CHAPTER 2

Demographic mechanisms determining the dynamics of the relative abundance of phases in biphasic life cycles

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ABSTRACT

Studies investigating the demographic traits that drive the patterns of phase dominance (the ploidy ratio) in isomorphic biphasic life cycles have not found an integrative solution. Either fertility or survival has been suggested independently as the main driver. Here we provide a global theoretical framework on how demographic mechanisms determine the ploidy ratio, unifying previous numerical and observational attempts at this question. The analytical solutions of both the ploidy ratio and its elasticities to model parameters of a stage/size structured model patterned after the life cycle of a marine alga were derived and analysed. A complex interaction among vital rates determines the patterns of phase dominance of biphasic life cycles. Three co-occurring processes, growth, fertility and looping may dominate the dynamics of the population, determining both its growth rate and ploidy ratio. Our analyses show that, in species where fertility is low, the ploidy ratio is highly elastic to looping transitions (survival, breakage and clonal growth). Consequently, the subtle morphological, ecophysiological and biochemistry phase differences that have been reported in isomorphic life cycles as not explaining the observed ploidy ratios, may, in fact, explain them if they translate into slight phase differences in looping transitions. In species where fertility is low, the looping dissimilarities between phases cannot be too high favouring simultaneously one phase, as the population structure would be completely dominated by that phase. In the case of ecological similarity between phases (equal looping and growth rates between phases), a ploidy ratio different from one can only be set by strong phase differences in fertility.

Keywords: Biphasic life cycle; demography; haploid-diploid; matrix modelling; ploidy ratio; population dynamics; structured population models.

INTRODUCTION

Sexual reproduction implies life cycles with some alternation between haploid and diploid phases, which may vary widely in size and duration. In haplont life cycles the diploid phase is restricted to the zygote, and vegetative development occurs in the haploid phase. In diplont life cycles the haploid phase is restricted to the gametes. Life cycles with alternating, well developed, haploid and diploid phases are less common in nature, but well represented in many algae, ferns, moss, and fungi. Marine algae, in particular, show complex life cycles that involve the alternation of free living haploid and diploid phases (Klinger 1993), which can be morphologically similar (isomorphic) or distinct (heteromorphic). In red algae, modified biphasic life cycles involving three phases are common. These include a haploid gametophyte, the carposporophyte, a short-lived phase which develops on top of the female gametophyte after fertilization and is dependent on it for nutrients (Kamiya and Kawai 2002) and a diploid tetrasporophyte that develops from carpospores. In conceptual terms, this particular cycle can be treated as a biphasic cycle as there are only two independent phases. Carpospores can be considered as a mitotic mechanism of increasing the reproductive output of fertilization.

The relative abundance of phases in marine algae, i.e. the ploidy ratios, has received increasing attention recently. The fact that in many species the phases are morphologically similar raised the question of what drives the observed variation of phase abundance. Thornber´s (2006) recent review revealed that many species-specific differences have been found in the functional properties of the isomorphic phases, namely in their adult survival, fertility, ecophysiology, resistance to herbivory and disease, and genetic population structure. However, no common pattern was found distinguishing the gametophyte from the sporophyte phases and it is not clear how most of those differences affect the ploidy ratio.

A few modeling attempts have been done to investigate the patterns of phase dominance of biphasic life cycles when there is ecological similarity between phases, i.e. no differences in demographic rates except spore production. Scrosati and DeWreede (1999) showed that the dominance of the gametophyte phase is the obvious consequence of the minimum theoretical spore output of each phase, i.e. one carpospore from every two gametophytes and four tetraspores per sporophyte. Thornber and Gaines (2004) showed that under the hypothesis of equal carpospore and tetraspore production the reproductive output of the gametophyte phase is half that of the sporophyte phase and a 1.4 gametophyte to tetrasporophyte ratio (H:D) is expected. Fierst et al. (2005) examined the role of fertilization success on the gametophyte-to-sporophyte ratio, concluding that gametophytes always dominate regardless of fertilization rate unless egg production (carpospores in the case of red algae) greatly exceeded meiospore production (tetraspores).

When ecological dissimilarity between phases is considered, as were the cases of the red algae populations of *Gracilaria gracilis* studied by Destombe *et al.* (1989) and Engel et al. (2001), *Mazzaella oregona* (Mudge and Scrosati 2003) and *Mazzaella parksii* (Scrosati and Mudge 2004), small reductions in the survival of one phase may decrease significantly its frequency. Numerical simulations of combinations of survival rate and fertility explained the variability of ploidy ratios observed across populations and over time. In the case of the three *Mazzaella* species investigated by Thornber and Gaines (2004), the gametophyte dominance observed in the field was better explained by differences in fecundity than in mortality rates between phases.

Previous research on the demographic traits that may sustain the evolution and stability of biphasic life cycles suggest that there is a range of conditions where the haploid-diploid cycle optimizes the advantages of both haploidy and diploidy (Hall 2000). Richerd et al. (1993) showed that biphasic life cycles may benefit from reducing the cost of sex, whenever it is high, as they reproduce sexually half as much relative to monophasic life cycles. Mable and Otto (1998) argue that it would then be expected that the cost of sex is reduced by increasing asexual reproduction. In fact, this vital rate may play an important role in the population dynamics of many seaweeds as has been observed in red algae (Santos 1995).

The ecological divergence among phases may be a condition for the evolution and stability of biphasic life cycles as Hughes and Otto (1999) showed. The haploid-diploid cycle will be favoured as long as the inter-phase competition among individuals is lower than the intra-phase competition, just like the conditions for coexistence in a two-species competition model. This means a trade-off in the ability of the phases to explore the environment differently. The work by Jenkins (1993) and Jenkins and Kirkpatrick (1994) emphasized the importance of ecological dissimilarity between phases (different phase mortality) on the evolution of phases. They showed that constant mortality rates that differ between the haploid and diploid phases lead to the evolution of the phase with lowest mortality and the extinction of the other.

Hughes and Otto (1999) found that slight differences were enough to favour the evolution and maintenance of biphasic life cycles through niche differentiation.

The aim of this work is to provide a theoretical framework for how demographic mechanisms determine the ploidy ratio of biphasic life-cycle species, unifying previous numerical and observational attempts to answer this question. The ploidy ratio demography will then be discussed under the perspective that niche differentiation between phases is necessary for the evolution and maintenance of biphasic life cycles as demonstrated by Hughes and Otto (1999). Previous authors (Scrosati and DeWreede 1999; Engel et al. 2001; Thornber and Gaines 2004; Fierst et al. 2005) have used a simple stage model with only one stage class in each phase of the biphasic life cycle to test numerical solutions for the effects of vital rates on the ploidy ratio. Here we derive the analytical solutions of the ploidy ratio of a more complex stage/size structured model as well as the ploidy ratio elasticities to the parameters of the model. The use of a more complex model unveils the effects of transitions among stages within both phases, which is not possible with a single stage model. The clonal growth from basal system, which allows the regeneration of the same phase, was included in the model as this demographic transition is possible in many life cycles. Previous reports emphasized the importance of this vital rate to the population dynamics of marine algae, in particular when recovering from disturbances (Santos 1995), and its effects on the ploidy ratio (Fierst et al. 2005). This transition contributes with new ramets to the population (*sensu* Harper 1980) rather than with new genets. To use the model developed here to simulate genet-based population dynamics this transition would have to be made equal to zero.

Scenarios of ecological differentiation between phases driven by dissimilarities in several traits of the life cycle are tested for their effects on the ploidy ratio. To do this, we used the ramet-based vital rates of a population of the red seaweed, *Gelidium sesquipedale* (Clemente) Thuret, estimated based on previously reported data (Santos 1993, 1994, 1995; Santos and Duarte 1996; Santos and Nyman 1998; Carmona and Santos 2006).

METHODS

The stage/size structured model

Male and female gametophytes are not discriminated in the model, thus assuming that their survival rates are equal. The males' gamete production was also assumed to be sufficient to fertilize all female gametes. Consequently, males and females were clustered into one state variable, the gametophytes, in which fecundity results from the fertilization rate and the number of gametophytes. To apply the model to the triphasic life cycles of red algae, the gametophyte fecundity is considered equal to the carposporophytes' mitotic production of carpospores. It must be noted that this pathway of the life cycle of red algae has the same effect of the vegetative reproduction processes of other algae such as apomeiosis, parthenogenesis, spore and propagule production, etc: they all contribute with new ramets to the population. Thus, the population dynamics of many algae need to be based on the ramet- rather than genet-demography, the latter being almost impossible to monitor in the field. This concept of clonal construction in plant population studies has been discussed previously for terrestrial plants (e.g. White 1985, Harper et al. 1986). The models developed here are ramet-based, i.e. the unit of the model is considered to be a ramet (units of construction of clonal plants) independently of being physically connected, or not, to the parental plant (*sensu* Harper, 1980).

A model with four state variables in each phase was developed, including a spore stage and three ramet size classes (Fig.1). Haploid ramets' size classes are stages "1", "2" and "3" whereas diploid ramets' size classes are stages "4", "5" and "6". If the fecundities of the lower size class of each phase is zero, then this class can be considered a juvenile stage. Vital rates representing transitions among size classes of each phase, such as growth, stasis and breakage were considered. Ramets that survive have one of three fates: to grow into a larger size class, to break into a smaller size class or to stay in the same size class (stasis). The transitions growth, (G_x), stasis, (St_x), breakage, (B_{xy}) and carpospore and tetraspore survival, (S_{carp} and S_{tet}, respectively), are probabilities and hence vary between 0 and 1. The spore survival rates include, in fact, not only their survival but a combination of probabilities such as spore settlement, spore germination and sporeling survival and growth to the lower size classes. The fertilities of each phase appear decomposed into adult fecundities and spore survival. The transitions fecundity (Fec_x) and clonal growth (CG_x) are production rates (new spores or ramets, respectively, produced by each existing ramet) and hence may vary between 0 and +∞.

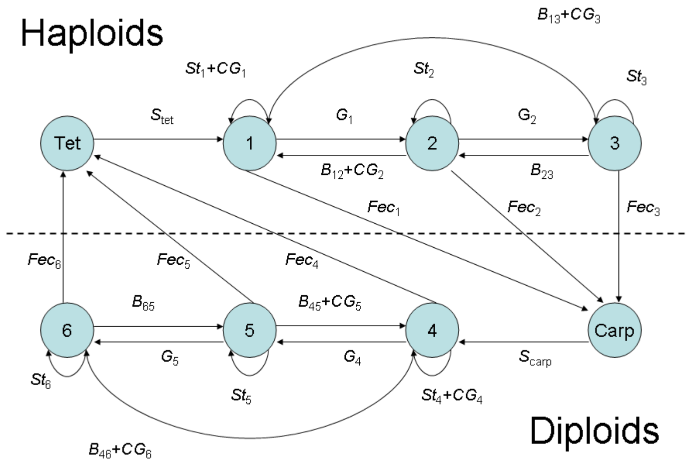

Figure 1 - Biphasic life cycle: (tet) tetraspores, (1, 2 and 3) haploid ramets' size classes, (carp) carpospores and (4, 5 and 6) diploid ramets' size classes. Arrows indicate: (CG) clonal growth, (Fec) fecundity, (Stet) tetraspore survival, (Scarp) carpospore survival, (G) growth, (St) stasis and (B) breakage.

The inherent matrix model assumptions are (Caswell 2001):

a) In each time step only the transitions represented in the model can occur and not any sequence of them.

b) The model is a first order Markovian process, i.e. the fate of a spore or a ramet in time t is only a consequence of its state at time t-1 and not of its state at any other time.

c) The model is deterministic, i.e. the transition values remain constant over time.

Further assumptions are also considered:

a) In each time step, ramets in each size class may only grow to the size class immediately above and produce recruits by clonal growth only to the first size class.

b) There is no spore dormancy, i.e. within each time step, a spore either germinates and grows to the first size class, or dies.

The matrix demographic model is represented by the 8 dimensional population vectors and the (8, 8) dimensional population matrix (equation 1):

$$\begin{bmatrix} Tet \\ 1 \\ 2 \\ 3 \\ \hline Carp \\ 4 \\ 5 \\ 6 \end{bmatrix}_{t+1} = \left[\begin{array}{cccc|cccc} 0 & 0 & 0 & 0 & 0 & Fec_4 & Fec_5 & Fec_6 \\ S_{tet} & \mathrm{St}_1 + CG_1 & B_{12} + CG_2 & B_{13} + CG_3 & 0 & 0 & 0 & 0 \\ 0 & G_1 & St_2 & B_{23} & 0 & 0 & 0 & 0 \\ 0 & 0 & G_2 & St_3 & 0 & 0 & 0 & 0 \\ \hline 0 & Fec_1 & Fec_2 & Fec_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \mathrm{S}_{\mathrm{carp}} & St_4 + CG_4 & B_{45} + CG_5 & B_{46} + CG_6 \\ 0 & 0 & 0 & 0 & 0 & G_4 & St_5 & B_{56} \\ 0 & 0 & 0 & 0 & 0 & 0 & G_5 & St_6 \end{array}\right] \times \begin{bmatrix} Tet \\ 1 \\ 2 \\ 3 \\ \hline Carp \\ 4 \\ 5 \\ 6 \end{bmatrix}_{t} \qquad \text{(eqn 1)}$$

Model analysis

The strong ergodic theorem demonstrates that for any primitive matrix such as those of any perennial biphasic life cycle, the population's long-term dynamics are determined by the demographic matrix's dominant eigenvalue λ_a and its corresponding right eigenvector w_a (Caswell 2001). If the long-term population structure of perennial algae is set by eigenvector w_a, then this will also be true for any function of the population's structure such as the haploid to diploid ratio (H:D):

$$H : D = \frac{w_{a1} + w_{a2} + w_{a3}}{w_{a4} + w_{a5} + w_{a6}} \qquad \text{(eqn 2)}$$

where w_{ai} is the component of the eigenvector w_a corresponding to state variable i. The eigenvector w_a can be deduced from the life-cycle graph (Caswell 2001).

An elasticity analysis was performed to reveal the relative response of the H:D to relative changes in matrix parameters. The analytical solutions of the elasticities of the H:D to the model parameters were deduced taking the partial derivatives of the model to its parameters (Caswell 2001). The results of the analytical solutions were always confirmed upon numerical simulations. Note that the solutions to both the H:D and its elasticities were not fully analytical as the population growth rate (λ) needs to be numerically determined.

Dynamics of the H:D elasticities

Numerical simulations were performed to assess the H:D elasticities' responses to both varying vital rates and dissimilarities of the life-cycle phases. The vital rates used for the initial numerical simulation were estimated from previous reports by Santos (1993, 1994), Santos and Duarte (1996), Santos and Nyman (1998) and Carmona and Santos (2006) on the demography of a population of an isomorphic, biphasic life cycle, red seaweed, *Gelidium sesquipedale*. A time step of one month was considered. The following demographic matrix (equation 3) was obtained from these sources, where the vital rates representing transitions among the ramets were considered equal between phases. To make sure that the numerical analysis performed here could be generalized, a wide range of matrix values were tested.

$$\left[\begin{array}{c|cccccccc}
 & \mathit{Tet} & 1 & 2 & 3 & \mathit{Carp} & 4 & 5 & 6 \\
\hline
\mathit{Tet} & 0 & 0 & 0 & 0 & 0 & 0 & 6651 & 13841 \\
1 & 0.0001 & 0.33 & 0.06 & 0.03 & 0 & 0 & 0 & 0 \\
2 & 0 & 0.18 & 0.53 & 0.06 & 0 & 0 & 0 & 0 \\
3 & 0 & 0 & 0.03 & 0.42 & 0 & 0 & 0 & 0 \\
\mathit{Carp} & 0 & 0 & 14754 & 30704 & 0 & 0 & 0 & 0 \\
4 & 0 & 0 & 0 & 0 & 0.0001 & 0.33 & 0.06 & 0.03 \\
5 & 0 & 0 & 0 & 0 & 0 & 0.18 & 0.53 & 0.06 \\
6 & 0 & 0 & 0 & 0 & 0 & 0 & 0.03 & 0.42
\end{array}\right] \qquad \text{(eqn 3)}$$

To avoid testing each of the thirty model parameters independently and one at a time (transitions of Fig. 1), lower level parameters for both haploid and diploid spore survival, growth, stasis, breakage and clonal growth were considered. For example, the haploid growth (G_1 and G_2) were all linked to the haploid growth lower level parameter (G_H) with the following algorithm: $G_1 = 1.379*G_H$ and $G_1 < 1$, while $G_2 = 0.204*G_H$. Any variation of this lower level parameter represents a proportional variation of each original growth parameter.

Manipulations were carried out for each lower level parameter changing the gametophytic and tetrasporophytic equally and at the same time while the other parameters were fixed. Parameters that contribute to survival were only varied within the range that makes biological sense, i.e. their sum could not be higher than 1. The growth and breakage lower level parameters were varied from 0 to 0.4, stasis lower level parameters were varied from 0 to 0.7 and the clonal growth lower level parameter was varied from 0 to 2. The fertilities were manipulated so that spore survival varied from 10^{-8} to 10^{0}, maintaining fecundities constant. Fertilities as low as 10^{-8} have been reported for seaweeds (Chapman 1984; Santos and Duarte 1996).

The effects of ecological similarity or dissimilarity on the H:D , i.e. equal or unequal vital rates for gametophytic ramets and tetrasporophytic ramets, were assessed keeping a constant ratio within gametophytic and tetrasporophytic lower level parameters. The dissimilarity levels tested were 0.1%, 1% or 10%.

To explore how the H:D may vary in biphasic species with different life history strategies, i.e. life histories dominated by fertility, growth or survival processes, we simulated theoretical demographic matrices varying spore survival from 10^{-1} to 10^{-8}, and randomly attributing values between 0 and 1 to the remaining lower level parameters (growth, stasis, breakage and clonal growth). Matrices with no biological meaning, such as those where survival exceeded 1 were not accepted for further analysis. As well, matrices where the population growth rate (λ) was outside the range 1 to 1.02 were also excluded, i.e. populations which are either decaying or growing too fast. The elasticities of both λ and H:D to fertility, growth and looping of the accepted matrices were then plotted in a triangular plot. Such plots of the elasticities of λ have been used for demographic matrices of plants and animals (see Caswell 2001). Each of the three axes represents the elasticity of λ or H:D to fertility, growth and looping. As the elasticities of λ always add up to 1, no further transformations were needed. However, the elasticities of the H:D always add up to 0. To force the H:D elasticities to add up to 1, the absolute values of the H:D elasticities were used and then weighted by their total sum.

RESULTS

Analytical solutions to the H:D

The analytical solution of the H:D of the stage/size structured model at steady state (see appendix I) is the product of three quotients (equation 4). The first quotient (Q_1), represents the effects of the forward paths within each phase (growth paths) on the H:D. The numerator (N_1) estimates the influence of forward paths on the abundance of gametophytic ramets whereas the denominator (D_1) estimates the same for tetrasporophytes. The second quotient (Q_2) represents the effects of the reproductive paths on the H:D. The numerator (N_2) estimates the influence of the tetrasporophytic reproductive paths on the relative abundance of the gametophytic ramets whereas the denominator (D_2) estimates the same for the gametophytes. The third quotient (Q_3) represents the effects on the H:D of looping paths within each phase, i.e. ramets which persist in the same phase through self-looping paths. The numerator (N_3)

estimates the influence of the tetrasporophytic looping paths on the relative abundance of the gametophytic ramets whereas the denominator (D_3) estimates the same for the gametophytes. The looping transitions are subtracted from one (see appendix I) and thus more looping of one phase has a negative effect on the relative abundance of the other phase.

$$\mathrm{H:D} = \frac{(\lambda - St_3).(\lambda - St_2) - B_{23}.G_2 + G_1.(\lambda - St_3 + G_2)}{(\lambda - St_6).(\lambda - St_5) - B_{56}.G_5 + G_4.(\lambda - St_6 + G_5)} \times$$

$$\times \sqrt{\frac{Fec_4.S_{tet}.[(\lambda - St_6).(\lambda - St_5) - B_{56}.G_5)] + G_4.[Fec_5.S_{tet}.(\lambda - St_6) + Fec_6.S_{tet}.G_5]}{Fec_1.S_{carp}.[(\lambda - St_3).(\lambda - St_2) - B_{23}.G_2)] + G_1.[Fec_2.S_{carp}.(\lambda - St_3) + Fec_3 S_{carp}.G_2]}} \times$$

$$\times \sqrt{\frac{[(\lambda - St_6).(\lambda - St_5) - B_{56}.G_5)].[\lambda - (St_4 + CG_4)] - [(B_{45} + CG_5).G_4.(\lambda - St_6) + (B_{46} + CG_6).G_5.G_4)]}{[(\lambda - St_3).(\lambda - St_2) - B_{23}.G_2)].[\lambda - (St_1 + CG_1)] - [(B_{12} + CG_2).G_1.(\lambda - St_3) + (B_{13} + CG_3).G_2.G_1)]}}$$

(eqn 4)

Analytical solutions to the elasticities

The analytical solutions of the elasticities of the H:D to each model parameter (p), include two types of terms, an explicit term (ET), when parameter p appears in the quotient Q_i of the analytical solution and an implicit term (IT), when parameter p is not present but its effect is exerted through λ, i.e. changes in the parameter affect λ which in turn affect any of the quotients. The total elasticity of the H:D to any parameter p is the sum of its explicit and implicit terms and represents the overall contribution of that parameter to an uneven H:D (equation 5):

$$\text{Elasticity of H:D to p} = \text{ExT of } Q_1 + \text{ExT of } Q_2 + \text{ExT of } Q_3 + \text{IT of } Q_1 + \text{IT of } Q_2 + \text{IT of } Q_3$$

(eqn 5)

Explicit terms of the H:D elasticities

The H:D elasticities explicit terms relative to the three quotients are presented in Table I. In many cases, one or two terms are null because that parameter does not appear in the respective quotient. Positive elasticities to a parameter represent a contribution to gametophytic ramets and to a Q_i quotient bigger than 1, while negative elasticities represent a contribution to tetrasporophytic ramets and to a Q_i quotient between 1 and 0. The results reveal that:

i. The fecundity and spore survival rates contribute only to the opposite phase's abundance.
ii. The growth rates contribute to the abundance of its own phase through forward paths (Q_1) and looping paths (Q_3), and to the opposite phase through reproductive paths (Q_2). This results in opposite contributions to the H:D
iii. The breakage, stasis and clonal growth rates contribute positively to the abundance of its own phase through looping (Q_3) and counteract the effects of both forward (Q_1) and reproductive (Q_2) paths.

Table I - Explicit terms of the H:D elasticities to gametophyte parameters.

of to	Q_1:	Q_2:	Q_3:
Fec_1:		$-\frac{Fec_1}{2D_2^2}\times$ $\times S_{carp}.[(\lambda - St_3).(\lambda - St_2) - B_{23}.G_2]$	
Fec_2:		$-\frac{Fec_2}{2D_2^2}\times S_{carp}.G_1.(\lambda - St_3)$	
Fec_3:		$-\frac{Fec_3}{2D_2^2}\times S_{carp}.G_1.G_2$	
S_{carp}		½	
G_1	$\frac{G_1}{N_1}\times(\lambda - St_3 + G_2)$	$-\frac{G_1}{2D_2^2}\times$ $\times S_{carp}[Fec_2.(\lambda - St_3) + Fec_3.G_2]$	$\frac{G_1}{2D_3^2}\times$ $\times[(B_{12} + CG_2).(\lambda - St_3) + (B_{13} + CG_3).G_2]$
G_2	$\frac{G_2}{N_1}\times(G_1 - B_{23})$	$-\frac{G_2}{2D_2^2}\times$ $S_{carp}(Fec_3.G_1 - Fec_1.B_{23})$	$\frac{G_2}{2D_3^2}\times$ $\times[B_{23}.(\lambda - (St_1 + CG_1)) + (B_{13} + CG_3).G_1]$
St_1			$\frac{St_1}{2D_3^2}\times[.(\lambda - St_3).(\lambda - St_2) - B_{23}.G_2]$
St_2	$-\frac{St_2}{N_1}\times(\lambda - St_3)$	$\frac{St_2}{2D_2^2}\times Fec_1.S_{carp}.(\lambda - St_3)$	$\frac{St_2}{2D_3^2}\times(\lambda - St_3).[\lambda - (St_1 + CG_1)]$
St_3	$-\frac{St_3}{N_1}\times(\lambda - St_2 + G_1)$	$\frac{St_3}{2D_2^2}\times$ $\times S_{carp}.[Fec_1.(\lambda - St_2) + Fec_2.G_1]$	$\frac{St_3}{2D_3^2}\times$ $\times\langle[\lambda - (St_1 + CG_1)].(\lambda - St_2) - (B_{12} + CG_2).G_1\rangle$
B_{12}			$\frac{B_{12}}{2D_3^2}\times G_1.(\lambda - St_3)$
B_{13}			$\frac{B_{13}}{2D_3^2}\times G_1.G_2$
B_{23}	$-\frac{B_{23}}{N_1}\times G_2$	$\frac{B_{23}}{2D_2^2}\times Fec_1.S_{carp}.G_2$	$\frac{B_{23}}{2D_3^2}\times G_2.[\lambda - (St_1 + CG_1)]$
CG_1			$\frac{CG_1}{2D_3^2}\times[(\lambda - St_3).(\lambda - St_2.) - B_{23}.G_2]$
CG_2			$\frac{CG_2}{2D_3^2}\times G_1.(\lambda - St_3)$
CG_3			$\frac{CG_3}{2D_3^2}\times G_1.G_2$

Note. - the explicit terms of the H:D elasticities to tetrasporophyte parameters are identical, but stage 1 is replaced by stage 4, 2 by 5 and 3 by 6, and the equations are multiplied by -1.

Implicit terms of the H:D elasticities

Each of the three parcels of the implicit terms of the H:D elasticity to parameter p (equation 4) can be further decomposed into one parcel for the numerator and one parcel for the denominator (Table II). The first term of every equation ($\partial\lambda/\partial$p) represents the sensitivity of λ to parameter p that is calculated as (Caswell 2001):

$$\frac{\partial\lambda}{\partial p} = \left(\bar{v}'.w'\right)_{ij} \qquad \text{(eqn 6)}$$

where w is the dominant right eigenvector, $\bar{\mathrm{v}}$ is the complex conjugate of the dominant left eigenvector and *i* and *j* are the row and column indexes of parameter p in the demographic matrix.

Table II - Implicit terms of Q_1, Q_2 and Q_3 to model parameter p.

Q1: $\mathrm{IE\ of\ N_1 + IE\ of\ D_1}$

Q2: $\mathrm{IE\ of\ N_2 + IE\ of\ D_2}$

Q3: $\mathrm{IE\ of\ N_3 + IE\ of\ D_3}$

N1: $\frac{\partial\lambda}{\partial p}.\frac{p}{N_1}\left(2\lambda + G_1 - St_2 - St_3\right)$

D1: $-\frac{\partial\lambda}{\partial p}.\frac{p}{D_1}\left(2\lambda + G_4 - St_5 - St_6\right)$

N2: $\frac{\partial\lambda}{\partial p}.\frac{p}{2.N_2^2}S_{tet}\left[Fec_4.\left(2\lambda - St_5 - St_6\right) + Fec_5.G_4\right]$

D2: $-\frac{\partial\lambda}{\partial p}.\frac{p}{2.D_2^2}S_{carp}\left[Fec_1.\left(2\lambda - St_2 - St_3\right) + Fec_2.G_1\right]$

N3: $\frac{\partial\lambda}{\partial p}.\frac{p}{2.N_3^2}\left[\left(2\lambda - St_5 - St_6\right)\left(\lambda - St_4 - CG_4\right) + \left(\lambda - St_6\right)\left(\lambda - St_5\right) - B_{56}.G_5 + G_4\left(B_{45} + CG_5\right)\right]$

D3: $-\frac{\partial\lambda}{\partial p}.\frac{p}{2.D_3^2}\left[\left(2\lambda - St_2 - St_3\right)\left(\lambda - St_1 - CG_1\right) + \left(\lambda - St_3\right)\left(\lambda - St_2\right) - B_{23}.G_2 + G_1\left(B_{12} + CG_2\right)\right]$

Unlike the explicit, the implicit terms to parameters from one life-cycle phase have the same sign as the corresponding elasticities to parameters of the other life-cycle phase. A positive variation in any parameter will increase the population growth rate, λ, which in turn will have a direct (not inverse) effect on the intrinsic elasticities of both life-cycle phases (the numerator and denominator of the quotients, Table II). The effect will have the same magnitude for both phases under ecological similarity of phases whereas it will be unbalanced in the case of ecological dissimilarity. Moreover, the implicit elasticities of N_i and D_i to parameter p can never reverse signs but their sum can. This means that, depending on the situation, an alteration in the population growth rate can benefit the gametophytic, the tetrasporophytic or neither ramets. The model behavior is described in appendix II.

Dynamics of the H:D elasticities

The analysis of the H:D elasticities is presented only for the gametophytic ramets as the tetrasporophytic ramets elasticities will have the same absolute values with opposite signs. The effects of varying the lower level parameters on the H:D elasticities are presented in Figure 2, decomposed in its three components: the Q_1, Q_2 and Q_3,terms of the H:D elasticities representing the growth, fertility and looping paths ratios, respectively. The elasticity to each model parameter individually is not presented. Rather, the elasticity to fertility (F), which is the sum of all the elasticities to gametophytic fertility, to growth (G), which is the sum of all the elasticities to gametophytic ramets' growth and to looping (L), which is the sum of all the elasticities to gametophytic looping, are presented.

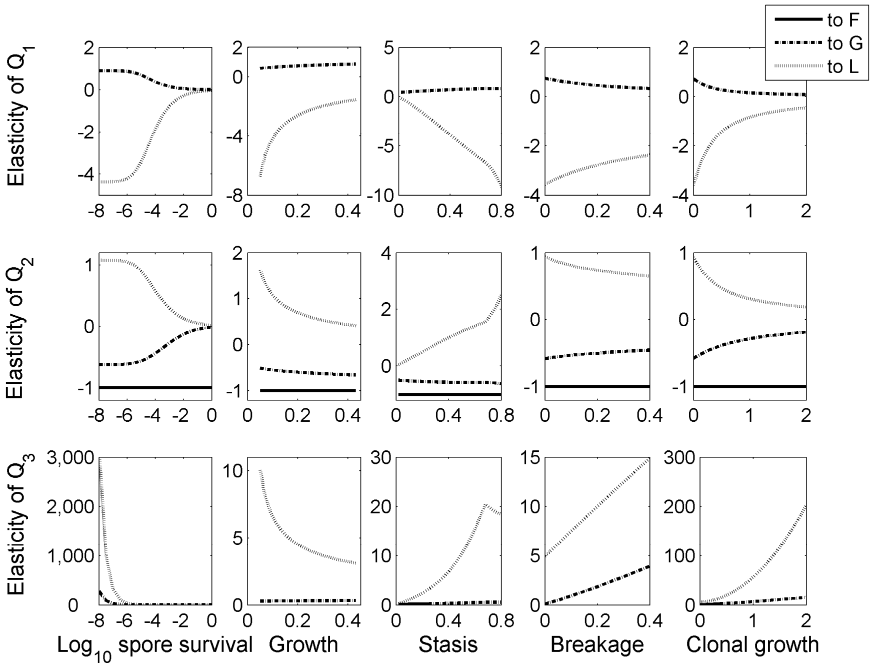

Figure 2 - Effects of varying the lower level parameters on the elasticities of the H:D (Q1, Q2 and Q3 terms) to the gametophytic ramets' fertility parameters (F), to the gametophytic ramets' growth parameters (G) and to the gametophytic ramets' looping parameters (L).

The analysis shows that when fertility (manipulated through spore survival) is low, the H:D is drastically affected by looping parameters through their direct effects on the looping paths ratio, Q_3 (Fig. 2). The elasticity of the H:D to looping when fertility is low is by far the highest of all elasticities, showing that in species with low fertilities very small differences in ramets' stasis, breakage or clonal growth among phases have major effects on the H:D. On the other hand, when fertility is high, the H:D elasticities are low, and thus the H:D is not much responsive to population parameters. High H:D elasticities to looping are also observed when the looping vital rates are high, in particular the clonal growth rates (Fig. 2), even though they are two orders of magnitude lower than the previous case.

The elasticities of the reproduction path (Q_2) to fertility parameters have the value of -1 in all simulations (Fig. 2). The influence of the fertility path on the H:D through the reproduction path Q_2 is negative because it contributes to the other phase. It is 1 because when fertility changes in a certain proportion it also changes in the exact same proportion the offspring of the other phase. As a change in fertility does not affect the population structure within each phase (contrary to the other population parameters) the whole phase numbers change in the same proportion of the fertility change.

Another interesting dynamics happens for the H:D elasticities to growth. These rates contribute to their own phase through the growth and looping paths and to the opposite phase through the fertility path, as shown both by the signs of the elasticities of Q_1, Q_2 and Q_3 to growth parameters and by figure 2. An example of the H:D response dynamics to growth, structured by size class, is shown in figure 3, plotted against spore survival ranging from 10^{-3} to 10^{-6}. The H:D of each size class was estimated simulating a tetrasporophytic ramets' growth 10% smaller than the gametophytic ramets' growth. In this case haploids dominate in bigger size classes (H:D > 1) whereas diploids dominate in smaller size classes (H:D < 1).

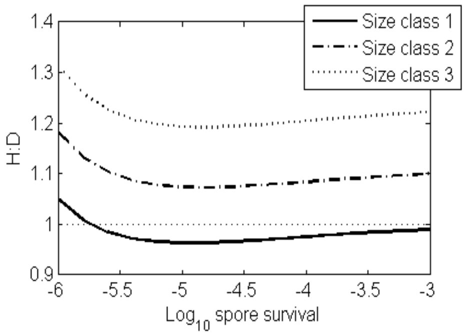

Figure 3. The H:D of each size class when tetrasporophytic ramets' growth is 10% smaller than the gametophytic ramets' growth and the spore survival ranges from 10^{-3} to 10^{-6}.

The effects of ecological dissimilarity between the isomorphic phases of biphasic life cycles on the H:D are further explored in Figure 4 in the case of varying fertility. The other lower level parameters are not presented, as their effects are negligible compared to fertility. As expected, the H:D is more uneven when dissimilarity increases. The major effects on the H:D derive from dissimilarities on the looping path when spore survival decreases (Fig 4, C). In this case, slight differences in the looping vital rates will have a drastic effect on the H:D. A looping dissimilarity of just 1% less in the diploid phase than the haploid was enough to reverse the ploidy ratio to 10:1 or even 100:1 given a sufficiently low fertility. Lower effects on the H:D (by one order of magnitude) derive from dissimilarities in the growth paths when spore survival decreases (Fig 4, B). On the other hand, when fertility is high, the H:D is not much affected by dissimilarities in the growth or looping paths (Fig 4, B and C). The dissimilarities on the fecundities affect the H:D, independently of the fertility level of the population (Fig. 4, A). This is because the elasticities of the H:D to fertility in each phase always add up to 1 (Fig. 2).

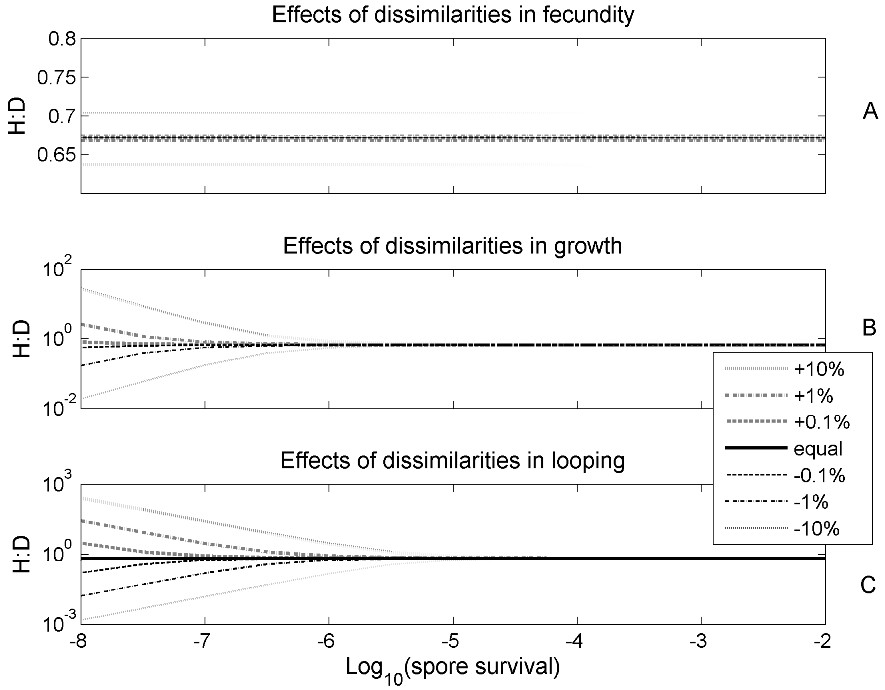

Figure 4. Effects of dissimilarities between phases in fecundity (F), growth (G) and looping (L) under varying fertility (spore survival) on the H:D. All the simulations were derived from the *Gelidium sesquipedale* null hypothesis of a 0.67 H:D. Ploidy dissimilarities (pd) of (±) 0.1%, 1% and 10%. $P_{haploid}=(1+pd)*P_{diploid}$, where P may be F,G or L, i.e the sum of all fecundities, growth or looping in a phase.

The triangular ordination of the elasticities of the population growth rate (λ) and H:D is presented in Figure 5 for hypothetical populations whose demographic matrices were manipulated to represent life strategies from those dominated by fertility, to those dominated by growth and to those dominated by looping. Each axis (one of the sides of the triangle) represents the percentage of the total elasticities of H:D or λ that is relative to an elasticity to F, G or L. The demographic matrix with the left-most coordinate in the triplot had the most fertility dominated life strategy and was simulated with a spore survival rate of $10^{-1.19}$. As spore survival was increased the accepted demographic matrices migrated towards the looping dominated corner of the plot (the right corner). The right-most demographic matrix was simulated with a $10^{-7.97}$ spore survival rate. The elasticities of H:D have the same behavior as the elasticities of λ, making a clear shift in the life-cicle dominance from fertility to survival. The H:D elasticities to the growth parameters are always lower than the λ elasticities to growth. This shows that the growth vital rates have a lower effect on the H:D than on the population growth rate.

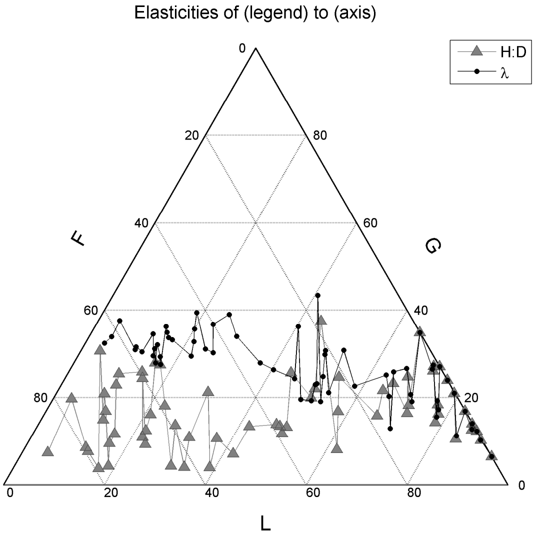

Figure 5. Triangular ordination of both H:D and population growth rate (λ) elasticities to fertility (F), growth (G) and looping (L) parameters of hypotetical populations.

DISCUSSION

This study provides the theoretical knowledge to assess the effects of intrinsic population processes on the ploidy ratio, including size/stage structure, vegetative recruitment and negative ramet growth (transitions to lower classes) effects. Previous numerical attempts to this question (Scrosati and DeWreede 1999, Thornber and Gaines 2004, Fierst et al. 2005) are included in this general model. In fact, the same numerical solutions of previous simulations are obtained with our stage/size structured model (results not shown).

The focuses of the previous attempts to assess the demographic traits that drive the patterns of phase dominance have been the sexual reproduction traits. We showed here that a complex interaction among vital rates determines the patterns of phase dominance of biphasic life cycles. Three co-occurring processes (quotients of equation 4) may dominate the dynamics of the population, determining, by themselves or in combination with the others, both its growth rate (λ) and its H:D: i) the flux of ramets to higher size classes within the same phase of the life cycle (the growth path), ii) the flux of ramets to the other phase of the life cycle (the fertility path) and iii) the looping flux within the same life-cycle phase, which includes both stasis, sequences of growth followed by breakage or clonal growth (the looping path).

In species whose demographics are dominated by fertility or by a gradient between fertility and growth, the H:D (and λ) is mainly determined by the fertility path whereas growth and looping fluxes have low contributions. In this case, the H:D elasticities to every vital rate are low and a H:D different than one can only be set when there are evident vital rate differences between phases. On the other hand, in species where fertility is low and loop-contributing vital rates are high, the fate of the ramets is the main factor regulating the population dynamics. In this case, the H:D is particularly elastic to looping within the same phase. The ploidy ratios of such species may be highly deviated from 1 with even slight phase differences in looping processes (survival, breakage and vegetative growth).

The models developed elsewhere to assess the demographic traits that drive the patterns of phase dominance in complex life histories have been focused on species with isomorphic phases, in particular the red algae (Scrosati and DeWreede 1999, Thornber and Gaines 2004, Fierst et al. 2005). Isomorphic phases are often considered to be ecologically similar, and thus to have similar vital rates in both phases. However, as stated above, our results show the importance of considering subtle differences in frond survival, breakage and vegetative growth between isomorphic phases as they can determine the dominance of one phase over the other. Thornber (2006) had already pointed out that these subtle differences should be taken into account. These can even reverse the phase dominance expected by the fertilities' ratio. This is a possible explanation for the gametophyte dominance of the Gris-Nez high-intertidal population of *Gracilaria gracilis* studied by Engel et al. (2001) in spite of the higher gametophyte fertility and no evident dissimilarities between phases. As expected, *G. gracilis* ploidy ratio elasticities to survival were much higher than to fertility, suggesting that slight differences in survival between phases may be ecologically relevant in determining the H:D and yet be very difficult to detect empirically.

Subtle, yet potentially significant, morphological differences have been detected in species with isomorphic life cycles, such as larger and less branched tetrasporophytic ramets of *Gelidium sesquipedale* (Santos and Duarte 1996) or differences in branch angle and a tendency for dichotomic vs proliferative primary branches in *Ceramium codicola* (Lewis and Lanker 2004). These may have consequences in terms of hydrodynamic forces acting on fronds and thus on frond breakage and/or survival. Slim differences in survival rates can also arise from differences in biochemical composition of fronds. Carrington et al. (2001) found that the gelling kappa-type carrageenans of the gametophytes' distal tissue of *Chondrus crispus* make them stronger, more extensible and stiffer than the tetrasporophytes' distal tissue composed of weaker nongelling lambda-type carrageenans. They further argue that the kappa-type carrageenans may also render gametophytes more resistant to desiccation and herbivory. Thornber et al. (2006) tested for herbivore selectivity among tissue types of the isomorphic red alga *Mazzaella flaccida*. They found important differential grazing by snails for gametophyte reproductive tissue over other tissue types that may play a role in algal population biology.

The above morphological, biochemical and physiological differences between phases may influence the competitive effect of one phase over the other. Hughes and Otto (1999) investigated these effects with a genetic model for the evolution of life cycles that incorporated haploid and diploid carrying capacities and relative competitive effects. They concluded that evolutionary stable haploid-diploid life-cycles may evolve as long as resource competition between haploids and diploids is lower than competition within each phase. This implies that there must be some degree of niche differentiation between phases. Hughes and Otto's (1999) model is spatially adimensional and is solved for steady state, resulting that niche differentiation is neither spatially nor temporaly resolved. It is a conditional differentiation where the two phases explore differentially the same environment at the same time. A trade-off is established between phases so that when one phase is better at a particular trait, the other phase is better at another. Shmida and Ellner (1984) suggested earlier the existence of conditional differentiation in the case of the coexistence of competing plant species. They predicted the coexistence of two ecologically similar plant species where one species emphasized fecundity and the other adult survivorship.

The trade-off associated to conditional differentiation that Hughes and Otto (1999) tested occured within survival. We showed that a slight missmatch in a trade-off within the looping path is enough to set a biased H:D, but it needs to be a wide missmatch within the fertility or growth path to have the same effect. Furthermore, a trade-off may also occur among distinct paths (fertility, growth and looping). For example, a small dissimilarity in survival (looping path) that has a strong effect on the H:D may be compensated by an opposing and large dissimilarity in growth. In populations with fertility dominated life-strategies where dissimilar growth rates between phases have significant contributions to both fertility and growth paths, the resulting change in phase dominance from smaller to bigger size classes (Fig. 3) has the potential to yield the necessary niche partition. Finally, if one phase benefits from the opposing phase's better ability to reproduce, this can not be balanced by the opposing phases better ability to survive. It would mean that the average ramet of the opposing phase would be better at allocating resources both to survival and reproduction, and this is not likely. Niche partitioning theory has been used for explaining the evolution of biphasic life cycles (Hughes and Otto 1999). This theory relies on models of competition (Lotka-Voltera) between two biological entities, in this case not species but the two phases of a life cycle. These models do not take population structure into account. As a consequence, when ramets of one entity grow faster their reproductive output will increase, as ramets will earlier become reproductive. If population structure is considered, faster growth of some ramets does not only contribute to an increase in reproductive output, but also to an increased relative density of reproductive ramets. Using niche partitioning theory in biphasic life cycles Hughes and Otto (1999) have not been able to access the role of growth rates, thereby overlooking a unique feature of biphasic life cycles with high reproductive output. In this type of life cycles a phase with higher ramet growth rates does not only contribute to its dominance in larger adults, as in the classical competition models, but also contributes to the dominance of the opposite phase in the smaller ramets, due to the connectivity between the two phases of the life cycle. This produces a negative feedback and should lead to a stable equilibrium for the coexistence of both phases of the life cycle even if competition between phases is high.