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The Science of Larval Dispersal and Its Implications for Marine Reserve Planning

For scientists who study the larvae of marine species, traditional theory has held that such offspring are relatively passive in their movement, riding ocean currents potentially great distances before settling in a new area of the sea. But recent research on larval dispersal has suggested that for many species, larvae may play a relatively active role in determining their own settlement area. Some larvae may even resist currents in order to stay in local waters, the home range of their parents, establishing a cycle of self-recruitment for the resident population.

Where MPA planners seek to protect marine species, the issue of long-distance dispersal or local retention of larvae can play an important role in guiding decisions on protected-area design. This month, MPA News examines the state of the science of marine larval dispersal and how MPA practitioners can account for dispersal in planning marine reserves.

Measuring larval dispersal

The marine organisms most often protected with MPAs live in shallow water, and the majority of shallow-water species have a two-phase lifecycle. Relatively sedentary adults, living on or near the sea bottom, produce larvae that exist largely in pelagic (mid- to surface-water) environments. The larvae eventually settle to the bottom and grow to be adults, starting the process over. Because many larval stages, particularly in the first weeks of life, are seemingly too small or undeveloped to contend with ocean currents, biologists have historically assumed passive dispersal to be the rule in determining settlement.

Challenging that rule has not been easy. The logistics involved in tracking very small larvae through a larval period lasting weeks or months can be difficult. "Unfortunately, there is little information about the mean dispersal of most marine larvae," said Steve Palumbi, a marine population biologist at Stanford University (US). "Larval dispersal is unmeasured in almost all important fishery species."

In the past decade, however, researchers have developed indirect ways of estimating dispersal distance, and have found indications of an apparent fondness for home among several marine species. As described by Palumbi in an article he co-wrote with Robert Warner in the journal *Science* (3 January 2003), evidence to challenge the passive dispersal theory has come mainly from two sources: advanced genetic monitoring of scattered marine populations, and chemical analysis of particular internal structures in larvae.

"By comparing the genes of individuals collected from different places, genetic analysis can help to underscore the way in which marine populations move around," wrote Palumbi and Warner. "Because every adult or larva or egg carries with it the genes it inherited from its parents, genetic variation can serve as a natural tag." When differences emerge from marine genetic data among populations - as researchers have found in several organisms, including species of shrimp, gobies, crabs, oysters, and mussels - the implications are strong that little population exchange has taken place. This in turn indicates short dispersal distances and self-recruitment, say Palumbi and Warner.

Paralleling this genetic research have been investigations of the chemical signature of otoliths and statoliths, small structures found in the balance organs of fish and mollusks that form layer upon layer through an organism's life. Each layer incorporates trace metals from the immediate surrounding marine environment, enabling researchers to track where larvae were hatched and how far they dispersed. Findings using this technique have been similar to those of the genetic research, say Palumbi and Warner. "[The] emerging empirical data obtained using two very different approaches are telling us the same thing: that in some times and places, marine larvae are capable of maintaining close links to home despite their proximity to the ocean highways of the sea."

(Direct study of larval dispersal is also possible, namely through the "mark and recapture" method: i.e., introducing a fluorescent mark into otoliths of developing fish embryos, allowing them to hatch in the field, then sampling the larvae at settlement. Developed by Geoffrey Jones and a team from James Cook University [Australia], this method has been used to indicate self-recruitment in a population of coral reef fish.)

How do some larvae stay so close to home? Biologist Jeffrey Leis of the Australian Museum, who studies the offspring of reef fish, says larvae can be very good swimmers, particularly as they enter their settlement stage. Of fish species on the Great Barrier Reef, he says, the fastest larvae are capable of swimming at speeds of over 60 cm per second (cm/s). With the mean current speed in the area being just 10-20 cm/s, these larvae can swim faster than the local water flow. "With swimming capabilities such as these, the average settlement-stage reef-fish larva could easily swim across the width of the Great Barrier Reef near Lizard Island [a distance of 50 km] in less than three days," said Leis. "This indicates considerable control over which reef it settles on at the end of its pelagic phase."

Larval fish have also displayed abilities to orient their movement according to an array of sensory cues - including smell, sight, and sound - and to control their vertical distribution in the water column, where differentials in currents can be significant. "It seems clear that by the end of the pelagic phase, larvae of reef fishes are behaviorally very competent and are able to greatly influence, if not totally control, their trajectories," said Leis.

Oceanographic currents still play an important role in the dispersal of larvae, however. Leis points out that when reef-fish larvae initially leave the reef as pelagic eggs or newly-hatched larvae, they are very close to being the passive particles that the traditional simplifying assumption on dispersal would have them to be: the larvae's impressive behavioral capabilities develop sometime later in the pelagic period, which can last 10-100 days. And local oceanographic factors, such as gyres, have been shown to wield significant effects on the dispersal of larvae. The passive dispersal theory therefore may represent more of an upper limit to dispersal, particularly for species with lesser swimming and orientation skills as larvae. "It is likely that the proportion of self-recruitment in marine populations will vary among locations, among times, and among species," said Leis.

Recommendations for reserve planning

The movement of larvae into and out of no-take marine reserves plays an integral role in determining whether reserves can sustain themselves, exchange larvae with other protected sites, or supplement surrounding fished areas. Therefore, although our scientific understanding remains very basic, the effective design of reserves and reserve systems requires some consideration of larval transport.

"Of course, we know very little about actual dispersal, beyond the evidence that in many cases it looks like it is much more limited than we once thought," said Warner, who co-authored the above-mentioned *Science* paper with Palumbi. (Warner is a biologist at the University of California, Santa Barbara [US].) "What this may mean is that local increases in larval production - for example, what you might get from local protection in a reserve - will have a local effect on recruitment. Thus reserves of proper size could be self-seeding." Assuming there is some spillover of self-seeding populations across the reserve boundary, Warner says this bodes well for local fishermen. "For fisheries that might be limited by the arrival of new recruits, this could be good news, because the same people who give up local areas to closures could also be the beneficiaries of local enhancement to nearby areas," he said.

Reserves are much more likely to support self-recruiting populations of short-distance dispersers than long-distance dispersers. (Bottom-living invertebrates generally disperse shorter distances than bony fish, although there are many exceptions.) As a result, although isolated reserves may protect some species, others - those with greater dispersal distances - will receive less protection. Therefore, networks of reserves may be necessary to protect the longer-dispersing species. Notably, the reserves in these networks need to be close enough for these protected populations to interact.

Said Warner, "The best advice I can offer is that, in networks, spacing reserves at a range of tens of kilometers from each other will likely result in good connectivity between reserves for many species, while ensuring adequate export to areas outside of protection." (In a perspective piece in the March 2001 issue of MPA News, Palumbi of Stanford also provided size suggestions for reserve networks based on considerations of larval dispersal [MPA News 2:8].)

Warner looks forward to improved computer modeling to help planners in their work. He is part of a large US-based group (the Partnership for the Interdisciplinary Study of Coastal Oceans, or PISCO) involved in research to test models of circulation in nearshore shallow-water environments, accounting for physical features like capes, headlands, and downstream eddies around islands, as well as capturing three-dimensional current flow and rudimentary larval behavior. "The eventual aim is to provide managers with models that can estimate larval dispersal and retention based on simple measures of local physical conditions (geography, bathymetry, tidal range) and simple measures of life history (pelagic larval duration, time of spawning)," said Warner.

Lower-technology methods for measuring dispersal and larval duration of individual species are accessible to most researchers (see box at end of article). MPA planners who don't have time to apply these tools may want to consider so-called "retention zones" as potential sites for MPAs. Such zones - areas that tend to accumulate larvae prior to settlement, often due to a re-circulating current - can be useful for designing self-recruiting reserves. Where water flows along a curved or bumpy coast, for example, it may separate from the coast and form a swirling eddy. Such eddies can range from 1-100 km or more in diameter, and often form around headlands or rocky promontories. Semi-enclosed bays or lagoons can offer a similar effect.

Callum Roberts, a marine biologist at the University of York (UK), says planners should not worry too much about the precise details of larval dispersal. "I do not think exact knowledge of larval dispersal will ever be critical to planning effective marine reserves, because reserves are designed to benefit the full spectrum of biodiversity," he said, noting that the case would be different for single-species protection efforts. "Every species has a different dispersal strategy, so any reserve placement is going to be good for some species and less good for others. We cannot hope to gather knowledge of all of those dispersal strategies to feed into reserve planning. And even if we did, this would simply highlight the trade-offs that have to be made regarding which species will gain most from particular reserve placements."

Roberts, who with Fiona Gell of the University of York has authored a new report on fishery effects of marine reserves (see the Notes & News section, this issue), says recent advances in the study of larval dispersal only serve to display how little we still know. "To overcome our ignorance, we must adopt the strategy used by investors," he said. "We need to create protected areas in networks that, averaged across all reserves, will accommodate the dispersal needs of all species and will continue to do so even as environmental conditions change. Like investors, we can make best guesses (using the latest science) about what places to include in our network portfolio, based on prevailing current regimes, habitat quality, species distributions and distance to other reserves, for example. By creating such risk-spreading networks, we hope that we will succeed in sustaining species and fisheries over the long term."

For more information

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An MPA News interview with **Jeffrey Leis**, providing background and literature citations relevant to his comments above, is available online.

Box: Low-cost methods for measuring larval dispersal

Wide implementation of high-tech tools for measuring larval dispersal, as described in the above article, may be years away. In many parts of the world, the technology is not readily available to researchers, and where it is, the cost or time required to conduct it can be prohibitive. For advice to researchers on how to measure larval dispersal using relatively low-cost methods, MPA News asked two experts: Rudolf Hermes of the Visayan Sea Coastal Resources and Fisheries Management Project (Philippines), and Jeffrey Leis of the Australian Museum.

"A good understanding of wind-driven surface (and near-surface) currents is essential - possibly overlaid by tidal currents, assuming that the MPA is nearshore," said Hermes. "The use of drift cards or miniaturized drogues should be considered." Drift cards and drogues are both floating devices designed to mimic the potential passive dispersal of larvae over time. Their final location is used to assume the direction of surface currents. Although these tools don't drift exactly like larvae and are restricted to riding surface currents, they can indicate the range of dispersal distances from several different release-points.

"A major shortcoming [of drift cards and drogues] is that neither the trajectory nor the time spent in transit until stranded or recovered can be known," said Hermes. "And only a general idea on directional movement can be deduced. This, however, may constitute a reasonable basis to address concerns on source-sink relations between potential sites," said Hermes. He estimates that drift cards - printed cards in waterproof plastic sheets connected with nylon to little floats - could be produced in a local community setting at US $0.50-$1.00 apiece.

Actual sampling of fish larvae in shallow inshore habitats can employ plankton traps, such as those that use light as an attractant, or plankton net tows, he said. "Transect stations across the shelf from inshore to offshore sites may provide an idea about larval movements," said Hermes, "but otherwise this methodology only results in 'snapshot' inventories and should be combined with the above-stated hydrographic activity."

Leis notes that although the sorting and identification involved in plankton studies can be labor-intensive, the actual sampling process is relatively easy, doesn't require expensive infrastructure, and can be done from small boats. "Plankton net tows, if properly designed, can give a strong indication - and in many cases a demonstration - of dispersal, retention or self-recruitment," he said. "What is required here is a good taxonomic base of knowledge, as it will be necessary to identify larvae species in most cases."

Leis agrees that light traps, as well as fixed channel nets and plankton purse seines, are useful for measuring the numbers of larvae that are about to settle. "Low-cost light traps can be assembled by researchers and are relatively inexpensive to operate," he said. "It is important to note, however, that each sampling method has limitations, and most are suitable only for comparisons of relative abundance among locations and times." He said, for example, that light traps can operate only at night, are highly selective in the species they capture, and may have their catch influenced by ambient light levels, current speed, and water turbidity, among other limitations. "Careful framing of questions and matching of the questions to sample gear advantages and limitations is required," he said. "It is often useful to combine different sampling methods."

For more information

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An MPA News interview with **Jeffrey Leis**, providing background and literature citations relevant to his comments above, is available online.

Box: Measuring larval spillover from a reserve (Taklong Island, Philippines)

Willy Campos, a biologist at the University of the Philippines in the Visayas, is measuring the dispersal of fish larvae to determine larval spillover occurring out of the Taklong Island marine reserve in the Philippines. MPA News asked him what challenges he had encountered in monitoring the spillover and how he met those challenges. The following is his reply:

"Our first concern was how and when to sample. Various methods, employing various net sizes (dimensions) and sampling durations (e.g., every tidal phase or cycle, or continuous over moon phases) have been reported in the literature. We were unable to actually test any in the field because of time and resource constraints. We eventually decided on using moored surface and bottom nets retrieved hourly during a tidal cycle (night) at the new moon phase, because this would give us information on how concentration and perhaps species composition varied with tidal stage. This in turn provided insights on the potential role of behavior (e.g. vertical movement) in the dispersal.

"Another concern was where to sample. We initially decided on what appeared to be a main path for water exchange between the shallow reserve area and the outside, and observed that movement at this location was always outward, regardless of tidal stage. To verify this, we conducted drogue studies covering a complete tidal cycle, using improvised drogues and handheld GPS units to record drift. From this we were able to confirm water movement within the reserve, and other important features, such as gyres forming at the shallow southern entrance (precluding outflux perhaps) and what appears as rather restricted movement in the area of the mangrove forest in the reserve. This made it clear that we needed to deploy nets at two sites simultaneously.

"The study is still ongoing and we intend to examine the effects of the spring-neap [strong tide-weak tide] cycle, new vs. full moon phases, and how these might vary with the monsoon seasons. We are still continuing the hourly sample interval."

For more information

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Box: For more on larval dispersal, MPAs...

For readers who want more information on larval dispersal and how it can affect the design of MPAs, two academic journals have recently published supplemental issues of relevance to the topic:

Bulletin of Marine Science, Vol. 70, No. 1, Supplement. January 2002. Titled "Open vs. Closed Marine Populations: Synthesis and Analysis of the Evidence". Edited by Robert Warner and Robert Cowen.

Ecological Applications, Vol. 13, No. 1, Supplement. March 2003. Titled "The Science of Marine Reserves". Edited by Jane Lubchenco, Stephen Palumbi, Steven Gaines, and Sandy Andelman. This issue of the journal is currently available free of charge on the web (in PDF format) at http://www.esapubs.org/esapubs/journals/applications_main.htm. Click your way through to Volume 13 (2003) of Ecological Applications, then click "Issue 1, Supplement".