










Thinking and managing outside the box: coalescing connectivity networks to build region-wide resilience in coral reef ecosystems

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Abstract As the science of connectivity evolves, so too limit recruitment by more than 50%. For demographic must the management of coral reefs. It is now clear that the connectivity to contribute to the resilience of coral reefs, spatial scale of disturbances to coral reef ecosystems is must function beyond the box of no-take reserves. Sparger and the scale of larval connectivity is smaller than typically, it must improve nursery habitats on or near reefs previously thought. This poses a challenge to the current and enhance the reproductive output of ecologically focus of coral reef management, which often centers on the important species throughout coral reef ecosystems. Spestablishment of no-take reserves (NTRs) that in practical protection of ecologically important species (e.g., are often too small, scattered, or have low stakeholder compliance. Fished species are generally larger and more fisheries that capitalize on the benefits of NTRs and abundant in protected reserves, where their reproductive maintain critical ecological functions are examples of potential is often greater, yet documented demographic measures that coalesce marine reserve effects and improve benefits of these reproductive gains outside reserves are the resilience of coral reef ecosystems. Important too is the modest at best. Small reproductive populations and limited necessity of local involvement in the management process dispersal of larvae play a role, as does the diminished so that social costs and benefits are properly assessed, receptivity to settling larvae of degraded habitats that can compliance increased and success stories accrued.

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Introduction

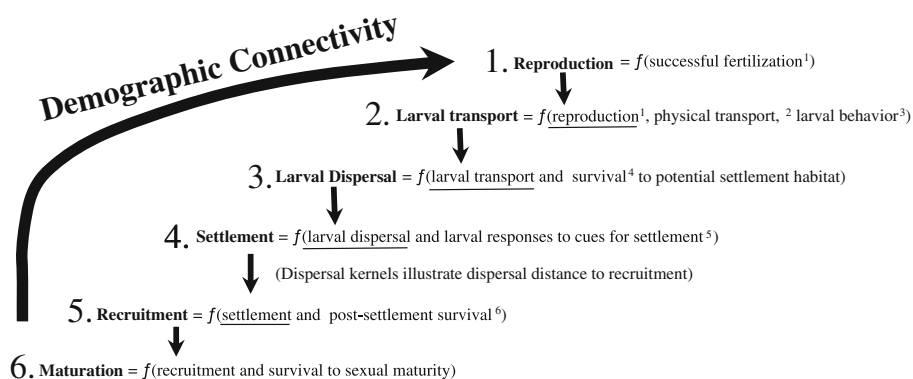
Connectivity and management of Caribbean coral reefs was the title of an influential paper published more than a decade ago (Roberts 1997). This paper concluded that sites supplied copiously from upstream reef areas will be more resilient to recruitment overfishing, less susceptible to species loss, and less reliant on local management than places with little upstream reef. Partnerships among nations were envisioned with the goal of developing large-scale connectivity networks among inter-dependent reserves. Clearly, connectivity was considered important for the management of coral reefs. However, since the publication of that landmark paper, much has changed in the science of connectivity, coral reefs, and their management (e.g., Sale et al. 2005; Mumby and Steneck 2008).

Over the past several decades, coral reefs have suffered from increasingly frequent and widespread coral mortality from diseases, coral bleaching, and algal overgrowth (Hughes 1994; Pandolfi et al. 2003, 2005). These factors resulting from global climate and atmospheric change, overfishing, and other insults work individually and synergistically to cause significant large-scale loss of coral cover. The decline in coral cover is best documented for the Caribbean Sea and Indo-Pacific Ocean (Gardner et al. 2003; Bruno and Selig 2007), but it is so severe and widespread that nearly a third of the world's coral species are now considered threatened (Carpenter 2004). Declining coral cover translates to declining habitats for many groups of reef-dwelling or reef-recruiting organisms, especially fishes (Jones et al. 2004; Garpe et al. 2006). Thus, a central challenge for confronting this coral reef crisis is to determine how to improve recovery of these beleaguered ecosystems.

Much is known about the factors influencing the scale and rates of disturbances on coral reefs, but surprisingly little about what controls their recovery and the role of larval connectivity in this process (Jennings 2001; Russ and Alcala 2004; Mumby and Steneck 2008). More is known about larval dispersal, or the physical and biological characteristics affecting larvae departing a reproductive source (Pineda et al. 2007), than about larval connectivity, or the linkage between a reproductive source and recruitment of larvae to a given area (Leis 2006; Gaines et al. 2007). Much connectivity research focuses on larval dispersal among natal and non-natal areas (Jones et al. 2009), a necessary first step, but what matters most for the management of coral reefs is demographic connectivity (sensu Kritzer and Sale 2004). Connectivity is much more than the biophysical coupling of larvae from reproductive populations to recruitment sites (i.e., steps 2 and 3 in Fig. 1). To sustain and grow, populations require an unbroken nexus among reproductive populations called demographic connectivity or reproductive population connectivity (sensu Kritzer and Sale 2004; Pineda et al. 2007, respectively).

The present review takes a larger view of demographic connectivity in reconsidering how connectivity links networks of no-take reserves (NTRs) and the important role that habitat receptivity plays in linking larval dispersal to population persistence. This paper focuses on reef corals, fishes, and lobsters because of their importance to coral reef structure, function, or economic value and because

Fig. 1 Six sequential steps leading to demographic connectivity (sensu Kritzer and Sale 2004). Each sequential step (boldface) is a function of several other processes (in parentheses) with supporting literature identified in footnotes. Explicit linkage among steps is illustrated with arrows. Modified from Pineda et al. 2007



¹ Fertilization success increases reproduction which in turn increases larval production

² Physical transport scales with larval duration (e.g., Shanks et al. 2003)

³ Larval behavior vertically and horizontally increases local retention (Leis 2006)

⁴ Larval mortality increases the probability of limiting dispersal (Cowen et al. 2000)

⁵ Settlement and metamorphosis is induced by local habitat cues (chemical: Morse and Morse 1991; Sweatman 1988; light, sound: Leis 2006)

⁶ Post-settlement survival declines due to lower recruitment potential for fish (Jones et al. 2004), lobsters (Butler et al. 2005) and corals (Box and Mumby 2007)

their larval durations and probably dispersal distances span the range of coral reef organisms. It concludes by proposing a broader spatial scale of management well beyond the relatively small oases of NTR protection currently used or proposed for the management of coral reef ecosystem. Because people are the critical part of ecosystems, it is suggested that social connectivity is also necessary for communicating results among stakeholders to develop incentives for supporting new ways to better sustain these ecosystems.

State of connectivity science for reef ecosystem management

As the frequency and intensity of adult mortality on reefs increase from coral bleaching, disease, and overfishing, the process of recruitment becomes increasingly important. As a result, connectivity, or the nexus between the production and eventual recruitment of dispersive propagules (e.g. larvae, spores or zygotes) becomes more important as we follow reproduction, larval transport disperses larvae as a function of local physical oceanography and larval behavior, which controls their depth, and influences their transport where currents are stratified. Larval mortality governs how far larvae effectively disperse from a reproductive population (step 3 in Fig. 1; Cowen et al. 2000). The dispersal distance from a reproductive source to where the larvae settle (step 4) is usually illustrated as a declining function with distance known as the dispersal kernel (Fig. 2). The dispersal kernel is a probability density function describing the spatial distribution of settlement. Post-settlement survival then determines the subset of individuals that recruit to benthic and ultimately reproductive populations (steps 5 and 6 in Fig. 1).

If populations are to persist or grow, recruitment must equal or exceed the rates of mortality (horizontal lines in Fig. 2). Generally, the demographically important rates of recruitment necessary to sustain populations (i.e., the portion of the curve above the horizontal line) occur nearer to the origin of dispersal kernels, whereas evolutionarily important rates for seeding distant populations to maintain gene flow and prevent local extinction extend further along the tail of the curve (Fig. 2). Connectivity distances vary for many reasons. For example, if a population suffers elevated mortality, its reproductive output and thus its range of sustaining levels of connectivity will decline (Fig. 2b).

Life expectancy (i.e., longevity) also influences the rate of recruitment necessary to sustain populations (Fig. 3). Short-lived fish require frequent recruitment to persist. Long-lived corals, in contrast, require much lower

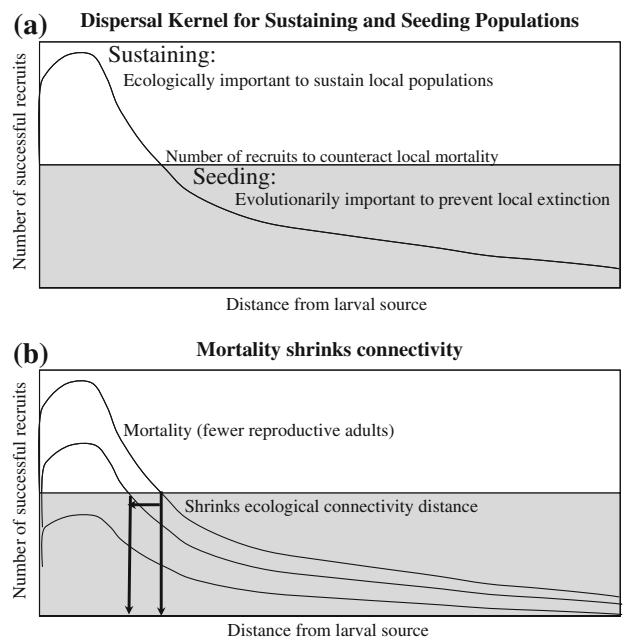


Fig. 2 Sustaining and seeding portions of dispersal kernels determine potential connectivity distance between reproductive populations and offspring. Horizontal lines identify the distinction between ecologically important recruitment necessary to balance against local mortality and evolutionarily important recruitment to balance against local extinction. Shrink dispersal kernels resulting from adult mortality (after Steneck 2006)

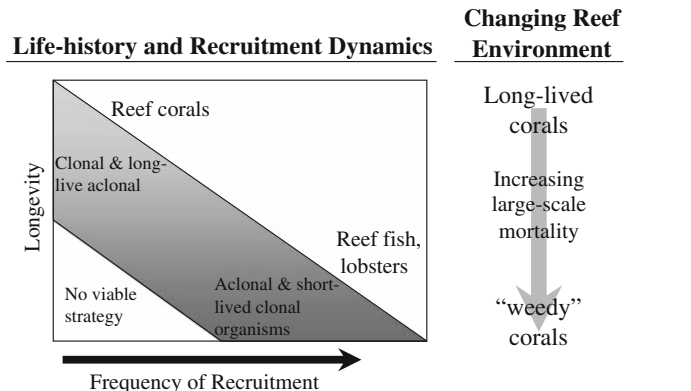


Fig. 3 Conceptual model illustrating tradeoffs between life history characteristics (e.g., average longevity) and the necessary recruitment for species persistence. Note that as the frequency of mortality increases for characteristically long-lived organisms such as corals, the frequency of recruitment must also increase to persist

frequency of recruitment. For example, in the Caribbean, dominant reef-building corals, such as species of the genus *Acropora*, had very low rates of recruitment even when they were hyper-abundant before their mass mortality from disease in the early 1980s (Rylands et al. 1983). These corals were long-lived (Fig. 3), large, and had a low probability of adult mortality (Hughes and Jackson 1985), and thus, they dominated shallow reef zones competitively (Lang 1974)

creating near-monocultures. However, as large-scale papers in this issue). Most studied are fishes that have tality events increased in frequency, the *Acropora* (and pelagic larval durations (PLD) of 10–60 days, in contrast to *Montastraea*) clonal strategy became less viable (Rogersthe short PLDs of corals (2 to 14-day larval durations) and and Miller 2006 Mumby and Steneck2008). Increased long PLDs of spiny lobsters (>200 days). Self-recruitment disturbance frequency may be shifting Caribbean reefs is more prevalent among reef fish than previously sus- toward assemblages of diminutive, short-lived corals thapected (e.g., Jones et al.1999 2005 Almany et al.2007). recruit frequently (e.g. *Agaricia*, *Porites*, and *Siderastrea*; Using stable Barium isotopes, Almany et al.2007) found Green et al.2008). This shift toward “weedy” corals in that 60% of the recruits of the orange clownfish and the Caribbean (Fig3) not only transforms reefs into diminu- vagabond butterfly fish rejoined their natal populations tive architecture, but also, due to the predominance oafter PLDs of less than a week to more than a month, brooding corals, will likely shorten demographically rele- respectively. Genetic studies in the Mediterranean mea- vant connectivity distances. sured over 66% self-recruitment in a littoral fish, *Tripterygion delaisi*, with a larval period ranging between 16 and 21 days (Carreras-Carbonell et al.2007). Using otolith microchemistry, Patterson et al.2005) determined that about 67% of damselfish, *Pomacentrus coelestis*,

Progress: scaling dispersal kernels

Recent research points to several reasons why dispersal kernels of marine larvae are smaller than previously thought (Jones et al.1999 Hughes et al.2000 Cowen et al. 2006 Steneck2006 Almany et al.2007). Most reflect the evolving perception of larval dispersal, but some are conducted in Kimby Bay, Papua New Guinea, for example, revealed by actual declines in dispersal kernels. The shift in Caribbean coral species composition and the commensurate rate change in life history strategy described above is an example of a temporal shift in dispersal potential of the coral community. Another reason results from the loss of large heavily fished individuals within populations of fish and invertebrates that typically produce a high per capita fraction of the young in natural populations (Bertelsen and Matthews2001). If adult fecundity declines, then so will the distance of sustaining levels of recruitment (Fig). Further, because pelagic larvae die as they disperse, average dispersal distances could be reduced by as much as half (Cowen et al.2000 Fig. 4a).

The critical level of settlement to sustain or grow populations (i.e., horizontal lines above shaded halves in Fig. 2) is not known for most reef organisms including corals. However, the range of sustaining rates of settlement will logically be nearer the reproductive source than will the maximum range of observed settlement. Accordingly, measurements of coral settlement with distance from an isolated reef (Helix Reef) found that over 70% of the corals settled within 300 m of the reproductive source (Sammarco and Andrews1988 1989). Further, as expected, spawning corals recruited farther from the source reef than did brooders (most of which recruited to the source reef) (Werner et al.2007) brings into question the long held notion that marine larvae disperse widely. Simulations of passive larval reef fish dispersal (i.e., no vertical migratory behavior) in flow fields without eddies suggest that peak recruitment generally occurs less than 100 km from the larval source. In the presence of coastal eddies, the same larvae recruit only about half this distance from the source. When diel and ontogenetic vertical migration by larvae is added, the distance shrinks further to less than 20 km (Fig. 4b).

The results of increasingly sophisticated biophysical and oceanographic modeling that includes small-scale turbulence (i.e., “eddies”) and larval behavior (Cowen et al.2008; Werner et al.2007) brings into question the long held notion that marine larvae disperse widely. Simulations of passive larval reef fish dispersal (i.e., no vertical migratory behavior) in flow fields without eddies suggest that peak recruitment generally occurs less than 100 km from the larval source. In the presence of coastal eddies, the same larvae recruit only about half this distance from the source. When diel and ontogenetic vertical migration by larvae is added, the distance shrinks further to less than 20 km (Fig. 4b).

Empirical support for short recruitment distance and applicability for management

Relatively few studies have succeeded in measuring connectivity distances for reef-dwelling species (see other the evolutionarily important long tail of the dispersal

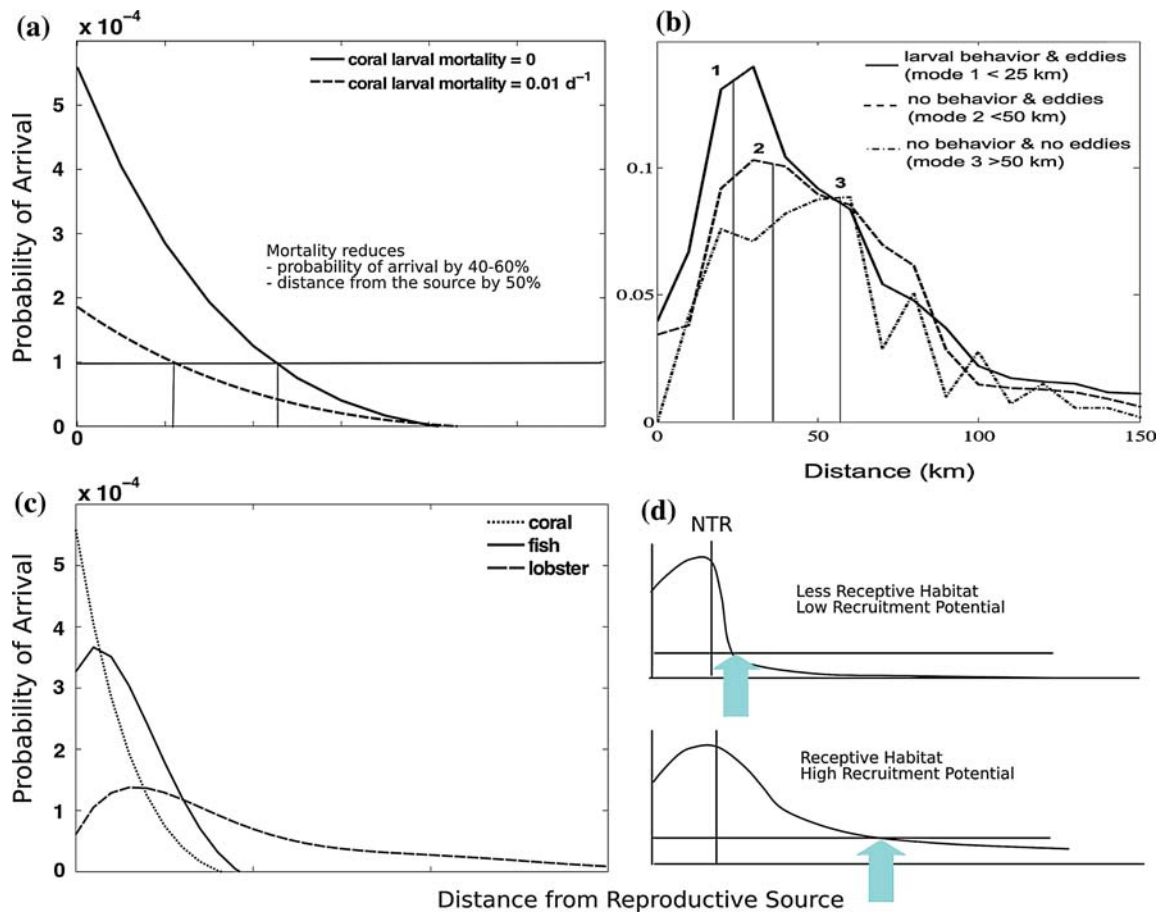


Fig. 4 Sensitivity analyses of factors that affect shapes of theoreticakernel for coral has a asymptotic shape with maximum larval delivery dispersal kernels integrated for multiple release locations and timeat or near the reproductive source, while kernels for fish and lobster and representing larval dispersal as defined in Fig. 2. b Effects of larval behavior and the presence of eddies on dispersal kernels for fish with a PLD of 30 days (a common convention; see Kinlan et al. 2005). Simulated from 48 localities in the Mesoamerican region (after Paris et al. 2007). c Effect of inter-phylectic differences on dispersal kernels of tropical regions and species (see Botsford et al. 2009) lobster, coral, and fish simulated for the Bahamian archipelago. The

kernel, whereas the ecologically and demographically 2009; McCook 2009). However, that design would be significant "sustaining" portion of the dispersal kernels is constrained by social landscapes and other factors making controlling local colonization is much smaller and more difficult or impossible in many local (Fig. 2a).

The variation in dispersal kernels, among ecologically and economically important reef organisms (e.g., short for corals, intermediate for fish, long for lobster), creates a serious problem for the design of effective networks of NTRs. For example, typical dispersal kernels modeled for many fished species increase in abundance, body size, and lobsters, fish, and corals suggest that fish and corals have ~50 and 70% shorter dispersal kernels, respectively, than lobsters (Fig. 4c). Designing networks of NTRs with a wide range of inter-reef distances could allow for the range of dispersal distances (Kinlan et al. 2005; Almany et al. 2009). The demonstrable positive aspects of NTRs include the protection of vulnerable species, biodiverse habitats, and ecological processes such as recruitment and predation within their borders (Mumby et al. 2006; Sweatman 2008). Many fished species increase in abundance, body size, and reproductive potential inside reserves (Palumbi 2001; Russ 2002; Gell and Roberts 2003; Nardi et al. 2004). However, we know of no empirical evidence of larval subsidies from NTR resulting in elevated population densities in adjacent NTRs or adjacent unprotected areas (Agardy et al. 2003).

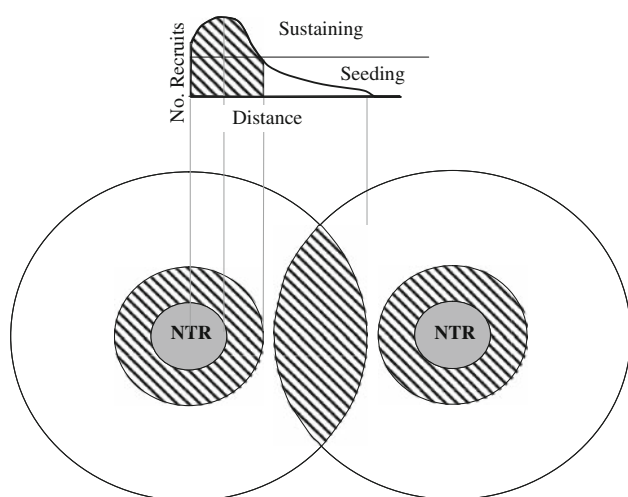


Fig. 5 Conceptual model for coalescing connectivity networks in which overlapping “seeding” tails of dispersal kernels could sustain populations (if other restrictions prevent overfishing outside the reserves). Cross-hatching represents “sustaining” zones in which recruitment exceeds local mortality. Upper inset diagram illustrates how a traditional dispersal kernel relates to a non-directional (radiating) pattern of larval dispersal

Willis et al. 2003; Sale et al. 2005). If NTRs provide larval subsidies sustaining and enhancing demographic connectivity among reserves and unprotected areas, recent research suggests the distances will be relatively short. Thus, it remains a management challenge to determine how to extend and coalesce such “recruitment effects” so they can be effective at the scale of entire coral reef ecosystems (Fig.

Closing the loop: the strong role of habitat for recruitment to adult populations

Abundant, competent larvae are a necessary, but insufficient condition for sustaining high rates of demographic connectivity. Increasingly important in coral reef ecosystems is the availability of settlement habitat of sufficient quality to facilitate settlement and post settlement success—called the “recruitment potential” of the benthos (sensu Steneck and Dethlefsen 1994, steps 4 and 5 in Figs. 4d). Studies of corals, lobsters, and fishes suggest that population declines ranging from 50 to 100% can occur when the recruitment potential of benthic habitats is diminished. Corals settling in hostile environments with high algal biomass (Birkeland 1977; Kuffner et al. 2006 reviewed by Birrell et al. 2008), appreciable sediment (Birrell et al. 2005), and an abundance of coralline algal species that shed their surface layer of cells can experience 75–100% mortality (Harrington et al. 2004). Lobsters settling into lagoonal sediment with little vegetation or crevice-bearing habitats suffer 50% higher rates of

mortality than those that settle into architecturally complex habitats (Butler et al. 2005). Fish recruitment in a NTR in Papua New Guinea declined by over 75% following the bleaching-induced loss of live coral cover (Jones et al. 2004). Indeed, the delivery of copious larvae to hostile settlement habitats can result in far lower rates of recruitment than areas where many fewer larvae arrive into receptive habitats, as has been demonstrated in studies of lobster in the Bahamas (Lipcius et al. 1997) and Florida (Butler et al. 1997). Thus, recruitment derived from any benefit afforded by larval spillover from NTRs will be most evident where the recruitment potential of the benthos is high and possibly undetectable where the recruitment potential is low.

Thinking and managing outside the box

Based in part on the assumption that larger NTRs will create larger larval spillover effects, the trend in management actions over the past decade has been toward larger proportions of reefs being placed into no-take protection (Roberts 1997; Hughes et al. 2003). This often meets increased or even insurmountable resistance from local fishing communities who subsist on fishing grounds previously closed for closure (McClanahan et al. 2006). However, even where human dependency is relatively low and where compliance is high, if as much as 20–30% of reef ecosystems are protected, 70–80% remain unprotected and often subject to displaced fishing effort that is refocused from protected areas (Mora et al. 2006). While there has been considerable effort and progress in understanding biophysical drivers of larval dispersal, other important ecological and social aspects of connectivity that influence the resilience of coral reefs often receives less attention.

Ecosystem connectivity

Demographically important “ecosystem connectivity” involves ontogenetic changes in habitat utilization. Mangroves and seagrass beds are nursery habitats for many reef-dwelling organisms such as lobsters (Butler et al. 2005) and reef fishes (Mumby et al. 2004), particularly in the Caribbean. For example, the association between some species of reef fishes, such as the largest Caribbean parrotfish (*Scarus guacamaia*) and mangroves is so strong that in regions where mangroves have been removed, this species of parrotfish has become locally extinct (Mumby et al. 2004). Yet, few NTRs designed to protect coral reef communities have been shown to also protect nearby non-fishing communities. In the Florida Keys National Marine Sanctuary, for example, there are 23 small (all <10 ha),

fully protected coral reef reserves scattered over the area are virtually impossible to overcome (Alcala and Russ 2006). Approximately 200 km long barrier reef tract, but only one 3,000 ha zone fully protects a portion of the adjoining non-reef habitat in the sanctuary.

Example 1: Philippine marine no-take reserves and local compliance

Social connectivity and compliance

In a very different sense, scientists, managers, and stakeholders exhibit little social connectivity and, consequently, most no-take reserves are ineffective because of low stakeholder compliance (Kelleher et al. 1995; McClanahan 1999; McClanahan et al. 2006). Social connectivity, or the flow of information among people, is as important as demographic connectivity, because socioeconomic and political factors drive the location and size of reserves (McClanahan 1999; Alcala and Russ 2006). Before there can be connectivity networks among NTRs, there must be social connectivity among stakeholders (Johannes-Alcala and Russ 2006). That is, stakeholders must buy-in to the concept. Social connectivity includes activities that bring communities together, reduce conflicts (Sala et al. 2002), create a conservation ethic, and maintain high compliance (White et al. 2006). The incentive for compliance is highest for local communities that reap direct benefits from their conservation activities (Agardy 2005). Effective community-supported activities include the establishment and patrol of NTRs (Russ and Alcala 2004) but also, limitation on the export of reef fish (Pennisi 1997), restrictions on fishing gear (McClanahan and Mangi 2004), temporal closure of fishing zones (Cinner and McClanahan 2006) or spawning aggregations (Johannes 2002), and development of ecotourism income (Alcala and Russ 2006). The success of these efforts will depend on how well they create and/or maintain incentives that improve the lives of the stakeholders and their families.

Finding the right social and ecological scales for management remains a challenge (Agardy 2005). Coordinated multi-scale conservation and management activities are needed at local scales and regional scales. With the Local Government Code of 2001 in Indonesia and similar codes for the Philippines (see Example 1), regional laws empower local communities to be responsible for implementing, monitoring, and enforcing regulations (White et al. 2006). The incentives to comply are directly tied to successes in local fishing communities. The achievement of such management initiatives are only now coming to light (see Example 1). Although there has been progress in social-ecological co-management of reef ecosystems, many countries poverty is so widespread that the immediate needs of fisherman outweigh the future benefits attributable to a conservation ethic. Such poverty traps

No-take reserves require partnerships among and within local fishing communities, scientists, and governing bodies.

These partnerships are based on shared information and trust. They are essential for what we call "social connectivity" and without them compliance is often lacking. The Philippines provides an excellent example. In the early 1970s, the establishment of marine NTRs based upon community-based management began in the Philippines and Sumilon and Apo Islands. Stakeholders (local fishing communities and local government units) were involved in the process of reserve establishment from the very beginning. The process began with community meetings where information on local problems (e.g., overfishing, "out-sider" access to their local fishery resources) and views on possible solutions were solicited. Later, scientists and managers explained to fishers in these communities the life techniques, the benefits of conservation (e.g., tourism income), and possible solutions to local problems such as NTRs. This social connectivity was vital in fostering a sense of ownership of the reserves and in empowering the local fishing communities to take control of their own destinies by encouraging the formation of local marine management committees and the establishment of local government legislation to protect reserves (Alcala and Russ 2006).

The founding of the Sumilon and Apo NTRs had a much wider impact than simply being the first of a network of hundreds of new NTRs that sprang up across the country. Their establishment influenced the formulation of the Local

Government Code of 1991 and the Fisheries Code of 1998, legislation which ensured that every coastal municipality in the Philippines now had a say in how their marine resources were managed. This was a major shift in national policy that empowered coastal communities and allowed for co-management between local and national governments of inshore marine resources.

As a result, Filipinos have a high level of satisfaction with the use of NTRs as fisheries management tools, and Alcala and Russ (2006). For example, fishers at Apo Island were asked in formal surveys in 1986, 1992, and 2000, whether their catch had changed since the establishment of the NTR. A high percentage (67–100%) of fishers believed that catch at Apo Island had increased since the reserve was implemented (Alcala and Russ 2006). These local fishers adopted a management scheme that reduces their

access to fishing grounds. Key reasons for this are perceived incentives of fishery benefits through spillover of adult fish and increased income from tourism. Proposed and employed to bolster reproductive stocks of exploited reef fish, foremost among them being NTRs (Coleman et al. 2000). The near universal increase in the abundance of large individuals within well-protected NTRs, some of which protect spawning aggregation sites, is encouraging. Yet, the great majority of coral reefs are not NTRs with good compliance. Furthermore, the enhanced larval subsidy produced by the few functional NTRs that teem with big fish, corals, and lobsters is often only a drop in the bucket given the huge unprotected areas into which larvae recruit and the high mortality of larvae and new recruits. Management measures that capitalize on the reproductive benefits of NTRs in ways that integrate those benefits across the entire ecosystem are crucial to pre-coral, this might be achieved by managing for low algal biomass through the protection of herbivore populations from over-exploitation (Mumby et al. 2006; Birrell et al. 2008; Mumby and Steneck 2009). In some places in the Pacific, this was accomplished by virtually halting the export of harvested reef fish. This protects highly valued large parrotfish from over-exploitation for Asian markets (Pennisi 1997). Similarly, parrotfishes and other herbivores have been preserved in Bonaire, in the Caribbean, by only allowing hook and line fishing for carnivores (Bruckner and Bruckner 2003; Kramer 2003). Coral bleaching that kills corals and thus reduces fish recruitment for some species cannot be prevented. Most attempts to remediate such lost habitats have failed or have been too small to be effective. In contrast, there have been successes in remediating nursery habitats that restore ecosystem connectivity. These include efforts to re-establish seagrass beds damaged by vessel groundings or mass die-offs, rebuilding of mangrove-fringed shorelines impacted by development, and the restoration of structure-forming sponge and coral communities in hard-bottom communities devastated by episodic bleaching and harmful algal blooms (Butler et al. 2005).

Enhancing reproductive potential across the seascape

Managing habitats outside reserves is necessary, especially nursery habitats that nurture the typically more vulnerable individuals. But this alone is not likely to coalesce and expand the connectivity of NTR networks for species subject to unchecked fishing pressure outside reserves where spawning stocks have been severely depleted. The loss of large, ecologically, and reproductively important individuals to over-harvesting on coral reefs and elsewhere is well documented (Birkeland and Dayton 2005) and has diminished the population connectivity by reducing the number of potential dispersers (e.g., Fig. 2b). A number of management measures (e.g., gear limits, size limits, total individual catch limits, and area closures) have been

Example 2: Expanding larval subsidy: NTRs

Minimum size limits are an important and near universal element of every fishery management scheme, but the added establishment of a maximum size limit for allowable catch creates what is referred to in fishery circles as a "slot-limit." Slot-limits are a familiar and successful management tool for preserving and rebuilding spawning stocks in freshwater (e.g., Nordwal et al. 2008) and some coastal fisheries (e.g., Vaughan and Carmichael 2002), yet have not seen widespread use in the management of exploited species on coral reefs. The premise that slot-limits bolster reproductive output is based on straight-forward demographics and common biological attributes shared by many exploited reef species with type III survivorship. Among such species, bigger individuals experience lower rates of natural mortality, provide stronger ecological interactions and produce many more, often exponentially more, larvae than smaller individuals. Among tropical spiny lobsters, for example, large individuals have low natural mortality and larger females produce exponentially more eggs per clutch but also more hatchlings (i.e., spawning events) per annum than small females (MacDiarmid and Sainte-Marie 2006). Larger, ecologically, and reproductively important individuals to often older individuals may also sire larvae of higher quality (e.g., greater energetic reserves, larger size, faster growth) whose larval and post-settlement survival are higher than smaller, younger individuals as has been demonstrated in temperate (Berkeley et al. 2004; Berkeley et al. 2006) and tropical (Kerrigan 1997; Bergenijs et al. 2002) fish. For species that undergo sequential hermaphroditism

(e.g., Serranidae groupers) or in those where male size can limit fertilization success through sperm limitation (e.g., spiny lobster; MacDiarmid and Butler 1999), slot limits should apply to males as well as females.

Implementation of slot-limit regulations is potentially less contentious than other management regulation because, in most cases where fishing pressure is high stakeholders are not forced to surrender a resource that they currently have access to, the big fish, lobsters, conch, or other species that have already been fished out. Enforcing the protection of large individuals as they return to the system is the eventual problem, but no more difficult to enforce than minimum size limits currently in place in many areas. As with all regulations, success depends on compliance. If stakeholders see value in slot-limits they will have the incentive to support this management initiative (as occurred with the clawed lobster fishery in Maine Acheson and Steneck 1997). Of course, slot-limits can be achieved more easily for some species than for others. Fishes subject to barotrauma upon capture from deep water (e.g., hyper-extension of swim bladders in some fish) are poor candidates, as are species that experience reproductive senescence. Nevertheless, size-selective hooks and traps can work with this group. Slot-limits could work well for reef fisheries because they are shallow (without barotrauma) and fishers can see many of the species they fish (e.g., spiny lobster, conch).

Of particular appeal for coral reef fishery management is an approach that combines ecosystem- and fishery-based management tools via the implementation of NTR net-size at which 50% of females are reproductive. Mean works along with fishery slot-limits. Alone, populations protected within NTRs will be too few and too small to yield enough the spillover of larvae or large reproductive individuals into adjacent heavily fished areas and thus will not appreciably increase the reproductive output of the population. However, if slot-limits protecting the largest individuals are added to this scenario, a considerable fraction of the large individuals that spill out of fishing and NTR could survive and eventually proliferate throughout unprotected areas, enhancing reproductive output of these species throughout the ecosystem.

To explore the potential effectiveness of slot-limits when combined with a network of NTRs as an approach to enhancing reproductive potential throughout the ecosystem, a simple life-table model for one of the Caribbean case for tropical spiny lobsters although perhaps not for most economically important reef fisheries—the Caribbean temperate species (MacDiarmid and Sainte-Maure 2006) spiny lobster, *Panulirus argus* was applied (Fig 6).

For this demonstration, the assumptions were a hypothetical self-recruiting population (as would be expected if Fig. 6). Egg production is further improved over time by slot-limits and NTRs were established Caribbean wide with a typically low larval and early benthic recruit survival (survival probability = 0.0004). Then generally accepted age-specific demographic parameters such as

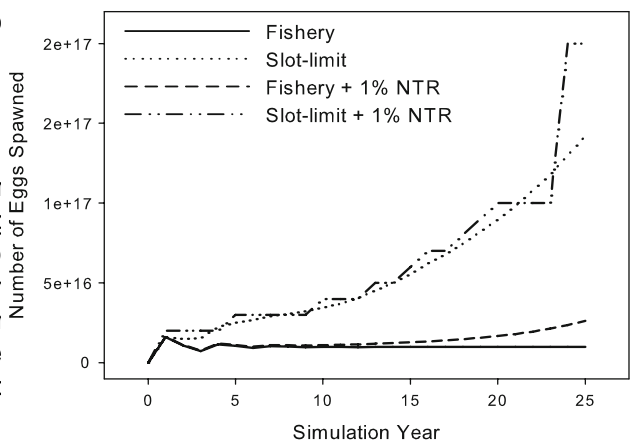


Fig. 6 Reproductive output of a hypothetical population of Caribbean spiny lobster (*Panulirus argus*) over 25 years simulated in an age-structured matrix model under four different management scenarios: an intensively fished population (Fishery), a fished population that also includes NTRs covering 1% of the area (Fishery+ 1% NTR), a fished population under slot-limit catch regulation but no NTRs (Slot-limit), and a fished population under slot-limit catch regulation with NTRs covering 1% of area and assuming that 5% of adult lobsters in NTR immigrate into the adjacent fished area (Slot-limit + 1% NTR)

natural mortality, fishing mortality, and fecundity for *P. argus* that are currently used for stock assessment in south Florida (SEDAR US Stock Assessment Panel 2015) were applied. In this region, ~1% of the adult lobster population resides in NTRs. The minimum size limit for harvest is 76 mm carapace length (CL), which is also the minimum size at which 50% of females are reproductive. Mean fishing mortality outside reserves is estimated to be 0.40, which is believed to sustain the fished population at 20% of the estimated spawning biomass of an unfished population. An age-structured matrix model (Gotelli 1995) was used to compare the trajectories of lobster population growth and reproductive output (i.e., annual production of eggs of the largest individuals) over 25 years under four scenarios of fishing and NTR (Fig 6). The slot-limit regulation considered in this example prohibits the catch of lobsters >76 mm CL (i.e., current minimum size limit) and those >100 mm CL, which currently comprise only 11% of the population in south Florida. An assumption made in this simple model is that size or age has no effect on larval survival, which appears to be the case for tropical spiny lobsters although perhaps not for temperate species (MacDiarmid and Sainte-Maure 2006).

The benefit of adding a maximum size limit to the reproductive output of this type of population is striking (Fig. 6). The inclusion of even a small NTR network protecting just 1% of population with minimal adult spill-over (5% of adult NTR population). More theoretical and empirical studies on other species and particular management

- Coleman FC, Koenig CC, Huntsman GR, Musik JA, Eklund AM, Kinlan BP, Gaines SD, Lester SE (2005) Propagule dispersal and the scales of marine community process. *Divers Distrib* 11:139D148
- McGovern JC, Chapman RW, Sedberry GR, Grimes CB (2000) Long-lived reef fishes: the grouper-snapper complex. *Fisheries* 25:14D28
- Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science* 287:857D859
- Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311:522D527
- Fenner D, Banks K (2004) Orange cup coral *Favosites* invades Florida and the Flower Garden Banks, Northwestern Gulf of Mexico. *Coral Reefs* 23:505D507
- Gaines SD, Gaylord B, Gerber LR, Hastings A, Kinlan BP (2007) Connecting places: the ecological consequences of dispersal in the sea. *Oceanography* 20:90D99
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958D960
- Garpe KC, Yahya SAS, Lindahl U, Ohman MC (2006) Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Mar Ecol Prog Ser* 315:237D247
- Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol Evol* 18:448D455
- Gotelli N (1995) A primer of ecology. Sinauer Associates, Sunderland, MA, USA, p 206
- Green DH, Edmunds PJ, Carpenter RC (2008) Increasing relative abundance of *Porities astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Mar Ecol Prog Ser* 359:1D10
- Harrington LK, DeWath Fabricius G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:2437D3437
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547D1551
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. *Ecol Monogr* 55:141D166
- Hughes TP, Baird AH, Dinsdale EA, Moltschaniwkyj NA, Pratchett JE, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. *Ecology* 81:2241D2249
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden JR (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929D933
- Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol Evol* 20:381D386
- Jennings S (2001) Patterns and prediction of population recovery in marine reserves. *Rev Fish Biol Fish* 10:209D231
- Johannes RE (2002) The renaissance of community-based marine resource management in Oceania. *Ann Rev Ecol Syst* 33:317D340
- Jones GP, Milicich MI, Emslie M, Lunow C (1999) Self-recruitment in a coral reef fish population. *Nature* 402:802D804
- Jones GP, McCormick MJ, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251D8253
- Jones GP, Planes S, Thorrold SR (2005) Coral reef fish larvae settle close to home. *Curr Biol* 15:1314D1318
- Jones GP, Almany GR, Russ GD, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* (this issue)
- Kelleher G, Bleakley C, Wells S (1995) Global representative system of marine protected areas, vol 4. The World Bank, Washington
- Kerrigan BA (1997) Variability in larval development of the tropical reef fish *Pomacentrus amboinensis* (Pomacentridae): the parental legacy. *Mar Biol* 127:395D402
- Kramer PA (2003) Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA program (1997D2000). *Atoll Res Bull* 496:1D57
- Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish Fish* 5:131D140
- Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar Ecol Prog Ser* 323:107D117
- Lang J (1974) Interspecific aggression by scleractinian corals: Why the race is not only to the swift. *Bull Mar Sci* 23:260D279
- Leis JM (2006) Are larvae of demersal fishes plankton or nekton? *Adv Mar Biol* 51:59D141
- Levin LA (2006) Recent progress in understanding larval dispersal: new directions and digressions. *Integr Comp Biol* 46:282D297
- Lipcius RN, Stockhausen WT, Eggleston DB, Marshall LS Jr, Hickey B (1997) Hydrodynamic decoupling of recruitment, habitat quality and adult abundance in the Caribbean spiny lobster: source-sink dynamics? *Mar Freshw Res* 48:807D816
- MacDiarmid AB, Butler MJ (1999) Sperm economy and limitation in spiny lobsters. *Behav Ecol and Sociobiol* 46:14D24
- MacDiarmid AB, Sainte-Marie B (2006) Reproduction. In: Phillips B (ed) *Lobsters: biology, management, aquaculture and fisheries*. Blackwell Publishing, Oxford, pp 45D77
- McClanahan TR (1999) Is there a future for coral reef parks in poor tropical countries? *Coral Reefs* 18:321D325
- McClanahan TR, Mangi SC (2004) Gear-based management of tropical artisanal fishery based on species selectivity and capture size. *Fish Manag Ecol* 11:51D60
- McClanahan TR, Marnane MJ, Cinner JE, Kiene WE (2006) A comparison of marine protected areas and alternative approaches to coral-reef management. *Curr Biol* 16:1408D1413
- Almany GR, Connolly SR, Heath DD, Hogan JD, Jones GP, McCook LJ, Mills M, Pressey RL, Williamson DH (2009) Connectivity, biodiversity conservation, and the design of marine reserve networks for coral reefs. *Coral Reefs* (this issue)
- McCook LJ, Almany GR, Day J, Green A, Jones GP, Leis JM, Planes S, Russ GR, Sale PF, Thorrold SR (2009) Management under uncertainty: guide-lines for incorporating connectivity into the protection of coral reefs. *Coral Reefs* (this issue)
- Mora C, Andrefouet S, Costello MJ, Kranenburg Rollo A, Vernon J, Gaston KJ, Myers RA (2006) Coral reefs and the global network of marine protected areas. *Science* 312:1750D1751
- Morse DE, Morse ANC (1991) Enzymatic characterization of the morphogen recognized by *Agaricia humilis* (scleractinian coral) larvae. *Bio Bull* 181:104D122
- Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol Evol*. doi:10.1016/j.tree.2008.8.06.011
- Mumby PJ, Edwards AJ, Arias-Gonzalez EJ, Lindeman KC, Blackwell PG, Gall A, Gorczyńska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* 427:533D536
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffe RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98D101
- Nardi K, Jones GP, Moran MJ, Cheng YW (2004) Contrasting effects of marine protected areas on the abundance of two exploited reef fishes at the sub-tropical Houtman Abrolhos Islands, Western Australia. *Environ Conserv* 31:160D168

- Nordwal F, Lundberg P, Eriksson T (2008) Comparing size-limit strategies for exploitation of a self-thinning stream fish population. *Fish Manag Ecol* 7:413–424
- Palumbi SR (2001) The ecology of marine protected areas. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer Associates Inc, Sunderland, MA, pp 509–530
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman JH, Paredes G, Warner RR, Jackson BC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E (2005) Are US Coral reefs on the slippery slope to slime? *Science* 307(18):1725–1726
- Paris CB, Cherubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Mar Ecol Prog Ser* 347:285–300
- Patterson HM, Kingsford MJ, McCulloch MT (2005) Resolution of the early life history of a reef fish using otolith chemistry. *Coral Reefs* 24:222–229
- Pennisi E (1997) Brighter prospects for the world's coral reefs? *Science* 277:491–493
- Pineda J, Hare JA, Sponaugle S (2007) Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20:22–39
- Roberts CM (1997) Connectivity and management of Caribbean coral reefs. *Science* 278:1454–1457
- Rogers CS, Miller J (2006) Permanent phase shifts or reversible declines in coral cover? Lack of recovery of two coral reefs in St. John, US Virgin Islands. *Mar Ecol Prog Ser* 306:103–114
- Russ GR (2002) Yet another review of marine reserves as reef fishery management tools. In: Sale PF (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, Amsterdam, pp 421–444
- Russ GR, Alcala AC (2004) Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138:622–627
- Rylaarsdam K (1983) Life histories and abundance patterns of colonial corals on Jamaican reefs. *Mar Ecol Prog Ser* 13:249–260
- Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PW (2002) A general model for designing networks of marine reserves. *Science* 298:1991–1993
- Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. *Trends Ecol Evol* 20:74–80
- Sammarco PW, Andrews JC (1988) Localized dispersal and recruitment in Great Barrier Reef corals: the helix experiment. *Science* 239:1422–1424
- Sammarco PW, Andrews JC (1989) The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. *Limnol Oceanogr* 34:896–912
- Scheffer M, Westley FR (2006) The evolutionary basis of rigidity: locks in cells, minds and society. *Ecology and Society* 12:36
- SEDAR US Stock Assessment Panel (2005) Assessment of spiny lobster, *Panulirus argus*, in the southeastern United States: stock assessment. NOAA, South Atlantic Fishery Management Council, North Charleston, SC, 97 pp
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecol Appl* 13:S159–S169
- Steneck RS (2006) Staying connected in a turbulent world. *Science* 311:480–481
- Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476–498
- Sweatman HPA (1988) Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. *J Exp Mar Biol Ecol* 124:163–174
- Sweatman HPA (2008) No-take reserves protect coral reefs from predatory starfish. *Curr Biol* 18:598–599
- Vaughan DS, Carmichel JT (2002) Estimating improvement in spawning potential ratios for South Atlantic Red Drum through bag and size limit regulations. *N Am J Fish Manage* 22:895–906
- Verner FE, Cowen RK, Paris CB (2007) Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. *Oceanography* 20:54–69
- White AT, Gomez E, Alcala AC, Russ G (2006) Evolution and lessons from fisheries and coastal management in the Philippines. In: McClanahan T, Castilla J (eds) *Fisheries management: progress towards sustainability*. Blackwell Publishing, Oxford, UK, pp 88–108
- Willis TJ, Millar RB, Babcock RC, Tolimieri N (2003) Burdens of evidence and the benefits of marine preserves: putting Descartes before the horse? *Environ Conserv* 30:97–103