

FERTILIZATION SUCCESS CAN DRIVE PATTERNS OF PHASE DOMINANCE IN COMPLEX LIFE HISTORIES¹

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Many algal life cycles alternate between two free-living generations. Life histories in which the two generations look identical (isomorphic) are common, particularly in the Rhodophyta. Reports of natural populations dominated by one generation of the life history have sought explanation in terms of phase-specific differences in mortality and reproductive output, yet in many cases identification of these adaptations has been elusive or inconsistent with predictions. We hypothesized that the gametophyte-to-sporophyte ratio of ecologically equivalent isomorphs could result from variation in fertilization rate. We developed two models to test this hypothesis: one representing a generalized isomorphic life history and the other specific to red algae with a *Polysiphonia*-type life history. Fertilization rate affected the gametophyte-to-sporophyte ratio, especially at low fertilization rates. In the general model, gametophytes dominated the population regardless of fertilization rate unless egg production greatly exceeded meiospore production. In the red algal model, phase dominance depended on the combination of fertilization rate and the number of carpospores produced per fertilization. The generational composition of model multiphasic algal populations results from their inherent reproductive characteristics and the dynamic environment to which fertilization and mortality rates are tied.

Key index words: algae; fertilization; gametophyte dominance; isomorphic; life history; population structure; sporophyte dominance

Life cycles that consist of an alternation of generations occur in many groups of algae and plants and provide opportunities for phase-specific adaptations to environments that vary in space and time. Several hypotheses have been proposed to explain different distributions of alternate generations. In the case of heteromorphic algae, there is compelling evidence for adaptive trade-offs between crustose and upright phases. Crusts resist or tolerate disturbance (grazing

and abiotic factors) better than upright fronds but grow more slowly and usually are poor competitors (Littler and Littler 1980, Lubchenco and Cubitt 1980, Slocum 1980, Dethier 1981, Steneck and Dethier 1994). Crusts, having much longer life spans than fronds, are a source of genetic continuity over long temporal scales.

Life cycles that alternate between isomorphic generations occur in all major macroalgal groups. Isomorphic life histories occur in a few orders of phaeophyceans and ulvophyceans but predominate among orders of Florideophyceae in which the phenomenon has been most studied. In at least 18 genera comprising 34 species of isomorphic red algae there are populations dominated by one phase of the life history or a spatial separation of phases (Edwards 1973, Mathieson and Burns 1975, Craigie and Pringle 1978, Norall et al. 1981, DeWreede and Green 1990, Scrosati 1998, Thornber and Gaines 2004). Intertidal populations of *Chondrus crispus* Stackhouse, the most frequently cited example, often consist of 80%–90% gametophytes, whereas nearby subtidal populations are dominated by tetrasporophytes (Mathieson and Prince 1973). Instances of dominance by one phase in natural populations have prompted explanations similar to those proposed for differences among heteromorphs, although the adaptive trade-offs between isomorphs are less apparent.

Tests of hypotheses of phase dominance from distribution and abundance patterns and correlations implicitly assume a 1:1 ratio between haploid and diploid adults in the absence of adaptive differences (but see Thornber and Gaines 2004). This assumption may not apply, even when phases within a species are ecologically equivalent, because zygotes and meiospores are not always produced in equal numbers (Scrosati and DeWreede 1999). There are several potential reasons for the disparity. Gametangia and sporangia may be differentially abundant on their respective thalli. These structures also produce different numbers of their respective products. Meiotic spore production ranges from four (tetraspores per tetrasporocyte in red algae and in unilocular sporangia of some phaeophyceans) to greater than 256 per sporangium (in other phaeophyceans) (Graham and Wilcox 2000). Similarly, gametangia are abundant, and some plurilocular sporangia produce many gametes per gametangium. The production of gametes and spores is most equitable in ulvophytes in which gametangia or sporangia develop

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from typical vegetative cells with equivalent numbers of gametes and zoospores per cell (Stratman et al. 1996). Finally, the ratio of zygotes to meiospores may be reduced by low fertilization rates as one or both sets of gametes are transported through environments that hamper syngamy. In the Florideophyceae, however, fertilization is internal, and the cloning of zygotes during carposporophyte development may produce several thousand carpospores from a single fertilization. The null model 1:1 ratio further assumes that any disparity in propagule production is meaningless because so many more are produced than can survive. The validity of this assumption is questionable because large reproductive investments of many algae suggest that making more propagules is adaptive. Model populations of red algae with 1:1 sex ratios show that the production of four tetraspores for every carpospore (Scrosati and DeWreede 1999), or even equal fecundity of females and sporophytes (Thornber and Gaines 2004), is sufficient to cause gametophytic dominance.

Experimental tests of phase-specific adaptive differences between isomorphic generations have met with limited success. The hypotheses most frequently invoked concern differences in postsettlement mortality between phases due to differences in physiology, mechanical properties, susceptibility to endophytic infection, or herbivores (Mathieson and Norall 1975, Bhattacharya 1985, Hannach and Santelices 1985, Buschmann and Santelices 1987, Buschmann and Bravo 1990, Correa and McLachlan 1992, Carrington et al. 2001, Lindgren et al. 2003, Thornber and Gaines 2004). Most such studies found no differences between phases or found differences contrary to predictions from natural patterns. In *C. crispus*, however, tests of infection by some endophytes (but not others) provide partial support for patterns of gametophytic dominance of intertidal populations (Correa and McLachlan 1992). Lower mortality rates of tetrasporophytes (Bhattacharya 1985), similar breaking forces at the base of the stipe (Carrington et al. 2001), and similar consumption by herbivores of each phase (Lindgren et al. 2003) are inconsistent with gametophytic dominance in *C. crispus*. Several other studies examined reproductive output and/or survival of spores of each phase as factors influencing phase dominance in nature (Destombe et al. 1989, 1990, 1993, Scrosati and DeWreede 1999, Engel et al. 2001, Thornber and Gaines 2004). Diploid carpospores of *Gracilaria verrucosa* (now *G. gracilis* [Stackhouse] Steentoft, Irvine & Farnham) have higher survival rates than do tetraspores and may explain tetrasporophytic dominance (Destombe et al. 1993). None of these hypotheses adequately explains the patterns of phase dominance observed in all natural populations of a species. In the case of the red alga, *Mazzaella splendens* (Setchell & Gardner) Fredericq (formerly *Iridaea cordata*), the dominant life history phase at two sites switched from gametophyte to tetrasporophyte during a 21-month span (DeWreede and Green 1990). However, no such shifts have been ob-

served in the congener, *M. flaccida* (Setchell & Gardner) Fredericq (Thornber and Gaines 2003). In theory, only slight differences are necessary for selection to favor the evolution of biphasic life cycles through niche partitioning (Hughes and Otto 1999), but none that completely explains patterns observed in nature has been found.

Our objective was to examine the role of fertilization success on the gametophyte-to-sporophyte ratio in model populations of macroalgae. We developed a model algal population in which isomorphic phases were ecologically equivalent and tested whether varying reproductive characters, including fertilization rate, can cause a deviation from the expected null model of a 1:1 ratio of gametophytes to sporophytes. Fertilization rates vary widely among algae (Kain and Bates 1993, Santelices 2002), so there is reason to hypothesize that they contribute to phase distributions. This variation is due to both differences in reproductive traits and environmental factors, such as water motion. For example, some algae achieve high fertilization rates by releasing gametes only when there is little or no flow (Serrão et al. 1996, Engel et al. 2001).

We further developed the model to represent the triphasic life cycle of a florideophycean alga, which often exhibit phase dominance in natural populations. Scrosati and DeWreede (1999) and recently Thornber and Gaines (2004) developed models of a red algal life cycle that showed the inherent differences in spore production, in part due to dioecy, in an alternation of generations favored gametophytes when fertilization rate is 100%. Here, we explored the simultaneous effects of fertilization rate and carpospore versus tetraspore production on the gametophyte-to-sporophyte ratio. We also used our model to examine density-dependent versus density-independent fertilization rates, the effects of perturbations on outcomes of phase dominance, and the relative strengths of fertilization rate versus phase-specific mortality rates in determining phase dominance.

THE MODEL

The general model. To model a haploid-diploid life cycle, we derived two equations, one representing the diploid (sporophyte) phase and the other the haploid (gametophyte) phase. The general form represented an isomorphic alternation of generations in which the abundance of each phase increased with new recruits produced by the alternate phase but was limited by local resources in a density-dependent manner. The model is nonspatial, deterministic, and has stationary parameters.

The rate of change of the gametophyte population ($dG \cdot dt^{-1}$) is equal to the difference of two products: the recruitment rate of gametophytes from sporophytes (b_G) times sporophyte abundance (S_t) minus the mortality rate of gametophytes (d_G) times gametophyte abundance (G_t):

$$dG \cdot dt^{-1} = b_G \cdot S_t - d_G \cdot G_t \quad (1)$$

The recruitment rate of gametophytes, b_G , is a function of meiospore production times their survival. Specifically,

$$b_G = \rho_s \cdot \lambda_s \cdot \alpha_G \quad (2)$$

where ρ_s is the sporangial density per frond, λ_s is the meiospores per sporangium, and α_G is the survivorship through the gametophytic juvenile stage. The mortality of adult gametophytes (d_G) shows density dependence at a rate equal to q_G .

The overall equation for gametophytes is:

$$dG \cdot dt^{-1} = \rho_s \cdot \lambda_s \cdot \alpha_G \cdot S_t - q_G \cdot G_t \quad (3)$$

The equation representing the gametophyte population and the model output includes both males and females. To account for the fact that only female gametes are fertilized (i.e. assumed that the species is dioecious), reproductive parameters for gametophytes were multiplied by the parameter, p_F , which represents the proportion of gametophytes in the population that is female. All analyses presented in this study assume a 1:1 ratio of males to females; hence, $p_F = 0.5$ (see equations with parameters for birth rate of sporophytes below).

The equation for the number of sporophytes in a population was derived in a similar manner as for gametophytes. The rate of change of sporophytes ($dS \cdot dt^{-1}$) is also expressed as a difference of two products: the recruitment rate of sporophytes (b_S) from gametophytes times gametophyte abundance (G_t) minus the mortality rate of sporophytes (d_S) times sporophyte abundance (S_t):

$$dS \cdot dt^{-1} = b_S \cdot G_t - d_S \cdot S_t \quad (4)$$

The recruitment rate of sporophytes is

$$b_S = p_F \cdot \rho_G \cdot \lambda_G \cdot F \cdot \alpha_S \quad (5)$$

where p_F is the proportion of female gametophytes, ρ_G is the density of oogonia per individual, λ_G is the number of eggs per oogonium, F is the fertilization rate of oogonia, and α_S is the survivorship through the sporophytic juvenile stage. Like gametophytes, the mortality of adult sporophytes (d_S) is assumed to be density dependent at a rate equal to q_S . The overall equation for sporophytes is

$$dS \cdot dt^{-1} = (p_F \cdot \rho_G \cdot \lambda_G \cdot F \cdot \alpha_S) \cdot G_t - q_S \cdot S_t \quad (6)$$

Isomorphic red algal model. The model representing isomorphic red algae differs from the general model in several ways. The diploid phase is termed a tetrasporophyte, and parameters are symbolized with the subscript T. Because there is only one oogonium produced per carpogonium, $\lambda_G = 1$, and the total number of oogonia in the population is simply the number of female gametophytes ($G_t \cdot p_F$) times the number of fertile carpogonia per female (ρ_G). However, zygotes are cloned in the carposporophyte phase, yielding many carpospores that can potentially result in many tetrasporophytes per fertilization. The model incorporates a cloning rate parameter (m)

to determine carpospore number in b_T , the recruitment rate of tetrasporophytes parameter.

$$b_T = (p_F \cdot \rho_G \cdot F \cdot m) \cdot \alpha_T \quad (7)$$

In the Florideophyceae, each sporangium (i.e. tetrasporangium) typically yields four tetraspores, so the population of tetraspores equals four times the product of tetrasporangial density per frond and tetrasporophyte abundance. Hence, for the red algal model,

$$b_G = 4 \cdot \rho_T \cdot \alpha_G \quad (8)$$

where ρ_T and α_G equal tetrasporangial density and survivorship through the gametophytic juvenile stage, respectively.

In addition to density-dependent mortality, in this model we also incorporated a density-independent mortality rate, q_D , such that

$$d_G = q_G + q_D \quad (9)$$

and

$$d_T = q_T + q_D \quad (10)$$

to test the effect of perturbations on populations. As expected under the null hypothesis of no difference between isomorphs, the rate was equal for gametophytes and tetrasporophytes.

The equations for gametophytes and tetrasporophytes are, respectively,

$$dG \cdot dt^{-1} = \rho_T \cdot 4 \cdot \alpha_G \cdot T_t - (q_G + q_D) \cdot G_t \quad (11)$$

$$dT \cdot dt^{-1} = (p_F \cdot \rho_G \cdot F \cdot m \cdot \alpha_T) \cdot G_t - (q_T + q_D) \cdot T_t \quad (12)$$

Mortality rates in Eqs. 11 and 12 above pertain only to established individuals. There were sources of mortality to reproductive phases, including aborted propagules, propagules that were never released, and those that did not recruit. These factors are represented as constants in both the general and red algal models (Table 1).

MODEL RESULTS AND SIMULATIONS

Fertilization rates required for a 1:1 phase ratio. A null model of a 1:1 ratio of life history phases implies that gametophytes and sporophytes are ecologically equivalent. In such a case mortality rates for juveniles and adults can be both assumed equal and the model equations solved for equal-sized gametophyte and sporophyte populations at equilibrium. For the general model, the fertilization rate that yields a 1:1 ratio of phases is

$$F = \frac{\rho_S \cdot \lambda_S}{p_F \cdot \rho_G \cdot \lambda_G} \quad (13)$$

(for $0 < p_F < 1$). Thus, the fertilization rate necessary to yield a 1:1 ratio is sensitive to the ratio of spore-to-egg investments. Greater fertilization rates are needed to maintain a 1:1 phase ratio when meiospore production per sporophyte exceeds oogonial

TABLE 1. Red algal model parameter values used in simulations.

Parameter	Default value	Source
Abort rate	0.9	Kaczmarek and Dowe 1997
Cloning rate	1024	Boney 1960a,b, Boney 1960a,b, Kaliaperumal et al. 1986, Hughes and Otto 1999
Death rate	Density dependent	
Disturbance death rate	0	
Fertilization rate	Variable	Kain and Bates 1993, Kaczmarek and Dowe 1997, Destombe et al. 1990
Juvenile survival rate	Density dependent	
Oogonia (carpogonia) density	10 ²	Boney 1960a, Avila et al. 1999, Engel et al. 2001
Proportion female	0.5	
Release rate	0.6	Kain and Bates 1993
Settlement rate	0.01	
Sporangia (tetrasporangia density)	(carpogonia density) ^{1.96}	Boney 1960a, Avila et al. 1999, Hughes and Otto 1999, Engel et al. 2001

production by females. Similarly, for florideophycean red algae,

$$F = \frac{4 \cdot \rho_T}{P_F \cdot \rho_G \cdot m} \quad (14)$$

In red algae, both the production of just four meiospores per sporangium and numerous carpospores from the cloning of zygotes reduces the fertilization rate of carpogonia needed to yield a 1:1 ratio. Using values for reproductive characters representative of a typical red alga (Table 1) and assuming an even sex ratio yields a 1:1 phase ratio at a 65% rate of fertilization of carpogonia. Gametophytes should be more abundant at <65% fertilization, whereas tetrasporophytes should be more abundant at rates >65%. Parameter values for the red algal model were based on the literature for algae with an isomorphic (i.e. *Polysiphonia*-type) life cycle (Table 1). Therefore, the ranges of parameters used for the model and findings of the model represent values that occur in natural systems but are not specific to one genus or species.

Relationship between phase ratio and fertilization rate. Assuming equal mortality rates of juveniles and adults for both phases, the model equations can be solved at equilibrium for the ratio of gametophytes to sporophytes. The solutions for the general and red algal models, respectively, are

$$x = \sqrt{\frac{\rho_S \cdot \lambda_S}{P_F \cdot \rho_G \cdot \lambda_G \cdot F}} \quad (15)$$

$$x = \sqrt{\frac{4 \cdot \rho_T}{P_F \cdot \rho_G \cdot F \cdot m}} \quad (16)$$

for $0 < p_F < 1$, where x equals the scalar that expresses the gametophyte-to-sporophyte ratio.

The solutions indicate that the ratio of gametophytes to sporophytes varies nonlinearly with fertilization rate. Specifically, in the general model it is proportional to the square root of the reciprocal of fertilization rate, and in the red algal model it is proportional to the square root of the reciprocal product

of fertilization and cloning rates. Consequently, gametophyte-to-sporophyte ratios are most sensitive to fertilization rate at low egg-to-spore production ratios (general case) or low cloning rates (red algal case).

Consider the simplest case, where oogonia and sporangia are produced in equal abundance on their respective fronds with one egg per oogonia and four meiospores per sporangium. Assuming a 1:1 sex ratio, 100% fertilization of eggs (and one zygote per egg), the expected ratio of gametophytes to sporophytes is 2.8, the same value as in the matrix model of Scrosati and DeWreede (1999). (The ratio of 1.4 reported by Thornber and Gaines (2004) represents the case where carpospore and tetraspore production are equal.) Greater gametophyte-to-sporophyte ratios are associated with lower fertilization rates as expected. Thus, gametophytic dominance is expected at typical fertilization rates (i.e. <100%) when sporangial abundance is similar to, or exceeds, oogonial abundance with three exceptions. First, in the general model, sporophytic dominance can occur if the number of eggs produced per oogonium greatly exceeds the number of meiospores produced per sporangium (Fig. 1A). Second, in the red algal model, sporophytic dominance can arise if cloning produces many carpospores (i.e. high m) per zygote (Fig. 1B). For instance, tetrasporophyte abundance exceeds that of gametophytes at fertilization rates >17% when 2¹² carpospores are produced per zygote. Third, mechanisms of asexual propagation (not included in our models) of sporophytes can generate sporophytic dominance.

For red algae, published data are few and highly variable, but on average tetrasporangia are much more abundant than carpogonia on their respective fronds (Table 1) (M. Guiry, C. Maggs, and J. West, personal communication). Likewise, data for carpospore production are few and highly variable, but the values we chose are representative of the range reported for red algae (Table 1).

Conditions for persistence of founder populations. We also evaluated the red algal model equations with respect to boundary conditions for persistence of founder populations of either phase. The persistence

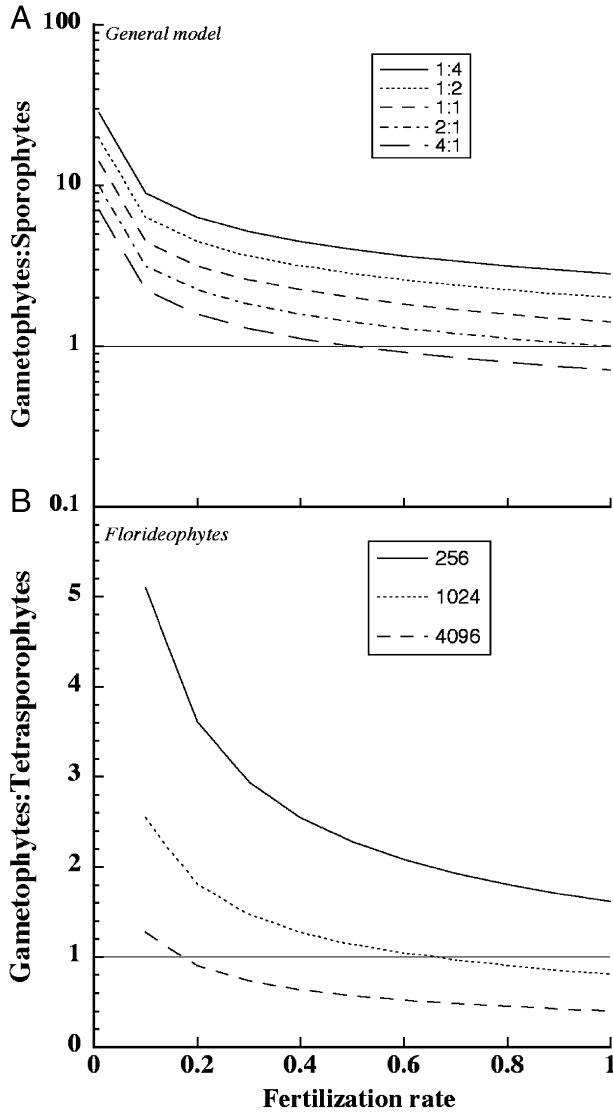


FIG. 1. The effect of fertilization rate on the ratio of gametophytes to sporophytes in the (A) general model at egg- to-spore ratios of 1:4 (solid line), 1:2 (narrow dashed line), 1:1 (medium dashed line), 2:1 (medium-narrow dashed line), and 4:1 (broad dashed line) and (B) red algal model at carpospore production rates of 256 (solid line), 1024 (narrow dash), or 4096 (broad dash) per zygote. We used the median value (2^{10}) of carpospore production per cystocarp from the distribution of reported values and up to two orders of magnitude less (2^8) and more (2^{12}) than the median. The ratio of tetrasporangia to carpogonia per thallus used in these simulations represented the geometric mean of the distribution of ratios of these cell types reported in the literature (Table 1).

of founder populations requires that both $dG \cdot dt^{-1}$ and $dS \cdot dt^{-1} \geq 0$.

Case i: sporophyte founder populations: Consider a founder population of sporophytes at time 0 that releases spores shortly after arrival. Sporophyte abundance in year 0 cannot increase further because no gametophytes are available to reproduce. Gametophyte abundance in the following year will increase

if the following condition holds:

$$\rho_T \cdot 4 > \frac{q_T}{\alpha_G} \quad (17)$$

In other words, meiospore production must exceed the ratio of sporophyte mortality to juvenile gametophyte survivorship. Intuitively, greater spore production is necessary either in cases of high sporophyte mortality or low survivorship of gametophytic recruits. Assuming the tetrasporophyte founders die after year 0 and survivorship of gametophytic recruits is approximately 10^{-3} , then at least 250–500 tetrasporangia are necessary to generate both a male and female gametophyte for the next generation. Thus, a single fecund tetrasporophyte can found a population of gametophytes. For the gametophyte population to contribute new sporophytes to subsequent generations (assuming $\alpha_G = \alpha_T$), the fertilization rate of carpogonia must satisfy the following (for $p_F < 1$):

$$F > \frac{q_T^2}{\rho_G \cdot \rho_T \cdot 4 \cdot P_F \cdot m \cdot \alpha^2} \quad (18)$$

A greater number of fertilizations are necessary either when tetrasporophyte mortality is high or when fecundity is low. Substitution of parameters with values conservative for a red alga ($q_T = 0.875$, $\rho_G = 50$, $\rho_T = 2.14 \times 10^3$, $p_F = 0.5$, $m = 1024$, and $\alpha = 10^{-3}$) suggest that persistence of tetrasporophytes requires that 3.50 per 1000 carpogonia be fertilized. Assuming fertilization rate is density independent, this rate would correspond to, on average, one of every six (or 17%) female gametophytes fertilized. Using the higher default values for reproductive characters from Table 1 corresponds to 4.5% of female gametophytes fertilized. Assuming default values and a spatially implicit model of density-dependent fertilization [$F = (G \cdot (0.167)^{-1} \cdot K)^2$, where G = number of gametophytes, K = carrying capacity, and 0.167 is a scalar generating a frond density of $1/\text{cm}^2$] requires approximately 213 female gametophytes needed for sporophyte persistence.

Case ii: gametophyte founder populations: In the case of a population founded by male and female gametophytes, fertilization is necessary to create sporophytes in the coming generation according to the following:

$$F > \frac{q_G}{P_F \cdot \rho_G \cdot \alpha_T \cdot m} \quad (19)$$

Greater fertilization rates are necessary for sporophyte persistence either when gametophyte mortality is high or fecundity is low. Using default values for a red alga suggests that the formation of 1.71 zygotes per 100 carpogonia (i.e. 1.71%), which assuming $\rho_G = 100$, corresponds to >1.71 fertilizations per female being necessary to establish tetrasporophytes. Assuming density-dependent fertilization, a fertilization rate of 1.71% corresponds to approximately

1307 female gametophytes/m² being necessary to establish a tetrasporophyte population.

Model simulations. Our model simulations assume an even sex ratio and populations having a single reproductive generation per year. Therefore, each cycle through the model represented one generation or 1 year. The model sampled the population weekly, and parameter values were evenly distributed over the course of a year.

Sensitivity to initial conditions. We tested whether the effect of fertilization rate on phase ratio was sensitive to the starting ratio at two densities: the carrying capacity (K) and $0.125 \cdot K$. We varied the starting ratio of gametophytes to sporophytes between 10^{-4} and 10^4 (using the following exponents to the base 10: -4, -3, -2, -1, -0.301, -0.125, 0.097, 0.176, 1, 2, 3, 4) with the total number of adults summing either to K or $0.125 \cdot K$. At each starting ratio, we varied the fertilization rate between 10% and 100% and the time series of the abundance of gametophytes and sporophytes was followed to equilibrium. In the case of the general model, a 1:1 ratio of egg to spore production was used. In the case of the red algal model, default parameter values were used (Table 1).

Results—general model: Despite different starting abundances, each phase converged on an abundance corresponding to a specific fertilization rate (Fig. 2). By the fifth generation, populations reached equilibrium and any effect of the initial phase ratio had disappeared. Moreover, in each simulation the equilibrium abundances of the phases for a particular fertilization rate corresponded to a gametophyte-to-sporophyte ratio that closely approximated that given by the analytical solution at equilibrium (Figs. 1A [the 1:1 case for 20%, 60%, and 100%] and 2). This was the case for populations summing to both K and $1/8K$ (latter data not shown).

Results—red algal model: Similarly, using the red algal model, initial differences in the modeled populations disappeared within the first few years. Abundances of gametophytes and sporophytes converged on ratios that corresponded to specific combinations of fertilization and cloning rates (Fig. 3). As for the general case, the outcomes of simulations corresponded closely to the analytical results of the model at equilibrium. At fertilization and cloning rates of 20% and 256 carpospores per zygote, respectively, the gametophyte-to-sporophyte ratio approximated the equilibrium solution ratio of 3.6, whereas at the higher cloning rate of 4096 carpospores per zygote, tetrasporophytes were 1.1 times the abundance of gametophytes (cf. Figs. 1B and 3).

Perturbation analysis. Simulations using default values for the red algal model (Table 1) were allowed to proceed to steady state and then perturbed to examine resilience of the modeled population at different fertilization rates. The perturbations consisted of 75% mortality in a pulse (over one fourth of a year). We applied perturbations in five different sce-

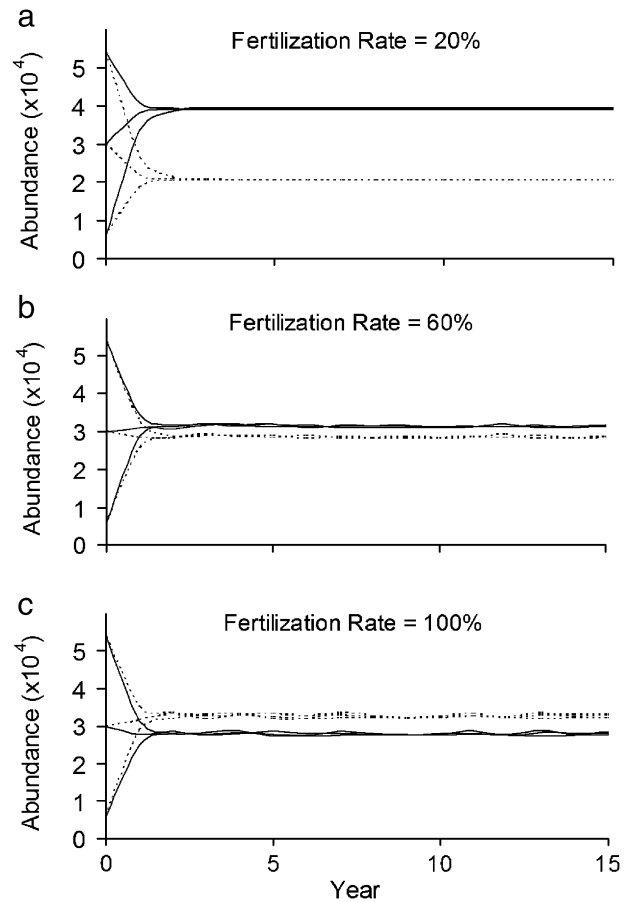


FIG. 2. Time series showing the abundance of gametophytes (solid lines) and sporophytes (dashed lines) in the general model using a 1:1 ratio of eggs to spores and different starting ratios. Abundances of each phase were compared at fertilization rates of (a) 20%, (b) 60%, and (c) 100% of oogonia. For clarity, only three (starting ratios 1:100, 1:1, 100:1, gametophytes to sporophytes) simulations representative of all 12 starting ratios examined are shown in each plot. The sum of the initial abundances of gametophytes and sporophytes equaled the carrying capacity.

narios: 1) perturbations to both gametophyte and tetrasporophyte populations over a range of fixed fertilization rates, a perturbation to either 2) gametophyte or 3) tetrasporophyte populations over a range of fixed fertilization rates, and a perturbation to either 4) gametophyte or 5) tetrasporophyte populations with a density-dependent fertilization rate.

Results: A pulse disturbance to both life phases had no effect on the ratio of gametophytes and tetrasporophytes in the population after 2 years (Fig. 4). A pulse disturbance to gametophytes caused a transient increase in the abundance of tetrasporophytes. Likewise, a pulse disturbance to tetrasporophytes transiently increased gametophyte abundance. Perturbations had the same effect in models with and without density-dependent fertilization rates (data not shown).

Effect of differential mortality rates. Previous research on phase dominance of isomorphic algae

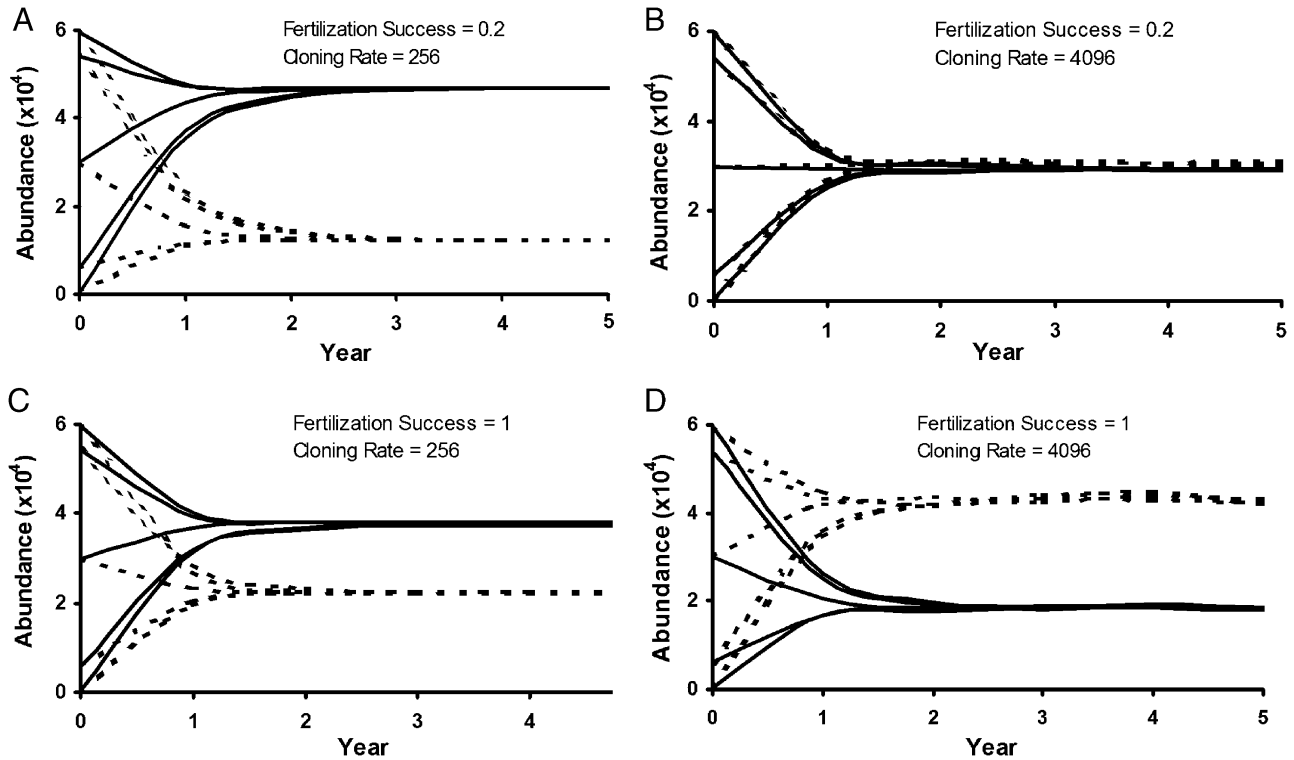


FIG. 3. Time series showing the abundance of gametophytes (solid lines) and sporophytes (dashed lines) in the red algal model using different starting ratios. Abundances of each phase were compared at fertilization rates of either 20% (A and B) or 100% (C and D) of carpogonia and cloning rates of either 256 (A and C) or 4096 (B and D) carpospores per zygote. For clarity, only three (starting ratios 1:100, 1:1, 100:1, gametophytes to tetrasporophytes) simulations representative of all 12 starting ratios examined are shown in each plot. The sum of the initial abundances of gametophytes and tetrasporophytes equaled the carrying capacity.

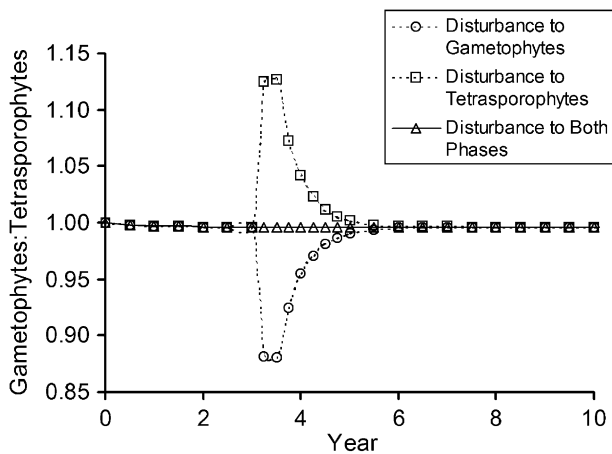


FIG. 4. The effect of a pulse (equivalent to a duration of one season of a year) disturbance causing 75% mortality on the ratio of gametophytes to tetrasporophytes over time. Mortality was inflicted either on gametophytes (circles), tetrasporophytes (squares), or both phases simultaneously (triangles).

suggested that adaptive differences between isomorphic adults generated the observed phase ratios in natural populations. The interplay between phase-specific ecological differences and fertilization rates

may generate a 1:1 ratio of isomorphs at some fertilization rates, causing real differences between phases to go undetected. To test whether fertilization rate can compensate for adaptive differences between phases, we assigned different density-dependent mortality rates to gametophytes and tetrasporophytes and searched for rates of fertilization that yielded a 1:1 ratio of phases. Mortality rates were varied from $q = 0.8((G + T) \cdot K^{-1}) + 0.1$ to $q = 0.4((G + T) \cdot K^{-1}) + 0.1$.

Results: Dominance by either phase or a 1:1 ratio was possible in any of the scenarios tested depending on the fertilization rate (Fig. 5). Overall, each phase was more abundant when the other phase had enhanced mortality, but fertilization rate affected phase ratios as described above. When gametophyte mortality rates were twice that of tetrasporophytes, a 1:1 phase ratio was observed with 20% fertilization. Likewise, when mortality of tetrasporophytes was twice that of gametophytes, a 1:1 phase ratio was observed at a fertilization rate of 68%. Despite phase-specific mortality rates, phase dominance was dependent on fertilization rate. With equal mortality rates, generations were equally abundant with a fertilization rate of 37%, with gametophytes dominating at lower fertilization rates (<37%) and tetrasporophytes dominating at greater rates (>37%).

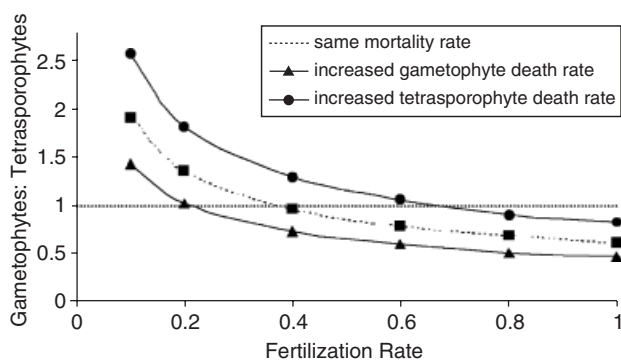


FIG. 5. The effect of fertilization rate on the ratio of gametophytes to tetrasporophytes when mortality rates of life history phases are equal (squares), biased against gametophytes (triangles), or biased against tetrasporophytes (circles). Dashed line indicates a 1:1 ratio of gametophytes and sporophytes.

DISCUSSION

Predominance of one phase of an alternating life cycle has often been taken as evidence of ecological or physiological disparity between isomorphic generations (Mathieson and Burns 1975, Bhattacharya 1985, Carrington et al. 2001). The results of our modeling experiments suggest that fertilization rate and reproductive output can create a disparity in abundance of isomorphic generations and, either separately or in concert with, phase-specific adaptations can potentially generate any phase ratio. Our model and its results both complement and build on models by Scrosati and DeWreede (1999) and Thornber and Gaines (2004) that demonstrated the inherent production of four tetraspores for every carpospore, or equal spore production coupled with dioecy, generated gametophytic dominance. Specifically, our model extends the topic to isomorphic life histories in general and accommodates variation in fertilization rate as well as egg-to-spore (or carpospore-to-tetraspore in red algae) ratios and shows how the combination of reproductive characteristics and mortality rates can lead to dominance by either or neither phase.

In the isomorphic red algae that exhibit phase dominance, the abundant phase in nature is generally consistent throughout a taxonomic order (Table 2). Reproductive traits are used, in part, to define orders of the class Florideophyceae, and the coincidence suggests that reproductive variables, like fertilization rate, densities of gametangia and sporangia, and carpospore production, may be a primary cause of phase dominance in nature. We found no reports of phase dominance or lack thereof in isomorphic brown or green algae and can only assume that the possibility has not been studied. It seems reproduction, especially fertilization rate, is a good place to look for hypothetical explanations for phase dominance in any taxon with a complex life history.

Variability in fertilization rates. Fertilization rates must vary among species and among sites or times within a species for the fertilization rate hypothesis to

adequately explain cases of phase dominance in nature. Evidence exists for variation in average rates of fertilization among species, and spatiotemporal variation in fertilization rates due to environmental variation is likely. Several brown and green algal taxa exhibit synchronizing mechanisms, potentially causing mass spawnings (Clifton 1997, Pearson and Brawley 1998, Clifton and Clifton 1999) or pheromones (Müller et al. 1971) that enhance fertilization success (Serrão et al. 1996). To date, only pheromones in the Ectocarpales have been found, but no synchronizing mechanisms have been reported among species with isomorphic life histories. The range of published fertilization rates among red algae is 7%–90%, and average values reported are approximately 50% (Sheath and Hambrook 1990, Hambrook and Sheath 1991, Kain and Bates 1993, Kaczmarek and Dowe 1997, Engel et al. 2001). Lower natural fertilization rates of red algae are likely due to the lack of chemotaxis or motile spermata (Searles 1980), but overall, fertilization rates of red algae vary over a similarly wide range as those reported for taxa with external fertilization (Santelices 2002). Within species, data collected during natural spawning events show high variance among individuals in the proportion of females fertilized (Leviton and Peterson 1995, Engel et al. 1999). Intertidal algae found on wave-swept shores may experience fluctuations in fertilization rate dependent on spatial and temporal variability in water motion. Lower fertilization rates are predicted in areas of swifter or turbulent water flow (Denny 1988, Denny and Shibata 1989, McNair et al. 1997), and there is a trend of gametophytic dominance in areas subject to wave action and disturbance (Mathieson and Burns 1975, Craigie and Pringle 1978, May 1986, Lazo et al. 1989, Nelson 1989, Lindgren and Aberg 1996, Carrington et al. 2001). The results of our model are consistent with these findings: Gametophytes dominate at lower fertilization rates, which may explain patterns observed on many wave-swept shores. Exceptions to the pattern of exposed shores dominated by gametophytes (Dyck and DeWreede 1995, Shaughnessy et al. 1996, Mudge and Scrosati 2003) may represent candidates for studies of phase-specific adaptations favoring tetrasporophytes.

Comparison between models assuming density-independent versus density-dependent fertilization rates confirms that more individuals are required to found populations if fertilization is density dependent. Similarly, it is more difficult for unfertilized gametophytes to found populations than for carpo- or tetrasporophytes. If fertilization rate in natural populations is density dependent, as has been determined for some brown algal species (Serrão, E. A. personal communication), then the likelihood of persistence of a founder population depends on the phase that arrives first. Assuming that our model of density-dependent fertilization success is more realistic than one based on density-independent fertilization, the sensitivity to

TABLE 2. Phase dominance in red algal taxa.

Order	Species/author	Dominant phase	References
Gigartinales	<i>Chondrus crispus</i> Stackhouse	Gametophyte/ similar proportions	Mathieson and Burns 1975, Craigie and Pringle 1978, Wright 1981, Bhattacharya 1985, Chopin 1986, McLachlan et al. 1988, Lazo et al. 1989, Dudgeon and Johnson 1992, Lindgren and Aberg 1996, Carrington et al. 2001
	<i>Gigartina skottsbergii</i> Setchell & Gardner	Gametophyte	Piriz 1996, Zamorano and Westermeier 1996, Avila et al. 1999
	<i>Hypnea</i> spp.	Tetrasporophyte	Rao 1970, Mshigeni 1976, Schenkman 1989, Reis and Yoneshigue-Valentin 2000
	<i>Mazzaella affinis</i> (Harvey) Fredericq	Gametophyte	Abbott 1980
	<i>M. cornucopiae</i> (synonym of <i>M. laminarioides</i>)	Gametophyte	Scrosati 1998
	<i>M. flaccida</i> (Setchell & Gardner) Fredericq	Gametophyte	Thornber and Gaines 2004
	<i>M. laminarioides</i> (Bory de Saint-Vincent) Fredericq	Gametophyte	Hannach and Santelices 1985, Luxoro and Santelices 1989, Thornber and Gaines 2004
	<i>M. leptorynchos</i> (J. Agardh) Leister	Gametophyte	Abbott 1980
	<i>M. splendens</i> (Setchell & Gardner) Fredericq	Gametophyte	Dyck et al. 1985, Hannach & Santelices 1985, DeWreede and Green 1990, Dyck and DeWreede 1995, Thornber and Gaines 2004
	<i>Sarcothalia crispate</i> (Bory de Saint-Vincent) Leister	Gametophyte	Avila et al. 1996
Gracilariales	<i>Gracilaria arcuata</i> Zanardini	Tetrasporophyte	Kaliaperumal et al. 1986
	<i>G. blodgetti</i> Harvey	Tetrasporophyte	Gerung et al. 1997
	<i>G. bursapastoris</i> (Gmelin) Silva	Tetrasporophyte	Hoyle 1978
	<i>G. coronopifolia</i> J. Agardh	Tetrasporophyte	Hoyle 1978
	<i>G. corticata</i> (J. Agardh) J. Agardh	Tetrasporophyte	Kaliaperumal et al. 1986
	<i>G. edulis</i> (Gmelin) Silva	Tetrasporophyte	Umamaheswara Rao 1973
	<i>G. foliifera</i> (Forsskål) Borgesen	Tetrasporophyte	Umamaheswara Rao 1973
	<i>G. gracilis</i> (formerly <i>G. verrucosa</i>) (Stackhouse)	Tetrasporophyte/similar proportions	Abbott 1980, Destombe et al. 1989, 1990, 1992, Engel et al. 1999, 2001
	Steentoft, Irvine & Farnham		
	<i>G. sjoestedtii</i> Kylin	Tetrasporophyte	Abbott 1980
<i>G. sordida</i> Nelson	Tetrasporophyte	Nelson 1989	
Ceramiales	<i>Ceramium</i> spp.	Tetrasporophyte	Edwards 1973
	<i>Acanthophora nayadiformis</i> (Delile) Papenfuss	Tetrasporophyte	Cecere et al. 2000
	<i>Delesseria sanguinea</i> (Hudson) Lamouroux	Tetrasporophyte	Kain and Bates 1993
	<i>Membranoptera alata</i> (Hudson) Stackhouse	Tetrasporophyte	Norall et al. 1981
	<i>Odonthalia dentate</i> (Linnaeus) Lyngbye	Gametophyte	Kain and Bates 1993
	<i>Phycodrys rubens</i> (Linnaeus) Batters	Tetrasporophyte	Norall et al. 1981
	<i>Polysiphonia lanosa</i> (Linnaeus) Tandy	Tetrasporophyte	Norall et al. 1981
	<i>Polysiphonia lanosa</i>	Gametophyte	Kaczmarska and Dowe 1997
	<i>Pilota serrata</i> Kützing	Tetrasporophyte	Norall et al. 1981
	<i>Gelidium microdon</i> Kützing	Tetrasporophyte	Neto 2000
Gelidiales	<i>Gelidium robustum</i> (Gardner) Hollenberg & Abbott	Tetrasporophyte	Barilotti 1971
	<i>Pterocladia capillacea</i> (Gmelin) Santelices & Hommersand	Tetrasporophyte/subtidal gametophyte	Neto 2000
	<i>Audouinella violacea</i> = <i>A. hermannii</i> (Roth) Duby	Similar proportions	Korch and Sheath 1989

initial conditions may help to explain phase dominance in some algae. Likewise, the composition of a founder population also may explain phase dominance. This is supported by data for populations of *Chondrus crispus*. In the St. Lawrence estuary, *C. crispus* populations experience frequent catastrophic disturbance and are the only intertidal populations of this species to exhibit a 1:1 phase ratio rather than a predominance of game-

tophytes (J. McLachlan, personal communication). Sporophytes (carpo- or tetra-), rather than gametophytes, are likely to be the ecologically significant phase for long distance dispersal and founding of populations because they establish in the absence of mates.

Impact of reproductive output. The modulating effect that egg-to-spore production has on the relationship between fertilization rate and phase ratio has

implications for the structure and dynamics of populations. Shifts in production ratios in the direction favoring meiospores increased the sensitivity of the phase ratio to low fertilization rates. Given the tremendous influence of environmental factors, principally water motion, on fertilization rates of marine and freshwater algae, we suggest that production ratios favoring gametes may reduce temporal variability in the ratio of life history phases and in population growth. Because theory predicts similar energetic costs for the production of gametes and spores (Bell 1997), the allocation of reproductive investments in favor of gamete production, in addition to mechanisms that increase fertilization rates (Müller et al. 1971 Serrão et al. 1996, Clifton 1997), would appear to be adaptive.

Similarly, the carposporophyte phase of a floridophycean life history may represent an adaptation to minimize the effects of both low and variable fertilization rates (Searles 1980). The cloning of the zygote amplifies the production ratio of carpospores relative to tetraspores, and our model suggests that increasing this ratio dampens the effect that fertilization rate and, hence, stochastic environmental factors have on population structure and growth. Searles (1980) argued that the carposporophyte phase compensates for characters that contribute to low fertilization success, although the higher than expected fertilization rates among a few red algae recently called this hypothesis into question (Santelices 2002). This question cannot be resolved without directly comparing the demographies and fertilization ecologies of rhodophytes with and without carposporophyte stages. Nevertheless, our model indicates that increasing carpospore output dampens the effect that variation in fertilization rate has on population structure and dynamics. We suggest that the evolution of the carposporophyte was selectively favored because increased carpospore output at all fertilization rates reduces the influence of fertilization rate on population structure and growth.

A comparison of the general and red algal models shows that a 1:1 phase ratio or sporophyte dominance among ecologically equivalent isomorphs is more likely to occur in red algae at moderate fertilization rates probably typical of most macroalgae. For brown and green algae, sporophyte dominance among isomorphic species is expected to occur only when egg production vastly exceeds that of spores and high fertilization rates are achieved. The differences between these taxa may be relevant to the greater incidence of isomorphy among florideophytes.

Distinguishing between causes of phase dominance. We concur with Scrosati and DeWreede (1999) that the use of distribution and abundance patterns as a basis for inferring adaptive differences that underlie phase dominance is problematic. For instance, Thornber and Gaines (2004) reported gametophytic dominance in populations of *Mazzaella flaccida* based on comparing the observed overall average of 72% gametophytes with an expected value (assuming

equal carpospore and tetraspore production) of 59%. However, models that differ from that of Thornber and Gaines (2004) only by assuming equal production of carpogonia and tetrasporangia in the simplest case (ours and that of Scrosati and DeWreede 1999) have an expected null value of 74% gametophytes, remarkably close to the observed value for *M. flaccida*. Clearly, the choice of null model for reproductive effort can influence the conclusions.

In any case, phase dominance may result from differences in spore production between generations (Scrosati and DeWreede 1999, Thornber and Gaines 2004) or fertilization rate (this study) and not from phase-specific adaptations that confer different mortality rates, as often hypothesized but infrequently demonstrated. Conversely, when ratios approximate 1:1, the assumption that there are no phase-specific differences may be incorrect because the interaction of environmental factors with life history traits could counterbalance and effectively mask adaptive differences.

Adaptive differences between isomorphic generations of a life history can be identified only by combining experimental tests with data of phase ratios that differ from the ratios predicted based on life history traits. Rigorous and sophisticated experiments that involve reproductive stages *in situ* (Serrão et al. 1996, Engel et al. 1999, Dudgeon et al. 2001) can be coupled with classical approaches and models to unravel causes underlying patterns of phase dominance.

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