

Population dynamics and stage structure in a haploid-diploid red seaweed, *Gracilaria gracilis*

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Summary

1 Many red seaweeds are characterized by a haploid-diploid life cycle in which populations consist of dioecious haploid (gametophyte) and diploid (tetrasporophyte) individuals as well as an additional diploid zygote-derived sporangium (carposporophyte) stage. A demographic analysis of *Gracilaria gracilis* populations was carried out to explore and evaluate the population dynamics and stage structure of a typical haploid-diploid red seaweed.

2 Four *G. gracilis* populations were studied at two sites on the French coast of the Strait of Dover. Survival, reproduction and recruitment rates were measured in each population for up to 4 years. Eight two-sex stage-based population projection matrices were built to describe their demography.

3 All four populations were characterized by high survival and low recruitment rates. Population growth rates (λ) were similar between populations and between years and ranged from 1.03 to 1.17. In addition, generation times were found to be as long as 42 years.

4 Sex and ploidy ratios were variable across populations and over time. Female frequencies ranged from 0.31 to 0.59 and tetrasporophyte frequencies from 0.44 to 0.63. However, in most cases, the observed population structures were not significantly different from the calculated stage distributions.

5 Eigenvalue elasticity analysis showed that λ was most sensitive to changes in matrix transitions that corresponded to survival of the gametophyte and tetrasporophyte stages. In contrast, the contribution of the fertility elements to λ was small. Eigenvector elasticity analysis also showed that survival elements had the greatest impact on sex and ploidy ratios.

Key-words: algal demography, eigenvector elasticity analysis, ploidy ratio, sex ratio, two-sex projection matrix model

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Introduction

Marine algae show a wide diversity of life cycles, spanning the continuum of the relative importance of the growth and development of haploid and diploid phases: haploid, haploid-diploid and diploid cycles are all represented in seaweeds (De Wreede & Klinger 1988; Valero *et al.* 1992; Bell 1994). However, little is known about the

demographic characteristics and consequences of the complexities of these life histories.

Matrix population models can accommodate complex life cycles and integrate both population dynamics and population structure, which are determined by the vital rates (mortality, recruitment, reproduction, growth) associated with the different stages of a life cycle. Projection of these matrix models elegantly summarizes the consequences of the stage-specific vital rates in terms of population structure and population growth rate, or mean population fitness (Caswell 1989; Stearns 1992). While matrix models have been developed for different life cycles found in marine algae (Ang & De Wreede 1990), they have been applied to only a handful of

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species (e.g. Ang & De Wreede 1990, 1993; Ang *et al.* 1990; Åberg 1992; Chapman 1993; Santos 1993; Santos & Nyman 1998). In addition, although many of these species are dioecious, all of these models are one-sex linear models – as are most matrix models of plant or animal species (but see Bierzychudek 1982; Meagher 1982; Cipollini *et al.* 1994; Legendre *et al.* 1999) – thereby ignoring at least some of the dynamics associated with sexual reproduction, that is, that male and female fertility are interdependent. Furthermore, the dynamics and determinants of the relative frequencies of the different phases of the more complex algal life cycles have been largely unexplored.

Red seaweeds typically have complex haploid-diploid life cycles that are sometimes referred to as triphasic. The three phases are a diploid (tetrasporophyte) phase, a haploid (gametophyte), usually dioecious phase and an additional diploid, zygote-derived sporangium (carposporophyte) phase. While the gametophyte and tetrasporophyte stages are independent, the carposporophyte stage develops on the gametophyte thallus. As in all sexual life cycles, the three phases are interconnected through meiosis and syngamy. Meiosis takes place on the tetrasporophyte plants, giving rise to haploid tetraspores. Tetraspores develop into gametophytes, which produce gametes by mitosis. Fertilization (syngamy) occurs on the female gametophyte and the fertilized female gamete develops into a carposporophyte. Cystocarps are macroscopic hemispherical swellings observed on the surface of female branches, within which the carposporophyte produces thousands of diploid carpospores. Finally, completing the cycle, each carpospore can develop into a tetrasporophyte. Thus, the alternating haploid and diploid phases in most haploid-diploid red algae occur as biologically distinct stages. Paradoxically, the recruitment and the relative frequencies of the gametophyte stage depend on the vital rates of the tetrasporophyte stage, and *vice versa* (Destombe *et al.* 1989).

Populations of the red haploid-diploid alga *Gracilaria gracilis* consist of four readily observable stages: cystocarps, tetrasporophytes, female gametophytes and male gametophytes. Thus this species provides an excellent opportunity to explore the demography of a typical red seaweed life history. Moreover, using stage-specific vital rates as matrix elements, a matrix model approach to the study of population dynamics allows a finely tuned evaluation of the interplay between phases. Specifically, analysis of matrices provides insight into the contribution of the various stage-specific life history parameters to population fitness and to population stage structure. Eigenvalue elasticity analyses measure the fitness responses of a population to small changes in the matrix elements (Caswell 1989; for review see Benton & Grant 1999). By extension, the eigenvector elasticity analysis measures the effect of small changes in the matrix elements on the population structure, i.e. on the ploidy (tetrasporophyte:gametophyte) ratio and the sex (female:male) ratio.

The aim of this paper is to explore and evaluate the population dynamics and stage structure of a typical red seaweed, *G. gracilis*. Vital rates were measured for up to 4 years in four populations located in the Strait of Dover. The ultimate consequences of spatial and temporal variation in these vital rates are investigated using two-sex matrix models that accommodate the tetrasporophyte, gametophyte and carposporophyte stages. Using eigenvalue elasticity analyses, we identify the demographic parameters that most influence population fitness. Further, we develop an eigenvector elasticity analysis of population structure to explore the effects of small proportional changes in the matrix elements on sex and ploidy ratios.

Methods

STUDY SPECIES AND POPULATIONS

In *Gracilaria gracilis*, the tetrasporophytic, female gametophytic and male gametophytic individuals are isomorphic. The thallus is an erect system of deciduous spaghetti-like branches that grow from the holdfast, fixing the individual to the substrate. Male and tetrasporophytic individuals can be distinguished by their reproductive structures, which are readily visible under a dissecting microscope, while female individuals are recognized by the presence of cystocarps.

This study was carried out in the Strait of Dover region, where previous studies have established that reproductive maturity, growth and cystocarp production reach a maximum in August–September (Destombe 1987; Destombe *et al.* 1988, 1989). After September, branches weaken and break off, and all three types of individual are quiescent in the winter months. New branches grow back in the spring (March–April). Reproductive structures – tetrasporangia (the site of meiosis) in tetrasporophytes, and gametangia in gametophytes – are uniformly distributed along the branch and are produced as the branch grows (Kling & Bodard 1987). Each tetrasporangium produces four tetraspores and the primary sex (female:male) ratio of tetraspores is 1:1. Male gametangia develop into concave male crypts, each producing thousands of male gametes. Female reproductive structures produce a single gamete. Cystocarps reach maturity *c.* 1 month after fertilization; the carpospores are liberated over 6–10 weeks (Lefebvre *et al.* 1987). Cystocarps do not survive from year to year and are lost when the female branches senesce. Likewise, there is no spore bank: tetraspores and carpospores either settle or disintegrate (cf. Destombe *et al.* 1992). Spores that settle and germinate form a basal holdfast and the first branches appear after *c.* 3 weeks (Destombe *et al.* 1993). However, these recruits are not detectable before the following year, when they reach *c.* 2 cm in length.

G. gracilis individuals occupy intertidal rock pools where they remain immersed at ebb tide. The rocky intertidal zone in the study area is a dynamic landscape composed of bedrock, rock outcrops and sand. Rock

Table 1 Characteristics of the four tide pools studied

Pool	Tide level*(m)	Pool surface area (m ²)	No of plants sampled†	Census years
GNH	2.8	4.5	208	1995/96/97/98
GNL	1.3	14.0	115	1997‡/98
AuH	4.9	17.5	164	1996/97/98
AuL	2.3	16.5	67	1996/97/98

*Above chart datum according to <http://www.shom.fr>; the mean tide level is 4.91 m on the French coast of the Strait of Dover.

†Over period of study. Not all individuals were necessarily alive at one time. ‡Census carried out in June. All other censuses took place in September.

pools are patchily distributed; those occupied by *G. gracilis* are found below the mean tide level. Four rock pools, each containing a group of plants described as a population, were studied at Cape Gris-Nez (50°53' N, 1°35' E) and at Audresselles (50°49' N, 1°35' E), 3 km further south, on the French coast of the Strait of Dover. Two rock pools were selected at different tide levels at each site (Table 1). High and low populations are, respectively, noted as GNH and GNL at Gris-Nez and AuH and AuL at Audresselles. Due to differences in the slope of the shore, GNH and GNL are separated by a distance of 25 m, while AuH and AuL are separated by 100 m.

DEMOGRAPHIC CENSUSES

Plants within the rock pools were mapped relative to a pair of fixed points. In this study, we followed individual plants (genets), delimited by the branches arising from a single holdfast. It is often difficult to distinguish genets of algae (e.g. Åberg 1989; Lindgren *et al.* 1998), but for *G. gracilis*, previous studies have confirmed, with genetic markers, that branches of a common holdfast are genetically identical while branches arising from different holdfasts are genetically distinct (Wattier *et al.* 1997; Engel *et al.* 1999). To estimate the vital rates, between two and four censuses were carried out, once a year, in each population (see Table 1).

At every census, maximum thallus length and maximum thallus diameter were recorded for each individual observed in the rock pool. Total individual biomass was represented by the volume of a cylinder of this length and diameter. For *G. gracilis*, as for other algal species (e.g. Åberg 1990; Lindgren *et al.* 1998), this estimate is non-destructive, easy to make in the field and significantly correlated with dry weight ($R^2 = 0.87$; $P < 0.0001$; $n = 74$). Due to the deciduous nature of branches, measurements taken at the end of the growing season estimate the current year's growth. As the production of gametangia and tetrasporangia is also a function of branch growth in *G. gracilis* (see above), volume provides an index of both annual net growth and fecundity (i.e. gamete or spore production). Finally, several branches of each individual were sampled and examined under a dissecting microscope to establish the ploidy level and sex of each individual based on the observed reproductive structures.

To assess the total number of cystocarps produced by a population, we counted, for every female, the cystocarps found on the 10-cm distal extremity of three branches. Cystocarp production was estimated for each female by multiplying the average number of cystocarps cm⁻³ of thallus (assuming a branch diameter of 1 mm) by the total volume of the female individual. The sum of the individual female cystocarp production estimates thus gives an estimate of the number of cystocarps produced by one population during one reproductive season (cf. Destombe 1987).

A total of 554 individuals was sampled in the four populations (Table 1). The field data provided detailed information on the fate of each individual plant in each pool from one year to the next. From these data, we built eight stage-based population projection matrices.

POPULATION PROJECTION MATRICES

Matrix construction

Matrices were constructed on the basis of a life-cycle diagram representing four stages of a rhodophyte haploid-diploid life cycle: cystocarps (*C*), tetrasporophytes (*T*) and female (*F*) and male (*M*) gametophytes (Fig. 1a). (Letters are used as subscripts to indicate the respective stages throughout the rest of the paper.) Males were explicitly included in the matrix in order to fully explore the dynamics of population structure in terms of sex and ploidy ratios.

For the construction of the matrices, we made two assumptions: (i) censuses were carried out after the production of cystocarps and (ii) mortality took place before reproduction. Stage-specific reproductive output entries (*f*) were calculated as functions of recruitment into the following stage, i.e. as effective fertilities. Cystocarp fertility (f_{TC}) was calculated by dividing the number of tetrasporophyte recruits in year $t + 1$ by the number of cystocarps produced in year t . Likewise, tetrasporophyte fertilities (f_{FT} and f_{MT}) were based on the recruitment rates of females and males. Finally, male and female fertilities (f_{CF} and f_{CM}) were assumed to be frequency-dependent; that is, each depends on the relative abundance of the other sex. The fertility functions were derived from the number of cystocarps produced in one reproductive season (n_C) using the harmonic mean birth function (Caswell 1989):

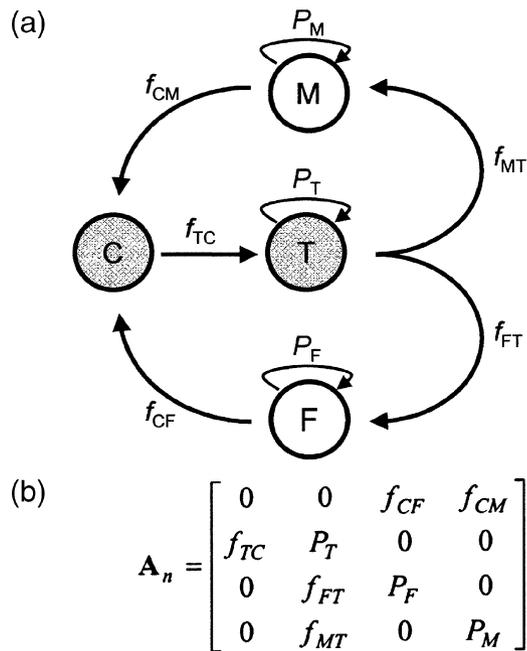


Fig. 1 Life-cycle graph for *Gracilaria gracilis* (a) and its corresponding population projection matrix (b). Circles represent the different stages included in the model (filled = diploid stages; C = cystocarp, T = tetrasporophyte; open = haploid stages; F = female gametophyte, M = male gametophyte) and arrows represent the possible transitions (a_{ij}) from stage class j to stage class i over 1 year's time. Matrix elements (a_{ij}) are subdivided into fertility (f) and survival (P).

$$n_C = \frac{2kn_F n_M}{n_F + n_M}$$

where k is the clutch size, or the average number of cystocarps produced by one male and one female gametophyte, and n_F and n_M are the number of females and males, respectively. Thus male and female fertility, respectively, are given by:

$$f_{CF} = \frac{kn_M}{n_F + n_M} \quad \text{and} \quad f_{CM} = \frac{kn_F}{n_F + n_M}$$

The dynamics of a *G. gracilis* population can thus be described by the non-linear projection matrix \mathbf{A} (Fig. 1b), the elements a_{ij} of which represent the transitions from stage j to stage i over 1 year. The corresponding projection equation is given by:

$$\mathbf{n}(t+1) = \mathbf{A}_n \mathbf{n}(t)$$

where the vector $\mathbf{n}(t) = [n_C \ n_T \ n_F \ n_M]$, represents the numbers in each of the four stage classes and the subscript n indicates that \mathbf{A} depends on n_F and n_M .

CALCULATING POPULATION PARAMETERS

As \mathbf{A}_n is continuous and frequency-dependent, a non-trivial equilibrium population structure exists that can be obtained directly from the life cycle graph using the z-transform method (Caswell 1989). The population growth rate at equilibrium, λ , is obtained from the characteristic equation:

$$1 = \frac{f_{TC}}{\lambda(\lambda - P_T)} \left[\frac{f_{FT} f_{CF}}{(\lambda - P_F)} + \frac{f_{MT} f_{CM}}{(\lambda - P_M)} \right] \quad \text{eqn 1}$$

Bootstrap confidence intervals for λ were obtained using the bias-corrected percentile method (Caswell 1989) with a bootstrap sample size of 5000.

The relative stage distribution at equilibrium is given by the dominant right eigenvector \mathbf{w} :

$$w_C = 1$$

$$w_T = \frac{f_{TC}}{\lambda - P_T}$$

$$w_F = \frac{f_{TC} f_{FT}}{(\lambda - P_T)(\lambda - P_F)} \quad \text{eqn 2}$$

$$w_M = \frac{f_{TC} f_{MT}}{(\lambda - P_T)(\lambda - P_M)}$$

As at equilibrium f_{CF} and f_{CM} are themselves functions of \mathbf{w} , equations 1 and 2 must be solved simultaneously to obtain λ and \mathbf{w} . From these stable stage distributions, we obtained the relative proportions of the tetrasporophyte, and female and male gametophyte stages.

The stage-specific reproductive values are given by the dominant left eigenvector, \mathbf{v} :

$$v_C = 1$$

$$v_T = \frac{f_{CF} f_{FT}}{(\lambda - P_T)(\lambda - P_F)} + \frac{f_{CM} f_{MT}}{(\lambda - P_T)(\lambda - P_M)}$$

$$v_F = \frac{f_{CF}}{(\lambda - P_F)}$$

$$v_M = \frac{f_{CM}}{(\lambda - P_M)}$$

Reproductive values express the probable contribution of a stage class to future population growth through current and expected reproduction.

The damping ratio (ρ) is a measure of how fast a population will converge to the stable stage distribution and is defined as the dominant eigenvalue (λ_1) divided by the absolute value of the largest subdominant eigenvalue (λ_2) (Caswell 1989).

Finally, using the methodology presented by Caswell (1989) it is possible to obtain an expression for the mean generation time (i.e. mean age of parents of offspring produced at stable stage distribution) (\bar{A}) in t he stable population. For the life cycle presented in Fig. 1 we obtain:

$$\bar{A} = -\lambda \sum_i \frac{\partial L_i}{\partial \lambda} \Big|_{\lambda=\lambda_1} \quad \text{for } i = 1, 2$$

where

$$L_1 = \frac{f_{TC} f_{FT} f_{CF}}{\lambda(\lambda - P_T)(\lambda - P_F)} \quad \text{and}$$

$$L_2 = \frac{f_{TC} f_{MT} f_{CM}}{\lambda(\lambda - P_T)(\lambda - P_M)}$$

Eigenvalue elasticity analysis

Eigenvalue elasticities (e_{ij}) are calculated by measuring the proportional change in λ caused by proportional changes in one of the a_{ij} matrix elements (Caswell 1989, equation 6.38, p. 132).

Eigenvector elasticity analysis

As we were interested in exploring the effects of small changes in the matrix elements on the sex and ploidy ratios, we developed an eigenvector elasticity analysis. We measured the relative changes in the stable stage distribution (w) when small changes were made to the matrix elements. We proceeded as follows. Matrix element a_{ij} was multiplied by a factor (x) close to, but smaller than, unity. Population growth was simulated from $t = 0$ to $t = 200$, and a new stable stage distribution (w') was obtained. Elasticities of the matrix elements equal the change in the frequency of females (s_{ij}) or the frequency of diploids (g_{ij}):

$$s_{ij} = \frac{\frac{w_F}{w_F + w_M} - \frac{w'_F}{w'_F + w'_M}}{1 - x}$$

$$g_{ij} = \frac{\frac{w_T}{w_T + w_F + w_M} - \frac{w'_T}{w'_T + w'_F + w'_M}}{1 - x}$$

where $1/(1 - x)$ is a scaling factor correcting for the absolute size of factor x . Factor x was first set to 0.99 and then the process was repeated with a factor closer to unity (0.999, 0.9999, etc.) until the s_{ij} and g_{ij} values converged to stable values (5 significant digits). As cystocarp production remains constant in the simulations, a change in the initial values of f_{CF} and f_{CM} has no effect on the final stable matrix. We thus performed an elasticity analysis on k . We decreased k by the same factor used for the matrix elements and proceeded as above. The subsequent change in the sex ratio (i.e. s_k) was divided evenly among f_{CF} and f_{CM} so that s_{CF} , $s_{CM} = 0.5s_k$. As we are dealing with relative frequencies which add up to unity, the sum of the s_{ij} 's, and of the g_{ij} 's, is zero. However, absolute values cannot be compared between matrices.

STATISTICAL ANALYSES

ANOVAS were used to test for differences in volume, survival and recruitment according to sex, census year (or interval) and population. The factor population was designated random while census year (or interval) and stage were treated as fixed factors. Volume was tested using a three-way ANOVA with replication. The data set was balanced by taking a random sample of 10 individuals per stage from census years 1997 and 1998 for all four populations. Survival and recruitment were

tested using a three-way ANOVA without replication. Only data from the 1996–97 and 1997–98 census periods of the GNH, AuH and AuL pools were selected to obtain balanced data sets. Error terms were defined based on three-factor mixed model expected mean squares, although the three-way interaction could not be tested as there are no replicates. The assumption of homogeneity of variances was tested with Cochran's test (Winer *et al.* 1991). Fourth-root (volume) and arcsine (survival probabilities) transformations successfully reduced significantly heterogeneous variances.

Results

POPULATION DYNAMICS

Vital rates

We used individual volume to assess annual net growth and fecundity. Figure 2 shows the mean volume of tetrasporophytes, females and males for each population and year. The three-factor ANOVA showed two significant interactions, between stage and population and between population and year (Table 2); as the interactions involved all three main effects, these are not discussed individually. Males were almost always smaller than females and tetrasporophytes. Females were either smaller than (in populations GNL and AuL) or similar in size to tetrasporophytes (populations GNH and AuH) (Fig. 2). The mean size of individuals increased from 1997 to 1998 in GNH and AuL, but decreased in the GNL and AuH populations. This pattern suggests that net growth (or fecundity) typically shows yearly variation but that there were no regional-scale environmental events that affected all populations similarly. This yearly variation in size is probably caused by small-scale, stochastic, pool-level processes.

Survival was high for all three types of individual in all the populations and census periods (mean survival probability \pm SE, %CV: tetrasporophytes, 0.98 ± 0.01 , 1.5%; females, 0.96 ± 0.02 , 6.5%; males, 0.95 ± 0.02 , 4.5%; $n = 8$). These survival rates did not differ significantly between stages, between years, or between years within populations (Table 3).

At least one individual was recruited into each stage at all census intervals in all populations (mean 5.29 recruits stage⁻¹ years⁻¹, SE 0.66) (Fig. 3). Recruitment was more variable than survival (%CV, tetrasporophytes, 33.7%; females 35.0%; males, 27.8%; $n = 8$). Some of this variation can be explained by population-specific yearly variation (significant population \times census interval interaction, Table 3) which precludes interpretation of the significant population main effect. Overall recruitment increased from the 1996–97 to the 1997–98 census interval in the GNH population while it decreased in the AuH population (Fig. 3). Neither the stage factor nor any interactions including stage accounted for any significant variation. Further, the variation in recruitment

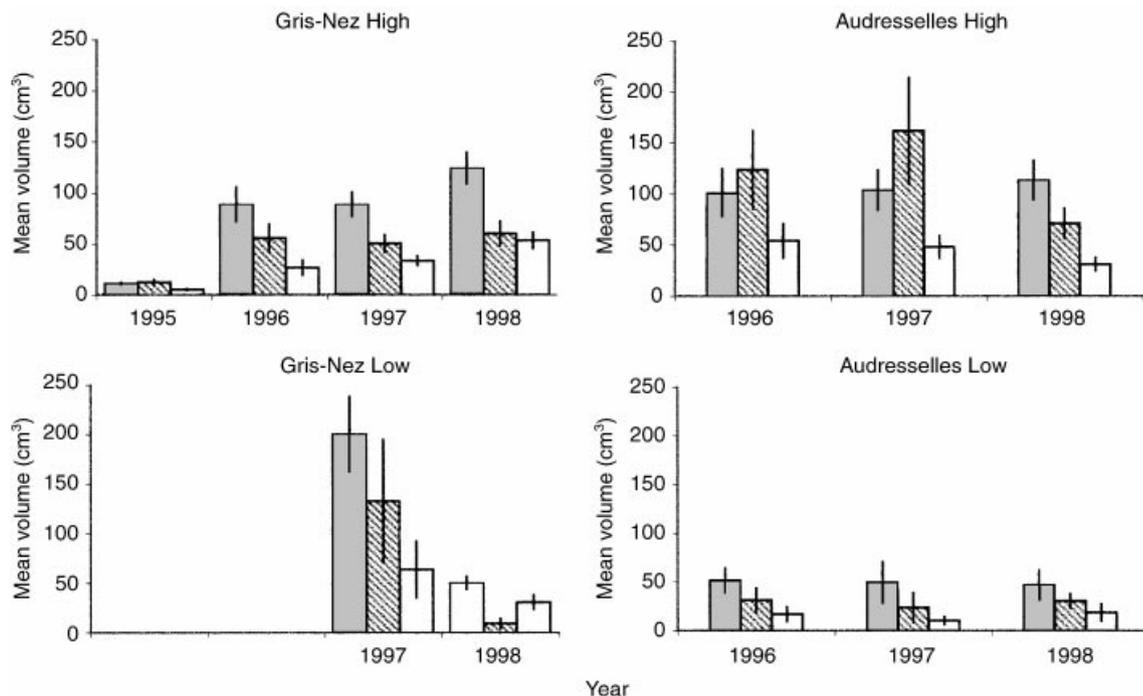


Fig. 2 Mean volume of all three types of *Gracilaria gracilis* individuals for all four populations in each census year. Grey bars = tetrasporophytes; striped bars = females; white bars = males. Data are raw means \pm 1 SE.

Table 2 ANOVA on volume of *Gracilaria gracilis* male and female gametophyte and tetrasporophyte individuals in four pools and 2 census years

Source	d.f.	MS	F	P	Tested over
Population	3	3.90	3.94	0.009	Error
Census year	1	0.51	0.07	0.806	Pop. \times Year
Stage	2	8.13	2.99	0.126	Pop. \times Stage
Pop \times Census year	3	7.16	7.23	< 0.001	Error
Pop \times Stage	6	2.72	2.75	0.014	Error
Census year \times Stage	2	1.37	0.88	0.462	Year \times Stage \times Pop.
Census year \times Stage \times Pop.	6	1.56	1.57	0.155	Error
Error	216	0.99			
Total	239				

Table 3 ANOVAs on survival and recruitment rates of *Gracilaria gracilis* male and female gametophyte and tetrasporophyte stages

Source	d.f.	Survival			Recruitment (number m ⁻²)			Tested over
		MS	F	P	MS	F	P	
Population	2	0.0013	0.10	0.908	1.930	142.40	< 0.001	Error
Census interval	1	0.0288	2.96	0.227	0.194	0.35	0.615	Pop. \times Census
Stage	2	0.0389	3.99	0.112	0.036	2.43	0.204	Pop. \times Stage
Pop. \times Census	2	0.0097	0.73	0.536	0.559	41.23	0.002	Pop. \times Census \times Stage
Pop. \times Stage	4	0.0098	0.74	0.614	0.015	1.10	0.465	Pop. \times Census \times Stage
Census \times Stage	2	0.0075	0.57	0.607	0.017	1.25	0.379	Pop. \times Census \times Stage
Pop. \times Census \times Stage	4	0.0133			0.014			
Total	17							

was not correlated with total spore production. Total cystocarp production (n_C) in year t was not correlated with the number of tetrasporophyte recruits in year $t + 1$ (Spearman rank correlation; $r = 0.49$, $P > 0.05$,

$n = 8$), nor was the mean volume of tetrasporophytes correlated with the number of gametophyte recruits (Spearman rank correlation, $r = 0.500$, $P > 0.05$, $n = 8$).

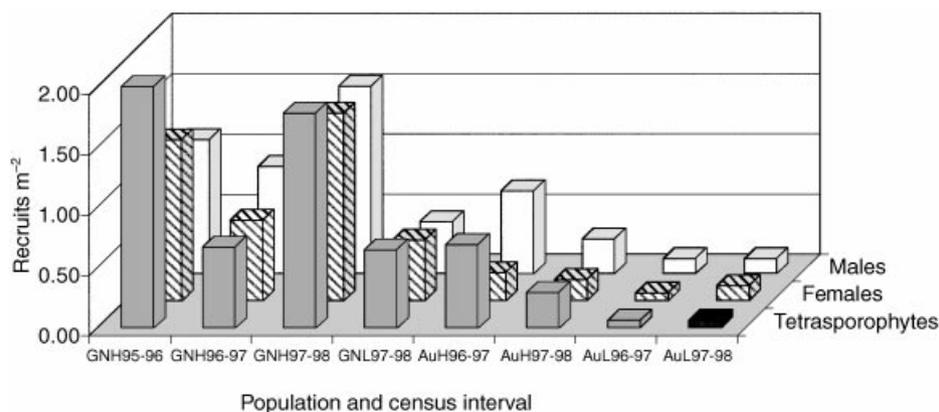


Fig. 3 Recruitment in *Gracilaria gracilis* according to stage, expressed as density of recruits for each pool/census year combination.

Table 4 Demographic parameters of the eight *Gracilaria gracilis* population/census-interval combinations (matrices). λ , population growth rate (upper and lower bias-corrected 95% confidence intervals); \bar{A} , mean generation time (in years); ρ , damping ratio

Pop	Census interval	λ	\bar{A}	ρ
GNH	1995–96	1.091 (1.03–1.14)	21.263	1.118
	1996–97	1.040 (1.00–1.08)	42.399	1.067
	1997–98	1.092 (1.04–1.15)	18.072	1.114
GNL	1997–98	1.172 (1.05–1.24)	11.810	1.331
AuH	1996–97	1.167 (1.08–1.22)	13.891	1.167
	1997–98	1.040 (1.00–1.08)	23.818	1.096
AuL	1996–97	1.044 (1.00–1.14)	32.490	1.062
	1997–98	1.031 (1.00–1.11)	27.091	1.051

Population projection

Population growth rates (λ) were always greater than unity, whatever the population and census period (Table 4). There were only small differences in λ between populations or years: all of the values fell within the confidence intervals of all other populations and/or census intervals (Table 4). Thus, growth rates of populations of *G. gracilis* are similar and stable across a range of tide levels in the Strait of Dover region.

In comparison with the growth rates, the mean generation times were much more variable (Table 4). The average length of time that it takes to complete the haploid-diploid cycle, whatever the starting point, varied between 12 and 42 years. Closer inspection revealed that the generation times were negatively correlated with per-capita recruitment rates (modelled as effective fertilities) (Spearman rank correlation, $r = -0.976$, $P < 0.001$, $n = 8$; data not shown). Thus variability in generation times reflects the large variability in recruitment.

The damping ratios were low, suggesting that the convergence of the populations to the predicted

equilibrium stage distributions is quite slow (Table 4).

Population structure

The frequencies of females and diploids (i.e. sex and ploidy ratios) observed were relatively stable in populations from year to year (Table 5). Over all populations, sex and ploidy ratios ranged from 0.31 to 0.59 and from 0.44 to 0.63, respectively. Given that factors controlling sex determination are known to segregate in a Mendelian fashion (van der Meer 1990), we tested the probability of obtaining the observed frequencies of females within the gametophyte subpopulation against expected cumulative binomial frequencies. Only the Gris-Nez populations (GNH and GNL) showed skewed sex ratios that were always biased in favour of males (Table 5). Similarly, we tested the probability of obtaining the observed frequencies of tetrasporophytes over the total population, assuming no phase dominance. Only the GNL population showed skewed ploidy ratios. Tetrasporophytes were over-represented in both years (Table 5).

The projected stage distributions indicated that cystocarps dominate the stable stage structure; the gametophyte and tetrasporophyte stage proportions are in the order of 10^{-4} (results not shown). However, we were mainly interested in the dynamics between the perennial stages. The equilibrium sex and ploidy ratios showed considerably more variation from matrix to matrix than the observed ratios. The frequencies of females among the gametophyte subpopulations ranged from 0.25 to 0.79 and the frequencies of tetrasporophytes ranged from 0.27 to 0.57 (Table 5). Observed female frequencies were almost always greater than those at projected equilibrium (Table 5). Further, equilibrium sex ratios were consistently skewed in favour of the sex with the higher survival probability, whatever the tetrasporophyte fertility values, suggesting that survival dynamics are most important (data not shown). On the other hand, equilibrium frequencies of diploids were always smaller than those observed in the

Table 5 Population structure of *Gracilaria gracilis* in tide pools and comparison of observed and projected sex and ploidy ratios. Δ = difference between observed and equilibrium projected ratios. G = log likelihood ratio values obtained when comparing the three-stage (excluding cystocarps) observed with equilibrium (projected) population structure. n_C = number of cystocarps produced, n_T = number of tetrasporophytes, n_F = number of females, n_M = number of males; sex ratio $n_F/(n_F + n_M)$; ploidy ratio, $n_T/(n_T + n_F + n_M)$

Population	Year	Stage				Sex ratio			Ploidy ratio			
		n_C	n_T	n_F	n_M	Observed	Projected	Δ	Observed	Projected	Δ	G
GNH	1995	107 640	72	32	52	0.38*			0.46			
	1996	435 248	78	36	57	0.39*	0.42	+0.04	0.46	0.43	-0.03	0.678
	1997	406 451	81	38	60	0.39*	0.39	0.0	0.45	0.42	-0.04	0.844
	1998	594 864	87	45	64	0.41	0.61	+0.22	0.44	0.39	-0.06	<u>18.874</u>
GNL	1997	672 595	57	11	25	0.31*			0.63*			
	1998	30 427	65	16	29	0.36*	0.45	+0.14	0.59*	0.57	-0.06	2.021
AuH	1996	566 965	67	30	26	0.54				0.54		
	1997	858 629	77	34	38	0.47	0.25	-0.29	0.52	0.41	-0.13	<u>23.165</u>
	1998	564 090	80	37	39	0.49	0.56	+0.09	0.52	0.50	-0.02	1.576
AuL	1996	82 008	30	16	11	0.59			0.53			
	1997	74 117	31	17	12	0.59	0.61	+0.02	0.53	0.44	-0.09	1.313
	1998	163 776	31	19	13	0.59	0.79	+0.20	0.49	0.27	-0.26	<u>20.275</u>

*Significantly different from a 1:1 ratio, two-tailed binomial distribution probability $P < 0.05$; underlined G values are significant, all at $P < 0.001$.

Table 6 Relative reproductive values of *Gracilaria gracilis* cystocarp, male and female gametophyte and tetrasporophyte stages according to pool and census interval. The largest value for each pool-interval combination is indicated in bold

Stage	GNH			GNL	AuH		AuL	
	1995–96	1996–97	1997–98	1997–98	1996–97	1997–98	1996–97	1997–98
Cysto.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tetrasp.	0.364	0.505	0.426	0.374	0.299	0.423	0.503	0.512
Female	0.289	0.283	0.287	0.289	0.537	0.360	0.332	0.244
Male	0.347	0.212	0.287	0.337	0.165	0.216	0.166	0.244

populations (Table 5). Using the log likelihood ratio, G , we compared the observed and calculated stage distributions. The results show that observed population structures were generally close to those expected at equilibrium (Table 5). Only three population/census-interval combinations showed significant departure from the calculated equilibrium distribution. In general, the differences were due to changes in the overall structure of the population. AuH1996–97 and AuL1997–98 showed large differences between observed and equilibrium sex and ploidy ratios, while GNH1997–98 showed substantial divergence primarily in the sex ratio (Table 5).

Reproductive values

The highest reproductive values were associated with the tetrasporophyte stage in all but one case (AuH1996–97, Table 6). Within the gametophyte stage, females had reproductive values larger than or equal to males in six out of eight matrices. In general, populations have similar reproductive patterns across tide levels, sites, and in time.

ELASTICITIES

Eigenvalue elasticity

The highest elasticity values were consistently associated with survival terms for all three stages (Fig. 4). Conversely, the elasticities of fertility elements were low (ranging from 0.01 to 0.09). The tetrasporophyte stage showed the highest relative contribution (i.e. total elasticity) to population growth rate compared with either of the gametophyte stages, and frequently with both of the other stages combined (Fig. 4). Thus, the elasticity analysis indicates that in *G. gracilis* populations, survival is the most important component of population growth, while the transition between stages (i.e. fertility) plays a relatively minor role. Furthermore, population growth appears to be more sensitive to small changes in the tetrasporophyte stage than in the gametophyte stages.

The elasticities of the female and male fertilities were always equal, as were the two tetrasporophyte fertility elasticities. This is a direct consequence of the harmonic mean fertility function we employed: female and

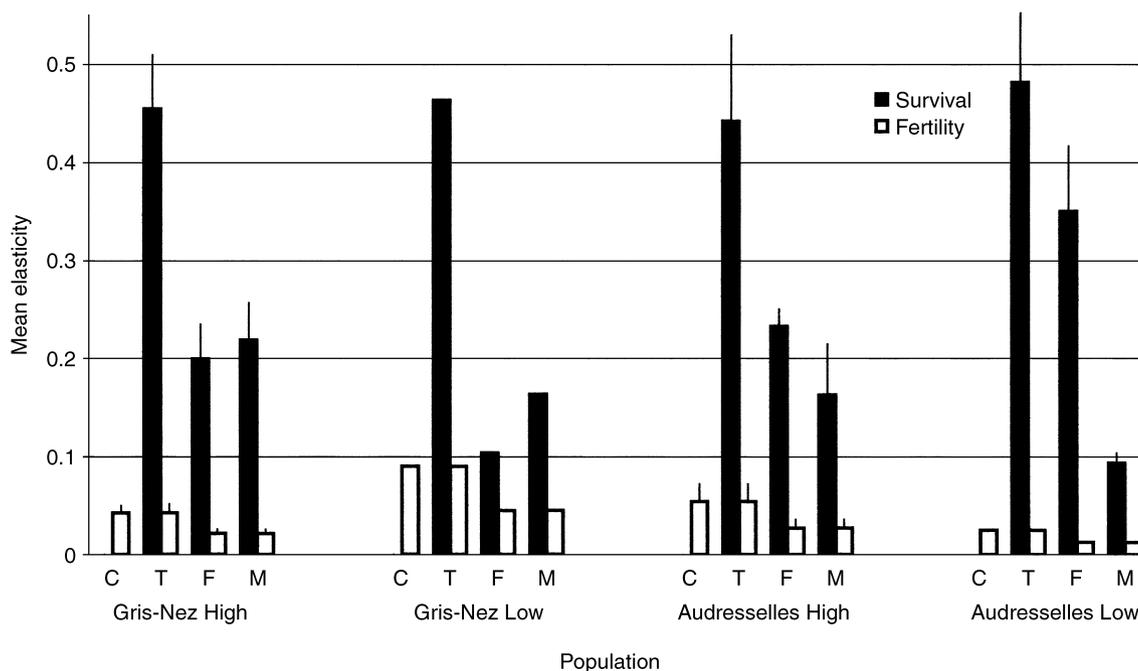


Fig. 4 Eigenvalue elasticity values of the eight *Gracilaria gracilis* matrices. White bars = fertility components and black bars = survival components. Data are means \pm 1 SE. C = cystocarp, T = tetrasporophyte, F = female gametophyte, M = male gametophyte.

male fertilities are interdependent. Thus male and female fertilities and production rates (through tetrasporophyte fertility) contribute equally to the population growth rate.

Eigenvector elasticities

As observed in the eigenvalue elasticity analysis, the highest absolute eigenvector elasticity values were consistently associated with the three survival terms, while the fertility terms generally showed values at least one order of magnitude smaller (Fig. 5). This indicates that the equilibrium sex and ploidy ratios are most sensitive to small changes in survival of tetrasporophytes, and female and male gametophytes. While the ploidy ratio was most sensitive to the stage with the highest survival probability overall, the sex ratio was most sensitive to the gametophyte stage with the highest survival probability (data not shown).

Interesting patterns emerge when we consider the sign of the change in sex or ploidy ratio due to a perturbation in a specific life cycle stage. Here we explored the effect of a perturbation corresponding to a decrease in the stage-specific parameters. A positive value in Fig. 5 represents a corresponding decrease in the ratio; likewise, a negative value corresponds to an increase in the ratio. For all of the matrices, the perturbation of female survival (P_F) and tetrasporophytes' production of females (f_{FT}), decreased the frequency of females, while the opposite was true for a perturbation of male survival (P_M) and tetrasporophytes' production of males (f_{MT}). However, the effects of a perturbation of tetrasporophyte survival (P_T), cystocarp fertility (f_{TC}), and gametophyte fertilities (f_{CF} and f_{CM}) depended on the sex ratio at equilibrium. When the equilibrium frequency of females

for unperturbed matrices was less than 0.50, a perturbation of P_T , f_{TC} , f_{CF} or f_{CM} decreased the frequency of females, while the opposite was true when the sex ratio was skewed in favour of females. In fact, all four elements concern the survival and production of the diploid phase, and as such, they have an indirect impact on the production of females and males. It follows that an increase in the tetrasporophyte stage increases the production of gametophytes. This has a relatively greater and positive impact on the less-abundant sex.

All perturbations of terms associated with the production of tetrasporophytes and tetrasporophyte survival decreased the frequency of tetrasporophytes. Increases in the frequency of tetrasporophytes were generally observed when perturbing those terms concerning production of gametophytes and gametophyte survival. However, the absolute impact of the terms concerning the over-represented sex was higher than for the less abundant sex (Table 6 and Fig. 5; compare GNH with GNL). Furthermore, where equilibrium sex ratios were very highly skewed (AuH1996–97 and AuL1997–9, see Table 6), the frequency of tetrasporophytes decreased when negatively perturbing elements concerning survival and production of the less-abundant sex (Fig. 5). Consequently, a shift towards balanced sex ratios results in an increase in the frequency of tetrasporophytes at equilibrium. Therefore the dynamics of sex ratios can affect ploidy ratios.

Discussion

Our results demonstrate that *G. gracilis* is a long-lived perennial alga. Populations are characterized by modest growth rates which reflect a combination of features:

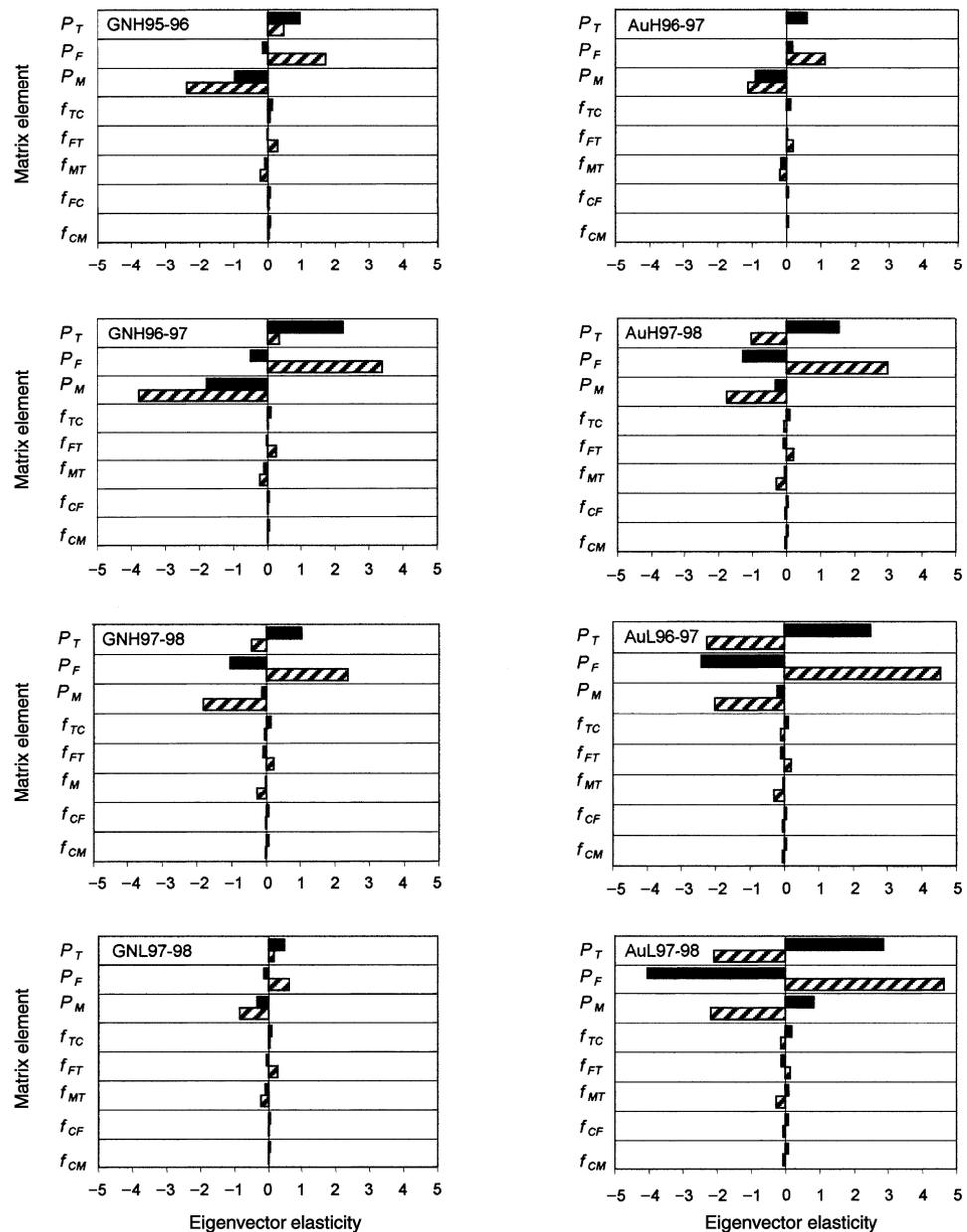


Fig. 5 Results of eigenvector elasticity analysis of the eight *Gracilaria gracilis* matrices. Black bars = ploidy ratio elasticities; striped bars = sex ratio elasticities. For definition of the matrix elements, see Fig. 1. The values on the right hand side of the graphs show that a perturbation that decreases (or increases) a matrix element will decrease (increase) the frequencies of tetrasporophytes or females. The values on the left hand side show that a perturbation that decreases (increases) a matrix element will increase (decrease) the frequencies of tetrasporophytes or females.

high survival, low recruitment and long generation times. Further, the dynamics of different *G. gracilis* populations in the Dover Strait region were similar even though populations differed in terms of density, height on the shore and population structure. Indeed, population growth rates varied very little between populations and were stable in time in spite of significant variation in recruitment and in population structure.

G. GRACILIS: A LONG-LIVED PERENNIAL SEAWEED

The population growth rates obtained for *G. gracilis* are similar to those reported for other long-lived

perennials, i.e. close to unity (perennial herbs, e.g. Bierzychudek 1982; Meagher 1982; Valverde & Silvertown 1998; trees and palms, Alvarez-Buylla *et al.* 1996; brown seaweeds, Ang & De Wreede 1990; Åberg 1992; and a red seaweed, Ang *et al.* 1990). Likewise, *G. gracilis* showed survivorship rates as high as or higher than those reported for perennials (*op cit.*). At an average survival rate of 0.96, 10% of a cohort will theoretically survive for at least 55 years. Furthermore, survivorship did not differ between stages, populations or years (Table 3). On the other hand, recruitment, while far from negligible, was low. This low recruitment was reflected in the long generation times we obtained for *G. gracilis*: c. 20 years will elapse before an individual

replaces itself, completing the haploid-diploid life cycle. While recruitment showed significant yearly variation in populations, this variation did not result in substantial differences in the rates of population growth (Table 4). As in herbaceous perennial plants which possess subterranean perennating organs, the holdfast of *G. gracilis* ensures survival not only over the unfavourable season but also for longer periods of time. Indeed, some individuals did not produce any sizeable branches over a given census period. These quiescent individuals do not participate in reproduction but contribute to population resilience.

A comparison of the elasticity matrices of > 80 terrestrial plant species representing a wide range of life histories revealed that, in long-lived perennials, survival is the most important component of population growth while fertility and/or growth are considerably less important (Silvertown *et al.* 1993, 1996). Similarly, the eigenvalue elasticity analysis of the *G. gracilis* matrices showed that survival had the highest elasticities whereas fertility elasticities were generally low. Other long-lived algal species show similar patterns. *Ascophyllum nodosum* (Åberg 1992), *Sargassum siliquosum* (Ang & De Wreede 1990) (both Phaeophyceae, Fucales) and *Gelidium sesquipedale* (Rhodophyta, Gelidiales) (Santos & Nyman 1998) show fertility elasticities that are several orders of magnitude smaller than their survival elasticities. In shorter-lived algal species, such as *Laminaria longicuris* (Phaeophyceae, Laminariales) (Ang & De Wreede 1990) and *Fucus distichus* (Phaeophyceae, Fucales) (Ang & De Wreede 1993), fertility elasticities took on relatively greater values although they were still lower than survival elasticities. A classification of marine algae according to a functional-form, algal-successional framework (Littler & Littler 1980, 1984), defines opportunistic forms, predation-tolerant forms and disturbance-tolerant forms. This classification has at least superficial parallels with the successional trajectory that is inscribed in the demographic triangular ordination of the fertility, growth and survival elasticities (Silvertown *et al.* 1996; Franco & Silvertown 1997). The trajectory runs from the fertility vertex (short-lived pioneer/opportunistic) species up to the growth vertex (longer-lived competitive/predation-tolerant species) back down to the survival vertex (long-lived climax/disturbance-tolerant species). *G. gracilis*, along with the other long-lived species, would be placed near the climax/disturbance-tolerant vertex based on its perenniality, low recruitment, low population growth rates and resilience to disturbance.

VARIATION IN RECRUITMENT AND FECUNDITY

Variation in volume showed similar stochastic yearly variation within populations to that of recruitment. Spore production and individual volume are inextricably linked in *G. gracilis*: tetrasporophytes can produce more than 750 000 tetraspores cm⁻³ of branch and one

cystocarp produces up to 6000 carpospores (Destombe 1987). This intimate connection may seem to suggest that recruitment would be a direct consequence of fecundity. Nevertheless, recruitment was not correlated with the production of spores. That is, factors influencing the variation in the dispersal, settlement, germination and growth of released spores were not correlated with factors influencing the variation in fecundity (indexed by volume). The ecophysiological conditions that favour spore establishment in algae may be highly complex, including factors such as temperature, photoperiod, salinity, grazers, inter- and intraspecific competition and sand dynamics (burial and scour) (for review see Santelices 1990) and hydrodynamic regimes that create spatial and temporal unpredictability (for review see Denny & Shibata 1989). Nonetheless, a positive correlation between fecundity and fertility may exist: large individuals with high fecundity may enjoy high reproductive success in years of either high or low recruitment.

Many marine organisms show high temporal variability in recruitment (e.g. marine invertebrates, Gotelli 1991; Hughes *et al.* 1999; algae, Reed *et al.* 1988; Åberg 1992; for review on marine organisms with a planktonic phase see Caley *et al.* 1996). Nevertheless, despite the weak contribution of fertility to the population growth rate, recruitment is important for long-term population stability (Reed *et al.* 1988; Gotelli 1991; Ang & De Wreede 1993), as without recruitment, populations eventually go extinct.

SEX AND PLOIDY RATIO DYNAMICS

It was not feasible to incorporate both size and life history stage into our matrix model. In our study we were primarily interested in the demographic behaviour of the different stages in rock pools (discrete population units) in which the fate of the individual plants was followed (thereby avoiding fecundity approximations). Accordingly, the number of individuals sampled was dependent on the specific rock pool studied and this unit could not be replicated. As a consequence, while individual size (volume) was measured, the incorporation of size classes within each of the stages would have reduced the sample size and thus the precision of our estimates of demographic parameters. Therefore the life cycle graph that we developed was less complex than that suggested for triphasic algal life histories by Ang & De Wreede (1990). However, we extended their triphasic model to include the male gametophyte stage, thereby generating a two-sex model. In doing so, we were able to explore the dynamics of all the types of individual that are found in populations, and more specifically, the dynamics of the sex and ploidy ratios in a typical red algal life cycle. A two-sex model causes female and male fertilities to be interdependent (Caswell & Weeks 1986). While the true birth function of *G. gracilis* gametophytes is unknown, we chose the harmonic mean function to describe the interdependence of male and female fertilities as it agrees with evolutionary sex ratio theory (Fisher 1930).

The observed sex ratios showed little temporal variation within populations. However, the sex ratios differed between populations: two of the four populations showed skewed sex ratios, and both were male-biased. Adult sex ratios may be biased due to environmental variation and differential mortality of the two sexes. Indeed, variation of sex ratios between populations of many dioecious plants, mosses and algae has been attributed to differential herbivory of juveniles (e.g. Cipollini & Whigham 1994), density effects (e.g. Bond & Maze 1999), to height on the shore (e.g. Norall *et al.* 1981; Williams 1995), or differential mortality (e.g. Shaw & Gaughan 1993). Sex ratios in dioecious algae vary from unity to female-biased (Norall *et al.* 1981; De Wreede & Klinger 1988; Kain (Jones) & Destombe 1995); only rarely are they male-biased (one report, in Kain (Jones) & Destombe 1995). The unanticipated male bias at the Gris-Nez site may be due to subtle differences in transient population dynamics, differential herbivory and/or differential juvenile survival at this site. Nonetheless, although the low number of populations studied does not allow explicit testing of environmental correlates, we discerned no trends that would suggest that female frequencies varied with tidal level or population density (Tables 1 and 5). Alternatively, the male bias may be caused by a genic sex ratio distorter, although none have been documented for an algal species (for review see Werren & Beukeboom 1998).

The eigenvector elasticity analysis sheds some light on the relative importance of the different vital rate parameters in the determination of the sex ratio. Interestingly, we found that (adult) survivorship, and not fertility (a term that included juvenile survival), of all three individualized stages was the most important component of sex ratios. In addition, the eigenvector analysis revealed some interesting dynamics. Perturbations of the production and survival of tetrasporophytes resulted in variations in sex ratio that depended on the equilibrium female frequency. Moreover, this was true regardless of the relative values of the f_{FT} and f_{MT} terms (i.e. gametophyte recruitment). Thus, small increases in the parameters concerning the tetrasporophyte stage can indirectly influence the sex ratio in favour of the less abundant sex.

The observed ploidy ratios were even more stable in time than the sex ratios. Three of the four populations showed balanced ploidy ratios (Table 5). Among the isomorphic red algae, ploidy ratios range from gametophyte-biased to tetrasporophyte-biased (e.g. Norall *et al.* 1981; De Wreede & Klinger 1988; Destombe *et al.* 1989; Kain (Jones) & Destombe 1995; Lindgren & Åberg 1996; Scrosati 1998). Some studies have shown that ratios vary according to tidal levels, with the frequency of tetrasporophytes decreasing with increasing height on the shore (Craigie & Pringle 1978; Norall *et al.* 1981). In addition to differential mortality (or recruitment) according to environmental or ecological factors, the skewed ploidy ratios could be due to asexual reproduction in at least some of the above-cited studies.

As only one population (GNL) showed significantly skewed ploidy ratios, it was not possible to attribute variance in ploidy ratios to ecological factors such as tidal level. Further, vegetative propagation is unlikely in *G. gracilis* (Destombe *et al.* 1992; Wattier *et al.* 1997; Engel *et al.* 1999).

The projected ploidy ratios were in general quite similar to the observed ratios. Two of the three cases of significant departure from projected structure involved dramatic differences in the observed and projected ploidy ratios; both were skewed in favour of gametophytes (Table 5), whatever the sex ratio. Destombe *et al.* (1989) and Lindgren & Åberg (1996) suggested that juvenile survival was a determining factor of ploidy ratios observed in the field. However, this study shows that the balance of ploidy ratios, as observed for the sex ratios, is due mainly to survival dynamics and not to fertility (analogous to juvenile survival) dynamics. The eigenvector analysis demonstrated that, in general, a small increase in gametophyte survival would decrease the frequency of tetrasporophytes and vice versa.

The equilibrium sex and ploidy ratios and their elasticities obtained from our two-sex model are contingent on the model's assumption of frequency-dependent fertility. While one-sex linear models or two-sex models employing birth functions other than the harmonic mean may give different results, the magnitude of the actual difference is not easy to predict. In an exploration of the population dynamics of birds using a one-sex linear model and two-sex models with various birth functions, Legendre *et al.* (1999) showed that differences between two-sex frequency-dependent and one-sex linear models were especially pronounced in short-lived species. Their results suggest that the high survival rates demonstrated in *G. gracilis* would render the conclusions based on a variety of birth functions (linear and non-linear) qualitatively comparable. Nevertheless, independent data would be necessary to test the assumptions behind birth functions.

Stable stage structure of the haploid and diploid phases has been reported in studies of matrix models that have been applied to other haploid-diploid species, including a heteromorphic species, *Laminaria longicurvis* (Ang & De Wreede 1990) and two isomorphic rhodophytes, *Gelidium sesquipedale* (Santos & Nyman 1998) and *Mazzaella splendens* (as *Iridaea splendens*, Ang *et al.* 1990). In *Laminaria*, the sporophyte stage is macroscopic while the gametophyte phase is microscopic. The stable stage structure of *L. longicurvis* was largely dominated by the gametophyte stage (Ang & De Wreede 1990). The isomorphic red alga *G. sesquipedale* propagates by vegetative means. Matrix model projections showed that the tetrasporophyte stage comprised less than 1% of the stable stage structure (Santos & Nyman 1998). As the vegetative dynamics were modelled using the same parameters for the haploid and diploid phases, gametophyte dominance was attributed to successful, albeit limited, recruitment of tetraspores (Santos & Nyman 1998). On the contrary, while the haploid and

diploid phases alternate in dominance seasonally in *M. splendens* (Ang *et al.* 1990; Dyck & De Wreede 1995), projections of the tetrasporophyte-dominant season showed that the frequencies of diploids stabilized to *c.* 50% (Ang *et al.* 1990). Thus even with slightly different demographic dynamics, this exclusively sexual red alga showed similar equilibrium ploidy ratios to those that we found in *G. gracilis*.

While population growth rates showed no spatio-temporal variation, equilibrium population structure varied substantially from year to year in at least three populations. Although the survival rates were not significantly different from year to year, both elasticity analyses showed that subtle changes in the survival rates had the biggest impact on population fitness and on population structure. It is interesting to note that minor differences in survival may result in very different equilibrium population structures (data not shown, but see Table 5). Therefore, changes in adult survival that are too minor to be detected statistically may contribute to the observed biases in sex and ploidy ratios. Alternatively, these biases may be transitory and reflect past population dynamics.

The low damping ratios in *G. gracilis* are typical of long-lived perennials with long generation times (Doak & Morris 1999) and indicate that convergence to equilibrium structure is slow (Table 4). Thus the small differences that resulted in very different projected population structures will not be immediately reflected in the observed population structure (Table 5). In addition, even subtle variation in survival and recruitment dynamics will probably prevent populations from reaching the extreme projected sex and/or ploidy ratios. Comparing the observed population structures in this study with those observed in 1985 in GNH and GNL (in Destombe *et al.* 1989) and in AuH in 1990 (in Richerd 1993) shows that population structure has changed relatively little in 8 years. In these surveys, sex ratios were 0.458, 0.513 and 0.618 and ploidy ratios were 0.438, 0.485, 0.553 for GNH, GNL and AuH, respectively. Only the GNL population showed trends opposite to the ones reported in this study, suggesting that perhaps this population is experiencing different dynamics from the others. Unfortunately, it is difficult to speculate further on these differences in sex and ploidy ratios since only one census period was recorded for this population.

Conclusion

The demographic model developed in this study allowed exploration of the population dynamics and structure of a red haploid-diploid seaweed. The results revealed little spatiotemporal variation in the dynamics of populations found in one geographical region, providing valuable insight into demographic processes at a local (i.e. small) scale. There is nevertheless a need to carry out intensive, hierarchical sampling at several spatial scales (e.g. Hughes *et al.* 1999) to determine large-scale

patterns as well as the impact of putative local ecological correlates, such as density or height, on the shore.

While most population matrix models previously developed for red haploid-diploid seaweeds incorporate both haploid and diploid phases (e.g. Ang & De Wreede 1990; Ang *et al.* 1990; Santos & Nyman 1998), the dynamics of ploidy ratios are rarely discussed (but see Scrosati & DeWreede 1999). Our two-phase, two-sex model took into account both phases and both sexes within the haploid phase, providing an opportunity to explore the dynamics of not only ploidy ratios but also sex ratios. Indeed, our analysis of the stable stage structure showed that the dynamics of sex and ploidy ratios depend, for the most part, on adult survival, and may be interdependent. This integrative two-sex, two-phase approach to the study of the population demographic structure of red haploid-diploid seaweeds is particularly promising for future studies addressing the evolution and maintenance of the haploid-diploid life cycle with respect to other types of cycle.

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