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Impact of Dragraking on the Reproductive Capacity of Southern Gulf of St. Lawrence Irish Moss (Chondrus crispus)

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ABSTRACT

A non-harvested bed of Chondrus crispus (Rustico) showed, year round, a greater carposporangial reproductive capacity than a dragraked bed (Miminegash). The former had a lower frond density but larger plants which were the major sources of reproduction. Although carposporangial sori had a greater area and were more often full in Miminegash, their reproductive capacity was higher in Rustico due to their higher number per frond and sample unit. All the studied parameters did not show significant (P=0.05) difference for tetrasporophytes, resulting in an equal overall tetrasporangial reproductive capacity in both locations. However, before dragraking season started it had a high potential in Miminegash. Class 4 appeared to be determinant to assume reproduction. As no harvesting technique can, at the moment, preserve individuals of this class, a 1-mo delay of the present opening date of the fishing season is suggested to improve bed reproductive potential. Besides, the much higher tetrasporangial reproductive capacity over that of carposporangial sori could explain the gametophytic dominance of the population.

RÉSUMÉ

La capacité de reproduction des carposporocystes de Chondrus crispus est plus importante dans un champ inexploité (Rustico) que dans un autre, exploité par des dragues à rateaux (Miminegash). Le premier a une densité de frondes inférieure mais possède des plantes plus développées qui contribuent davantage de la reproduction. Bien que les carposporocystes aient une surface plus grande et soient plus souvent pleins à Miminegash, leur capacité de reproduction est plus importante à Rustico en raison de leur plus grand nombre per fronde et per unité d'échantillonnage. Aucune différence significative (P=0.05) n'est observée dans les paramètres étudiés pour les tétrasporophytes, ce qui conduit à une égale capacité de reproduction globale des tétrasporocystes dans les deux sites. Cependant, cette dernière montre un grand potentiel à Miminegash avant que la saison de pêche débute. La Class 4 apparaît déterminante pour assumer la reproduction. Comme il n'existe pas, pour l'instant, de technique de récolte qui préserve les individus de cette classe, un détai d'un mois de la date actuelle d'ouverture de la saison de pêche est suggéré pour une meilleure gestion de la ressource. En outre, la plus grande capacité de reproduction des tétrasporocystes, par comparaison aux carposporocystes, pourrait expliquer la prédominance gamétophytique de la population.

INTRODUCTION

The perennial red seaweed Chordrus crispus Stackhouse (Irish moss) is the basis of an important marine plant fishery in the Canadian Maritime Provinces (MacFarlane 1964; Ffrench 1971; Pringle 1976). It is generally the second largest fishery, on a value-per-species basis, after lobster (P.E.I. Dept. of Fisheries and Labour 1985) in Prince Edward Island. The crop is processed for the colloid, carrageenan, whose gelling, thickening, and stabilizing properties are used in industries such as food-processing, pharmaceuticals, and cosmetics (Chopin 1986).

Problems in attaining a stable annual yield arose in 1971 in Marine Plant Harvesting District 1 (MPHD 1), the single most productive Irish moss fishery in the northwestern Atlantic (Pringle 1981). The decrease in annual yields occurred following an increase in both fishing pressure (Pringle and Semple 1984) and fishing power without a concomitant resource management plan (Pringle 1986). It was shown that resource abundance controlled annual yields (Pringle 1981) and that the mean annual frond size in the crop was significantly less than that in other marine plant harvesting districts (Pringle and Sharp 1986), suggesting growth overharvesting. Furthermore, Pringle and Semple (1984) noted patches of prime substrate (sandstone ledge), barren of macrophyte cover for up to 7 yr. The barren areas represented up to 21% of this ledge in certain commercial dragraked beds. Pringle and Semple (1984) hypothesized that this long-term condition may be the result of recruitment overharvesting.

Considerable information has been published on C. crispus reproductive phenology in France (Kopp 1975; Chopin 1985), in New England (Prince and Kingsbury 1973; Mathieson and Burns 1975), and in the Canadian Maritime provinces (MacFarlane 1968; Bhattacharya 1985). However, little data are available on the reproductive capacity of C. crispus. The present study was designed to yield quantitative data on aspects of reproduction in southern Gulf of St. Lawrence C. crispus beds. We test, in particular, the null hypothesis that the reproductive capacity is significantly ($P \leq 0.05$) different between a commercial dragraked bed (Miminegash) and a commercially important, non-dragraked bed (Rustico; fronds are cropped via wave shock and ice scouring and harvested as "storm toss" [Pringle and Mathieson 1986]).

MATERIALS AND METHODS

We define the reproductive capacity of C. crispus as the amount of reproductive material (expressed as the area of reproductive sori) per unit area (0.25 m^2) of ocean bottom (within the bounds of both study sites) over a 12-mo period. Reproductive capacity was calculated from the following parameters: frond density, frond biomass, and number, area, and state of fullness of reproductive sori per frond. Samples were collected from beds (Fig. 1) at Miminegash (Cape Gage and Pleasant View Reef) and Rustico (Orby Head). The latter bed was dragraked only during 1969 and 1970, after which dragraking was banned in 1971 (Craigie and Pringle 1978). Collections were made monthly during spring and summer and bimonthly thereafter. Dynamic ice conditions did not permit January Miminegash collections. Three transects, running perpendicular to the shore through the C. crispus beds, were established at each site. Three stations on each transect (the inner, middle, and outer regions) were designated. Three sample units were haphazardly chosen at each station by dropping a 0.25 m^2 quadrat frame (that size deemed most efficient by Pringle [1984]) from the diver tender. The macroalgae in each quadrat were hand-collected by divers and carefully placed in a fine-mesh sampling bag. They were transferred to plastic bags, stored in a cooler on the boat, and later (no more than 5 h) frozen at -30°C until sorting. The method of frond removal underestimates the density of Class 1 fronds. The impact on our estimates of reproductive capacity will be nil, as this class has never been observed to be reproductively mature.

The fronds in a sample (combination of all sample units per site per collection) were initially separated into three categories: 1) entire fronds of _C. crispus_; 2) torn pieces ("torns") of _C. crispus_; and 3) "other" algae. _C. crispus_ fronds were sorted into five classes, based on number of dichotomies and frond length, using a slightly modified version of the classification of Sharp et al. (1986):

Class 1 - non-dichotomous fronds

Class 2 - fronds with up to three dichotomies and a frond length less than 10 cm, or fronds with any number of dichotomies and a frond length less ≤ 6 cm

Class 3 - fronds with four or five dichotomies and a frond length between 6 and 10 cm

Class 4 - fronds with more than five dichotomies and a frond length between 6 and 10 cm

Class 5 - fronds with any number of dichotomies and a frond length greater than 10 cm

Fronds within each class were sorted into three groups: 1) fructified female gamtophytes; 2) fructified tetrasporophytes; and 3) non-fructified fronds (which likely included male gametophytes). The number of fronds in each group was scored. Up to ten specimens were haphazardly chosen from each of the first two groups; the number of reproductive sori per frond, and their state of sorus fullness (a subjective assessment using the following categories: empty, partially empty, and full), were determined for each individual. One reproductive sorus per chosen frond was subjectively assessed as a "typically sized" sorus for that frond. Its area was determined and then multiplied by the number of sori on the frond, to give an estimate of the frond reproductive capacity. The mean frond reproductive capacity was calculated for all chosen fronds per reproductive type and per frond class for each sample unit. This value was multiplied by the corresponding number of mature fronds per sample unit to estimate the class reproductive capacity per sample unit. The mean class reproductive capacity per sample was determined by averaging the class sample unit reproductive capacity. The mean annual class reproductive capacity was determined by summing the mean class sample values and dividing them by the number of samples. This procedure was followed for each frond class of both reproductive types. The mean overall sample reproductive capacity was determined by summing the mean sample class values. The mean overall annual reproductive capacity was determined by summing the mean overall samples values and dividing them by the number of samples. Following 72 h of drying at 80°C, dry weight (biomass) of each group was measured.

Usual statistics (mean, standard deviation, etc.) and normality analyses were carried out with the packaged computer programs in Statistical Package for the Social Sciences (Nie et al. 1975). All distributions were normal; thus, the parametric Student t-test was employed to determine significant differences ($P \leq 0.05$) between means. Percentages were transformed in arcsin to permit statistically significant ($P \leq 0.05$) differences to be delineated (Sokal and Rohlf 1969). Relationships between characteristics were assessed using a regression analysis (Nie et al. 1975).

RESULTS

Frond density

C. crispus total frond density per 0.25 m^2 was significantly greater (Fig. 2) in Miminegash (699.5; Table 1) than in Rustico (544.7) due to a greater abundance of Classes 1 and 2 individuals; these were the most abundant classes in both locations. Frond density peaked in late summer. Classes 4 and 5 fronds were most abundant in June and September in Miminegash, with decreases in early summer and during autumn, to reach a minimal level in winter. There was only one peak (July) in Classes 4 and 5 abundance in Rustico. There were significantly ($P \leq 0.05$) more Classes 1, 2, and 3 fronds in Miminegash, but more Class 4 fronds in Rustico (Table 1). The mean number of Class 5 fronds was not statistically ($P=0.05$) different between the two locations.

The density of carposporangial and tetrasporangial bearing fronds over time (Fig. 3), exhibited a bimodal pattern for both locations, with maxima in early summer and autumn. Carposporangial minima occurred in early spring and July; tetrasporangial in August. Class 4 fronds had the highest incidence of fructification at both locations. There were significantly ($P \leq 0.05$) more Classes 2, 4, and 5 carposporangial bearing fronds in Rustico than in Miminegash (Table 1), but more mature Class 3 tetrasporaphytes at the latter site. Overall, carposporangial bearing fronds were 1.8 times more dense at Rustico (33.0) than at Miminegash (18.3), but the density of mature tetrasporphytes at the two sites was similar (20.1 and 22.6 respectively). The percentage of fronds bearing reproductive sori was always low. Carposporangial bearing fronds were 2.3 times more frequent in Rustico (6.1%) than in Miminegash (2.6%). However, the frequency of mature tetrasporophytes between the two sites was similar (3.7% and 3.2% respectively).

Frond Biomass

Total frond biomass over the study period showed two maxima (June and September) in Miminegash, and one (July) in Rustico (Fig. 4). Overall, the mean biomass was significantly greater in Rustico (48.62 g; Table 2) than in Miminegash (41.36 g), due in part to significantly greater numbers of larger fronds in Rustico. Classes 4 and 5 provided most of the biomass in Miminegash only during spring and early summer, whereas at Rustico these classes dominated the biomass production year round.

Annual variations in the biomass of both carposporangial and tetrasporangial bearing fronds (Fig. 5) followed a similar pattern to that of frond density (r=0.87) (Fig. 3). Total biomass of both Classes 2 and 3 fronds was always much lower than that of Classes 4 and 5 fronds, except in autumn and winter in Miminegash. The biomass of Classes 2, 4, and 5 fronds bearing carposporangial sori was significantly ($P \leq 0.05$) greater in Rustico than in Miminegash; the reverse was the case for Class 3 tetrasporangial bearing fronds (Table 2). Overall, the biomass of carposporangial bearing fronds per 0.25 m^2 was 2.6 times greater in Rustico (9.73 g) than in Miminegash (3.68 g). There was no difference ($P=0.05$) between these sites in the biomass of tetrasporangial bearing fronds. The percentage contribution of Classes 2 and 3 reproductively mature fronds to the total biomass of these classes was low at both sites. However, 50.6% of the total Class 5 biomass at Rustico was contributed by reproductively mature fronds.

Number of Reproductive Sori Per Frond

Carposporangial and tetrasporangial sori occurred on Classes 2 to 5 fronds; Class 1 fronds were never reproductive. The mean number of reproductive sori per frond increased markedly with each class (Fig. 6). The mean number of tetrasporangial sori per frond per class was always higher than that for carposporangial sori. There was little seasonal difference in mean number of reproductive sori per Classes 2 and 3 fronds at either site, which was in contrast to that of the Classes 4 and 5 fronds. The pattern in the seasonal distribution of number of carposporangial sori per frond was unimodal in both locations, with minimal numbers in July (Fig. 7). The seasonal pattern in number of tetrasporangial sori per frond was bimodal at both sites, with peaks in June and November. The mean number of carposporangial and tetrasporangial sori per frond per class was greater at Rustico than at Miminegash: the former by a factor of 1.9; the latter by a factor of 1.3 (Table 3).

Number of Reproductive Sori Per 0.25 m^2

The seasonal pattern in mean number of carposporangial and tetrasporangial sori per 0.25 m^2 (Fig. 8) resembled (r=0.86) that of cystocarpic and tetrasporic frond biomass (Fig. 5). However, at Miminegash the September carposporangial sorus maxima of Classes 4 and 5 fronds were of the same order as that of June; in Rustico, the tetrasporangial sorus maxima of these classes were in November instead of September. The number of reproductive sori per 0.25 m^2, contributed per frond class, increased exponentially (Fig. 9). There were significantly ($P \leq 0.05$) greater numbers of carposporangial sori per 0.25 m^2 contributed by each frond class at Rustico than at Miminegash (Table 3). Overall, there were 3.5 times more carposporangial sori per 0.25 m^2 at Rustico (3,406.8) than at Miminegash (974.4). The mean number of tetrasporangial sori per 0.25 m^2 in June was much higher at Miminegash than at Rustico (Fig. 10); however, from late summer and during winter this number was larger in Rustico due to a higher density of tetasporangial bearing Classes 4 and 5 fronds (Fig. 3), and a higher number of tetrasporangial sori per frond (Fig. 7). Thus, there was no significant difference ($P=0.05$) between the two sites either within each class or overall (Table 3).

Area of Reproductive Sori

There was a significant (P≤0.05) temporal component to the variation in area of both carposporangial and tetrasporangial sori at both Rustico and Miminegash. The pattern was similar in each class; hence, site data were combined (Fig. 11). Carposporangial sori peaked in area in June and September; it was minimal in August and late autumn/winter. The seasonal pattern in tetrasporangial sorus area was unimodal with the largest sori occurring in June. For both types of sori, there was no correlation between area and either frond class or number of sori per frond (r=0.15). Carposporangial sori from Miminegash fronds were significantly (P≤0.05) larger in all frond classes than those from Rustico fronds (Table 4); overall, they were 16% larger. There was no difference (P=0.05) in overall tetrasporangial sorus area between the two study sites.

Reproductive Area Per Unit Area of Bed (Reproductive Capacity)

The seasonal carposporangial sorus area pattern (Fig. 12) was bimodal at both locations; maxima in Miminegash occurred in June and September; minima occurred in mid summer (July/August) and late autumn/winter. Carposporangial sorus area in Rustico followed a similar pattern except that the spring maximum occurred earlier (May). Variation in tetrasporangial sorus area for both Miminegash and Rustico followed the same seasonal pattern as that for carposporangial sorus area. Contributions to the overall reproductive capacity by Classes 2 and 3 fronds was low compared to Classes 4 and 5 fronds (Fig. 13). With the exception of tetrasporophytes from Rustico, there was an increase in reproductive capacity by Class 5 fronds over Class 4 fronds. The reproductive capacity of Rustico's Classes 2, 4, and 5 carposphorophyte bearing fronds was significantly (P≤0.05) larger than those from Miminegash; overall carposporangial reproductive capacity was greater by 58% in fronds from Rustico (Table 4). The reproductive capacity of Miminegash-derived Classes 3 and 5 tetrasporophytes was significantly (P≤0.05) greater than those from Rustico. Nevertheless, there was no significant difference (P=0.05) between the overall reproductive capacity of tetrasporophytes from Miminegash and Rustico (Table 4).

Fullness State of Reproductive Sori

Seasonal variations in fullness of reproductive sori for each frond class at each location were similar for both carposporangial and tetrasporangial sori; therefore, data for all classes were combined (Fig. 14). Partially empty carposporangial sori were abundant for most months but June in Miminegash, and from April to July in Rustico. This was coincidental with the seasonal pattern of the incidence of empty carposporangial sori in both Miminegash and Rustico. The incidence of full carposporangial sori never attained more than 17.5% (May) in Miminegash fronds and 6.8% (April) in Rustico fronds. The remainder of the year at both sites, with the exception of November at Miminegash, the incidence of full carposporangial sori was low. The seasonal pattern of partially empty tetrasporangial sori showed two maxima (June and September), and two minima (spring and August) in Miminegash. The percentage of empty tetrasporangial sori followed an opposite pattern as observed for carposporangial sori. As well, the incidence of full tetrasporangial sori was low (except in late summer/early autumn). Bimodality was not observed in Rustico; the pattern was similar to that of carposporangial sori. However, incidences of partially empty and empty tetrasporangial sori vary markedly from May to June and January to April. Full tetrasporangial sori increased in incidence from 0.3% in May to 12% in August/September, whereafter the incidence declined to low levels from November through April.

The fullness state of both carposporophytes and tetrasporophytes was remarkably similar between the two study sites (Table 5). For example, overall the percentage of empty carposporangial sori was about 31% at both locations; the percentages of partially empty carposporangial and tetrasporangial sori were not different. The incidences of full carposporangial and tetrasporangial sori were significantly greater at Miminegash (4.8% and 6.3%) than at Rustico (3.2% and 4.5%), however, and the frequency of empty tetrasporangial sori in Rustico (30.8%) and Miminegash (28.2%) was similar.

DISCUSSION

The results of the study suggest rejection of the null hypothesis that C. crispus reproductive capacity, measured as sporangial area, is not significantly ($P=0.05$) different between intensely dragraked (Miminegash) and non-dragraked (Rustico) beds (Fig. 12 and 13; Table 4). Assuming carpospore production is directly related to cystocarpic area, we found that this production in a non-dragraked bed was greater, by a factor of two, over that in a dragraked bed. This was in spite of the latter bed having significantly ($P\leq0.05$) greater overall frond density (Table 1) and with the female gametophytes bearing significantly (≤0.05) larger cycstocarps (Table 4). The potential for greater carpospore production in non-dragraked beds was due to the following: first, the density was higher by a factor of three for those frond classes with significantly greater carpospore reproductive capacity (Table 1); and secondly, these fronds were heavier by about a factor of three (Table 2) which is likely why cystocarpic sorus density per frond was greater by a factor of two (Fig. 6; Table 3).

Of interest is the observation that tetraspore reproductive capacity was not significantly ($P=0.05$) different between dragraked and non-dragraked beds (Fig. 12 and 13; Table 4). This was no doubt due to both bed types having a similar density of equal-sized (dry weight) tetrasporophytes. The first seasonal peak in tetrasporangial reproductive capacity occurred in early June in the dragraked bed versus July in the non-dragraked bed. Were they both to have occurred in July, then the non-dragraked bed would likely have had a greater tetrasporangial reproductive capacity, as many of the larger fronds would have been cropped prior to the peak in tetraspore formation.

Nevertheless, given that Classes 4 and 5 fronds have the largest tetrasporic reproductive capacity (Fig. 13), that these larger fronds are generally selected for by dragrakes, and that the peak in tetrasporangial reproductive capacity is in June in Miminegash at the initiation of the harvest, it is surprising that tetrasporic reproductive capacity is similar between dragraked and non-dragraked beds. The direct reason for this phenomenon is the overall equal density of tetrasporangial bearing fronds in both dragraked and non-dragraked beds (Table 1). In fact, there were double the number of tetrasporangial bearing Class 3 fronds in the dragraked bed! The causes of this can only be speculated on.

The preharvest ratio (i.e. the 1940's) of the densities of cystocarpic to tetrasporangial bearing fronds in the dragraked district is not known. This ratio in 1985/86 in the non-dragraked bed was approximately 2:1, in the dragraked bed it was approximately 1:1. If the preharvest ratios were 2:1 in the dragraked beds, this suggests that there has been a selection in the dragraked beds for those fronds with the potential for carpospore formation. Could it be that the tetrasporophyte is more resistant to dragraking? Diploid dominance under rigorous environmental conditions has been noted in other benthic algal taxa (see Pringle 1986 for a partial review).

Unfortunately, emperical data on the spore production required to maintain viable macroalgal beds, whether harvested or unharvested, are not available. We do know that _Chondrus_ germling recruitment on outplant blocks in Marine Plants Harvesting District (MPHD) 1 (Miminegash) took years longer (Pringle unpubl. data) than in the handraked MPHD 12 beds (southwestern Nova Scotia) (Pringle and Semple 1980). As well, we have observed areas that have been barren of _C. crispus_ for many years (Pringle and Semple 1984).

Given this lack of data, the declining biomass levels, the intense harvest pressure, and the persistent barren areas we suggest that all should be done to maximize spore production within the commercial fishery of MPHD 1. The most obvious solution would be to close the fishery during the period of peak spore production. The present season opens June 11. June was the single most important month for reproductive capacity (Fig. 12) for both carpospores and tetraspores. Reproductive capacity in July and August was low (Fig. 12).

To summarize, in MPHD 1 there is an intense harvest. The harvest technique selects for the large frond classes. These frond classes have the largest reproductive capacity. The harvest begins June 11, the time of peak reproductive capacity and just prior to peak biomass levels (if MPHD 1 biomass levels would have peaked in July at the time of peak biomass levels in MPHD 3). To maximize both spore production and biomass levels it is recommended that the season opening be moved back. In 1985 a late June/early July opening would have enhanced both spore production and biomass levels.

CONCLUSION

1. Reproductive capacity was significantly greater in the non-dragraked, than the dragraked, bed.

2. For the year studied, the season opening date (June 11) in MPHD 1 (heavily dragraked) coincided with peak production of both carpospores and tetraspores.

3. Little is known about the spore recruitment process. It is known that areas have persisted in the barren mode for up to 7 yr in MPHD 1. Also, the rate of germling recruitment on cement substrates is much lower than in southwestern Nova Scotia beds. Thus, there is concern about recruitment overharvesting.

RECOMMENDATION

It is recommended that in the development of the management plan for MPHD 1, methods such as season opening date manipulation, leaving beds fallow, etc., should be considered in an attempt to enhance spore production.

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Table 1: Mean number and percentage of fronds per 0.25 m², in Miminegash (M) and Rustico (R) in the different frond classes. Asterisks indicate significantly (P≤0.05) different values between the two locations.

	Class 1		Class 2		Class 3		Class 4		Class 5		All Classes	
	M	R	M	R	M	R	M	R	M	R	M	R
Number of fronds 0.25 m⁻²	*163.9	*69.8	*341.8	*274.3	*94.2	*73.4	*72.1	*97.1	*27.4	*30.1	*699.5	*544.7
Number of carposporangial bearing fronds 0.25 m⁻²			* 3.9	* 6.1	4.0	4.0	* 6.5	*15.1	* 3.9	* 7.8	* 18.3	* 33.0
Number of tetrasporangial bearing fronds 0.25 m⁻²			3.3	2.5	* 4.4	* 2.4	10.7	11.0	4.1	4.2	22.6	20.1
Percentage of carposporangial bearing fronds 0.25 m⁻²			1.1	2.2	4.2	5.4	9.0	15.6	14.2	25.9	* 2.6	* 6.1
Percentage of tetrasporangial bearing fronds 0.25⁻²			1.0	0.9	4.7	3.3	14.8	11.3	15.0	14.0	3.2	3.7

Table 2: Mean dry weight and percentage of fronds per 0.25 m^2, in Miminegash (M) and Rustico (R) in the different frond classes. Asterisks indicate significantly ($P \leq 0.05$) different values between the two locations.

	Class 1		Class 2		Class 3		Class 4		Class 5		All Classes	
	M	R	M	R	M	R	M	R	M	R	M	R
Dry weight (g) fronds 0.25 m^{-2}	*0.81	*0.32	9.37	8.07	*7.37	*5.18	*13.61	*19.60	*10.20	*15.44	*41.36	*48.62
Dry weight (g) of carposporangial bearing fronds 0.25 m^{-2}			*0.20	*0.35	0.41	0.37	* 1.40	* 3.91	* 1.67	* 5.10	* 3.68	* 9.73
Dry weight (g) tetrasporangial bearing fronds 0.25 m^{-2}			0.19	0.15	*0.54	*0.25	2.69	3.04	2.22	2.72	5.64	6.17
Percentage dry weight of carposporangial bearing fronds 0.25 m^{-2}			2.1	4.3	5.6	7.1	10.3	20.0	16.4	33.0	8.9	20.0
Percentage dry weight of tetrasporangial bearing fronds 0.25 m^{-2}			2.0	1.9	7.3	4.8	19.8	15.5	21.8	17.6	13.6	12.7

Table 3: Mean number of reproductive sori per frond and per 0.25 m^2, in Miminegash (M) and Rustico (R) in the different frond classes. Asterisks indicate significantly ($P \leq 0.05$) different values between the two locations.

	Class 2		Class 3		Class 4		Class 5		All Classes	
	M	R	M	R	M	R	M	R	M	R
Number of cystocarpic sori $frond^{-1}$	* 16.9	*22.1	23.1	23.7	*52.6	*86.7	*76.6	* 90.2	*42.3	*80.7
Number of tetrasporangial sori $frond^{-1}$	42.0	43.1	63.3	73.9	*145.9	*180.1	*295.1	*428.1	*136.6	*181.3
Number of cystocarpic sori 0.25 m^{-2}	* 79.3	*165.8	*103.8	*143.2	*386.3	*1431.8	*384.6	*1658.4	*974.4	*3406.8
Number of tetrasporangial sori 0.25 m^{-2}	164.4	150.2	319.9	297.1	1953.6	2192.2	2181.1	2118.1	5022.8	4775.9

Table 4: Mean area of reproductive sori, and reproductive capacity of the different frond classes in Miminegash (M) and Rustico (R). Asterisks indicate significantly ($P \leq 0.05$) different values between the two locations.

	Class 2		Class 3		Class 4		Class 5		All Classes	
	M	R	M	R	M	R	M	R	M	R
Carposporangial sorus area (mm^2)	* 1.14	* 1.03	* 1.36	* 1.15	* 1.28	* 1.13	* 1.56	* 1.16	* 1.33	* 1.12
Tetrasporangial sorus area (mm^2)	* 0.86	* 0.97	1.00	0.95	* 1.08	* 1.01	* 1.22	* 0.97	1.04	0.97
Carpospore reproductive capacity (mm^2 0.25 m^{-2})	* 88.57	*174.37	143.11	152.49	*538.47	*1486.62	*728.13	*1761.35	*1498.28	*3574.83
Tetraspore reproductive capacity (mm^2 0,25 m^{-2})	154.18	172.97	*348.24	*245.09	2438.58	2186.75	*3047.87	*1888.76	5988.81	4493.57

Table 5: Mean percentage of fullness state of reproductive sori, in Miminegash (M) and Rustico (R) in the different frond classes. Asterisks indicate significantly ($P \leq 0.05$) different values between the two locations.

Reproductive type	Fullness type	Class 2		Class 3		Class 4		Class 5		All Classes	
		M	R	M	R	M	R	M	R	M	R
Cystocarpic	Empty	30.2	29.0	29.6	32.6	32.1	34.9	*34.9	*27.2	31.6	31.3
	Partially empty	61.2	65.9	64.5	61.7	65.5	63.6	*61.8	*70.6	63.6	65.5
	Full	*8.6	*5.1	5.9	5.7	2.4	1.5	3.3	2.2	*4.8	*3.2
Tetrasporic	Empty	*27.6	*34.6	*33.8	*40.7	27.9	26.4	*22.5	*29.8	*28.2	*30.8
	Partially empty	63.8	58.6	60.3	57.6	65.7	67.9	*73.0	*67.4	65.5	64.5
	Full	8.6	6.8	*5.9	*1.6	6.5	5.7	4.6	2.8	*6.3	* 4.5

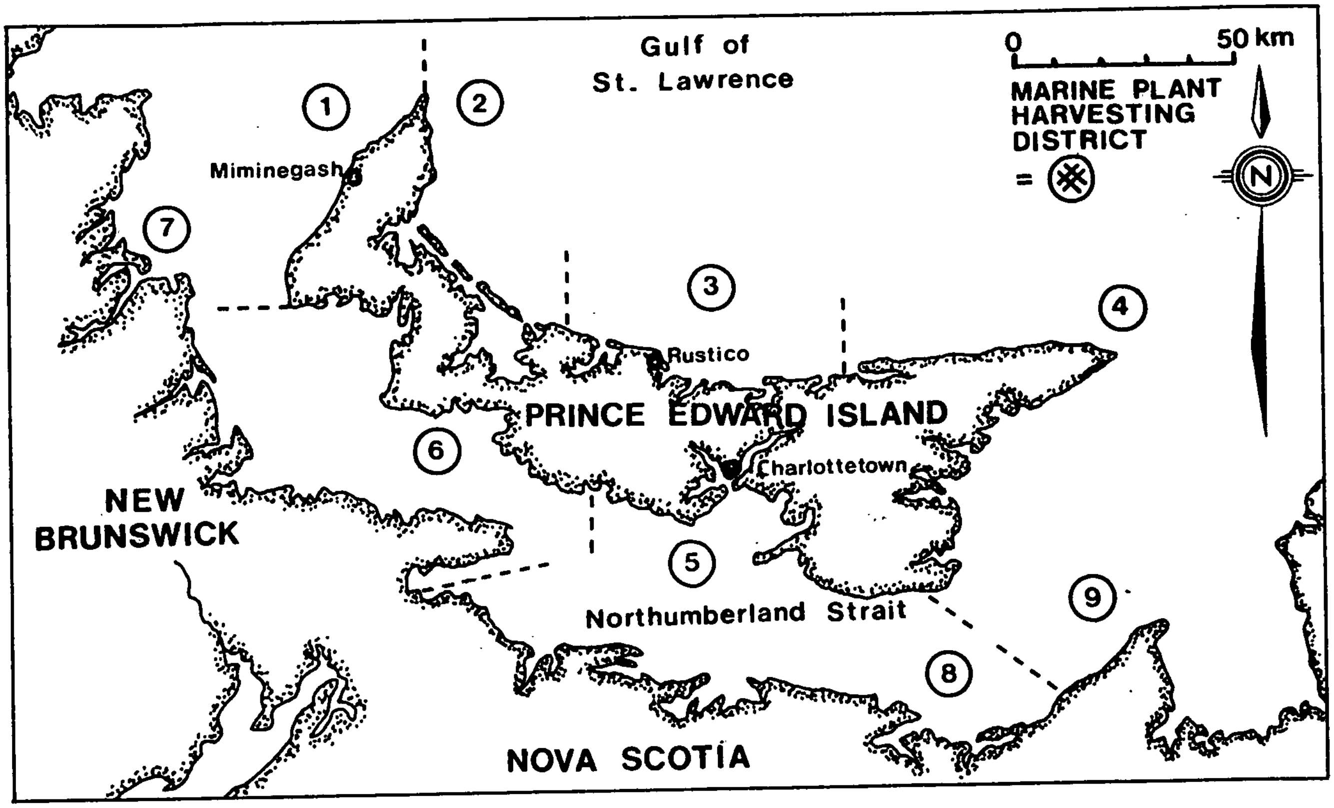

Fig. 1. Location of the study sites in Prince Edward Island: Miminegash (MPHD 1, dragraked) and Rustico (MPHD 3, non-dragraked).

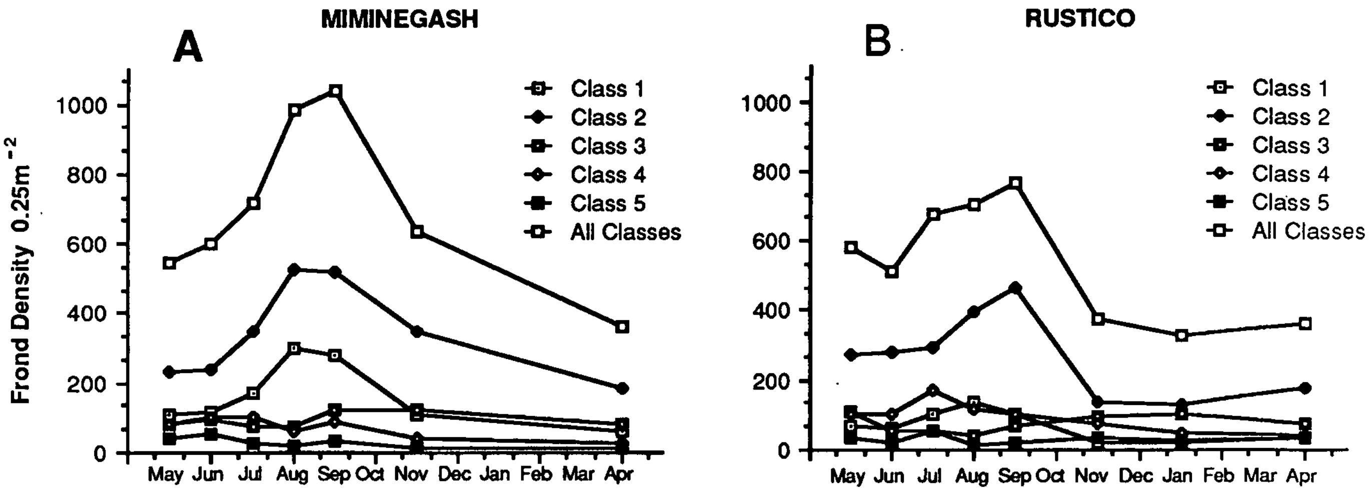

Fig. 2. Frond class density for the period May 1985 to April 1986 at Miminegash and Rustico.

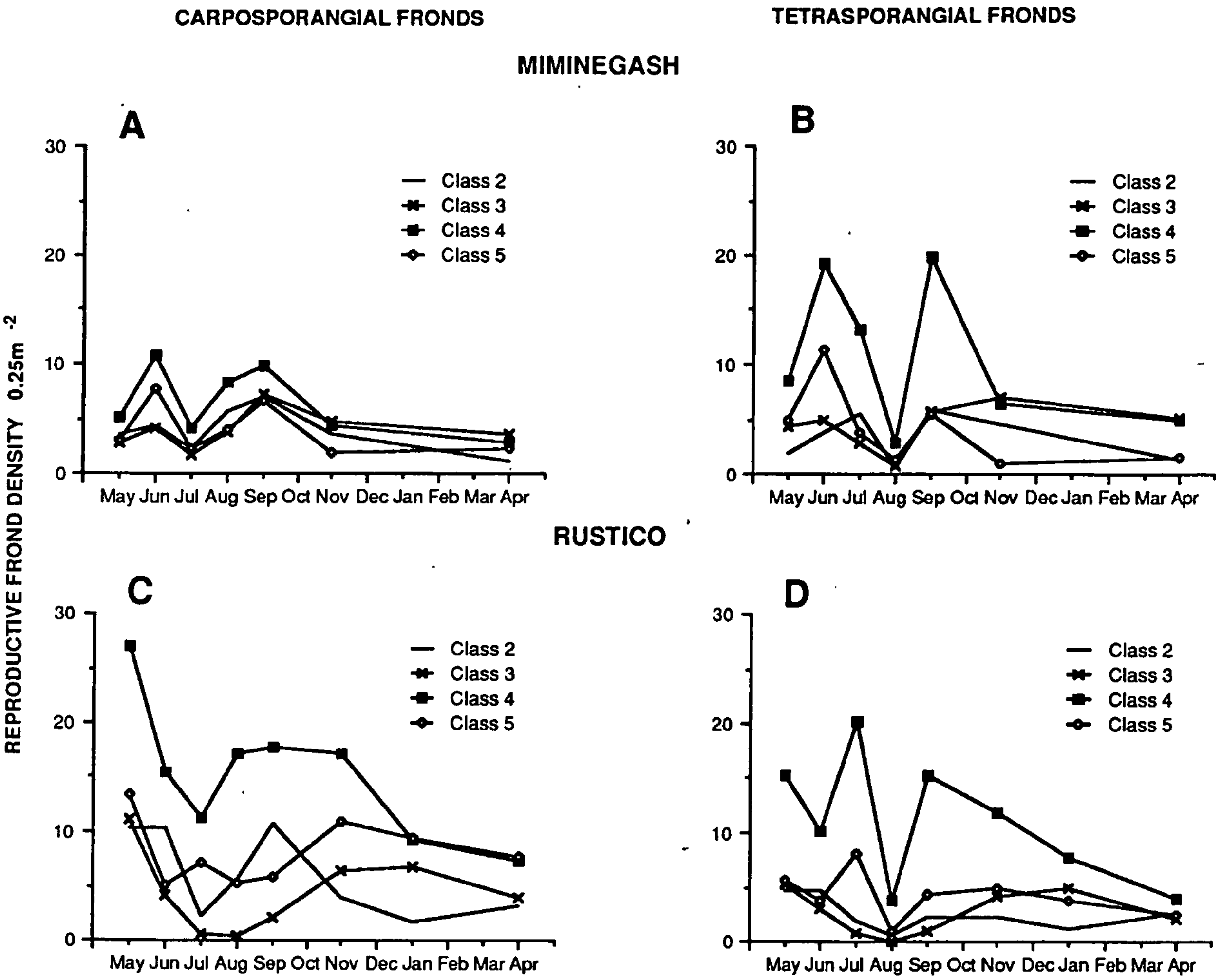

Fig. 3. Mean density of carposporangial and tetrasporangial fronds from May 1985 to April 1986 at Miminegash and Rustico.

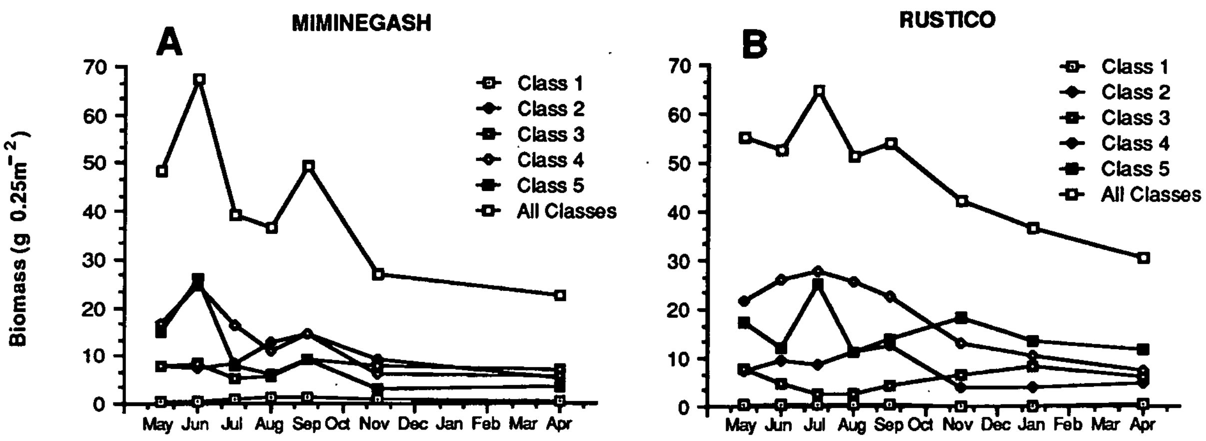

Fig. 4. Frond class biomass for the period May 1985 to April 1986 at Miminegash and Rustico.

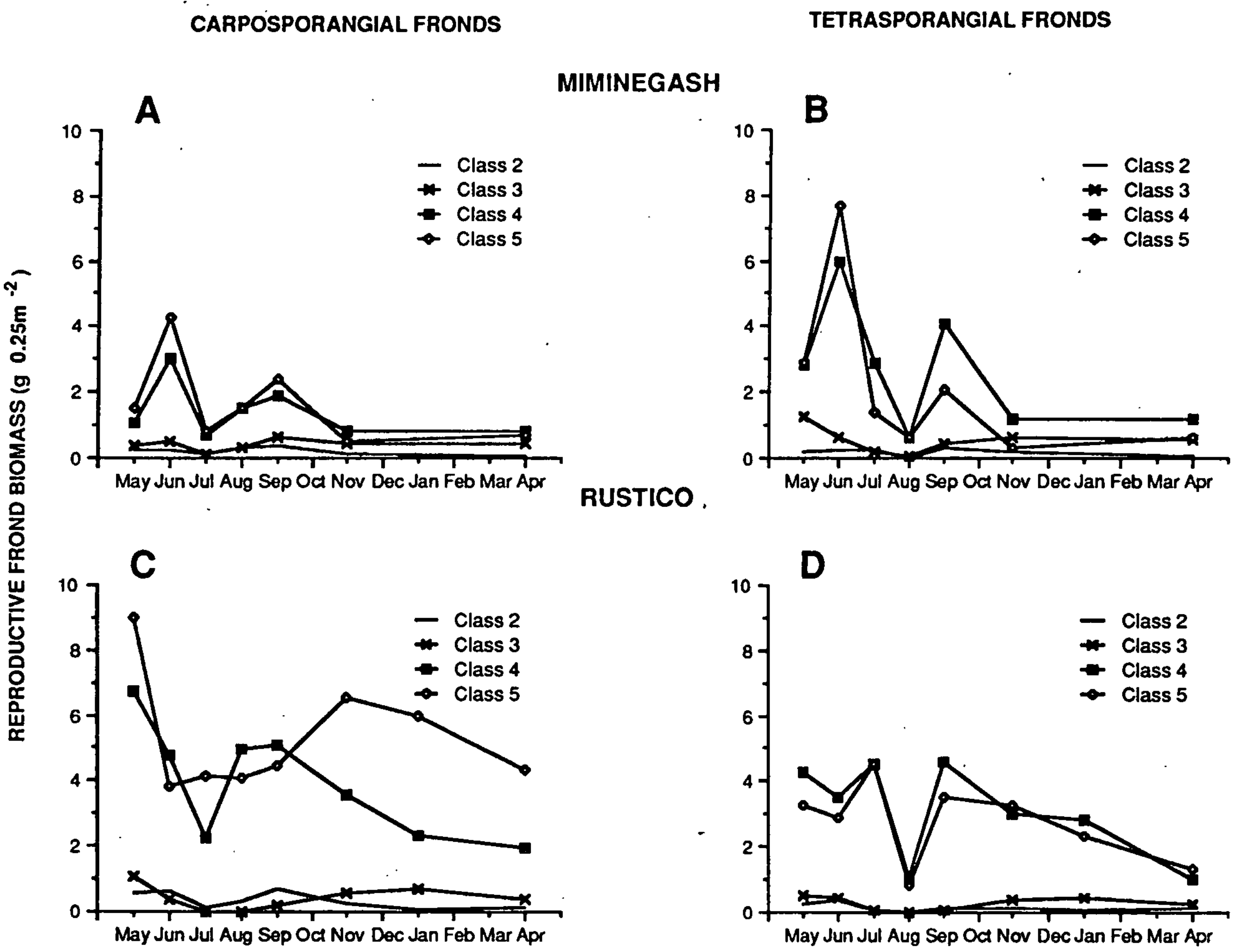

Fig. 5. Mean biomass of carposporangial and tetrasporangial fronds from May 1985 to April 1986 at Miminegash and Rustico.

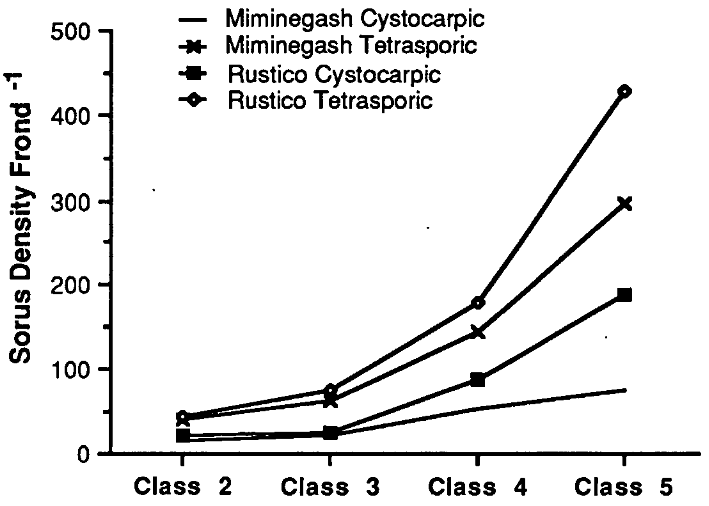

Fig. 6. Mean sorus density for each of Frond Classes 2 to 5 at both Miminegash and Rustico.

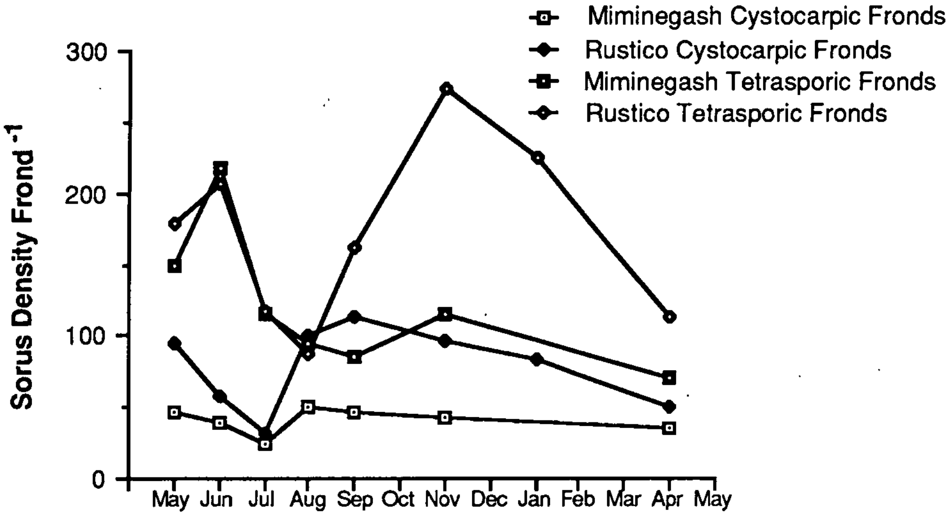

Fig. 7. Mean sorus density per frond for each reproductive type and sample from May 1985 to April 1986 at both Miminegash and Rustico.

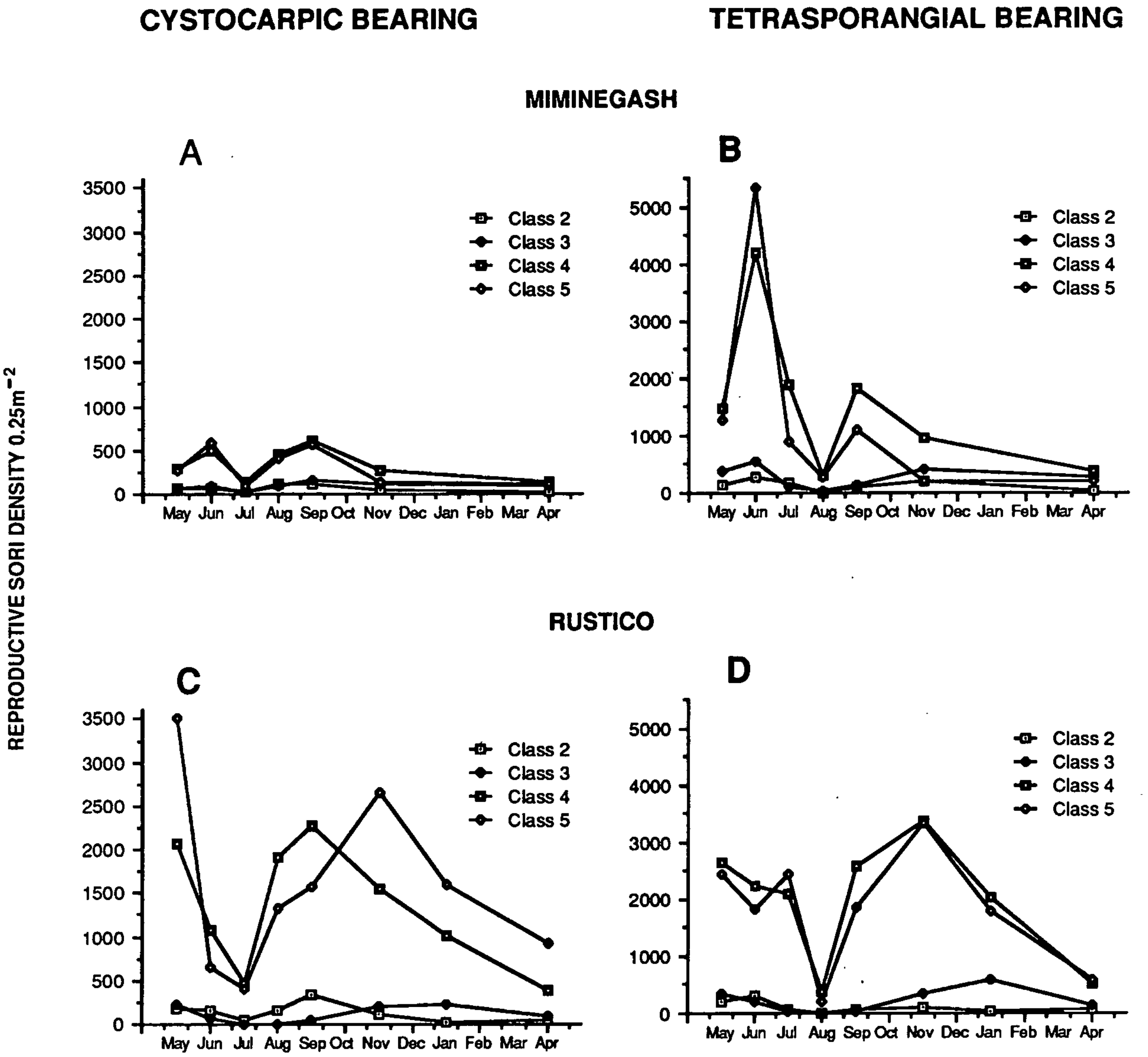

Fig. 8. Mean reproductive sorus density for each frond class and sample (Miminegash and Rustico) between May 1985 and April 1986.

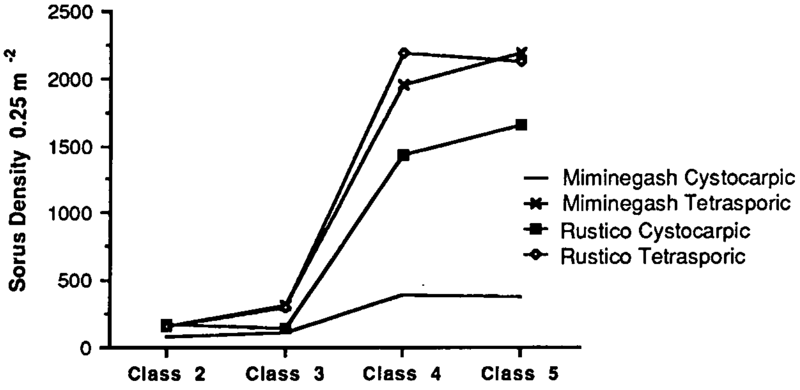

Fig. 9. Mean sorus density per 0.25 m^2 for Frond Classes 2 to 5 for each reproductive type at both Miminegash and Rustico.

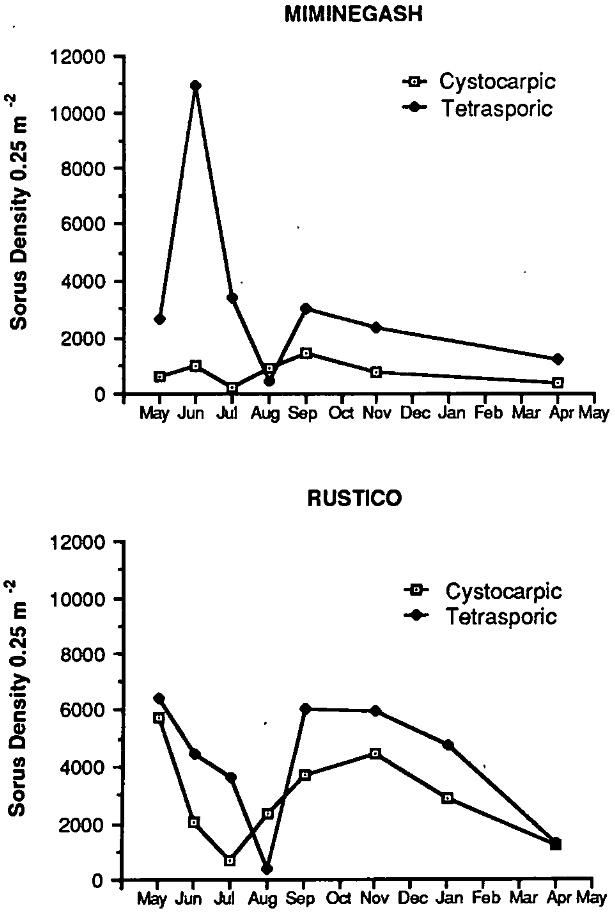

Fig. 10. Mean sorus density per 0.25 m^2 for each reproductive type from May 1985 to April 1986 at both Miminegash and Rustico.

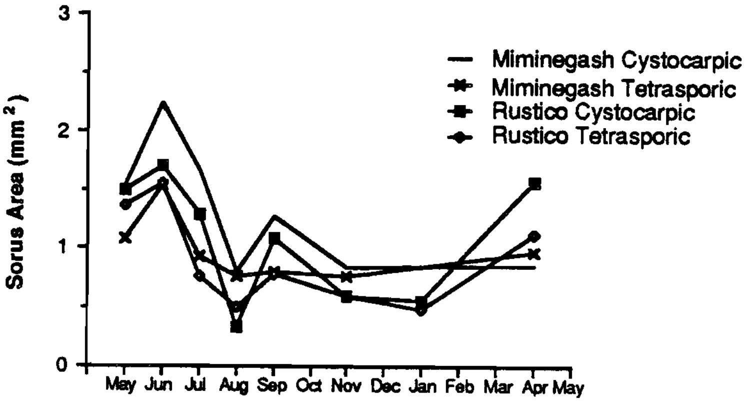

Fig. 11. Mean sorus area (square millimeters) per sporangial type from May 1985 to April 1986 at both Miminegash and Rustico.

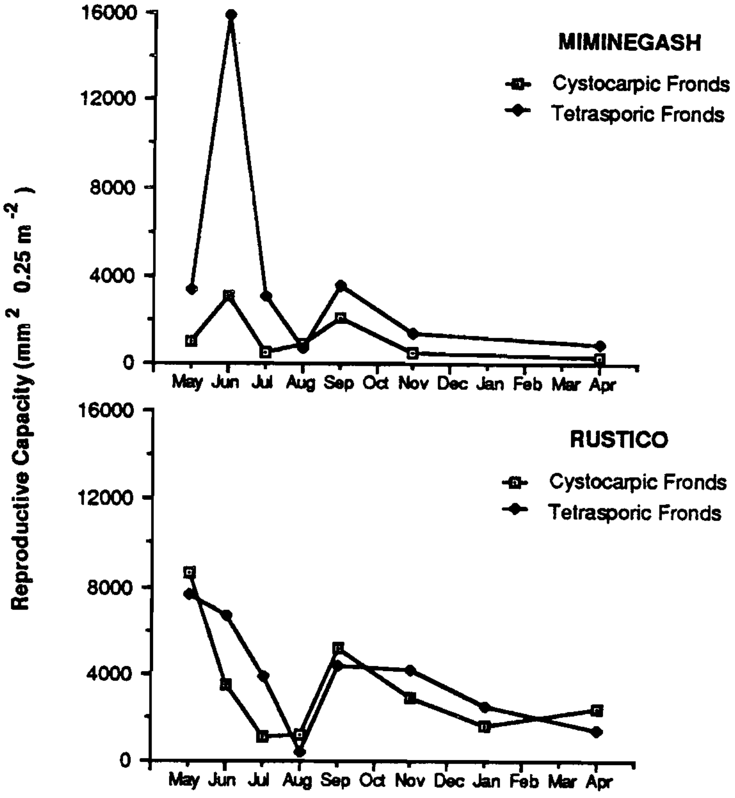

Fig. 12. Mean reproductive capacity (square millimeters $0.25m^{-2}$) per sporangial type from May 1985 to April 1986 at both Miminegash and Rustico.

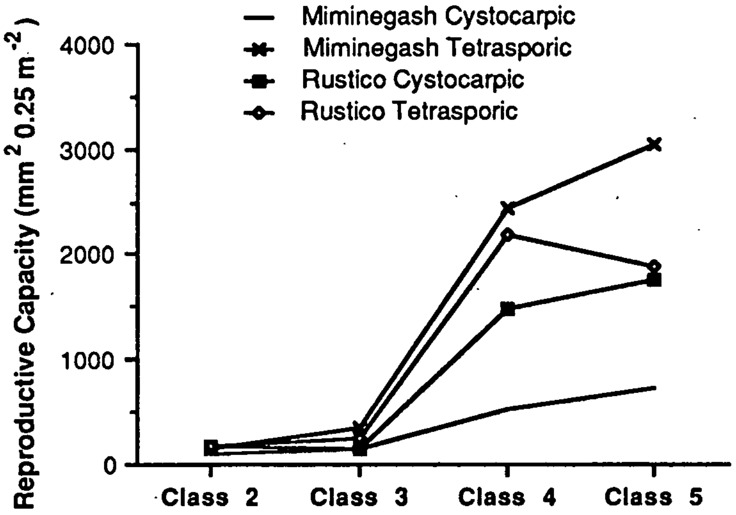

Fig. 13. Mean reproductive capacity (square millimeters 0.25 m^{-2}) for each of Frond Classes 2 to 5, both at Miminegash and Rustico.

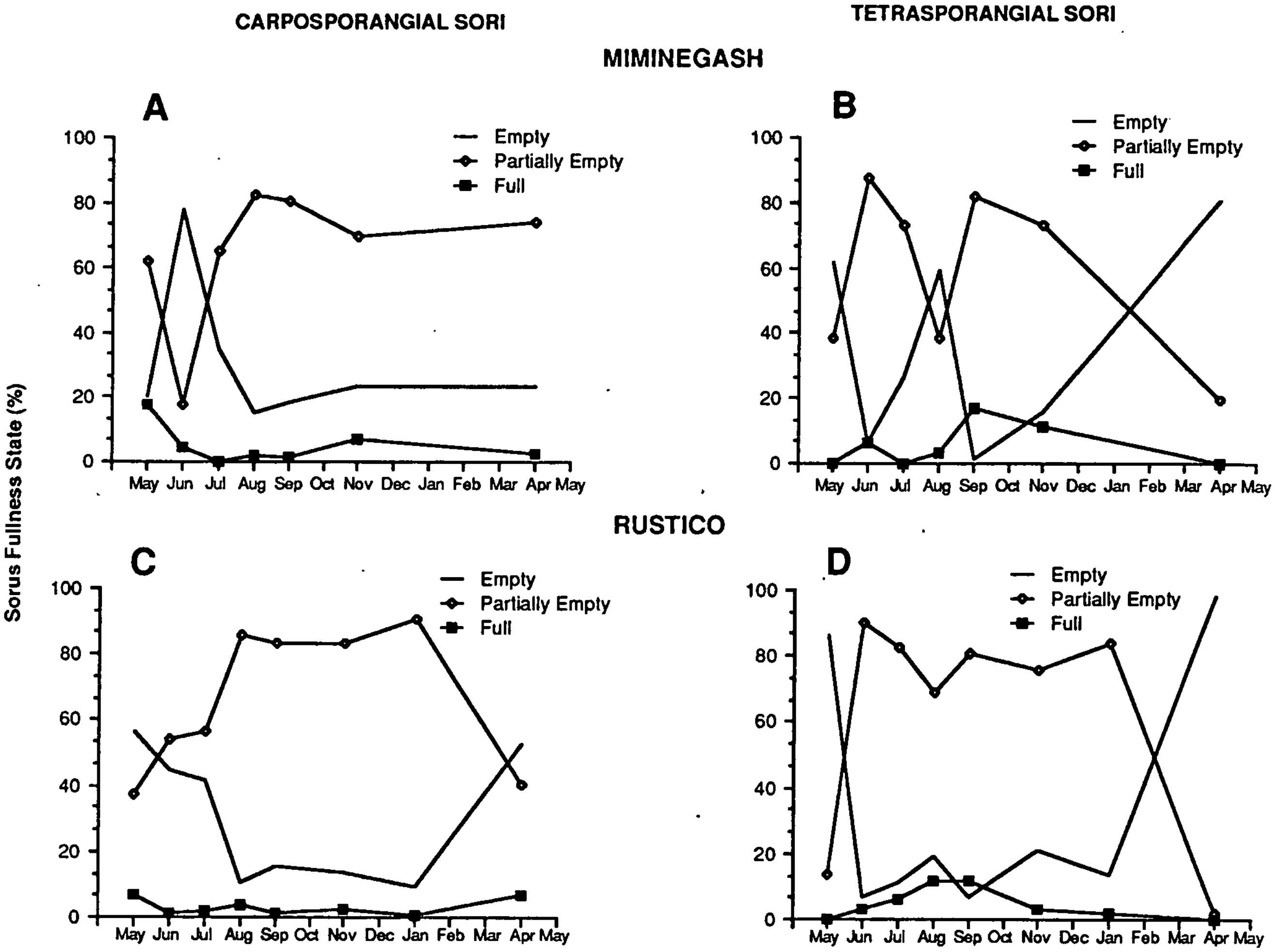

Fig. 14. Fullness state of carposporangial and tetrasporangial sori from May 1985 to April 1986 at Miminegash and Rustico.