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Reproductive Ecology of *Chondrus crispus* (Rhodophyta, Gigartinales) from Nova Scotia, Canada

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Abstract

Spore production and viability were studied in *Chondrus crispus* based on monthly samples from June to October 1991 at Tor Bay on the Atlantic coast of Nova Scotia. Random collection of fronds showed a gametophyte : tetrasporophyte ratio of about 3 : 1. Two reproductive periods were distinguished based on number and diameter of cystocarps and number of tetrasporic sori g^{-1} frond weight, with reproductive fronds in June and July having larger and fewer cystocarps, and fewer tetrasporic sori g^{-1} than fronds collected from August to October. The pattern of daily spore release was variable among months. Spore viability varied between monthly means of 4–16% for carpospores and 6–26% for tetraspores, with maximum viability in June and August for carpospores and tetraspores, respectively. Variation in spore viability occurred at all levels: among cystocarps or tetrasporangial sori on the same frond, among different fronds, and among months. Such variation provides additional levels of complexity that need to be more fully explored if the extent and timing of spore production to actual reproductive success in *C. crispus* (or any other seaweed) is to be fully understood.

Introduction

On cold-temperate North Atlantic coasts, *Chondrus crispus* Stackhouse, or Irish moss, is one of the most common seaweeds. It is found from Labrador to New Jersey in the western Atlantic, and from Norway to Morocco in the eastern Atlantic (MacFarlane 1968). It has a significant ecological as well as commercial importance, the latter resulting from the presence of carrageenan in its cell walls (McLachlan 1991). Consequently, ecology and reproduction of *C. crispus* have received considerable attention in both North American (*e. g.*, Prince and Kingsbury 1973 a, b, Mathieson and Burns 1975, Craigie and Pringle 1978, Tveter-Gallagher *et al.* 1980, Mathieson 1982, 1989, Bhattacharya 1985, Lazo 1987, Chopin *et al.* 1988, McLachlan *et al.* 1988, Pringle and Semple 1988, Lazo *et al.* 1989 and Lazo and McLachlan 1989) and European populations (*e. g.*, Pybus 1977, Fernández and Menéndez 1990, 1991 a, b, Chopin and Floc'h 1992, Gutiérrez and Fernández 1992).

The plant or clump (after Lazo 1987) of *Chondrus crispus* consists of a crustose holdfast from which numerous dichotomously branching, foliose fronds or ramets arise (McLachlan *et al.* 1989). Clumps can develop from more than one spore, as a result of sporeling coalescence (Tveter and Mathieson 1976, Tveter-Gallagher and Mathieson 1980). In order to understand the reproductive ecology of *Chondrus crispus*, Lazo and McLachlan (1989) and McLachlan *et al.* (1989) pointed out the necessity of investigating the relationship among fronds within reproductive clumps rather than simply studying fronds regardless of where they come from in the population.

In this study we have focused on the relationships between reproductive and non-reproductive fronds within cystocarpic and tetrasporic clumps in an intertidal popu-

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lation of *C. crispus* from Nova Scotia, Canada. We have examined changes in cystocarps and tetrasporic sori on a monthly basis, and daily release and viability of respective spores over a five-month period. We also analyzed the variation of spore viability within fronds of the same clump, amongst clumps of the same life history phase and between life history phases, in order to provide a better picture of the reproduction of this species.

Material and Methods

Samples of *Chondrus crispus* were collected monthly from the intertidal zone at Tor Bay, Guysborough County (lat. 45°11' N, long. 61°21' W), on the Atlantic coast of Nova Scotia, Canada, from June through October 1991. The study site is moderately exposed and has a gentle slope with a substratum of large granitic boulders. All clumps came from the lower intertidal zone, below the region of conspicuous fucoid cover. Gametophyte : tetrasporophyte (G/T) ratios were determined monthly based on a minimum of 100 haphazardly-collected fronds using the resorcinol test (Garbary and De Wreede 1988). The reproductive stage of clumps was studied by collecting all of the fronds of cystocarpic and tetrasporic clumps. Clumps were selected based on the presence of reproductive structures. The number of fertile and non-fertile fronds in each clump was enumerated, and the wet weight of every frond recorded (to the nearest 0.001 g). Cystocarps and tetrasporic sori were counted, and cystocarp diameter measured.

Spore viability was estimated monthly using cystocarpic and tetrasporic fronds collected haphazardly in the field (only one frond per clump). Segments of 5−10 fronds (containing 1 cystocarp or 2−4 tetrasporic sori each) with seemingly mature, but unreleased spores were placed individually in chambers of 25-celled plastic repli-boxes (Sterilin, Hounslow, U. K.) containing 6 mL of modified von Stosch medium (Guiry and Cunningham 1984) with 5 mg L^{-1} GeO_2, at 15 °C, 16 : $\overline{8}$ h (light : dark), and a photon flux density of 20 μE m^{-2} s^{-1} using cool-white, 40-w fluorescent tubes. Spore release was recorded each morning for six days, and the plant fragment was transferred to a new chamber in the repli-box. Germination was assayed three days after spore release using an inverted microscope. Spore germination was recorded as positive, based on the occurrence of at least one cell division or changes in color and shape (*e. g.*, expansion on one side of spore) indicating development.

Values of various measurements were analyzed using *t*-tests and one-way analyses of variance (ANOVA), followed by the Tukey test (Zar 1984). When heteroscedasticity was detected according to Bartlett's test, nonparametric Kruskal-Wallis one-way ANOVA was performed, followed by nonparametric multiple comparisons (Zar 1984). Statistical analyses were done using SYSTAT 5.0 (Wilkinson 1989).

Results

Gametophyte : tetrasporophyte ratio

The gametophyte : tetrasporophyte (G/T) ratio showed only minor variation throughout the five-month study period. Monthly values were between 72−78% for gametophytes and 23−28% for tetrasporophytes and are within the expected errors of the sampling procedure.

Reproductive stage of clumps

Fertile cystocarpic and tetrasporic clumps occurred in all months. Cystocarpic clumps were less frequent in August, when only a single reproductive clump was found after an extensive search. Except for the August cystocarpic clump with only 12 fronds, cystocarpic and tetrasporic clumps respectively had monthly mean values of 49−82 and 42−66 fronds, which were not significantly different between themselves ($p > 0.01$). Fertile fronds for both phases were less numerous than non-fertile ones in all clumps (Table I). The monthly mean percentage (in number) of reproductive fronds was highly variable in cystocarpic clumps (7 to 33%) but much more stable in tetrasporic clumps (20 to 26%), and the overall mean values for all clumps of the two phases did not differ

Table I. Monthly values for cystocarpic and tetrasporic clumps (mean ± s. d.). Number of clumps analysed indicated in parentheses.

Month	Number of fertile cystocarpic fronds (%)	Weight of fertile cystocarpic fronds (%)	Number of fertile tetrasporic fronds (%)	Weight of fertile tetrasporic fronds (%)	Frond number in cystocarpic clumps	Frond number in tetrasporic clumps
June	28.1 ± 22.8 (7)	48.8 ± 28.5	25.3 ± 17.6 (9)	58.7 ± 25.5	59.4 ± 39.3	57.9 ± 32.8
July	7.4 ± 4.0 (4)	37.2 ± 16.1	23.9 ± 12.4 (5)	72.7 ± 19.8	83.0 ± 49.1	41.4 ± 26.9
August	33.3 (1)	97.4	20.4 ± 11.3 (7)	68.7 ± 12.0	12.0	38.9 ± 32.3
September	24.7 ± 11.1 (4)	88.8 ± 6.4	25.6 ± 7.7 (6)	64.1 ± 17.2	49.0 ± 49.8	65.7 ± 30.7
October	16.2 ± 10.0 (4)	66.9 ± 15.0	20.7 ± 10.0 (4)	57.0 ± 21.5	70.7 ± 8.3	49.3 ± 19.2
Mean	21.2 ± 16.6 (20)	60.6 ± 27.5	23.4 ± 12.4 (31)	64.0 ± 19.5	61.8 ± 39.2	53.4 ± 28.5

Table II. Monthly weights of fertile and nonfertile fronds from female gametophytic and tetrasporophytic clumps (mean ± s. d.). In parentheses, number of fronds.

Month	Fertile cystocarpic fronds (g)	Nonfertile cystocarpic fronds (g)	Fertile tetrasporic fronds (g)	Nonfertile tetrasporic fronds (g)
June	0.88 ± 0.88 (70)	0.20 ± 0.32 (346)	0.66 ± 0.70 (108)	0.16 ± 0.27 (416)
July	1.45 ± 1.80 (24)	0.20 ± 0.39 (305)	0.99 ± 0.85 (39)	0.15 ± 0.39 (168)
August	4.34 ± 2.11 (4)	0.06 ± 0.04 (8)	0.85 ± 0.71 (56)	0.09 ± 0.14 (276)
September	2.14 ± 2.05 (32)	0.06 ± 0.11 (164)	0.50 ± 0.35 (35)	0.13 ± 0.16 (291)
October	1.50 ± 1.81 (46)	0.11 ± 0.30 (237)	0.72 ± 0.73 (322)	0.09 ± 0.13 (162)
Mean	1.43 ± 1.67 (176)	0.16 ± 0.32 (1066)		0.13 ± 0.24 (1309)

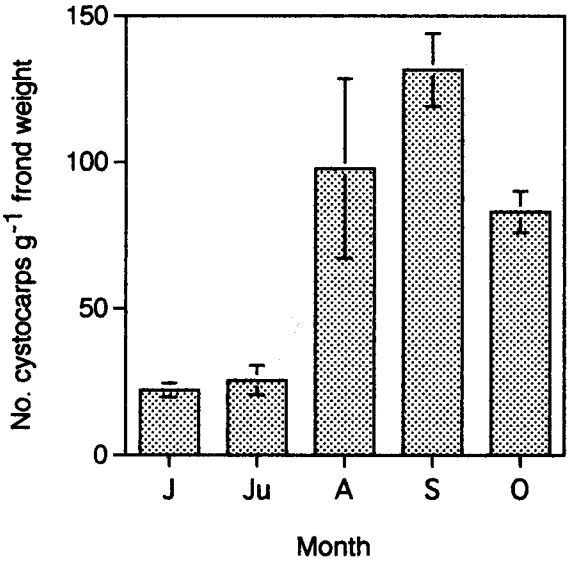

Fig. 1. Mean number of cystocarps g^{-1} of frond weight from June to October (mean ± s. e.).

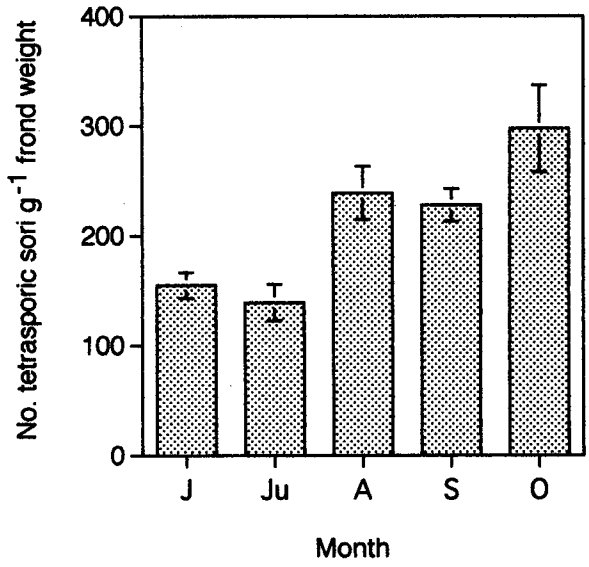

Fig. 3. Mean number of tretrasporic sori g^{-1} of frond weight from June to October (mean ± s. e.).

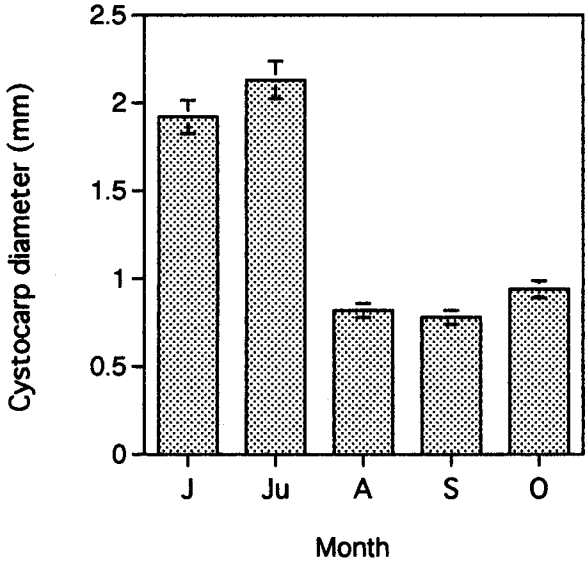

Fig. 2. Mean diameter of cystocarps from June to October (mean ± s. e.).

significantly ($p > 0.01$). The relative contribution to clump biomass of fertile fronds was higher in most clumps (Table I). Maximum monthly means were 97% and 73% for cystocarpic and tetrasporic clumps, respectively, and the mean values for all clumps were not significantly different between phases ($p > 0.01$).

Wet weight of fertile cystocarpic fronds varied from 0.020 g to 9.898 g, while that of fertile tetrasporic fronds varied from 0.012 g to 4.819 g. Weight of non-fertile fronds ranged from 0.001 g (limit of balance resolution) to 4.086 g and 3.115 g in cystocarpic and tetrasporic clumps respectively. Fertile cystocarpic fronds were significantly heavier than fertile tetrasporic fronds ($p < 0.01$), but non-fertile cystocarpic fronds were not significantly different in weight from non-fertile tetrasporic ones ($p > 0.01$) (Table II).

Production of cystocarps and tetrasporic sori

Monthly mean number of cystocarps (Fig. 1) was significantly different among months ($p < 0.05$), and Tukey's multiple comparison distinguished two groups ($p < 0.05$):

1. clumps from June–July, with an average production of 23 ± 21 cystocarps g^{-1} of frond weight; and

2. clumps from August to October, with a mean of 102 ± 59 cystocarps g^{-1}.

Mean diameter of cystocarps (Fig. 2) was also significantly different among months ($p < 0.05$), and two groups were resolved ($p < 0.05$) using Tukey's test:

1. June–July (mean = 2.0 ± 0.5 mm); and

2. August to October (mean = 0.9 ± 0.2 mm).

In both periods, there was no relationship between cystocarp diameter and frond weight. Mean number of tetrasporic sori (Fig. 3) was also significantly different ($p < 0.05$) among months. Two temporal groups were identified ($p < 0.05$):

1. June–July (mean = 151 ± 116 sori g^{-1} of frond weight); and

2. August to October (mean = 244 ± 174 sori g^{-1} of frond weight).

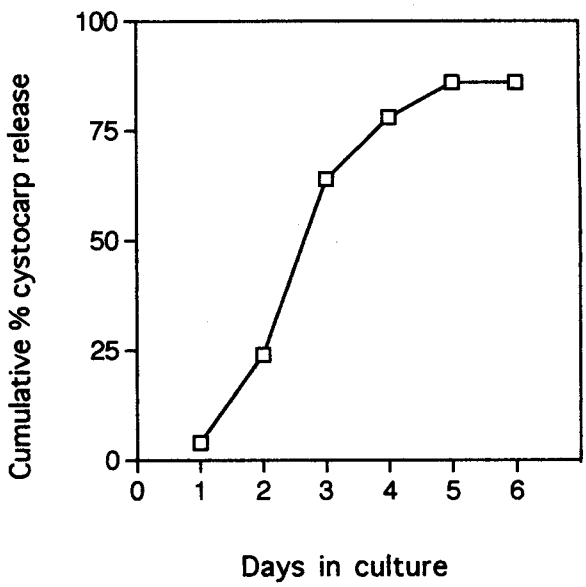

Fig. 4. Cumulative percentage release of cystocarps in relation to days in culture.

Release and viability of carpospores and tetraspores

Between 0 and 20% of cystocarps in culture released carpospores the first day for all monthly samples, while the cumulative percentage of release by the sixth day was 40–70% for June–July, and 80–90% for August to October. Cumulative release pattern was a sigmoidal curve for all months (Fig. 4). The pattern of daily release was variable among months (Fig. 5A–E), and, after pooling all data, the highest number of cystocarps releasing carpospores was observed in the third day (Fig. 5F). Cumulative daily release of tetraspores showed two patterns: between June and August, percentage of sori releasing tetraspores in the first day was 45–65%, compared with only 20–40% in September–October. By the sixth day, however, both groups presented cumulat-

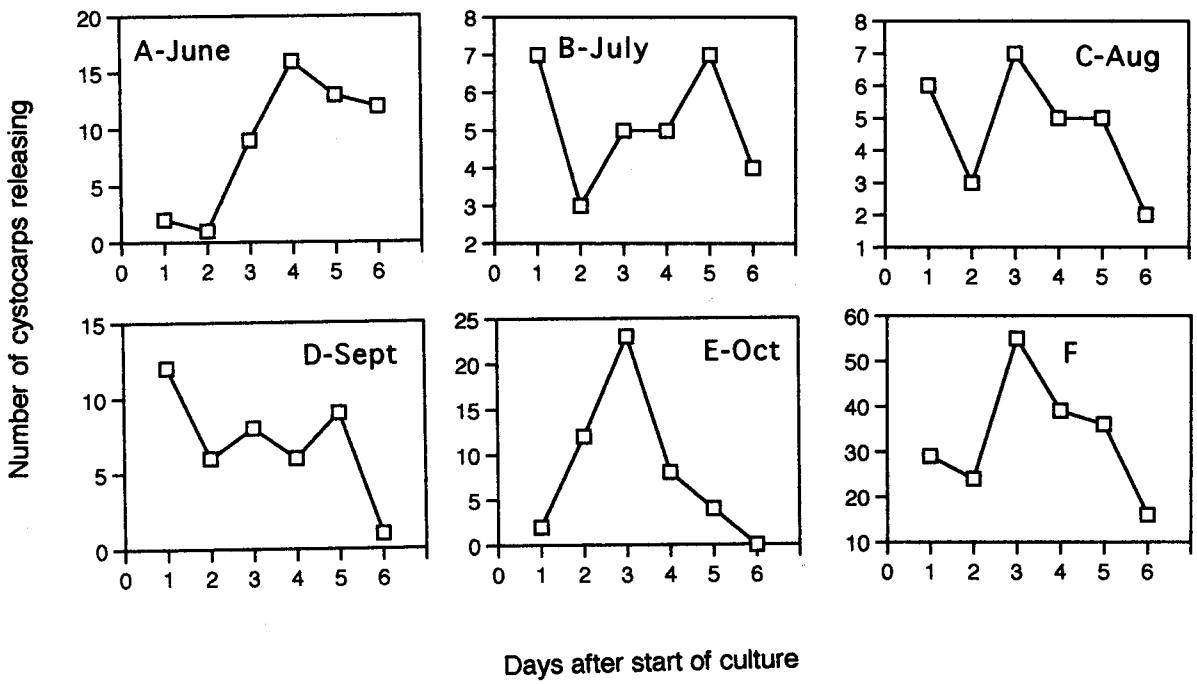

Fig. 5. Frequency of spore release from cystocarps with respect to day in culture based on individual months from June to October (A–E) and combined monthly data (F).

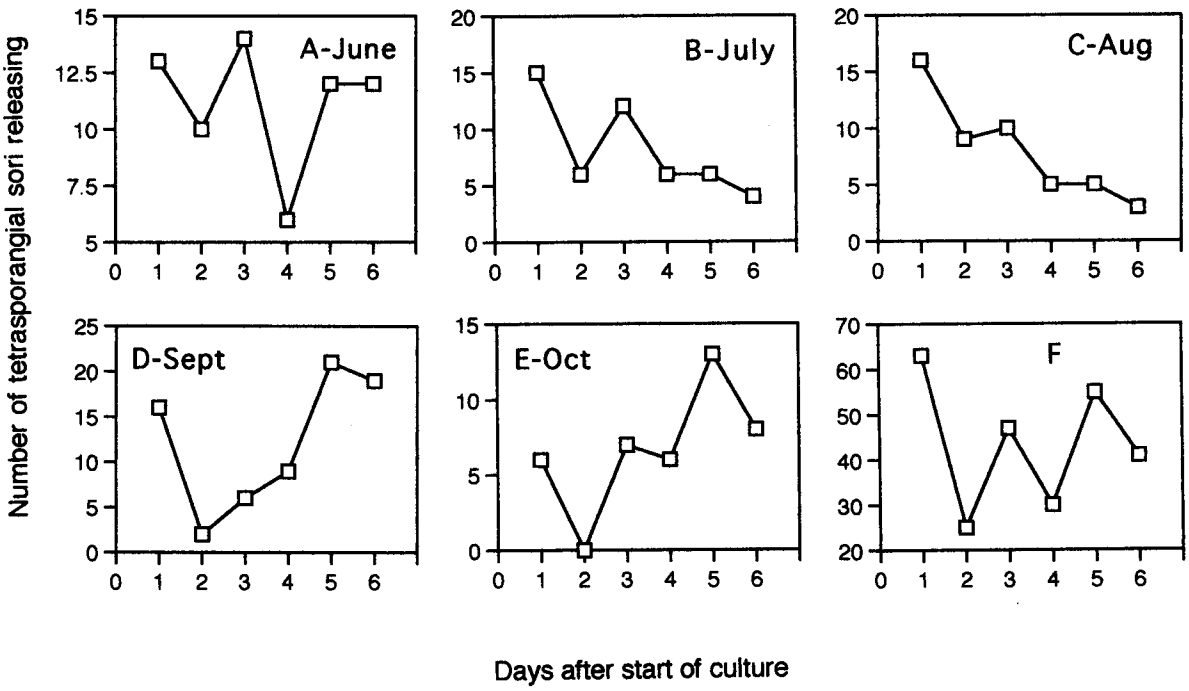

Fig. 6. Frequency of spore release from tetrasporic sori with respect to day in culture based on individual months from June to October (A–E) and combined monthly data (F).

ive percentage of release between 92–100%. The pattern of daily release of tetraspores was variable among months (Fig. 6A–E), but the pooled data revealed several peaks with alternating high and low means (Fig. 6F).

Viability of carpo- and tetraspores was extremely variable both within and among fronds, ranging from 0–100%. However, monthly mean viability was usually low (Figs 7, 8). Mean viability of carpospores (Fig. 7) did not show significant differences among months ($p > 0.01$). Average viability of tetraspores (Fig. 8) was significantly different among months ($p < 0.01$). Mean viability in September was significantly lower than in June–August. The overall viability of tetraspores (15%) for June–October was significantly higher than for carpospores (9%) ($p < 0.01$).

There were no significant differences among mean daily viability of carpospores ($p > 0.01$), but day of release had an effect of mean tetraspore viability ($p < 0.01$). Those released in the sixth day had a significantly lower viability ($p < 0.01$) than those released in the second day.

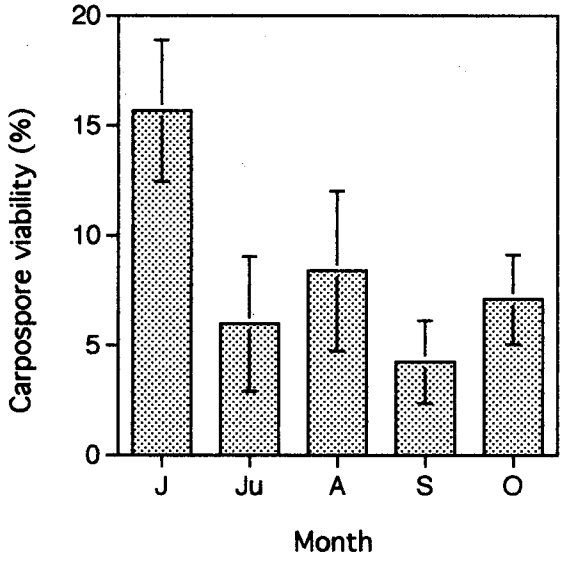

Fig. 7. Monthly mean viability of carpospores (%) from June to October (mean ± s. e.).

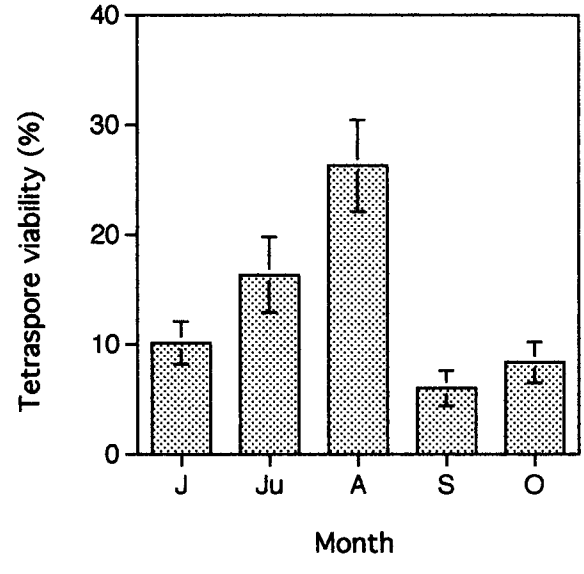

Fig. 8. Monthly mean viability of tetraspores (%) from June to October (mean ± s. e.).

Discussion

The gametophyte : tetrasporophyte (G/T) ratio for *Chondrus crispus* at Tor Bay was similar to that reported previously for the Atlantic coast of Nova Scotia (McLachlan 1991, McLachlan and Lewis, unpublished) and to the ratio found in independent studies, that included samples from Tor Bay in 1989 and 1993 (McLachlan and Garbary, unpublished). The temporal stability of this ratio at any particular site is to be expected, as *C. crispus* is a perennial species that retains its fronds throughout the year. Bhattacharya (1985) also reported little inter-monthly variation in a year round study of a population from southwestern Nova Scotia.

The predominance of gametophytes in our intertidal population of *C. crispus* might be explained by the proposal of McLachlan (1991). He suggested that the hard and stable substratum in the littoral zone of the Atlantic coast of Nova Scotia and the morphology of the clumps was conducive to population maintenance mainly by vegetative growth from the holdfasts rather than by germination of spores. Different ecophysiological properties between the two reproductive phases (*e. g.*, endophyte susceptibility, Correa and McLachlan 1991) may make the gametophytes more competitive than tetrasporophytes, thus becoming the more numerous phase in the intertidal level. These populations on the Atlantic coast of Nova Scotia have different G/T ratios to those in the Gulf of Saint Lawrence, where the ratio is typically 1 : 1 in subtidal populations (Lazo *et al.* 1989, Craigie and Pringle 1978, but see Chopin *et al.* 1988 for exception). Further field studies are needed to see if tetrasporophytes are more abundant than gametophytes at the lower limit of distribution of the Tor Bay population (probably in the subtidal region). Such a change in relative phase abundance with depth has been described for *C. crispus* from other populations (Mathieson and Burns 1975, Craigie and Pringle 1978).

Fronds of *C. crispus* in the Gulf of St. Lawrence with two or more dichotomies were classified as reproductively mature fronds (Lazo and McLachlan 1989). A large proportion of fronds may be mature; however, only a small percentage is reproductive at any time (Lazo *et al.* 1989). The fact that non-fertile fronds are always present, and always more numerous than fertile fronds indicates that reproductive clumps are dynamic structures, where the largest reproductive fronds are lost at the same time as new non-fertile fronds are formed. The instantaneous frequencies of reproductive fronds are expected to be variable, and the longer the frond is associated with the clump, the greater the number of expected reproductive structures.

As shown in our results, the number of cystocarps and tetrasporic sori per frond increased in August, and fronds maintained these higher values in September and October. This period of the year is coincident with peaks in water and air temperature, but possible environmental factors affecting changes in reproductive features need to be tested in further experimental field studies. It is also possible that carpospore production in June–July and August–September–October is similar, because of the significant difference in cystocarp size during the two periods. Regardless of this, the single fertile cystocarpic clump that we found in August suggests that this is a transition month between two distinct reproductive periods.

Seasonal maxima in formation of reproductive structures appear to be population specific. Chopin *et al.* (1988) described a peak in number of cystocarps per frond in June in populations from Prince Edward Island, whereas Prince and Kingsbury (1973 b) observed an increase in percentage of fronds bearing cystocarps during August and September in Massachusetts. In European populations, Fernández and Menéndez (1991 b) also recorded the maximum number of cystocarps per frond in August, as well as the highest average volume of cystocarps in spring. Environmental or genetic factors that account for these differences remain to be established. From our data and personal field observations, it is likely that most of the cystocarpic fronds present in July disappeared by August. This would account for the fact that the few cystocarpic fronds observed in August had new and smaller cystocarps. We have no information as to whether these groups of reproductive fronds belong to the same or different clumps as those bearing cystocarps in early summer. It is possible that wave action removed all cystocarpic fronds between July and August. This explanation is consistent with observations of Bhattacharya (1985) who reported that the largest fertile fronds tagged in April had been mostly detached by August. Production of new cystocarps in July and August was also observed by Mathieson (1982) in New Hampshire. Our observations are consistent with these previous studies; however, the seasonal differences in cystocarp numbers and sizes introduce a new level of complexity into understanding the reproductive biology of *C. crispus*.

Seasonal production of tetrasporic sori is also population specific. Prince and Kingsbury (1973 b) and Chopin *et al.* (1988) also observed an increase in reproduction between August and October. However, this differs from observations by Bhattacharya (1985) and Mathieson (1982) who described constancy in number of tetrasporic sori per frond thoughout the year, in southwestern Nova Scotia and New Hampshire, respectively.

The higher values of daily release of tetraspores with respect to those for carpospores was expected, since

each tetrasporic frond fragment put into the culture boxes contained more than one sorus, while cystocarpic frond fragments only contained one cystocarp each. The pattern of daily spore release was highly variable for both phases among months. However, when pooling monthly data separately for both phases, a unimodal curve was found for carpospore release, whereas tetraspore release showed three peaks of maximum discharge in the study period. Release of both kind of spores has been observed in laboratory conditions up to 30 days after initiation of the cultures (Tasende and Fraga 1992). Monthly mean viability of carpospores and tetraspores was low in our study, never reaching 30%. Such low values suggest that reproduction by spores does not contribute much to the maintenance of this intertidal population. This agrees well with McLachlan's (1991) hypothesis mentioned previously. However, longer-lasting field studies and quantification of spore production are needed to confirm this idea. In populations from New Hampshire, Mathieson (1982, 1989) observed maximum discharge and viability of carpospores and tetraspores in summer, but reported much higher values of viability than those reported here. The difference between both data sets may rely on the different methods employed to estimate viability. In his studies, Mathieson (1982, 1989) used neutral red to monitor viability, instead of counting actively germinating spores; thus discrepancies may partially reflect differing methods for quantification. In future experiments, the influence of different culture media on spore germination should also be taken into account, as this has been shown to be a source of variation in experiencies with *C. crispus* from Spain (Tasende and Frage 1992).

Our studies on spore viability have important implications for the understanding of algal phenology in general. Many seasonal ecological studies only report the presence/absence of reprodutive structures in a population. Similar to Prince and Kingsbury (1973 b), our observations suggest that even when a reproductive structure is present, it can be highly variable in terms of abundance, and the reproductive units produced may have vastly different viabilities (also see Hoffmann and Camus 1989). In our area, cystocarps and tetrasporangia have been recorded for *C. crispus* throughout the year, and in laboratory culture at 10 °C the respective spores were viable the year round (Bhattacharya 1985). At 5 °C or less, discharged spores failed to germinate (McLachlan, unpublished), indicating that water temperatures on the Atlantic coast of Nova Scotia (Edelstein *et al.* 1969) from December to June are unsuitable for spore germination, and *in situ* spore germination would be thus limited to the warmer months (June to November). Both spore types were viable throughout this period. The considerable variability in release and viability of spores found here (see also Pacheco-Ruiz *et al.* 1989) suggests a complex relationship between the presence (and abundance) of reproductive structures and patterns in spore release and viability. Thus, simple counts of sporangia, or even measures of spore production do not adequately model reproductive potential. Whether the variation we observed is a reflection of internal physiological control within fronds and clumps, or represents stochastic processes remains to be determined.

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