

Mesoamerican reef spawning aggregation as sources: A review of the state of connectivity research and future priorities for science and management

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ABSTRACT

The life history of most marine organisms includes an obligate period of pelagic larval dispersal. Migration to spawning areas and pelagic dispersal is 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 scientific review into four sections 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, and it is still 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 their connectivity, are likely to provide an important contribution to reversing the decline in fisheries throughout the Gulf of Mexico and Caribbean Region.

KEYWORDS: transient spawning aggregation, connectivity, marine protected area, reef fish

INTRODUCTION

Caribbean reef-ecosystem-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 areas networks that effectively recognize and protect all of the important taxa and species with all of their varied life history strategies (Roberts, 1997). The task is enormous and well beyond the scope of this review which focuses on reef fish that spawn in transient aggregations as an important example for connectivity studies and their management applications.

Most large Caribbean reef fish species form transient spawning aggregations at specific times and locations (Domeier and Colin, 1997). These fish often produce pelagic larvae that float on ocean currents for weeks, before settling into suitable juvenile habitat (Leis, 1987). Therefore, in order to promote the sustainable use 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).

For these species, where total annual reproductive output occurs locally, the aggregation sites are clearly worthy of protection and management (Johannes, 1999). 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 position. The connectivity between reef fish spawning aggregations and nursery areas is perhaps the most important scientific gap in marine protected areas network designs. Mora and Sale (2002) define connectivity as the demographic connection between populations of species due to the migration of individuals (especially larvae) between them. The goal of this paper is to describe the status of the science of connectivity studies with particular focus on the Mesoamerican Reef (Fig. 1), outline future research needs, and offer recommendations for applications of this research for management in the near and longer term.

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, 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, Carter et al., 1994; Fine, 1990, Aguilar-Perrera and Aguilar-Davila, 1996, Sala et al., 2001).

Intensive fishing at these and other sites have 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, provide documentation of 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 have been documented to spawn there at all times of the year (Fig. 2A) (Heyman 1996; Heyman and Requena 2002; Graham and Castellanos 2003; Heyman et al. 2001; 2005, Heyman unpublished data). Similar examples are found throughout Belize (7 of the 16 documented sites are illustrated in Fig. 2B) as documented by the members of the Belize National Spawning Aggregations Working Committee and Heyman and Requena (2002).

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, Guanaja, Honduras. Claro & Lindeman (2003) provide a comprehensive set of examples from Cuba gathered from fishermen interviews. Many of the Cuban sites documented 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 6 other transient spawning species aggregated for spawning there as well. Riley's Hump in the Dry Tortugas provides a similar example from Florida, known to harbor spawning aggregations of mutton snapper, *Lutjanus analis*, but also several Serranid and Carangid species, similar to Gladden Spit (Peter Gladding, personal communication). Sosa-Cordera et al. (2002) documented 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 following similar seasonal, lunar, and diel patterns 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 suggest a thorough analysis of the timing and location of spawning aggregations throughout the region. Further, there is an urgent need for year-round multi-species characterizations at sites that are known to harbor one species and believed to harbor others. If further support to this hypothesis could be garnered, managers could close 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 (G.o.B. 2003a) and a closed season implement for Nassau grouper during December – March (G.o.B. 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.

Oceanographic and biophysical models applied to connectivity

Constructing realistic hydrodynamic models to study biological connectivity near Caribbean reefs is a challenging task. Models need to include various forcing mechanisms on

different scales such as tides, winds, runoff from rivers, and remote influence from offshore currents and eddies. The 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 the tidal currents along the reef represent only a relatively small portion of the 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 barrier reef are often uncorrelated 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; Sheng and Tang, 2003; Oey et al., 2003; Ezer et al., 2003, 2005; Romanou et al., 2004; Richardson, 2005).

Modeling the impact of eddies on the flow and biological connectivity near the MBRS 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 MBRS and its connection with the western Caribbean Sea used a z-level model with a high-resolution nesting (Sheng and Tang, 2004; Tang et al., 2006) and in another case a terrain-following model with a curvilinear grid (Ezer et al., 2005), which also includes assimilation of eddies. However, some model deficiencies still remain unresolved, as suggested later in this review.

Below are examples that aim to 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 the Gulf of Honduras (GOH). On top of the seasonal cycle (associated with the thermal structure of the upper ocean), one can see a higher frequency variability (associated with mesoscale eddies) that dominate the record. Interannual 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 4 years), but further research to understand those variations and the possible consequences for coral reef connectivity are needed.

An example of the westward propagation of cyclonic (low SSHA) and anticyclonic (high SSHA) is shown in Fig. 4; a similar pattern of eddies with irregular frequency appears throughout the 13 years 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 Lagoon). On the other hand, if an anticyclonic anomaly 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.

While there are no observations to verify the model results, the simulations clearly demonstrate the crucial role played by eddies in affecting biological connectivity. Note that dispersion calculations conducted by Tang et al. (2006) using seasonal forcing (but no eddy assimilation) show quite different patterns than 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 discrepancy in the coastal flows between the two models. These studies emphasize the need for coordinated efforts to compare between different 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 climatic changes and its influence on the local circulation can also provide useful insights. Finally, and most importantly are the new efforts that couple physical models with biological aspects of the larvae to study biophysical aspects of connectivity (e.g., Paris and Cowen, 2004; Cowen et al. 2006, Paris et al. 2004; 2005; Warner et al., 2000; Tang et al. 2006; Sheng et al. 2004).

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 visible 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 WCS model output indicate a potential physical barrier to connectivity between the northern and southern MBRS (Fig. 6).

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 the 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 the 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 mechanisms for the near-reef currents. Unfortunately, there is seldom available a sufficient number and extent of appropriate physical time series and drifter data for effective model validation, and although there usually is an abundance of satellite imagery, long duration between sequential overpasses, large ground pixels/swaths, and the presence of clouds usually means that the satellite imagery by itself should never be used as a sole source for connectivity model validation.

Thus, a solid understanding of the local physical oceanography and flow variability at the spawning aggregation sites and along the adjacent MesoAmerican barrier reef is essential for successful connectivity modeling. In the case of the MesoAmerican barrier reef, time series current measurements have been conducted intermittently 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 local bottom. The locations 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 towards the north or south with speeds 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 is show 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 Figs. 7a and 7b 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 course bathymetric data which may influence their results. Accurate bathymetric data is particularly important at the time and location of spawning aggregation sites, as it influences the initial trajectory of spawned materials. 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 (Figs. 2a, 8a,b). Surveys of detailed small-scale topography (e.g. Ecochard et al., 2003a, b; Heyman et al., in press) can be incorporated into very high-resolution numerical models to study the local circulation near fish aggregation sites. In addition to direct measurement of sea-bottom with single beam echosounders 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 to incorporate into biophysical models of connectivity.

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 towards 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 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).

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 the 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 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, the connectivity between various populations. Most important are otolith microchemistry and marking larvae with radio isotopes.

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. Salient and Gold, 2005; Kuhner et al., 1995).

These type 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 MBRS 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 each side 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 each side 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 the otoliths illustrate specific chemical signals of water bodies through which they travel from spawning to recruitment (Swearer et al., 1999; Jones et al., 1999, Thorrold et al., 2002; Rooker and Secor, 2005). A promising new approach for empirical connectivity studies is based on marking larvae with radio isotopes. Larval otoliths can be tagged with radio isotopes by injecting the 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 for Caribbean ecosystem management. We predict that within 10 years, networks of marine reserves will be designed with extensive use of the research reviewed within this paper. With an extensive regional management program already in place and a great deal of modeled and empirical data already collected, the MBRS region provides an excellent site to test these relatively new techniques and their applications in management.

Summarizing the needs for priority observations and research, we submit the following:

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 species and taxa and identify barriers to and corridors that enhance connectivity
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 data – altimeter and ocean color particularly
9. reduce grid size of biophysical models

Human Connectivity

In analyzing the lessons learned from experiences in the conservation and management of spawning aggregation sites as sources in the Mesoamerican Reef, we found that the human component was critically important. The efforts that lead to national closure of 11 sites involved myriad fishermen and technicians in the collection and analysis of data. It is 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 meeting in Xel Ha, 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 populous 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 to the successful management of spawning aggregations as sources in Belize.

Political Connectivity

Directly linked to the idea of human connectivity expressed above, is political connectivity. Scientists and NGOs have a bad habit of “preaching to the converted” or discussing issues of concern without including key policy makers. The Belize Fisheries Department and the Minister of Fisheries in 2002, Mr. Dan Silva, was intimately involved with the development of the science, public awareness raising, involvement of fishermen, and training exercises. The Minister himself participated in training exercises in 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 GCFI and spoke at the podium to conclude the spawning aggregation workshop in November 2002 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 processes, 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 at the Fishermen’s Festival the following day in Southern Belize. . . and he did! (Fig. 9b).

SUMMARY OF RECOMMENDATIONS AND CONCLUSION

It is recommended that resource managers can and should identify and protect multi-species spawning aggregations and critical nursery grounds for reef fishes. In conclusion, there is an increasing need for regional accords and actions that recognize and embrace human, political, oceanographic, and biological connectivity towards the management of Caribbean marine resources. This paper has identified a variety of research avenues that will produce results that will be applicable to reef fish management at local, national, and regional scales. The timing of 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 transcend physical and political boundaries. Their conservation depends on regional collaboration and policy harmonization.

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LITERATURE CITED

- Aguilar-Perrera, A., and W. Aguilar-Dávila. 1996. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), in the Mexican Caribbean. *Environmental Biology of Fishes* 45:351-361.
- Andréfouët, S., P.J. Mumby, M. McField, C. Hu, F.E. Müller-Karger. 2002. Revisiting coral reef connectivity. *Coral Reefs* 21: 43-48.
- Armstrong, B. N. 2003. Currents along the Mesoamerican Barrier Reef, Western Caribbean. M.S. Dissertation, University of South Carolina.
- Candela, J., S. Tanahara, M. Crepon, B. Barnier and J. Sheinbaum. 2003. Yucatan Channel flow: observations versus CLIPPER ATL6 and MERCATOR PAM models. *Journal of Geophysical Research* 108(C12): doi: 10.1029/2003JC001961.
- Carter, J., G.J. Marrow, and V. Pryor. 1994. Aspects of the ecology and reproduction of Nassau grouper, *Epinephelus striatus*, off the coast of Belize, Central America. *Gulf and Caribbean Fisheries Institute* 43: 64-111.
- Carton, J. A. and Y. Chao, 1999. Caribbean Sea eddies inferred from TOPEX/POSEIDON altimetry and a 1/6° Atlantic Ocean model simulation. *Journal of Geophysical Research* 104(C4): 7743-7752, doi: 10.1029/1998JC900081.
- Claro, R. and K.C. Lindeman. 2003. Spawning aggregation sites of snapper and grouper species (Lutjanidae and Serranidae) on the insular shelf of Cuba. *Gulf and Caribbean Research Institute* 14(2): 91-106.
- Coleman, F.C., C.C. Koenig, G.R. Huntsman, J.A. Musick, A.M. Eklund, J.C. McGovern, R.W. Chapman, G.R. Sedberry, and C.B. Grimes. 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries* 25(3): 14-21.
- Cowen, R. K., K.M.M. Lwiza, S. Sponaugle, C.B. Paris, and D.B. Olson. 2000. Connectivity of marine populations: open or closed? *Science* 287: 857-859.
- Cowen R.K., C.B. Paris CB and A. Srinivasan. 2006. Scaling connectivity in marine populations, *Science* 311: 522-527.
- Domeier, M.L and P.L. Colin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. *Bulletin of Marine Science* 60(3): 698-726.
- Ducet, N., P.Y. Le Tron, and G. Reverdin. 2000. Global high-resolution mapping of ocean circulation from TOPEX/Poseidon and ERS-1 and -2. *Journal of Geophysical Research* 105(C8): 19,477-19,498, doi: 10.1029/2000JC900063.
- Ecochard, J.L.B., W.D. Heyman, N. Requena, and E. Cuevas. 2003a. *Adaptive Bathymetric System (ABS)*. The Nature Conservancy. Arlington, VA. Available at: www.conserveonline.org.
- Ecochard, J.L.B., W.D. Heyman, N. Requena, E. Cuevas, and F.B. Biasi. 2003b. *Case Study: Mapping Half Moon Caye's Reef Using the Adaptive Bathymetric System (ABS)*. The Nature Conservancy. Arlington, VA. Available at: www.conserveonline.org.
- Ezer, T. and G.L. Mellor. 2000. Sensitivity studies with the North Atlantic sigma coordinate Princeton Ocean Model, *Dyn. Atmos. Ocean*, 32: 185-208.
- Ezer T., L.-Y. Oey, H.-C. Lee and W. Sturges. 2003. The variability of currents in the Yucatan Channel: Analysis of results from a numerical ocean model. *Journal of Geophysical Research* 108(C1), 3012, doi: 10.1029/2002JC001509.

- Ezer, T., D.V. Thattai, B. Kjerfve and W. Heyman. 2005. On the variability of the flow along the Meso-American Barrier Reef System: A numerical model study of the influence of the Caribbean Current and eddies. *Ocean Dynamics*. 55: 458-475.
- Fine, J.C. 1990. Groupers in love: spawning aggregations of Nassau groupers in Honduras. *Sea Frontiers* 36, 42-45.
- Government of Belize (G.o.B). 2003a. Statutory Instrument No. 161 of 2003. Fisheries (Spawning Aggregation Site Reserves) Order, 2003. 161, 1-8.
- Government of Belize (G.o.B). 2003b. Statutory Instrument No. 161 of 2003. Fisheries (Nassau Grouper Closed Season) Order, 2003,
- Graham, R.T. and D.W. Castellanos. 2005. Courtship and spawning of Carangid species in Belize. *Fishery Bulletin* 103: 426- 432.
- Hey, J. and R. Nielsen. 2004. Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. *Genetics* 167: 747-760.
- Heyman, W.D. 1996. *Integrated coastal zone management and sustainable development for tropical estuarine ecosystems: A case study of Port Honduras, Belize*. Ph.D. dissertation. University of South Carolina, Columbia, SC.
- Heyman, W.D., J-L.B. Ecochard, and F.B. Biasi. Low-cost bathymetric mapping for tropical marine conservation – a focus on reef fish spawning aggregation sites. *Marine Geodesy* in press.
- Heyman, W.D., R.T. Graham, B. Kjerfve, and R.E. Johannes. 2001. Whale sharks, *Rhincodon typus*, aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series* 215: 275-282.
- Heyman, W.D., B. Kjerfve, K.L. Rhodes, R.T. Graham, and L. Garbutt. 2005. Cubera snapper, *Lutjanus cyanopterus*, spawning aggregations on the Belize Barrier Reef over a six year period. *Journal of Fish Biology* 67: 83-101.
- Heyman, W.D. and N. Requena. 2002. Status of multi-species spawning aggregations in Belize. The Nature Conservancy. Arlington, Virginia. www.conserveonline.org.
- Hu, C., E.T. Montgomery, R.W. Schmitt and F.E. Muller-Karger. 2004. The dispersal of the Amazon and Orinoco River water in the tropical Atlantic and Caribbean Sea: Observation from space and S-PALACE floats. *Deep-Sea Research II*, 51: 1151-1171.
- Intelman, S.S. 2006. Comments on the hydrographic and topographic LIDAR acquisition and merging with multibeam sounding data acquired in the Olympic Coast National Marine Sanctuary. Marine Sanctuaries Conservation Series ONMS-06-05. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Sanctuary Program, Silver Spring, MD.
- Johannes, R.E. 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends in Ecology & Evolution* 13(6): 243-246.
- Jones, G.P., M.J. Milicich, M.J. Emslie and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature* 402: 802-804.
- Kingsford, M.J., J.M. Leis, A. Shanks, K.C. Lindeman, S.G. Morgan, and J. Pineda. 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* 70(1) Suppl. 309-340.
- Kjerfve, B. 1981. Tides of the Caribbean Sea. *Journal of Geophysical Research* 86(C5):4243-4247.

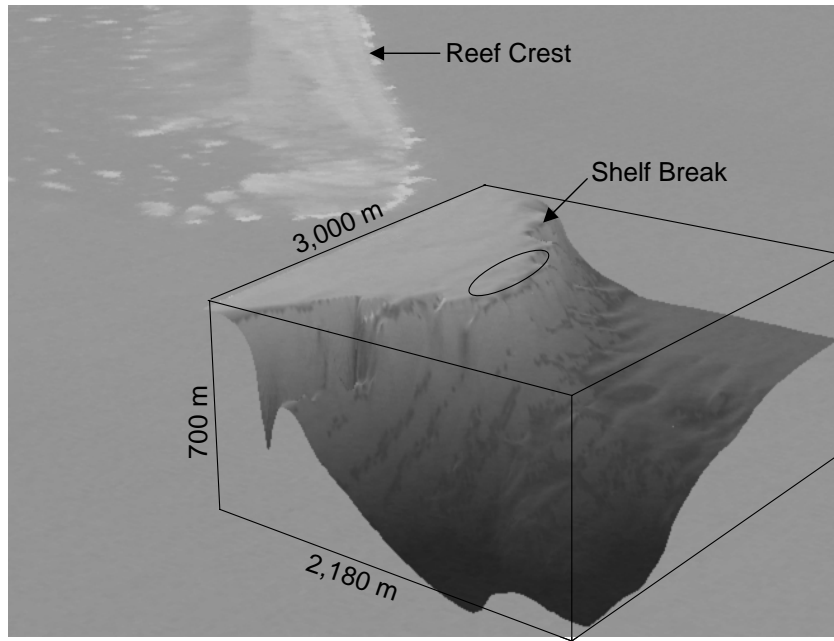
- Kuhner, M.K., J. Yamato and J. Felsenstein. 1995. Estimating effective population size and mutation rate from sequence data using Metropolis-Hastings sampling. *Genetics* 140: 1421-1430.
- Leis, J.M. 1987. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). In *Tropical Snappers and Groupers* (Polovina, J.J. & Ralston, S., eds.), pp. 189-238. Boulder, CO: Westview Press.
- Leis, J.M. and R. Fisher. 2006. Swimming speed of settlement-stage reef-fish larvae measured in the laboratory and in the field: a comparison of critical speed and in situ speed. In: Y. Suzuki, T. Nakamori, M. Hidaka, H. Kayanne, B.E. Casareto, K. Nadaoka, H. Yamano and M. Tsuchiya (eds) *Proceedings of the 10th International Coral Reef Symposium, Okinawa* 438-445.
- MacDonald, A. 2005. New developments increase use of airborne LIDAR bathymetry. *Sea Technology* September: 46-48.
- Mora, C. and P. Sale. 2002. Are populations of coral reef fish open or closed? *Trends in Ecology and Evolution* 17: 422-428.
- Murphy S. J., H. E. Hulbert and J. J. O'Brien, 1999. The connectivity of eddy variability in the Caribbean Sea, the Gulf of Mexico, and the Atlantic Ocean. *Journal of Geophysical Research* 104(C1): 1431-1453, doi: 10.1029/1998JC900010.
- Oey L.-Y., H.-C. Lee and W. J. Schmitz, 2003. Effects of winds and Caribbean eddies on the frequency of loop current eddy shedding: A numerical model study. *Journal of Geophysical Research* 108(C10): 3324, doi: 10.1029/2002JC001698.
- Oey, L.-Y., T. Ezer, D.-P. Wang, S.-J. Fan and X-Q. Yin, 2006. Loop Current warming by hurricane Wilma. *Geophysical Research Letters* 33, L08613, doi: 10.1029/2006GL025873.
- Oey, L.-Y., T. Ezer, D.-P. Wang, X-Q. Yin and S.-J. Fan, 2007. Hurricane-induced motions and interaction with ocean currents. *Continental Shelf Research*. In press.
- Paris, C.B. and R.K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography* 49(6): 1964-1979.
- Paris, C.B., R.K. Cowen, R. Claro and K.C. Lindeman. 2005. Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. *Marine Ecology Progress Series* 296: 93-106.
- Richardson, P.L., 2005. Caribbean Current and eddies as observed by surface drifters. *Deep-Sea Research* 52:429-463.
- Roberts, C.M. 1997. Connectivity and the management of Caribbean coral reefs. *Science* 278(5342): 1454-1457, doi 10.1126/science.278.5342.1454.
- Romanou, A., E.P. Chassignet and W. Sturges, 2004. The Gulf of Mexico circulation within a high resolution numerical simulation of the North Atlantic Ocean. *Journal of Geophysical Research* 109, CO1003, doi: 10.1029/2003CJ001770.
- Rooker J.R and D.H. Secor (eds.). 2005. Connectivity in the life cycles of fishes and invertebrates that use estuaries. *Estuarine, Coastal and Shelf Science* 64:1-148.
- Sadovy, Y. 1994. Grouper stocks of the western central Atlantic: the need for management and management needs. *Proceedings of the Gulf and Caribbean Fisheries Institute* 43:43-64.
- Saillant, E. and J.R. Gold. 2005. Population structure and effective size of Gulf red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico. *Fishery Bulletin* 104(1):136-148.

- Sala, E., R. Starr, and E. Ballesteros. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* 26(10):23-30.
- Sheng J. and L. Tang. 2003. A numerical study of circulation in the western Caribbean Sea. *Journal of Physical Oceanography* 33: 2049-2069.
- Sheng J. and L. Tang, 2004. A two-way nested-grid ocean circulation model for the Meso-American Barrier Reef System. *Ocean Dynamics* 54: 232-242.
- Sosa-Cordero, E., A. Medina-Quej, R. Herrera, and W. Aguilar-Dávila. 2002. Agregaciones reproductivas de peces en el Sistema Arrecifal Mesoamericano: Consultoría Nacional – Mexico. Informe preparado para el consultor internacional, Research Planning Inc., y Proyecto SAM-Banco Mundial-Belice.
- Sponaugle, S., R.K. Cowen, A. Shanks, S.G. Morgan, J.M. Leis, J. Pineda, G.W. Boehlert, M.J. Kingsford, K.C. Lindeman, C. Grimes, and J.L. Munro. 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. *Bulletin of Marine Science* 70(1) Suppl.: 341-375.
- Swearer, S.E., J.E. Caselle, D.W. Lea, and R.R. Warner. 1999. Larval retention and recruitment in an island population of coral reef fish. *Nature* 402:799-802.
- Tang, L., J. Sheng, B.G. Hatcher and P.F. Sale. 2006. Numerical study of circulation, dispersion, and hydrodynamic connectivity of surface waters on the Belize shelf. *Journal of Geophysical Research* 111, C01003, doi:10.1029/2005JC002930.
- Taylor, M.S. and M.E. Hellberg. 2003. Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* 299: 107-109.
- Thattai, D.V. 2003. Modeling the hydrometeorology and circulation in the Gulf of Honduras and the Mesoamerican Lagoon, western Caribbean. PhD Dissertation, Department of Geological Sciences, University of South Carolina, 122 pp.
- Thattai, D., B. Kjerfve and W. D. Heyman. 2003. Hydrometeorology and variability of water discharge and sediment load in the inner Gulf of Honduras, Western Caribbean. *Journal of Hydrometeorology* 4: 985-995.
- Thorrold, S.R., G.P. Jones, M.E. Hellberg, R.S. Burton, S.E. Swearer, J.E. Neigel, S.G. Morgan, and R.R. Warner. 2002. Quantifying larval retention and connectivity in marine populations with artificial and natural markers. *Bulletin of Marine Science* 70(1) Supplement: 291-308.
- Warner, R.R., S.E. Swearer, and J.E. Caselle. 2000. Larval accumulation and retention: implications for the design of marine reserves and essential fish habitat. *Bulletin of Marine Science* 66(3): 821-830.
- Whaylen, L, C.V. Pattengill-Semmens, B.X. Semmens, P.G. Bush, and M.R. Boardman. 2004. Observations of a Nassau grouper, *Epinephelus striatus*, Spawning Aggregation Site in Little Cayman, Cayman Islands, Including Multi-Species Spawning Information. *Environmental Biology of Fishes* 70(3): 305-313. doi:10.1023/B:EBFI.0000033341.57920.a8
- Wright, J.M. and P. Bentzen. 1994. Microsatellites: genetic markers for the future. *Reviews in Fish Biology and Fisheries* 4: 384-388.



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

(a)



(b)

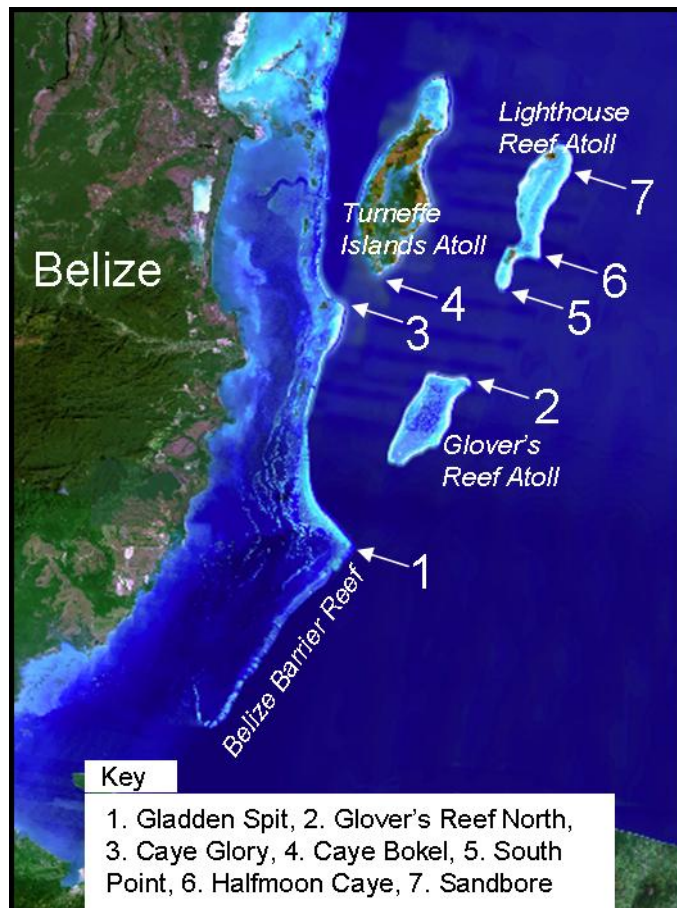


Fig. 2. (a) Gladden Spit, showing the location of the multi-species spawning aggregations in relation to the shelf break and the bend in the reef (from Heyman et al., 2006) (b). The locations of 7 documented multi-species spawning aggregation sites in Belize.

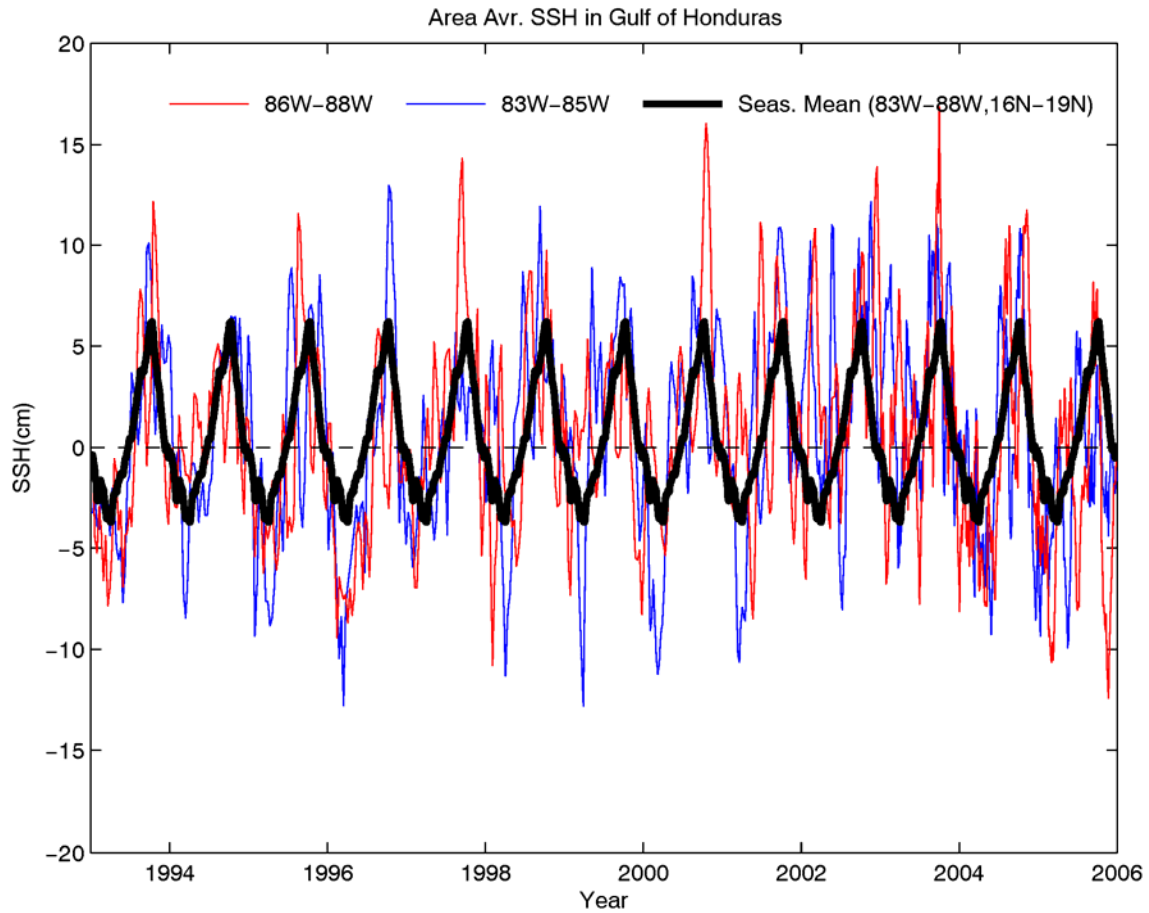


Fig. 3. Time series of sea surface height anomalies from satellite altimeter data averaged over the western (red line) and mid (blue line) GOH. The mean seasonal cycle averaged over the 13-year record is indicated by the heavy line. The fact that the two sub-regions are out of phase with each other is due to the propagation of eddies from one region to another.

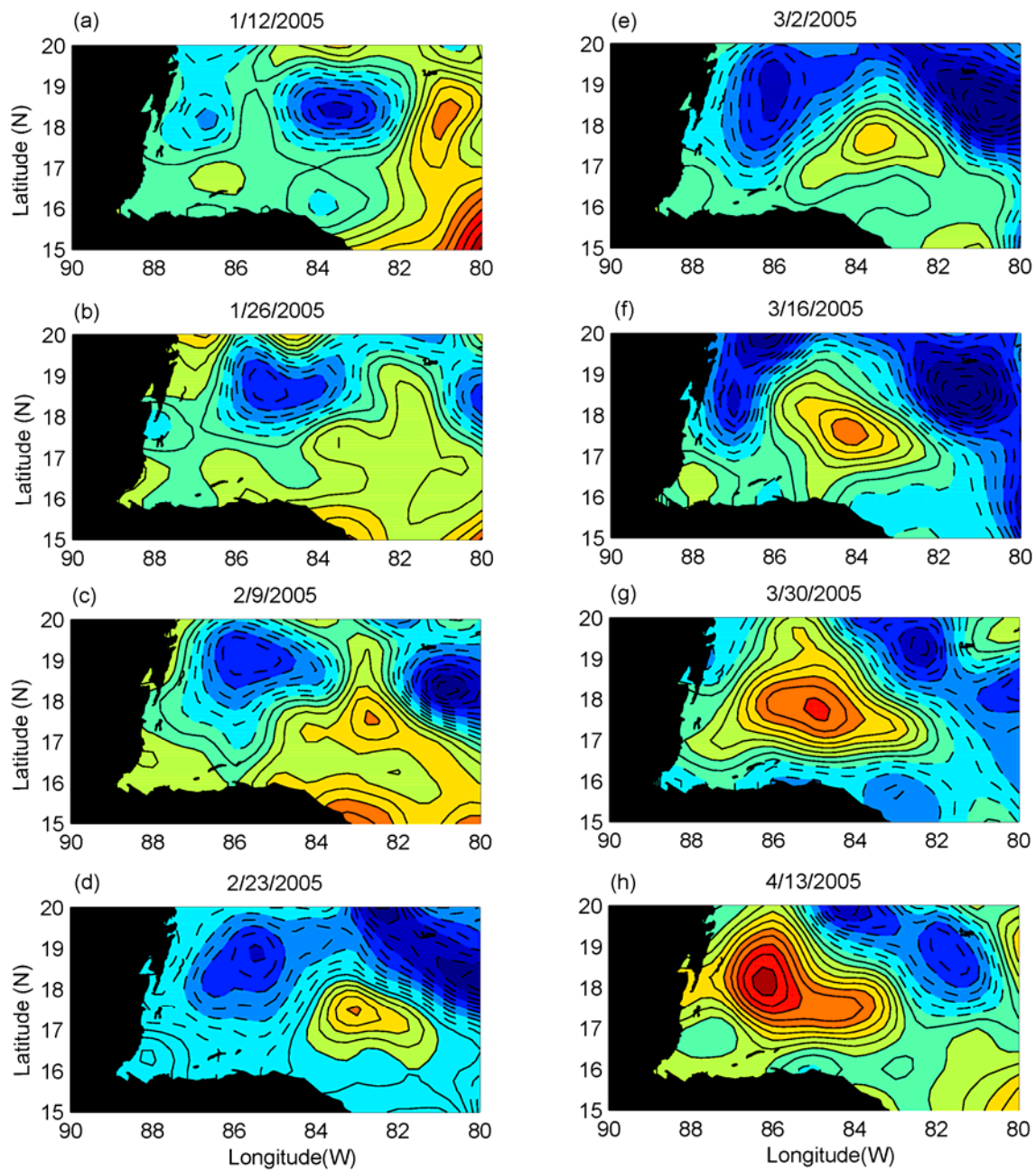


Fig. 4. Sea surface height anomaly from altimeter data in the GOH. The 2-weekly images demonstrate the westward propagation of cyclonic (negative/blue SSHA, a-d) and anticyclonic (positive/red SSHA, e-h) features. Contour interval is 2 cm.

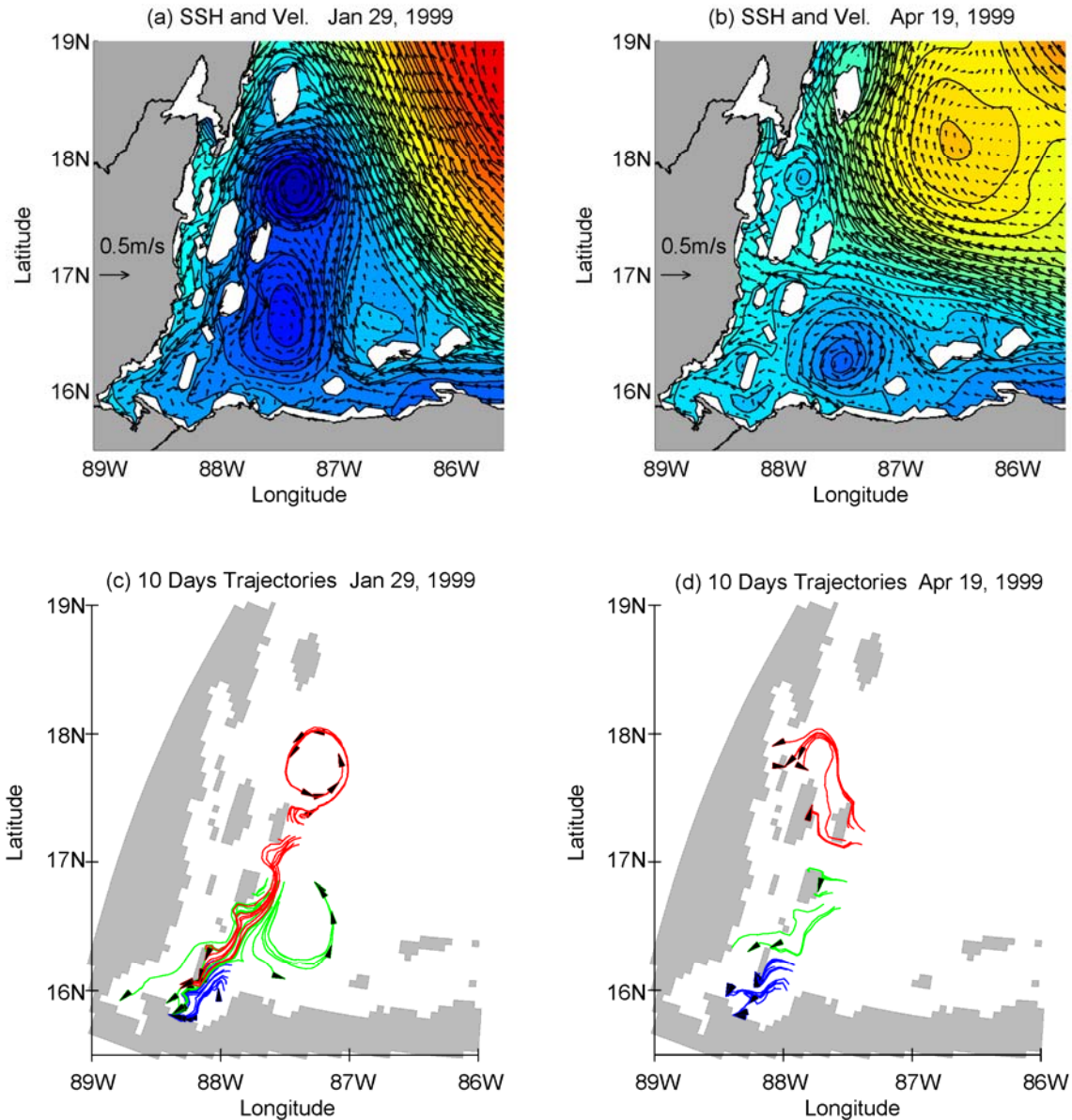


Fig. 5. Model simulations (Ezer et al., 2005) of sea surface height (blue/red for low/high) and surface velocity for (a) January and (b) April, 1999, when a cyclonic and an anticyclonic anomalies, respectively, were observed near the MBRs. (c) and (d) show the trajectories of passive tracers released 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.

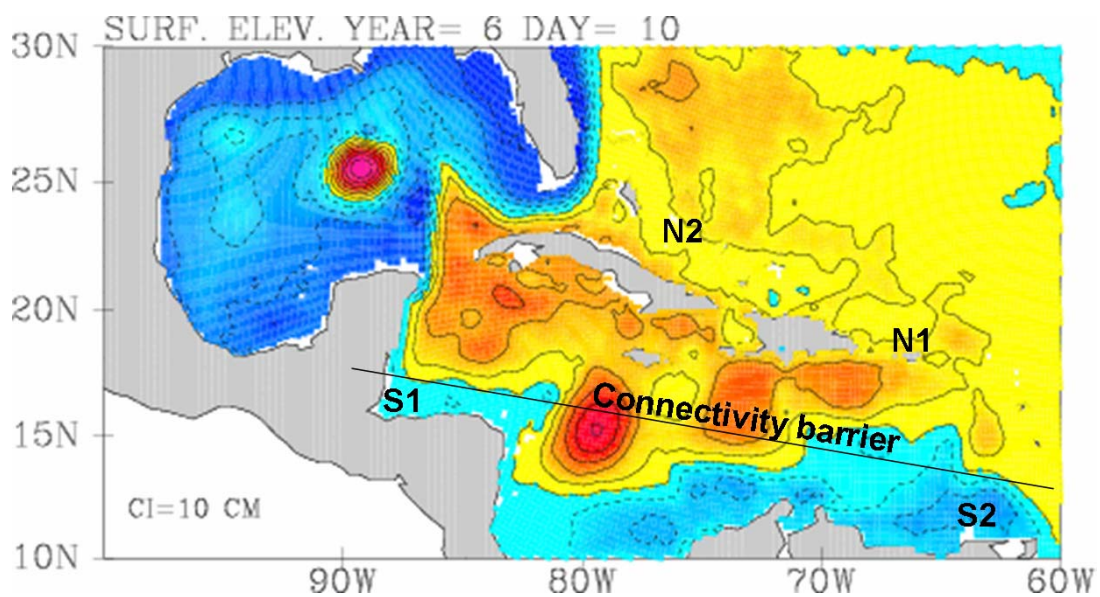


Fig. 6. Shown is an example of a synoptic sea surface height field with blue/red shades represent low/high values (from the Ezer and Mellor, 2000 model). A barrier to connectivity may be created along the MBRS where cyclonic eddies diverge from anti-cyclonic eddies. Inter-reef connectivity is likely 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.

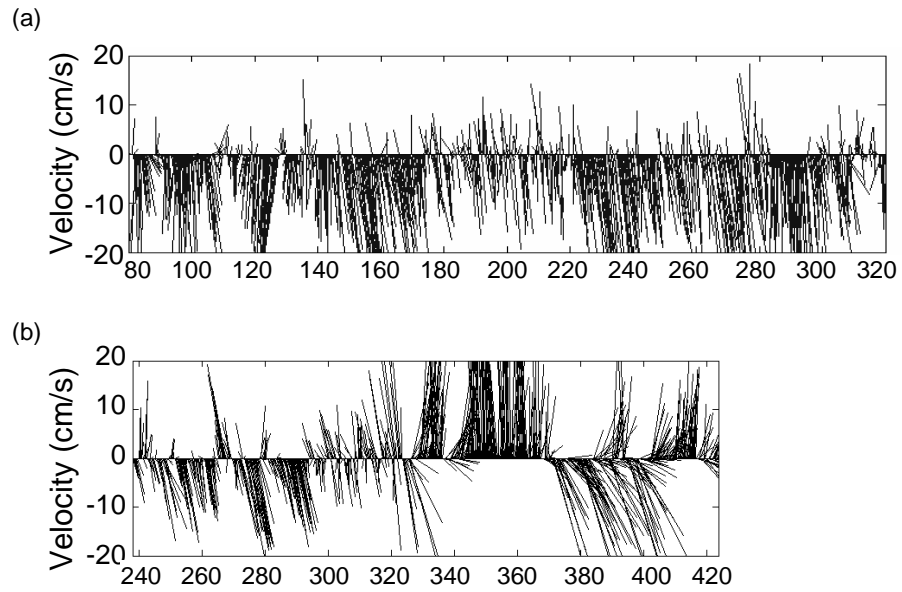


Fig. 7. Stick diagrams showing the measured speed and direction of currents at the shelf break at 26m depth at (a) Gladden Spit, Day 80-30 in 2000 and (b) Lighthouse Reef Atoll, Day 240 in 2000 until day 80 in 2001.

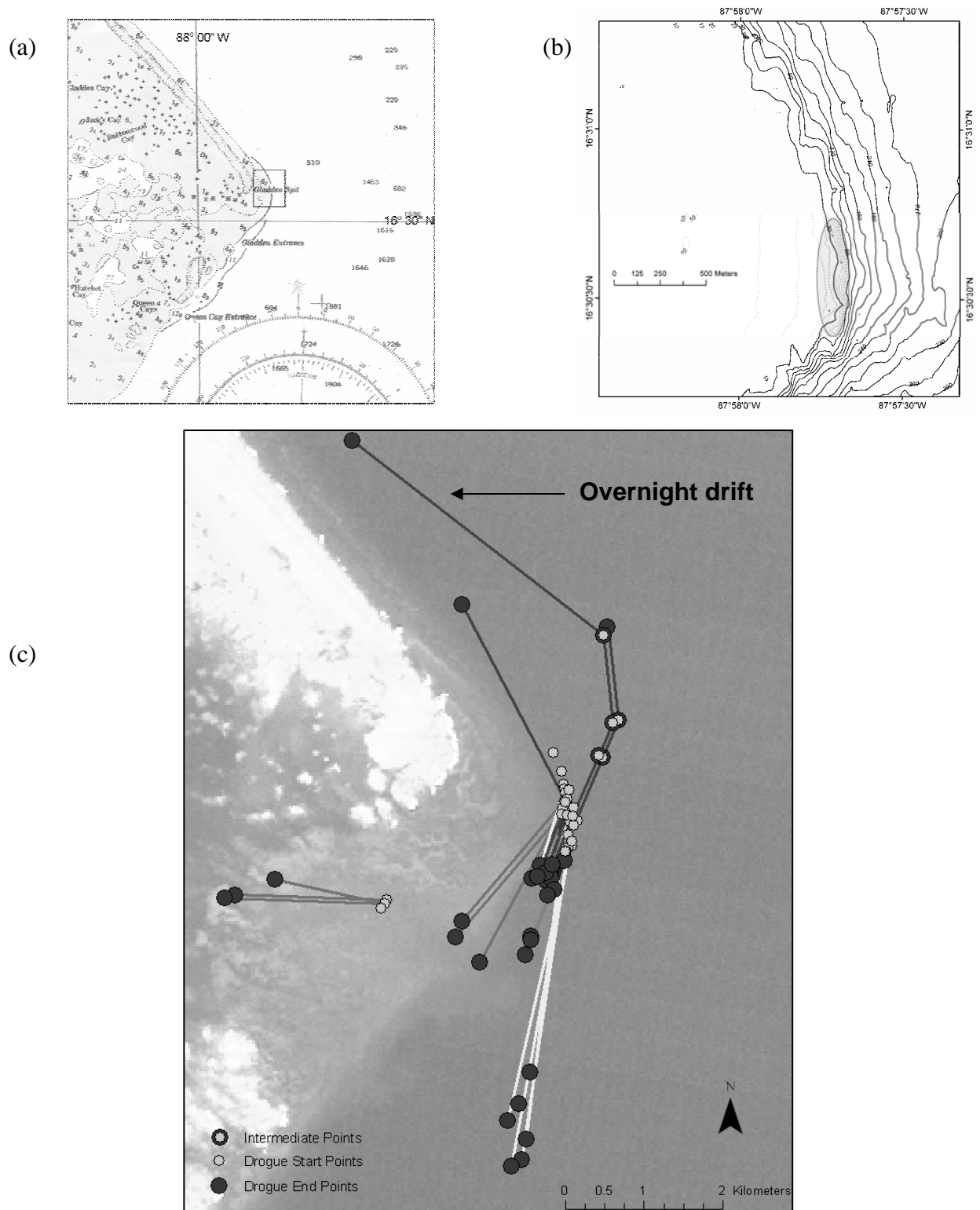


Fig. 8. (a) Bathymetric chart of Gladden Spit. (b) Detailed bathymetry derived from inexpensive mapping efforts (Heyman et al. in press) (c) Drogues (modeling eggs) move away from spawning site in multiple directions illustrating the initial trajectory of spawned materials.

(a)



(b)

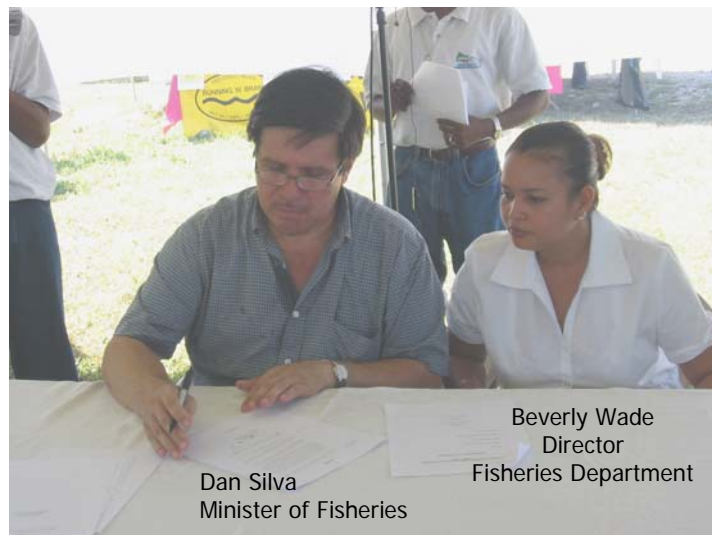


Fig 9. (a) Minister of Fisheries for Belize in 2002, Mr. Dan Silva, seeks guidance from patriarch fishermen as NGO leaders, Fisheries Department Head and others observe. (b) Historic legislation signed to protect Nassau grouper and their multi-species spawning aggregation sites.