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Coral Reef Targeted Research & Capacity Building for Management

Preserving Reef Connectivity

A Handbook for Marine Protected Area Managers

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Citation: P.F. Sale, H. Van Lavieren, M.C. Ablan Lagman, J. Atema, M. Butler, C. Fauvelot, J.D. Hogan, G.P. Jones, K.C. Lindeman, C.B. Paris, R. Steneck and H.L. Stewart. 2010. Preserving Reef Connectivity: A Handbook for Marine Protected Area Managers. Connectivity Working Group, Coral Reef Targeted Research & Capacity Building for Management Program, UNU-INWEH.

Edited by: Lisa Benedetti

Cover photo: Commonwealth of Australia (GBRMPA)

ISBN: 978-1-9213-17-06-4
Product code: CRTR 004/2010
Editorial design and production: Currie Communications, Melbourne, Australia, May 2010.

Contents

Acknowledgements

This handbook is a product of the Coral Reef Targeted Research & Capacity Building for Management Program (CRTR) – an international development project funded by the Global Environment Facility (GEF), implemented by the World Bank, and executed by the University of Queensland, and numerous partners including the United Nations University – Institute for Water, Environment and Health (UNU-INWEH), which managed the Connectivity Working Group. I thank the many members of the CRTR Connectivity program who acted as authors, provided images or advice, or helped in other ways to bring it to fruition.

This handbook has been produced by the CRTR Connectivity Working Group, with the assistance of UNU-INWEH and CRIOBE (Le Centre de Recherches Insulaires et Observatoire de l'Environnement de Polynésie Française), which hosted a workshop: Connectivity in Coral Reef Systems Lessons to Date and Goals for the Future in Moorea, French Polynesia, March 2009, during which planning of this handbook was finalized. We also benefited from discussions, provision of detailed information and images by the following workshop participants: Jesús Ernesto Arias González, CINVESTAV-Unidad Merida, Mexico; Paul H. Barber, University of California, USA; Michael Berumen, Woods Hole Oceanographic Institution, USA; Brian Bowen, University of Hawaii, USA; Michael L. Domeier, Marine Conservation Science Institute, USA; Cécile Fauvelot, Université de Perpignan, France; Daniel Heath, University of Windsor, Canada; Serge Planes, Université de Perpignan, France; Tonya Shearer, Georgia Institute of Technology, USA; and Hannah L. Stewart, Department of Fisheries and Oceans, Canada. I would also like to thank Alina M. Szmant, University of North Carolina at Wilmington, USA.

I am also grateful to all members of the Connectivity Working Group who have consistently worked to ensure that the information we provided has been accurate and up-to-date. I thank Gabrielle Sheehan at Currie Communications and Adam Cusack at Cusack Design for their patience and their creativity in getting this handbook designed and finalized, Melanie King at the University of Queensland, who worked many miracles, and particularly Hanneke Van Lavieren and Lisa Benedetti at UNU-INWEH, who worked tirelessly as final editors to turn the drafts into this polished, professional product.

Peter F. Sale
UNU-INWEH

The decline of the coastal ocean and why this handbook exists

The coastal ocean environment provides enormous value in fishery and other products, as well as ecosystem services like coastal protection, water purification, and locations for ports, harbors, urban centers, tourist destinations, and numerous recreational pursuits. Coastal environments can also cleanse the soul, stimulate the mind, and restore the body. But 40% of all people live within 50 km of a coast, and our enthusiasm for coastal living is creating ever more environmental damage.

Unfortunately, current management practices in most coastal regions are ineffective, and to continue them will endanger the coastal economies and ecosystems that support over one half of the world's population. The trend for coastal ocean ecosystems over recent decades has been one of progressive decline in the face of growing human population, rising demand for coastal resources, and increasing use of the coastal environment. Today, climate change is adding to the pressures on the coastal environment, further stressing ecosystems there.

Figure 1. The coastal ocean environment provides enormous value in fishery and other products, as well as ecosystem services like coastal protection, water purification, and locations for ports, harbors, urban centers, tourist destinations, and numerous recreational pursuits. Coastal environments can also cleanse the soul, stimulate the mind, and restore the body. Photo: Hanneke Van Lavieren

The decline of coastal environments has become a particularly significant problem for many tropical countries with coral reefs. In these areas, reefs often contribute to the major component of GDP because of their importance to tourism and fisheries. They also provide an important protein food source and help support a traditional way of life for coastal peoples.

This handbook tackles one specific concern when contemplating effective management of coastal marine environments – the issue of connectivity. Marine protected areas (MPAs) have become an important management tool, particularly in tropical regions, and connectivity is an important consideration in the effective design of MPAs and MPA networks. Connectivity issues are also involved in most other aspects of coastal management for two reasons: first, water moves and transports items such as sediments, nutrients and pollutants considerable distances; and second, most marine organisms also move within the water stream, transporting themselves between places. Our goal is to assist MPA managers and others in understanding and applying the concept of connectivity in their work. In this way, we hope to help managers strengthen their ability to tackle the challenging task of sustaining coastal marine environments. This would help protect fisheries and other goods and services they provide.

How to use this handbook

This handbook contains a summary of the science of coral reef connectivity and guidance on how to use this information to aid in making management decisions. Although it has been written for coral reef managers, decision makers and others who may be involved in reef management efforts, the science discussed is relevant to managers of coastal waters in all oceans. Much of the science of connectivity remains to be discovered, however, substantial scientific research effort is currently underway to address knowledge gaps and translate this science into practice for improving reef management.

This handbook describes what we mean by "connectivity", and discusses the various uses of this term. Most attention is given to populational connectivity – the extent of connection among local populations of a species – because it is both the most difficult type of connectivity to deal with and because it is the least effectively used in current management practices. Populational connectivity comes in two forms: evolutionary (genetic) connectivity and demographic (ecological) connectivity. The first is concerned with genetic differences in different populations of the same species. This can be informative when considering long-term (evolutionary) and large-scale biogeographic dispersal patterns of organisms. It can also be useful for managers wanting to assess the genetic uniqueness of populations when making decisions concerning biodiversity preservation. In contrast, demographic connectivity involves the extent of linkage that occurs among nearby local populations of a species due to the exchange of individuals. This type of connectivity is most important for marine protected areas (MPAs), and particularly no-take fishery reserves (NTRs), when making decisions concerning design and management, and when trying to determine the optimum amount of reef habitat to protect when conservation or precautionary fisheries management is the objective. Other forms of connectivity relate to the transmission of nutrients, pollutants, or other items between locations, by passive transport via water currents. These are also important for managers, but easier to understand and apply because transmission is due solely to physical processes.


Figure 2. South Water Caye, Belize. Photo: Ron Schaasberg

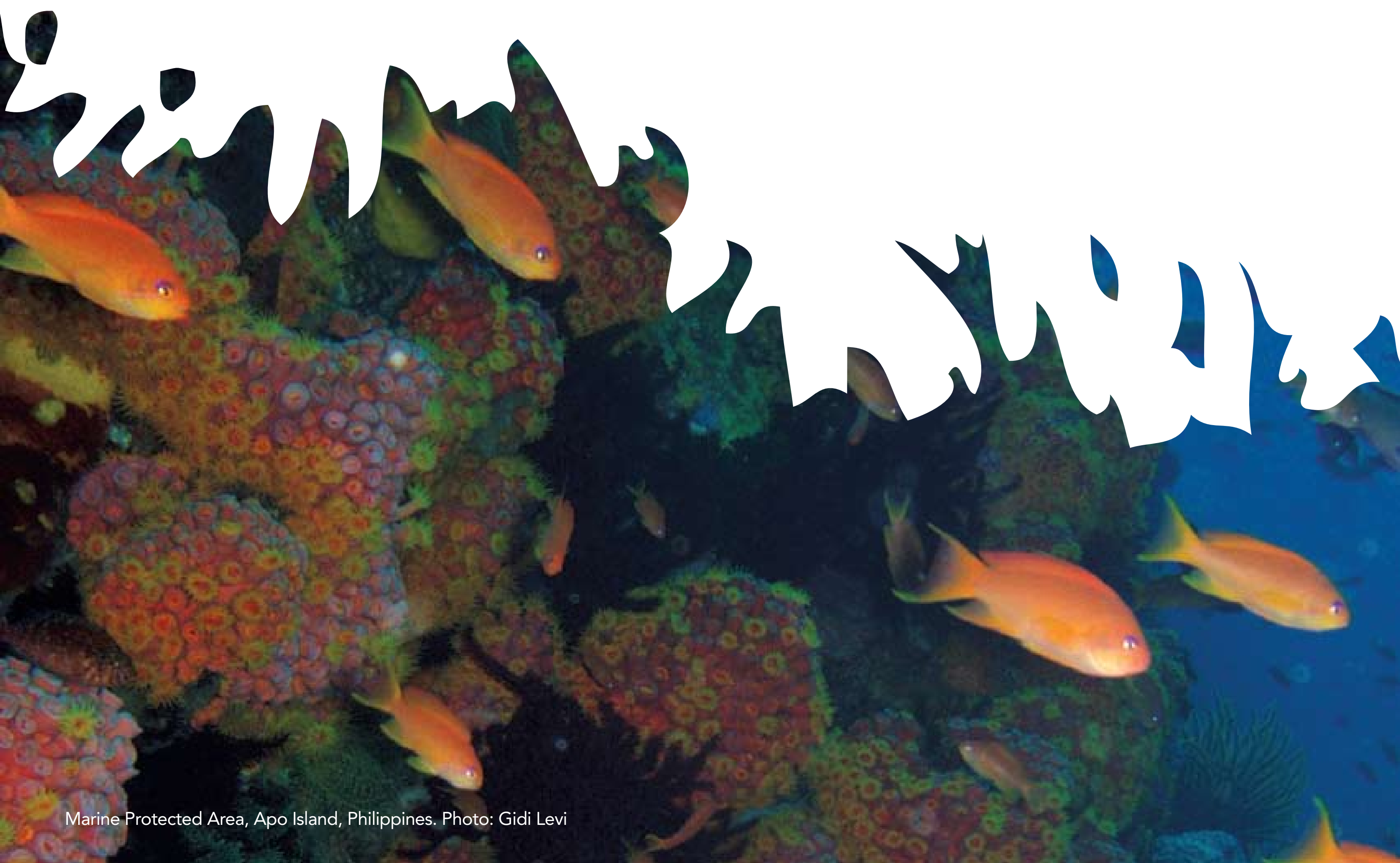
This document provides a summary of what is currently known about the science of connectivity and the techniques and tools used for measuring connectivity for different types of organisms (e.g., corals, fish and lobster). It also highlights the gaps in our knowledge and offers suggestions and advice on how to use what connectivity information is available. A strong plea is made for scientists and managers to establish close working collaborations and use management activities in an adaptive management context to simultaneously advance the scientific understanding of connectivity, while also using the best available knowledge to guide current management decisions.

This handbook has been written to make the science as accessible as possible to managers with varying levels of scientific background or expertise. For those who do not have time to read the entire document, key points are summarised on "Message boards". Also provided is a list of useful contacts within the Coral Reef Targeted Research & Capacity Building for Management Program (CRTR) and citations to relevant scientific literature for those who wish to delve further into the currently active field of connectivity research.

Section 1
What is connectivity?

In this section you will find:

The particular importance of populational connectivity



Marine Protected Area, Apo Island, Philippines. Photo: Gidi Levi

1. What is connectivity?

Coral reefs are patchily distributed habitats found throughout oceanic environments which provide a mechanism for transport among them. So are mangroves, seagrass beds, and other coastal environments. Each local patch of any of these environments will support populations of particular organisms if they are big enough to do so. Thus, the patchy distribution of habitat results in a pattern of numerous and more-or-less isolated local populations of each species characteristic of that region, i.e., more-or-less isolated because individual coral reefs and other habitat patches are seldom so remote that there is no movement of organisms among them. This movement is one form of connectivity.

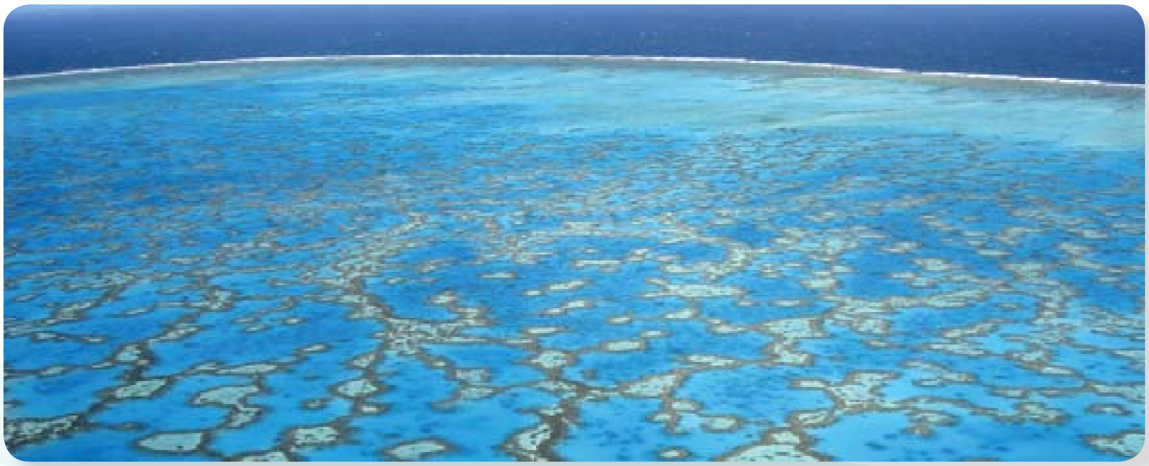


Figure 3. Patchy reef formation Great Barrier Reef, Australia. The patchy distribution of coral reef habitats subdivides populations on many spatial scales. Photo: Ove Hoegh-Guldberg

Connectivity is the flux of items between location types that are the same or different (e.g., reefs and/or seagrass beds). It exists for nutrients, sediments, pollutants, and individual dispersing organisms, i.e., any item that has the potential to move among and between reefs and other environments. In the context of coastal management, the effective transfer of individuals (usually pelagic larvae) between local populations is one of the most important, and certainly the most difficult form of connectivity to quantify. While the transfer of non-living materials, such as sediments or pollutants, is likely to be determined primarily by local and regional hydrodynamics, we know that the transfer of organisms is more complex. This is because passive transport will likely be modified by the sensory and behavioral capabilities of individual larvae. Effective transfer among populations also requires successful establishment within breeding populations, so connectivity among populations cannot be measured by focusing on dispersal patterns alone but must also include successful recruitment to the receiving population.

Box 1. Types of populational connectivity

Populational connectivity comes in two forms:

1) **Evolutionary (genetic) connectivity:** the amount of gene flow occurring among populations over a timescale of several generations. It determines the extent of genetic differences among populations.

2) **Demographic (ecological) connectivity:** an exchange of individuals among local populations that can influence population demographics and dynamics. It can include:

- Exchange of offspring between populations through larval dispersal;
- Recruitment of juveniles and survival of these juveniles to reproductive age;
- Any large-scale movement of juveniles and adults between locations.

1.1 The particular importance of populational connectivity

The transfer of individuals between populations allows for the transfer of genes. It is therefore useful to make a distinction between the two kinds of connectivity that influence populations, evolutionary and demographic connectivity. Relatively low exchange of individual organisms can still allow for a sufficient level of gene transfer and thus can result in genetically similar populations. Whereas at exceptionally low levels of exchange, populations tend to slowly diverge genetically through processes like genetic drift, mutation, and differential selection. Over time, these populations can become separate species.

The low levels of exchange that maintain genetic similarity among neighboring populations is called evolutionary (genetic) connectivity. This exchange, perhaps one or two individuals per generation, is usually far too low to have any measurable effect on population growth rates i.e., demographically, they are insignificant exchanges. At somewhat higher rates of exchange, populations remain quite similar genetically, and the rates of arrival and departure of individuals are high enough that they have a measurable impact on the rates of growth for each population. In these cases, we are referring to demographic (ecological) connectivity.

Evolutionary and demographic connectivity are equally important considerations in coastal management, but they are important in quite different ways. A manager whose primary goal is biodiversity conservation will be particularly interested in the patterns produced by evolutionary connectivity. That is, conservation decisions are frequently based on whether a particular population is taxonomically unique; absence of evolutionary connectivity usually permits this. As well, patterns of evolutionary connectivity among locations can help reveal underlying patterns of gene flow, which may reveal likely biogeographic events in the recent past or near-term future.

When demographic connectivity exists amongst populations, they can influence each other's patterns of growth or decline. This occurs when the number of individuals exchanged per generation is great enough to have a measurable impact on the population growth rate in one or each of the exchanging populations. A primary concern for many managers is ensuring that fisheries are sustainable or that coral reefs which are being managed for tourism can continuously support the normal range of species. These managers will be primarily interested in demographic connectivity. MPAs known as no-take fishery reserves should be designed with due consideration for this type of connectivity, as should networks of such reserves.

Message board

- The use of MPAs and MPA networks as a management tool has become widespread, particularly in tropical regions, and connectivity is considered a critical component in their design.
- Evolutionary and demographic connectivity are equally important considerations in coastal management, but they are important in quite different ways.
- In the context of coastal management, the effective transfer of individuals (usually pelagic larvae) between local populations is one of the most important, and certainly the most difficult form of connectivity to quantify.
- Much of the science of connectivity remains to be discovered, however, substantial scientific research effort is currently underway to address knowledge gaps and translate this science into practice for improving reef management.

Section 2
What processes cause connectivity?

2

In this section you will find:

Water moves, often in mysterious ways

Most marine organisms have pelagic larvae

Many marine organisms move about after larval life is over

Colony of *Favites halicora* spawning. Photo: James Guest

2. What processes cause connectivity?

2.1 Water moves, often in mysterious ways

The marine environment is bathed in water, a medium which is seldom at rest. Movement of water can transport items, such as plants and animals, from one place to another. Organisms such as kelp, oysters or corals, which are securely fastened to the substratum, may not move, but water will flow past and provide them with food and nutrients. Organisms that are not securely fastened, such as fish, jellyfish, killer whales or crabs, may be transported by the masses of water within which they are swimming. Indeed, in the open ocean, if an organism does not possess the equivalent of a Global Positioning System (GPS) fix of its location, or an external reference such as the view of a distant island, it cannot sense that it is being transported.

Figure 4. Gyre or eddie formation behind a reef, Bowden Reef, Australia. Oceanographic processes such as these gyres and eddies and their variability over time and space greatly determines the patterns of connectivity through larval dispersal among locations. Photo: James Oliver, Reef Base

Movement of oceanic water is brought about by various factors; the earth's rotation, wind, tides, and friction against continental margins. It is also affected by changes in water salinity or temperature. That is, water of a particular salinity and temperature will have a specific density, and so a mass of water of the same salinity and temperature tends to move as a single unit. Adjacent water masses that differ slightly in temperature or salinity can remain as distinct layers over considerable periods of time until mixing at edges averages out differences and causes them to merge together. As surface waters warm because of heat from the sun, they become less dense and rise while cooler waters sink. At the same time, evaporation due to heat from the sun causes surface waters to become more saline. Increasing salinity makes water more dense and likely to sink below deeper layers.

Putting all these factors together, we can see the ocean as a complex of adjacent patches of water moving relative to each other, both horizontally and vertically. The scale of these patterns of movement begins with the tiniest eddies only centimeters in size, to broad-scale, long-lasting currents or rotational gyres (large eddies) that can be hundreds of kilometers wide and travel thousands of miles. The Gulf Stream is an example of an enormous river of ocean water that moves from the Caribbean through to the Florida Strait, up along the eastern coast of North America, and ultimately to the shores of northern Europe. It plays a major role in transporting heat from the tropics towards the poles, as do comparable large-scale currents in other ocean basins.

When a moving water mass comes into contact with a continental margin, a mid-ocean island, or a coral reef, frictional forces modify the patterns of movement resulting in upwellings, refraction of waves, and places of intense wave action or calm lee conditions. The complexity of ocean movement has become increasingly apparent with the development of more sophisticated ocean observation instruments. Broad-scale surface movement patterns are readily seen with various satellite imaging systems, while vertical movements can be detected using a variety of devices that can be deployed on the ocean floor, moored in midwater or towed by vessels. Along with the improved understanding of hydrodynamic patterns and processes has come greater ability to accurately model these patterns. This is the environment in which all marine organisms spend their lives.

Ocean movement becomes most complex near coastlines as this is where the forces moving parcels of water come up against the relatively immovable substratum and shoreline (e.g., shelf edges, reefs, banks, islands, headlands, and beaches). This interaction creates upwellings, refraction and breaking of waves, and transport of sediments via long-shore currents. River discharge introduces less saline water into oceanic waters. It first floats above the more saline layers, but then slowly mixes via eddy diffusion. Discharge from large rivers, such as the Orinoco in the Caribbean, can generate a plume of low-salinity surface water that extends thousands of kilometers out from the river mouth, and transports sediments, nutrients and pollutants, as well as dispersive phases of some organisms across those distances. On coasts lacking rivers, there may be extensive, but more diffuse discharge of fresh water (and associated nutrients and pollutants) via surface run-off or groundwater. In many reef regions, coastal landscapes are made up of heavily eroded limestone (often fossil reefs), riddled with underground streams that can discharge large quantities of freshwater several kilometers out from shore. This creates upwellings that are sometimes visible from the surface. Tidal patterns, which are essentially slow period waves, are also distorted by interactions of the water mass with shallow bathymetry or a shoreline. This interaction results in variations in tidal height and timing from place to place along coastal areas. Tides alter local sea level on a regular diurnal cycle, the extent and pattern of which depend upon the location, and these alterations can modify patterns of water movement due to currents and waves as water becomes alternately deeper or shallower. It is the integrated result of each of these separate processes that determines the actual movement patterns of water near a reef or coast, and the manner in which water moves will determine the patterns of connectivity amongst locations.

2.2 Most marine organisms have pelagic larvae

With the exception of some large predators, marine organisms of reefs and other coastal habitats are relatively sedentary throughout the majority of their lives. While larger whales and sharks, and some turtles, can travel distances on ocean basin scales, many common reef sharks and larger groupers spend their lives moving kilometers rather than hundreds of kilometers. There are also numerous small reef fishes that remain within the space of an average living room for an entire lifespan. For example, many small gobies that are commensals on branching acroporid corals, and some damselfish that shelter among coral branches, spend their lives within the immediate vicinity of a single coral colony. In addition to these mobile but relatively sedentary species, reef environments feature a wide range of species that are sessile – the corals themselves, and a wide variety of taxa including tube worms, sponges, barnacles, ascidians, and algae permanently attached to the substratum.

This sedentary or sessile lifestyle is abandoned during early life as the great majority of reef species experience pelagic larval stages and produce pelagic eggs. When eggs are shed into the water column, and larvae remain in the mid-water layers for days to weeks, extensive dispersal is very likely. Indeed, a widely accepted argument for why reef organisms produce pelagic larvae is that this is essential for dispersal. In a world which changes over time, the organism that is more capable of dispersing offspring is most likely to persist because no site remains permanently suitable for occupancy by any particular species.

Message board

- The complexity of ocean movement has become increasingly apparent with the development of more sophisticated ocean observation instruments.
- The manner in which water moves will determine the patterns of connectivity amongst locations.
- Most marine organisms of reefs and other coastal waters are relatively sedentary throughout the majority of their lives. This sedentary or sessile lifestyle is abandoned during early life as the great majority of reef species experience pelagic larval stages and produce pelagic eggs.
- In a world which changes over time, the organism that is more capable of dispersing offspring is most likely to persist because no site remains permanently suitable for occupancy by any particular species.

2.2.1 Spawning on that special night of the year

Since water movement patterns vary through time, for organisms that place their eggs or larvae into the water column there will be some times that are better than others to do this – eggs deposited at those times will be favored either because they will be dispersed along better trajectories or because they will suffer less predation en route. This, and the associated fact that reproductive effort is normally more successful when members of the same species reproduce at the same time, has resulted in many species exhibiting quite precise timing of spawning activities. These events are frequently tied to tidal cycles (spawning typically occurs as tides begin to ebb – this facilitates eggs being taken away from the reef and its hungry planktivores), including monthly peak spring tides and sometimes the most extreme spring tides of the year. The mass spawning of Great Barrier Reef corals is a well-known example. Here, the majority of broadcast spawning species time their spawning so that it occurs the same one or two nights a year, usually 4-5 nights following the November new moon, and the strongest spring tide of the year. Sometimes, there is a smaller spawning event one month later.

Figure 5. The main cues for spawning appear to be ocean temperature, the lunar cycle and tides. On calm days following a mass coral spawning event, spawn slicks (and thus larval dispersal) can be tracked from the air. Photo: Charlie Veron

Some fish species spawn daily throughout much of the year, with spawning occurring at the daytime high tide. Other species show semi-lunar or lunar cycles of spawning once or twice a month, again over several months. Still others are known to spawn during a 2-3 week period at a specific time of the year (usually centered around strong spring tides). Among organisms which brood eggs, such as damselfishes and some crustaceans, the hatch of eggs is closely timed. In several damselfish species it has been confirmed that egg hatch occurs shortly after dusk during the spring tide. In such cases, spawning is also closely synchronized, but at a time which results in egg release at the most opportune time.

2.2.2 Larval behavior

This section briefly reviews the biology of larval stages. Far from being "embryonic" or "developing" organisms, larvae are fully functional, well adapted to pelagic life, and selected for abilities which allow them to find suitable juvenile habitat at the end of larval life.

Pelagic eggs behave much like small particles with a set buoyancy. On calm days, corals eggs are positively buoyant and can form a visible scum at the waters surface. Newly hatched larvae are usually quite limited behaviorally, but not incapable. For example, coral planula larvae are able to modify buoyancy, thereby moving higher or lower in the water column, and perhaps able to take advantage of current patterns at specific depths. Among fish, newly hatched larvae are both physically weak and small enough that water viscosity becomes a major factor in determining sinking rates or mobility. Many possess greatly elongated fin rays or other filaments that likely function to impede sinking through this viscous medium (Leis 1991).

Figure 6. A Caribbean spiny lobster (*Panulirus argus*) larva. These long-lived larvae spend over six months in the plankton, during which they are potentially dispersed thousands of kilometers. Yet, recent connectivity research shows that their vertical migratory behavior may reduce this dispersal to a few hundred kilometers, which in turn may double their successful settlement in coastal nurseries. Photo: Mark Butler

Even when quite young, larvae can be found at specific depths (and change depth according to time of day and age). This indicates that they are capable of adjusting buoyancy and can thereby move vertically within masses of water. However, coral reef larvae do not remain small and behaviorally limited. Although they are largely at the mercy of water movement at early stages, as they grow they develop limited locomotory capacity and an ability to control buoyancy permitting vertical movement, potentially permitting selection of water masses moving in specific directions. While most reef fish species have larval lives that last about one month, some remain in larval form for up to three or four months. Surgeonfish larvae, at the end of their 2-3 month larval life, can swim at speeds of 36 to 42 cm per second. When maintaining 13.5 cm per second, they can continue swimming for over 194 hours without food, effectively covering a distance of 94 km (Stobutzki and Bellwood 1997, Hogan et al. 2007). There is also some evidence that they can swim in specific directions, changing orientation according to particular cues.

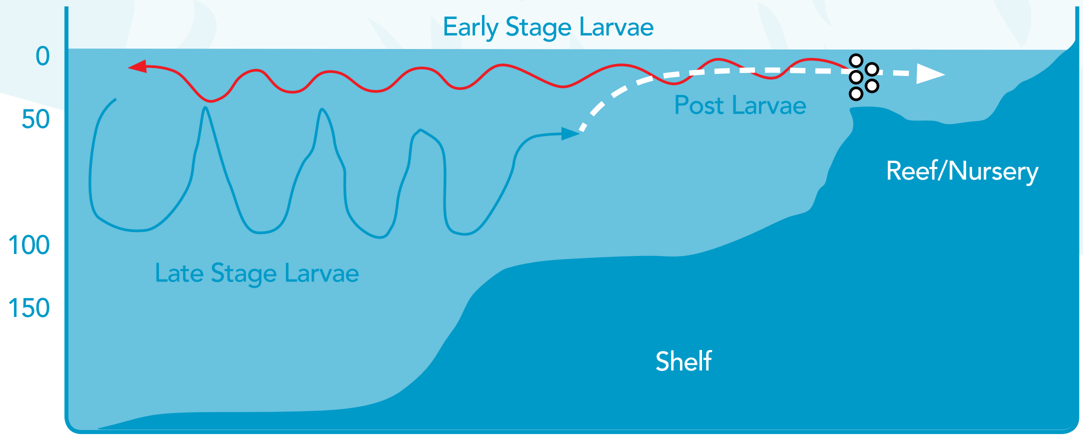


Figure 7. This figure summarizes the spawning and larval/postlarval dispersal and behavior of Caribbean spiny lobster (*Panulirus argus*), and indeed most spiny lobsters. Larvae hatch from eggs that are carried by adult females to reef edges at night while falling tides disperse the hatched larvae offshore (white circles). Early stage larvae are attracted to light, so remain in the surface waters (< 50 m) although they move up and down in the water column each day in response to light (diurnal or diel vertical migration). Late stage larvae avoid light, and remain in deeper waters (> 50 m), an age dependent behavior referred to as "ontogenetic vertical migration", but also engage in diurnal vertical migration with greater amplitude because they are stronger swimmers. Near continental shelf edges, larvae metamorphose to the last stage puerulus postlarvae. These larvae are transported by tides but also swim towards coastal nurseries following chemical signals. Credit: Mark Butler

Fish are not the only reef organisms that show remarkable changes in behavioral ability during larval life. The Caribbean spiny lobster (*Panulirus argus*) passes through more than twenty moults over its long six month larval life, during which its preference for depth and pattern of daily vertical migration changes as it develops (Goldstein et al. 2008). The final larval stage, the puerulus postlarva, is a non-feeding, rapidly swimming phase capable of swimming for 2-4 weeks at speeds up to 15 cm per second. It does so while negotiating a path that can be tens of kilometers long from the open ocean to vegetated coastal nurseries, which it detects using chemical cues (Goldstein and Butler 2009).

2.2.3 What larvae see, hear, smell, and taste – the cues to finding reefs

A dispersive phase would not be very adaptive, nor make sense, if larvae were to only drift passively or swim in random directions. Coral reefs are not common and occupy a mere 0.1% of the world's oceans, and we should expect that the larvae of reef and other inshore species will have well developed sensory capabilities able to detect suitable habitat by the time they complete larval life. However, identifying these sensory capabilities is not simple because late-stage larvae are at a period where development is very rapid, and many undergo substantial metamorphosis as soon as they reach inshore habitat. This makes studies of their physiology and behavior very difficult because they cease being larvae almost as soon as they are caught! Nevertheless, scientists have been able to make some progress in this area of research.

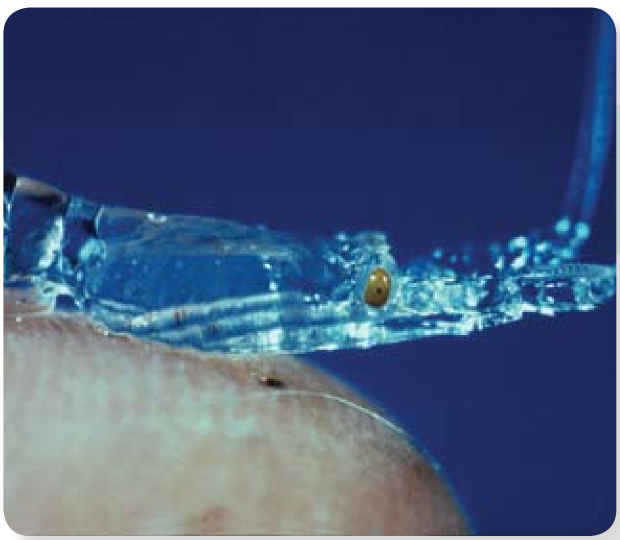


Figure 8. The final peurulus postlarval stage of the Carribean spiny lobster (*Panulirus argus*). The lobster larvae uses chemical and pressure cues to locate back-reef nurseries as it swims from the open sea to complete its complex life cycle. Photo: William Herrnkind

Even towards the later stages of larval life, coral planula larvae only have limited locomotory ability. However, they do show discriminatory capacity and clear preference for some substrata over others as sites for settlement. This discriminatory capability, also common in other invertebrates (e.g., barnacles and oysters), is due to their ability to respond to specific chemical cues from suitable substratum in order to successfully settle and attach permanently.

Among fishes, there is limited but growing evidence that they can use hearing and odor in the selection of suitable juvenile habitat. This is largely based on behavioral research where larval fish are given a choice and subsequent responses are observed. Some of this work has involved placing simple floating Y mazes in marine study sites, and later putting larvae into the structure to test whether they swim in the direction of the reef. This would infer whether they are able to detect the reef's presence.

Some physiological studies have confirmed that late stage larvae have "ears" that detect noise (chiefly breaking waves) created by reefs. Recent studies by Gerlach et al. (2007) in the southern Great Barrier Reef, have very convincingly demonstrated that larval cardinalfishes (Apogonidae) and damselfishes (Pomacentridae) are able to detect the odor of reef water and actively choose to swim in water from their home reef rather than in water of the open ocean or neighboring reefs (Atema et al. 2002, Gerlach et al. 2007). It has also been found that this ability is used differently by the two species. For example, genetic analyses of the population structure of several nearby reefs demonstrated that the Doederlein's cardinalfish, *Ostorhinchus doederleini*, and not the neon damselfish, *Pomacentrus coelestis*, shows strong homing behavior to particular reefs (Gerlach et al. 2007). Presumably, the damselfish uses its home odor recognition to discriminate reef water from non-reef water to help find its way back to reef habitat. Both these families care for their eggs, and the offspring only become pelagic at hatching, the time at which they are first exposed to environmental odor and have a functional olfactory organ. Therefore, this ability to recognize and respond to home odor may be a form of imprinting. Similar imprinting may cause the strong attraction of clownfish larvae, *Amphiprion percula*, to the odor of tree leaves, which is thought to help them identify a preferred inshore settlement habitat (Dixson et al. 2008).

It should not be surprising that cardinalfish show selective preference for the home reef. Much earlier research, also done in Australia, has shown that damselfish of the genus *Dascyllus*, which exist as small groups occupying single heads of branched coral, are capable of discriminating and favoring coral colonies containing conspecifics rather than other species of *Dascyllus*, or no fish at all, when settling to juvenile habitat at night. Related experiments using the Y maze showed that fish could detect and respond to the odor of conspecifics (Sweatman 1988).

Figure 9. The larval phase of coral reef fishes was once considered a black box. Larvae come in all shapes and sizes and seem to be designed for going places, but what they do and where they go in the 3-dimensional oceanic environment has been shrouded in mystery. Through the use of new technologies, these mysteries are rapidly being solved. Credit: C.M. Guigand & R.K. Cowen, Rosenstiel School of Marine and Atmospheric Science, University of Miami

While there is clearly an enormous amount to learn about how pelagic larvae find home reefs, the results of investigations to date are clear. Dispersive pelagic larvae do not drift aimlessly in the ocean. They use their varying behavioral and sensory capabilities to minimize the extent of dispersal, and in many species, are active agents in ensuring successful return to reef habitat, and to specific microhabitats that will be suitable for juvenile life.

2.2.4 Connectivity through larval dispersal

The fact that most reef species experience a pelagic larval phase means that the majority of adult reef organisms exist as local breeding groups (local populations) that occupy suitable habitat and are predominantly inter-connected by larval dispersal. On scales of tens of kilometers or less, there is considerable mixing as larvae disperse from one population to another. However, on scales of hundreds of kilometers, populations are largely isolated demographically (though still linked genetically). The details of the patterns of dispersal and larval exchange vary among species, so that some taxa disperse only over quite limited distances, while others disperse more widely. At present we only have limited information detailing these differences, yet it is already clear that different species breeding at the same time, and in the same location, can show markedly different dispersal patterns during larval life. This can be attributed to variations in larval phase duration, behavior, and sensory capabilities (Gerlach et al. 2007).

The details of the patterns of dispersal and larval exchange vary among species, so that some taxa disperse only over quite limited distances, while others disperse more widely.

Some important conclusions can be drawn with respect to larval dispersal. The first is that connectivity amongst populations of reef species is primarily, or (for sessile species) exclusively, due to dispersal during larval life. Secondly, for the majority of reef species that have been studied, demographic connectivity has been shown to act on scales of up to tens of kilometers, rather than on scales of hundreds of kilometers or more. Therefore, the concept of a demographically well-connected population across the Caribbean, or along the length of the Great Barrier Reef, does not apply. Genetic (evolutionary) connectivity operates at larger spatial scales because the rare individual larva will occasionally get transported far beyond its usual dispersal range. If MPAs are intended to play a role in fisheries management, the smaller scale of demographic connectivity should be taken into account in the design of MPA networks. This type of connectivity can also be informative when considering extensive reef destruction caused by bleaching, crown-of-thorn outbreaks, and major hurricanes, because it defines the distance over which natural re-seeding of reef habitat is likely to occur.

Message board

- The fact that some times are better than others to place eggs or larvae into the water column, and the associated fact that reproductive effort is normally more successful when members of the same species reproduce at the same time, has resulted in many species exhibiting precise timing of spawning activities.
- Many reef organisms show remarkable changes in behavior and appearance during larval life.
- Among fishes, there is limited but growing evidence that they can use hearing and odor in the selection of suitable juvenile habitat.
- Many reef organisms show discriminatory capacity and clear preference for some substrata over others as sites for settlement. They often do this by responding to the chemical characteristics of a surface.
- Connectivity amongst populations of reef species is primarily, or sometimes exclusively, due to dispersal during larval life.
- For most reef species, demographic connectivity has been shown to act on scales of up to tens of kilometers, rather than on scales of hundreds of kilometers or more. If MPAs are intended to play a role in fisheries management, the smaller scale of demographic connectivity should be taken into account in the design of MPA networks.

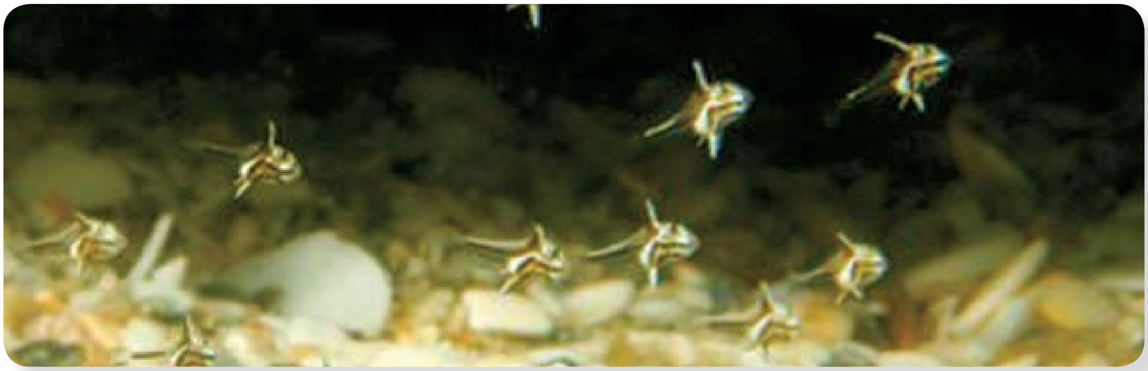
2.3 Many marine organisms move about after larval life is over

The largest part of the lives of most marine organisms is not spent as larvae at sea, but as juvenile and adult forms, associated with the bottom in various manners throughout life. Life after settlement from the larval phase varies developmentally and ecologically among different species. If not eaten by a marine predator or man, individuals of many species can survive for decades and occupy many different habitats throughout life.

2.3.1 Settlement and recruitment

The transition from a pelagic oceanic environment to a benthic reef habitat, during which the relationship between the organism and its environment changes radically, is a particularly dangerous phase in any marine organism's life. Settlement of larvae to reef habitats occurs in many different ways among fishes and invertebrates and is typically sporadic, nocturnal and/or cryptic. This parameter is difficult to measure so ecologists tend to sample recruitment (animals which settle and survive) quite soon after settlement. The term recruitment, in the broadest sense, means the addition of new individuals to populations or to successive life-cycle stages within populations. In more specific terms, 'recruitment' can have several different meanings:

Larval Recruitment: New individuals being added to a population by arrival of incoming larvae to bottom habitats. Figure 10a. Newly settled larvae (8-12 mm). Photo: D.B. Snyder



Inter-habitat Recruitment: Individuals arriving at a later-stage habitat - not the first larval settlement event, but a later habitat shift. Figure 10b. Photo: Gerald Nowak/WaterFrame/Specialist Stock

Fishery Recruitment: Individuals reaching a size at which they are first retained by specified fishing gears (i.e., when they enter the fishery). This can occur many years and habitats after larval recruitment. Figure 10c. Photo: Photoshot/VISUM/Specialist Stock

Credit for figure: Kenyon C. Lindeman

Following the settlement stage, movement between habitats may happen one or more times during the development of some species, including grunts, and sometimes never in others like damselfishes.

2.3.2 Movement between habitats and coastal development

Many coastal areas contain a wide array of habitats, including vegetation, hardbottom, or reefs, which occur along shallow to deep gradients along coastal shelves. Some remarkable connections exist among marine animals and habitats, especially when considering the life cycles of the fishery species we humans feed upon. For some species, a single habitat within a complex seascape is sufficient to complete an entire life cycle. Many other species however, move between habitats at different temporal and spatial scales. Some habitats are critical to the early developmental stages, survival and growth, of many species of fish, lobster, and shrimp, while others serve as spawning and feeding grounds. Marine organisms may also make repeated migrations between habitats on various time scales, especially daily and seasonal. Daily shifts typically involve nightly feeding migrations between feeding and resting habitat every 12 hours. For example, daily movement and habitat use patterns have been shown for goatfish (Mullidae) and grunts (Haemulidae), which undertake crepuscular foraging migrations between daytime reef and nocturnal sand flat habitats (Meyer et al. 2000). In some fish species, these daily shifts can lead to direct transfer of nutrients between seagrass feeding habitats and mangrove and reef resting habitats.

Some remarkable connections exist among marine animals and habitats, especially when considering the life cycles of the fishery species we humans feed upon.

Adult population size depends upon the successful survival of developing, bottom-associated early life stages. Even under the best natural conditions, individuals at these stages are often subject to extremely high mortality rates. Predators frequently feed on nocturnally migrating prey, and any human-caused disruption to pathways between habitats can increase mortality rates. Access to shelter and food provided by critical inshore habitats is essential for survival. Unfortunately, important habitats (e.g., nurseries or those visited for daily feeding) used by the youngest fishes and other reef organisms are often in shallow areas that are vulnerable to human impact.

Figure 11. Spiny lobster (*Panulirus argus*), the most important fishery resource in the Greater Caribbean, changes habitats several times during growth. Larvae settle in shallow vegetation while juveniles migrate to hard bottom habitats, and eventually to deeper reefs. Other important species in the Caribbean that move among habitats, often into deeper waters, over the course of post-settlement life include groupers, snappers, conch, sea turtles, porgies, parrotfishes, grunts, and jacks. Photo: Mark Butler

Figure 12. The Queen conch (*Strombus gigas*) is an important fishery species in the Caribbean. The positive effect of reserves is not confined within the "borders" of a reserve because conch larvae produced within reserves have been found to drift outside of reserve boundaries and seed surrounding areas (Stoner et al. 1996). Photo: Ron Schaasberg

Many coastal areas in coral reef regions are being developed for tourism with a focus on rapid and speculative coastal growth. The Caribbean for example, represents some of the world's most concentrated coastal tourism, with places like Cancun, Mexico, at the doorway to the southeast U.S., processing 5 million tourists annually.

Coastal development, pollution and natural events can work together to alter or damage important inshore habitat used by developing fishes, lobster and other organisms, e.g., making inshore habitat no longer suitable for juveniles and disrupting vital pathways between these and offshore habitats. Moreover, any negative impact during an organism's early life stages could indirectly affect the abundance of adults and the food webs they are embedded in. In addition, although not well studied, modest alterations to coastal environments may disrupt daily or seasonal migratory patterns. This could lead to reduced populations or local extirpation of fishery species which could in turn impact fisheries that operate in deeper waters where environmental conditions appear unchanged.

Protection of crucial habitat required by developing fish species can be a very cost-effective management approach for enhancing fishery production. When an MPA is designed to protect even just one or a few species, it is critical to have information concerning the specific migration patterns and habitat requirements of that species. In order to be effective, the MPA or MPA network must be large enough to encompass all these habitats as well as the daily and seasonal migration routes of the species they aim to protect.

In nearly all regions, the use of the Environmental Impact Assessment (EIA) procedure to assess the potential threat of coastal development has been inadequate and poorly managed. Causes for this include:

Figure 13. Dubai, UAE. Most marine fishes and invertebrates use more than one habitat throughout their lives. Coastal development can make inshore habitats no longer suitable and disrupt vital pathways between these and offshore habitats. Photo: iStockphoto

- Conclusions are not always based on sound scientific information;
- Absence of independent, third-party peer-review of documents;
- No control over natural spatial or temporal variations;
- Lack of community participation;
- Poor coordination.

Given the often poor quality of impact assessment, it is not surprising that many projects proceed despite having severe deleterious impacts on connectivity, and ultimately the ecological functioning of coastal marine systems. Political pressure that encourages development and corruption in the approvals process is simply making this situation worse.

Box 2. *Turbinaria* in French Polynesia – connectivity and colonization via dispersal of adults

While larval dispersal is of primary importance to reef species, dispersal of detached adult organisms through passive drift on ocean and wind-driven currents or by hitching rides on other drifting organisms can also play an important role in maintaining connectivity and colonization of new locations. Individuals which have already reached adult stage have higher survival rates than larval forms. Also, since they are reproductively mature, they can establish new populations immediately upon arrival in a new location. Adults are also generally larger and more evident to reef managers than minute larval forms, and their arrival into a new area may be more obvious. It is important to remember that invasive or nuisance species that disperse in this manner can also pose a serious threat to reef ecosystems.

Figure 14. A detached, floating frond of the tropical brown alga *Turbinaria ornata* in the lagoon of Moorea, French Polynesia. Photo: Hannah L. Stewart

For example, the current spread of the alga *Turbinaria ornata* across French Polynesia, shows the potential for connectivity achieved by adults and the challenges this can pose to reef managers. This large widespread Indo-Pacific macroalga traditionally occurred in only a few areas within the French Polynesia. However, since the early 1980s it has been spreading and becoming so abundant that it is now considered an invasive species and is displacing coral in many reefs throughout this region (Stewart 2008).

Thalli of *Turbinaria* grow attached to reefs, but as they reach sexual maturity, they become buoyant and their attachment to the substratum weakens (Stewart 2006). Following storms, large rafts of detached thalli are blown away and drift from island to island (Martinez et al. 2006). Detached thalli are able to maintain fertility and viability even after floating for 3 months (perhaps even longer) (Stiger and Payri 1999). During this time, fertilization events occur (motile male gametes find eggs in female thalli) at least once a month. Young germlings are released from the parent plant, and then become established successfully across the reef, creating new populations of the alga. Examination of the genetics of *Turbinaria* reveals that there is very little genetic differentiation across the French Polynesia, perhaps a result of the high connectivity between populations maintained by this drifting dispersal mechanism.

It has been observed that a diverse assemblage of invertebrates and algae drift passively along in association with rafts of *Turbinaria* (Stewart and Meyer, unpublished data). As large floating rafts of *Turbinaria* are relatively recent in French Polynesia, it may present a new mechanism of connectivity in the region. Researchers have only begun investigating the potential impact on the connectivity of these associated species.

Increasing numbers of this alga are causing severe problems. In addition to shading, abrading and outcompeting coral for reef space, floating thalli damage fishing nets and fish harvest, clog motors, rot on beaches, and are negatively affecting the tourism industry. The impact on reef nutrient dynamics due to the increase in algal biomass has yet to be determined. Researchers have been searching in vain for economic incentives to harvest this alga (e.g., cosmetic or pharmaceutical), and local fishing groups are beginning to organize *Turbinaria* removals in an attempt to abate its spread. As reefs increasingly face shifts from coral to algal dominated systems, this type of whole adult connectivity, that is characteristic of many algae, could become increasingly important to consider in coastal management.

2.3.3 Spawning migrations

During yearly spawning migrations, the adults of many grouper, snapper, and other species, undergo large scale oceanic movements. Some undergo migrations of hundreds of kilometers, although most travel much shorter distances; this can involve weeks of travel between differing habitats until suitable spawning sites are reached. These annual events utilize important bottom habitats, and specific sites and routes, in order to broadcast egg and larval stages that are largely independent of the reef during pelagic stages. The resulting spawning aggregations represent some of the most concentrated numbers of adult reef fish that can be seen around the world. Not surprisingly, these groups are very susceptible to fishing pressure. The fate of eggs and larvae generated from these migrations can substantially determine the level of connectivity of fishes among differing habitat systems. The relative degree of such connectivity is a critical determinant in the population structure of a target species, and a key factor when developing coherent spatial management policies.

Box 3. Spawning aggregations and connectivity

With respect to spawning aggregations, connectivity occurs through two distinct mechanisms:

1) The movement of fish as eggs and larvae from a spawning aggregation site to settlement sites via dispersal;

2) The movement of adults from normal residence sites (= "catchment area") to spawning sites.

Both must be studied to determine the relationship of a particular spawning aggregation or site to its surrounding area.

Figure 15. Some fish species such as these Nassau groupers, *Epinephelus striatus*, gather at specific spawning grounds each year where they are extremely vulnerable to overfishing. These spawning aggregation sites should be incorporated in no-take reserves to protect these fish at this vulnerable stage. Photo: Enric Sala

Figure 16. This mature Sweetlips (*Plectorhinchus albovittatus*) has a fully ripe ovary that almost fills its body cavity, but was captured at a spawning aggregation site in Palau. Larger, older fish are notably fecund because their larger body cavities permit a great expansion of ovary size as eggs mature. Photo: Patrick L. Colin

Message board

- Settlement of larvae to reef habitats occurs in many different ways among fishes and invertebrates and is typically sporadic, nocturnal and/or cryptic.
- Remarkable connections exist between animals and habitats. These connections are central to the ecological functioning of coastal habitats and to the production of their environmental goods and services.
- Coastal development, pollution and natural events can work together to alter or damage important inshore habitats used by developing fishes, lobster and other organisms, e.g., making inshore habitats no longer suitable for juveniles and disrupting vital pathways between these and offshore habitats.
- When an MPA is designed to protect even just one or a few species, it is critical to have information concerning the specific migration patterns and habitat requirements for those species.

Section 3
Using connectivity in management

In this section you will find:

Marine protected areas

MPA networks

What MPA networks cannot do

The value of coastal marine ecosystems

Marine park managers, Akumal, Mexico.
Photo: Miguel Angel Maldonado, Centro Ecológico Akumal

3. Using connectivity in management

3.1 Marine protected areas

Faced with widespread decline in ocean health, many nations are turning to marine protected areas (MPAs) as a tool to manage the most important marine habitats and species. Many "types" of MPAs have been developed to serve different purposes in diverse ways. They can range from no-take reserves (NTRs), which are small areas where all extractive activities (e.g., fishing) are prohibited in order to conserve target species or sensitive habitat, to extensive marine management areas (MMAs), which have a single comprehensive management plan that often includes spatial zoning to permit different management tools, including NTRs, in different locations. MMAs are an attempt to integrate the management of many species, habitats, and uses within a specific region.

MPAs fill some or all of the following roles:

- Sustain fisheries by providing insurance against stock collapse; act as a buffer against recruitment failure, and possibly also provide centres for propagule and adult dispersal to surrounding fished areas (recruitment subsidy and spillover respectively);
- Conserve marine ecosystems and biodiversity;
- Protect attractive habitats and species on which sustainable tourism can be based;
- Contribute to the scientific knowledge of marine species, communities and ecosystems, by providing relatively undisturbed sites for research, and ecological benchmarks against which to measure human impacts;
- Preserve genetic diversity;
- Protect cultural diversity (e.g., sacred places, shipwrecks and lighthouses).

Figure 17. School of yellow goatfish (*Mulloidichthys martinicus*). NTRs greatly reduce fishing pressure on animals living within their borders and tend to maintain higher population levels of some species. Photo: Robert Steneck

Figure 18. The once abundant Elkhorn coral (*Acropra palmata*) is considered one of the most important reef-building corals in the Caribbean and Florida Keys. It is now listed as an endangered species on the IUCN Red List and in Appendix II of CITES. Since 1980, an estimated 90-95% have been lost due to disease, storms and bleaching. While NTRs can act to protect and enhance habitat and ecosystem recovery they cannot solve all management problems for species such as these. Photo: Robert Steneck

Confusion over MPA terminology complicates the dialogue about whether, when, and how these management tools should be used. Likewise, MPAs having similar names can sometimes differ fundamentally in their effectiveness in protecting habitats and resources. For example, there is a widespread misperception that all MPAs are "no-take" because most are not. Box 4 lists and defines the most frequently used terms that define the various types of MPA used today. The remainder of this section focuses on no-take reserves.

Box 4. MPA Definitions

A bewildering array of names are used for marine protected areas (MPAs). Below, the most common definitions are given with specific focus on no-take reserves and MPA networks.

Marine protected area (MPA)

Any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment (IUCN/WCPA 1994).

A geographical defined area, which is designated or regulated and managed to achieve specific conservation objectives (UN CBD 1992).

According to the IUCN, an MPA also has to follow the IUCN definition for a Protected Area (PA): A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (IUCN/WCPA 2008).

Marine management area (MMA)

These are usually relatively large, legally delineated locations in the (coastal) ocean that are intended to be under active management for purposes of conservation or resource management. They are frequently subdivided, or zoned, to provide for different patterns of management at different locations. Some of their zones are usually no-take fishery reserves.

No-take fishery reserve (NTR)

No-take fishery reserves (NTRs) are also referred to as marine reserves, no-take areas, or ecological reserves. NTRs are a special category of MPA within which extractive fishing activities are regulated (usually not permitted). Within some NTRs, all biological resources are protected through prohibitions of fishing and removal, disturbance, or harm to any living or non-living marine resource, except when necessary for monitoring or research (Lubchenco et al. 2003).

Some NTRs restrict access and/or other activities (e.g., pollution, construction, research, boating and diving) that may adversely impact resources, processes or the ecological and cultural services they provide. Others restrict only extractive activities.

Marine and coastal protected area (MCPA)

Any defined area within or adjacent to the marine environment, together with its overlying waters and associated flora, fauna, and historical and cultural features, which has been preserved by legislation or other effective means, including custom, with the effect that its marine and/or coastal biodiversity enjoys a higher level of protection than its surroundings (UNEP-WCMC 2008). An MMA adjacent to a coast, and associated terrestrial protected areas, would comprise an MCPA.

MPA "network" or "system"

The use of "network" and "system" can be confusing as neither term has a globally accepted definition, and because they are often used interchangeably with the same meaning in the same document. The commonly used definition for an **MPA network** is: a collection of individual MPAs or reserves operating cooperatively and synergistically, at various spatial scales and with a range of protection levels that are designed to meet objectives that a single reserve cannot achieve alone (IUCN/WCPA 2008). Although there are exceptions, the word "system" tends to be used most frequently for terrestrial protected areas, whereas the term "network" is more prevalent when discussing MPAs (UNEP-WCMC 2008).

3.1.1 The no-take fishery reserve

Closing parts of the ocean to fishing, so that fish stocks are preserved, holds great intuitive appeal. In many regions of the world, one of the main arguments used to justify new MPAs is the claim that they help maintain or replenish depleted fisheries stocks in surrounding waters. By prohibiting (or sometimes severely restricting) fishing activities, no-take fishery reserves (NTRs) serve as the only type of MPA which can assist fisheries management, whether by operating singly or as several reserves in an MPA network. Some NTRs may also restrict access and/or other activities, such as development, construction, research, boating and diving.

Since fishing pressure on animals living within NTR borders is greatly reduced, these areas help promote fish survival and reproduction even if the surrounding area is severely over-fished. They also tend to maintain higher population levels of site-attached species and help protect site-attached ecological functions such as spawning aggregations. Furthermore, by serving as refuges for heavily fished species, NTRs can protect overfished species from local extinction. However, none of these effects directly impacts the populations of the fished species in the surrounding area.

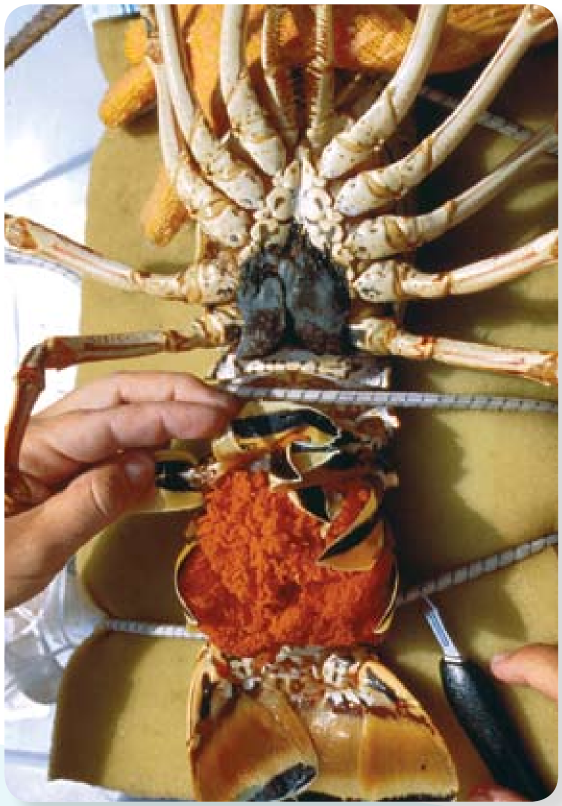


Figure 19. The underside of a female Caribbean spiny lobster (*Panulirus argus*) showing the black, tar-like spermatophore deposited by a male which will fertilize the bright orange eggs attached to her abdomen. In fished areas, small spiny lobsters may produce a few hundred thousand eggs, while large females protected in MPAs can produce millions of eggs in each of several clutches. Photo: Mark Butler

Demographic connectivity in marine populations is key to the fisheries-management role of no-take reserves because it provides a mechanism for reserves to enhance fish production outside borders (Kritzer and Sale 2004). Because of connectivity, reserves may supplement a fishery population in the surrounding fished area if some of the production within is exported as spillover or recruitment subsidy. This argument is often used to convince fishing communities to support the introduction of NTRs, yet supporting evidence remains limited. Unfortunately, it is technically very challenging to demonstrate recruitment subsidy, and for slow-growing late-maturing fishes and invertebrates, any positive effects of NTRs may not be evident until many years after establishment. Hence there is a need for long term protection and monitoring, coupled with well-designed experiments, to quantify spillover and recruitment subsidy if the full benefits of a reserve are to be revealed.

Empirical studies have shown, to varying degrees, four changes inside (Mumby et al. 2006) and/or outside (Roberts et al. 2001, Russ et al. 2003) NTRs that may benefit fished populations outside reserves. These changes include:

1) Increased reproductive output within the NTR because of increases in fish abundance, spawning biomass, mean age, and body size;

2) Higher net export of juveniles and adults to surrounding fished areas (“spillover”);

3) Higher net export of eggs and larvae to surrounding fished areas (“recruitment subsidy”); and

4) Protection and recovery within the reserve of both the habitat and entire ecosystems on which fished species depend.

3.1.2 Protection of a portion of the population

There is some compelling evidence that NTRs help protect animals within borders from the effects of fishing. Any well-managed NTR that is large enough to cover the majority of an individual organism's movements will come to hold denser populations of older and larger individuals. This can be attributed to increased survivorship resulting from reduced fishing impacts. In planning such reserves, consideration should be given to the specific habitat requirements of individuals at different life stages, and the extent of daily or seasonal movements. Ideally, an NTR should also be large enough that a reasonable proportion of target species larvae will complete pelagic life stages and settle within the NTR borders. Even if the NTR confers a good level of protection for individuals inside, if a sufficient area is not covered, the target population inside the NTR may end up depending on reproduction outside NTR borders for replenishment. Overfishing would then lead to declines in abundance both within and outside the reserve.

> *Our relative lack of scientific information on matters such as the correct size, spacing or placement of no-take reserves limits our ability to predict the effects that a proposed no-take reserve will have on surrounding fisheries or biodiversity conservation.*

For this reason, the appropriate size (and sometimes shape) of an NTR should depend upon the geography of a region (presence of required habitat), the hydrodynamics, and the habits of the target species. It follows that an NTR cannot simultaneously be optimal in size and placement for a broad suite of species, unless habits and habitat requirements are similar. However, there is currently insufficient information about this for most reef species so it is not yet possible to dictate minimum size requirements by species. Nor do we yet have enough information on the precise benefits of creating networks of neighboring NTRs, rather than stand-alone reserves. Still, available evidence shows that organisms within NTRs attain greater longevity and larger sizes, which indicates that even small reserves a few hectares in area provide protection for many site-attached reef species. What remains to be discovered is whether these small reserves can continue to sustain viable populations in the face of continued over-fishing beyond borders.

3.1.3 Spillover and recruitment subsidy

Protection of a portion of the fishery population, as insurance against fishery collapse or species extinction, is one benefit of no-take reserves. More important, is if the protected population is able to significantly enhance productivity of the fished populations beyond reserve borders. Connectivity should lead to this enhancement through sustained net export of target species biomass from the reserve to surrounding areas. The fact that this net export should be sufficient to also compensate for the loss of fishing area is also important, and frequently forgotten. However, precise assessment of such export functions is technically and logistically difficult, and recruitment subsidy has rarely been demonstrated (Russ 2002, Sale et al. 2005).

Although evidence for spillover is increasing, the mechanisms that encourage adult fish movement from reserves to fished areas remains poorly understood (Abesamis and Russ 2005). Spillover is often assumed to be driven by density-dependent processes. Density-dependent movement occurs when the rate and directionality of individual movement changes with population density (Sutherland et al. 2002). This is often thought to be driven by high rates of aggressive interactions within denser populations. To cause spillover by this mechanism, measurable density differences between the reserve and surrounding area are necessary, and it is also likely that the density within the reserve needs to approach the carrying capacity of the local environment before spillover can occur. Spillover is generally assumed to be a very local process that can enhance fishing success close to no-take reserve boundaries, but not far from them.

A special situation somewhat analogous to spillover occurs if the reserve is established over the nursery habitat of a species. In such a case, enhanced survival of organisms would be expected as a result of habitat protection (e.g., from destructive fishing gears, such as traps or trawls) than from lack of fishing pressure. Only in instances where a fishery targets juveniles, or takes these as by-catch, would direct protection from fishing lead to enhanced survival. Still, so long as enhanced survival results, a protected nursery habitat would likely yield a greater number of fish that reach an age where they are able to leave nursery grounds for adult habitat. This would lead to enhanced production out of the reserve to support a fishery that targets mature fish, thereby having a more widespread positive impact on fishing success when compared to the effect of spillover between protected and unprotected patches of the same (adult) habitat.

Recruitment subsidy should affect fishing yield at further distances from reserve boundaries. Denser populations of larger (and therefore more fecund) individuals inside a reserve can be expected to produce larger numbers of larvae, many of which will disperse beyond the boundaries of all but the largest reserves. There have been few experimental demonstrations of dispersal kernel shapes to date, but in theory, it should be possible to use such data on a target species, together with data on local geography and oceanography, to calculate the optimal size and spacing of individual and networks of no-take reserves. Until the science progresses to this point, we are limited to making estimates, such as that for typical reef fish species where demographically important recruitment subsidy might extend from 10-30 km beyond the borders of a no-take reserve.

The spatial scale of connectivity and its resolution is a critically important issue for management of reef fisheries using NTRs or NTR networks. The resolution of connectivity also has important implications when trying to gain a fundamental understanding of the structure and dynamics of these communities, and of the appropriate scales at which to mount management interventions. For example, if larvae are predominantly retained at local (kilometer) spatial scales, local scale management may be effective, but if larvae disperse further, management will need to be similarly scaled up if it is to be effective. The task of defining dispersal patterns for important fishery species will demand carefully designed experiments that include spatially large-scale sampling of organisms. Such experiments will be most feasible if they are implemented jointly by managers and scientists in the context of adaptive management.

> *To conserve biodiversity, regardless of the particular history of establishment, an effective management program should be put in place across the full network, including the space between NTRs, and should encompass the coastal marine ecosystem and land areas that affect it.*

3.2 MPA networks

Because of connectivity, a set of MPAs (usually NTRs) in a given region may operate ecologically as a network with individual organisms dispersing from one NTR to the other as well as from one NTR to the surrounding area. Critical for success, the details of dispersal patterns will help determine the appropriate scale of an NTR network. That is, NTRs within a network must be close enough so that there is some exchange of individuals. Moreover, it can be expected that an NTR network will be functionally more effective than an equivalent number (and area) of NTRs operating in isolation. This expectation exists because demographic connectivity among NTRs within a network presumably confers resilience to individual populations, in the same way that dispersal processes within a metapopulation confer greater resilience to local subpopulations.

MPA networks have been widely advocated for the conservation of marine biodiversity, protection against natural and human disturbances including overfishing, and as a tool to increase resilience of coastal ecosystems and their ability to adapt to climate change. However, the theory supporting their benefits is still incomplete, and in any event, the lack of comprehensive data on the connectivity of target species would preclude formal application of theory into network design. At present, it can only be anticipated that benefits occur, and that networks should be planned so that neighboring NTRs are separated from 10-30 km apart; an ideal scale for most target reef species (this is essentially the same approach to be taken when establishing single NTRs for fisheries management).

In practice, MPA networks develop in one of two ways: as separately established and managed NTRs augmented with additional NTRs interspersed as needed, or as regional-scale marine management areas zoned to include an appropriate number and spacing of NTRs. To conserve biodiversity, regardless of the particular history of establishment, an effective management program should be put in place across the full network, including the space between NTRs, and should encompass the coastal marine ecosystem and land areas that affect it.

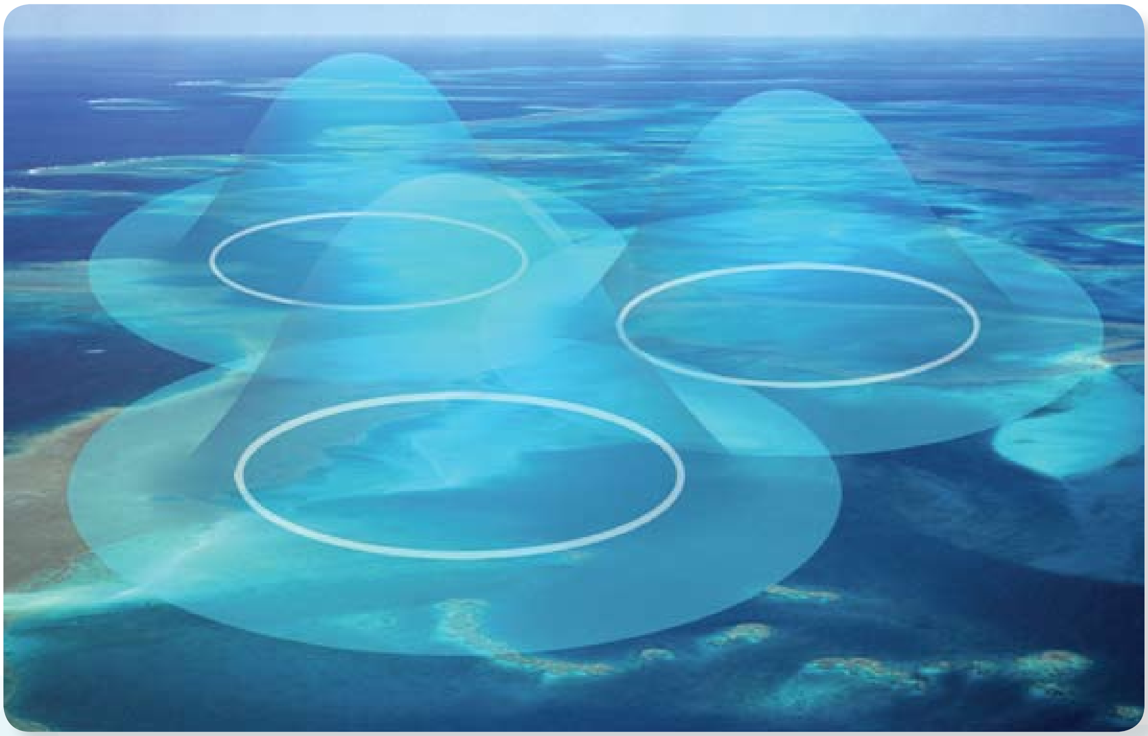


Figure 20. The size and spacing of no-take reserves with respect to dispersal distance of the species of interest. The white circles represent reserve boundaries while the dome shape represents the pattern of larval dispersal (higher numbers of larvae occur at the birthplace, i.e., within the reserve, and gradually decrease in number with distance). Reserves intended for:

1) Conservation: should be large enough to retain a substantial portion of larval dispersal to ensure adequate self-recruitment;
2) Fisheries enhancement: should be sized and spaced so that a significant proportion of larvae can disperse to surrounding fished areas. If reserves are to function as a network they must be spaced close enough to ensure connectivity via larval dispersal.

Credits: Photo, Commonwealth of Australia (GBRMPA); Graphics, Zeke Pesut

3.2.1 Metapopulation dynamics, sources and sinks

Coral reefs are inherently patchy and fragmented habitats, and many reef organisms exist as spatially distinct local populations connected by an unknown degree and distance (Kritzer and Sale 2004). The level of connectivity among local reef populations will essentially determine whether they function as isolated "almost closed" populations, as metapopulations where the dynamics of separate populations are buffered by recruitment subsidy from nearby populations, or as spatially discontinuous but otherwise unitary populations with no particularly interesting demographic substructure. Of the three, metapopulations are the least understood, but in theory possess increased resilience at the single local population level because of the exchange of individuals. Much of the developing theory of MPA networks hinges on the expectation that connectivity among MPAs within a network confers resilience comparable to that which exists within a metapopulation. This resilience should make the MPAs within such networks less susceptible to decline if overfishing, or other factors, impact populations outside MPA borders. In general, connectivity between subpopulations should increase in a species-specific way as distance decreases. Knowing the level of connectivity among a set of nearby populations is important for understanding the demographics of each population. For dispersing organisms, the spatial arrangement of populations and/or prevailing patterns of water movement may make certain populations consistent sources or sinks. Sink populations are those that fail to replenish themselves and are only saved from extinction by the dispersing surplus of other populations (sources). It is not uncommon in discussions of metapopulation theory to assume the presence of both population types. It is also likely, however, especially when hydrodynamic patterns are variable, that few if any populations can be permanently labelled as sources or sinks. Still, source populations should be considered intrinsically more important to the functioning of a metapopulation because they are self-sustaining and are best able to subsidize recruitment to other populations.

Determining the factors that determine whether an NTR functions as a source or sink population for a particular species is directly relevant to the science and design of marine reserve networks. Currently, these factors have not yet been clearly identified, and verifying whether an NTR functions as a source or sink will require sampling of species production and dispersal over several years. At this stage it can only be stated that certain preconditions may favor source or sink status. For example, a consistent physical oceanography, which might change seasonally but consistently through time, is essential for permanent source or sink status, i.e., uniform oceanography leads to consistent patterns of larval dispersal. In a variable oceanographic setting, most populations likely spend some time as sources. Also, for most habitats, an up-stream location with a consistent oceanography should ensure source population status. However, this will not guarantee the strength and viability of a source. On the other hand, although not always the case, a down-stream location permits the existence of sink populations. Also, a population occupying marginal habitat, or consistently experiencing higher than usual fishery-independent mortality, is more likely to be a sink.

Figure 21. Buoys can be used to delineate the borders and zones of a marine reserve. Photo: Miguel Angel Maldonado, Centro Ecológico Akumal

Despite our current inability to specify status, there is a general consensus on how best to maximize the effectiveness of an MPA network in a region where source and sink populations are present. This consensus has resulted in a set of “principles” that are reasonable, but have not been validated, and are virtually impossible to apply:

1) A network in which reserves are placed in source habitats will be superior to one that places reserves at random locations or in sink habitats;

2) The importance of source-sink population structure is increased if the MPA network displaces rather than reduces fishing effort;

3) Appropriate siting of MPAs becomes increasingly important as the proportion of the environment consisting of poor-quality (sink) habitat increases;

4) If the environment contains directional currents, the spatial location of reserves will be critical to population enhancement.

If reef species are distributed as consistent source and sink populations, this arrangement should be recognized when setting up an MPA network. Just as in instances where lack of knowledge of dispersal patterns for target species precludes a precise and objective set of decisions on NTR size, so too the lack of information on source-sink dynamics, or even whether consistent source-sink dynamics exist, precludes objective decisions on NTR placement in a network. Nevertheless, even though these science gaps need to be filled, an MPA network should not be designed without reference to these important demographic issues. Overall, efforts to advance science in the context of designing

Figure 22. Environmental education and awareness programmes aimed at stakeholders and users of marine areas are an important part of coastal management. Photo: Miguel Angel Maldonado, Centro Ecológico Akumal

and implementing new networks should be encouraged. Again, this will require that scientists and managers work together in a long-term adaptive management process in which setting up a network becomes a way of testing ideas about the effectiveness of the choices made. It is regrettable that the use of MPAs as fishery management tools has proceeded as far as it has with so little concern about the lack of sound demographic science to underpin it, but there are excellent opportunities to work towards redressing this problem in the course of improving reef fishery management.

It is regrettable that the use of MPAs as fishery management tools has proceeded as far as it has with so little concern about the lack of sound demographic science to underpin it, but there are excellent opportunities to work towards redressing this problem in the course of improving reef fishery management.

Beyond metapopulations, coral reef communities are now increasingly being viewed as metassemblages (or metacommunities) in which each species exists in its own metapopulation. Thus, a single location represents one node within each metapopulation, and the metassemblage comprises a spatial overlay of individual metapopulations. In a metassemblage, metapopulations are organized on different spatial scales depending on the dispersal properties of a species. Here, species interactions can be particularly rich. The theory of metassemblages is not well developed, and any attempt to apply it to MPA network design, or management of reef communities, relies on a scanty and feeble set of rules of thumb. While managers operate in this theory-free state, there is considerable scope for population ecologists to build the needed theory, and introduce it into management regimes.

3.3 What MPA networks cannot do

Marine protected areas, and particularly NTRs and NTR networks, are valuable tools for reef managers. NTRs protect target species from fishing mortality, and also protect habitat from fishery-related degradation. Other types of MPAs provide limited to solid protection against other forms of site-specific human impact. However, the strong advocacy for the use of MPAs has obscured the fact that they are not the only tool that reef managers need, nor even the best tool for every task. Fisheries management in particular, is a complex task that cannot be solved by the application of a single tool.

Furthermore, the establishment of MPAs is rarely followed by good management and enforcement. Many MPAs exist on maps and in legislation but offer little real protection. Often referred to as "paper parks", these sites represent a failure to protect resources and ecosystems. Adding more of these paper parks does nothing for conservation or fisheries management. In fact, the ineffective deployment of minimal funds and few personnel to provide the semblance of management, represents a depletion of resources that could have been used to properly manage MPAs in other areas.

Box 5. No-take reserves can be ineffective

Some circumstances where NTRs will be ineffective:

1) Highly mobile species will be poorly served by any form of MPA unless a substantial portion of their habitat lies within MPA boundaries. Thus, fisheries for reef-associated pelagics, and more widely-ranging demersal species, are unlikely to be sustained by the creation of an NTR network unless the NTRs are exceptionally large or numerous. Otherwise, individuals will spend most of their time outside reserve borders and be subject to fishing.

2) Fishery species which experience a critical life stage within nursery habitats degraded by pollution or coastal development will not be sustained by an NTR that only protects adult habitat. The lack of suitable nursery habitat becomes a bottleneck that restricts production and limits replenishment to the adult fish population.

3) NTRs are also an ineffective fishery management tool in regions where pollution or other general activities are degrading habitat and reducing the NTRs capacity to support the target species. Habitat quality will continue to degrade inside as well as outside the NTR and the fishery will likely decline.

4) To be optimally effective in sustaining a particular fishery, the spacing and sizing of NTRs in a network must reflect the dispersal characteristics of the target species. It also follows that an NTR network cannot be simultaneously optimal for several target species, especially if they each have very different patterns of dispersal as larvae. That is, one size does not fit all.

5) In most cases, the introduction of NTRs results in redistribution rather than reduction of fishing effort from the now protected to remaining unprotected locations. In circumstances where fishing effort is greater than that which is sustainable and overfishing continues unchecked, the target species will likely continue to decline in size, age and abundance. While NTRs provide some insurance and mitigation against overfishing, poor fishing practices will eventually lead to fishery collapses. If fisheries are to be sustainable, imposition of other controls on fishing effort and catch must occur in combination with NTRs.

Finally, and perhaps most importantly,

6) NTRs which are not managed to ensure that compliance with regulations is enforced, will not fulfill their intended role. Under these circumstances, NTRs will not be free from fishing mortality, target species will not survive longer within borders, increase in production of offspring will not occur, and there will be no net spillover or recruitment subsidy to surrounding areas.

Message board

- Coral reefs are inherently patchy and fragmented habitats, and many reef organisms exist as spatially distinct local populations connected by an unknown degree and distance.
- Demographic connectivity in marine populations is key to the fisheries-management role of no-take reserves because it provides a mechanism for reserves to enhance fish production outside borders.
- If fishing pressure on animals living within NTR borders is greatly reduced, these areas can help promote fish survival and reproduction even if the surrounding area is severely over-fished.
- Ideally, an NTR should be large enough so that a reasonable proportion of the target species larvae will complete pelagic life stages and settle within the NTR borders.
- NTRs within a network must be close enough so that there is some exchange of individuals. Here, dispersal patterns determine the appropriate scale of NTR networks.
- Best estimates indicate that neighbouring NTRs should be from 10-30 km apart, a reasonably appropriate scale of connectivity structure for most target reef species.
- The spatial arrangement of populations and/or prevailing patterns of water movement can make certain populations consistent sources and others sinks for dispersing organisms.
- Sink populations are those that fail to replenish themselves and are only saved from extinction by the dispersing surplus of other populations (sources).
- There is a need for long term protection and monitoring of NTRs, coupled with well-designed experiments, to quantify spillover and recruitment subsidy if the full benefits of a reserve are to be revealed.
- MPAs are only effective if well managed and enforced. They are not the only tool that reef managers need, nor even the best tool for every task.

3.4 The value of coastal marine ecosystems

Healthy marine resources require healthy, intact ecosystems. Marine and coastal ecosystems are highly productive and support communities and economies by delivering various goods and services (e.g., food security, clean water, recreational opportunities and other benefits).

It is estimated that by 2050, 91% of the world's coastlines will be affected by development. Many coastal areas of developing countries are dominated by "sun and beach" tourism with a focus on rapid coastal growth. Development often proceeds because it seemingly brings jobs and revenue in the short-term. But the long-term costs of inappropriate development in lost ecosystem goods and services, degraded local cultures, and other neglected impacts are estimated to be far greater.

A number of major economic activities are by definition coastal:

- Recreational and commercial fisheries;
- Ports and shipping;
- "Sun and beach" tourism;
- Community recreational services;
- Nature and adventure tourism;
- Onshore construction, including seawalls, groins, and other structures to protect shores.

Many coastal businesses and recreational activities rely heavily on the natural and non-market services that healthy coastal habitats provide. These services include shoreline protection, fish nursery grounds, and destinations for valuable tourist industries.

Figure 23. Ocean habitat types are connected by the movements of juvenile and adult organisms and through the transfer of materials and nutrients. These connections should be considered in the design of MPAs and MPA networks. Photo: Stillpictures

Figure 24. Many coastal businesses and recreational activities rely heavily on the natural, non-market services that healthy coastal habitats provide. Sustainably managed coastal eco-systems serve many recreational, family and cultural purposes. Photo: Stillpictures

It is necessary for all coastal communities, local businesses, coastal managers and governments to recognize that it is business-smart to conserve coastal habitats and the wide network of industry and ecosystems they support, because this will ensure compounded returns on investments through time.

3.4.1 Maintaining habitat corridors and economic services

The habitats which link the various life stages of species across continental shelves are vital for healthy fishery and ecosystem functioning. Unfortunately, although maintaining ecosystem function is important for economic production in coastal areas, it is poorly understood. A mangrove, seagrass or reef habitat can be seriously damaged due to coastal developments that block, divert, slow, or enhance water flow (and transfer of substances) from one habitat to another, even if construction occurs some distance away.

The last century has witnessed extensive modification of our coastal ecosystems. Individuals, communities, business entities, environmental scientists, management and regulatory agencies, and governments need to work together so that these impacts can be successfully managed. We need to apply the best science based on the best information available to ensure that effective policy decisions are made, and that all groups accept resulting management decisions. This requires thinking on time-scales which last longer than an election cycle.

Box 6. Major coastal economic activities

To achieve more sustainable management of coastlines, communities, governments and managers should insist on taking the following actions:

- Anticipate and plan for changes in coastal habitats on 5 to 20 year time scales;
- Anticipate cumulative impacts, i.e., coastal development is a continuous process and negative impacts can build up over time;
- Provide incentives so that coastal enterprises adopt sustainable business practices;
- Ensure that all coastal stakeholders are publicly involved in decision making;
- Avoid urban sprawl by applying strict zoning rules to land use plans;
- Adopt best practices in waste management to reduce coastal pollution;
- Acquire objective and comprehensive environmental assessments for coastal development proposals;
- Use independent environmental experts to evaluate proposals for coastal development.

Sustainably managed coastal communities serve many recreational, family and cultural purposes and are wise investments for future generations.

3.4.2 Alleviating poor connectivity

There are many reasons one population of a reef species may not be connected to others in the same region. For example, distance and current patterns may limit the supply of larvae dispersing into a population. Further to this, lack of suitable settlement habitat may reduce the success of arriving larvae. Also, where population size has been reduced, whether by direct harvest or by indirect impacts on needed resources, the Allee effect, which limits reproductive effectiveness within sparse populations, may also reduce or eliminate connectivity (Stephens et al. 1999). In species that have sparsely distributed populations, the number of larvae being produced is limited as there is a lower likelihood of successful fertilization. This is especially true for species that release gametes directly into the water column. Where populations have severely declined, this reproductive failure may lead to local extinction of that species.

Aggregating and restocking are management options which can help restore viable populations of reef organisms (Bell et al. 2008). For example, aggregating remnants of a population into no-take zones can be used as a low cost intervention to alleviate the Allee effect. When populations have been decimated, restocking with hatchery-reared individuals may be an effective option. In cases where reduction in suitable settlement habitat limits reproductive success, stabilizing substrates to improve habitat quality may help attract new recruits (Raymundo et al. 2007). Although aggregation and restocking serve as local solutions to local problems, if applied across a region where a species population has declined, they offer cost-effective ways to strengthen local reproduction and rebuild connectivity. Restoration of connectivity among populations is a desirable goal because of the way it improves resilience to local perturbations in population number.

Message board

- Sustainably managed coastal ecosystems serve many recreational, family and cultural purposes and are wise investments for future generations.
- Where population size has been reduced, whether by direct harvest or by indirect impacts on needed resources, the Allee effect, which limits reproductive effectiveness within sparse populations, may also reduce or eliminate connectivity.
- Although aggregation and restocking serve as local solutions to local problems, if applied across a region where a species population has declined, they offer cost-effective ways to strengthen local reproduction and rebuild connectivity.

Section 4
The science of connectivity

In this section you will find:

Methods for defining larval dispersal patterns

Larval biology, behavior and sensory capabilities

Determining migration patterns following larval life

Current knowledge of connectivity

Coral Reef, Gili Islands, Indonesia. Photo: Andrew Dansie

4. The science of connectivity

4.1 Methods for defining larval dispersal patterns

Demographic connectivity arises from the dynamic interactions between geographically separated populations due to dispersal of individuals among them. In the marine environment, pelagic organisms are often very mobile and populations can be kept connected on very large spatial scales by adult movement. For coastal and benthic species, such as those inhabiting coral reefs, interactions between breeding populations mostly take place through natal dispersal (Sugden and Pennisi 2006) during the pelagic larval phase. This interaction also occurs for some species through spawning migrations or other post-settlement movements (Box 3). Thus, populational connectivity depends both on seascape (i.e., currents and habitat patches) and the life history of a particular organism.

4.1.1 Biophysical models of larval dispersal

4.1.1.1 Why do we need numerical modeling?

Since most coastal species disperse during the larval phase, one could predict that the measurement of natal dispersal and larval exchange among patchy populations would give an accurate assessment of connectivity. However, difficulties arise when attempting to make direct observations of small pelagic larvae. Empirical methods for tracking larvae (e.g., plankton surveys, otolith tagging, and genetic comparisons) are limited to snapshots in time and space, and to specific larval linkages and populations. Numerical modeling is a unique approach which generates a full spectrum of connectivity patterns and provides estimates of important dispersal characteristics (see Box 7: Characteristics of a Modern Biophysical Connectivity Model). In the end, a combination of techniques is needed to achieve a robust assessment of population networks. Despite this, numerical modeling remains a key tool for mechanistic understanding of the complex processes involved in population connectivity (Werner et al. 2007). A particular strength of models in an era of climate change, is their use in predictive analyses, i.e., they can generate hypotheses revealing the importance of particular processes, and unanticipated or nonlinear effects.

4.1.1.2 What kind of models do we need?

To capture important physical (e.g., transport and dispersion by water masses and eddies) and biological processes (e.g., growth, mortality, swimming ability, and response to gradients), the use of coupled biophysical models is imperative (Werner et al. 2007). Access to near real-time remotely sensed ocean observation data, in combination with increased computational ability, now allows for a better understanding of oceanic processes and much improved 3-D ocean models. On the biological side, the use of individual trajectories (Individual Based Models, IBMs) can provide more realistic results as they allow for simulation of species specific behavior during a given phase of larval life. Connectivity models should also incorporate uncertainties in physical (e.g., stochastic Lagrangian models, LSM) and biological (e.g., stochastic mortality) features, otherwise the value of the output can be limited. A "good" connectivity modeling system should generate all the dispersal characteristics that are missing in empirical data (i.e., spatial and temporal gaps, see Box 7: Characteristics of a Modern Biophysical Connectivity Model). It should also be directly coupled to gene flow models and compared with genetic structures derived from population studies. Such models are powerful hypothesis-testing tools that can address management questions including what is the best placement and size for a marine protected area (MPA)?

4.1.1.3 Model resolution and validation

Spatial resolution in connectivity models is critical because the emphasis is placed on spatial patterns (i.e., where are source and sink populations?). Ocean General Circulation Models (OGCMs, e.g., the hybrid coordinate ocean model (HYCOM), Mercator) now operate on regional scales and archived data on "live" servers are the source for biophysical models of reef larval dispersal (Cowen et al. 2006). The coupling of OGCM output with stochastic particle-tracking tools simplifies the set-up of these models. Recent studies have shown that the spatial scales of larval exchange may be in the order of only a few kilometers for some reef organisms (e.g., Almany et al. 2007, Jones et al. 2009) and that early development of larval sensory and behavioral abilities plays a major role in driving recruitment (Irisson et al. 2004, Paris and Cowen 2004). Models that better simulate the local topography and initial dispersal patterns are constantly being improved (e.g., the regional ocean modeling system (ROMS) and the Princeton ocean model (POM)). Temporal resolution in a model is also important because larval dispersal is usually seasonally discrete and because emphasis is placed on temporal patterns in climate modeling. Thus, beyond the spatial resolution requirements of OGCMs in connectivity studies, we also need long time-series data recorded over past decades as a baseline for forecasting. This could then be used with coupled climate-OGCM models to assess the effects of climate change on ocean stratification and larval dispersal.

Validation of each component within the coupled model should occur using available physical data (e.g., satellite-derived sea surface temperature (SST) and sea surface height (SSH), Acoustic Doppler time series from Ocean Observing Systems, surface floats and drogues) and by comparing dispersal outputs against the patterns of field sampled biological data (e.g., plankton surveys, genetic fingerprinting, recruitment time series, and other biological tracers such as chemical signatures in fish otoliths). A well validated biophysical model can then become a very powerful tool for hypothesis testing in connectivity research. Without doubt, our understanding of connectivity will grow most effectively through consistent long-term comparisons of modeling and empirical studies.

Box 7. Characteristics of a modern biophysical connectivity model

The Multi-Scale Connectivity Modeling System, developed at the University of Miami, is proving effective in a number of studies which examine the connectivity of reef organisms. This system is capable of providing detailed model output on all three connectivity features likely to be of interest – dispersal distance, advection/diffusion, and dispersal kernel shape.

Distance

Information on larval dispersal distance can be obtained from spatially explicit numerical models that incorporate both the hydrodynamics and individual behavior of larvae. The model system simulates larval pathways and gives an exact measure of total displacement for each individual. Given that we are interested in the shortest path from the start (spawning) to the end point (settlement) of individual trajectories, migration distance is typically estimated as the average of a group of larvae dispersing from a spawning output (Paris et al. 2007).

Advection/diffusion

Advection is the mean transport of a group of larvae, while diffusion is the variance around that mean direction and distance due to individual larval differences (Okubo and Levin 1989). Biophysical models that solve for individual movements resulting from eddy activity and larval behavior (e.g., feeding, swimming, and sinking) can readily be used to provide the direction and spread of dispersion either (in one dimension) as a Gaussian distribution (Botsford et al. 1994, Hastings and Botsford 2006) or (in 2-D) as a cloud of particles (Paris et al. 2005, Cowen et al. 2006). Largier (2003) estimated mean advection due to hydrodynamics to be in the order of 10-100 km for a 30-day larval duration. This researcher also found that advection decreased with increased diffusion and that all larvae would be exported from the local region before settlement (i.e., no local retention). However, in another study, when larval behavior was introduced, advection decreased significantly while diffusion remained unchanged (Paris et al. 2007). Diffusion may actually increase if larvae exhibit random (i.e., non-oriented) swimming patterns as this may enable them to reach more habitat patches (Armsworth and Roughgarden 2005). Nonetheless, increased diffusion can dilute the number of settling larvae at any given location while directed movement concentrates settlement at specific locations. Overall, the Multi-Scale Connectivity Modeling System can input spatially explicit values of eddy diffusivity, extracted from the OGCM, to improve the advection/diffusion computation.

Dispersal kernel

This function gives the probability distribution of the location of an individual as a function of its spawning location and time since dispersal commenced. In nature, dispersal is asymmetrical due to the unevenness of water current patterns and recruitment habitats. Thus, reasonable biophysical models should generate dispersal shapes that change with life history traits. Due to the stochastic nature of IBMs, the relative frequency of all possible outcomes tends to stabilize at given values and gives a good estimate of the dispersal kernel of successful dispersal (Cowen et al. 2006). In addition, stochastic fluctuations from the mean trend are also well represented in such IBMs. Dispersal kernels can be represented in one dimension (i.e., probability of arrival vs. distance), or in 2-D (i.e., transition probability matrix). In highly fragmented habitats, such as coral reefs, modeling 2-D dispersal kernels allows the analysis of individual movement patterns between population patches (Bode et al. 2006, Cowen et al. 2006). In both forms, dispersal kernels also provide the relative level of local recruitment, an important value for the persistence of populations (Levin et al. 2003, Hastings and Botsford 2006).

The Multi-Scale Connectivity Modeling System (CMS) incorporates a variety of species-specific biological and site-specific physical data to provide output that is specific to a particular organism and region. Relevant time periods include the duration of the pre-hatching egg stage (hours-days), larval stage (days-months), spawning season (months), and reproductive life-time of adults (years). Values of velocity (advection) and eddy diffusivity (diffusion) are averaged over these time scales (Botsford et al. 2002). In this way, the variability of larval dispersal and settlement can be modeled at different time scales, as appropriate for the target organism (Paris et al. 2002). For example, climatology data can help predict connectivity patterns that can be expected in a region for a particular month. The CMS is forced by realistic currents (time and space variable) and by appropriate demographic parameters to simulate dispersal kernels and resulting settlement patterns with a level of detail that far exceeds what is possible with current empirical methods (Cowen et al. 2000).

A dispersal kernel can be uni- or multi-modal, depending on the life history of an organism, the degree of habitat fragmentation, and the oceanography and geomorphology of a region. The spatial arrangement and distance between coral reef patches, atolls, or archipelagos of the habitat layer in the CMS plays a definite role in the final shape of the kernel. For example, for long distance dispersers or organisms with variable pelagic larval duration that can significantly extend beyond the competency period, the distribution may be multi-modal, which suggests a greater likelihood of such larvae crossing large habitat gaps. Species with large dispersal potential (i.e., long pelagic larval duration) show bimodality in the dispersal kernel since they have the ability to recruit either close to the natal place by moving into deeper waters where the current is not as strong, or to recruit to distant reef locations if they are dispersed too far from home. This is indeed the case for spiny lobster larvae (Butler et al. in review).

Most mortality takes place during the pelagic larval stage (Cushing 1990).This effectively limits the distance over which meaningful dispersal can occur (Cowen et al. 2000) and therefore the pattern and scale of connectivity. These complexities are currently being explored so that spatially-explicit larval mortality predictions can be improved. Specifically, the larval-tracking model (see IBM Module Box 8) will be linked to a Nutrient-Phytoplankton-Zooplankton (NPZ) model. The latter can be used to determine food availability for larvae; this affects larval growth and mortality rates. A growth function will also be used to determine the larval duration of individuals, i.e., if a larva has sufficient food and grows faster, its pelagic duration will be shorter, and its survivorship will increase.

In metapopulation models, it is common practice to use species-specific dispersal distances to predict the exchange of individuals between habitat patches. The influence of patch distribution on arrivals can also be explored in larval exchange models. Adult effects can be modeled, by adding or removing marine reserves (Botsford 2001). This changes the spatial pattern of production so that the impacts of dispersal model outputs can be explored.

Box 8. Components of the Multi-Scale Connectivity Modeling System

The Multi-Scale Connectivity Modeling System (CMS) is designed to model abiotic and/or biotic particles, movement, growth and survivorship. It also takes into account the interactions of these factors with nutrients, predator-prey fields, the pelagic physical environment (temperature, salinity, currents) and benthic habitat (production, proximal cues for settlement, carrying capacity). These processes extend across coastal to oceanic ecosystems and can be modeled by independent functional units with data and information flowing from the physical environment to progressively higher trophic levels over multi-decadal time scales. The CMS downscales simulation output from basin to coastal scale circulation models, integrates geochemical NPZ models, and fully couples the Individual Based Models of larval transport and recruitment which can eventually be fed back into climate models. The CMS is thus inter-disciplinary in essence and represents a novel framework to efficiently integrate several applications generating output in any kind of resolution and spatial format. The CMS employs two widely used community tools, the Earth System Modeling Framework (ESMF) and the Open Project for Network Data Access Protocol (OPeNDAP), to overcome technical problems related to information exchange between different models and data management. The multi-scale CMS includes six primary modules as follows:

1) Oceanographic Module

Ocean Generalized Circulation Models (HYCOM, ROMS, etc.) provide the underlying velocity fields in 3-D which move both passive and active particles from shallow coral reef habitats to the coastal ocean and back.

2) Seascape Module (Habitat Matrix)

This module represents both the spawning and settlement locations of larvae and is associated with particular habitat for the target species and region. For example, the seascape for coral reef organisms is derived from remote sensing of coral reefs (Andréfouët et al. 2006). First, habitat polygons are buffered to a distance representing the ability of larvae to sense settlement habitat, following Paris et al. (2005). The seascape is then further partitioned into discrete polygon units (or nodes) using a tolerance level which defines the resolution of the habitat matrix.

3) Biological Module

This module accounts for both the adult reproductive strategy (e.g., spawning time, location, frequency, and production) and the larval traits (e.g., competency period, pelagic larval duration (PLD), mortality rate and swimming behavior (e.g., buoyancy, vertical migration, and orientation), from the egg to settlement stage. This module uses the life history characteristics of a species and serves to simulate larval movement other than that caused by current-induced advection. For example, in a larval damselfish model, particles are moved passively in the shallowest water layers up to the flexion stage, after which they move in a vertical migration scheme following Paris and Cowen (2004) until they reach a stage where they are competent to settle. Settlement occurs when the particle trajectory encounters a reef polygon. The reproductive strategy is then simulated by the particle release scheme. In order to find significant results, simulations use a series of particle releases from each source node (spawning location).

4) Nutrient-Phytoplankton-Zooplankton (NPZ) Module

This module runs online with the Oceanographic Module since it is affected by climatology (e.g., wind, heat flux, and sun irradiation determine the depth of the mixed layer, photosynthesis, and in turn zooplankton density). Daily output of zooplankton (typically small copepods) is coupled offline to the Biological Module to parameterize larval mortality and compute larval growth (and pelagic duration) over time and space. The phytoplankton component of this module can be validated through satellite ocean color images.

5) Individual-Based Module (IBM)

Individual particles (larvae) are moved by the 3-D current (see Oceanographic Module), a specific behavior, including survivorship (see Biological Module), and subgrid-scale turbulence. The underlying base of the IBM module is a Lagrangian Stochastic Model (LSM). A stochastic model is a tool for estimating probability distributions of potential outcomes by allowing for random variation in one or more inputs over time. A Lagrangian model uses a moving frame of reference as particles move. Because circulation in coastal spawning areas is complex and typically characterized by both mesoscale and small-scale eddies, the Lagrangian statistics used in the stochastic particle-tracking scheme should be spatially-explicit (Paris et al. 2007).

6) Matrix Module

The typical output in this model uses square matrices called connectivity or transition probability matrices. In order to describe a system at ecological scales, the proportion of successful recruits must reflect the recruitment rates (i.e., number of recruits per generation) required to replenish the local population to a minimum of zero growth (Cowen et al. 2006). Such recruitment rates can be estimated a posteriori to match adult mortality rates using simple population growth models. Similarly, demographic connectivity models can be a posteriori scaled by production (e.g., relative spawning biomass per unit population, or proportion of adult habitat in each population), which can be approximated by the area of each node (see Seascape Module). Because connectivity models are by nature spatially explicit, the LSM algorithm is coupled with the Seascape Module. This serves to delineate the suitable settlement habitat along an individual particle path. It is also important to incorporate uncertainties into the connectivity model (e.g., stochastic Lagrangian model (LSM), stochastic mortality) otherwise the analytical value of the Matrix Module is limited.

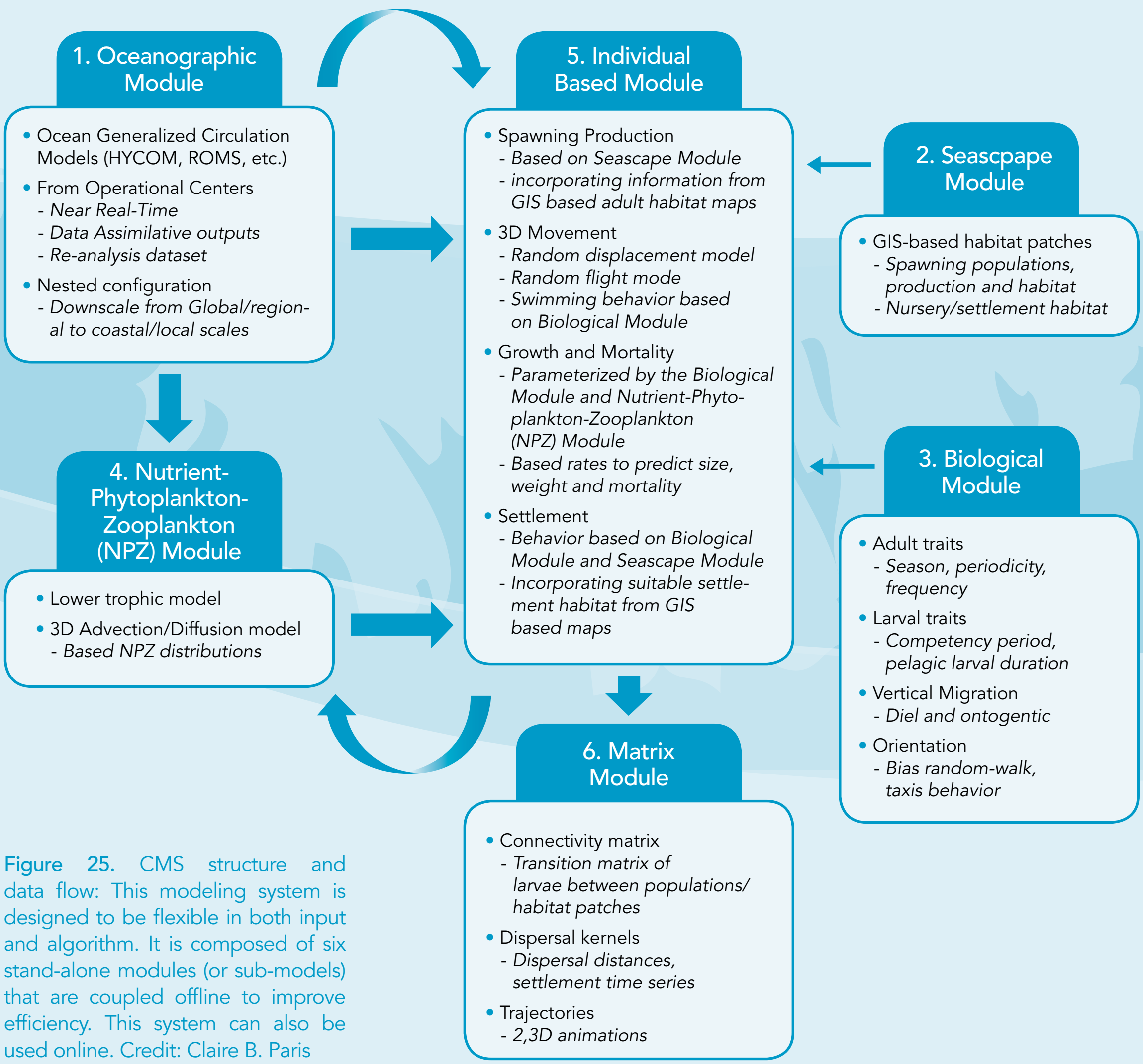


Figure 25. CMS structure and data flow: This modeling system is designed to be flexible in both input and algorithm. It is composed of six stand-alone modules (or sub-models) that are coupled offline to improve efficiency. This system can also be used online. Credit: Claire B. Paris

4

Message board

- Empirical methods for tracking larvae (e.g., plankton surveys, otolith tagging, and genetic comparisons) are limited to snapshots in time and space, while numerical modeling is a unique approach which generates a full spectrum of connectivity patterns and provides estimates of important dispersal characteristics.
- A well validated biophysical model can become a very powerful tool for hypothesis testing in connectivity research and our understanding of connectivity will grow most effectively through consistent long-term comparisons of modeling and empirical studies.
- The Multi-Scale Connectivity Modeling System incorporates a variety of species specific biological data and site-specific physical data to provide output that is specific to an organism and region.
- A particular strength of models in an era of climate change, is their use in predictive analyses, i.e., they can generate hypotheses revealing the importance of particular processes, and unanticipated or nonlinear effects.

4.1.2 Genetic analyses of populations and individuals

4.1.2.1 Evolutionary versus ecological connectivity

Populations of coral reef species can be geographically separated at distances ranging from a few meters (e.g., invertebrates inhabiting specific coral heads) to thousands of kilometers (e.g., species present on both the western and eastern Pacific). If these populations are isolated from each other (i.e., no exchange of individuals or genes) for an extended period of time, they evolve independently through natural selection and genetic drift (random changes in gene frequency). Ultimately, this isolation can lead to genetically different populations and the rise of new species. Conversely, if populations regularly exchange migrants (and genes), the flow of genes will keep them genetically similar. This process of gene exchange drives evolutionary (genetic) connectivity and corresponds to the rate of gene flow occurring among populations over a timescale of several generations. In contrast, ecological (demographic) connectivity refers to the actual exchange of individuals occurring at spatial scales that can influence population demographics and dynamics. It includes larval dispersal, recruitment of juveniles, and the survival of these juveniles to reproductive age. This form of connectivity among populations will measurably influence the amount of recruitment to a population, the number of breeding individuals in a location and the amount of biomass available to a fishery.

It is important to differentiate between these two types of connectivity because the rates of migrant exchange necessary to connect populations ecologically need to be much higher in magnitude than those which connect populations in an evolutionary sense. That is, there can be highly relevant evolutionary connectivity between populations even if they experience such low levels of exchange that ecological connectivity is essentially absent.

Environmental managers, particularly those responsible for managing MPAs, usually ask questions that are related to ecological connectivity rather than evolutionary connectivity. For example, are MPAs in a network adequately connected? What is the maximum geographic distance at which they will remain ecologically connected? Are populations within MPAs self-sustaining? What is the output of an MPA to surrounding exploited areas? And, how far can the larvae supplied by an MPA be exported?

Questions which instead concern evolutionary connectivity, such as whether a particular population is sufficiently distinct genetically to warrant special conservation effort are also important, but less frequent. In the following section, we will therefore focus on genetic tools and analyses that can be used to answer questions concerning ecological connectivity.

4.1.2.2 Patterns in population differentiation

Connectivity among populations, within MPAs or not, can be estimated indirectly by examining the genetic variation of individuals sampled from spatially discrete populations. Indeed, populations may differ in the presence of alternative gene forms (alleles) that constitute heritable diversity among conspecific individuals. Populations may also differ in the frequency of these alleles, and in associations between alleles (genetic linkages). Under the assumptions of population genetics theory, the number of migrants exchanged per generation can be indirectly estimated from the standardized variance in allele frequency among local populations. The pitfall of this approach is that it only paints an average picture of dispersal patterns because it sums up the varied dispersal characteristics that might occur from year to year. Unfortunately, it also does not distinguish between contemporary (on-going) and historical gene flow, since indirect methods cannot distinguish between the exchange of 100 individuals once every 100 generations and the exchange of 1 individual every generation. Moreover, one migrant that settles and enters a local breeding population per generation is enough to prevent the accumulation of large genetic differences, while ten migrants per generation are enough to prevent all but minor genetic differences from developing. Therefore, these indirect genetic surveys are too insensitive to detect ecological connectivity among populations when little to no genetic variation is detected. In marine realms, this is often the case when considering the spatial scales that concern MPAs.

Recently, more sensitive molecular and statistical techniques have been developed to make direct estimates of ecological connectivity in marine populations. These rely on the assignment of individuals (usually offspring) to populations of origin (assignment methods) or to specific parents (parentage analysis). These approaches are conceptually similar to evidence obtained from using physical or chemical/environmental tags (see Section 4.1.3.3).

4.1.2.3 Genotype assignment of offspring to source populations

In individual-based assignment methods, an individual is assigned to one of many possible populations, based on the expected frequency of its genotype at multiple genetic loci. As opposed to the indirect methods presented above, assignment methods allow for estimates of present-day connectivity. However, when applied at spatial scales relevant to an MPA framework, the potential problems of these tests are that: (1) in some cases these methods require that all possible sources have been sampled and; (2) putative source populations must be sufficiently genetically differentiated (i.e., migration among source populations is low). Indeed, it has been shown that as the dispersal rate among populations increases, genetic differentiation between populations decreases, and the ability to distinguish the source population of an individual becomes more problematic (Saenz-Agudelo et al. 2009). Therefore, individual-based assignment tests may be most useful in determining patterns only when there is low connectivity. Several examples in the literature have demonstrated the utility and versatility of assignment tests to detect ecological connectivity in marine organisms. However, for many marine species, genetic subdivision may be too low for accurate assignment.

Figure 26. An estimate of the proportion of self-recruited versus dispersed larvae in cohorts of the bicolor damselfish (*Stegastes partitus*) was made using genotype assignment analysis at two reefs located in Turneffe atoll in the Mesoamerican Barrier Reef System (MBRS). Photo: John E. Randall

4.1.2.4 Parentage analysis

Parentage analysis can provide a finer-scale assignment test than those analyses which assign individuals to putative source populations. In this form of analysis, individuals are assigned to a single parent or parent pair, where the most likely parent is selected from a pool of potential parents. It allows the determination of an individual's natal origin if the parent's location at the time of conception is known. This method is particularly suitable to an MPA framework as it provides data on present-day dispersal events. For assignment tests and parentage analyses, the use of highly polymorphic (many alleles) and species specific genetic markers (such as microsatellite markers) is required. This may be problematic because the development and characterization of such markers is rather expensive and time consuming. Aside from this, there are two main drawbacks specific to parentage analyses: (1) the location of the parents at the time of conception must be known (this may be difficult to determine for some large mobile species); and (2) that assignment success declines dramatically as the number of candidate parents sampled decreases. Therefore, a high proportion of the adult population must be sampled and genetically processed, making this a difficult and costly approach. Parentage analysis would be most useful when using species for which microsatellite markers are already available, and for which the number of adults is low enough that nearly all possible parents can be sampled.

4.1.3 Use of chemical signals to identify source locations

4.1.3.1 Otoliths, statoliths and other useful structures

Figure 27. Otoliths and mussel shells have been used by researchers to find possible source locations of larvae. These structures grow in proportion to an animal's body, and the chemicals which make up the composition of these hard parts are taken in by the animal from the surrounding water. Photo: IStockphoto

Many marine organisms have hard body parts, including bones, shells, scales, otoliths and statoliths. Otoliths and statoliths are calcified stone-like structures used by fish and crustaceans for hearing and/or orientation. Most of these structures are primarily made up of calcium minerals (e.g., mollusc shells, fish otoliths and invertebrate statoliths are almost entirely composed of calcium carbonate). These structures grow in proportion to an animal's body in a process by which calcium compounds are incorporated into the structure daily. The chemicals which make up the composition of these hard parts are taken in from the surrounding water. Otoliths are 97% calcium carbonate, however, other elements are also incorporated into the hard structures, such as strontium, magnesium, barium, lead and others (Campana 1999). Because these chemicals come from the environment, structures like otoliths can be used as a record of where an animal has been in its lifetime.

4.1.3.2 Natural signals defining source locations

Many studies have used natural chemical signatures to differentiate between coastal habitats, i.e., to distinguish between estuaries and coastal habitats among reefs, and between reefs and mangroves (Chittaro et al. 2005, Gillanders 2005, Becker et al. 2007, Ruttenberg et al. 2008, Kingsford et al. 2009). In addition to this, otoliths and mussel shells have been used by researchers to define possible source locations of larvae (otoliths: Swearer et al. 1999; mussel shells: Becker et al. 2007). To do this, researchers sample animals from a particular reef, mangrove forest, or estuary, and then analyze the otoliths or shells from these animals. By sampling organisms from numerous reefs and other coastal habitats, scientists can create a "chemical map" of the coastal ecosystem. If there are enough chemical differences between the reefs and other habitats, then it may be possible to tell where animals of unknown origin (e.g., a recently dispersed larva) are from. The otolith/shell chemistry of unknown animals are then compared to that of animals from known locations on the chemical map and unknowns are assigned to the most likely site. If the otolith or shell chemistry of a dispersed larva matches the chemistry of individuals from a known location, and only that location, it is possible to say with a level of certainty that the larva was spawned in that habitat.

4.1.3.3 Labeling otoliths with distinct chemical tags

Researchers have also developed techniques to mark otoliths and other hard parts with chemical tags. These artificial tags are powerful because they are unique and do not occur naturally, and can be used to track the movement of individuals between and among coastal habitats. When a tagged individual is re-caught, there is no doubt of its origin. For example, this method has been used by various researchers to track fish dispersal (Jones et al. 1999, Almany et al. 2007). The principle is simple; the investigator introduces a tag to the adults or young of a study organism and the tag is incorporated into the otoliths or other hard parts. Studies have used tetracycline antibiotic and barium isotopes to tag larvae prior to dispersal away from natal habitat (Jones et al. 1999). After a certain period of time, the investigator collects juvenile animals that have dispersed and then checks for the presence of tags. When a tag is detected, the investigator can determine the animal's origin and how far it traveled.

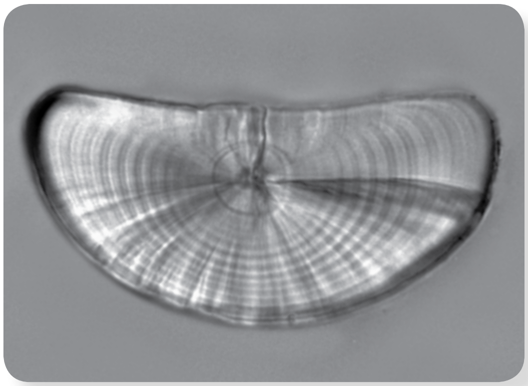


Figure 28. Researchers have developed techniques to mark otoliths and other hard parts with chemical tags to track the movement of individuals between and among coastal habitats. Studies have used tetracycline antibiotic and barium isotopes to tag larvae prior to dispersal from natal habitats. Photo: Evan D'Alessandro and Su Sponaugle, RSMAS, University of Miami

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- Environmental managers, particularly those responsible for managing MPAs, usually ask questions that are related to ecological connectivity.
- If populations are isolated (i.e., no exchange of individuals or genes) for a large amount of time, they evolve independently through natural selection or genetic drift (random changes in gene frequencies in a population), ending up as genetically differentiated populations.
- If populations regularly exchange migrants (and genes), the flow of genes between populations will keep the populations genetically similar.
- Sensitive molecular and statistical techniques have been developed to make direct estimates of ecological connectivity in marine populations. These rely on the assignment of individuals (usually offspring) to populations of origin (assignment methods) or to specific parents (parentage analysis).
- In individual-based assignment methods, an individual is assigned to one of many possible populations, based on the expected frequency of its genotype at multiple genetic loci.
- Parentage analyses allows for the determination of an individual's natal origin if the parent's location at the time of conception is known.
- Otoliths and mussel shells have been used by researchers to define possible source locations of larvae. A "chemical map" of coastal ecosystems is constructed from otolith/shell chemistry of animals from known locations, and larvae from unknown locations are matched to this map.
- Researchers have developed techniques to mark otoliths and other hard parts with chemical tags. An investigator can use tags to track the movement of organisms between and among coastal habitats.

4.2 Larval biology, behavior and sensory capabilities

The study of larval biology is still in its infancy when compared to the study of adult reef organisms. Small size, difficulty of live capture, and the fact that larvae of many species tend to commence settlement and become juveniles immediately after being captured and placed into a bucket all account for the lack of progress. Nevertheless, some headway is being made, particularly for reef fishes.

Figure 29. Examples of experimental collectors used in spiny lobster connectivity studies to capture postlarvae as they recruit to back-reef nursery habitats. The above photo is a Witham-type collector used to collect Caribbean spiny lobster. The below photo shows an experimental apparatus designed to attract Caribbean lobster postlarvae and then provide housing for them in crevice structures as they grow larger. Photo: Mark Butler (above); Unknown (below)

4.2.1 Duration of larval life

For most taxa, larval life duration can only be determined by using rearing experiments. For example, as reported in (Section 2.2.2), the larval life duration of the Caribbean spiny lobster was recently determined to be 6 months. However, given that many taxa are able to prolong larval life once they reach a stage where they can settle and become juveniles, these experiments often only provide minimal estimates of larval duration. One challenge is that it is seldom possible to rear larvae in conditions that mimic the open ocean sufficiently to prevent settlement as soon as the organism is competent.

For reef fish, larval duration can be assessed without the need for rearing. This is because fish otoliths provide a record of age, and most species have a recognizable mark which identifies the time of individual settlement and metamorphosis to the juvenile stage. In fact, there is now an abundance of data reporting larval duration in reef fish, based on otolith microstructure. Duration can range from a minimum of 7-10 days in *Amphiprion* and some Apogonidae, to a duration of 100 days in various surgeonfishes (Acanthuridae) and some other taxa. In all species that have been studied, there is some flexibility in the time to settlement, as well as some interesting studies that show the effects of age, size, or condition during larval life on post-settlement survival and growth.

4.2.2 Response to habitat cues

In addition to the studies of olfaction and hearing reported earlier (Section 2.2.3), there have been a considerable number of experimental studies that reveal many reef species are capable of making precise microhabitat choices at the time of settlement. The simplest of these experiments provide patches of differing habitat types (e.g., live coral, dead coral, or sand) and then record which type is selected by settling organisms. In some of these studies it has also been possible to identify the specific cues used by responding larva. Thus we now know that oyster larvae are attracted to specific chemicals in oyster shell, that a number of coral species preferentially settle close to various species of crustose coralline algae, and may be particularly attracted to the species *Titanoderma prototypum*, presumably also in response to specific chemical cues, and that some reef fishes respond to odor of conspecifics, or more generally to reef habitat. In most cases, the cues are used for short-distance, final-decision, responses right around the time of settlement. (The use of odor by cardinalfishes to recognize a home reef is the only such chemical response that could be guiding the larva when it is still some distance from the source of the cue.)

It is undoubtedly true that marine organisms use more than one cue during larval stages, and that specific cues are used at different stages upon return to juvenile and adult habitat. It is also true that cues can sometimes be very specific. If these specific cues are absent, settlement may not occur. For example, clownfish larvae, *Amphiprion percula*, show strong preferences for the odor of specific tree leaves as well as for specific anemone hosts which help them identify suitable settlement habitat in anemones close to island shores. Further research will undoubtedly reveal a large number of cues, some precise, some broader, used by larval organisms at specific phases of their journey, and in specific environments.

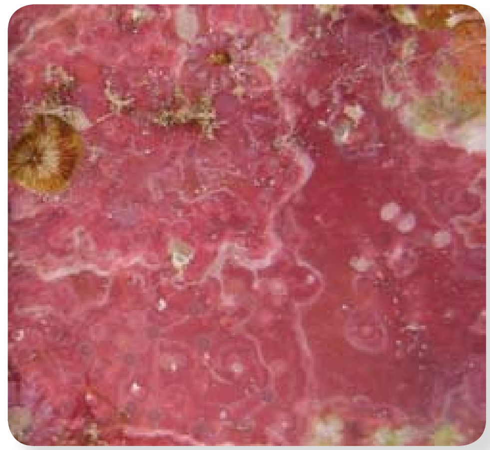


Figure 30. All reef species are capable of making precise microhabitat choices at the time of settlement. A number of coral species prefer to settle close to crustose coralline algae species, and may be particularly attracted to *Titanoderma prototypum*, presumably in response to specific chemical cues. Photo: Robert Steneck

4.2.3 Swimming abilities

Recently, there has been considerable interest in the swimming abilities of reef fish larvae. Partly because these abilities are so different when compared to the larvae of temperate fish species; the latter having been the primary focus of previous fish physiological and behavioral research. Reef fish larvae are generally strong swimmers exhibiting both speed and endurance. Indeed, many of these species can swim more or less indefinitely at speeds of 13 cm per second, or 6-10 body lengths per second – comparable to an Olympic swimmer doing the 100 m freestyle in 7-11 seconds instead of the 46.91 second current world record (no human could swim indefinitely at even the 46 second pace). The Caribbean spiny lobster larva is also no slouch swimming at 15 cm per second for 2-4 weeks. It is clear that some reef species, or perhaps many, have larvae that at least by the end of larval life, are capable of swimming so rapidly that they can overcome prevailing currents as well as travel considerable distances.

4.3 Determining migration patterns following larval life

Habitat use at settlement is poorly understood in many invertebrate and fish species. Areas where newly settled and juvenile stages are recorded are often called nursery habitats. However, the correct definition of a nursery habitat should be that habitat in which the early life stages of a particular species occurs, and that in which it shows superior survivorship and growth. A good nursery habitat must provide the bio-physical necessities (e.g., abundant food and good water quality) that promote efficient growth rates. Criteria to assess relative habitat values for early life stages would help identify potential nursery habitats more precisely.

Methods for evaluating movement among habitats have traditionally been based on physical tagging of individuals and repeated collection of these individuals over time. Although a wide array of tags have been developed, there is a surprising absence of comprehensive tagging information for most of the economically and ecologically significant coastal marine fishes and invertebrates. For example, detailed studies of even frequently occurring behaviors, such as daily feeding migrations, are not common. However, new advances in tagging technology have arisen with some recent focus on the use of digitally tracked transmitter tags. These have allowed for the creation of precise movement maps, particularly if the habitats were mapped beforehand and are available as digitized GIS files.

Despite considerable potential, the mapping of pre-spawning and post-spawning migration patterns of aggregating fishes is also an area of little directed research. We know that some aggregating fishes can be highly concentrated during annual migration through channels and inlets simply because the fishing industry tells us so. In fact, peak fish landings have been achieved by using targeted netting during pre-spawning "runs". Figure 31 shows how cross-shelf spawning migrations of lane snapper (*Lutjanus synagris*) in Cuba were severely impacted commencing in the mid-1970s, when fishers began using channel nets to target spawning runs.

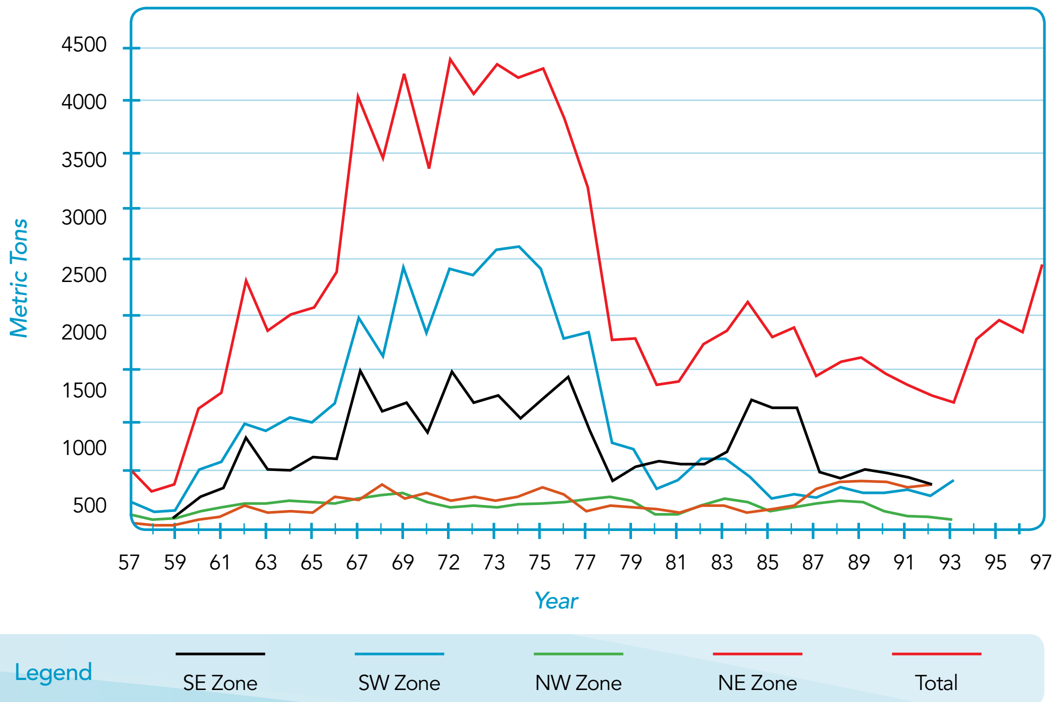


Figure 31. Sometimes we can learn about spawning migration routes and spawning aggregation sites from the fishing industry. The above graph shows marked reduction in landings of lane snapper *Lutjanus synagris* in Cuba from several locations in 1978. This reduction in landings was due to the use of intensive channel netting on spawning migration paths in the previous years. Credit: Paris et al. 2005.

4.4 Current knowledge of connectivity

4.4.1 Historical context and recent advances

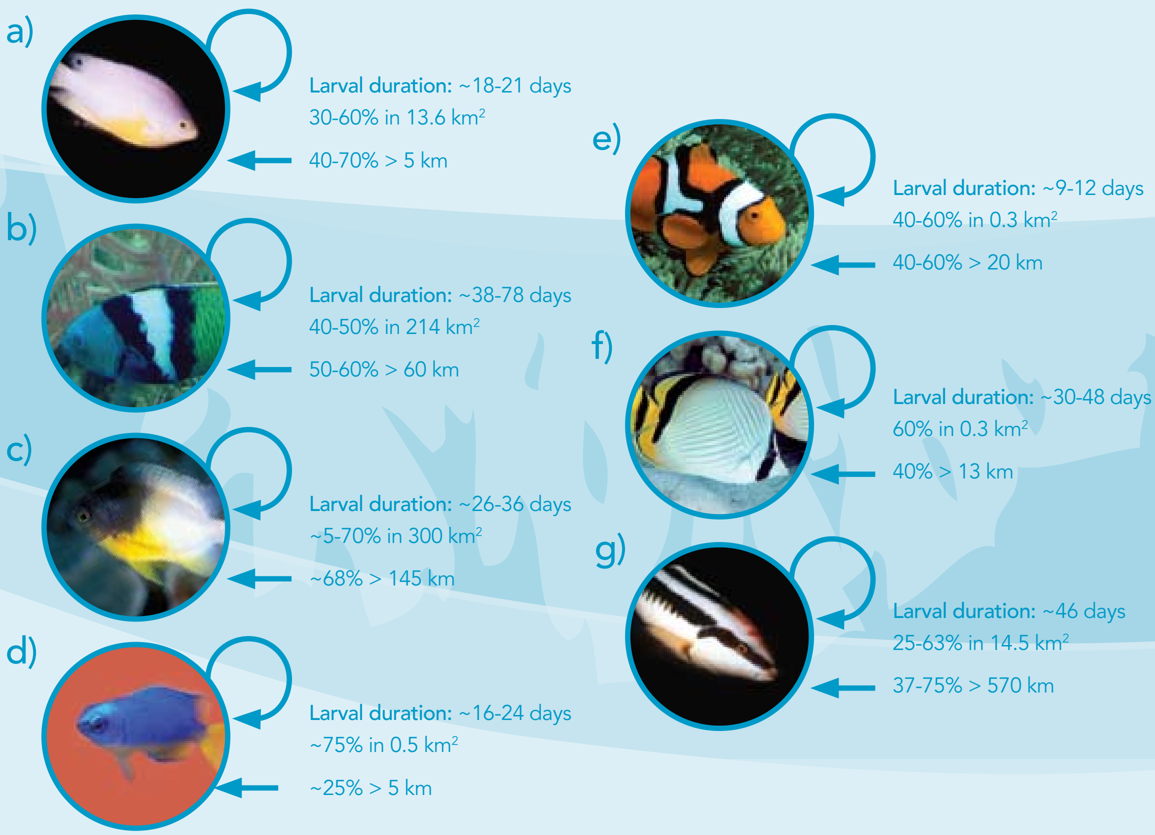
The lack of information on how far marine larvae disperse has historically been an impediment to managing marine populations and designing MPA networks (Sale et al. 2005). However, the science of larval connectivity is advancing rapidly and the large gaps in our knowledge are gradually being filled (Jones et al. 2009). With the application of many new approaches (see Section 4.1), our grasp of the extent of larval connectivity has changed dramatically in the last 10-15 years. In turn, this is increasing our understanding of how current MPA networks operate and how they may be better designed in the future.

Prior to the late 1990s, it was generally assumed that because of their small size, marine larvae are passively transported among spatially discrete populations by prevailing water currents. Individual populations were considered "open", where most of the juveniles were added to a population by passive transport of larvae from other places. Early hydrodynamic models, based on passive particles, predicted dispersal distances over 100s of kilometers far (e.g., Roberts 1997). However, by the end of the millennium, information began to emerge that not all marine larvae are transported such long distances. Biological attributes of larvae and information on larval behavior began to be incorporated into dispersal models. Finer scales and more realistic models predicted much higher levels of local retention of larvae near natal sources, although some long distance dispersal could also be expected (Cowen et al. 2000, 2006). Information from new methods for estimating larval dispersal, including otolith microchemistry, larval tagging, genetic assignment tests, and parentage analysis, all indicated ecologically significant levels of self-recruitment on scales much smaller than once predicted (see review by Jones et al. 2009).

The emerging view is one of a dispersal curve with a substantial portion of the recruitment occurring close to home, and a long tail that includes a substantial number of long-distance dispersers. The exact scale of dispersal significant to population dynamics and resource management is still an issue since a complete dispersal curve has not yet been described for any species (Botsford et al. 2009). However, it is thought that both larval retention and connectivity are likely to play a role in local population dynamics. In coral reefs for example, coral and fish studies provide evidence of both extremely local scale patterns of self-recruitment (at scales of less than 1 km) and ecologically significant connectivity among reefs at scales of 10s of kilometers (and in some cases 100s of kilometers) (Jones et al. 2009).

Percent self-recruitment (the proportion of recruitment to a local population that is derived from adults in that population) provides a useful index for the degree to which a local marine population may be considered "open" or "closed" (Jones et al. 2009). For a range of fish species associated with tropical islands, there is increasing evidence for significant self-recruitment in the range of 30-70% (Box 9). Importantly, while % self-recruitment figures in the 30-70% range are common, no evidence of either 0 or 100% self-recruitment has been documented (Jones et al. 2009). Estimates of distance between the focal island and nearest other island represent minimum estimates of how far immigrant larvae have travelled (Box 9). These dispersal distances range from ~5 km in the case of *Pomacentrus coelestis* at Lizard Island to ~570 km for *Coris picta* at Lord Howe Island. These extremes suggest that ecologically significant connectivity can occur over large distances and may increase as the geographic spacing of suitable habitat increases.

Box 9. Estimates of self-recruitment and connectivity for a range of fish species associated with tropical islands



a) ***Pomacentrus amboinensis***, Lizard Island, Great Barrier Reef. Jones et al. (1999); James et al. (2002). Methods: Tetracycline tagging; Biophysical modelling. **b)** ***Thalassoma bifasciatum***, St. Croix, Caribbean. Swearer et al. (1999); Hamilton et al. (2008). Method: Otolith microchemistry. **c)** S***tegastes partitus***, Barbados, Caribbean. Paris et al. (2002); Paris & Cowen (2004). Method: Biophysical modelling. Photo: John E. Randall **d)** ***Pomacentrus coelestis***, Lizard Island, Great Barrier Reef. Patterson et al. (2005). Method: Otolith microchemistry. **e)** ***Amphiprion percula***, Kimbe Island, PNG. Almany et al. (2007); Planes et al. (2009). Methods: Barium tagging; Parentage analysis. Photo: Brian Donahue **f)** ***Chaetodon vagabundus***, Kimbe Island, PNG. Almany et al. (2007). Method: Barium tagging. Photo: Paul Asman **g)** ***Coris picta***, Lord Howe Island, Australia. Patterson & Swearer (2007). Method: Otolith microchemistry. Credit for figure: Geoffrey P. Jones

While there are still limited data, it is clear that many populations appear to rely on both a local supply of juveniles and recruitment from other populations. The ability of individual populations to replenish themselves by either self-recruitment or immigration confers a high level of resilience as they may be able to persist with recruits from either home or away (Almany et al. 2007).

4.4.2 Biological factors affecting dispersal distance

Modeling data suggest that a range of biological factors can affect actual dispersal distance, including pelagic larval duration, larval survivorship, swimming speed and direction (e.g., Cowen et al. 2000, 2006). However, many of these generalizations remain to be tested by independent methods. For example, the spread in percentages of self-recruitment show little relationship with mean pelagic larval duration (Box 9). In a single study, Almany et al. (2007) found the same high level of self-recruitment on a small island for two reef fishes; the benthic spawning orange clownfish *Amphiprion percula* with a 9-12 day larval duration and the pelagic spawning vagabond butterflyfish *Chaetodon vagabundus*, with a 30-48 day pelagic larval duration.

Figure 32. Measuring coral recruitment with settlement plates. Photo: Robert Steneck

Although one would expect higher self-recruitment for geographically larger source populations, this is not indicated by the current data (Box 9). To some extent, the absence of this pattern probably reflects differences among the techniques used and the spatial scale at which they discriminate self-recruitment. While larval tagging and parentage analyses provide the finest scale picture for sites less than 15 km^2 (Jones et al. 1999, 2005, Almany et al. 2007), otolith microchemistry and biophysical modeling are probably more suitable for discriminating larval retention and connectivity among larger, more distant populations (Swearer et al. 2002, Patterson et al. 2005, Patterson and Swearer 2007, Hamilton et al. 2008). Cross-validation of these techniques is therefore required before absolute % self-recruitment figures can be considered reliable.

Isolated reefs may be expected to exhibit higher levels of self-recruitment than those in reef archipelagos since the low probability of finding suitable habitat may place a premium on staying close to home. However, some recorded estimates of % self-recruitment appear to be unrelated to distance of nearest habitat. For example, *Pomacentrus coelestis* exhibited 75% self-recruitment at Lizard Island in the Great Barrier Reef, which has many other reefs in close proximity (Patterson et al. 2005), whereas *Coris picta* at isolated Lord Howe Island exhibited 25-63% self-recruitment (Patterson and Swearer 2007).

4.4.3 Implications for MPA design and function

Some key issues for MPA design and function include whether individual MPAs are partially self-sustaining, to what extent they are connected to fished populations, and how connected they are to other MPAs across a network. However, for existing MPA networks, the details of these different factors remain relatively unknown. Evidence that currently active MPAs may be self-sustaining, has come from new methods of tagging larvae (Jones et al. 1999, 2005, Thorrold et al. 2006, Almany et al. 2007, Williamson et al. 2009) and the application of genetic parentage analysis (Jones et al. 2005, Planes et al. 2009, Saenz-Agudelo et al. 2009). These techniques have altered past perceptions about how close to home pelagic fish larvae can settle. For example, Jones et al. (1999) used tetracycline tagging of larvae to show that 30-60% of ambon damselfish recruitment (*Pomacentrus amboinensis* – Box 9) to Lizard Island (Great Barrier Reef -GBR) came from resident adults. This island is now a core no-take reserve in the northern GBR lagoon. Modeling studies not only confirmed this level of self-recruitment, but also showed that Lizard Island is strongly connected to adjacent islands (James et al. 2002) and may also be an important source of larvae to the southern GBR (Bode et al. 2006). Hence, not only is this northern reserve self-sustaining, it may also be an important source of larvae to many other reefs further downstream.

Evidence shows that even relatively small MPAs may be self-sustaining. A recent field study showed that a high proportion of juveniles (~60%) of two fish species recruiting to a small isolated island MPA, were progeny from resident adults (Almany et al. 2007). In another study, genetic parentage analysis using hypervariable nuclear DNA sampled from juveniles and prospective parents, successfully measured the exact dispersal distances of individual larvae (Jones et al. 2005, Planes et al. 2009, Saenz-Agudelo et al. 2009). Parentage analysis has not only confirmed that a large number of fish recruits inside small MPAs are spawned locally, but also that larvae can disperse distances in excess of 30 km, from one MPA to another (Planes et al. 2009).

Once we reach a point where dispersal kernels have been fully described, the size and spacing of individual reserves can be adjusted according to specific goals. Generally it is expected that longer dispersal distances will be an argument for larger (for significant self-replenishment) and more widely spaced reserves (while maintaining significant connectivity) (Jones et al. 2007, Almany et al. 2009). In any case, populations that are primarily self-sustaining (e.g., isolated islands) and/or important sources of larvae (e.g., upstream sites) will be a high priority in MPA site selection.

Box 10. Methods for measuring coral larval dispersal

In order to be proactive in restoring coral reefs, managers need to know where coral larvae could come from so that degraded reefs can be re-seeded. However, it has been difficult to determine actual coral transport and connectivity patterns without the use of extrapolations from population genetics and hydrographic models. Difficulties in measuring coral connectivity arise because coral larvae are:

- Very small (< 1 mm in length);
- Difficult to collect from plankton without damaging them;
- Difficult to ID to individual species.

In addition, newly settled coral recruits are almost invisible so they are difficult to sample or monitor.

Innovative techniques are being developed to directly measure coral larval transport:

1) Enzyme-Linked Immunosorbent Assay (ELISA)

Is used to detect and positively identify larvae in plankton as they disperse. It can also be used to assess the richness of a larval pool in any given area during the time frame surrounding spawning. These assays are currently being improved to make them more quantitative. Results could provide both assessment of larval supply originating from healthy reefs and supply of larvae reaching any given target reef. This method is easy to learn and relatively inexpensive.

2) Magnetic beads

Can be used to track dispersal of larval cohorts. Small magnetic beads are constructed to be of similar size and density of a biological target (= mini drift beads). The beads are then deployed at a specific location within a spawning mass. Magnetic collectors deployed at various distances from that point source (kms to 100s of kms) will then passively accumulate the magnetic beads. Collectors sampled at various times after spawning provide a record of the number of beads recovered at different distances from the source. This technique is useful for any detailed study of dispersal of small particles in a water column and can display actual dispersal patterns of coral larva mimics. This data can then be used to validate dispersal models.

To use these techniques for management purposes we need the following information:

1) Biological characteristics:

- Development pattern of each species (passive vs. active behavior);
- Time to competency (days to weeks);
- Duration of competency (days to weeks).

2) Physical determinants:

- Hydrographic patterns of source and receiving areas;
- Weather during larval period;
- Distribution and distance between source and receiving sites;
- How cohorts of larvae disperse over time and space.

4.4.4 Conclusions and challenges

The proliferation of larval connectivity studies in the last 10-15 years, at scales ranging from individual reefs to several hundred kilometers, has revealed a number of interesting patterns. Levels of connectivity among reef populations clearly range from high levels of self-recruitment within a small area to significant dispersal at scales of 10s of kms, and sometimes in excess of 100s of kms. Also, variation in dispersal distance within fish species is likely to be large, and the differences do not appear to be closely related to pelagic larval duration. Geographic isolation and spacing of reefs may therefore have a greater influence on dispersal than individual species characteristics.

The likely wide variation in dispersal distance should contribute to the resilience of local populations. It allows for considerable flexibility in the design of MPA networks when trying to achieve sustainable harvesting and biodiversity conservation. If the geographic setting has a greater influence than species characteristics on connectivity levels, optimizing MPA design for the majority of species may not be an insurmountable problem. Optimal design will be best approached using fine-grained biophysical models applied to a particular geographic setting, supplemented with independent verification of dispersal and connectivity for representative species, using individual identification techniques (e.g., larval tagging, parentage analysis, etc.).

Despite the substantial research effort that has already taken place, large gaps in our knowledge concerning the extent of larval connectivity remain. A full description of a dispersal kernel has not yet been achieved for any coral reef species. Demographically relevant levels of larval connectivity may be modified by the availability of recruitment habitat (Jones et al. 2007) and a suite of post-recruitment processes (Hamilton et al. 2008, Steneck et al. 2009). As the magnitude and scale of coral reef degradation increases, any resilience provided by broad dispersal kernels and MPA networks will quickly erode. Until demographic connectivity is fully quantified, our understanding of human impact on reef organisms, and the tools needed to effectively manage reefs, will be limited.

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- Some key issues for MPA design and function include whether individual MPAs are partially self-sustaining, to what extent they are connected to fished populations, and how connected they are to other MPAs across a network.
- The lack of information on how far marine larvae disperse has historically been an impediment to managing marine populations and designing MPA networks.
- With the application of many new approaches our grasp of the extent of larval connectivity has changed dramatically in the last 10-15 years. However, the exact scale of dispersal significant to population dynamics and resource management is still an issue since a complete dispersal curve has not yet been described for any species.
- Studies reveal that many reef species are capable of making precise microhabitat choices at the time of settlement, during larval stages, and that specific cues are used at different stages upon return to juvenile and adult habitat.
- Mapping of pre-spawning and post-spawning migration patterns of aggregating fishes is also an area of little directed research.
- Percent self-recruitment provides a useful index for the degree to which a local marine population may be considered “open” or “closed”.
- Coral and fish studies provide evidence of both extremely local scale patterns of self-recruitment (at scales of less than 1 km) and ecologically significant connectivity among reefs at scales of 10s of kilometers (and in some cases 100s of kilometers).
- Evidence that existing MPAs may be self-sustaining has come from new methods of tagging larvae and the application of genetic parentage analysis.

Section 5
Integrating connectivity with management today

In this section you will find:

Only limited data are now available on connectivity of marine species

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Species differ in the spatial scales at which they are connected, and connectivity patterns are also transient through time

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Management of coastal marine species is ultimately management of people

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Rules of thumb for incorporating connectivity information into management

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Fishing boats, Puerto Morelos, Mexico. Photo: Hanneke Van Lavieren

5. Integrating connectivity with management today

5.1 Only limited data are now available on the connectivity of marine species

Despite considerable effort by many scientists over the last two decades, only limited data on the connectivity of marine species exists today. Coral reef species may be better known than others in this respect, as much of the available information has been derived from coral reef studies. Although a number of innovative techniques have been developed, the nature of the question ensures that all techniques, with the exception of biophysical modeling, require relatively intensive fieldwork at numerous sites over extended periods of time. For example, any study using a genetic parentage or assignment approach, or otolith tag technique to determine connectivity in a fish species, will require extensive sampling of newly recruited juveniles (or of soon to settle larvae) over a spatial scale of at least 100 km. This is necessary to ensure that adequate numbers from an appropriate geographic range are collected so that clear patterns of dispersal can be characterized. Furthermore, the sampling effort will likely need to be contemporaneous in order to capture the correct cohort of newly settled recruits (those bearing tags). Undertaking such work would require a large team or considerable funds to support travel of a small team throughout the study region. Furthermore, it would be difficult to find funding for such studies from conventional research granting agencies. On the other hand, a partnership between scientists and managers could solve the problem of broadly distributed sampling (if the managers are distributed at sites across the region) while ensuring that the data collected will be available promptly to the managers who need them. If there was ever an area of research that would benefit from scientist/manager partnerships, pinning down precise estimates of connectivity patterns for specific species is it.

> *If ever there was an area of research that would benefit from scientist/manager partnerships, the effort to pindown precise estimates of connectivity patterns for specific species is it.*

Still, while the sparse data are being augmented by new research, management has to make do with what is currently available. "Rules of thumb" suggested throughout this handbook, offer managers a reasonable guess as to the optimal approach when making management decisions involving connectivity. These should be applied, but with clear recognition that they are current best estimates, rather than rigorously founded scientific data. The good news is that there are now some reasons for optimism. Regularities across species and regions are emerging as new data are collected, and this may make a manager's tasks less complex than it might have been previously. For example, empirical and modeling work are now suggesting that the physical geography of available habitat in a region has a major role in determining connectivity patterns among sites. That is, while species with radically different larval biology will not respond in the same way to a particular geography, species with moderately similar larval biology will disperse in very similar patterns across that landscape. This apparent regularity means that it will not likely be necessary to research the connectivity patterns of each species of interest, and also that it may be possible to design sets of NTRs that serve a number of target species in a close to optimal manner. The problem remains however, that we have sensitive techniques, and considerable amassed data for fish species, but far fewer techniques or connectivity data available for corals, lobster, other invertebrates, and algae.

Waving our arms about while talking about apparent regularities, or general patterns, is not an appropriate way to deal with the paucity of data on connectivity. The sooner scientists and managers commence a serious effort to answer the difficult questions, such as what is the optimum size for an MPA, the better off our science and management of coral reefs will be.

Box 11. Climate change and connectivity

Climate change is causing significant changes in sea surface temperatures, ocean circulation, ocean chemistry, weather patterns (e.g., cyclones, storms, and rainfall) and sea levels. These changes will likely affect many key ecological processes such as population connectivity among reef ecosystems. At the same time, the degree of this connectivity will influence the ability of coral reef organisms to adapt to these changes because high connectivity will allow for the exchange of favorable genotypes which are more resilient to the effects of climate change, while facilitating recovery from localized damage caused by storms and bleaching.

Our understanding of the potential impacts of climate change on the connectivity of reef populations is incomplete. However, we have evidence which suggests the following potential effects on reef fish populations (Munday et al. 2009):

- Higher water temperature can lead to changes in timing of reproduction, reduced reproductive output and shorter pelagic life stages.
- Changes in ocean currents can alter the dynamics of larval supply and affect planktonic productivity, this may affect the number of larvae surviving the pelagic stage and their settlement ability.
- More intense cyclones will increase the rate of reef destruction, while warmer temperatures will enhance the frequency and severity of coral bleaching. Both factors will lead to loss and fragmentation of reef fish habitat unless reef-building and repair processes can keep pace.
- Changes in ocean chemistry (ocean acidification) are likely to reduce the capacity of coral populations to recover from bleaching or storm damage thus increasing the risk that reef fish habitat will be reduced.
- Rising sea level can alter larval dispersal patterns due to changes in water movements and currents.

These potential impacts will vary from place to place as well as over time. Changes in the spatial and temporal scales of connectivity have implications for management of coral reef ecosystems. For example, although far from certain, evidence suggests that climate change will likely reduce the dispersal distance of reef organisms chiefly by shortening larval duration. This means that the size and spacing of MPAs may need to be strategically adjusted if reserve networks are to retain their efficacy into the future.

5.2 Species differ in the spatial scales at which they are connected, and connectivity patterns are also transient throughout time

Even with the limited data now available, we know that species with substantially different larval biology may respond very differently to a particular geography and water movement patterns. Also, species with larger adult home ranges will respond quite differently to species that are sedentary or sessile as adults. For these reasons, although a particular MPA management regime may be "more or less" optimal for a number of species, it may not be optimal for all. Managers who seek to design MPA networks must begin by choosing goals, and these goals will frequently be species specific, or sometimes "functional group" specific. However, it should be remembered that as much as we may desire a management regime that serves the needs of all fishery targets, or even all species, this has always been impossible. Management can only be improved when the limitations of the management actions are explicitly recognized.

Management can only be improved when the limitations of the management actions are explicitly recognized.

An additional problem is that current empirical data reveal that connectivity patterns are temporally variable in response to temporally variable oceanography. This complicates the task of determining connectivity patterns experimentally because the results will always be time-dependent. Modeling offers a way to move beyond this limitation because a model can be run under oceanography characteristic of different time periods, and this would generate answers about the extent of such temporal variation. Temporal variation will likely ensure that there are rarely places in which populations can exclusively be classified as either source or sink, and that there are commonly places in which the majority of populations are alternately source and sink. Much of the developing theory on management of regions containing source and sink populations may start to be seen as esoteric, compared to the usual real world situation. Finally, temporal variation also likely means that for fisheries management, MPA networks will turn out to be relatively blunt-edged tools rather than the razor-sharp instruments envisioned by some advocates. This reinforces the argument that fisheries management is a difficult task requiring the application of many, rather than a single tool.

Figure 33. *Montastrea faveolata*. There are a number of sensitive techniques, and considerable amassed data for fish species, but far fewer techniques or connectivity data are available for corals, lobster, other invertebrates or algae Photo: http://coralpedia.bio.warwick.ac.uk/en/corals/montastraea_faveolata.html

The focus of connectivity research has been centered on larval dispersal for a number of obvious reasons. However, this interest has revealed just how little we know about the movement of juveniles and adults of most reef species. There is need for new research on this topic, and a need to ensure that juvenile and adult movements are catered for in management plans so that the preservation of important corridors and the protection of critical habitats is ensured. The use of NTRs for fisheries management is not simply a case of placing NTRs of appropriate size and spacing across a region. It also requires that protected sites are positioned to maximally benefit target species by protecting critical linkages between nursery and adult habitat, protecting spawning habitat, and catering to the needs of organisms that move beyond protected habitat borders.

5.3 Management of coastal marine species is ultimately management of people

Ultimately, reef managers are managers of people, or more specifically, managers of the negative impact that humans can have on the species and habitats concerned. While fisheries management is by no means the only role for coral reef managers, it is an important and difficult task because in most reef regions, coastal fisheries are intensively exploited by a mixed commercial/artisanal fishing community which uses a range of techniques to harvest a broad suite of species of differing biology. The complexity of fisheries makes its management particularly problematical, and overexploitation and need to reduce effort makes the challenge extreme.

Figure 34. Management of coastal marine species is ultimately management of human activities. Photo: Andy Hooten

In developing countries where the fishing industry is characterized by a high diversity of target species and a wide array of fishing gears, species-based fisheries management strategies such as restricting landed catch to a recommended size, using closed seasons, and limiting catch, will be necessary in many instances even if NTRs are also used. Examples include the hook-and-line fishery for groupers and snappers or fisheries which target invertebrates such as sea urchins and giant clams.

> *Our management of coral reef systems would improve immensely if we simply started enforcing the regulations that already exist in most jurisdictions.*

Area-based and spatially explicit management approaches, however, are more common and certainly more expedient for managing multi-gear and multi-species fisheries. Defining fishing zones where only specific fishing gears may be used is a common practice in countries in southeast Asia and Africa (McClanahan and Mangi 2004, Ablan and Garces 2005). Establishing "no-take" zones which are expected to function as fisheries reserves is a strategy that seems to have high compliance when well managed (Russ and Alcala 1999). In such circumstances, information about connectivity becomes essential to decision-making.

Ultimately, management must be implemented so that it really changes the way humans impact coastal ecosystems. Catch limits, size limits, and closed seasons can all reduce fishery exploitation, but only if they are rigorously enforced. NTRs and NTR networks can also function to help manage reef fisheries, but again, only if regulations are rigorously enforced. Despite the need for new science to better delineate connectivity in coral reef systems, our management of coral reef systems would improve immensely if we simply started enforcing the regulations that already exist in most jurisdictions. An awareness of connectivity, and particularly of how it can show that inappropriate activities in one location can have deleterious consequences at other locations, provides added ammunition for those who want to fight for better coastal and reef management.

In a world in which climate is changing rapidly, with consequences that are not yet fully apparent, it will be more important than ever to ensure that coral reef and other coastal ecosystems are managed as effectively as possible.

Figure 35. In developing countries where mixed commercial/artisanal fishing communities use a range of techniques to harvest a broad suite of target species, species-based fisheries management strategies such as minimum fish sizes, closed seasons, and catch limits, will often be necessary even if NTRs are also used. Photo: Yvonne Sadovy

In a world in which climate is changing rapidly, with consequences that are not yet fully apparent, it is more important than ever to ensure that coral reefs and other coastal ecosystems are managed as effectively as possible. Only in this way will they have any likelihood of possessing the resilience that will be needed to adapt successfully to climate change.

Message board

- We have sensitive techniques, and considerable amassed data for fish species, but far fewer techniques or connectivity data available for corals, lobster, other invertebrates, and algae.
- Although a particular MPA management regime may be "more or less" optimal for a number of species, it may not be optimal for all.
- Temporal variation in connectivity patterns complicates the task of experimentally determining connectivity patterns.
- Ultimately, reef managers are managers of people, or more specifically, of the negative impact that humans can have on the species and habitats concerned.
- An awareness of connectivity, and particularly of how it can show that inappropriate activities in one location can have deleterious consequences at other locations, provides added ammunition for those who want to fight for better coastal and reef management.

Rules of thumb for incorporating connectivity information into management

Note: These rules of thumb can be applied, but only with recognition that they serve as current best estimates, rather than rigorously defined scientific principles.

1) Set clear goals

- Managers who seek to design MPAs and/or MPA networks must begin by choosing management goals; these will frequently be "species" specific, or sometimes "functional group" specific and may relate to fisheries enhancement, biodiversity conservation, habitat protection or other objectives. Although a particular management regime may be optimal for a number of species, it may not be optimal for all.

2) Apply a systems approach

- Think big; manage entire coastal regions rather than isolated protected areas.
- Recognize patterns of connectivity within and among ecosystems, including linkages among coastal habitats (e.g., reefs, seagrass, mangroves and wetlands), linkages between these and "upstream" terrestrial and freshwater habitats, linkages to activities taking place in coastal zones (e.g., tourism development), and dynamic processes (e.g., currents and rivers).
- Include entire biological units and a buffer zone around the core area of interest.

3) Incorporate different aspects of connectivity into network design

I. Larval dispersal:

- Within a network, aim for NTRs that are of a size which ensures that a reasonable number of individuals of the target species complete all life stages within natal NTR borders.
- Aim for a network that provides for a wide range of dispersal distances between protected areas.
- Take into account that the larval dispersal distance of some species is smaller than previously thought and that local retention of reef fish larvae is prevalent.
- MPAs should be placed within 10-30 km from each other to capture effective connectivity for most target reef species.
- Variable spacing is better than uniform spacing when networks consist of several small reserves rather than a few large reserves (as long as they are within the 10-30 km range).

II. Movement in later life:

- To protect a range of species within an MPA or MPA network, the range of juvenile and adult movement patterns should be considered.
- Spawning migration routes and habitats required at different life stages, and daily or seasonal pathways used by target species, should be protected.
- Ultimately, an MPA network that protects species with more extensive adult movement patterns will likely also protect more sedentary species.

III. Habitats:

Protect habitats that are important for maintaining connectivity including:

- Critical habitats: habitats that are critical during the target species life cycle (e.g., nursery grounds, nesting and spawning sites).
- Refugia: areas protected from disturbances; these may serve as sources of propagules for recolonization of damaged sites.
- Isolated sites: these often have endemic and unique assemblages, low genetic diversity, small populations and low connectivity (e.g., remote oceanic reefs); these characteristics make them less resilient to disturbance (McCook et al. 2009).

- Consider the potential impacts of coastal development, pollution and other human activities on near shore habitats as well as on crucial pathways used by reef organisms during their life cycle.

IV. Water movement:

- In areas where currents are complex (e.g., eddies or reverse flows), an even spread of MPA locations is recommended.
- Certain populations can act as consistent sources and others as sinks for dispersing organisms. In areas where currents are strongly directional, MPAs sited in upstream locations will be more likely to support recruitment to other management areas.
- Anticipate that climate change may lead to changes in current regimes, and ensure that legal instruments governing the MPA network make provisions for change in the spatial pattern of management in the future.

4) Conduct targeted research to fill information gaps

- Because the scientific base supporting environmental management is weak, a strong plea is made for scientists and managers to establish close working collaborations and use management activities in an adaptive management context to simultaneously advance the scientific understanding of connectivity, while also using the best available knowledge to guide current management decisions.
- Research programs associated with either the development of MPAs and MPA networks, or with improving their effectiveness, should include studies of population connectivity (e.g., larval biology, behavior and dispersal of targeted species).

5) Manage buffer zones and surrounding areas

- Protecting the species and habitats located within the "invisible" boundaries of an NTR is not sufficient by itself. Sustainable fisheries practices and good environmental quality in surrounding non-reserve areas are also necessary for achieving healthy ecosystem processes and linkages. Monitoring and management outside MPA boundaries is essential.

6) Use models together with field research

- Optimal MPA network design is best approached using fine-grained biophysical models applied to specific geographic settings and supplementing these models with independent field studies of dispersal and connectivity of representative species (e.g., studies using individual identification techniques like larval tagging, parentage analysis, etc.).

7) Ensure enforcement and monitoring

- Ensure compliance with management plan regulations, and monitor long term impacts on protected habitats and organisms so that the effectiveness of management efforts can be measured.

8) Educate

- Educate and inform coastal communities, management agencies and governments on the concept and importance of maintaining connectivity in coastal ecosystems.

9) Be adaptive

- Scientists and managers should work together in long-term adaptive management programs in which setting up a network or taking other management action provides an opportunity to test the effectiveness of actions and the underlying science.
- Use new information and understanding of connectivity in management programs as it emerges, while recognizing that we will never have the full picture of how coastal systems function.
- Adapt coral reef ecosystem management to climate change impacts on connectivity processes as they occur.

References

Abesamis, R.A, and G.R. Russ, 2005. Density-dependent spillover from a marine reserve: long-term evidence. Ecological Applications 15: 1798-1812.

Ablan, M.C.A., and L.R. Garces, 2005. Exclusive economic zones and the management of coastal fisheries in the South China Sea. In: Ebbin, S., A. Sydnes, and A.H. Hoel (Eds.), A sea change: the exclusive economic zone and governance institutions for living marine resources. Springer, pp. 136-149.

Almany, G.R, 2007. Population connectivity and conservation of marine biodiversity. Oceanography 20: 100-111.

Almany, G.R., M.L. Berumen, S.R. Thorrold, S. Planes, and G.P. Jones, 2007. Local replenishment of coral reef fish populations in a marine reserve. Science 316: 742-744.

Almany, G.R., S.R. Connolly, D.D. Heath, J.D. Hogan, G.P. Jones, L.J. McCook, M. Mills, R.L. Pressey, and D.H. Williamson, 2009. Connectivity, biodiversity conservation, and the design of marine reserve networks for coral reefs. Coral Reefs 28: 339-351.

Andréfouët, S., S. Ouillon, R. Brinkman, J. Falter, P. Douillet, F. Wolk, R. Smith, P. Garen, E. Martinez, V. Laurent, C. Lo, G. Remoissenet, B. Scourzic, A. Gilbert, E. Deleersnijder, C. Steinberg, S. Choukroun, and D. Buestel, 2006. Review of solutions for 3D hydrodynamic modeling applied to aquaculture in South Pacific atoll lagoons. Marine Pollution Bulletin 52: 1138-1155.

Armsworth, P.R., and J.E. Roughgarden, 2005. The impact of directed versus random movement on population dynamics and biodiversity patterns. American Naturalist 165: 449-465.

Atema, J., M.J. Kingsford, and G. Gerlach, 2002. Larval reef fish could use odour for detection, retention and orientation to reefs. Marine Ecology Progress Series 241: 151-160.

Becker, B.J., L.A. Levin, F.J. Fodrie, and P.A. McMillan, 2007. Complex larval connectivity patterns among marine invertebrate populations. Proceedings of the National Academy of Sciences 104: 3267-3272.

Bell, C., S.W. Purcell, and W.J. Nash, 2008. Restoring small-scale fisheries for tropical sea cucumbers. Ocean and Coastal Management 51: 589-593.

Bode, M., L. Bode, and P.R. Armsworth, 2006. Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. Marine Ecology Progress Series 308: 17-25.

Botsford, L.W., C.L. Moloney, A. Hastings, J.L. Largier, T.M. Powell, K. Higgins, and J.F. Quinn, 1994. The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. Deep-Sea Research Part II: Topical Studies in Oceanography 41: 107-145.

Botsford, L.W., 2001. Physical influences on recruitment to California current invertebrate populations on multiple scales. ICES Journal of Marine Science 58: 1081-1091.

Botsford, L.W., C.A. Lawrence, M.F. Hill, A. Hastings, and K.S. McCann, 2002. Dynamic response of California current populations to environmental variability. American Fisheries Society Symposium 32: 215-226.

Botsford, L.W., J.W. White, M-A. Coffroth, C.B. Paris, S. Planes, T.L. Shearer, S.R. Thorrold, and G.P. Jones, 2009. Measuring connectivity and estimating resilience of coral reef metapopulations in MPAs: matching empirical efforts to modeling needs. Coral Reefs 28: 327-337.

Butler, M.J. IV, C.B. Paris, J.S. Goldstein, H. Hirokazu Matsuda, and R.K.Cowen, (in review). Behavior constrains the dispersal of long-lived spiny lobster larvae, submitted to Limnology and Oceanography, December 2009.

Campana, S.R., 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188: 263-297.

Chittaro, P.M., P. Usseglio, B.J. Fryer, and P.F. Sale, 2005. Using otolith microchemistry of *Haemulon flavolineatum* (French Grunt) to characterize mangroves and coral reefs throughout Turneffe Atoll, Belize: difficulties at small spatial scales. Estuaries and Coasts 28: 373-381.

Cowen, R.K., K.M.M. Lwiza, S. Sponaugle, C.B. Paris, and D.B. Olson, 2000. Connectivity of marine populations: Open or closed? Science 287: 857-859.

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

Cushing, D.H., 1990. Recent studies on long-term changes in the sea. Freshwater Biology 23: 71-84.

Dixson, D.L., G.P. Jones, P.L. Munday, S. Planes, M.S. Pratchett, M. Srinivasan, C. Syms, and S.R. Thorrold, 2008. Coral reef fish smell leaves to find island homes. Proceedings of the Royal Society of London, Series B 275: 2831-2839.

Gerlach, G., J. Atema, M.J. Kingsford, K.P. Black, and V. Miller-Sims, 2007. Smelling home can prevent dispersal of reef fish larvae. Proceedings of the National Academy of Science 104: 858-863.

Gillanders, B., 2005. Using elemental chemistry of fish otoliths to determine connectivity between estuarine and coastal habitats. Estuarine, Coastal and Shelf Science 64: 47-57.

Goldstein, J.S., H. Matsuda, T. Takenouchi, and M.J. Butler IV., 2008. A description of the complete development of larval Caribbean spiny lobster *Panulirus argus* (LATREILLE, 1804) in culture. Journal of Crustacean Biology 28: 306-327.

Goldstein, J.S., and M.J. Butler IV., 2009. Behavioral enhancement of onshore transport by postlarval Caribbean spiny lobster (*Panulirus argus*). Limnology and Oceanography 54: 1669-1678.

Hamilton, S.L., J. Regetz, and R.R. Warner, 2008. Postsettlement survival linked to larval life in a marine fish. Proceedings of the National Academy of Sciences of the United States of America 105: 1561-1566.

Hastings, A., and L.W. Botsford, 2006. Persistence of spatial populations depends on returning home. Proceedings of the National Academy of Sciences of the United States of America 103: 6067-6072.

Hogan, J.D., R. Fisher, and C. Nolan, 2007. Critical swimming speed of settlement-stage coral reef fishes from the Caribbean: A methodological and geographical comparison. Bulletin of Marine Science 80: 219-231.

Irisson, J.O., A. Levan, M. de Lara, and S. Planes, 2004. Strategies and trajectories of coral reef fish larvae optimizing self-recruitment. Journal of Theoretical Biology 227: 205–218.

IUCN/WCPA, 1994. Guidelines for protected area management categories, Gland, Switzerland.

IUCN/WCPA, 2008. Guidelines for applying protected area management categories, 3rd draft of revised guidelines.

James, M.K., P.R. Armsworth, L.B. Mason, and L. Bode, 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. Proc. B., Royal Society of London, 269: 2079-2086.

Jones, G.P., M.J. Milicich, M.J. Emslie, and C. Lunow, 1999. Self-recruitment in a coral reef fish population. Nature 402: 802-804.

Jones, G.P., M. Srinivasan, G.R. Almany, 2007. Population connectivity and conservation of marine biodiversity. Oceanography 20: 100-111.

Jones, G.P., G.R. Almany, G.D. Russ, P.F. Sale, R.S. Steneck, M.J.H. van Oppen, and B.L. Willis, 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28: 307-325.

Kingsford, M.J., J.M. Hughes, and H.M. Patterson, 2009. Otolith chemistry of the non-dispersing reef fish *Acanthochromis polyacanthus*: cross-shelf patterns from the central Great Barrier Reef. Marine Ecology Progress Series 377: 279-288.

Kritzer, J.P., and P.F. Sale, 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries 5: 131-140.

Largier, J.L., 2003. Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13: 71-89.

Leis, J.M., 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes. In: P.F. Sale, (Ed.), The ecology of fishes on coral reefs. Academic Pres, San Diego, pp. 183-230.

Levin, S.A., H.C. Muller-Landau, R. Nathan, and J. Chave, 2003. The ecology and evolution of seed dispersal: A theoretical perspective. Annual Review of Ecology, Evolution, and Systematics 34: 575-604.

Lubchenco, J., S. Palumbi, S. Gaines, and S. Andelman, 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13: 3-7.

Martinez, E., K. Maamaatuaiahutapu, C. Payri, and A. Gamachaud, 2006. *Turbinaria ornata* invasion in the Tuamotu Archipelago, French Polynesia: ocean drift connectivity. Coral Reefs 26: 79-86.

McClanahan,T.R, and S.R. Mangi, 2004. Gear-based management of a tropical artisanal fishery based on species selectivity and capture size. Fisheries Management and Ecology 11: 51-60.

McCook, L.J., G.R. Almany, J. Day, A. Green, G.P. Jones, J.M. Leis, S. Planes, G.R. Russ, P.F. Sale, and S.R. Thorrold, 2009. Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. Coral Reefs 28: 353-366.

Meyer, C.G, K.N. Holland, B.M. Wetherbee, and C.G. Lowe, 2000. Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, Parupeneus porphyreus, in a marine reserve. Environmental Biology of Fishes 59: 235-242.

Mumby, P.J., C.P. Dahlgren, A.R. Harborne, C.V. Kappel, F. Micheli, D.R. Brumbaugh, K.E. Holmes, J.M. Mendes, K. Broad, J.N. Sanchirico, K. Buch, S. Box, R.W. Stoffle, and A.B. Gill, 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311: 98-101.

Munday, P.L., J.M. Leis, J.M Lough, C.B. Paris, M.J. Kingsford, M.L. Berumen, and J. Lambrechts, 2009. Climate change and coral reef connectivity. Coral Reefs 28: 379-395.

Okubo, A., and S.A. Levin, 1989. Diffusion and Ecological Problems: Modern Perspectives, Springer NY, pp. 469.

Paris, C.B., R.K. Cowen, K.M.M. Lwiza, D.P. Wang, and D.B. Olson, 2002. Objective analysis of three-dimensional circulation in the vicinity of Barbados, West Indies: Implication for larval transport. Deep Sea Research 49: 1363-1386.

Paris, C.B., and R.K. Cowen, 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnology and Oceanography 49: 1964-1979.

Paris, C.B., R.K. Cowen, R. Claro, and K.C. Lindeman, 2005. Larval transport pathways from Cuban spawning aggregations (Snappers; Lutjanidae) based on biophysical modeling. Marine Ecology Progress Series 296: 93-106.

Paris, C.B., L.M. Cherubin, and R.K. Cowen, 2007. Surfing, spinning, or diving from reef to reef: effects on population connectivity. Marine Ecology Progress Series 347: 285-300.

Patterson, H.M., M.J. Kingsford, and M.T. McCulloch, 2005. Resolution of the early life history of a reef fish using otolith chemistry. Coral Reefs 24: 222-229.

Patterson, H.M., and S.E. Swearer, 2007. Long-distance dispersal and local retention of larvae as mechanisms of recruitment in an island population of a coral reef fish. Austral Ecology 32: 122-130.

Planes, S., S.R. Thorrold, and G.P. Jones, 2009. Larval dispersal connects fish populations in a network of marine protected areas. Proceedings of the National Academy of Sciences of the United States of America 106: 5693-5697.

references

Raymundo, L.J., A.P. Maypa, E.D. Gomez, and P. Cadi, 2007. Can dynamite-blasted reefs recover? A novel, low-tech approach to stimulating natural recovery in fish and coral populations. Marine Pollution Bulletin 54: 1009-1019.

Roberts, C.M., 1997. Connectivity and management of Caribbean coral reefs. Science 278: 1454-1457.

Roberts, C.M., J.A. Bohnsack, F. Gell, J.P. Hawkins, and R. Goodridge, 2001. Effects of marine reserves on adjacent fisheries. Science 294: 1920-1923.

Russ, G.R., and A.C. Alcala, 1999. Management histories of Sumilon and Apo marine reserves, Philippines and their influence on national marine resource policy. Coral Reefs 18: 307-319.

Russ, G.R., 2002. Yet another review of marine reserves as reef fishery management tools. In: Sale, P.F. (Ed.), Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp. 421-444.

Russ, G.R., A.C. Alcala, and A.P. Maypa, 2003. Spillover from marine reserves: the case of *Naso vlamingii* at Apo Island, the Philippines. Marine Ecology Progress Series 264: 15-20.

Ruttenberg, B.I., S.L. Hamilton, and R.R. Warner, 2008. Spatial and temporal variation in the metal otolith chemistry of a Hawaiian reef fish: prospects for measuring population connectivity. Canadian Journal of Fisheries and Aquatic Sciences 65: 1181-1192.

Saenz-Agudelo, P., G.P. Jones, S.R. Thorrold, and S. Planes, 2009. Estimating connectivity in marine populations: an empirical evaluation of assignment tests and parentage analysis at different spatial scales. Molecular Ecology 18: 1765-1776.

Sale, P.F., R.K. Cowen, B.S. Danilowicz, G.P. Jones, J.P. Kritzer, K.C. Lindeman, S. Planes, N.V.C. Polunin, G.R. Russ, Y.J. Sadovy, and R.S. Steneck, 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution 20: 74-80.

Steneck, R.S., C.B. Paris, S.N. Arnold, M.C. Ablan-Lagman, A.C. Alcala, M.J. Butler, L.J. McCook, G.R. Russ, and P.F. Sale, 2009. Thinking and managing outside the box: Coalescing connectivity networks to build region-wide resilience in coral reef ecosystems. Coral Reefs 28: 367-378.

Stephens, P.A., W.J. Sutherland, and R.P. Freckleton, 1999. What is the Allee effect? Oikos 87: 185-190.

Stewart, H.L., 2006. Ontogenetic changes in buoyancy, breaking strength, extensibility and reproductive investment in a rafting macroalga *Turbinaria ornata* (Phaeophyta). Journal of Phycology 42: 43-50.

Stewart, H.L., 2008. The role of spatial and ontogenetic morphological variability in the range expansion of the tropical brown alga, *Turbinaria ornata*. Integrative and Comparative Biology 48: 713-719.

Stiger, V., and C.E. Payri, 1999. Spatial and seasonal variation in the biological characteristics of two invasive brown algae, *Turbinaria ornata* (Turner) J. Agardh and *Sargassum mangarevense* (Grunow) Setchell (Sargassaceae, Fucales) spreading on the reefs of Tahiti (French Polynesia). Botanica Marina 42: 295-306.

Stobutzki, I.C., and D.R. Bellwood, 1997. Sustained swimming abilities of the late pelagic stages of coral reef fishes. Marine Ecology Progress Series 149: 35-41.

Stoner, A.W., and M. Ray, 1996. Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production. Fishery Bulletin 94: 551-565.

Sugden, A., and E. Pennisi, 2006. When to go, where to stop. Science 313: 775.

Sutherland, W.J., J.A. Gill, and K. Norris, 2002. Density-dependent dispersal in animals: concepts, evidence, mechanisms and consequences. In: Bullock, J.M., R.E. Kenward, and R.S. Hails (Eds.), Dispersal ecology. Blackwell Publishing, Malden, Massachusetts, USA, pp. 135-151.

Swearer, S.E., J.E. Caselle, D.W. Lea, and R.R. Warner, 1999. Larval retention and recruitment in an island population of a coral-reef fish. Nature 402: 799-802.

Swearer, S.E., S.R. Thorrold, J.S. Shima, M.E. Hellberg, G.P. Jones, D.R. Robertson, K.A. Selkoe, G.M. Ruiz, S.G. Morgan, and R.R. Warner, 2002. Evidence for self-recruitment in benthic marine populations. Bulletin of Marine Science 70: 251-272.

Sweatman, H.P.A., 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. Journal of Experimental Marine Biology and Ecology 124: 163-174.

Thorrold, S.R., G.P. Jones, S. Planes, and J.A. Hare, 2006. Transgenerational marking of embryonic otoliths in marine fishes using barium stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 63: 1193-1197.

UN Convention on Biological Diversity, 1992. http://www.cbd.int/convention/convention.shtml

UNEP-WCMC, 2008. National and regional networks of marine protected areas: A review of progress. UNEP-WCMC, Cambridge.

Werner, F.E., R.K. Cowen, and C.B. Paris, 2007. Coupled biophysical models: Present capabilities and necessary developments for future studies of population connectivity. Oceanography 20: 54-69.

Williamson, D.H., G.P. Jones, S.R. Thorrold, and A.J. Frisch, 2009. Transgenerational marking of marine fish larvae: stable isotope retention, physiological effects and health issues. Journal of Fish Biology 74: 891-905.

Other useful references

Methods Manual: Selected methods for monitoring coral reef fish, juvenile corals and spiny lobster post-larvae. CRTR, UNU-INWEH. 2007.

Van Lavieren, H., 2009. The science of no-take fishery reserves: A guide for managers. CRTR and UNU-INWEH Brochure.

A handbook for the conservation & management of reef fish spawning aggregations. SCRFA.

A

Appendices

Appendix 1

Acronyms

CBD	Convention on Biological Diversity
CMS	Multi-Scale Connectivity Modeling System
CRIOBE	Le Centre de Recherches Insulaires et Observatoire de l'Environnement de Polynésie Française
CRTR	The Coral Reef Targeted Research and Capacity Building for Management Program
ELISA	Enzyme-Linked Immunosorbent Assay
ESMF	Earth System Modeling Framework
GIS	Geographic Information System
GPS	Global Positioning System
HYCOM	Hybrid Coordinate Ocean Model
IBM	Individual Based Model
IUCN	International Union for Conservation of Nature
LSM	Stochastic Lagrangian Model
MCPA	Marine and Coastal Protected Area
MMA	Marine Management Area
MPA	Marine Protected Area
NPZ	Nutrient-Phytoplankton-Zooplankton
NTR	No-take (fishery) Reserve
OGCM	Ocean General Circulation Model
OPeNDAP	Open Project for Network Data Access Protocol
PLD	Pelagic Larval Duration
POM	Princeton Ocean Model
ROMS	Regional Ocean Modeling System
UNU-INWEH	United Nations University - Institute for Water, Environment and Health

Appendix 2

Key definitions

Adaptive management – A resource management program in which management actions are deliberately used as experimental manipulations of the managed system to test predictions of alternative models. In this way, scientific understanding is expanded and management becomes more effective.

Allee effect – The limitation on spawning success that can occur when the numbers of reproductive individuals present has been reduced sufficiently, by harvest or by indirect impacts, to make finding a mate more difficult.

Benthic – Relating to the close proximity to the substratum/bottom of a sea or to the organisms that live there.

Chemical signatures – Pattern of trace chemical abundances present in an otolith or other anatomical structure which is characteristic of organisms that have lived at a particular location.

Commensal – Symbiotic relationship in which one species benefits from living within, or in close proximity to a second species which is unaffected by this relationship.

Connectivity – Linking of places or populations through movement of organisms, nutrients, pollutants or other items between them. For the various forms of connectivity please refer to Box 1.

Conspecific – Member of the same biological species.

Planula larva – Flat, free-swimming, ciliated planktonic larval form produced by corals and other cnidarians.

Dispersal – Movement of individual organisms away from a starting location, such as the site where they were spawned. Dispersal may be active or passive.

> **Dispersal curve** – Equals the dispersal kernel.
>
> **Dispersal kernel** – Gives the probability distribution of the location of an individual as a function of its spawning location and time since dispersal commenced. A dispersal kernel can be uni- or multi-modal, depending on the life history, the oceanography and geomorphology of the region, and the degree of habitat fragmentation.
>
> **Natal dispersal** – First movement of an organism from its birth site.
>
> **Larval dispersal** – Spread of larvae from a spawning source to a settlement site.

Flexion – Larval life stage for fish (start of notochord flexion to completion of notochord flexion).

Gaussian distribution – Theoretical frequency distribution for a set of variable data, usually represented by a bell-shaped curve symmetrical about the mean. Also called a normal distribution.

Genetic drift – Process of change in the genetic composition of a population due to chance or random events rather than by natural selection, resulting in changes in allele frequencies over time.

Genetic locus – Location of a gene (or of a significant sequence) on a chromosome.

Genetic marker – Gene or DNA sequence having a known location on a chromosome and associated with a particular trait.

Genotype – Genetic constitution (the genome) of a cell, an individual or an organism. The genotype is distinct from its expressed features, or phenotype.

Homing behavior – Place of birth (or natal origin) is called home. Homing is a common feature in fish, where species return to their place of birth to reproduce.

Imprinting – Rapid learning process by which a newborn or very young animal establishes a behavior pattern, typically of recognition and attraction to another animal of its own kind or, as used here, to a particular habitat feature.

Metapopulation – A population that exists as a set of spatially subdivided local subpopulations interconnected by immigration and emigration. The subdivided reef habitat, and life histories with pelagic larval dispersal and relatively sedentary adults, make it likely that many reef organisms exist as metapopulations in which the overall population is composed of many separate sub-populations connected by larval dispersal.

Metassemblages/Metacommunities – A community formed of species which each occur as metapopulations.

Ontogenetic – Of or relating to the origin and development of individual organisms.

Otolith – Minute calcareous structures found in the inner ear of fish and certain lower vertebrates.

Parentage analysis – By analysing individual genotypes, individuals are assigned to one single parent or parent pair selecting the most likely parent from a pool of potential parents. It allows for the determination of an individual's natal origin if the parents' location at the time of conception is known.

Progeny – Offspring or descendants considered as a group.

Propagules – The fertilized eggs or larvae which will give rise to the next generation.

Puerulus postlarvae – Non-feeding, rapid swimming final larval stage of lobster. The puerulus is a transitional stage which bridges the planktonic and benthic phases of the life cycle. It is a short-lived (ca 3–4 weeks), non-feeding stage (ca 30 mm long) which then swims across the continental shelf toward the shore. When the puerulus reaches shallow water near the shore, it settles.

Recruitment – Addition of a new cohort of young animals to a population. In marine species, recruitment is often measured at the age when animals complete the dispersive larval stage, or at the (later) age when maturity is reached and individuals join the breeding population.

Recruitment subsidy – Enhancement of production of a fishery species within fished locations surrounding one or more no-take reserves, owing to the net export of pelagic larvae from the reserve.

Self-recruitment – Addition of a new cohort (age group) of juveniles to a local population due to the production of larvae by that population.

Sessile – Permanently attached or fixed (to substrate); not free-moving.

Spawning aggregation site – Traditional site to which fish of a particular species return each year to reproduce.

Spawning migration – Movements of organisms to and from spawning grounds.

Spillover – Emigration of adults and juveniles across MPA borders.

Statolith – The calcareous objects that occur within the statocyst or balance organ of crustaceans.

Transmitter tag – Digitally tracked tag.

Appendix 3

CRTR Connectivity Working Group members

Peter Sale, United Nations University, Canada

Ma. Carmen Ablan Lagman, De la Salle University, Philippines

Jesús Ernesto Arias González, CINVESTAV Unidad Merida, Mexico

Mark Butler, Old Dominion University, USA

Mary Alice Coffroth, State University of New York, USA

Robert Cowen, University of Miami, USA

Bret Danilowicz, Georgia Southern University, USA

Geoffrey P. Jones, James Cook University, Australia

Kenyon C. Lindeman, Florida Institute of Technology, USA

Serge Planes, Universite de Perpignan, France

Barry Ruddick, Dalhousie University, Canada

Yvonne Sadovy, The University of Hong Kong, China

Enric Sala, Scripps Institution of Oceanography, USA

Robert Steneck, University of Maine, USA

Alina Szmant, University of North Carolina at Wilmington, USA

Simon Thorrold, Woods Hole Oceanographic Institution, USA

Appendix 4

Contributing author details

Ma. Carmen Ablan Lagman
Associate Professor, Biology Department
De La Salle University Manila
2401 Taft Avenue, Manila
1004 Philippines
Email: ma.carmen.lagman@dlsu.edu.ph

Jelle Atema
Professor of Biology
Boston University Marine Program
5 Cummington Street, BRB 307
Boston, MA 02215, USA
Email: atema@bu.edu

Mark Butler
Professor, Department of Biological Sciences
Old Dominion University
Norfolk, VA 23529-0266, USA
Email: mbutler@odu.edu

Cécile Fauvelot
Chargée de Recherche
Institut de Recherche pour le Développement (I.R.D.)
UR 227 - 'Biocomplexité des écosystèmes coralliens de l'Indo-Pacifique' Université des Antilles et de la Guyane
DYNECAR (EA 926), Biologie marine
Campus de Fouillole BP 592
97159 Pointe-à-Pitre cedex, Guadeloupe
Email: cecile.fauvelot@ird.fr

J. Derek Hogan
Postdoctoral Research Associate
Department of Ecology and
Evolutionary Biology
Tulane University
400 Lindy Boggs Building
New Orleans, LA 70118, USA
Email: dhogan2@tulane.edu

Geoffrey P. Jones
Professor, School of Marine and Tropical Biology
ARC Centre of Excellence for Coral Reef Studies
James Cook University
Townsville, QLD 4811, Australia
Email: geoffrey.jones@jcu.edu.au

Kenyon C. Lindeman
Research Professor, Dept. of Marine &
Environmental Systems
Florida Institute of Technology
150 W. Univ. Blvd.
Melbourne, FL 32901, USA
Email: lindeman@fit.edu

Claire B. Paris
Assistant Professor
Rosenstiel School of Marine & Atmospheric
Science Divisions of Applied Marine Physics
University of Miami
Operations Building, Room 24
4600 Rickenbacker Causeway
Miami, FL 33149, USA
Email: cparis@rsmas.miami.edu

Peter F. Sale
Assistant Director, Coastal Zones
United Nations University - Institute for Water,
Environment and Health (UNU-INWEH)
1047 Brandy Crest Road, RR#1
Port Carling, ON P0B 1J0, Canada
Email: sale@uwindsor.ca

Robert Steneck
Professor, Marine Biology
Oceanography and Marine Policy
School of Marine Sciences
University of Maine
Darling Ctr, Walpole, ME 04573, USA
Email: steneck@maine.edu

Hannah L. Stewart
Former: UMS 2978 CNRS - EPHE
Centre de Recherche Insulaire et
Observatoire de l'Environnement (CRIOBE)
BP 1013 - 98 729, Papetoai, Moorea
Polynésie Française
Present: Research Scientist - Benthic Ecology
Department of Fisheries and Oceans Canada
West Vancouver Lab - 4160 Marine Drive
West Vancouver, B.C. V7V 1N6, Canada
Email: hannah.stewart@dfo-mpo.gc.ca

Hanneke Van Lavieren
Programme Officer, Coastal Zones
United Nations University - Institute for Water,
Environment and Health (UNU-INWEH)
175 Longwood Road South, Suite 218
Hamilton, ON L8P OA1, Canada
Email: vanlav@inweh.unu.edu

authors

Further information

The United Nations University – Institute for Water, Environment and Health is a member of the United Nations University family of organizations. It is the UN Think Tank on Water created by the UNU Governing Council in 1996 to strengthen water management capacity, particularly in developing countries, and to provide on the ground project support. UNU-INWEH's Coastal Programme focuses on improvement of scientific understanding to foster sound decision making for sustainable coastal marine management. This is directly linked to capacity development efforts to address critical gaps, achieved through diffusion of scientific research and promotion of human and institutional capacity.

United Nations University – Institute for Water, Environment and Health (UNU-INWEH)
175 Longwood Road South, Suite 204 Hamilton, ON L8P OA1 Canada

Telephone: +1 905 667 5511 Facsimile: +1 905 667 5510
Email: contact@inweh.unu.edu
Internet: www.inweh.unu.edu

The Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program is a leading international coral reef research initiative that provides a coordinated approach to credible, factual and scientifically-proven knowledge for improved coral reef management. The CRTR Program is a partnership between the Global Environment Facility, the World Bank, The University of Queensland (Australia), and approximately 40 research institutes & other third parties around the world.

Coral Reef Targeted Research & Capacity Building for Management Program
C/- Global Change Institute
The University of Queensland St Lucia QLD 4072 Australia

Telephone: +61 7 3365 4333 Facsimile: +61 7 3365 4755
Email: info@gefcoral.org
Internet: www.gefcoral.org

The decline of coastal environments is a critical problem for many tropical countries with coral reefs. These reefs frequently provide a major component of GDP through their support of fisheries and tourism, while also providing important protein food for coastal communities, and supporting a traditional way of life for coastal peoples. Preserving Reef Connectivity: A Handbook for Marine Protected Area Managers tackles one specific issue in the effective management of these important coastal marine environments – the issue of connectivity. Connectivity is a measure of the degree of connectedness among nearby places and among local populations of a species.

This handbook summarizes the relevant science on connectivity and provides advice on the use of connectivity information to strengthen reef management. While targeted to coral reef managers, the advice will be of value to all managers of coastal waters. Our goal is to assist MPA managers and others in understanding and applying the concept of connectivity in their work. In this way, we hope to help managers better execute their challenging task of sustaining coastal marine environments and the fishery and other environmental goods and services they provide.

After an introductory section and one that clarifies the multiple meanings of the word "connectivity" the handbook includes sections on the processes that cause connectivity, the ways in which connectivity is important to management, the underlying science that is informing us about connectivity, and on ways in which to build information about connectivity into management planning and action. Emphasis is placed on the demographic connectivity among local populations because that is the aspect of connectivity most difficult to evaluate, and most important for day-to-day management of coastal waters.

Knowledge about connectivity, and particularly an understanding of how this knowledge can be extended through the collaboration of scientists and managers in an adaptive management framework will make the tasks of coastal marine managers easier. Application of this knowledge will make the tasks more successful. In a world in which climate is changing rapidly, with consequences that are not yet fully apparent, it will be more important than ever to ensure that coral reef and other coastal ecosystems are managed as effectively as possible.

To be truly effective in sustaining biodiversity and ecosystem functioning, while also sustaining coastal fisheries, coral reef management must incorporate ideas of connectivity into planning and action. Talking about connectivity must give way to coordinated adaptive management programs that advance our understanding of this subject, while using the best science now available to guide management actions. In our rapidly changing world, we have to put in place the best possible local management if we are to provide coral reefs with the capacity to weather global threats.