

Gigartinales symposium

Demographic models to simulate the stable ratio between ecologically similar gametophytes and tetrasporophytes in populations of the Gigartinaceae (Rhodophyta)

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SUMMARY

In populations of the Gigartinaceae (Rhodophyta), gametophytes often predominate numerically over tetrasporophytes. Several hypotheses have been proposed to explain this dominance, based on the usually implicit assumption that the stable ratio between gametophytes and tetrasporophytes (G:T ratio) should be 1 if both reproductive phases are ecologically similar. We developed demographic models to test this assumption, for which we considered that both phases are ecologically similar. Defining ecologic similarity for most demographic rates is relatively straightforward, except for rates of spore output. The first set of models considered the same spore output per thallus of both phases as representing ecologic similarity. Model iterations led to stable G:T ratios of 1 for triennial and for perennial thalli, regardless of the initial G:T ratio, but not for annual thalli with initial G:T ratios different from 1. However, equal spore output may not represent ecologic similarity, due to size differences between carpospores and tetraspores. The second set of models considered the lowest possible spore output for each phase, according to the life history of this family: only one carposporangium, with one carpospore, is produced from every two gametophytes and only one tetrasporangium, with four tetraspores, is produced by every tetrasporophyte. Model iterations led to stable G:T ratios of 2.8 for most cases, a ratio of 1 being obtained only every 2 years for annual thalli with an initial G:T ratio of 1. Increasing absolute spore output, without altering the relative output between phases and incorporating density-independent mortality through a matrix model, given the same mortality rate for both phases, did not modify results. We suggest that the combination of both modeling and field research may uncover more rapidly than otherwise the most relevant ecologic differences between phases, if any, that underlie the G:T ratio observed for a given population.

Key words: demography, gametophyte, Gigartinaceae, matrix models, Rhodophyta, tetrasporophyte.

INTRODUCTION

Populations of red algae in the Florideophycidae are generally composed of two independent life-history phases, gametophytes and tetrasporophytes. For members of the Gigartinaceae (Gigartinales), including the ecologically and economically important genera *Chondracanthus*, *Chondrus*, *Gigartina*, *Iridaea*, *Mazzaella*, *Rhodoglossum*, and *Sarcothalia* (Hommersand *et al.* 1993), a numerical dominance of gametophytes is common on a whole-habitat basis and/or on an annual basis (Mathieson and Burns 1975; Craigie and Pringle 1978; Mathieson 1982; Bhattacharya 1985; Dyck *et al.* 1985; Hannach and Santelices 1985; May 1986; Lazo *et al.* 1989; DeWreede and Green 1990; Bolton and Joska 1993; Scrosati *et al.* 1994; Dyck and DeWreede 1995; González and Meneses 1996; Lindgren and Åberg 1996; Piriz 1996; Zamorano and Westermeier 1996; Scrosati 1998). Numerical dominance of tetrasporophytes seems to be restricted to smaller spatial or temporal scales in this family and has been reported only for a few species (Hansen and Doyle 1976; Dyck *et al.* 1985; Lazo *et al.* 1989; DeWreede and Green 1990; Bolton and Joska 1993; Phillips 1994; Dyck and DeWreede 1995).

Some of the studies that reported numerical dominance of gametophytes suggested that such dominance results from ecologic differences between the two life-history phases. Specifically, differences in spore production, spore settlement, spore germination, sporeling survival, growth rates, resistance to environmental conditions, susceptibility to herbivores, holdfast perennation,

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Communicating editor: S. C. Lindstrom.

Received 14 January 1999; accepted 20 May 1999.

and apogamy have been proposed as mechanisms leading to gametophyte dominance (Bhattacharya 1985; Hannach and Santelices 1985; May 1986; Lazo *et al.* 1989; Luxoro and Santelices 1989; Fernández and Menéndez 1991; Scrosati *et al.* 1994; González and Meneses 1996; Lindgren and Åberg 1996; Piriz 1996; Zamorano and Westermeier 1996). A few of these hypotheses were experimentally tested in the laboratory and results showed a variable degree of predictive power. Although usually not explicitly stated, the above line of thought implies that the stable ratio between gametophytes and tetrasporophytes (G:T ratio) would be 1 were both reproductive phases ecologically similar. The objective of this paper is to use demographic models to test this assumption.

MATERIALS AND METHODS

The models describe population growth in a discrete manner and apply to ecologically similar phases, which can be interpreted as phases that affect, and are affected by, the environment similarly. Model assumptions are:

1. Same spore viability (100%) for both phases.
2. Same reproductive maturation rates (thalli become fully reproductive 1 year after spore germination).
3. Same reproductive periodicity (thalli release spores once a year until death).
4. Same longevity (different values were considered, as shown below).
5. Competition among thalli does not occur; density-dependence was not considered.

For spore output rates (fecundity rates, which are equal to fertility rates when spore viability is 100%), one way to conform to ecologic similarity is to assume the same production of spores per thallus for both phases. For example, a thallus releasing 100 spores per unit area will impact the environment differently from a thallus releasing only 10 spores, once recruits grow and compete with other organisms. Given the life history of the Gigartinales, we could assume that each tetrasporophyte produces four tetraspores, which is the lowest possible number, considering one meiosis event in only one tetrasporangium, with 100% spore viability. As only female, not male, gametophytes produce carpospores, we should assume that each female gametophyte produces eight carpospores to keep the same spore output per thallus (eight spores per female-male pair of thalli = four spores per thallus) as tetrasporophytes. The models consider that species of the Gigartinales are generally dioecious (M. H. Hommersand, pers. comm., 1998), although some exceptions occur, such as *Chondrus crispus* Stackhouse, for which 'a few cystocarpic plants from Sidmouth, Devon, contained small patches of elongate surface cells near the apex that appeared to function as spermatangial initials' (Fredericq *et al.* 1992).

To make the demographic simulations, we consid-

ered different longevities: annual, triennial, and perennial thalli, with the same longevity for both reproductive phases for each case. Longevity estimates for thalli of the Gigartinales are poor, so the three longevities selected here cover the broadest possible range. Models are:

$$G_t = 4T_{t-1} \text{ and } T_t = 4G_{t-1} \text{ (for annual thalli)} \quad (1)$$

$$G_t = G_{t-1} + 4T_{t-1} - 4T_{t-4} \text{ and}$$

$$T_t = T_{t-1} + 4G_{t-1} - 4G_{t-4} \text{ (for triennial thalli)} \quad (2)$$

$$G_t = G_{t-1} + 4T_{t-1} \text{ and } T_t = T_{t-1} + 4G_{t-1}$$

$$\text{(for perennial thalli)} \quad (3)$$

where G = gametophyte density, T = tetrasporophyte density and t = time (years). We ran the models under different initial G:T ratios (0.5, 1, and 2).

The preceding models have been based on one interpretation of ecologic similarity. The specifics of this concept change when different organisms and processes are considered. For example, if spores are considered as food for filter feeders, the generally larger size of carpospores compared with tetraspores makes for ecologic dissimilarity, even if gametophytes and tetrasporophytes show the same spore output per thallus.

Another approach to modeling ecologic similarity is to consider the simplest life-history sequence. For this case, while each tetrasporophyte still produces four tetraspores, which give rise to two female and two male gametophytes, only one carposporangium with one carpospore is produced by every female gametophyte. Ecologic similarity here consists in both phases carrying on the life history in the simplest possible manner. Incorporating this assumption in place of that assuming the same spore output per thallus, models are:

$$G_t = 4T_{t-1} \text{ and } T_t = 0.5G_{t-1} \text{ (for annual thalli)} \quad (1')$$

$$G_t = G_{t-1} + 4T_{t-1} - 4T_{t-4} \text{ and } T_t = T_{t-1} + 0.5G_{t-1} - 0.5G_{t-4} \text{ (for triennial thalli)} \quad (2')$$

$$G_t = G_{t-1} + 4T_{t-1} \text{ and } T_t = T_{t-1} + 0.5G_{t-1} \text{ (for perennial thalli)} \quad (3')$$

We also ran these models under different initial G:T ratios (0.5, 1, and 2).

Then, we incorporated density-independent mortality in the models, applying the same rate of mortality to both phases, 0.33 year^{-1} (i.e. one-third of the thalli die each year), although this could have been any other value. We considered the second set of assumptions referred to previously. For annual thalli, applying the same density-independent mortality rate to both phases is equivalent to multiplying the parameters of (1') by the same constant, so the stable G:T ratios would not change. However, to incorporate density-independent mortality for triennial and for perennial thalli, the models need to be more complex than (2') and (3'). We built matrix models (Ang and DeWreede 1990; Tuljapurkar and Caswell 1997), separating the gametophytes into male and female thalli and each reproductive phase

into age classes. For simplicity, only triennial thalli will be considered further here. The life-history model that we used, showing the transition probabilities that link the appropriate age classes, appears in Fig. 1. The actual transition matrix and population vector appear in Fig. 2. For matrix models like ours, the initial G:T ratio given by the column vector has no effect on the stable G:T ratio.

RESULTS AND DISCUSSION

For models assuming the same spore output per thallus for both phases, stable G:T ratios depended on the

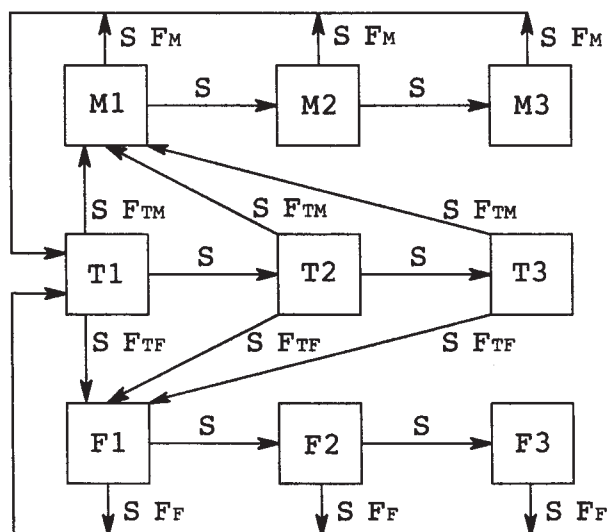


Fig. 1. Life-history diagram used to design the matrix model for triennial thalli. M, male gametophytes (numbers indicate age class); T, tetrasporophytes; F, female gametophytes; S, survival rate (0.67 year^{-1}); F_{TM} , rate of production of male gametophytes (fertility rate) from each tetrasporophyte (2 year^{-1}); F_{TF} , rate of production of female gametophytes from each tetrasporophyte (2 year^{-1}); F_F , rate of production of tetrasporophytes from each female gametophyte (0.5 year^{-1}); F_M , rate of production of tetrasporophytes from each male gametophyte (0.5 year^{-1}).

(a)									(b)			
0	0	0	0	0	0	0	$S F_{TM}$	$S F_{TM}$	$S F_{TM}$	M1		
S	0	0	0	0	0	0	0	0	0	M2		
0	S	0	0	0	0	0	0	0	0	M3		
0	0	0	0	0	0	0	$S F_{TF}$	$S F_{TF}$	$S F_{TF}$	F1		
0	0	0	S	0	0	0	0	0	0	F2		
0	0	0	0	S	0	0	0	0	0	F3		
$S F_M$	$S F_M$	$S F_M$	$S F_F$	$S F_F$	$S F_F$	$S F_F$	0	0	0	T1		
0	0	0	0	0	0	0	S	0	0	T2		
0	0	0	0	0	0	0	0	S	0	T3		

Fig. 2. (a) Transition matrix and (b) population vector used for modeling populations of triennial thalli. M, density of male gametophytes (numbers indicate age class); F, density of female gametophytes; T, density of tetrasporophytes. Other symbols are as in Fig. 1.

details of each case. Iterations of (1) resulted in a continuous annual alternation of two G:T ratios (0.5 and 2) for initial G:T ratios of 0.5 and 2. For an initial G:T ratio of 1, the stable G:T ratio was 1. For longer-lived thalli, [i.e. using (2) and (3)], the G:T ratio followed damped oscillations until it stabilized at 1, regardless of the initial G:T ratio. The results remained the same as a result of increasing initial density of thalli, but without modifying the initial relative density between phases, or as a result of increasing spore output per thallus, but without modifying the relative output between phases. These simulations show that it is possible to expect stable G:T ratios different from 1 for ecologically similar phases, contrary to common expectations, although this difference from 1 was obtained only for annual thalli. A possible example of an annual species is *Mazzaella heterocarpa* (Postels *et* Ruprecht) Fredericq, whose fronds are completely absent for almost half a year in Barkley Sound, western Canada, although no data are available on possible holdfast perennation (R. Scrosati and R. E. DeWreede, pers. obs.).

For models based on the basic life history, stable G:T ratios also depended on the details of each case. Iterations of (1') resulted in a continuous annual alternation of two G:T ratios that depended on the initial G:T ratio. Values oscillated between 0.5 and 16 with an initial ratio of 0.5, between 1 and 8 with an initial ratio of 1, and between 2 and 4 with an initial ratio of 2. For (2') and (3'), the G:T ratio followed damped oscillations until stabilizing at 2.8, regardless of the initial G:T ratio. The stable G:T ratio also remained the same after increasing the initial density of thalli, but without modifying the relative density between phases, or by increasing individual spore output, but without modifying the relative output between phases. Under the assumptions made for this second set of models, it is not possible to achieve a stable G:T ratio of 1.

Based on the calculation of the stable age distribution, regardless of the initial G:T ratio, the stable G:T ratio was also found to be 2.8 for the matrix model for triennial thalli.

Matrix models such as the present one could be taken as a baseline against which G:T ratios of natural populations can be compared. By altering parameters of the model and thus reducing the similarities between the life history phases, natural G:T ratios can be simulated. In natural populations, such differences between phases may result from the effects of factors such as resistance to herbivores and pathogens, irradiance, photoperiod, desiccation, nutrient concentration, apogamy, and apomeiosis. The combination of the natural range of variation of all of these factors results in virtually infinite possibilities for the stable G:T ratio for a given population. To illustrate the effects of these factors on the stable G:T ratio, we modified the magnitude of some of them differently for each phase, but imposing only one modification at a time, using the matrix model for triennial thalli.

For example, considering only changes in survival rates:

1. If the survival rate of female gametophytes (or male gametophytes) is set to 0 for 1-year-old thalli (but allowing them to reproduce before dying), the stable G:T ratio decreases to 2.5.

2. If the survival rate of tetrasporophytes is set to 0 for 1-year-old thalli (but allowing them to reproduce before dying), the stable G:T ratio increases to 3.8.

Considering only changes in spore output rates:

1. If the spore output rate of female gametophytes (or male gametophytes) increases to 1 (twice the original rate), the stable G:T ratio decreases to 2.0.

2. If the spore output rate of tetrasporophytes increases to eight (twice the original rate), the stable G:T ratio increases to 4.0.

As stated, possible results are virtually infinite using matrix models. A stable G:T ratio of 1 is one of those possibilities, but it will only result with phases that differ ecologically in some respect.

How might these conclusions affect the preliminary interpretation of field data on the relative abundance of gametophytes and tetrasporophytes for a given population? *Mazzaella cornucopiae* (Postels *et* Ruprecht) Hommersand offers a good example. This species occurs abundantly in the high intertidal zone of rocky areas of Barkley Sound that are close to the open ocean (Kim 1995; Scrosati 1998). For one population we studied, analyses of frond samples using the resorcinol test (Garbary and DeWreede 1988; Shaughnessy and DeWreede 1991) gave G:T ratios of 3.3 in April 1994, 2.1 in May 1995 and 2.6 in December 1995 (Scrosati 1998). Under the assumption that the stable ratio between ecologically similar phases should be near 1, the above ratios would call for an explanation for the departure from 1 by identifying possible ecologic differences between phases. However, the observed G:T ratios seem to oscillate close to 2.8, which, instead, suggests that gametophytes and tetrasporophytes may be ecologically similar, in light of results of simulations with the second set of models presented herein.

However, even if an observed G:T ratio is close to the expected value of 2.8, significant ecologic differences may still exist between phases. A given ecologic factor may favor one phase, but another factor may favor the other phase in a way that counterbalances the effects of the first factor. Thus, it is necessary to examine the demographic traits of both phases and factors affecting them in order to fully understand the mechanisms underlying a G:T ratio for a given population. In fact, for *M. cornucopiae*, some ecologic differences between phases have been reported for a population from the coast of Oregon (Olson 1990), with gametophytes being more resistant to desiccation and tetrasporophytes more resistant to grazing by limpets.

Overall, we conclude that:

1. Ecologic similarity between gametophytes and tetrasporophytes may be defined in more than one way in terms of spore output rates.

2. A stable G:T ratio of 1 should not be expected as the only alternative when gametophytes and tetrasporophytes are ecologically similar, under our assumptions.

3. It is necessary to evaluate demographic rates for both phases and the effects of relevant ecologic factors on them to understand the causes of a G:T ratio for a given population.

For this purpose, the interaction between field work and modeling is important. For example, given an observed G:T ratio and preliminary field observations on the dynamics of a population, manipulation of suspected relevant model parameters may indicate the most likely necessary changes between phases (in fertility, survivorship, etc.) that lead to such a ratio. This, in turn, provides a basis for further field research. As field studies yield more data on relevant demographic rates, the assumptions and theory inherent in the models can be further examined. Such an iterative process should enhance both field and theoretical understanding.

ACKNOWLEDGEMENTS

We are grateful to the Phycological Society of America for funding the symposium, Current developments in the Gigartinales, organized by R. E. DeWreede during the 52nd annual meeting of the society, held on 3–8 August 1998 at the Northern Arizona University, Flagstaff, Arizona, USA. Natural Sciences and Engineering Research Council grant 5–89872 to R. E. DeWreede supplied some resources used to gather data for this paper.

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