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THE EXTENT AND SPATIAL SCALE OF CONNECTIVITY AMONG REEF FISH POPULATIONS: IMPLICATIONS FOR MARINE PROTECTED AREAS DESIGNATED FOR FISHERIES ENHANCEMENT

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ABSTRACT Enthusiasm for the use of no-take marine protected areas (MPAs) as management tools for the protection and enhancement of coral reef fishes is widespread. However, evidence that such marine reserves actually enhance fishery yields is limited, primarily because of difficulties in quantifying the exchange of individuals—especially larvae—between local populations within and outside the protected area. Knowledge of the extent and spatial scale of this connectivity is of vital importance for the effective design and implementation of marine reserves intended as fishery management tools. We review our current understanding of connectivity among coral reef populations, including the role of important determining factors such as pelagic larval duration, larval behavior, and hydrodynamics. We also discuss artificial and natural tagging methods that potentially can be used to track movements of larvae between marine reserves and surrounding waters. To illustrate the application of such methods, we discuss ECONAR (Ecological CONnections Among Reefs), a new, regional-scale research project designed to measure the extent of connectivity among populations of coral reef fishes in the Mesoamerican Barrier Reef System.

Marine Fisheries in Peril

A recent, but major, revelation in our quest to understand nature is that humans dominate the world's ecosystems (Vitousek et al. 1997a). Through a variety of mechanisms, including habitat alteration, exploitation, exotic species introductions, and atmospheric emissions, humans have negatively influenced population, community, and ecosystem dynamics (Vitousek 1994, Williamson 1996, Botsford et al. 1997, Vitousek et al. 1997a-c, Jackson 2001), making it difficult for the world's flora and fauna to persist (Langston 1998). The extent of this human domination is clearly illustrated by changes in the world's fisheries resources. Quite simply, many historically important commercial and recreational fisheries are in a state of peril (Murray et al. 1999). In fact, commercial fishing has caused nearly a quarter (22%) of the world's pelagic marine stocks to become overexploited and brought an additional 44% of them to the brink of overexploitation (Botsford et al. 1997). In addition, long-term historical data suggest that these negative impacts have been long-standing (Jackson et al. 2001). The situation is no less dire on coral reefs. Roughly 58% of the world's coral reefs are considered at risk, owing, in part, to destructive fishing practices and overexploitation (Bryant et al. 1998).

Sadly, the continued decline of many marine fisheries, both pelagic and coastal (e.g., associated with coral reefs), cannot be attributed to turning a "blind eye" to the problem. On the whole, resource management agencies have recognized that fisheries around the world are in trouble, and have responded with seemingly appropriate management plans implemented to remedy the situation. These attempts at management, however, have been largely unsuccessful, especially for reef systems (Plan Development Team 1990, Roberts and Polunin 1991, Bohnsack and Ault 1996, Roberts 1997b, Guénette et al. 1998, Russ 2002, Sale 2002). Reasons for the continued decline of reef fisheries around the world are numerous and include: 1) a reliance on inappropriate, traditional management approaches that pretend fishers exploit single targets, while having no impacts on the ecosystem that sustains those species, 2) a lack of ecological information pertinent to understanding species life histories, as well as reef fish population and community dynamics, 3) an inability to understand, predict, and therefore regulate human behavior, 4) a failure to integrate the diversity of skilled personnel (i.e., ecologists, physical oceanographers, and resource managers) necessary for the development of appropriate management plans, and 5) insufficient funds to collect monitoring data or to enforce imposed fishery regulations (Plan Development Team 1990, Roberts and Polunin 1991, Bohnsack and Ault 1996, Roberts 1997b, Guénette et al. 1998, Russ 2002, Sale 2002).

Owing to the failure of traditional fisheries management approaches, a growing interest in use of spatially explicit management techniques has developed during the past two decades (Guénette et al. 1998, Murray et al. 1999, Sale 2002). In particular, the use of marine reserves as fishery management tools has been widely advocated and frequently implemented (Plan Development Team 1990, Roberts and Polunin 1991, Bohnsack and Ault 1996, Russ 2002). Although the concept of marine reserves as a management option is not new, first explored by Beverton and Holt during the 1950s (see Guénette et al. 1998), their establishment definitely is a contemporary phenomenon, demonstrating exponential growth since the early 1900s (World Conservation Monitoring Center Protected Areas Database; http://www.wcmc.org.uk/protected_areas/data/un_eanalysis.htm). By 1997, close to 600 marine-related protected areas > 1,000 ha in size had been established worldwide, of which, more than 400 included coral reefs (Bryant et al. 1998). Further, when considering all MPAs, even those of postage stamp size, as well as those unmanaged "paper parks" that are of dubious value, their numbers likely range into the 1000s (Sobel 1993).

MARINE RESERVES AS FISHERY MANAGEMENT TOOLS

Marine refuges are seductive tools that seem to promise much. The potential benefits of marine reserves are diverse (Plan Development Team 1990, Bohnsack and Ault 1996, Murray et al. 1999), ranging from the protection of biodiversity and ecosystem function, and the enhancement of fish populations (e.g., improved abundance, age structure, fecundity, and/or intraspecific genetic diversity), to the fulfillment of more human-oriented goals (e.g., "minimally disturbed" areas for research and education, simplified enforcement areas for fisheries management, areas for "non-consumptive" economic uses). Of relevance to this paper, is the claim that marine reserves can enhance fisheries via protection of spawners and spawning habitat from the direct and indirect effects of exploitation (Plan Development Team 1990, Roberts and Polunin 1991, Murray et al. 1999).

Protecting fish within the boundaries of a marine reserve does not directly enhance yields. There are two hypothesized ways in which an MPA can augment exploitable yields outside its boundaries, both of which stem from the accumulation of fish biomass within the no-take (or reduced-take) zone (Plan Development Team 1990, Roberts and Polunin 1991, Murray et al. 1999). The first is through 'spillover', or the net outward migration of fish, which originally recruited to (or spent their early life within) the marine reserve. Conceivably, this spillover effect should occur as a result of heightened competition for resources (e.g., food, habitat) within the reserve, stemming from increased survivorship. The second, and presumably more important form of fishery augmentation is termed 'subsidy'. With enhancement of both size and age structure, population fecundity within the marine reserve should increase, given the strong, positive (typically exponential) relationship between size/age and fecundity (Plan Development Team 1990, Carr and Reed 1993). In turn, if pelagic larvae are dispersing or being advected out of the reserve (i.e., into the region still open to fishing), heightened gamete production within the reserve should result in an increased supply (or subsidy) of these larvae to fished populations.

Although marine reserves can effectively enhance species richness within their borders (see Crowder et al. 2000 for a review), there is surprisingly little evidence showing they enhance fisheries (Roberts and Polunin 1991, Carr and Reed 1993, Dugan and Davis 1993, Crowder et al. 2000, Russ 2002). Much evidence has accrued demonstrating that fish within the borders of marine reserves achieve higher abundances, grow to larger sizes, and reach older ages than fish still subject to the fishery (see Plan Development Team 1990, Roberts and Polunin 1991, Carr and Reed 1993, Dugan and Davis 1993, Crowder et al. 2000, and Russ 2002 for reviews). Some evidence also exists, which demonstrates that spillover can enhance yields from regions immediately adjacent ($\leq$1 km) to marine reserve borders (Alcala and Russ 1990, Russ and Alcala 1996, Crowder et al. 2000, McClanahan and Mangi 2000). No investigation, however, has actually quantified the numbers of juveniles and adults that leave marine reserves, and we are still uncertain as to whether the amount of spillover compensates for the removal of the reserve from the available fishing ground (Roberts and Polunin 1991, Dugan and Davis 1993, Crowder et al. 2000, Russ 2002). Roberts et al. (2001) present data they claim as clear evidence that marine reserves do enhance adjacent fisheries. They document, for the Soufrière Marine Management Area, significant increases in biomass of five fishery families both inside and outside the reserve (3-fold, and 2-fold respectively in the three years following implementation), as well as significant increases, in the immediate vicinity of the reserve, in total trap fishery catch (46% increase for large traps and 90% increase for small traps) and CPUE (36% for large and 80% for small traps). However, these seemingly impressive data, suggesting very substantial spillover effects, include no controls for

natural variation in recruitment, biomass or yield, and provide no evidence that spillover has caused the improvements seen outside the reserve borders.

Even more troubling is the fact that the subsidy effect remains completely untested. Subsidy is expected to be a far more substantial effect of a marine reserve than is spillover (Watson et al. 1997) because larvae will travel further outside of reserve boundaries than juvenile and adult fishes with home ranges that typically are less than 1 km in diameter (Sale 1980, Roberts and Polunin 1991, McClanahan and Mangi 2000). Unfortunately, we know of no empirical study of a marine reserve that has even demonstrated a subsidy exists, let alone quantified its extent.

If we are to continue to promote marine reserves as an effective fisheries management tool, we must demonstrate that they enhance fish yield in surrounding waters by an amount that is greater than the yield now excluded from the fishery by the establishment of the reserve. Otherwise, the implementation of marine reserves is simply a way of forcing a reduction in effort while pretending to do something more. We, therefore, urgently need to document the extent of subsidy and spillover.

Recognizing that our understanding of subsidy, and hence connectivity among reef fish populations, is limited primarily by our limited knowledge of larval dispersal (Doherty and Williams 1988, Leis and McCormick 2002, Sale 2002), our goals for this paper are to consider the various processes that influence larval dispersal, to review the techniques that may elucidate the extent of the resulting connectivity, and to introduce one current research project representing the type of regional-scale, multidisciplinary approach that is going to be necessary, if definitive estimates of connectivity are to be obtained. The goal of quantifying connectivity must be recognized as of primary importance both for improved fundamental understanding and for more effective management using marine reserves as fishery management tools.

IMPORTANCE OF LARVAL DISPERSAL

Most coral reef fishes follow an indirect model of development (Balon 1990), wherein there is a prominent larval stage followed by settlement on a reef and metamorphosis into the juvenile stage. Because larvae of many reef fishes are pelagic, for a period ranging from days to months (Brothers et al. 1983, Wellington and Victor 1989, Carr and Reed 1993), long-distance dispersal of larvae has been viewed as likely, thereby causing reef fish populations to be viewed as open metapopulations (Sale 1980, Carr and Reed 1993, Caley et al. 1996, Roberts 1997a). In addition, because pelagic larvae are typically small in size, and thus likely at the mercy of their physical environment, knowledge of large-scale hydrodynamic processes (e.g., mean current patterns) and pelagic larval duration (PLD) seemed primarily what was necessary to make predictions about larval dispersal, and hence connectivity among reefs (Williams et al. 1984, Hourigan and Reese 1987, Roberts 1997a). While the importance of connectivity for understanding the demography of marine populations has been broadly acknowledged (e.g., Carr and Reed 1993, Ogden 1997, Roberts 1997a, Warner et al. 2000, Crowder et al. 2000), the difficulty of measuring it—and possibly the force of other agendas—has meant that those responsible for establishing marine reserves have done so primarily without reference to objective estimates of connectivity.

Recently, our scientific view of coral reef systems has begun to change. The emphasis on long-distance dispersal of larvae has been replaced by arguments for the importance of retention (i.e., self-recruitment; Shultz and Cowen 1994, Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000, Leis and McCormick 2002). Four lines of evidence can explain this paradigm shift (also see Leis and McCormick 2002).

1. As we are only now beginning to appreciate, reef fish larvae are strong, competent swimmers with highly developed sensory systems (Stobutzki and Bellwood 1994, 1997, Stobutzki 1998, Leis and Carson-Ewart 2001, Leis and McCormick 2002), enabling them to actively choose the direction in which they move (Leis and Carson-Ewart 1998, 2001, Leis and McCormick 2002). While hydrodynamic processes will dictate the direction of movement of newly hatched larvae, laboratory and *in situ* investigations have shown that larvae can swim in a directed manner and orient themselves toward reefs that are not in the direction of currents (Leis and Carson-Ewart 1998, 2000, Leis and McCormick 2002). In addition, several field-validated biophysical models of larval movement among reefs have demonstrated that information on both hydrodynamic features and larval behavior is necessary to understand larval distribution patterns (Wolanski et al. 1997, Cowen et al. 2000).

2. It is now recognized that small- and meso-scale hydrodynamic processes, which dominate in the immediate vicinity of the reef complex, might be more important than large-scale processes in influencing larval dispersal (see Cowen 2002 for a review). Interestingly, many of these smaller-scale processes tend to promote retention rather than dispersal from a reef, as suggested

by both empirical and numerical modeling studies (Shultz and Cowen 1994, Black et al. 1991, Cowen 2002).

3. The small, but growing, number of spatial studies of reef fish genetics indicates a large degree of genetic heterogeneity among local populations (Bell et al. 1982, Planes 1993, Planes et al. 1994). In fact, in a recent review of studies on coral reef fish genetics, Planes (2002) found significant genetic divergence among local populations in 36 of the 38 species examined, suggesting that larval (or even adult) dispersal rarely has operated to homogenize them.

4. The only two empirical field studies that have attempted to quantify larval dispersal (i.e., Jones et al. 1999, Swearer et al. 1999) present evidence showing self-recruitment can be equally as important as dispersal to understanding coral reef fish population structure.

These findings have major implications for the use of marine reserves as fishery management tools. If retention is important, we cannot set up marine reserves assuming that larvae will be broadly dispersed, according to simple rules that combine PLD and mean ocean currents. Patterns of dispersal of larvae may be strongly dependent on local details of hydrography and geography, in combination with details of larval behavior. In turn, dispersal may be constrained to regional or local scales, and therefore, several small reserves scattered throughout a region may be more effective than a single larger one (Leis and McCormick 2002). Clearly, there is an urgent need to build our understanding of connectivity so that it can be used as a tool to design useful marine reserve networks.

INNOVATIVE TECHNIQUES TO QUANTIFY DISPERSAL AND CONNECTIVITY

Multiple factors, including PLD, hydrodynamic features, and larval behavior, can interact to regulate larval dispersal. Because we are still in our infancy in understanding these interactions (Cowen 2002, Leis and McCormick 2002), there is the risk that a comprehensive understanding of connectivity may not be within our grasp, at least for the foreseeable future. We need increased effort on all fronts (larval biology, sensory capabilities and behavior, detailed hydrodynamic studies), and concerted efforts to integrate these approaches. Further development of biophysical models will be essential as tools for testing hypotheses (e.g., Cowen et al. 2000), as well as to aid in this integration.

While a comprehensive understanding of connectivity must be a long-term goal, we are fortunate that, owing to recent technological advances, we can begin to quantify connectivity without necessarily understanding the suite of causal mechanisms. Below, we discuss a traditional tagging approach for evaluating dispersal, and afterwards, two innovative approaches that hold more promise for quick estimates of extent of larval exchange.

Tagging Studies

The clearest way to identify larval dispersal patterns would be to track the movements of numerous individuals using some type of artificial tag (e.g., Passive Integrated Transponders (PIT) tags, Floy tags, pop-up satellite archival tags, radio-transmitters). Such approaches have proven quite successful in identifying home ranges, migration routes, and horizontal and vertical distribution patterns of juvenile and adult fishes in both freshwater and marine systems (e.g., Parker 1992, Zabel et al. 1998, Auer 1999, Anras et al. 1999, Smithson and Johnston 1999, Bolden 2000). Unfortunately, however, these technologies are not yet available in forms appropriate for small-bodied organisms, such as fish eggs and larvae. Even if they were, high mortality rates (>99%) and dilution effects during pelagic stages might make their use impractical.

As a potential alternative to these expensive (or impractical) methods, artificial tagging techniques have been developed, wherein otoliths—calcium-carbonate concretions of the inner ear—are marked with fluorescent dyes, such as tetracycline or alizarin (see Table 1 in Geffen 1992). To date, this technique has primarily been used to quantify survival of hatchery-reared fish, as well as to validate daily increment deposition on otoliths, which then can be used to age fish (Geffen 1992, Yamashita et al. 1994, Secor et al. 1995). However, in the only larval fish tagging study attempted in a marine system, Jones et al. (1999) used this technique (i.e., oxytetracycline marking of embryos in nests) to demonstrate that retention (self-recruitment) of a damselfish, *Pomacentrus amboinensis*, to reefs at Lizard Island (Great Barrier Reef) might be equally, if not more, important than larval immigration to the reefs.

Unfortunately, the utility of artificial tags is limited, owing to high larval mortality, and hence low recapture rates (e.g., only 15 of ~10 million marked individuals were recaptured by Jones et al. (1999)). This can reduce confidence in estimates of self-recruitment (range in Jones et al. (1999) was 15% to 60%). In addition, this technique seems only appropriate for nest-guarding species with benthic eggs or larvae (e.g., Blenniidae, Gobiidae, Pomacentridae, Apogonidae), not broadcast spawners found in the families Serranidae, Lutjanidae,

Haemulidae, Labridae, and Acanthuridae. Clearly, making use of a natural tag, which would eliminate any need to mark fish, seems an ideal way to quantify connectivity for any species of fish.

Genetics

Quantifying genetic relatedness among fish both within and among reefs offers one such approach. If some sort of open (metapopulational) structure exists and larval exchange occurs among reefs, then we would expect populations to be homogeneous relative to reefs that do not exchange individuals. Although several empirical investigations have demonstrated that larval exchange among reefs can occur (e.g., Swearer et al. 1999), 95% (n = 36 of 38) of the studies that have examined genetic structure among local reef fish populations found significant genetic heterogeneity among them (Planes 2002), indicating that dispersal was low enough that panmixis had not occurred (or possibly that differential selection was occurring).

Despite the benefit of not needing to mark fish, the use of genetics as a tool to quantify connectivity has its drawbacks. First, choosing an appropriate technique is not a straightforward endeavor, owing to tradeoffs among cost, ease of use, and the potential to discriminate among populations. For example, most genetic studies of coral reef fishes have explored differences among local populations using protein electrophoresis (i.e., variation in allozymes; Planes 2002). Although a fairly straightforward, quick, and inexpensive technique, protein electrophoresis has two potential limitations. First, this method presupposes that differences in allelic frequencies among populations are due solely to gene flow (i.e., dispersal) and random divergence associated with genetic drift. This assumption, however, is not realistic because natural selection, as well as historical contact, can be influential (Planes 2002). Second, and more importantly, whereas a result of genetic dissimilarity among local populations is clear evidence of a lack of exchange of individuals among them, a result of genetic homogeneity might not be real. Because not all DNA codes for proteins, protein electrophoresis can underestimate genetic variation among populations, resulting in apparent homogeneity (Planes 2002).

Alternatively, one may choose to use restriction fragment length polymorphisms, random amplified polymorphic DNA, minisatellites and microsatellites, or DNA sequences to explore genetic differences among local populations. Although Planes (2002) views microsatellites as "the future tool for population genetics" because microsatellite systems are highly variable and are not under the influence of selection, this technique is expensive, time-consuming, and plagued with problems with regard to analysis and interpretation (Planes 2002). See Parker et al. (1998) and Planes (2002) for a more detailed discussion of the advantages and disadvantages of these genetic techniques.

The second major drawback with using genetics to explore connectivity is that the information required to properly design marine reserve networks might not be provided. Indeed, genetics has the potential to determine whether two (or more) populations are mixing (homogeneity) or not (heterogeneity). However, an exploration of genetic structure cannot quantify the magnitude (or rate) of exchange of individuals between populations because only a few exchanges can lead to genetic homogeneity (Allendorf and Phelps 1981, Hartl and Clark 1997, Planes 2002). Thus, even if two populations were found to be genetically similar (i.e., homogeneous), we still would not be able to tell whether the lack of genetic divergence was due to an exchange of 10 or 10,000 individuals per year between them. And unfortunately, it is this information (i.e., the rate and magnitude of mixing) that has been the critical limiting element in models attempting to determine how marine reserves will influence fish population dynamics. As such, although genetics can be useful for determining the extent of connectivity via larval dispersal, it cannot be used as the only tool, especially if populations appear homogeneous.

Otolith microchemistry

The developing ability to accurately measure trace concentrations of elements in otoliths of fish offers another potential way to explore connectivity that does not require artificial tagging (Campana 1999, Thresher 1999, Swearer et al. 1999, Thorrold et al. 2001, Thorrold and Hare 2002). This technique, however, has an advantage over genetics in that it allows the magnitude (or rate) of exchange between local populations to be quantified.

Because otoliths are metabolically inert, and therefore do not undergo chemical resorption (unlike other calcified structures in fish), and because they grow incrementally throughout the life of the fish, their microchemistry serves as a permanent record of the environment experienced by fish (Campana 1999, Thresher 1999). Thus, the progeny of disparate local populations should have differential incorporation of elements (e.g., strontium, barium, lead, manganese, magnesium) into otoliths, assuming that water chemistries vary among locations. In turn, by collecting a sample of newly settled recruits to a reef and comparing the chemistry of the otolith core (which should be related to water chemistry at the natal

site) to the chemistry of post-settlement growth rings (which should be related to water chemistry at the resident reef), one should be able to 1) determine the proportion of settlers (or even spawners) that were produced locally versus those that arrived from elsewhere (sensu Gillanders and Kingsford 1996, Swearer et al. 1999), and 2) identify from where the immigrants to a particular reef were produced (sensu Gillanders and Kingsford 2000, Thorrold et al. 2001), assuming that microchemical "signatures" from other production areas are known. Such information would be of obvious value for marine reserve network design.

This technique has mainly been used to identify migration routes and spatial (stock) structure of freshwater, anadromous/catadromous, and marine fishes (Campana et al. 1999, Limburg 1995, Begg et al. 1998, Thorrold et al. 1998; see Campana 1999, Thresher 1999, and Thorrold and Hare 2002 for reviews). However, it also has been used to quantify the degree of connectivity among local populations of weakfish (*Cynoscion regalis*) by quantifying the degree of philopatry (natal homing) to estuaries located along the Atlantic coast (Thorrold et al. 2001). In addition, Swearer et al. (1999) used otolith microchemistry to determine whether larval dispersal or retention (i.e., self-recruitment) was more important to understanding recruitment patterns to coral reefs surrounding St. Croix, U.S. Virgin Islands. Although Swearer et al. (1999) found both to be important, depending on whether recruitment was occurring to the windward or leeward side of the island, no attempt was made to identify the natal origin of the immigrating larvae. Thus, despite its promise, this technique has not yet been used to quantify connectivity among populations from two or more reefs.

PRESCRIPTION FOR QUANTIFYING CONNECTIVITY: ECONAR AS AN EXAMPLE

Despite widespread recognition that quantifying larval dispersal, and hence connectivity, is vital for proper design of marine reserve networks, no study has yet attempted to quantify connectivity between two or more reefs. Likely, this is so because of complexities involved with such an undertaking. Clearly, effective research projects aimed at quantifying connectivity will require collaboration among scientists from numerous disciplines, including hydrologists, geneticists, ecologists, and geochemists. In addition, because larval dispersal might be extensive, and therefore, will not adhere to jurisdictional boundaries, the most informative collaborations seemingly will need to conduct field work on a regional scale and involve scientists (and resource managers) from one or more countries. Certainly, this will further the need for long-term planning and coordination.

We are currently undertaking a research project called ECONAR, for Ecological CONnections Among Reefs, which is focused on identifying the extent of connectivity among reef fish populations residing along the Meso-American Barrier Reef System (MBRS) off the coast of Central America. Our project's objectives are as follows. First, at reef sites in both Belize and Mexico, we seek to characterize spatio-temporal patterns of recruitment (settlement), which are a consequence of larval dispersal and the distribution of natal sites (i.e., sources of larvae). Second, we seek to build detailed analytical models of water flow (in the upper 100 m) in the region. Because small-scale hydrodynamic features (e.g., convection eddies) can be as important to understanding larval dispersal (or lack thereof) as large-scale processes (e.g., long-shore currents), we are nesting fine-scale models of water flow for each of our primary field sites (i.e., Turneffe Islands, Belize and Banco Chinchorro, Mexico) within a coarse-scale, regional model. This modeling effort will be built from remotely sensed data of sea surface characteristics, as well as archived data of topography and habitat types. Third, we will use empirical collections of newly settled fish to 1) identify characteristics of the pelagic larval phase (e.g., PLD, growth rates), and 2) determine whether those settlers were produced locally or elsewhere. Information on PLD will be obtained from otoliths, and will be combined with hydrodynamic models to determine the potential range of dispersal distances that fish might have endured. To identify natal origins of new settlers, we will use information obtained from otolith microchemistry (using solution-based and laser-based inductively coupled plasma-mass spectrometer), genetics (using microsatellites), and growth rate analyses (sensu Swearer et al. 1999). Importantly, conducting all of these analyses on the same individuals collected from sites among geographically separated reefs will allow us to determine the performance of each technique relative to the others. We are confident that this three-pronged approach to evaluate specimens, coupled with the monitoring of settlement patterns, will allow us to discriminate larvae from different source areas. In addition, a comparison of these results to transport vectors derived from our hydrodynamic models will provide evidence on the importance of passive dispersal to inter-reef connectivity.

While we know that ECONAR will make only a modest contribution to understanding questions relat-

ing to connectivity, it has three attributes that could make it a model for future projects.

ECONAR is multi-disciplinary

Seven principal investigators are involved in the project, including two reef fish ecologists, two fish geneticists, one geochemist, and two physical oceanographers. In addition to several graduate students, two post-docs are involved, one to assist with ecological aspects of the project and the other with building the hydrodynamic models. With this diversity of expertise, we will be able to blend contemporaneous ecological data with detailed physical models to test questions relating to connectivity.

ECONAR is regional in scope

Our field sites are a set of seven locations around the rim of Turneffe Atoll, Belize, and a set of six locations around the rim of Banco Chinchorro, Mexico. In Belize, we are working in conjunction with the University of Belize Institute for Marine Studies at their Calabash Caye facility. In Mexico, we are collaborating with Dr. J. Ernesto Arias, CINVESTAV-IPN, as well as with the managers of the Banco Chinchorro Biosphere Reserve. Furthermore, ECONAR has been specifically designed to interface with a much larger, international development project funded by the World Bank that is dedicated to improving the sustainability of environmental management in the region of the MBRS, stretching from the southern Yucatan of Mexico, through Belize and Guatemala to the Bay Islands of Honduras. ECONAR will directly contribute to some aspects of the environmental monitoring component of the World Bank project, while we, in turn, benefit from some of its monitoring efforts.

ECONAR is a multi-scale investigation

Past research has demonstrated that processes that influence recruitment, and hence population, dynamics can vary both spatially and temporally (Caley et al. 1996, Caselle and Warner 1996, Sponaugle and Cowen 1997, Swearer et al. 1999, Cowen 2002). As such, we have designed our project to test mechanisms of connectivity at multiple spatial and temporal scales. For example, with the aid of our collaborators, we will be able to explore questions of connectivity at both the regional (Chinchorro versus Turneffe) and local (sites within each atoll) scales. Similarly, by sampling at both long (annual) and short (daily to weekly to monthly) time scales, we also will be able to explore inter-annual variation in larval dispersal.

SUMMARY AND CONCLUSIONS

While the movement by resource managers to supplement, or even abandon, traditional forms of fisheries management, in favor of the creation of marine reserves has produced important benefits both ecologically and socially, not all proposed benefits of such reserves have been realized. Most notably, we still do not know whether marine reserves can fulfill their role as fisheries enhancement devices because 1) no study has quantified whether the spillover from such reserves offsets losses to the fishery caused by the establishment of no-take areas, and 2) no study, as of yet, has demonstrated that a measurable subsidy through larval dispersal from the reserve even occurs. This latter uncertainty is especially disturbing because fisheries enhancement in the form of larval subsidy is theorized as being more important than spillover.

The primary reason for this lack of understanding has been the difficulty with tracking larval dispersal, and hence connectivity, among reefs inside and outside of marine reserves. Owing to new technological advances, however, that allow individual larvae to be tracked via artificial (e.g., fluorescent marking of otoliths) and natural (e.g., genetics, otolith microchemistry) tags, our ability to quantify connectivity in a fashion useful to marine reserve network design should be quite rapid. This will especially be so, if these technologies are incorporated into multi-disciplinary, multi-scale projects that operate at a regional scale (e.g., ECONAR).

Given that we now have the tools to begin to understand connectivity, we must stop paying it lip service and actually begin to quantify it. For, until we understand the extent of connectivity among reefs, we will not be able to design marine reserve networks that benefit fisheries. Likewise, until we devise projects that use these innovative techniques to explore the utility of current marine reserve networks, we cannot say for certain that they benefit the fisheries they are supposed to protect. This last point is especially critical when considering that, more likely than not, marine reserves have been "sold" as fishery enhancement devices to developing countries with weak economies that revolve around artisanal and commercial fishing. Although we agree with Crowder et al. (2000) that marine reserve networks should continue to be established because of other potential benefits, we do not feel that they should be promoted as fisheries enhancement tools in the absence of evidence. By continuing to do so, we, as scientists and resource managers, risk losing credibility that will be vital for future efforts

to gain support necessary to properly implement networks that are based on sound information.

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