

# Population modelling of *Gelidium sesquipedale* (Rhodophyta, Gelidiales)

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## Abstract

A matrix population model of *Gelidium sesquipedale*, a commercial agarophyte from the Northeast Atlantic, was developed based on demographic data obtained during two years in a commercial stand of Cape Espichel, Portugal. *G. sesquipedale* individuals were classified into categories such as life cycle phase, spores, juveniles and adult frond size, because the species vital rates, fecundity, fertility, survival, growth and breakage depend on them. We also exemplify the use of a user-friendly modelling software, Stella, to develop a structured-population model. This is the first time this software has been used to model the demography of seaweed populations. The Stella model developed here behaved very similarly to the matrix model, because of its particular construction, which causes the forcing functions to be discrete rather than continuous.

The relative importance of spore recruitment and vegetative growth of new fronds in both population growth and population structure was investigated. Elasticity analysis suggests that vegetative recruitment is the most important demographic parameter controlling population growth together with survival and transitions between juveniles (1–6 cm fronds) and class 1 fronds (6–9 cm fronds). On the other hand, sexual reproduction may, by itself, efficiently control the relative proportion of gametophytes and tetrasporophytes in the population, even though its contribution to recruitment is extremely small. A 40% difference in the growth rates of gametophyte and tetrasporophyte submatrices resulted from natural differences in spore recruitment rates.

### Introduction

*Gelidium sesquipedale* is a red alga which grows in the Northeast Atlantic and is industrially exploited for its agar (Santos & Duarte, 1991; Melo, 1998). The species has a clonal type of construction in which a system of erect fronds develops from a system of small, intermingled and ramified prostrate axis. It typically forms dense stands of clumped fronds in which it is impossible to separate individuals, i.e. independent fronds that arise from different prostrate systems. This is a difficulty for population growth studies where individuals must be defined and identified in the field. Following previous population studies of *G. sesquipedale* (Santos, 1994, 1995) an individual here is defined as an erect frond, independent of the prostrate system.

Two types of population models were developed for seaweeds. Production models that simulate the dynamics of the total density or biomass of the population (Silverthorne, 1977; Seip et al., 1979; Seip, 1980a, 1980b) and structured population models, such as difference equation matrix models (Nyman et al., 1990; Åberg, 1992a, 1992b; Ang & De Wreede, 1993) or differential equation models (Nisbet & Bence, 1989). In this kind of models, individuals are classified into categories that can be age, size or developmental stage. The rational for this classification is that the



Breakage + Vegetative Reproduction

*Figure 1.* Conceptual model of each life cycle phase, tetrasporophyte and gametophyte, of *Gelidium sesquipedale*.

vital rates, fecundity, survival and growth depend on one (or more) of those categories. Santos (1994) and Santos & Duarte (1996) showed how the vital rates of *G. sesquipedale* fronds such as growth, breakage, mortality and fecundity, are related to frond size. Two structured-population models were developed for this commercial species. Santos (1993) assessed its best harvest strategy using a matrix model, and Duarte & Ferreira (1997) used a differential equation model to simulate the population productivity. For comprehensive information on the theory and methods on both discrete and continuous structured-population models, the reader is referred to the excellent books of Caswell (1989) and Tuljapurkar & Caswelll (1997).

One objective of this work is to exemplify the use of a modelling software based on differential equations, Stella, to develop a structured-population model. The Stella software has not been used previously to model seaweed populations. It is userfriendly, requiring relatively little knowledge of differential equations. The user needs only to draw the life cycle conceptual diagram and the program will then construct the differential equations that regulate the fluxes of individuals among the state variables and calculate them by iterative processes.

The relative importance of spore recruitment and vegetative growth of new fronds in the population dynamics of most seaweeds, is unclear (Santelices, 1990). The latter is considered to be the most important process of *G. sesquipedale* population recovery from disturbances such as commercial harvest or storms (Santos, 1994). Other objective of this work is to assess the intrinsic mechanisms that regulate the dynamics of *G. sesquipedale* populations, such as

the relative importance of sexual versus vegetative recruitment on both population growth and population structure. The sensitivity of population growth to vital rates variation, will also be investigated.

## Conceptual model

*G. sesquipedale* has a triphasic life cycle with two independent, isomorphic phases, the tetrasporophyte diploid phase that produces haploid tetraspores by meiosis, and the gametophyte haploid phase that produces male and female gametes (Dixon, 1959). The fertilisation of the female gamete takes place in the female thallus, as well as the development of the zygote into the carposporophyte diploid phase. This phase is never independent of the female thallus and develops into the cystocarps that produce diploid carpospores that in turn develop into tetrasporophyte fronds. These fronds produce tetraspores that develop into gametophyte fronds closing the cycle.

Both models developed here consider only the two independent life cycle phase, the steps related to the production of *G. sesquipedale* gametes, fertilisation, and development of the casposporophyte phase were not considered. A diphasic life cycle was thus modelled in which tetrasporophytes produce tetraspores that develop into gametophytes that produce carpospores that in turn develop into tetrasporophytes. Gametophyte fecundity is thus the number of carpospores produced per frond in the cystocarps.

The underlying conceptual model of Figure 1, was the basis of both matrix and Stella models. The *G. sesquipedale* population models are based in two of these submodels, one for the gametophyte generation the other for the tetrasporophyte generation. These submodels are linked by the tetraspores and carpospores categories which develop into, respectively, the gametophyte generation and the tetrasporophyte generation.

## Estimation of demographic parameters

The transition probabilities among stages and size classes were estimated based on previous work on the population biology of a *G. sesquipedale* stand off Cape Espichel, central Portugal, from August 1989 to August 1991 (Santos, 1994, 1995; Duarte & Ferreira, 1997). Transition probabilities among size classes corresponding to frond growth and breakage, as well as the size specific vegetative recruitment, i.e. the contribution of each size class to the juvenile class through

*Table 1.* Size-specific fecundity (number of spores produced per individual) of *Gelidium sesquipedale* from August 1989 to August 1991. Fecundity was zero in the other periods of time. Size class limits include highest value: class 1 from 6 to 9 cm, class 2 from 9 to 13, class 3 from 13 to 19 cm and class 4 higher than 19 cm.

Date	Game	tophytes			Tetras	porophy	tes	
	1	2	3	4	1	2	3	4
September 1989	0.4	5.0	5.0	8.0				
October 1989					0.7	1.3	2.5	5.7
January 1990					1.5	2.8	5.1	11.9
March 1990					33.2	61.7	113.8	265.6
May 1990					5.8	10.8	19.9	46.4
June 1990					1.6	3.0	5.6	13.1
July 1990					0.0	0.0	0.1	0.1
December 1990					1.3	2.4	4.5	10.4
January 1991	12.8	172.7	172.7	281				
April 1991					0.5	0.9	1.7	4.0



Figure 2. Gelidium sesquipedale distribution error (DE) and sample error (SE) for determining length classes. Each value shows the sum of the distribution error within potential length classes. Arrows show the upper limits of selected classes.

the development of erect axis from the prostrate system of erect fronds, were calculated based on Santos (1994, 1995) and on Duarte & Ferreira (1997). Because gametophytes and tetrasporophytes are isomorphic and only distinguishable when fertile, which is not a common event (Santos & Duarte, 1996), the transition probabilities were estimated independently of the life cycle phase. In the models developed here, we considered the same transitions for gametophytes and tetrasporophytes. Thus, the only differences among phases are on fecundity, the number of tetraspores or carpospores produced per frond, and on fertility, the probability of a spore to develop into a juvenile. Both size-specific fecundity (Table 1), and fertility values  $(4.7 \times 10^{-5}$  for tetraspores and  $2.1 \times 10^{-6}$  for carpospores) were estimated based on Santos & Duarte (1996).

#### Width of size categories

An important factor in the construction of sizestructured population models is determining the appropriate size class width. If too few size classes are chosen, then the individuals inside each class will not have a stable distribution and the transition probabilities will depend on the distribution shape. The assumption that all individuals in the same category have the same transition probabilities is then violated. Using too many classes results in each class containing too few individuals and thus in a higher sample error of parameter estimates. These two problems were designated 'error of estimation' and 'error of distribution' by Vandemeer (1978), who first proposed an algorithm for attaining balance between both extremes. Moloney (1986) revised and extended this algorithm, allowing for differences in transition probabilities among subpopulations and census periods. Here we used Moloney's algorithm to define the size class width (frond length) of G. sesquipedale population models

(Figure 2). As the minimum size for reproduction was previously found to be 5.4 cm for tetrasporophytes and 6.9 cm for gametophytes (Santos & Duarte, 1996), we considered the juvenile class of both gametophyte and tetrasporophyte phases to include all fronds shorter than 6 cm (including this value). The selected size classes for adult fronds were (including the higher value): class 1 from 6 to 9 cm, class 2 from 9 to 13, class 3 from 13 to 19 cm and class 4 higher than 19 cm (Figure 2). Classes were selected so that the total error, the distribution error plus the sample error, was low, and that the total number of size classes was four.

#### The matrix model

The general matrix model form, which can be adapted for age, size or stage classified populations, is in matrix notation:

$$n_{t+1} = An_t$$

where  $n_t$  and  $n_{t+1}$  are column vectors representing the structure of the population at time t and t+1, whose elements are the numbers of individuals in each category, and A is a transition matrix containing demographic data, the vital rates fecundity, survival and growth, which describes the transition probabilities within q categories during one time interval. Each of the elements of A, describe the probability of one individual moving between categories, in the time interval considered.

The asymptotic dynamics of the transition probabilities matrix A is determined by its maximal eigenvalue,  $\lambda_1$ , and its corresponding right and left eigenvectors:

$$A n = \lambda_1 n$$
$$v'_1 A = \lambda_1 v'_1$$

the right eigenvector, *n*, represents the stable stage distribution and the left eigenvector,  $v_1$ , gives the reproductive values, i.e., the relative contributions of each stage in the initial population to future population growth (Caswell, 1989). If  $\lambda_1 > 1$ , classes grow exponentially and so does total population size; if  $\lambda < 1$ , the population will decrease exponentially towards extinction; if  $\lambda = 1$ , the population will remain constant.

Changing environmental conditions and consequent time variation of vital rates are incorporated into the matrix projection model by using a sequence of matrices to represent each successive time period. We constructed a matrix projection model for *G. sesquipedale* using a sequence of 17 matrices covering the period from August 1989 to August 1991. Time periods range in length from one month (most cases) to four months (one case). We divided the population into twelve classes based on stage and size, in this order: carpospores (C), juvenile gametophytes (JG), four size classes of adult gametophytes (G1–G4), tetraspores (T), juvenile tetrasporophytes (JT), four size classes of adult tetrasporophytes (T1–T4). A transition matrix was constructed as follows:

	С	JG	G1	G2	G3	G4	Т	JT	T1	T2	Т3	T4
С	0	0	$f_{G1}$	$f_{G2}$	$f_{G3}$	$f_{G4}$	0	0	0	0	0	0
JG	0	P <sub>jgjg</sub>				$P_{jg4}$	P <sub>jgt</sub>	0	0	0	0	0
G1	0						0	0	0	0	0	0
G2	0						0	0	0	0	0	0
G3	0						0	0	0	0	0	0
G4	0	$P_{4jg}$				P44	0	0	0	0	0	0
Т	0	0	0	0	0	0	0	0	$f_{T1}$	$f_{T2}$	$f_{T3}$	$f_{T4}$
JT	P <sub>jtc</sub>	0	0	0	0	0	0	P <sub>jtjt</sub>				$P_{jt4}$
T1	0	0	0	0	0	0	0					
T2	0	0	0	0	0	0	0					
Т3	0	0	0	0	0	0	0					
T4	0	0	0	0	0	0	0	$P_{4jt}$	•	•		P44

where f are the fecundity values for each class (gametophyte or tetrasporophyte) and P are the transition probabilities among classes. Columns of the transition matrix represent the class to which an individual belongs at the beginning of the time period; rows represent the class in which the individual resides at the end of the time period.

As indicated by the dotted lines, the above transition matrix can be partitioned into 4 submatrices as:

where G and T describe, respectively, the transitions among gametophytes and the transitions among tetrasporophytes, and C and Ts are all zeros except one value in each, respectively on row 8, column 1, and on row 2, column 7, that is the probability of a spore to become a juvenile of next phase. The only connection between the two submatrices G and T is through the spore fertility matrices C and Ts. In many of the 17 periodic transition matrices the fecundity entries (in the first row of C, and in the first row of Ts) are zero, because spores are not produced in every time period (Table 1).



*Figure 3.* Reduced Stella model of *Gelidium sesquipedale* population. In the full model, tetrasporophytes and gametophytes are further classified into four size classes each. See text for further explanation of the model.

Multiplying the matrix containing the transition probabilities at time t by the column vector representing the structure of the population at time t:

С	
JG	
G1	
G2	
G3	
G4	
Т	
JT	
T1	
T2	
T3	
T4	

gives a column vector representing the structure of the population at time t+1.

Matrix entries were estimated to four decimal places. Eigenvalues and eigenvectors for the two annual and the bi-annual matrices were calculated to six digit accuracy using Maple V (Waterloo Maple Software). Since any constant multiple of an eigenvector is again an eigenvector corresponding to the same eigenvalue, we have scaled the eigenvectors to 1.

The damping ratio, a measure of how fast a population will converge to the stable stage distribution was calculated as (Caswell, 1989):

$$\rho = \lambda_1 / |\lambda_2|$$

the dominant eigenvalue divided by the second largest eigenvalue.

The sensitivity of the dominant eigenvalue to changes in the entries of the projection matrix are measured by calculating the matrix product of the left eigenvector with the right eigenvector (Caswell, 1978). De Kroon et al. (1986) introduced the concept of elasticity which is a proportional measure of sensitivity, making easier the comparison of sensitivities of transition probabilities and fertilities which are measured on different scales. The elasticity matrix was obtained by multiplying each entry of the sensitivity matrix by the corresponding entry of the projection matrix, then dividing each product by the dominant eigenvalue.

# The Stella model

Figure 3 shows a reduced Stella model of the *G. sesquipedale* population. The state variables (boxes) represent the numbers of individuals in each stage. The fluxes among boxes are the numbers of individuals that flow from one stage to the other in each time step. These flows are regulated by forcing functions, the transition probabilities among stage/size classes. In this particular model the forcing functions are not a function of time but constant for each time step. Their values were estimated for each time step.

Both gametophyte and tetrasporophyte stages of the full model used in simulations are further classified into four size classes each of which is the same of the matrix model. All possible transitions among classes were considered. The transition probabilities that regulate the fluxes among stage/size classes are the same transition probabilities of the matrix model. The diagram of the full model is not showed because it becomes too complex to be understandable.

The Stella model developed here is very similar to a discrete matrix model because of its particular construction which causes the forcing functions to be discrete rather than continuos through time. Transition probabilities are entered in the model as fixed values for each time interval. If the models were perfectly tuned, there would be no differences between them. However, Stella models do not have the limit properties of matrix models that allow its dynamics to be summarised in a few statistics, easy to calculate, such as population growth rate (main eigenvalue), population stable structure (right eigenvector correspondent to the main eigenvalue) and reproductive values (left eigenvector correspondent to the main eigenvalue). The asymptotic behaviour of the Gelidium sesquipedale population will be analysed below with the matrix model while the transient behaviour of the population will be analysed with the Stella model.

The population growth rates assessed with the Stella model at the end of the first year and at the end of the second year, were calculated as the rate between the simulated population density at the end of the period over the initial value. Elasticity analysis of population growth rate was done by varying the forcing functions of 10% and 50%. It is important to test the elasticity at two or more levels of parameter changes as the relation between a parameter and a state variable is rarely linear (Jorgensen, 1994).

## Results

#### Matrix model

The population dynamics for the two year period are modelled by the biannual matrix obtained by multiplying all 17 matrices in reverse order. The first and seventh rows of the product matrix are exactly zero because in some time periods no spores were produced. Entries of the following matrices with the first non-zero digit beyond the third decimal place are written in 'scientific notation', using e–n in place of  $10^{-n}$ .

	С	JG	G1	G2	G3	G4	Т	JT	T1	T2	Т3	T4
С	0	0	0	0	0	0	0	0	0	0	0	0
JG	2e-10	0.33	0.33	0.30	0.25	0.20	1e-5	1e-4	2e-4	2e-4	2e-4	3e-4
G1	1e-10	0.16	0.17	0.15	0.13	0.10	7e-5	7e-5	9e-5	1e-4	1e-4	1e-5
G2	6e-11	0.09	0.09	0.08	0.07	0.05	4e-6	4e-5	5e-5	5e-5	5e-5	7e-5
G3	6e-12	0.009	0.010	0.009	0.007	0.006	4e-7	4e-6	5e-5	6e-6	5e-6	8e-6
G4	6e-12	0.009	0.009	0.009	0.007	0.006	4e-7	3e-6	5e-6	5e-6	5e-6	7e-6
Т	0	0	0	0	0	0	0	0	0	0	0	0
JT	4e-7	2e-6	2e-6	3e-6	2e-6	3e-6	1e-10	0.22	0.23	0.21	0.18	0.14
T1	2e-7	8e-7	9e-7	9e-7	8e-7	1e-6	3e-11	0.09	0.09	0.08	0.07	0.05
T2	7e-8	7e-8	9e-8	1e-7	1e-7	3e-7	2e-12	0.04	0.04	0.03	0.03	0.02
Т3	9e-9	4e-9	7e-9	1e-8	1e-8	3e-8	5e-14	0.005	0.005	0.004	0.004	0.003
T4	2e-8	6e-9	1e-8	2e-8	3e-8	6e-8	0	0.009	0.009	0.008	0.007	0.006

Differences in the gametophyte matrix compared with the tetrasporophyte matrix are due to differences in sexual reproduction (fecundity and fertility), because all the other vital rates are the same for both generations.

The dominant eigenvalue for the biannual matrix is  $\lambda = 0.589$ . The corresponding stable stage distribution is:

С	0
JG	0.55
G1	0.28
G2	0.15
G3	0.02
G4	0.02
Т	0
JT	9.8e-6
T1	3.5e-6
T2	9.0e-7
T3	7.7e-8
T4	2.0e-7

The model predicts a stable population distribution concentrated in the gametophyte classes. This is due to the relative size of the transition probabilities from spores to juveniles. The transition probabilities from carpospores to juvenile tetrasporophytes were estimated to be  $2.1*10^{-6}$ . From tetraspores to juvenile gametophytes the probabilities were estimated to be  $4.7*10^{-5}$ . Both probabilities are small, but the latter probability is more than 20 times as large as the former. Hence, the tendency for the matrix model to predict the population to stabilise predominantly in the gametophyte classes. In the calculated stable population distribution vector the entries for spores was exactly zero. Spores were only produced during a few months of the period studied (Table 1). The model assumes that within one month spores either disappear or



Length of simulation

*Figure 4.* Simulation of the total density (gametophytes + tetrasporophytes) of each *Gelidium sesquipedale* size class through time. Sixteen simulations correspond to a two year period. Size class limits are: juveniles <=6 cm; class 1 <=9 cm; class 2 <= 13 cm; class 3 <= 13 cm; class 4 > 19 cm.



*Figure 5.* Observed and simulated growth rates of *Gelidium* sesquipedale population through time. The first 17 simulations correspond to the two year period when population was monitored.

grow into juveniles. Consequently, the model predicts no spores to be present in the long run.

The damping ratio was  $\rho = 0.589/0.357 = 1.65$ , indicating that the population does not converge very rapidly to the stable distribution.

#### Reproductive value

At the limit, the asymptotic behaviour of the population represents only the gametophyte classes because all tetrasporophytes flow into the other generation. Consequently, the tetrasporophyte reproductive values are extremely small, and will not be showed. The relative contribution of each gametophyte class in the initial population to future population growth is:

JG	0.23
G1	0.23
G2	0.21
G3	0.18
G4	0.14

The reproductive values indicate that smaller classes make larger relative contributions to future population growth. The reproductive value of carpospores could not be assessed because the spore entries of the product matrix were zero.

#### Elasticity analysis

The following elasticity matrix shows only the gametophyte size class entries, rounded to three decimal places. Spore entries are exactly zero. Tetrasporophyte entries (not shown) are extremely small, on the order of  $10^{-9}$  or less:

	JG	G1	G2	G3	G4
JG	0.307	0.157	0.078	0.007	0.005
G1	0.157	0.081	0.040	0.004	0.003
G2	0.078	0.040	0.020	0.002	0.001
G3	0.007	0.004	0.002	0	0
G4	0.005	0.003	0.001	0	0

The elasticity matrix indicates that *G. sesquipedale* population growth rate is most sensitive to the probability of staying in the juvenile class (survival + vegetative recruitment of juveniles), and to transitions between juveniles and size class 1 adults. Both growth and breakage transitions between the same classes have the same elasticity values.

## Stella model analysis

Simulated population growth of the Stella model, calculated as the ratio of population density in time t over the initial population density, was quite similar to the limit population growth rate of the matrix model, respectively, 0.569 and 0.589. This indicates that the population density will decrease in the future providing the vital rates remain the same. Figure 4 shows the sharp density decline of all classes of the population. At the 40th run, two and a half times the period of this study (2 y, 16 time steps), the population will be close to extinction.

Simulated and observed growth rates presented in Figure 5 show that only in a few time intervals, mainly in the first year, was population growth higher than one. The simulated population growth compares well with the observed one. It decreases continuously through time after the period of the study.



*Figure 6.* Observed (full lines) and simulated (dashed lines) densities of each *Gelidium sesquipedale* size class, through the two year period when population was monitored. Each simulation corresponds to the time period of each periodic matrix. 1. Aug/Sep 89; 2. Sep/Oct 89; 3. Oct89/Jan 90; 4. Jan/Mar90; 5. Mar/Apr 90; 6. Apr/May 90; 7. May/Jun 90; 8. Jun/Jul 90; 9. Jul/Aug 90; 10. Aug/Sep 90; 11. Sep/Dec 90; 12. Dec90/Jan 91; 13. Jan/Apr 91; 14. Apr/May 91; 15. May/Jun91; 16. Jun91/Jul 91; 17. Jul/Aug 91. Error bars are the confidence limits (p=0.05) of observed values. Size class limits are: juveniles <= 6 cm; class 1 <= 9 cm; class 2 <= 13 cm; class 3 <= 13 cm; Class 4 > 19 cm.

In order to assess if the model describes correctly the dynamics of the *G. sesquipedale* population, the time variation of category densities, estimated from Santos (1995) field data, were compared with model simulations (Figure 6). Simulations show the same general trends observed in the *G. sesquipedale* population, except for larger individuals, of size class 4, in the second year of the field study. Stella model simulations predict, for the second year, a peak in February followed by a continuos decline of size class 4, whereas observed values for this period are zero. *G. sesquipedale* fronds of this size class (> 19 cm) were not present in the quadrats sampled in Santos (1995) density surveys. On the other hand, plants of this size were tagged and monitored through time (Santos, 1994). The fit of observed vs. simulated frond densities of size class 4 is generally difficult to assess because of high errors due to low number of cases.

Simulated densities of size classes 1 and 2 are, respectively, higher and lower than observed for June to August 1990 period. This suggests that the combined effect of the model parameters, growth, breakage and mortality, in this period of time, underestimates the flow of fronds from size class 1 to size class 2.

#### Elasticity analysis

Elasticity analysis of population growth rate was done by varying the forcing functions of 10% and 50%. Tetrasporophytes elasticities are the same as those of



*Figure 7.* Harvest yields of *Gelidium sesquipedale* at Cape Espichel commercial zone. Yields are expressed in dry weight.

gametophytes, the only difference between submodels being fecundity and fertility. The population growth rate sensitivity to sexual reproduction is zero for both generations. In the matrices presented below, the sensitivity values of one category to itself are the values of sensitivity to variations in the mortality rate of that category. The sensitivity values of the gametophyte phase is shown below:

+10%	VegRec	J	G1	G2	G3	G4
J	0.439	- 0.193	0	0	0	0
G1		0.018	-0.070	0 0	0	0
G2		0	0	- 0.0	35 0	0
G3		0	0	0	-0.	018 0
G4		0		0	0	0
+ 50%	VegRee	: J	G1	G2	G3	G4
J	8.561	-0.42	-0.02	0	0	0
G1		0.07	-0.25	0	0	0
G2		0	0	- 0.09	0	0
G3		0	0	0	-0.04	0
G4		0		0	0	-0.02

The growth rate of the *G. sesquipedale* population is very sensitive to vegetative recruitment to the juvenile stage. It is also sensitive to mortality rates, particularly of juveniles and class 1 individuals.

## Discussion

One of the great advantages of matrix models is that their analysis is easy, at least for density-independent linear models like the one developed here. Due to the limit properties of the matrices, all the complex demographic information can be condensed into a few statistics such as population growth rate, reproductive values, stable distribution and damping ratio (Groenendael et al., 1988; Caswell, 1989). Easy to use formulas were also developed by Caswell (1978) and de Kroon et al. (1986) to assess how does the growth rate respond to changes in the vital rates (sensitivity and elasticity analysis). These statistics describe the long term dynamics of the population as a result of the asymptotic behaviour of these type of matrices (irreducible and primitive, see Caswell, 1989).

The growth rate of the *G. sesquipedale* matrix model is very low,  $\lambda = 0.589$ , indicating that if vital rates remained the same the population would rapidly decrease to extinction. Previous work on the frond dynamics and on the population structure of this stand supports this result (Santos, 1994, 1995). The accumulated effects of extreme environmental conditions which occurred during this period of time and the commercial harvest are responsible for the collapse of commercial harvest the year after this study (Figure 7).

The *G. sesquipedale* population modelled with Stella behave similarly to the matrix model. Population categories showed an asymptotic behaviour, decreasing continuously with time (Figure 4). Although the population growth rate at the end of the study period was very similar to the matrix population growth rate, these values cannot be really compared because the former represents a punctual growth of the population while the later represents its long term, asymptotic, growth. The average simulated growth of the population throughout the study period was 0.91, and it decreases continuously through time (Figure 5).

The damping ratio for the *G. sesquipedale* transition matrix is small ( $\rho = 1.65$ ), indicating that the rate of convergence to the population stable structure is slow. Damping ratios much larger than one have been reported for species of *Sargassum, Laminaria* and *Ascophyllum*. (Ang & De Wreede, 1990; Åberg, 1992a). There is some evidence that the damping ratio of plant (Caswell, 1986) and seaweed populations (Åberg, 1992a) decreases with increasing  $\lambda$ , fast growing populations or species will converge slower, but the available data on this statistic is small.

An unresolved question in many *Gelidium* species is the relative proportion of gametophyte (haploid) and tetrasporophyte (diploid) individuals in the population, with consequences to their population dynamics due to potential fitness differences between haploids and diploids. The life cycle phase of a frond is only evident when it is fertile. Fertile gametophytes are generally much less than fertile tetrasporophytes (0.2% and 2% of total fronds, see Santos & Duarte, 1997 and



*Figure 8.* Simulations of *Gelidium sesquipedale* Juveniles and Class 1 densities through time, using the Stella model with fixed vegetative recruitment. Error bars are the confidence limits (p=0.05) of observed values. Time periods of each simulation and size class limits as in Figure 6.

references therein), but that does not mean that the proportion of gametophytes in the population is lower than tetrasporophytes. We showed here that sexual reproduction may, by itself, efficiently control the relative proportion of gametophytes and tetrasporophytes in the population. When analysing the gametophyte and tetrasporophyte submatrices their eigenvalues are, respectively, 0.589 and 0.357. This 40% difference in the growth rates can only be accounted by sexual reproduction, because all other transitions among categories of the matrix model were the same. Life cycle generation differences in sexual reproduction contribution to recruitment may be responsible by themselves, even if the other vital rates are the same, for the differences in the relative abundance of gametophytes and tetrasporophytes. It is unknown if vital rates such as frond survival and frond growth differ between the two isomorphic generations of G. sesquipedale.

The common pattern in seaweeds in which fecundity is a function of size is that the reproductive value increases with size (Ang & De Wreede, 1990; Åberg, 1992a; Ang & De Wreede, 1993). *G. sesquipedale* reproductive values show that the contribution of smaller fronds to population growth rate is higher than bigger ones. This reflects the great importance of vegetative recruitment in the dynamics of this population. Smaller size classes have more individuals and thus contribute more with new fronds arising from their prostrate systems.

Vegetative recruitment rates were measured through time for two years and thus incorporate the time varying dynamics of recruitment. In both models, vegetative recruitment in each time step was considered proportional to the frond numbers of each size class, assuming that more erect fronds mean more prostrate axis and thus more potential to give rise to new erect fronds. The consequence of this is that, in each time step, the vegetative contribution to the juvenile class depends of the simulated population for that time step, which is different from the observed one (Figure 6). The vegetative recruitment input in the models is thus different from the observed. In the Stella model it is easy to avoid this by making the vegetative recruitment input independent of the size class density of the same time step. Fixed inputs in each time step were added to the juvenile category. Simulations of this model fit better the observed population structure, particularly for juveniles and class 1 (Figure 8). Simulations of other classes do not differ much from the model in which vegetative recruitment is proportional to class density. The long term behaviour of the fixed vegetative recruitment model is different, the population rather than decreasing continuously, slowly increases until it stabilises (Figure 9). This suggests that small differences in vegetative recruitment have a great impact on population behaviour.

The elasticity analysis of both models showed that population growth is more sensitive to variations in the transitions associated with smaller categories, particularly vegetative recruitment, juveniles and class 1 survival, and transitions between juveniles and class 1. This is not surprising, because the logic behind this analysis implies that population growth rate will be most sensitive to alterations in transitions from abundant classes to classes possessing high reproductive values (Caswell, 1989). An important application of this is that commercial harvest should be selective for bigger fronds. As it is done, by divers that pluck the fronds by hand (Santos & Duarte, 1991), it is not. On the other hand, mechanical cutters would select for bigger fronds, supporting the results of Santos (1993)



*Figure 9.* Simulation of total *Gelidium sesquipedale* frond density using the Stella model with fixed recruitment. The first 17 simulations correspond to the two year period when population was monitored.

who suggested that this would be a better harvest strategy.

Both the development of new erect fronds from the prostrate system, and juveniles and class 1 survival are the most important vital rates regulating the *G. sesquipedale* population dynamics. Consequently, the estimation of these demographic parameters is crucial. This is a powerful application of elasticity analysis, to indicate which parameters should be more accurately estimated.

To improve the understanding of G. sesquipedale population dynamics, more effort should be done in understanding what triggers the development of new erect fronds from the prostrate system. Unfortunately, almost nothing is known about these cylindrical, colourless, and ramified branches, which adhere to the substrate by rhizoidal attachments. Other intrinsic factors controlling the G. sesquipedale population dynamics should also be introduced in future models. These are the density-dependent suppressed growth of smaller fronds which seems to occur in G. sesquipedale (Santos, 1995), and the historical effects of frond breakage on its future growth (Santos, 1994). This last issue cannot be modelled with matrix models because they assume that the matrix describes a first order Markov process, i.e. the transition probabilities during the time interval t to t+1, depend only upon the state an individual is in, at time t, and not upon its state at any previous point in time (Caswell, 1989).

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