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Field, culture and cytological studies of *Porphyra carolinensis* COLL et COX (Bangiales, Rhodophyta) from North Carolina

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The morphological life history of *Porphyra carolinensis* has been studied in the field and laboratory culture. Cross-gradient light-temperature culture in 10:14 and 14:10 LD cycles was utilized to investigate the effects of photon flux, temperature and daylength on growth and reproduction. Conchospore release appeared to be controlled by a requirement for a combination of short photoperiod and low temperature. The blade phase was found to grow and reproduce itself by monospores throughout the year. Four chromosomes occur in conchocelis, conchospores, carpospores, spermatia, and vegetative cells of the foliose phase.

Key Index Words: *Bangiophyceae*; *cytology*; *North Carolina*; Porphyra; *reproductive seasonality*; *Rhodophyta.*

The life history of *Porphyra* species typically includes a conspicuous blade phase which alternates with a microscopic filamentous conchocelis phase (COLE and CONWAY 1980). The blade phase is usually reported to be an annual with a summer maximum of growth and reproduction at higher latitudes (MUMFORD 1975) and a winter-spring maximum in lower latitude temperate waters (EDWARDS 1969, BIRD *et al.* 1972, KAPRAUN and LUSTER 1980, HAWKES 1981).

Previous field studies in coastal North Carolina (34°N lat.) indicated that *Porphyra carolinensis* (COLL and COX 1977) seems to have a phenology unique for warm temperate species, with the blade phase growing and reproducing throughout the year (KAPRAUN 1980).

This communication presents the results of field, culture and cytological studies conducted to determine the life history of *Porphyra carolinensis* and its responses to photon flux, temperature and daylength which are responsible for the phenology observed in nature.

Materials and Methods

Monthly observations on the growth and phenology of *Porphyra carolinensis* were made on a rock jetty at Masonboro Inlet, Wrightsville Beach, North Carolina from November 1983 to May 1985. Blades were examined microscopically in the laboratory for the presence of reproductive cells. Blade areas with monospores and carpospores were exised and kept in culture to determine germination pattern. Unialgal cultures were grown in an enriched seawater medium (salinity 34-36‰) modified after Von STOSCH (KAPRAUN 1970). GeO_2 was used to control diatom growth (LEWIN 1966). Blue-green algal contaminants were treated with 100 units Penicillin G per m*l* of medium (PAGE 1973).

Two sets of apparatus were utilized for the culture studies. Photon flux, photoperiod

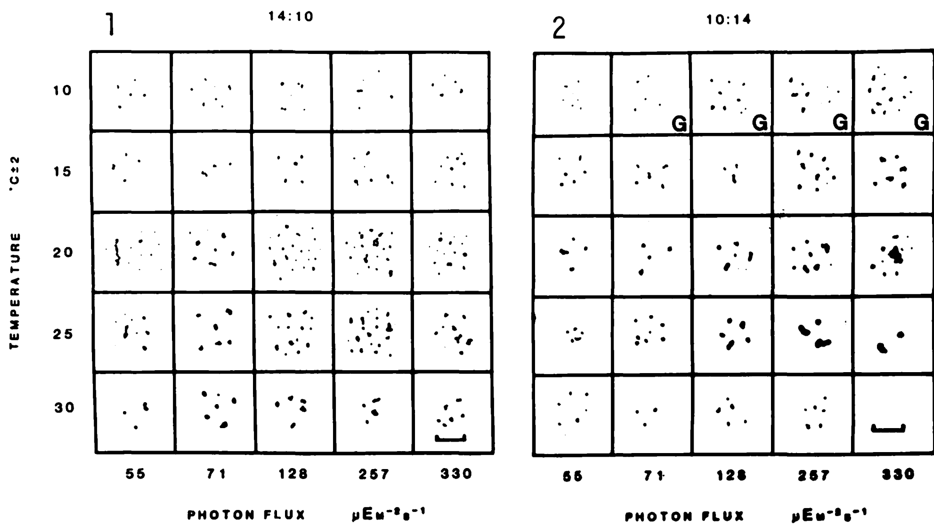
and temperature effects on growth and reproduction were studied using a cross-gradient light-temperature apparatus (EDWARDS and VAN BAALEN 1970) which permited the simultaneous culture of the isolates in 25 combinations of the two parameters (Fig. 1). Photoperiods used were 14 : 10 and 10 : 14 LD. Culture vessels were 15× 60 mm, and contained 25 ml medium.

Conchocelis for culture experiments came from subcultured spores of blades collected in nature January 18, 1983 and maintained at 18 : 6 LD, 20°C and 55 $\mu Em^{-2}s^{-1}$ photon flux. In the first experiment, ten tufts of conchocelis were put in each vessel and cultured for 21 days. The medium was changed every 6-8 days. These cultures were then examined microscopically to determine their relative growth and degree of conchosporangial production. In the replicate experiment, five tufts of conchocelis were put in each vessel and cultured for 55 days (Figs. 1 and 2). The medium was changed every 3-4 days. These cultures were studied to determine the effects of photon flux, photoperiod, and temperature on conchospore release and development.

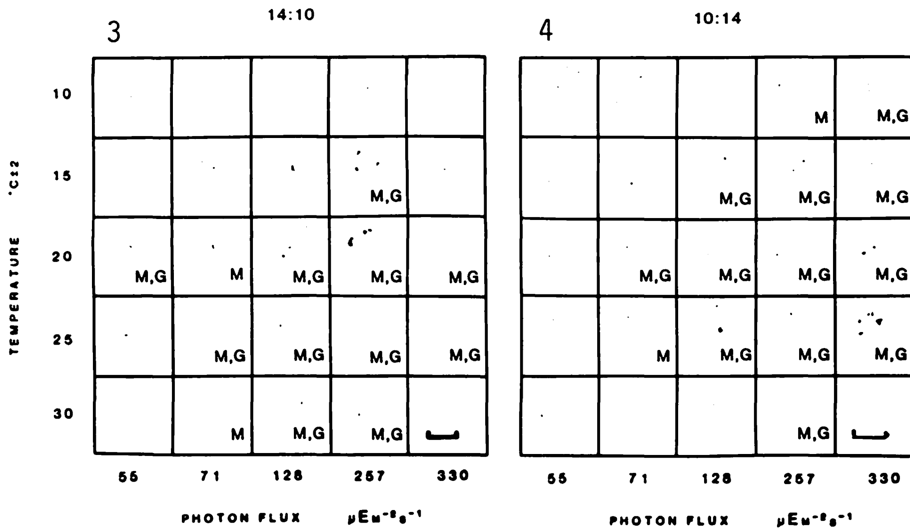
Germlings were grown from monospores of blades collected on November 20, 1983 and maintained at 12 : 12 LD, 15°C and 45 $\mu Em^{-2}s^{-1}$. Three to five germlings were put in each vessel and cultured 24 days in the initial experiment and 39 days in the replicate. These cultures were then examined to determine growth and sporulation patterns (Figs. 3 and 4). Illumination was provided by Phillips TL 34 cool white fluorescent tubes. Photon flux ranged from 55-330 $\mu Em^{-2}s^{-1}$ and was measured with a Lambda I. Cor. PAR (Photosynthetic Active Radiation) quanta meter.

Incubators with light sources as described above were used to maintain isolates and to study the life history under varying temperature, photoperiod, and quantum flux combinations (Tables 2 and 3).

Chromosome counts were made using a procedure modified after AUSTIN (1959) in vegetative and sporulating sections of mature blades, germlings, conchocelis and conchosporangia. Conchocelis from culture and blades collected in nature were fixed at 1 h intervals beginning 1 h before sunset (or dark cycle) and continuing for five h,



Figs. 1 and 2. Growth and reproductive responses of *Porphyra carolinensis* conchocelis phase to photon flux densities and temperature regimes after 55 days. Fig. 1. 14 : 10 LD. Fig. 2. 10 : 14 LD. (Photon flux densities, temperature gradient, and scale in Fig. 1 apply to Figs. 2-4, Scale = 1 cm). G = germling development.



Figs. 3 and 4. Reproductive response of *Porphyra carolinensis* blade phase to photon flux densities and temperature regimes after 32 days. Fig. 3. 14 : 10 LD. Fig. 4. 10 : 14 LD. G = germling development, M = monospores.

and again beginning at sunrise (or light cycle) and continuing for four h. Material was fixed in 3 : 1 absolute ethanol-glacial acetic acid and left overnight. Fixed material was stored in 70% ethanol, hydrolized in 1 N HCl for 10 min at room temperature, rinsed in distilled water, and stained in 2% acetocarmine or aceto-orcein for 2-3 h prior to squash preparation. Documentation was made by both microphotographs and camera lucida drawings using an Olympus BH 2-RFK microscope.

The geographical range of *Porphyra carolinensis* was investigated by examining herbarium specimens from the following herbaria: University of South Florida-Tampa (USF), University of Michigan-Ann Arbor (MICH), and the University of North Carolina-Wilmington (WNC).

Daylength was calculated from sunrise and sunset data for 34°N lat. (US DEPT. COMM. 1984). Water temperature data for Wrightsville Beach for the period November 1983 to May 1985 were made available by the Laque Center for Corrosion Technology.

Results

Field observations: *Porphyra carolinensis* was found on upper eulittoral and lower supralittoral rocks every month of the study. Maximum abundance and blade development were observed from November to April (Fig. 5). Monospore production from blade

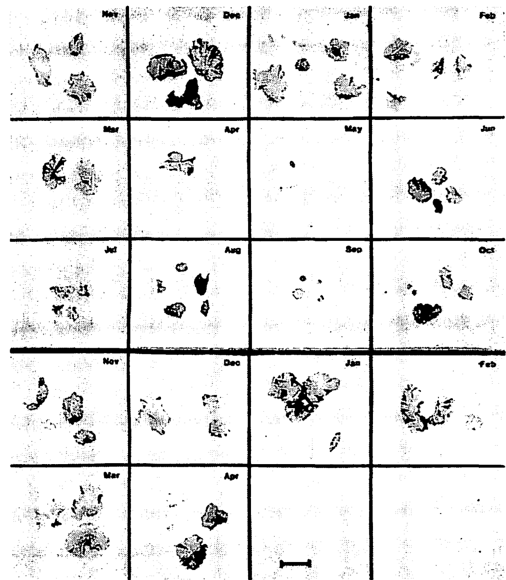


Fig. 5. Seasonal variation in the blade phase (herbarium specimens) of *Porphyra carolinensis* from Masonboro Inlet, November 1983-March 1985. Scale = 2 cm.

margins occurred continuously while carpospore and spermatium formation coincided with the November-April period of maximum vegetative growth (Table 1, Fig. 6). Subsequent development of monospores followed in the laboratory revealed that all surviving monospores germinated in a bipolar manner to produce blades except in the collections of 12 June and 16 July, 1984 when fewer than 1% of the monospores germinated to produce conchocelis. Unipolar germination was observed for all surviving carpospores.

Table 1. Sporulation of *Porphyra carolinensis* blades collected in nature (November 1983-March 1985).

Date	Water Temperature °C	Daylength (hr : min)	Carpospores	Spermatia	Monospores
Nov. 20	16	10 : 15	+	+	+
Dec. 19	14	9 : 48	+	+	+
Jan. 14	9	10 : 04		+	+
18	7	10 : 08	+	+	+
Feb. 02	9	10 : 30	+	+	+
17	12	10 : 59	+	+	+
Mar. 16	12	12 : 01	+	+	+
31	16	12 : 34	+		+
Apr. 26	18	13 : 25			+
May 10	21	13 : 49			+
16	20	13 : 58			+
June 12	26	14 : 25			+
July 16	27	14 : 13			+
Aug. 08	28	13 : 40			+
Sept. 23	21	12 : 07			+
Oct. 25	24	11 : 01			+
Nov. 24	18	10 : 10	+	+	+
Dec. 19	15	9 : 52	+	+	+
Jan. 19	8	10 : 12	+	+	+
Feb. 07	9	10 : 42	+	+	+
Mar. 08	17	10 : 46	+		+
20	13	12 : 07	+		+

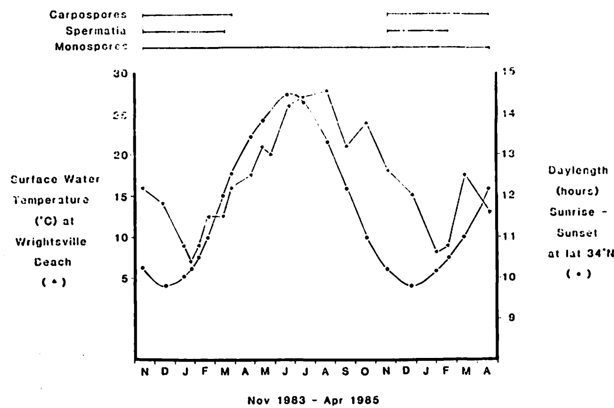


Fig. 6. Phenology of *Porphyra carolinensis* correlated to monthly water temperature and daylength (November 1983-April 1985).

Cross-gradient culture: In both cross-gradient conchocelis experiments, growth and conchosporangial production occurred in all photon flux-temperature combinations under both 10 and 14 h days. In the second experiment, which was initiated with a smaller amount of inoculum, reproduction by fragmentation was especially pronounced at 20°C in all flux densities. After 55 days, conchospore release and subsequent blade germling development were observed only in 10 h days at 10°C and photon flux densities of 71-330 $\mu Em^{-2}s^{-1}$ (Figs. 1 and 2).

In both cross-gradient blade experiments, growth and reproductive responses were similar in 10 and 14 h days. Germlings survived in all photon flux and temperature combinations except at 30°C. After 32 days, monospore production and blade germling development appeared to increase with increasing temperature in 14 h days (Fig. 3), and was observed in only one culture dish at temperatures below 20°C. In contrast, monospore production and blade germling development appeared to increase with photon flux in 10 h days (Fig. 4), and was observed through all temperatures tested (10-30°C).

The relationship of sporulation in cultured conchocelis and subsequent spore development to irradiance in both cross-gradient photoperiods is summarized in Fig. 7. Although conchospore release and blade development were observed through a wide range of irradiance (quantum doses of 2.56-12.9 $Em^{-2}day^{-1}$), both phenomena occurred only at 10°C in 10 h days. A combined photoperiodic and temperature requirement is implicated.

Incubator experiments: Additional tests to determine the effect of temperature and photoperiod on conchospore release confirmed the results of the cross-gradient experiment: only a combination of 10°C and 10 h days among the parameters tested produced conchospore release (Table 2).

Additional tests were conducted to induce both uni- and bipolar germination of blade monospores in cultured material as had been observed in nature. In the parameters tested only bipolar germination was observed (Table 3).

Blade morphology: *Porphra carolinensis* was recently distinguished from the other *Porphyra* species on the North American Atlantic coast and recognized as a new species (COLL and COX 1977). The reported diagnostic features include: blades monostromatic with 1 plastid per cell, microscopically dentate margins, marginal monospores, carpospores and spermatia formed in adjacent marginal patches on the same blade, carpospores in packets of 16 in two tiers, spermatia in packets of 32 in four tiers.

In general, blades examined in this study show the same morphological features (Figs. 8-10) previously reported for this species (COLL and COX 1977, KAPRAUN 1980). However, we found the division sequence and final number of cells in mature carposporangia and spermatangia to differ from

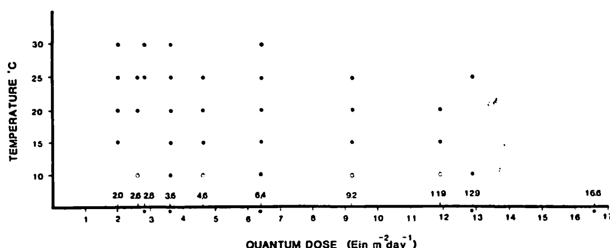


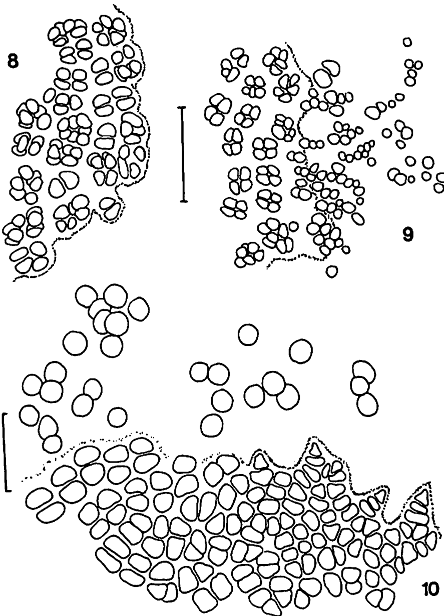
Fig. 7. Maximum developmental stage reached by conchocelis at various quantum dose rates in 14 : 10 (*) and 10 : 14 (other) : ● = conchosporangial development in <50% of inoculum: ○ = conchospore release and blade germling development.

Table 2. Release of conchospores under various conditions of photoperiod and temperature after 28 days.

L : D	Temperature (°C)	Photon flux ($\mu Em^{-2} s^{-1}$)	Conchospore release	Development
18 : 6	20	52	−	
12 : 12	15	30	−	
10 : 14	26	130	−	
10 : 14	10	43	+	Bipolar

Table 3. Development of monospores released from germlings under various photoperiods and temperatures after 14 days.

L : D	Temperature (°C)	Photon flux ($\mu Em^{-2} s^{-1}$)	Germling development	
			Bipolar	Unipolar
18 : 6	20	52	+	−
12 : 12	15	30	+	−
10 : 14	25	130	+	−
10 : 14	10	43	+	−



Figs. 8-10. Formation of reproductive cells on blade margin. Scale=50 μm. Fig. 8. Carpospore formation. Fig. 9. Spermatia formation. Fig. 10. Monospore formation. Note dentate margin.

the accounts given by COLL and COX (1977). The division sequence in a mature carposporangium results in the formation of eight carpospores in two tiers (Fig. 11) instead of 16 as previously reported. Apparent cases of 16 carpospores we observed are assumed to be artifacts of recent vegetative divisions producing small daughter cells in close proximity. The carposporangial division sequence begins with a planar division (Fig. 11). In contrast, at least two vertical divisions occur before the first planar division in spermatangia (Fig. 12). The division sequence in a mature spermatangium results in the formation of 32 spermatia in two tiers (Fig. 12) instead of four as previously described.

Carposporangia and spermatia typically occur on the same blade, and though generally in different areas, they have been observed in close association. Even in these cases, they are easily distinguished since carposporangia gain pigment and become darker than the surrounding vegetative cells, while spermatia lose pigment and are almost clear.

Using the criteria designated by KUROGI (1972) as having taxonomic significance, a comparison was made of *P. carolinensis* with the descriptions of other *Porphyra* species reported for the North and South Atlantic coasts (ROSENVINGE 1909, TAYLOR 1957, 1960, GAYRAL 1958, 1966, CONWAY 1964a,

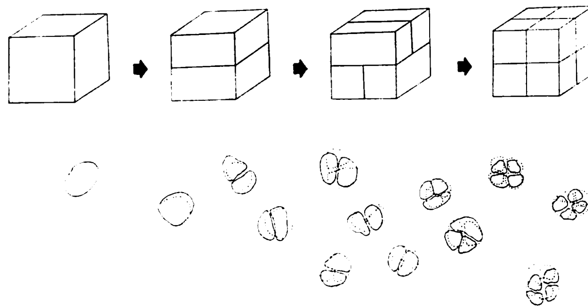


Fig. 11. Division sequence in the formation of a mature carposporangium of eight carpospores.

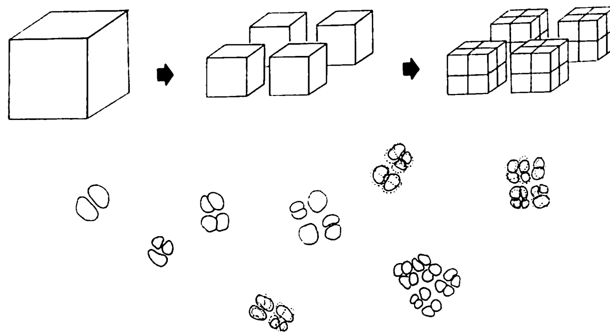


Fig. 12. Division sequence in the formation of a mature spermatangium of thirty-two spermatia.

1964b, ARDRÉ 1970, OLIVEIRA FILHO and COX 1975, COLL and OLIVEIRA FILHO 1976, COLL and COX 1977, KORNMANN and SAHLING 1977, JOHN *et al.* 1979). Despite the minor differences between the observations in our study and the original description by COLL and COX (1977), we are in agreement with their conclusion that *Porphyra carolinensis* is distinct from other Atlantic species.

Geographical distribution: The known distribution of *Porphyra carolinensis* includes coastal, stenohaline habitats in North and South Carolina, and northern Florida. It is possible that the range of this species could include suitable habitats in Virginia and Bermuda, but we were unable to confirm this with the herbarium specimens available.

Representatiue specimens: FLORIDA. Marine Land, coquina rock, 31 March 1978, R. MCINTOSH and C. DAWES (as *Porphyra leucosticta*), USF 131070. NORTH CAROLINA. Kure Beach, coquina rock, 2 Sept. 1971, D. KAPRAUN, WNC 9537; Wrightsville Beach, jetty rocks, 18 Dec. 1971, D. KAPRAUN, WNC 7907. SOUTH CAROLINA. Myrtle Beach, pilings, 20 July 1985, W. FRESHWATER, WNC 16557.

Life history: Culture studies have produced a functional life history for *Porphyra carolinensis* from filamentous conchocelis to macroscópic blade and back to conchocelis (Fig. 13). Monospores from blades develop in bipolar fashion to produce the blade phase (Fig. 14). Carpospores from blades develop in unipolar fashion to produce conchocelis (Fig. 15a-d). Conchocelis filaments from conchosporangia (Fig. 15e) under all environmental conditions tested, but conchospore release occurs only in cold temperatures under short day conditions. Conchospores

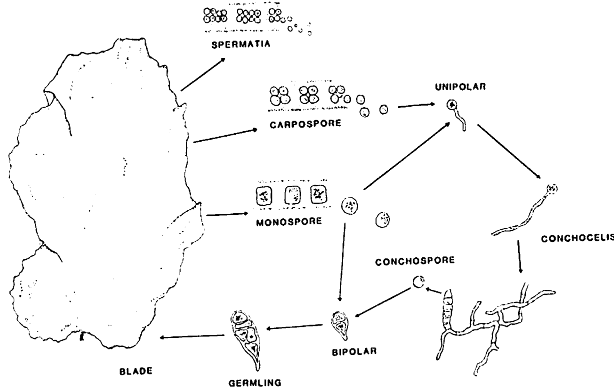


Fig. 13. Life history of *Porphyra carolinensis.*

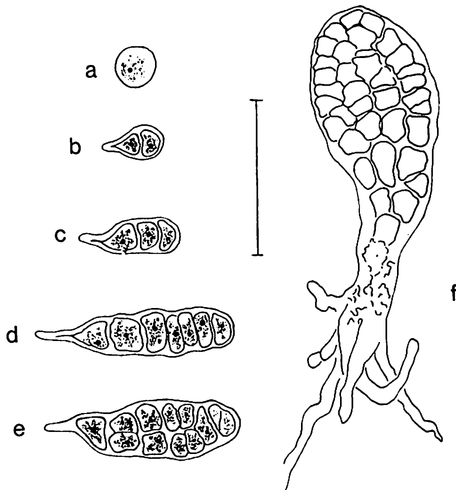


Fig. 14. Bipolar development of monospores and blade germling formation. Scale=50 μm.

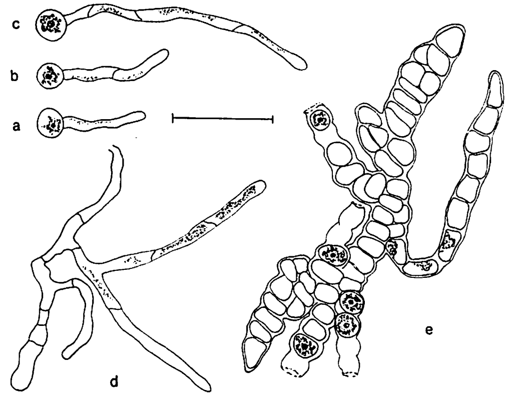


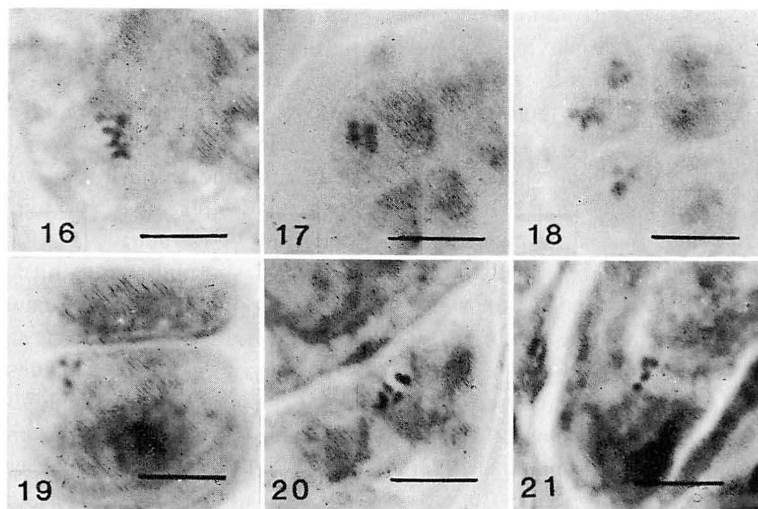
Fig. 15. Unipolar development of carpospores and conchocelis formation. Scale=50 μm.

develop in a bipolar fashion to produce blades, thus completing the life cycle. Spermatia are apparently vestigal.

Cytological observations: Four chromosomes were found in mitotic prophase cell divisions in conchocelis, conchospores, carpospores, spermatia, and vegetative cells of the blade phase (Figs. 16-21). In general, adequate mitotic figures were found in actively growing material from all fixation periods. Aceto-orcein was found to be superior to acetocarmine as it was less likely than the latter to stain cytoplasm and obscure chromosomes.

Discussion

Conchocelis phase: Individually or in combination, temperature, photon flux and photoperiod have been implicated in the control of conchospore formation and release in *Porphyra* species (KUROGI and AKIYAMA 1966, DRING 1967, RENTSCHLER 1967, KAPRAUN and LUSTER 1980). In this study, conchospore formation did not appear to be dependent on photon flux density. However, a temperature effect was apparent with maximum conchospore formation at 20 and 25°C in both 10 and 14 h days. Conchospore release and subsequent blade germling de-



Figs. 16–21. Chromosomes of *Porphyra carolinensis*. Scale=5 μm. All chromosomes are mitotic. Fig. 16. Vegetative blade cell anaphase with four pairs of chromosomes. Figs. 17 and 18. Four prophase chromosomes in spermatia. Fig. 19. Carposporangium with three visible chromosomes. The fourth is below the plane of focus. Figs. 20 and 21. Conchosporangia with four chromosomes (Fig. 20. Late metaphase. Fig. 21. Prophase).

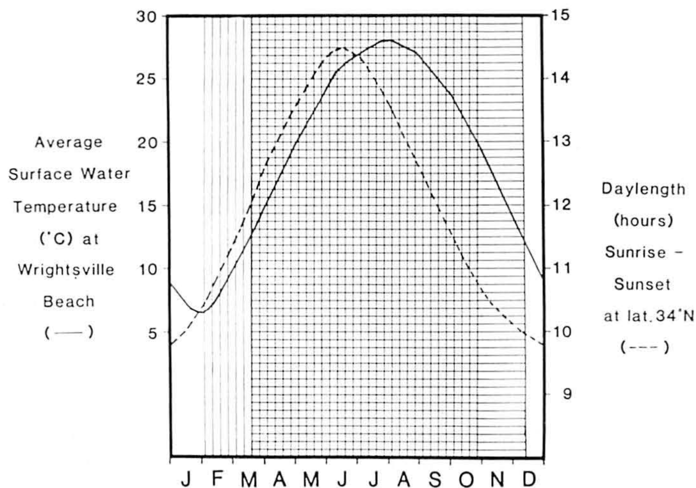


Fig. 22. Relationship between conchospore release and daylength or seawater temperature at Wrightsville Beach. Vertical lines indicate inhibition by daylength, horizontal lines by temperature.

velopment were controlled by a combination of low temperature (10°C) and short days (10 h). Previous studies of other *Porphyra* species have demonstrated a similar disparity between environmental parameters which promote conchospore induction and release (KUROGI and HIRANO 1956, KUROGI and AKIYAMA 1966, LÜNING 1980).

In *P. carolinensis*, the pathway leading to conchospore release is opened in short days only within a rather narrow temperature interval, around 10°C, with complete inhi-

bition at 15°C or less. Only from mid-December to early February are daylength and temperature in the appropriate range for the process of blade formation from conchospores to occur (Fig. 22). Thus, the "window" for blade reseeding via conchocelis is rather small, and would be even smaller in years when water temperatures remain above normal through the winter. Since blade formation via blade monospore production does not seem to be inhibited by any ambient combination of temperature and photoperiod, it can be surmised that this accessory means of reproduction is of critical importance to the continued survival of this species in local waters.

Blade phase: Investigations of the importance of environmental parameters on sporulation in the blade phase of *Porphyra* species have demonstrated considerable variation among the species investigated. IWASAKI (1961) found *P. tenera* blades remained vegetative in 8 h days, but formed carpospores in 13 h light. In contrast, several species have been found to produce both carpospores and spermatia through a wide range of temperatures and daylengths (BIRD *et al.* 1972, EDWARDS 1969, KAPRAUN and LUSTER 1980). Apparently, in these cases a maturation sequence or "ripening" rather than an environmental stimulus controls the initiation of sporogenesis.

In this study, both carpospore and spermatium formation showed a distinct seasonality in field collected material (Fig. 6). Comparison of sporulation patterns with water temperature and photoperiod data suggests a threshold of 16°C and 10.5 h days is required to initiate both carpospore and spermatium formation. Sporogenesis is subsequently inhibited as temperatures rise above 16°C, but continues in daylengths approaching 12.5 h. This strongly suggests that vegetative cells, once induced by photoperiod, may continue to undergo sporogenesis under inappropriate (non-inducing) daylengths. Unfortunately, there are few experimental data to correlate with these field observations. We have been successful only once in our attempts to induce sporulation in laboratory grown blades in any of our experimental conditions. Usually the rapid erosion resulting from monospore formation seems to prevent tissue from maturing and initiating sporogenesis. However, blades placed in aerated flasks at 16°C, 100 $\mu Em^{-2}s^{-1}$, and 10 : 14 LD after 14 days produced spermatia and initiated carpospore divisions. These environmental parameters coincide with the values predicted above.

Porphyra carolinensis blades produce two distinct spore types capable of germination: 1) monospores from single undivided vegetative cells, and 2) carpospores arising in packets of eight. Carpospores invariably develop in unipolar fashion to produce the conchocelis phase. This developmental sequence is typical of most *Porphyra* species (CHEN *et al.* 1970, BIRD *et al.* 1972, HAWKES 1977, KAPRAUN and LUSTER 1980).

In contrast, *P. carolinensis* monospores usually, but not invariably, develop in bipolar fashion to produce the blade phase. Of the *Porphyra* species which produce monospores from large blades (CONWAY and WYLIE 1972, HAWKES 1977, OGAWA and LEWMANOMONT 1978), only the two species investigated in North Carolina have been shown to have the flexibility of both uni- and bipolar monospore development (KAPRAUN and LUSTER 1980).

Cytology: Four chromosomes (N=4) were found in all phases of the life history of *P. carolineusis* confirming the absence of sexuality and meiosis in this species. Interestingly, the other two local *Porphyra* species, *P. rosengurtii* (KAPRAUN and LUSTER 1980) and *P. leucosticta* (unpublished data), also lack an alternation of ploidy levels. Elsewhere, the presence of both haploid and diploid nuclear phases has been shown to be a common occurrence. YABU (1975) reported haploid and diploid numbers for most of the 19 species investigated in Japan. On the west coast of North America, MUMFORD and COLE (1977) found haploid and diploid numbers in three of seven species studied. All three species of *Por-*

phyra in the North Atlantic which have been examined cytologically possess haploid and diploid phases (MAGNE 1952, GIRAUD and MAGNE 1968, KITO *et al.* 1971).

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フレッシュウォーター，D. W.・カプラウン，D. F.：ノースカロライナ産 *Porphyra carolinensis* COLL et COX（紅藻ウシケノリ目）の野外，培養および細胞学的研究

北米ノースカロライナ産の *Porphyra carolinensis* の生活史について，野外と室内培養で研究した。光周期 10L : 14D および 14L : 10D のもとで種々の光強度と温度を組合せ，光強度，温度および日長が生長と生殖に及ぼす影響を調べた。殻胞子の放出は，短日条件と低温の組合せを必要とすることにより御制されていること，葉状体の生長と単胞子による増殖が年間を通して行われていることが明らかになった。また，糸状体，殻胞子，果胞子，精子，葉状体の栄養細胞の染色体数は，いずれも4であった。（米国ノースカロライナ大学生物科学部）