Morphology, reproduction and development of *Hypoglossum hypoglossoides* (Stackhouse) Collins & Hervey (Ceramiales, Rhodophyta) from the south and southeastern Brazilian coast

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ABSTRACT – (Morphology, reproduction and development of *Hypoglossum hypoglossoides* (Stackhouse) Collins & Hervey (Ceramiales, Rhodophyta) from the south and southeastern Brazilian coast). *Hypoglossum hypoglossoides* (Stackhouse) Collins & Hervey is reported for the first time from the infralittoral of São Paulo and Santa Catarina states. The species was already reported to the states of Rio de Janeiro, Espírito Santo and Bahia as *Hypoglossum tenuifolium* (Harvey) J. Agardh var. *carolinianum* Williams. A detailed description of the morphology and reproduction is given based on field-collected material. Unialgal cultures were initiated from tetraspore germination, and growth rates of gametophytes were determined under different conditions of temperature, photoperiod and irradiance. Gametophytes grew well between 15 to 30 °C, 14L:10D and 10L:14D photoperiods and irradiance from 20 to 120 μmol photons.m⁻².s⁻¹, but presented low percentage of fertile plants in low temperature (15 °C). Gametophytes cultured in laboratory developed only male reproductive structures. Physiological responses of *H. hypoglossoides* indicate that the species is well adapted to temperature and light variations which could explain its range of vertical (6-26 m depth) and latitudinal distribution (from Fernando de Noronha to Santa Catarina) as well as the absence of sexual reproduction in the southern limit of its distribution.

Key words - Delesseriaceae, development, Hypoglossum hypoglossoides, reproduction, Rhodophyta

RESUMO – (Morfologia, reprodução e desenvolvimento de *Hypoglossum hypoglossoides* (Stackhouse) Collins & Hervey (Ceramiales, Rhodophyta) da costa sul e sudeste do Brasil). *Hypoglossum hypoglossoides* (Stackhouse) Collins & Hervey é descrito pela primeira vez para o infralitoral dos estados de São Paulo e Santa Catarina. A espécie já foi descrita para os estados do Rio de Janeiro, Espírito Santo e Bahia como *Hypoglossum tenuifolium* (Harvey) J. Agardh var. *carolinianum* Williams. Uma descrição detalhada da morfologia e reprodução da espécie é apresentada com base em material de campo. Cultivos unialgais foram estabelecidos a partir da germinação de tetrásporos e a taxa de crescimento de gametófitos foi determinada em diferentes condições de temperatura, fotoperíodo e irradiância. Os gametófitos toleraram as variações de temperatura de 15 a 30 °C, fotoperíodos de 14L:10E e 10L:14E e irradiâncias de 20 a 120 μmol fótons.m⁻².s⁻¹, mas apresentaram baixa percentagem de plantas férteis quando cultivados em baixa temperatura (15 °C). Gametófitos cultivados em laboratório desenvolveram somente estruturas masculinas. As respostas fisiológicas de *H. hypoglossoides* indicam que a espécie está bem adaptada às variações de temperatura e luz, o que pode explicar a sua ampla distribuição vertical (6-26 m de profundidade), distribuição latitudinal (Fernando de Noronha a Santa Catarina), assim como a ausência de plantas férteis no seu limite sul de distribuição.

Palavras-chave - Delesseriaceae, desenvolvimento, Hypoglossum hypoglossoides, reprodução, Rhodophyta

Introduction

The genus *Hypoglossum* Kützing is represented by 28 species, mostly from warm waters (Wynne & Kraft 1985, Wynne & Ballantine 1986, Zheng 1998,

Wynne & De Clerck 2000, Stegenga *et al.* 2001). It is characterised by having initials of all third-order cell rows reaching the margin of blades, carposporangia formed in chains, tetrasporangia produced from cells of second and third-order rows, and absence of intercalary divisions (Womersley & Shepley 1982).

The genus is represented in Brazil by three species, the present one (Oliveira Filho 1969, Yoneshigue 1985, as *Hypoglossum tenuifolium* (Harvey) J. Agardh var. *carolinianum* Williams), *H. anomalum* Wynne & Ballantine (Horta & Oliveira 2001) and *H. tenuifolium* (Harvey) J. Agardh var. *tenuifolium* (Cordeiro-Marino & Guimarães 1981).

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The relatively broad vertical and latitudinal distribution of *Hypoglossum hypoglossoides* in Brazil led us to study the effects of light and temperature on its growth and reproduction. Additionally we present a detailed description of the morphology and reproduction of *H. hypoglossoides*.

Material and methods

Collections were carried out by scuba diving (6-26 m), in the south and southeastern coast of Brazil. Field-collected plants were preserved in formalin 4% in seawater, stained with aniline blue 1%, acidified with 1N HCl, and mounted in 50% Karo Syrup. The photographs were taken on a standard Leica microscope. The studied specimens were deposited as slides (PH) in the Phycological Herbarium of the University of São Paulo (SPF), Brazil.

For laboratory culture studies, fertile tetrasporophytes were collected at Rapada Island, Ubatuba, SP (23°26' S and 44°54' W), in April/1999, at around 10 m depth. Voucher specimens were deposited in the herbarium of Institute of Botany, Brazil (access number: SP 355789). Unialgal cultures were initiated by tetraspore germination, and cultivated in Von Stosch's enriched seawater (VSES) at full strength (Edwards 1970) with vitamin concentrations reduced to 50%. Germanium dioxide (1.0 mg.L⁻¹) was added to the VSES to supress diatom growth. Standard culture conditions were: salinity 30 ± 1 psu, temperature of 24 ± 2 °C, 40.0-50.0 µmol photons. m⁻².s⁻¹ provided by cool-white fluorescent lamps with 14L:10D photoperiod (light:dark cycle), without aeration. Photon irradiance was measured with a LI-COR 250 quantameter equipped with underwater quantum sensor (LI-192 SA, LI-COR, Inc.). Culture medium was renewed weekly.

The effects of temperatures of 15, 20, 25 and 30 °C under photoperiod of 14L:10D (light:dark cycle) and temperatures of 20 and 30 °C under photoperiod of 10L:14D (light:dark cycle) were tested under photon irradiances of 40.0-50.0 μ mol photons. $m^{-2}.s^{-1}$. The experiment of photon irradiance variation (from 20 to 120 μ mol photons. $m^{-2}.s^{-1}$) was conducted at 20 °C and 14L:10D photoperiod. Other experimental conditions were the same as those described above for unialgal cultures. Each treatment was tested with three replicates of 10 gametophytic blades (3-5 mm length) inoculated into 250 mL conical flasks containing 150 mL of VSES.

Measurements of blade length and observation on reproductive structures, as well as medium renewal were made weekly. Growth rate was calculated as [ln(L_t . L_o^{-1}). t^{-1}].100%, where L_o is the initial blade length, L_t is the blade length after t days, and t is the number of days. Growth rates were calculated after 21 days, when plants were in a vegetative phase. Analysis of variance with one factor was performed on growth rate data.

Results

Hypoglossum hypoglossoides (Stackhouse) Collins & Hervey, Proc. Amer. Acad., Arts Sci. 53:116. 1919.

Basionym: *Fucus hypoglossoides* Stackhouse, Nereis Britannica 3:76. 1802 ("1801").

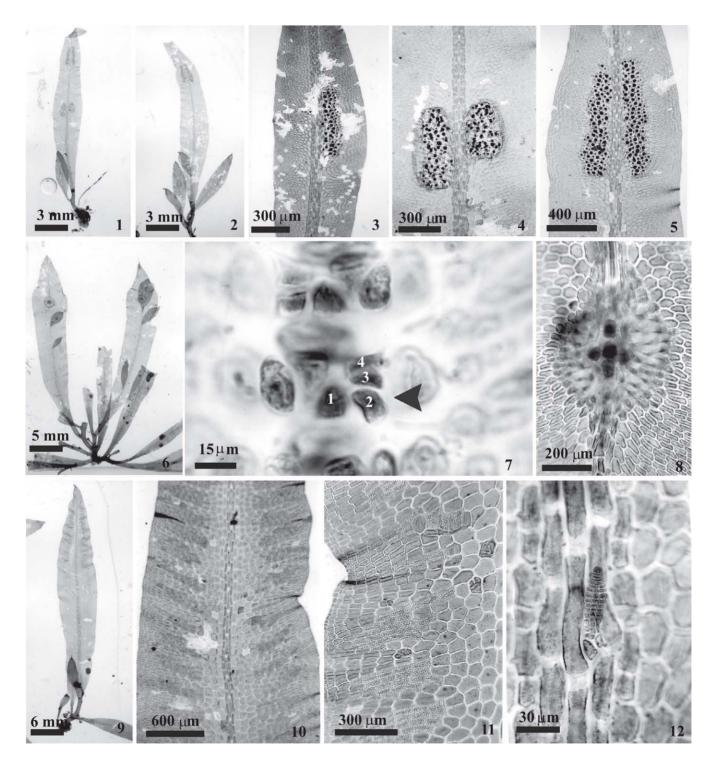
Studied material: BRAZIL: RIO DE JANEIRO: Emboassica Island, X-1998, *P. Horta* (PH 28); Porcos Island, X-1998, *P. Horta* (PH 118-125). SÃO PAULO: Rapada Island, IV-1999, *P. Horta* (PH 12); Queimada Grande Island, VII-1997, *P. Horta* (PH 491); Laje de Santos, XI-1998, *P. Horta* (PH 492). SANTA CATARINA: Arvoredo Island, I-1998, *P. Horta* (PH 495).

Field material description - Rosy delicate plants, 1-4 cm in height, growing erect as epiphyte or epilithic on rock or shell fragments. Blade monostromatic except at the midrib, 1-3 mm wide at the median portion and 0.3-0.7 mm at the base. Cortication restrict to the basal cylindrical portions. Branches single or in opposite pairs originating from the midrib axial cell. Midrib with elongated axial cells, 105-225 µm long; in superficial view midrib with three cells on the distal portion and five cells on the basal portion. The monostromatic region is made out by second and third-order rows, composed of irregular hexagonal cells disposed obliquely to the margin in surface view. All cells of the second-order rows give rise to third-order rows (type-1 apex). Growth in length takes place by transversely dividing apical cell in the terminal portion of each branch.

Tetraporangia tetrahedrally divided, 22-54 μm in diameter, randomly distributed in one-two pairs of opposite sori or in unilateral sori, 0.6-1.5 mm long and 150-380 μm wide. Lateral pericentral cells are not directly involved in tetrasporangia formation (figures 1-5).

Gametangial thalli dioecious. Female plants with procarps distributed along the midrib, with four-celled carpogonial branch L-shaped, with the second cell larger than the others with ca. 7 μ m in diameter. Cystocarp projecting on the midrib, in series or isolated, 330-820 μ m in the larger diameter. Carposporangia with 29-58 μ m in the larger diameter (figures 6-8). Spermatangial sori oblique, distributed along both sides of midrib, originated from cells of second and third-order filaments. Male plants are usually smaller and less branched (figures 9-12).

Germination of tetraspore and tetrasporeling development in laboratory culture - Tetraspores attach and soon divide into two unequal cells, one of which becomes the rhizoid initial and the other divides to



Figures 1-12. Morphology and reproduction of *Hypoglossum hypoglossoides* from field-collected material. 1-2. General aspect of tetrasporic plants. 3-5. Detail of tetrasporangial sori. 6. General aspect of female plant. 7. Detail of four-celled carpogonial branch, with the second cell larger than the others (arrowhead). 8. Detail of a cystocarp, showing four gonimoblast initial cells. 9. General aspect of a male plant. 10-11. Different aspects of spermatangial sori. 12. Young branch produced from midrib.

produce an axial cell row (figures 13-16); pericentral cells are cut from the third to the fifth segments behind the apical cell (figures 17-21).

Development of gametophytes in laboratory culture -Growth rates of gametophytes varied from 5.2%.d⁻¹ to 7.7%.d⁻¹, with the highest growth rate at 30 °C/10L:14D (figure 22). However, the differences among treatments were not significant (F = 0.52). Gametophytes developed spermatangial sori after three weeks of culturing in all treatments (figure 23), and the highest percentage of male plants was induced by 20 °C/ 10L:14D, and high temperature (30 °C) in both photoperiods. Low percentage of male plants was observed at 15 °C (figure 23). Development of spermatangial sori was observed in all gametophytes cultured under irradiances from 20 to 120 µmol photons. m⁻².s⁻¹ after three weeks. Growth rates of fertile male gametophytes varied from 1.9%.d-1 to 3.0%.d⁻¹ (figure 24). However, differences among treatments were not significant (F = 0.74).

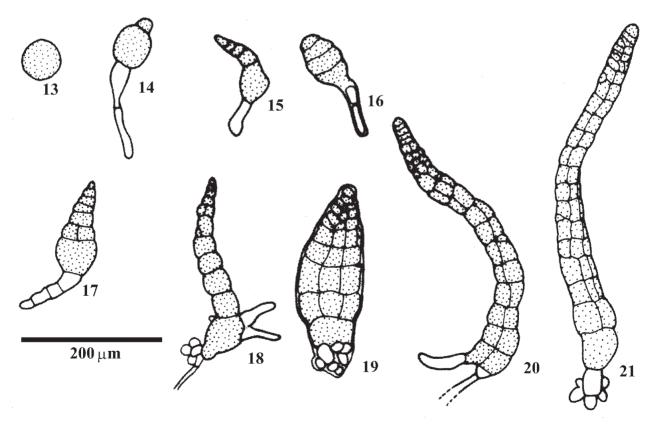
In cultured male gametophytes, spermatangial sori are produced on both sides of the midrib and are separated by rows of sterile cells (figures 25-26). Some sterile cells divided and gave rise to new erect blades (figures 27-28) resembling the early stages of tetrasporeling development (figures 19-21). Carpogonial branches were not observed in our cultures and the life-history of *Hypoglossum hypoglossoides* was not completed in laboratory.

Discussion

Our plants fit well in the genus *Hypoglossum*, exhibiting its diagnostic features of a third-order cell row produced from every cell of the second-order row, blades typically elongated and attenuated, and tetrasporangia arranged irregularly in sori (Wynne & Ballantine 1986, Wynne 1988).

Our material of *Hypoglossum hypoglossoides* presents type-1 apex (sensu Wynne *et al.* 1989), corticated midribs at least in lower portions of blades, tetrasporangia in linear sori separated from the midrib of ordinary blades by sterile cells and sori present mostly in both sides of the midrib (Wynne 1984, Schneider & Searles 1991, Schneider 2000, Wynne & De Clerck 2000).

Among the 26 species listed in the key proposed by Wynne & De Clerck (2000), the taxon with great



Figures 13-21. Tetraspore germination and tetrasporeling development of Hypoglossum hypoglossoides in laboratory conditions (salinity of 30 ± 1 psu, temperature of 24 ± 2 °C, photon irradiance of 40.0-50.0 µmol photons. m⁻².s⁻¹, 14L:10D photoperiod, and culture medium with Von Stosch's nutrient solution). 13. Liberated tetraspore. 14-21. Different stages of tetrasporeling development with one to seven-days old.

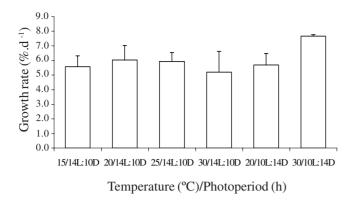
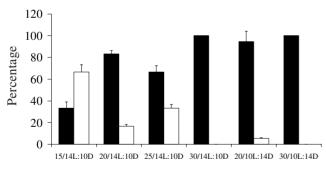


Figure 22. Growth rates of gametophytic blades of *Hypoglossum hypoglossoides* cultured in different temperatures and photoperiods for three weeks. Each data point is the mean of three replicates. Experiment was conducted in salinity of 30 ± 1 psu, photon irradiance of $40.0\text{-}50.0 \,\mu\text{mol}$ photons. m⁻².s⁻¹, and culture medium with Von Stosch's nutrient solution.

similarity to our specimens is *Hypoglossum* androlamellare Wynne & De Clerck. However, this species, described from Tanzania, presents spermatangial sori in a chevron arrangement, whereas in *H. hypoglossoides* the male structures are represented by interrupted or continuous sori.

Hypoglossum imperfectum Stegenga, Anderson & Bolton (Stegenga *et al.* 2001), recently described to



Temperature (°C)/Photoperiod (h)

Figure 23. Development of reproductive structures on gametophytic blades of $Hypoglossum\ hypoglossoides$ cultured in different temperatures and photoperiod for five weeks. Percentage corresponds to the number of blades with reproductive structures per total number of blades. Experiment was conducted in salinity of 30 ± 1 psu, photon irradiance of 40.0-50.0 µmol photons. $\text{m}^{-2}.\text{s}^{-1}$, and culture medium with Von Stosch's nutrient solution. $\square = \text{Non fertile}$ plants; $\blacksquare = \text{Male plants}$.

South Africa, differs from our specimens by its prostrate habit and incomplete third-order cell rows, while *H. hypoglossoides* has erect frond with all third-order cell row reaching the thallus margin.

The material identified as *Hypoglossum* tenuifolium var. tenuifolium by Cordeiro-Marino & Guimarães (1981) differs from our specimens because third-order cell rows are not produced from every cell of the second-order rows.

The plants referred as *Hypoglossum tenuifolium* (Harvey) J. Agardh var. *carolinianum* Williams from the coasts of Espírito Santo (Oliveira Filho 1969), Bahia (Oliveira *et al.* 1979, Nunes 1998), and Rio de Janeiro (Yoneshigue 1985, Pedrini *et al.* 1992) are better placed into *H. hypoglossoides*. This variety was considered as a synonym of *H. hypoglossoides* by Wynne & Ballantine (1986) due to the fact that all cells of the second-order rows give rise to the initial cells of the third-order rows.

Our material was frequent in all the studied area, being found from 6-26 m depth. Tetrasporangial and sexual plants were found in Rio de Janeiro and in the northern localities of São Paulo state. Fertile plants were not found at Santa Catarina state which corresponds to the southern limit of *Hypoglossum hypoglossoides* distribution in western Atlantic. These data could be related to the temperature responses of cultured gametophytes, which presented lower percentage of male plants in low temperature (15 °C).

Gametophytes of *Hypoglossum hypoglossoides* tolerated the tested variations of temperature, photoperiod and irradiance. Our experimental data show

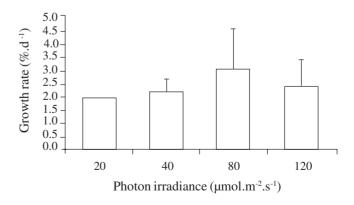
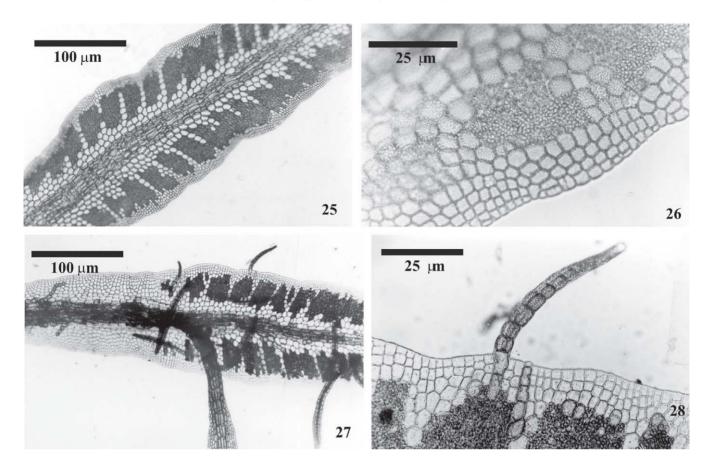


Figure 24. Growth rates of gametophytic blades of *Hypoglossum hypoglossoides* cultured in different photon irradiances for three weeks. Each data point is the mean of three replicates. Experiment was conducted in salinity of 30 ± 1 psu, temperature of 24 ± 2 °C, 14L:10D photoperiod, and culture medium with Von Stosch's nutrient solution.



Figures 25-28. Cultured male gametophytes of $Hypoglossum\ hypoglossoides$ in laboratory conditions (salinity of 30 ± 1 psu, temperature of 24 ± 2 °C, photon irradiance of 40.0-50.0 µmol photons. m⁻².s⁻¹, 14L:10D photoperiod, and culture medium with Von Stosch's nutrient solution). Figure 25. General aspect of blade with spermatangial sori. 26. Detail of a spermatangial sorus. 27. General aspect of a blade with the formation of new erect thalli. 28. Detail of the formation of new erect blades.

that *H. hypoglossoides* is well adapted to the temperature and light variations expected to be found in its regions of occurrence in Brazil. The range of temperature tolerance of *H. hypoglossoides* (from 15 to 30 °C) is similar to the data obtained for other Brazilian red algae as *Hypnea cornuta* (Lamour.) J. Agardh and *Pterocladiella capillacea* (S.G. Gmel.) Santel. & Hommers. (Yokoya & Oliveira 1992), and colour strains of *H. musciformis* (Wulfen *in* Jacqu.) J.V. Lamour. (Yokoya *et al.* 2003).

The tetraspore germination pattern described in the present study corresponds to the "Ceramium-type" (Dixon 1973), and is similar to the germination pattern observed for *Hypoglossum nipponicum* Yamada (Notoya 1986) and *H. rhizophorum* Ballantine & Wynne (Ballantine & Wynne 1988).

A "Polysiphonia-type" life-history was expected for our plants as have been determined for other

Delesseriaceae genera (Yarish & Edwards 1982, Kamiya et al. 1995, West et al. 2001), and for species of Hypoglossum (Notoya 1986, Ballantine & Wynne 1988). Nevertheless, the life-history of H. hypoglossoides was not completed because only male plants were produced from the tetrasporederived plants. Cultured gametophytes of H. nipponicum and H. rhizophorum were dioecious, and developed approximately equal numbers of male and female plants (Notoya 1996, Ballantine & Wynne 1988). Deviation observed in H. hypoglossoides could be related to the lack of aeration in the cultures. The occurrence of spermatangia and tetrasporangia in carpospore-derived plants and only spermatangia in tetraspore-derived plants of Gracilaria chilensis Bird, McLachlan & Oliveira were related to the presence or absence of aeration, and these results could be explained by the interference of environmental factors in genetic expression of the spores (Plastino & Oliveira 1988). Similarly, genetic characteristic or specific environmental conditions could regulate the reproductive development of *H. hypoglossoides*, as the occurrence of exclusive asexual reproduction in some populations of *Caloglossa leprieurii* (Montagne) G. Martens (West *et al.* 2001).

The present study describes for the first time the occurrence of *Hypoglossum hypoglossoides* from the littoral of São Paulo and Santa Catarina states, the latter being its southern limit in the American Atlantic.

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