

A TIME COMMITMENT HYPOTHESIS FOR SIZE-DEPENDENT GENDER ALLOCATION

TROY DAY¹ AND L. W. AARSSSEN²¹*Department of Mathematics and Statistics, Queen's University, Kingston, Ontario K7L 3N6, Canada**E-mail: dayt@mast.queensu.ca*²*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada**E-mail: aarssenl@biology.queensu.ca**Key words.*—Differential mortality, environmental sex determination, gender, sex ratio.

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In many species of plants, gender expression is correlated with size. Usually large plants are “more female” than small plants (Policansky 1981, 1987; Bierzychudek 1982, 1984a,b; Lovett Doust and Cavers 1982; Schlessman 1987, 1988, 1991; Pickering and Ash 1993), but the reverse is sometimes seen in wind pollinated species (see Burd and Allen 1988; de Jong and Klinkhamer 1994; Lundholm and Aarssen 1994). Models that predict evolutionarily stable sex ratios have been developed to explain this phenomenon (Freeman et al. 1980; Charnov 1982, ch. 4, 16; Lloyd 1983; Lloyd and Bawa 1984; Charnov and Bull 1985; Schlessman 1988; de Jong and Klinkhamer 1989, 1994; Bulmer 1994, ch. 10), and the majority of these are derived from Ghiselin's (1969) size-advantage hypothesis for sequential hermaphroditism in animals. This hypothesis postulates that the sexes each have different reproductive successes (RS) at different sizes, and that the sex whose relative rate of gain of RS with size is greatest should be expressed by large individuals. For example, if females gain RS more quickly with size than males, then large individuals should be female. Many of these models predict an abrupt transition from all male to all female allocation at a threshold size (i.e., diphasy; e.g., see Charnov 1982, ch. 4, and Schlessman 1988 for a review).

When applying this hypothesis to flowering plants it is usually suggested that females have a higher energetic cost of reproduction relative to males as a result of the resource requirements for seed and fruit development (Bierzychudek 1984b; Lloyd and Bawa 1984; Schlessman 1988, 1991; de Jong and Klinkhamer 1994). Larger plants are believed to have greater resources or resource gathering potential and consequently, the increase in RS with size is greatest for females.

Here we discuss a simple alternative evolutionary explanation that is frequently overlooked. Much available evidence suggests that mortality rate (per unit time) in plants is strongly correlated with size (Harper 1977; Gross 1981; Mithen et al. 1984; Silvertown and Lovett Doust 1993). The smallest plants in a population inevitably sustain the highest mortality rates, with mortality often declining substantially as size increases. Additionally, the female function of plants usually requires a longer reproductive *time commitment* relative to the male function as a result of the time required for fruit production. These two factors combine to create a selective regime promoting the evolution of a positive correlation between femaleness and size.

The reasoning is simple. Suppose the smallest plants have the highest mortality rate. Then because the probability of dying early in the season is high when small, often there will not be sufficient time for female reproduction. The likelihood of reproductive success when small will be greater for males than females because pollen production and dispersal occur relatively fast. Thus, the female function will gain the most from an increase in size. Under this time-commitment hypothesis one would expect natural selection to favor the gender allocation rule, if small be male, if large be female. Although this prediction is the same qualitative one made by models based on energetic costs, it is not widely appreciated that this alternative explanation exists. Given that it is based on demographic and reproductive characteristics that appear to be quite common, we suggest that it deserves further attention. Additionally, we suggest that this time-commitment hypothesis can also explain instances of environmental sex determination (Charnov and Bull 1977), whereby plants in good quality sites are more female than plants in poor quality sites.

From the above verbal argument however, it is difficult to determine whether diphasy or a graded gender transition is expected. Consequently, we present a simple mathematical model to address this question, and to clarify the conditions under which our verbal argument is valid. The model also allows a more detailed prediction of the expected pattern of gender expression and therefore suggests potential ways in which this hypothesis might be tested empirically.

THE MODEL

Consider a hermaphroditic, herbaceous plant that begins growth at the start of the season. If the species is perennial, then it may attain a size that is greater or smaller than its size the previous season. For simplicity, however, we neglect any correlation between a plant's size from one year to the next. We assume that every plant can be placed into one of N size classes and that the proportion of available resources devoted to male and female function is dependent on this size (see Table 1 for notation). Each size class can exhibit an allocation strategy anywhere from all male to all female.

Note that the number of ovules and pollen grains produced by a plant of size s (i.e., $F[s, \beta_s]$ and $M[s, \beta_s]$) depends on plant size in two ways. First, F and M depend on size through β_s , which denotes the proportion of resources devoted to male function by a plant of size s . Second, we allow F and M to

TABLE 1. A list of notations. Note that the last two functions are dependent on size through mortality rate $\mu(s)$.

N	number of size classes
α	the N -dimensional vector of ESS allocation strategies for each size
α_s	the s th element of α
β	the N -dimensional vector of mutant allocation strategies for each size
β_s	proportion of available energy allocated to male function for a plant of size s ; $\beta_s \in [0,1]$. It is the s th element of β
$f(\beta)$	a function specifying how ovule output depends on allocation strategy; $f(\beta) \in [0,1]$ and $f(0) = 1$, $f(1) = 0$
$m(\beta)$	a function specifying how pollen output depends on allocation strategy; $m(\beta) \in [0,1]$ and $m(0) = 0$, $m(1) = 1$
$\xi(s)$	a function specifying how ovule and pollen output depend directly on size
$M(s, \beta_s)$	number of pollen grains produced by a plant of size s ; $M(s, \beta_s) = \xi(s)m(\beta_s)$
$F(s, \beta_s)$	number of ovules produced by a plant of size s ; $F(s, \beta_s) = \xi(s)f(\beta_s)$
$\theta(s)$	frequency of size class s ; $\sum \theta(s) = 1$
$\mu(s)$	mortality rate; a decreasing function of size
τ	length of time required to complete male function (i.e., length of male reproductive period)
$\gamma\tau$	length of time required to complete female function ($\gamma > 1$; i.e., female function requires more time)
$p_s(t)$	probability density of the time of mortality
$P_s(t)$	probability of living at least until time t ; $P_s(t) = \int_t^\infty p_s(u)du$

depend directly on plant size, because a change in size will likely alter ovule and pollen output even when the allocation strategy β , is held constant. For example, suppose a plant divided its resources equally between the two gender functions regardless of its size (i.e., $\beta_s = 0.5$ for all s). Total ovule and pollen output might nonetheless increase with an increase in size because the total amount of resources available to the plant might increase. Indeed, the energetics-based models for size-dependent gender allocation that do predict increasing femaleness with increasing size do so because they assume such increases in resource availability have a greater relative effect on the female function. Therefore, to isolate the effect of size-dependent mortality on gender expression, we assume that there are no such differences in the way plant size directly affects the two gender functions. For simplicity we further assume that F and M are of the form $F(s, \beta_s) = \xi(s)f(\beta_s)$ and $M(s, \beta_s) = \xi(s)m(\beta_s)$ where $\xi(s)$ specifies the direct size dependence. This form implies that the trade-off relationship between ovule and pollen production (i.e., the $f[\cdot]$, $m[\cdot]$ trade-off) is the same for all size classes. This trade-off can be depicted by a graph of m versus f that is parameterized by the allocation proportion β (Fig. 1; see Charnov 1982). Because this curve is the same for all size classes, we take our focus on hermaphrodites to imply that it is concave down (Fig. 1, curve a; see Charnov et al. 1976; Charnov 1982; Brunet 1992).

Now consider a large, panmictic population just after winter. Each individual grows until sexual maturity, but by chance individuals differ in size giving a distribution of sizes $\theta(s)$ at the beginning of the reproductive season. Variation in

size might result from random environmental effects during growth, for example. Suppose that male and female reproduction commence at the same time. We assume that no size change occurs during reproduction so that the mortality rate $\mu(s)$ is constant for each size class. This gives,

$$p_s(t) = \mu(s)e^{-\mu(s)t}$$

$$P_s(t) = e^{-\mu(s)t}$$

where $p_s(t)$ is the probability density of the time of mortality and $P_s(t)$ is the probability of living at least until time t ; that is, $P_s(t) = \int_t^\infty p_s(u) du$. For simplicity we suppose that a plant gains the full benefit of male function if it survives the entire length of the male reproductive period, τ , and gets zero benefit from the male function otherwise. Similarly, a plant gains the full benefit of both male and female function only if it survives the entire length of the female reproductive period, $\gamma\tau$ (recall $\tau < \gamma\tau$). This last assumption implies that the payoff of each gender occurs at a point in time. Later we relax this assumption.

To determine the ESS gender allocation strategy for each size class (Maynard Smith and Price 1973; Maynard Smith 1982) consider a population at the ESS, represented by the N -dimensional vector of size-dependent strategies, α (bold symbols identify vectors). What is the fitness of an individual that uses a slightly altered, mutant strategy, β ? The mutant will be of size s at maturity with probability $\theta(s)$. With probability $P_s(\gamma\tau)$, it will gain fitness through both gender functions and with probability $P_s(\tau) - P_s(\gamma\tau)$ it will gain fitness through male function only. Equating male RS with the number of ovules fertilized, the expected fitness of this mutant strategy is

$$W(\beta, \alpha) = \sum_{s=1}^N \theta(s)[P_s(\gamma\tau) \cdot (\text{female fitness} + \text{male fitness}) + (P_s[\tau] - P_s[\gamma\tau]) \cdot \text{male fitness}]$$

or

$$W(\beta, \alpha) = \sum_{s=1}^N \theta(s)[P_s(\gamma\tau)(F[s, \beta_s] + M[s, \beta_s] \cdot \Phi) + (P_s[\tau] - P_s[\gamma\tau])M[s, \beta_s] \cdot \Phi], \quad (2)$$

where Φ is the number of ovules per pollen grain. Expression (2) simplifies to

$$W(\beta, \alpha) = \sum_{s=1}^N \theta(s)F(s, \beta_s)P_s(\gamma\tau) + \sum_{s=1}^N \theta(s)M(s, \beta_s)P_s(\tau) \cdot \Phi, \quad (3)$$

where

$$\Phi = \frac{\sum_{s=1}^N \theta(s)F(s, \alpha_s)P_s(\gamma\tau)}{\sum_{s=1}^N \theta(s)M(s, \alpha_s)P_s(\tau)}. \quad (4)$$

Bulmer (1994, pp. 231–232) presents an analogous derivation for environment-dependent gender allocation in a patchy habitat.

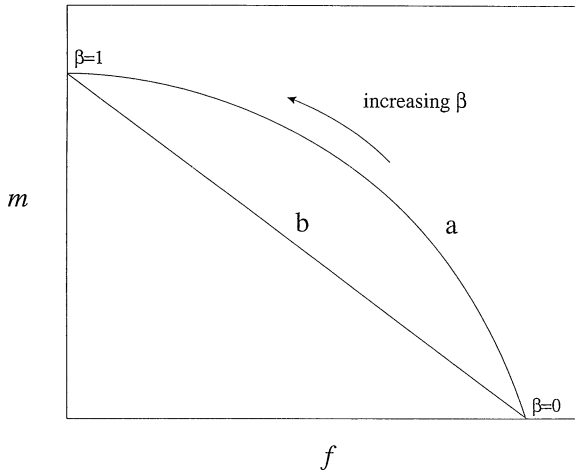


FIG. 1. The m versus f trade-off curve, parameterized by β . Curve (a) models a nonlinear trade-off between pollen and ovules and curve (b) models a linear trade-off.

Now if α is an ESS, all mutant strategies β must be less fit than α in an α -population. This implies that equation (3), as a function of β , has a maximum at $\beta = \alpha$. Each element of β must lie in the interval $[0, 1]$, and therefore the ESS strategy is characterized as follows: (1) for a size class to have an intermediate allocation strategy as an ESS, we require $\partial W/\partial \beta_s|_{\beta=\alpha} = 0$; and (2) for a size class to have an all-female or all-male allocation strategy as an ESS, we require $\partial W/\partial \beta_s|_{\beta=\alpha} < 0$ or $\partial W/\partial \beta_s|_{\beta=\alpha} > 0$, respectively. These conditions must hold for each size class $s = 1 \dots N$. Calculating the derivative in these conditions using equation (3) and the definitions of the functions F , M , and P_s gives

$$\frac{\partial W}{\partial \beta_s} \Big|_{\beta=\alpha} = \theta(s) \left[\frac{\partial F}{\partial \beta_s} P_s(\gamma\tau) + \frac{\partial M}{\partial \beta_s} \Phi P_s(\tau) \right]_{\beta=\alpha} \quad (5a)$$

$$= \theta(s) \left[\frac{df}{d\beta_s} \xi(s) e^{-\mu(s)(\gamma\tau)} + \frac{dm}{d\beta_s} \xi(s) \Phi e^{-\mu(s)\tau} \right]_{\beta=\alpha} \quad (5b)$$

Now using the derivative (5b) in the ESS conditions and noting that $df/d\beta$ is negative gives:

(1) mixed gender if: $|dm/df| = \exp(-\mu[s]\tau \cdot [\gamma - 1])/\Phi$, (6)

where $|dm/df|$ is the absolute value of the slope of the m versus f graph (Fig. 1);

(2) all female if: $|dm/df| < \exp(-\mu[s]\tau \cdot [\gamma - 1])/\Phi$; (7)

or

all male if: $|dm/df| > \exp(-\mu[s]\tau \cdot [\gamma - 1])/\Phi$. (8)

To make sense of these conditions, note that they are evaluated at the ESS, and therefore the number of ovules per pollen grain, Φ , is constant. Also, by our choice of the form of $F(s, \beta_s)$ and $M(s, \beta_s)$, the derivatives on the left-hand side of equations (6)–(8) are independent of size. Therefore, because the right-hand side of equations (6)–(8) is strictly increasing, for equality to hold in equation (6) across a range of sizes, $|dm/df|$ must increase as size increases. From Figure 1a it can be seen that allocation to male function must therefore decrease with increasing size. Thus, for those size classes

with an intermediate ESS, size will be positively correlated with femaleness. It is also possible for an all-female or all-male strategy to be an ESS if conditions (7) or (8) hold for some range of sizes. From Figure 1a equation (7) can hold only for the largest sizes and equation (8) for the smallest. If a single gender strategy is to be an ESS, big plants will be female and small plants will be male (see also Charnov and Bull 1985).

DISCUSSION

Here we have used the framework of condition-dependent sex ratio evolution to demonstrate that the different reproductive time commitments of female versus male function can explain the positive correlation between femaleness and size. This result can be viewed as another example of Ghiselin's (1969) size-advantage hypothesis. Here the female function requires a greater time investment than the male function. Therefore when size, and hence survivorship, increases, the female function has the highest relative rate of gain in RS. Before discussing the biological implications of this result, we discuss some of the simplifications in our formulation.

The form chosen for the ovule and pollen output functions (i.e., $F[s, \beta_s] = \xi[s]f(\beta_s)$ and $M[s, \beta_s] = \xi[s]m(\beta_s)$) led to the useful simplification whereby the left-hand side of equations (6)–(8) is independent of s . This allowed us to use the same m, f trade-off curve for all size classes. This form incorporates a large number of plausible possibilities, but we point out that our results are not necessarily restricted to this case. Other forms for these functions can be envisioned whereby the left-hand side of equations (6)–(8) is not independent of s . Similar conclusions may result, however in such cases it is often more difficult to obtain simple analytical results. We have restricted attention to this simple, yet plausible, form in an attempt to make the exposition more transparent.

For simplicity, our formulation also made the assumption that the pay-off of each gender follows an all-or-none rule. While this is a reasonable approximation in many instances, it is worth considering how to relax this assumption. Figure 2a plots the proportion of the total potential pay-off of each gender that is realized for increasing values of the time of mortality under the all-or-none rule. The male and female curves are step functions at τ and $\gamma\tau$, respectively, because the plant will realize all of the benefit of these genders if it survives to these times and none otherwise. Figure 2b depicts two such functions that are more general. Here if the plant dies prior to completion of its male or female function (τ or $\gamma\tau$, respectively), it still obtains some reproductive success through each. In the appendix we show how the above model can be extended to include such functions and we derive conditions for our results to hold.

What gender expression patterns do we expect to observe under this hypothesis? If mortality rate is a strictly decreasing function of size, then there will always be a size class with mixed gender expression. The range of sizes exhibiting single versus mixed gender strategies is determined by two factors (Fig. 3). First, the curvature of the m, f curve (Fig. 1a) determines the distance between f^* and m^* in Figure 3. Changing this will produce a corresponding change in the gender

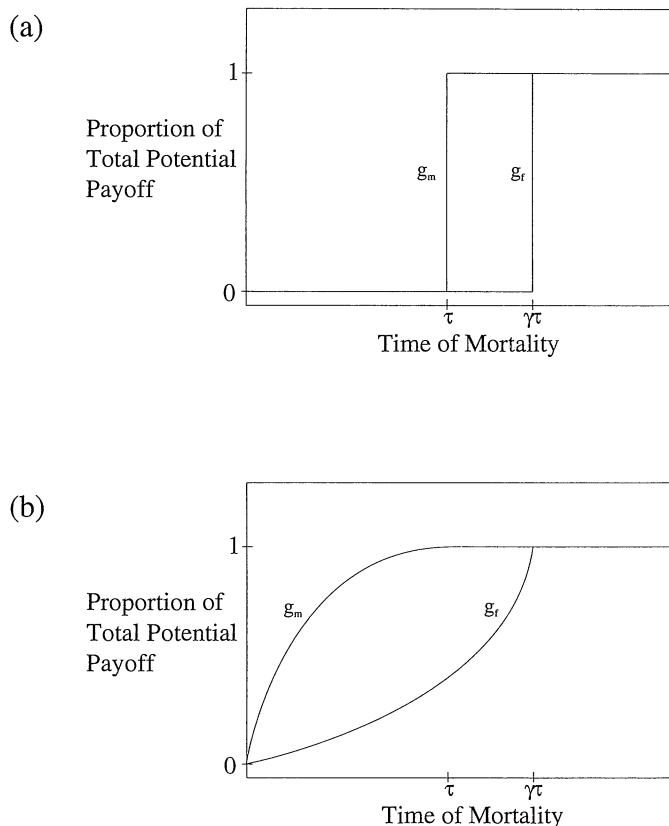


FIG. 2. The proportion of total potential pay-off for each gender as a function of the time of mortality; g_m is the male function and g_f the female function; (a) the all-or-none assumption of reproductive pay-off; (b) a more general pair of functions for the schedule of reproductive pay-off.

strategy ranges on the size axis of Figure 3. Second, changing the steepness of the curve in Figure 3 (e.g., by changing the steepness of $\mu[s]$) will also alter the gender strategy ranges on the size axis. All such alterations will result in a size class with mixed gender expression. Note however, that the range of sizes that exhibit mixed gender may be too small to distinguish from diphasy in practice. Thus all else being equal, plants whose mortality rate decreases very rapidly with size, or whose pollen-ovule trade-off is nearly linear (Fig. 1b) should have gender expression patterns that look essentially like diphasy.

It is also interesting to ask how predictions change if there are a small number of relevant size classes. If, for example, mortality rate is roughly a step function of size with one step, then the population can be effectively categorized into two size classes. In this situation, there are two possible allocation patterns. Either one of the size classes uses a mixed male-female strategy and the other uses a single gender strategy, or the small size class is male and the large size class is female. Determining which of these is expected would require some knowledge of the pollen-ovule trade-off relationship as well as the size-mortality relationship.

Previous treatments of size-dependent gender allocation have relied primarily on an argument for a higher energetic cost of reproduction incurred by females (Bierzychudek 1984b; Lloyd and Bawa 1984; Schlessman 1988, 1991; de

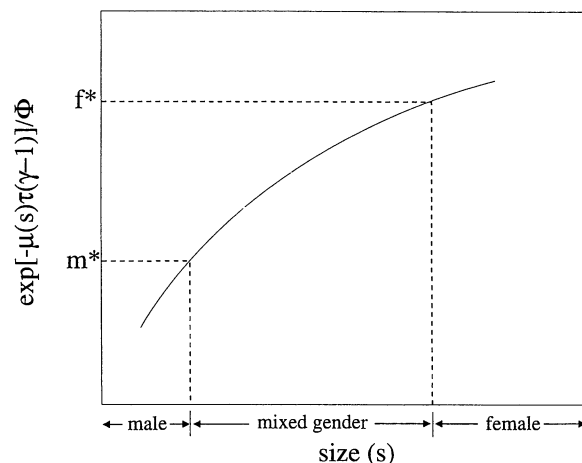


FIG. 3. A hypothetical graph of the right-hand side of equations (6)–(8) against size, s ; f^* and m^* are the maximum and minimum absolute value of the slope embodied by the m/f trade-off curve (Fig. 1, curve a as $\beta \rightarrow 0$ and $\beta \rightarrow 1$, respectively). The function $\exp[-\mu(s)\tau(\gamma - 1)]/\Phi$ and these values determine the range of sizes that exhibit single-versus mixed-gender strategies. Note that because size is discrete, the curve will actually be stepped. However, by employing a large number of size classes the curve can be made arbitrarily close to that shown.

Jong and Klinkhamer 1994). Some of this earlier work has also been directed toward other condition-dependent gender allocation strategies. For example, it is often believed that plants with environmental sex determination (Charnov and Bull 1977) tend to be more female in good versus poor quality sites (Freeman et al. 1976, 1981; Lovett Doust and Cavers 1982; Zimmerman 1991; see Bierzychudek and Eckhart 1988 for a review). One explanation for this is a greater female energetic cost of reproduction. Our results suggest that this pattern can also be explained simply by site differential mortality rates. Assuming that mortality rate is a decreasing function of site quality (which is likely), good quality sites should contain plants that are more female than poor quality sites. Note that this hypothesis does *not* involve gender-based differential mortality rates (see Bierzychudek and Eckhart 1988). The model and analysis are formally the same, but the variable s is now interpreted as site quality. Again this pattern results from a greater female reproductive time commitment.

At present, there is little data available to thoroughly test the above hypothesis. Numerous demographic studies of the relationship between size and mortality exist, but none to our knowledge links mortality during the growing season to gender expression. Given the ubiquity of a negative size-mortality relationship however, we believe the present hypothesis warrants attention. We hasten to note however, that it need not be exclusive to hypotheses based on energetic costs. Rather it may simply constitute an additional factor favoring the evolution of size-dependent gender expression. Indeed, larger time commitments will often entail larger energy commitments as well. Nonetheless, it might prove easier to address empirically, as it is probably simpler to measure differences in time investments than differences in energetic investments.

Similarly, given that mortality rates in poor quality sites are high, a time commitment hypothesis is a simple expla-

nation for many patterns of environmental sex determination as well. Thus, an investigation of the correspondence between size-dependent mortality and gender expression as well as site-dependent mortality and gender expression would be worthwhile.

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APPENDIX

Here we generalize the results of the text to allow more general g_m and g_f functions and to derive conditions on these functions for the above results to hold. First, note that the probability of mortality between times t and $t + dt$ is $p_s(t)dt$, where $p_s(t)$ is given by equation (1). The fitness of a β -mutant if this occurs is given by

$$W(\beta, \alpha) = \sum_s \theta(s) [g_f(t)F(s, \beta_s) + g_m(t)\Phi M(s, \beta_s)]. \quad (A1)$$

Therefore, the expected fitness of a β -mutant is given by

$$W(\beta, \alpha) = \int_0^\infty p_s(t) \left\{ \sum_s \theta(s) [g_f(t)F(s, \beta_s) + g_m(t)\Phi M(s, \beta_s)] \right\} dt, \quad (A2)$$

which can be rewritten to give

$$W(\beta, \alpha) = \sum_s \theta(s) F(s, \beta_s) \int_0^\infty p_s(t) g_f(t) dt + \sum_s \theta(s) \Phi M(s, \beta_s) \int_0^\infty p_s(t) g_m(t) dt \quad (A3)$$

Equation (A3) is a generalization of equation (3) of the text. Note that if g_f and g_m are step functions, as in Figure 3a, then

$$\int_0^\infty p_s(t) g_f(t) dt = \int_{\gamma\tau}^\infty p_s(t) dt = P_s(\gamma\tau). \quad (A4)$$

From (A3) it can be seen that the generalization of the right-hand side of equations (6)–(8) is

$$\int_0^\infty p_s(t) g_f(t) dt / \int_0^\infty p_s(t) g_m(t) dt. \quad (A5)$$

This is the expected proportion of the total potential output through the female function divided by the expected proportion of the total potential output through the male function for size class s . For the results of the text to hold under this generalization, we require that

(A5) be an increasing function of size, s . In other words, the ratio of female to male success must increase with size. This is simply a version of Ghiselin's size-advantage hypothesis. Alternatively, since μ is decreasing in s we require that (A5) be decreasing in μ .

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GENETIC EVIDENCE FOR LONG TERM PERSISTENCE OF MARINE INVERTEBRATE POPULATIONS IN AN EPHEMERAL ENVIRONMENT

RONALD S. BURTON

*Marine Biology Research Division, Scripps Institution of Oceanography,
University of California at San Diego, La Jolla, California 92093-0202*

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Understanding the ecology and evolution of species requires that we know the relationships between individuals currently extant in a population and conspecifics previously occupying the same geographic locale. In the case of marine invertebrate species with free-swimming larval and/or adult stages, such relationships are rarely known. From a natural history perspective, it is commonly assumed that dispersing larvae (and/or adults) result in population structures characterized by a nearly complete lack of local recruitment. Larval dispersal would then effectively homogenize the gene pool resulting in negligible differentiation of geographically separated populations. However, genetic analyses of several species with planktonic larvae have revealed unexpectedly high levels of population differentiation on either local or regional spatial scales (e.g., Burton 1983; Johnson and Black 1982, 1984; Reeb and Avise 1990; Watts et al. 1990; Karl and Avise 1992; Lewis and Thorpe 1994; Edmands, et al. 1996).

Dispersal itself is not the only problem we face in determining if today's populations are descended directly from the local conspecific populations of the past. A second, perhaps less widely discussed problem involves the temporal stability of certain marine habitats. For example, some patches of rocky intertidal habitat are irregularly inundated with sand making much of the hard substrate required by many intertidal invertebrates unavailable. Similarly, high intertidal pools are seasonally subjected to complete desiccation or, at the other extreme, transformation into freshwater pools by drought or storms. When present, such habitats are typically inhabited by a diversity of species. Knowing the origin of colonists reestablishing such populations is central to understanding the ecology and evolution of species living in ephemeral marine habitats.

Regardless of the factors complicating our understanding, it is generally difficult to address problems of the temporal relationships of conspecific populations of marine organisms. Even vigilant monitoring of populations (including physical marking of individuals) can only directly relate post-recruit-

ment age classes. For this reason, genetic tools have taken a lead role in the analysis of population structure. Unfortunately, levels of genetic differentiation among conspecific populations are often insufficient to allow direct assessment of population persistence. Most marine invertebrates lack sharp geographic differentiation, with the vast majority of genetic variation being distributed within rather than between populations. In some cases, however, strong differentiation has been observed and these situations provide opportunities to determine if today's populations are descended directly from the local population of the past. For example, Piertney and Carvalho (1995) documented large monthly fluctuations in allelic frequencies in populations of the intertidal isopod *Jaera albifrons*; they concluded that while occupying the same rock, the assemblages of animals sampled over monthly intervals differed more than could be attributed to within-population genetic change. Hence, animals sampled at a given time were frequently not closely genetically related to those collected at the same location only months earlier. Lessios et al. (1994) reported that allozyme frequencies were stable in nine out of ten isopod (*Exocirolana* sp.) populations studied over a two-year time frame. In the tenth population, changes in allelic frequencies were again so dramatic that extinction and subsequent recolonization of the particular beach was the most likely explanation for the genetic data. While substantially more data are needed to determine if the 10% turnover rate observed in two years is typical in this system, it is important to note that even this relatively low rate of population extinction and recolonization would predict that only 7% of populations would persist for half a century. Such expectations have important ramifications for both ecology and evolution and lie at the center of current discussions of the significance of "metapopulation" dynamics (e.g., Hanski and Gilpin 1991).

Another approach to understanding the temporal persistence of populations is exemplified by several studies comparing allelic frequencies among size or age classes within and between populations (KoeHN et al. 1980; Johnson and