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Importance of Metapopulation Connectivity to Restocking and Restoration of Marine Species

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We examine the impact of spatial processes on the efficacy of restocking in species with varying forms of population or metapopulation structure. Metapopulations are classified based on spatial complexity and the degree of connectedness between populations. Designation of effective restocking sites requires careful attention to metapopulation dynamics; populations in the metapopulation can differ dramatically in demography and connectivity, and the sites they occupy can vary in habitat quality. Source populations, which are optimal for restocking, can be distinct geographically and may be a small percentage of the metapopulation. Sink areas, where restocking is almost certain to be fruitless, can nonetheless serve as productive locations for habitat restoration since larvae from source reefs are likely to recruit to these areas. Effective restocking of metapopulations is most likely to be attained by selection of optimal source populations; inattention to metapopulation dynamics can doom restoration efforts with marine species.

Keywords   metapopulation dynamics, source-sink dynamics, restocking, restoration

INTRODUCTION

The dynamics of marine species vary at various spatial scales (Menge and Olson, 1990; Doherty and Fowler, 1994) such that marine populations with dispersive stages should be regarded as metapopulations with interconnected subpopulations (Hanski and Gilpin, 1997). Dispersive stages in species with complex life cycles (*sensu*, Roughgarden et al., 1988) sever the link between reproduction and recruitment at local scales; connectivity among subpopulations is an emergent and vital characteristic of marine species (Doherty and Fowler, 1994).

Marine species are also likely to reside in "source" and "sink" habitats (Lipcius et al., 1997, 2001a, 2005; Fogarty, 1998; Crowder et al., 2000; Tuck and Possingham, 2000). Populations that

occur in "sink" habitats are unable to contribute sufficient numbers of juveniles or adults to the spawning stock to balance mortality. In contrast, populations that occur in "source" habitats contribute an excess of individuals to the spawning stock to maintain populations in source and in sink habitats (Pulliam, 1988). We employ this established population-dynamics definition of sources and sinks, which emphasizes habitat quality and its effects on demographic rates (Pulliam, 1988), rather than that whereby sources and sinks pertain to origins and destinations, respectively, of dispersive stages (Roberts, 1997, 1998; Cowen et al., 2000).

Exploitation has drastically reduced the abundance and distribution of several marine fish and invertebrate populations through overfishing and habitat destruction (Pauly et al., 1998; Watling and Norse, 1998; Jackson et al., 2001). Restocking and stock enhancement can potentially mitigate these impacts and augment stocks (Bell et al., 2006). Here we focus on the influence of metapopulation structure upon restocking of exploited marine populations, with emphasis on spawning stock and recruitment.

We progress from populations to metapopulations, sub-dividing these into population or metapopulation types based primarily on spatial complexity and the degree of connectedness between populations.

Recruitment processes regulate population fluctuations (Thorson, 1950; Sale, 1982; Connell, 1985; Gaines and Roughgarden, 1987; Doherty, 1991; Gaines and Bertness, 1993). Hence, significant advances in the use of restocking and stock enhancement to conserve and restore exploited species demand examination of their potential to augment recruitment (Carr and Reed, 1993; Morgan and Botsford, 2001; Botsford et al., 2003). A central goal of our discourse is thus to identify ecological processes critical to improving recruitment of exploited species at the metapopulation level. In the examples, we emphasize restoring spawning biomass of exploited species to the level needed to achieve persisting populations and metapopulations capable of yielding regular harvests. We assume that a sustainable level of recruitment depends upon an adequate abundance of the spawning stock, even if the functional relationship between spawning stock and recruitment only holds at low population levels (Rothschild, 1986; Myers et al., 1995). We are not concerned with recruitment at moderate to high spawning stock levels where populations are neither threatened nor endangered, and where the spawning stock-recruitment relationship is variable (Rothschild, 1986).

Although the influence of metapopulation dynamics on marine species has been recognized (Crowder et al., 2000; Lipcius et al., 2001a, 2005; Botsford et al., 2003), scientists have not classified the different ways by which population or metapopulation structure may drive the success of restocking. We therefore emphasize the impact of spatial processes upon the efficacy of restocking in species with different forms of population or metapopulation structure.

Isolated Self-Replenishing Populations

Self-replenishing populations can have significant metapopulation connectivity, but in the simpler cases described below we deal with isolated self-replenishing populations, including (1) resident populations, (2) migratory populations, and (3) ontogenetically disjunct populations (Lipcius et al., 2005). A resident, isolated self-replenishing population is one that has little interchange with other populations and is dependent on its own reproductive output for recruitment (Figure 1). This model appears to be appropriate to coral reef fish, such as bluehead wrasse, *Thalassoma bifasciatum*, (Swearer et al., 1999), other species in the Caribbean (Cowen et al., 2000), and damselfish on the Great Barrier Reef (Jones et al., 1999). Despite the apparently simple structure of self-replenishing populations, which should facilitate restocking efforts, augmentation of such populations through release of hatchery-reared juveniles will nonetheless be sensitive to factors such as habitat quality, habitat degradation, natural disturbance, invasive species, and climate change.
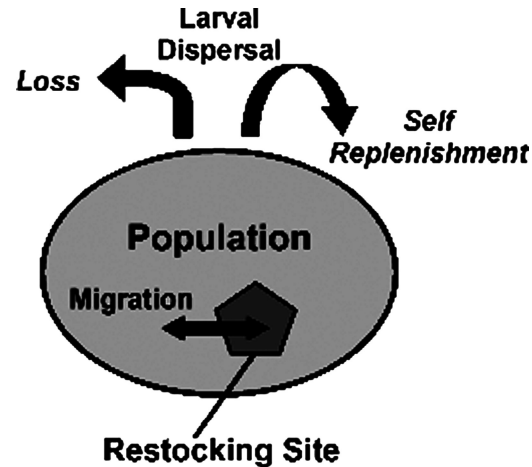

Figure 1 Isolated, self-replenishing populations. "Resident" isolated populations display little movement of juveniles and adults, and there is a low probability that individuals would move out of restocking sites. In contrast, individuals of species with "migratory" isolated populations move outside restocking areas, which renders them susceptible to exploitation.

Exploited species with resident populations include trochus (*Trochus niloticus*) in the Pacific (Heslinga et al., 1984) and the hard clam (*Mercenaria mercenaria*) in the Atlantic (McCay, 1988). Populations of both species have been depleted through overexploitation, and restocking efforts were conducted in collaboration with fishers to protect a relatively sizeable fraction of the habitat for discrete populations of each species. Some populations did not increase significantly after these efforts, and subsequent investigations indicated that restocking of these populations had been performed in marginal habitats where the reproductive contribution of the snails and clams was negligible (Heslinga et al., 1984; McCay, 1988). Further restocking efforts have identified various habitat characteristics that influence the success of trochus and hard clam releases (Bell et al., 2005), e.g., habitat quality of sites to which adults were translocated and which must be considered in restocking.

The next level of complexity involves isolated self-replenishing populations whose individuals exhibit moderate to extensive migrations or movements during their life cycle. Restocked individuals might be expected to migrate from the areas where they are released to unprotected habitats where they are exploited and do not contribute to the spawning stock. The effectiveness of restocking such species varies directly with the rate of movement between habitats due to the increased susceptibility of the population to exploitation of emigrants from protected areas (Polacheck, 1990). For instance, whereas a resident, nearly sedentary species may only require restocking of 20% of the unexploited spawning stock, restocking levels for a highly migratory species may need to be >60% (Polacheck, 1990). Furthermore, emigration rates of dispersing juveniles and adults will generally be greater from small than large release areas due to their larger edge to area ratios (Attwood and Bennett, 1995) such that restocking should generally be attempted in larger areas, where the likelihood of emigration is lower.

There are two different cases related to vagile populations, one in which individuals of all ages can move large distances (migratory), and another in which only certain sex or age classes undergo migrations (ontogenetically disjunct). An example of the former is the northern cod (*Gadus morhua*), which undergoes seasonal migrations; all members of the population move onshore during the spring and summer and offshore in the fall before aggregating along the continental shelf in winter (Guénette et al., 2000). If one were to attempt restocking of cod juveniles, the restocking areas would have to be connected to very large protected areas (up to 80% of fishing grounds) where the adults produced by restocking would be safe from exploitation (Guénette et al., 2000). Otherwise, the juveniles and adults produced by restocking would be susceptible to displaced fishing effort in unprotected areas due to the highly migratory nature of cod. For species that undertake migrations, meaningful restocking and stock enhancement demands either massive restocking areas or, more reasonably, a comprehensive approach whereby restocking is combined with other restoration approaches such as marine reserves and traditional fishery catch or effort controls (Lipcius et al., 2005).

Ontogenetically disjunct populations are those in which different life-history stages (besides larvae and post-larvae) reside in disjunct habitats, including, for instance, species whose juveniles make use of nursery habitats distant from mating or spawning grounds (Figure 2). Common examples of this life history include the wide diversity of invertebrates (e.g., blue crab, *Callinectes sapidus*) and fishes (e.g., Nassau grouper, *Epinephelus striatus*) that use distinct spawning grounds, where they may be
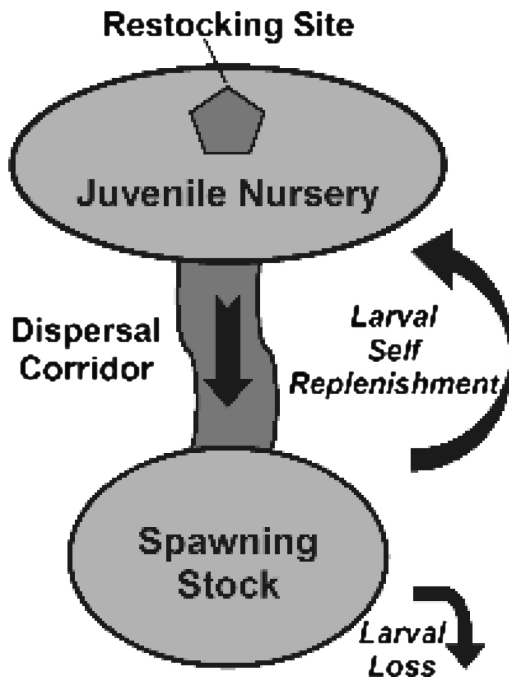

Figure 2 Ontogenetically disjunct populations. These populations also have limited interchange with other populations but exhibit habitat segregation during their life cycle—individuals move across different habitats as they develop and mature. Juveniles in restocking sites emigrate before they reach maturity.

especially vulnerable to exploitation. At this level of complexity, we must consider not only the protection of individuals in restocking areas, but also the adults in the spawning grounds and within dispersal corridors that link augmented nursery areas or feeding habitats with the spawning grounds (Hines et al., 2008).

A prime example of an ontogenetically-disjunct self-replenishing population is the blue crab in Chesapeake Bay. The blue crab life history involves reinvasion of shallow-water nurseries by post-larvae from the continental shelf, followed by growth and dispersal throughout the tributaries and shallow waters of the inner bay. Mating occurs in the tributaries and inner bay. Mature, mated females then migrate to the bay's mouth to spawn the egg masses, hatch the eggs, and release larvae in the higher salinities of the lower bay. Hence, juveniles, subadult females, and mature males are distributed throughout the bay, whereas mature females migrate to the lower-bay spawning grounds (Lipcius et al., 2001b; Seitz et al., 2001; Hines et al., 2008).

In Chesapeake Bay, the blue crab spawning stock declined by 80% after 1992 (Lipcius and Stockhausen, 2002). A large sanctuary was subsequently implemented to protect the spawning stock in >75% of the spawning grounds (Lipcius et al., 2003) and migratory routes of adult females (Lipcius et al., 2001b). The sanctuary was effective in protecting mature females occurring within it (Lipcius et al., 2001b, 2003; Lambert et al., 2006a) but did not restore the spawning stock due to continued heavy exploitation outside the spawning grounds (Lambert et al., 2006b). Therefore, effective restocking for this species will require protection of juveniles released in nursery habitats, mature crabs in mating habitats, and females along migratory corridors to the spawning sanctuary (Hines et al., 2008).

At a smaller spatial scale, restocking must be implemented with information on patterns of advection and recruitment of young juveniles. In the case of the blue crab in Chesapeake Bay, seagrass meadows provide important settlement habitat, food, and refuge for post-larvae and young juveniles (Lipcius et al., 2007). In the York River, seagrass beds have declined substantially. Beds that existed 12–25 km upriver from the mouth have disappeared. A model for planktonic post-larval behavior was coupled with a three-dimensional hydrodynamic transport model to investigate spatial variation in the efficacy of seagrass restoration and juvenile blue crab augmentation (Stockhausen and Lipcius, 2001). Recruitment was much higher in some locations (e.g., seagrass beds on the northern shore of a tributary) due to spatial variation in transport processes. Landscape-level spatial patterns of seagrass habitat interacted with transport processes and juvenile migration behavior to determine recruitment, and should be considered when evaluating population impacts of habitat restoration or juvenile restocking.

Another example of the susceptibility of restocking to life history traits is the elimination of spawning aggregations of long-lived serranid fishes throughout the Caribbean (Coleman et al., 2000). The Nassau grouper is a case in point; it migrates from widespread shallow reef and seagrass habitats to discrete locations to spawn. Groupers in these aggregations are easily
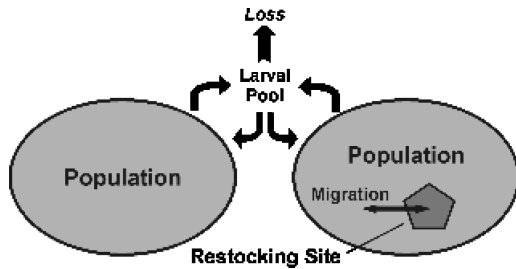
Figure 3 Balanced metapopulations consist of populations with significant interchange, whether at larval, juvenile, or adult stages, and which have approximately equivalent demographic rates (births, deaths, immigration, and emigration), including larval exchange.

exploited because they concentrate over small areas (e.g., hundreds to thousands of fish per ha) during narrow windows of the lunar cycle, and have been fished to local extinction in many locations (Coleman et al., 2000). If one were to restock juvenile grouper while leaving the spawning aggregations unprotected, the restocking effort would fail. Ontogenetically disjunct species such as the blue crab and Nassau grouper require protection in all critical habitats and at all exploitable stages to limit the inevitable redirected exploitation in areas outside restocking habitats.

Metapopulations

When dealing with metapopulations, we confront the vagaries of transport and dispersal processes (Grantham et al., 2003; Largier, 2003; Shanks et al., 2003). The simplest metapopulation setting deals with populations that reside in habitats that do not differ substantially in quality and which contribute equally to the larval pool (Figure 3). In this case, the challenges to restocking are equivalent to those for isolated self-replenishing populations (Figures 1 and 2). In more intricate metapopulations, the origins and destinations of larvae differ among populations (Figures 4 and 5) and can be expected to determine the most efficient allocation of restocking activities among populations.

One species that characterizes a complex metapopulation is the Eastern oyster (*Crassostrea virginica*), whose populations have declined dramatically in Chesapeake Bay, the Western Atlantic, and Gulf of Mexico (Rothschild et al., 1994; Kirby, 2004). The Eastern oyster is well suited for restocking and stock
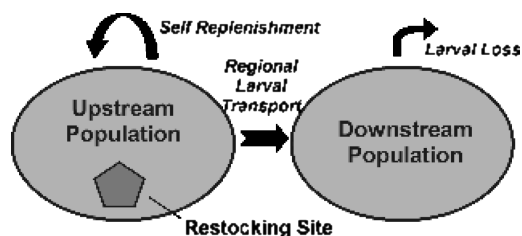

Figure 4 Directional metapopulations are those in which demographic rates are approximately equivalent for all populations, but where larval exchange is uneven and directional. Restocking in upstream populations will produce adults in both upstream and downstream populations, whereas restocking in downstream populations will not produce adults for upstream populations.
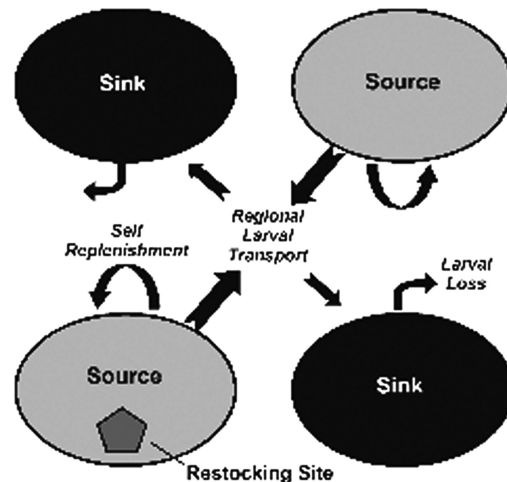

Figure 5 Directional source-sink metapopulations are those where demographic rates differ significantly and substantially between populations, and whose larval exchange is uneven. Restocking in habitats of source populations will increase abundance in more than the source population, whereas restocking in habitats of sink populations will be fruitless.

enhancement due to its sedentary juveniles and adults. In the Lynnhaven River System (LRS) of lower Chesapeake Bay, a three-dimensional hydrodynamic model was used to define the optimum oyster reefs (= populations) for restocking and stock enhancement. Simulated larvae were then "released" from 45 potential sites and the destinations of larvae tracked. A network connectivity analysis demonstrated that populations on oyster reefs in the LRS metapopulation could be grouped into five types (Figure 6). Most importantly, relatively few (7 of 45) of the populations were "sources" (Figure 6b), which self-replenish while concurrently contributing larvae to most (>50%) of the remaining populations and are therefore optimal for restocking of broodstock. The second type was a closed population, which self-replenishes (Figure 6c) while contributing few larvae to the remainder of the metapopulation. Larvae that did not return to the natal populations were advected out of the system and lost to the metapopulation. A large proportion of the populations (13 of 45 reefs) inhabited sink reefs (Figure 6d), whose populations produced larvae that either died before settlement or were advected out of the system. Although these reefs would not be suitable for broodstock restoration, many were in locations that received numerous larvae from source reefs and which would therefore be suitable sites for habitat restoration. Also, oyster populations on restored sink reefs would not be expected to contribute larvae to the metapopulation, but they could improve water quality through their filter feeding and enhance habitat quality for structure-dependent species. A smaller fraction of the metapopulation was composed of populations at "exporter sinks," whose larvae did not return to the natal reef and which did not receive larvae from any other reefs (Figure 6e). Larvae released from these reefs recruited to other reefs, so that they might be suitable sites for one-time broodstock restoration to jump-start the metapopulation. The final reef type was a "putative source," comprising a large proportion of the metapopulation
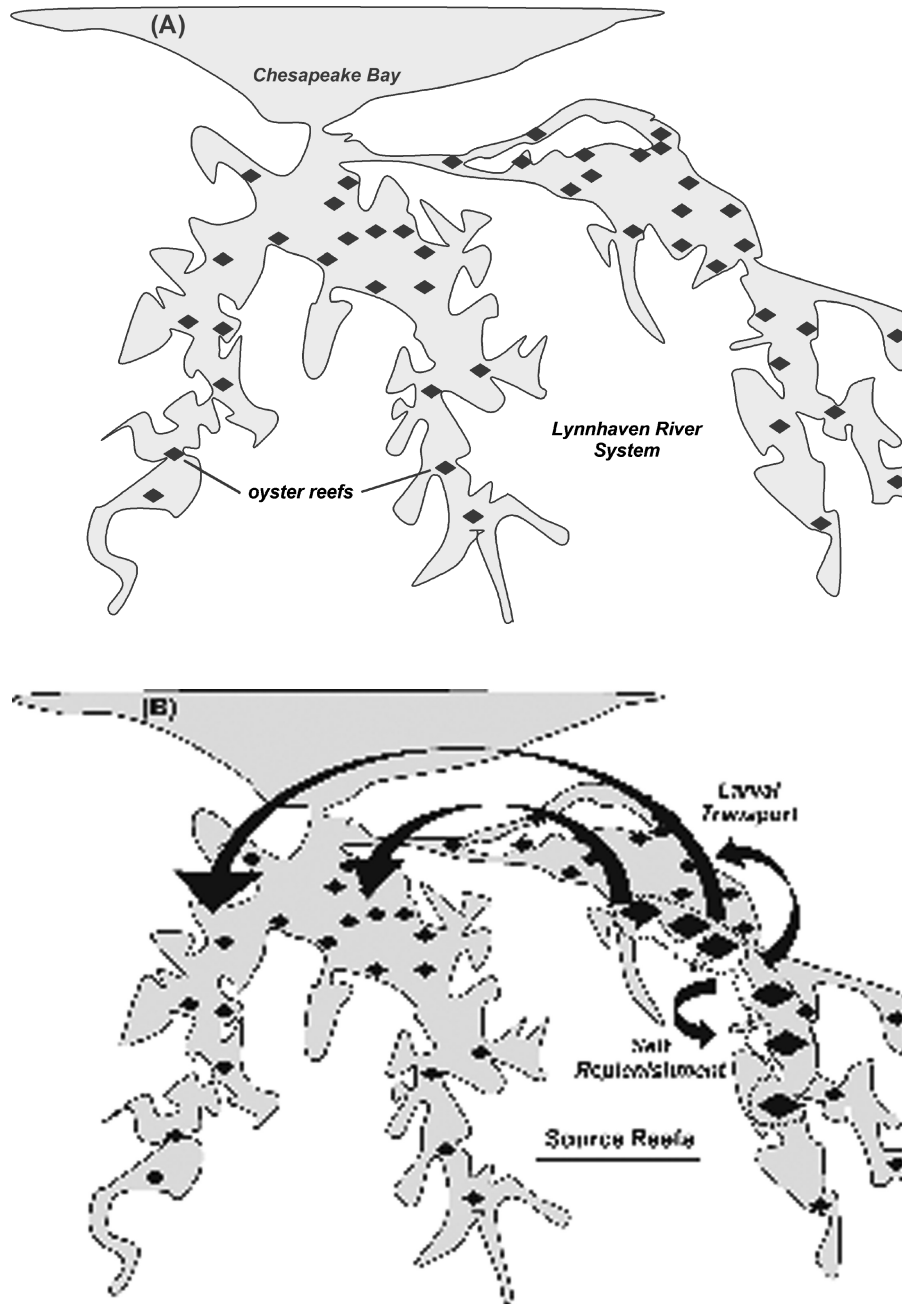
Figure 6 Population (oyster reef) types in a metapopulation of the Eastern oyster in the Lynnhaven River system of Chesapeake Bay, as determined by a network connectivity analysis (Lipcius et al., unpublished data). (a) The metapopulation consisting of 45 oyster reefs harboring individual populations interconnected through larval dispersal; (b) Source reefs support populations that self replenish and which contribute substantial numbers of larvae to most of the remaining 45 populations, except Exporter Sink reefs; (c) Self-replenishing closed reefs do not contribute larvae to other populations—their larvae either settle back on the natal reef or are advected out of the system; (d) Sink reefs harbor populations whose larvae are advected from the system and which depend on immigrating larvae from source reefs; (e) Exporter sink reefs do not receive larvae, though larvae released from these reefs settle on many other reefs of the metapopulation—these reefs support the growth of transplanted oysters, but they were never natural reefs due to the lack of larval settlement; (f) Putative source reefs sustain populations that may or may not self replenish, depending on hydrodynamic conditions, and which can produce larvae that will settle on other reefs in the metapopulation. *(Continued)*

(14 of 45 reefs; Figure 6f). These reefs did not consistently self-replenish or provide larvae to other reefs. Changing environmental conditions could alter these reefs to reliable sources or to sinks. Thus, they are questionable as broodstock restoration sites, though there would be a reasonable likelihood of success, depending on the environmental setting. These reefs might also be suitable sites for reef habitat restoration in the absence of broodstock augmentation.
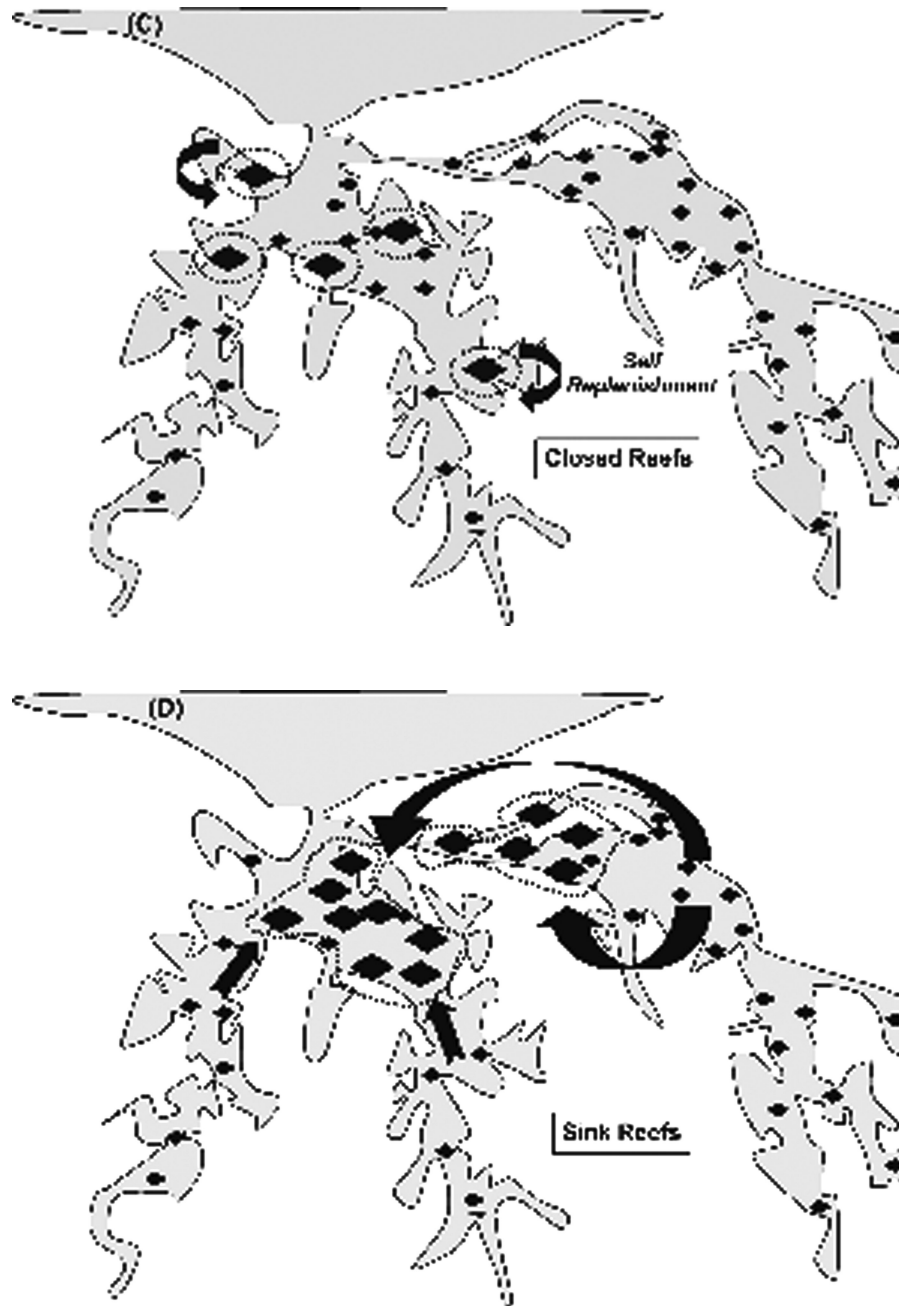
Figure 6   (Continued)

Another species typifying metapopulation structure is the red sea urchin, for which the impact of transport processes upon metapopulation dynamics similarly depends upon the details of transport (Wing et al., 1995; Morgan et al., 2000; Morgan and Botsford, 2001). As in the Eastern oyster, the relative benefits of restocking different populations in the metapopulation would be dictated by population connectivity patterns.

Variation in demographic rates of populations increases the complexity of metapopulations further (Figure 5). For example, the structures and demographic rates of rock lobster *Jasus edwardsii* populations vary noticeably around Tasmania (Gardner

et al., 2000), yet these populations are linked as a metapopulation by larval dispersal. In southern populations, growth rates and reproductive output are substantially lower than those of northern populations, such that adults in the southern populations contribute little to the metapopulation larval pool. Consequently, attempts at restocking of the metapopulation through releases in the southern "sink" region would fail, whereas corresponding endeavors in the northern "source" habitats would likely be quite successful. Recently, translocation of lobsters from the southern region to northern restocking sites was simulated in a population model (Gardner and Van Putten, 2008). Egg production of the northern population was increased, indicating that effective
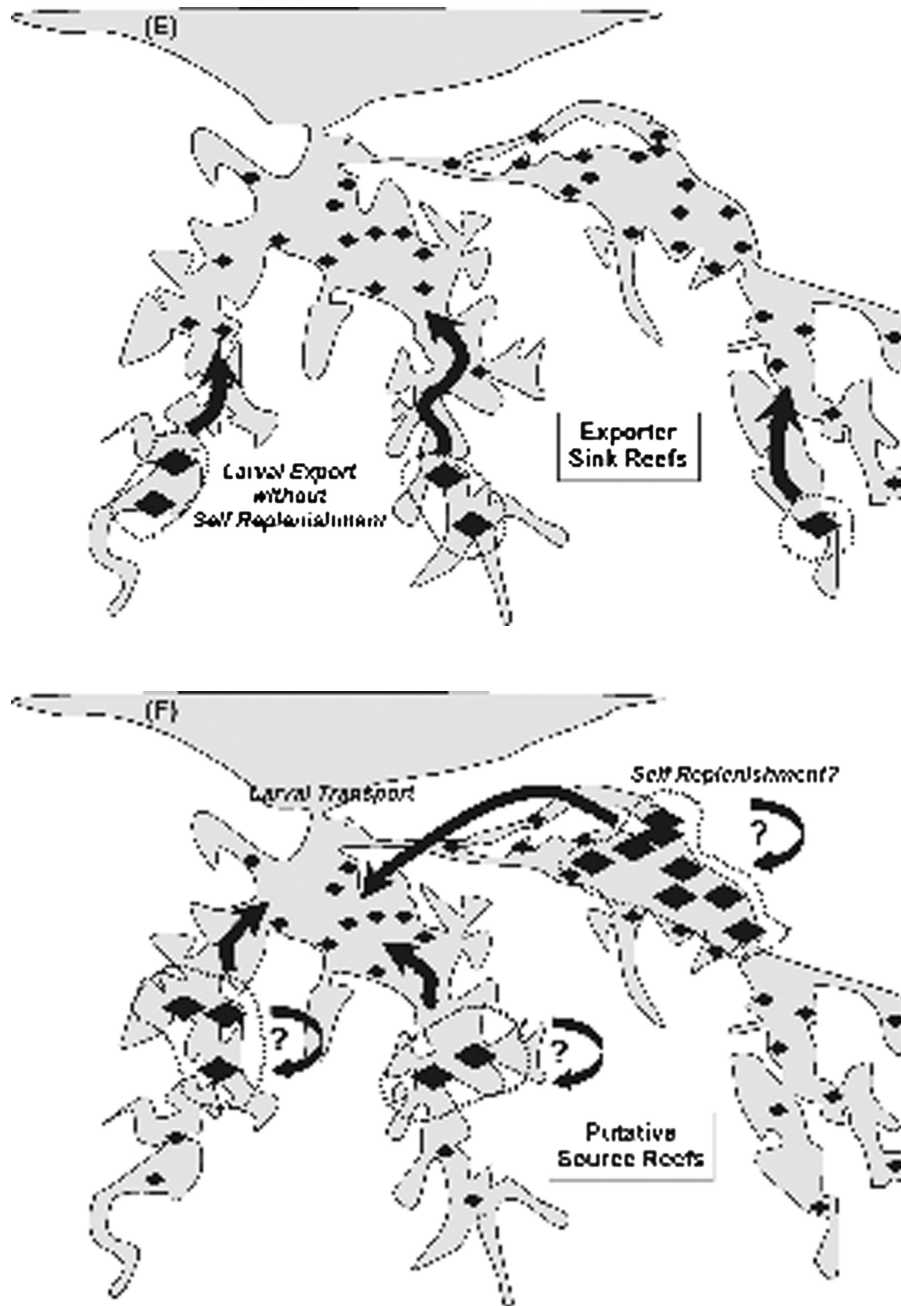
Figure 6 (Continued)

restocking of the metapopulation can be accomplished through translocation of lobsters from sink to source populations.

Another example is provided by investigations of populations of the Caribbean spiny lobster (*Panulirus argus*) at four locations in Exuma Sound, Bahamas (Lipcius et al., 1997, 2001a; Stockhausen et al., 2000). The four locations are separated by 60–150 km from each other, such that reproductively active individuals at the four locations are distinct, but the populations at these locations are linked as a metapopulation through larval dispersal. Sites of origin and settlement of spiny lobster post-larvae were modeled using field measurements of geostrophic

flow and gyral circulation, which drive larval transport in Exuma Sound. Most larvae produced at two of the four locations (Figure 7: Great Exuma Island and Cat Island) were advected to a single site with poor habitat quality and low adult abundance. The remaining two sites of origin (Figure 7: Exuma Cays Land and Sea Park and Eleuthera Island) produced larvae that were advected to all four locations. Restocking efforts at the latter two sites would improve metapopulation recruitment, whereas efforts at the former sites would be unfruitful. In this complex scenario, the spiny lobster metapopulation was characterized by spatially-distinct transport processes and source-sink dynamics
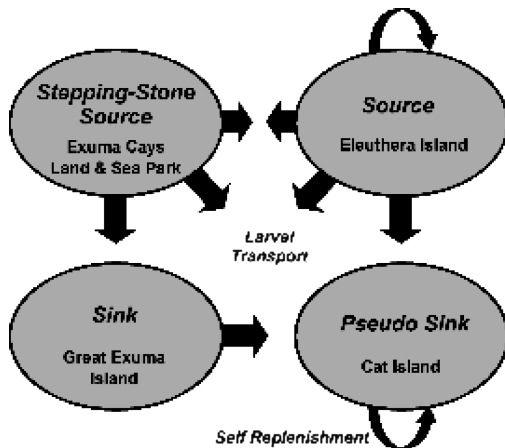
Figure 7 Synopsis of metapopulation connections for the four sites simulated in the Exuma Sound metapopulation of Caribbean spiny lobster. Arrows indicate sites that release larvae which settle in significant numbers at recipient sites. Looping arrows indicate sufficient larvae for self-replenishment.

(Figure 5). One of the former sites (Figure 7: Great Exuma Island) had excellent habitat quality and was therefore a prime candidate for restocking, but it contributed little to recruitment in the metapopulation because most larvae produced there were either expelled from the metapopulation or transported to a distant site with poor nursery grounds (Figure 7: Cat Island). Hence, restocking efforts at only two of the four sites (Figure 7: Exuma Cays Land and Sea Park and Eleuthera Island) would be suitable for metapopulation recruitment, with the best site being Eleuthera Island which also self replenished. In selecting an optimal location for restocking, the best strategy was one that used information on larval transport and habitat quality.

CONCLUSIONS

Selection of restocking sites requires careful attention to the interplay between metapopulation dynamics, habitat quality, and recruitment processes. Populations can differ dramatically in demography, habitat quality available to them, and connectivity patterns (Figures 5, 6 and 7). Source populations, which are optimal for restocking efforts, can be distinct geographically and may be a small percentage of the metapopulation. Sink areas, where broodstock restocking is almost certain to be fruitless, can nonetheless benefit from habitat restoration because larvae from source reefs are likely to recruit to these areas. Optimal metapopulation augmentation is most likely to be attained by making releases into source populations while allowing exploitation of sink populations linked to the sources via larval dispersal. Failure to investigate metapopulation dynamics can doom restocking programs for marine species.

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