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Effects of temperature and salinity on spore germination and sporeling development in South American agarophytes (Rhodophyta)

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Spores of five *Gracilaria* species and of *Pterocladia capillacea* (Gmelin) Bornet et Thuret were cultivated under different temperature and salinity conditions in the laboratory. The results show that temperature and salinity are limiting factors in the process of spore germination and sporeling development in *Gracilaria* species, but not in tetraspores of *P. capillacea*, which germinated under all conditions tested. Carposporelings of *G.* aff. *verrucosa*, *G. verrucosa* (Hudson) Papenfuss and *G. chilensis* Bird, McLachlan and Oliveira were distinct in their responses to temperature tolerance range and temperature optima. Carposporelings of *G.* aff. *verrucosa*, *G. tenuifrons* Bird and Oliveira, and *Gracilaria* sp. from various habitats (rocky shore, lagoon, and estuary, respectively) presented different degrees of tolerance to variation in salinity. Spores of these species lysed when submitted to salinities lower than 15‰ and those incubated on salinities higher than 50‰ germinated only if previously attached to the substratum. Comparative experiments with carposporelings and tetrasporelings of *G.* aff. *verrucosa* showed that the latter are more sensitive to variation in temperature and salinity. The results indicate that commercial cultivation based on spore propagation should be preceded by tests for tolerance range to variations of temperature and salinity for each selected species, once these factors can limit the spore germination and sporeling development.

Key Index Words: *agarophytes*—Gracilaria—Pterocladia—*salinity*—*sporeling development*—*temperature.*

Intensive exploitation of natural beds of Gracilariaceae and Gelidiaceae for agar production has brought about depletion in several regions of South America (Oliveira 1981, Alveal 1986). As a consequence mariculture has been proposed as an alternative to supplement the production of raw material for the industry (Oliveira 1984). In order to provide rational support for mariculture, basic information about the biology of suitable species is under investigation.

A number of authors have studied the influence of environmental factors on the growth and reproduction of *Gracilaria* spp. (e.g. Causey *et al.* 1946, Stokke 1957, Simonetti *et al.* 1970, Edelstein *et al.* 1976, McLachlan and Bird 1984, Bird and McLachlan 1986), and of *Pterocladia capillacea* (Gmelin) Bornet et Thuret (e.g. Santelices 1978 and Berchez 1985). However the information is concerned only with adult plants, without consideration about spore and sporeling development. The scarcity of information on the effects of temperature and salinity on red algal spore survival and development can be seen in the extensive revision by Santelices (1990).

This paper presents observations on the effects of temperature and salinity on spore germination and sporeling development in some of the more important species of agarophytes from South America.

Materials and Methods

Fertile plants of five *Gracilaria* species (Fig. 1) and of *Pterocladia capillacea* were collected from a variety of sites (Table 1), and transported to the laboratory in an insulated container. Voucher specimens were deposited at the herbarium of the Departamento de Botânica (SPF), Instituto de Biociências, Univer-

Table 1. Locations and collecting dates of the species studied.

SPECIES	LOCALITY	COORDINATES TEMPERATURE RANGE	DATA
Gracilaria chilensis Bird, McLachlan & Oliveira	Tubul River Chile	37°14'S 73°25'W 10–18°C	November 1987
Gracilaria verrucosa (Hudson) Papenfuss	Puerto Madryn Argentina	42°46'S 65°02'W 06–17°C	March 1986
Gracilaria tenuifrons Bird & Oliveira	Rio Una, Valença (BA) Brazil	13°22'S 39°05'W 23–30°C	December 1987
G. aff. *verrucosa*	Ubatuba (SP) Brazil	23°26'S 45°04'W 18–28°C	April 1987 November 1987
Gracilaria sp.	Lagoa de Araruama (RJ) Brazil	22°51'S 42°21'W 22–26°C	November 1987
Pterocladia capillacea (Gmelin) Bornet et Thuret	Ubatuba (SP) Brazil	23°26'S 45°04'W 18–28°C	January 1988 May 1988

sidade de São Paulo, Brazil.

Small segments of fertile thalli were excised (Fig. 2), brushed in sterile seawater under a stereomicroscope, and put on cover slips in Petri dishes containing sterile seawater. Twenty-four hours after release, spores were collected by two methods. By first method, cover slips inserted beneath fertile thalli with attached spores were transferred directly to other Petri dishes. By second method, unattached spores were transferred with Pasteur pipettes to other Petri dishes containing cover slips, and it was used in all treatments except for ones of *Gracilaria* spores incubated in salinities higher than 45‰, when the first method was used. In all cases spores were inoculated in 40 ml seawater enriched with Provasoli's solution (after McLachlan 1973) at concentrations of 5 and 20 ml·l^{-1} for the temperature and salinity experiments respectively.

Temperature experiments were carried out in growth chambers (FANEM, modelo 347-G), at temperatures of 14, 18, 22, 26 and 30°C.

The salinities tested ranged from 5 to 60‰, at intervals of 5‰. Seawater (32±2‰) was sterilized and concentrated by freezing. Gradual melting provided low (0–20‰), intermediate (25–40‰) and high (45–80‰) salinity stocks, which were mixed to obtain any salinity desired. The final salinity was checked with a refractometer (American Optical) and the seawater was filtered (Millipore, 0.45 μm).

Temperature and salinity experiments were carried out in duplicate under the following conditions: photon flux density 35–40 μmol·m^{-2}·s^{-1} provided by cool-white fluorescent lamps on a light/dark cycle of 16/8 hours, temperature 23(±3)°C for salinity experiments, and salinity 32(±2)‰ for temperature experiments. Germanium dioxide (1 mg·l^{-1}) was used to suppress diatom growth when necessary.

Spore germination was observed periodically and media exchanged weekly. Sporeling development was assessed by measurements of basal disc diameter, or by length of erect frond for *Gracilaria* species, and by length of the larger axis for *P. capillacea* sporelings.

Factorial analysis of variance was conducted on the data of sporeling development, and Student t significance test was used to compare tetrasporeling and carposporeling development.

Results

Spore size and germination pattern—Data for the diameter of recently released spores of the species studied are presented in Table 2. The Brazilian plants of *Gracilaria* presented smaller carpospores than those of *G. chilensis* and *G. verrucosa* (Table 2). Germination patterns of carpospores and tetraspores correspond to "*Dumontia* type", after Chemin (1937), or "typus discalis mediatus", after Inoh (1947). After attachment, the first divi-

Table 2. Diameter (μm) of recently released tetraspores (T) and carpospores (C).

SPECIES	TYPE	x±s*	maximum	minimum
Gracilaria chilensis	C	34.2±4.3	40.8	28.8
Gracilaria verrucosa	C	34.3±3.8	40.8	28.8
Gracilaria tenuifrons	C	21.0±1.4	24.0	19.2
G. aff. *verrucosa*	C	22.8±1.6	26.4	21.6
	T	21.6±1.2	22.8	20.4
Gracilaria sp.	C	21.0±1.4	21.6	19.2
Pterocladia capillacea	T	24.1±4.2	38.0	19.0

* x±s=average±standart error (n=30).

sion takes place in a median plane forming a two celled sporeling. Subsequently, one of the resultant cells divides perpendicularly to the first median division, this is followed by a division in the undivided cell, forming a four celled stage (Fig. 3). Several divisions take

Table 3. *Gracilaria* aff. *verrucosa*–Comparison between tetrasporeling and carposporeling development assessed by measures of basal disc diameter (d) and length of erect frond (l), after 10 days on different temperatures (T) and after 14 days on different salinities (S). The Student's t significance test (p=0.05) was used to compare the experiments.
Initial diameter of tetraspores=(21.6±1.2 μm) and carpospores=(22.8±1.6 μm), n=30.

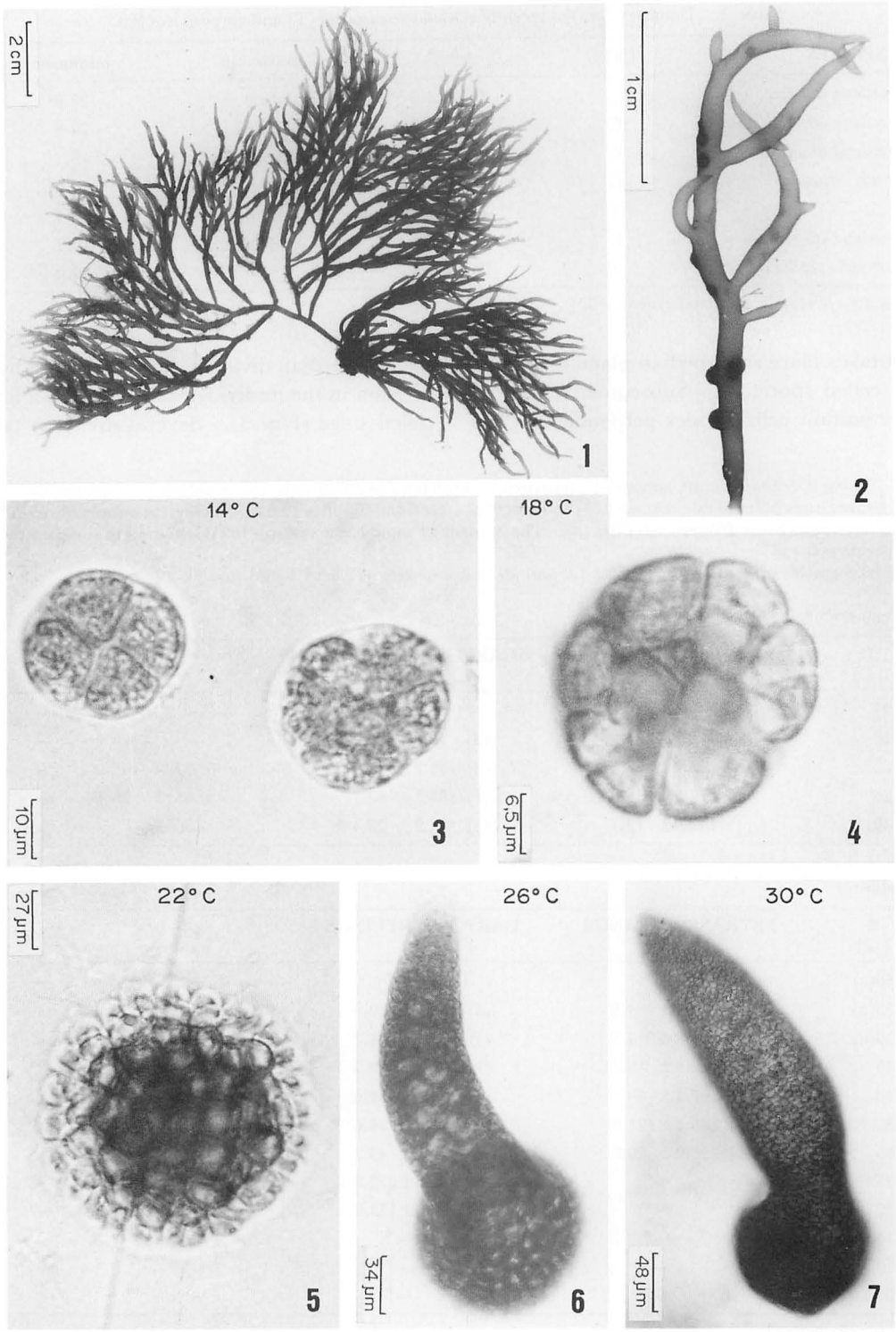
(Temperature)

T (°C)	TETRASPORELINGS (μm)	CARPOSPORELINGS (μm)	t	p=0.05
14	—*	—*	—	—
18	—*	(d) 38.0± 3.5	—	—
22	(d) 84.9± 8.2	(d) 103.2± 4.4	−10.7709	s.
26	(l) 179.5± 58.8	(l) 187.5± 32.7	− 0.6513	ns.
30	(l) 152.9± 42.7	(l) 197.9± 28.4	− 4.8063	s.

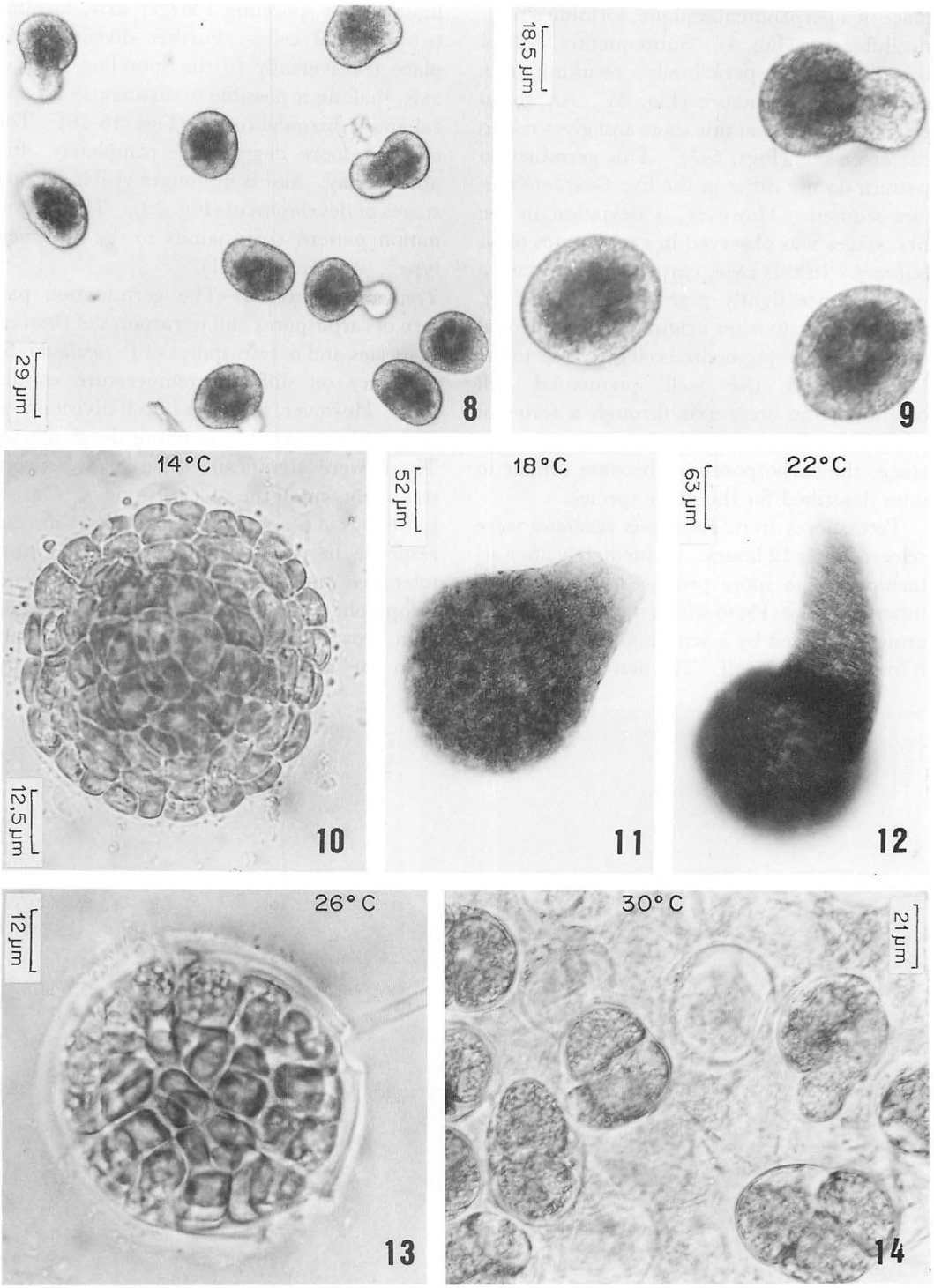
(Salinity)

S (‰)	TETRASPORELINGS (μm)	CARPOSPORELINGS (μm)	t	p=0.05
60(a)	—*	—*	—	—
55(a)	(d) 52.9± 4.8	(d) 57.6± 20.4	− 1.2284	ns.
50(a)	(d) 84.8± 4.3	(l) 165.3± 24.2	−17.9387	s.
45	(d) 112.4± 9.3	(l) 201.8± 49.2	− 9.7793	s.
40	(l) 257.1± 69.7	(d) 119.7± 51.6	8.6780	s.
35	(l) 386.1±121.0	(l) 185.5± 34.6	8.7305	s.
30	(l) 286.2± 20.6	(l) 391.9± 43.2	−12.0965	s.
25	—*	(l) 631.5±222.8	—	—
20	—*	(l) 380.6±175.9	—	—
15	—*	—*	—	—
10	—**	—**	—	—
05	—**	—**	—	—

*; sporelings dead
**; spores lysed after 10 minutes
a); spores attached on cover slips before the incubation on tested salinity.
s. and ns.; significant and non significant differences.



Figs. 1–7. *Gracilaria* aff. *verrucosa*. 1, General aspect of plants with cystocarps; 2, detailed of a branch with cystocarps; 3–7, Carposporelings cultured on different temperatures after 7 (3–4) and 14 days (5–7). Numbers on the top represent the temperature tested. Initial diameter=(23.8±2.3)μm, n=30.

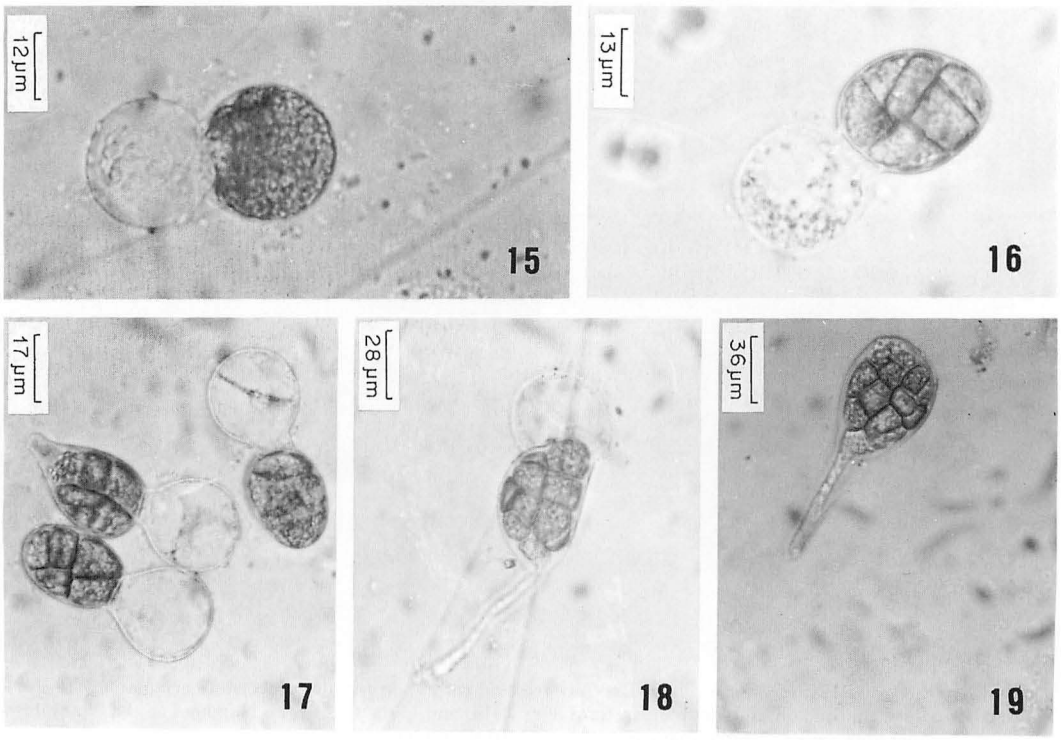


Figs. 8–14. *Gracilaria chilensis*. 8–9, Recently released carpospores in the process of germination; 10–14, Carposporelings cultured on different temperatures after 7 (14) and 14 days (10–13). Numbers on the top represent the temperature tested. Initial diameter=(34.2±4.3)μm, n=30.

place in a perpendicular plane, forming a multicellular disc (Fig. 4). Subsequently, cells of this disc divide periclinally, resulting in a dome-shaped structure (Fig. 5). An apical cell is established at this stage and gives rise to the erect axis (Figs. 6-7). This germination pattern do not differ in the five *Gracilaria* species studied. However, a deviation in the first stages was observed in carpospores of *G. chilensis*. In this case, carpospores produce a protuberance lightly pigmented (Figs. 8-9), and the first division originates two unequal cells. The less pigmented cell gives rise to the holdfast and the well pigmented cell originates the erect axis through a series of periclinal and anticlinal divisions. In this stage, the carposporelings become similar to ones described for the other species.

Tetraspores from *Pterocladia capillacea* were released after 12 hours. Immediately after attachment, the spore produces a lateral protuberance (Fig. 15) to which the protoplast migrates, followed by a septation which isolates it from the spore wall. The first division is oblique to the sporeling's larger axis, forming two unequal cells. Further divisions take place transversally to the sporeling's larger axis, making it possible to distinguish an apical and a rhizoidal region (Figs. 16-18). The original spore degenerates completely after about 7 days, and is no longer visible in later stages of development (Fig. 19). This germination pattern corresponds to the "*Gelidium* type", after Inoh (1941).

Temperature responses—The germination pattern of carpospores and tetraspores of *Gracilaria* species and of tetraspores of *P. capillacea* did not vary on different temperature conditions. However, the rates of cell divisions varied, influencing the sporeling development. There were significant differences between treatments in all the species studied. Carposporelings of *Gracilaria* spp. displayed a distinct response in terms of range of temperature tolerance and optima temperatures for development. *G. verrucosa* (Argentina) presented a broader range of temperature tolerance than the other *Gracilaria* species, and car-



Figs. 15–19. *Pterocladia capillacea*. Different stages of development of tetrasporelings.

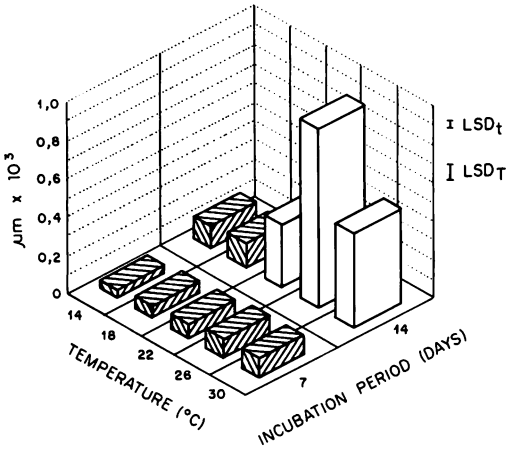


Fig. 20. *Gracilaria verrucosa*–Argentina. Development of carposporelings under different temperatures. Initial diameter=34.3±3.8 µm, n=30. Factorial ANOVA F=80.88***, LSD_t and LSD_T (p=0.05)=less significance difference for time (t) and temperature (T) respectively. Hatched column=basal disc diameter, and empty column=length of erect frond.

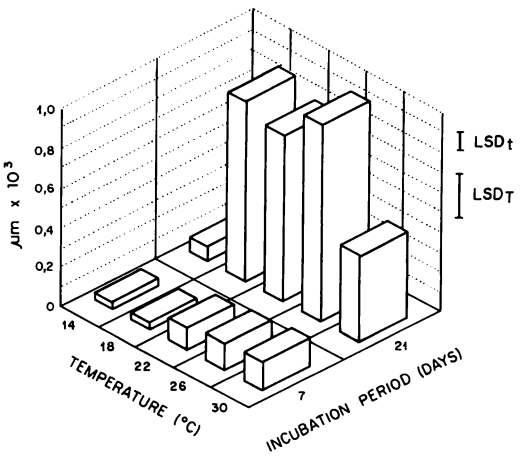


Fig. 22. *Pterocladia capillacea*. Development of tetrasporelings under different temperatures. Initial diameter of tetraspores=(24.1±4.2)µm, n=30. Factorial ANOVA F=19.74***, LSD_t and LSD_T (p=0.05)=less significance difference for time (t) and temperature (T) respectively.

posporelings survived on temperature variations from 14 to 30°C, with maximum growth at 26°C (Fig. 20). A high number of carpospores of *G.* aff. *verrucosa* (Brazil) submitted to 14 and 18°C did not attach to the substratum and did not germinate; a few germinated up to the stage of 4-8-celled, and died after 10 days at 14°C. At the 18°C development went on to more advanced stages but sporelings died after 14 days. Carposporelings survived on temperatures of 22 to 30°C, and developed the erect axis at temperatures of 26 and 30°C (Figs. 6-7). The optimum temperature for sporeling development in this species was 30°C. Carposporelings of *G. chilen-*

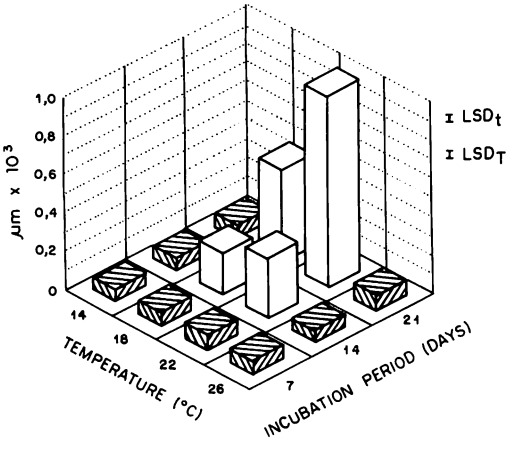


Fig. 21. *G. chilensis*. Development of carposporelings under different temperatures. Initial diameter=43.2±4.3 µm, n=30. Factorial ANOVA F=259.70***, LSD_t and LSD_T (p=0.05)=less significance difference for time (t) and temperature (T) respectively. Hatched column=basal disc diameter, and empty column=length of erect frond.

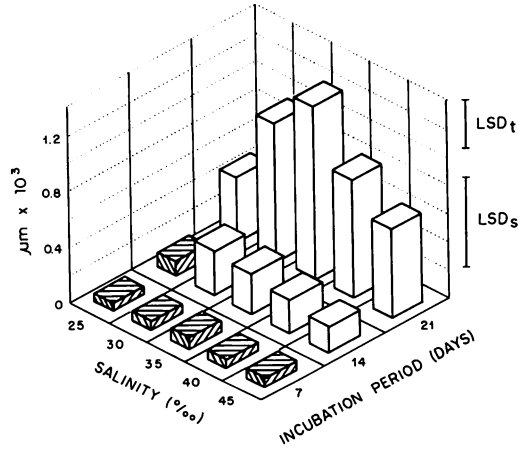


Fig. 23. *Gracilaria* sp. Development of carposporelings under different salinities. Initial diameter=21.0±1.2 µm, n=30. Factorial ANOVA F=3.85*, LSD_t and LSD_S (p=0.05)=less significance difference for time (t) and salinity (S) respectively. Hatched column=basal disc diameter, and empty column=length of erect frond.

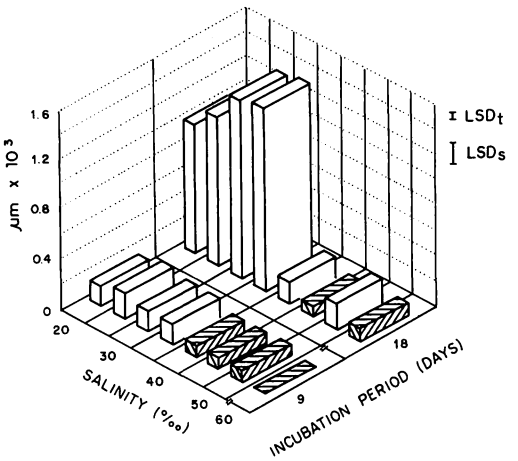


Fig. 24. *Gracilaria tenuifrons*. Development of carposporelings under different salinities. Initial diameter=21.0±1.4 µm, n=30. Factorial ANOVA F=87.54***, LSD_t and LSD_S (p=0.05)=less significance difference for time (t) and salinity (S) respectively. Hatched column=basal disc diameter, and empty column=length of erect frond.

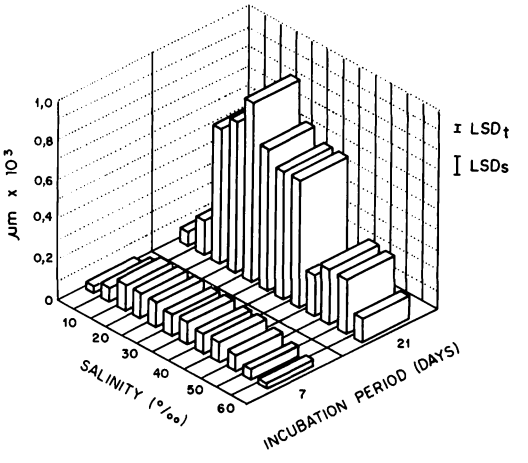


Fig. 25. *Pterocladia capillacea*. Development of tetrasporelings under different salinities. Initial diameter of tetraspores=(24.1±4.2)µm, n=30. Factorial ANOVA F=25.51**, LSD_t and LSD_S (p=0.05)=less significance difference for time (t) and salinity (S) respectively.

sis (Chile), however, did not develop well in the high temperatures tested; carpospores submitted to 30°C germinated only up to the stage of 2-4-celled (Fig. 14), and died after 7 days. Carposporelings submitted to 14 and 26°C grew slowly, and the erect axis did not develop after 21 days (Figs. 10 and 13). The optima temperature for carposporeling development in this species were 18 and 22°C (Figs. 11, 12 and 21). A comparison of the responses of tetraspores and carpospores for the same species (*G.* aff. *verrucosa*—Brazil) is given in Table 3, where it may be seen that the carposporelings presented a broader tolerance than the tetrasporelings. The temperature optima for development were 30°C for carposporelings and 26°C for tetrasporelings.

Pterocladia capillacea tetrasporelings presented the broadest tolerance to temperature, growing over the entire ranges tested (Fig. 22). However the extreme values of temperature were not favorable to development, and tetrasporelings grew better between 18 and 26°C.

Salinity responses—The different salinity conditions did not alter the germination pattern of carpospores and tetraspores of *Gracilaria* species and of tetraspores of *P. capillacea*, but influenced the sporeling development. Carposporelings of *Gracilaria* sp. tolerated variations in salinity from 25 to 45‰, and developed better at 30-40‰ (Fig. 23). Free carpospores (obtained following second method) inoculated at 50-60‰ did not attach to the substratum but stayed alive for 14 days. Few carpospores germinated at salinities of 50-55‰, but developed multicellular disc with irregular shapes. Carposporelings of *G. tenuifrons*, however, tolerated salinities from 20 to 60‰ (Fig. 24) although they developed better between 20-35‰. Normal carposporelings developed even at 50-60‰, but only when they originated from attached carpospores (first method).

Comparative salinity responses of tetrasporelings and carposporelings of *G.* aff. *verrucosa* are presented in Table 3. Tetrasporelings were more sensitive to low salinities (significant at p=0.05), and did not survive in salinities lower than 30‰. Tetraspores germinated in and tolerated salinities from 30 to 50‰, with maximum growth at 30-40‰. However, carposporelings tolerated a broader range of salinity variation, from 20 to 55‰, with maximum growth at salinities of 20-40‰. Spores from these three *Gracilaria*

species lysed when incubated in salinities lower than 15‰.

Tetrasporelings of *P. capillacea* growing at salinities of 5 and 10‰ presented irregular shapes, lighter colour and rhizoids, surviving 21 days on these conditions. Tetrasporelings grew better at salinities from 15 to 40‰ (Fig. 25).

Discussion

The germination pattern of carpospores and tetraspores of *Gracilaria* species described here is in accordance with the observations made by Oza and Krishnamurthy (1967), Ogata *et al.* (1972), Oza (1975), Bird *et al.* (1977), Mshigeni and Wevers (1979), Oliveira and Plastino (1984) and Plastino (1985). The deviation observed on germination pattern of *G. chilensis* carpospores is similar to the descriptions made by Plastino and Oliveira (1988) for the same species. There are not references whether other species of *Gracilaria* presents this type of deviation on germination pattern.

The germination pattern of tetraspores of *P. capillacea* is in agreement with observations made by Oliveira and Paula (1974) for the same species and by Inoh (1941), Chihara and Kamura (1963) and Paula *et al.* (1988) for other species of Gelidiaceae.

The results show that temperature and salinity are critical factors on spore germination and sporeling development in the species of *Gracilaria* studied here. Bird *et al.* (1977) have already reported on the importance of temperature for spore germination in *Gracilaria* sp. (afterwards identified as *G. tikvahiae* McLachlan by McLachlan (1979) from the Maritime Provinces of Canada). Observations that carposporelings of *G.* aff. *verrucosa* and *G. verrucosa* present maximum growth in higher temperatures are in agreement with those reported by Mshigeni and Wevers (1979) for *G. corticata*, and by Friedlander and Dawes (1984) for *G. foliifera* var. *angustissima*. On the other hand, carpospores of *G. chilensis* were sensitive to the highest temperature tested here (30°C). Of the species studied this *Gracilaria* is the best adaptated to cold water conditions.

Temperatures for better development of carposporelings of *G. chilensis* and of *G. verrucosa* are between 18-22°C and 22-26°C respectively; these are higher than the ranges of temperature variation found in their habitats (Mayer 1981, McLachlan and Bird 1984). These results suggest that the field temperature regime in the regions where the species lives is not always the most favorable for spore germination, and this might influence the reproductive pattern of the population. Romo and Alveal (1979) observed only tetrasporophytic plants in a population of *G. verrucosa* from Reyes Island (Concepcion Bay), and suggested that this population reproduces only vegetatively because this region does not have temperatures favorable to spore germination.

As regards salinity responses, it is observed that spores of the *Gracilaria* species studied did not germinate in salinities above 50‰, and that they lysed in salinities lower than 20‰, while unattached spores did not germinate on salinities higher than 50‰. Salinity tolerance is obviously variable with the species as shown by Friedlander and Dawes (1984), who reported growth of carpospores of *G. foliifera* var. *angustissima* at salinity variation ranging from 5 to 35‰. Muñoz *et al.* (1984) reported growth from 5 to 55‰ for carposporelings of *G. verrucosa*, although 5 and 15‰ show low survival of plants due to lysis of the carpospores.

Experiments devised to compare responses of carpospores and tetraspores in *G.* aff. *verrucosa* showed that tetraspores are more sensitive than carpospores, both to temperature and salinity variations. This observation may be related to the cellular ploidy of the phases, since diploid cells are supposed to be more tolerant than haploids to environmental variations. This observation may explain the predominance of tetrasporophytic phase in natural populations, as observed by Hoyle (1978), Pinheiro-Joventino and Bezerra (1980), Ludewigs (1984) and Plastino (1985), in different species of *Gracilaria*. This is also generally assumed for other genera of red al-

gae (e.g. Dixon 1973), although the explanation is not as simple as that (cf. Santelices 1990).

Temperature and salinity in the range tested here are not inhibitory to tetraspore germination of *Pterocladia capillacea*, which survived all tested conditions. This is perhaps to be expected, as the population studied comes from the intertidal zone and is therefore subject to a broader variation of temperature and salinity.

On the practical side, the results of our experiments indicate that the use of spores for the mariculture of *Gracilaria* spp. should be preceded by careful studies of their tolerance to temperature and salinity variations, since these factors are limiting to spore germination and sporeling development. They also show that on what concerns spore germination and early stages of development, species of *Gracilaria* from Chile and Argentina could be cultivated in some areas of the Brazilian coast.

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Nair. S. Yokoya・Eurico. C. Oliveira*: 南アメリカ寒天藻（紅藻植物門）の胞子発芽とその後の発達におよぼす温度と塩濃度の影響

オゴノリ属5種およびオバクサの胞子を種々の温度と塩濃度の下で培養した。その結果，温度と塩濃度が胞子発芽とその後の発達過程の律速因子となること，オバクサの四分胞子は調べたどの条件下においても発芽することが示された。*Gracilaria* aff. *verrucosa*，オゴノリ及び *G. chilensis* の果胞子発芽体は温度耐性と最適温度が他のものとは異なっていた。*G.* aff. *verrucosa, G. tenuifrons* の果胞子発芽体，成育環境の異なった場所（磯，磯の水溜り，河口）から採集した *G. sp.* の果胞子発芽体において，それぞれの塩濃度変化に対する耐性の度合は異なっていた。これらの種の胞子は15‰より低い塩濃度では分解し，50‰以上では基質へ付着している場合だけ発芽した。*G.* aff. *verrucosa* の果胞子発芽体と四分胞子発芽体を用いた比較実験から，四分胞子発芽体が果胞子発芽体よりも温度と塩濃度の変化に対して敏感であることが示された。これらの結果は，胞子を用いて商業的に栽培する場合には，その種の温度・塩耐性の範囲をあらかじめ調べておくべきである。なぜなら，これらの因子は胞子発芽とその後の育成を制限するからである。(Instituteo de Botânica, Secretaria do Meio Ambiente, C. Postal 4005, 01061–970 São Paulo, Brasil, *Instituto de Biociencias e Centro de Biologia Marinha, Universidade de São Paulo, C. Postal 11461, 05422–970 São Paulo, Brasil)

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