

**Connectivity and the evolution of self-recruitment mechanisms  
in marine populations**

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ABSTRACT

In evolutionary terms, a species cannot evolve from an isolated stock unless a mechanism exists that ensures that a reasonable proportion of its offspring repopulates the natal area. Thus, in a marine demersal environment, a closed ontogenetic gyre or loop is essential for the development of a core stock of a species. Larvae that are lost from such a gyre either die, settle in areas in which they cannot successfully replenish themselves or settle in an area in which another stock can be established. Stocks can be connected by occasional influxes of larvae from other areas and the stocks will thus form a genetically similar metapopulation. If one or more component stocks of the metapopulation become wholly isolated as a result of changes in oceanographic conditions, another new species will evolve. If evolutionary processes have favored the adoption of life stages and behavioural traits that enhance self-recruitment, a corollary will be that most demersal marine areas must be largely inhabited by locally spawned stocks and that few recruits can be expected to arrive from adjacent areas unless they are very close and directly up-current. Consequently, marine protected areas that are surrounded by grossly depleted fish stocks will take a very long time to develop significant spawning stock biomasses of exploited species.

INTRODUCTION

Much has been written in recent years about the degree to which individual stocks (sometimes called local populations) of benthic marine fish and invertebrates are replenished by their own progeny, as opposed to being repopulated to a significant degree by propagules produced by distant components of a metapopulation (Johannes 1978, Leis 1991, Roberts 1997, Jones et al 1999, Swearer et al 1999, Crowder et al 2000, Cowen et al 2000). Much attention has been paid to the mechanisms that might enable larvae or post-larvae to return to their natal sites. However, singularly little attention seems to have been given to the evolution of self-recruitment mechanisms and the implication of such adaptations for the management of stocks and the location of marine protected areas and fishery reserves.

Here I argue that all shelf-dwelling marine benthic species must have evolved from single stocks that were able to replenish themselves with their own progeny. This is because any population that becomes reproductively isolated from the main stock or stocks of a species can only evolve into a new species if it has relatively strong adaptations that enable it to replenish itself. Alternatively, it would have to be situated in a very favorable oceanographic gyre. All adaptations that further enhanced the stock's ability to replenish itself would be rapidly adopted. This stock would then become the *core* stock of a new species. As it originated from an isolated stock it presumably would be fairly uniform genetically. If propagules from the core stock managed to settle elsewhere and form another largely self-replenishing stock, then a metapopulation would come into being. While the core stock would be self-replenished to a very high degree, other components of the metapopulation would have rates of self-replenishment ranging from high to zero.

## THE EVOLUTION OF SELF-REPLENISHING MECHANISMS

The earliest forms of marine animal life, either planktonic or benthic, presumably reproduced by simple fission. Self-recruitment, therefore, was not a problem and parts of planktonic stocks would only have been extinguished if they were carried by currents into adverse environments. Later life forms presumably had simple, short-lived, larvae such as planulae and the early reproductive mechanisms must have been suited to maximizing settlement of larvae in the natal area or nearby. They would have functioned best in enclosed or semi-enclosed bodies of water such as lagoons or estuaries or deep ocean areas in which circulation rates or exchange rates were negligible and a significant proportion of larvae were retained close to the parent stock.

However, for those animals that colonized relatively shallow benthic habitats of continental or island shelves with significant ocean currents, the difficulties of retaining significant numbers of propagules would have increased. Larvae that drifted passively would be swept away from their natal habitat and the stock would never be replenished. Larvae that were carried out of a self-replenishing ontogenetic gyre would either be taken into deep water and perish or settle in new habitats far from the parent stock. Therefore, every stock of a marine benthic species that became isolated from the main stock of a species would evolve into a new species only if it had the ability to replenish itself, failing which it would have rapidly become extinct. That ability might have depended on a biological adaptation or on a fortuitous oceanographic gyre. This initial population would have become the *core* stock of the species. Propagules that were swept away from the core stock and settled successfully, would become a *peripheral* stock if they were able to replenish themselves. Alternatively, they might form a *terminal* stock that was able to survive but, if able to breed, be unable to replenish itself because of unfavorable circulation patterns. Thus, metapopulations would have come into being, inter-connected by occasional or frequent exchanges of propagules (Figure 1). A metapopulation can be defined as a population that consists of a number of spatially separated stocks (such as those inhabiting different reefs or island ecosystems) that are connected to a greater or lesser degree by interchange of propagules. If one or more component stocks of this metapopulation became isolated as a result of oceanographic changes, then another new species might evolve.

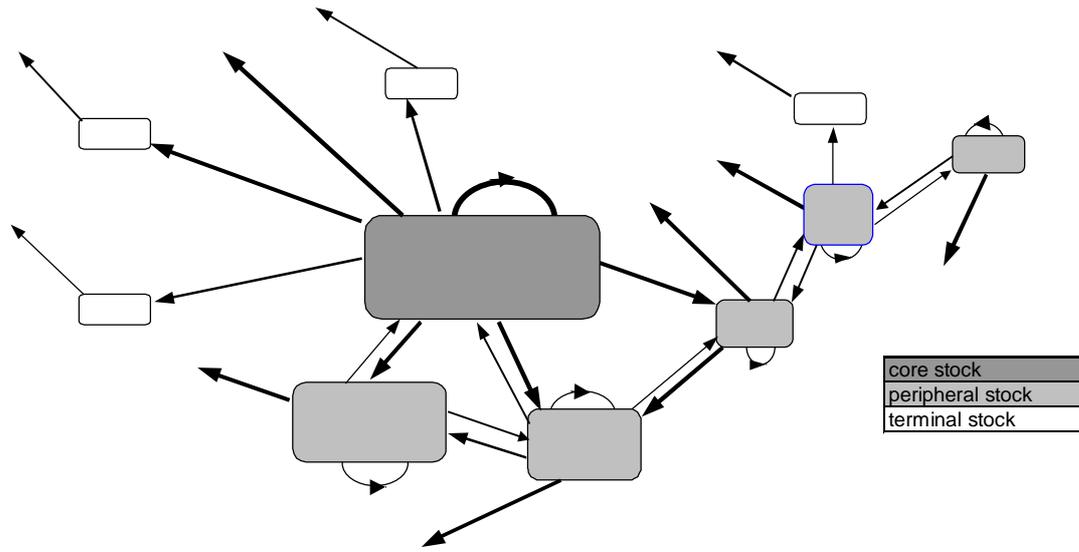
A core stock will inhabit some relatively central area within the distributional range and be characterized by having a high rate of recruitment ( $R$ ) relative to spawning stock biomass ( $SSB$ ). Peripheral stocks would have  $R/SSB$  ratios ranging from very high to nearly zero. Terminal stocks would be those that have zero self-replenishment because of oceanographic conditions.

During the course of evolution a number of reproductive strategies have evolved in demersal marine organisms that clearly serve to reduce the chances of dispersal of propagules. These include viviparity (some fishes), passage of most larval stages within an egg capsule (many gastropods, squid, octopus, lobsters, some sharks) and brooding of eggs in nests (damsel fish), pouches or brood chambers (some oysters, ascidians, sea horses) or egg masses (pipefish, apogonids). However, these are all relatively uncommon and represent advanced adaptations. For most shallow, marine, benthic animals one or more relatively long-lived planktonic larval stages are the norm and this is at odds with the apparent need to ensure that individual stocks are effectively replenished. They appear to function more effectively for dispersal of the species. The possible reasons for the evolution and maintenance of a pelagic stage in reef fishes has been comprehensively discussed by Bonhomme and Planes (2000). Their arguments apply equally to most other marine benthos.

However, if this phenomenon of a planktonic and, for some species, a later pelagic larval phase is placed in its evolutionary context it makes more sense. Larvae produced by any core stock needed to survive and return, at some stage, to their natal habitat. Drifting in the plankton might have advantages in terms of release from predators and the availability of planktonic food, but disadvantages in terms of self-replenishment. However, it is suggested that all marine larvae have behavioral, sensory or morphological adaptations that will, *if oceanographic conditions are right*, enhance their ability to return, with some degree of success, to their natal habitats. For many species, ontogenetic movements from nursery areas to adult habitat make this a three-stage process and spawning migrations from the adult habitat may add another dimension to the ontogenetic gyre.

The "Fundamental Theorem of Natural Selection" (Fisher 1930) states that a population will very rapidly assimilate any adaptation that gives an organism a greater chance of reproducing itself. This is a

mathematical fact. Consequently, it is likely that seemingly useless or ineffective features of an animal's behaviour or morphology might only make sense in the context of the original core stock. For other stocks, the adaptations might be effective to some degree or be quite useless or even fatal. But that is irrelevant as long as the core stock is replenished. Of course, adaptations that are more widely useful to component stocks of a metapopulation will also be rapidly adopted. It is not argued that core stocks will be unfailingly replenished year after year. Variability in ecological conditions is still the main factor affecting successful settlement of year-classes and order-of-magnitude variations in settlement rates are normal events in most species (Coe 1956, Munro and Bell 1997).



**Figure 1.** Hypothetical structure of a metapopulation consisting of a core stock with strong self-replenishment, peripheral stocks with variable self-replenishment and terminal stocks that are unable to replenish themselves.

Thus the 'core' stock is simply the original stock and, for a species with a continuous distribution over a wide area, might be the only stock. If the core stock in a metapopulation was eliminated by oceanographic changes this might lead to the extinction of the species. Alternatively, if the original adaptations that ensured a high degree of self-replenishment were still effective, one or more of the other stocks might take up that role. Species that are very rare will be those that have lost their core stock and survive only by chance replenishment of local stocks by random events.

Although it should be possible to identify a core stock because it will be one of those with the highest rates of recruitment relative to its spawning stock biomass ( $R/SSB$ ), this would not be an absolute rule because a stock might have high recruitment from elsewhere simply by virtue of its oceanographic situation. For example, a terminal stock of a tropical species in North Carolina waters might get high rates of settlement of larvae that have become entrained in the Florida current, but not survive well and never reproduce successfully. Also, areas with high topographic complexity, such as the Bahamas, might also be favored in terms of retention of larvae, simply because of the eddies and gyres that are caused by physical features. Ratios of  $R/SSB$  would be fairly easily measurable by underwater visual censuses of SSBs and by monitoring settlement rates of post-larvae with light traps or abundances of pre-recruits in small-meshed Antillean fish traps (Munro 1999, Munro and Watson 1999).

#### THE CARIBBEAN SITUATION

The rather limited array of species of fish and invertebrates that inhabit the Caribbean presumably evolved from an even more limited number of species that inhabited the area when the Caribbean

became isolated from other coralline tropical seas. Metapopulations of these species are now mostly quite widespread in the Caribbean, from Trinidad to Bermuda. The shallow demersal benthic species separate into insular and shelf species with obvious differences in the ease with which post-larvae will be able to find suitable habitats at settlement. Species that inhabit isolated habitats such as coral reefs, mangroves, sea grasses or rocky shores must have more difficulty in finding their natal habitat, or any other suitable habitat, than those that inhabit broad soft-bottom shelves.

If the foregoing arguments are correct, all Caribbean species, and particularly the reef-dwelling insular species, must have adaptations that assist the return of propagules to their natal reefs or, at least, to suitable shallow habitats. The degree to which larvae are exchanged between islands or reef areas will depend on proximity, oceanographic conditions and chance (Cowen et al 2000). However, apart from exceptional situations, the evolutionary imperative will dictate that most successful settlers or recruits will be returning to the general area where they originated, if not to their natal reefs.

The effect of heavy fishing will be to reduce spawning stock biomasses (SSBs) and weaken or break connections between Caribbean metapopulations. Severe over-fishing can reduce the SSBs to zero or negligible levels and reduce the influx of post-larvae to similar levels (Munro 1999, Munro and Watson 1999). When marine protected areas (MPAs) are created in seriously over-exploited areas, the build-up of stocks in the MPAs can be expected to be a very lengthy process.

Isolated islands can be expected to be "on their own" in terms of recruitment; whereas island chains and continental shelf populations will be to some degree interconnected, with terminal populations at the limits of the distribution of many species. On the basis of the arguments presented here it seems clear that marine protected areas are needed throughout the Caribbean. Given the prevailing currents, the stocks of vulnerable reef fish, such as groupers, in the eastern Caribbean would be particularly vulnerable to being extinguished by overfishing. In cases of severe overfishing, the benefits of fishery reserves for rebuilding SSB of high-value species, e.g., groupers, could be augmented by responsible restocking programs (Munro and Bell, 1997) to "fast-track" the creation of viable numbers of reproductive fish.

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