CHAPTER 4

Responses of the haploid to diploid ratio of isomorphic biphasic life cycles to time instability

ABSTRACT

Most previous modelling of the haploid-to-diploid ratio (H:D) in biphasic life cycles relied on estimates of the stable population growth rate and structure. This is a type of analysis that projects the average population dynamics given current conditions. However, the environment is hardly constant but has both periodic and random instabilities over-imposed. It was the objective of this work to unveil how the H:D responds to time instability, and thus to launch the basis for future research on the adaptation of isomorphic biphasic life cycles to unstable environments. It was found that ploidy phase dissimilarities on the demographic matrix and in the initial population structure both cause an inevitable H:D time variability as a consequence of the life cycle structure and independent of the environmental seasonal cycle. The specificities of these H:D time series depend on the type of life strategy and ploidy dissimilar vital rates. Furthermore, ploidy dissimilar fertility or growth rates cause a cyclic oscillation of the H:D that hardly matches the seasonal cycle. If there is a ploidy fitness ratio associated to the environment seasonal cycle, then the misfit between these two cycles may be problematic to isomorphic biphasic life cycles. This should not happen with ploidy dissimilarities in the ramet looping rates (stasis, breakage and clonal growth, all respective to survival) because these induce a H:D variability which is monotonical and directly proportional to the ploidy looping ratio.

Keywords: Biphasic, demographic matrix, G:T, H:D, isomorphic, life cycle, time variability, transient trajectory.

INTRODUCTION

In demographic models, provided that the life cycle is irreducible, i. e. all the stages contribute to at least one other stage, and that the transitions among stages do not vary with time or density (stable environment, density independence), the population will approach asymptotically a stable population structure and growth rate (Caswell 2001). Until stabilization the population trajectory will generally oscillate around a central tendency given by the asymptotic stable trajectory. It is called the transient phase, during which the population trajectory and dynamics are determined both by the life cycle properties and by the initial population structure (Caswell 2001). Most of the analyses on demographic models of haploid-diploid life cycles have focused on the stable population growth and structure (Richerd et al 1993, Hughes and Otto, 1999, Hall 2000) These are projections of the population structure at steady-state would the vital rates remain the same, which are very helpful at determining the populations dynamics but must not be confounded with forecasting. This is also the particular case of the analyses of the reasons why the H:D of species with biphasic life cycles vary, in particular when phases appear to be isomorphic and thus are expected to be ecologically undifferentiated (Engel et al 2001, Thornber and Gaines 2004, Fierst et al 2005, second chapter, third chapter). The H:D time variability has been documented in seaweed species (Engel et al 2001, Otaiza et al 2001, Thornber and Gaines 2003, Scrosati and Mudge 2004a and b, and Dyck and deWreede, 2006). Furthermore, the environment is not constant and stable environmental conditions are not likely to occur. In those particular cases when the environment is stable long enough the population might attain the stable population structure, but most often the variant environment may be expected to drive a natural population from one transient phase to another. Therefore, it is reasonable to expect populations of biphasic life-cycle algae species to endure more time at an unstable transient trajectory than at a stable one, highlighting the relevance of understanding the dynamics of the transient phase.

The main questions investigated in this work are “What is the H:D variability under transient conditions?” and “How this variability relates to the different life strategies, i.e. those dominated by fertility, looping or growth?”. The second chapter showed how these three co-occurring processes modulate the dynamics of populations of biphasic life cycle species, determining both their growth rates and ploidy ratios. In order to assess these questions, the H:D variability was simulated using the previous developed models in the second and third chapters and imposing a differentiation between the haploid and diploid abundances in the initial population structure and/or a conditional differentiation on fertility, growth or looping rates between ploidy phases. Hughes and Otto (1999) showed the importance of conditional differentiation between phases (their ability to explore the environment differently) in order to avoid the extinction of one phase through evolutionary time. The oscillatory properties of the transient phase of the H:D such as its duration, wave amplitude and wave length, were then analyzed and related to the three basic life strategies, i.e. those dominated by fertility, growth or looping.

METHODS

The matrix demographic model

The model used in this study (equation 1) is based in the biphasic life cycle, stage/size structured model previously used in the second chapter for the study of the H:D dynamics of perennial algae in the stable population structure, for which the vital rates were observed to be adequately aggregated into three groups: the fertility vital rates (F), the growth vital rates (G) and the looping vital rates (back to the same ploidy) (L). It is a ramet based model, which means the units of the adult stages are the individual fronds that may rise from the same holdfast. The matrix demographic model is represented by the 8 dimensional population vector and the (8,8) dimensional population matrix (equation 1). The gametophytes were separated into tetraspores and state (size) variables 1, 2 and 3, whereas tetrasporophytes were separated into carpospores and state (size) variables 4, 5 and 6. The growth vital rates (g), the looping vital rates (l), and the spores' survival (ss) are probabilities and hence vary between 0 and 1. These add up to survival, which cannot be higher than 1. There are two ways a ramet may loop back, it may stay on the same size class (stasis) or it may break to a smaller size class. The probability of stasis was considered to be 0.75 (6/8 for size class 3 and 3/4 for size class 2, equation 1) and the probability of breakage to smaller stages equal to 0.25 (1/8 from size class 3 to 2 plus 1/8 from 3 to 1; 1/4 from 2 to 1, equation 1). These probabilities were based on the analysis of the vital rates of the red seaweed *Gelidium sesquipedale* (Santos and Nyman, 1998). It was verified that the model results were not significantly altered when other probabilities were considered. The fecundity transitions (fec_x) are production rates and hence vary between 0 and $+\infty$.

The dissimilarities of fecundity, growth and looping transitions between phases were introduced in the model by d_F, d_g, and d_l, respectively, which represent the proportion of the diploid vital rates relative to the haploid. Model assumptions are: (i) in each time step only the transitions represented in the model can occur, (ii) the model is a first order Markovian process, (iii) the model is deterministic and (iv) the projection time is one month.

$$\left[\begin{array}{cccc:cccc} 0 & 0 & 0 & 0 & 0 & d_F \times fec_4 & d_F \times fec_5 & d_F \times fec_6 \\ ss & l & l/4 & l/8 & 0 & 0 & 0 & 0 \\ 0 & g & 3l/4 & l/8 & 0 & 0 & 0 & 0 \\ 0 & 0 & g & 6l/8 & 0 & 0 & 0 & 0 \\ \hdashline 0 & fec_1 & fec_2 & fec_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & ss & d_L \times l & d_L \times l/4 & d_L \times l/8 \\ 0 & 0 & 0 & 0 & 0 & d_G \times g & d_L \times 3l/4 & d_L \times l/8 \\ 0 & 0 & 0 & 0 & 0 & 0 & d_G \times g & d_L \times 6l/8 \end{array}\right] \times \left[\begin{array}{c} Tet. \\ 1 \\ 2 \\ 3 \\ \hdashline d_{ss}.Carp. \\ d_1.4 \\ d_2.5 \\ d_3.6 \end{array}\right] \qquad \text{(eqn.1)}$$

Several thousand different deterministic demographic matrices were tested and compared. Each of them was assembled by randomly choosing their matrix entries under the following conditions:

(i) fecundities were given a fixed value of 100 to the smaller size class, 500 to the medium and 1000 to the larger. The values themselves were chosen arbitrarily with the sole objective to reflect the fact fecundity increases exponentially with ramet size. Still, care was taken to keep the values of the fecundities simple yet close to the values observed by Santos and Nyman (1998).

(ii) spore survival (ss) could range from 10^{-6} to 10^{0}. These encompass the spore survival range observed for most seaweeds and were further expanded to the highest survival possible (10^{0}=1=100%). Testing a wide range of spore survival was fundamental because the H:D dynamics varies extremely with the amount of fertility output (Fierst et al 2005, second and third chapters)

(iii) growth (g) and looping (l) could range from 0 to 1. These were chosen to test the vital rates in a wide range of values.

(iv) The dissimilarity coefficients d_F, d_G and d_L were tested for values between 0 and 2, i.e. the diploid rates were from 0% to 200% of the haploid rates. Still, coefficients largely apart from 1 (100%) were only tested, and may only reasonably be expected, over fertility rates (d_F). These coefficients were fixed and not randomly selected.

It was also tested for the effects on the H:D variability of dissimilarities between ploidy phases in the initial population structure. These were imposed by means of the dissimilarity coefficients d_S, d_1, d_2 and d_3, which set the initial proportionality of the diploid stage abundances relative to the haploid stage abundances for the spores and size classes 1, 2 and 3. These coefficients were fixed and not randomly selected.

Life strategies of demographic matrices

The population's growth rate (λ) and the elasticities of both λ and H:D to fertility, growth and looping were estimated for every demographic matrix produced. Then, the matrices which both population growth and survival rates were credible for natural populations, i.e. population growth varying between 1 and 1.11 and survival ≤1, were selected for further analysis. These were plotted in triangular plots (see Franco and Silverthorne 1996, Oostermeijer et al 1996, second and third chapters) of the elasticities of λ to fertility (F), growth (G) or looping (L) parameters. In these plots,.demographic matrices (populations) with different combinations of elasticities to F, G and L, are distributed within the triangle. The populations much more elastic to only one type of vital rates are located closer to the respective vertices of the triangle.

Analytical solution of the transient phase

The population's structure and abundance at a given time t is given by the vector N_t, which is a function of the eigenvalues (λ_i) and eigenvectors (w_i) of the population's demographic matrix and the coefficients for the initial conditions (c_i):

$$N_t = c_a\lambda_a^t\begin{bmatrix} w_1 \\ w_2 \\ \dots \\ \dots \\ w_8 \end{bmatrix}_a + c_b\lambda_b^t\begin{bmatrix} w_1 \\ w_2 \\ \dots \\ \dots \\ w_8 \end{bmatrix}_b + \dots + c_h\lambda_h^t\begin{bmatrix} w_1 \\ w_2 \\ \dots \\ \dots \\ w_8 \end{bmatrix}_h \qquad \text{(eqn.2)}$$

The c coefficients enable the initial population's vector (N_0) to be written as a linear combination of the eigenvectors (Caswell 2001). This can be seen if time t is set to 0 in equation (2). The eigenvalues (λ), eigenvectors (w) and c coefficients have two possible forms: as a strictly real set or as a set of complex conjugated pairs. In the first case they can be written exactly as in equation (2) or transposed to polar coordinates, in which $c_i = \gamma_i * \text{sen}(\rho_i)$ and $w_i = \sigma_i * \text{sen}(\omega_j)$. In the latter case the complex conjugated pair (equation 3.a) can be rearranged with the eigenvectors and c coefficients in Cartesian coordinates or with the eigenvectors and c_i coefficients in polar coordinates (equation 3.b),

$$c_a\lambda_a^t\begin{bmatrix} w_1 \\ w_2 \\ \dots \\ \dots \\ \\ w_8 \end{bmatrix}_a + \bar{c}_a\bar{\lambda}_a^t\begin{bmatrix} \bar{w}_1 \\ \bar{w}_2 \\ \dots \\ \dots \\ \\ \bar{w}_8 \end{bmatrix}_a \quad ; \quad 2\left|\lambda^t.\gamma\right|.\left(\cos(\theta t)\begin{bmatrix} |\sigma_1|.\cos(\rho-\omega_1) \\ |\sigma_2|.\cos(\rho-\omega_2) \\ \dots \\ |\sigma_8|.\cos(\rho-\omega_8) \end{bmatrix} - \sin(\theta t)\begin{bmatrix} |\sigma_1|.\sin(\rho+\omega_1) \\ |\sigma_2|.\sin(\rho+\omega_2) \\ \dots \\ |\sigma_8|.\sin(\rho+\omega_8) \end{bmatrix}\right)$$

(eqn.3a) (eqn.3b)

where λ and θ are the ith eigenvalue's module and angle, γ and ρ are respectively the c_i coefficient's module and angle, and σ and ω_j are the module and angle of the eigenvector's entry w_{ji}.

Once the form of the analytical solution was formulated, the demographic transient dynamics was assessed from the sub-dominant eigenvalues and eigenvectors and from the c coefficients. The sub-dominant eigenvalues are the biases from the central tendency of the population growth rate and the sub-dominant eigenvectors are the biases from the central tendency of the population structure. The central tendency is given by the dominant eigenvalue and eigenvector. Thus, there knowledge is still fundamental for the analysis of the transient phase. Each c coefficient for the initial population structure is also the coefficient for the initial momentum of its bias (the corresponding eigenvector). These initial momentums were converted to the relative initial momentums. Their formulas were $\gamma_b/\sum\gamma_i$ for the real sets and 2* $\gamma_b/\sum\gamma_i$ for the complex conjugate sets. The persistence rate was estimated as $|\lambda_b|/\lambda_a$, where λ_b is a sub-dominant eigenvalue whereas λ_a is the dominant eigenvalue. This is the inverse of the damping ratio proposed by Caswell (2001). The persistence rate shows the rate at which the initial momentum persists and thus the highest it is, the longest the population is at its transient phase. The oscillatory properties of the transient trajectories were fully defined by the eigenvalues (for the persistence rate), eigenvectors (for the population structure) and c coefficients (for the initial momentum). In Appendix IV is presented a detailed explanation of these metrics and how they interact to yield a determined transient trajectory of the population growth rate and H:D.

Responsiveness analysis

It was evaluated how responsive were the oscillatory properties of the transient trajectory to dissimilarities between ploidy phases. This was done by estimating the following:

(i) Elasticity of the persistence rate ($|\lambda_b|/\lambda_a$);

(ii) Elasticities of the phase ratios within the eigenvector (σ_i/σ_{i+4}). The amplitudes of the oscillations of each stage were given by the respective entry in the eigenvector. Yet, it was more feasible and interesting to test and present the ratio between the amplitudes of the ploidy correspondent stages;

(iii) Sensitivity of the relative initial momentum ($\gamma_b/\sum\gamma$). In the absence of any kind of ploidy dissimilarities some γ diverged zero only at very low decimal places and it was due to precision error. The elasticities were automatically set aside as they required this value in the denominator.

It was estimated the elasticities and sensitivities to the ploidy phase dissimilarities in the demographic matrix (d_F, d_G, d_L) and in each stage of the initial population vector (d_S, d_1, d_2 and d_3) changing these independent variables by 0.01 from an initial value of 1 (i.e: no dissimilarities). The initial population vector was always N_0=[1 1 1 1 1 1 1 1].

RESULTS

The demographic matrices were represented in the triangular plot using their relative elasticities of λ to F, G and L as coordinates and giving a colour scale to the persistence rates of the sub-dominant eigenvalue (fig.1). It can be seen that both fertility and survival life strategies (respectively in the F and L lower corners of the triangle; these are the F and L domains) had high persistence rates, which meant that, in the absence of density dependency, any population with one of these strategies (in one of these domains) would have its populations subject to long transient phases. There were no demographic matrices with growth dominated life strategies. However, where the growth relevance was higher (closer to the upper horizontal edge) the transient phase could also be long.

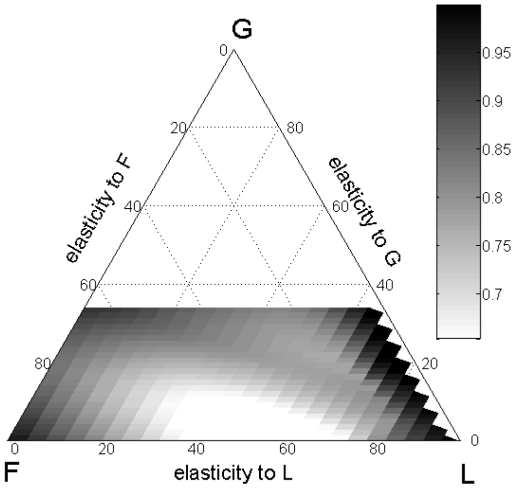

Figure 1 – Overall persistence rate (color scale) plotted upon the triangular ordination of the λ elasticities to fertility (F), growth (G) and looping (L). The coordinate of a point in each axis is given by a line parallel to the lines that intercept the axis coming from its right side.

So, for the sake of synthesis this area was considered the growth domain, although it was somewhat abusive to call it that. Separating these F, G and L domains there was a well marked area of lower persistence rates where the transient phase was short and its dynamics little significant. To this area slipped the populations with demographies between fertility and looping dominated. Each of these domains of the ternary plot with a high persistence rate was associated to a different sub-dominant set of eigenvalue, eigenvector and c coefficient (fig.2). So, the three types of life strategies had different transient phase characteristics with different responses to dissimilarities among life cycle phases.

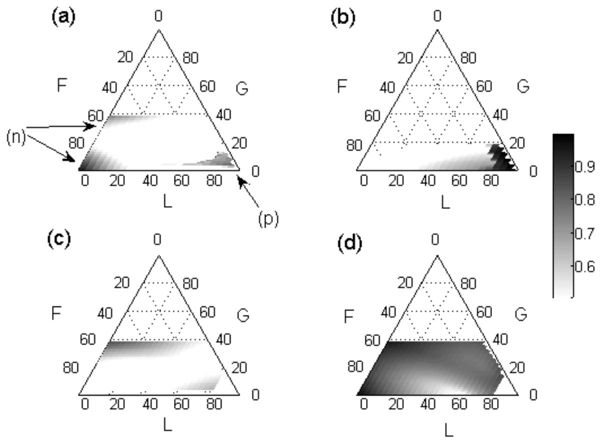

Figure 2 –Persistence rates (color scale) of the specified sets plotted upon the triangular ordination of the λ elasticities to F, G and L. The coordinate in each axis is given by a line parallel to the lines that intercept the axis coming from its right side. (a) Real and Equal Set, (b) Real and Symmetric Set, (c) Complex Conjugate and Equal Set and (d) Complex Conjugate and Symmetric Set. The (a) with (n) a negative and (p) a positive eigenvalue.

Subdominant sets of eigenvalues, eigenvectors and c coefficients

For the several thousand demographic matrices analysed the dominant eigenvalue, eigenvector and c coefficient were always strictly real and positive. This was the expected from an irreducible primitive life-cycle. Moreover, there were typically four types of sets of subdominant eigenvalues, eigenvectors and c coefficients that determine the duration, the wave amplitude and the wave length of the transient phase of the population trajectory. One of the ways to characterize these sets was as either strictly real or complex conjugated pairs. The other way was according to the eigenvector's equality or symmetricity for the correspondent stage/size classes of both phases of the life cycle (w_i and w_{i+4} in equations 2 and 3). What type of sets did occur, which was the sub-dominant one, how fast did each of them fade way and which were their oscillatory characteristics, depended on the type of life strategy and the magnitude of the ecological dissimilarity between ploidy phases. The four possible types of sets were:

1. *Real and equal*

This was a set of a strictly real eigenvalue, eigenvector and c coefficient (ex: equation 1a of Appendix V). As this set had its imaginary components null its formulation could be simplified to the real components (ex: equations 1b and 1c of Appendix V). The eigenvector was equal for the correspondent stage/size classes of both ploidy phases of the life cycle ($\omega_{i+4}= \omega_i$) and thus $\cos(\omega_i)=\cos(\omega_{i+4})$. The eigenvalue and the entries in the eigenvector could be positive or negative, thus splitting the set into two sub-types:

1.1. *With a negative eigenvalue*

Its persistency rate shows it was only important in the fertility domain (fig.2a). The eigenvector had a structure that alternated positive and negative signs for the consecutive stages within each phase (equation 1 of Appendix V). It was the same period of its real, negative eigenvalue as it was raised to t. So, with time each size class also alternated between being favoured or prejudiced with that same period of 2. This set simulated pulses of individuals that went up the demographic structure of the population, from spores to the bigger ramets (see the sequence of pulses in fig.3 A, B and C). These pulses were caused by the most immediate production of offspring. This is the shortest, fastest path of growing to the first size class and immediately to reproduce, resulting in a loop with a size of four transitions which took four time steps (4t) to revolve. However, as each phase started with its own offspring there were two simultaneous symmetric pulses resulting in an oscillation with a period of half the time (2t) the loop took to complete itself. These pulses were more prevailing the higher the relative fecundities of the smaller size classes (fig.3 D). Ecological dissimilarities brought a bias between complementary entries in the eigenvector ($\sigma_i \neq \sigma_{i+4}$), which gave a phase a cycle with a wider amplitude (fig.3 A, B and C). However, when it was estimated its linear combination with the dominant set it resulted that the ploidy phase abundances always kept the same proportionality (fig.3E) and so the H:D did not cycled. It meant that the Real Equal Set with a negative eigenvalue could only carry information about the component of these pulses that was even between phases. As a consequence, for simulations in the fertility domain where there were no dissimilarities imposed, this set showed the highest initial relative momentum. It was always about twice the relative momentums of the other sets.

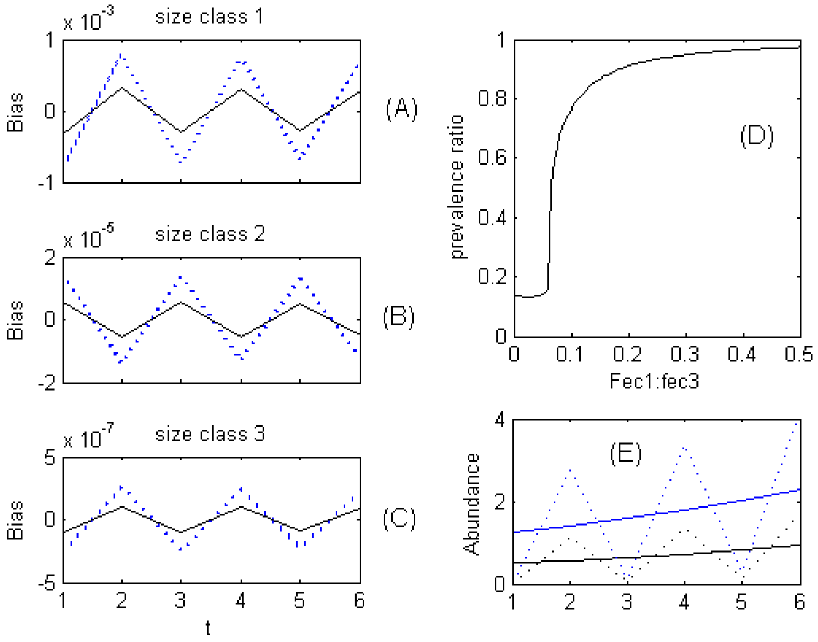

Figure 3 – Real Equal Set with a negative eigenvalue. In A, B and C the black solid line is haploids and the blue dotted line is diploids. The bias in each size class was standardized to the bias in the spores. In E the black lines are haploids, the blue lines are diploids, the solid lines are the central tendency given by the Dominant Set and the dotted lines are the linear combination of the Dominant Set with the Real and Equal Set.

1.2. With a positive eigenvalue

Its persistence rate shows it was only of moderate importance in the looping domain (fig.2a). This set did not produce any periodic alternation in the bias ($\theta=0$). It simply faded away monotonically with time. Ecological dissimilarities produced a bias from the central tendency that always overrated the abundance of the same ploidy phase (although fading away). The favoured ploidy phase was always the same as the favoured by the dominant set and it was always favoured in that same amount.

2. Real and symmetric

This set was only relevant for the populations in the looping domain, where it had a very high persistence rate (fig.2b). This was a set with a strictly real eigenvalue, eigenvector and c coefficient (ex: equation 2 of Appendix V). The eigenvalue was always positive ($\theta=0$) and the eigenvector had symmetrical signs for the correspondent stage/size classes of both phases of the life cycle ($\omega_{i+4}= \pi+\omega_i \Rightarrow \cos(\omega_{i+4}) = \cos(\pi+\omega_i) = -\cos(\omega_i)$). Thus it was produced a bias from the central tendency that permanently favoured a phase in detriment of the other. Under ecological similarity $\sigma_i=\sigma_{i+4}$ but the c coefficient was null ($\gamma=0$) and so this set turned obsolete (it was switched off). With phase dissimilarities either on the demographic matrix or in the initial population vector, both $\sigma_i \neq \sigma_{i+4}$ and the c coefficient became non null ($\gamma\neq0$) bringing a momentum to a set (it was switched on) that was responsible for a monotonical transition to stability (fig.4). Often, more of these sets did occur with lesser relevance in the transient dynamics but still enough to eventually make the transition not monotonical (as was the case of size class 3 in fig.4). The linear combination of the real symmetric sets simulated the ploidy uneven component of the slow diffusive flow of individuals up the population structure.

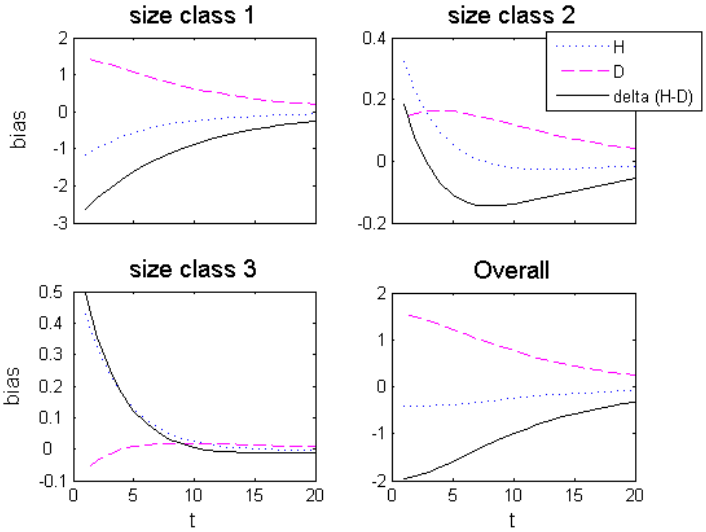

Figure 4 – Trajectory of the linear combination of the real symmetric sets. Simulation in the looping domain with i=-3.8, g=0.05 and l=0.96. Dissimilar L with d_L = 0.9. λ_b/λ_a=0.88, λ_c/λ_a=0.76, λ_d/λ_a=0.67. $\gamma_a/\sum\gamma_i$=0.095, $\gamma_b/\sum\gamma_i$=0.093, $\gamma_c/\sum\gamma_i$=0.172, $\gamma_d/\sum\gamma_i$=0.253.

3. Complex conjugate and equal

This set was very important close to growth domain where it showed a high persistence rate, and lesser important in the looping domain (fig.2c). It was a set of a complex conjugate pair of eigenvalues, eigenvectors and c coefficients (ex: equation 3 of Appendix V). The eigenvectors were similar for the correspondent stage/size classes of both phases of the life cycle. When the pairs were added they yielded a strictly real set in the form of equation 3b that preserved the equality of signs between correspondent stage/size classes of both phases ($\omega_{i+4} = \omega_i \Rightarrow \cos(\omega_{i+4}) = \cos(\omega_i)$). The structure of the added eigenvectors, together with the added complex conjugate eigenvalues, produced a bias from the central tendency that, as time passed, alternated in favouring some size classes in detriment of the others. This set simulated pulses of individuals that went up the demographic structure of the population, from spores to the bigger ramets. The pulses were caused by the bulk production of offspring. This was growing to the larger, more fecund ramets and once there, to reproduce. However, reproduction was not restricted to the biggest ramet size class and thus the average breeder was slightly below 3 ramet size units. It resulted that the average number of transitions in the bulk loop was slightly below eight and thus it took slightly below eight time steps (8t) to revolve. However, as each phase started with its own offspring, there were two symmetric loops generating individuals in two simultaneous pulses, resulting in an oscillation with a period of half the time (slightly below 4t) each loop took to revolve (fig.5). This periodicity was simulated by an eigenvalue with an angle θ in the complex plane of approximately ±π/2 (fig.6).

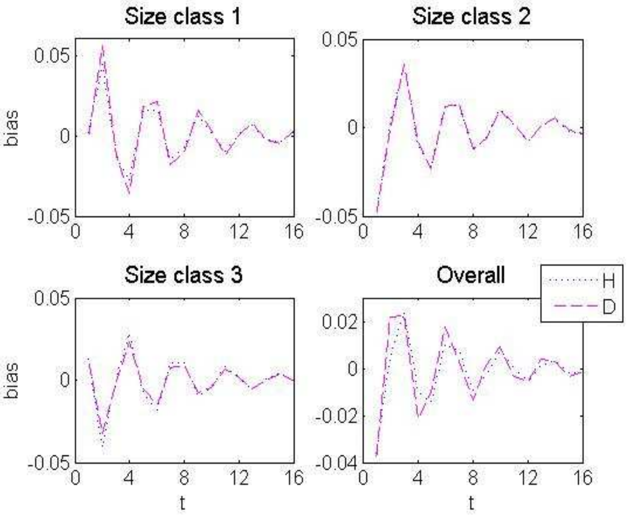

Figure 5 – Bias to the central tendency given by the complex conjugate equal pair of eigenvectors, eigenvalues and c coefficients. Simulation in the growth domain with i=-3, g=0.8 and l=0. This was the demographic matrix with the highest elasticity to G. Dissimilar G with d_G=0.8. Persistence rate = 0.84.

The more concentrated the fecundities were in one size class the higher the persistence rate of the pulses ($|\lambda_i|/\lambda_a$), as individuals diffused less through other paths. The more the initial population was concentrated in one size class the bigger the relative initial momentum of the pulses ($2\gamma_b/\sum\gamma_i$). The σ_i and σ_{i+4} were always approximate despite the amount of dissimilarities between ploidy phases (fig.6). Hence, the amplitudes of the pulses were always very close between the haploid and diploid population structure (fig.5). This proved that this set was only competent for simulating the component of the pulses that was even between ploidy phases. Furthermore, the eigenvalues, eigenvectors and c coefficients responded to dissimilarities changing the absolute value of their entries (λ, σ and γ) while their angle in the complex plane (θ, ω_i and ρ) exhibited insignificant differences (fig.6 but not shown for the c coefficients). It proves dissimilarities change the initial momentum, prevalence rate and amplitude of the pulse but not its period.

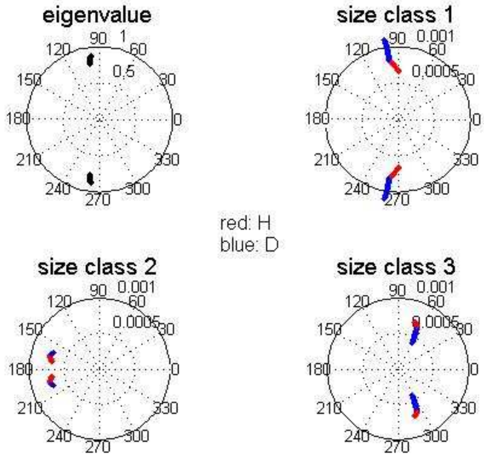

Figure 6 – Polar plots of the complex conjugate equal pair of eigenvectors and eigenvalues. In the eigenvalue is plotted λ_b and θ_b whereas in size class ‘i’ is plotted σ_i and ω_i in red and σ_{i+4} and ω_{i+4} in blue. Simulation in the growth domain with i=-3, g=0.8 and l=0. Dissimilarities tested for d_G from 1 to 0.6 at intervals of 0.02.

4. *Complex conjugate and symmetric*

This set was particularly important in the fertility and in the growth domains but also in the transition from the growth to the looping domain, though with a lesser relevance (fig.2d). This was a set of a complex conjugated pair of eigenvalues, eigenvectors and c coefficients (ex: equation 4 of Appendix V). The eigenvectors were symmetric for the correspondent stage/size classes of both phases of the life cycle. When the pairs were added they yielded a strictly real set in the form of equation 3b that preserved the symmetricity of signs between correspondent stage/size classes of both phases ($\omega_{i+4} = \pi+\omega_i \Rightarrow \cos(\omega_{i+4}) = \cos(\pi+\omega_i) = -\cos(\omega_i)$). This structure, together with the complex conjugated pair of eigenvalues, produced a bias from the central tendency that, as time passed, alternatively favoured some size classes in detriment of others, thus also simulating pulse flows. However, as the signs of the added eigenvector entries were complementary between ploidy phases, these pulses were out of phase but synchronized between ploidy phases (fig.7); meaning that the peaks of one phase were the sinks of the other phase.

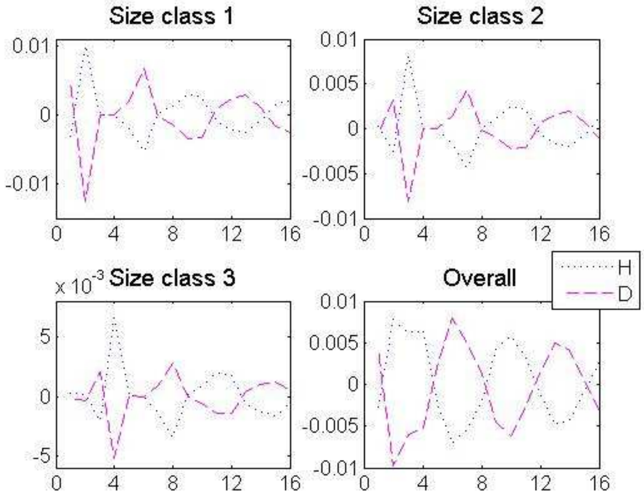

Figure 7 – Bias to the central tendency given by the complex conjugate symmetric pair of eigenvectors, eigenvalues and c coefficients. Simulation in the growth domain with i=-3, g=0.8 and l=0.01. This was the accepted demographic matrix with the higher elasticity to G. Dissimilar G with d_G=0.8. Persistence rate = 0.95.

When simulated in the growth domain these eigenvalues had an angle θ in the complex plane that was half the angle of the complex conjugate equal eigenvalues, thus causing an oscillation with double the period. That was because this complex conjugate symmetric set was only simulating the uneven component of the pulse flow of individuals through the bulk loop in the life cycle. The flow of the unbalance is similar to the flow of a single un-paralleled pulse. However, when simulated in the fertility domain these eigenvalues had an angle θ in the complex plane that was half the angle of the negative real equal eigenvalue. That was because this complex conjugate symmetric set was only simulating the uneven component of the pulse flow of individuals through the shortest loop in the life cycle. So, whatever the life strategy domain and the ploidy uneven pulse flow, the unbalance between ploidy phases was always represented by the complex conjugated symmetric set.

Dissimilarities in the vital rates had little effect in the angle of the eigenvalues, eigenvectors and c coefficients in the complex plane and basically resulted in the change of their absolute values (λ, σ and γ). This proves that dissimilarities did not change the period of the oscillation but rather its amplitude (σ), initial momentum (γ) and prevalence rate (λ). In particular, in the absence of dissimilarities between ploidy phases in both the demographic matrix and the initial population vector, this set was switched off by a null c coefficient (thus, null momentum).

Having presented the dynamics of this set it is now important to reveal that there were usually two of these sets for a given demographic matrix. One related to the shortest loop in the life cycle and the other related to the bulk loop. Which set started stronger and damped away slower depended on the population's stand in terms of fertility *vs* growth domain.

Effects of dissimilarity between ploidy phases

The c coefficients, being different or equal to zero, were like a switch that turned on and off the symmetric sets according to the presence or absence of ploidy dissimilarities. A ploidy even population structure could not be given by the linear combination that contained a ploidy uneven eigenvector. On the other hand, a ploidy uneven population structure could hardly be given by a linear combination exclusively of eigenvectors that tended to be ploidy even. Besides switching on and off, when dissimilarities were imposed, the equal sets reduced their relative initial momentums (the negative sensibilities) while the symmetric sets increased them (the positive sensibilities). This was a consequence of the symmetric sets replacing the equal sets in simulating the flows. Increasing the ploidy dissimilarities also increased the wave amplitude of the uneven component of the flow. Nevertheless, as the oscillations of the size classes were out of phase, these tended to smooth the bias in the overall abundances of the phases (figures 4 and 7).

The responsiveness of the oscillatory properties of each set was only tested in the F, G or L domains where it was previously found relevant (Table I). When in the particular case of the real and symmetric set in the looping domain there were actually several sets of this type. Therefore, it was estimated the sensitivity of the sum of their relative initial momentums ($\sum\gamma_b/\sum\gamma$).

Table I – Responsiveness of the several sets. (a and e) with i=-2, g=0.01 and l=0.05 (a) λ=0.95, θ=πrad and relative persistence rate=0.9. (b and c) with i=-3.8, g=0.02 and l = 0.96 (b) λ = 0.75, θ=0rad and relative persistence rate=0.75. (c) λ=[0.98 0.79 0.63 0.01], θ=[0 0 0 0]rad and relative persistence rate=[0.94 0.76 0.6 0.01]. (d and f) with i=-3, g=0.8 and l=0.01, (d) λ=0.88, θ=±1.71rad and relative persistence rate=0.84. (e) λ=1.001, θ=±1.52rad and relative persistence rate=0.95. (f) λ=0.99, θ=±0.89rad and relative persistence rate=0.95. (g) with i=-3.4 g=0.04 and l=0.91, λ=0.82, θ= ±0.024rad and relative persistence rate=0.81.

to of	d_F:	d_G:	d_L:	d_{ss}	d_1	d_2	d_3
Real and equal set in the fertility domain (a)							
λ_b/λ_a	0.007	-0.002	-0.011	0	0	0	0
σ_2/σ_5	0.499	-0.002	0.011	0	0	0	0
σ_3/σ_6	0.499	-0.992	0.028	0	0	0	0
σ_4/σ_8	0.499	-1.973	0.044	0	0	0	0
γ_b/γ_a	10^{-4}	0.001	0.001	-0.001	-10^{-4}	-0.002	0.003
Real and equal set in the looping domain (b)							
λ_b/λ_a	-0.034	-0.004	-90	0	0	0	0
σ_2/σ_5	0.499	1.499	0.476	0	0	0	0
σ_3/σ_6	0.499	2.514	1.389	0	0	0	0
σ_4/σ_8	0.499	1.499	2.307	0	0	0	0
γ_b/γ_a	-0.004	0.008	0.001	-10^{-5}	0.1	-0.156	0.056
Real and symmetric sets in the looping domain (c)							
λ_b/λ_a	-0.031	-0.012	-0.007	0	0	0	0
σ_2/σ_5	0.499	1.250	17.9	0	0	0	0
σ_3/σ_6	0.499	0.147	13.9	0	0	0	0
σ_4/σ_8	0.499	-0.845	10.8	0	0	0	0
$\sum\gamma_b/\sum\gamma$	0.268	0.226	13	10-4	0.039	0.163	0.364
Complex conjugate equal set in the growth domain (d)							
λ_b/λ_a	-0.021	0.046	-0.004	0	0	0	0
σ_2/σ_5	0.499	1.004	-0.003	0	0	0	0
σ_3/σ_6	0.499	0.005	-0.0002	0	0	0	0
σ_4/σ_8	0.499	-0.985	0.001	0	0	0	0
γ_b/γ_a	-0.071	-0.188	-0.002	0.0001	-0.145	-0.29	-0.111
Complex conjugate symmetric set in the fertility domain (e)							
λ_b/λ_a	0.011	-0.011	-0.012	0	0	0	0
σ_2/σ_5	0.499	0.0006	-0.001	0	0	0	0
σ_3/σ_6	0.499	-0.989	-0.001	0	0	0	0
σ_4/σ_8	0.499	-1.970	-0.002	0	0	0	0
γ_b/γ_a	0.235	0.007	0.008	10^{-4}	0.03	0.148	0.148
γ_b/γ_a	0.194	0.16	0.002	10^{4}	0.14	0.17	0.143

(continues)

(continued)

Complex conjugate symmetric set in the growth domain (f)							
λ_b/λ_a	-0.006	0.014	-0.002	0	0	0	0
σ_2/σ_5	0.499	0.793	-0.0001	0	0	0	0
σ_3/σ_6	0.499	-0.204	-0.005	0	0	0	0
σ_4/σ_8	0.499	-1.193	-0.009	0	0	0	0
Complex conjugate symmetric set in the looping domain (g)							
λ_b/λ_a	-0.032	-0.005	0.054	0	0	0	0
σ_2/σ_5	0.499	0.968	8.719	0	0	0	0
σ_3/σ_6	0.499	-0.308	0.489	0	0	0	0
σ_4/σ_8	0.499	-1.295	-4.275	0	0	0	0
γ_b/γ_a	0.366	0.36	13.1	10^{-4}	0.213	0.239	0.007

The eigenvalues and eigenvectors are exclusively determined by its associated demographic matrix. This is a known algebra theorem. Therefore, both the relative persistence rates and the phase ratios within the eigenvectors were only elastic to changes in the demographic matrix and not in the initial population structure. On the contrary, the c coefficients are determined by both the demographic matrix and the initial population structure. Therefore the relative initial momentums were sensitive to dissimilarities anywhere. The properties of the transient phase were always much more responsive to a particular type of vital rate when in its respective life strategy domain. This was particularly evident for the looping rates, to which the transient phase was much more elastic when in the looping domain.

The phase ratio within the eigenvectors always had 0.499 elasticities to dissimilarities in fertility. This is the same as the constant 0.5 elasticity of the H:D to fertility analytically determined in the second chapter, the difference being the precision error in the current numerical estimates. Dissimilarities in looping rates induced a change in the phase ratio contrary from the change induced by dissimilarities in fertility rates. Dissimilarities in growth induced a change in the phase ratio of the smaller ramets contrary to the change in the phase ratio of the bigger ramets. All this is also in accordance with the previous findings in the second chapter. It is important to retain that the elasticities of the phase ratio within the eigenvector to the dissimilarities were tested increasing the diploid rates and abundances. Therefore, an increase in diploid fertility contributed to an increase in haploids abundance and thus an increase on the phase ratio (positive elasticity). On the other hand, an increase in diploid growth or looping contributed to an increase in diploids abundance and thus a decrease on the phase ratio (negative elasticity).

Systematization of the transient trajectory

The transient trajectory could be perfectly resumed by the several distinct sets of eigenvalues, eigenvectors and c coefficients, each representing a different types of flow of individuals (or model units) up the population structure within each ploidy phase. These were either slow diffusive flows or fast pulse flows, and ploidy even or uneven. Therefore, the transient trajectory could also be classified by identifying which were the important sets in each life strategy domain.

1. *In life-strategies in the fertility domain*

These populations had their transient trajectories characterized by pulses of ramets that came with a short wave length (4t). These pulses were the production and flow of the offspring through the shortest loop in the life-cycle. When two simultaneous pulses occurred, starting at equivalent stages of each phase, the population numbers had long-lasting oscillations with half the period (2t). The component of these pulses that was even between ploidy phases was given by the Real and Equal Set. Nevertheless, dissimilarities between phases either in the life-cycle or in the initial population structure caused the two parallel pulses to oscillate with different amplitudes resulting in a H:D oscillation with double that period (4t; see fig. 8a). This component of the oscillation was given by the Complex Conjugated Symmetric Set. The persistence of these pulses through the shortest loop in the life cycle was increased by dissimilarities between ploidy phases in fertility rates; but it was reduced by dissimilarities between ploidy phases in growth or looping rates because these enhanced the effects of the uneven flow of individuals through other paths and loops. As a matter of fact, the pulse flow of individuals through the main loop was also present and had a higher prevalence rate. However, it always came with a very low initial momentum which made it meaningless.

2. *In life-strategies in the growth domain*

These populations had their transient structures characterized by long-lasting pulses of ramets coming with a big wave length (approximately 8t) and originated by the production and flow of the offspring through the bulk loop in the life-cycle. As most of the offspring production was done by bigger ramets the bulk loop in the life-cycle had a higher number of transitions which took more time to complete. When two simultaneous pulses occurred, starting at equivalent stages of each phase, the population structure suffered oscillations with a period of approximately 4t. This was simulated by the complex conjugated and equal set. In the advent of dissimilarities between ploidy phases the H:D oscillated with double that period (fig. 8b). This was due to the uneven flow of individuals, which was mainly simulated by the complex conjugate and symmetric set. Dissimilarities between ploidy phases in fertility or growth rates had a moderate effect on the initial strength of the uneven component of these pulses and a low effect in the rate at which they prevail. However, dissimilarities in the growth rate of the ramets severely biased the flow of the individuals to the bigger size classes and thus greatly affected the amplitude of the H:D oscillations. Although the transient phase was dominated by the pulse flow through the main loop, in the advent of recolonization the first pulse of individuals was through the shortest loop in the life cycle. Hence the odd initial oscillation seen in fig.8b.

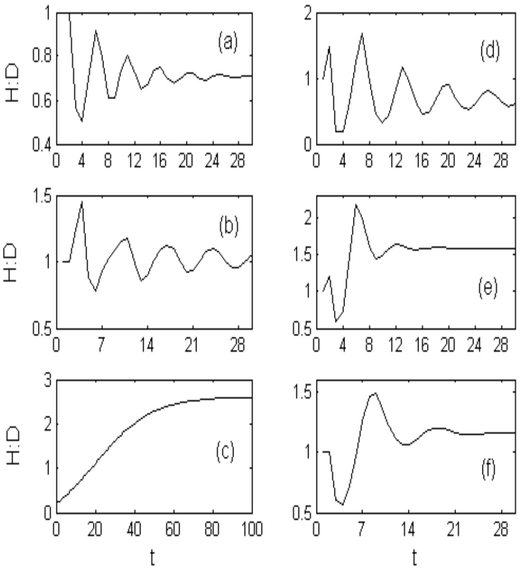

Figure 8 –H:D transient trajectories with the life strategy in: (a) fertility domain with i=-2, g=0.08, l=0.05, d_F=0.5, d_G=1, d_L=1; (b) growth domain with i=-3, g=0.8, l=0.01, d_F=1, d_G=0.8, d_L=1; (c) looping domain with i=-3.8, g=0.01, l=0.96, d_F=1, d_G=1, d_L=0.95, d_{spore}=4, d_1=4, d_2=4 and d_3=4. (d) between the fertility and the growth domain with i=-2.5, g=0.5, l=0, d_F=0.5, d_G=0.5, d_L=1 (e) between the fertility and the looping domain with i=-2.5, g=0.05, l=0.5, d_F=2, d_G=1, d_L=0.7; (f) between the growth and the looping domain with i=-3, g=0.3, l=0.5, d_F=1, d_G=1.5, d_L=0.7.

3. In life-strategies in the looping domain

These populations had their transient trajectories dominated by the slow monotonical transition from the initial structure to the stable structure (fig.8c), which originated from the slow diffusion of individuals through the life cycle. This was simulated by the linear combination of the real symmetric sets (fig.4), the real equal set with a positive eigenvalue and the dominant set. All the features of this transient trajectory were extremely responsive to dissimilarities in looping rates and little responsive to anything else. Notice from figure 8c the difference between the dissimilarities imposed in the looping rates and the imposed upon the initial population structure. A shift in phase dominance (like in fig.8c) could only be attained if the phase that dominated the initial population structure was opposite to the phase that dominated the stable population structure. A particular situation did occur when l was decreased slightly and g was increased slightly (eg. l=0.87 and g=0.1). In these cases the survival rate was still in the vicinity of 1, the population was still dominated by looping but the real sets gave way to the complex conjugated sets. However, these new subdominant complex eigenvalues had θ very close to 0. These sets were replacing the real symmetric ones copying their dynamics and role. Thus, in practice, everything stood the same.

4. In life-strategies in the transition from the fertility to the growth domain

In these populations the pulse flow of individuals through the shorter loop in the life cycle prevailed in the first few instances but soon merged with and gave way to the pulse flow through the main loop. This could be observed from the H:D cycle where an initial period of approximately 4 was gradually overwhelmed by a longer period that asymptotically tended to approximately 8 (fig.8d). However, the amplitude of the oscillations decayed fast and the progression of this shift rapidly became veiled.

5. In life-strategies in the transition from the fertility to the looping domain

These populations had the pulse flow of individuals through the shortest loop in the life cycle merged with the slow diffusive flow of individuals throughout the life cycle until its settlement at the stable population structure. It resulted in a short lasting transient phase with the population attaining its stable structure soon after restart. Therefore, also the H:D oscillation with a 4t wave length quickly damped away to the H:D at steady-state (fig.8e).

6. In life-strategies in the transition from the growth to the looping domain

These populations had the pulse flow of individuals through the bulk loop in the life cycle merged with the slow diffusive flow of individuals throughout the life cycle until its settlement at the stable population structure. It resulted in a short lasting transient phase with the population attaining its stable structure soon after restart. Therefore, also the H:D oscillation with a 8t wave length quickly damped away to the H:D at steady-state (fig.8f).

DISCUSSION

The present work demonstrated biphasic life cycles show an H:D variability in their transient trajectories in the presence of ploidy phase dissimilarities in the demographic matrix and/or initial population vector. The transient trajectories are very specific to the type of life strategy adopted by the species as they are originated by specific demographic processes. These are simulated by specific eigenvectors, eigenvalues and c coefficients extracted from the demographic matrix and initial population structure. It was found that species which invest mainly in fertility exhibit high frequency H:D oscillations that damp away fast. It is due to the flow of individuals through the shorter, faster loop in the life-cycle. Species that invest mainly in growth exhibit lower frequency H:D oscillations that damp away slower. It is due to the flow of individuals through the main loop in the life-cycle. Species that invest mainly in looping (corresponding to investment in survival) exhibit no H:D oscillations but rather a slow monotonical transition. It is due to the slow diffusive flow of individuals through the life cycle. Species that lye in the transitions between two life strategies exhibit transient trajectories with the conjugation of the specific features from each type.

The present work showed the H:D may vary over time solely due to the own structure of the life cycle. In fact, even if the environment is generally stable, any punctual time instability in the population structure or demographic matrix shall generate and H:D time variability. All it takes is dissimilarities between ploidy phases in (i) the vital rates and/or (ii) in the initial population structure. Thus, a cyclic time variation of the H:D in a particular population, as observed by Thornber and Gaines (2003), can not be automatically taken as evidence of seasonality. Likewise, a change in the H:D over a period of 12 years (Scrosati and Mudge 2004a) should not be immediately taken as evidence that the population is evolving to a new situation. Relatively to point (i) dissimilarities between ploidy phases were found over the fecundity rates by Scrosati et al (1994), Gonzalez and Meneses (1996), Santos and Duarte (1996), Thornber and Gaines (2004) and Thornber et al (2006). These could be seasonal, herbivory dependent and could possibly be due to their differential cytological process of gametes/spore production. Dissimilarities between ploidy phases were also found for spore performance by Destombe et al (1989), Scrosati et al (1994), Gonzalez and Meneses (1996), Garza-Sanchez et al (2000), Carmona and Santos (2006), Roleda et al (2008) and Pacheco-Ruíz et al (2011), and for ramets growth and survival rates by Destombe et al (1989), Gonzalez and Meneses (1996), Carmona and Santos (2006), Thornber et al (2006), Vergés et al (2008) and Pacheco-Ruíz et al (2011) which are possibly due to conditional differentiation. Relatively to point (ii) a population structure may get biased from its stable structure whenever there is a perturbation in the population effectives. It may happen following environmental extreme events or extreme grazing or competition events, provided they affect ploidy phases differentially. One particular situation that conjugates points (i) and (ii) is when the demographic matrix changes, as it implies that the population structure at the time of change is the initial population structure of a new run. There are several ways this situation is likely to occur: it may be a change in the vital rates inside the survival or the fertility sub-block of the demographic matrix, due to seasonality; or it may be reproductive asynchrony of the spore/gametes donor population, which was already reported for *Gelidium sesquipedale* (Santos and Duarte 1996)

This work has demonstrated that, in an environment that is spatially homogeneous (there was no spatial discretization in the model) and tends to be stable through time, ploidy dissimilarities in either fertility or growth rates alone are able to create cyclic time niche partitions that damp away with time. However, as long as punctual extreme events arrive, even at low frequencies, it may be enough for these ploidy dissimilarities to generate over the time dimension the niche partition necessary for the evolution and stability of biphasic life cycles. On the other hand, ploidy dissimilarities in a particular looping rate alone (basically in surviving or clonal growing) are not able to do this and need a counter weight. If a phase is beneficed by looping in a particular environmental condition, the other phase should either be (i) beneficed by looping at an alternative environmental condition, or (ii) beneficed by fertility, growth or a different aspect of looping at the same environmental conditions. To support this statement, in the simulations of looping dominated life strategies with ploidy dissimilarities imposed over looping rates, a shift in ploidy dominance only occurred when the initial H:D was opposite to the asymptotic H:D. While the latter H:D was imposed by ploidy dissimilarities in looping rates, the former H:D could only be imposed by ploidy dissimilarities in fecundity or spore performance. Furthermore, if this counter-weighting occurs in life strategies not so much dominated by looping, the shift from the initial to the asymptotic H:D is expected to go through a cyclic alternation of ploidy dominance that dumps away with time, as exemplified in figure 8 (e and f).

The argumentation of the cyclic oscillations promoting the necessary conditions for the evolution and stability of biphasic life cycles may be twisted around or have to be restricted to the absence of a seasonality that affects the demographic matrix. This is because the oscillations are induced by the own life cycle structure, which may induce an H:D evolution miss-fitted to the environmental cycle. Supposing the environment changes to a situation where a ploidy phase is fitter than the other because it reproduces or grows better. If the environmental cycle has a periodicity wider than the one imposed by the life cycle structure, there is only an increase in the average population fitness for a restricted amount of time. After that, the own life cycle structure and not the environment, forces the population to shift to the lesser fit phase. The population may come around this problem if the wavelength of the oscillation induced by the life cycle is wider than the seasonality. In such case, while the seasonal conditions are better for a particular ploidy phase the phase dominance imposed by the life cycle structure shall always fit. The seasonal conditions better for the opposite phase appear prior to the population entering a time sequence with the dominance of the lesser fit phase,. When the environmental change occurs the population starts a new oscillation with the dominance of the greater fit phase and the process is repeated. Awareness about this possibility is fundamental for future theoretical research about the evolution and stability of biphasic life cycles. The outcome of the modelling essays may be strongly dependent on the duration of the simulated shorter and/or main loops of the life cycle relative to the seasonality. This problem should not occur with ploidy dissimilarities only in the survival rates. In such case the H:D evolution should always be directly proportional to the ploidy fitness ratio. All these possibilities become particularly relevant for the species which were documented to seasonally shift their H:D, their ploidy dissimilarities, or were simply reported to have a time variable dynamics. Such were the cases of *Gracilaria verrucosa* (Destombe et al 1989), *Chondrus crispus* (Scrosati et al 1994), *Chondracanthus chamissoi* (Gonzalez and Meneses 1996), *Gelidium sesquipedale* (Santos and Duarte 1996), *Mazzaella cornucopiae* (Scrosati 1998), *Sarcothalia crispata* (Otaiza et al 2001), *Pterocladiella capillacea* (Servière-Zaragoza and Scrosati 2002), *Mazzaella splendens* (Dyck and DeWreede 2006), *Gelidium pusillum* (Prathep et al 2008), *Gracilaria gracilis* (Martín et al 2010) and *Grateloupia turuturu* (Araújo et al 2011), showing seasonality is worldwide in isomorphic biphasic life cycles.

Thornber and Gaines (2003) reported the H:D geographical and time variability for *Mazzaella flaccida*. They later found the average H:D of *Mazzaella flaccida* could only be justified by their observed ploidy dissimilarities in fertility rates, whereas the geographical variability of its H:D could only be justified by their observed ploidy dissimilarities in survival rates (Thornber and Gaines 2004). Vieira and Santos (*accepted*) generalized that H:D geographical variabilities such as the observed by Thornber and Gaines (2003) could easily be set by ploidy dissimilarities in looping rates provided its life strategy is dominated by survival; whereas it could hardly be set by ploidy dissimilarities in fertility rates, whatever the life strategy. However, the survival rates of *Mazzaella flaccida* reported by Thornber and Gaines (2004) dismiss any claim for it to be a survival strategist. Thus, if indeed are ploidy dissimilarities in looping rates to set the H:D, these must also be conspicuous. To this matter, clonal growth is a looping rate with a tremendous potential to set an uneven H:D (Vieira and Santos 2010), which was reported to be conspicuously ploidy dissimilar (Destombe et al 1989) but that has tendentiously been neglected. It is noteworthy that the H.D of *Mazzaella flaccida* observed by Thornber and Gaines (2003) at both Piedras Blancas and Vandenberg with a fine temporal resolution show an outstanding match to the transient H:D patterns predicted by the current model for life strategies in the transition between fertility and survival dominated with ploidy dissimilarities in both types of vital rates. The periodic oscillations at Piedras Blancas closely fitted the yearly cycle only at the beginning and damped away fast; but not at Vandenberg. Furthermore, at Piedras Blancas, there seams to occur a slow change in the central tendency of the H:D from slightly below 1 to slightly above 1.The overwhelming difference in the oscillation period of Vandenberg relative to Piedras Blancas is possible if the ramets there survive more, get older, attain bigger sizes or get sexually mature latter. Still, these are just suppositions and need be experimentally demonstrated. A related situation was reported by Gonzalez and Meneses (1996) in what seems to be a conditional differentiation of the ploidy phases of *Chondracantus chamissoi* involving different types of vital rates. These authors observed that tetraspores were better than carpospores at settlement and germination whereas tetrasporophytes were better than gametophytes at growing and reproducing.