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Evolutionary ecology: how to reconcile pelagic dispersal with local adaptation

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Abstract. Because of dispersal, many marine organisms exist in a series of local populations spanning a wide variety of different physical environments. Recruitment is often sporadic, and thus the age structure and density of the population are also highly unpredictable. Rates of gene flow may be high, and this can inhibit local genetic differentiation. How can local adaptation occur when the environments that young or adults will face are so variable and unpredictable? One solution is phenotypic plasticity, a set of specific responses to cues in the environment that indicate local conditions critical to fitness. In some cases local populations may be very finely tuned to the local environment. Other environmental factors simply cannot be predicted by adults. For such cases, fixed responses are the best solution, averaged over the dispersed range of the species. Such fixed responses may be highly maladaptive at many local levels. Their validity cannot be interpreted in studies that restrict themselves to a few localities. The relative roles of local genetic differentiation, phenotypic plasticity, and large-scale fixed responses in determining behavior and morphology should be a function of the selective regime, the degree of larval dispersal (and hence the gene flow among populations), and the detection abilities of the benthic individuals. Phenotypic plasticity may most likely occur in species with widely dispersed larvae and good sensory capabilities. In contrast, corals may employ a strategy of simply varying the phenotypes of their young, as do some plant species.

Introduction

One definition of evolutionary ecology is the study of adaptive responses to the environment. The diversity of life histories and behavior that we see in nature are interpreted as evolutionary solutions to problems posed by a diversity of environments. For example, the optimal balance between present and future reproduction may be an evolved response to the age-specific probability of mortality; foraging group size may be an adaptation to the intensity of predation; or the size of young may represent a compromise made by the parents between the conflicting advantages of size and number of offspring, set by the environmentally determined relationship between size and fitness (these and many other examples are summarized in Krebs and Davies 1991; Cockburn 1991; Stearns 1992).

A problem faced in many models in evolutionary ecology is that populations are exposed to variable environments, which complicates the development of local adaptations. This problem is particularly acutein many marine organisms because they have distinct bipartite life cycles in which the larval stage is highly dispersive and adults are quite sedentary. Larvae are small and often planktonic, and large-scale oceanographic processes may be important in determining the patterns of settlement. This has several fundamental effects on the ability of organisms to adapt to local environments.

First, such species may exist in a series of local populations spanning a wide variety of different physical environments. Depending on depth and locale, young may find themselves in areas of high or low food supply, and physical factors such as light, current, and turbulence may differ radically over relatively short distances. In fishes, planktonic larval durations often range between 30 and 60 days (Victor 1991), which can potentially lead to very broad dispersal.

Second, because recruitment is often sporadic (e.g., Shulman 1985; Victor 1986; many other examples in Sale 1991), the demographic environment (in terms of both age structure and density) is highly unpredictable. Natural recruitment rates in coral reef fishes have been documented to vary tremendously from one time period to another, leading to large differences in the resultant adult population density (Doherty and Williams 1988; Doherty 1991). Depending on the timing of arrival relative to other pulses of recruitment, a young individual may find itself to be at the large or the small end of a size distribution, and relative size can have profound effects on access to food, mates, or other resources (Schultz and Warner 1989).

Third, the rates of gene flow are high, and this can inhibit local genetic differentiation. Using neutral markers, several studies have demonstrated a lack of geographic genetic structure among marine species with extensive dispersal phases (summarized in Avise 1994; see also Shulman and Bermingham 1995; Doherty et al. 1995). It is important to realize that the extent of gene flow sufficient to produce panmixia in neutral alleles does *not* preclude the evolution of local adaptation (Maruyama 1972; Endler 1977; Holt and Gaines 1992). The degree to which local genetic adaptation can occur depends on the intensity of local selection, the temporal consistency of local selection, and the extent to which at least some offspring are retained in the same area (Holt and Gaines 1992). With an obligate long-term pelagic larval phase, many coral reef fish populations may be completely open, with no local retention (Warner and Hughes 1988); this would preclude local genetic differentiation except by within-generation selection. Also, as noted, the sporadic nature of recruitment may lead to extreme temporal variation in demographic environments and their associated selection intensities.

Unfortunately, fieldwork in evolutionary ecology often depends on the assumption that the population being studied has achieved genetically based solutions to long-standing problems posed by the local environment. How can we expect to see local adaptation when the environments that the next generation will face are so variable and unpredictable? If local genetic adaptations cannot be expected, are there fatal flaws in evolutionary ecological investigations of highly dispersive marine species?

Here, I outline two general solutions to the problem of local adaptation in the absence of genetic differentiation. The first, phenotypic plasticity, can actually be used to enhance studies of evolutionary ecology. The second solution, consisting of generalized responses that *on average* convey the highest fitness, can only be interpreted on scales that are much larger than are now commonly studied in evolutionary ecology.

Phenotypic plasticity

In many cases, life-history or behavioral responses are mediated through reaction norms, a set of specific responses to cues in the environment that indicate local conditions critical to fitness (Stearns and Koella 1986; West-Eberhard 1988; Zhivotovsky et al. 1996). The same factors that impede local genetic differentiation, mentioned already, give rise to selection for phenotypic plasticity (Warner 1980, 1991).

There are many examples of extreme plasticity in marine organisms, such that local populations are very finely tuned to the local environment (Warner 1991). For example, in the bluehead wrasse (*Thalassoma bifasciatum*), a common coral reef fish of the Caribbean, the predominant mating system can change from lek-like, where females migrate to spawn in an area occupied by closely adjacent territorial males, to harem-like, where females do not migrate and mate with a local dominant male, to completely promiscuous, where nearly all mating is within massive, non-aggressive groups of similar-sized males and females (Warner and Hoffman 1980a; Fitch and Shapiro 1990; Warner 1995). Strikingly, all of these mating systems can be found within a few hundred meters of each other, depending on the size and demography of a local population and the economic defendability of mating sites (Warner 1984b).

In some species, plasticity is so pervasive and responsive that the plasticity itself can be used to test alternative hypotheses on the adaptive significance of a particular trait (Warner 1991). While most hypotheses propose some longer-term solution to a persistent environmental challenge, plasticity represents a set of specific responses to a specific array of environments. The environmental factors to which a particular species responds in the short term should often be the same as those that shape differences between species over evolutionary time. Thus phenotypic plasticity allows a manipulative, experimental approach to testing hypotheses about fitness and adaptive significance. For example, experiments have shown that the variable mating system of the bluehead wrasse described already is due to the effects of variation in population density on the economic defendability of mating sites, and it is not due to differences in the distribution of mating sites themselves (Warner and Hoffman 1980b, Warner 1988). Warner (1991) provides other examples of this approach.

The degree to which an organism can respond with phenotypic plasticity depends on its response capabilities and on the availability of appropriate cues (Moran 1992). It is important to note (especially if manipulative experiments are planned) that the cues involved need not be the actual factor affecting fitness, but instead an easily measured correlate of the actual factor. For example, in studies of the social control of sex change in coral reef fishes, it appears that the decision of an individual to change sex is often mediated by aggression received from larger individuals (Ross 1990). In this case, aggression received is a strong predictor of the likelihood of successful spawning as a male, and thus is used as a reliable cue.

There are many cues available to mobile, active species like most coral reef fishes. Relative size, sex ratio, population density and size, prevailing current directions and speeds, and the spatial and temporal distribution of food and shelter are all factors that can strongly vary from habitat to habitat, affect the fitness of adults, and can be easily detected. We know that fish species are capable of responding to many of these factors (e.g., food distribution: Ebersole 1980; relative size: Ross et al. 1983; relative size and sex ratio: Robertson 1972; Shapiro 1980; current direction: Warner 1986; population size and distribution: Aldenhoven 1986; Sakai in press). It is also possible that habitat-specific mortality rates can be estimated by a fish through simple observation of predators, direct experience of failed predation attempts, or witnessing predation of others. However, there have been no investigations into whether life-history or behavioral traits are altered in response to such factors.

Generalist phenotypes

There are many other local environmental factors (especially those that will affect dispersing young) that are simply unpredictable by adults. In this case, behaviors and life histories often represent a response that is more fit than any other, *averaged over the dispersed range of the species*. Such "rules of thumb" will evolve when the fitness consequences of a particular trait are undetectable or costly to detect, or if the environment changes too rapidly to allow conditional adjustments (Lloyd 1984; Seger and Brockman 1987). The monomorphic or generalist phenotype that evolves is strongly affected by the fitness returns in different environments. Especially for temporal variation, we expect traits that maximize the geometric mean fitness (Moran 1992). Note that such a strategy often means that the arithmetic mean fitness will be maintained at an intermediate level. In fact, these generalized traits may be highly maladaptive in some habitats, and cannot be easily interpreted in studies that restrict themselves to a few localities. It is these sorts of distribution-wide adaptations that cause the greatest potential problems for studies in evolutionary ecology, but these problems can be overcome if the approach takes the proper scale.

A good example of the contrast between local and global adaptation is the explanation of the existence of primary males in the bluehead wrasse. The majority of individuals in this species start life as females and eventually change sex into large, brightly colored terminal-phase males. However, there are also primary males that actively spawn in groups while small, and also change into terminal-phase males when they grow large (Warner et al. 1975). What maintains this alternative life-history in the population? Originally, it was thought that these primary males coexist with the sex-changers in frequency-dependent equilibrium at a local level (Warner et al. 1975; Charnov 1982a,b). However, it soon became clear that in smaller populations, primary males had much lower lifetime reproductive success than did sex-changers, and conversely, terminal phase males do relatively poorly on the largest reefs (Warner and Hoffman 1980a; Warner 1984a, 1995). Studies that were constrained to single populations could not explain the coexistence of these two types. In contrast, an approach that explicitly took into account the relative contributions of all reef sizes to the larval pool was quite successful in predicting the proportion of the population that should be comprised of primary males (Warner and Hoffman 1980a; Warner 1984b).

In many cases, individuals of many coral reef species never leave a local area as adults (Sale 1980), and thus they have no information about the oceanographic conditions that their dispersing young will face. Studies that concentrate on the fitness associated with behaviors affecting dispersing young may often show maladaptation if they focus on one or a few localities. For example, Appledoorn et al. (1994) showed that dispersal of *T. bifasciatum* eggs (simulated by drogues) from one reef in Puerto Rico ended in inhospitable nearshore areas when they were launched from mating sites during the normal spawning period (see also Shapiro et al. 1988). Bluehead wrasses do not leave their home reefs as adults (Warner and Hoffman 1980a), and settle as juveniles after a weeks-long period of pelagic life (Victor 1986). Since the adults were likely themselves to be products of other reefs with different downstream characteristics, it should not be surprising that no local adaptation had occurred. Selection can only act on the average fate of eggs over many reefs, and the adaptive significance of spawning at particular sites should be studied at the same scale.

This and a companion study clearly demonstrate the idea that conditional responses can only evolve in circumstances where there are local cues for adaptive behavior. As outlined already, spawning at particular times or places did not appear to result in any advantage in terms of the eventual fate of dispersing eggs. However, spawning sites did appear to provide an advantage in terms of dispersal of eggs immediately following release (Hensley et al. 1994). One could predict that the latter result should be observable on every reef studied, because immediate consequences can be assessed by adults, while the longer-term and greater-distance fitness consequences of the timing and location of mating must be studied as averages over a larger scale.

The importance of the scale over which selection acts illuminates an interesting aspect of the study of local adaptation. While many hypotheses on the adaptive significance of reproductive events make reference to physical processes such as transport and dispersal, the physical parameters themselves are seldom measured. Instead, the physical environment is inferred from almanacs and tide tables, using common assumptions about relationships between predicted events (e.g., moon phase or tidal height) and relevant physical conditions (e.g., current speeds and directions). There is increasing awareness that these assumptions may not hold under local conditions, and that an almanac may not be an adequate substitute for actually measuring physical parameters (Roberts et al. 1977; Marsh et al. 1982; Wolanski and Hamner 1988). However, it is also important to realize that the large-scale average predictions found in almanacs and tables may actually be a *better* predictor of local behavior than local conditions. Local conditions themselves may be a very poor predictor of the eventual fate of dispersed young. In this case, a general "rule of thumb" may provide higher average fitness than any conditional response to local circumstances (Lloyd 1984; Ebenman 1992; Moran 1992).

There are many examples of behaviors that appear to be predictable from lunar and tidal tables (Morgan and Christy 1994, and Morgan 1996 are particularly good examples), but there are few if any explicit comparisons of the relative strength of local versus more global cues. We have recently completed such a comparison for the daily timing of spawning in the bluehead wrasse on patch reefs in Tague Bay lagoon, in St. Croix, US Virgin Islands (RR Warner, CW Petersen, DY Shapiro, unpublished). In this species, spawning takes place daily, over a discrete period of about 110 min (Warner et al. 1975). The average time of spawning varied from day to day in a strongly periodic fashion, occurring as early as 11:00 or as late as 17:30. The cycle of spawning times had a period of 13–14 days, suggesting some relationship with the lunar or tidal cycles. At the same time that we were measuring the timing of mating, we used current meters to record local current speed and direction, as well as depth (tidal height). If the timing of spawning on a local reef were an adaptation to local conditions, we would expect a strong correlation between our measured physical data and the mean spawn time. However, by far the best correlates of local spawning times were the time of highest tidal amplitude and lunar phase, both of which were taken from standard tables. The local physical variables actually had a low, nonsignificant correlation with the tabular data, since depth, current speed and direction in this semi-enclosed lagoon were strongly affected by local winds.

These data indicate that individuals may be responding to large-scale physical characteristics rather than local conditions. In the eastern Caribbean, one of the daily flood tides is almost invariably the flux of highest amplitude, especially during periods when the actual magnitude of the amplitude is high. Regardless of the reef on which they are found, bluehead wrasses in Tague Bay tend to advance the time of spawning on successive days, a few hours ahead of the time of the preceding extreme low tide. This maintains spawning in the period of maximum tidal flux, as predicted by the tide tables. The fact that there is only a weak correspondence of this time to actual current speeds on the reef may be irrelevant, because local conditions are not a good predictor of the general conditions that dispersing eggs would encounter. In fact, there was a much better match of current speeds and predicted tidal amplitudes on the outer forereef, under more oceanic conditions. In other words, the timing of mating in this species may be highly adaptive, but the adaptation should properly be viewed as a response to conditions that prevail over a larger geographic range of the species rather than specific conditions in one small area of local habitat.

I stress that these generalized responses are particularly important when considering aspects of fitness where local environmental conditions provide little or no information, for example regarding the subsequent oceanic conditions affecting dispersing young. In contrast, we have also been able to show that those aspects of reef structure that potentially influence the survival of adults (such as the vertical profile of the reef) affect the timing of spawning on a local level. The effect here is strong enough that reefs only tens of meters apart can have distinctly and predictably different spawning schedules (RR Warner, CW Petersen, DY Shapiro, unpublished).

Discussion

In any benthically associated marine species, the relative roles of genetic differentiation, phenotypic plasticity, and large-scale adaptation in determining behavior and morphology should be a function of (1) the spatial and temporal heterogeneity of selective environments, (2) the degree of larval dispersal, and (3) the response abilities of the benthic individuals. If the local fitness consequences of a particular trait expression are strong and temporally consistent, local genetic differentiation can occur as long as the population is at least partially closed (that is, as long as there is sufficient return of locally-produced young). If broad dispersal is the rule and populations are essentially open (no return of locally produced young), individuals may respond conditionally if cues to a proper response are available and the organism is capable of detecting them. Plasticity may also arise in response to temporally variable environments, even if the population is closed. Otherwise, generalized responses are expected.

I emphasize that any of these types of responses can be studied in evolutionary ecology. Both local differentiation and phenotypic plasticity can be used in comparative tests over relatively few populations; some forms of plasticity have the added advantage of permitting manipulative field experiments within populations. Generalist phenotypes need to be interpreted over broader scales, with some knowledge of the distribution of environments and their associated fitness consequences.

Problems of interpretation arise when the method of study does not suit the particular trait. For example, populations with fixed traits are not likely to respond in adaptive ways to novel environmental manipulations. Nor can we expect necessarily to see positive fitness consequences of particular traits in particular environments, if those traits simply represent the best average response over a broad range. Similarly, generalist phenotypes may not show sufficient variation to be of use in comparative studies across species ranges. Of course, in many cases, we do not know the nature of the response before a study is undertaken. However, our conclusions (especially regarding negative results) should be tempered with a consideration of the congruence of the study method used with the type of trait investigated.

My examples and reasoning have focused on species with the potential for extensive interchange between distant populations, characteristics shared by most coral reef fishes and many invertebrates. Such extensive gene flow does not appear to be the case for some other reef organisms, most notably not for corals themselves (e.g., Ayre and Dufty 1994). Larval durations of many corals are often a matter of minutes or hours, and average dispersal distances are on the order of meters to hundreds of meters (Sammarco and Andrews 1988, 1989). At first consideration, this would be expected to promote a considerable degree of local genetic differentiation. However, the rate of local differentiation should be inversely related to the longevity of the organisms, and corals live (often in fragmented form: Ayre and Willis 1988) for very long periods (Hughes and Jackson 1980; Potts 1984). The combination of long lives and pervasive vegetative reproduction may slow the process of selection across generations, and thus selection may only result in the predominance of the best-adapted clone among a limited set of candidates.

Another aspect of coral life history has considerable implications for evolutionary ecology, morphology, and taxonomy. Corals, like plants, may have a relatively limited sensitivity to those cues in the environment that correlate with fitness of particular morphological, life-historical, or behavioral strategies. Lloyd (1984) has suggested that this is why conditional strategies are uncommon in plants. He also suggests that when faced with a variable environment, plants may evolve what he calls ”multiple responses” as a strategy. That is, plants may produce a variety of morphologies or life-histories among their young, gambling that one of a proper type will settle into a favorable environment. It has been exceedingly difficult to sort through the relationships between morphology and species in corals (Hughes et al. 1992); perhaps this diversity of form is the same multiple-response strategy that Lloyd has identified in plants (see Ayre and Willis 1988). If so, studies that relate form to habitat within species will provide a rich source of information for studies in life-history and functional morphology.

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