In the Bahamas, Nassau grouper settled exclusively in clumps of macroalgae and not in seagrass or on sand; postsettlement fish (25–35 mm total length, TL) resided within the algae clumps, early juveniles (60–150 mm TL) resided adjacent to the algae, and juveniles (>150 mm TL) colonized natural and artificial patch reefs in areas apparently removed from the postsettlement and early juvenile habitat (Eggleston 1995, Eggleston et al. 1998, Grover et al. 1998, Dahlgren & Eggleston 2001). The relationship between the health of nursery areas and recovery rates of adult populations at tFSA sites remains unclear; however, it is likely that the condition of both of these essential habitats will have an impact on overall population recovery.

Owing to the recent history of extirpation of some once very productive tFSAs and the vulnerability of many tropical species that aggregate to spawn, we concur with Sadovy et al. (2008) and advocate caution in communicating the locations of newly found or unprotected tFSAs. Information in the present review, however, was gained entirely from well-known and documented tFSAs. Predicting the location of tFSAs can create the risk of exposing undisturbed spawning stocks to opportunistic and severe fishing and rapid depletion before evaluation of sustainable management options takes place. Conversely, sites unregulated because they are unknown to environmental managers can also be vulnerable to overexploitation. From the perspective of science-driven, ecosystem-based management, fully detailed maps and descriptions of tFSAs are crucial to understanding the broader ecological patterns and processes operating within a region and between regions.

This review highlighted future directions for research, monitoring and management of Caribbean tFSAs. In the Caribbean region, enforcement capacity may be greater than in many remote areas of the Pacific but is still rather limited. Data sharing can be an essential component for management of regional or national resources, as demonstrated in Belize (Heyman 2011). By sharing information on site ecology and habitat maps, as well as enforcement techniques, legislation and policies, and techniques and tools for research, scientists, fishing communities and environmental managers can learn from others' successes and challenges.

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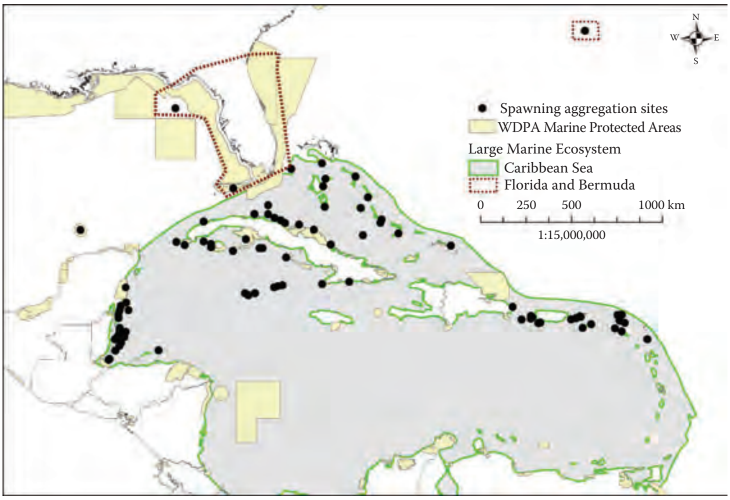
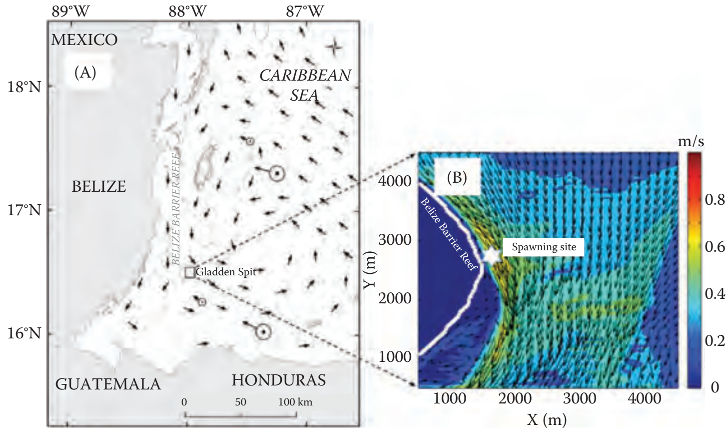


Colour Figure 1 (Kobara, Heyman, Pittman & Nemeth)



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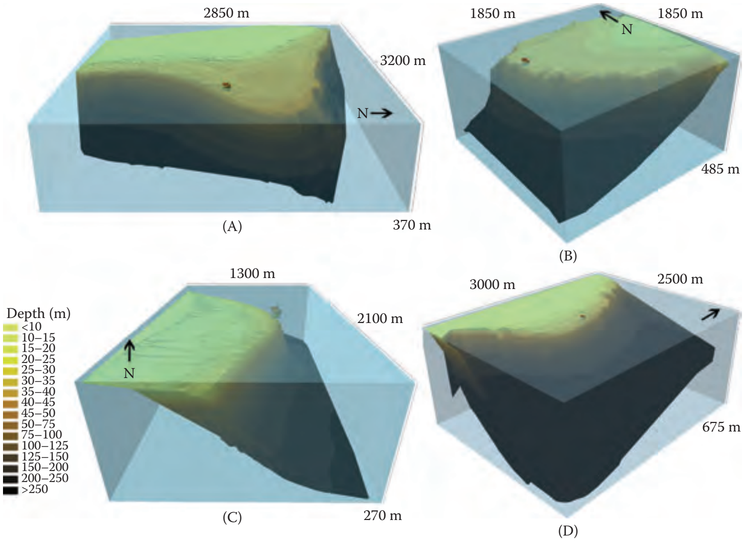

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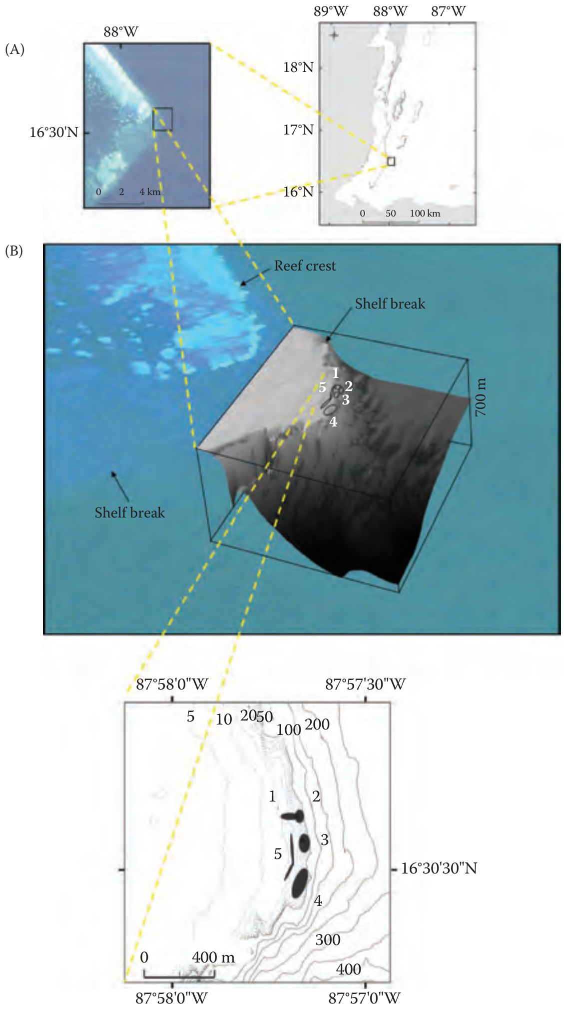
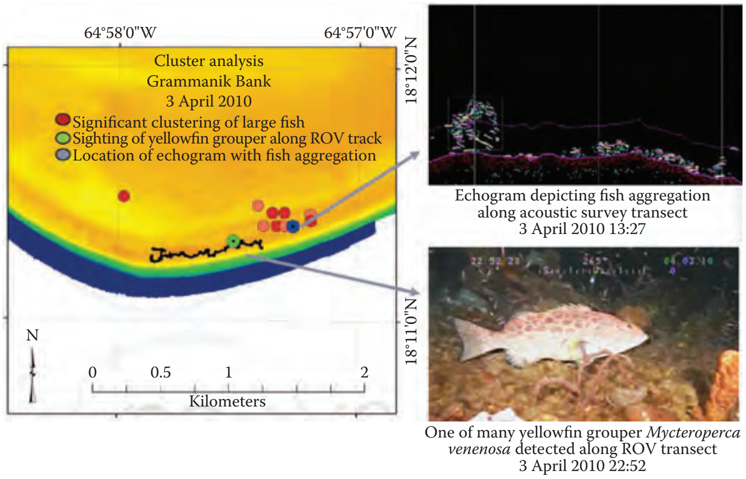


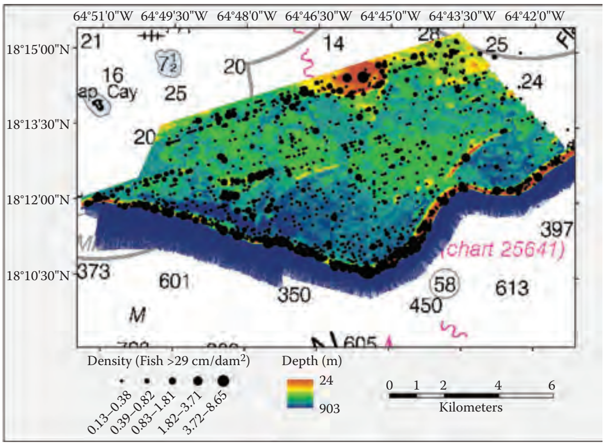
Colour Figure 8 (Kobara, Heyman, Pittman & Nemeth)



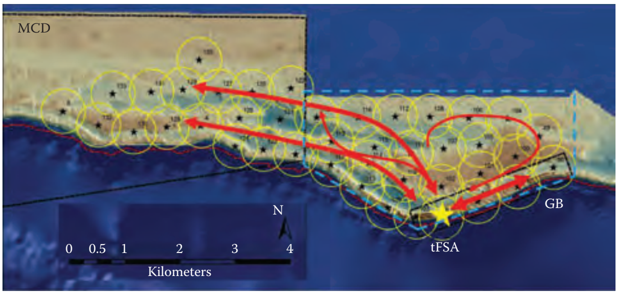
Echogram depicting fish aggregation along acoustic survey transect 3 April 2010 13:27

One of many yellowfin grouper *Mycteroperca venenosa* detected along ROV transect 3 April 2010 22:52

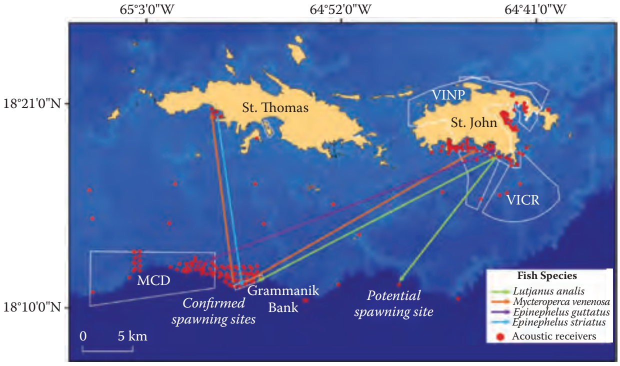
Colour Figure 9 (Kobara, Heyman, Pittman & Nemeth)



Colour Figure 10 (Kobara, Heyman, Pittman & Nemeth)



Colour Figure 11 (Kobara, Heyman, Pittman & Nemeth)



Colour Figure 12 (Kobara, Heyman, Pittman & Nemeth)