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EVOLUTION OF LOCAL RECRUITMENT AND ITS CONSEQUENCES FOR MARINE POPULATIONS

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ABSTRACT

Advantages of dispersal on the scales that are possible in a long pelagic larval period are not apparent, even for benthic species. An alternative hypothesis is that wide dispersal may be an incidental byproduct of an ontogenetic migration from and then back to the parental habitat. Under this hypothesis, the water column is a better habitat than the bottom for early development. Because the parental area is often an especially favorable habitat for juveniles and adults, selection may even favor larval retention or larval return rather than dispersal. Where larval capabilities and currents permit, a high percentage of recruits may then be produced from local adults. Expected consequences of a high proportion of local recruitment are stronger links between stock and recruitment, greater vulnerability to recruitment overfishing and local modifications of habitat, greater local benefits from fishery reserves, and possibly more localized adaptation within populations. Export of some larvae is consistent with a high proportion of retained or returning larvae, could stabilize populations linked by larval exchange, and provide connectivity between marine reserves. Even a small amount of larval export could account for the greater gene flow, large ranges, and long evolutionary durations seen in species with long pelagic larval stages.

The companion papers in this series indicate that local recruitment and retention of locally produced larvae may occur commonly in marine species with pelagic larval stages (Hellberg et al., Sponaugle et al., Swearer et al., Warner and Cowen, this issue). In this paper we first explore evolutionary hypotheses that reconcile the advantages of local retention with the maintenance of a pelagic larval stage. We then discuss evolutionary and demographic consequences of recruitment near the parental area, including the consequences for marine conservation. These consequences depend on the magnitudes of dispersal and local recruitment. The incidental dispersal associated with long pelagic larval periods has substantial genetic consequences even while a high proportion of local recruitment has substantial demographic consequences.

THE EVOLUTIONARY BASIS FOR LOCAL RECRUITMENT

THE FUNCTION OF A PELAGIC LARVAL STAGE: DISPERSAL OR MIGRATION?

Pelagic larvae of marine animals are certainly capable of dispersing away from parents and siblings. Offshore distributions of larvae suggest spectacular transport (Johnson, 1960; Scheltema, 1988). Because larvae travel far from parents, it is often assumed that many settle far from their parents. Oceanographic data on advection and eddy diffusion indicate the potential for dispersal. Dispersal distances of tens to hundreds of kilometers could be easily attained within the observed weeks or months of larval development. Because larval dispersal over long distances can and often does occur, it is tempting to

conclude that selection maintains long pelagic larval periods in life histories because of advantages of dispersal.

On closer inspection, however, large-scale dispersal during a long pelagic period looks more like a byproduct than the result of selection for dispersal. As discussed below, life histories and environmental patterns do not suggest benefits from such dispersal on time scales of decades. Instead, dispersal can remove larvae from benthic areas where they could survive as juveniles or reproduce as adults. Thus there is no reason to assume advantages from large-scale dispersal of larvae. Instead, selection may favor recruitment near parents and thus in a favorable environment. Widely dispersed larvae may be an incidental byproduct of an ontogenetic migration into the water column that is favored for other reasons. In terms of selection within populations, the dispersal that occurs could be neutral or disadvantageous.

If our arguments are correct, then we might expect that many of the recruits to a local area result from local production, where larval capabilities and currents permit (Schultz and Cowen, 1994; Secor et al., 1995; Jones et al., 1999; Swearer et al., 1999; Cowen et al., 2000; Armsworth et al., 2001). Retention near the parental area is one means of such local recruitment; return to natal areas from growth and development in more distant waters is another. The observed wide dispersal of larvae may often represent the tails of distributions centered near parental areas, or perhaps a distant migration followed by a return closer to the parental area. Migration for early life in the pelagic habitat, rather than widespread dispersal, may be the function of the pelagic larval stages of benthic or demersal marine animals (Strathmann, 1982; Sinclair, 1988). The degree of local recruitment may depend on how far the larvae migrate from the parental area, their behavioral capabilities, and currents throughout the water column (Kingsford et al., this issue; Sponaugle et al., this issue).

ARE THERE SPECIFIC ADAPTATIONS FOR DISPERSAL IN LARVAE?

Larvae of animals that are pelagic for their entire life history are often similar to pelagic larvae of animals that are benthic as juveniles and adults (Strathmann, 1985). For example, benthic and pelagic gastropods have veligers, benthic barnacles and pelagic copepods have nauplii, and there are no consistent differences between the larvae of pelagic and benthic fishes. Thus the larval morphologies likely represent requirements for pelagic life rather than specific adaptations for dispersal. An otherwise sedentary life is not a necessary condition for the persistence of pelagic larvae in life histories because larval stages persist in species that can disperse as well by other means. Because larvae are widespread among pelagic and benthic species alike, a parsimonious explanation of the function of larvae should apply to both. Feeding larvae, which have the longest pelagic durations, may simply be an efficient means of turning a small egg into a larger juvenile (Vance, 1973). To demonstrate that larvae are a necessary means of dispersal among subpopulations of pelagic adults, one needs to show that larvae are better equipped for this role than juveniles or adults.

Some larval traits are consistent with advantages to obligate dispersal on smaller scales of tens of meters to kilometers. The timing of larval release of many species occurs during strong tidal flows enhancing initial transport from parental areas (Morgan, 1995a; Hovel and Morgan, 1997), and subsequent upward swimming toward the light and against gravity by young larvae further ensures dispersal from the parent (Thorson, 1964). Some larvae that hatch from broods or egg masses are dispersed away from the parental site

even though there is no apparent barrier to developing competence at hatching. Precompetent release without larval growth could be interpreted as purely an adaptation for dispersal because in these cases a precompetent period offers no other apparent benefits. For example, larvae of the nudibranch *Phestilla sibogae* hatching from egg masses near corals are initially habituated and unresponsive to the settlement stimulus from the coral. They become increasingly dishabituated during the next 5 h away from the coral stimulus and increasingly responsive when re-encountering the stimulus (Hadfield and Scheuer, 1985). The habituation could be a mechanism forcing dispersal from the coral head occupied by parents. Such dispersal is often brief, lasting from seconds to hours, but larvae of the nudibranch *Adalaria proxima* hatch up to 2 d before becoming competent to settle even though they do not require food for development (Todd et al., 1998). If their dispersal is as reported for other invertebrate larvae (Shanks et al., in press), they may travel up to a kilometer from the parental site. To our knowledge this is the maximum pelagic larval period for which there are no apparent advantages other than dispersal. Longer periods of pelagic development without growth are found in animals that spawn eggs into the plankton. Pelagic development from egg to first feeding or competence could result from constraints on benthic retention and protection of embryos (Lee and Strathmann, 1998).

HYPOTHESIZED FUNCTIONS OF DISPERSAL

Do hypothesized selective advantages of dispersal plausibly match the life histories and populations of benthic animals, and do these hypothesized advantages require long-distance travel? It is difficult to envision dispersal as a function for larvae in species with pelagic adults and easy to imagine that larvae are necessary for dispersal in species with sessile or sedentary adults. The hypothesized functions of larval dispersal have therefore been based almost exclusively on benthic species. Offspring of benthic animals could be leaving a parental site to select proper habitat, to find unoccupied sites, in response to a locally deteriorating environment, to found new populations, or to engage in bet hedging in a varying environment.

Habitat Selection.—Some dispersal necessarily accompanies habitat selection. For sessile or sedentary animals, a pelagic larva may provide the mobility necessary for such selection among habitats. However, to select a habitat, a larva must be developmentally competent to settle. The competent period permits selection of sites or times of settlement (Doyle, 1975; Sponaugle and Cowen, 1994), but duration of competence may be determined by the balance of risk of settling at a suboptimal site or time versus risk of mortality during continued pelagic development (Doyle, 1975).

If habitat selection were the sole reason for sending larvae away from the sea bed, then larvae should be released ready to settle. Indeed, pelagic periods of larvae released from benthic protection are usually brief unless feeding and growth is required for development to competence. Long competent periods may compensate for long precompetent periods of feeding larvae. Larvae dispersed farther from favorable habitat while precompetent may require more time to encounter it while competent (Jackson and Strathmann, 1981). Modal dispersal distances for larvae released at competence are short, often less than 10 m. For larvae released by brooding ascidians, observed dispersal distances have been similar to distances for sperm (Grosberg and Quinn, 1986; Grosberg, 1991), less than 1/200 of the distances for rafting adults (Worcester, 1994), and less than the distances for passively dispersed non-swimming larvae (Bingham and Young, 1991). These short dispersal distances suggest that longer pelagic periods occur because eggs

are released into the pelagic environment rather than provided with benthic protection or because the larvae must feed and grow before becoming competent to settle.

Finding Unoccupied Sites.—In a crowded environment, simply finding unoccupied habitat may require some dispersal (Motro, 1983). Given the evidence for recruitment limitation and unsaturated adult habitats in many marine species (Connell, 1985; Caley et al., 1996), it is unclear how often the presence of juveniles and adults actually reduces the fitness of new settlers. Often, the advantages of unoccupied habitat could be obtained within meters to kilometers of parents, obviating selection for long distance dispersal. Also, after pelagic periods exceeding a week, many larvae preferentially settle near conspecific adults.

Locally Deteriorating Environment.—One possible advantage of dispersal is escape from locally deteriorating conditions. Many terrestrial animals disperse when the parental environment is deteriorating but remain closer to the parental site when conditions are favorable (Olivieri and Gouyon, 1997). For many marine animals, however, pelagic development is an obligate part of reproduction, and a pelagic larval period is rarely a facultative response to crowding or other deterioration in the parental environment.

One possible exception is colonial animals that reproduce sexually when the colony runs out of space for growth, thereby increasing the potential for dispersal to less crowded conditions (Harvell and Grosberg, 1988). However, many colonies begin producing larvae long before this limit is reached. Another exception is those rare poecilogonous animals that change reproduction from non-feeding to feeding larvae upon adult starvation, thereby increasing the time spent in the plankton and the probability of dispersing to areas where food is more plentiful (Krug, 1998).

More commonly, adults obligately produce pelagic offspring whenever they reproduce. If these larvae were a means of escaping locally deteriorating conditions, then it would follow that the parental areas are deteriorating relative to other areas likely to be encountered through dispersal. Moreover, an advantage from long distance larval dispersal (tens of kilometers) requires that parental areas be usually deteriorating on a large spatial scale.

What might cause routine deterioration of parental sites? Increases in parasites and pathogens are one possibility. Dispersal of offspring could reduce offspring's exposure to parasites and pathogens infecting the parental population, but dispersal could also result in a net export of larvae from areas with few parasites (and highly fecund parents) to areas with many parasites. Dispersal could aid escape from pathogens if dispersed larvae have a higher probability of arriving with different genetic defenses and thereby avoid the virulence associated with local adaptation of parasites to host genotypes (Edmunds and Alstad, 1978; Lively, 1999). Spatial and temporal patterns of infection could also favor dispersal as a form of bet hedging (see below). What we doubt, on present evidence, is that selection for breaking cycles of transmission commonly favors dispersal of larvae on scales of tens to hundreds of kilometers.

Since parental habitats do not appear to be deteriorating or fully occupied on scales of tens of kilometers each generation, we infer that an obligate long pelagic larval period greatly exceeds the requirements of leaving a crowded or deteriorating parental area.

Founding New Populations.—In the long run, large favorable areas deteriorate, other areas become favorable, and colonization of new sites may be the only means of avoiding extinction. However, obligate large-scale dispersal of larvae in each generation is not the most effective means of colonizing new areas. Colonizing requires that the animals first

reach a location and then populate it. Larvae dispersed on a large scale can reach many sites, but if the settlers continue to reproduce with dispersing larvae, they export their offspring rather than populating the site. Animals with shorter routine dispersal distances may reach new locations more rarely but are better colonists once they reach the site (Strathmann, 1974; Johannesson, 1988).

Bet Hedging.—If favorability of each area changes over time, such that good areas are not consistently good and bad areas are not consistently bad, then animals that spread sibling offspring over a larger area could damp generation-to-generation variation in success and thereby gain a relatively greater rate of increase over time (Cohen, 1967; Strathmann, 1974). The advantage derived from spreading larvae diminishes with increasing spread. Mothers are ‘sampling’ sites with their dispersed offspring, and each further extension of sampling provides less additional reduction in generation to generation variation. In contrast, with consistently favorable and unfavorable areas, the spread of siblings over larger areas results in a net transfer from good to bad areas (Palmer and Strathmann, 1981; Holt and McPeck, 1996).

For bet hedging to favor widespread dispersal of sibling larvae, the favorability of large benthic areas for survival and reproduction of recruits must often change rank. A world favoring such bet hedging would have a high spatial correlation of favorability (large areas good or bad) but low temporal correlation (large areas not consistently good or bad; Palmer and Strathmann, 1981). Although there are few good data on spatial and temporal variation in favorability over large regions and long times, the available observations suggest that over tens of generations, there is sufficient consistency in rank of quality of benthic areas to select against obligate and large scale spread of siblings in each generation.

As an example, we assume spatial variation in the abundance of corals to be an indication of environmental variability or predictability and thus of the patterns of variability that a dispersing cloud of larvae is likely to encounter as the larvae move and settle farther and farther from the point of release. Abundances could reflect favorability because of proximity to conspecifics for mating or availability of prey or hosts. Alternatively, abundances could reflect unfavorability for animals excluded by the corals. Hughes et al. (1999) sampled 18 reefs from north to south along the Great Barrier Reef with 4 sites on each and 10 transects at each of the 72 sites (Hughes et al., 1999). This design allowed calculation of variances for pairs of transects that were all at the same depth and habitat (1 m, reef crest) and separated by (1) a few meters at a site, (2) a kilometer or two on the same reefs, (3) about 10 km between reefs in the same sector, and (4) 200 to 1800 km between sectors. A nested ANOVA showed that 50–70% of the total variation in abundances occurred among replicates at a site and among sites on the same reef. Almost no variation (typically 0–10%) occurred at the intermediate scale, among reefs. Generally, 30–50% of the variation occurred at the largest scale, among sectors.

To apply the results to bet hedging, we must add assumptions about temporal variation so that the pattern can be extended over generations of dispersal. Assuming low temporal correlations for coral abundance, dispersal within reefs could confer advantages from bet hedging, but the advantages would diminish as a sibling cohort of larvae added settling sites and would diminish greatly with spread of larvae among reefs. Spread of larvae over the largest scale (sectors) is unlikely because of larval duration and survival; but if it occurred, little advantage would be gained because adjacent transects are likely to be as

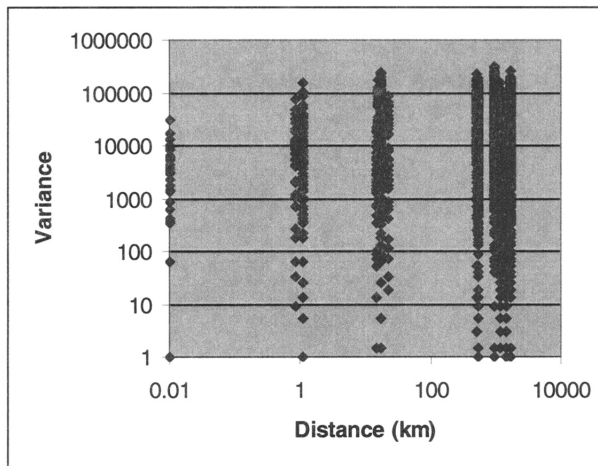


Figure 1. Variances in percentage cover of corals among pairs of transects that were separated by a range of distances (meters to >1000 km) on the Great Barrier Reef, Australia. Note that dispersing larvae will encounter similar variation in adult cover at small, medium, and large scales.

different as transects separated by >1000 km (Fig. 1). Thus for bet hedging, an averaging of good and bad habitats is as likely to be found nearby as far away.

Advantages from bet hedging will decline even more rapidly with increasing scale of spread if temporal consistency for spatial variation is greater on the larger scales. Recruitment is an example of temporal correlation at large spatial scales. In a meta-analysis of 23 studies of recruitment by corals along 2000 km of coastline on the east coast of Australia, recruitment measured over the 20 year span of studies was highly predictable at a regional scale, being 2 orders of magnitude lower at higher latitudes than at the central Great Barrier Reef (Hughes et al., 2002). The temporally consistent pattern appears to be driven by regional variation in fecundity. Similar regional-scale patterns in recruitment are inferred for the west coast of the USA, driven by patterns of upwelling (Ebert and Russell, 1988).

Thus far, evidence is against the hypothesis of advantageous bet hedging from wide dispersal of offspring. Are there other possibilities? Environmental features that might reduce temporal correlation on large spatial scales are catastrophes such as hurricanes striking different coastal areas. Parasites and pathogens might also have such effects. Chaotic population dynamics also could favor dispersal (Holt and McPeck, 1996). Combinations of species differing in dispersal could be stable when either species in isolation could be invaded and replaced by other dispersing organisms (Cohen and Levin, 1991; Ludwig and Levin, 1991). If a coastline has consistently favorable and unfavorable sites, but advection of pelagic larvae varies from one generation to the next, then spreading sibling larvae could provide bet hedging benefits (Strathmann, 1974). Although the spread of larvae is rich in demographic possibilities, sites are often consistently ranked over large spatial scales and over many generations in such features as adult abundance, density of recruits, suitability of substratum, and production of food and thus do not suggest a consistent advantage to bet hedging (Palmer and Strathmann, 1981; Parrish et al., 1981; Connell, 1985; Menge et al., 1997; Connolly and Roughgarden, 1998; Hughes et al., 2000). On present evidence, long pelagic larval periods fit none of the hypothetical functions of dispersal.

HYPOTHESIZED FUNCTIONS OF MIGRATION

Why should long larval periods persist if not for dispersal? One hypothesis is that the pelagic larval period is simply a migration away from and back to the bottom (Strathmann, 1982). Under this hypothesis, return to the parental area could be favored at least as much as transport to other areas. Here we discuss three hypotheses of advantages from a larval migration to the pelagic environment: a migration away from adult habitat may (1) exploit a nutritionally advantageous environment, (2) avoid predation, or (3) break cycles of parasitism.

For each hypothesis, selection could favor an ontogenetic migration into the water column and back to the bottom because of size or stage dependent advantages of different habitats. The same hypotheses apply to larval migration from estuaries and reefs to open coastal waters and back (Johannes, 1978; Strathmann, 1982; Morgan, 1990). In one model, the habitat that minimizes the ratio of instantaneous mortality rate to instantaneous growth rate changes with size, and growing animals switch habitats to minimize this ratio (Werner and Gilliam, 1984). We can add that size is not the only change from egg to adult-like juvenile. Embryos and early stage animals are intrinsically limited in their capabilities, but as cells multiply and differentiate, an animal's capabilities change. These limitations could result in stage-dependent advantages of different habitats.

Feeding.—Planktonic food near the seabed is augmented by benthic diatoms and meiofauna (Muschenheim and Newell, 1992; Judge et al., 1993) and can be at least as abundant as in the rest of the water column, but for some small organisms, the pelagic environment may provide better sources of nutrition than the benthos. Greater growth rates have been reported for pelagic than for settled stages of butterflyfishes and lobsters (Fowler, 1989; James-Pirri and Cobb, 1997). Food can be depleted when the density of benthic suspension feeders is high and vertical mixing near the bottom is low, as has been noted for diverse habitats (Buss and Jackson, 1981; Peterson and Black, 1987; Fréchette et al., 1989). Suspension feeding by small larvae may not be as effective near the seafloor as it is in the water column; the benthic nauplii of most benthic copepods do not suspension feed, unlike the pelagic nauplii of copepods and barnacles (Hicks and Coull, 1983). Data on growth rates of small animals that are adapted to a range of benthic and pelagic habitats are needed to test whether growth is greater in the water column or on the sea bed.

Where in the pelagic environment can the most nutrition be obtained? Coastal regions are among the most productive regions of the ocean, and estuaries have even higher densities of potential prey (phytoplankton and zooplankton) than do adjacent coastal waters (Denman and Powell, 1984; Rissik et al., 1997). Food limitation for copepods is more likely to occur offshore than in more productive estuaries, bays and nearshore coastal waters (Huntley and Boyd, 1984). Barnacle and fish larvae retained near spawning areas appear to grow more rapidly and settle at larger sizes than those that have moved offshore (Gaines and Bertness, 1992; Swearer et al., 1999). Thus shallow coastal waters may provide a better food supply for young larvae, and a larval migration to regions farther offshore may negate this advantage.

Predation.—The idea that pelagic development carries eggs and young away from benthic areas where predators are concentrated has a long history (e.g., Randall and Randall, 1963; Robertson and Hoffman, 1977). Planktivorous animals are abundant near reefs, estuaries and other nearshore environments and pose a danger to pelagic juveniles that remain very near to parental areas (Johannes, 1978; Morgan, 1990). Greater survival in

the plankton also could account for pelagic development of prefeeding embryos and non-feeding larvae, for which habitat is unimportant for growth. For these, the hypothesis predicts greater survival away from the bottom than at the bottom.

We know of few data for comparing predation on small animals in benthic and pelagic environments (Strathmann, 1982; Shapiro et al., 1988). Sampling planktonic larvae has provided estimates of mortality (Strathmann, 1985; Rumrill, 1990; Lamare and Barker, 1999). These estimated mortality rates are greater than those for benthic embryos that are protected from predators in broods or egg masses (Strathmann, 1985; Rumrill, 1990; Petersen, 1990; Warner et al., 1995), but benthic embryos and larvae that are not in protected aggregations may not fare so well (Warner et al., 1995).

Indirect indications are suggestive but inconclusive. Since predators can be concentrated near the sea bed and along shorelines, a migration into the open water column may confer safety. Although mortality rates of postmetamorphic juveniles are often lower than for larvae (Houde, 1987; Rumrill, 1990), mortality rates in the first day of postsettlement life (estimated from Gosselin and Qian, 1997) are similar to those estimated for planktonic larvae (Strathmann, 1985; Rumrill, 1990), with mortality rates declining with postsettlement age. This pattern of mortality estimates is consistent with Werner and Gilliam's (1994) model for optimal size for changing habitat, although it is also consistent with high risk at settlement followed by lower mortality in the benthic habitat. Body mass scaling of production/biomass ratios and respiration rates suggest that predation risk is reduced at small body sizes for both meiofauna and zooplankton, possibly greater for meiofauna (Banse and Mosher, 1980; Banse, 1982), but the data are insufficient to indicate which of them has the smaller ratio of mortality rate to growth rate. Reviews of data have been insufficient to test the mortality hypothesis, and comparative studies for habitat-specific tests are needed. These studies could include comparisons of mortality of small benthic and small pelagic animals of similar size and form, such as benthic and pelagic nauplii of copepods.

We have simplified the discussion by addressing growth and mortality separately, but the two factors combine to render a habitat better or worse for a given size or stage of feeding larva. Larvae that remain near inshore parental habitats may contend with more numerous predators but develop more rapidly in food-rich waters near favorable habitat for settlement. In contrast, larvae that migrate offshore may find fewer predators but also less food and must locate a suitable settlement site at the end of a long trip. Coexisting species differ, with some larvae migrating short distances between the parental area and nearshore waters whereas others are exported far offshore (Epifanio, 1988; Morgan, 1995b). In shallow-water crabs, the distance that larvae migrate is correlated with differences in larval size and defenses (Morgan, 1987, 1989, 1990). Larvae released on nocturnal ebb tides disperse from predator-rich shorelines under the cover of darkness into deeper waters during the first hours after they are released (Morgan, 1995a; Hovel and Morgan, 1997). Thereafter, behaviors of well defended larvae foster short distance migrations in bays, estuaries and nearshore coastal waters, whereas those of comparatively poorly defended larvae favor migration far onto the continental shelf and back. Interspecific comparisons of larval production and settlement have shown that larvae that develop offshore may recruit to adult populations as reliably as do larvae that remain near the parental habitat (Hovel and Morgan, 1997; Christy and Morgan, 1998). Thus, a range of migrations occurs within the same array of habitats revealing a variety of evolutionarily stable

strategies. It remains to be demonstrated whether species that develop in estuaries recruit to the parental estuary more than do those that develop on the continental shelf.

Parasitism.—The pelagic larval stage may break cycles of parasitic transmission because of the migration into the water column. Here we emphasize effects of a pelagic larval stage that are not dependent on dispersal among benthic sites.

Transmission of parasites occurs in the pelagic environment with hosts that are large or concentrated, as with trematode metacercariae in chaetognaths (Pearre, 1976), hyperiid amphipods in salps, ctenophores, and medusae (Madin and Harbison, 1977; Laval, 1980), *Metophrya* ciliates in chaetognaths (Kudo, 1966), and larval tapeworms in jellyfish (Dollfus, 1931). Dense phytoplankton blooms have been terminated by the epidemic spread of host-specific viruses (Suttle et al., 1990; Milligan and Cosper, 1994). In contrast, it is much more difficult for parasites to spread in a sparsely distributed population of pelagic larval hosts.

Migration into the water column could break transmission because pelagic larvae are very small, dispersed in three dimensions, and often scarce. As a result, pelagic larvae are less suitable hosts for the parasites of the subsequent benthic stages. Large parasites simply cannot use very small hosts. Small hosts provide smaller resources for production of numerous infectious propagules. Parasites that can profitably infect marine larvae are small, such as protozoans, bacteria and viruses, and these require a high host density threshold for effective transmission (Bailey, 1957; Stiven, 1968; Kuris and Lafferty, in press), a condition rare for larvae (Strathmann, 1996). Consistent with this, we found no reports of epidemics sweeping through larval populations in nature, although epidemics occur in cultures with sustained high host densities (Aquacop, 1977; Nicolas et al., 1992). In contrast, mass marine mortalities have been documented for many benthic or demersal molluscs, echinoderms and fishes (Dungan et al., 1982; Lessios, 1988; Lafferty and Kuris, 1993; Harvell et al., 1999).

Larval stages can be parasitized, but apparently not by agents that will also be effectively transmitted to adults (Rigby and Dufour, 1996). Metamorphic and habitat discontinuities, perhaps in concert with very low larval densities, may prevent transmission of disease. We know of no examples of infectious diseases transmitted across pelagic larval phases from adult to juvenile populations. If they exist, they are not commonplace.

GENERAL CONCLUSIONS: MIGRATION VS DISPERSAL

The preceding hypotheses of migration advantages are not yet strongly supported by data on survival and growth, but they are not yet rejected either. At present, the migration hypothesis is supported largely by deficiencies in the alternative hypothesis of dispersal advantages of a long pelagic stage. Regardless of the form of the migration hypothesis, there are no apparent advantages for extending the migration beyond the nearest favorable habitat for larvae. If the ontogenetic migration is simply between habitats, it does not matter if the larvae return to the parental area or another as good. If, however, the probability of reaching an area as favorable as the parental one is low, then pelagic larvae should be either retained near the parental area or returned to it. The degree to which they are returned or not depends on both the movement of the water and capabilities of the larvae (Bonhomme and Planes, 2000; Armsworth et al., 2001). Less transport confers proximity to settlement areas (Kingsford et al., this issue, Sponaugle et al. this issue).

A migration with complete fidelity to the parental area could be disadvantageous in the long term, but some incidental 'leakage' of offspring from the parental area is unavoidable even with continuing selection within populations for endogenous recruitment of pelagic larvae. This leakage, though selected against, may be sufficient to spread risk from local catastrophes among descendants, as long as catastrophes are infrequent.

CONSEQUENCES OF ENDOGENOUS RECRUITMENT TO PARENTAL SITES

Some marine larvae are transported long distances from parental sites, as exemplified by numerous examples of both offshore transport of larvae and larval range extensions, but a larger portion than previously suspected may return to the parental area (Jones et al., 1999; Swearer et al., 1999; Sponaugle et al., this issue; Swearer et al., this issue). If an unexpectedly large proportion of pelagic larvae of benthic or demersal animals returns to the parental area, what are the evolutionary and demographic consequences?

MACROEVOLUTIONARY CONSEQUENCES

Macroevolutionary hypotheses based on larval type have predicted that species with longer larval periods have greater geographic and stratigraphic ranges and are less prone to extinction and speciation than those with non-feeding or brooded larvae. Some studies support some or all of these predictions (Jablonski, 1986); in some the reverse is true (Edinger and Risk, 1995); and in others there is no relationship (Bouchet, 1981). In the Neogene gastropod genus *Nassarius*, greater species durations and geographic ranges occurred in species with feeding larvae (Gili and Martinell, 1994), yet speciation and extinction rates were not enhanced with non-feeding larvae. There appears to be substantial overlap in species durations between 'dispersed' species and those with non-feeding or brooded larvae. For example, nine of 31 species (29%) of nassariid gastropods with feeding larvae had species durations similar to those with non-feeding larvae (Gili and Martinell, 1994). In Jablonski's (1986) study, 13 of 49 taxa inferred to have feeding larvae (27%) had species durations that were less than or equal to the median value for taxa without feeding larvae, but only 8 of 50 taxa inferred to lack feeding larvae (16%) had species durations that exceeded or equaled the median value for taxa with feeding larvae. In Hansen's (1978) study, 5 of 13 species with feeding larvae (38%) had species durations similar to species without. Hansen (1978) interpreted the overlap in durations of species with and without feeding larvae in terms of environmental tolerances, but degree of larval retention might also play a role.

Macroevolutionary predictions based on developmental mode have assumed equivalence between larval mode and distance that recruits are dispersed. Recruitment of pelagic larvae to the parental area could weaken this assumed correlation, but how much of the larval pool needs to be retained to make a macroevolutionary difference? In other words, does a smaller proportion of larvae dispersed long distances affect the macroevolutionary consequences of a pelagic larval stage? Even if there is a substantial shift in the proportion of larvae that recruit to the parental population, there still may be no effect on predicted macroevolutionary consequences, as long as some of the larvae are dispersed long distances.

Thus, for a particular species, larval retention may not be consistently high enough to prevent a wide range or long duration, even though it may result in high rates of endogenous recruitment.

Can one test the prediction that species with greater larval retention show smaller geographic ranges, shorter species durations, and greater rates of speciation and extinction? Ideally, one would compare evolutionary rates within monophyletic groups that show both larval retention and large-scale dispersal, or among sister clades that strictly show one or the other pattern, but we see no clear basis for evaluating larval retention versus broad-scale dispersal in fossil species.

MICROEVOLUTIONARY CONSEQUENCES: LOCAL ADAPTATION AND MOSAIC EVOLUTION

Local recruitment sufficient for strong demographic consequences does not preclude genetic exchange sufficient to reduce genetic differentiation among populations. In many taxa of marine invertebrates, species with a pelagic larva exhibit greater genetic homogeneity over greater distances than do those without, but populations with long pelagic larval periods can also exhibit genetic differences among sites (Palumbi, 1995, for review). Local recruitment can be added to the list of factors (including local differences in post-settlement selection) that could produce genetic differences among populations, despite pelagic larval periods of days or weeks.

If reduced larval dispersal resulted in reduced genetic exchange among populations, it could increase possibilities for local adaptation. The possibility of local adaptation contrasts with the expected microevolutionary consequences of broad dispersal across variable habitats. If populations were truly open with no possibility of local feedback, then adaptations would either be fixed, representing the best strategy averaged over the dispersal range of the species, or phenotypically plastic, if the proper local environmental cues were detectable by newly arrived individuals (Warner, 1991; Morgan, 1991; Morgan and Christy, 1994).

Also, the demographic consequences of local recruitment suggest particular microevolutionary consequences. Downcurrent populations of the bluehead wrasse on St. Croix received large numbers of recruits, sufficient for local density-dependent population regulation (Caselle and Warner, 1997; Caselle, 1999). The large downcurrent recruitment pulses were retention events; the proportion of locally retained recruits was much higher in pulses, comprising up to 70% of the recruiting cohort (Swearer et al., 1999). If large recruitment pulses often represent retention, then high-density marine populations (that themselves resulted from large recruitment events) may also represent populations that are self-seeding and therefore capable of undergoing local adaptation. Local adaptation can occur under some circumstances of high rates of gene flow from immigration (Holt and Gomulkiewicz, 1997; Gomulkiewicz et al., 1999). Local retention could provide the intergenerational feedback to allow local adaptation to occur and could also lead to high population densities in which additional components of selection are present. Processes operating in larger, denser local populations can be important in the evolution of species characteristics and tolerances, simply because these populations are large (Holt, 1996).

DEMOGRAPHIC CONSEQUENCES

If there is a connection between retention and high recruitment levels, then areas conducive to larval retention may also be areas in which post-settlement density-dependent processes are important in local population regulation. In contrast, other areas with more distant sources of young may experience chronically low supply and be recruitment-limited (*sensu* Doherty, 1983, Victor, 1983). Attempts to classify populations or species as recruitment-limited vs density-regulated are less useful than identification of the times

and places in which local marine populations experience predominantly one or the other of these regulation mechanisms (Warner and Hughes, 1988; Caley et al., 1996; Morgan, 2000). The degree of local retention may be directly related to the mechanism of local population regulation. If particular physical features are associated with retention, then these may provide a working hypothesis about local densities and mechanisms of regulation. For example, the contrast between upcurrent, low-retention reefs and downcurrent, high-retention reefs in St. Croix suggests that the downcurrent ends of islands may have higher densities and thus be more likely to be regulated by reef-based processes.

Populations with and without some degree of local retention show profoundly different dynamics. If all recruits come from elsewhere, the population size responds linearly to increased inputs of recruits in the absence of density-dependent mortality (e.g., Warner and Hughes, 1988; Hughes, 1990). Although the external recruits are added periodically and temporarily stored in the population (*sensu* Warner and Chesson, 1985), they do not multiply over several generations. In contrast, if all recruits are locally-derived offspring, the population responds geometrically to increased or decreased birth rates.

Where local recruitment dominates, the addition of a few external recruits has little effect on the size of a local population or its long term growth rate. Some clonal taxa show an interesting variant on this dynamic, where asexually produced offspring are retained locally and sexually-derived larvae are dispersed. In this case, larval dispersal may be important evolutionarily, but its demographic role in maintaining local populations can be far exceeded by 'self-seeding' of asexual offspring (e.g., Hughes and Tanner, 2000).

As a local population increases in size, per capita recruitment from an outside source will tend to fall as the number of recruits arriving is divided by a growing number of pre-established individuals. Consequently, recruitment can appear to be density-dependent and to regulate local population size around an equilibrium, even in the absence of density-dependent mortality (Warner and Hughes, 1988). However, without some source of density dependence, the global production of recruits would walk randomly to zero or grow exponentially, given enough time. In reality, true density dependence in birth or death rates is likely to occur somewhere (in one or more sub-populations or in the plankton) and random walks to zero recruitment are unlikely to occur. Furthermore, asynchrony of dynamics in partially open local populations is a well-established mechanism of global stabilization or regulation (e.g., Crowley, 1981; Palmqvist and Lundberg, 1998). For example, the coexistence of competing species is promoted by fluctuations in per-capita rates of recruitment that must increase at low densities (Warner and Chesson, 1985). Reeve (1988) and Murdoch et al. (1992) also examined this phenomenon in a meta-population context and concluded that temporal density-dependence due to fluctuating per capita migration rates could be a stabilizing influence, under conditions that are likely to occur in nature. Population theory and model predictions in this area need empirical testing.

Most empirical tests of recruitment-limitation have been highly localized. In small-scale studies, most populations are open. However, even a modest scaling up has suggested that populations are partially closed (Jones et al., 1999; Swearer et al., 1999). Tests of the role of self-seeding and meta-population theory are possible with organisms with short-lived or easily manipulated larvae, such as tunicates or brooding fish.

MANAGEMENT CONSEQUENCES

Fishery Management.—In a locally recruiting population, the loss of larger and more productive members of the local population through intense fishing will directly reduce recruitment. In essence, local retention of young results in geographically smaller management units. Management itself may be simplified due to fewer losses from export, less dependence on importation of recruits whose parents are under differing management regimes, and tighter stock-recruitment relationships. On the other hand, populations with extensive larval retention are more vulnerable to recruitment overfishing and loss due to catastrophe.

The juveniles of many fishery species use nearshore habitats affected by coastal construction. Even when negative human effects on a habitat and an associated assemblage of animals can be documented, conclusions on the population-scale significance of the impact are usually constrained by limited knowledge of population sizes and the connectivity of local and adjacent populations. It is equally difficult to evaluate the effects of mitigation projects or other regulatory tools without knowledge of the degree to which local populations are dependent on their own recruitment (Lindeman and Snyder, 1999). The more open the population, the greater the probable capacity to recover from significant local anthropogenic impacts.

Marine Reserves.—Reserve planning involves several spatial scales, including (1) the size and shape of individual reserves and (2) the potential for connectivity, or lack thereof, among multiple reserves. The identification of ontogenetic migration paths of larvae, juveniles, and adults can suggest reserve boundaries and also the distribution of reserve networks. Regardless of whether the objective of a reserve is conservation of biodiversity or fisheries management, all design theory must include assumptions about the source of recruits into the reserve and the fate of young produced by the reserve (Roberts et al., in press). If larval retention is more common than previously supposed, how might this affect reserve design?

Obviously, the ability of a reserve to sustain its own biodiversity would reduce concerns about the dependence of reserve populations on supplies of recruits from elsewhere. Identifying physical features that may be associated with enhanced local retention will be important for placement of reserves. In fishery reserve design, multispecies spawning aggregation sites are particularly important examples (Lindeman et al., 2000). The diversity of spatial scales of local recruitment for co-occurring animals and plants and the multispecies nature of many fisheries suggests difficulties in fitting one network to all species. This problem is not as severe as it first appears, because differing processes may work for different species within a single reserve network. For example, one function of connectivity of reserves is protection against local extinction, and organisms differing in dispersal and local recruitment can persist locally by quite different means. For species with a long pelagic larval period, connectivity and persistence can result from larvae that are routinely leaked beyond presumed population boundaries and between reserve sites even when there is substantial local recruitment. Such leakage also may enhance fisheries outside reserves. For species with little or no transport of larvae, persistence can result from much rarer transport between reserves because of a higher capacity for local recruitment (Dethier and Strathmann, submitted; Shanks et al., in press).

CONCLUSION

Assumptions of selective advantages of long-distance dispersal by pelagic larvae of benthic animals are unsupported by existing evidence. An alternative hypothesis is that the pelagic environment is favorable for unprotected, early-stage animals. In this view, a long pelagic development is an ontogenetic migration into the pelagic environment and back to the benthos. This migration hypothesis proposes short-term selection for pelagic larval stages while implying no advantage or disadvantage from larval dispersal. In addition, we expect the parental locale to be better than most sites reached after long pelagic drift and therefore predict selection for local recruitment to the extent that currents and larval capabilities permit. This migration hypothesis is consistent with new evidence for local recruitment in marine populations with feeding pelagic larvae. Substantial local recruitment is consistent with incidental dispersal, which exceeds that favored by natural selection. Incidental dispersal is consistent with and may account for evolutionary consequences of a long pelagic larval development, even while local recruitment has substantial demographic consequences.

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