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POPULATION DEMOGRAPHICS IN SPECIES WITH BIPHASIC LIFE CYCLES

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Abstract. We develop and test models for the population dynamics of species that undergo regular alternations of generations between independent, free-living, haploid and diploid phases. The models are patterned after the dioecious, haploid–diploid lifecycle of many marine algae. If the two phases have equal demographic rates, all models (with or without density dependence) predict a stable distribution with a ratio of $\sqrt{2}$:1 (~60% haploids and 40% diploids). We find that observable deviations from this distribution can occur when the demographic rates (mortality, fecundity) between phases vary widely. Field surveys of three macroalgal species with independent, free-living haploids and diploids, *Mazzaella flaccida*, *M. laminarioides*, and *M. splendens*, reveal a consistent pattern of haploid dominance that significantly exceeds this null model expectation (72%, 76%, and 66%, respectively). These species also exhibit significant variation in haploid frequency among sites. We estimated the per capita fecundity and mortality rates for each phase of both *M. flaccida* and *M. laminarioides* and used this information to address two basic questions: (1) Which parameter better explains the overall high relative haploid abundance for each species? and (2) Which parameter better explains the variation in relative haploid abundance among sites?

Differences in haploid and diploid mortality rates did not explain the high relative abundance of haploids for either *M. flaccida* or *M. laminarioides*. However, differences in fecundity rates between phases were consistent with the high relative abundance of haploids for *M. flaccida*; diploids usually had significantly higher per capita fecundity rates than haploids. For *M. laminarioides*, there were no significant differences in fecundity rates between phases.

For *M. flaccida*, among-site variation in relative abundance of haploids can be explained by differences in mortality rates. The relative abundance of haploids was positively correlated with the ratio of diploid:haploid mortality rates; the sites with the highest ratio of diploid:haploid mortality had the highest percentage of haploids. Differences in mortality rates for *M. laminarioides*, and fecundity rates for *M. flaccida* and *M. laminarioides*, could not explain the observed variation in haploid abundance among sites.

Key words: *algae; diploid; fecundity; haploid; isomorphic life cycle;* Mazzaella flaccida; Mazzaella laminarioides; Mazzaella splendens; *mortality; population dynamics.*

INTRODUCTION

Although complex life cycles are found in a wide variety of taxa, the population dynamics of species with complex life cycles are, in general, poorly understood. Complex life cycles can include developmental changes where individuals undergo substantial morphological changes as they age (e.g., larval vs. adult forms in many invertebrate and vertebrate groups), or they can involve obligate alternations between distinct life stages (e.g., the free-living haploids and diploids of many plant and algal taxa). All phases of these life cycles can influence overall population dynamics, but the magnitude of these effects can vary widely (Ebenman 1992, Wing et al. 1995, Schmitt and Holbrook 1996). Understanding the population dynamics of these species is necessary before larger-scale ecological and evolutionary questions about complex life cycles can be addressed.

There are several major phylogenetic groups (e.g., algae, fungi, ferns) whose life cycles consist of alternating generations of separate, free-living individuals with different ploidy levels and modes of reproduction. One of the more intriguing examples is the haploid–diploid life cycle, where there is an alternation between free-living haploid and diploid individuals.

In the typical diploid dominated life cycle of most plant and animal taxa, diploid adults produce gametes by meiosis, which subsequently fuse to form a new diploid individual. This haploid stage undergoes no (or limited) somatic development and never becomes an independent, functional organism. In a haploid–diploid life cycle, however, mature diploid individuals produce haploid spores through meiotic division. These spores develop (without fusion) into haploid adults. Depend-

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ing upon the species, these haploid adults are either monoecious or dioecious. When mature, haploid adults produce female and/or male gametes, which subsequently fuse to produce new diploid individuals. Thus, each phase is dependent upon the other for species persistence, and the population dynamics of each phase are closely linked to those of the other phase.

The morphological similarity of the two phases varies dramatically in haploid–diploid species. In some species, the two phases are morphologically indistinguishable (isomorphic), and in others the two phases are quite dissimilar (heteromorphic). Indeed, until techniques were developed that allowed the culturing of entire algal life cycles, some haploid and diploid forms of the same algal species were classified as different species, often in different families (West 1972). Variants of these life cycles are pervasive in all divisions of macroalgae; in this study, we focus upon algal species with isomorphic life cycles.

Starting with the simplest case of an obligate alternation of different life stages, one obvious question arises: what will be the relative abundance of the two adult forms? Isomorphic species are an intriguing group, since the two phases are frequently found living in close proximity in the same habitat. One might assume that haploid–diploid species with isomorphic, ecologically equivalent, adult life stages should have approximately equal numbers of haploids and diploids. Following this logic, it has been argued that simple population surveys could be used to examine the relative advantage of haploid vs. diploid states, and deviations from a 1:1 haploid–diploid ratio have been used to infer the advantages of haploidy vs. diploidy (Hansen 1977, May 1986, Dyck and DeWreede 1995). In addition, the relative advantages of haploids vs. diploids in terms of such issues as energy efficiency, rates of evolutionary change, expression of mutations, and DNA repair have long been debated (Crow and Kimura 1965, Bernstein et al. 1981, Kondrashov and Crow 1991, Perrot 1994). Isomorphic species provide a unique opportunity to test among these competing hypotheses, but only after the correct haploid–diploid equilibrium ratio has been determined.

Recently, the 1:1 assumption has begun to be challenged (Destombe et al. 1989, Scrosati and DeWreede 1999), because most isomorphic algal species are dioecious (and not monoecious). All diploids produce both male and female spores via meiosis, but only their female haploid offspring actually produce young. Diploids thus face an inherent demographic cost of producing males, and the costs of spore production vs. gamete production should affect the relative abundance of the two life stages (Bell 1994, Mable and Otto 1998).

What will happen to the relative abundance of haploids and diploids if the two phases are not ecologically equivalent? Per capita mortality and fecundity rates are assumed to be equal for isomorphic species, but this is not always true in field populations (Allender 1977, May 1986, Luxoro and Santelices 1989, Engel et al. 2001). The effects of differing demographic rates on predicted haploid–diploid ratios also need to be considered for these models.

A variety of haploid–diploid ratios have been reported for field populations of isomorphic algal species. Some studies report a dominance of diploids (Hansen and Doyle 1976, Norall et al. 1981, DeWreede and Green 1990), others find a dominance of haploids (Dyck et al. 1985, Hannach and Santelices 1985, May 1986), and still others find similar numbers of diploids and haploids (Hay and Norris 1984, Destombe et al. 1989). Conducting these surveys is challenging, because the different life stages are often indistinguishable morphologically when not reproductive. By using simplifications such as only counting adults that are reproductive (which is fraught with potential biases—only a fraction of the population is reproductive at any given point in time and different life history stages may reproduce at different times of the year), many of these existing field surveys may provide a misleading picture of the population structure of haploid–diploid species in the field. There are also few studies that replicate surveys of haploids and diploids spatially and/or temporally (but see Dyck et al. 1985).

The wide variability in haploid–diploid ratios of field populations where all individuals are included indicates that there may be ecologically important differences between mortality and/or fecundity rates of haploids and diploids. However, few studies combine field surveys with demographic studies to determine the relative effects of mortality and fecundity on population structure (but see Engel et al. 2001).

To address the above theoretical and empirical issues, we first develop and then test a new, more general set of population models that explore the dynamics of species with haploid–diploid life cycles. We use these models to provide a general conceptual framework that predicts expected equilibrium proportions of haploid and diploid individuals. Our starting focus is on the null life cycle model in which the phases have equal demographic rates; we then explored the consequences of varying the relative per capita fecundity and/or mortality rates on haploid–diploid ratios. We evaluated these predictions against spatially and temporally replicated field surveys for haploid–diploid ratios of three species of isomorphic marine algae.

In the second part of our study, we measured mortality and fecundity at several sites for *Mazzaella flaccida* and *Mazzaella laminarioides*. These sites spanned the natural range of variability in haploid–diploid ratios. We used these studies to address two issues about the regulation of haploid–diploid ratios in each species:

First, what is (are) the mechanism(s) responsible for the significant overabundance of haploids? Do haploids have lower mortality rates or lower fecundity rates than diploids?

Second, what is (are) the mechanism(s) responsible for the significant variation among sites in the degree of haploid overabundance? Does the advantage/disadvantage of haploids relative to diploids change predictably from site to site in a manner consistent with variation in the degree of haploid overabundance?

Models of Haploid–Diploid Populations

Exponential growth

The expected abundances of haploids and diploids have been modeled for populations with nonoverlapping generations and/or those with exponential growth (Destombe et al. 1989, Richerd et al. 1993, Scrosati and DeWreede 1999). The findings from the Richerd et al. 1993 model are summarized in Appendix A. Further progress requires a more general framework that predicts patterns of abundance across a broader range of ecological conditions. We begin with a simple, discrete, time model of an exponentially growing population with alternating haploid and diploid individuals. This and subsequent models developed here are a first step towards understanding the dynamics of species with haploid–diploid life cycles. In all of our models we make four key assumptions: (1) all female gametes are assumed to be fertilized—i.e., male gametes are never limiting (Engel et al. 1999); (2) spores produced by diploids are assumed to have a 50:50 sex ratio, as is true for many species of red and brown algae (van der Meer and Todd 1977, van den Hoek et al. 1995); (3) demographic rates do not vary through time; and (4) there is an obligate alternation of independent, free-living, haploid and diploid phases within the life cycle. With this last assumption, we ignore two complications of this basic life cycle that are found in some algal taxa: (a) asexual looping of either phase, which is rare in the family of species (Gigartinaceae) used for this study (Kim 1976); and (b) a third life cycle stage (carposporophyte). Most species of red algae have a more complicated haploid–diploid life cycle with a third small diploid phase that lives as a parasite on the female haploid blade. This third phase produces multiple diploid spores from a single fertilized female gamete and can serve to enhance the fecundity of female haploids (Searles 1980). We do not include this life stage explicitly in our models, but we return to the issue of altered fecundities to examine their likely population consequences (see *Discussion* for implications of the model assumptions).

Initially, we assume that haploids and diploids have equal demographic rates, which yields the following three-stage, discrete time, population model:

$$F_{t+1} = F_t + \frac{g}{2}U_t - dF_t \tag{1}$$

$$M_{t+1} = M_t + \frac{g}{2}U_t - dM_t \tag{2}$$

$$U_{t+1} = U_t + gF_t - dU_t \tag{3}$$

where F, M, and U are the number of female haploids, male haploids, and diploids, respectively at time t, g is the per capita fecundity rate, and d is the per capita mortality rate.

Since there is no density dependence in this model, the population either grows (if $g > d\sqrt{2}$) or declines (if $g < d\sqrt{2}$) exponentially. A steady-state, non-zero, population size is only achieved with the conditions of $g = d\sqrt{2}$.

However, as with the exponential growth of age-structured populations, the ratio of the abundance of different stages eventually reaches a stable equilibrium (Caswell 1982). This convergence on a constant haploid–diploid ratio can be found by expressing Eqs. 1, 2, and 3 in matrix form

$$N_{t+1} = \mathbf{A}\mathbf{N_t} \tag{4}$$

where

$$\mathbf{A} = \begin{pmatrix} s & 0 & \frac{g}{2} \\ 0 & s & \frac{g}{2} \\ g & 0 & s \end{pmatrix} \tag{5}$$

$$s = 1 - d \tag{6}$$

and

$$\mathbf{N_t} = \begin{pmatrix} F_t \\ M_t \\ U_t \end{pmatrix}. \tag{7}$$

The population will grow exponentially at a rate of $1/2(\sqrt{2}g + 2s)$, which is the dominant eigenvalue of this system (Caswell 1982). The stable stage structure of this model is given by the dominant eigenvector:

$$\begin{pmatrix} 1 \\ 1 \\ \sqrt{2} \end{pmatrix}.$$

This vector describes the relative frequencies of female haploids, male haploids, and diploids, respectively, that the population will eventually reach, and is independent of initial conditions.

Logistic growth

We now ask whether the predicted dominance of haploids in exponential models holds in population models with density dependent regulation of fecundity and mortality rates. This is a more realistic scenario, since most populations will reach some maximum size due to environmental constraints. We start with a logistic growth model by letting the fecundity and mortality rates be linear functions of the total population size. For example, g, the constant per capita reproductive output from Eq. 1 is replaced by $[g - k_g(F_t + M_t + U_t)]$, a declining function of population size. As was the case in the exponential model, the per capita demographic rates are first assumed to be identical for

haploids and diploids. Because haploids and diploids are assumed to occupy the same ecological niche, all individuals contribute equally to the density dependence. Since the number of males and females is equal at each timestep, only the equations for female and diploid population size will be written below.

With density dependence in both fecundity and mortality, the model becomes:

$$F_{t+1} = F_t + \frac{U_t}{2}[g - k_g(F_t + M_t + U_t)] - F_t[d + k_d(F_t + M_t + U_t)] = M_{t+1} \quad (8)$$

$$U_{t+1} = U_t + F_t[g - k_g(F_t + M_t + U_t)] - U_t[d + k_d(F_t + M_t + U_t)] \quad (9)$$

where k_g and k_d are the strength of density dependence for per capita fecundity and mortality, respectively.

Solving for the total population size N (where $N = F + M + U$) at equilibrium yields

$$\hat{N} = \frac{g - \sqrt{2}d}{\sqrt{2}k_d + k_g}. \quad (10)$$

From the above equation, the number of females at equilibrium is

$$\hat{F} = \frac{g - \sqrt{2}d}{(2 + \sqrt{2})(\sqrt{2}k_d + k_g)}.$$

Since there are equal numbers of males and females, the fraction of haploids is therefore

$$\frac{2\hat{F}}{\hat{N}} = \frac{2}{2 + \sqrt{2}}.$$

This fraction of haploids is equivalent to the ratio of $\sqrt{2}$ haploids:1 diploid found in the above models without density dependence. This equilibrium was found to be stable for a range of ecologically relevant parameter values, as is true of similar discrete models of populations with more simple life cycles. As in the discrete-time, logistic, population model, however, the equilibrium population size becomes unstable as per capita rates of fecundity increase and/or mortality decrease substantially.

Logistic growth, differing demographic rates

The previous models are built upon the assumption of equal demographic rates for the two phases. How do the conclusions change when we relax this assumption? Adding different demographic rates to the logistic population model (Eqs. 8 and 9) yields the following system of equations:

$$F_{t+1} = F_t + \frac{U_t}{2}[g_U - k_g(F_t + M_t + U_t)] - F_t[d_F + k_d(F_t + M_t + U_t)] = M_{t+1} \quad (11)$$

$$U_{t+1} = U_t + F_t[g_F - k_g(F_t + M_t + U_t)] - U_t[d_U + k_d(F_t + M_t + U_t)]. \quad (12)$$

It should be noted that the density-dependent terms (k) might also vary between the phases. The steady-state solution to this model can be solved analytically; however, it is exceedingly complex and offers little insight. Thus, we turn to numerical simulations for clarity.

We ran the population simulations with a range of demographic parameters ($0.1 < g < 2.0$, $0.2 < d < 1.0$) that yielded stable equilibria in the simpler logistic model discussed above (Eqs. 8 and 9). We continued the simulations until the haploid–diploid ratio converged to four decimal places; if a simulation did not converge to an equilibrium, we did not include its results. We report the converged value as the equilibrium haploid–diploid ratio. To display the results graphically (Fig. 1), we express the difference in mortality rates between haploids and diploids as the ratio d_U/d_F; differing fecundity rates are expressed as g_U/g_F. As expected, the haploid–diploid ratio matches the null model prediction when demographic rates are equal. When haploids have a lower mortality ($d_U/d_F > 1$) or lower fecundity ($g_U/g_F > 1$) than diploids, the haploid frequency rises.

In addition to highlighting the direction of population change arising from differences in haploid and diploid performance, Fig. 1 also shows how different the life stages must be in order to generate a given deviation from the null expectation. Surprisingly, differences in mortality or fecundity have to be substantial to generate even a 10% shift in haploid frequency. Since haploid and diploid stages must alternate, advantages of one stage over the other are dampened compared to the situation where stages can reproduce themselves. The expected haploid frequency is especially insensitive to differences in mortality rates. Across a range of demographic rates, haploid and diploid mortality rates must differ by a factor of four to generate a noticeable shift in haploid frequency. With equivalent fecundities ($g_U/g_F = 1$) and a lower mortality of diploids ($d_U/d_F = 0.25$), the percentage of haploids at equilibrium ranges from 0.45 to 0.57. Similarly, with equivalent fecundities ($g_U/g_F = 1$) and a lower mortality of haploids ($d_U/d_F = 4.0$), the percentage of haploids ranges from 0.62 to 0.71 (Fig. 1). (The range of values is due to the numerical values of fecundity used in the simulations.) With mortality differences greater than these, the populations frequently become unstable (Appendix B).

The equilibrium frequencies are more sensitive to differences in fecundity rates. The change in equilibrium haploid frequency generated by a two-fold change in fecundity is similar to that produced by a four-fold change in mortality (Fig. 1). Thus, small to moderate ecological differences between the different, obligately cycling, life stages of a haploid diploid species should have relatively small influences on the equilibrium structure of the population. Similarly, field populations with consistently large deviations from the null expec-

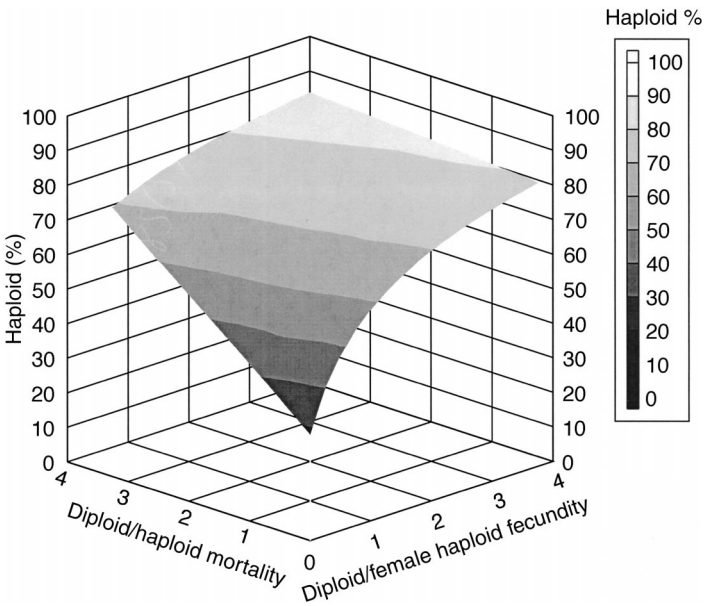

FIG. 1. The relationship between varying ratios of haploid and diploid per capita mortality and fecundity rates and the percentage of haploids at equilibrium. The curve represents a variety of per capita fecundity and mortality rates. When the per capita rates are equal (i.e., the ratios are both 1), the population has 59% haploids, as expected from our null model. The proportion of haploids at equilibrium rises if diploids have higher fecundity and/or mortality rates than haploids.

tation of 59% haploids imply large differences in the demographic performance of haploids and diploids.

FIELD STUDIES

Methods

Study species.—To examine how closely field data match with our model predictions, we studied three species of common intertidal red algae, *Mazzaella flaccida* (Setchell et Gardener) Fredericq, *M. laminarioides* (Bory) Fredericq, and *M. splendens* (Bory) Fredericq. *M. flaccida* and *M. splendens* are found along the Pacific coast of North America, and *M. laminarioides* is found along Pacific coast of Chile. These are among the few species with an isomorphic life cycle where nonreproductive haploids and diploids can be distinguished with a simple chemical test, which separates haploids and diploids based upon differences in their carrageenan content (Santelices and Norambuena 1987, Garbary and DeWreede 1988).

Field surveys.—We surveyed populations of *M. flaccida* at seven to 10 rocky intertidal sites ranging from northern Oregon to central California during August and September yearly from 1997 to 2000 and *M. splendens* at six to 10 of the same or nearby sites yearly from 1997 to 1999 (Table 1). *M. laminarioides* was sampled at six to 10 sites in central Chile during January of 1999 and 2000 (Table 1). Sites were sampled yearly to determine the amount of interannual variability in haploid abundance. For *M. flaccida*, we sampled a subset of the sites bimonthly to examine more frequent changes. There was little monthly variation in the population structure (Thornber and Gaines 2003). All sites included suitable rocky reef habitat and were selected to provide a broad geographical distribution.

Approximately 200 individuals of each species were sampled at a site, with individuals sampled every 10 cm along two 10-m haphazardly laid transects. We recorded the number of reproductive individuals of each phase, and we took small tissue samples of nonreproductive individuals for subsequent chemical testing. Variation between the two transects was not large; the average standard deviation for the percentage of haploids found was 5.1. If the population had an actual distribution of 59% haploids, a sample size of 200 should be able to estimate the haploid frequency with a standard error of 3.5%.

Demographic studies.—To test our model predictions, we measured mortality and fecundity rates for each phase for *M. flaccida* and *M. laminarioides*. For both species, sites were selected from those sampled previously to represent a range of naturally occurring haploid proportions: 55–83% for *M. flaccida* and 74–95% for *M. laminarioides*. We selected seven sites for *M. flaccida* and six for *M. laminarioides* (Table 1). We always sampled in the middle (along the tidal height gradient) of each population to get a representative measure of mortality and fecundity for each site.

Mortality rates: M. flaccida *and* M. laminarioides.—For each species, individuals were initially haphazardly selected and were relocated during each subsequent survey by triangulating the distances from sets of three permanent stainless steel bolts anchored into the rock at each site. Individuals that disappeared (no blades or crustal holdfast evident) between surveys were recorded as dead.

Approximately 150 *M. flaccida* individuals were first identified at each of six sites (Table 1) during early June 1999. Censuses were repeated during both late August 1999 and May 2000. To examine temporal consistency, a different set of 150 individuals was selected during May 2000 and checked during August 2000 at seven sites (Table 1). Of these 150 surveyed each year,

TABLE 1. Field sites used and years sampled for each parameter.

Site name	Location	Parameter		
		Haploid (%)	Mortality	Fecundity
Cape Meares	45°29′ N, 123°57′ W	S 97, 98		
Boiler Bay	44°50′ N, 124°03′ W	F 97, 98, 99, 00 S 97, 98, 99	F 00	F 00
Strawberry Hill	44°15′ N, 124°6′ W	S 97, 98		
Cape Blanco	42°50′ N, 124°33′ W	F 97, 98, 99, 00 S 97, 98, 99	F 99, 00	F 99, 00
Harris Beach	42°03′ N, 124°33′ W	F 97, 98, 99 S 98		
Patrick's Pt.	41°08′ N, 124°9′ W	F 97, 98, 99, 00 S 97, 98, 99	F 99, 00	F 99, 00
Glass Beach	39°27′ N, 123°48′ W	F 97, 98, 99, 00 S 97, 98	F 99, 00	F 99, 00
Jug Handle	39°22′ N, 123°48′ W	F 97, 98, 99, 00	F 99, 00	F 99, 00
Duxbury Reef	37°53′ N, 122°41′ W	F 97, 98, 99 S 97, 98, 99		
Hopkins	36°38′ N, 121°55′ W	F 97, 98, 99 S 97		
Piedras	35°40′ N, 121°17′ W	F 97, 98, 99, 00 S 98, 99	F 99, 00	F 99, 00
Vandenberg	34°43′ N, 120°36′ W	F 97, 98, 99, 00 S 98, 99	F 99, 00	F 99, 00
Punta Talca	30°92′ S, 71°62′ W	L 99		
Los Moilles	32°23′ S, 71°48′ W	L 99		
Quintay	33°20′ S, 71°63′ W	L 99		
Laguna Verde	33°17′ S, 71°63′ W	L 99		
El Quisco	33°30′ S, 71°62′ W	L 99, 00	L 00	L 00
ECIM	33°49′ S, 71°59′ W	L 99, 00		L 00
Las Cruces	33°50′ S, 71°59′ W	L 99, 00	L 00	L 00
Pelancura	33°51′ S, 71°59′ W	L 99, 00	L 00	L 00
Matanzas	33°97′ S, 71°82′ W	L 99, 00	L 00	L 00
Punta de Lobos	34°43′ S, 71°98′ W	L 99, 00	L 00	L 00

Note: Algal species are abbreviated as follows: F, *M. flaccida*; L, *M. laminarioides*; S, *M. splendens*. Years sampled are abbreviated from 1997–2000.

~75 reproductive individuals of each phase were followed at both Piedras and Vandenberg. At all other sites, because there were few to zero reproductive individuals at the time of the initial census (<1 in 50), 150 nonreproductive individuals were selected and their phase was subsequently determined. Because individuals can switch multiple times between being reproductive or nonreproductive (depending upon the presence/absence of reproductive fronds), our sampling design was appropriate (see *Results*).

The major period of growth and reproduction of *M. flaccida* occurs from late spring to early fall (Foster 1982; C. Thornber, *unpublished data*). Tracking mortality rates during this period of time is appropriate; if mortality rates of the phases differ during the summer before they can reproduce, the subsequent relative production of haploid and diploid spores will be affected. (The two southernmost sites had reproductive individuals present year-round, although larger individuals were present during the summer.) Also, regrowth from inconspicuous holdfasts is rare for *M. flaccida*; depending upon the site, 9–19% of the locations of individuals that had disappeared by the August 1999 census had an individual of the same phase present during May 2000. This may either represent regrowth from a holdfast, or new recruitment; thus these data are likely overestimations of the percentage of individuals regrowing from holdfasts that are inconspicuous or invisible to the naked eye.

Mortality rates were also calculated for *M. laminarioides* individuals. We followed ~50 reproductive female haploids and 50 reproductive diploids at each of five sites (all except ECIM) from January until April 2000. Seasons of growth and reproduction are not as clearly defined for *M. laminarioides*; studies have documented varying patterns of plant size and reproduction throughout the year (Hannach and Santelices 1985, Gomez and Westermeier 1991, Santelices and Martinez 1997). However, this study represents a first attempt to document mortality rates in *M. laminarioides*.

To determine if haploid and diploid mortality rates differ significantly in a manner consistent with the average haploid dominance of sites (i.e., diploid > haploid mortality), we compared mortality rates between the phases with a contingency analysis (JMP v4.0.4; SAS, Incorporated, Cary, North Carolina, USA). To explain the variation in relative haploid abundance among sites, we regressed the mean (1999 and 2000) three month diploid/haploid mortality rate against the mean (1999 and 2000) percentage of haploids found at each site.

Fecundity rates: M. flaccida *and* M. laminarioides.—Per capita diploid and female haploid fecundity rates of both species were determined by calculating the number of spores produced per individual (haploid spores for the diploids, and diploid spores for the female haploids) from the total reproductive blade area and spore density of each individual. It should be noted that in red algae, each fusion of a male and a female haploid gamete quickly develops into a small swelling (cystocarp) on the female haploid blade. This cystocarp is filled with thousands of diploid spores produced via mitotic divisions that will become new free-living diploids when they mature. Because this spore production derives from the nutritional contributions of the female haploid, we express haploid fecundity as the number of diploid spores produced in cystocarps.

In *Mazzaella*, calculating fecundity rates is a multistep procedure. Each individual can have one to several flat, oval-shaped blades arising from a common holdfast, and each blade can potentially bear spores. Spores are packaged in small reproductive structures (cystocarps on haploids, sori on diploids) that are found across the entire blade surface. Thus, for an individual alga, the area of the reproductive blades, the size and number of reproductive structures on these blades, and the number of spores per structure all contribute to an individual's fecundity. Prior to these studies, for each species, we determined the relationships between blade length/width and area, and between sorus size and the number of spores, from previously collected blades (Appendix C).

Field estimates of fecundity.—Reproductive haploids and diploids of *M. flaccida* were collected at seven sites during August 1999, and July, August, and October 2000 (Table 1). Additional collections were made during February and May 2000 at the only sites with reproductive individuals at that time of year (Piedras and Vandenberg); these data yielded similar results to the other months and are not discussed further here. Reproductive haploid and diploid *M. laminarioides* individuals were collected during January 2000 at six sites in Chile (Table 1).

At each site, a total of 40 reproductive haploids and diploids (20 of each) were collected along two transect lines laid haphazardly through the population. The two lines were placed at least 30 m apart from each other, and both were placed within the middle (of the tidal height gradient) of the population at each site to maintain consistency (e.g., individuals at the upper intertidal limit may be smaller due to desiccation stress). Individuals were collected at regular intervals along each line (every 1 m for *M. flaccida*, every 0.5 m for *M. laminarioides*). To determine the per capita reproductive area, the length and width of each reproductive blade on each individual was recorded and subsequently calculated. To determine the size and density of the reproductive structures, a piece of tissue $\sim 3 \times 6$ cm was removed from the middle of one reproductive blade per individual and preserved in silica gel. Tissue samples were subsequently rehydrated in the lab prior to analysis.

Four to six replicate images per tissue sample were analyzed with NIH Image (available online)[2] to determine the size of each reproductive structure in each image (image size = 90.75 mm^2). We calculated the total number of spores in each image by using the reproductive structure area–spore number relationships (Appendix C). Spore totals were used to determine the average number of spores per 90.75-mm^2 image of reproductive tissue for each individual. Per capita fecundity was then calculated from the product of the total reproductive blade area per plant, and the average spore density.

To determine if haploid and diploid fecundity rates differ significantly in a manner consistent with the haploid dominance in the field (i.e., diploid $>$ haploid fecundity), we compared reproductive blade area, spore density, and per capita fecundity rates among sites and between phases with two-way mixed model ANOVAs. (Each sampling date was analyzed separately, because blade size can vary widely during different seasons.) To explain the among-site variability in haploid abundance, we regressed the ratio of diploid to haploid fecundity against the percentage of haploids at each site.

Results

Field surveys.—The three species exhibit different patterns of haploid/diploid dominance, ranging from a pattern near the null expectation (*M. splendens*, Fig. 2A) to patterns of extreme haploid relative abundance (*M. flaccida*, *M. laminarioides*; Fig. 2B, C). The overall site mean for *M. splendens*, averaged across all years and sites, was 64% haploids (1 SE = 2.77, $n = 24$ site estimates with a total of 3831 individuals). Although the mode of this distribution is centered on the null expectation, a few high-frequency haploid sites cause the overall distribution to be significantly different from the null expectation of 58.6% (G test, $P < 0.001$). Yearly means fluctuated from 64% to 70% to 55% (1997, 1998, and 1999, respectively). Part of the interannual variation may be attributable to unavoidable differences in accessibility to sites that were sampled due the low intertidal distribution of *M. splendens*.

The extent of haploid overabundance is more striking in *M. flaccida* (Fig. 2B). Averaged across all years and sites, haploids comprised 72% of all individuals (1 SE = 1.79, $n = 37$ site estimates with a total of 7203 individuals), which is significantly different from the null model prediction of 58.6% (G test, $P < 0.001$). Unlike the *M. splendens* data, the entire distribution of *M. flaccida* is shifted towards higher levels of relative haploid abundance. This pattern was fairly consistent among years ($\bar{x}$ = 71% in 1997, 76% in 1998, 73% in 1999, and 68% in 2000). The distribution of sites was

[2] URL: ⟨http://rsb.info.nih.gov/nih-image/index.html⟩

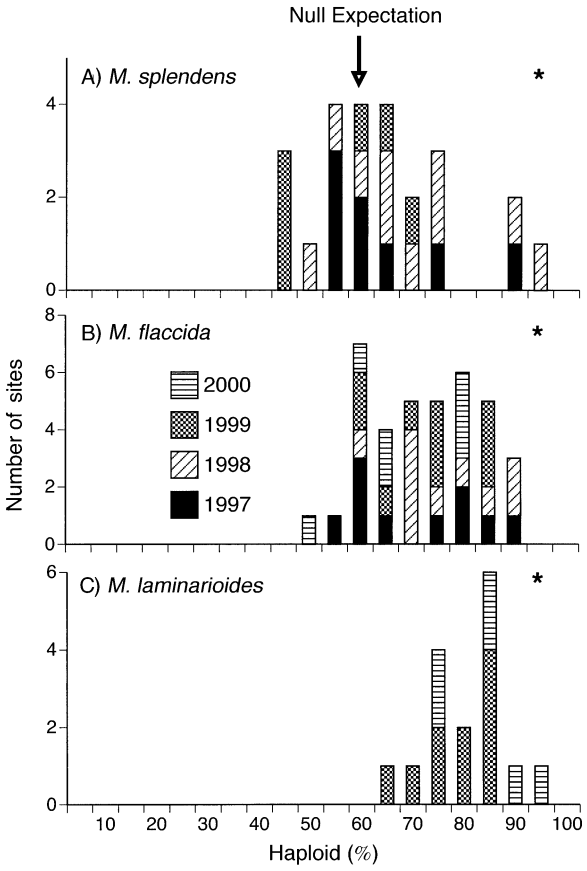

FIG. 2. The percentage of haploid individuals at several intertidal sites for three algal species: (A) *M. splendens* during the summers of 1997, 1998, and 1999; (B) *M. flaccida* during the summers of 1997, 1998, 1999, and 2000; (C) *M. laminarioides* during the austral summers of 1999 and 2000. Each bin spans 5 percent; for example, the bin labeled 60 includes all sites with 57.5–62.49 percent haploids. A star (*) indicates when the mean percentage of haploids is greater ($P < 0.001$) than the null model prediction.

strongly skewed to higher haploid levels than would be predicted from the null model; only three out of thirty-seven populations had haploid percentages lower than the null expectation.

Haploid dominance in *M. laminarioides* was even more extreme than that seen in *M. flaccida* (Fig. 2C). *M. laminarioides* had an overall mean of 80% haploids (1 SE = 2.0, $n = 10$ site estimates with a total of 3143 individuals), which is significantly different from the null model prediction of 58.6% (G test, $P < 0.001$). Yearly means were 78% for 1999 and 84% for 2000. None of the 24 site means were smaller than the null expectation.

Mortality rates: M. flaccida.—Per capita mortality rates of *M. flaccida* differed significantly among sites and occasionally between phases (Fig. 3, see Appendix D for statistical tables and more detailed graphs). From June to August 1999, *M. flaccida* individuals showed significant differences in mortality between phases ($\chi^2_{[1]} = 6.690$, $P = 0.0097$; Fig. 3A, Appendix D). Per capita mortality rates were higher in haploids (0.49) than in diploids (0.38). However, when these individuals were rechecked during May 2000, mortality rates did not differ between phases ($\chi^2_{[1]} = 2.729$, $P = 0.0985$; Fig. 3B, Appendix D). Different individuals that were tracked from May to August 2000 also did not differ significantly in mortality between phases ($\chi^2_{[1]} = 2.790$, $P = 0.0949$; Fig. 3C, Appendix D). These results indicate that differences in mortality cannot explain the overall high haploid abundances found at sites.

By contrast, differences in the mean three-month mortality rates between phases were consistent with the among-site variability in haploid percentage. As diploid mortality increased relative to haploid mortality across sites, the percentage of haploids also increased ($r = 0.64$, $P = 0.12$; Fig. 4A). Removing the one site that had severely unbalanced numbers of each phase (17 diploids, 133 haploids) strengthens the correlation ($r = 0.96$, $P = 0.003$); due to the small sample size of diploids, it is plausible that the recorded mortality rate may not reflect true diploid mortality at this site.

Mortality rates: M. laminarioides.—Per capita mortality rates of *M. laminarioides* did not differ signifi-

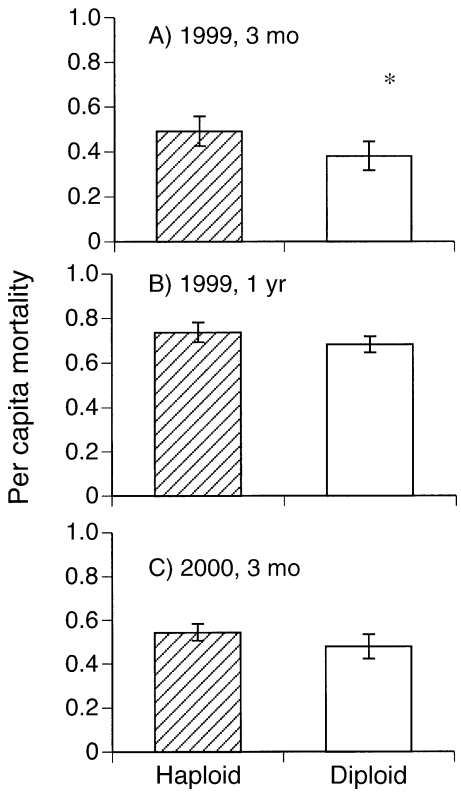

FIG. 3. Per capita mortality rates of haploid and diploid *M. flaccida* individuals (means ± 1 SE): (A) Individuals marked in 1999 and checked after 3 mo; (B) individuals marked in 1999 and rechecked after 1 yr; (C) individuals marked in 2000 and checked after 3 mo. An asterisk (*) indicates significant difference between phases ($P < 0.05$).

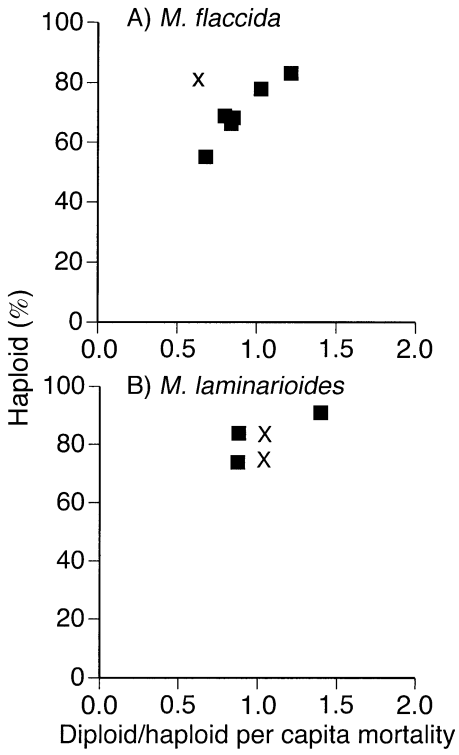

FIG. 4. (A) The relationship between relative mortality rates and the percentage of haploids found at each site for *M. flaccida* data averaged for 1999 and 2000. Excluding the one outlier (represented with an X, see *Results*), there is a significant relationship ($r = 0.96$, $P = 0.003$); including all sites yields $r = 0.64$, $P = 0.12$. (B) The relationship for *M. laminarioides* data for 2000; the two sites in which all individuals died are each represented by an X. This correlation was not statistically significant when three ($r = 0.81$, $P = 0.39$) or all five ($r = 0.72$, $P = 0.17$) sites were included.

cantly between phases ($\chi^2_{[1]} = 0.001$, $P = 0.975$; Appendix D). At two sites (Las Cruces and Pelancura), all individuals died due to overexposure from a series of exceptionally calm, sunny days in late January; even the small crustal holdfasts of individuals were bleached white. The other three sites were more wave-exposed and thus did not suffer the same fate; only these three sites are graphed and compared statistically here (including all five sites in the analysis reveals no significant difference between phases or among sites). Because per capita mortality rates did not differ between phases, differences in mortality rates cannot explain the high relative haploid abundance in *M. laminarioides* at these sites.

Differences in mortality rates also cannot explain among-site variation in haploid abundance for *M. laminarioides*. Unlike *M. flaccida*, there was no significant relationship between the diploid/haploid mortality ratio and the relative haploid abundance at the three sites ($n = 3$, $r = 0.81$, $P = 0.39$; Fig. 4B), or when all five sites were included ($r = 0.72$, $P = 0.17$) for *M. laminarioides*.

Fecundity rates: M. flaccida.—Reproductive blade area did not differ significantly between phases in three of the four months examined (two-way ANOVAs, $P > 0.12$ for each; Fig. 5A–D); during July 2000, the reproductive area of haploids was significantly larger than that of diploids ($F_{1,6} = 14.834$, $P = 0.008$). There was no significant difference in area between phases when all months were averaged together ($t_{60} = 1.186$, $P = 0.25$). Statistical test results and more detailed graphs for all fecundity measurements can be found in Appendix E.

Spores were significantly denser on diploid than on haploid blades during each month surveyed ($P < 0.05$ for each; Fig. 5E–H); on average, there was a twofold difference in spore density (4.2×10^5 vs. 2.3×10^5 spores per 90 mm^2). It is this difference in spore density that is responsible for the difference in per capita fecundity between phases. In two of the four months sampled (August and October 2000), diploids had significantly higher per capita fecundity rates than haploids ($F_{1,6} = 20.895$, $P = 0.004$ and $F_{1,5} = 15.630$, $P = 0.011$; Fig. 5I–L; Appendix E). During August 1999 and July 2000, fecundity rates were statistically indistinguishable between haploids and diploids ($F_{1,6} = 3.069$, $P = 0.13$ and $F_{1,6} = 5.047$, $P = 0.066$, respectively) although the trends were in the same direction (diploids > haploids). When all months were averaged together, diploids had 50% more spores than haploids ($t_{60} = 2.231$, $P = 0.03$).

Differences in fecundity rates between phases did not appear to contribute to among-site variation in haploid abundance. There was no significant correlation between the diploid:haploid fecundity ratio and the fraction of haploids at each site ($r = 0.1$, $P = 0.80$).

Fecundity rates: M. laminarioides.—There was no significant difference in reproductive blade area, spore density, or per capita fecundity between haploid and diploid individuals of *M. laminarioides* ($P > 0.11$ for all; Appendix E; Fig. 6). These results are inconsistent with the hypothesis that haploid dominance is due to higher diploid fecundity. Because these data are from one sampling date, and this species is known to be reproductive throughout the year (Hannach and Santelices 1985, Luxoro and Santelices 1989), the influence of fecundity differences in *M. laminarioides* must be interpreted with caution.

Differences in fecundity rates among sites were also inconsistent with the spatial variation in haploid abundance for *M. laminarioides*. There was no correlation between the diploid:haploid fecundity ratio and the relative haploid abundance at sites ($r = 0.22$, $P = 0.67$).

DISCUSSION

All of the issues addressed in this paper are focused around the larger question of the relative advantages of haploids and diploids within a complex life cycle. There is a wide body of literature on the evolution and persistence of life cycles that include free-living hap-

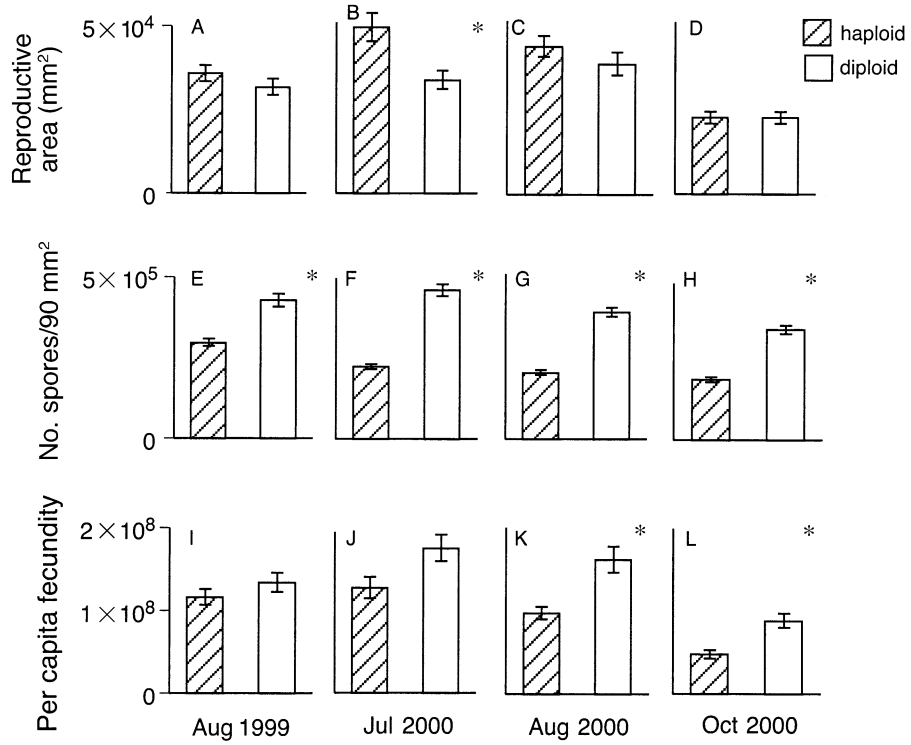

FIG. 5. Per capita fecundity rates for *M. flaccida* haploid and diploid individuals, plotted by sampling date (means ± 1 SE): (A–D) mean reproductive blade area (mm²); (E–H) mean density of spores on blades; (I–L) mean per capita fecundity, calculated for each individual from its reproductive blade area and spore density. Each set of four figures corresponds to individuals sampled in August 1999 and in July, August, and October 2000, respectively. An asterisk (*) indicates a significant difference between phases ($P < 0.05$).

loid and diploid phases (e.g., Kondrashov and Crow 1991, Perrot et al. 1991, Jenkins and Kirpatrick 1995, Hughes and Otto 1999). Haploids can have advantages over diploids through reduced mutational loads (Crow and Kimura 1965) or lower nutritional requirements (especially in unicellular organisms), because the DNA content is half that of diploids (Lewis 1985). By contrast, diploids can potentially mask deleterious mutations more effectively than haploids (e.g., Perrot et al. 1991), and they can adapt more quickly to new environment (Bell 1982). Given these differences, genetic models commonly predict that life cycles with such multiple phases are evolutionarily unstable (see Mable and Otto 1998).

Despite such model predictions, multiphasic life cycles are common and found in a wide variety of taxa (e.g., algae, fungi, hydrozoans, mosses). One hypothesis that has been proposed is that the phases can exploit different ecological niches (Stebbins and Hill 1980). This has been found in yeasts (Banuett and Herskowitz 1994, Sia et al. 2000) and mosses (Hobbs and Pritchard 1987), and is also readily apparent in algae with heteromorphic life cycles (Lubchenco and Cubit 1980, Slocum 1980). This hypothesis may also be important for algal species with isomorphic life cycles, as isomorphic haploids and diploids may differ in ways that are morphologically subtle, but ecologically significant (Destombe et al. 1989, Engel et al. 2001). Recent theoretical work has demonstrated that slight differences in demographic rates between the phases of isomorphic species can promote the stability of multiphasic life cycles (Hughes and Otto 1999).

Model predictions

The development of robust population models for isomorphic haploid–diploid species is an important first step for interpreting varying abundances of haploids and diploids in the field. The null population model we developed predicts that a distribution of 59% haploids and 41% diploids is expected for dioecious species with equivalent per capita demographic rates. Our results show that deviations from this null prediction will occur when there are large, ecologically significant (at least twofold) differences in demographic rates between the phases.

Our models include several assumptions about the basic population biology of isomorphic species that may affect the haploid–diploid ratio; four of these assumptions merit further discussion. First, our models assume that male gametes are unlimited, and thus all female gametes are fertilized (see *Models of haploid–diploid populations: Exponential growth*). Since red

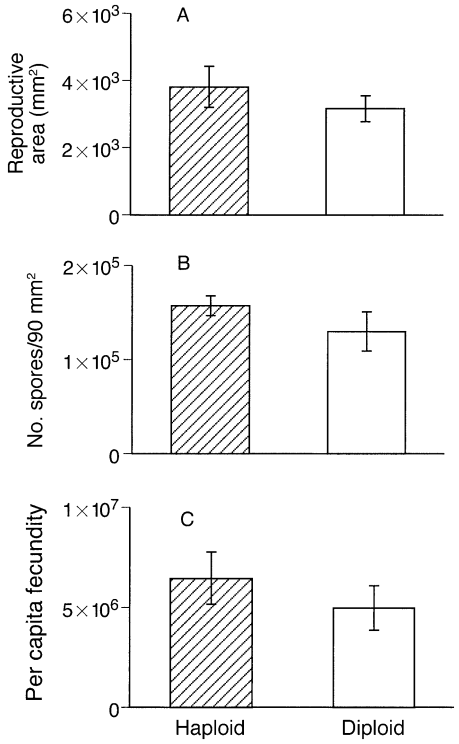

FIG. 6. Per capita fecundity rates for *M. laminarioides* haploid and diploid individuals (means ± 1 SE): (A) mean reproductive blade area (mm²); (B) mean density of spores on blades; (C) mean per capita fecundity. $P > 0.05$ for each panel.

algal male gametes do not have flagella, it is plausible that fertilization success may limit female fecundity. If fertilization success is not close to 100%, haploid fecundity (as measured by diploid spore production) should decrease and the proportion of haploids expected should increase. Fertilization success has rarely been examined in algae, but male gametes were found to be nonlimiting for fertilization of the red alga, *Gracilaria gracilis* (Engel et al. 1999). Second, the presence of the small diploid (carposporophyte) phase on the female blade can serve as a mechanism to effectively increase female fecundity (Searles 1980). Since multiple carpospores are produced asexually from a single fertilized gamete, haploid fecundity is effectively increased. This should result in a relative decrease in haploids as a fraction of the total population. Third, the asexual looping of one phase (apomeiosis) may affect the relative proportion of the phases, if one phase is able to produce itself (not the other phase) via reproduction. Apomeiosis has been shown to be rare in *M. splendens* (Kim 1976, DeWreede and Green 1990) but has not been tested in *M. flaccida* or *M. laminarioides*. Fourth, we assume that populations are density dependent. During August and October 2000, we found a highly significant negative correlation between density and per capita fecundity for both haploids and diploids of *M. flaccida* ($r = 0.8$, $P = 0.021$ and $r = 0.92$, $P = 0.009$, respectively; Thornber and Gaines 2003). Although we did not find a significant relationship between density and per capita mortality, this may be because microscopic spore and/or macroscopic recruitment mortality is the density-regulated step, as there is a finite amount of suitable rocky intertidal habitat available.

Explanations of field patterns

There are three classes of explanations for the widespread overabundance of haploids in the field, relative to model expectations. First, the models may ignore some key feature of the life cycle (see previous paragraph). Second, the null expectation for proportion of haploids is an equilibrium prediction. Disturbance or chance events could perturb populations away from this equilibrium value, and the observation of deviations in field populations could reflect transient states of recovery. However, if the observations were a reflection of nonequilibrium populations, we should not expect any bias in pattern of relative abundance. Excess diploid abundance should be as common as excess haploid abundance unless haploids and diploids are differentially susceptible to disturbances (which would violate the assumption of haploids and diploids being ecologically equivalent). Only eight of the 84 populations sampled had haploid fractions lower than the null expectation, and six of the eight were for *M. splendens*, the species that most closely met model predictions. For the other two species, the extent of haploid overabundance was so consistent that it is difficult to envision the patterns simply reflecting nonequilibrium dynamics.

The final, most plausible, explanation for the dominance of haploids is that the two phases differed in their per capita mortality and/or fecundity rates despite their morphological similarity. In this study, we found differences in both mortality rates and fecundity between haploid and diploid life stages, although their patterns and effects varied among species. For *M. flaccida*, the strong dominance of haploids throughout the species range was consistent with significant differences in fecundity rates among the life stages (diploid > haploid when the phases differed). Overall, diploid adults had substantially higher average fecundity than haploids, which leads to the numerical dominance by the stage with poorer average performance. Sites with the highest diploid/haploid mortality rate had the highest percentage of haploid individuals (Fig. 4A), suggesting that differences in mortality rates between phases may be responsible for some of the subtle, yet important, intersite variation in haploid relative abundance in *M. flaccida*.

Demography of haploid/diploid species

Few previous studies have been conducted on haploid:diploid ratios on the three *Mazzaella* species dis-

cussed here. *M. splendens* populations in Vancouver exhibit an alternation of haploid dominance in summer and diploid dominance in winter (DeWreede and Green 1990, Dyck and DeWreede 1995). However, seasonal data for *M. flaccida* indicates that this species does not exhibit these shifts in population structure (Thornber and Gaines 2003).

Previous studies on mortality and fecundity rates in isomorphic algal species have yielded conflicting results. In *Padina japonica* and *Gracilaria verrucosa*, diploids have lower per capita mortality than haploids (Allender 1977, Destombe et al. 1989); both *Gracilaria gracilis* and *M. splendens* have similar mortality rates between the phases (May 1986, Engel et al. 2001), mirroring our results for *M. flaccida*. Also, as we found for *M. flaccida*, fecundity was higher for diploids in *G. gracilis* and *G. verrucosa* (Hughes and Otto 1999, Engel et al. 2001), although no fecundity differences have been found for *Hypnea cervicornis, H. chordacea* (Mshigeni 1976), *Mazzaella laminarioides* (Luxoro and Santelices 1989), and *Plocamium cartilagineum* (Kain 1982). Few studies have examined both mortality and fecundity rates for a particular species (but see Destombe et al. 1989, Engel et al. 2001), which is necessary for understanding their effects on haploid:diploid field ratios.

Possible mechanisms for differences in fecundity between phases

In this study, *M. flaccida* diploids had significantly higher fecundity rates than haploids, due to a higher density of spores on diploid blades. There are several possible mechanisms that could be responsible for this diploid advantage, including reduced susceptibility to herbivory when grazing has sub-lethal effects (Buschmann and Santelices 1987), an increased allocation of resources towards reproduction (Santelices and Martinez 1997), or constraints on fertilization. In *M. flaccida*, some herbivores (e.g., the turban snail *Tegula funebralis*) prefer haploid reproductive tissue to diploid reproductive tissue, which could selectively decrease haploid fecundity as only the outermost cell layers (including spores) are removed during grazing (C. S. Thornber, *unpublished data*). Limits on fertilization success may be due to a lack of male gametes; it may also occur via venereal diseases, because the fusion of gametes occurs only on the haploid phase (W. Rice, *personal communication*), though venereal diseases have not yet been reported in algae.

Importance of microscopic stages

In this study, we focused on the combined mortality of juveniles and adults, and the fecundity (spore production) of adults as potential explanations for the strong dominance of haploids in the field. Although these two factors could explain some of the dominance of haploids for *M. flaccida* (via fecundity rates) and some of the spatial variation in haploid relative abundance (via mortality rates), they could not explain any of the patterns observed in *M. laminarioides*.

What could account for the excessive haploid dominance in *M. laminarioides*? One possible explanation is that performance differences between haploids and diploids occur in parts of the life cycle that we did not examine, such as the microscopic spores that are produced by each phase. For *M. laminarioides*, haploid adults released significantly more spores than diploid adults (Luxoro and Santelices 1989). However, no differences in spore settlement and germination rates between the phases of *M. laminarioides* were found in that study. No data on spore mortality or dispersal exist for *M. flaccida*, but in the red algal *Gracilaria verrucosa*, haploid spores showed higher mortality but greater dispersal capability than diploid spores (Destombe et al. 1989, 1992). Thus, if spores from haploids vs. diploids differ substantially in any of these traits, the underlying cause of haploid dominance would have been undetected by our measurements.

The degree of spore dispersal in *Mazzaella* could also influence the haploid:diploid ratio of populations. If spores produced at one site do not recruit back to the same site, local fecundity differences between the phases would not have a large influence on the local recruitment differences between the phases. Spore dispersal in red algae is generally considered to be low; red algal spores lack flagella and spore viability is usually less than 48 h with dispersal distances from 2–10 m (Santelices 1990), but this has been found to range up to 96 h for swimming spores of the brown algae *Macrocystis pyrifera* and *Pterygophora californica* (Reed et al. 1992). The dispersal distance of *M. flaccida* or *M. laminarioides* spores has not been investigated, but spores of the latter species did not survive in suspended solutions for more than 50 h (Luxoro and Santelices 1989), suggesting a potential for dispersal among localized populations.

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APPENDIX A

A description of the Richerd model is presented in ESA's Electronic Data Archive: *Ecological Archives* E085-046-A1.

APPENDIX B

An examination of the stability of the logistic models is presented in ESA's Electronic Data Archive: *Ecological Archives* E085-046-A2.

APPENDIX C

A description of the process used to determine blade area from length/width vs. area regressions is presented in ESA's Electronic Data Archive: *Ecological Archives* E085-046-A3.

APPENDIX D

A table showing the results of chi-square likelihood tests and graphs of haploid and diploid per capita mortality rates is presented in ESA's Electronic Data Archive: *Ecological Archives* E085-046-A4.

APPENDIX E

A table and graphs showing results of two-way mixed-model ANOVA for *Mazzaella flaccida* and *Mazzaella laminarioides* reproductive blade area, spore density, and per capita fecundity are presented in ESA's Electronic Data Archive: *Ecological Archives* E085-046-A5.