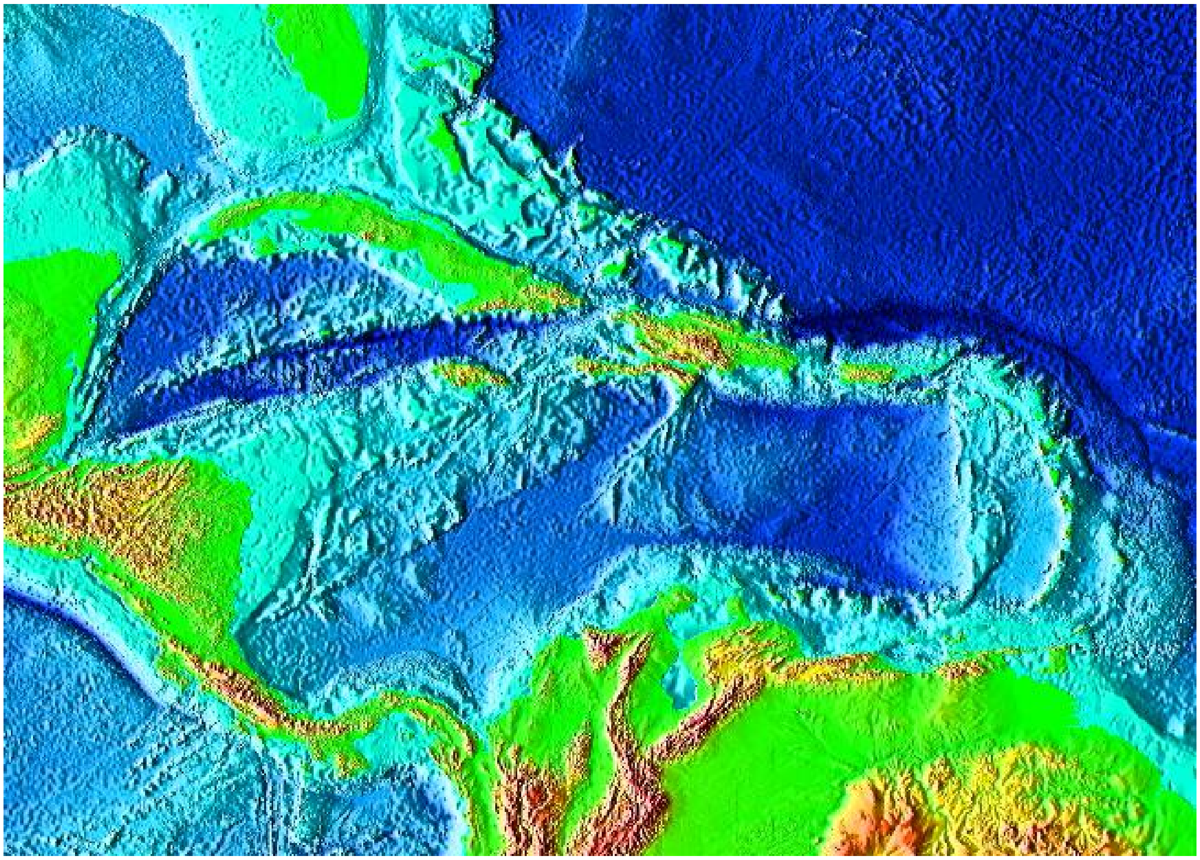
Marine Sanctuaries Conservation Series ONMS-08-07

Caribbean Connectivity: Implications for Marine Protected Area Management



Proceedings of a Special Symposium
9-11 November 2006
59th Annual Meeting of the Gulf and Caribbean Fisheries Institute
Belize City, Belize

U.S. Department of Commerce
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Office of National Marine Sanctuaries

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About the Marine Sanctuaries Conservation Series

The National Oceanic and Atmospheric Administration's National Ocean Service (NOS) administers the Office of National Marine Sanctuaries (ONMS). Its mission is to identify, designate, protect and manage the ecological, recreational, research, educational, historical, and aesthetic resources and qualities of nationally significant coastal and marine areas. The existing marine sanctuaries differ widely in their natural and historical resources and include nearshore and open ocean areas ranging in size from less than one to over 5,000 square miles. Protected habitats include rocky coasts, kelp forests, coral reefs, sea grass beds, estuarine habitats, hard and soft bottom habitats, segments of whale migration routes, and shipwrecks.

Because of considerable differences in settings, resources, and threats, each marine sanctuary has a tailored management plan. Conservation, education, research, monitoring and enforcement programs vary accordingly. The integration of these programs is fundamental to marine protected area management. The Marine Sanctuaries Conservation Series reflects and supports this integration by providing a forum for publication and discussion of the complex issues currently facing the sanctuary system. Topics of published reports vary substantially and may include descriptions of educational programs, discussions on resource management issues, and results of scientific research and monitoring projects. The series facilitates integration of natural sciences, socioeconomic and cultural sciences, education, and policy development to accomplish the diverse needs of NOAA's resource protection mandate.

Caribbean Connectivity:
Implications for Marine Protected Area Management

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COVER

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, 59th 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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Executive Summary

Tropical marine ecosystems in the Caribbean region are inextricably linked through the movement of pollutants, nutrients, diseases, and other stressors, which threaten to further degrade coral reef communities. The magnitude of change that is occurring within the region is considerable, and solutions will require investigating pros and cons of networks of marine protected areas (MPAs), cooperation of neighboring countries, improved understanding of how external stressors degrade local marine resources, and ameliorating those stressors.

Connectivity can be broadly defined as the exchange of materials (e.g., nutrients and pollutants), organisms, and genes and can be divided into: 1) genetic or evolutionary connectivity that concerns the exchange of organisms and genes, 2) demographic connectivity, which is the exchange of individuals among local groups, and 3) oceanographic connectivity, which includes flow of materials and circulation patterns and variability that underpin much of all these exchanges. Presently, we understand little about connectivity at specific locations beyond model outputs, and yet we must manage MPAs with connectivity in mind. A key to successful MPA management is how to most effectively work with scientists to acquire the information managers need.

Oceanography connectivity is poorly understood, and even less is known about the shape of the dispersal curve for most species. Dispersal kernels differ for various systems, species, and life histories and are likely highly variable in space and time. Furthermore, the implications of different dispersal kernels on population dynamics and management of species is unknown. However, small dispersal kernels are the norm - *not* the exception. Linking patterns of dispersal to management options is difficult given the present state of knowledge.

The behavioral component of larval dispersal has a major impact on where larvae settle. Individual larval behavior and life history details are required to produce meaningful simulations of population connectivity. Biological inputs are critical determinants of dispersal outcomes beyond what can be gleaned from models of passive dispersal.

There is considerable temporal and spatial variation to connectivity patterns. New models are increasingly being developed, but these must be validated to understand upstream-downstream neighborhoods, dispersal corridors, stepping stones, and source/sink dynamics. At present, models are mainly useful for providing generalities and generating hypotheses. Low-technology approaches such as drifter vials and oceanographic drogues are useful, affordable options for understanding local connectivity.

The "silver bullet" approach to MPA design may not be possible for several reasons. Genetic connectivity studies reveal divergent population genetic structures despite similar larval life histories. Historical stochasticity in reproduction and/or recruitment likely has important, long-lasting consequences on present day genetic structure.

Within the region, there are several important bio-geographic boundaries such as the mouth of the Amazon basin and the Mona Passage. Several species have similar dispersal potential, but

varying genetic structures; the genetic breaks in different geographic locations indicates that larval duration, geographic distributions, and oceanographic currents are poor predictors of population structure. There is increasing evidence of local-scale larval retention. Empirical studies suggest that connectivity may be more localized than previously thought.

The Caribbean region shares common threats such as tourism, sewage, overdevelopment, cruise ships, and movement of organisms. Stressors to marine communities in the region can only be managed by working together to build bridges of understanding by supporting research and discussion on this important topic. Connecting scientists and managers will require engaging in tactical, specific actions involving panmixis of disciplines and new standards for conservation products.

Because seascapes outside of MPAs are degraded by habitat loss, sewage, and coastal development, connectivity is rarely on the minds of most MPA managers. Rather, managing for localized stressors typically dominates agendas, but to effectively conserve marine ecosystems Caribbean-wide will require reaching across borders.

Knowledge of connectivity will help in deciding whether to create a single large or several small MPAs in a particular location. In complex seascapes, species are flexible in their use of habitat. Some have ontogenetic migrations where different habitats are used at different stages of their life. Habitat use is variable across families and species, with cross-shelf location as well as habitat type often being important in determining the distribution of reef fishes.

Many species depend upon nursery habitats during early life history, but this is not always an obligate relationship. The relative importance of nursery habitats to sustain reef fish populations is not known. Therefore, it is difficult to estimate the minimum nursery area required to conserve populations. Acquiring direct information on the importance of particular habitats for various species is often difficult, though advancements in techniques such as acoustic tagging and stable isotope ratios are improving our ability to understand demersal connectivity. Reef fishes move from inside to outside the boundaries of MPAs. Movement of fishes is influenced by the underlying seascape, with certain habitat features appearing to act as inhibitors to movement.

The ability of an ecosystem to recover from disturbance may be influenced by habitat connectivity. Ontogenetic mechanisms of ecosystem connectivity may increase the resilience of Caribbean reefs to climate-induced changes such as hurricane disturbance. Particular habitats such as seagrass and mangrove may play a functional role in maintaining connectivity in the Caribbean.

Protection of multi-species spawning aggregations throughout the Caribbean region is recommended. Spawning aggregations are extremely vulnerable to overfishing. Scientific evidence suggests that spawning locations may function to retain larvae; if so, then spawning aggregations should be managed as separate stocks.

Contents

Introduction

Rikki Grober-Dunsmore[1] **and Brian D. Keller**[2]

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Understanding connectivity among coral reef ecosystems is fundamental to conserving marine biodiversity and fisheries resources in the Caribbean. Because many marine protected areas (MPAs) are envisioned to enhance and conserve marine ecosystems on a scale larger than their boundaries, improving our knowledge of how connectivity functions and the implications of connectivity across time scales, spatial scales, and species is crucial for managing MPAs. However, connectivity is poorly understood and little is known about gene flow or the transport of diseases, nutrients, and sediments throughout the region. Consequently, predicting the effects of MPAs on local and regional populations is challenging. Strong connectivity among areas implies that local populations and conditions may depend on processes occurring elsewhere. If this is the case, local management initiatives may be ineffective in providing localized benefits, and an increase in the scale of management may be necessary. If connectivity across large spatial scales is the norm, then populations may straddle political boundaries and stressors emanating from one country may have negative consequences on ecosystems in another country. The development of management strategies to ensure region-wide sustainability of marine ecosystems is complex and will require input from fisheries scientists, oceanographers, resource managers, and fishers in the Caribbean and Gulf of Mexico.

The purpose of this symposium was to share cross-cutting research and management approaches for understanding biological connectivity in the Caribbean Sea and Gulf of Mexico and to provide a forum for resource managers and the academic community to address questions on how to apply scientific information to better manage MPAs in the region. The primary goals of the symposium were to 1): provide a forum for information-sharing and feedback between scientists conducting research on marine connectivity and resource managers who are managing resources at a local or regional scale, 2) provide hands-on training opportunities in technologies and approaches for predicting connectivity in the Caribbean region, and 3) provide a synthesis of the information available and future research recommendations on Caribbean connectivity at local and regional spatial scales.

This three-day symposium included of two keynote speakers (*Billy Causey* and *Peter Sale*), five invited theme speakers (*Bob Cowen*, *Iliana Baums, Georgina Bustamante, Rich Appeldoorn,* and *Will Heyman*), and contributed oral and poster presentations. A poster session was held on November 9th (see Schedule, below). Oral presentations and panel discussions took place on November 10th. The final day of the symposium was dedicated to a technical training workshop on tools for assessing connectivity. The symposium themes were: 1) oceanographic connectivity, 2) connectivity in population structure, 3) linking research on connectivity with MPA management, 4) demersal connectivity, and 5) spawning aggregations. This proceedings volume is organized around these primary themes, and includes contributed papers followed by summaries of oral presentations and panel discussions; we included summaries of the panel discussions because these were major elements of each of the five themes. Abstracts of oral and poster presentations have been published elsewhere (Acosta 2007).

The plenaries by Billy Causey and Peter Sale discussed, from their unique perspectives, that although we may never completely understand connectivity we need to manage areas using the best available scientific information. Presentations in the oceanographic connectivity session and poster presentations addressed a number of fundamental and applied topics ranging from modeling population connectivity (Cowen et al. *summary of oral presentation*; see also Cowen et al. 2006; Treml et al. *summary*), the importance of larval behavior (Paris et al. *summary* and *contributed paper*), and empirical approaches to understanding connectivity (Criales et al. *abstracts* in Acosta 2007; Glazer et al. *summary*; Pizarro et al. *abstract* in Acosta 2007). This section includes additional contributions on dispersal of queen conch larvae (Delgado et al. *contributed paper*) and the distribution of surgeonfish larvae in the eastern Caribbean (Oxenford et al. *contributed paper*).

Presentations on the topic of connectivity in population structure addressed genetic connectivity (Baums et al. *summary*; see also Baums et al. 2005, 2006, Hellberg 2007; Paris et al. *contributed paper*; Perez et al. *abstract* in Acosta 2007; Richards et al. *abstract* in Acosta 2007; Rocha *summary*) and modeling approaches (Butler et al. *summary*; see also Paris et al. 2005; Ralston and O'Farrell *abstract* in Acosta 2007) to better understand the scales at which populations should be managed and the potential connectivity between management units.

In the session about linking research on connectivity with MPA management, various presentations addressed how information on connectivity could be integrated to better manage local areas and networks of MPAs. Examples including the World Heritage Program (Bustamante and Paris *contributed paper* and *summary*), the Costa Maya (Quintana Roo, Mexico) (Reveles *summary*), and the west coast of the U.S. (O'Farrell *summary*) were presented. This section also includes a presentation from the training workshop about use of the Integrated Coral Observing Network by MPA managers (Hendee et al. *abstract*).

Talks and posters presented under the demersal connectivity theme examined movement of fishes throughout ontogeny, which highlighted the importance of incorporating various habitat types in spatial management schemes. During early life history stages, nursery habitats play a crucial role in the distribution of reef fishes (Aguilar et al. *abstract* in Acosta 2007; Appeldoorn et al. *summary*; Baltz et al. *abstract* in Acosta 2007; Nagelkerken *summary*; see also Nagelkerken et al. 2001; Schärer et al. *abstract* in Acosta 2007). Movements of fishes relative to MPA boundaries and MPA efficacy were discussed (Pina et al. *contributed paper* and *summary*; Lindeman *summary*), and consequences of connectivity for coral reef resilience was presented (Mumby *summary*).

The spawning aggregations theme examined spatially explicit information on the movements of adult fishes during reproduction. An overview of the role of adult reproductive events on population structure was presented (Heyman et al. *contributed paper* and *summary*), and examples of data from the U.S. Virgin Islands (Nemeth et al. *contributed paper* and *summary*) and the Cayman Islands (Semmens et al. *summary*) suggested that predictable spatial and temporal patterns to spawning movements may help resource managers understand connectivity among disparate locations.

Following the oral presentations for each of the major themes, a panel was formed including the speakers and representative resource managers from the Caribbean region, during which the audience participated in an interactive roundtable dialogue. During these discussions, the focus of inquiry was to determine how the scientific information presented could best be integrated into actual marine conservation initiatives. The panels encapsulated broad-based expertise and collectively had considerable experience in dealing with understanding the implications of connectivity to resource management. The panel on oceanographic connectivity consisted of Bob Cowen, Eric Treml, Claire Paris, and Gabriel Delgado. The panel on connectivity in population structure consisted of Iliana Baums, Luiz Rocha, Mark Butler, Martha Prada, and Maria Criales. The panel on linking research on connectivity with MPA management consisted of Georgina Bustamante, Mike O'Farrell, Mark Butler, Frank Muller-Karger, Marion Howard, and Barbara Reveles. The panel on demersal connectivity consisted of Rich Appeldoorn, Ivan Nagelkerken, Hazel Oxenford, Fabian Pina, Rikki Grober-Dunsmore, and Ken Lindeman. The panel on spawning aggregations consisted of Will Heyman, Rick Nemeth, Brice Semmens, and Dwight Neal.

The Symposium Organizing Committee included Brian Keller, Billy Causey, and Sarah Fangman (NOAA Office of National Marine Sanctuaries) and Rikki Grober-Dunsmore (National Marine Protected Areas Center). Sarah Fangman took notes for summaries of oral presentations and panel discussions.

Acknowledgments

We thank the Executive Committee of the Gulf and Caribbean Fisheries Institute (GCFI) and the sponsors (National Ocean Service, NOAA) whose financial and technical support made this symposium possible. Specifically, Bob Glazer, Alejandro Acosta, and Gabriel Delgado were vital in terms of logistics before, during, and after the symposium. Friendship and dedication to efforts such as these is greatly appreciated and we thank all of the participants, presenters, and audience for making this a highly successful, engaging symposium. Thank you.

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Baums, I.B., M.W. Miller, and M.E. Hellberg. 2006. Geographic variation in clonal structure in a reef-building Caribbean coral, *Acropora palmata*. Ecol. Monogr. 76: 503-519.

Cowen, R.K., C.B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. Science 311: 522-527.

Hellberg, M.E. 2007. Footprints on water: the genetic wake of dispersal among reefs. Coral Reefs 26: 463-473.

Nagelkerken, I., S. Kleijnen, T. Klop, R.A.C.J. van den Brand, E. Cocheret de la Morinière, and G. Van der Velde. 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: a comparison of fish faunas between bays with and without mangroves/seagrass beds. Mar. Ecol. Prog. Ser. 214: 225-235.

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. Mar. Ecol. Prog. Ser. 296: 93-106.

Schedule of Poster and Oral Presentations

Thursday, November 9, 2006

Poster session afternoon and evening

A. Aguilar-Perera and R.S. Appeldoorn

Variations in juvenile fish density along the mangrove-seagrass-coral reef continuum in southwestern Puerto Rico

D. Baltz, J. Maiaro, A. Roth, and A. Arrivillaga

Patterns of habitat use by early life history stages of fishes in Placencia Lagoon, Belize: Connecting marine reserves and nursery habitat

M.M. Criales, J.A. Browder, C Mooers, M.B. Robbleee, H. Cardenas, and T. Jackson

Implications of tidal transport and internal tides on the cross-shelf transport of pink shrimp larvae at the Southwest Florida Shelf

M.M. Criales, C. Andrade, T.N. Lee, E. Williams, and A. Lopez

Lagrangian measurements in the southwestern Caribbean and its implications for larval transport

P. Fanning, H.A. Oxenford, and R.K. Cowen

Swimming deep: new evidence of acanthurid larval dispersal at depth in the eastern Caribbean

C. Paris, C. Guigand, J. Olivier Irisson, and R. Fisher

Orientation With No Frame Of Reference (OWNFOR): An in situ system to detect and measure orientation in pelagic reef fish larvae

R. Perez-Enriquez, G. Mendoza, and T. Gutierrez

Gene flow of Queen conch* Strombus gigas *in the Mexican Caribbean

V. Pizarro, S. Lonin, and J.C. Thomason

Connections between coral reefs: trajectories of coral larvae in the Caribbean Sea

S. Ralston and M. O'Farrell

Spatial variation in fishing intensity and its effect on yield

V.P. Richards, M.B. Debiasse, and M.S. Shivji

Comparative phylogeography, dispersal strategy, and biodiversity in three commensal invertebrates and their host sponge

M. Schärer, M. Nemeth, and R. Appeldoorn

Ontogenetic connectivity of grunts and snappers within an isolated seascape

Friday, November 10, 2006

Symposium Presentations and Discussion Panels

Each speaker below will provide a **10 minute** talk that addresses highlights of work, management implications of results, how results can be applied at various spatial and technological scales, and what is needed in future to link research and management. Discussion following presentations.

8:30 am Opening welcome
Billy Causey (NOAA) and Rikki Grober-Dunsmore (NOAA)

9:00 Keynote address: **Peter Sale**
Connectivity: What it is, how to measure it, why it is important for management

9:30-10:40 Oceanographic Connectivity (Bob Cowen, panel lead)

Panel Members: Bob Cowen, Gabriel Delgado, Claire Paris, Eric Treml

9:30 Bob Cowen
Modeling population connectivity of coral reef fishes within the greater Caribbean
9:40 Eric Treml
A graph-theoretic approach for evaluating marine population connectivity
9:50 Claire Paris
Surfing, spinning, or diving from reef to reef: how does it affect population connectivity?
10:00 Bob Glazer
When low-tech is enough: Using drift vial and plankton studies to develop restoration strategies
10:10-10:40 ***Discussion with panel***

10:40-11:40- Connectivity in Population Structure (Iliana Baums, panel lead)

Panel members: Iliana Baums, Mark Butler, Maria Criales, Martha Prada, Luiz Rocha

10:40 Iliana Baums
From small to large and present to past: scales addressed by genetic connectivity studies
10:50 Luiz Rocha
The importance of sampling across environmental gradients in connectivity studies
11:00 Mark Butler
Connectivity in Caribbean spiny lobster: The tail of the dispersal kernel?
11:10-11:40 ***Discussion with panel***

11:40-12:40 Linking Research on Connectivity with MPA Management (Georgina Bustamante, panel lead)

Panel members: Georgina Bustamante, Marion Howard, Frank Muller-Karger, Mike O'Farrell, Barbara Reveles

11:40 Georgina Bustamante
Marine World Heritage Sites in the wider Caribbean: How research data on biological connectivity can document the "outstanding universal value" of new nominations
11:50 Barbara Reveles
Sustainability and tourism in the Costa Maya: Their influence in Natural Protected Areas of Quintana Roo
12:00 Mike O'Farrell
Added uncertainty with marine reserves: Identifying and understanding the sources
12:10-12:30 ***Discussion with panel***

LUNCH 12:30-1:30

1:40-2:40- Demersal Connectivity (Rich Appeldoorn, panel lead)

Panel members: Rich Appeldoorn, Ken Lindeman, Ivan Nagelkerken, Hazel Oxenford, Fabian Pina

1:30 Rich Appeldoorn
Patterns of habitat use and tagging studies in a complex coral reef ecosystem: Toward understanding habitat connectivity through ontogenetic migration
1:40 Ivan Nagelkerken
Connectivity between non-estuarine mangroves, seagrass beds, and coral reefs by fishes?
1:50 Fabian Pina
Movement of adult fish in the Jardines de la Reina Marine Reserve, Cuba
2:00 Peter Mumby
The effects of mangroves on the resilience of coral reefs
2:10 Ken Lindeman
Connectivity texture and the need for cross-cultural panmixis
2:20-3:10 ***Discussion with panel***

3:10- 3:45-Spawning Aggregations (Will Heyman, panel lead)

Panel members: Will Heyman, Dwight Neal, Rick Nemeth, Brice Semmens

3:10 Will Heyman
Reef fish spawning aggregations as sources: Science and management
3:20 Rick Nemeth
Regional coupling of red hind spawning aggregations to oceanographic processes in the eastern Caribbean
3:30 Brice Semmens
Defining the biogeography of a spawning aggregation to inform marine reserve planning and evaluation in the Cayman Islands
3:30- 4:00 ***Discussion with panel***

Opening Remarks and Welcome and Introduction to the Symposium

Billy D. Causey[1] and Rikki Grober-Dunsmore[2]

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[2]*National Marine Protected Areas Center, Santa Cruz, CA.* Present address: *University of the South Pacific, Suva, Fiji Islands* dunsmore_r@usp.ac.fj

Opening Remarks (*Summary*)

The die-off in 1983 of the important grazing sea urchin, *Diadema antillarum*, created an awakening to connectivity in the Caribbean, Gulf of Mexico, and the Florida Keys. We realized we had to start thinking differently about how we were managing our sites, considering spatial scales much larger than the areas we were managing.

Lessons learned:
- Consider appropriate scales
- Use appropriate tools
- Start working with our neighbors

Now we have satellite drifter information about ocean circulation and we know much more about regional connectivity. For example, we can look at the Mississippi River plume and see how it impacts the Florida Keys. We now have the tools (remote sensing included), but we also have models and we can look more effectively at how different regions affect each other.

We need to use the positive aspects of connectivity to our advantage. By understanding physical connections, we can start looking outside the areas we are managing and start to look for the benefits of connectivity.

Welcome and Introduction to the Symposium (*Summary*)

Questions that managers propose need answers:
- How can information on Caribbean connectivity be applied to address resource management questions concerning MPAs (e.g., source-sink between MPAs, MPA design and siting, monitoring coordination between MPAs)?
- What is the current state of knowledge in each area of research to be discussed in this symposium?
- What are future research directions that are needed to address critical resource management needs?
- How can this information be scaled technologically (low tech - high tech) to answer resource management questions?
- What information can resource managers provide to improve on our current knowledge?

Keynote Address:

Connectivity: What It Is, How It Is Measured, and Why It Is Important For Management of Reef Fishes

Peter F. Sale[1] **and Jacob P. Kritzer**[2]

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Abstract

Numerous field studies have documented the sedentary habits of most species of fish on coral reefs. This habit of staying put, and a strong tendency to associate with specific types of habitat, jointly result in reef fish species being distributed patchily across the available environment at a range of spatial scales. Local aggregations function as breeding groups that may be more or less isolated demographically from nearby groups of the same species, and the set of local groups is probably best represented as a metapopulation. Current studies of connectivity are attempts to quantify the extent of interconnection among local groups, a topic of considerable importance because of the growing prevalence of spatially based management approaches, such as the use of no-take marine reserves. Such management approaches should be based on sound knowledge of the spatial scales at which local groups are interconnected. In a similar way, communities of fish on coral reefs can best be thought of as metassemblages (or metacommunities), in which each of the individual species present at a local site represents one node in its own metapopulation, with the proviso that the metapopulations may well exist on different spatial scales. To date, the consequences of metassemblage structure for interspecific interactions have scarcely been explored. A number of recent reviews have focused on each of these topics. Our goal is to unify those topics, linking spatial arrangement to connectivity and metapopulation structure, relating these to management, and exploring methodological options for advancing knowledge of connectivity in these organisms.

Introduction

The ecology of fishes in coral reef systems has been studied directly ever since the advent of SCUBA as a scientific tool, to the extent that it is hard to imagine anyone being successful at reef fish ecology without being equipped to use such methods. More recently, reef fish ecology has become more sophisticated. The laboratory has come to be an integral component, as researchers glean important new insights by examining the structure and composition of otoliths, the histology of gonads, the biochemistry and physiology of individual fish, and molecular make-up of DNA. But in its early days, our knowledge primarily advanced through field observation and experimentation. Those simple and often crude approaches yielded a wealth of knowledge about species' movements, habitat relationships, and interactions with one another that could never have been uncovered in the laboratory (Sale 2004; Kritzer and Sale 2006a). The understanding gained has direct application in efforts to manage reef fisheries sustainably, and for conservation. It is also likely that this understanding can be fruitfully exported to many other aquatic environments. This paper integrates what is known about the spatial relationships of

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 12-26 *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, 59th 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.

coral reef fishes and the connectivity among local populations, and relates this to management issues. There is a growing need for greater understanding of spatial organization, particularly at a time when coral reef fisheries are putting increased pressure on target populations, and spatially explicit management approaches are being promoted as the best way to manage these systems sustainably.

Use by Fishes of the Coral Reef Habitat

Coral reefs provide a rich diversity of habitat types, patchily distributed on spatial scales ranging from centimeters to hundreds or thousands of kilometers. The fishes that associate with coral reefs universally respond to this spatial mosaic, many showing pronounced associations with specific types of habitat. The high degree of habitat specialization was noted in the first significant paper on reef fish ecology (Hiatt and Strasburg 1960), and exists despite the fact that life histories of all but a handful of reef fishes include a pelagic larval phase lasting from several days to several months. Following settlement from the larval stage to the reef, fish are found almost exclusively in the "correct" habitat for that species and age class, even though adjacent patches of different habitat are close by and swimming amongst them could be achieved in seconds or minutes (Leis and McCormick 2002).

The spatial scale at which fish respond to the reef habitat depends on the scale of daily movements, which, in turn, is strongly linked to the sizes of the fish (Sale 1978). Scales vary from 1 m^2 for some small gobies or damselfishes to several hectares for larger groupers, sharks or other species. Some of the latter may also migrate to traditional spawning sites as much as 100 or more km away from the home range. However, tagging studies have repeatedly shown that even among larger and/or more mobile species of the lutjanid, lethrinid, serranid, scarid, acanthurid, and mullid families, it is rare for individuals to move more than 500 m (Kritzer and Sale 2006a). Thus, most reef fish species can be expected to move about over an area of reef that falls somewhere between 100 m^2 and 1 hectare. Overall, reef fish are so sedentary that it becomes quickly apparent to the diving scientist that the same individuals are present in the same neighborhoods day after day over months and years. These strong associations of individual fishes with specific places on the reef have also permitted the development of complex social and mating patterns including defense of permanent, individual territories, haremic mating systems, trap-lining among scattered food sources, culturally transmitted knowledge of traditional spawning sites, cleaning stations that attract fish of many different species, and interspecific cooperative foraging (e.g., Petersen and Warner 2002 and references therein).

The close association with habitat and the tendency to be sedentary become particularly important demographically when the spatial scale at which they are expressed interacts with the scale at which larval dispersal occurs. It then becomes appropriate to think in terms of local populations within which reproduction occurs, but with some leakage of dispersive larvae to become immigrants to neighboring populations. While it is logical that this scale must be larger than the scale at which individuals of most reef species restrict their individual movements (post-settlement), researchers are not currently able to specify the scale that is appropriate. Still, given that larval durations are typically 20 to 40 days, and that hydrodynamics should ensure mixing over scales of many square kilometers, the critical feature in determining appropriate scales likely will be the spatial patchiness of the reef habitat in a particular region, rather than the patterns of daily movements of the resident species. It follows that patterns of organization of a species into neighboring populations will vary geographically for reasons that have rather little to do with the fish and a lot to do with geological history of coral reefs. It also follows that, within reef fish populations, random mating should be the last mating system to expect. Instead, reef fishes will tend to mate with their nearest neighbors, often on scales of meters. It should ultimately become possible to specify the spatial scale at which populations (as groups of mating individuals) are arrayed for a particular species. This will require information on patterns of larval dispersal, habitat specificity, post-settlement movements, and patchiness in abundance of post-settlement individuals of that species, but it will also be very dependent on patterns of patchiness in habitat in the region of interest.

Metapopulations and "Functional" Metapopulations

Cowen et al. (2006) recently modeled likely connectivity of reef fish species using sophisticated individual-based modeling of dispersing larvae in a hydrodynamic field replicating five years of history in the Caribbean, and with coral reef habitat identified as 260 nodes (10 x 50 km) in this region. While there was some variation across the region, they found, overall, high levels of self-recruitment (i.e., from within the 10 x 50 km nodes), and demographically meaningful immigration effectively limited to distances less than 100 km. On average, ~21% of recruiting larvae came from within the node, and recruitment from more than 100 km away was trivial. Whether or not their predictions are correct depends greatly on the assumptions they made concerning behavior of larvae, and in the accuracy of their hydrodynamic and dispersal models, but their predictions are the best to date, and do provide some likely boundaries to thinking about spatial structure in these systems.

Using the predictions of Cowen et al. (2006) it is possible to visualize the following scenarios for a species. In a region where coral reef habitat is distributed as a set of patches (reefs) of 10 kilometer scale (diameters of 10-50 km), separated by >1 km and <100 km of non-reef habitat, it is very likely that the fish that occupy a single patch constitute one sub-population within a metapopulation made up of the full set of patches and their fish. In locations where the patches of suitable habitat are smaller and closer together, or for species with somewhat greater dispersal abilities, the sub-populations may each encompass two or more adjacent habitat patches. In places where the coral reef habitat is arrayed as a small set of reefs very well separated from each other (100 km or more apart), or for species with somewhat more restricted dispersal abilities, it is possible that there is no effective metapopulation and the fishes on each reef function as a single, if slightly leaky, population. These three possibilities are diagrammed in Fig. 1. All three are represented in many locations around the world, both because the pattern of distribution of coral reef habitat is highly variable geographically when looked at on a 10-100 km scale, and because dispersal abilities of species undoubtedly differ.

There are many locations where the reef habitat is more or less contiguous over distances of several hundred km – many sections of the Great Barrier Reef, the Mesoamerican Barrier Reef of the western Caribbean, and scattered locations in Indonesia, the Philippines, and elsewhere come to mind. In these, there is no clear division of environment into separated patches, yet the sedentary behavior of the fishes ensures that reproduction is spatially constrained. Kritzer and Sale (2006a) suggested that in such situations it may be appropriate to think in terms of *functional metapopulations*, by recognizing subsets of adjacent locations within the overall region of reef habitat as effectively separate local populations (Fig. 1). The resident fish of each subregion breed within it, and the subregions are of sufficient size that there is significant self-recruitment to them (perhaps the 21% of total recruitment that Cowen et al. (2006) report). But in a functional metapopulation, there are no visible boundaries to the subregions and their contained subpopulations. Indeed, unless hydrodynamics and larval behavior are far less variable through time than we expect, the subdivision of the overall region is essentially arbitrary in location while still being explicit in subunit size. Despite the lack of objective definition of individual subpopulations, this approach does capture the localized nature of reproductive activity, and would be useful in analysis of any spatially explicit management system, such as the use of no-take fishery reserves, that was to be introduced. It also provides a useful way of adequately accounting for spatial variation in rates of recruitment, survivorship and growth, and therefore for variation in population size, density and structure. These are regularly present in reef fish populations, although there has been relatively little attention to them from population modelers (but see Kritzer and Davies 2005). We anticipate that models using a functional metapopulation structure will become necessary if the properly effective design of networks of marine protected areas (MPAs) becomes a fishery management goal.

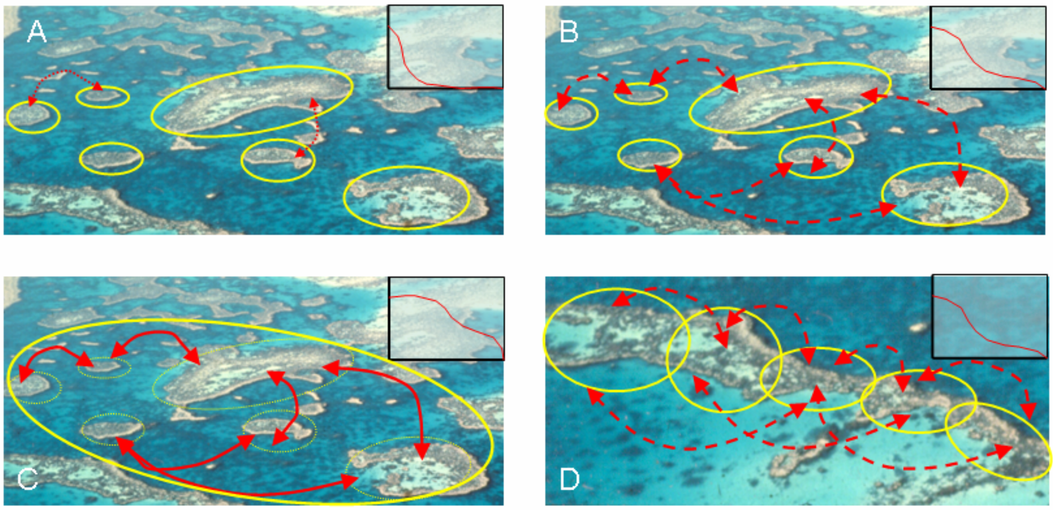

Fig. 1. Each panel shows a patchy array of reef habitat, some of which is occupied by a reef fish species (ovals = local aggregations of fish). Dispersal (chiefly by larvae) among sites is shown by arrows, graded to show slight (A), moderate (B, D) or extensive exchange (C). Mean scale of dispersal is shown as a graph of proportion of larvae (y axis) against distance from source (x axis) in upper right corner of each panel – mean dispersal distance is least in A, intermediate and identical in B and D, and greatest in C. Cases A, B, and C differ only in the scale of dispersal relative to the scale of patchiness of habitat, yet yield essentially independent local populations (A), a metapopulation (B) in which local populations are sufficiently connected by dispersal for some interaction, and a single, but subdivided, population (C), occupying a number of patches of habitat. Case D is typical of regions where coral reef habitat is more contiguous, yet the spatially explicit mating pattern and scale of larval dispersal still provide a functional metapopulation even though patch structure is primarily an analytical construct.

The simulations of Cowen et al. (2006), and the accumulated information on the breeding biology and larval ecology of reef fish species permit making of more-or-less explicit predictions concerning the sizes of sub-populations and the proximity needed for them to function as metapopulations. However, while progress is encouraging, we have a considerable way to go and diagrams such as in Fig. 1, even if given explicit scale and species name, remain cathedrals built on a rather silty plain. What is missing is direct information on the extent of connectivity among local populations of reef fish species. Such information is scant, and very difficult to acquire. Yet there are reasons to believe that acquiring it should be a crucially important step if management and conservation of reef fish systems is to be enhanced.

Methods for Gaining Information on Connectivity

Demographic connectivity, the extent of interconnection among local populations of a species, is connectivity achieved through the exchange of individuals among the populations. By this we mean both the movement of individuals between populations, and their successful establishment as participating members of the population they join (Kritzer and Sale 2006b). Demographic connectivity is thus distinguished both from evolutionary connectivity which is due to the movement of genes among populations, and from other forms of connectivity among ecological systems due to the movement of nutrients, pollutants, and so on. Directly measuring demographic connectivity among populations of most marine species is a particularly challenging task. Most of the connectivity in these species is through the dispersal of larval stages rather than the movements of older organisms, and larval stages are both difficult to tag, and as likely as not to fail to survive to the settlement stage.

Approaches taken by coral reef ecologists have included use of genetic, or even morphological, differences among populations, simulation modeling of larval dispersal, direct observation of dispersing larvae, tracking of drifters intended to mimic larvae, use of natural tags in the form of genetic sequences or of chemical signals taken up from the spawning location, and direct chemical tagging of larvae (Sale and Kritzer 2003). Each method has its advantages and disadvantages. All have proved demanding to apply given the usual durations of larval life, the complexity of current streams around complex reef topography, and the fact that over 99% of larvae are expected to fail to survive to settlement. Detailed understanding of demographic connectivity requires use of multiple methods.

Genetic analysis of populations has a long history, and modern molecular approaches permit very sensitive discriminations of relatedness of populations. Nevertheless, genetics focuses on genes, and populational differences in gene frequencies can be due to several factors, only one of which is pattern of movement of individuals among them (Mora and Sale, 2002). Genetic discrimination of populations can readily provide information about demographic connectivity, but it does not measure this explicitly. In particular, neighboring populations that have very similar genetics may have only slight or much more extensive exchange of larvae. Genetic methods that evaluate the relatedness of individual larvae to putative parental populations seem the most powerful for connectivity studies.

Modeling studies enable the combining of sophisticated analysis of hydrodynamics, and data on the behavior of dispersing larvae, in exercises whose scale in space and time is only limited by CPU time available. However, while they can generate interesting, and detailed results, their statements about demographic connectivity are only as accurate as the assumptions built into the underlying code. While hydrodynamic models have progressed greatly, they are still limited, particularly when it comes to modeling water flow in close proximity to complex topography especially in shallow waters (Tang et al. 2006). Dispersing coral reef larvae begin and end their journeys precisely in such shallow, topographically complex boundary layers. Models for the behavior of the dispersing larvae remain far more primitive than the hydrodynamic models upon which they run. Larvae are rarely passive, neutrally buoyant particles, and their behavior is made more complicated by the fact that it changes, and grows in complexity during larval life (Sale and Kritzer 2003). Eggs fertilized in mid-water at the edge of the reef are rather different to recruiting surgeonfish larvae, 2 to 3 months later. The latter are highly capable swimmers, with excellent hearing, sight, olfaction, and, almost certainly, lateral line sensitivities. Models of dispersal are only now beginning to incorporate these ontogenetic changes (Leis and McCormick 2002; Cowen et al 2006). Needless to say, reef ecologists remain a long way from being able to define how larvae respond to the cues offered by their environments (Myrberg and Fuiman 2002). Do reef fishes, for example, detect reef habitat from 9 km away and swim towards it, as they are assumed to do in the model of Cowen et al. (2006)? Or do they respond at substantially different distances, or in far more complex ways? While recent modeling studies provide exciting glimpses of what may be happening, there will need to be many more basic studies in the sensory physiology and behavioral biology of larval stages, at all stages during larval life, before the things that make them not passive particles can be fully captured. Results of modeling studies can usefully guide the behavioral and physiological research because even in their current crude state, dispersal models can generate boundary conditions (Armsworth 2000).

Direct observation is limited by the sizes of larvae and the duration of their larval journeys. Leis and colleagues (Leis and Carson-Ewart 1999, 2001; Leis et al. 1996) have pioneered this approach for reef fish, but may have gone almost as far as it is possible to go, at least with the present understanding of the problem. Direct observation may be a lot more useful for organisms with very short-lived larvae that settle within hours of spawning, and may certainly be useful for capturing the details of the initial and terminal stages of the journey – those portions for which oceanographers have the least detailed understanding of hydrodynamics. The tracking of drifters is an allied method, although most drifters are entirely passive and all are much larger than any marine larvae. With large size they do not necessarily move in the current stream in the way larvae would, even if the larvae had behavior as limited. Attempts to build 'smart' drifters or drifters that are scaled more closely to larvae do occur from time to time, and these approaches should be encouraged more than they currently are in the competition for funding.

The use of natural tags was initially exclusively a use of genetic tags, but in recent years studies that make use of natural trace-element chemistry of the otoliths of fish have also been used (Swearer et al. 1999; Thorrold et al. 2001). The approach in either case is to identify a feature of the larva that ties it to its natal population (for genetic tags), or to its natal location (for chemical tags). These approaches show real promise, although they both are restricted to situations in which there is sufficient background variation against which to map the patterns of genetics or chemistry exhibited by individual larvae. These are discussed further below.

The use of artificial tags is clearly the definitive way of tracking individual larvae from starting to finishing site. The tags are unique, and were applied to larvae at a particular place and time. Every settled larva that exhibits the tag must have come from that place and time. That the larvae are so small at hatching does make this a challenging approach, but G.P. Jones and colleagues are demonstrating the power of this approach, and generating interesting data on connectivity in the process (Jones et al. 1999; Thorrold et al. 2006). Tagging, using natural or artificial genetic or chemical tags, is going to be the essential technique for validating the results of dispersal models, while modeling, once more fully validated, will become the methodology that will extend the results of a small number of logistically difficult tagging studies to a more comprehensive understanding of demographic connectivity among coral reef populations.

Why Demographic Connectivity Is Important

Field data are quite solid in confirming that the great majority of reef fish species are sedentary both because that is their nature and because the patchy environment imposes spatial structure on their movements. The overwhelming majority of species have extended pelagic lives as larvae. There are three possible population structures: 1) larval dispersal is sufficient to overcome the localization of adult movements so that the population is homogeneous over a large area even though spatially patchy in occurrence, 2) the extent of larval dispersal is such that local populations are essentially demographically separate, but connected as a metapopulation, and 3) dispersal is so ineffective that local aggregations on patches of reef habitat really are independent demographic units. These three possibilities demand quite different management approaches both locally and regionally, particularly if a spatially explicit management of fishing effort is planned. The actual situation can only be identified with knowledge of the extent of connectivity relative to the patchy distribution of groups of adults.

While there is a fundamental scientific interest in knowing which scenario applies, the real importance of connectivity lies in the fact that in these shallow coastal environments, the use of various types of MPAs, especially no-take marine reserves, is being very widely advocated, and implemented, as the best solution to sustainable management and conservation. Unfortunately, while managers attempting to design and implement networks of MPAs are frequently well aware of the intrinsic importance of knowledge of connectivity patterns to designing them effectively, there are currently very few studies that explicitly set out the dispersal patterns for any species in any region. As a consequence, managers must design by best guesstimate. Sale et al. (2005) recently called attention to this problem – one that becomes ever more severe as the enthusiasm for MPAs grows, and some advocates increasingly gloss over the real difficulties in gaining connectivity data. While there are a number of other problems to be solved if MPAs are going to fulfill many of the expectations set out for them, the lack of objective data on dispersal patterns and connectivity has to be one of the most important impediments to building a science of management using MPAs. Coordinated programs of experimental implementation of MPAs, coupled with a rigorous supporting scientific framework, usually termed adaptive management, can be a powerful means of building this science, and should be encouraged. Arm waving, usually with glossy brochures clenched tightly, and PowerPoint presentations ready for anyone who cares to watch, are not a long-term solution to this problem, yet there is too much money being spent in proselytizing about the virtues of MPAs as management tools, and not enough effort going into building up the basic science. Fortunately, there is growing realization that more science is needed, and a number of research groups are attempting to move forward on methods for defining connectivity.

Some Preliminary Results for Reef Fishes on the Mesoamerican Barrier Reef

Since 2001, we have participated in a multidisciplinary study of connectivity in fishes on the Mesoamerican Barrier Reef along the western Caribbean shores of Mexico's Yucatan, Belize, Guatemala, and Honduras. The project has focused primarily on the common damselfish, *Stegastes partitus* (Poey), the bicolor damsel, and has attempted to integrate ecology, genetics, otolith chemistry, and hydrodynamics to advance understanding of its connectivity. This common small reef fish is a typical damselfish: during the several-month breeding season, males prepare and defend nests inside shells and under overhangs, and court females. Males care for the eggs and protect them from predators for the 3.5 days it takes them to hatch. Reproductive activity is synchronized on a lunar cycle with successive clutches spawned 3-5 days following the full moons (Knapp 1993). Larvae hatch in the early evening, swim up to the surface waters, and commence a pelagic existence which lasts 29-35 days (Wilson and Meekan 2002). At the close of larval life, recruits settle to suitable reef habitat where, if they survive, they will reach maturity in 5 or so months, and live for several years. This life history pattern ensures that reproductive activity is scattered throughout the habitat of the fish (shallow back- and fore-reefs with a coral-dominated substratum), and occurs over a substantial portion of the year. This is typical of the majority of reef fish species, and the bicolor has the advantage that it is abundant, easily recognized, and not subject to a fishery. The task has been to determine the structure of the bicolor populations in Mesoamerica.

Reef fish are particularly attractive targets for studies of connectivity because, unlike invertebrate larvae, in addition to offering genetic tags, fish possess otoliths that both provide considerable information on the larval life of the individual and offer a convenient location in which to look for chemical tags (Sale and Kritzer 2003). Because the otolith grows by daily deposition of calcium carbonate, it provides both a record of age and growth, and a temporally explicit record of the trace element composition of the waters occupied at each stage in life. By sampling the otolith close to its core, one theoretically captures the elemental composition of its natal environment, while samples from the outer edge define the chemistry of the site where it was captured as a young recruit (Campana and Thorrold 2001). Our goal for this species was to develop an extensive record of rates of recruitment to reef sites, and collect samples of fish recruiting to each site for genetic and chemical analysis to define likely natal origins. Some of this work is already published, but much remains to be completed and the following is an interim report of results. Ours is not the only multidisciplinary approach to this problem, and our experience has revealed difficulties in measuring connectivity as well as provided some results.

The field sampling program operated each summer (late May to late August) from 2001 to 2005, and attempted to sample a suite of 21 reef locations nearly contemporaneously during the week following new and full moons. Logistics and limitations of funding constrained the design, and it was maximally implemented in only one year. Sites were distributed as six at Banco Chinchorro and three near Mahahual in Mexico's southern Yucatan, seven at Turneffe Atoll offshore from Belize City, and five at Roatan, in Honduras' Bay Islands. Sampling was most complete over the five years at Turneffe Atoll, which is approximately 50 km from north to south. The seven sites were distributed around its outer boundary. Each site was sampled by censusing eight belt transects, 1 x 30 m, set out haphazardly at each of a shallow (3-5 m) and a deep (10-15 m) permanent station. Fish were sampled using a 1-m wide T-bar to delineate width, and a 30-m PVC tape that was deployed as the transect was swum. All fish of 18 species that were small enough to have settled during the previous two weeks were counted. With field teams in Mexico, Belize, and Roatan, it was possible to census all sites within about five days. In addition to censuses of recruitment, the field teams made collections of up to 20 recruits of each of 10 species (limited by rates of settlement), using small spears, nets, and clove oil to narcotize fish and facilitate capture. Collected fish were put on ice until return to shore, and then preserved directly in 95% ethanol for subsequent otolith and genetic analysis.

Results for the bicolor damsel are typical of most species monitored. Recruitment varied substantially among collection times and among sites, suggesting that successful completion of larval life was a markedly variable event across the spatial and temporal scales of the study. Such a result is the norm for reef fish species and hardly surprising. Because the oceanographic team-members were developing a hydrodynamic model for the region (Tang et al. 2006), it was possible to map locations where water exchange during summer months was high, and places where water tended to be retained longer. As well, the hydrodynamic model generated hypotheses concerning likely paths of connectivity within the region, and likely rates of transport if transport was effectively passive. At present, final data analyses (R. Fisher, unpubl. data) are being done that are expected to permit associating some proportion of the variation in recruitment to a suite of environmental aspects including summer residency time of the water, microhabitat, wind strength and direction during the preceding week and so on. To the extent that variation in recruitment is successfully associated with such factors, this component of the study will mark an advance over prior studies of recruitment.

Additional analyses (J.D. Hogan, unpubl. data) are being undertaken to determine the overall coherency, or synchrony, of the recruitment data. (Coherency refers to the extent to which recruitment follows similar temporal patterns at groups of sites, and the spatial distribution of coherent sites.) These studies should generate hypotheses concerning the likely factors driving larval dispersal, the extent to which hydrodynamics determines larval dispersal, and the spatial scale at which larvae are associated during pelagic life.

Somewhat more progress has been made in the studies that use natural genetic or chemical tags to deduce natal origins of recruited fish. However, both genetic and chemical approaches have revealed that these techniques are going to be somewhat harder to implement routinely than might at first appear.

It is known that otoliths incorporate trace elements haphazardly as they are being formed, that the incorporated elements are trapped and not reactivated later in life, and that trace elements get to the otolith (as do calcium and carbonate) by traveling from the environment via gills to blood stream, then to endolymph of the otic capsule, and finally to the otolith (Campana and Thorrold 2001). At each of these three transitions, elemental transport is likely not passive. For that reason, any study that uses otolith elemental chemistry as a natural tag cannot simply compare otolith chemistry to water chemistry from different sites (Thorrold and Hare 2002). Hence, it has long been known that using chemical tags will require measurement of otolith core chemistry as a signal for (unknown) natal site chemistry, and otolith edge chemistry as a signal of otolith chemistry from fish living at known (collection) sites. Our studies have demonstrated that, in the offshore carbonate reef environments studied, the situation is still more complicated.

The natural variation in elemental composition in these calcium carbonate-dominated environments is sufficient for discriminating fish from nearby sites, but the variation among sites is transient (Chittaro et al. 2004, 2005, 2006b). To use otolith chemistry to identify natal origins, it is therefore necessary to make two sets of collections separated by approximately the duration of the larval stage. The edge chemistry of fish from collection #1 defines the otolith chemistry at the suite of sampled sites around the collection date. The core chemistry of fish from collection #2 is then compared to the map of site chemistries defined by collection #1. Fortunately, our fortnightly samples of fish provided several possible pairs of collections one larval duration (approximately one month) apart. However, there is a further complication. This is that the otoliths of some (perhaps all) fish show a strong maternal influence on trace elemental composition during the days when the larva is feeding primarily on yolk reserves. In particular, concentrations of manganese are strongly elevated. This phenomenon was first reported by Brophy et al. (2003) for Atlantic herring, and work in Sale's lab has reported this in several freshwater species (Ludsin et al. 2006), in bicolor damselfish, and in French grunt, *Haemulon flavolineatum* (Desmarest) (Chittaro et al. 2006b). Preliminary data on likely interconnections among sites at Turneffe used core data but discounting elements such as manganese that showed evident spikes at the core (Chittaro et al. 2006a). Current work (J.D. Hogan, unpubl. data) is sampling otolith chemistry five days outside the core and just inside the otolith edge on a large sample of bicolor damsels, using the argument that by five days, larval otoliths are being formed without significant maternal effects and the larvae are still likely to be relatively near to the natal site. By sampling just inside the otolith edge, it is anticipated that water chemistry in the pelagic environment but relatively close to the site of settlement (and collection) of the specimen is being characterized. The interim conclusion is that the use of natural trace element chemistry still holds promise as a tag for natal origins, but it requires more complex procedures than originally anticipated. Indeed, it may turn out that this approach is only useful in locations where an unusual, and persistent environmental chemistry tags the fish being produced. Such locations were not sought out in this study, but researchers interested in using this approach for connectivity studies would be well advised to seek out locations of unusual chemistry whether natural or due to anthropogenic pollution.

Genetic methods are substantially better developed than are those using otolith chemistry, but even here researchers have learned that simple approaches provide limited data on demographic connectivity. To begin with, it is necessary to use genetic markers that are likely to be evolving rapidly (Hellberg 2006). Otherwise, all populations with some degree of connectivity will already contain all genotypes. Thus, while use of mtDNA sequences can be useful in many genetic studies, these can seldom be used in tests of demographic connectivity. Populations with trivial levels of connectivity will still exhibit homogeneity of mtDNA sequences, as will populations that are very strongly connected by larval dispersal. Use of slowly evolving markers, and the straightforward comparison of populational genotypic frequency are appropriate when seeking patterns of evolutionary connectivity, but the time-scales involved are such that the results usually say little about demographic processes.

What does appear promising is to use rapidly evolving microsatellite markers, and to apply various genetic parental assignment techniques to assign individual recruits to the population from which they are most likely to have originated. Further, such tests can be more powerful if a greater number of markers is used. Our initial work with the bicolor damsel made use of eight recently identified microsatellite markers (Williams et al. 2003), while developing additional markers for future more detailed work. An initial populational genetic analysis (Hepburn et al. in press) revealed, as expected, that the bicolor damsel undergoes high levels of larval dispersal along the Mesoamerican Barrier Reef with little evident genetic structure. Structure was detected at smaller (30 km) but not at larger (100 km) spatial scales, and this is likely driven by stochastic dispersal coupled with micro-geographic effects. We anticipate that temporal instability may be a fundamental characteristic of connectivity patterns in coral reef fishes, given the processes that drive larval dispersal. This further complicates attempts to characterize connectivity patterns.

A preliminary parental assignment analysis used samples of fish from the 21 sites, augmented by a collection in August 2003 from a set of 22 sites along the Belize Barrier Reef, and the southern Yucatan shore. This analysis (C. Mora, unpubl. data) was hampered by the small sizes of the collections used to characterize adult populations, but has suggested some plausible patterns of connectivity, most of which are among sites <30 km apart. Current work is seeking to extend this effort with a more robust data set collected during 2005.

While our published results to date are preliminary, it appears likely that relatively large-scale, multidisciplinary approaches such as ours are likely to be the most appropriate ones for gaining direct measurements of connectivity among reef fish populations. The work with the bicolor damsel has demonstrated that both genetic and otolith features can be used to identify sources of recruited larvae, but that both are far from routine tests. Parental assignment requires relatively large samples of fish (100 per site) from numerous separate locations taken over a few days to a couple of weeks to characterize the populations and a follow-up collection of recruits from sites of greatest interest a month later. The otolith chemistry approach requires smaller samples, but again two sets from each location a month apart, and must deal with the fact that otolith core formation is chemically different to the process later in larval life. Both techniques are technically challenging once material is back at the lab. As a consequence, these are unlikely to become methods routinely applied, but rather will be methods used for critically important species, or to validate modeling approaches.

Groups of Coexisting Species – Metassemblages

If rather little is known about the spatial structuring of reef fish populations, still less is known about the organization of reef fish communities. If each of the species present in a region is organized as a metapopulation, then the group of species takes on a complex structure of overlain metapopulations. Such a structure has been termed the metacommunity or metassemblage (the latter term seems linguistically preferable). While metassemblages have been mentioned, nobody has yet done much to explore the ramifications of their complex, multi-scaled structure. Hubbell (2001) has provided an introduction to metassemblages within his Unified Neutral Theory, and Karlson (2006) has provided definitions, and likely ramifications for population and community processes from a marine perspective.

In the simplest case, in which the component species are sufficiently similar in life history traits that their larvae disperse to a similar extent in the same environment, the metassemblage is a set of species sharing the same spatial scale of organization, and, in all probability, the same set of habitat patches. Even in this simple case, the demographic traits of the various species may vary quite differently across the various habitat patches, so that their interactions may have dramatically different outcomes from place to place.

In the majority of cases, however, the life-history traits of the various species will vary substantially with the result that the metapopulation structure of each species (assuming for now that all are present as metapopulations) may be quite different. This will only increase the complexity of interspecific interactions. Overall, exploration of the consequences of spatial structure needs to be encouraged, and may best be pursued using simple models of fish communities. The interactions among species that are possible in such systems are likely to be far richer and more varied than in the case of simple, coexisting, isolated populations, and more effective fishery management or ecosystem conservation will only be possible with far more information on such interactions than is currently available. In this respect, scientists working with fish communities may be able to make original and significant additions to metapopulation theory – a field of study that has been driven by terrestrial studies, and one that has yet to explore the community-level ramifications of metapopulation structure.

Future Directions

There is a real need for sound data on the patterns of connectivity among populations of coral reef fishes. Their generally sedentary behavior, and their usually strong association with specific habitats in a decidedly patchy world, coupled with the lengthy pelagic larval lives of most species make it very likely that most species are distributed in some form of metapopulation; however, it is impossible to look at patterns of distribution of fish in space and draw sound conclusions about the spatial scale or the population richness of the metapopulation present. To do that requires information about the scale of dispersal of the larval stages, and thus the connectivity among local groups. Nor can observation of patterns of distribution of the fish confirm that a metapopulation structure is present in any particular case. There will be cases of isolated populations, and of broadly distributed but spatially subdivided populations in addition to true metapopulations.

The precise nature of the spatial structure of a reef fish species depends on the relationship between the spatial pattern of dispersion of the fish, and the pattern of dispersal of the larval stage. Knowledge of larval dispersal is in its infancy because this is a complex process driven by the synergistic effects of variable hydrodynamics, and the sensory capabilities and behavior of the larvae. The hydrodynamics are not completely understood given that they include movement of water in close proximity to complex topography and in shallow seas. Larval behavior is poorly known both because larvae are rapidly changing in abilities as they mature, and study of their behavior is made difficult by the fact that they do their behavior while thinly distributed in the open ocean. Nevertheless, a number of groups are working in innovative ways to gradually build an empirical understanding of the process of larval dispersal for specific cases. Long term, such data will inform the increasingly sophisticated models of larval dispersal. These will become sufficiently precise that they can be deployed routinely to calculate demographic connectivity for fish of specific characteristics in a region of particular geography and oceanography.

The nature of the interactions among coexisting species of reef fish can be expected to be far more complex than those in simple, traditional models of unitary, coexisting populations. It is very likely that fish distributed across a common region of reef environment are distributed as sets of overlapping metapopulations, probably arrayed on quite different spatial scales, and there is no information yet available on the demographic and competitive consequences of such a complex spatial structure. Since the use of no-take marine reserves and other spatially explicit techniques is gaining importance as a tool for management, and since the effectiveness of reserves depends upon them being scaled appropriately to the spatial scale of the target species, there are going to have to be decisions, explicitly or implicitly made, regarding which species are to be the targets of management, and which will have to come along for the ride as best they can. Given that most coral reef fisheries are multi-species ones, and that fisheries management in these environments is closely tied to management for conservation of the reef ecosystem, this need for target species that will carry others with them has always been present, but the complex spatial structures increase the need to make these decisions appropriately. Clear answers on how best to proceed are not yet available, however it is clear that there is a need for substantial effort to build a science robust enough to help guide informed management decisions (Sale et al. 2005). There is real urgency to make progress if marine protected areas and similar spatially explicit management techniques are to fulfill the promise claimed for them.

As noted at the beginning, coral reefs are one of the environments in which there already exists considerable knowledge about the spatial organization of fish populations. Results obtained in this environment are certain to be able to inform research in environments where the challenges to determine patterns of spatial structure of populations are far greater. It would be unwise to assume that coral reefs are a special case, and that a similarly robust science guiding the effective use of spatially explicit management is not urgently needed elsewhere, wherever fish are strongly associated with components of a patchy physical environment. Such systems may be far more common than ones in which fish are distributed in simple ways, not tied to habitat features.

Acknowledgments

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Discussion

Question: You are making a big leap of faith that we understand things (wind, current, etc.) but you don't talk about it – what do you think about observing systems? Should we be more concerned regarding physical factors driving the dispersal if we are concerned about connectivity?
Sale: It depends on what you are trying to determine. The world's oceans don't move simply. However if all you want to know is where the animals come from that arrive here, all that is important is where they come from – without knowing about how they do it – in the long term, obviously we need the physical information in order to make models.

Comment: There is a discrepancy between what you said in the first slide vs. the last where you said guessing is irresponsible – please comment on that. Also, when talking about size of reserves – take it one step further and talk about networks.
Sale: Two good points – the difference between the "angry" slide and the later part of the talk: I was trying to be less angry. Lots of people are doing a lot of talking about connectivity, suggesting that we actually understand it – and therefore we can convey our understanding as we draw lines on map (for protection). But we need to acknowledge that we are drawing lines on the map without all the information. As for networks – I agree the sizing and spacing of reserves and how that relates to connectivity relates to whether we address connectivity or not.

Q: Why are we not seeing sustained partnerships between science and managers?
Sale: I think it comes down to trust. I think it's due to the fact that there have been bad experiences in the past. Scientists have talked to managers, got their help to do science, disappeared and produced science in obscure journals and then never get the information to the manager. Additionally, some managers offer their help and support, but then they are too busy to follow through. However, change is coming. A greater number of scientists recognize that they need to get their work out – and a greater number of managers know that they need help.

Comment: Many scientists are constrained by the traditional requirements for reaching tenure (i.e., not encouraged to conduct applied research). In order to facilitate better collaboration between scientists and managers we need to change the scientific judgment process – that is, it takes a lot of time to help managers. Conducting applied research and providing information for management needs to be a part of tenure decisions.
Sale: Tenure decisions (i.e., recognizing importance of applied work) are changing slowly.

Billy Causey: There are fringes both in the communities of managers and scientists – and the idea of trust is very important. We need to take the information scientists are giving us and rely on it. Also, scientists are publishing in newspapers and there are managers that aren't listening. We have to move forward with the best information we have – and we have to develop trust between scientists and managers.
Sale: There are two kinds of trust and we need to be able to trust them both: the data and the individuals. Managers must be able to understand what the scientists can contribute.

Oceanographic Connectivity

Do Queen Conch (*Strombus gigas*) Larvae Recruiting to the Florida Keys Originate from Upstream Sources? Evidence from Plankton and Drifter Studies

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Abstract

Effective marine restoration programs require an understanding of the origin of recruits to the population. However, not all managers have access to the emerging technologies that may provide definitive answers to this vexing issue. In these cases, low-tech methods may help elucidate the source of recruits. We present the results from plankton trawls and from a drift vial study designed to determine the origin of queen conch (*Strombus gigas*) larvae recruiting to the Florida Keys. Plankton surveys were conducted during the peak of the spawning season from May through August in the Florida Keys, Dry Tortugas, and Florida Straits. The drift vials were released in late June at four sites in Mexico with queen conch aggregations and at three sites in the Florida Straits (as a proxy for Cuba). We concluded that few conch larvae arrive in the Florida Keys from upstream sources. The plankton trawls showed that queen conch larval densities in the Dry Tortugas and the Florida Straits were very low (0.52 and 1.08 veligers · 100 m^{-3}, respectively) while concurrent larval density in the Keys was significantly higher (6.82 veligers · 100 m^{-3}). Only 4.1% of the 2,500 drifters released in Mexico were recovered. However, the great majority of the recoveries were retained in Mexico within the competency period of a queen conch larva (one month). Of the 1,500 vials released in the Florida Straits, 10% were recovered. All but one bypassed the Florida Keys and were recovered from Miami Beach to points north. Based on these findings, we concluded that most of the larvae found in the Keys originated from the Keys and that the system is dependent on local recruitment. Therefore, restoration efforts should target local spawning populations. Despite the well-described drawbacks associated with using drifters, we argue that there is still value in the data they provide and that these data coupled with plankton surveys can be used to address key management issues.

Introduction

Effective restoration strategies require the identification and conservation of source populations. For marine species with a planktonic life-history stage, traditional views argued for long-distance

Delgado, G.A., R.A. Glazer, D. Hawtof, D. Aldana Aranda, L.A. Rodríguez-Gil, and A. de Jesús-Navarrete. 2008. Do queen conch (*Strombus gigas*) larvae recruiting to the Florida Keys originate from upstream sources? Evidence from plankton and drifter studies. Pages 29-41 *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, 59th 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.

transport as the likely mechanism for dispersal from natal areas to distant metapopulations (Scheltema 1971). More recently, as criticism of this paradigm grew and new technologies were developed, the pendulum swung, resulting in a widespread acceptance of local retention as a significant force in supplying recruits (Cowen et al. 2000, 2003, 2006; Lindeman et al. 2001; Swearer et al. 2002; Taylor and Hellberg 2003). This is especially true in hydrographically complex systems and with species exhibiting behavioral traits that counter advection from natal populations (Sponaugle et al. 2002; Paris and Cowen 2004). However, identifying source populations within the geographic distribution of a marine species has remained elusive. Recently, emerging technologies such as otolith microchemistry, hydrodynamic modeling, satellite imagery, and the use of genetic markers have provided more sophisticated approaches to answer this basic question (Palumbi et al. 2003; Levin 2006). Unfortunately, these techniques require significant technical and financial capacity, often beyond the reach of many managers in developing countries.

Even when these methods are employed, the results are often perplexing. For example, Morales (2004), using nuclear DNA, showed that disparate queen conch (*Strombus gigas*) metapopulations from Antigua and the Florida Keys were more closely related than metapopulations spatially juxtaposed to either of these sites. Given the hydrodynamics in the Caribbean and the geographical distance between these locations, this particular conclusion is suspect. In this vein, managers are often reluctant to employ management strategies without the certainty that their approaches will result in the desired effects, especially considering that they may impact stakeholders' social or economic welfare.

We applied the results from two commonly employed approaches to address an important local resource management issue. Specifically, we coupled the results of plankton surveys for queen conch larvae and the results of drifter studies to address a question that will ultimately drive our restoration program: What component of queen conch larvae recruiting to the Florida Keys originates from outside the Keys system? If the conch population in the Keys is dependent on recruitment from upstream sources, then regional management of the resource is necessary. However, if the population is reliant on self-recruitment, then local restoration efforts will be more efficacious.

Methods

Plankton Surveys

In Florida, queen conch reproduction has been observed year round in years with warm winters; however, in years with typical annual water-temperature profiles, reproduction begins in March and ceases in late October with peak reproduction occurring from June through August (Delgado et al. 2004). Thus, we conducted plankton surveys from May through August (1996, 1998, 2000-2002; Table 1) to determine the abundance of queen conch larvae found within the Florida Keys (FK) system in relation to larvae found outside of the Keys (i.e., the Dry Tortugas region and the Florida Straits) (Fig. 1). All plankton surveys in FK were conducted in the shallow backreef zone over known queen conch spawning aggregations and approximately 1.5 km offshore of the reef in waters about 30 m deep where there are no aggregations. The Dry Tortugas region (DT) contained plankton trawls conducted from approximately 15 km west of Key West through Dry Tortugas National Park. The plankton trawls in the Florida Straits (FS) were made along a transect 113 km south of the Dry Tortugas to just north of Cuban territorial waters in July 1996 and along a transect 80 km south of Key West in August 2002 (Table 1; Fig. 1). We sampled less frequently in DT and FS compared to FK because of the budgetary and logistical constraints in reaching these remote locations.

Table 1. The number of plankton trawls conducted from 1996 to 2002 in the Florida Keys (FK), the Dry Tortugas region (DT), and the Florida Straits (FS).

	FK	DT	FS
1996			
July	--	14	10
1998			
June	14	--	--
July	4	--	--
August	12	--	--
2000			
May	20	--	--
June	44	--	--
July	24	--	--
August	45	6	--
2001			
June	2	--	--
July	4	--	--
August	5	--	--
2002			
May	4	--	--
June	23	19	--
July	28	3	--
August	22	--	17
Total	**251**	**42**	**27**

In each of these surveys, a 0.5-m-diameter, 202-micron-mesh plankton net (Sea-Gear Inc., Melbourne, FL) was towed behind a vessel at about 1.5 m · sec^{-1}. Trawls were conducted in the first meter of the water column where conch larvae are known to be most common (Barile et al. 1994; Stoner and Davis 1997). The distance traversed during each trawl was determined by using a calibrated flowmeter (General Oceanics, Miami, FL) suspended in the mouth of the plankton net. The distance traversed multiplied by the area of the mouth of the net represented the volume of seawater sampled. All samples were collected in daylight and preserved with 5% formalin in seawater. Location was determined using a Global Positioning System (GPS).

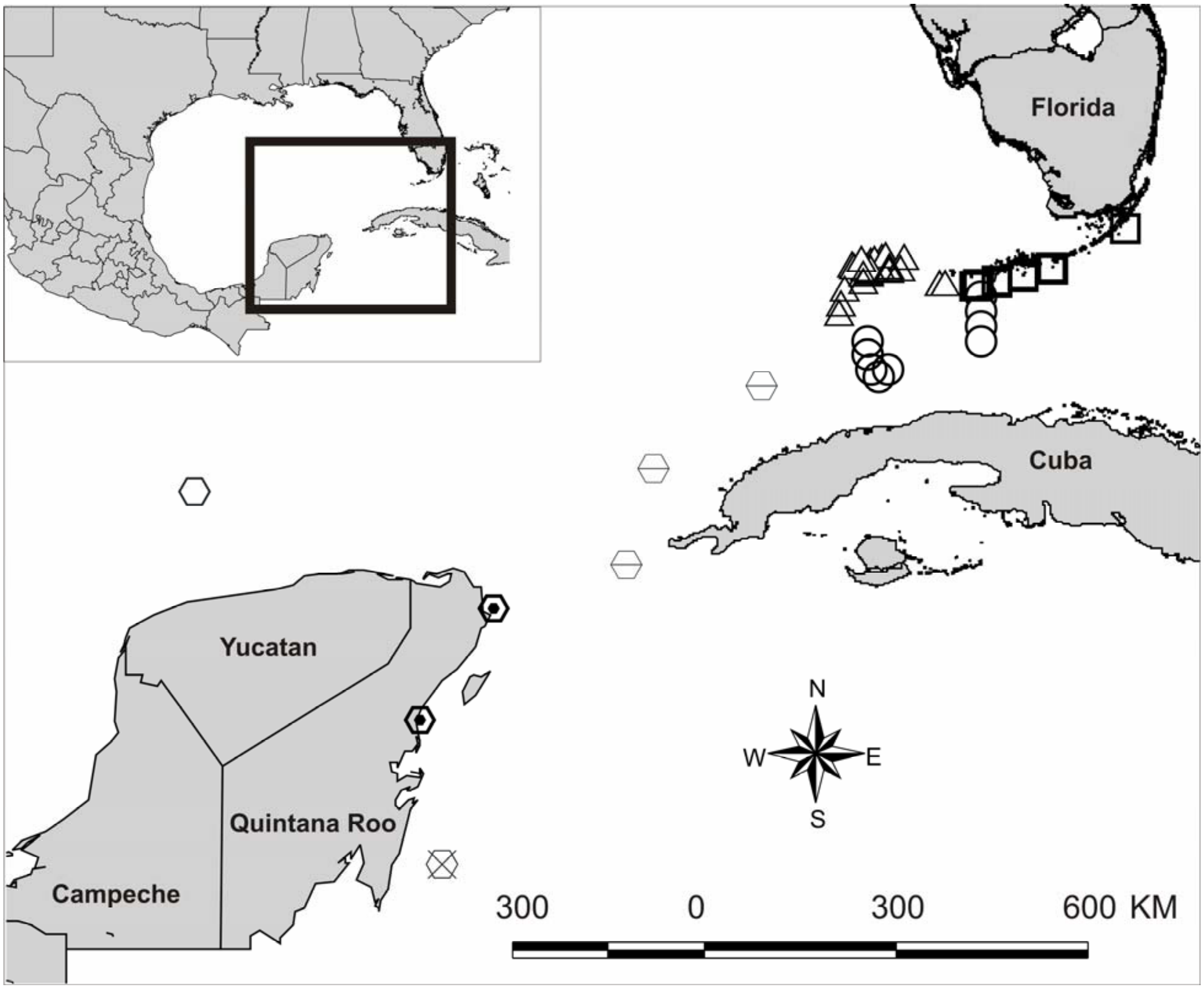

Fig. 1. Queen conch plankton trawl and drift vial release sites. Open squares represent plankton trawl sites within the Florida Keys system (FK), open triangles represent plankton trawl sites in the Dry Tortugas region (DT), and open circles represent plankton trawl sites in the Florida Straits (FS). The hexagons signify drift-vial release sites: hexagons bisected by a horizontal line symbolize the three release sites in the Florida Straits, the hexagon with an X symbolizes the Banco Chinchorro release site, the hexagons with a dot in the middle symbolize the two release sites in NE Quintana Roo (Xel-Ha is to the south; Isla Mujeres is to the north), and Alacranes Reef is symbolized by the open hexagon.

Queen conch larvae were sorted using 20x dissecting microscopes and were identified using the criteria of Davis et al. (1993). Additionally, each conch larva was measured using an optical micrometer and was classified as early- (< 500 µm), mid- (500 to 900 µm), or late-stage (> 900 µm) following the size classification of Stoner et al. (1996). Size-specific density data were used to interpret larval production and transport (Stoner et al. 1996). We interpreted early-stage density as a measure of production and late-stage density as a measure of recruitment. The larval density in each sample was calculated as the number of queen conch veligers per unit volume of seawater sampled (no. · 100 m^{-3}). We compared queen conch larval densities from upstream sources (DT and FS) with larval density in FK by using the nonparametric Kruskal-Wallis test because variances were not homogeneous and the data resisted transformation. Tests were run on SPSS 11.0 (SPSS, Chicago, Illinois). Results were considered significant if $p < 0.05$.

Planktonic Drifters

In late June 2004, we conducted a drift-vial study to examine the trajectory of passive particles entrained in the FS as well as particles originating from known queen conch spawning aggregations in Mexico. We selected late June because this corresponds to the peak in queen conch reproduction (Aldana Aranda et al. 2003; Delgado et al. 2004) and is also the month with the highest density of newly hatched (i.e., early-stage) conch larvae (de Jesús-Navarrete 2001; this study). We released a total of 4,000 scintillation vials (clear-glass with polyethylene caps, 60 mm x 25 mm) at seven sites (Fig. 1). We released 500 drifters at each of the three sites in the FS (Fig. 1). At Banco Chinchorro, we released 1,000 drifters, while 500 vials were released at each of the following sites: Xel-Ha (NE Quintana Roo), Isla Mujeres (NE Quintana Roo), and Alacranes Reef in the Gulf of Mexico (Fig. 1).

Queen conch larvae are positively phototaxic and remain near the water surface throughout most of their planktonic phase (Barile et al. 1994). In addition, conch veligers are relatively passive, with minimal diurnal vertical migration (Barile et al. 1994; Stoner and Davis 1997). Therefore, to mimic the vertical location of queen conch larvae as much as possible, we put approximately 16 g of sand in each vial to ensure that the top of the vial's cap was at the water surface. A note on waterproof paper, printed in English and Spanish, was placed inside the vial with instructions for the individual who found it to e-mail or call a toll-free telephone number to report the date, location, and the unique alphanumeric code identifying the vial's place of release. Prior to the initiation of this study, we provided press releases to local news sources to promote awareness of the experiment. To encourage people to report recoveries, rewards were offered based on a random drawing from the returns.

Results

Plankton Surveys

The density of early-stage queen conch larvae in our plankton trawls ranged from 0.0 conch · 100 m^{-3} to 50.9 conch · 100 m^{-3} with an overall mean of 1.38 conch · 100 m^{-3}. The Kruskal-Wallis test showed a statistically significant difference in early-stage larval density among our three sampling areas ($\chi^2 = 34.16$, df = 2, $p < 0.001$). No early-stage veligers were found in FS, and the density in FK was two orders of magnitude higher than that in DT (Table 2).

Mid-stage larval densities also varied from 0.0 conch · 100 m^{-3} to 50.9 conch · 100 m^{-3}; the overall mean was 1.60 conch · 100 m^{-3}. There was a statistically significant difference in mid-stage larval density among our three sampling areas ($\chi^2 = 22.89$, df = 2, $p < 0.001$). The density of mid-stage larvae in FK was ten times higher than in DT or FS (Table 2).

Late-stage larval density in our plankton trawls ranged from 0.0 conch · 100 m^{-3} to 126.9 conch · 100 m^{-3}, with an overall mean of 2.53 conch · 100 m^{-3}. As with the other two veliger stages, there was a statistically significant difference in late-stage density among our three sampling areas ($\chi^2 = 18.89$, df = 2, $p < 0.001$). Once again, the density in FK was an order of magnitude higher than in the other sampling areas (Table 2).

Table 2. The mean density (no. · 100 m^{-3}), with 99% confidence limits, of early-, mid-, and late-stage queen conch larvae found in our plankton trawls in the Florida Keys (FK), Dry Tortugas region (DT), and the Florida Straits (FS).

	Mean	99% C.I. Lower Bound	99% C.I. Upper Bound
Early-Stage			
FK	1.76	0.94	2.59
DT	0.02	-0.03	0.06
FS	0.00	--	--
Mid-Stage			
FK	1.98	1.04	2.93
DT	0.20	-0.15	0.55
FS	0.18	-0.16	0.52
Late-Stage			
FK	3.07	1.15	5.00
DT	0.30	-0.17	0.78
FS	0.90	-0.41	2.21

Pooling the three different stages together, to analyze total density, yielded similar results. The Kruskal-Wallis test showed that there was a statistically significant difference in larval queen conch density ($\chi^2 = 51.14$, df = 2, $p < 0.001$), with the density in FK almost seven times higher than in FS and more than ten times higher than in DT (Fig. 2).

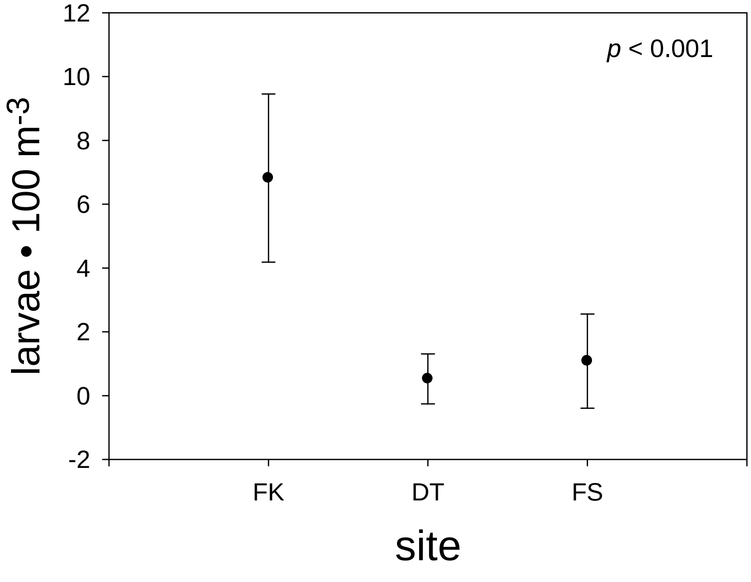

Fig. 2. Mean density (no. · 100 m^{-3}), with 99% confidence limits, of queen conch larvae (all stages combined) found in our plankton trawls in the Florida Keys (FK), Dry Tortugas region (DT), and the Florida Straits (FS).

Planktonic Drifters

A total of 254 drift vials were recovered (6.4%). Of the 1,500 vials released in the FS, 151 were recovered (10%). Of those, 113 were recovered in the first month after release (75%; we report the one-month time period because this reflects the maximum larval duration for a queen conch larva). There were comparatively fewer returns from the Mexican releases; 103 of the 2,500 drifters were recovered (4.1%), with 65% of those recovered within the first month.

The most recoveries originated from the FS release site closest to FK (Fig. 1); 131 of the 500 were recovered (26.2%), with 86% of those recovered within the first month. All of the recoveries came from points north of FK (i.e., Miami Beach to Jupiter, FL). The other two release sites in the FS yielded much fewer recoveries. Only 20 drifters were reported from those two sites, all after one month. Almost all the recoveries were reported from northern Florida to North Carolina, with one notable exception: one drifter was recovered within Bahia Honda State Park in the lower Florida Keys.

Only 3% of the Banco Chinchorro drifters were recovered (30 of 1,000). All were retained in Mexico, more specifically, in Cancun, Tulum, and Uvero in the state of Quintana Roo. Most of the vials (80%) were recovered within one month.

The two release sites in NE Quintana Roo had a combined recovery rate of 6.2% (62 of 1,000). Most of the vials were retained within Mexico; however, 22.6% (14 of the 62) were recovered in Texas. Almost 90% of the drifters recovered in Mexico were found within one month, whereas the Texas recoveries were found three to four months after release. Most of the recoveries from Xel-Ha (48 of 49) were retained in Quintana Roo, with one vial recovered near Galveston, TX. All of the recoveries from Isla Mujeres (a total of 13) were found in Texas near the border with Mexico.

There were very few recoveries from Alacranes Reef; only 11 of the 500 drifters were found (2.2%). None were found in Mexico. Ten of the vials were recovered in Texas, with the earliest found three months after release. One of the vials was recovered more than six months after release near Palm Beach in eastern Florida.

Discussion

Our plankton surveys demonstrated that there was very little queen conch larval supply from upstream sources (i.e., DT and FS) relative to the larval abundance within FK, at least at the time our study was conducted. Furthermore, the drift-vial experiment demonstrated that most of the drifters released in FS bypassed FK and were found further north, corroborating the results of two previous studies: a low-tech drifter study conducted in June 1963 (Sims and Ingle 1966) and a high-tech computer simulation of lutjanid larval transport from May to August 1984 (Paris et al. 2005). Consequently, we consider the queen conch population in the Keys as mostly self-recruiting. Based on this conclusion, a restoration strategy in south Florida must seek to protect local reproductive output (and, hence, larval supply) by conserving the local spawning stock. If the goal is to enhance larval output and therefore supply, the strategy must increase the density of spawning-aged individuals in low-density aggregations and/or increase the overall abundance of the spawning stock.

The prolonged recovery of the queen conch population in FK also argues for a closed system that is dependent on self-recruitment. In 1986, all queen conch harvest in Florida was prohibited because of a significant decline in abundance, and recovery was very slow until 2000, when a more rapid recovery began (Glazer et al. in prep.). The sluggish recovery in FK has been attributed to limitations in larval supply (Stoner et al. 1996) and to depensatory processes (i.e., Allee effects) that resulted from the low density of spawning individuals (Stoner and Ray-Culp 2000; Glazer et al. in prep.). This is consistent with the complicated system of mesoscale and sub-mesoscale gyres and eddies that regularly develop along the Keys reef tract, effectively entraining larvae and depositing them back onto settlement habitats (Lee et al. 1992; Lee et al. 1994; Lee and Williams 1999; Sponaugle et al. 2005). The slow recovery of the Keys conch population stands in contrast to the rapid recovery of populations that are presumably more open and/or fed by recruits originating from populations that are not fished (e.g., Turks and Caicos Islands: Bené and Tewfik 2003; Northern Cays of Colombia: M. Prada, pers. comm., February 2007).

Although it is likely that most conch larvae originating outside Florida bypass the Keys, it is also incontrovertible that some larvae from upstream are deposited and survive in the Keys, thereby making contributions to the genetic structure of the local population (Mitton et al. 1989; Campton et al. 1992). Significantly, the one drift vial released in FS and found within FK was recovered in an area with a sizable conch population (i.e., Bahia Honda). It is also likely that episodic hydrodynamic events may facilitate deposition of non-local larvae to the reef tract, especially in the upper Keys, where the Florida Current approaches the reef more closely (Sponaugle et al. 2005; D'Alessandro and Sponaugle 2006). In fact, most of the drifters that reached FK from outside Florida in the Sims and Ingle (1966) study were recovered in the upper Keys. Thus, upstream sources may play a greater role in recruitment events in the upper Keys compared to other regions within FK (i.e., lower Keys), where longer-lived events (e.g., the Pourtales Gyre) may more efficiently entrain and deposit locally produced larvae (Lee et al. 1992; Lee et al. 1994; Lee and Williams 1999).

In the past, conch populations in the Keys may have been more influenced by recruits from upstream sources than they are now. Historical documents detail the recovery of conch from a die-off in the Key West region in the mid-1940s and the subsequent reopening of the fishery within a decade (Key West Citizen 1952). Because the die-off was so severe that locals had to resort to obtaining conch from the Bahamas, we infer that the relatively quick recovery may have been influenced by recruits from upstream populations. We hypothesize that larval influx from upstream sources is currently greatly diminished, probably as a result of Caribbean-wide overfishing of queen conch stocks (Theile 2001). Consequently, there has been a shift in the origin of larval recruits from a mixture of upstream and locally produced larvae to a greater reliance on local sources.

Our study examined recruitment relative to queen conch issues in the Keys; however, we believe that these results can be applied to other species, particularly those with limited active larval behavior (e.g., swimming, homing), including the numerous coral species inhabiting the Florida Keys reef tract. With coral cover rapidly declining in south Florida (Gardner et al. 2003), we believe that a coral recovery and restoration program should parallel that for queen conch by focusing on ensuring sufficient reproductive output within the Keys to provide larval supply back to the system.

For a larval organism to become available to a downstream population, a larva must effectively disperse from the natal population into currents that facilitate transport and recruitment. The extensive deposition of drifters from Miami Beach northwards compared with the lone drifter recovered within the Keys supports the case for a relatively impermeable barrier, at least to passive particles, along what we term the Florida Current Shear (Fig. 3). This shear serves to direct larvae past the Keys system, particularly during the summer (Paris et al. 2005), when the Florida Current is at its period of maximum flow (Lee and Williams 1999). However, the Florida Current Shear may be more porous for species with more active larval behavior. For example, many larval fish have advanced homing behavior that facilitates recruitment to nearshore settlement habitat (Montgomery et al. 2001; Atema et al. 2002; Mora and Sale 2002). The same is true for many species of larval lobster (Jeffs et al. 2005).

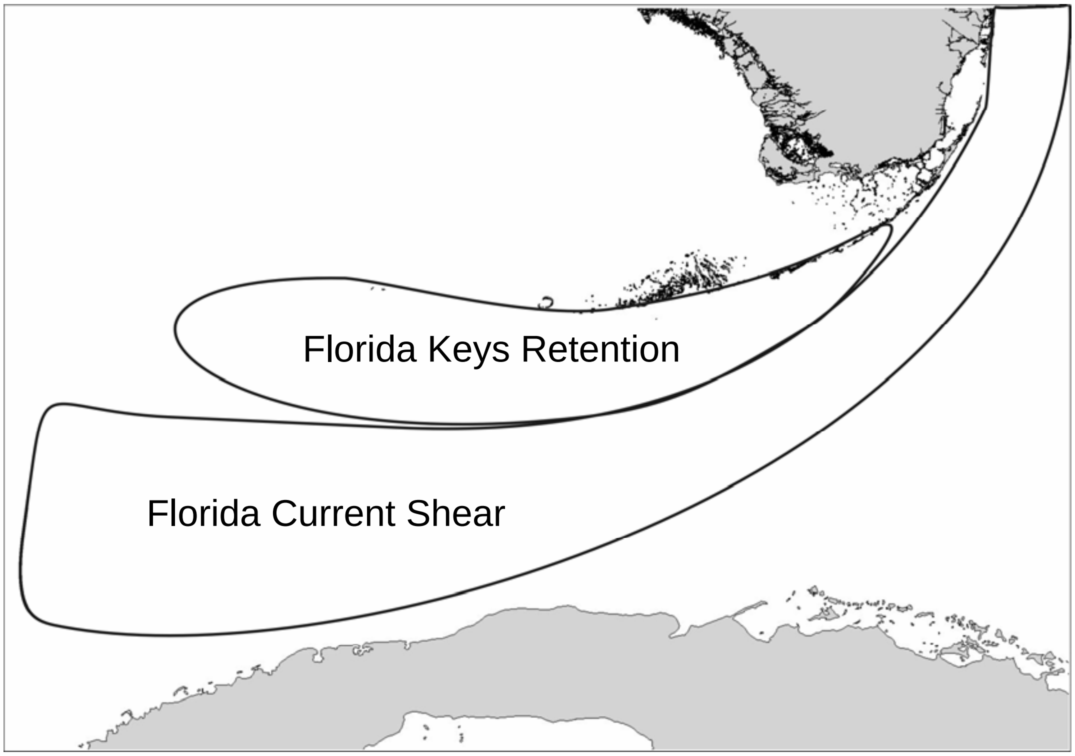

Fig. 3. Map showing the hypothesized Florida Current Shear model. Delineations are not meant as definitive boundaries and are intended for illustrative purposes only.

Despite the limited number of early-stage queen conch larvae collected in DT (to our knowledge, there are no large breeding aggregations of queen conch in this region), it is probable that this region serves as a source of larvae to FK for a variety of other species. In 1999-2000, a similar drift-vial study examined the fate of larvae originating from a significant mutton snapper (*Lutjanus analis*) spawning aggregation at Riley's Hump in DT and determined that this area provides recruits to FK (Domeier 2004). Sims and Ingle (1966) also had numerous returns in FK from the drifters they released near DT. Partly as a result of the Domeier study, the snapper aggregation is now protected from fishing, illustrating how these simple methods can be incorporated into progressive management regimes. Because of the previous studies, we included the Dry Tortugas as part of the Florida Keys system within our Florida Current Shear model (Fig. 3).

Our drift-vial study demonstrated that the queen conch populations upstream from Florida may also have retentive mechanisms, a theory supported at Banco Chinchorro by plankton surveys conducted in 1997-1998, where larval conch densities exceeded those in FS (during this study) by an order of magnitude (de Jesús-Navarrete 2001). In addition, all of the recovered drifters released at Banco Chinchorro and the majority of recovered drifters released in NE Quintana Roo were found in Mexico in areas that have or had queen conch aggregations and within the competency period for queen conch larvae. This is consistent with genetic studies that show that queen conch populations around the Yucatan Peninsula are very similar (Tello-Cetina et al. 2005). Larval dispersal models further reinforce this contention by suggesting that ecologically significant numbers of larval recruits are only available 50 to 100 km away from their origin, and that Mexico is isolated from Florida (Cowen et al. 2006). Nevertheless, larval sources in Mexico (e.g., Alacranes Reef) may play a role in episodic recruitment events in the Gulf of Mexico as shown by the drifters recovered in Texas.

When compared with the current tools employed in larval-dispersal studies, the approaches described in this study were relatively simple and unsophisticated. Like all methods, they have drawbacks. For one, both the plankton surveys and the drifters serve as “snapshots” of conditions at the time of the study, making it prudent to be cautious when applying the results more broadly. Furthermore, there were large temporal gaps and an unbalanced design in the plankton sampling. In the case of the drifters, it is assumed that the larvae they mimic behave as passive particles, an assumption not true for many marine larvae. In addition, trajectories and time spent in the water before recovery are only estimates. Despite these limitations, drifter studies have been widely used to model dispersal (Tegner and Butler 1985; Steinke and Ward 2003), and we feel that the disposition of the vials still provided valuable information relative to larval dispersal and deposition, especially considering the limited active behavior of conch veligers. Overall, we feel that our conclusions are supported when the data are examined collectively and compared with the existing literature on hydrodynamics in the region.

Our abilities to exploit more sophisticated approaches were limited by budgetary constraints, as is likely the case with many managers facing similar issues. These studies were accomplished with little capital outlay and with the assistance from a large cadre of volunteers. We feel that in the spirit of Occam’s Razor (i.e., the principle of simplicity), these approaches provided us with sufficient information to make informed decisions on how to best approach restoration of queen conch in the Keys. Based on these results, we have begun implementing a local restoration program that focuses on increasing the density of adult conch in breeding aggregations above minimum thresholds to facilitate reproductive encounters (i.e., mating) as well as increasing the abundance of adults in these aggregations to boost larval production and supply. Further research and monitoring (e.g., recruitment studies) will determine the ultimate success of this restoration strategy.

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Spatial Distribution of Surgeonfish (Acanthuridae) Pelagic Larvae in the Eastern Caribbean

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Abstract

A total of 896 surgeonfish (Acanthuridae) larvae were collected in 32 pelagic samples at 24 locations during the FAO Lesser Antilles Pelagic Ecosystem (LAPE) Project survey (April-May 2006). Larval sizes ranged from 9-41 mm indicating late-stage acronurus larvae. Large catches of acanthurid larvae (in excess of 100 individuals in a single sample) were collected to windward (NE) of the Lesser Antilles island chain more than 200 km from the nearest reef and to leeward (NW) of the islands over 50 km from reef habitat. Collection depths ranged from 39-576 m. Using mean catch per tow as an index of abundance, the highest density of both *Acanthurus* sp. and *A. bahianus* occurred in the 100-150 m depth interval. These accumulations of larvae are deeper than previously reported for this family, and coincident with, or slightly above, the depth of the chlorophyll *a* maximum and a high-salinity layer. These observations indicate that pelagic acanthurid larvae are capable of significant offshore dispersal, probably in association with the North Brazil Current retroflection eddies that typically pass northward along the eastern edge of the Lesser Antilles. The high concentration of larvae below 100 m and distribution down to 576-m depth confirms the strong swimming capability, especially of late-stage acronurus larvae, and indicates preferred use of sub-surface water masses in open ocean. This emphasizes the importance of taking vertical distribution into account when developing hydrodynamic oceanographic models for predicting reef fish larval dispersal and connectivity of Caribbean coral reefs, especially in strongly vertically-stratified waters.

Introduction

For coral reef fishes with a pelagic larval stage, predicting patterns of dispersal and connectivity remains a major challenge (Cowen et al. 2000; Cowen 2002; Mora and Sale 2002; Thorrold et al. 2002), and yet understanding the extent to which fish populations and reefs are connected is key to the appropriate design of marine protected areas and in general for effective management and conservation of coral reefs (Fisher et al. 2000; Leis 2002; Irisson et al. 2004; Cowen et al. 2006).

Larval dispersal, assumed in earlier work to be simply determined by pelagic larval duration (PLD) and patterns of water movement (e.g., Williams et al. 1984; Booth and Beretta 1994; Roberts 1997) is now recognized to be driven by multiple, complex factors and mediated to a lesser or greater degree by larval behavior (Cowen and Castro 1994; Armsworth et al. 2001; Paris and Cowen 2002; Leis and McCormick 2002; Kingsford et al. 2002). The extent to which larval behavior influences whether recruits are retained or dispersed is likely to be highly

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variable, taxon-specific, location-specific, and to depend on the temporal and spatial scale over which the question is posed (Mora and Sale 2002; Sponaugle et al. 2002; Swearer *et al.* 2002). For the vast majority of reef fish species this is simply not known. Field studies of reef fish larvae in open water are limited partly because reef fish larvae are sparse/patchy, small, and difficult to follow, and relatively few studies have used multiple sampling devices that allow determination of vertical distribution (Leis 1991a; Hogan and Mora 2005). Lack of empirical data on larval reef fish behavior and over-simplification of the many factors affecting dispersal or retention has hindered accurate predictions of reef fish dispersal (Mora and Sale 2002), though recent modeling efforts have incorporated more realistic physical and biological parameters (e.g., Cowen et al. 2006).

The focus of this study is the spatial distribution of larval surgeonfishes (Acanthuridae), a family of relatively large and common herbivores with an obligate association with coral reefs (Choat and Bellwood 1991), occurring throughout the tropics, and thought to be particularly important in the Caribbean as primary herbivores (Ogden 1976; Hay 1984) and even of commercial value in heavily fished reefs (e.g., Munro 1983; Mahon 1993; Sary et al. 1997). A few studies have examined the behavior of late- and settlement-stage acanthurid larvae in situ (e.g., Great Barrier Reef: Leis 1991b; Sancho et al. 1997; Leis and Carson-Ewart 2000; Caribbean: Sponaugle and Cowen 1996) and in the laboratory (Stobutzki and Bellwood 1997; Fisher et al. 2005), but most observations have been restricted to small numbers, to late settlement-stage larvae, and/or to neritic waters. Others have reported on distribution of acanthurid larvae (e.g., Burgess 1965; Sale 1970; Cha et al. 1994; Powell et al. 2000) but again, these studies are restricted to small samples and a limited geographical scale. None have examined the horizontal and vertical distribution of acanthurid larvae in open ocean off the Lesser Antilles island chain in the eastern Caribbean, an area of particular interest for Caribbean reef connectivity, being the most up-current archipelago of the Caribbean region.

Methods

Research Cruise

Data for this study were collected during the Food and Agriculture Organisation - Lesser Antilles Pelagic Ecosystem (FAO-LAPE) survey cruise onboard the *RV Celtic Explorer* from 26 April – 22 May, 2006. A full report of the research cruise is given in Fanning (2006).

Trawl Sampling

Mid-water sampling of fish and invertebrates took place at 44 selected locations along 40 stratified zig-zag transects across the Lesser Antilles (Fig. 1a). Sampling between 18-592-m depth was achieved by mid-water trawling with a single cod-end herring net (for shallow sets only) or with a multi-purpose trawl fitted with an acoustically operated multi-sampler with three cod-ends that could that could be opened and closed sequentially at target depths to sample discrete (20-30 m) depth intervals. As such, a total of 95 discrete depth samples were taken. Trawling time was 20-30 min at a speed of 3.5 knots (1.8 m sec^{-1}).

All catches were sorted immediately after they were brought onboard. Acanthurid larvae were identified to species wherever possible, weighed to the nearest 1 g, counted, and measured individually to the nearest 0.1 mm with calipers.

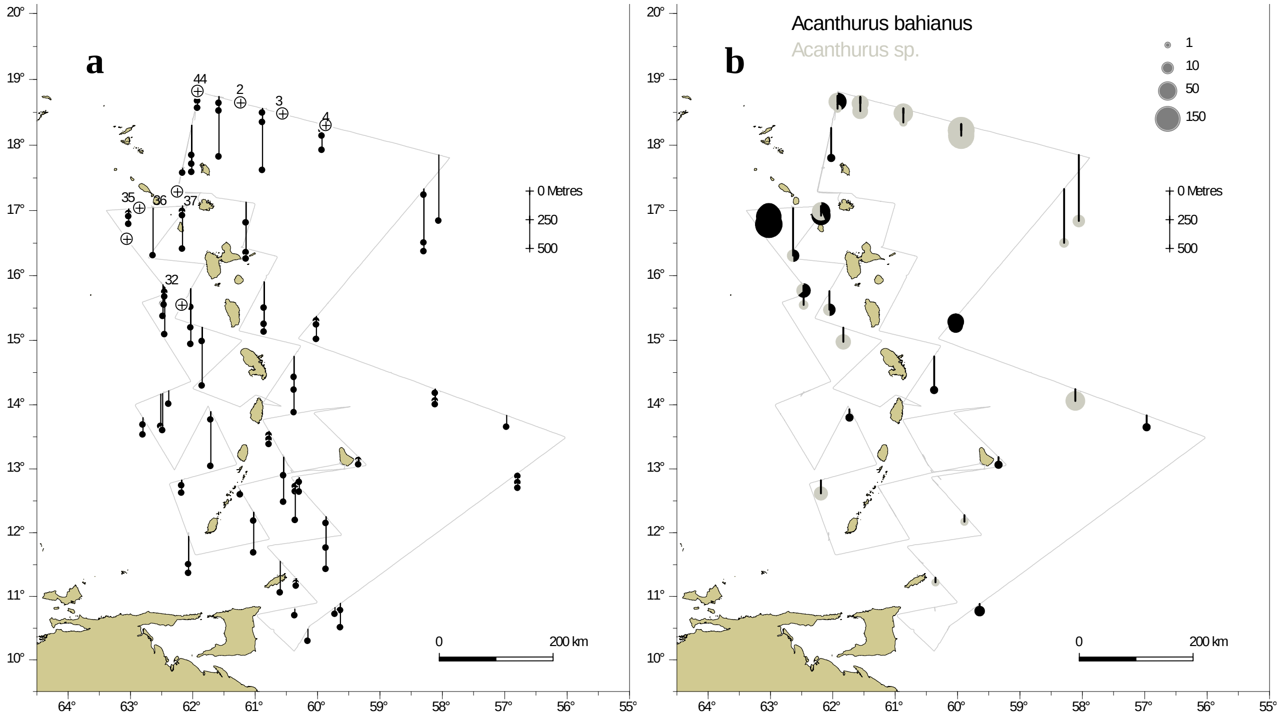

Fig. 1. Map of the Lesser Antilles island chain showing cruise transects and locations and depths of: **a** - all pelagic trawl sets (fishing station numbers and selected adjacent oceanographic stations with CTD casts are also indicated); **b** - catches of acanthurid larvae per trawl net (indicated by relative size of filled circles). *Acanthurus* sp. refers to *A. chirurgus* and/or *A. coeruleus*.

Oceanographic Sampling

Salinity and temperature depth profiles to 500 m and 1500 m were taken at pre-selected stations along the transects with a Seabird 911 conductivity-temperature-depth (CTD) probe. An in situ fluorescence profile, giving an index of chlorophyll *a* concentration, was also measured down to 500 m at the CTD 500-m stations using a Sea Tech FL500 fluorometer.

Results

Species and Larval Size

Two species could be reliably separated, the ocean surgeon, *Acanthurus bahianus* (based on the presence of a long second dorsal fin spine), and a second species that differed from *A. bahianus* but could not be identified to species (either *A. chirurgus* or *A. coeruleus*) and was therefore classified as *Acanthurus* sp.

Acanthurid sizes ranged from 9-41 mm (overall mean: 25.4 mm), indicating late-stage acronurus larvae. *A. bahianus* were slightly smaller (mean size: 20.4 mm) than *Acanthurus* sp. (mean size: 30.0 mm) (Fig. 2).

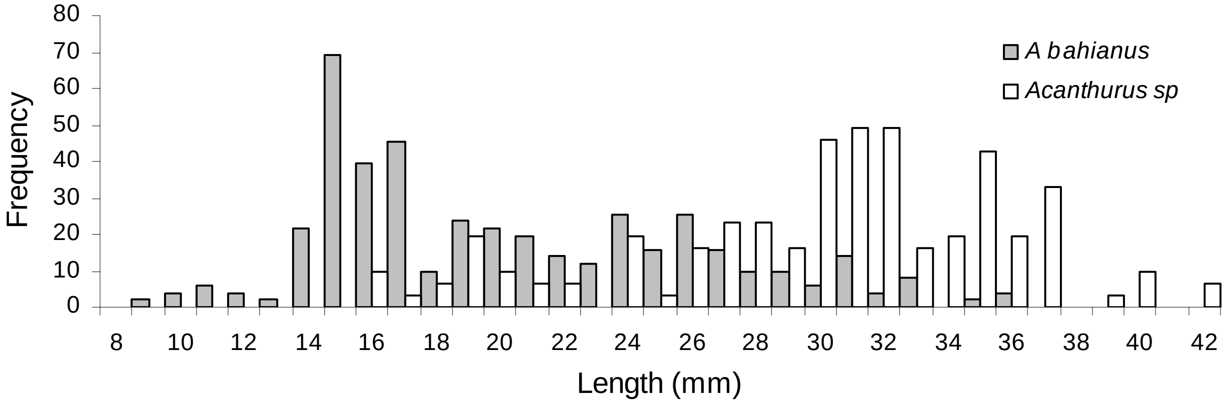

Fig. 2. Size-frequency of acanthurid larvae taken by pelagic mid-water trawls in the Lesser Antilles. *Acanthurus* sp. refers to *A. chirurgus* and/or *A. coeruleu*s.

Horizontal Distribution

A total of 896 acanthurid larvae (436 *A. bahianus* and 460 *Acanthurus* sp.) were collected in 32 of 95 pelagic samples at 24 of 44 locations across the Lesser Antilles, giving an overall mean catch rate of 9.3 larvae per net tow for the entire area (Fig. 1b). Large catches (>100 individuals in a single sample) were collected to windward (NE) of the Lesser Antilles island chain more than 200 km from the nearest reef, and to leeward (NW) of the islands over 50 km from reef habitat. Some larvae were found in excess of 350 km from the nearest reef and to windward of the islands (Fig. 1b), i.e., to the longitudinal limits of the sampling effort. Occurrence of acanthurids in the southern part of the survey area was relatively low compared with the northern part (Fig. 1a, b).

Vertical Distribution

Larvae were found at depths ranging from 39-576 m and large accumulations of larvae were found in sub-surface waters between 50 and 150 m depth (Table 1). Using mean catch per net tow as an index of abundance, the highest densities of both *A. bahianus* and *Acanthurus* sp. occurred in the 100-150 m depth interval. This coincided with, or was slightly above the deep chlorophyll *a* maximum and a layer of highly saline water with salinities in excess of 37 psu and temperatures of 22-25 ^{o}C (Fig. 3).

Discussion

The horizontal distribution of acanthurid larvae over the Lesser Antilles up to 350 km from the nearest island confirms that pelagic larvae of *Acanthurus* spp. are capable of significant offshore dispersal, away from natal reef areas into open ocean. This is not altogether surprising for a family with pelagic eggs and a comparatively long pelagic larval duration (PLD is 44-69 d for *A. bahianus*, Sponaugle and Cowen 1996; 44-83 d for *A. triostegus*, Randall 1961; McCormick 1999). Furthermore the specialized morphology (acronurus larva) suggests adaptation to long periods of pelagic life (Schultz and Cowen 1994; Cowen and Sponaugle 1997).

Table 1. Abundance of acanthurid larvae by depth strata over the Lesser Antilles, showing the number of net trawls (sets), the total numbers of larvae collected and the catch rate.

Depth (m)	No. sets	Total catch			Mean catch per net tow		
		A. bahianus	*Acanthurus* sp.	All	*A. bahianus*	*Acanthurus* sp.	All
30-50	16	94	60	154	5.9	3.8	9.6
50-99	21	180	175	355	8.6	8.3	16.9
100-149	15	155	209	363	10.3	13.9	24.2
150-199	8	3	5	8	0.4	0.6	1.0
200-399	19	2	0	2	0.1	0.0	0.1
400-599	16	3	11	14	0.2	0.7	0.9
Overall	95	436	460	896	4.6	4.8	9.4

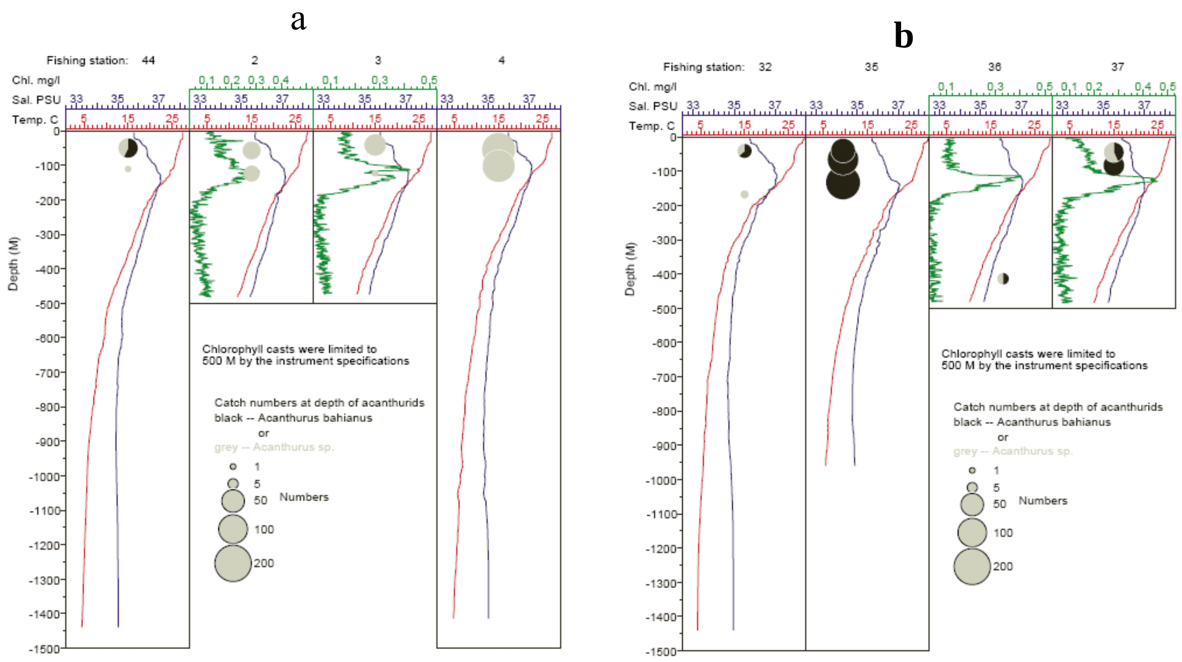

Fig. 3. Conductivity, temperature, depth-profiles (CTD 500 m and CTD 1500 m) at selected oceanographic stations in the Lesser Antilles showing typical water mass characteristics for open ocean areas with high abundance of acanthurid larvae. **a** - shows oceanographic stations sampled along the most northerly transect to the windward (NE) of the island chain, **b** - shows stations to the leeward (NW) of the islands. Locations of fishing stations and adjacent oceanographic stations are shown in Fig. 1a. *Acanthurus* sp. refers to *A. chirurgus* and/or *A. coeruleus*.

Very few studies have reported on the horizontal distribution of acanthurid larvae for comparison, and all are relatively limited in geographical scope. For example, Powell et al. (2000) reported a small number (n = 11) of early stage acanthurid larvae along an onshore-offshore transect in Onslow Bay, North Carolina, approximately 40-80 km from shore, but did not indicate at which stations along the transect they were found. Sale (1970) studied the distribution of larval Acanthuridae off Hawaii and found *A. triostegus* to be more abundant at an offshore station (48-58 km offshore) than a nearshore station (4.8-8 km from shore) off Oahu, corroborating the results reported here of higher densities offshore. However, no study has reported Acanthuridae so far from the nearest reef as in the present study, although other reef fish larvae have been collected several hundred km from reef habitat (Leis 1984; Victor 1987; Clarke 1995). These findings contrast with the more restricted reef fish larval dispersal patterns reported in other studies. For example, Ramirez-Mella and Garcia-Sais (2003) reported that reef fish larval dispersal was restricted to a maximum of 46 km from shore off La Parguera, Puerto Rico, and Cowen et al. (2006) suggested that ecologically relevant reef fish larval dispersal is likely to be under 140 km from most source reefs in the Caribbean for many species, based on a model of surface currents coupled with estimates of larval mortality. The exceptions are likely to be in areas of either high directional flow or in the vicinity of eddies carrying larvae offshore (e.g., Lobel and Robinson 1986; Sponaugle et al. 2005).

The vertical distribution of acanthurid larvae observed in this study, with high concentrations of larvae below 100 m and distribution down to 576 m depth indicates strong swimming capability of late-stage larvae, and also indicates preferred use of sub-surface water masses in the open ocean of the Lesser Antilles sub-region. That acanthurid larvae are strong swimmers is corroborated by several laboratory and field studies that have highlighted the swimming capabilities of *Acanthurus* spp. and placed them among the strongest swimmers of larval reef fishes (Sancho et al. 1997; Stobutzki and Bellwood 1997; Leis and Carson-Ewart 2000; Fisher et al. 2005). They are reported to be capable of sustained horizontal swimming speeds well in excess of ambient currents (Leis and Carson-Ewart 2000) and, in the laboratory, have demonstrated the ability to swim 95 km in 8 d (Stobutzki and Bellwood 1997).

Surprisingly little information exists on vertical distribution of reef fish larvae in oceanic waters (Cowen 2002; Leis and McCormick 2002; Hogan and Mora 2005), even though the outcome of predicted dispersal can vary enormously with depth (Cowen and Castro 1994; Cowen and Sponaugle 1997; Leis 2002; Paris and Cowen 2004). A few studies have examined vertical distribution in Acanthuridae, and these suggest that the larvae are generally restricted to the upper 100 m of the water column. For example, acanthurid larvae off Florida were found to be most abundant above 100 m (Burgess 1965). This was corroborated by Cha et al. (1994) who reported 69% of *Acanthurus* spp. larvae were found in the upper 25 m of the Florida Current and none were found below 50 m, although sampling occurred to 200 m. Acanthurid larvae have been found in the upper 100 m of the water column in the Caribbean Sea and Gulf of Mexico (Belyanina 1975; cited in Leis 1991a). Sale (1970) found *A. triostegus* in surface (0-20 m deep) and deep (85-120 m) hauls off Oahu, but recorded no significant difference in abundance at these two depths. Sale (1970) also suggested that larval acanthurids were primarily limited to the upper 100 m off Hawaii, based on stomach content analysis of tuna species with different forage depths. Oceanic mid-water trawl samples at discrete depths in the Banda Sea, Indonesia, revealed relatively high abundance of acanthurid larvae in the 0-100 m stratum, only 4 specimens in the deeper stratum (100-300 m), and none below 300 m (Soewito and Schalk 1990). Leis (1991b) investigated vertical distribution of pelagic fish larvae including Acanthuridae in the shallow Great Barrier Reef lagoon off Lizard Island, but sampling was restricted to the upper 20 m. Collections of larval fish off Barbados indicate that acanthurids are uncommon (Powles 1975) and restricted to the upper 50 m (Cowen, unpubl. data). Thus, the findings of the present study are remarkable in terms of the depths these acanthurid larvae were found with peak numbers generally deeper (100-150 m) than most earlier reports and maximum depths (>500 m) well in excess of any earlier report. Most larvae we collected were found within the high-salinity layer, near the chlorophyll maximum, but no explicit relationship with water mass was clear. The deepest larvae collected were in water as low as 10º C, though most were collected above the thermocline and therefore in temperatures more typical of coral reef fish.

While our observations may seem to support the broad-distribution, open-population, end of the larval-dispersal spectrum, it is likely that larvae windward (NE) of the island chain are being dispersed in association with large gyral motions of the anticyclonic North Brazil Current retroflection eddies that typically pass northward along the eastern edge of the Lesser Antilles (Goni and Johns 2001; Fratantoni and Glickson 2002). As such, larvae are likely to be retained in the Lesser Antilles for some time and perhaps returned to coastal waters during the passage of these eddies, as has been determined for Barbados (Cowen et al. 2003). Likewise, leeward (NW) accumulations of larvae may be entrained in complex eddies typically associated with strong circulation pushing through island passages (Molinari et al. 1981; Garrafo et al. 2003). The suggestion that retention and return of acanthurid larvae to shore occurs and is not entirely passive was made several decades ago (Randall 1961; Sale 1969). Indeed, Sale (1970) reported that the accumulation of acanthurid larvae at the offshore station in Hawaii was a consequence of larvae being entrained in a large current gyre 100 km in diameter and extending to 300 m depth that would sweep larvae within 25-50 km of the coast of Oahu every 5-6 d, providing a possible opportunity for self-recruitment if coupled with active directional swimming.

A mechanism for larval fish retention is reported for Barbados involving current flow around the island forced by topography of the island ridge and coupled with downward movement throughout ontogeny ensuring transport of late settlement-stage larvae onshore (Cowen and Castro 1994; Cowen et al. 2003; Paris and Cowen 2004). Further support for retention or return of acanthurid larvae to source reefs rather than broad dispersal was provided by Planes et al. (1996) and Planes and Fauvelot (2002) who reported strong genetic stratification of ocean populations of *A. triostegus* across the Pacific, indicating limited dispersal and self-recruitment in this species.

In summary, our observations stress the importance of taking vertical distribution of larvae and vertical stratification of ocean currents into account when developing dispersal models. The cause for the deep occurrence of acanthurid larvae is not clear from this study, though finding food in association with the chlorophyll maximum is one possibility. Alternatively, vertical migration to deeper waters may be a means of mediating the dispersal outcome for these fish, with the normal outcome being retention closer to shore and/or return to coastal environments. Many of the larvae in this study caught long distances offshore might be returned if eddy circulation is favorable. However, it is also feasible that many, if not all of these larvae were captured in a non-recruitment favorable event and were lost to the population.

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Orientation with No Frame of Reference (OWNFOR): A Novel System to Observe and Quantify Orientation in Reef Fish Larvae

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Abstract

A central question in marine ecology today is to understand the spatial scales over which populations are connected by larval dispersal. Although coral reef fish larvae develop strong behavioral capabilities during the processes of dispersal (e.g., vertical migration, swimming), the influence of these capabilities on survival depends on the ability of larvae to orient in the open ocean. Yet, behavioral mechanisms by which reef fish larvae achieve successful recruitment from blue waters to coral reefs are still unknown. We describe a novel system designed to detect and quantify the orientation of larval coral reef fish in the pelagic environment, where they have no apparent frame of reference to navigate. The Orientation With No Frame Of Reference (OWNFOR) system is deployed at sea and drifts while videotaping the movement of a larva placed within a clear, circular arena. The data are then treated with a combination of open-source programs that track particles and analyze orientation using circular statistics. We demonstrate that (1) this system successfully detects orientation behavior and (2) the shape of the behavioral arena and appropriate statistical treatments minimize the impact of the semi-enclosure on quantifying larval bearing. This observational approach provides a means of assessing the abilities of larvae to orientate during ontogeny and of testing cues, representing a breakthrough in the field of larval ecology. Such behavioral data will provide critical inputs to a new generation of biophysical larval dispersal models that are vital to achieve a better understanding of larval connectivity in marine systems.

Introduction

Most coral reef fishes have a dispersive larval stage that might distance them from reef predators (Johannes 1978). This dispersive stage ends when the well-developed larva leaves the pelagic environment and settles onto coral reef habitat. The supply rate of larvae is critical for the structure of reef populations and is recognized as an important factor in their management (Sale and Kritzer this issue). With the increasing trend toward the implementation of a network of marine protected areas (MPAs) designed to enhance spawning production and to maximize the number of larvae settling within the network, an understanding of the connectivity of marine populations through larval dispersal and recruitment patterns has become an area of critical concern. Understanding population connectivity is one of the most important and challenging goals in ecology, evolution, and conservation (Steneck 2006). There has been considerable

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investment in high-resolution numerical simulations of currents from basin-scale circulation to small hydrodynamic features around coral reefs (Wolanski and Sarenski 1997; Chassignet et al. 2006; Cherubin et al 2007; Ezer et al 2005). Taking advantage of these models, spatially explicit biophysical models have been used to determine the trajectories of individual larvae from a population in realistic flow fields (Werner et al. 2001; Paris et al. 2002, 2005; Cowen et al. 2000, 2006). Yet, a major question in marine ecology is how the larval stages of benthic marine organisms behave while in the pelagic environment, long prior to settlement, because their behavior could considerably influence their dispersal trajectories (see Cowen 2002, for review). Recent advances in the study of the sensory system of reef fish larvae (see Myrberg and Fuiman 2002; Montgomery et al. 2006, for review), of their vertical migration (Paris and Cowen 2004) and of their swimming behavior (Leis 2006, for review) have demonstrated that larval reef fishes have considerable capabilities that enable them to actively control their position in the ocean at relatively large scales. Late-stage larvae may navigate toward suitable settlement sites by responding to a variety of gradients of environmental stimuli (Kingsford et al. 2002) and even early-stage fish larvae can exhibit directed horizontal or vertical motion (Fisher et al. 2000; Paris and Cowen 2004). However, the realized impact of such behavior remains unclear. For larvae to have a significant impact on their dispersal they must be capable of orientation, possibly using a variety of different cues (Stobuski and Belwood 1998; Leis and Carson-Ewart 2003; Leis 2006).

To investigate the ability of reef fish larvae to orientate during ontogeny, we present a new concept for behavioral observations in the pelagic environment. The notion is that larvae have no apparent frame of reference to orientate in open waters. Presumably, larvae may not sense the direction of the water mass in which they are embedded (Galileo 1632) to avoid being swept downstream, nor are they able to see the coral reefs or the seafloor that would provide a visual frame of reference for navigation back home or to the nearest coral reef. Our main goal is to observe larvae in their natural settings and detect whether they actively swim in a non-random direction while the current moves them. This contribution describes the Orientation With No Frame of Reference (OWNFOR) system and tests its capacity to record data on orientation. The effectiveness of the system depends on the success in recording true orientation. Because fish larvae are known to display a rheotactic behavior (Stobutzki and Bellwood 1994; Hogan and Mora 2005), usually swimming against the current, it is important that the system drifts exactly locked in the current (i.e., with no drag). Furthermore, the larva's movement is altered near the edges of the arena and might bias its orientation behavior by holding the larva in a specific location. Thus, in addition to demonstrate an orientation versus random movement, we need to show that the larva has no position preference within the circular arena.

Materials and Methods

OWNFOR

The observational system is designed to detect and quantify orientation behavior of larval fish in their natural settings using the concept of a float. The structural frame is equipped with drogue panels, a surface global positioning system (GPS), a compass, a reference marker, a digital video camera, a small environmental sensing system (i.e., conductivity-temperature-density, CTD), and a circular (38 cm ∅, 10 cm deep), and a semi-enclosed behavioral arena (Fig. 1). A larva placed inside the arena is filmed while the system drifts at sea. The frame is half-submerged along the side of the boat to introduce the specimen before it is released (Fig. 1E). The boat motors downstream and the engine is turned off during the behavioral trial. The system is recovered and the larva is replaced for the next deployment. The video recording system looks down on the arena, as well as on the reference marker to enable corrections on the recorded larval trajectory and the compass to obtain orientation data in a fixed cardinal reference (Fig. 1D). The recording is done in progressive scanning mode (30 frames s^{-1}) for maximum resolution per image (0.3 mm pixel^{-1}). The video data (i.e., Mini DV tape) are retrieved after a set of deployments (Fig. 2A, 3B). To test this novel system, pre-settlement reef fish were captured in light traps on French Reef (Key Largo), collected at sunrise and immediately used in the trials. We first deployed OWNFOR at 20 m below the surface, near the 50-m isobath, off Key Largo on June 8, 2006. After examination of the video, the seafloor was visible, providing the larva a visual frame of reference for navigation (Fig. 2B). For the purpose of testing larval fish orientation with no visual cue, the bottom depth of the test release sites was always $\geq$ 60 m as larvae may see the dark outline of reef patches from as far as 30 m (Lara 2001).

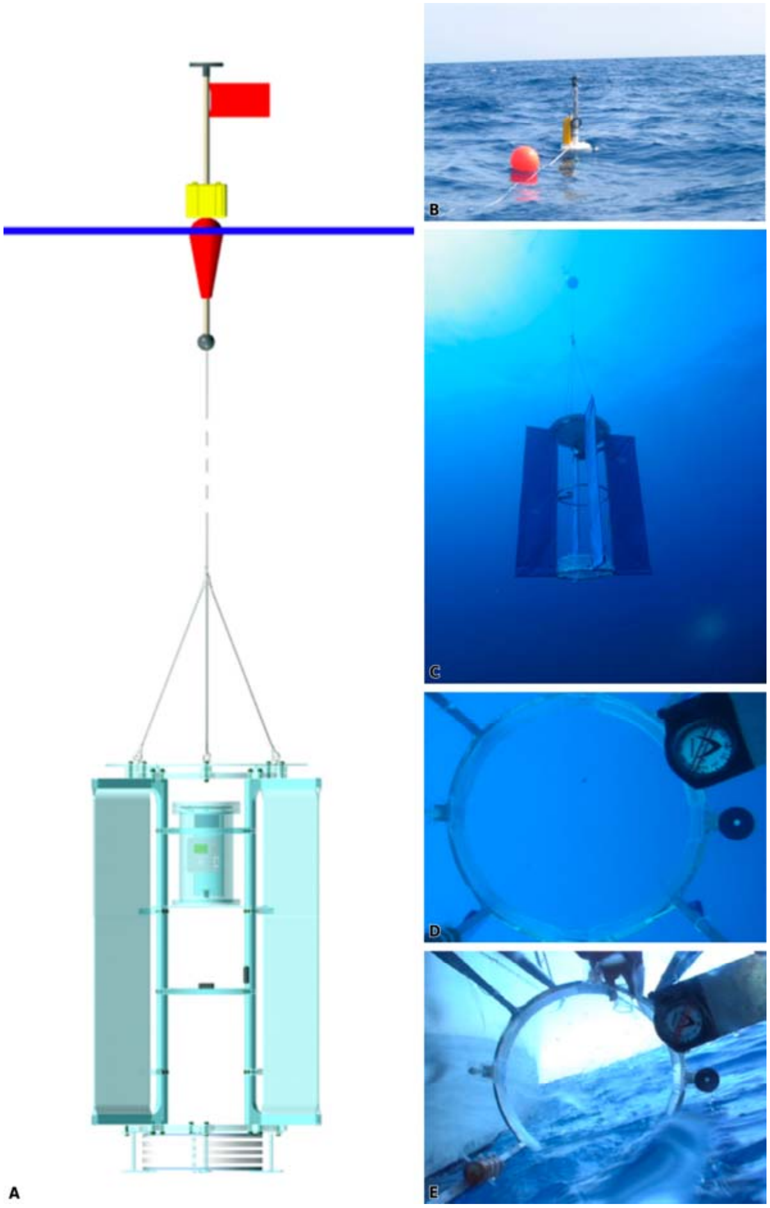


Fig. 1. Orientation With No Frame Of Reference (OWNFOR) system: A) schematic view of the system deployed at sea; B) the surface bouy is equipped with a GPS antenna and data logger to record the drifting track of the system; C) the underwater drifting unit is linked to the surface buoy via a line, a small sub-surface buoy, and three bridles and is made of four aluminum bars and three rings holding the drogues, a circular arena (made of optically clear acrylic sheets on the top and bottom and a 300 µm Nytex® mesh on the periphery, attached with velcro), and a digital video camera (Sony Handycam DCR-PC350®) housed in a pressure vessel (Ikelite Underwater Systems Inc.); D) view from the camera looking down on the behavioral arena with the larva (in the red circle), a compass and a reference marker; E) a larva is placed in the arena by opening the mesh, while the system is half-emerged along the boat and setup for a new trial.

Movement Analysis

In order to describe and compare orientation behaviors, the convention is directionality in the swimming bearings (Leis et al. 1996). However, in a circular arena the larva is bounded and orientation is associated with two types of behavior: the larva will either (1) continue to swim along the edge then swim back toward its preferred direction, in which case swimming direction indicates orientation, or (2) stop and stay in the preferred direction, in which case the larval position indicates the orientation. To capture those behaviors, we need a good representation of the trajectory of the larva for each observation. The video is sub-sampled to 0.6 mm pixel^{-1} and 1 image s^{-1} because it is sufficient to resolve the movement of the pigmented post-flexion larvae used in these experiments (mean standard length = 4.5 mm) with typical mean swimming speed of 10-15 cm s^{-1} (Leis 2006). The position of the larva is manually recorded with *Image J®,* an Open Source Software (OSS) for image analysis. Based on this OSS, we developed a program called *BlueBidule* (http://rsmas.miami.edu/personal/cparis/ownfor/doc/bluebidule.html) to automatically perform video processing (i.e., denoising, sub-sampling), tracking (i.e. tracks calibration, tracking of the larva, the fixed reference point and the compass, tracks corrections), the statistical analyses, and the visualization.

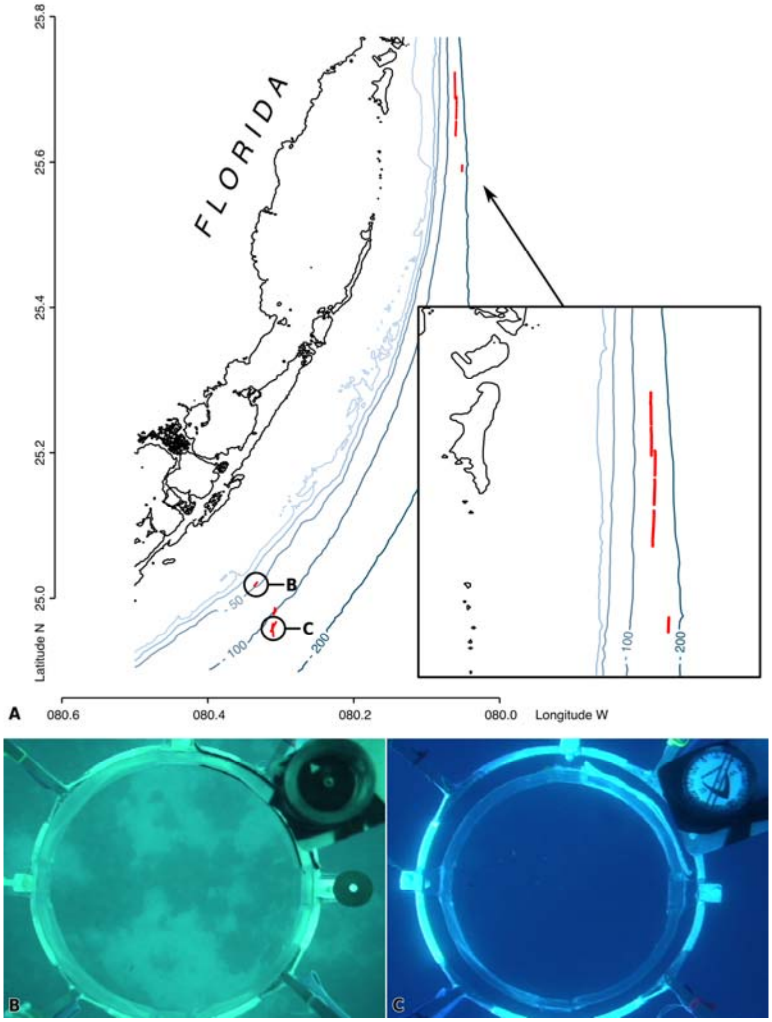


Fig. 2. OWNFOR deployments: **A)** drift trajectories of the system deployed at 20 m from the surface during June 16, 2005, offshore Biscayne Bay (Miami) and during September 9, 2005, offshore Key Largo (Florida Keys); Snapshots of the arena during a deployment in ca. 40 m **(B)** and 100 m **(C)** waters. Note that the coral reef is visible in **(B)**, giving a visual point of reference to the larva on its drift and, in this case, a direct visual cue of settlement habitat.

Circular Statistics

The circular shape and symmetrical design of the arena is ideal to perform circular statistics (Batschelet 1981). The bearings of vectors between the center of the aquarium and the position of the larva (or the swimming direction) are extracted from the trajectory data. Because we are interested in the orientation in a cardinal reference, magnetic north as determined by the compass is automatically recorded to correct the larval trajectory from warp caused by changes in the float direction and/or rotation. The angular component of the compass position is subtracted from the angular component of the position of the larva, on each frame. Swimming distances are then computed between two successive frames only when the larva is detected on both, and converted to instantaneous swimming speeds. Those bearings (positions and directions) are regarded as unit vectors and their sum vectors are computed. Their bearings are the mean angle of each dataset and their norm describes the strength of the directionality of the data. We can compute :

$$r = \frac{||\vec{V}||}{N}$$

where N is the number of observations and V the sum vector. If the positions are evenly distributed in the aquarium or if swimming direction is random, the sum vector will be small. In contrast, if the larva is more frequently present in one portion of the arena or if it swims more often toward one direction, the sum vector will be longer and pointing in this direction. As a direct consequence, the closer it is to one, the less random the observations. Hence, the sum vector captures the behaviors we want to detect and quantify. The mean bearing is then tested for directionality with Rayleigh's test for uniformity and the null hypothesis is rejected if the sum vector (r) is not significantly different from one. As in all statistical frameworks, this technique assumes that observations are independent from each other. This may be true for swimming directions but not for position (Fig. 4). Therefore, we use partial bootstrapping by computing statistic descriptors on a subset (i.e., 5%) of independent position data and repeat this process 1000 times for each larva (Fig. 3D). The percentage of sub-sampling is chosen as the largest percentage for which independent data are obtained.

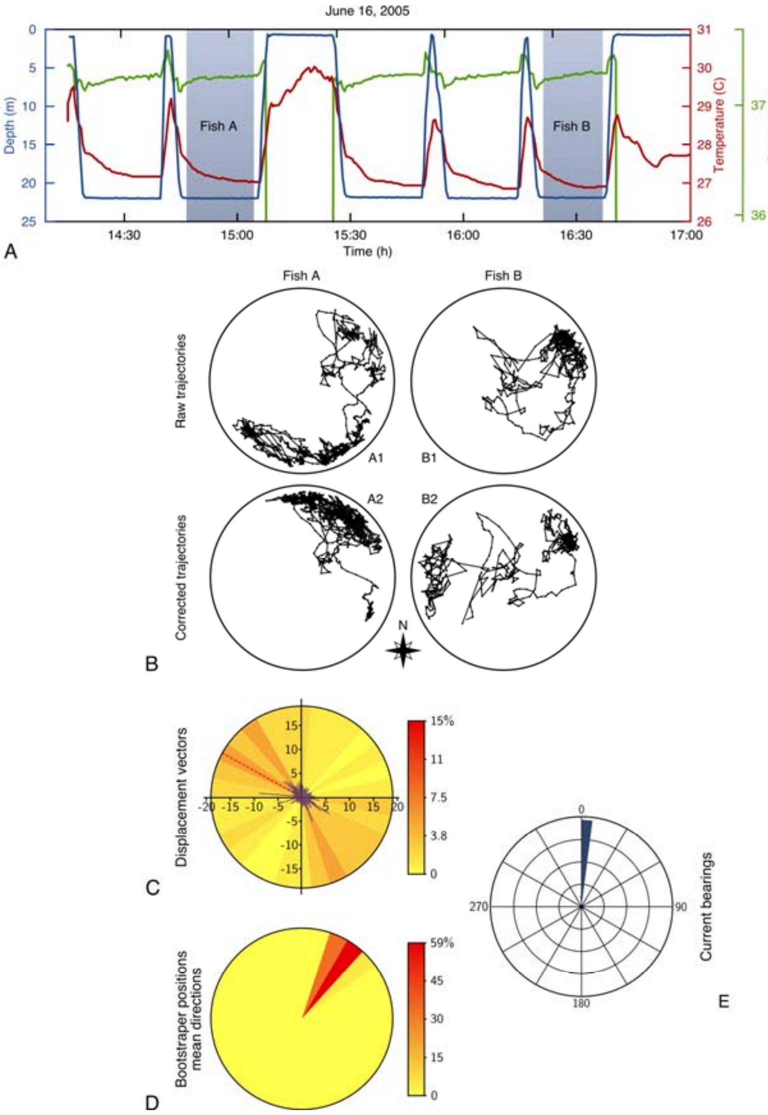


Fig. 3. Detection and quantification of orientation behavior: **A)** Depth, salinity and temperature profile of a series of five deployments of the OWNFOR system offshore Key Largo, Florida Keys; **B)** trajectories of larvae *A* and *B* before and after compass correction, showing that larva *A* orientate while larva *B* does not (the analysis of larva *B* is stopped); **C)** displacement vector of larva *A* plotted from the center of the arena with mean direction indicated by the red dashed line; **D)** mean direction associated with the bootstrapped positions of the random subset of positions of larva *A* ; **E)** rose diagram of the current direction. The Florida Current flowed mostly northward at 1.6 m s^{-1} on June 16, 2005.

Results

Detection of Orientation Behavior

A total of eighteen 20-minute trials with larvae from four families (Apogonidae, Balistidae, Pomacentridae, Monacanthidae) were used for the analyses. Based on the analyses of positions, sixteen out of eighteen trials showed significant concentration of larvae positions. From those, eight were identified as true orientation, two as artefactual concentrations and the rest could not be discriminated. There seemed to be a taxonomic effect on orientation, but we did not have enough larvae from each taxon to robustly document this effect nor to document differences in bearings between species. An example of discrimination between orientation versus non-orientation is given in Fig. 3. A larva that orients keeps a steady position relative to a cardinal reference, regardless of the direction of the drift or of the rotation of the system (e.g., larva A, Fig. 3B). Alternatively, a larva that does not orient shows either a random position with regard to a bearing, and/or preference for a section of the arena (e.g., larva B, Fig. 3B). The drift of the apparatus revealed the steady direction of the Florida Current during the trials (Table 1, Fig. 2). However, none of the larvae oriented directly opposed to this drift (i.e., rheotaxis behavior), indicating that there was no detectable flow in the arena and that the device was well locked in the current, a fundamental criterion to provide the natural settings of the pelagic larva (i.e., no frame of reference in relation to the direction of the current).

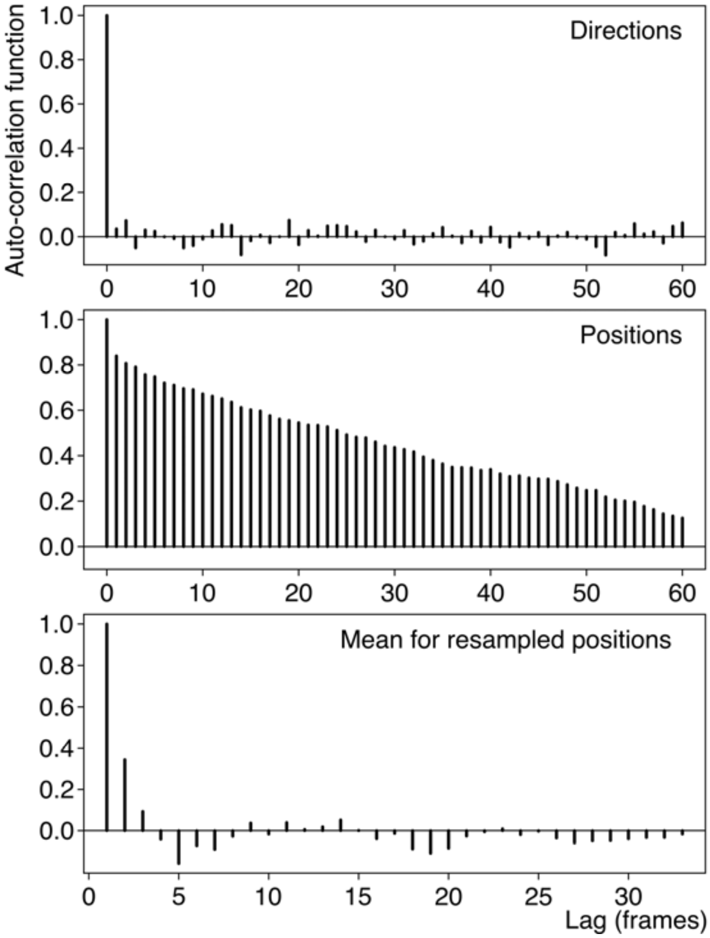


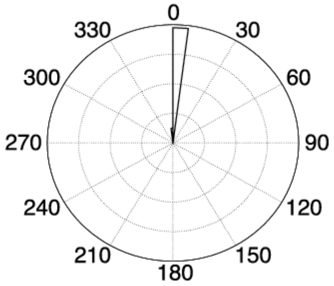
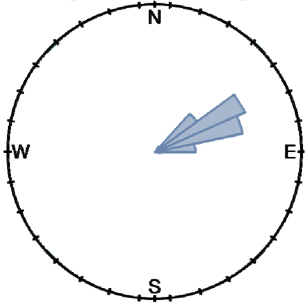
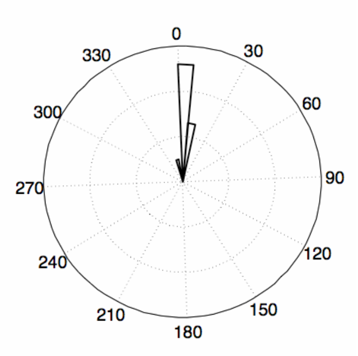
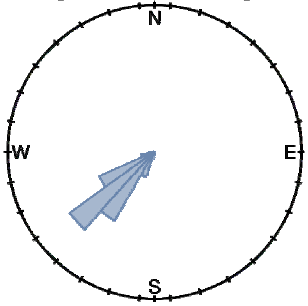
Fig. 4. Autocorrelation values for directions (independent), positions (strongly dependent), and bootstrapped positions (independent).

Quantification of Orientation

If the larva swims directionally, the displacement vectors are concentrated around the sum vector of directions (red dotted line, Fig. 3C) and Rayleigh's test for direction data is likely to reject the null hypothesis of lack of orientation. However, the swimming directions of most larvae (similar to larva A, Fig. 3C) did not differ from a uniform distribution of swimming directions. This is explained by the relatively small size of the arena in comparison with the average cruising speed of a reef fish post-flexion larva (e.g., 15 cm s^{-1}, Stobuski and Bellwood 1994; Leis and Carson-Ewart 1997, Bellwood and Fisher 2001, Fisher and Wilson 2004). Alternatively, orientation was detectable in position data for at least

50% of the trials, where many mean angles calculated from bootstrapped positions are close to each others (Fig. 3D). Examples of significant bearings of larvae and the direction of the current in which they were set to drift are given in Table 1.

Table 1. Examples of the direction of the OWNFOR drift in the Florida Current and the corresponding bearings of damselfish (Pomacentridae) larvae. The influence of each larva orientation behavior on its trajectory is shown in Fig. 5.

Deployment Date / Time	Frequency Distribution of Current Direction [range of bearing]	Probability Distribution of Larval Position [range of bearing]
June 16, 2005 / 14:21 Offshore Miami, Biscayne Bay **Fish larva A**	[353° - 3°] 	[34.5° - 99.5°] 
Sep. 2, 2005 / 10:02 Offshore Key Largo, Florida Keys **Fish larva B**	[351° - 10°] 	[190.3°-257.4°] 

Orientation and Dispersal

The influence of orientation behavior for the two larvae in Table 1 is shown based on the observed range of swimming speeds measured in the laboratory (Fisher 2005). The trajectory of larva *A* departs quickly from the passive drift, with a zonal displacement ranging from 100-450 m in *ca.*15 minutes (or 10-43 km in 24 hours, Fig. 5). This deviation is even more remarkable as this larva orientated generally in the current with only a small angular deviation of 30-70 degree from the strong northward flow (*ca.* 160 cm s^{-1}). The faster the larva swims, the larger the deviation from the passive trajectory, but the distance traveled by the larva relative to the bottom increases (i.e., dispersal distance increases). Alternatively, for larva *B* released off Key Largo (in slower current *ca.* 90 cm s^{-1}) and orienting by and large against the current, a small difference in bearing has a large effect on its deviation from the passive trajectory. In this case, the greater the swimming speed, the smaller the dispersal distance. For larva B, a combination of both higher swimming speed and angular deviation from the current axis can bring larva *B* onto the reef in less than 24 hours.

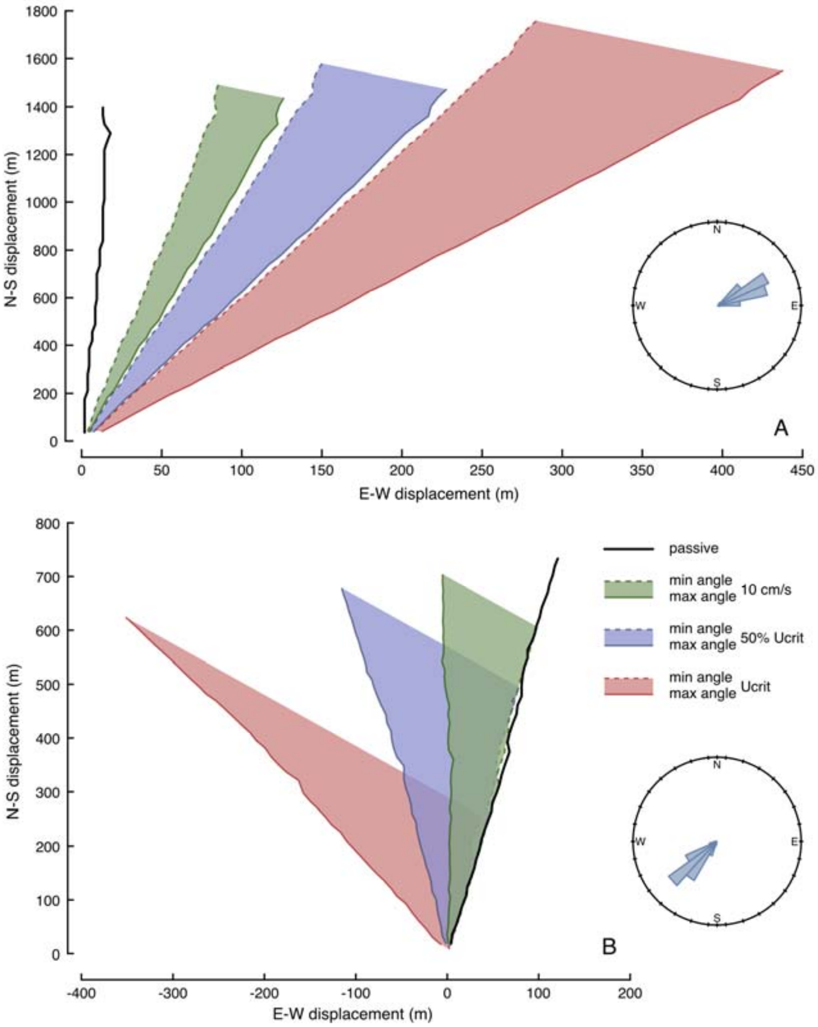


Fig. 5. Influence of orientation behavior on larval trajectory depicted by the passive and active trajectories of two damselfish larvae (from Table 1), **A)** larva *A* released offshore Miami in a 1.6 m s^{-1} northward flowing Florida Current, and **B)** larva *B* released offshore Key Largo in a slower current (*ca.* 0.9 m s^{-1}). When larval orientation is mainly with the current, swimming speed becomes important to deviate from the passive trajectory, even with a small angular deviation from the current axis. When orientation is largely against the current, the angular deviation from the current axis becomes as critical as swimming speed. In both scenarios, we used the critical speed of a pre-settlement damselfish (i.e. Ucrit 37.6 cm s^{-1}, Fisher 2005). The passive drift indicates the direction of the current and the pie chart the larva's bearing during a 15-minute trial.

Discussion

Although preliminary, this dataset provided substantial evidence that the novel concept and system (OWNFOR and BlueBidule Software) successfully captures and measures *in situ* orientation behavior in reef fish larvae with minimal disturbance. In effect, orientation was detected in the symmetrical arena using circular statistics, an efficient tool in dispersal ecology (Bullock et al. 2001). Independent orientation measures such as those obtained from divers following late-stage larvae (Leis et al. 1996) should be carried in parallel to check the constancy of results. For these trials, we used settlement stage larvae caught in light traps, but in the future we intend is to use pelagic larvae captured in the open ocean, as well as reared larvae to describe the ontogeny of orientation in the early life history of reef fish.

Swimming behavior has been measured in flume tanks where larvae swim against a current (Fisher and Bellwood 2003; Fisher et al. 2000; Hogan and Mora 2005; Stobutzki and Bellwood

1997). However, Fisher and Bellwood (2003) have come closer to measuring undisturbed swimming speeds (or routine speed) in a still tank. Although larvae were more active during the day than at night, they swam at speeds far less than their critical speeds (Fisher and Wilson 2004). Similarly, the OWNFOR system may allow measurements of *in situ* swimming speeds of the earlier stages, when swimming behavior might not be affected by the enclosure. Vertical swimming behavior has also been observed in reef fish larvae (Cowen 2002; Paris and Cowen 2004; Leis and Carson-Ewart 2001). However the time scales at which vertical swimming behavior occurs is in the order of several hours (i.e., diel vertical migration) or days and weeks (i.e., ontogenetic vertical behavior). OWNFOR was deployed at depths corresponding to observed depth ranges at developmental stage (Paris-Limouzy 2001; Cowen 2002). The effect on orientation of OWNFOR deployment depth relative to the depth of the thermocline and pycnocline should be further tested.

Fish larval swimming capabilities hint at an active behavioral influence on recruitment. Yet without environmental awareness (e.g., direction of the land masses in relation to their position) and orientation, this potential cannot be materialized into successful recruitment. It is therefore crucial to identify the cues involved in orientation (Montgomery et al. 2000, 2001). This new system brings a platform to test a series of isolated and combined sensory cues such as solar compass, sound (Tolimieri et al. 2004; Simpson et al. 2004), magnetic field (Lohmann et al. 2004), and chemicals (Atema et al. 2002; Gerlach et al. 2007). The device can also be deployed at different distances from the reef to measure the sensory envelope of pelagic larvae, which represents an important parameter in larval dispersal and recruitment models (Paris et al. 2005; Cowen et al. 2006). Here we demonstrate that orientation has profound implications for modeling larval dispersal (Fig. 5), most likely changing patterns of population connectivity (Cisco et al. 2007) and conservation strategies (Leis 2002).

There is room for improvement of this first, yet successful OWNFOR version. For example, the entire system can be built in clear polycarbonate (transparent to visible light) to eliminate any possible visual signal that would have a positive (i.e., attract) or negative (i.e., scare) effect on behavior; infrared lights can be implemented for night-time experiments for the study of orientation in late-stage larvae settling at night (Stobutzki and Bellwood 1998; Sponaugle et al. 2002). This observational system can also be applied to a large array of marine organisms. The success of this exploratory approach, together with rapid development of remote sensing and camera technologies, will help to catalyze innovative advances in the field of larval ecology. This system provides information vital to our understanding of the potential for these larvae to influence their dispersal patterns using active behavior.

Acknowledgements

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Modeling Population Connectivity of Coral Reef Fishes within the Greater Caribbean

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Summary of oral presentation

Larval supply driven by –
- Production of eggs (adult population size)
- Larval survival (food, predation)
- Larval transport (currents, behavior, habitat)

Larval transport contributes to:
- Population variability
- Population persistence
- Population dynamics (scaling)

How to determine dispersal in marine systems?
- Direct measurement – tag young, survey recruits
- Indirect measurement – genetic markers, natural (chemical) marker
- Modeling – physical circulation model, biological (behavioral) linkage

What is the shape of the dispersal curve, how do kernels differ for various systems, species and life histories?
Over what distance are larvae typically dispersed?
What are the implications of different kernels on population dynamics and management of species?

Over what scale does larval transport occur? Evolutionary vs. ecological:
- Evolutionary – a few individuals per generation required for gene homogeneity
- Ecological – many orders of magnitude more transport than for evolutionary

Modeling – ocean circulation model; input forcing mechanisms; GIS with geographic information; biological model; blended with stochastic model – outputs: connectivity matrices, dispersal kernels, graph theory.

Behavioral component of larval dispersal has major impact on where the larvae settle.

Lots of regionality in the Caribbean – i.e. Turks and Caicos/Bahamas are strongly connected, but not so connected to other areas.

Conclusions & Caveats:

- Model suggests that typical larval dispersal distances may be quite limited
- Biological inputs are critical determinants of dispersal outcomes
- Spatially and temporally explicit sources of variation exist in dispersal outcomes
- Models are useful but caution…
- Models need to be validated
- Models are useful for sensitivity analyses to identify most important parameters and processes
- As such, they are useful for generating hypotheses for efficient field experimentation

Abstract:

Cowen, R.K., C.B. Paris, and A. Srinivasan. 2007. Modeling population connectivity of coral reef fishes within the greater Caribbean. Proc. Gulf Carib. Fish. Inst. 59: 624.

A Graph-Theoretic Approach for Evaluating Marine Population Connectivity

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Summary of oral presentation

Modeling connectivity – to determine the probability of larvae dispersing to a specific area.

Graph theory – relationships between entities; e.g. in ecology looking at food web dynamics.

Graph properties and metrics:
- Upstream/downstream neighborhood analysis
- Shortest paths and average paths
- Betweenness measures (bottlenecks)
- Identify likely routes
- Robustness and resilience
- Community structure

Modeling dispersal neighborhoods (upstream and downstream); provides information for managing these communities. Can identify gateway reefs; critical stepping-stones; potential sources and sinks.

Abstract:

Treml, E.A., P.N. Halpin, and D.L. Urban. 2007. Graph-theoretic approach for evaluating marine population connectivity. Proc. Gulf Carib. Fish. Inst. 59: 625.

Surfing, Spinning, or Diving From Reef to Reef: How Does It Affect Population Connectivity?

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Summary of oral presentation

Individual level: what are the physical-biological interactions that contribute to successful dispersal?

Looked at:
Physical – jets and fronts, eddies & filaments, turbulence & diffusion
Biological – ontogenetic vertical migration & mortality

Different combinations of physical and biological conditions result in very different dispersal patterns.

Individual larval behavior and life-history details are required to produce meaningful simulations of population connectivity.

Abstract:
Paris, C.B., L.M. Chérubin, A. Srinivasan, and R.K. Cowen. 2007. Surfing, spinning, or diving from reef to reef: How does it change population connectivity? Proc. Gulf Carib. Fish. Inst. 59: 626.

When Low-Tech Is Enough: Using Drift Vial and Plankton Studies to Develop Restoration Strategies

Robert A. Glazer[1], Gabriel A. Delgado[1], David Hawtof[1], Dalila Aldana Aranda[2], Luis Rodríguez-Gil[3], and Alberto de Jesús-Navarrete[4]

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[3]*Instituto Tecnológico de Mérida*
[4]*El Colegio de la Frontera Sur*

Summary of oral presentation

Queen conch (*Strombus gigas*): Important to emphasize the life cycle in understanding restoration strategies.

What component of recruitment originates upstream?
If a significant proportion of the local stock originates locally, where to do we target local restoration?

Where do larvae originate? They have found little coming in (larvae), but there are lots in the Keys. Therefore recruitment must be influenced by local production.

Conducted release studies over known conch sites. Eastern Sambo releases ended up going northeast along the Keys (including Molasses Reef) and up to Miami. Releases from Molasses reef: everything went north; nothing was found in the Keys. Therefore restoration efforts should target the Lower Keys.

Larval production is higher in the Upper Keys than in the Middle and Lower Keys.

Nearshore conch are non-reproductive; offshore are reproductive. The two groups are separated by Hawk Channel – juveniles cannot cross.

Translocating conch into reserves to enhance the spawning stock – using hydrographic information to inform location selection.

Abstract:
Delgado, G.A., R.A. Glazer, D. Hawtof, D. Aldana Aranda, L Rodríguez-Gil, and A. de Jesús-Navarrete. 2007. When low-tech is enough: Using drift vial and plankton studies to develop restoration strategies. Proc. Gulf Carib. Fish. Inst. 59: 627.

Panel Discussion: Oceanographic Connectivity

Question: What percentage of the time are larvae in the surface layer?
Bob Glazer: 100% of the time; diurnal migration of a couple of centimeters.

Q: So the behavior of the vials matches the behavior of the larvae?
Bob Glazer: I think it is as close as we can get. Coral larvae are probably better – but these larvae are pretty passive.

Q: If the larvae dispersed such a short distance what is the dominant factor determining transport?
Bob Glazer: Other scientists are studying water movement, and we collaborate to use their data.
Bob Cowen: There is a very strong wind component – surface drifters are impacted by this – deeper water would be transported differently.
Bob Glazer: Also – this is a snapshot and should be recognized as such.

Q: Where is the ecological dispersal coming from? Dispersal kernel that showed that was below demographic levels of larval supply – how would that population replenish itself?
Bob Cowen: I was trying to show that a single-source population – larvae would be lost to that population, not a sink – would require subsidy.

Brian Keller for Claire Paris: Was your talk a call for more empirical studies of larval behavior?
Claire Paris: There are a lot of studies needed on larval behavior – not only on the early stages. What we don't know is when the larvae start to swim toward shore. So yes, there is a lot to do regarding understanding larval behavior. We have parameterized these behaviors for some species.

Peter Sale – Comment: Early research focused a lot on behavioral studies of reef fishes. In the 1970s, that went out of favor. We need to get back at looking at behavior – particularly for the larvae.

Q: What about predation – can you combine prey and predator to look at mortality?
Claire Paris: We can use the models to look at larval mortality; however, we don't know if in the tropics this is a cause of mortality. We need to look at trophic dynamics. It is possible to do it right now – the problem is that the sensitivity of the model is so great that we can't put any numbers on it as we wouldn't know if it was correct – it would take a lot of validation work.

Q: Isn't there more trust between scientists and MPA managers than between the politicians who draw the lines?
Bob Glazer: I believe that politicians are driven by economics. There is a lot of work that needs to be done related to the economic valuation of these MPAs. Politicians need to understand the economic advantage of the MPAs and then they can bring that information to their constituencies.

Q: Are there generalities that can be made across trophic and taxonomic groups in terms of larval behavior?

Bob Cowen: Dispersal distances are shorter than genetics might suggest. The few runs that we've done have been centered on fish that are typical (30-45 d larval durations). To generalize now is a little premature – we see a lot of variation in the vertical distribution, huge variations in the visual fields and we haven't fully tested these models. I would be hesitant to generalize, but that is where we are going (to be able to generalize).
Claire Paris: Theoretically we could do that with the models I use – the problem is that we don't have enough information to make those generalities.

Q: How do we match the scales to management decisions?
Bob Cowen: Management stock sizes in many areas have been established based on genetic information. The concept was based on an understanding that larval dispersal was on the order of 100s to 1000s of kilometers. In that case we were managing stocks across entire ocean basins. Information coming out of the models is that we're down to 100s of km and sometimes smaller scales. That's directly applicable to managers. In the Caribbean where there are many jurisdictions, it will help that we're talking about smaller areas. Next step – more realistic design of MPA networks. Our current knowledge may be useful to test the existing networks – and test the predictions of our models.
Claire Paris: When we talk about distances – we have to remember that this is a heterogeneous habitat – so the reserve doesn't have to be 100km long – we may only have to protect the reproduction to sustain the metapopulation.
Bob Cowen: Eric Treml gave a great example of an analysis that can be used to help in the design of a networked MPA. Bob Glazer also gave a nice example of the empirical, as well as knowledge of models, to solve a very specific problem. Both are examples of using the advances to manage.
Bob Glazer: There is an increase in production as you increase the population – so there is an advantage – you can design a reserve such that you can maintain harvest outside the area as if the reserve weren't there.

Connectivity in Population Structure

Segregation of Queen Conch, *Strombus gigas*, Populations from the Yucatan Peninsula, Mexico

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Abstract

Despite active conservation measures, slow recovery of Queen conch (*Strombus gigas*) is a growing concern in the Caribbean. Although conventional expectations presume that *S. gigas* populations are largely connected, we present results using larval drift patterns from the Yucatan peninsula in Mexico that suggest otherwise. Spatial-temporal patterns of veliger larvae in the field and simulated spatial distributions of larval stages are used to determine the degree of segregation of the *S. gigas* population from Alacranes Reef on the North Yucatan from those of the Mexican Caribbean coast. Isolation of the Alacranes population is evident, driven by high retention on Campeche Bank, separate from the highly variable larval transport of the Yucatan Current traveling along the Mexican Caribbean coast and eventually into the Loop Current. We believe our conclusions to be robust because the calculated probability that veliger originating from Alacranes Reef settle in Florida is null, while a small fraction of larvae produced north of the Mexican Caribbean coast periodically reaches the Lower Florida Keys. Although low levels of connectivity through this long-distance dispersal may not be sufficient to replenish the downstream populations, gene flow could prevent differentiation of the Florida Keys and Mexican Caribbean Queen conch populations. This work constitutes a fundamental step in understanding the structure of *S. gigas* populations from Mexico, which can facilitate the recovery of individual populations, the persistence of the species in the region, and the proper management of its local, historical fisheries. Detailed larval dynamics (e.g., behavior, growth, mortality, settlement) and mapping of population networks at the regional and wider Caribbean scales will be an extension of this work.

Introduction

The Queen conch, *Strombus gigas* (Gastropoda: Caenogastropoda: Strombidae), has been of economic importance since pre-Columbian times (Baqueiro 1997). Presently, it is a significant marine resource for many Caribbean countries and has been subject to considerable fishing pressure, greatly reducing the overall size of the population (Brito-Manzano and Aldana-Aranda 2004). Since the 80's, commercial catch has increased in response to the international market. In the Caribbean region, the Queen conch is the second most important fishery after spiny lobster (CITES 2003). In Jamaica, *S. gigas* is the most important fishery in both value and catch, but as for most Caribbean countries, the Queen conch fishery is second only to the spiny lobster (*Panulirus argus*) in economic importance (García-Moliner 1996). From 1992 to 1998, the mean

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annual catch of *S. gigas* in the Wider Caribbean was 7,369 tons (T). Following this period, annual catches dwindled from 5,554 T in 1999 to 4,598 T in 2000 and 3,132 T in 2001. Due to the high fishing pressure exerted upon most of its populations, several stocks have been reduced to levels where the population can no longer recover, and commercial fishing is no longer functional. Conch was included in the Convention on International Trade in Endangered Species (CITES; Appeldoorn 1992) of Wild Fauna and Flora in 1992, and in 1994, the Queen conch was added to the International Union for the Conservation of the Nature's (IUCN) Red List.

Following the pattern of other Caribbean countries, Queen conch abundance in Mexico has also diminished. A decline that took place in the Yucatan from 1985 to 1987 led to the closure of that fishery (Pérez-Pérez and Aldana-Aranda 2000). Presently, there is a temporal ban during peak spawning season, from March 1st to October, a harvest quota of 30 T for Chinchorro Bank and 12 T for Cozumel, and a minimum capture size of 22 cm total length (TL). In spite of these measures, for the most part the distribution of Queen conch in the area remains confined to Marine Protected Areas (MPAs). Given the uniform nature of the conservation measures for the area, one might expect a uniform response from the population, but this does not appear to be case, as evidenced by discrepancies between Alacranes Reef, a rare population on Campeche Bank, and Cozumel and Chinchorro Bank situated on the Caribbean coast (Aldana-Aranda *et al*. 2003a, b).

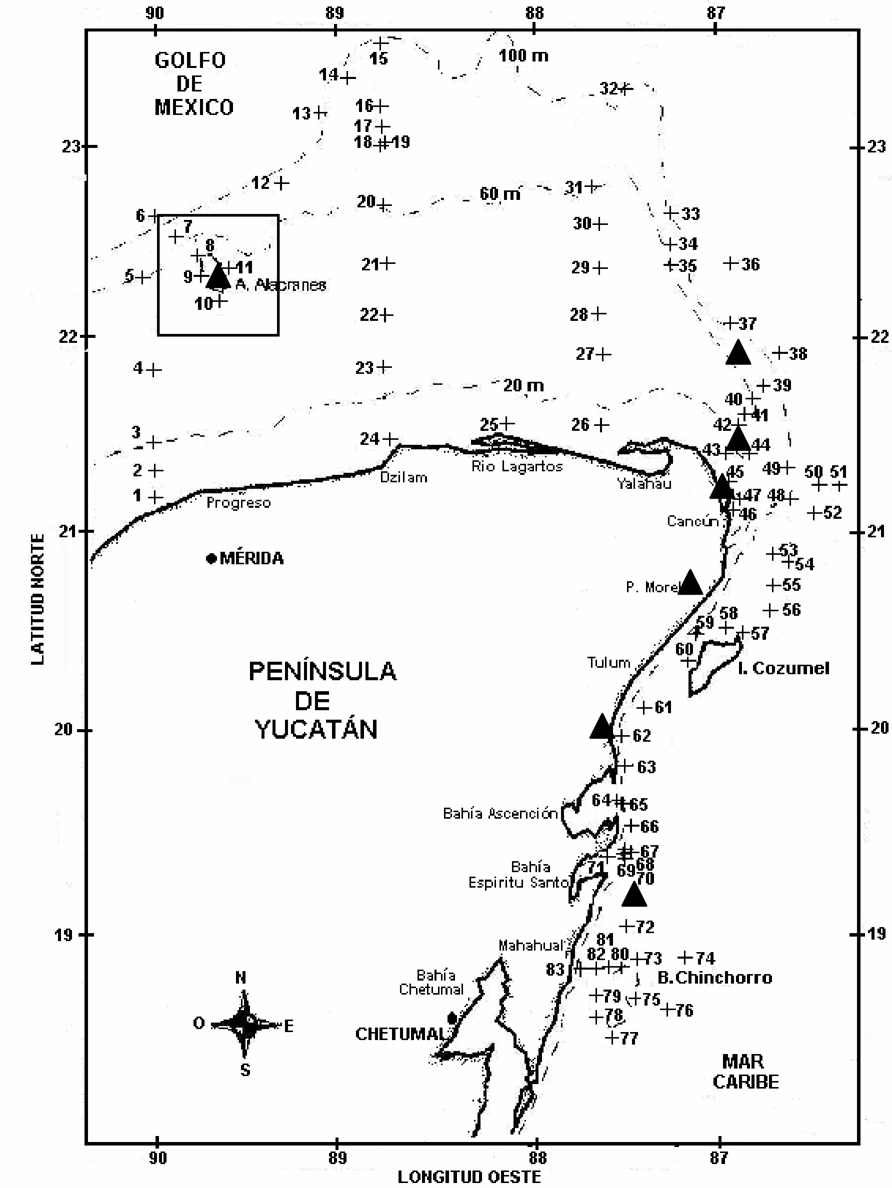
The population of *S. gigas* in Alacranes Reef was almost depleted after 1988. Recent studies still report relatively low abundances at Alacranes Reef varying from 0.015 m^{-2} to 0.001 m^{-2} (Pérez-Pérez and Aldana-Aranda 2000; Pérez-Pérez, 2004). In contrast, despite relative lack of enforcement, the *S. gigas* population situated at Chinchorro Bank has remained relatively stable. These observations suggest that Alacranes reef may be disconnected from other populations of *S. gigas* along the Caribbean coast. Effective management of these populations could be greatly enhanced by a better understanding of larval movements.

According to a theory developed by Stoner (1997), currents carrying larvae from the Yucatan Peninsula to the Bahamas and Florida could also provide larval drift between the Mexican Caribbean coast and the North Yucatan Peninsula. The interactions of the flow with *S. gigas* life history traits (or genetically inherited attributes) may play a large role in the outcome of the distribution of adults. Studies of the abundance of larvae have been carried out in Florida and the Bahamas (Stoner et al. 1992, 1996; Glazer and Berg 1994; Posada and Appeldoorn 1994; Stoner and Ray 1996; Stoner 1997; De Jesús-Navarrete and Aldana-Aranda 2000) with the intention to protect larval sources of *S. gigas*. However, little is known about their transport dynamics and the relationship between densities of *S. gigas* larvae and ocean circulation has never been explored.

This study examines Queen conch larval transport along the Mexican coastline with the goal of testing Stoner's null hypothesis that geographically separated *S. gigas* populations are linked. Our major objectives are to (1) describe patterns of larval dispersal around the Yucatan Peninsula and potential transport to Florida, the Bahamas, and Cuba; (2) estimate the degree of segregation of the Alacranes Reef population from those of the Mexican Caribbean; and (3) identify likely larval sources in the Yucatan Peninsula. To accomplish these objectives, we use both field studies and biophysical modeling, taking into account *S. gigas*' life history traits (e.g., adult reproductive season, larval developmental stages, pelagic duration). As a first step, we use field observations to corroborate the model predictions, and then we use the model to estimate larval linkages.

Study Area

The Yucatan Peninsula is characterized by a large continental shelf, approximately 175,945 km^2, mostly occupied by the Campeche Bank. The northeastern edge of the Bank is delineated by the 200 m isobath, whereas the conventional western and eastern boundaries are 94^{o}W and Cabo Catoche, respectively. The geological characteristics of the continental shelf of the Yucatan Peninsula allow differentiating two distinct marine regions: (1) the Mexican Caribbean coast with a narrow shelf, bordered by back reef lagoons, shallow bays, and banks; and (2) the Campeche Bank with a wide shelf and a single small bank, the Alcranes Reef, located at the edge of the 60 m isobath (Chávez 1994). The study area at the north of the Yucatan Peninsula is limited to the area situated between the 5 m and 50 m isobaths (Fig. 1).



ALACRANES REEF

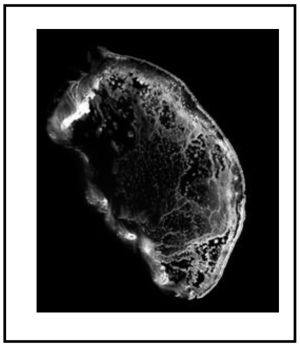


Fig. 1. Study area: Position of the 83 sampling sites in the North Yucatan Peninsula and in the Mexican Caribbean during the months of March, July, and October 2001. Dotted lines represent isobaths (20, 60, 100 m). The insert shows the Alacranes lagoonal reticulated reefs located at the edge of the 60 m isobath, sole home of the Queen conch (*Strombus gigas*) on the Campeche Bank. (image insert from Millennium Coral Reef Mapping Project, IMaRS). The major National Protected Areas (INE SEMARNAT 2002) for *S. gigas* are indicated with a triangle.

The eastward flowing Caribbean Current veers northwestward as it impinges on the margin of the Yucatan peninsula and becomes the Yucatan Current. The Loop Current enters the Gulf of Mexico through the Yucatan Current and exits through the Florida Straits as the Florida Current. Eddy motions that dominate the eastern Yucatan Basin, with a cyclone-anticyclone pair, slowly translate westward and feed into the Yucatan Current (Richardson 2005). Thus, transport in the vicinity of the Yucatan Channel is highly variable (Abascal et al. 2003; Centurioni and Niiler 2003), while the flow at the shelf edge is controlled by a regular shift of the Loop Current maximum velocity (Cherubin et al. 2005). The surface transport in the Yucatan Channel is characterized by the main inflow of the Yucatan Current into the Gulf of Mexico and the outflows along the Cuban and Mexican sides. The Loop Current oscillates, shifting to the center of the channel as the transport increases and moving back to the west when the inflow increases. The deep outflow (toward the Caribbean Sea) also increases on one or both sides of the Yucatan Current as a response to the Yucatan Current inflow (toward the Gulf of Mexico, Cherubin et al. 2005). This outflow occurs approximately at the level of the cape of the continental margin (ca. 22^{o}N, 86.5^{o}W, nearby the group of stations 38-41 in Fig. 1), the surface expression of which can translate into a convergence zone. On average, the Yucatan Current flow is relatively weak from November to February and becomes stronger from May to Aug (Tang et al. 2006).

In the Yucatan region, spawning of *S. gigas* occurs from March to October, with one (Frenkiel and Aldana-Aranda, unpublished) to six spawning events per female (Pérez-Pérez y Aldana-Aranda 2000), producing benthic egg masses. Veliger larvae hatch at a minimum size of 250 µm and have a maximum size of 1200 µm at settlement (Davis et al. 1993). Larvae become competent to metamorphose between 20-24 d after hatch, but metamorphosis can occur as early as 12-14 d or as late as 25-60 d (Davis and Dalton 1991; Davis et al. 1993; Brito-Manzano and Aldana-Aranda 2004). The pelagic larval duration is of 30 d on average, but larvae remain in the water column up to 60 d according to Stoner et al. (1997a; Table 1). Veligers are usually found in the upper 5 m of the water column, but despite their limited horizontal swimming, they are capable of vertical migration (Stoner 1997; Stoner and Smith 1998; Fuchs and Mullineaux 2004).

Table 1. Biological factors of *S. gigas* larva in laboratory conditions.

Mean size at hatching	354 ± 15 µm	Davis et al. (1993)
Size range at settlement	952-1258 µm	Davis (1994)
Growth rate	21.5 µm day^{-1}	Brito-Manzano and Aldana-Aranda (2004)
Maximum time in the water column	40-60 days	Davis et al. (1990) Stoner et al. (1997a)

Materials and Methods

Observations

This area was covered by three oceanographic surveys from the Marine Secretary from the north of Chuburná Puerto and Cabo Catoche during March, July, and October of 2001. Plankton was sampled at 83 stations located between 21°30'N-23°42'N and 90°00'W-87°00'W and sea surface temperature and salinity were recorded. Near surface (1 m) plankton tows were made at each site using a Bongo net with a 0.61-m diameter opening and 302-µm mesh size. Tow durations were 15 min at 1 $m \cdot s^{-1}$ and volume filtered was measured using a calibrated flow meter suspended in the mouth of the net. Plankton samples were preserved in a 5% neutral formaldehyde-seawater mixture (Stoner and Davis 1997a).

In the laboratory, the entire volume of each plankton sample was sorted for *Strombus* veligers using a dissecting microscope (20 x). Positive identifications for *S. gigas* were made following the descriptions of Davis et al. (1993). Veligers were counted and shells were measured for total length with a calibrated ocular micrometer. According to Davis et al. (1993) and De Jesus-Navarrete and Aldana-Aranda (2000) larvae were divided in two size classes of shell length (SL) and aged using growth rates obtained in the laboratory (Brito-Manzano and Aldana-Aranda 2004): pre-competent larvae < 700 µm SL, ≤ 20 days, and the competent larvae > 700 µm LS, ≥ 21 days.

Biophysical Modeling and Simulation

To simulate larval conch transport, we used the velocity field from a layered ocean circulation model, the North Atlantic HYbrid Coordinate Ocean Model (HYCOM; http://hycom.rsmas.miami.edu). HYCOM is forced using real daily wind data from the European Center for Medium-Range Weather Forecasts (ECMWF) and bottom topography from a digital terrain data set with 5' latitude-longitude resolution (ETOPO5). The coastal boundary for the topography data was set at the 10-m isobath. The model resolution is 1/12 degree (~ 7 km) and its domain encompasses the study region. Daily velocity field output from HYCOM is archived and coupled offline with a Lagrangian particle tracking algorithm, incorporating (1) a biological model that invokes conch larval traits (i.e., pre-competent and maximum competency period), adult spawning strategies, and recruitment habitat (Paris et al. 2005; Baums et al. 2006; Cowen et al. 2006), and (2) a Geographic Information System (GIS) that represents the Queen conch adult and settlement habitat. The GIS data was developed using reef locations provided by the Millennium Coral Reef Mapping Project (http://imars.usf.edu/corals), buffered at a distance of 5 km and split using a tolerance level of 10 km. There are a total of 1,915 polygons for the Wider Caribbean: 60, 5, 50, and 355 reef polygons shape the Mexican Caribbean coast, Alacranes Reef, the Florida Keys, and the Bahamas, respectively. Particles (virtual larvae) are released from spawning locations and are moved by the underlying velocity field while they check the GIS layer at each time step. Individual particles are active in the sense that their behavior is conditional on their ontogenetic stage. For example, if the particle is competent and its trajectory intercepts a suitable settlement habitat (polygon), it sinks and settles. Otherwise, it continues its drift until its path crosses a nursery habitat (polygon) or until it reaches the end of the pelagic duration. If the particle has reached its maximum competency period (here set to 40 d) without finding a polygon, it is removed from the system (i.e., dies). Daily natural larval mortality is not accounted for in this model. A series of simultaneous releases are initiated in the upper layer of the model (0-20 m) with a monthly frequency (February-March) from all polygons within the Yucatan Peninsula region (i.e., 65 polygons). A total of 100 particles per polygon were released each month (526,500 virtual larvae). We also released virtual larvae during March, July, and October from the 83 stations sampled. In this scenario, the number of particles released at each station was scaled by the observed veliger densities, while the particle 'age' at release corresponded to the mean developmental stage of the sample. The source and receiving polygon for individual successful virtual larva was recorded to build connectivity matrices (Cowen et al. 2006) and estimate the probability of larval exchange between and among regions. The time of arrival of individual virtual larva in each polygon was also recorded to compute settlement frequencies. Time series were used to describe the temporal patterns and levels of settlement each region.

Results

Spatio-temporal Abundance and Size of Queen Conch Larvae

Observations on the North Yucatan Shelf (stations 1-37, Fig. 1) – During the month of March 2001, 50% of the 31 stations sampled yielded 68 larvae, with a maximum density of $1.8 \cdot 10^{-1}$ m^{-3} at station 4, about 100 km south of Alacranes Reefs (Fig. 2C). Mean density was $0.28 \cdot 10^{-1}$ m^{-3} and size ranged from 520-990 µm (mean 774 µm), with a tendency toward competent larvae. In July, 17% of the 12 sites yielded few pre-competent larvae (four larvae, maximum density $0.07 \cdot 10^{-1}$ m^{-3}, mean size 512 µm). In October, 30% of the 17 stations sampled yielded 18 larvae with a maximum density of $0.1 \cdot 10^{-1}$ m^{-3} at station 27 north of Cabo Catoche. Most larvae were competent with a size range of 670-970 µm (mean 873 µm).

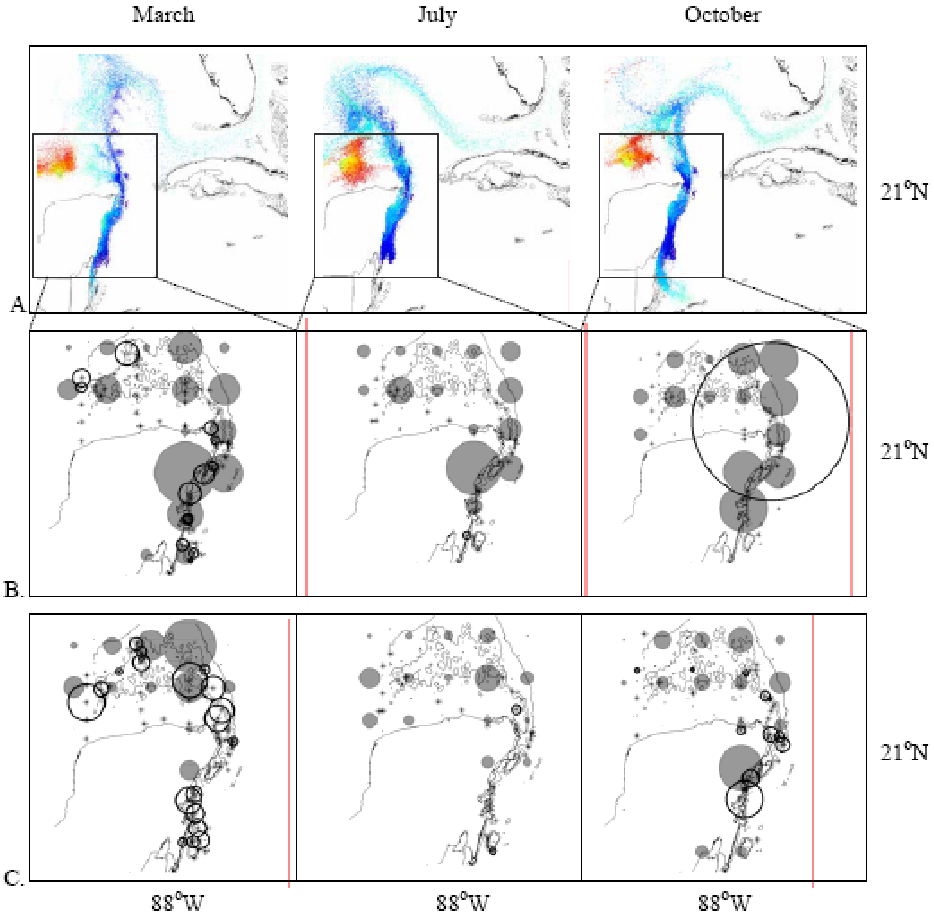


Fig. 2. **A**) Simulated dispersal of *S. gigas* larvae released during the first day of March, July, and October. Color gradients indicate dispersal in days from spawning events of Alacranes Reefs (yellow » red = post-hatch » competent larvae) in the North Yucatan Peninsula, and along the Mexican Caribbean Coast (lt blue » dk blue = post-hatch » competent larvae). **B**) Modeled (filled grey circles) and observed (hollow black circles) distribution patterns of pre-competent (1-20 d old, size < 700 µm) *S. gigas* larvae. **C**) Modeled and observed patterns of competent larvae (21-40 d old, size > 700 µm). Stars indicate stations sampled during each monthly survey. The virtual larvae have a pre-competent, passive period of 20 d, while the maximum pelagic duration is 40 d. Daily larval mortality is not included.

Observations along the Mexican Caribbean Coast (stations 38-83, Fig. 1) – During March 2001, 57% of the 30 stations sampled yielded 82 larvae with a maximum density of $0.9 \cdot 10^{-1}$ m^{-3} at station 66, between the Espirito Santo Bay and Ascension Bay (Fig. 2C). Size ranged from 350-990 µm with a tendency toward early stage larvae (mean 645 µm). Mean density was 0.17 larvae$\cdot 10^{-1}$ m^{-3}. In July 17% of the 18 stations sampled yielded only six larvae. Similar to the North Yucatan Peninsula, mean density was very low (0.01 larva$\cdot 10^{-1}$ m^{-3}), but larvae were competent (mean size 825 µm, range 680-970 µm; Fig. 2C). In October, 60% of the 16 stations sampled yielded the largest number of larvae (n = 1,642) with a maximum density of $43.2 \cdot 10^{-1}$ m^{-3} in a single patch of 1,402 larvae at station 40, northeast of Holbox Island at the cape (Fig. 2B). Catches were composed of both early- and late-stage larvae and sizes ranged from 520-990 µm (mean size 783 µm, mean density $1.93 \cdot 10^{-1}$ m^{-3}).

On average, there are less early larvae than late larvae, which is counter-intuitive since mortality rates should decrease the number of larvae by orders of magnitude with age (Houde 1987; Brito-Manzano and Aldanana-Aranda 2006). This indicates that there might be net selectivity.

Modeled Dispersal around the Yucatan Peninsula – Larval dispersal from the Mexican Caribbean coast is variable and extends south to the northern atolls of the Belize Barrier Reef, and north to the lower Florida Keys (Fig. 2A). On the other hand, dispersal from the North Yucatan is limited and less variable. Throughout the spawning season of the Queen conch, the model predicts high retention around Alacranes Reef (Fig. 2A). In July, higher northward transport of the Yucatan Current in the simulations produced lower larval densities (Fig. 3), especially of competent larvae along the eastern edge of the Peninsula (Fig. 2C).

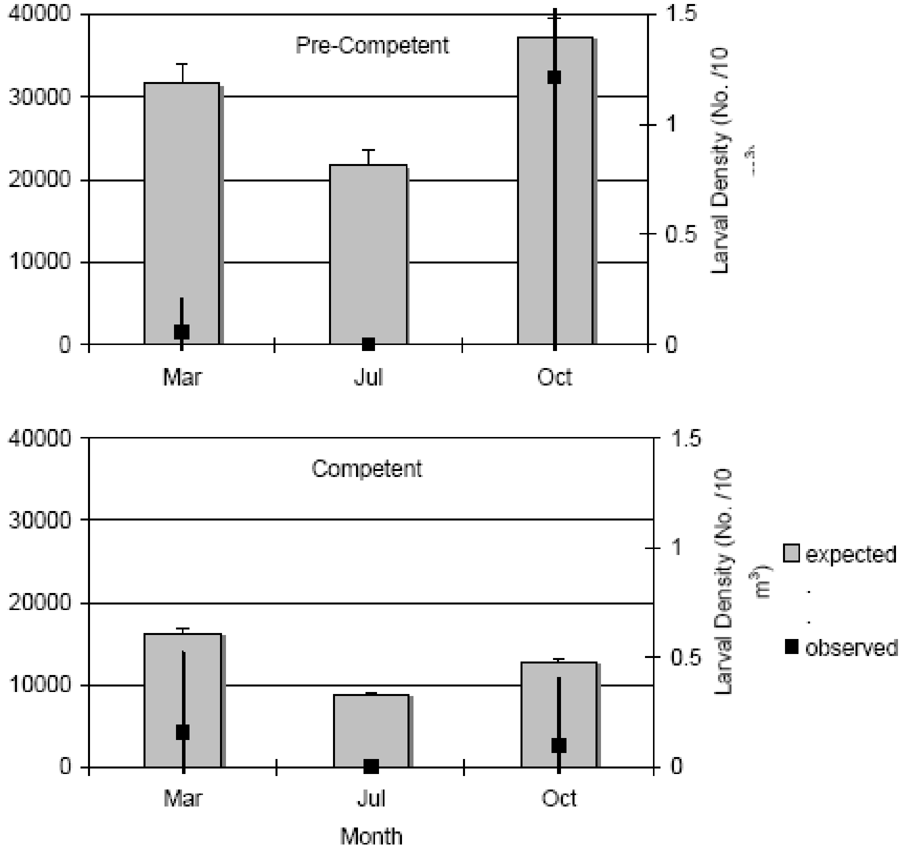


Fig. 3. Average temporal trends of pre-competent and competent conch larvae around the Yucatan Peninsula from **A**) point observations at stations (black squares) and **B**) modeled distributions (grey bars). Mean and standard deviation are calculated from the stations sampled and the binned distribution (black circles and filled grey filled, respectively, in Fig. 2). Data were not transformed in relative percentage to keep the statistical information on the variability of modeled versus empirical data (i.e., higher variability in observations).

Comparison of Observed and Modeled Distributions of Larval Stages – Observations and predictions agree well early in the reproductive season (March), when early stages are found in both locations with an noticeable separation between the Mexican Caribbean the western part of Campeche Bank, near Alacranes Reef (Fig. 2B). More advanced larvae are predominant in the North Yucatan (Fig. 2C). This is an indication that both sub-regions are sources, but advection is stronger in the Mexican Caribbean. Monthly patterns are also well predicted by the model, with lower densities during July (Fig. 3), when currents along the Mexican Caribbean are swifter (Tang et al. 2005). Observed larval densities were low everywhere around the Yucatan Peninsula (Fig. 2B-C and 3). In addition to higher dispersal, atmospheric conditions may have been unfavorable for the larvae (e.g., strong trade winds or a tropical depression). Veliger larvae are presumably more abundant near the surface during calm seas (Barile et al. 1994; Stoner and Davis 1997b), but they sink in turbulent conditions (Fuchs and Mullineaux 2004; Fuchs et al. 2007). It is possible that Queen conch larvae may have moved deeper to avoid the surface and affected the regional-scale sampling (both the Campeche bank and the Caribbean coast). During October, *S. gigas* densities increased in both models and observations, but observations were much patchier. Late in the reproductive season, however, 1,660 larvae were caught, 1,402 of which at a single station (n = 33). This rare catch was composed of a mixture of larvae from 10-30 d after hatch (520 -890 µm), indicating that they had been accumulating in that area for more than 10 d, or they could have been actively aggregating and transported there (D. Aldana-Aranda, pers. obs.). The model did not predict accumulation of larvae in a small area such as through eddies. Yet virtual larvae from 20- to 30-d old were accumulated along a strong frontal convergence (Fig. 2B). According to the model, this large larval patch could have contributed to recruitment during November in the Dry Tortugas, but not as an unusual larger recruitment peak (Fig. 4B). Altimetry data showed small eddies forming along the western edge of the Loop Current, especially at the level of the cape formed by the edge of the continental shelf on the eastern Campeche Bank (Fig. 5). A combination of larval vertical behavior in convergence zones may create large patches of larvae as those observed in October (Shanks 1983, 1986). Such rare events are worthy of more research as they could influence extinction risk.

When the model is run repeatedly (i.e., monthly spawning frequency) in a probabilistic mode rather than predictive, the spatial pattern of larval densities was reestablished (Fig. 6). Thus we are confident that the biophysical model is consistent with the observations and can be used to estimate larval exchanges between regions.

Larval Exchange Between Sub-regions – There is high connectivity within sub-regions (i.e., the Mexican Caribbean and the North Yucatan) and clear isolation of Alacranes Reef from all other locations of the study area (Fig. 7). The population of Alacranes Reef is principally self-recruiting and disconnected. The Mexican Caribbean population(s) exports a small fraction of *S. gigas* to Florida (ca.12% of successful recruits), Cuba, (ca. 4%), and the Bahamas (<1%), but none to Alacranes Reef. About 82% of the successful larvae settle within the sub-region, the southern part of the Mexican Caribbean (MCS) appears to be a large source to the north (MCN, Fig. 7).

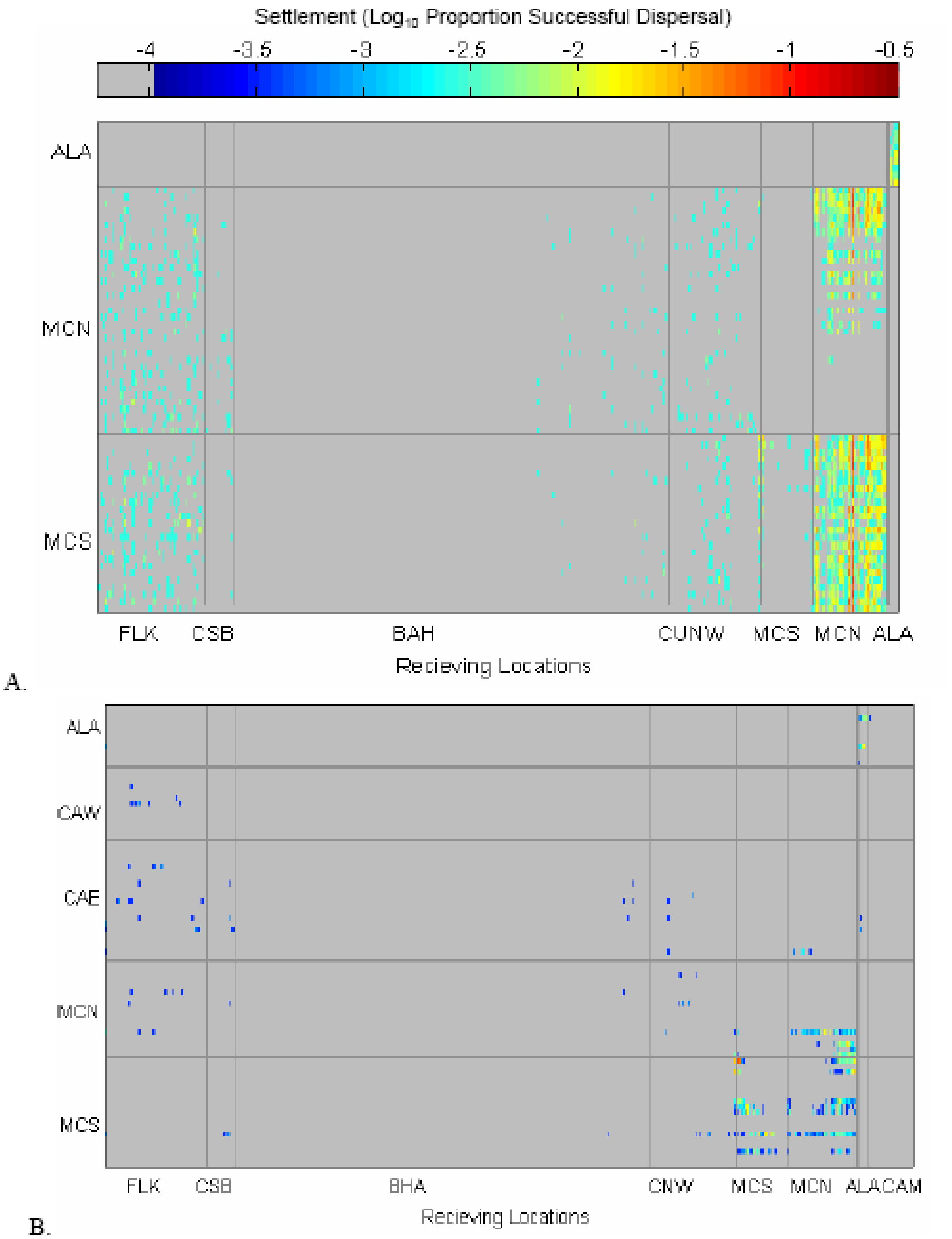


Fig. 4. Connectivity matrices between *Strombus gigas* populations from the Yucatan Peninsula (i.e., Mexican Caribbean coast and Alacranes Reef) and populations of the Florida Keys, the Bahamas, and northwest Cuba estimated from **A**) homogeneous monthly (Feb.-Oct.) spawning events from 65 reef locations (i.e., polygons or 10 km x 5 km reef-unit) of the Yucatan Peninsula and from **B**) scaled production, initializing larval transport from observed distributions of pre-competent and competent larvae sampled from 83 stations in March, July, and October. The contents of a single matrix element describe the probability of individual larvae making the transition from the source population (Y-axis) to the destination population (X-axis) computed over the reproductive season. The matrix is sparse, where gray area represents regions of no connectivity and color-code indicates levels of connectivity from high (red) to low (blue). There is evidence of higher connectivity within populations (e.g., within the Mexican Caribbean) and isolation of the Alacranes Reef, principally self-recruiting and disconnected from all other locations in the study area. The source and receiving locations are: Alacranes (ALA); Mexican Caribbean South (MCS, from Ascension Bay to Chinchorro Bank); Mexican Caribbean North (MCN, from north of

Ascension Bay to Contoy Island); Campeche Bank East and West (CAM, CBE, CBW); the Florida Keys (FLK); Cay Sal Bank (CSB); the western Bahamas (BAH); Cuba North West (CUNW).

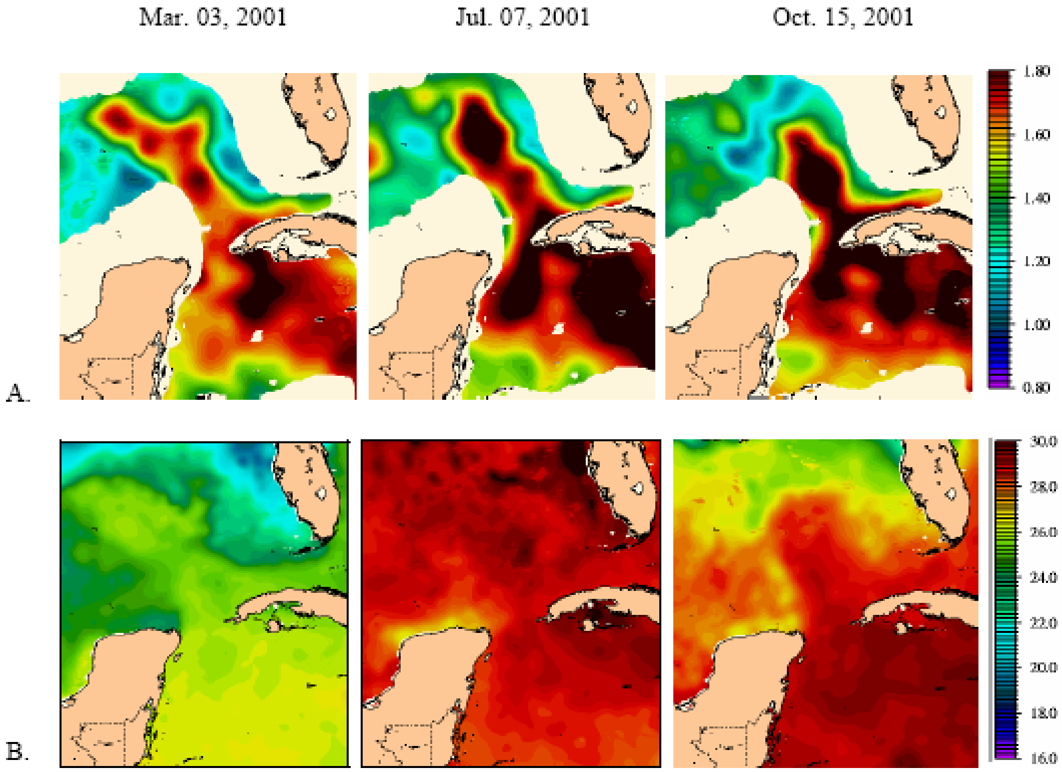


Fig. 5. Sea surface conditions during the Queen conch oceanographic surveys: MODIS combines satellite and in situ data with the Navy Coastal Ocean Model (NCOM) to create an analysis of: **A**) sea surface height and **B**) temperature structure of the ocean. From March to October of 2001, the Yucatan Current flowing into the Gulf of Mexico intensified, creating a stronger deep outflow to the Caribbean Sea (Cherubin et al. 2005), as indicated by a cold front along the eastern edge of the Campeche Bank in October.

<u>Simulated Settlement</u> – Homogeneous simulated spawning from reef locations (60 along the MCC, five at Alacranes Reef) around the Yucatan Peninsula generates a seasonal settlement pattern along the Mexican Caribbean, but relatively constant settlement in Alacranes Reef (Fig. 4A). When settlers are predicted from field larval densities, a seasonal pattern emerges in Alacranes, where most settlers arrive during the spring (Fig. 4B). This pattern is out of phase with settlement in the Mexican Caribbean, and is a direct result of the spatial and temporal differences in the presence of real larvae around the Yucatan Peninsula, indicating that the two populations have separated dynamics. When homogeneous spawning is simulated, July and September spawning events yielded the highest recruitment peaks in August and October, respectively. On average, the number of recruits per unit area was significantly different between Alacranes (0.2-1.2 km^{-2}) and the Mexican Caribbean (0.2-1.4 km^{-2}, Fig. 4). On the other hand, abundance of *S. gigas* settling in the Florida Keys and originating from the Yucatan Peninsula was always an order of magnitude lower (0.06-0.4 km^{-2}, Fig. 4).

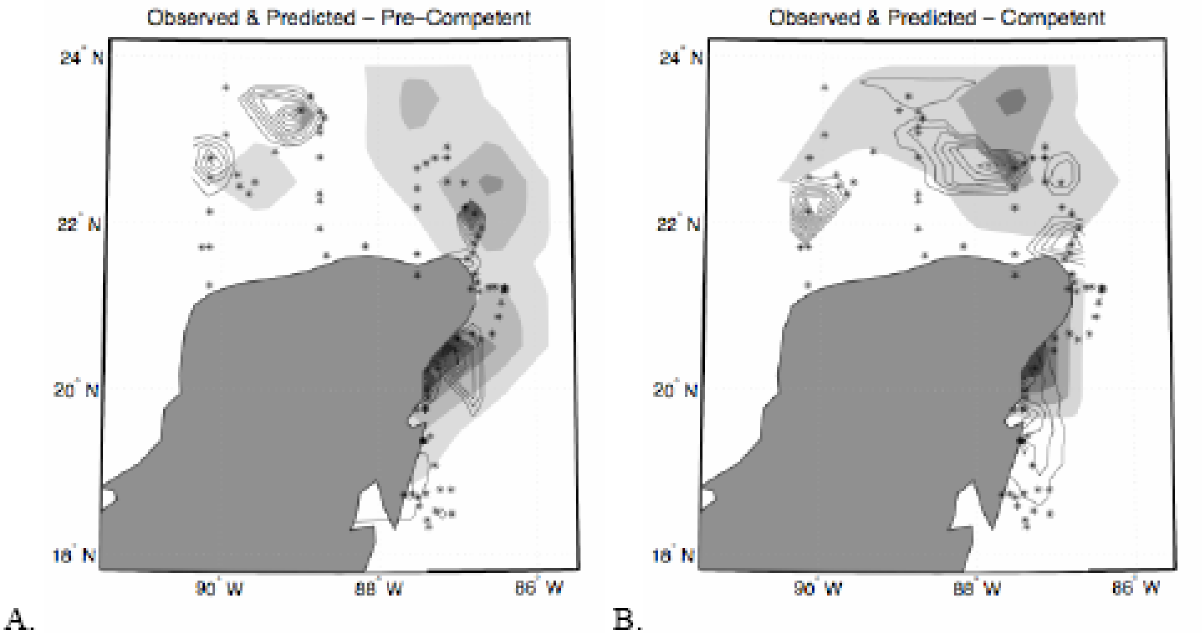


Fig. 6. Mean distribution (shaded surface) of predicted *S. gigas* larvae from monthly spawning (February to October) compared to mean observed distribution (March, July, and October sampling; contour lines) for **A**) pre-competent and **B**) competent stages. Type I error is low, i.e., the model does not predict the presence of larvae in areas where they were never caught, such as along the North Yucatan coast. In both observed and predicted distributions, early larvae (1-20 d post hatch) were found along from the Mexican Caribbean to the cape of the Peninsula, as well as around Alacranes, with a distinct break between the two regions. Older larvae (21-30 d) moved northwards along the Mexican Caribbean coastline, slightly west of Alacranes, and were also found along the northern edge of the Yucatan continental shelf. Although general patterns appeared to be reproduced well by the model, a value of a Mantel correlation comparing the two patterns was low, presumably due to the slight geographical shift between observed and predicted centers of distributions (r = 0.1 and 0.2, respectively).

Discussion

Many marine invertebrates show a dual life history where settled adults produce dispersing larvae. The planktonic nature of *S. gigas* veliger larvae suggests that ocean currents would quickly cause panmixis over large spatial scales and prevent isolation of populations. However, slow recovery of the Queen conch in the Caribbean, especially in Alacranes Reef and Florida, contradicts this panmixis hypothesis. While ocean currents are a major force in larval dispersal and genetic studies do not show population structure in the Caribbean (Sobel et al. 1988; Mitton et al. 1989; Zamora-Bustillos 2001), this study shows far greater isolation than hypothesized by Stoner (1997). As a consequence, *S. gigas* populations could develop genetic differences that can only be resolved by using fast-evolving genes (e.g., Baums et al. 2005).

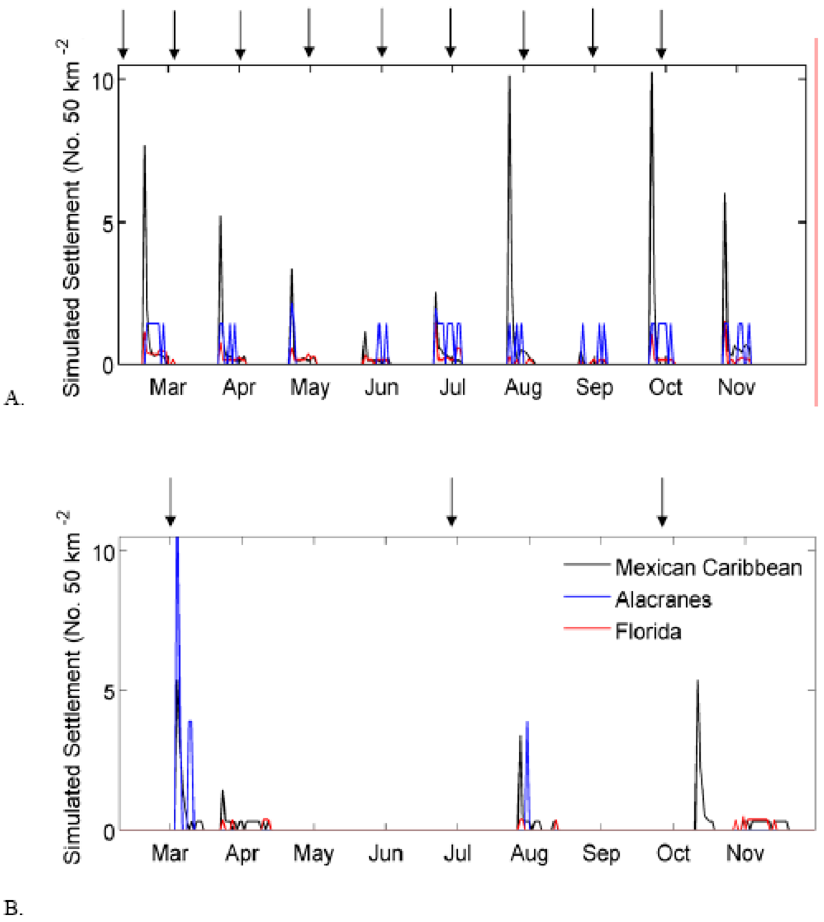


Fig. 7. Time series of simulated recruitment from **A**) homogeneous monthly (Feb.-Oct.) spawning events of *S. gigas* populations from a total of 65 reef locations (i.e., polygons or 10 km x 5 km reef-unit, 60 reef-units along the Mexican Caribbean, five at Alacranes Reef) and **B**) scaled production, initializing larval transport from observed distributions of pre-competent and competent larvae sampled from 83 stations in March, July, and October. Arrows indicate release times (simulating spawning events); maximum larval duration was set to 40 d.

Segregation of Alacranes Reef

According to Stoner et al. (1996, 1997), early larval stages originate from the local breeding population, while upstream populations generate advanced stages. This criterion does not hold for Alacranes Reef, where the population is isolated from the Mexican Caribbean and is by-and-large self-recruited. Isolation appears to be driven by the strong and highly variable Yucatan Current (Centurioni and Niiler 2003) and the life history traits of *S. gigas*, forming a bio-oceanographic barrier (sensu Baums et al. 2006) to the mixing of veligers from Alacranes Reefs and the Mexican Caribbean. Such a barrier may not exist for other organisms with lengthy pelagic durations, such as lobsters. In addition, the simulated settlement time series of the two populations are decoupled, indicating that they have entirely independent dynamics (Levins 1969). Alacranes Reef and the Mexican Caribbean thus consist of discrete, local breeding populations, where migration (i.e., the virtual exchange rate of individuals) has no real effect on their local dynamics (Hanski and Simberloff 1997). Although larval drift could contribute to the colonization of areas where populations have been banished (Stoner et al. 1996), the restoration rate in Alacranes Reef is so low that it has not been reflected in the recovery of the *S. gigas* population.

Connectivity between the Yucatan Peninsula and Other Regions

This study suggests that Alacranes Reef may not be a source for the South Florida *S. gigas* population. The lower Florida Keys may occasionally receive a small fraction of recruits from the Mexican Caribbean. The strength of the Yucatan Current as well as the northward intrusion of the Loop Current seems to control the level of exchanges. However, this long-distance dispersal may not sustain the Florida populations. In fact, the Florida populations of *S. gigas* have been under a total catch ban since 1985, but have not shown signs of recovery (García-Moliner 1996). Hence, self-recruitment becomes essential to their persistence (Hastings and Botsford 2006).

The southern Mexican Caribbean, including Chinchorro Bank, appears to be an important source of *S. gigas* larvae and a corridor for populations located on either sides (i.e., the northern coast of Quintana Roo and the northern Belize Barrier Reef). De Jesús-Navarrete and Aldana-Aranda (2000) found a high percentage (89%) of early-stage larvae (244 – 780 µm) in Chinchorro Bank, and hypothesized that this site is a potentially important source of veliger *S. gigas* to other sites of the Quintana Roo coast, and possibly to Florida. Here we do not find evidence that Chinchorro Bank contributes recruits to Florida, but it is most probably a source for the Mexican Caribbean coast. Indeed, the model indicates that potential source locations of *S. gigas* for the Mexican Caribbean are located from Chacala and Tulum (south of Cozumel) to Xcalak (Bahia Chetumal), including Chinchorro Bank, and from Puerto Madero and Majahual to Xcalak (north of Ambergris Cay). However, locations between Puerto Madero and Majahual to Xcalak seed only the northern portion of Quintana Roo. De Jesús-Navarrete and Aldana-Aranda (2000) also indicated that competent larvae were found in Cayo Lobo, south of Chinchorro Bank and assumed that they might have come from distant sources in Belize (up to ca. 900 km). Yet, throughout the *S. gigas* reproductive season, alongshore currents can reverse, allowing larval drift from the Quintana Roo coast toward the south, including part of the Belize Barrier Reef (Fig. 2A, Mar. and Oct.). Detailed larval linkages are worth investigating further to map networks of *S. gigas* populations within the Mesoamerican region.

Conservation of Strombus gigas *in the Caribbean*

One of the fundamental concepts of metapopulation theory is that the persistence of a species depends on its existence as the sum of a set of local populations, largely independent but yet interconnected by migration. Risk of extinction from an unpredictable physical environment and/or strong interactions between species is minimized by such a population structure (Harrison and Taylor 1997). This may be the case for the lower Florida Keys population, which is connected via low but downstream dispersal from the Mexican Caribbean. Connectivity between local populations in the wider Caribbean will prescribe the scale at which the *S. gigas* metapopulation should be defined. Indeed, if retention is a common phenomenon for *S. gigas* in the Caribbean, then the exchange rate of veligers between isolated locations would be low enough to fit the metapopulation critical assumptions. The latter explains the fact that the Queen conch has a wide distribution of fragmented populations in the Caribbean and yet may maintain genetic continuity (Apperldoorn 1994). Thus, conservation measures should take into account local networks of sub-populations. Isolated populations such as that of Alacranes Reef have a higher risk of extinction and should be protected and managed separately.

Model and Sampling Constraints

In general, observations of larval conch around the Yucatan peninsula agree well with the transport model, where higher abundances in the Mexican Caribbean are found when the model predict lower levels of exchange via the Loop Current. However, there are two major differences between observed and predicted mean densities. First, patchiness is higher in the observed data, indicating that active aggregation may play an important role in the transport and settlement of *S. gigas* larvae. Studies of larval behavior are needed to introduce individual movements in the model's algorithm (Paris et al. this issue). A combination of larval vertical behavior in convergence zones may create large patches of larvae as those observed in October (Fig. 2B). These types of rare events warrant further research as they could potentially influence extinction risk. Second, the model always predicts higher abundance of pre-competent virtual larvae, whereas observed densities of early and late *S. gigas* larvae are not significantly different (Fig. 3). Since daily mortality rate is not accounted for in the biophysical model, the decrease in expected larval abundance is due to transport out of the study domain, acting to increase apparent mortality (i.e., advective + natural mortality). Older larvae should be sparser due to high levels of larval mortality during the pelagic phase (Houde 1987). In the laboratory, Brito-Manzano and Aldana-Aranda (2004) have observed *S. gigas* mortality rates ranging from 63-74%. Thus, either older veligers are coming from exceptionally productive upstream sources or, most likely, there is a strong net selectivity for older larvae.

This work shows that the model is currently not suitable for providing instantaneous predictive snapshots, unless near-real-time systems are used when assimilating data, or the physical environment is sampled with and at the same scales as the plankton. If the biophysical model is run in a probabilistic mode, however, with high temporal frequency of dispersion simulations, the spatial predictions of mean sampling are revealed (Fig. 6), but it is important to bear in mind the probabilistic nature of the results. Another complication arises when sampling stations are too far apart and cannot resolve the size of the patches (Paris and Cowen 2004). To capture such small-scale biological variability and processes, sampling at a larger spatial scale and higher frequency is required. To validate small spatial-scale aspects of model predictions, sampling should be increased ideally to a frequency less than the average larval duration, hence capturing the same larvae along their developmental stages from one sampling cycle to the next (e.g., Paris and Cowen 2004).

Summary

Queen conch populations from the North Yucatan Peninsula and the Mexican Caribbean are segregated, with major isolation of the Alacranes Reef, while spawning entities along the Mexican Caribbean are highly inter-connected. Isolated populations, such as that of Alacranes Reef, have a higher risk of extinction and should be protected and managed separately.

This study does not support Stoner's hypothesis of long-distance larval linkages between Queen conch populations in the Caribbean. Simulations reveal a weak connectivity of the Mexican Caribbean with the lower Florida Keys. Yet, there are no significant exchanges with the Bahamas and clear isolation of the North Yucatan Peninsula.

Although the biophysical model reproduces temporal trends in larval densities well, there is mismatch in snapshots of spatial distribution when the model is run in a predictive mode due to the stochastic nature of biological processes. However, the biophysical modeling is able to provide an accurate probabilistic geographic distribution of larvae, estimating relative recruitment magnitude. Biological factors such as aggregation in fronts (Shanks et al. 2000), sinking in turbulence (Fuchs et al. 2007), and mortality (Cowen et al. 2000; Paris et al. 2007) must play a large role in determining absolute levels of settlement.

Acknowledgements

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From Small to Large and Present to Past: Scales Addressed by Genetic Connectivity Studies

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Summary of oral presentation

What do patterns of dispersal mean in terms of management options?
Panmixia: all individuals interbreed freely *or* restricted movement

Genetic markers –
MtDNA Sequencing – successful in fish, not in corals/sponges – one locus. Microsatellites – DNA electrophoresis – resolve small spatial scales even for coral – large sample sizes required

Larvae life history and behavior is important in dispersal (ex. Mona Passage)
Only currents that have remained constant for a very long time are relevant

Direction of gene flow:

- Separating past from present
- IM models for sequencing data
    Eastern Pacific: direction of gene glow across open ocean
- Bayesian assignment methods, msats

Silver Bullet Approach to Reserve Design:

- Divergent population genetic structures despite similar larval life histories
- Importance of historical stochasticity in reproduction and/or recruitment
- Long lasting effects on present day genetic structure

“Model species” concept flawed?

Genetic analyses can distinguish past isolation from present gene flow – bridging the gap
Multi-locus genotyping can be used to detect migration events on ecological time scales
How many migrants does a population need to sustain itself?

Abstract:

Baums, I.B., C.B. Paris, and L.M. Chérubin. 2007. Bio-oceanographic filter to larval dispersal in a reef-building coral. Proc. Gulf Carib. Fish. Inst. 59: 628.

The Importance of Sampling across Environmental Gradients in Connectivity Studies

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Summary of oral presentation

Most reef organisms have two-phase life history – dispersing pelagic larval stage; sedentary adult phase.

Little attention is paid to different ecological habitats and how they structure populations.

Amazon River mouth – freshwater output from Amazon (50-60 times as great as flows from the Mississippi River) creates a barrier between eastern South America (Brazil) and the Caribbean/south Atlantic. Assumption was that this is a barrier for reef fish and reef fish organisms.

Ecological differences between Brazilian reefs and Caribbean reefs. Brazil: Lots of sediment from the coast washes into the reef. Coral communities are very different. Low coral diversity. Mainly built by calcareous algae. Caribbean reefs: high coral diversity, built by hermatypic corals.

Looked at *Halichoeres* – PLD 27-30 days, and most are influenced by same biogeographic barriers.

Strong structure between Brazil and the Caribbean with *Halichoeres bivittatus*
Two DDP lineages, one formed by Brazil and the Caribbean and the other by Florida and Bermuda; so they are crossing the barrier readily, but they don't get to Northeast Florida, Georgia and South Carolina.

Only a population level differentiation was observed between Brazil and the Caribbean; thus the Amazon is not a strong barrier to this species

Halichoeres radiatus: two populations – Caribbean and Brazil – found two island populations off coast of Brazil that were more related to Caribbean populations than mainland Brazil. More similar to the reefs in the Caribbean than to 200 km away on the coast of Brazil. Populations in Brazilian oceanic islands are identical to those in the Caribbean, thus the Amazon is again, not a strong barrier to this species.

All species have similar dispersal potential, but varying genetic structures, and genetic breaks in different geographical locations, indicating that larval duration, geographic distributions and oceanographic currents are poor predictors of population structure.

Abstract:

Rocha, L.A. 2007. The importance of sampling across environmental gradients in connectivity studies. Proc Gulf Carib. Fish. Inst. 59: 629.

Connectivity in Caribbean Spiny Lobster: The Tail of the Dispersal Kernel?

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Summary of oral presentation (provided by Mark Butler)

Spiny lobsters are the target of one of the most valuable fisheries in the Caribbean, with commercial landings valued at ~$500M US. Despite its economic importance and the widely held view that larval dispersal results in a pan-Caribbean population structure, studies of connectivity in spiny lobster have been hampered by:

(a) Poor population structure resolution using genetic techniques
(b) No known natural or artificial tags for larvae
(c) Long pelagic larval duration

Spiny lobsters indeed have one of the longest larval durations of any species in the Caribbean, although its exact duration has, until our recent studies, only been a guess. However, as we have heard from previous presentations, larval behavior often has a large impact on dispersal patterns. Although it has long been assumed that spiny lobster larvae disperse throughout the Caribbean because of their long pelagic larval duration, it is possible that larval behavior may too constrain spiny lobster dispersal.

Our studies utilize the bio-physical oceanographic modeling approach developed by Bob Cowen and Claire Paris, and we incorporate into the model information on spawning and larval behavior. In addition, we have initiated the first empirical test of those models by establishing, with the assistance of numerous partners around the Caribbean, a network of stations to monitor postlarval lobster recruitment with which we can compare model predictions. However, the models have limitations.

Working with colleagues in Japan, the first break-through in this study was the first successful rearing of *Panulirus argus* from egg to settlement as an early benthic juvenile (mean 174 days; range 140-198 d). That larval rearing break-through also permitted us to conduct studies of stage-specific larval vertical movement, wherein we examined larval response to light intensity and spectra indicative of various depths in the sea (0, 25, 75, and 100 m). We discovered that at about 100 days lobster larvae make a major transition from surface layer (< 25 m) to deeper waters (75-100 m). These results from laboratory experiments match well data that we collected based on oceanographic sampling on monthly cruises between Miami and Bimini from which we obtained larvae at different depths.

We also conducted laboratory experiments to determine if postlarval lobsters can detect coastal chemical cues that might help them orient toward shore and, if so, how far offshore they can detect those cues. Postlarvae are attracted to odors produced by the red macroalgae *Laurencia* spp., do not respond to the odor of seagrass (*Thalassia testudinum*), and avoid seawater of low (25 psu) or high (45 psu) salinity. Postlarvae also are attracted to coastal water sources with diminished response at 30 km, with water from 50 km offshore used as a control. A separate set of laboratory studies showed that postlarvae also use pressure as a cue so that they only settle at shallow depths < 7 m. This is evidence that postlarvae indeed use coastal chemical cues to orient shoreward and use both chemical and pressure cues to help them arrive in appropriate nursery habitat.

These results have been incorporated into a Lagrangian particle model linked with the Hybrid Coordinate Ocean Model (HYCOM) to generate initial predictions of connectivity among Caribbean regions. Preliminary simulations indicate that larval behavior plays a significant role in reducing the mean dispersal distance of lobster four-fold over simulations of passively dispersing larvae. Also, significant retention and possible self-recruitment appears possible in some regions, even in this species with long-lived larvae. For example, when spawning takes place at Glovers Atoll, Belize, a majority of the larvae are retained in the gyre off northern Honduras - even considering a species with a 6-mo larval duration. However, spawning that takes place at Ambergris Cay just to the north of Glovers Atoll leads to larvae that are transported out of the local system and up into the Gulf of Mexico and northern Caribbean (e.g., Florida, Bahamas, Cuba).

We have more detailed simulations planned that incorporate spawning biomass and timing, and we also intend to test model predictions against empirical estimates of recruitment patterns, as noted earlier. Once completed, we believe that this information will be of significant value to managers throughout the Caribbean who are tasked with managing one of the Caribbean’s most important and iconic fisheries.

Abstract:

Butler, M. R. Cowen, H. Matsuda, J. Goldstein, and C. Paris. 2007. Connectivity in Caribbean spiny lobster: the tail of the dispersal kernel? Proc. Gulf Carib. Fish. Inst. 59: 630.

Panel Discussion: Connectivity in Population Structure

Q (Peter Sale): You are talking about genetic relationships among fish populations; some genetic similarity was due to movement of fish between locations; some was due to genetic movement. Is there a way to differentiate between organism movement that affects gene selection or selection operating in two locations, so you get the same genes selected?
Mark Butler: I don't think we can test for that. In subtropical Florida – the tropical fishes get there, but they don't survive the cold water. This was a temporal snapshot of what was happening. We sampled in consecutive years – unique habitat in Bermuda. Influenced by warm waters of the Gulf Stream, but high latitude. Nearshore reefs – temperature drops. Reef fish populations inside are poor relative to the offshore populations. Collected juveniles and adults both inshore and offshore. Juvenile populations are identical – from the same larval pool. The other populations are different. Winter water temperature drops – those that can't survive cold water all die. The subtropical lineage survives in the cold water.

Q: Whole picture for the population from Brazil, Colombia, Panama, etc. We deployed buoys – could see link between Colombia and Honduras for 88 days. Can you tell me something about that?
Mark Butler: The data we showed is just a snapshot of what we intend to do. The model encompasses the entire Caribbean. We are going to add spatial and temporal variability in the entire Caribbean. In that particular case – in places close by – you still can have retention in some regions. There is more to come on that.

Q (Bob Glazer): Regarding the history of the Florida lobster fishery: given complex political structure, how can we ever hope to manage if we every see declines in the population for a species that is mixing throughout the Caribbean?
Mark Butler: It may not be mixing throughout the Caribbean as we've always believed. The answer is a political one. Once we know more about connectivity we hopefully will have more efforts toward better management. Everyone assumes that there are untouched deepwater spawning stocks – but these are tropical – there are no deepwater stocks that are going to save you. I think the best thing is to protect spawning populations. I would put a slot limit on lobsters – put the large lobsters off limits. Establish a maximum size limit throughout the Caribbean.

Q: Iliana, how large is a "large sample"? When you have one clone in a reef system, is there a reduction in the ability to sexually reproduce?
Iliana Baums: Statistic modeling studies have shown that you should have at least 50 samples for each population for what you are looking at. Then the question is, "What is a population?" We assume a dive site is a population. Two further considerations: if you have large populations – 50 is probably on the low end. Ghost populations – if you have a Caribbean-wide study, you are only going to study a few populations, in Bayesian test, the populations you haven't sampled may have a large influence on that population. As for clonal structure – there are consequences – *A. palmata* is a hermaphrodite; however, it doesn't self-fertilize. Needs input from sperm or eggs from the outside, or whole larvae from the outside. Therefore those reefs haven't received outside influence or there is strong selection against outside settlement. Clonal plants shift energy toward asexual production at the margin.

Q: When you said there are no deepwater lobster populations what did you mean? Could you clarify what depth you are talking about?
Mark Butler: It is not a function of depth – it's temperature. 10 degrees C is the lowest temperature they can tolerate. There is a temperature barrier.
Follow up: My understanding is that there is some deep-water fishing for spiny lobster (over 100 feet).
Mark Butler: that is not very deep – I guarantee that the temperatures are over 10 degrees C wherever you find spiny lobster.

Comment about collaboration and scientists – when you are dealing with genetics – you must collect within many areas in the region – but you need to get a permit. The people issuing permits do not always they understand why it's important. Therefore we need to extend partnerships between scientists and managers specifically for taking samples for specific studies.

Q (Billy Causey): We see a growth form of plating *Montastraea* in the Flower Garden Banks and Veracruz, Mexico. In the Keys, we only see it in the Tortugas. Are these genetically similar – or just is this just a morphological similarity?
Iliana Baums: You have hit upon a shortcoming of coral genetics. My first guess is that you are seeing a morphological variance. There are no genetic differences between growth forms. The short answer is, I don't know.

Comment (Iliana Baums): I have found that acquiring permits for sampling is very difficult. As a result, we have no samples for very important regions in the study.

Linking Research on Connectivity with MPA Management

Marine Population Connectivity and its Potential Use for the Nomination of New World Heritage Sites in the Wider Caribbean

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Abstract

The ecoregional boundaries of the Tropical Northwestern Atlantic Coastal Biogeographic Province (or Wider Caribbean) are changing as connectivity in marine populations is being investigated in the region. In the past decade, field and modeling studies of larval dispersal suggest that the scales of population connectivity are smaller than previously thought as most settlers come from less than 50-100 km for many reef-related species. This new scientific information raises each nation's (or group of neighboring nations) responsibility for managing its own marine resources in a sustainable way, and reduces potential "outsourcing" from upstream countries and ecoregions. Based on new findings of limited larval dispersal, this paper recommends a more-partitioned ecoregional scenario in the Wider Caribbean and discusses its application in gap analysis of a particular rank of marine protected area known as World Heritage Site. The existing sites are analyzed in the ecoregional context and new sites are proposed using the current marine population connectivity information to document their ecoregional significance. The use of this information for the transboundary management of marine resources is also suggested.

Introduction

Of the more than 180 natural World Heritage Sites (WHS), only 30 are associated with marine protected areas and even less are predominantly nominated for their marine features. In the Wider Caribbean, the only true marine WHS is the Belize Barrier Reef. In addition, the Pitons Management Area (St. Lucia), Sian Ka'an Biosphere Reserve (Mexico), the Desembarco del Granma National Park (Cuba), and Everglades National Park (U.S.) WHS contain coastal components. The World Heritage Center has a mandate to promote better representation of marine sites in the Caribbean. With the assistance of a large group of experts, an analysis of potential marine WHS in the tropics was conducted (Hillary and Max 2003). The ecoregional division of each tropical region of the world was used as the geographic basis to conduct the analysis to select potential sites. In particular, the Latin America and Caribbean group stated that sites in small islands might be less likely to become marine WHS than other regions of the world. This claim was mostly based on the difficulty of documenting the criterion of "outstanding universal value" of sites that are smaller and less conserved than analogous sites in other parts of the world with different biogeographic and socioeconomic conditions.

Bustamante, G., and C.B. Paris. 2008. Marine population connectivity and its potential use for the nomination of new World Heritage Sites in the wider Caribbean. Pages 97-112 *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, 59th 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.

This paper uses the most recent information on biological connectivity to propose an ecoregional scenario that can be used to document the ecological significance of potential marine WHS as a proof of its “outstanding universal value.” This suggestion was previously discussed at the Regional Training Workshop for the Caribbean on Marine World Heritage organized by the UNESCO’s Heritage Center, in Soufriere, St. Lucia.

Geographic and Biogeographic Scenarios

The Caribbean is the largest marginal sea of the Atlantic Ocean. It is closed off by the continental masses of South America and Central America to the south and west, and is connected to the North Atlantic Ocean via the Lesser Antilles and the Windward Passages to the east and the Gulf of Mexico via the Yucatan Strait to the north. It consists of a succession of 5 basins: Grenada, Venezuelan, Colombian, Cayman, and Yucatan. In the western Caribbean, the Cayman Basin, located between the Nicaragua Rise and the Cayman Ridge, has depths of more than 5000 m, while the Gulf of Honduras is 2000 m deep within close proximity of the Mesoamerican Barrier Reef system (MBRS) stretching for more than 1000 km from the northeastern region of the Yucatan (Mexico) to the Bay Islands (Honduras). The Yucatan Basin lies between the Cayman Ridge and the Yucatan Channel. The variable bathymetry is an important factor in the formation of eddies that move the water mass through the western Caribbean Sea (Fig. 1).

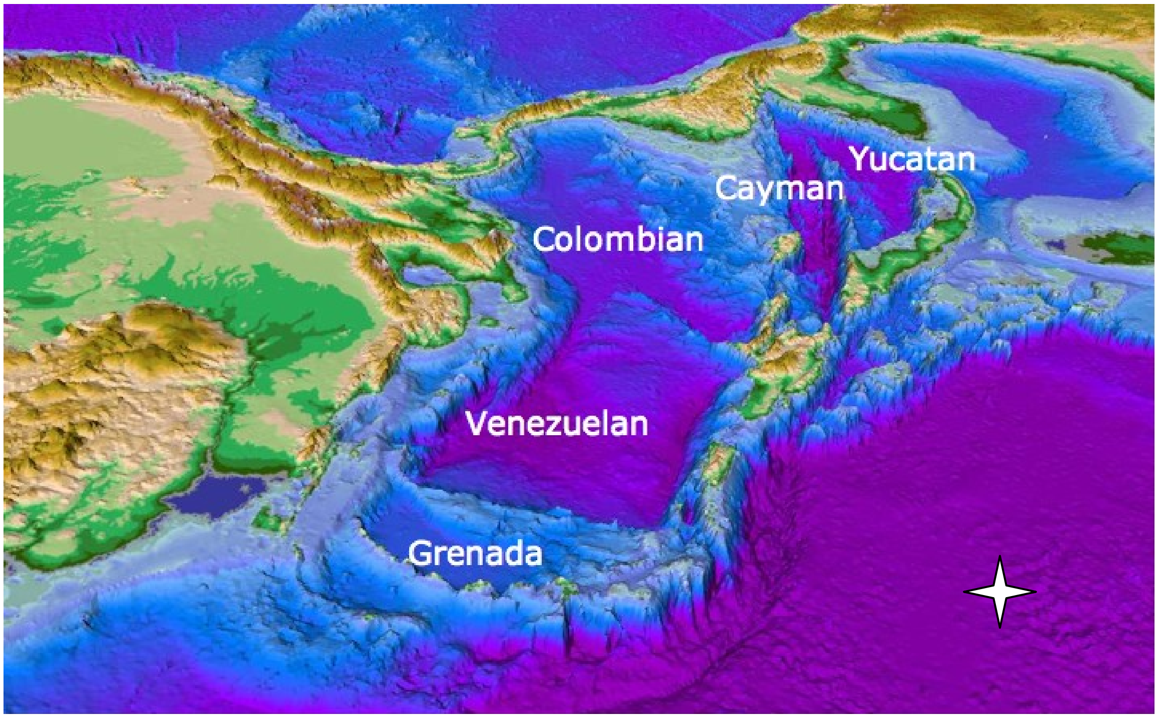

Fig. 1. The Caribbean basins: Topography of the Wider Caribbean region derived from satellite data. The Cayman Basin has depths of more than 5000 m, while the Gulf of Honduras, located where the Yucatan and Cayman basins merge, has waters as deep as 2000 m just within 15 km of the Mesoamerican Barrier Reef System stretching for more than 1000 km from Mexico to the Bay Islands in Honduras. North is to the right.

The ocean current system originates with the Equatorial Current, which branches into the Guiana Current as it hits Brazil. One part of this current remains windward of the Lesser Antilles and later the Bahamian Archipelago, to form the Antilles Current. The other part penetrates through the southern portion of the Lesser Antilles, running offshore to the eastern Venezuelan shelf. At the shelf, the current mixes with freshwater runoff from major rivers, the Magdalena (Colombia), the Orinoco (Venezuela), and the Amazon (Brazil) with annual discharges of several million to hundreds of millions of cubic meters each. The Magdalena river interacts with oceanic circulation in the southwestern Caribbean, while the Orinoco plume flows first northward along the South American coast and then influences the islands of the southern Lesser Antilles and the Greater Antilles. During the high runoff period or wet season, estuarine waters flow west-northwestward.

Water moves westward and northward through the Caribbean up the coast of Central America (the Caribbean Current), funneling first through the passage between the nothwest end of the Honduras shelf and Pedro Bank (southwestern Jamaica), and then through the Yucatan Channel. At the Gulf of Mexico, the Yucatan Current deflects to the west forming the Loop Current that turns abruptly back to the east and south through the Straits of Florida into the Florida Current and eventually the Gulf Stream.

The general geological structure of the Caribbean Basin generates a wide array of marine environments that include deep troughs and oceanic tongues, gulfs and bays, and shallow-water areas at shelves and banks. The submarine shelves are generally wider in some continental countries (e.g., Belize, northern Yucatan of Mexico, Honduras, and Nicaragua), and in the large archipelagoes of Cuba and the Bahamas, while in the Lesser Antilles they are very narrow and drop off a few hundred meters away from the coast.

The overall circulation pattern is shaped by dominant winds, coastal orientation, and sea bottom topography that combine to form meanders, eddies and gyres an nearshore counter-currents. The complex circulation influences the way propagules are dispersed from the places they originate to the place they settle. However, connections of species populations and ecosystems across the region also influenced by biological interactions with the environment and are still the subject of investigations (Paris et al. *this volume*).

There have been different attempts to delineate biogeographic regions in the Wider Caribbean. The division of the Caribbean into ecoregions has more than an academic interest. It is fundamental information to understand the connections of populations and ecosystems across the region and to plan conservation measures that can be effective and long lasting. Ideally, we would like to understand the spatial dynamics of the organisms that reside in the area that we intend to manage. Available information is still very limited, and is the focus of research projects and conservation programs in the region. While these questions are being investigated, conservation scientists and planners use ecoregional divisions as surrogates to identify likely biological connections. By doing this, it is assumed that the ecosystems and populations contained in certain ecoregions are more related biologically than with other areas and thus are used as approximate geographic units for conservation planning.

The ecoregional division proposed by Sullivan Sealey and Bustamante (1999) has been revised as more information has become available, particularly on habitat distribution. Among the most notable research efforts in ecoregional assessment are the ecoregional classification and conservation assessments conducted for the Mesoamerican Reef Region (Kramer and Kramer 2002), Cuba (Areces et al. 2004), Central America (Calderon et al. 2003), the Caribbean continental coast of Colombia (Alonso et al. 2007), and the status of reefs of the region (Burke and Maidens 2004).

In 2004, The Nature Conservancy (TNC) proposed a new division of the Tropical Northwest Atlantic Coastal Biogeographic Province (further discussed by Spalding et al. 2007). Eight marine planning units were delineated. The boundaries of these regions were drawn by Chatwin et al. (2004) based on existing information on West Atlantic surface water circulation along with seasonal temperature and salinity variability, which revealed a number of persistent features that influence coastal environmental conditions and geomorphology. In particular, the existence of re-circulation gyres that provide a barrier for larval dispersal were identified in the West Caribbean (Mesoamerican Reef area) and the Southwest Caribbean marine ecoregions. In addition to this oceanographic information, the underlying geological structures was used to subdivide the Central Caribbean marine ecoregion from the South and Central American continental areas, resulting in four marine ecoregions, namely, the Greater Antilles, West Caribbean, Southwest Caribbean, and South Caribbean marine ecoregions. The stable carbonate platforms of the Bahamian archipelago separate this ecoregion from that of the Lesser Antilles, a highly complex volcanic island-arc system that sits between the North and South American and Caribbean plates. The Gulf of Mexico marine ecoregion encompassed most of Gulf, but did not include the Southwestern Florida shelf or the Northwestern Cuban shelf. The Exclusive Economic Zone (EEZ) boundaries were used to position marine ecoregional boundaries, particularly over open deep water where there were few biophysical or geologic features present. This was also done to aggregate, where possible, countries into a single marine ecoregion rather than have their national boundaries subdivided into different marine ecoregions. Exceptions to this included Cuba, Dominican Republic, Colombia, and Mexico (see Chatwin et al. 2004). This bio-regionalization was included in the “Global coastal and marine biogeographic regionalization” as a support tool for the implementation of the Convention on Biological Diversity (CBD) Programmes of Work and presented at the CBD Conference of the Parties in Curitiba, Brazil, 20-31 March, 2006 (UNEP/CBD/COP/8/INF/34) further elaborated by Spalding et al. (2007).

Research efforts on ocean circulation and larval dispersal for the wider Caribbean (Cowen et al. 2000, 2003, 2006; Andrade and Barton 2000; Paris et al. 2002, 2004, 2005, *this volume*; Colin, 2004; Thattai et al. 2005, 2007; Ezer et al. 2005; Sale et al. 2005; Baums et al. 2006; Cherubin et al. 2007) have provided important insights on how biological and oceanographic barriers and linkages operate in the wider Caribbean (Appendix I).

Despite differences in methodology and approaches, the full range of spatial and temporal variability of oceanographic conditions and larval behavior is not captured. Robust estimation of spatial probabilities of larval dispersal for multiple species and from a variety of spawning sites still requires higher resolutions, coupled with biophysical models (Werner et al., 2007).

Findings from these studies suggest a new ecoregional scenario or units of biological connectivity of the Tropical Western Atlantic Coastal Biogeographic Province (or wider Caribbean) (Fig. 2), a significant departure from the nine ecoregions proposed by Spalding et al. (2007) for this Province. There are some interesting highlights, namely:

- a bio-oceanographic barrier divides the Bahamas into two units
- the MBRS region may have a division at approximately the Mexico-Belize border
- there is limited larval exchange between Honduras and Nicaragua, Costa Rica and Panama, Panama and Colombia, and Colombia and Venezuela
- the San Andres and Providencia Archipelago may play the role of a corridor for the replenishment of Jamaican reef related populations
- despite potentially high larval retention, the Lesser Antilles islands are weakly connected to one another forming a large, fragmented unit of biological connection from Trinidad and Tobago to Puerto Rico
- the Mona Passage represents a seasonal barrier to dispersal between Puerto Rico and Hispaniola

This new representation with 15 units suggests that the ecoregional scenario of the Caribbean is more complex and divided than previously estimated.

A- Florida; B - N Central Cuba- Cay Sal; C - Bahamian; D. Hispaniola; E - Puerto Rico – Lesser Antilles; F- S Caribbean; G - Continental Colombia; H - Panama-Costa Rica; I - Colombian Archipelago & Jamaica; J - Nicaraguan Rise Islands; K - Gulf of Honduras; L - Mexican Caribbean; M - NW-S Cuba & Cayman Islands; N - Campeche Bank; O - Guianan

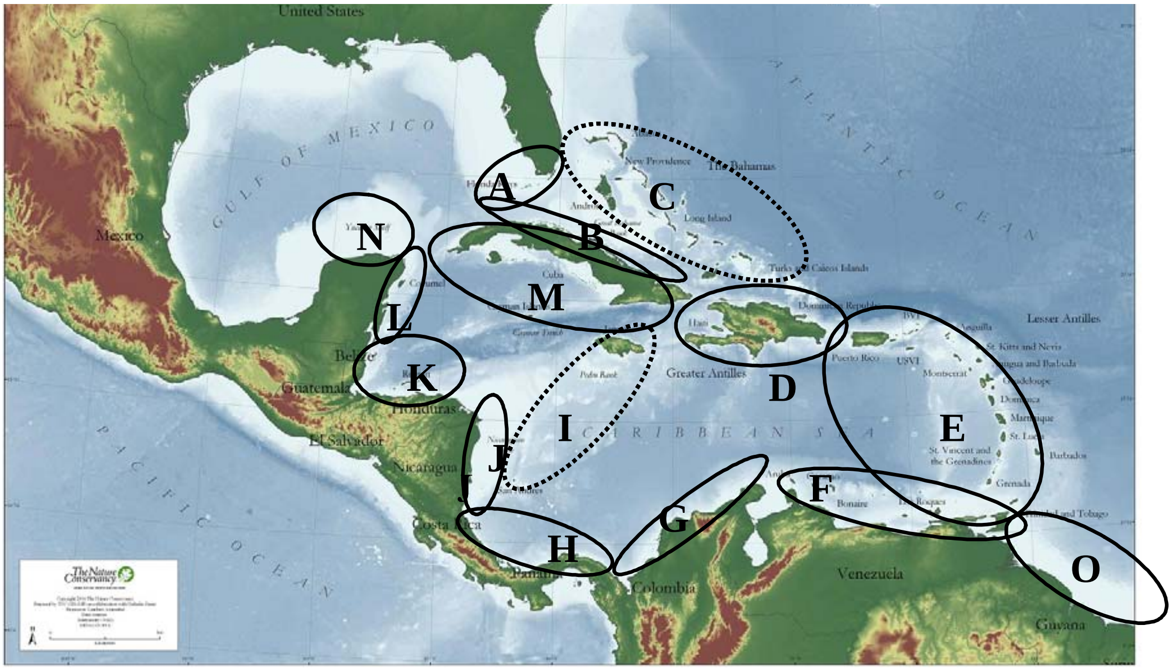

Fig. 2. Tentative units of biological connectivity (enclaves or marine ecoregions) of the Wider Caribbean, or Tropical Northwest Atlantic Coastal Biogeographic Province based on a combination of data from Colin (2004); Paris et al. (2005); Cowen et al. (2006) and others (see text for more detail). Ovals with dotted lines depict less documented or potential additional division.

Definition of "Outstanding Universal Value" for Marine WHS in the Caribbean

The Operational Guidelines for the Implementation of the World Heritage Convention (http://whc.unesco.org/en/guidelines) define sites with Outstanding Natural Value as:

(vii) containing superlative natural phenomena or areas of exceptional natural beauty and aesthetic importance;
(viii) be outstanding examples representing major stages of earth's history, including the record of life, significant on-going geological processes in the development of landforms, or significant geomorphic or physiographic features;
(ix) be outstanding examples representing significant on-going ecological and biological processes in the evolution and development of terrestrial, fresh water, coastal and marine ecosystems and communities of plants and animals;
(x) contain the most important and significant natural habitats for in situ conservation of biological diversity, including those containing threatened species of outstanding universal value from the point of view of science or conservation.

The Convention states that *outstanding universal value* denotes "natural significance that is so exceptional as to transcend national boundaries and to be of common importance for present and future generations of all humanity." These attributes for marine sites should be assessed based on their biogeographic context.

Gaps in the Wider Caribbean Marine WHS

To provide a basis for analyzing gaps in WHSs within this ecoregional scenario, existing WHSs with coastal and marine components in the Wider Caribbean, together with internationally recognized protected areas (UNESCO Biosphere Reserves and RAMSAR sites) and no-take areas (Lindeman and Appeldoorn 2003) were listed (Table 1, located after **Literature Cited**).

Habitat Representation

Extended Coral Reef Tracts and Archipelagos **–** There is only one WHS on a large coral reef barrier system: the Belize Barrier Reef System. However, several other outstanding coral reef systems have potential as candidates for marine and the "white-water-to-blue-water" type of WHS. Indeed they meet the following criteria: 1) outstanding biological and geological value; 2) relatively high conservation status; 3) threatened by current or potential intensive use (tourism and fishing); 4) includes no-take areas; 5) a focus for local, national and international conservation efforts and organizations; and 6) located in different marine ecoregions with poor WHS representation. Among these areas are the following: The Reefs of Southern Cuba (included in the WHS Preliminary List), Chinchorro Bank; The Bahamian Archipelago; The San Andres and Providencia Archipelago; The Southwest Caribbean Islands (from Bonaire to Los Roques); and the Florida Keys.

Marine–Upland Linkages – Four WHSs have a major land component with little adjacent marine areas: Alejandro de Humboldt National Park, Desembarco del Granma National Park (both in the northeastern and southeastern regions of Cuba, respectively), Pitons Management Area (St. Lucia), and Sian Ka'an Biosphere Reserve (Mexico). The latter does not extend enough to include valuable nearby reef habitats, fish spawning sites, and seabird nesting grounds, so expansion of this site will benefit its long-term conservation.

On the other hand, the Belize Barrier Reef System does not include enough area of other types of marine and coastal ecosystems (mangrove, coastal wetlands, upland watersheds), spawning aggregations, and nursery grounds necessary to ensure its long-term viability and is the only existing WHS in the Gulf of Honduras marine ecoregion. The inclusion of nearby marine reserves within the Belize site may increase the ecological value of the site and its contribution to the conservation of its marine ecoregion.

The Río Plátano Marine Reserve (Honduras) and the Everglades National Park (USA) are mostly wetlands and so have a limited coverage of coastal marine environments. The recently designated Tortugas Ecological Reserve (2001; part of the Florida Keys National Marine Sanctuary) has outstanding coral reef formations and is the spawning ground for several fishes and invertebrates. This Reserve may also provide larvae for marine populations of South Florida, along with the set of highly protected marine zones situated along the Florida Keys Reef Tract within the Florida Keys National Marine Sanctuary. Such a series of protected sites would provide a good coverage for the protection of the marine biodiversity of an entire marine ecoregion.

Ecoregional Significance

Ecoregions or Biologically-Connected Areas Without WHSs – Despite the importance of their marine reserves, many areas have no WHSs. This gap could be filled with the nomination of WHSs in the following promising areas: the southern or northern coasts of the Dominican Republic (Hispaniola marine ecoregion), the San Andres and Providencia Archipelago (for the Jamaica-Colombian Archipelagos marine ecoregion), the Cuban southern reefs (within the South Cuba-Cayman Islands marine ecoregion), and the area between Curaçao and Los Roques (Southwest Caribbean ecoregion). The Central Bahamian region also has potential and could be considered as soon as the Bahamas becomes a signatory party of the World Heritage Convention. Other ecoregions with little island components may also have opportunities of new marine WHSs as more data on population connectivity becomes available (Fig. 2).

Few WHSs in Large Marine Ecoregions – The Puerto Rico–Lesser Antilles ecoregion has only one WHS, the Pitons Management Area that includes most of Soufriere Marine Management Area (SMMA). The vulnerability of fish recruitment in the small islands of the Lesser Antilles as well as the encouraging results of the SMMA in the resolution of user conflicts and restoration of fish communities and coral reef health (Roberts et al. 2001) suggest that small but well-managed costal protected areas in the Lesser Antilles can have a significant impact on marine resource restoration. The use of the WH convention as an international tool to promote the effective management of individual or serial marine protected sites in this ecoregion may have a notable impact on marine resource restoration of the entire ecoregion. Among the sites with potential to be considered in the tentative list are the Saba Marine Park and Bank (serial), The Grenadines (serial transboundary) and maybe in the U.S. Virgin Islands, and Guadeloupe (Fig. 2).

Guianan Marine Ecoregion – There are no WH sites in this ecoregion. An ongoing effort of creating a regional network of MPAs may be a good basis to examine the potential for a serial transnational marine WHS in the coastal areas of Guyana, Suriname, and French Guyana.

Potential New Marine/Insular WH Sites in the Tropical Northwestern Atlantic Coastal Biogeographic Province

Based on the recommendations of the consultation process developed five years ago that culminated in the expert workshop held in Vietnam in 2002 (Hillary and Max 2003), along with the examination of data from different marine protected areas in the wider Caribbean and the biological connectivity information, we propose a list of at least 10 sites (new and expansion of existing) that have potential to be nominated in the near future (Fig. 3):

- Reef System of Southern Cuba
- Expansion of Everglades National Park with the Tortugas Ecological Reserve and other Preservation Areas of the Florida Keys National Marie Sanctuary
- Saba Marine Park and Bank (Netherland Antilles)
- The Grenadine Islands (serial transboundary site in Grenada and St Vincent and the Grenadines
- Islas del Caribe Sur (Curazao and Bonaire, Netherland Antilles; and Las Aves and Los Roques, in Venezuela) (serial and transboundary)
- Seaflower MPAs (San Andres and Providencia Archipelago, Colombia)
- Expansion of Belize Barrier Reef System WHS (Belize)
- Expansion of Sian Ka'an WHS (Mexico) with the inclusion of the Chinchorro Bank BR (Mexico)

The data used to examine these attributes and how the sites meet criteria vii, viii, ix and x of the Heritage Convention were presented by the first author (G. Bustamante) and discussed at a regional workshop[1]. Unfortunately, not all sites are in the same condition to meet the challenge of managing a WHS up to the standard required. It is encouraging that for most sites there is a high level of scientific information, as well as local and international attention. Recent regional surveys on the effectiveness of marine reserves (Appeldoorn and Lindeman 2003) and coral reef protected areas (Burke and Maidens 2004), among others, show similar results.

The above list of proposed sites should be taken only as an attempt to create a platform for discussion as well as promote the attention of the local conservation communities (governmental and non-governmental) on the importance of nominating WHSs using the scientific information on biological connectivity to document ecoregional significance.

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[1] "New opportunities of marine World Heritage Sites in the wider Caribbean: ecoregional scenario, natural value and potential new sites". Report by Georgina Bustamante discussed at the First Regional Training Workshop for the Caribbean on Marine World Heritage, Soufriere, St Lucia, March 2006.

E – Expanded sites: Everglades - Dry Tortugas; Sian Ka'an; Belize Barrier Reefs System.

N – New potential sites: Cuban Caribbean Reefs; Banco Chichorro; Saba; Guadeloupe; Grenadines; Is. Caribe Sur; Seaflower

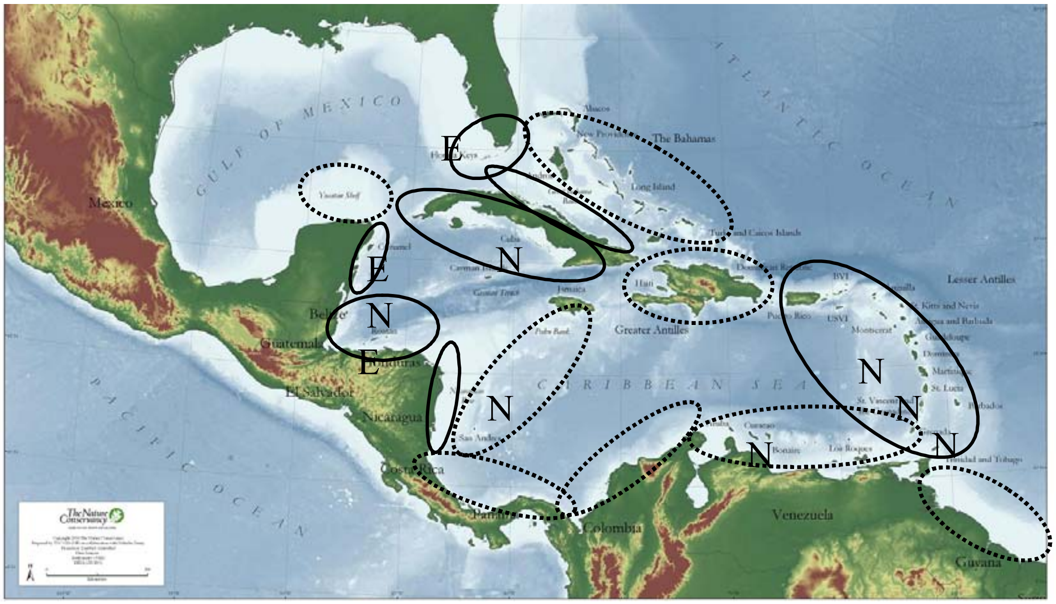

Fig. 3. Potential new WHSs of marine and island value in the Tropical Northwestern Atlantic Coastal Biogeographic Province (or wider Caribbean).

This information is also significant for the successful implementation of the Convention for the Protection and Development of the Marine Environment in the Wider Caribbean (Cartagena Convention, in force since 1986), which promotes regional cooperation for the management of the coastal and marine resources of the region, in particular, for meeting the objectives of the Convention's Protocols on biodiversity (SPAW Protocol) and land-based sources of pollution (LBS Protocol), as it will assist in the creation of effective networks of marine protected areas and eventually in the designation of World Heritage Sites. Information on biological connectivity is required for effective large-scale conservation planning and resource management, including networks of marine protected areas. Nevertheless, little has happened on this respect. The clock is ticking as we approach to the deadline (2012) for creating effective networks (or systems) of MPAs. Research data is not conclusive, but the Caribbean region is ready to use valuable (and expensive) research data to accomplish this objective. This paper is another attempt of taking this precious information out of the "science" closet.

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Table 1. World Heritage Sites and Biosphere Reserves with marine or coastal jurisdiction, and RAMSAR sites within the different marine ecoregions of the Tropical Northwest Atlantic Coastal Biogeographic Province as of June 2006.

No.	**Connectivity units (enclaves, or marine ecoregions)**[a]	**Geographic limits**	**Existing WHS**	**Marine Biosphere Reserves and** *RAMSAR* **sites**	**Marine reserves or no-take areas (or MPAs where they are located)** [b]
A	S Florida	From Dry Tortugas N to Palm Beach, and Tampa, Florida	Everglades National Park	*Everglades and Dry Tortugas* (USA)	Looe Key, John Pennekamp and Dry Tortugas (Florida Keys); Crocodile Sanctuary of the Everglades N.P.
B	N Central Cuba- Cay Sal	From Matanzas to the most eastern end of Cuba	Humboldt N.P (Cuba)	Gran Humedal del Norte de Ciego de Ávila, *Cuchillas de Toa* (Cuba)	Lanzamillo Pajonal Fragoso, Rincón de Guanabo, (Cuba)
C	Bahamian	The Bahamas, and Turk and Caicos Is	None	*Inagua National Park* (Bahamas);, *North, Middle and East Caicos* (Turk and Caicos Is.)	Berry Is.; Exuma Cays, N Abaco Cays, S Eleuthera, N Bimini (The Bahamas); Admiral Cockburn, Bell Sound, Chalk Sound, Colombus Landfall MNP, E Bay Is., Fort George Land Sea Natl. Park (LSNP), Grand Turk Cays LSNP, Lake Catherine NR, North, Middle and East Caicos NR, NW Point MNP, East Harbour Lobster and Conch Reserve, Princess Alexandra NR-Little Water, Donna and Mangrove Cays, S Creek NP, Vine Point and Ocean Hole NR, W Caicos, Pigeon Pond and Frenchman NR, and Princess Alexandra LSNP
D	Hispaniola	Dominican Republic, Haiti and Mona Is. (Puerto Rico)	None	*None*	Jaragua, Parque Nacional del Este (Dominican Republic); Mona Is. (Puerto Rico)

E	Puerto Rico and E Caribbean Is.	From Puerto Rico east and southeast Grenada and Barbados	Pitons Management Area (St. Lucia)	*Guanica* (Puerto Rico); *Virgin Islands* (St. John, U.S.Virgin Is.); *Western Salt Ponds of Anegada* (British Virgin Is.); *Codrington Lagoon* (Antigua and Barbuda); *Archipel de la Guadeloupe, Grand Cul-de-Sac Marin de la Guadeloupe (French Antilles); Mankoté Mangrove, Savannes Bay* (St. Lucia); *Graeme Hall Swamp* (Barbados)	Cas Cay/Mangrove Lagoon MR and Wildlife Sanctuary (MRWS), St. James MRWS, Hind Marine Conservation District, Compass Point Pond MRS (USVI); Wreck of the Rhone, Horseshoe Reef (British VI); Grand Cul-de-Sac Marin, Petite Terre, St. Martin; S. Barthelemy (French Antilles) Soufriere Marine Management Area, Maria Is., Anse Chastanet (St. Lucia); Desecheo Is., Canal Luis Pena-Culebra and Tres Palmas Marine Reserve (P. Rico), Saba, St. Eustatius (N.A), Cades Bay, Palester Reef, Diamond Reef (Antigua and Barbuda); Soufriere-Scottshead Marine Reserve (Dominica); Tobago Cays (St.Vincent and the Grenadines); Saba, St Eustatius (N.A.); Barbados M.R. (Barbados); Tobago Cays (Grenada)
F	S Caribbean	Venezuela coast and offshore islands, and Aruba, Curazao, Bonaire, and Trinidad and Tobago	None	*Archipielago Los Roques, Parque Nacional Medanos del Coro, Cuare, La Tacarigua, and Laguna La Restinga* (Venezuela); *Klein Bonaire Island and adjacent sea; Het Gotomeer, De Slagbaai, Het Lac, Het Pekelmeer* (Netherland Antilles); *Het Spaans Lagoen* (Aruba); *Buccoo Reef / Bon Accord Lagoon Complex, Nariva Swamp, Caroni Swamp* (Trinidad and Tobago)	Cuare, Los Roques, Las Tetas de Maria Guevara, Laguna de las Marites, Medanos del Coro NP, Las Aves WF, Laguna de Tacarigua NP, Cienaga Olivitos WR, Mochima NP, La Laguna La Restinga MP, San Esteban NP, Cienagas de Juan Manuel, Aguas Blancas y Aguas Negras, and Morrocoy (Venezuela); Buccoo Reef (Trinidad and Tobago), Bonaire MR (Bonaire).
G	Continental Colombia	Colombia continental coast	None	*Cienaga Grande de Santa Marta*	El Conchal El Mono Hernandez, Corales del Rosario and San Bernardo
H	Panama -Costa Rica	Coastal areas of Panama and Costa Rica	None	Gandoca-Manzanillo, *Humedal Caribe Noreste* (Costa Rica), *La Amistad, San San-Pond Sak* (Panamá);	
I	Jamaica – Colombian Archipelago	Jamaica and San Andres and Providencia Is. (Colombia)	*None*	*Palisadoes - Port Royal Black River Lower Morass,* *Portland Bight* (Jamaica); *Seaflower* (Colombia)	Old Providence McBean Lagoon, Seaflower BR (San Andres and Providencia Archipelago, Colombia); Montego Bay M.P; Negril M.P.; Ocho Rios M.P., Bogue Fish Sanctuary; Bowden Fish Sanctuary (Jamaica)
J	Nicaraguan Rise	Nicaraguan coast and offshore islands; islands off eastern portion of Honduras	Rio Platano (Honduras)	*Río San Juan; Cayos Miskitos* (Nicaragua);	**0**

K	Gulf of Honduras	Belize, Guatemala and most of Honduras	Belize Barrier Reef System (Belize),	Sarstoon Temash (Belize) Punta de Manabique (Guatemala); Gandoca-Manzanillo, Tamarindo and Terraba-Sierpe; National Park Jeanette Kawas, Punta Izopo, Barras Cuero y Salado (Honduras);	Corozal Bay, Zapodilla, Laughing Bird Caye, Glover's Reef, Blue Hole, Half Moo Caye, Caye Caulker, Port of Honduras, Hol Chan, Bacalar Chico (most of them are seasonal reserves at spawning aggregation sites) in Belize; Cayos Cochinos (Honduras)
L	Mexican Caribbean	From Cabo Catoche, NW corner of Yucatan, S to the Mexican-Belizean border	Sian Ka'an Biosphere Reserve	*Banco Chinchorro*, Arrecifes de Xcalak, Isla Contoy, Arrecife de Puerto Morelos; Playa Tortuguera, X'cacel-X'cacelito; Arrecifes de Cozumel	Sian Kaan, Puerto Morelos, Arrecifes de Cozumel, Is Contoy, Banco Chinchorro, Arrecifes de Xcalac,
M	NW-S Cuba & Cayman Islands	Northwestern and southern portions of the Cuban shelf, and the Cayman Is.	Desembarco del Granma National Park (Cuba)	*Buenavista, Baconao, Cienaga de Zapata*, Ciénaga de Lanier y Sur de la Isla de la Juventud, Humedal Delta del Cauto; *Peninsula de Guanahacabibes* (Cuba) *and* Central Mangrove Wetland, Little Sound, Ponds and associated Marine Zones (Cayman Is.)	Cayos Ana Maria, Maria La Gorda, Cayo Largo del Sur, Punta Francés, Jardines de la Reina, Guanahacabibes, Cienaga de Zapata (Cuba); W End Marine Park Zone (MPZ), 7-mile Bridge MPZ, Cayman Kai MPZ, Cayman Is Marine Park System, Dick Sessinger Bay MPZ, Hawksbill Bay MPZ, George Town MPZ, Spanish Bay Reef MPZ, NW Point MPZ, Preston Bay MPZ, Bloody Bay-Piasons MPZ.
N	Campeche Bank	Northern Yucatan shelf	None	*Ría Lagartos, Ría Celestún*; Dzilam, Sistema Arrecifal Veracruzano; Laguna de Términos, Yum Balam	Laguna de Terminos
O	Guianan	From the Guyana-Venezuela border to the French Guiana-Brazil border	None	Coppernamemonding (Suriname)*;* *Kaw* (French Guyana)	Connetable Is.(French Guyana) (and others)

[a] Marine ecoregions or units of marine population biological connectivity were defined using data provided in Appendix I .

Appendix I. Major findings on biological and physical interactions in the Caribbean.

Type of finding	**References**
Atlantic water entering the Caribbean basin: Cyclonic and anticyclonic gyres move north of 15º N with several eddies passing through the Antillean Arc (via Anegada and St Lucia Passages, and north of Trinidad) in different seasons, all traveling northward along the Central Caribbean. There is evidence that a large part of these eddies originate in the equatorial region at the retroflexion of the North Brazil Current, and make there way northwestward and, some of them, manage to pass through the gaps between the Lesser Antilles into the Caribbean. Once inside the Caribbean, they reformed and continue their way northwestward.	
Circulation within the Caribbean Basin: Cyclonic eddies in the Gulf of Honduras originated near the Nicaraguan Rise propagate westward along the coast of Honduras. These eddies may play an important role in the connectivity processes and associated biological transports. On average, an eddy takes approximately 10 months to transit from the Lesser Antilles to the Yucatan Channel, with values as short as 7 months and as long as 17 months. Another eddie passes through the Windward Passage and travels along the Cayman Sea exiting via the Yucatan Strait six month later. Almost all eddies dissipate at the Nicaragua Rise as they collide against the shoals and banks. In the W Caribbean Sea (from the Mesoamerican Reef system to W Cuba) the mean flow is characterized by a southeast-northwest flow accompanied by as many as five cyclonic gyres along the Honduran coast in the Gulf of Honduras each with diameter 50-150 km, and by the propagation of an anticyclonic eddy with a 300 km diameter southeast of the Yucatan Channel. A typical mesoscale eddy travels approximately 220 km in 30 days, which means that it could take up to 10-12 months to cross the entire area W Caribbean Sea from SE to NW.	
Marine larval dispersal	
• Although larval dispersal have the potential for long-distance dispersal, evidence is mounting that it may be limited and the ecological significant numbers for settlers are in the scale if 50 to 100 km for most species with a relatively high rate of local retention from adjacent locations;	
• The Panama-Colombia gyre is a broad circulation that limits the connection between the Colombia Basin and the Cayman Sea. These research results indicate that some kind of a barrier for larval dispersal exists between the S Caribbean and its central and NW part.	
• Based on the damselfish *Stegastes partitus* larvae distribution in Barbados, it was concluded that larval retention is favored; if some downstream location were receiving heavy fishing pressure (e.g., 40% of the population is being removed each year), then in order to sustain such fishing pressure, recruitment to the local population must be subsidized from upstream sources to the tune of about 40% of the total required, pre-fishery recruitment rates.	Cowen 2001
• There are considerable levels of self-recruitment in Cuban snapper populations, in particular, those from the southern and north central regions. For northern snapper populations, larvae end up mostly in the southern Bahamas (specifically Cay Sal Bank). A small lag in peak spawning times among species produces high recruitment variability among species.	Paris et al. 2005
• Using data on the presence of 25 species of *Elacatinus* (a small reef dweller goby fish), blue angelfish, yellow stingray, hamlets, and other species, as well as data on	Collin 2004

drifter tracks throughout the Caribbean Sea, it was found a disruption of connectivity in the Central Bahamas that generates some separation between Little Bahama and Central Bahama Banks, and the SE Bahamas islands and Turk and Caicos; a "filter barrier" between Dominican Republic and Puerto, at the Mona Channel; another disruption off the Guajira peninsula (Colombia); a separation between Colombia and Panama; an apparent breaking point close to the Mexico-Belize border; a strong local circulation pattern within both Gulf and Honduras and in southern Cuba-Cayman area.	
• Based on biophysical modeling of larval dispersal, marine populations larval dispersal in the region seems to operate like this: - The W and E Caribbean are moderately isolated from each other along a meridian break centered at about 67º to 70ºW, from W Puerto Rico south to Aruba off the coast of Venezuela, which may constitute an ecological barrier from the Colombian gyre area to the west; - the NE Caribbean (Puerto Rico and Leeward Is.) is relatively isolated from the reminder of the E Caribbean; - the Leeward Is. are self-recruited and constitute a sink for north-south larval exchange of the Windward Is.; - there is westerly exchange along the southern Windward Is. and those along the coasts of South America; - the Bahamas and the Turks and Caicos Is. form an enclave of high connectivity largely isolated from the reminding Caribbean region except for minor exchange the north Cuba and Haiti; - the Belize and Honduras coasts are weakly isolated from the N Mesoamerican Barrier Reef system, but strongly isolated from the islands along the coast of Nicaragua to the east and south; - the Hispaniola and Jamaica is a mixing zone among several of the regions; - two ecoregions, the Windward Islands and the Mexican Caribbean and Campeche Bank are recruitment-limited (below the necessary for replenishing populations); while the rest receive sufficient recruits; - Caribbean-wide self recruitment varies from 9% (off Mexico) to almost 57% (off Colombia in proximity to a semi-permanent Panama-Colombia gyre); and - The contribution to South Florida larval recruitment from Mexico is relatively low.	Cowen et al. 2006

Marine World Heritage Sites in the Wider Caribbean: How Reserch Data on Biological Connectivity Can Document the "Outstanding Universal Value" of New Nominations

Georgina Bustamante

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Summary of oral presentation

Using biological data on connectivity. The former view was that there is a one-way road from SE to NW in the Caribbean.

Broadcast spawners "go out" in search of oceanic conditions while they are still "at home" (shelf waters) so they can minimize energy.

Decline in fisheries abundance (1980s & 1990s). Severe decline of resources. Overfishing rampant; fishing on spawning aggregations.

In 90s: "We are all connected"
Politically correct by being all biologically connected?
The Caribbean is one unit of biological connection

Now, we understand that there is no one-way road for larvae. Instead, there are complex paths with strong eddy activity.

Fish larval dispersal is more restricted than previously thought. Management decisions based on open population models might overestimate the level of population exchange. Such overestimates might lead to a false sense of security of managers of downstream resources.

Countries in this region are identifying aggregation sites and establishing protection.

High rates of retention of snapper larvae from spawning aggregations in SW-SE and N Central Cuba. Mutton snapper larvae recruit mostly locally with some degree of export to neighboring locations. Therefore managers must not depend on recruitment from other areas – they must manage their own resources.

Distribution of cleaning gobies – identified barriers that produce enclaves with very limited connectivity between areas.

Demonstrating "outstanding universal value" of the marine World Heritage Site new nominations:

If the site is designed and managed to protect critical species, habitats, and ecological processes of the entire ecoregion, then this ecoregional significance should be considered an attribute to demonstrate “outstanding universal value,” instead of examining (comparing with) the site value in the context of an entire biogeographic province or the entire world (comparing Pacific apples with Caribbean oranges).

Developed new map of units of biological connectivity based on information for fish. Proposing this map serves better than previous attempts to map bioregions in the Caribbean and Gulf of Mexico.

Looked at the units and where there are existing coastal/marine, wetland, and terrestrial World Heritage Sites. Several of the units contained no World Heritage Sites.

Conducted analysis of areas to identify gaps in World Heritage Site representation in the region. The Puerto Rico-Lesser Antilles ecoregion has only one World Heritage Site and was not inscribed for its marine value. Therefore more sites are needed considering this vulnerability.

Marine-upland linkages – the Belize Barrier Reef system lacks sufficient mangrove, coastal wetlands, upland wetlands, etc.

Developed a list of potential new sites for establishment as World Heritage Sites, including proposing the Everglades be expanded to include the Dry Tortugas. Also proposing adding marine reserves and other MPAs to Belize system.

There are many sites in the region with interest in establishing new World Heritage Sites.

Suggestions:
Managers: let’s use demographic connectivity data to benefit; scientists: let’s make demographic connectivity data better; conservation organizations: let’s build bridges; donor agencies: fund research on demographic connectivity more; GCFI members: provide a regular forum, web page, etc.

Abstract:
Bustamante, G., and C. Paris. 2007. Marine World Heritage Sites in the wider Caribbean: How research data on biological connectivity can document the “outstanding universal value” of new nominations. Proc. Gulf Carib. Fish. Inst. 59: 631.

Marine World Heritage Sites in the wider Caribbean: How research data on biological connectivity can document the “outstanding universal value” of new nominations 114

Sustainability and Tourism in the Costa Maya: Their Influence in Natural Protected Areas of Quintana Roo

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Summary of oral presentation

Oil and tourism industries pressuring this area (Yucatan). Explosion of development in Quintana Roo. 1000% increase in population. 540% increase in development in six years. Destroying mangroves, coral. Loss of biodiversity, loss of nursery areas, many life cycles affected; huge pressure on resources.

Yucatan doesn't have river sources of water – sources are underground. Concern that wastewater is going into the ground – where the water sources are…

$21M US for mega cruise ship dock. Tourism doesn't benefit locals – and their resources are being impacted.

2001 started the increase. In June 2004 they "celebrated" 1 millionth passenger.

Increased tourism results in increased demands for resources.

Estimated 17-20 employees per hotel room.

Tourists staying spend $300 US; cruise ship passengers only spend $25 US.

Managers also have to respond to hurricanes and shipwrecks.

Land-use program "Costa Maya" POET (= zoning regulations). Has an environmental management unit – have to achieve certain goals for each unit. Don't have enough information to know how to manage resources sustainably.

Need more research: water pollution, water temperature, currents.

Need information put in a way that serves politicians making decisions and for general social awareness.

Abstract:

Reveles González, B. 2007. Costa Maya sustainability and tourism and its influence in natural protected areas in Quintana Roo. Proc. Gulf Carib. Fish. Inst. 59: 632.

Added Uncertainty With Marine Reserves: Identifying and Understanding the Sources

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Summary of oral presentation

"…MPAs can serve to hedge against inevitable uncertainties, errors, and biases in fisheries management."

New uncertainties with reserves come primarily from connectivity.

- Larval connectivity
- Juvenile/adult connectivity
- Economic connectivity

Three ways to partition uncertainty in fisheries:
1. Measurement error
2. Model choice error
3. Implementation error

Measurement error:

- Data are imperfect
- Can be quantified in a variety of models
- May not change with reserves

Model choice error

- New dependence on connectivity
- What types of connectivity are important for various stocks?
- What are proper parameter values for dispersal distance, home range size, etc.?
- How do we represent shifts in fishing effort?

Implementation error

- Choice of limits for exploitation uncertain
- These exist with or without reserve management

Synthesis:

- Measurement error: same; wouldn't necessarily increase with reserves
- Model Choice error: could increase, due to uncertainty in connectivity
- Implementation Error: same

Reserves do not eliminate uncertainty!

Integrating Near Real-Time Data for Coral Reef Ecological Forecasting

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Abstract

The National Oceanic and Atmospheric Administration (NOAA) has committed to integrating ocean data from a variety of sources into an Integrated Ocean Observing System, and to work toward operational ecological forecasting as part of its ecosystem approach to management. Consistent with this, NOAA's Coral Reef Conservation Program has committed to integrating coral data from a variety of sources for the specific benefit of coral reef researchers and marine protected area (MPA) managers. NOAA's Atlantic Oceanographic and Meteorological Laboratory, together with its NOAA and University of Miami partners, are contributing to this goal through their Integrated Coral Observing Network (ICON) project. ICON provides web-based software to integrate satellite, monitoring station (in situ), and radar data sources in near-real-time, and utilizes an inference engine (artificial intelligence software) to provide ecological forecasts using some or all of these data. The capabilities of ICON software are currently being focused upon one area in particular, Molasses Reef in the Florida Keys National Marine Sanctuary, to provide proof-of-concept and to provide a "discovery prototype" for consideration by the MPA managers assembled at the GCFI conference. Feedback to ICON developers from MPA managers, based upon their own specific management requirements and priorities as well as knowledge of the prototype capabilities, is essential to set priorities and enable additional ICON software engineering specifically tailored to MPA managers' needs. Featured in the prototype are several levels of user access: layperson, researcher, site maintainer, MPA manager, and software developer colleague. Depending upon user access, information products can include recent and historical single-source and integrated data output, custom graphics output, and ecological forecasts for coral bleaching, coral spawning, upwelling, pollution impacts, and larval drift.

Extended Abstract:

Hendee, J., L. Gramer, D. Manzello, and M Jankulak. 2007. Integrating near real-time data for coral reef ecological forecasting. Proc. Gulf Carib. Fish. Inst. 59: 525-528.

Panel Discussion: Linking Research on Connectivity With MPA Management

Q: Mike, you are talking about uncertainty in models, but you aren't talking about what is gained by the reserves. Didn't take into account that you can use reserves to inform management.
Mike O'Farrell: Agreed – probably could have been more upfront of what I was discussing. I was referring to a system where no reserves exist to inform decisions. The reserves that are there are so small that there is no network effect. We have very little information to go on regarding how populations will benefit.
Follow up: If you were to implement a larger system, you could test the effects before it is too late.
Mike O'Farrell: You are right. Generating the political will to do that is difficult, however.

Q (Sarah Frias-Torres): You are facing a tsunami of tourism development, but you mentioned that cruise liners make all the money and don't give back to the community. Someone has to give permits – so how is that happening? You mentioned we have to give information to managers so they can make good decisions, but they don't always make those good decisions!
Barbara Reveles: Regarding permission for piers – we have a state department environmental secretary. Not so clear sometimes who gives the permission. There is a lot of money, under the table perhaps. This is one of the main issues. In Mexico this is everywhere – in the U.S. and other countries, too. We should bring the politicians to that kind of discussions. We have to work a lot with those kinds of people – with the fishermen, the people that live there. We aren't bringing those to the table that have the power to make the changes.

Q (Brian Keller): If we managed to pepper the Caribbean with World Heritage Sites what would the potential benefits be?
Georgina Bustamante: This tool is not going to solve all the problems, but we've heard from those in the countries that they believe it will help. First it will focus the attention of the world. It's a jewel, and a matter of pride. They bring resources to the sites. If you can document that your WHS is good for management effectiveness of the site, but also that it contributes to the management and conservation of the ecoregion, that will bring more benefits. Tourism will come as well. Of course there are two sides to the tourism coin. Healthy environments are more and more scarce, making jewels desirable to tourists. There must be protection and legislation.
Barbara Reveles: There is a political benefit, too. The government must sign on to this. The government will not touch the World Heritage Site in Quintana Roo. There is a WHS in the Galapagos – and it is being reviewed and may lose its status. This is a tool we can use to protect these areas.

Q: What is the difference between the WHS and biosphere reserve status? What are the consequences of having both designations? What are the trade-offs with these two designations?
Georgina Bustamante: WHS are jewels – they are unique in the world. WHS become political issues in the country. There is a difference between being a biosphere reserve and a WHS – if a biosphere reserve can have a community inside the protected area.
Marion Howard: Biosphere reserves are established to help with sustainable development – not just conservation. They look at linkages between conservation and sustainable use.

Q: Are there models you can look at and apply them to developing sites?
Barbara Reveles: I have met with a Carnival Cruise Ships representative. He asked me to provide information – and we are going to start trying to involve them in conservation, and to show them how they are affecting our resources. These companies are everywhere – and it is the same everywhere. They don't have environmental concerns – these people that are involved in the cruise ships. We have to stop them, and to convince the government that is better to get people that want to stay for a week, and that are concerned with the natural environment.
Georgina Bustamante: Years ago we (GCFI) were just a group of scientists, then we started bringing more fishermen and managers. Trying to influence what they do and how they work. Evidently that is not enough. Maybe we need to do more – not sure how much more we can do – even now our meetings are crowded and we have to turn away workshop proposals. Maybe next year we should bring politicians and administrators. We need to reach out to the right people.

Q: Going beyond the intrinsic value of conservation, but that doesn't mean the same to all. Are you aware of any business plans that describe the value of these resources over time if they are protected vs. destroyed due to short-term interests? If it can be presented in dollar terms, it could be more appealing to businesses.
Georgina Bustamante: There are some efforts trying to get to the values of the reefs, but it is hard and it's a large value.
Marion Howard: A lot of work is being done around the world regarding economic valuation of ecosystems. When you try to take the information from different sites – you aren't sure how accurate, plus it may not have application in the area where you are interested.

Comment (Peter Rubec): It gets back to governments, and corruption or diversion of money. Even though you do good science, if you don't address politics and the issue of revenue for management and implementation of protected areas. We need to get protected areas self-sustaining. If the things the tourists come to see disappear, then the tourists will disappear. We need to be concerned about coastal pollution and solutions. Maybe it's not GCFI's role to do this – but the NGOs need to start addressing these issues.

Q: Mike, if I understood your presentation, connectivity introduces new uncertainty. The assumption is that distribution of effort, therefore mortality, is spread equally among the area. That is an untrue assumption. Connectivity uncertainty is there but we're not acknowledging it.
Mike O'Farrell: That's true. Even before MPAs gained popularity in North America, people were studying connectivity as they realized the importance of it. I agree uncertainties are still there, as we usually don't have the data at fine enough resolution to see how patchy populations are over space and how fishing is distributed over space. The data are usually very gross.
Follow up: With regard to California and the Caribbean – serial depletion. There is some existing information on this for California and in the South Atlantic.
Mike O'Farrell: Serial depletions are seen as errors in models.

Demersal Connectivity

Movement of Adult Fish in the Jardines de la Reina Marine Reserve, Cuba

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Abstract

Most studies documenting spillover/exportation of reef fishes from marine reserves are based on indirect evidence (gradients of abundance and catch) and have been conducted on small reef fish of low commercial importance. This paper presents research on movement of large reef fishes of high commercial importance across the boundaries of a marine reserve (Jardines de la Reina Marine Reserve) and among various habitat types (reef crest and reef slope), using tagging techniques (dart tags and modified spearguns). Exportation of some reef fishes (*Mycteroperca bonaci, Epinephelus striatusi,* and *Lachnlaimus maximus*) was recorded; however, for most species exportation was low or non-existent and movement was documented in only 25% of all recaptures. Most movement occurred within the first 200 m of the marine reserve boundaries, and movement among habitats typically occured from the reef crest to the reef slope in one direction (*Epinephelus itajara, Caranx bartholomaei, Lutjanus cyanopterus, Ginglymostoma cirratum,* and *L. maximus*). Less movement was documented from the reef slope to the reef crest (*Mycteroperca tigris, L. cyanopterus,* and *Lutjanus analis*). Movement among habitats was always greater than movement within the same habitat. Changes in the continuity of habitat features and a reduction in the structural complexity of the habitat appeared to reduce movement of fishes.

Introduction

Movement of adult fish is a key issue because of its management implications for commercially and recreationally important reef fishes. The topic is particularly relevant for the management of marine reserves since acceptance of reserves is often linked to benefits associated with catching fish that move out of a reserve (Edgar and Barret 1999; Brouwer 2002; Griffiths and Wilke 2002; Willis et al. 2003; Palumbi 2004; Sale et al. 2005).

Fish movement is due to many reasons including ontogenetic movement (Meyer et al. 2000; Brouwer 2002; Watson et al. 2002; Palumbi 2004); movement associated with structural relief (Starr et al. 2002; Palumbi 2004), showing less mobility in structurally less-complex sites and when discontinuities (a break in the habitat) are found (Buechner 1987; Barrett 1995; Edgar and Barret 1999; Chapman and Kramer 1999; Eristhee and Oxenford 2001); spawning-related movements (Zeller and Russ 1998; Eklund and Schull 2001; Polunin 2002; Hilborn 2004); inter-habitat movement for differential use of resources (many fish find shelter in reefs and food in

Pina Amargós, F., G. González Sansón, A. Jiménez del Castillo, A. Zayas Fernández, F. Martín Blanco, and W. Acosta de la Red. 2008. Movement of adult fish in the Jardines de la Reina Marine Reserve, Cuba. Pages 121-138 *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, 59th 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.

seagrass beds) (Grigg 1994; Burke 1995; McFarland and Wahl 1996; Meyer et al. 2000); and may depend upon feeding habits where predators that actively seek their prey move longer than ambushers (Samoilys 1997, Zeller et al. 2003). Movement has been associated with tidal and diurnal cycles (Samoilys 1997), though not in all cases (Hobson 1972; Choat and Robertson 1975; Sale 1978; Russ 1991), and may also be associated with cleaning stations (Robertson 1974; Samoilys 1997). Furthermore, movement occurs seasonally (Jones 1981, 1984; Bryant et al. 1989; Rutherford et al. 1989; Matthews 1990).

Research on non-pelagic fish movement reveals some generalities. Fish caught and then released away from the catching site return almost exactly (and many times exactly) to the place where they were caught (Burke 1995; McClanahan and Kaundra-Arara 1996; McFarland and Wahl 1996; Meyer et al. 2000; McClanahan and Mangi 2000), seemingly because such sites are their refuge, resting, or sleeping sites (Bardach 1958; Beets and Hixon 1994; Eristhee and Oxenford 2001). Fish show a natural trend to dispersion with time (short trackings show less mobility than longer ones) (Bardach 1958; Edgar and Barret 1999). However, little is known about large reef fish, mainly in the Caribbean area, as most of the studies have targeted middle-size and small species (Johannes et al. 1995; Corless et al. 1996; Munro 1999; Chapman and Kramer 2000; Eristhee and Oxenford 2001), though in general large pelagic fish can move 1000s to 100s of km, large demersal reef fish can move 100s of km, and small demersal reef often move on the scale of meters (Palumbi 2004).

Movement across a marine reserve, unless demonstrated that such movement is the result of an abundance gradient (spillover effect), should be regarded as exportation. Various papers report exportation, but generally a scarce number of individuals cross the reserve boundaries and most of the mobility occurs in adjacent areas, dramatically decreasing as distance from such areas increases (Eristhee and Oxenford 2001; Zeller et al. 2003). Many studies do not focus on tagging and recapturing close to the reserves, thus missing exportation evidence due to the low resolution of the recorded distances, usually ranging from 500 m to kilometers (Samoilys 1997; Zeller 1997, 2002; Zeller and Russ 1998; Chapman and Kramer 1999). Another problem related to low detection of exportation could be linked to the low recapture rates of most of the studies (Samoilys 1997; Zeller and Russ 1998; Chapman and Kramer 2000; Zeller et al. 2003). Increase of recaptures has been emphasized as a key issue for strengthening conclusions (Munro 2000; Zeller et al. 2003), with a recommendation of the use of visual recaptures (resightings) as a way to accomplish such an increase (Samoylis 1997; Zeller 1998; Zeller and Russ 1998; Chapman and Kramer 1999).

Traditionally, mark-recapture studies with external tags have constituted the main method of examining fish movement (Zeller and Russ 1998; Zeller 1999). External tagging techniques, however, are known to have several limitations. The most important one is that data obtained are usually limited to knowledge on points of release and recapture, only allowing estimates of straight-line distances and time interval between these events and not providing information about exact distance traveled and detailed movement patterns (Zeller and Russ 1998; Zeller 1999). On the other hand, external tags can provide useful information when objectives are defined. As external tagging methods are less expensive techniques, more individuals can be tagged, providing good data about populations and communities (Zeller and Russ 1998; Eklund and Schull 2001; Zeller et al. 2003). External tagging techniques have been used in combination with telemetry to yield insights (Zeller and Russ 1998) or alone (Chapman and Kramer 1999; Munro 2000; Zeller et al. 2003).

The main goals of the present study were to assess site fidelity, intra- and inter-habitat movement, effect of discontinuity on mobility, and large-size fish exportation in the coral reefs of the Jardines de la Reina Marine Reserve, using traditional mark-recapture methods.

Materials and Methods

Study Area

The Jardines de la Reina Archipelago stretches along 360 km, from the Gulf of Guacanayabo to Casilda Bay, south of Cuba (Fig. 1). It is made up of 661 keys. The archipelago has three groups of keys, the most important of which is Las Doce Leguas (The Twelve Leagues), located in the westernmost end, south of the provinces of Ciego de Avila and Camaguey. Since 1996 about 950 km^2 were proclaimed as “Zone Under Special Regime of Use and Protection” (ZUSRUP), according to Resolution 562/96, from the Ministry of Fisheries. Inside ZUSRUP only lobster fishing and finfishing by Azulmar, a tourist operator, are allowed. Lobster is fished in a sustainable way and Azulmar, the only tourist operator in the area, catches about five tons, mainly of snappers and jacks, per year. Such sustainable and low fishing levels make the ZUSRUP equivalent to internationally known marine reserves, and it is termed a marine reserve in this paper.

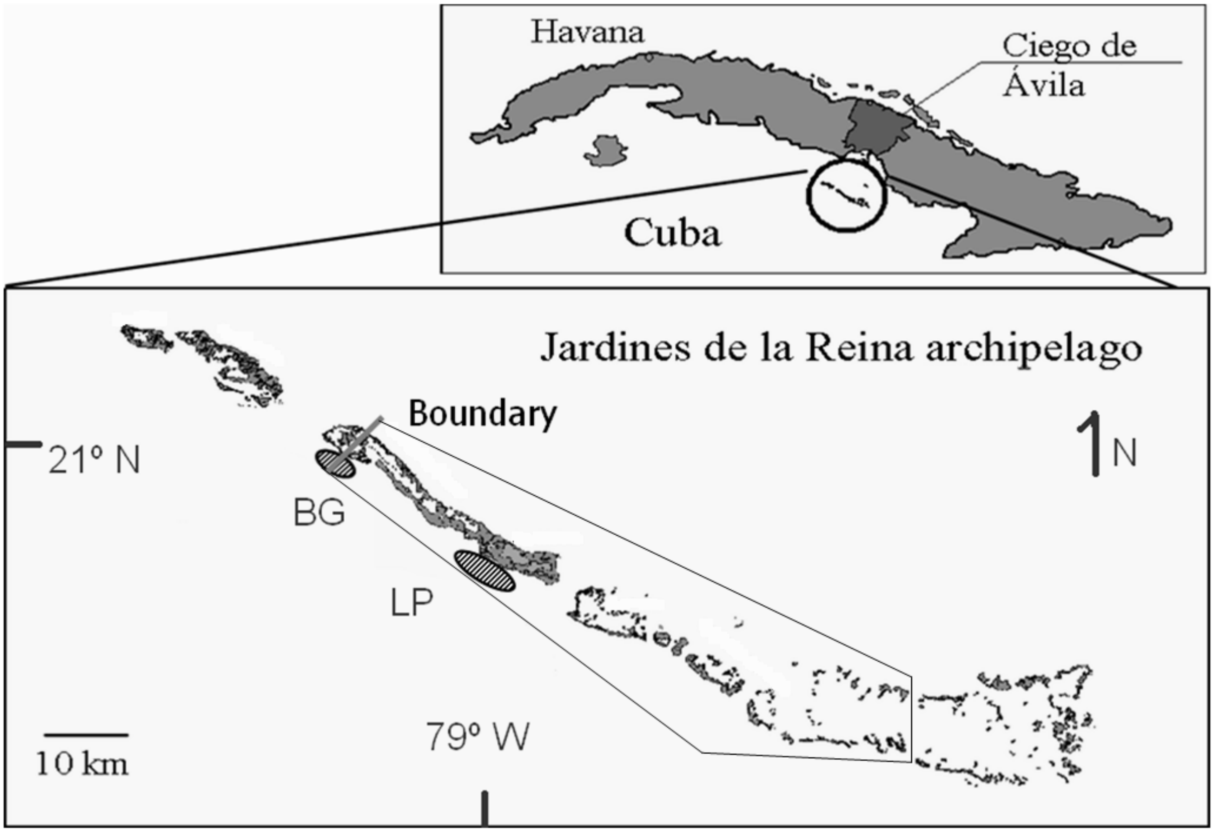

Fig. 1. Map of Jardines de la Reina archipelago and tagging sites. Bar elipses are BG and LP tagging sites. The continuous line is the Marine Reserve. “Boundary” is the west boundary of the Marine Reserve.

Tagging was carried out in the west boundary of the Jardines de la Reina Marine Reserve, located south of Cayo Grande, west of Boca de Guano key, and east of Boca Grande key, which will be termed Boca de Guano in the rest of this paper (BG, coordinates 20º 58’ N - 79º 10’ W) and in the area known as Los Pinos, south of Caballones key and east of the Caballones Pass, termed from here on as Los Pinos (LP, coordinates 20º 50’ N - 79º 00’ W) (Fig. 1). Intra-habitat Movements and movements across the boundary of the marine reserve were studied in BG. Intra- and inter-habitat movements were studied in LP. Distance between study sites is approximately 27 km. Field work was carried out during April and May, 2004. Intra-habitat movement means mobility in the same habitat (in our case reef crest or reef slope), while inter-habitat movement means mobility between these two habitats.

BG reef crest has a break of approximately 100 m in length (discontinuity). This discontinuity and the west boundary of the marine reserve coincide in location. The sector of the crest in the Reserve is well structured, with predominance of *Acropora palmata* (elkhorn coral). Depth of this sector is about 2–3 m. The reef crest outside of the Reserve is more fragmented and also has a predominance of *A. palmata.* Depth of this sector is of about 2 m. On the other hand, the BG reef slope has no discontinuity. Its depth ranges from 8 to 20 m, with high structural complexity and similar fish abundance along the study area.

The reef crest at LP is continuous, unlike the discontinuous reef crest at BG. The LP reef crest is predominantly *A. palmata* with patches of *Millepora complanata* (fire coral). Site depth is about 2–4 m. The LP reef slope (9–22 m deep) has similar features along the study area regarding structural complexity, although a discontinuity is located in the central part of this site (a little shelter – a steep wall about 10 m tall and 30 m long). Average distance between the reef crest and fore reef of LP is of about 150 m. The discontinuities observed at BG reef crest and at LP reef slope are usefull to assess their effects on fish mobility.

Sampling Method

To study fish movement across the marine reserve boundary, BG (crest and reef slope) was split into eight zones, 200 m each one, for a total of 1,600 m (Fig. 2) following the design of Zeller et al. (2003). The boundaries and the ends of the tagging zones were marked with surface buoys and the middle zones with bottom buoys.

To study inter-habitat movement at LP, the reef slope and reef crest habitats were color coded separately to determine which habitat a fish moved from. The LP study area was also divided into eight zones of 200 m, and the ends of the tagging zones were marked with surface buoys and the middle zones with bottom buoys. Tags with different colors were used in each zone. Color absorption in sea water and possible confusion between similar colors were taken into account for their selection and distribution. All the observers previously took underwater training covering different distances to identify colors.

Training was carried out during five days and 15 dives, with the participation of the four observers and a support diver. Three slates, each one with a different array of the 16 colors used, were prepared. The slates were never available for the observers out of water to prevent them from learning the array of tag colors. On each training dive, tag colors were identified from 5, 10, and 15 m distances by each observer. At the end of each dive, the support diver evaluated color identification, pointing out color confusion and recording efficacies to follow up evolution of identification skills in each observer.

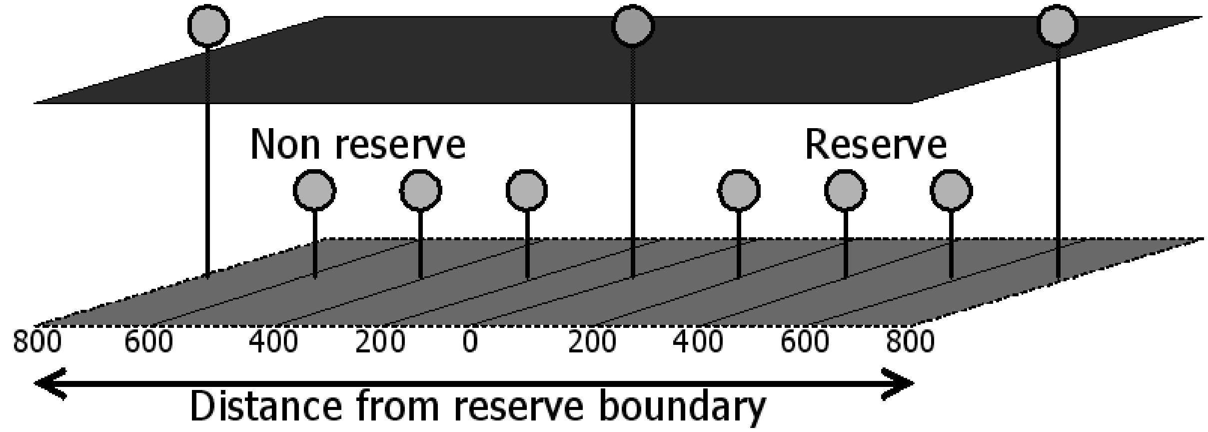

Fig. 2. Diagrammatic representation of the zones defined for tagging experiments (distances in meters).

Proper color identification improved remarkably with training at 5-m distance, reaching above 90% average by day four. Improvement was also evident for the other two distances, but was less dramatic than at 5 m and efficacies remained low (around 80% at 10 m and 60% at 15 m). Taking into account this fact, we decided to record recaptures only when distances between the observer and tagged fish were less than 5 m. Color confusion was more common between white-gray, yellow-orange, red-black-violet, and green-blue; therefore colors were distributed on each 200-m zone as follows (from west to east): yellow-green-violet-white-red-blue-gray-orange on BG and LP reef slope. The same distribution for bicolor tags on LP reef crest was followed to study inter-habitat movement. Separation of similar colors reduced likelihood of color confusion, under assumptions of high site fidelity of coral fish and that the likelihood of finding fish away from the tagging site decreased with distance. Most of the tagged individuals observed were recaptured because they allowed short-distance approach.

Recaptures were performed visually while tagging and were based solely on tag colors as it was impossible to read the numbers. Movement of tagged fish within the 200-m release and recapture zone is recorded as zero movement and when release and recapture points are located in different zones, movement distance is recorded in multiples of 200 m, according to the distribution of colors by zones. For example, a fish tagged in the “white zone” and recaptured in the same zone is recorded as 0 m movement, but if it is recaptured in the “orange zone” is recorded as a movement of 800 m.

Our sampling protocol prevented us from knowing detailed movement pattern, i.e., only linear distance from release to recapture points is recorded. Thus, information provided as movement is in fact the distance between these points, and this is the most relevant issue for our study.

Modified oleoneumatic spearguns were used for tagging with dart tags strengthened with steel wire (Floy Tag FT-1-94 tags), based on Sala et al. (2001) and Starr et al. (2007). This method was used after multiple attempts with fishing rods and traps, which resulted in low capture in some target species, very low recaptures in general, and high trap mortality. Experiments made it possible to determine that mortality due to immediate predation of released tagged fish caught in traps was 38% and 15% in those not tagged (Pina–Amargós unpublished data). Immediate mortality of fish tagged with spearguns was 6%. Tagging was performed in the seaward area (20-m wide) of the reef crests and in the reef slopes from top to bottom of the slope, width ranging from 10 to 30 m. To minimize fishing impact, tagging journeys were undertaken every other day in each site (BG and LP); 47 tagging journeys were carried out, 24 in BG and 23 in LP.

Besides dart tags, natural marks or tagging scars were used to complement successful tagging (Table 1).

Table 1. Types and percentages of tags by habitat.

Sites – Habitat	Amount of tags	Dart tags (percentage)	Natural or induced marks (percentage)
BG reef slope	535	412 (77)	123 (23)
BG reef crest	374	276 (74)	98 (26)
LP reef slope	290	226 (78)	64 (22)
LPP reef crest	304	226 (74)	78 (26)
TOTAL	1503	1140 (76)	363 (24)

Tagging effort focused on large-size fish and those of commercial importance, mainly for the fishing industry (Table 2). We tagged all species which met such criteria to obtain information on populations and community levels and to contribute to fill the gaps on large-size fish movement in the Caribbean. The species are treated in the results and discussion sections taking into account number of tagged and recaptured individuals.

Table 2. Target species.

Common name	**Latin name**	**Common name**	***Latin name***
Spotted Eagle Ray	*Aetobatus narinari*	Cubera Snapper	*L. cyanopterus*
African Pompano	*Alectis ciliaris*	Dog Snapper	*L. jocu*
Yellow Jack	*Caranx bartholomaei*	Tarpon	*Megalops atlanticus*
Crevalle Jack	*C. hippos*	Yellowmouth Grouper	*Mycteroperca interstitialis*
Horse-Eye Jack	*C. latus*	Black Grouper	*M. bonaci*
Bar Jack	*C. ruber*	Yellowfin Grouper	*M. venenosa*
Southern Stingray	*Dasyatis americana*	Tiger Grouper	*M. tigris*
Nassau Grouper	*Epinephelus striatus*	Lemon Shark	*Negaprion brevirostris*
Goliath Grouper	*E. itajara*	Rainbow Parrotfish	*Scarus guacamaia*
Nurse Shark	*Ginglymostoma cirratum*	Midnight Parrotfish	*S. coelestinus*
Margate	*Haemulon album*	King Mackerel	*Scomberomorus cavalla*
Hogfish	*Lachnolaimus maximus*	Great Barracuda	*Sphyraena barracuda*
Mutton Snapper	*Lutjanus analis*	Permit	*Trachinotus falcatus*

Data Analysis

Movement average distance for every species and movement across the boundary for BG and intra- and inter-habitat movement in LP were calculated. We also calculated the percentage of individuals that moved in respect to recaptured (resighted) ones per species (see formula). Only species with 10 or more recaptures were taken into account for site-habitat analysis.

$$Dmj = (\sum Dij)/Nj$$

Where:
Dmj = movement average distance of species j
Dij = movement distance i of species j
N = number of recaptures of species j

Applying this formula to the example of movement explained above, Dmj would be 400 m, as a result of two recaptures of 0 and 800 m movement distances of species j. Standard errors were calculated for movement average distances.

Results

1,503 individuals from 26 species were tagged and 640 individuals from 23 species were recaptured (42%). Yellowmouth Grouper, Permit, and King Mackerel were never recaptured (Table 3).

Table 3. Tagging summary by site and habitat.

Sites – Habitat	Tagged	Recaptures	Recapture percent
BG reef slope	535	232	43
BG reef crest	374	150	40
LP reef slope	290	129	44
LP reef crest	304	129	42
TOTAL	1503	640	42

Twelve species accounted for 91% of tagged individuals and 94% of recaptured individuals: Black Grouper, Yellowfin Grouper, Tiger Grouper, Nassau Grouper, Yellow Jack, Cubera Snapper, Dog Snapper, Rainbow Parrotfish, Mutton Snapper, Hogfish, Great Barracuda, and Tarpon.

Fish Movement at BG Reef Slope

Individuals of 14 species were recaptured. Black Grouper, Yellowfin Grouper, Tiger Grouper, Cubera Snapper, Great Barracuda, and Hogfish primarily remained at the study area. Most species (except Yellowfin Grouper and Tiger Grouper) moved 200 m or more (Table 4).

Exportation of adult fish from within the marine reserve to outside the reserve boundaries was observed in four of the species (Black Grouper, Yellowfin Grouper, Nassau Grouper, and Hogfish). However, individuals from outside the reserve also moved into the reserve. An equal number of fish moved into and out of the marine reserve (13%). Thus, one-quarter of the recaptures moved across the boundary, but net exchange was zero (Table 4). A gradient of movement was observed, with movement occurring in the boundary surroundings (200 m 57%, 400 m 25%, 600 m 4%, 800 m 10%, and 1,200 m 4%); no fish was recaptured beyond 1,200 m during the two months of work at BG.

Table 4. BG reef slope tagging results.

Species	No. of individuals tagged	No. of individuals recaptured	Recapture (%)	Average distance (± SE)	Export (%)	Import (%)
Yellowmouth Grouper	2	0	0	-	-	-
Black Grouper	30	20	67	240±45	10	0
Yellowfin Grouper	24	18	75	133±32	11	22
Tiger Grouper	28	16	57	150±22	0	0
Nassau Grouper	44	10	23	200±103	40	0
Goliath Grouper	1	0	0	-	-	-
Yellow Jack	24	4	17	200±0	0	50
Bar Jack	20	2	10	200±0	0	0
Cubera Snapper	18	18	100	244±64	0	11
Dog Snapper	10	0	0	-	-	-
Mutton Snapper	62	4	6	200±0	0	0
Nurse Shark	4	0	0	-	-	-
Margate	6	2	33	200±0	0	-
Rainbow Parrotfish	6	6	100	533±42	0	0
Spotted Eagle Ray	4	0	0	-	-	-
Permit	2	0	0	-	-	-
Hogfish	166	91	55	251±15	24	16
Great Barracuda	66	31	47	400±57	0	20
African Pompano	4	4	100	400±115	0	25
Southern Stingray	14	6	43	266±42	0	17

Fish Movement at BG Reef Crest

Individuals of 15 species were recaptured. Cubera Snapper, Dog Snapper, Rainbow Parrotfish, and Great Barracuda remained at the study area most of the time. In 23 recapture days no fish tagged in one side of the Reserve was observed in the other side (Table 5).

Table 5. BG reef crest tagging results.

Species	No. of individuals tagged	No. of individuals recaptured	Recapture (%)	Average distance (± SE)	Export (%)	Import (%)
Black Grouper	12	4	33	0	0	0
Yellowfin Grouper	4	4	100	0	0	0
Tiger Grouper	2	2	100	200±0	0	0
Nassau Grouper	4	0	0	-	-	-
Yellow Jack	10	1	10	200	0	0
Bar Jack	8	1	12	200	0	0
Horse-Eye Jack	10	2	20	0	0	0
Crevalle Jack	2	0	0	-	-	-
Cubera Snapper	10	14	140	0	0	0
Dog Snapper	30	58	193	96±25	0	0
Mutton Snapper	76	8	10	150±63	0	0
Rainbow Parrotfish	6	10	166	240±50	0	0
Midnight Parrotfish	2	4	200	200±0	0	0
Spotted Eagle Ray	6	2	33	200±0	0	0
Hogfish	104	10	10	160±27	0	0
Great Barracuda	74	26	35	262±33	0	0
Tarpon	14	4	28	200±0	0	0

Fish Movement at LP Reef Slope

Individuals of 12 species were recaptured. Yellowfin Grouper, Tiger Grouper, Nassau Grouper, Cubera Snapper, Dog Snapper, and Hogfish remained at the study area most of the time (Table 6).

Only four species (Tiger Grouper, Cubera Snapper, Mutton Snapper, and Great Barracuda) moved between the zones of this reef slope, the first eastwards and the rest westwards, for a movement of only seven individuals (5% of recaptures), a lot less than in similar habitat at BG (Table 6).

Reef slope movement toward the reef crest was very scarce. In 22 recapture days the movement of only one individual from three species (Tiger Grouper, Cubera Snapper, and Mutton Snapper) toward reef crest was observed, i.e., only 2% of the individuals tagged at the reef slope visited the reef crest (Table 6).

Table 6. LP reef slope tagging results.

Species	No. of individuals tagged	No. of individuals recaptured	Recapture (%)	Average distance (± SE)	Eastward movement (%)	Westward movement (%)	Movement towards reef crest (%)
Yellowmouth Grouper	2	0	0	-	-	-	-
Black Grouper	20	8	40	0	0	0	0
Yellowfin Grouper	24	14	58	57±40	0	0	0
Tiger Grouper	42	28	67	30±20	7	0	4
Nassau Grouper	31	10	32	0	0	0	0
Horse-Eye Jack	17	2	12	0	0	0	0
Cubera Snapper	20	14	70	71±40	0	14	7
Dog Snapper	24	14	58	0	0	0	0
Mutton Snapper	36	9	25	111±59	0	22	11
Nurse Shark	6	5	83	80±80	0	0	0
Margate	4	0	0	-	-	-	-
Rainbow Parrotfish	6	2	33	0	0	0	0
Spotted Eagle Ray	4	0	0	-	-	-	-
Hogfish	22	14	64	57±39	0	0	0
Great Barracuda	30	2	7	400±0	0	50	0
King Mackerel	2	0	0	-	-	-	-

Fish Movement at LP Reef Crest

Individuals of 16 species were recaptured. Yellowfin Grouper, Tiger Grouper, Yellow Jack, Dog Snapper, Hogfish, and Tarpon remained at the study area most of the time (Table 7).

More species (10) moved between the zones of LP reef crest than in the LP reef slope. This means that 26% of the recaptured individuals moved to the other zone (16% to the west and 10% to the east), i.e., about one-fourth, similar to the pattern of BG reef slope and a much larger per cent than that of BG reef crest and LP reef slope (Table 7).

Unlike movement from the reef slope to the reef crest, inverse movement was greater (9% of recaptures), with predominance of Yellow Jack and Hogfish (Table 7).

Table 7. LP reef crest tagging results.

Species	No. of individuals tagged	No. of individuals recaptured	Recapture (%)	Average distance (± SE)	Eastward movement (%)	Westward movement (%)	Movement towards reef crest (%)
Black Grouper	14	7	50	0	0	0	0
Yellowfin Grouper	27	18	67	44±30	0	11	0
Tiger Grouper	18	10	55	40±40	0	0	0
Nassau Grouper	8	3	38	0	0	0	0
Goliath Grouper	1	2	200	200±200	0	0	100
Yellow Jack	26	18	69	118±46	6	22	22
Crevalle Jack	3	1	33	0	0	0	0
Lemon Shark	1	2	200	400±0	0	100	0
Cubera Snapper	14	6	43	200±89	0	33	17
Dog Snapper	14	17	121	129±24	18	12	0
Mutton Snapper	40	7	18	29±28	0	0	0
Nurse Shark	9	6	67	133±84	0	33	17
Rainbow Parrotfish	11	3	27	133±133	33	0	0
Spotted Eagle Ray	4	0	0	-	-	-	-
Permit	2	0	0	-	-	-	-
Hogfish	43	19	44	21±21	7	0	21
Great Barracuda	51	8	16	125±65	12	25	0
Tarpon	19	14	74	229±51	38	38	0

Fish Movement: Comparisons among Species, Habitats, and Sites

Movement was highly variable among species, habitat, and sites (Fig. 3). In general, the most mobile species was Great Barracuda, followed by Cubera Snapper, Hogfish, and Tiger Grouper. The least mobile species were Dog Snapper, Yelowfin Grouper, and Black Grouper. However, species mobility was highly variable. For example, Cubera Snapper presented quite high mobility in general, and showed zero net movement at BG reef crest. Black Grouper showed zero mobility in three sites, but moved an average of 240 m at BG reef slope. The analysis by habitat and sites shows a trend to higher mobility at BG reef slope compared to other sites.

Fish Movement away from Study Sites

Five individuals from four species were recaptured out of the tagging sites during the year after field work. A Nassau Grouper tagged at LP moved about 5 km eastward in 11 months, while a Great Barracuda tagged at the same site moved westward 5 km in 9 months. A Tiger Grouper and a Dog Snapper tagged at BG moved eastward 16 km in 12 months and a Great Barracuda tagged at the same site moved also eastward 14 km in 10 months.

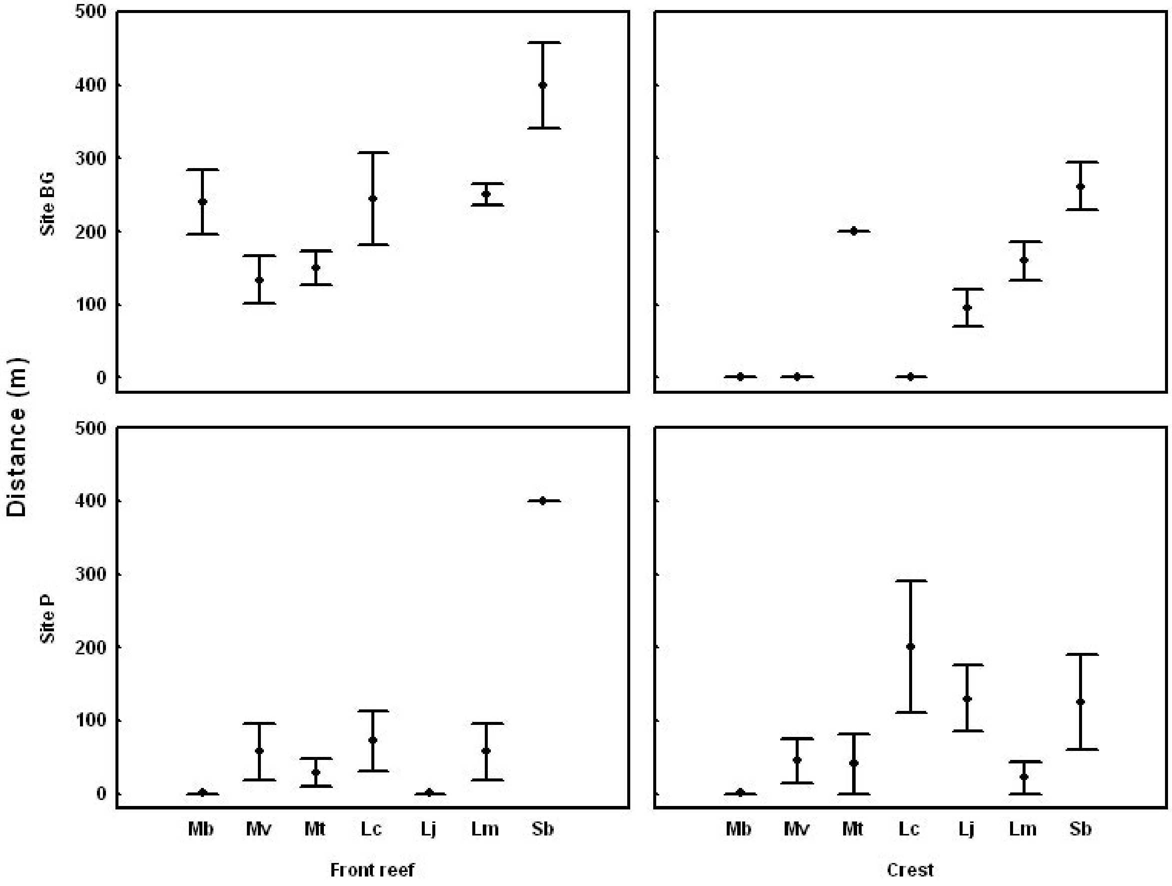

Fig. 3. Movement patterns among species, habitats, and sites. Legend: Mb (*Mycteroperca bonaci*), Mv (*Mycteroperca venenosa*), Mt (*Mycteroperca tigris*), Lc (*Lutjanus cyanopterus*), Lj (*Lutjanus jocu*), Lm (*Lachnolaimus maximus*), Sb (*Sphyraena barracuda*).

Discussion

This study supports previous studies that documented high site fidelity of studied species regardless of size (Eklund and Schull 2001; Zeller 2002; Griffiths and Wilke 2002; Willis et al. 2003; Zeller et al. 2003). Most species tended to move little (from 100 to 400 m), with most recaptures occurring at the tagging zone or in adjacent ones. However, both distance and movement propensity appeared to be species and site specific and highly variable.

Because of variability in movement, one can expect that some species will contribute more biomass to neighboring fishing areas through exportation (the case of Black Grouper, Yellowfin Grouper, Nassau Grouper, and Hog Fish at BG reef slope presented here) than others in a marine reserve. There may also be highly variable movement distances within species and between sites, perhaps dependent upon habitats within and outside the marine reserve.

In spite of the tendency for high site fidelity, some individuals were recaptured several kilometers away from tagging areas months later. This fact supports the hypothesis that reef fish move little as a rule and only a few individuals may move relatively long distances (Munro 2000; Griffiths and Wilke 2002; Willis et al. 2003).

Of the species studied, mobility distances are available for only Nassau Grouper, Mutton Snapper, Black Grouper, and Tarpon. Colin (1992) and Carter et al. (1994) detected movements up to 240 km for spawning Nassau Grouper, while Randall (1962, 1963) and Roberts et al. (1995) recorded movements of 4 km every 3 days, reaching a distance of 16 km during a 4-day observation period. In a day's time some Nassau Groupers moved in a 160 X 80 m rectangle, but returned to the refuge starting point once sunset approached (Carter et al. 1994), while others estimated daily movements up to 400 m (Sullivan and Garine-Wichatisky 1994). However, during spawning migration they can travel 30 km in less than 24 hours (Starr et al. 2007). On the other hand, movement of Mutton Snapper ranging from 29 to 298 km has been detected, seemingly related to spawning behavior, but the cause remains undetermined (Davis 1989; Bohnsack 1990; Begg et al. 1997; Gillanders et al. 2001; Patterson et al. 2001). In the case of Black Grouper, Lindholm et al. (2005) followed for months several ultrasonic tagged individuals, recording about 90% of recaptures on the tagging sites. The most mobile individual moved to a reef located 4 km away, returning to its home (tagging) site in a day´s time. Visits to another reef located 500 m away from the tagging site were also uncommon, returning to its home (tagging) site in a day´s time. Studies of Tarpon movement reveal high mobility. Fifty-six percent of ultrasonic tagged individuals stayed close to the tagging site (Boca Grande, Florida) a few hours after release, but the rest moved an average of 25 km away (Edwards 1998). Ault et al. (2005) reported movement up to 2,000 km in three months, with most of the reports on the order of hundreds of kilometers in this period. Research results on Nassau Grouper at time and space scales similar to those of our study match well with our results.

Due to the experimental design used in the present study, movements beyond 1,400 m with 200 m precision could not be detected. These are intermediate distances between those in the work of Zeller et al. (2003) (from 50 to 250 m) and others that used distances ranging from 500 m to some kilometers (Beinssen 1989; Beinssen and Beinssen 1991; Attwood and Bennett 1994; Zeller and Russ 1998; Chapman and Kramer 1999). Taking into account that many reef fish move at spatial scales of hundreds of meters, working at larger spatial scales could be the reason why many such studies have detected scarce or even no mobility. The high recapture rate, homogeneous tagging and recapture efforts averaging between 100 and 400 m for most species (quite lower than the 1,400-m maximum possible to be detected), and lack of relation between the release time after tagging and distance covered suggest that the scale used was right and that movement detected correctly represents mobility of the studied species at the time and spatial scales used, despite limitations of traditional external tagging.

Habitat discontinuity is one of the factors that affect fish mobility. Several authors have detected decreases of fish movement when discontinuities occur (Buechner 1987; Barrett 1995; Chapman and Kramer 1999; Edgar and Barret 1999; Eristhee and Oxenford 2001). This issue is quite evident in this work. Continuous habitat (BG reef slope and LP reef crest) experienced movements by approximately a fourth of tagged individuals, while at BG reef crest and LP reef slope movements were zero and 5%, respectively, presumably due to crest discontinuity and peculiar topography of reef slope, apparent barriers to fish movement.

Inter-habitat movements were scarce, similar to those within a discontinuous habitat. This could be for two main reasons. First, there could be a segregation of assemblages per habitat, i.e., no matter how close a reef crest or a reef slope is, each habitat will have its own fish assemblage with little inter-habitat movement, supporting the current idea that habitat type is an important factor in the composition of fish assemblages (Aguilar et al. 2004; Chittaro et al. 2005; Dorenbosch et al. 2005; Nuñez Lara et al. 2005). Second, movements during night or twilight hours, not sampled during this work, may have occurred as reported by several researchers (Hobson 1972; Ogden and Ehrlich 1977; Rooker and Dennis 1991; Burke 1995; Nagelkerken et al. 2000). These authors report diurnal movement of Haemulidae and Lutjanidae between mangroves, seagrass beds, and lagoonal patch reef, but research results on movement between adjacent reef crest and reef slope habitats were not available to be compared with our results.

Future studies using acoustic technology would provide exact distance traveled and detailed movement patterns and would be useful for future management. However, traditional external tagging is particularly appropriate for studying exportation or spillover in marine reserves and is cost-effective. Many recent studies about fish movement have used traditional external tags, using ultrasonic telemetry at the same time or later to detail or complete information gathered with traditional methods (Eklund and Schull 2001; Cooke and Philipp 2004; Ault et al. 2005; Starr et al. 2007). Zeller and Russ (1998) carried out a study using both methods to elucidate exportation or spillover. Several authors, however, have used only traditional tagging (Chapman and Kramer 1999; Munro 2000; Zeller et al. 2003).

Zeller et al. (2003) indicated as the possible cause of no detection of spillover the deterrent effect on fish produced by the manipulation of the gradient with spearguns. Effects of spearing have been documented, including increases in diver avoidance and “shyness” of fishes (Buxton and Smale 1989; Bohnsack 1998; Kulbicki 1998; Edgar and Barret 1999; Zeller et al. 2003). In the current study, at the beggining of tagging, abundance appeared to decline, but recovered after a period of time. Nevertheless, the use of this method could increase fish movement.

In summary, although fish mobility is species and site specific and very variable, our research yielded strong evidence that large reef fish show high site fidelity at short time scales while greater mobility at longer time scales is not supported by our data. Exportation of commercially important large adult fish was observed through the west boundary of the Jardines de la Reina Marine Reserve, although net exchange was zero due to bidirectional movement of one-fourth of the studied assemblage. Less mobility between habitats or between patches of the same habitat (separated by discontinuities) than in a single continuous habitat was also detected.

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Patterns of Habitat Use and Tagging Studies in a Complex Coral Reef Ecosystem: Toward Understanding Habitat Connectivity Through Ontogenetic Migration

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Summary of oral presentation

Marine reserves: Single large or several small or many large?

Habitat use by *Acanthurus bahianus* as it ages: moving offshore and switching from seagrass habitats to coral habitats. Did this for 28 species. Species within a family can behave differently. Yellowtail parrotfish (*Sparisoma rubripinne*) vs. bucktooth parrotfish (*Sparisoma radians*). Example of why you cannot lump by family to project habitat use patterns.

Also looked at comparative behavior of different seascapes. French grunts (*Haemulon flavolineatum*) in two different areas.

In complex seascapes: where do fish go, what pathways do they follow, what rules govern choice of direction?

Looked at French grunts (*H. flavolineatum*). Habitat shifts are size dependent.

In complex seascapes –

- most species show flexibility in habitat use
- most species showed ontogenetic migrations involving change in habitat use
- there are variations across species and families
- both habitat and cross-shelf location are important
- early juveniles use inshore seagrass/mangroves; inshore forereef coral habitats, offshore channel-axis coral habitats
- inshore forereefs important

Abstract:
Appeldoorn, R.S., B.L.K. Bouwmeester, K. Cerveny, K.A. Foley, and C.W. Recksiek. 2007. Patterns of habitat use and tagging studies in a complex coral reef ecosystem: Toward understanding habitat connectivity through ontogenetic migration. Proc. Gulf Carib. Fish. Inst. 59: 632-633.

Connectivity Between Non-Estuarine Mangroves, Seagrass Beds, and Coral Reefs by Fishes?

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Summary of oral presentation

Nursery hypothesis – do fishes leave nursery areas and migrate to the reef?
Nursery function -- nursery should have:

- Higher density
- Higher growth
- Higher survival
- Movement to adult habitat

As compared to other habitats

Should look at the total area, not just the unit area, even though fish densities may be lower.

Known: Many juvenile fish in mangroves and seagrass beds; adults on the reef; 100s of studies on single habitats (different methodologies, or no size data)
Unknown: degree of connectivity between ecosystems and the mechanisms of connectivity

Most of the existing studies do not look at linkages or connectivity

At least 50 Caribbean fish species with cross-shelf ontogenetic migration. 17 of 85 species are highly associated with mangroves when they were juveniles. Do they use alternative habitats if mangroves are not present? Bays with mangroves/seagrass beds have higher abundance and species richness.

Distance to nurseries – you would think that the adjacent reefs would have higher densities and that's what they found.

Size of nurseries – evidence that at different islands where mangrove area increased, you found increased density of certain species.

Areas with lower seagrass and mangrove habitats, there are significantly fewer of certain fish species (grey & yellowtail snapper, rainbow parrotfish, and others).

Shallow-water habitats (especially mangroves) are potential nursery habitats for various commercially important reef fish species in the Caribbean
The dependence on these habitats is high (but not obligate) for some species

Questions for MPA Design:
Contribution of mangroves/seagrass beds to coral reefs?
How large is contribution?
Degree of dispersal from nurseries in MPAS
Temporal & spatial variation?
Minimal values of essential (a) biotic variables
Minimum area of nursery and adult have in MPAs to sustain populations
What and Why to conserve?

Abstract:
Nagelkerken, I. 2007. Connectivity between non-estuarine mangroves, seagrass beds and coral reefs by fishes. Proc. Gulf Carib. Fish. Inst. 59: 633-634.

Movement of Adult Fish in the Jardines de la Reina Marine Reserve, Cuba

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Summary of oral presentation

- Various research on coral reef habitats detect spillover but…
- Many use indirect evidence (gradients of abundance through boundaries)
- Just one manipulates gradient of abundance (spillover vs. export)
- Many, primarily in the Caribbean, study the phenomenon on small/low commercially important species
- Not many study movement between habitats.

Jardines de la Reina marine reserve and proposed national park is located in the south central portion of Cuba.

3222 tagged specimens of 26 species; 1365 recaptures of 23 species (42%)

Movement of all species – ¼ of tagged community is moving in/out equally

Net export:
10 % Black Grouper
40% Nassau Grouper
8% hogfish

Little mobility past 600 meters; none past 1000 meters

Different species moved different distances – rainbow parrotfish was the most mobile, but it never crossed the border.

Movement between reef crest and fore reef:
Reef crest – 10%
Fore reef - 30%

Conclusions:
- Net movement through boundaries = 0
- Black grouper, Nassau grouper, hogfish show net export of biomass
- More movement on the first 200 m on each side of boundary
- Spillover detected
- More movement from reef crest to fore reef than from fore to crest

  - Habitat discontinuity reduces movement of fish

Abstract:

Pina Amargós, F., A. Jiménez del Castillo, A. Zayas Fernández, F. Martín Blanco, W. Acosta de la Red, and G. González Sansón. 2007. Movement of adult fish in the Jardines de la Reina Marine Reserve, Cuba. Proc. Gulf Carib. Fish. Inst. 59: 634.

The Effects of Mangroves in the Resilience of Reefs

Peter J. Mumby

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Summary of oral presentation

What are the ecological impacts of having increased numbers of fish?

Focus on parrotfish. What effect does increased density have on ecosystem function?

Need to understand functional role of grazing by these fishes.

Spatial simulation model to look at the effects of grazing on the ecosystem.

Parrotfish grazing has significant effect on coral – if you add additional grazing in certain conditions, you can stimulate reef growth.

Conclusions:
- Testing model assumptions straightforward, but predictions more difficult (scale and complexity of processes)
- Patterns of fish enrichment can differ dramatically from ecosystem consequences
- Need to combine empirical data on demographics with models of ecosystem function
- Mangrove-driven, increased grazing may enhance recovery rates of corals in some habitats but not all

Connectivity Texture and the Need for Cross-Cultural Panmixis

Ken Lindeman

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Summary of oral presentation

Management Realities

Hotels the size of cities are going into areas of the Caribbean; consider the land/water impacts…

Similar examples in Florida…

MPA networks are blooming in the region; however, there is an absence of enforcement.

Demersal and Larval Research

Larval connectivity is rarely on the mind of a MPA manager.

Many reef fishes we think of have discrete, single settlement events; other reef fish may have semi-continuous bottom associations.

So for some important families – larval connectivity can be based on demersal connectivity.

Better Connecting

Better connecting scientists and managers… in the Caribbean, they have been cross-pollinating for decades (along with NGOs)

From a macro view, they are both in the same or very similar culture already.

Political cultures routinely overrule our small elite culture.

Our culture is a science-management culture, but typically we're only getting 2/3 of the way down the pipe toward political intervention. We need to engage in tactical, specific actions involving panmixis.

Specific suggestions:

- New standards for what Conservation Products are: workshops, articles, and plans are tools and are rarely "end of the pipe" conservation products
- CV and tenure reform: a new section in CVs that bullets real conservation products e.g.
    - Statutory laws written or influenced
    - Administrative regulations, EIAs, management plans that were written or influenced

Would create incentive in our culture to go into the next culture.

In our culture, workshops that are needed:

- MPA enforcement
- MPA performance – demersal issues (spillover, habitat conservation, etc.)
- How to stop the rape of land use plans
- How to refine poor EIAs (reward those that do good EIAs)
- Coastal and fishery management in the post peak oil world

We need to:

Host workshops that are culturally panmictic
Use proven political campaign tactics to get all the way through the pipe.

Abstract:

Lindeman, K. 2007. Developmental patterns among MPAs of the northern Caribbean. Proc. Gulf Carib. Fish. Inst. 59: 635.

Panel Discussion: Demersal Connectivity

Q: I'm concerned that we're talking about physical and biological connectivity. There is also connectivity among mega developments. Colombia and Panama; widening of Panama Canal; Nicaragua building a canal; mega-ports in Belize and other areas. This is a challenge we have now and for the next decade. Please comment on this. What can we do to start being more proactive?
Ken Lindeman: I would suggest that some of the slides in the last presentation offered ideas – we need to have panels with lawyers, economists, businessmen, politicians. We need to develop a strategic array of activities. We need to use political campaigns. NGOs have been successful when they have established political campaigns.

Q (Sarah Frias-Torres): We run the danger of giving license to kill anything that is not an MPA. We have fancy MPAs everywhere, but everywhere else is getting destroyed. Shouldn't we also communicate the message that areas that aren't MPAs should also be taken care of?
Ken Lindeman: If we have an effective presence on land use and zoning – we can kill many birds with one stone – everything from habitat loss to sewage. MPAs and land use both.
Peter Mumby: Very important to have fisheries management at national scales outside of MPAs so you have the required amount of grazing outside of protected areas to maintain the complexity of structure. Maintaining certain fish in the ecosystem you maintain important parts of the ecosystem. If you assume that one of the reasons for MPAs is to create spillover, it isn't going to work if you don't have habitat within the MPA. The issues of water quality and habitat destruction that effects water quality – if you are going to have MPAs you have to protect the area around.

Comment: I don't think we can protect everything we want. There is too much pressure to develop. Need to bring the developers into the discussion. Need to stop encountering them in an adversarial way. Need to work with them. Need to figure out how to bring some of these people into the fold.
Ivan Nagelkerken: In one area of Bonaire there are zones which are well organized. Lot of people are employed in the benefit of the nature reserves. In Curaçao – it's a paper park. Everything gets destroyed. They set up same system (as Bonaire) in Curaçao – given to the government complete, and it was supported by the community. That was 11 years ago. It just needs to be passed by the legislature – but they keep postponing passage. Nature is not as strong of an economic industry as in Bonaire – it's not just about showing the politicians the issues and giving them the options – you need to have the economic motivators.

Q: We've heard about all kinds of connectivity. It is clear that the scale of connectivity among species is not equal. What networks of MPAs are we going to create – what size should serve all of the different species?
Ivan Nagelkerken: You have to figure out what your purpose is for your MPA. If you have an MPA for one species, you can have multiple MPAs for multiple species.
Rich Appledoorn: You have to go back to the general principals for MPAs. You need to have redundancy and replication to deal with different scale issues. It's very difficult to do this – must do it in a statistical way. Have to care for habitat. Core areas should go for those things most

affected by fishing. If you are looking at bulk of commercially important species people are targeting, you should focus on species with shorter duration larval stages.

Q: Habitats used by certain fishes are economically invisible on the landscape. Logical step: link the potential economic value of those habitats. It may be less than the development.

Peter Mumby: There is a fair bit of literature about valuing mangroves. It's not meant to value on a continuance scale – it tends to be either you have lots of mangroves or you have none. Needs to be more realistic. As you reduce the amount of habitat, what is the link to economics? Of course we're missing some important information for doing that. But people are trying to address these issues.

Ken Lindeman: Much of what has been done on this is usually on huge scales. If we get economists in our world – I think we could make great progress on this. What about economic evaluations that don't equal returns for development? I have nothing against development – lets just not forget 40 years of sustainable development science. The tsunami in the Indian Ocean demonstrated the incredible importance of mangrove habitats.

Rich Appledoorn: A lot of the negative things about functions aren't going into those calculations.

Spawning Aggregations

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, 59th 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).

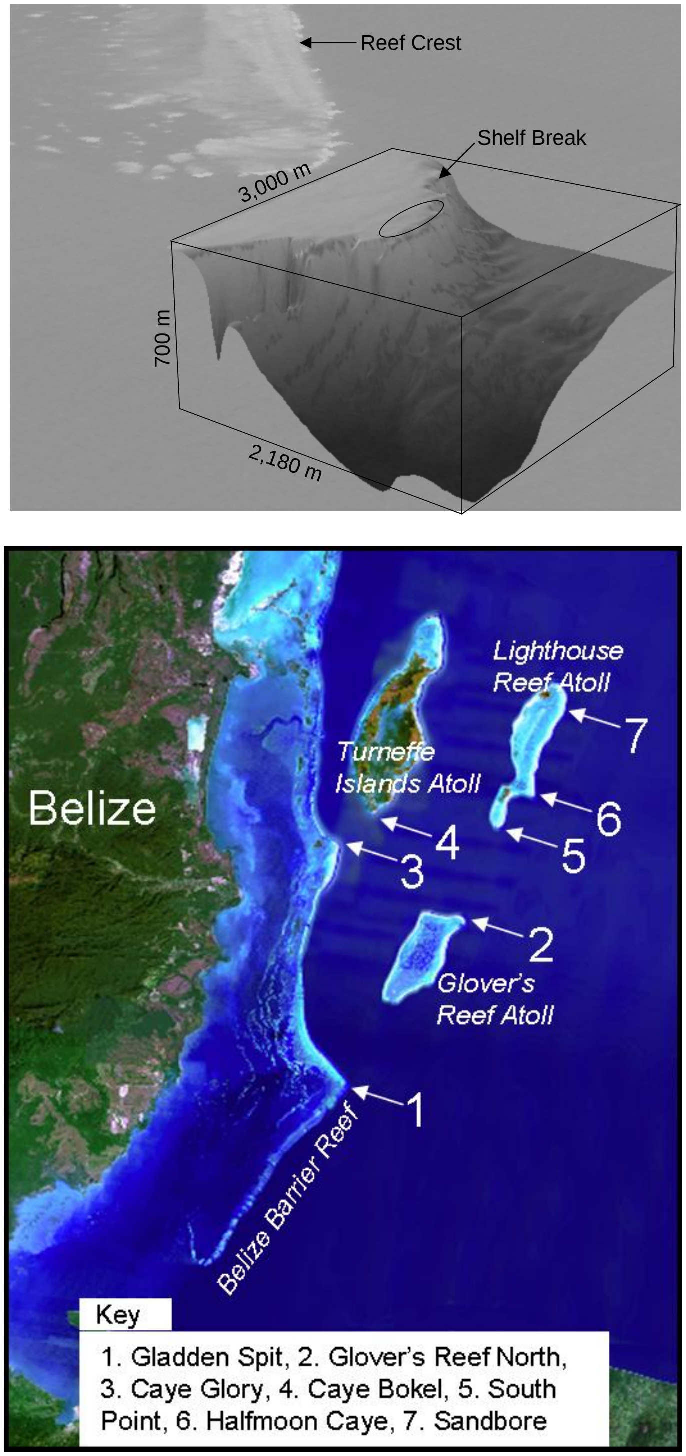

Fig. 2. (a: top) Gladden Spit, showing the location of the multi-species spawning aggregations (oval) in relation to the shelf break and the bend in the reef (from Heyman et al. 2007). (b: bottom) The locations of seven documented multi-species spawning aggregation sites in Belize.

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.

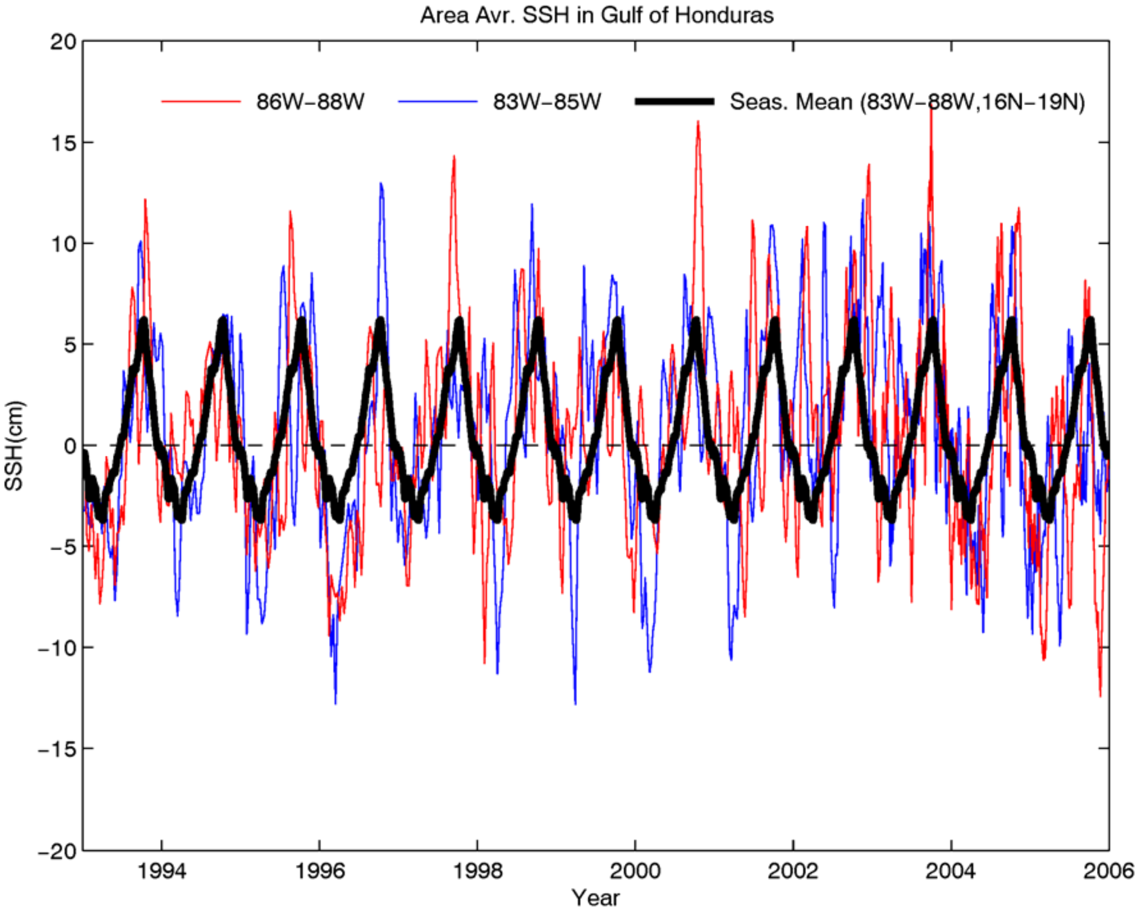

Fig. 3. Time series of sea surface height anomalies from satellite altimeter data averaged over the western (red line) and mid (blue line) Gulf of Honduras in the southern Mesoamerican Reef. The mean seasonal cycle averaged over the 13-year record is indicated by the heavy line.

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.

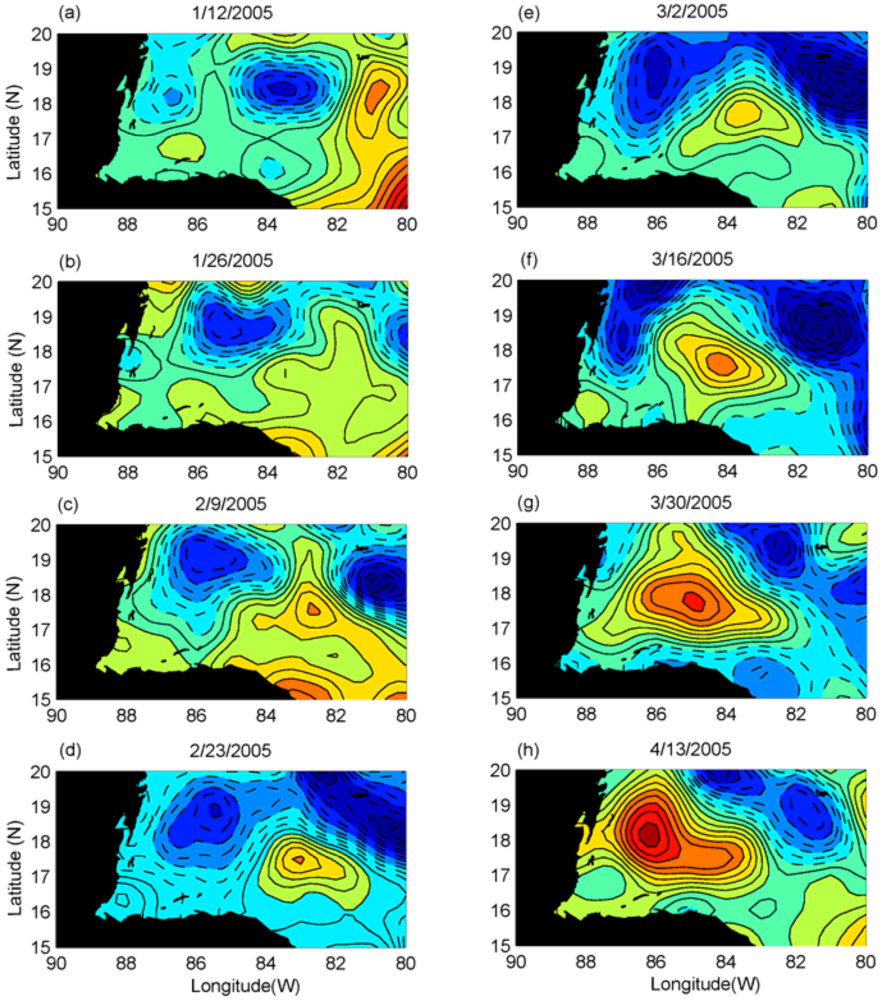

Fig. 4. Sea surface height anomaly from altimeter data in the southern Mesoamerican Reef. The 2-weekly images demonstrate the westward propagation of cyclonic [negative/blue SSHA, (a)–(d)] and anti-cyclonic [positive/red SSHA, (e)-(h)] features. Contour interval is 2 cm.

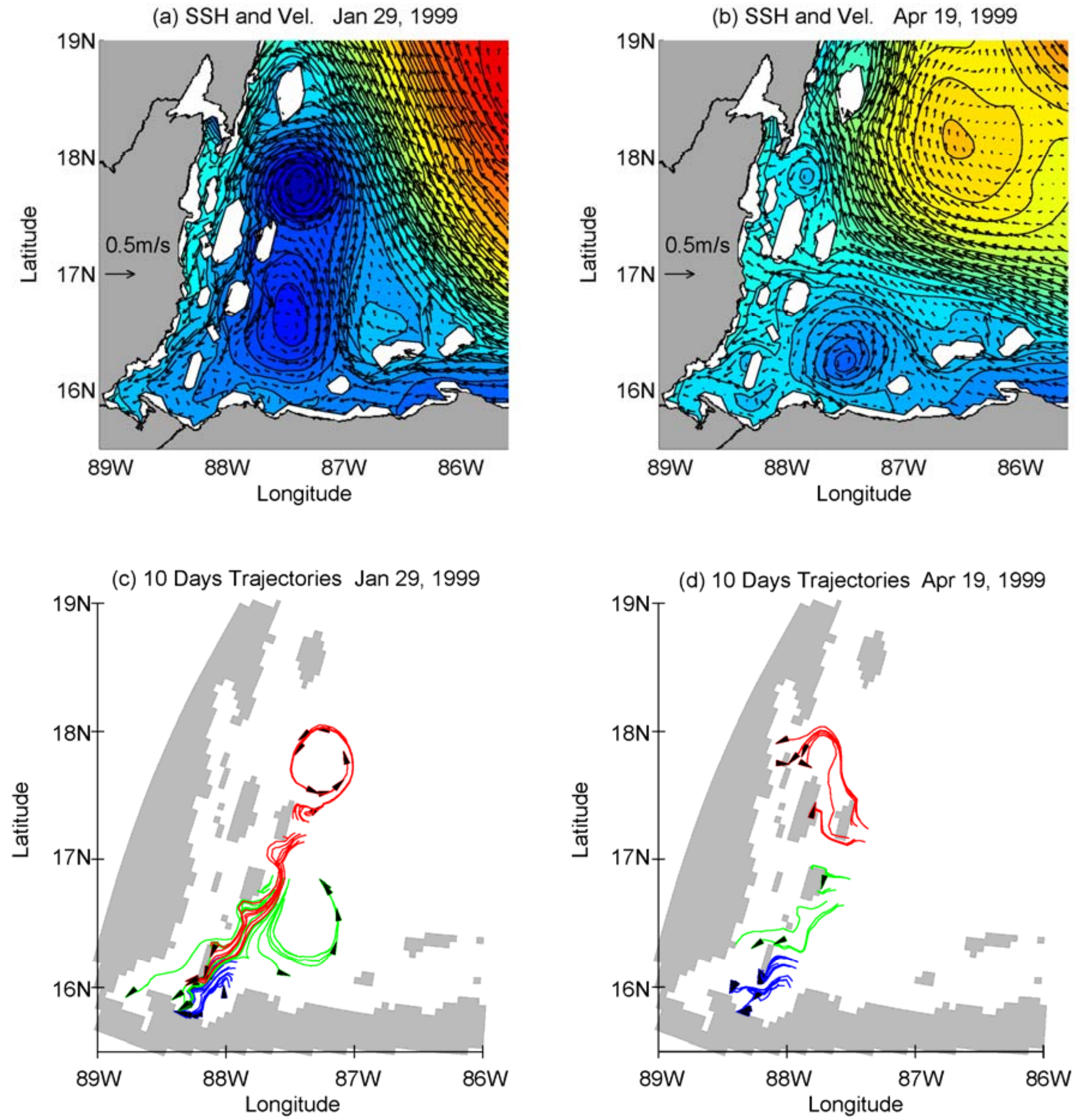

Fig. 5. Model simulations (Ezer et al. 2005) of sea surface height (blue/red for low/high) and surface velocity for (a) January and (b) April, 1999, when cyclonic and anti-cyclonic anomalies, respectively, where observed near the Mesoamerican Reef. (c) and (d) show the trajectories of modeled passive 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).

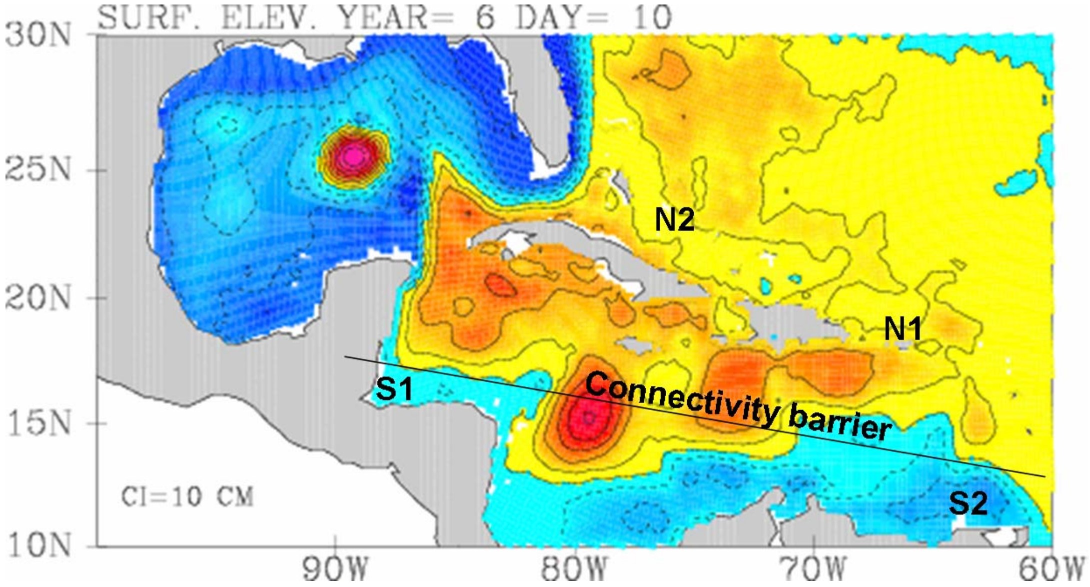

Fig. 6. Shown is an example of a synoptic sea surface height field with blue/red shades representing low/high values (from the Ezer and Mellor (2000) model). A barrier to connectivity may be created along the MAR where cyclonic eddies diverge from anti-cyclonic eddies. Inter-reef connectivity is likely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

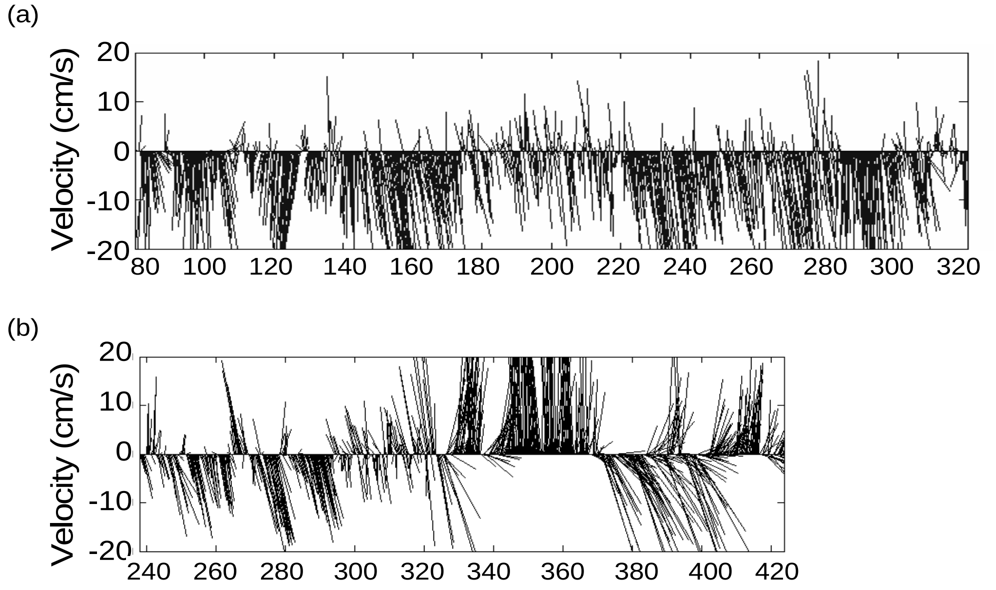

Fig. 7. Stick diagrams showing the measured speed and direction of currents at the shelf break at 26 m depth at (a) Gladden Spit (Site 1 in Fig. 2b) between Day 80-320 in 2000, 50 km to the northeast at (b) Halfmoon Caye, Lighthouse Reef Atoll (Site 6 in Fig. 2b) between Day 240 in 2000 and Day 80 in 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 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).

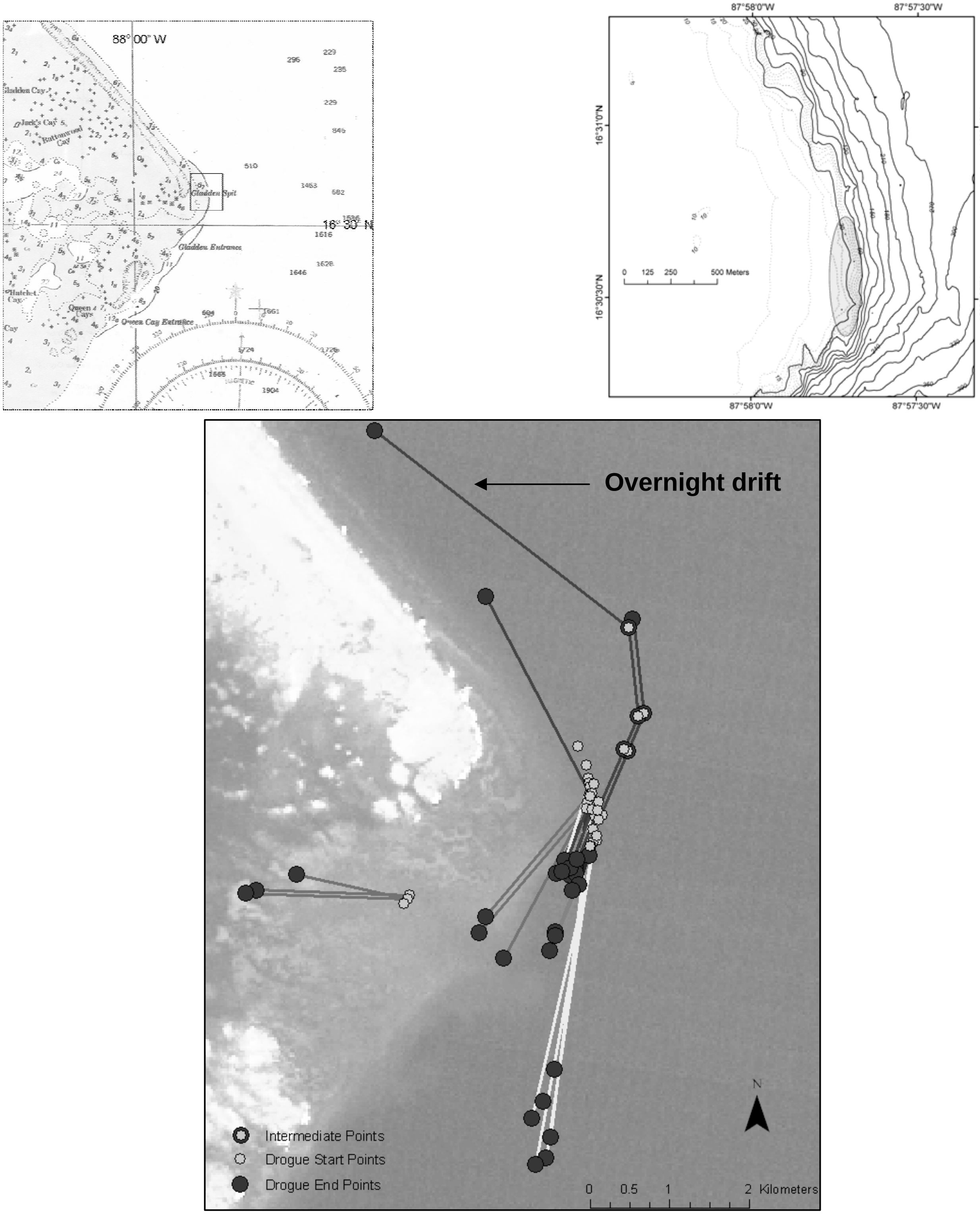

Fig. 8. (a: top left) Bathymetric chart of Gladden Spit. (b: top right) Detailed bathymetry derived from inexpensive mapping efforts (Heyman et al. 2007). (c: bottom) Davis-type drogues (simulating eggs) move away from spawning site in multiple directions illustrating the initial trajectory of spawned 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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Regional Coupling of Red Hind Spawning Aggregations to Oceanographic Processes in the Eastern Caribbean

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Abstract

Red hind (*Epinephelus guttatus*) in the eastern Caribbean form annual spawning aggregations during full moon periods between the months of December through February. Few studies have attempted to investigate what factors influence timing of spawning or selection of aggregation sites. From December 2005 through February 2006 three separate red hind spawning aggregation sites located in St. Thomas and St. Croix, U.S. Virgin Islands (USVI), and in Saba, Netherlands Antilles, were surveyed. These data were compared to seven years of previous research on red hind spawning within the USVI. At each site visual counts were conducted using SCUBA to estimate red hind density, the spawning population was sampled daily to determine female gonado-somatic index, and an acoustic Doppler current profiler (ADCP) was deployed during the spawning season to measure current speed and direction and water temperature. Sea water temperature was relatively uniform across the region. Average daily temperature below 25 m declined from 27.5ºC in December to 26.2ºC in February at all sites, and ranged from 26.5ºC to 26.7ºC during the week of the January full moon when fish were spawning. During the spawning season current speeds ranged from 7 to 21 cm s^{-1} in Saba (mean = 11.4 cm s^{-1} ± 2.42 s.d.), 8 to 30 cm s^{-1} in St. Croix (mean = 13.2 cm s^{-1} ± 3.58 s.d.), and 10 to 22 cm s^{-1} in St. Thomas (mean = 15.3 cm s^{-1} ± 2.98 s.d.). During the week of spawning in January, the average current speed near the reef remained the same or slowed and was 10.4 cm s^{-1} in Saba, 13.1 cm s^{-1} in St. Croix, and 15.3 cm s^{-1} in St. Thomas. General current direction the week before spawning was southwest at all sites. A week later, during spawning (i.e., around full moon) average current direction shifted to 260 (west) in St. Thomas, 196 (south-southwest) in St. Croix, and 178 degrees (south) in Saba. In each case the current would carry fertilized eggs and larvae onto the shelf. Data suggest that the location of spawning sites may be influenced by the presence of slower across-shelf currents that maximize retention of eggs and larvae. We also found that the majority of red hind within both St. Thomas and St. Croix spawning populations migrated up-current to their respective spawning aggregation sites. If eggs and newly hatched larvae drift slowly down current, they may be in the vicinity of adult home ranges at time of settlement. If this is occurring, then each red hind spawning aggregation may be composed of a distinct sub-population that is partly self-recruiting. Due to the vulnerability of spawning aggregations and their potential connection to sustaining the local population through self recruitment, it is critical that all spawning aggregation sites are protected from fishing and marine protected area (MPA) boundaries are appropriate for species-specific behavioral patterns. The knowledge that red hind spawning aggregations are extremely limited in space and time can be applied strategically to

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maximize the limited resources available for research, monitoring and enforcement and lead to more effective MPAs and potentially greater protection of spawning aggregations.

Introduction

Spawning aggregations consist of 100's to 1000's of fish and represent the primary mode of reproduction for large, commercially important species of groupers, snappers, and certain other species (Thresher 1984; Domeier and Colin 1997a). The formation of spawning aggregations along the edge of insular platforms may enhance connectivity among isolated subpopulations within a meta-population. Alternatively, the formation of annual spawning aggregations in a single location during very brief periods of time (i.e., < 1 wk) may synchronize the spawning population with specific oceanographic features that enhance retention and increase recruitment to natal areas. Regardless, these brief periods of annual reproduction are the most critical and most vulnerable life-history event for aggregating species that contribute to subsequent generations, sustain local or meta-populations, and support the fishery. While many environmental factors may negatively affect successful recruitment, over-fishing is by far the greatest danger that threatens long-term sustainability of spawning aggregations.

Intensive fishing on spawning aggregations has led to critical reduction or collapse of local grouper and snapper populations throughout the Caribbean, e.g., Belize (Heyman et al. 2001; Sala et al. 2001), Bermuda (Luckhurst 1996), Cuba (Claro and Lindeman 2003), Florida Keys (Lindeman et al. 2000), Mexico (Aguilar-Perera and Aguilar-Davila 1996), Puerto Rico (Shapiro et al. 1993; Sadovy et al. 1994), and the U.S. Virgin Islands (Olsen and LaPlace 1978). Fishery area closures have been established to protect fish spawning aggregations (Sadovy 1994; Bohnsack 1996; Domeier and Colin 1997b), but for over-fished aggregations, collapse of the aggregation had already occurred or recovery was very slow (Olsen and LaPlace 1978; Claro et al. 2001). Few examples exist of spawning aggregations that have been successfully protected (but see Nemeth 2005). A recent comparative analysis of two protected red hind spawning aggregations suggested that not only enforcement but also behavior of fish during the spawning season may be the two most important factors determining the effectiveness of marine protected areas (MPAs) (Nemeth 2005; Nemeth et al. 2006). In particular, movement of red hind in relation to closure size and placement of boundaries are critical to proper protection. Effective management of aggregating species requires a greater understanding of the factors and processes important for the formation of spawning aggregations, which may lead to the development of general models that can be applied more broadly. Because of the synchronized timing of some spawning aggregations (Nemeth et al. 2006), comparative studies at multiple spawning sites during the same time period have been logistically difficult, but are important for gaining a complete understanding of this complex life-history trait.

This paper summarizes previous research and presents new information on the similarities and differences in behavior, site characteristics, and oceanographic features of several red hind (*Epinephelus guttatus)* spawning aggregation sites. The primary purpose of this paper is to discuss the physical and biological factors that may be important for successful spawning and thus influence management decisions on the timing and placement of MPA boundaries. Understanding the oceanographic and biological connectivity among spawning aggregation sites may allow development of general approaches to managing red hind populations in the Caribbean.

Methods and Materials

Study Species

The red hind (*Epinephelus guttatus)*, a protogynous hermaphrodite, changes sex from female to male at 32 to 38 cm total length and reaches maximum length and age at 50 to 55 cm and 11 to 22 yr (Smith 1971; Thompson and Munro 1978; Luckhurst et al. 1992; Sadovy et al. 1992). *E. guttatus* aggregations consist of small haremic groups, which can occupy an area from 0.015 to 0.35 km^2 (Shapiro 1987; Shapiro et al. 1993; Nemeth 2005). In the USVI *E. guttatus* aggregations can occur from mid-December through February and spawning typically peaks the week before the full moon in January (Shapiro et al. 1993; Nemeth 2005). Spawning aggregations typically form on the top of deep coral reef ridges, which are located on or near the shelf edge (Colin et al. 1987; Beets and Friedlander 1999; Nemeth 2005).

Study Sites

Three red hind spawning aggregations sites were examined during their respective spawning seasons over a period of seven years. These sites were located in St. Thomas (December 1999 to February 2006) and St. Croix (December 2004 – February 2006), U.S. Virgin Islands and Saba (December 2005 – February 2006), Netherlands Antilles. All three sites were studied simultaneously from January to February 2006. The St. Thomas spawning aggregation site is located on the southern edge of the Puerto Rican shelf southwest of St. Thomas (18º 12’N, 65º 00’W) at 40 m depth. The St. Croix spawning site is located on the northeastern edge of Lang Bank (17º 49’N, 64º 27’W) at 35 m depth. The Saba spawning site is located on the northeastern edge of Saba Bank (17º 34’N, 63º 17’W) at 20 m depth. Detailed descriptions of these spawning sites are reported elsewhere (Nemeth 2005; Nemeth et al. 2007; Kadison et al. in press). Distances between sites ranged from 60 km to 150 km (Fig. 1).

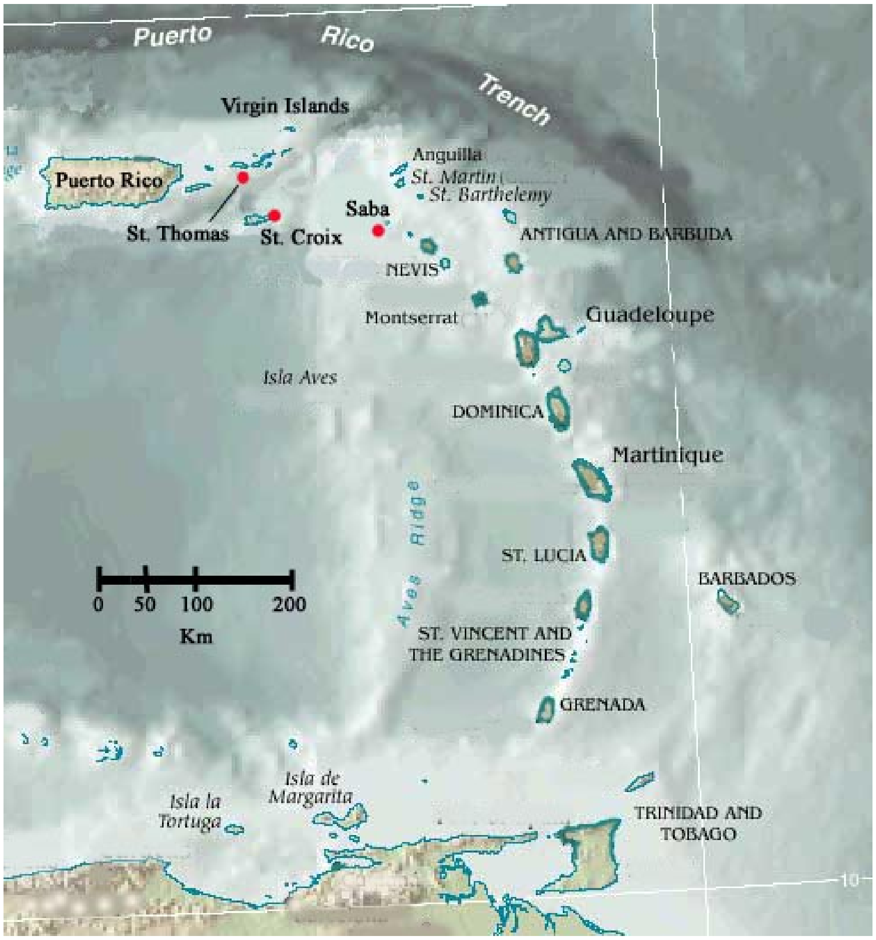

Fig. 1. Map of Eastern Caribbean showing location of three red hind spawning aggregation sites near the islands of St. Thomas, St. Croix, and Saba.

Data collected at each site included red hind density, length frequency, gender ratio, and gonadosomatic index (GSI). Red hind density was estimated with underwater visual surveys conducted along six to eight 30 x 2 m belt transects; statistical analysis of data was completed with either one-way ANOVA or Kruskal-Wallace test on ranks. Surveys were done between 0900 and 1630 on the days surrounding the full moon (Table 1), with transects placed haphazardly at the approximate center of each spawning aggregation site. Each spawning aggregation was sampled using either Antillean fish traps (6 cm mesh) or hand lines baited with squid. Each trap haul was marked with Garmin GPS so that the number and gender of fish caught at each trap location could be analyzed for spatial and temporal trends (Nemeth et al. 2007). Fish were measured to the nearest mm and gender was determined using ultrasound imaging (Whiteman et al. 2005) or by gently squeezing the body cavity above the vent to extract milt or possibly eggs. Before being released each fish was tagged in the dorsal musculature with a numerically coded anchor tag (Floy). At least six females were sacrificed per site per day when possible to determine gonadosomatic index. Ovaries of sacrificed fish were examined macroscopically and total body weight (±0.1g) and gonad weight (±0.01g) were recorded to determine fish GSI (gonad weight/somatic weight * 100).

Table 1. Full moon and sampling dates (and days) at the three spawning aggregation sites located in St. Thomas and St. Croix, USVI and in Saba, Netherland Antilles.

Site	December	January	February
Full moon date	15th	13th	13th
St. Thomas	13 – 15 (3)	11 – 16 (6)	10 – 13 (4)
St. Croix	(0)	12 – 15 (3)	9 – 11 (3)
Saba	12 – 17 (6)	11 – 16 (6)	10 – 13 (4)

In St. Thomas we also recorded seawater temperature and current speed and direction (Aanderaa RCM9) from April 2003 to September 2004. For the simultaneous study of the St. Thomas, St. Croix, and Saba spawning sites, acoustic Doppler current profilers (ADCP, Nortek 600 kH) were deployed in December 2005 to measure water temperature and current speed and direction. ADCPs were retrieved in late February and data were downloaded and analyzed for the 20-30 m depth range (Storm Ver. 1.04, Nortek AS).

Results and Discussion

Similarities between sites were found in the timing of movement, temporal, and spatial changes in sex ratios, annual and lunar predictability and environmental variables. Based on seven years of research on red hind spawning aggregations, several generalities can be made that might facilitate their management in the eastern Caribbean. Red hind spawning aggregations are strongly synchronized with the full moon cycle showing peaks in density in the days leading up to the full moon in January and occasionally February (Fig. 2). The greatest abundance of *E. guttatus* occurs on the spawning aggregation site when the January full moon falls 20 to 40 d after the winter solstice (i.e., from January 10 to 30). This occurred in 2006 and density of red hind within the St. Thomas, St. Croix, and Saba spawning aggregations peaked in January and was similar among sites ($H = 5.297$, $p = 0.06$) even though total population size varied considerably (ca. 80,000, 1,500, and 18,000, respectively (Nemeth et al. 2006; Kadison et al. in revision). Spawning population density in St. Thomas was significantly higher in February 2006 (Fig. 3), a difference which may be explained by the large size of this aggregation. An analysis of daily density in January showed that red hind in St. Thomas peaked two days before the full moon, whereas on Saba and possibly St. Croix peak densities occurred the day of or one day after the full moon, respectively (Fig. 4). GSI in Saba increased on the full moon (Fig. 5), which corresponded to peak density (Fig. 4), whereas St. Thomas and St. Croix GSIs showed little change. The predictability of *E. guttatus* spawning aggregations around the northeastern Caribbean and possibly across larger areas will be extremely beneficial for defining a seasonally protected area or a market closure in which a species is forbidden to be harvested during a particular time period as with conch, whelk and several species of snappers in the USVI.

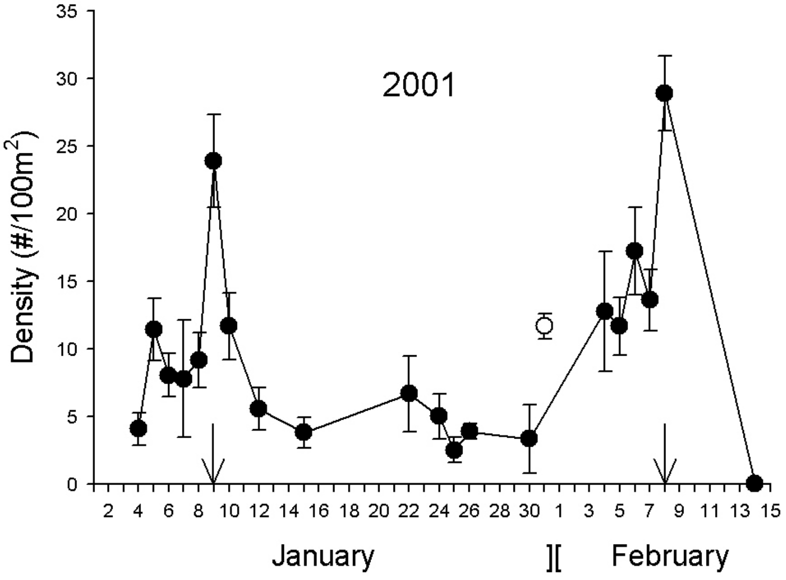

Fig 2. Red hind density (± SE) from January to February 2001 at the St. Thomas USVI spawning aggregation site. Arrows = date of full moon. White symbol = density of red hind 100 m off the primary spawning aggregation site in an area of small patch reefs, sand, and rubble. This habitat was sampled only once due to depth exceeding 45 m (modified from Nemeth 2005).

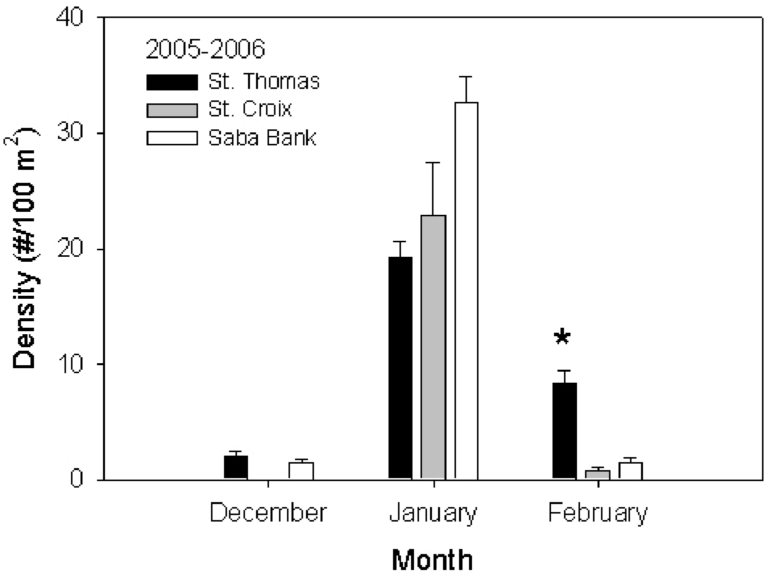

Fig. 3. Average density (± s.e.) of red hind at three spawning aggregation sites in December 2005 and January and February 2006 (*F = 14.148, p = 0.03). Full moon was on January 13.

Tag-recapture studies in St. Thomas and St. Croix found the majority of red hind migrated up-current to spawning aggregation sites at distances of 2 to 32 km (Nemeth et al. 2007). Based on geo-referenced trap catch data, gender-based behavioral patterns at all sites showed male red hind arrived to

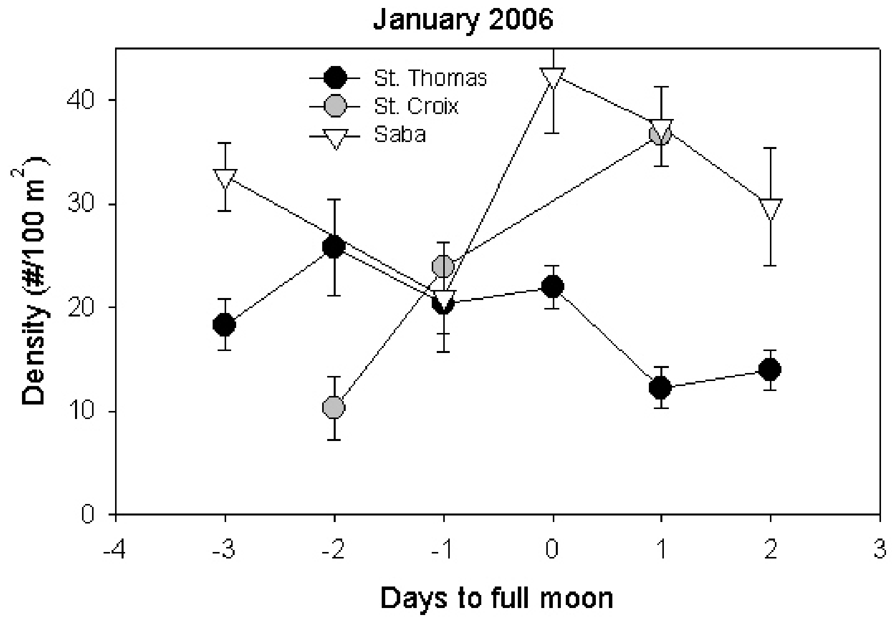

Fig. 4. Average density (± s.e.) of red hind at three spawning aggregation sites in January 2006 before and after the full moon (0 = Jan. 13th).

spawning sites before females, stayed longer than females and often remained on the aggregation site between January and February spawning peaks when they occurred. The majority of females arrived rapidly the week before the full moon and departed rapidly after spawning. Only the largest females within the spawning population remained on the spawning site between spawning peaks (Nemeth et al. 2007). Other individuals either departed the spawning site or moved to outlying areas (0.5 – 1 km) presumably to feed (Fig. 2). After the spawning season ended all red hind departed within a day with the largest males staying resident in deep offshore waters, whereas smaller males and females returned to mid-shelf or nearshore reefs (Sadovy et al. 1994b; Nemeth 2005; Nemeth et al. 2007). These gender-based behavioral patterns are extremely important to *E. guttatus* reproductive dynamics and their management. For example, if a closure is only implemented for a few weeks or a month, fish that remain on the spawning aggregation site between spawning peaks (i.e., the largest and most fecund males and females) will be more vulnerable to fishing mortality. Likewise, a seasonal closure may protect the spawning aggregation, but fishing in the area after the closure reopens may result in disproportional harvest of large males, skewing sex in subsequent years. Finally, if an area closure is too small (i.e., < 2 km^2) it may not protect the spawning population from harvest during daily or weekly movements associated with spawning particularly if migratory pathways are targeted by fishermen. The consistency and synchrony of movement and migration found for red hind will improve both the efficiency of planning research and monitoring programs and directing enforcement activities during critical time periods. These behavioral patterns must be factored into future studies and the design of fisheries regulations to ensure sustainability of spawning aggregation sites.

Oceanographic data from St. Thomas from 2003 to 2005 indicated that spawning typically occurred during annual and monthly periods of declining seawater temperature and slacking currents. Daily seawater temperature ranged from 26.0° to 27.5°C and average current speed 1 m above the reef at 40 m depth ranged from 2.5 to 3.5 cm sec^{-1} during the spawning season (Fig. 6). Seawater temperatures in 2006 were very similar among the three island spawning sites. Average daily water temperature declined from 27.5°C in December to 26.2°C in February at all sites, with water temperature at 26.5°C to 26.7°C during the week of the January full moon when fish were spawning (Fig. 7). Temperature profiles during the 2005-2006 spawning season in St.

Thomas showed less variability associated with the lunar cycle than in 2003-2004 (Fig. 7). The eastern Caribbean region warm water anomaly (Manzello et al. 2007), which started in summer of 2005 and continued through December 2005, may have inhibited the expansion of the upper mixed layer (35-40 m), where winter upper mixed layer (UML) off the south of St. Thomas is typically 70-90 m, reaching a maximum of 120 m in March (Idrisi et al. in prep.). The main mechanism for retention of spawned eggs on the south shelf is the tidal current, which extends to the bottom at the shelf edge when the UML includes at least the upper 40 m of the shelf waters. When the UML does not extend to the bottom of the shelf there is a greater probability of spawned eggs to be transported off-shelf (Idrisi et al. in prep.).

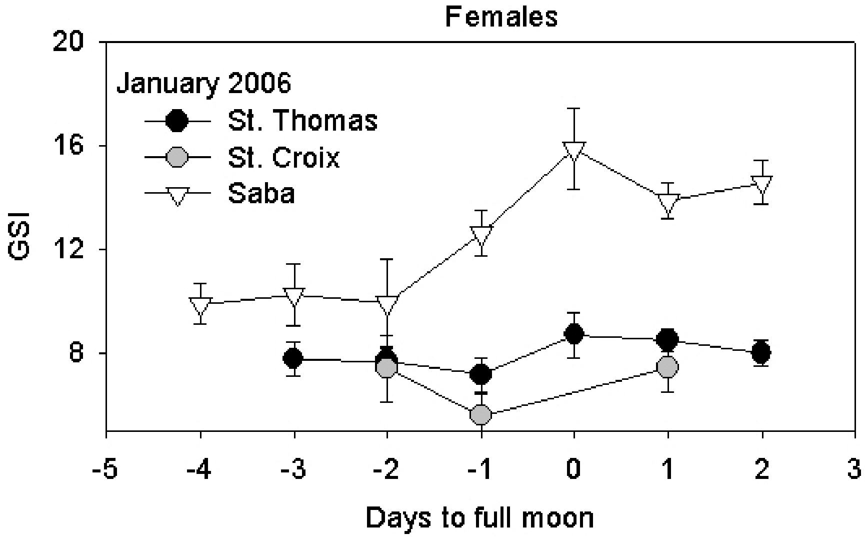

Fig. 5. Average gonado-somatic index (GSI) of female red hind at three spawning aggregation sites in January 2006 before and after the full moon (0 = Jan. 13th).

From 13 December 2005 to 14 February 2006 (approximate spawning season), current speeds ranged from 7 to 21 cm s^{-1} in Saba (mean = 11.4 cm s^{-1} ± 2.42 s.d.), 8 to 30 cm s^{-1} in St. Croix (mean = 13.2 cm s^{-1} ± 3.58 s.d.), and 10 to 22 cm s^{-1} in St. Thomas (mean = 15.3 cm s^{-1} ± 2.98 s.d.). During the week of spawning in January the average current speed tended to be the same or slower than at other times and was 10.4 cm s^{-1} in Saba, 12.8 cm s^{-1} in St. Croix, and 15.3 cm s^{-1} in St. Thomas. The week before spawning, the current direction near the bottom was 227 (southwest) in St. Thomas, 209 (southwest) in St. Croix, and 205 degrees (southwest) in Saba. During the week of spawning (i.e., around full moon) average current direction shifted to 260 (west) in St. Thomas, 196 (south-southwest) in St. Croix, and 178 degrees (south) in Saba (Fig. 8). In each case the changed current direction during the week of spawning would carry fertilized eggs and larvae onto the shelf (Fig. 9). If we assume spawning occurred on the full moon at all three sites, then we may be able to predict larval trajectories from fertilization through pre-flexion (~ 8 d) based on current speed and direction at the spawning site (Fig. 10). These trajectories were calculated using current speed and direction for fertilized eggs near the reef (25-40 m depth) for day one and surface currents (< 5 m) for pre-flexion larvae for days 2-8. In St. Thomas larvae would drift in a westerly direction until they encountered the islands of eastern Puerto Rico (Fig. 9). In St. Croix larvae would drift south about 10 km then WNW along the St. Croix shelf then SSE. On Saba, larvae would drift SSW for about 75 km before reversing direction back WNW. These data suggest that red hind larvae from the St. Thomas spawning site will most likely be retained on the Puerto Rican shelf. Larvae from St. Croix and Saba Bank may remain within the vicinity of the St. Croix shelf and Saba Bank due to reversal of currents especially if they encounter eddies or gyres. For these trajectories, we are making two major assumptions. The first assumes that the oceanographic data collected at the spawning site is representative of the water mass that has entrained eggs and pre-flexion larvae. The second assumption is that the swimming abilities of pre-flexion larvae are quite limited and movements would be largely current driven. During post-flexion larvae are stronger swimmers and thus are less influenced by local currents. We acknowledge that significant changes may occur in current speed and direction at any point along these trajectories and can be influenced by eddies, gyres or other oceanographic features as well as larval fish behavior. However, these data provide a first glimpse at how timing of spawning and the selection of multiple spawning aggregation sites within a region may be influenced by local current regimes.

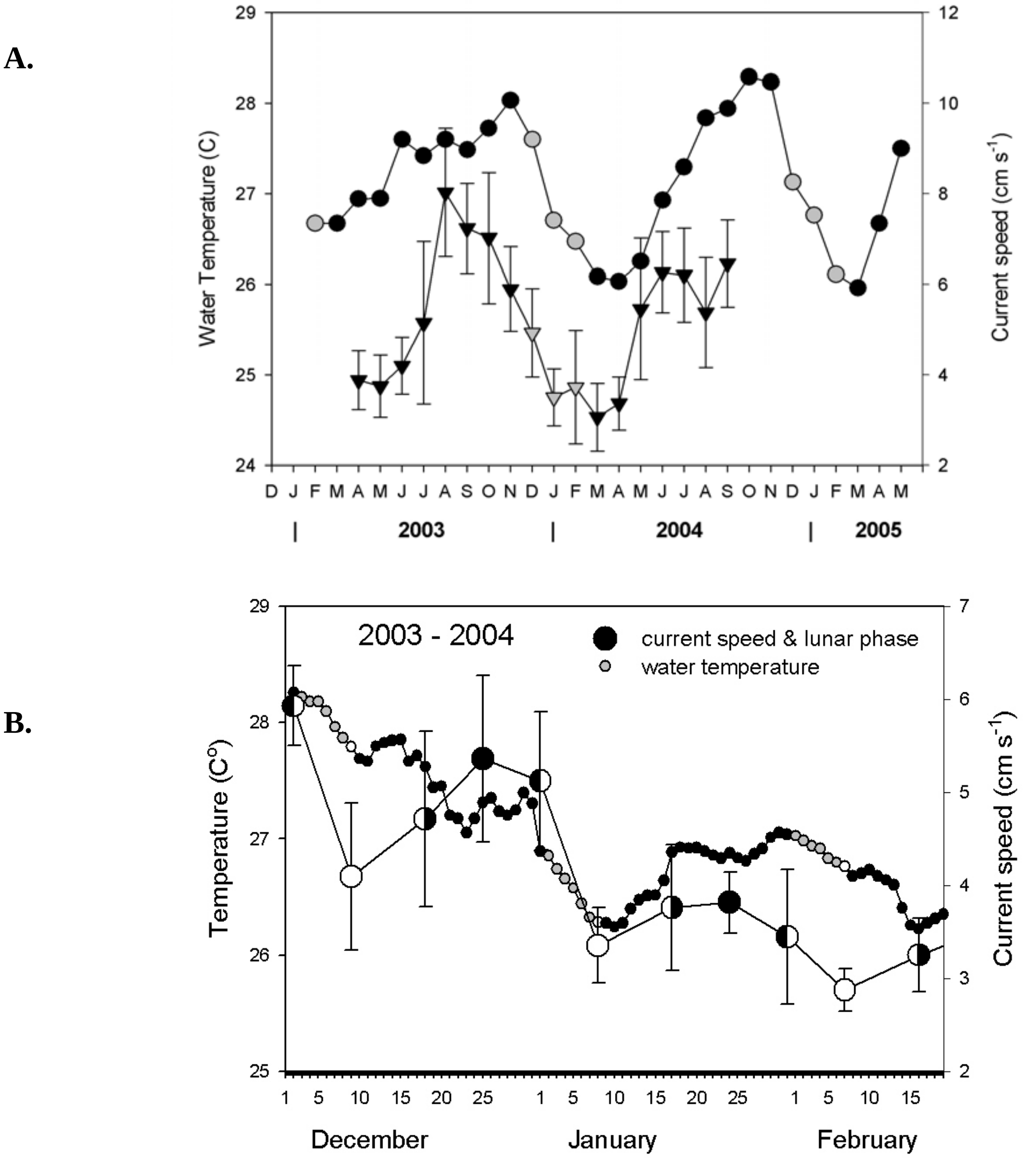

Fig. 6. (A) Monthly mean bottom seawater temperature (●) and current speed (▼) for the St. Thomas *E. guttatus* spawning site over a two-year period. Gray symbols = spawning months. (B) Daily mean bottom seawater temperature (● with gray symbols = spawning week and white = full moon), and average current speed ± SD calculated from the 7 days preceding each lunar symbol. (large ○, full moon = open circle, new moon = filled, quarter moons = half filled). Modified from Nemeth et al. 2007.

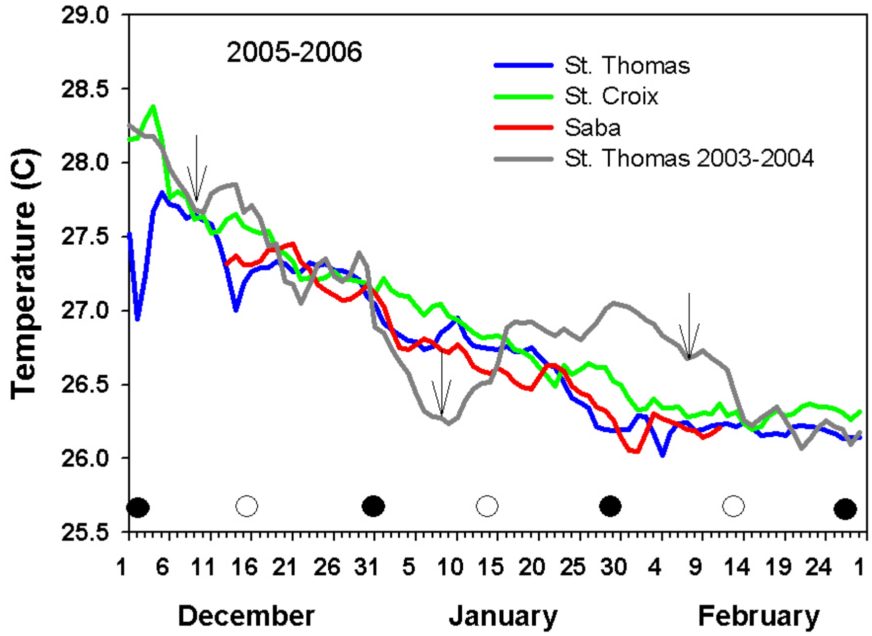

Fig. 7. Bottom sea water temperature profile at three spawning aggregation sites from December 2005 to February 2006 compared to temperature in St. Thomas during 2003-2004 spawning season. Open circle = full moon, closed circle = new moon, arrows = full moons in 2003-2004.

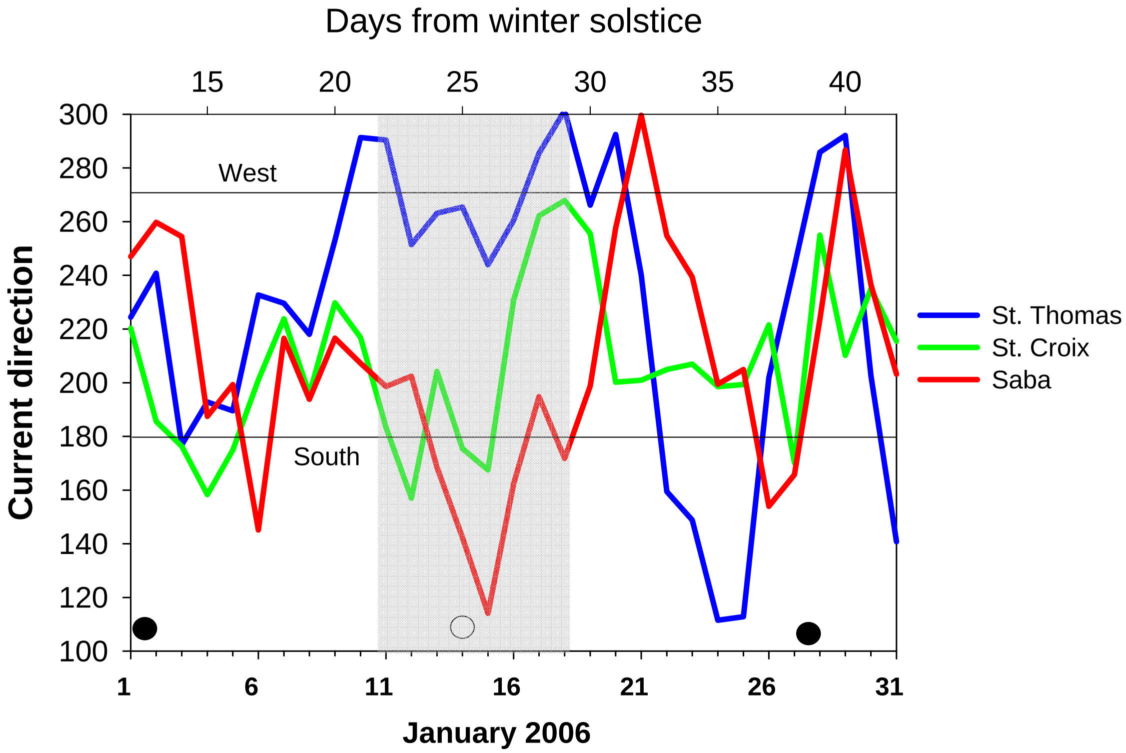

Fig. 8. Direction of ocean currents during January 2006 (primary spawning month) on three islands in the eastern Caribbean. Shaded area indicates approximate period of spawning and early egg and larvae drift. Open circle = full moon, closed circle = new moon.

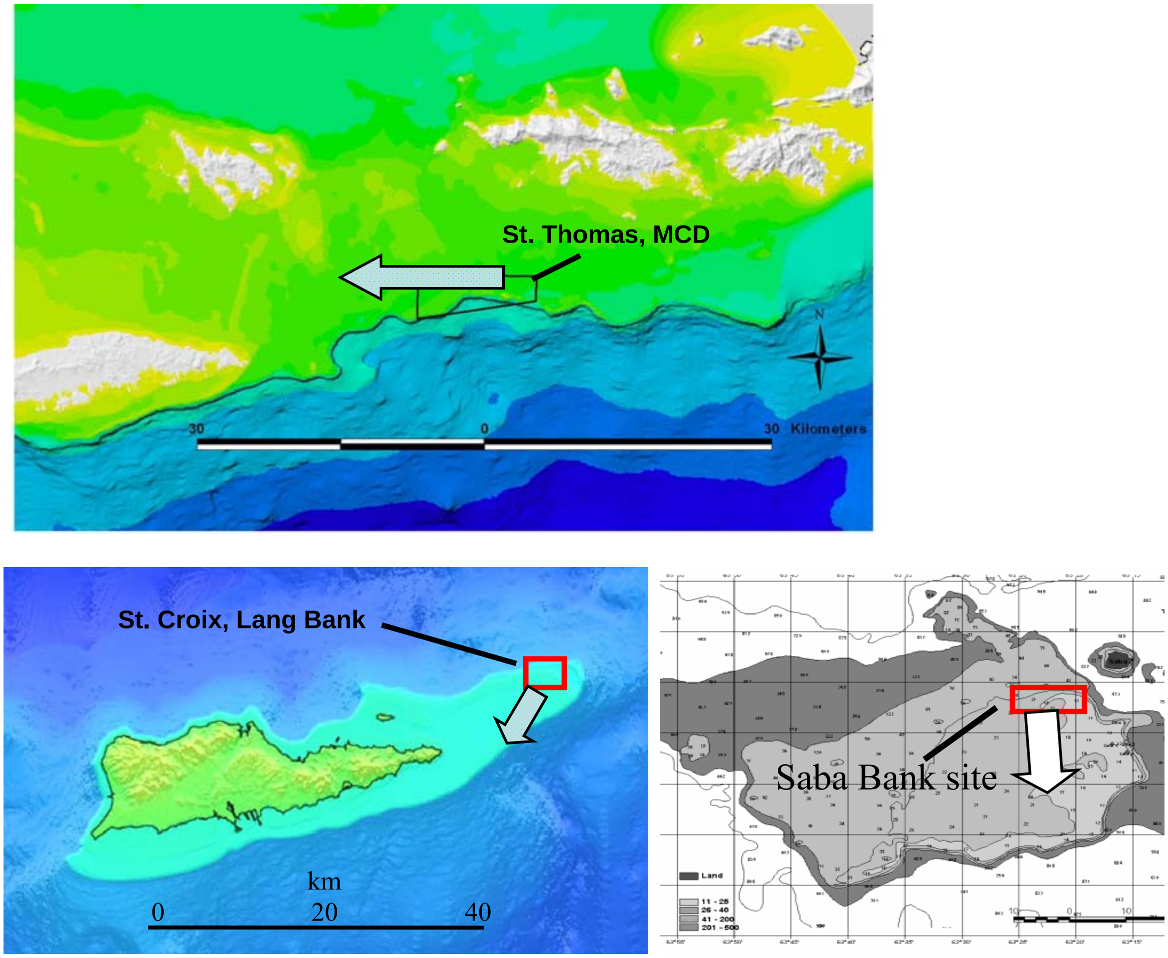

Fig. 9. Maps showing location of red hind spawning aggregation sites (rectangles) off St. Thomas, St. Croix, and Saba. Large arrows indicate general current direction during the week of spawning (i.e., a few days before and after the full moon in January).

Conclusions and Recommendations

This study found similarities in movement, migration, and oceanographic features among several distant red hind spawning aggregation sites within the eastern Caribbean. Many of the parameters found in the USVI were consistent with those found for *E. guttatus* and other Caribbean epinephelid species (Carter 1987; Colin et al. 1987; Colin 1992; Shapiro et al. 1993; Luckhurst 1998). The timing of red hind spawning aggregations was synchronized across large spatial scales, based on similar oceanographic features. Changes in the lunar cycles and seasonal declines in seawater temperatures and current speeds appear to initiate migration and synchronize arrival of *E. guttatus* to the spawning aggregation sites. Spawning of *E. guttatus* in the eastern Caribbean was restricted to brief periods between the winter solstice in December and the end of February when annual seawater temperature and current speed reach their minimum. While we cannot be certain why these particular sites have been selected by red hind for spawning or how long they have been used, the presence of slower across-shelf currents at all sites suggests that certain physical features may be consistent across multiple spawning aggregation sites. In the case of red hind, across-shelf currents may maximize retention of eggs and larvae and therefore enhance self recruitment at these three sites. More studies conducting simultaneous sampling will be necessary to elucidate the important features that define spawning aggregation sites.

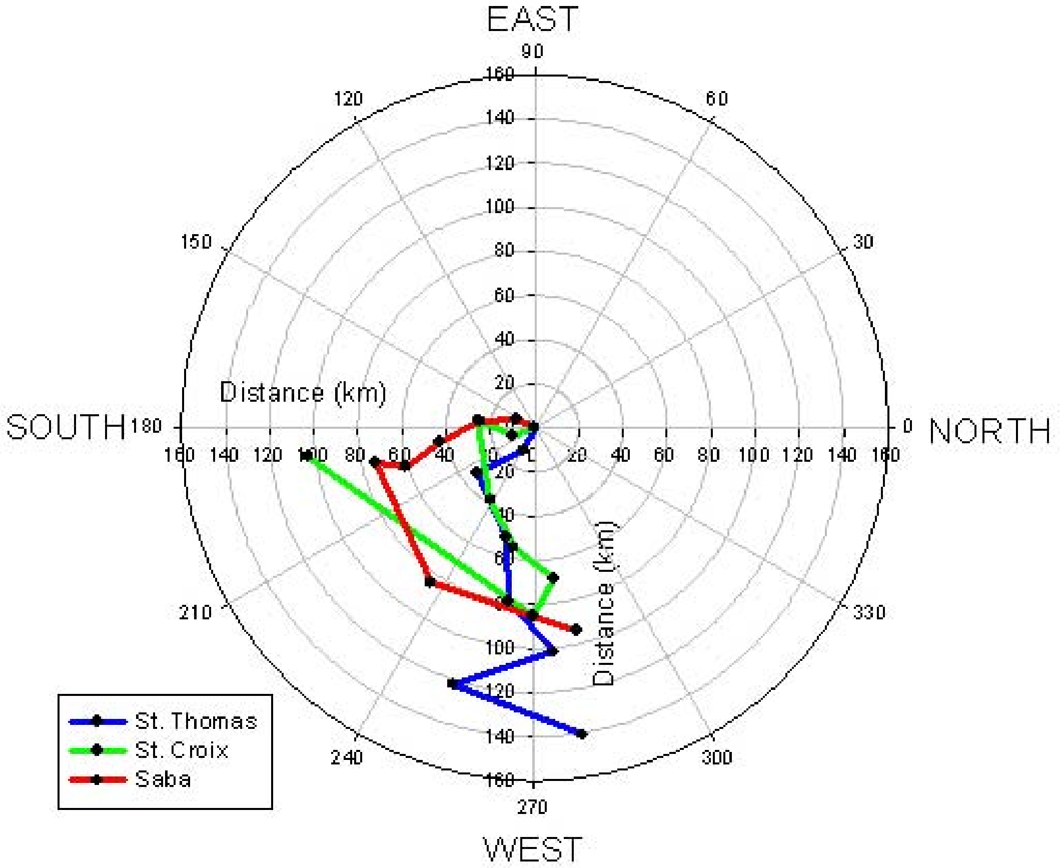

Fig. 10. Theoretical larval advection trajectories from fertilization at three spawning aggregation sites through pre-flexion stage (~ 8 d). Trajectories calculated from current speed and direction measured with ADCPs at spawning depth for day 1 and at 5 m depth for days 2-8.

We also found that the majority of red hind within both St. Thomas and St. Croix spawning populations migrated up-current to their respective spawning aggregation sites. These migration patterns will need to be confirmed for Saba, but they are consistent with *E. guttatus* in Bermuda (Luckhurst 1998) and Nassau grouper (*Epinephelus striatus*) in the Cayman Islands (Colin et al. 1987). These similarities in migration patterns suggest that red hind, and possibly other grouper species, may be composed of distinct sub-populations that are maintained largely through self-recruiting mechanisms (i.e., advection of eggs and newly hatched larvae toward adult home ranges). Under this scenario, if a local spawning aggregation site is overfished, reproductive output declines and a lack of self-recruitment may cause rapid depletion of the local sub-population within a distinct area of the shelf. This may explain why many spawning aggregations suddenly collapse and fail to recover (Sadovy and Domeier 2005).

Due to the vulnerability of spawning aggregations and the potential that local populations are sustained through self-recruitment, it is critical that all spawning aggregation sites are protected from fishing. Moreover, it is important that MPAs or other management initiatives, designed to protect reproductive adults, account for species- or gender-specific behavioral patterns. Identifying the migratory pathways and understanding the daily and weekly movements associated with spawning aggregations are critically important for accurately placing closure boundaries. The general knowledge that red hind spawning aggregations are restricted in space and time can be applied strategically to maximize the limited resources available for research, monitoring, and enforcement and lead to more effective MPAs and therefore greater protection of spawning aggregations. However, if fishery protected areas are too small or cannot be enforced or migratory pathways outside of MPAs are targeted by fishermen, seasonal catch bans may be just as effective at protecting the spawning population.

Acknowledgements

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Reef Fish Spawning Aggregations as Sources: Science and Management

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Summary of oral presentation

Belize: multi-species spawning aggregation sites inside reserves (Gladden Spit). Bathymetry data is limited, but appears to be at the shelf edge.

Where do the eggs go right after spawning? The models don't handle that very well. Where are the nursery habitats?

Human connectivity –
    Fishermen exchanges
    Regional information sharing

GCFI Annual Meeting at Xel Ha, 2002
Policy recommendation statement: spawning aggregation site protection throughout the Caribbean region

I hope we see a lot more participation next year from those who have power to make decisions and effect change.

We have a big head start, but lots of work to characterize and protect nursery grounds, aggregations, and adult migration.

Like to make headway in human and political connectivity.

Abstract:
Heyman, W., B. Kjerfve, and T. Ezer. 2007. Spawning aggregations as sources: The status of the science and its applications for management. Proc. Gulf Carb. Fish. Inst. 59: 635-636.

Regional Coupling of Red Hind Spawning Aggregations to Oceanographic Processes in the Eastern Caribbean

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Summary of oral presentation

Epinephelus guttatus – pair spawns in heremic groups. Study in St. Thomas, USVI.
Consistent spawning patterns over sites and years. Associated with the lunar cycle.
Movement of males and females also related to spawning timing.

Current meters placed at the spawning site – found temperature and current speed associated. Temperature lowest at spawning months. Association with the lunar cycle.

Do these oceanographic features help to synchronize movement patterns and reproduction at red hind spawning aggregation sites?

Primary spawning month was January (at St. Thomas, St. Croix, and Saba Bank). Expected to find the same synchronicity at St. Croix with the full moon. Didn't find the clean, dramatic increase as in previous years.

Current patterns at time of spawning were different at each island. They all serve to keep the eggs on the banks for each spawning location.

Conclusions:
Spawning aggregations on St Thomas, St Croix, and Saba formed during same lunar periods

Current patterns suggest that fertilized eggs are carried onto the shelf at each site

Managing Spawning Aggregations:
- SPAGs are extremely vulnerable to overfishing especially during peak aggregations
- Synchronized timing of spawning aggregations facilitates efficient research, monitoring, and enforcement when limited resources
- Spawning locations may function to retain larvae so SPAGs should be managed as separate stocks

Abstract:
Nemeth, R. E. Kadison, J. Blondeau, N. Idrisi, R. Watlington, K. Brown, and L. Carr. 2007. Regional coupling of red hind spaning aggregations to oceanographic processes in the eastern Caribbean. Proc. Gulf Carib. Fish. Inst. 59: 637.

Defining the Biogeography of a Spawning Aggregation to Inform Marine Reserve Planning and Evaluation in the Cayman Islands

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Summary of oral presentation

Project involved identifying the biogeography of a spawning aggregation.

Aggregations as "Black Holes" – large numbers of individuals and species brought together. Oftentimes they go to these sites and they don't return because they are harvested. Don't have a firm grasp of what the ecological features are of the seascapes where these fish aggregate.

Where are the fish coming from that are aggregating on the west end of Little Cayman? This is important information from a management context.

Nassau grouper – important because it is an ecological and social cornerstone. Historically abundant, top predator, large portion of regional fisheries catches (historically), highly valuable fishery.

Conservation status – aren't doing well in most places. Protected in Bermuda since 1970s, in FL since the early 1990s. Not showing significant recovery in the areas being protected.

Causes of decline – two main presumed causes: habitat loss (coincident with the decline of coral reefs) and overfishing (almost exclusively due to fishing on spawning aggregations).

Aggregations matter because:
- Typically solitary and territorial
- Better chance of egg and sperm meeting
- Presumably optimal location for population replenishment

There are few aggregations left –
- Historically 10s of 1000s of fish
- There are perhaps less than 10 known functional aggregations left
- "Large" aggregations are 1,000-2,000 fish

2001: Little Cayman spawning aggregation identified. Between 7,000-8,000 fish. In two years, fishers pulled out approximately 4,000. Existing protections will expire in 6 years unless the government can prove the protections are warranted.

What do we need to know to prove they are warranted?

- Where are they coming from?
- Do all fish aggregate every year?
- Do older fish aggregate more often?
- Are there any undiscovered aggregation sites?

This site is the only site known in the Caymans.

Used passive acoustics to address these questions. Tagged in 30 fish at the aggregation and 20 fish from other areas around Little Cayman.

Are able to track fish leaving aggregation site to its home site. Fish moved back and forth from spawning site to home site during spawning season.

Most of fish tagged at home sites – stayed at their home sites. Aggregation tagged fish – all but one went to a home site on the island.

Findings:

- No fish appeared to leave the island
- Fish equally from all areas of the island
- Half of the fish attended the aggregation more than once
- Males are more likely to come and go to the aggregation site
- Males were marginally more likely to participate in two aggregation cycles than females
- Bigger fish showed up earlier and stayed longer

In 2006 spawning season:

- All live individuals from last year returned
- Only two individuals tagged off the aggregation failed to attend

Answers to Our Questions:
Where are they coming from? Little Cayman
Do all fish aggregate every year? Yes, or nearly so
Do older fish aggregate more often? They stay longer
Are there any undiscovered aggregations? No, probably not for this island.

Abstrract:
Semmens, B.X., P.G. Bush, S.A. Heppell, B.C. Johnson, C.M.R. McCoy, S.K.E. Like, C.V. Pattengill-Semmens, S. Heppell, and L. Whaylen. 2007. Defining the biogeography of a spawning aggregation to inform marine reserve planning and evaluation in the Cayman Islands. Proc. Gulf Carib. Fish. Inst. 59: 638.

Panel Discussion: Spawning Aggregations

Q: Brice, the females that show up more than once, do they tend to be the larger females?
Brice Semmens: I would have to look at the data – my recollection is that there isn't a difference. Sex ratio for tagged was approximately 50:50 – so we only had 15 females from the aggregation site. So the sample size is low.

Q (Peter Sale): Looking at currents in relationship with temperature. Would you say that the dispersion of eggs is related to current patterns? Are current patterns before spawning influencing?
Rick Nemeth: Full moon could initiate hormones. Once they get on the aggregation, the full moon synch over a week or so. Dramatic temperatures and currents associated with the full moon may synch them more within a day or two of that spawning week. We're trying to answer that question in the next couple of years.

Q (Billy Causey): Has anyone ever described the physical components of an aggregation site? Seems to be some similarities among sites? Has anyone every described them?
Will Heyman: I haven't seen it in the literature. It's tricky – as you don't want to give away information to fishermen. But there does seem to be tremendous similarities between theses multi-species aggregation sites. We need to do that work, and one of my Ph.D. students is embarking on that.

Q: Brice, you had 8,000 fish and Cayman is 20 km long. That works out to 1 fish every 5 meters.
Brice Semmens: Yes. REEF has fisheries-independent data around the Caribbean. The relative abundance of Nassau grouper is 6-10x what there is in the Florida Keys. Therefore there are larger abundances in some areas.

Q: Current flow is such that most fish are returning to that aggregation. Are the spatial scales on the same order? Adults migrate 20-30 km to the west toward other islands. Is larval drift also in that direction?
Rick Nemeth: Haven't calculated how far the larvae would go in that direction. Interesting question to know if a single aggregation is self contained for that region.

Q: Dwight, as researchers and students and managers here, what recommendations would you have as we speak to our managers?
Dwight Neal: Worked at Belize Fisheries Department for 20 years. Also looked at these issues from the point of view of doing research. Also looked at it from the point of view of the managers. Couple of things seem to work:

1) You have to involve all the players (fishers, tourism operators, etc)
2) Have to make information available to people – if they don't have information they think you are trying to trick them, and are resistant to change
3) Limiting the kind of gear is important in aggregation areas; reduced the numbers of fish taken by limiting entry and gear type
4) Politicians aren't going to do something they think will be unpopular. If you are going to suggest something they think will be troubling, you need to take care.

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