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LOCAL RETENTION OF PRODUCTION IN MARINE POPULATIONS: EVIDENCE, MECHANISMS, AND CONSEQUENCES

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A major unanswered question in marine ecology is the degree of connectedness between local populations. Put another way, what proportion of young arriving into a local population are products of local production? What is the source of recruits for any local population, and where do the young produced in a local population go? The answers to these questions are unknown for most widespread species with a pelagic larval phase. Proper marine management depends on knowledge in this area: the efficacy of any reserve design, for example, is highly dependent on the degree to which it is reliant on other populations for recruitment, and the degree to which it supplies other areas.

Since most marine animals have a pelagic larval stage, the paradigm thus far has been to assume extensive dispersal and massive export (e.g., Thorson, 1950; Vance, 1973). In this view, connectivity is pervasive and extensive, with local populations receiving their young from the 'larval pool' to which most populations contribute. In such 'open' populations, recruitment is essentially independent of local production, and local dynamics are determined solely by recruitment and post-recruitment mortality (Warner and Hughes, 1988; Caley et al., 1996). To evaluate the appropriateness of this view, we convened a Working Group at the National Center for Ecological Analysis and Synthesis[1]. Our goal was to examine the evidence for open vs closed marine populations from a wide variety of viewpoints. The following fields were represented:

- Life-history characteristics of endemic species
- Genetic structure of marine populations
- Patterns of spread of introduced species
- Larval distributions, ecology and behavior
- Near-shore oceanography
- Marine paleoecology
- Empirical studies of recruitment
- Proximal effects of marine reserves

The entire group rapidly reached the consensus that evidence from a variety of fields indicated that local retention may be considerably more prevalent than previously thought, even in species with long larval durations. If such retention turns out to be a common feature of local marine population dynamics, this will require major reassessment of marine metapopulation models, fishery management schemes, marine reserve designs, and ideas about the mechanisms of marine speciation. Based on our deliberations of these issues, what follows in this special issue is a collection of papers representing the results of the Working Group's efforts to: (1) assemble the evidence, (2) examine the mechanisms, and (3) consider the consequences of local retention of production.

[1] Open vs Closed Marine Populations: Synthesis and Analysis of the Evidence. Convened by Robert Warner in October, 1999.

Scales of Interest and Definition of Terms

Because debates about ecological principles can easily get mired in semantics, the Working Group agreed that all the manuscripts would attempt to work at the same scale and to use similar terms with agreed-upon definitions, as follows.

What is meant by a *local* population? The spatial scale over which observations are made is obviously important. At the smallest scale (meters to 10s of meters), most populations are open in the sense that local production does not influence local recruitment. At the largest scale (a species range), all populations are closed. These facts should not deter us from asking questions about the degree of local retention at intermediate scales, however. The Working Group chose to focus on scales involving areas on the order of km to tens of km. Further, the connectivity issue over this spatial scale is focused on ecologically, or demographically, meaningful time scales (i.e., less than generation time). Therefore, we are primarily interested in time and space scales associated with the replenishment and maintenance of marine populations.

There were strategic and practical reasons for choosing the above spatial scale. First, given marine organisms with pelagic larval durations on the order of days to several weeks, and given average current speeds, the null model of passive particle transport would suggest that local production would disperse out of the area in question (e.g., Roberts 1997). That is, common assumptions would characterize marine populations at this spatial scale as open. Second, these are scales of practical interest to marine ecologists (in the sense that studies over such scales are logistically possible) and marine resource managers (in the sense that these scales encompass the sizes of most existing and proposed marine reserves; see Halpern, in press).

Another way to approach this question is to describe the spatial extent of successful dispersal from a particular area. If such a distribution encompasses the natal population, then self-recruitment occurs. Mean dispersal distances are critical parameters in many marine population models, including spatial fisheries management schemes and quantitative approaches to marine protected area design (e.g., Ruckelshaus and Hays, 1998, Botsford et al., in press) and the provision and protection of larval habitat (Carr and Reed, 1993). While the importance of knowing dispersal distances is widely acknowledged, the data have proven elusive.

The working group also concentrated on organisms with pelagic larval durations on the order of days to several weeks, precisely because these durations are common and we know little about the fate of larvae pelagic for these periods. It would be no surprise to find evidence of local retention in species with direct development, crawl-away larvae, or pelagic larval durations on the order of minutes or hours. Equally, cases of long-distance dispersal should be found in species with teleplanic larvae (sensu Scheltema, 1988) that are pelagic for many months. The unknown region in Table 1 encompasses the majority of marine benthic species and serves as the focus for our work.

For consistency across the articles in this series, the Working Group settled on a several definitions of common terms:

Given the scales of interest, a *local population* is a circumscribed area containing nonmigratory adults that reproduce within that area. The question then becomes: What proportion of recruitment into that area is the result of production by the local population? If this is very low, the local population tends to be open. If it is high, the local population is

Table 1. Characterizations of marine species by adult and larval movement, and the corresponding expectation regarding the degree of retention of local production. The question marks identify the main objects of investigation of the Working Group.

Adults:	Sedentary	Sedentary or localized			Highly mobile
Larval mode:	Brooded, crawl-away, or physically constrained	Short pelagic	Long pelagic	Very long	Pelagic
Local population:	Closed	?	?	?	Open

relatively closed. We realize that these are relative terms, but feel it is too early to be more quantitatively explicit.

Recruitment that results from retention of local production is termed *local* or *endogenous* recruitment. In contrast, recruitment that results from production in areas other than the local population is *non-local* or *exogenous* recruitment.

Connectivity is the degree to which local production results in recruitment to other populations. For any local population, connectivity could be characterized by (1) the proportion of recruitment into the local population that is endogenous; (2) the proportional contributions of other populations to recruitment into the local population, in a spatially explicit manner; and (3) the spatial distribution and proportional representation of the contributions of local production to exogenous recruitment in other populations.

Structure and Content of this Special Issue

The series of papers in this special issue consists of three parts: Evidence, Mechanisms, and Consequences. There are three papers in the Evidence section. Swearer et al. review and evaluate the sources of information we have brought to bear on the problem, providing the audience with a broad overview of the synthesis of the working group. In addition to this summary, Hellberg et al. organize the existing information on population genetics of marine organisms to evaluate connectivity. Much of the evidence covered in these papers is indirect. The most compelling evidence for local retention will come from studies using natural or artificial markers. Thorrold et al. review the attempts to use this latter approach, and provide a valuable guide for future work.

The Mechanisms section explores the physical and biological bases for larval retention: how can such small, seemingly helpless organisms remain near their source while in the pelagic environment? Kingsford et al. provide the essential background to this question, pointing out that larvae are quite competent pelagic organisms with a wide variety of sensory and motor capabilities. Sponaugle et al. discuss and evaluate biological and physical features that may be associated with local retention, with the aim of being able to predict a priori when and where such retention should occur. They also discuss how larval behaviors might interact with physical hydrographic features known to occur in nearshore environments.

The Consequences section consists of a single paper with two major themes: Strathmann et al. first reexamine the evolutionary basis of the pelagic larval phase: is it 'for' dispersal, or simply a migration to another environment? They then discuss the implications of local retention in marine populations on evolution (e.g., speciation, local adaptation) and on ecology (e.g., population dynamics and management).

Implications for Applied Ecology

As management and conservation schemes begin to focus on marine reserves and protected areas as key design elements, the degree of connectedness between local marine populations assumes critical importance. The paradigm of extensive dispersal and massive export inspires models that combine large-scale current estimates with known larval durations to predict patterns of connectivity (e.g., Roberts, 1997). These models often assume simple flow regimes and passive-particle larvae, and this may lead to large inaccuracies if nearshore physical processes and larval behaviors lead to local retention of young (Cowen et al., 2000). The evidence for a surprising amount of local retention that we review here suggests that it is still an outstanding question whether marine populations should be managed as open (i.e., strongly connected local populations, best approached through metapopulation models) or closed (i.e., dependent on local production, similar to many terrestrial systems).

Preservation of post-settlement feeding and spawning areas may have little effect on population sizes if presettlement processes are of critical importance in structuring marine assemblages. If many recruitment pulses are indeed retention events, as some recent evidence suggests (Swearer et al., 1999), then preservation of nearshore retention areas is as important as preservation of adult habitat. Also, extensive larval retention may require major reassessment of fishery enhancement models of marine reserves that depend on larval export for their effects.

Given these implications, we hope that this series of works will inspire further investigations in this critically important area. At the very least, we now have viable alternative hypotheses to the 'larval pool'.

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