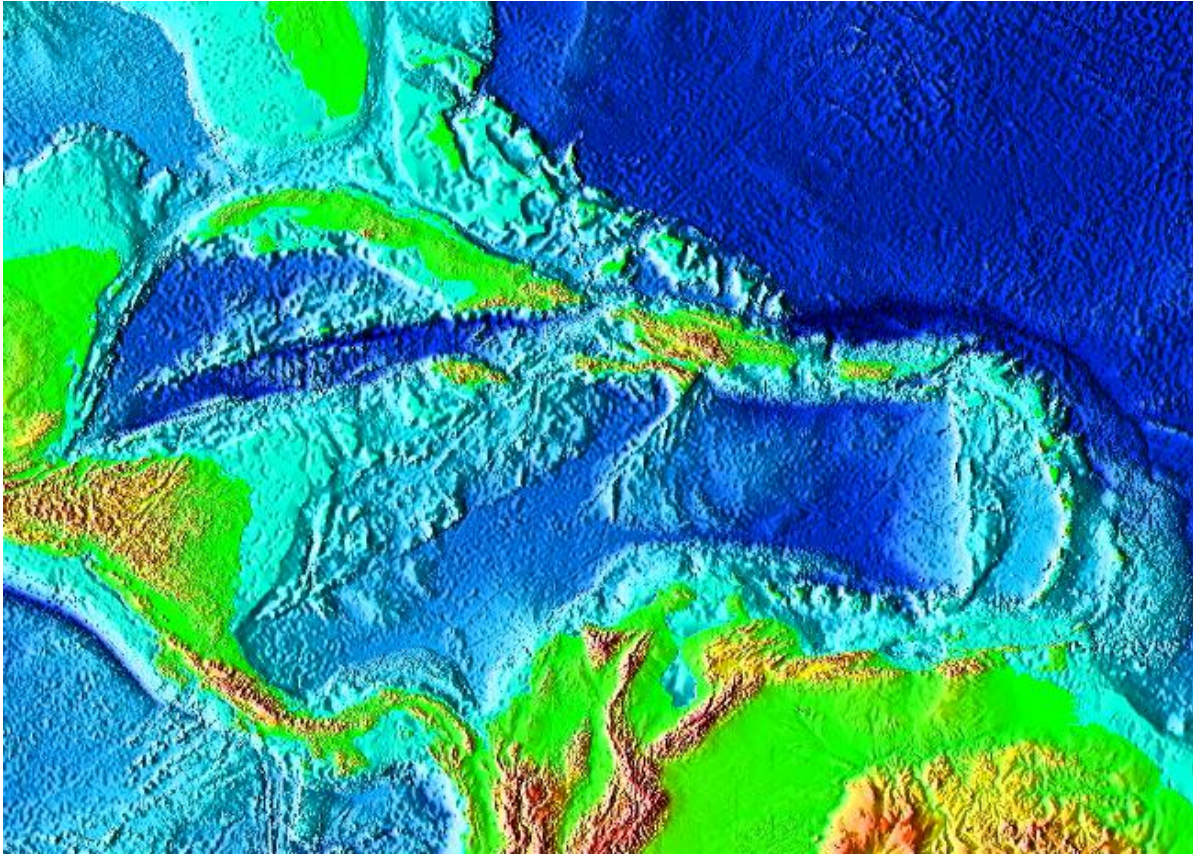


## Caribbean Connectivity: Implications for Marine Protected Area Management



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9-11 November 2006  
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Office of Ocean and Coastal Resource Management  
**Office of National Marine Sanctuaries**



November 2008

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# **Caribbean Connectivity: Implications for Marine Protected Area Management**

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Image of the Caribbean region showing major topographic and bathymetric features from southern Florida to the Greater and Lesser Antilles, part of Central America, and northern South America.

## **SUGGESTED CITATION**

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Example for a paper within the proceedings volume:

Sale, P.F., and J.P. Kritzer. 2008. Connectivity: What it is, how it is measured, and why it is important for management of reef fishes. Pages 16-30 *in* R. Grober-Dunsmore and B.D. Keller, eds. Caribbean connectivity: Implications for marine protected area management. Proceedings of a Special Symposium, 9-11 November 2006, 59<sup>th</sup> Annual Meeting of the Gulf and Caribbean Fisheries Institute, Belize City, Belize. Marine Sanctuaries Conservation Series ONMS-08-07. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD.

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## **Mesoamerican Reef Spawning Aggregations Help Maintain Fish Populations: A Review of Connectivity Research and Priorities for Science and Management**

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### **Abstract**

The life history of most marine organisms includes a period of pelagic larval dispersal. Migration to spawning areas and pelagic dispersal are often well beyond the home range of these organisms. Designing marine protected areas to include a broad range of taxa and their various dispersal patterns is an important and daunting challenge. This paper addresses the issue of connectivity for one set of species in a limited geographic area. We focus on transient spawning reef fish within the Mesoamerican Reef and their connectivity. We divide our review as follows: (1) ecological characterization of transient multi-species reef fish spawning aggregations, (2) oceanographic and biophysical modeling approaches for understanding connectivity, and (3) validation of models with observations. We conclude that the science behind connectivity is advancing rapidly on many fronts, but there are still large gaps. To date, it is largely impossible for managers to apply the results of these studies in specific cases. We further recognize that “human and political connectivity” may be as important for management as the science behind it. Managers, scientists, fishermen, and politicians can and should embrace connectivity as an important factor in regional fisheries and marine biodiversity management. The collaborative design and implementation of networks of marine reserves that include multi-species spawning aggregation sites, critical nursery habitat, and the connectivity between these elements, are likely to provide an important contribution to reversing the decline in fisheries throughout the Gulf of Mexico and Caribbean Region.

### **Introduction**

Caribbean reef-dwelling species have evolved a wide range of strategies for reproduction and larval dispersal. Pelagic larval dispersal times range from zero, for species that use internal fertilization and/or demersal eggs (e.g., conch or triggerfish), to several weeks for species that use broadcast spawning within aggregations (e.g., grouper and snapper), to several months for spiny lobster. The complex task for resource managers is to design marine protected area (MPA) networks that recognize and effectively protect all of the important taxa with all of their varied life-history strategies (Roberts 1997). The task is enormous and well beyond the scope of this review. We focus on reef fish that spawn in transient aggregations within the Mesoamerican Reef (Fig. 1) as an important example for connectivity studies and their management applications.

Heyman, W.D., B. Kjerfve, and T. Ezer. 2008. Mesoamerican reef spawning aggregations help maintain fish populations: A review of connectivity research and priorities for science and management. Pages 150-169 in R. Grober-Dunsmore, and B.D. Keller, eds. Caribbean connectivity: Implications for marine protected area management. Proceedings of a Special Symposium, 9-11 November 2006, 59<sup>th</sup> Annual Meeting of the Gulf and Caribbean Fisheries Institute, Belize City, Belize. Marine Sanctuaries Conservation Series NMSP-08-07. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Office of National Marine Sanctuaries, Silver Spring, MD.



Most large Caribbean reef fish species form transient spawning aggregations at specific times and locations (Domeier and Colin, 1997). These fishes often produce pelagic larvae that float on ocean currents for weeks before settling into suitable juvenile habitats (Leis, 1987). Therefore, in order to promote the sustainability of these species, it is important to understand the dynamic life history patterns, and the most vulnerable phases, places, and times, that form bottlenecks in their reproduction (Coleman et al., 2000; Warner et al., 2000).



**Fig 1.** The Mesoamerican Reef encompasses the Caribbean coastal waters of Belize, Guatemala, Mexico, and Honduras.

For these species, where total annual reproductive output occurs locally, the aggregation sites are clearly worthy of protection and management (Johannes 1999). We believe that MPA networks are the most effective tool for the conservation of spawning aggregations and the species that use this strategy. However, there exists only sparse information on the seasonal dynamics of Caribbean reef fish spawning aggregations and almost no data linking larval pathways from aggregation sites to nursery habitats. Fertilized gametes for most species are positively buoyant and are entrained in wind drift, wave drift, and ocean currents associated with mesoscale oceanic eddies. These passively transported eggs metamorphose into mobile larvae that are also transported by currents, but have the ability to actively modify their vertical and horizontal positions. The connectivity between reef fish spawning aggregations and nursery areas is perhaps the most important scientific gap in marine protected area network designs. We use the connectivity definition of Mora and Sale (2002), the demographic connection between populations of species due to the

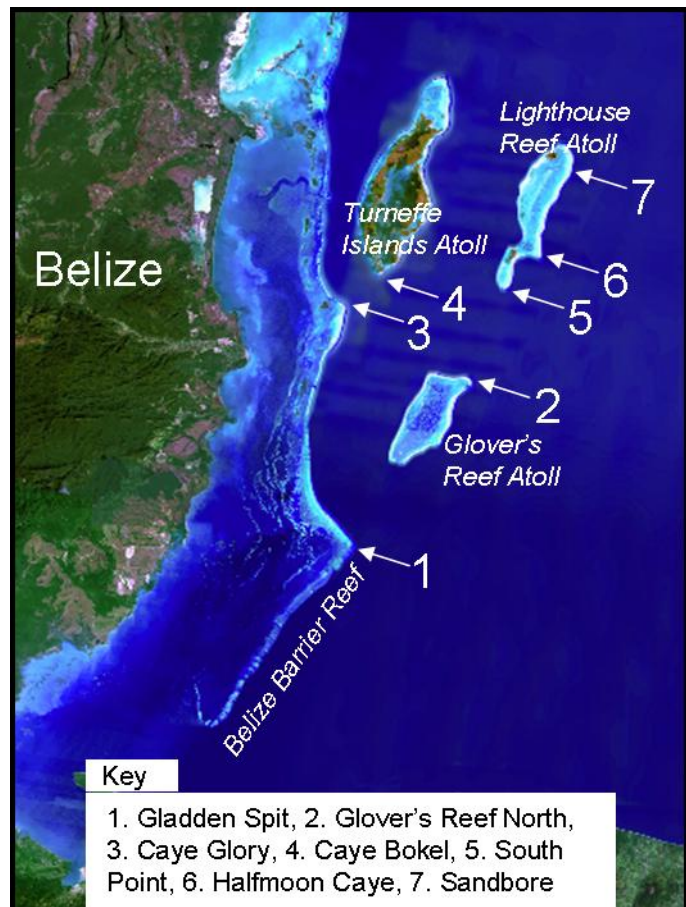
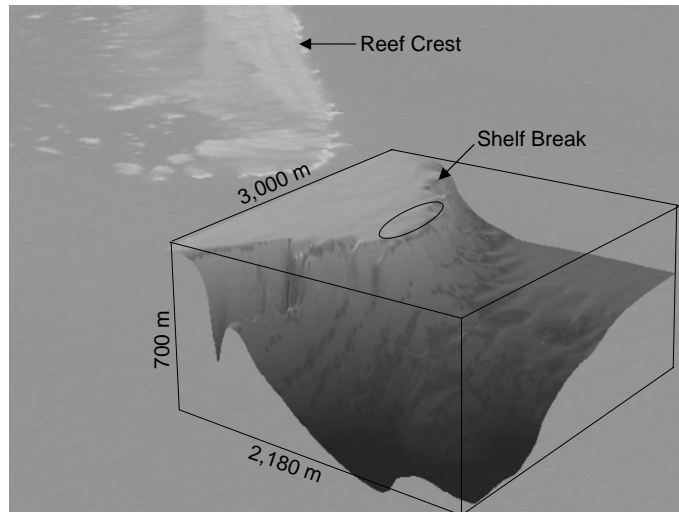
migration of individuals (especially larvae) between them. Even if connectivity pathways could be mapped in detail, implementation of the science within marine reserve networks is constrained by more practical realities. We therefore offer observations from our experiences of the human and political processes that govern marine reserve network implementation. The goals of this paper are to describe the status of the science of connectivity, outline future research needs, and offer recommendations on the applications of this research to management within real-world political systems.

**Review of Existing Science of Spawning Aggregations as Connectivity Sources**

*Ecological Characterizations of Transient Multi-species Reef Fish Spawning Aggregations*

There are several papers that document transient reef fish spawning aggregations within the Mesoamerican Reef (MAR), but the great majority of the papers provide field data from only a limited portion of the year. The majority of papers focus on serranid (grouper) species and of those, the most widely documented species is Nassau grouper, *Epinephelus striatus*, whose aggregations are best documented for the months of December and January (e.g., Craig 1969; Fine 1990; Carter et al. 1994; Aguilar-Perrera and Aguilar-Davila 1996; Sala et al. 2001). Intensive fishing at these and other sites has caused declines and in some cases localized extirpations throughout the Caribbean (Sadovy 1994).

In Belize, several sites that harbor *E. striatus* also harbor aggregations of other species. Sala et al. (2001), for example, describe an aggregation of *E. striatus*, but demonstrate that black grouper (*Mycteroperca bonaci*), yellowfin grouper (*M. venenosa*), and tiger grouper (*M. tigris*) also aggregate to spawn at the same location at nearly the same time. Gladden Spit is probably the best example of this phenomenon where 20+ species spawn there at all times of the year (Fig. 2a) (Heyman 1996; Heyman et al. 2001, 2005; Heyman and Requena 2002; Graham and Castellanos 2003; Heyman, unpublished data). Similar examples are found throughout Belize and seven of the 16 documented sites are illustrated in Fig. 2b (Belize National Spawning Aggregations Working Committee, pers. comm.; Heyman and Requena 2002).



**Fig. 2.** (a: top) Gladden Spit, showing the location of the multi-species spawning aggregations (oval) in relation to the shelf break and the bend in the reef (from Heyman et al. 2007). (b: bottom) The locations of seven documented multi-species spawning aggregation sites in Belize.

Transient multi-species reef fish spawning aggregations are more common than originally suspected and have been documented around the Caribbean. For example, Fine (1990) reports yellowfin and tiger grouper aggregate at the same location as Nassau and black grouper at Caldera del Diablo in Guanaja, Honduras. Claro and Lindeman (2003) provide a comprehensive set of examples from Cuba gathered from fishermen interviews. Many of the Cuban sites harbor several grouper and snapper species. Whaylen et al. (2004) provide a characterization of a Nassau grouper spawning site in the Cayman Islands, and documented six other transient spawning species aggregated for spawning there as well. Riley's Hump in the Dry Tortugas provides a similar example from Florida. The site is known to harbor spawning aggregations of both mutton snapper, *Lutjanus analis*, and also several serranid and carangid species, similar to Gladden Spit (Peter Gladding, pers. comm.). Sosa-Cordera et al. (2002) document 27 previously undocumented transient reef fish spawning aggregations sites along the Mexican Caribbean, the majority of which were multi-species sites with groupers and snappers. Many of the same species documented to spawn follow similar patterns - seasonal, lunar, and diel - to those at Gladden Spit. Given the importance of spawning aggregation sites for the maintenance of reef fish populations and the threats to their extirpation, we recommend a thorough analysis of the timing and location of spawning aggregations throughout the region.

#### *Oceanographic and Biophysical Models Applied to Connectivity*

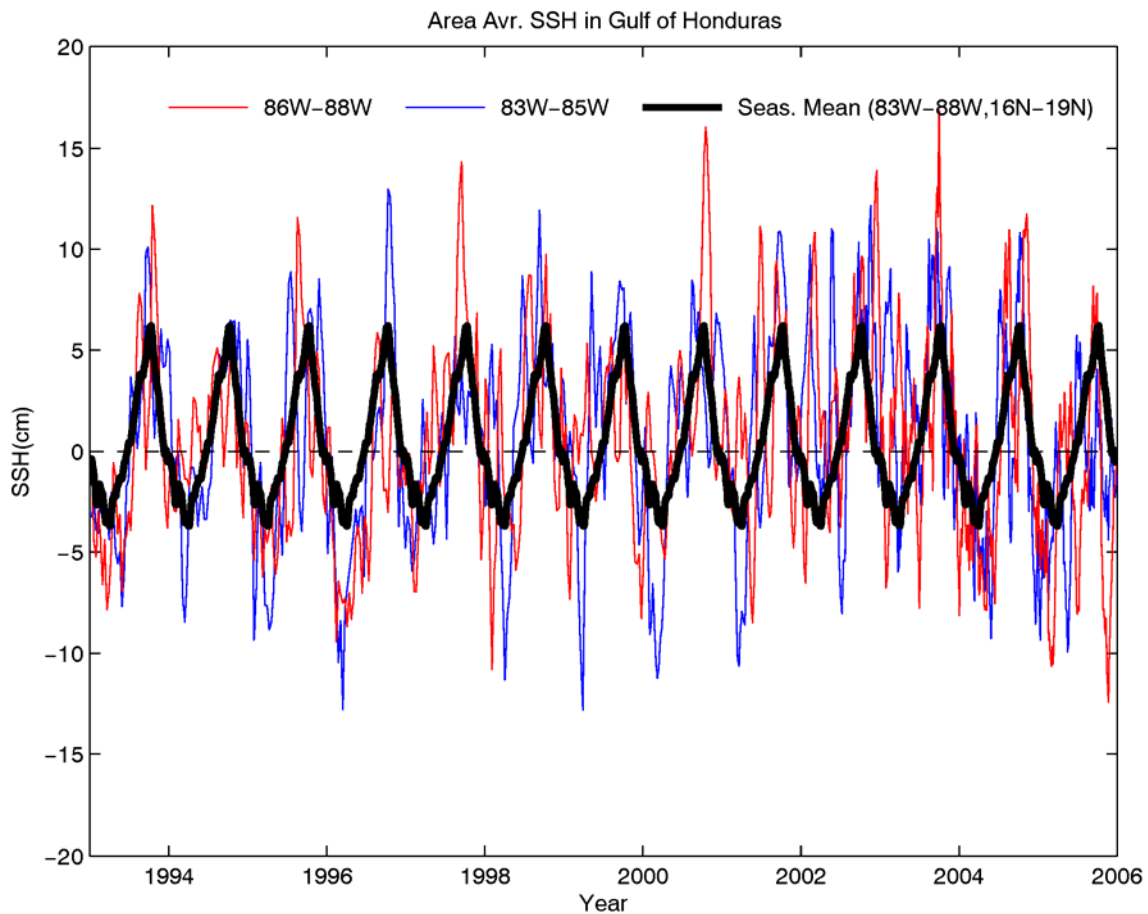
Constructing realistic hydrodynamic models to study biological connectivity near Caribbean reefs is a challenging task. Models include various forcing mechanisms on different scales such as tides, winds, runoff from rivers, and remote influence from offshore currents and eddies. Hydrodynamics and biological activities are also influenced by complex small-scale topography, and the sparsely available, long-term local observations in the region are usually insufficient for detailed model validations. Tides in the Caribbean Sea (Kjerfve 1981) can be simulated quite well (Thattai 2003; Ezer et al. 2005), but tidal currents along reefs represent only a relatively small portion of flow variability. Direct wind-driven currents may be important, especially during intense events such as tropical storms and hurricanes (e.g., see the simulated impact of Hurricane Wilma on the western Caribbean Sea by Oey et al. 2006, 2007), but surprisingly, surface currents adjacent to the Mesoamerican Reef are seldom correlated with the local wind (Armstrong 2003). Therefore, the question is, what drives the currents along the reef and how can these currents be simulated? Recent observations and model studies suggest that variations in the Caribbean Current and propagation of Caribbean eddies play a major role in this regional flow variability (Carton and Chao 1999; Murphy et al. 1999; Candela et al. 2003; Ezer et al. 2003, 2005; Oey et al. 2003; Sheng and Tang 2003; Romanou et al. 2004; Richardson 2005).

Modeling the impact of eddies on the flow and biological connectivity near the MAR is difficult for two main reasons. First, small-scale topographic features of significance to biological activities are much smaller (~10-100 m) than most high-resolution hydrodynamic models (~1 km grid size). Second, since the eddies are not predictable, even high-resolution ocean models with realistic wind forcing can only describe the statistical characteristics of the flow, but not the conditions at a particular location and time. One solution to alleviate the latter problem is to use data assimilation in the model. Recent attempts to model the flow near the MAR and its connection with the western Caribbean Sea used a z-level model with high-resolution nesting (Sheng and Tang 2004; Tang et al. 2006). Another approach used a terrain-following model with



a curvilinear grid (Ezer et al. 2005), which also includes assimilation of eddies. However, some model deficiencies remain unresolved, as suggested later in this review.

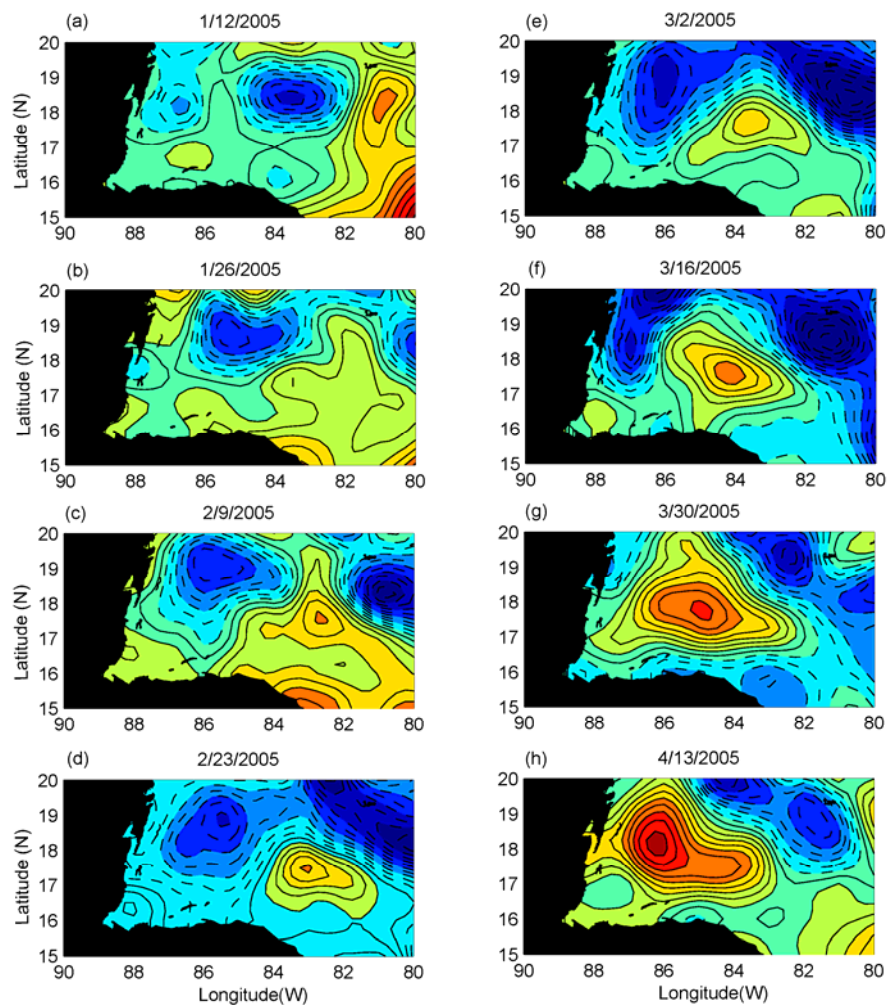
Below are examples that demonstrate the difficulty of modeling the variability in the region. Since long-term local observations are rare, we use an analysis of 13 years of altimeter data that combines several satellites (Ducet et al. 2000). Fig. 3 shows the variability of Sea Surface Height Anomaly (SSHA) in two regions, the eastern Gulf of Honduras (GOH) and the western GOH. The two regions are generally in phase with each other for the seasonal cycle (shown in a heavy black line) associated with the upper ocean's thermal structure, but they show different high-frequency variability associated with mesoscale eddies. Inter-annual variations and possible long-term climatic changes may also be found in the SSHA record (e.g., the apparent change in variability pattern over the last four years). Further research is needed to understand those variations and the possible consequences for coral reef connectivity.



**Fig. 3.** Time series of sea surface height anomalies from satellite altimeter data averaged over the western (red line) and mid (blue line) Gulf of Honduras in the southern Mesoamerican Reef. The mean seasonal cycle averaged over the 13-year record is indicated by the heavy line.

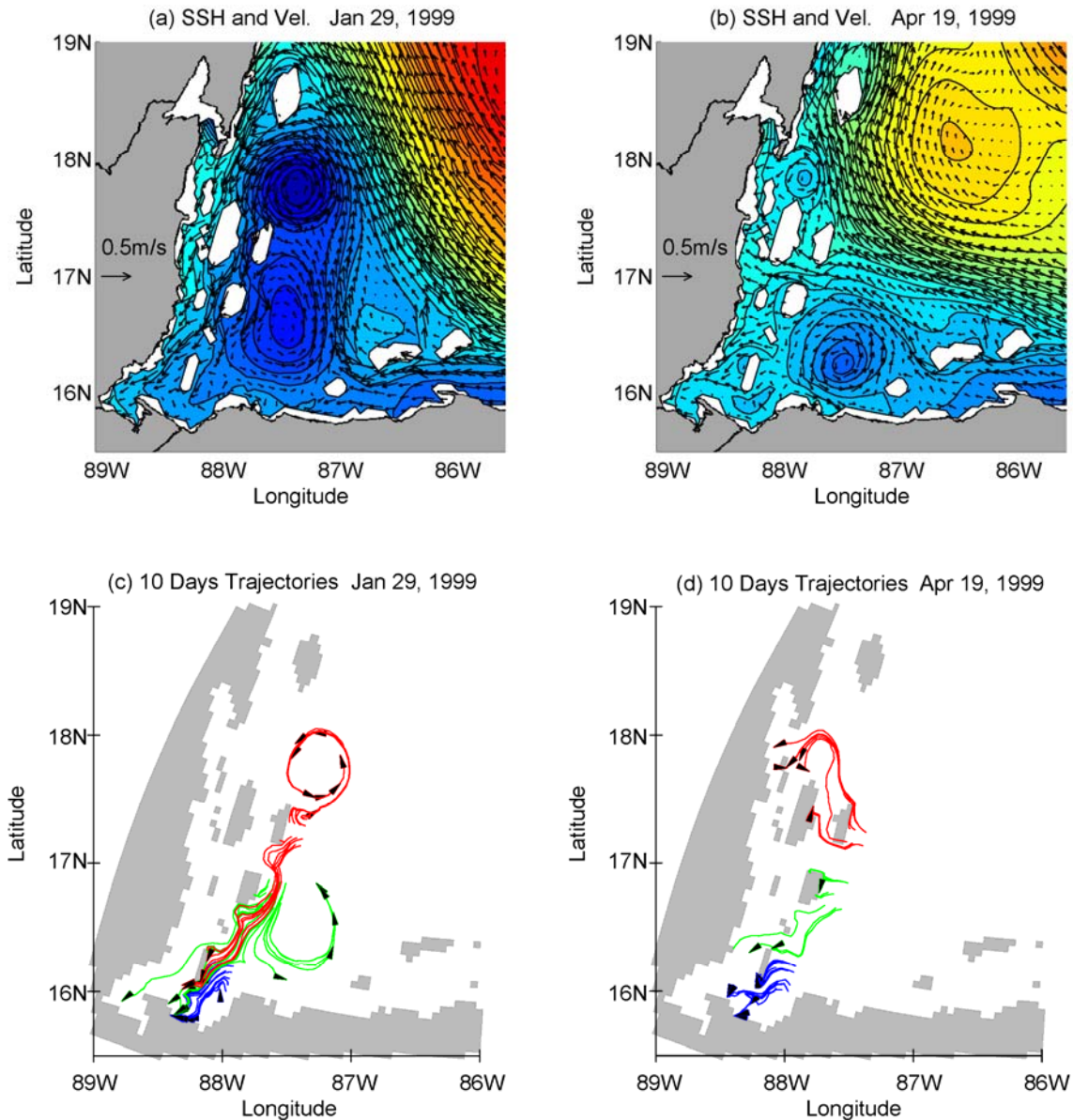
An example of the westward propagation of cyclonic (low SSHA) and anti-cyclonic (high SSHA) eddies is shown in Fig. 4; a similar pattern of eddies with irregular frequency appears

throughout the 13-year period. The dramatic influence of these types of anomalies on the flow near the MBRs has been diagnosed by assimilating SSHA into the model (Ezer et al., 2005), and is shown in Fig. 5a and 5b. The consequences for connectivity and the potential dispersal of eggs and larvae released near different reefs are shown in Fig. 5c and 5d. When a cyclonic anomaly is found near the reef (Fig. 5a and 5c) the Caribbean Current moves farther offshore, creating two cyclonic gyres outside the reef that can trap some eggs, but also results in a strong southward flow along the Belizean coast (in the Mesoamerican Reef lagoon). On the other hand, if an anti-cyclonic anomaly is found near the reef (Fig. 5b and 5d), the flow is mostly westward across the reef toward the lagoon, so no eggs are drifted offshore. Note that eggs released on two sides of the same reef may drift in opposite directions! If this persists for multiple generations, it can create stock separation, and thus a barrier to connectivity, which would allow for genetic differentiation of sub-populations of the same species to the north and south of the connectivity barrier.



**Fig. 4.** Sea surface height anomaly from altimeter data in the southern Mesoamerican Reef. The 2-weekly images demonstrate the westward propagation of cyclonic [negative/blue SSHA, (a)–(d)] and anti-cyclonic [positive/red SSHA, (e)–(h)] features. Contour interval is 2 cm.

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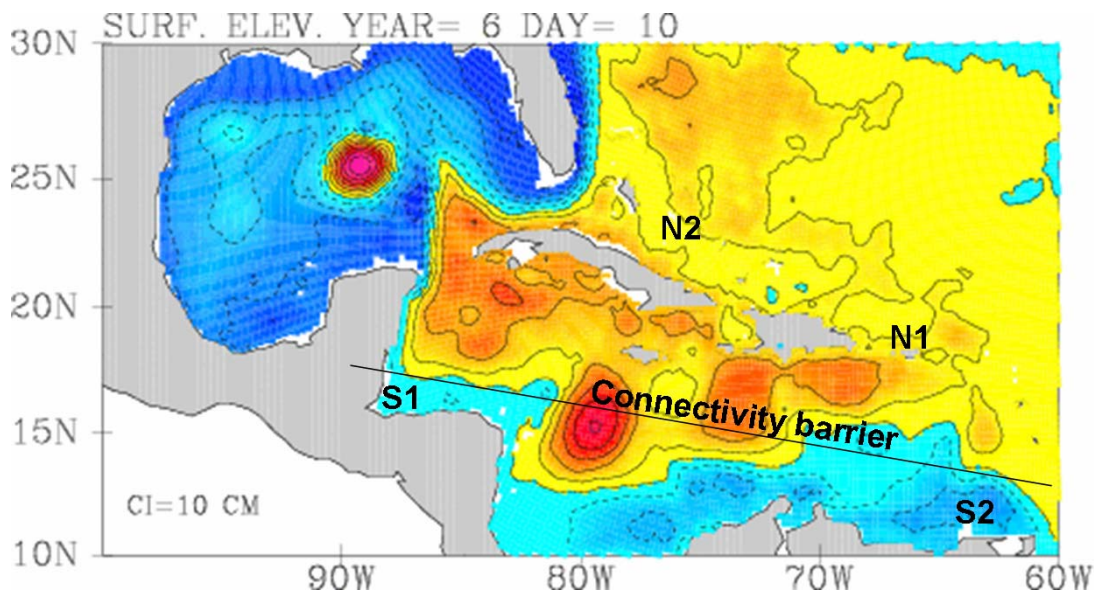
**Fig. 5.** Model simulations (Ezer et al. 2005) of sea surface height (blue/red for low/high) and surface velocity for (a) January and (b) April, 1999, when cyclonic and anti-cyclonic anomalies, respectively, were observed near the Mesoamerican Reef. (c) and (d) show the trajectories of modeled passive tracers released at the surface near reefs with known fish aggregations, and correspond to the velocity fields of (a) and (b). The model was initialized using observed altimeter data representing the two different periods.

While there are no observations to verify the model results, the simulations demonstrate the role of eddies in biological connectivity. Note that dispersion calculations made by Tang et al. (2006) using seasonal forcing (but no eddy assimilation) show quite different patterns from the Ezer et al. (2005) model. Moreover, the Tang et al. (2006) z-level model did not include the very shallow detailed topography of the Ezer et al. (2005) terrain-following model, resulting in a

discrepancy in the coastal flows between the two models. These studies emphasize the need for coordinated efforts to compare results between models and to verify models with observations.

Additional modeling approaches will be required before they can be directly applicable for management. Most of the existing models include relatively large grid cells, and could be reduced using higher-resolution nested models. Modeling the effects of river discharge and sediment transport (e.g., Thattai et al. 2003) can be useful for tracking the dispersion of river flows and eddy patterns, particularly by using ocean color sensors (Hu et al. 2004). Studying the impact of short-term catastrophic events such as hurricanes (Oey et al. 2006, 2007), as well as long-term climate change and its influence on local circulation, can also provide useful insights. Finally, and most importantly, are the new efforts that couple physical models with biological aspects of larvae to study biophysical aspects of connectivity (e.g., Warner et al. 2000; Paris and Cowen 2004; Paris et al. 2004, 2005; Sheng et al. 2004; Cowen et al. 2006; Tang et al. 2006).

In spite of the stochastic nature of marine currents, there are likely to be natural physical corridors that promote connectivity and/or boundaries that impede connectivity between marine populations that only become apparent after analysis of decadal variation. These corridors can enhance local recruitment or conversely provide separation between various populations (Cowen et al. 2000, 2006; Andréfouët et al. 2002). Regional management plans for various marine species must account for stock separation and differences. Initial observations of Western Caribbean Sea (WCS) model output indicate a potential physical barrier to connectivity between the northern and southern MAR (Fig. 6).



**Fig. 6.** Shown is an example of a synoptic sea surface height field with blue/red shades representing low/high values (from the Ezer and Mellor (2000) model). A barrier to connectivity may be created along the MAR where cyclonic eddies diverge from anti-cyclonic eddies. Inter-reef connectivity is likely to be enhanced within northern (N1 and N2) and southern (S1 and S2) regions, while inter-reef connectivity across the boundary is likely to be reduced or halted. These hypotheses can be tested using analysis of mitochondrial DNA.



*Physical Oceanographic and Bathymetric Observations Needed to Validate Connectivity Models*

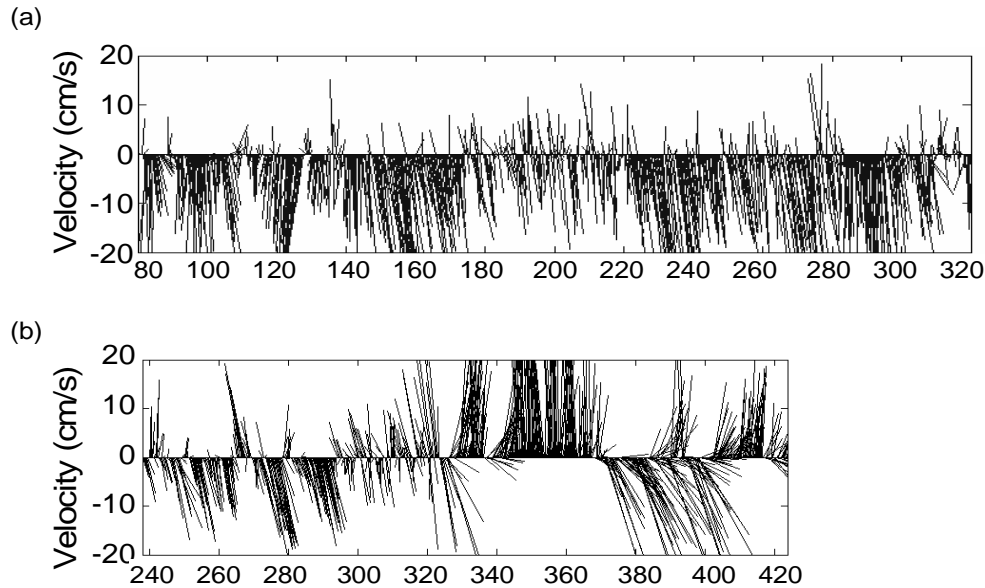
For numerical simulation models to be useful, they need validation. Such validation can be accomplished by time-series measurements of currents, salinity, water temperature, and water level; time-series measurements of wind speed and direction at several locations within the domain; Lagrangian measurements with drifter buoys; and sequential measurements from satellites of ocean temperature, color, and relative water level elevation by altimetry. Although the physical oceanographic measurements do not measure connectivity directly, they are essential for providing observational data to allow the validation of the large-scale behavior of simulated ocean currents and circulation. The drifter buoys can be very helpful in identifying the fine-scale flow for spawning clouds in the vicinity of reef features and provide confirmation of the influence of ocean eddies. The satellite imagery allows identification of water mass boundaries, influence of continental runoff, and the existence, propagation, and sense of rotation of mesoscale ocean eddies, which represent an important far-field forcing mechanism for near-reef currents. Unfortunately, a sufficient number and extent of appropriate physical time-series and drifter data are seldom available for effective model validation. Although there usually is an abundance of satellite imagery, there is generally a long duration between sequential overpasses, pixel size can be too large, and clouds can obscure images. Thus, satellite imagery should not be used as a sole source for connectivity model validation.

A solid understanding of local physical oceanography and flow variability at spawning aggregation sites and along the adjacent Mesoamerican Reef is essential for successful connectivity modeling. In the MAR case, time-series current measurements have been conducted intermittently over the period 1998-2005 at three locations just 1 km seaward of the reef, very near the shelf break in 22-30 m of water depth, using InterOcean S4 current meters moored 5 m above the bottom. The three locations are Lighthouse Reef, Gladden Spit, and the Sapodillas. The hourly measurements of current speed and direction (along with temperature, salinity, and water level) are of excellent quality. The data indicate approximately equal response to wind forcing and the occurrence of mesoscale ocean eddies with currents mostly flowing along the reef toward the north or south with speeds of 2-50 cm/s, with mean currents typically being 7 cm/s. Tidal current variability is in comparison small, (as shown in the simulations of Thattai 2003; Ezer et al. 2005) consistent with the relatively small local tidal range (Kjerfve 1981). Examples of the current flow at the Gladden Spit spawning location are shown in Fig. 7a and for Lighthouse Reef Atoll (Fig 7b) as a stick diagrams.

Note that oceanographic time-series measurements such as these can be used to help validate connectivity models. The data in Fig. 7a and b are taken from the south and north of the connectivity barrier illustrated in Fig. 6 and show current flow, largely in opposite directions, consistent with the maintenance of the barrier.

Most numerical modeling studies include only coarse bathymetric data, which may influence their results. Accurate bathymetric data are particularly important at the time and location of spawning aggregation sites since the initial trajectory of spawned materials can be affected. Model grids are often 3-8 km, while spawning aggregation sites at 30 m depth are often adjacent to steep walls and deep (>1,000 m) water depths (Fig. 2a, 8a, b). Surveys of detailed small-scale topography (e.g., Ecochard et al. 2003a, b; Heyman et al. 2007) can be incorporated into very high-resolution numerical models to study local circulation near fish spawning aggregation sites.

In addition to direct measurement of the sea-bottom with single beam echo-sounders described above, airborne sensors such as LIDAR can be used to map sea-bottom topography over relatively large areas with 1 cm depth accuracy (MacDonald 2005; Intelman 2006). These data can be extremely valuable when incorporated into biophysical models of connectivity.

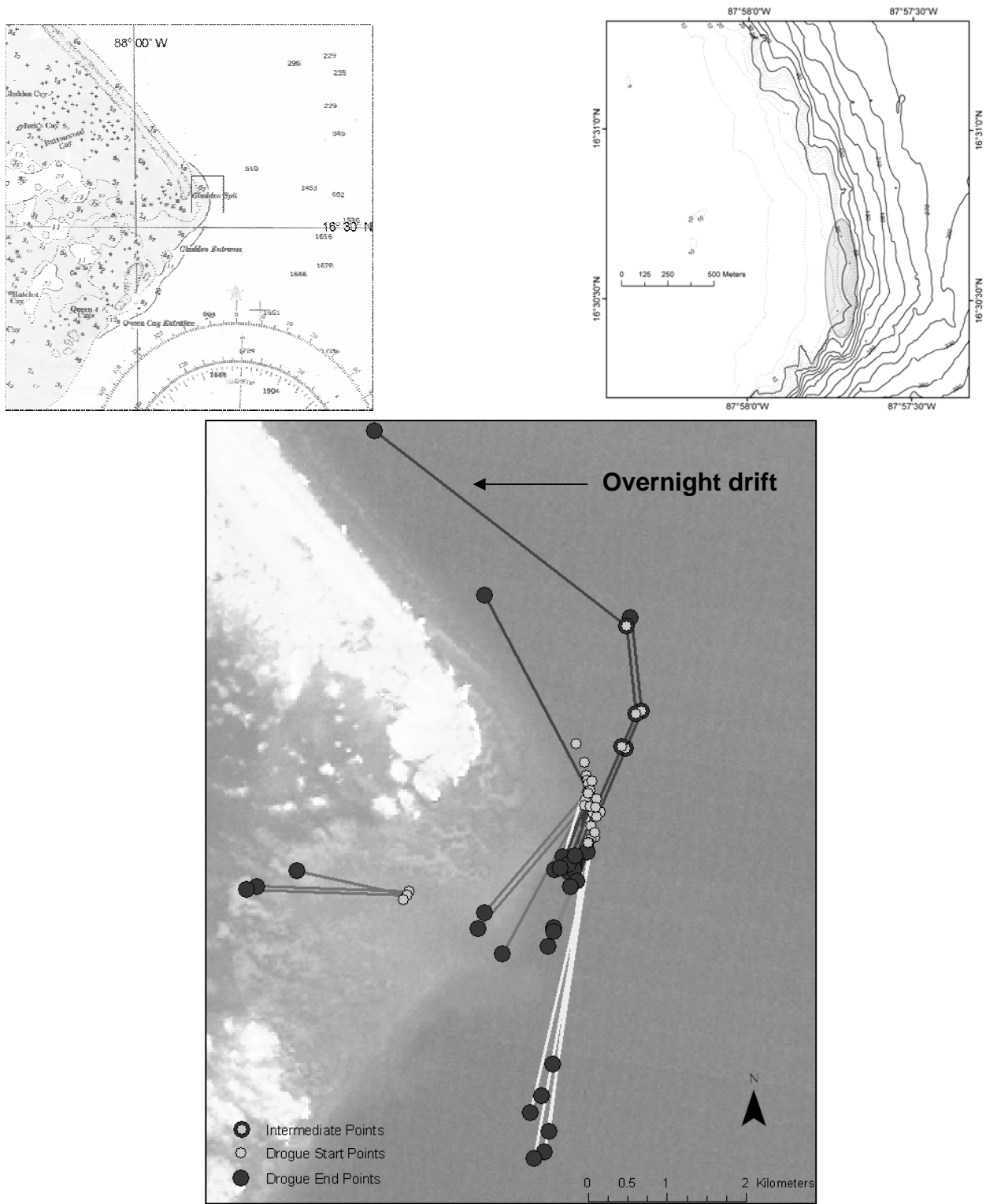


**Fig. 7.** Stick diagrams showing the measured speed and direction of currents at the shelf break at 26 m depth at (a) Gladden Spit (Site 1 in Fig. 2b) between Day 80-320 in 2000, 50 km to the northeast at (b) Halfmoon Caye, Lighthouse Reef Atoll (Site 6 in Fig. 2b) between Day 240 in 2000 and Day 80 in 2001. Gladden Spit is south of the proposed connectivity barrier illustrated in Fig. 6 so currents largely move south, driven by cyclonic eddies. The currents at Halfmoon Caye, 90 km to the northeast of Gladden Spit, reflect its position within the zone of the proposed connectivity barrier. Currents move to the south, consistent with currents at Gladden Spit, and to the north, where the northerly Caribbean Current dominates the influence of the cyclonic eddies near the coast.

#### *Biological Observations Needed to Validate Connectivity Models*

The dispersal of propagules generally starts with the passive transport of eggs. Passive transport can no longer be assumed after about 18-24 hours when eggs hatch into swimming larvae (Leis et al. 1987; Heyman et al. 2005). Some eggs, like those of Cubera snapper, float toward the surface and remain near or at the surface (Heyman et al. 2005). Others, like those of Nassau grouper, are less positively buoyant and can be suspended in mid water (C. Paris, pers. comm.). In all cases larval behavior and swimming ability increases with increasing age and size. Settlement stage larvae from 11 families had a mean in situ swimming rate of  $20 \text{ cm s}^{-1}$  (Leis and Fisher 2006). Larvae can swim over 10 km in a day in order to reach an appropriate area for settlement and recruitment (Sponagule et al. 2002; Paris et al. 2005).

## Caribbean Connectivity: Implications for Marine Protected Area Management



**Fig. 8.** (a: top left) Bathymetric chart of Gladden Spit. (b: top right) Detailed bathymetry derived from inexpensive mapping efforts (Heyman et al. 2007). (c: bottom) Davis-type drogues (simulating eggs) move away from spawning site in multiple directions illustrating the initial trajectory of spawned materials.

While a great deal of work has been done to model egg and larval movement from spawning aggregation sites, very few empirical studies actually show the pathway of larvae from spawning to recruitment. The initial trajectory of spawned materials from spawning aggregation sites has not been detailed sufficiently, and serves as an important input to connectivity models. Using Davis-type current drogues and plankton nets, the initial trajectory of spawned materials can be plotted at the time and location of spawning aggregations. Data collected at Gladden Spit illustrate the various speeds and directions that fertilized eggs move away from a spawning site (Fig. 8c). As mentioned above, since the grid size of most models is 3-8 km, the initial trajectory of eggs might not be included accurately. However, note that even without sufficient resolution, the simulated trajectories indicate a potential drift in the opposite direction from the same reef (Fig. 5c, d), that is surprisingly similar in nature to the observed local drift (Fig. 8c).

There exist several new techniques to measure, directly and indirectly, connectivity between various populations. Most important are genetic studies, otolith microchemistry analysis, and marking larvae with radioisotopes.

Genetic studies can be used to illustrate actual connectivity between spawning adults and juvenile recruitment (Taylor and Hellberg 2003). By analyzing statistical differences among microsatellites extracted from mitochondrial DNA, specific stocks and effective population sizes within a species can be differentiated (Wright and Bentzen 1994). Historical connectivity among populations, effective population size, exponential population growth rate, and migration rate between pairs of populations can be explored statistically (e.g., Kuhner et al. 1995; Salient and Gold 2005).

These types of research could be used to evaluate the validity of the connectivity barrier, illustrated in Fig. 6. Specifically, it is possible to test the hypothesis that gene flow of reef fish species is blocked by this physical barrier, but inter-site connectivity is enhanced within northern and southern areas.

The demographic and genealogical history of the MAR region can be explored by using a model of (partial) isolation, with migration, between pairs of closely related populations (Hey and Nielsen 2004). These analytical approaches can provide insights into the following questions: (1) Is there support for a model of historical connectivity, followed by isolation, between populations presently located south and north of the “connectivity barrier”? (2) What was the historical degree of connectivity among populations on opposite sides of the barrier and how long ago did it occur? (3) What is the degree or extent of connectivity, if it exists, between populations on opposite sides of the “connectivity barrier” and (4) What is the recent demographic history of each population (i.e., is each population expanding or declining in effective size)?

Natural and artificial markers embedded within the carbonate structure of larval otoliths can be used to validate connectivity models. The microchemistry of otoliths illustrates specific chemical signals of water bodies through which they travel from spawning to recruitment (Jones et al. 1999; Swearer et al. 1999; Rooker et al. 2001; Thorrold et al. 2002; Rooker and Secor 2005). A promising new approach for empirical connectivity studies is based on marking larvae with



radioisotopes. Larval otoliths can be tagged with radioisotopes by injecting markers into gravid parental females prior to spawning (Jones et al. 1999; Thorrold et al. 2002).

## **Discussion**

### *Connectivity Science and its Applications for Management*

Though directly applicable results will not be immediately available, resource managers and fishermen should work together with scientists to address the science of connectivity and its applications to Caribbean ecosystem management. We predict that in 10 years networks of marine reserves will be designed with extensive use of the research reviewed in this paper. With an extensive regional management program already in place and a great deal of modeled and empirical data already collected, the MAR region provides an excellent site to test these relatively new techniques and their applications in management.

We suggest that further research and observations are needed in order to increase the utility and focus of connectivity science for management planning. There are a variety of important vectors for research within biological and physical sciences. Since various groups may be best suited to address each of these in different places and at different times, the following list is submitted without order of priority:

1. identify and characterize important nursery habitats
2. characterize multi-species spawning aggregations
3. track initial trajectory and dispersal of eggs from spawning areas
4. map adult migration routes
5. map genetic distributions of various taxa and identify barriers to connectivity and corridors that enhance it
6. collect detailed bathymetric data for spawning and nursery areas
7. collect oceanographic data with time series at spawning areas
8. increase the use of remote sensing – particularly altimeter data and ocean color
9. reduce grid size of biophysical models

If pressed to prioritize, we suggest that detailed, year-round ecological characterizations of transient multi-species reef fish spawning aggregations would help the management community to understand the critical value of these areas for inclusion as core conservation areas within MPA networks. At this time, though several aggregations have been described in general terms, we are not aware of any published, year-round, field-based characterization of a multi-species spawning aggregation. Yet the conservation importance of such sites as critical life habitat is immeasurable. If and when multi-species aggregations are characterized, managers can close these areas year-round and implement closed seasons for particularly vulnerable species. This is exactly what was done for Belize when 11 multi-species spawning aggregation sites were closed year-round (Government of Belize 2003a) and a closed season was implemented for Nassau grouper during December-March (Government of Belize 2003b). This temporal and spatial overlap in legislation offers multi-species spawning protection at key sites and general seasonal protection, thus reducing costs and effort involved with management.

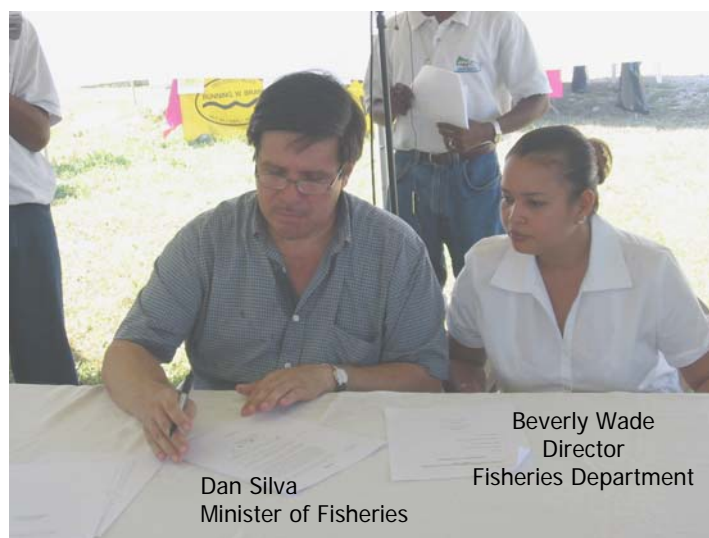
Since many reef promontories have been identified (even if not fully characterized) as multi-species spawning aggregation sites, these areas are likely to have similar oceanographic

conditions that might be revealed through coupled studies of physics and biology. Studies of the oceanographic influences on initial larval transport from spawning aggregations would also be highly desirable. We suggest the development and use of detailed, small-grid, nested oceanographic models created with high-resolution bathymetric data. These small-scale models could be used to generate conceptual models of flow patterns that could be produced with realistic far-field forcing. These models could be calibrated and refined with physical oceanographic data collected with current meters and drogues. Understanding the mechanism and dynamics of initial larval trajectory from reef promontory spawning aggregation sites would offer a vast increase in the predictive capacity of larger-scale connectivity models.

#### *Human and Political Connectivity*

In analyzing lessons learned from experiences in the conservation and management of spawning aggregation sites as connectivity sources in the Mesoamerican Reef, we found that the human component of the conservation process was critically important. The efforts that led to national closure of 11 sites involved myriad fishermen and technicians in the collection and analysis of data. It also involved exchanges between fishermen from one area within Belize to others, and from Belize to other countries – focusing on the plight of fisheries resources. Patriarch fishermen from all over the country provided their insights and experience to both scientists and policy makers. Public hearings and public service announcements on television and radio were aired to raise awareness of the issues, prior to and following the signing of legislation. Over 20 fishermen from Belize participated in a spawning aggregations workshop at the Gulf and Caribbean Fisheries Institute (GCFI) meeting in Xel Ha, Mexico, November 2002, immediately prior to legislation being signed. Public hearings on the general and specific plans for the reserves were held and reserve boundaries were negotiated with fishermen. Other countries of the MAR have had less-focused attention, have yet to raise the level of awareness sufficiently in the populace, and are thus still lagging behind Belize on aggregation protection and management. In sum, a multi-organizational collaborative effort with wide public support seems to have been a key element to the successful management of spawning aggregations in Belize.

Directly linked to the idea of human connectivity expressed above, is political connectivity. Scientists and non-governmental organizations (NGOs) have a bad habit of “preaching to the converted” or discussing issues of concern without including key policy makers. In 2002, the Belize Fisheries Department and the Minister of Fisheries, Mr. Dan Silva, were intimately involved with the development of the science, public awareness campaign, and field-training exercises. The Minister himself participated in training exercises at Lighthouse Reef and Glover’s Reef, attended meetings, and met often with patriarch fishermen to discuss their specific concerns (Fig. 9a). In preparation for the signing of legislation, the Minister attended the GCFI meeting in November 2002. Minister Silva delivered the concluding remarks at the spawning aggregation workshop with a historic statement and announcement. He called for bold action by politicians in an era of declining marine resources. He challenged NGOs and scientists to include policy makers more closely in their conservation initiatives, since it is the Minister’s ultimate responsibility to develop and sign legislation. He ended with the announcement of his plan to sign historic legislation, which he did the following day in southern Belize (Fig. 9b), creating a network of protected spawning aggregation sites and a closed season for Nassau grouper (Government of Belize 2003a, b).



**Fig 9.** (a: top) Minister of Fisheries for Belize in 2002, Mr. Dan Silva, seeks guidance from patriarch fishermen as NGO leaders, Fisheries Department Head, and others observe. (b: bottom) Historic legislation signed to protect Nassau grouper and their multi-species spawning aggregation sites.

Based on the experiences in Belize and the Mesoamerican Reef, solid conservation and management rests heavily on physical and biological science, but also requires intensive involvement of stakeholders at all levels, including high-level politicians.

### Summary of Recommendations and Conclusion

It is recommended that resource managers can and should identify, characterize, and protect transient, multi-species spawning aggregation sites and critical nursery grounds for reef fishes. There is an increasing need for regional accords and actions that recognize and embrace human, political, oceanographic, and biological connectivity toward the management of Caribbean marine resources. This paper has identified a variety of research avenues that will be applicable to reef fish management at local, national, and regional scales. The utility of these products will not be immediate, but should be pursued nonetheless. Perhaps most important is to recognize that reef fishes represent common property resources whose ecology transcends physical and political boundaries. Their conservation depends on regional collaboration, policy harmonization, and bold action.

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