These scales of propagule dispersal are enormous relative to comparable patterns on land. Comparing seaweeds and marine angiosperms with terrestrial plants, one can see that plant dispersal distances in the sea are at the upper end of the distribution of dispersal distances seen for plants on land. The potential for long-distance dispersal of the spores of seaweeds and seeds of marine angiosperms may be greater than that of many of their terrestrial counterparts just as it is for marine animal larvae, because it is far easier to stay suspended in water than in the air, particularly if the propagule is large. Marine plants do not have to rely on dispersal by animals to transport offspring large distances.

DISPERSAL AND INVASIONS

The scale and pattern of dispersal plays a fundamental role in species invasions. Species have a range that bounds where they occur on the planet. These ranges are not static, however. If the factors that control a species's range change, the range can expand. This can happen when climate changes make previously inhospitable areas hospitable, or when barriers to movement break down. Over evolutionary time scales, species ranges can change frequently (e.g., as a result of glacial cycles). In recent decades, the pace of changes in species ranges has accelerated dramatically as a variety of human activities have moved species to parts of the planet where they previously did not occur. Such exotic introductions have occurred in all habitats, and rocky shores are no exception. The means of introductions are diverse, including fouling on the bottom of ships, larval transport in the ballast water of ships, aquaculture, and the aquarium trade. Often such exotic introductions occur at a single location. If the introduction is successful, the exotic species can spread from the location in its new home. This subsequent spread of an exotic often depends more on its natural dispersal abilities rather than continued transport by human patterns.

The rates of spread of marine exotic species can be rapid, since their natural dispersal distances can be large. Expanding range edges that move many tens of kilometers per year are not uncommon. Surprisingly, the rates of spread of seaweeds and other species with relatively modest average dispersal distances can also be quite large—far in excess of their average dispersal distance. These patterns highlight the importance of the extremes of dispersal distances rather than the average. A seaweed may have an average dispersal distance of only a few hundred meters, but some spores may be able to disperse tens of kilometers in a single jump. These individuals are the extreme tails of the distribution of dispersal distances, and they can be orders of magnitude larger than the average. For seaweeds, one of the reasons that the extreme tails can be such large distances is the presence of alternative forms of dispersal. Spores can disperse directly by drifting. They can also be dispersed when adult plants are ripped from the shore and raft in surface currents. If these rafting plants eventually land on a distant rocky shore, they can release spores that have been effectively dispersed great distances from where the parental plant grew. Invertebrates that grow on seaweeds can disperse by such rafting as well. Rates of spread of exotic seaweeds are often as fast as those of invertebrates with long-lived planktonic larvae. This suggests that the rare long-distance dispersal events can often play as important a role as the average.

SEE ALSO THE FOLLOWING ARTICLES

Algal Biogeography / Biodiversity, Global Patterns of

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DISPERSAL, MEASUREMENT OF

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The apple may not fall far from the tree, but it is an open question just how far marine offspring move away from their parents. Thus, measurement of dispersal involves determining the extent to which individual organisms move away from a starting population to a destination. In marine systems, dispersal often takes place during the larval or juvenile phase of an organism's life cycle. Determination of larval and juvenile dispersal distances and determining the percentage of a particular cohort that have dispersed away from their birthplace rather than being retained are important factors in understanding how particular populations are replenished with the next generation of young. It also helps to build an understanding of how separate populations might be connected by larval dispersal (Fig. 1). Despite the fact that dispersal distances remain unmeasured for most marine species, quantifying the extent of population connectivity is vitally important in conservation and management of marine fishery resources, because planners need to identify which populations are most important in promoting the local persistence of marine species. In this way, reserve planners can identify those areas that require maximal protection and can map out an effective network of marine reserves that are connected by larval dispersal and thus are capable of supporting one another.

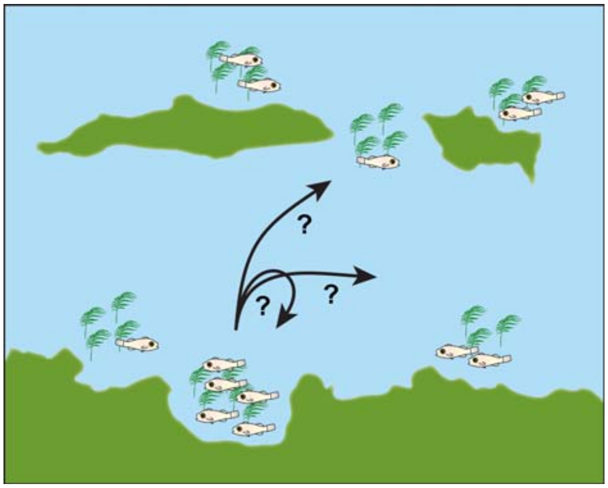

FIGURE 1 In this hypothetical shoreline with offshore islands, individual fish larvae are released from their birth population. Their dispersal trajectory is unknown and the connectedness of local populations, therefore, is unknown.

CHALLENGES AND APPROACHES

The challenges associated with measuring larval dispersal distance and percent retention are formidable. Larvae are typically microscopic, making direct observation impractical (Fig. 2). Further, they can exhibit complex behaviors (swimming, vertical migration) and can be advected away by oceanic currents and turbulent mixing processes. Scientists have employed artificial tagging techniques to track them directly but more commonly use indirect methods such as natural tagging (e.g., genetics, calcified tags) and modeling to estimate dispersal distances and extent of retention.

FIGURE 2 This barnacle larva (nauplius stage) is microscopic and nearly transparent, as is common for most marine larvae. Directly tracking this individual larva from its site of production to its settlement location would be a formidable challenge. Copyright Wim van Egmond/Visuals Unlimited.

ARTIFICIAL TAGGING

Artificial tagging is the only way to unequivocally measure dispersal distance when larvae move further than they can be followed directly. Larvae can be immersed in solutions containing marker chemicals such as fluorescent compounds (tetracycline, calcein), elemental tags (strontium, rare earth elements), or radioactive isotopes (^{65}Zn, ^{85}Sr) that typically tag calcified structures. They can also be artificially marked with novel DNA sequences using transgenic methods, thus producing a genetic tag. Larvae are then released from a source population and recaptured at a destination of interest, where they are screened for presence of the artificial tag. Recapture at the destination location is difficult because the probability of recovering a tagged larva can be exceedingly small as a result of high mortality rates and diffusive processes that can dilute their concentrations substantially. These factors make artificial tagging costly, time-consuming, and of limited effectiveness in most situations.

Rather than measuring dispersal distances, artificial tags have more typically been used to estimate rates of larval retention to their source population. Scientists combine the number of tagged larvae recaptured, relative to the total number of tagged and untagged larvae captured at the release site, with estimates of the percentage of larvae tagged at the release site to estimate the rate of retention. Because of the exceedingly low recapture rates of tagged larvae, the accuracy of such estimates is typically quite limited.

NATURAL TAGGING

Natural tagging approaches take advantage of population-specific tags generated either by naturally occurring genetic variation among populations or by variation in environmental conditions. Every larva is effectively tagged, and this eliminates the problems arising from diffusion of tagged larvae and low recapture rates.

One natural tagging approach censuses differences and similarities in allele frequencies of particular genes among populations. When allele frequencies are different among populations, the aggregate of populations is said to exhibit genetic structure. The magnitude of genetic structure can provide an estimate of the extent of larval exchange among populations and allow estimates of dispersal distances, but there is a large amount of uncertainty in interpreting data. Because even a small amount of gene flow can homogenize genetic structure among populations, estimates of per-generation connectivity can be impossible to assess. When dispersal distances are large, genetic approaches typically cannot determine variability in the extent of larval exchange over the short time scales relevant to resource management but instead can provide information about long-term average gene flow over many generations. Genetic estimates of dispersal have nonetheless provided very useful information about general trends in larval dispersal. For example, genetic estimates of dispersal distance typically support a correlation between realized dispersal distance and dispersal potential (measured as pelagic larval duration).

Alternative genetic approaches that can provide information on a per-generation time scale derived from paternity analysis. These techniques rely upon the ability to sample most potential parents in a sampling area, and thus are useful over small spatial scales where all adults can be readily located.

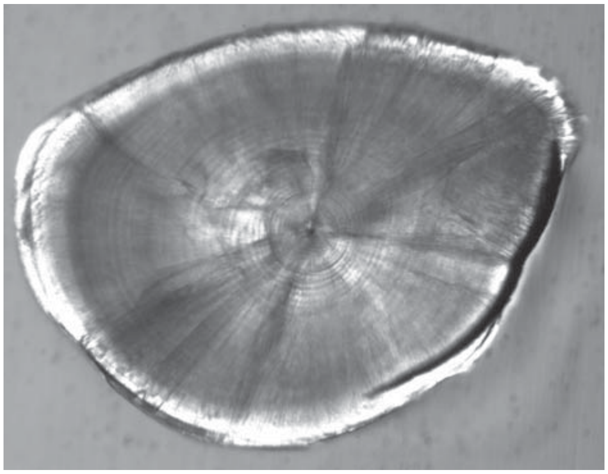

FIGURE 3 The calcified otolith (ear stone) of bony fish can act as a "flight recorder" of the environmental history experienced by larval fish at their birth location and during their dispersal phase. Otoliths can thus act as naturally induced tags of birth location. Photograph by Michael Sheehy.

Environmentally induced tags rely upon variation in environmental conditions, such as gradients in temperature or salinity or in metal concentrations in seawater to generate site or region specific tags. This variation in environmental factors is thought to generate variation in the chemical composition of calcified structures formed by dispersing larvae, such as otoliths (ear stones) of teleost fish, statoliths of molluscs, and larval shells of molluscs (Fig. 3). These calcified structures, then, potentially record environmental history in discrete time slices for the entire time period that the structure is forming. In some species, calcified structures are formed before larvae are released into the ocean currents, and so these structures can act as natural tags of birth location. Fish scientists have examined trace elements present in the otolith to reconstruct migration and dispersal patterns and to identify spawning grounds and juvenile nursery habitats.

To take advantage of either genetic tagging or environmentally induced tagging, scientists must first determine the spatial scale at which tags are generated. For example, if each population along a stretch of coast were genetically distinct from one another and therefore produced larvae that were uniquely tagged with their birth population's tag, a scientist could easily track larvae collected at any particular location back to its birthplace by simply analyzing the unique genetic tag. On the other hand, if distinctive genetic tags were present only in groups of populations separated by distances greater that 100 km, a researcher might, at best, be able to assign a larva's birthplace within a 100-km range. The ability to answer questions about larval exchange is therefore limited to that spatial scale at which variation in the tags occurs. Thus, successful application of any natural tag to identify source population information typically requires a complete characterization of the spatial and temporal variability in the tags. For both genetic and environmentally induced tagging approaches, there can be a large amount of uncertainty in interpreting the variation in tags among locations.

MATHEMATICAL MODELING

Using mathematical modeling, scientists can predict the trajectory and distance traveled by larvae released from a hypothetical location. Modelers can incorporate into their mathematical equations a large number of variables influencing larval dispersal, such as oceanography (current direction/speed, presence of eddies/complex flow fields), larval duration, mortality in the plankton, and larval competency duration. Estimating dispersal outcomes using models can be particularly valuable to determine the relative importance of these variables on dispersal outcomes.

Some models assume that larvae act as passively floating particles despite the knowledge that larvae can exhibit complex behavior (such as vertical migration and swimming). Estimating dispersal using models relies upon the acceptance of a number of assumptions about the parameter values of variables influencing dispersal.

SEE ALSO THE FOLLOWING ARTICLES

Genetic Variation, Measurement of / Larval Settlement, Mechanics of / Monitoring: Techniques

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DISTURBANCE

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The term "disturbance" refers to the displacement, damage, or death of organisms caused by an external physical force or condition or incidentally by a biological entity. Physiological or mechanical stress that does not result in tissue loss or death would not be considered a disturbance, although such stress is a common precursor to disturbance. The force or condition that causes disturbance is referred to as the agent of disturbance. Disturbance affects the structure and dynamics of intertidal populations and communities in a variety of ways. By displacing, damaging, or killing resident organisms, disturbance may (1) free up limiting resources, particularly space, for exploitation by colonists or survivors and thereby reset the successional state of the assemblage, (2) promote or hinder the coexistence of competitors, and (3) disrupt or enhance the influence of positive interspecific interactions. The nature and consequences of these effects depend on characteristics of both the disturbance regime and the affected organisms and assemblages.

COMMON AGENTS OF DISTURBANCE ON ROCKY SEASHORES

Common agents of physical disturbance on rocky seashores include wave forces; impact or abrasion by wave-borne objects such as cobbles, logs, or ice; extremes of air or water temperature; and desiccation associated with long periods of exposure at low tide. Abrasion by suspended sand or burial under deposited sand is an important agent of disturbance in areas where sandy beaches are contiguous with areas of hard substrate.

Biological entities also cause disturbance on rocky seashores. Biological disturbance occurs when organisms (other than targeted prey) are damaged, displaced, or killed by activities of animals or by algal fronds whiplashing rock surfaces. Examples of disturbance caused by animals include the bulldozing of sessile invertebrates or algae from the interior of territories maintained by limpets (Fig. 1) and the crushing and abrasion of invertebrates and algae by seals as they haul out onto emergent rocks to rest. Some authors also refer to the negative impacts of predation, herbivory, and parasitism as biological disturbance. It is, however, useful to distinguish between these trophic interactions and the phenomena just described, because the patterns and consequences of the two can be quite different.

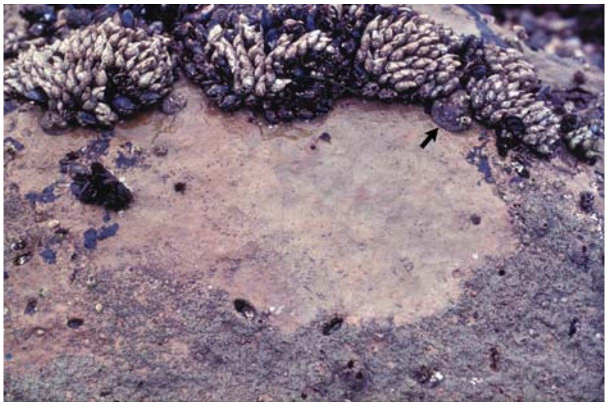

FIGURE 1 Defended territory of an owl limpet (*Lottia gigantea*). The limpet (at arrow) has bulldozed barnacles, smaller limpets, and other sessile space competitors from its territory (lighter-colored central area). This behavior maintains open space, promoting the recruitment of diatoms and early successional algae on which the owl limpet grazes. Photograph by. [AUQ1]