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Growth and reproductive phenology of *Pterocladiella capillacea* (Rhodophyta: Gelidiales) from the southern Adriatic Sea

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Abstract

Growth, external morphology and reproductive phenology of a southern Adriatic population of *Pterocladiella capillacea* from a marine cave were investigated. Production of new uprights from creeping axes was limited to late autumn–winter; upright growth in length and branching order increase reached their maxima in late summer. Tetrasporic fronds were dominant from June to September, with a peak in July, while cystocarpic uprights were rather rare and recorded in August only. Two stable, distinct morphotypes occurred in this population at two sampling sites exposed to different daily photon irradiances. Uprights from the more illuminated site were regularly pinnate, with numerous closely packed lateral branches, representing the best-known phenotype of the species; in contrast, uprights from the more shaded inner site had very long and narrow axes, greater intervals between first-order branches and lower branching order. Statistical analysis demonstrated that upright growth in length and branching was significantly different at the two sites; upright biomass in the more illuminated site was generally higher because of the higher orders of branching.

Keywords: Adriatic Sea; phenology; *Pterocladiella capillacea*.

Introduction

External morphology is the most frequently described trait of the Gelidiales (e.g., Akatsuka 1982, Santelices 1990, 1998, Hommersand and Fredericq 1996, Santelices and Hommersand 1997, Shimada and Masuda 2002, Xia et al. 2004, Millar and Freshwater 2005) and it is often used to separate genera and species. However, considerable morphological variability shown by most Gelidiales renders this taxonomic criterion impractical in the absence of extensive field studies. Such variability is generally correlated with ecological, seasonal and geographical conditions. Both Dixon (1966) and Stewart (1968) suggested that external factors could not only affect the physiological activity of axial and cortical cells, but also modify both position and shape of previously formed branches, as well as the potential life span of the upright fronds. Moreover, it is common knowledge that clonal gelidialean seaweeds are difficult to identify, especially when vegetative, because different species often occur in the same habitat with stolons that are sometimes entangled and anastomosed, and their uprights can be very similar in shape, size, color and branching. This can seriously flaw floristic and ecological work, even though morphology of the attachment system and the characteristics of rhizoid ontogeny have proven useful diagnostic and conservative taxonomic characters at the genus level (Perrone et al. 2006).

Among the Gelidiales, *Pterocladiella capillacea* (Gmelin) Santelices *et* Hommersand (transferred from *Pterocladia* J. Agardh, Santelices and Hommersand 1997) has long suffered a chaotic taxonomy due to its great morphological variability.

Morphological variants of *Pterocladiella capillacea* described by Dixon (1966) and Stewart (1968) (as *Pterocladia*) are commonly found on Italian coasts, viz., (1) scarcely and sparsely branched thalli, (2) pinnate and bipinnate forms, and (3) older plants with repeating regenerations (cf. Felicini and Perrone 1994).

Pterocladiella capillacea from southeastern Italy has been subjected to numerous studies (Felicini and Arrigoni 1967, Calabrese and Felicini 1970, Felicini 1970, 1992, 1993, Felicini and Perrone 1972, 1986), some of which demonstrated that in lab-cultures thallus morphogenesis is strongly affected by light intensity, with irradiances lower than 10 μmol photons m^{-2} s^{-1} giving rise to long, narrow, scarcely branched thalli (Felicini et al. 2002).

Qualitative observations carried out throughout several years in a cave locally named Grotta della Regina (Adriatic Sea, southeastern Italy), where *Pterocladiella capillacea* is a component of the marine flora, highlighted the constant occurrence of two morphotypes of this species within the same population. The two forms characterize two distinct zones in the belt: a morphotype representing the species, as it is more often described, colonizes most parts of the rocky wall toward the cave opening; a second morphotype, corresponding to thalli experimentally cultured under low irradiance, lives in the inner part of the cave. In the intermediate zone, transition forms are present.

Our objective was to undertake a quantitative study on growth and reproductive phenology of this population, to investigate what environmental factors might affect thallus morphology and to make phenological comparisons

of *Pterocladiella capillacea* from a temperate area with relevant studies from other latitudes.

Materials and methods

Study site

The Grotta della Regina is a small marine cave located at Torre a Mare, to the south of the city of Bari (south-eastern Italy). Its width ranges from approximately 8 m (at the entrance) to approximately 13 m (at approximately 10 m from the entrance) and maximum height is approximately 5 m above sea level. The cave's central basin is almost triangle shaped, with the apex towards the entrance, and it is delimited by a wave-cut surface (+20 cm above sea level) that can be walked upon (Figure 1). From the step edge of this surface a SE oriented vertical rocky wall runs to the basin bottom (-1.60 m) where *Pterocladiella capillacea* is established and forms a dense belt, 50–70 cm high, with pure stands extending over the cave opening.

After a year of observations and surveys of environmental parameters in the *Pterocladiella capillacea* population two sampling sites were selected, corresponding to the zones in which the two morphotypes appeared well distinct (3 m apart on the same rocky wall) and were exposed to permanently different daily photon irradiances. The inner site in the cave (site 1) is never exposed to direct sunlight; the outer site (site 2) received direct sunlight for approximately 4–6 h.

Values of light and temperature were recorded at a depth of approximately 25 cm thrice a month, throughout the year, with a portable photometer-thermometer (Hansatech, King's Lynn, UK). Measurements were made on a sunny day between 10:00 h and 12:00 h. At site 1, photon irradiance varied between a minimum of 3 μmol m^{-2} s^{-1} in January and a maximum of 10 μmol m^{-2} s^{-1} in August; at site 2, where photon irradiance was always measured in shaded areas, it varied between a minimum of 11 μmol m^{-2} s^{-1} in January and a maximum of 26 μmol m^{-2} s^{-1} in August (Figure 2). Throughout the year, seawater temperature was quite similar at the two sites; the lowest value was 10°C in December, the highest, in August, was 28°C (Figure 2).

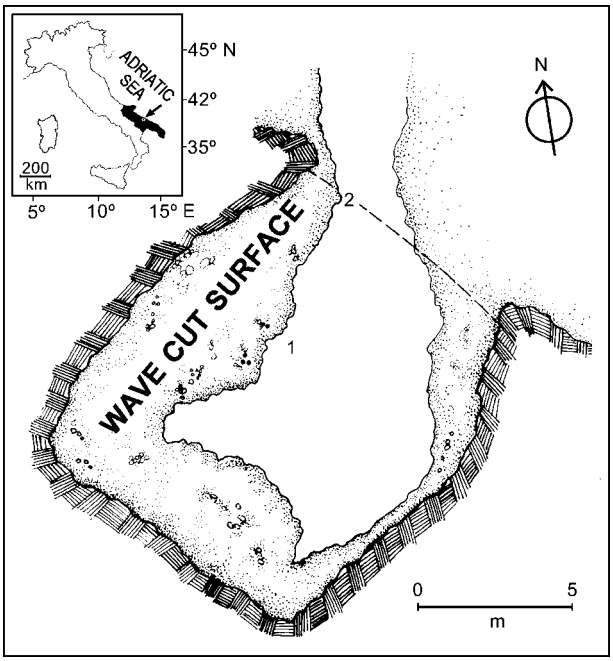


Figure 1 Plan of the Grotta della Regina (Italy, Adriatic Sea; 41°05′ N; 16°59′ E) showing the two collection sites (site 1 and site 2).
Dashed line indicates the outer limit of the cave roof. The inset panel shows a map of Italy with location of the study site (arrow).

Tide tables for the last decade were consulted. On this coast, the highest tidal amplitude is approximately 30 cm. Relative intensities of water movement were measured at each sample site as erosion rates of plaster balls (Doty 1971) and were almost the same at the two sites.

Grazing pressure was not assessed; rare unidentified annelids (Polychaeta) live on *Pterocladiella* and are uniformly distributed in the belt. In our aquaria, the youngest parts of thallus could be cut into small pieces up to 1 mm long.

Field sampling and laboratory procedure

Sampling methodology was established on the basis of population type and species size (cf. Lobban et al. 1985). The smallest area for the estimation of biomass and density was a 25-cm^2 quadrat. Every month, 10 quadrats were randomly selected from each study site, sampled and marked out with stakes to avoid sampling them again in later months. In each quadrat, all uprights of *Pterocladiella capillacea* (erect fronds cut off, using a scalpel, at the stipe bases where they arise from creeping axes) were collected, placed in Teflon-lined vessels and taken to the laboratory. All uprights were counted and total wet biomass (to the nearest mg) was then determined for each quadrat. Freshly collected samples were used for biometrics and morphological observations and then some of them were preserved in 4% formalin/seawater and some kept as herbarium specimens.

For 1 year (2005–2006), the following parameters were recorded every month for 50 randomly selected uprights from the two sites: length of the main axis, branching order, interval between first-order branches and width of the main axis measured 1 cm from the apex. Reproductive stage (vegetative, tetrasporic and cystocarpic) was also assessed by the presence/absence of reproductive organs observed under a stereomicroscope. Length of tetrasporic uprights and the interval between branches bearing cystocarps of female gametophytes were measured. The positions of tetrasporangia and cystocarps were also recorded.

Statistical analysis

All data collected were tested for normality and homogeneity prior to statistical treatment. The effects of sampling period as well as of sampling site on upright length, biomass and density were evaluated by two-way analysis of variance (ANOVA), followed by the Student-Newman-Keul's (SNK) multiple comparisons. Biomass was plotted against upright density on a bilogarithmic scale for all of

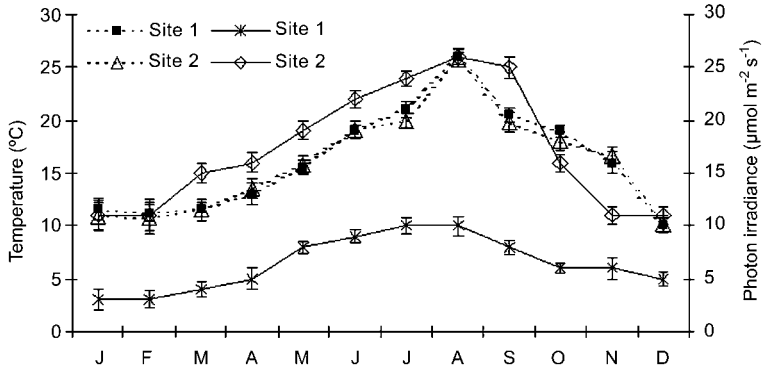


Figure 2 Monthly means of temperatures (dashed lines) and photon irradiances (at site 2, periods of minimal illumination are excluded) (solid lines) at both study sites (±SD, n=3).

the quadrats. For both sites, the strength of the linear association between $\log_{10}$ (biomass) and $\log_{10}$ (upright density) was assessed using the Pearson correlation coefficient (r). A t-test for unpaired samples was performed to compare first-order branch mean interval, main axis mean width and mean length between sterile and fertile uprights. The association between variables, such as sampling period, sampling site, branching order and reproductive stage, were evaluated using contingency tables and the χ^2-test. When necessary, stratification by time was made and the Cochran-Mantel-Haenszel test (CMH χ^2) was used. All data were analyzed using the statistical software SAS (SAS Institute Inc. 1999–2000, SAS Program for Windows Release 8.01. Cary, NC, USA).

Results

Growth and external morphology

Site 2 uprights were regularly pinnate, with numerous, short and closely packed lateral branches, representing the best-known phenotype of the species. Occasionally, approximately 50% of the uprights collected at this site had pale, bleached or damaged apices, especially after low spring tides, probably because of temporary exposure to full sunlight. Due to this loss of apical parts, the uprights were frequently characterized by many regenerated axes. Traces of regeneration also occurred at the stipe level where several marks close to one another in serial succession were often found.

Site 1 uprights, in contrast, had a more irregular morphology, viz., longer and narrower main axes, greater interval between first-order branches and lower branching order. Distal parts of both the main axis and lateral branches very often grew into terete axes curving downward and reattaching to the substratum, giving rise to secondary prostrate axes (Figures 3–6).

A two-way ANOVA testing upright length variation by month and site showed highly significant effects (Table 1); in particular, the interaction between sites and months was significant and demonstrated that the effect of site on plant length differed by month (Figure 7). During winter, there was no site effect on length; in all other seasons, site 1 plants were larger.

In the site 1 size class frequency distribution (Figure 8), there was a shift towards the highest length classes (9–12 cm) in the period from May to October. At site 2, intermediate length classes (5–8 cm) were the most frequent in all months of the year. At both sites, the smallest length classes (1–4 cm) were present from November.

Monthly data on branching order for uprights at the two sites were divided into four seasonal groups: November–January, February–April, May–July and August–October. In Figure 9, the variation of branching order of uprights from both sites is depicted for each season. At site 1, uprights with second- and third-order branching progressively increased during the year. At site 2, uprights with third order branching were the most abundant. The difference in the branching order between uprights from sites 1 and 2 was significant over time (CMH χ^2=179.21, $p<0.0001$).

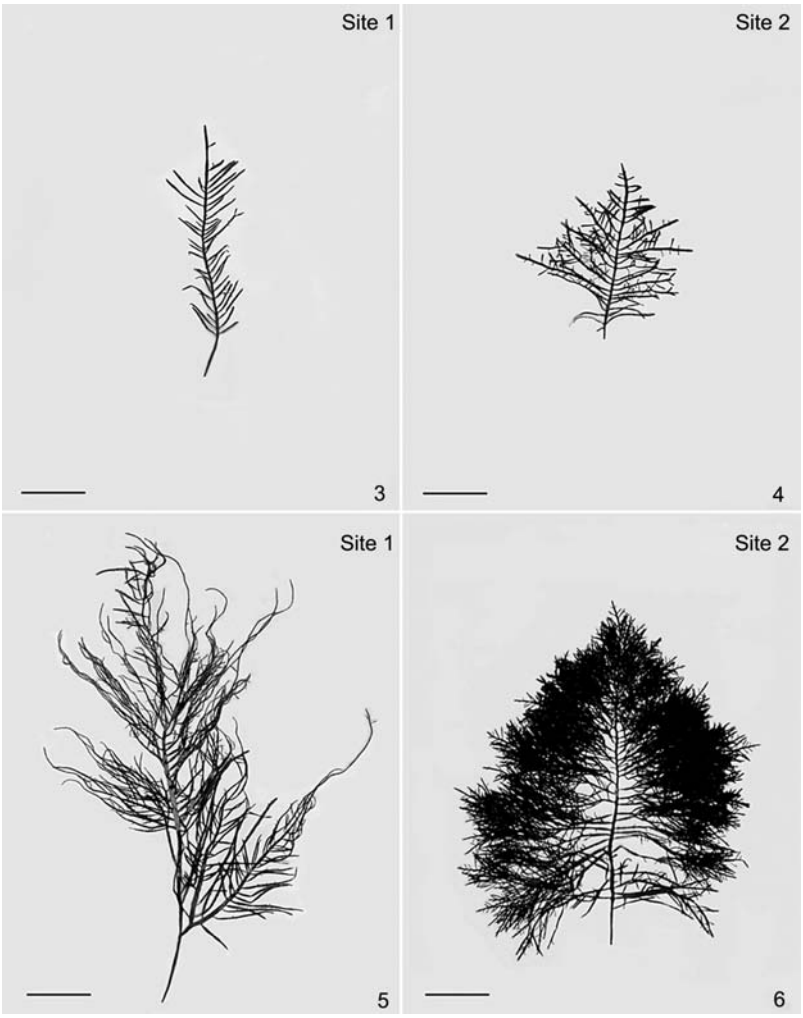
The interval between first-order branches was larger for uprights from site 1 than for uprights from site 2 (mean value: 18.6 vs. 3.48 mm, t=19.2, $p<0.001$). Minimum and maximum values ranged between 16 and 21 mm for uprights from site 1 and between 2 and 5 mm for those from site 2.

The main axis of uprights from site 2 was wider than from site 1 (mean width: 1.8 vs. 0.8 mm, t=9.95, $p<0.001$). At site 2, width ranged between a minimum of 1.5 mm in late summer–early autumn and a maximum of 2 mm in the remaining months of the year. At site 1, width varied between 0.5 and 1 mm in the same periods.

Biomass and density

A two-way ANOVA carried out to test biomass variation with respect to months and sites showed a highly significant interaction between sites and months, and significant main effects (Table 1). The effect of site on biomass varied by month (SNK test, Figure 10). Biomass of uprights from site 2 was higher than that of uprights from site 1 in each month (Figure 10), but the difference was smallest in winter months.

There were significant effects of site and month as main effects on density of uprights, but no interaction between the two factors (Table 1). However, differences in density were small, and SNK tests did not detect site effects within any month of the year (Figure 11).



Figures 3–6 *Pterocladiella capillacea*: distinct morphology of uprights at the two sites.
(3–4) Upright spring habit at sites 1 and 2, respectively. Scale bar=2 cm. (5–6) Upright late-summer habit at sites 1 and 2, respectively. Scale bar=2 cm.

Table 1 *Pterocladiella capillacea*: effects of site and time on upright length, biomass and density.

Dependent variable	Factor	df	MS	F	p
Length	Site	1	1977.36	756.93	<0.0001
	Month	11	271.67	104.00	<0.0001
	Site×month	11	53.96	20.66	<0.0001
	Error	1176	2.61		
Biomass	Site	1	382236.43	46180.33	<0.0001
	Month	11	16716.05	2019.57	<0.0001
	Site×month	11	3569.39	431.24	<0.0001
	Error	216	8.28		
Density	Site	1	6.16	37.98	<0.0001
	Month	11	95.06	586.13	<0.0001
	Site×month	11	0.42	2.57	0.0045
	Error	216	0.16		

Two-way ANOVA: df, degrees of freedom; MS, mean square; F, ANOVA F-statistic; p, type I probability error.

For both sites, logarithmically transformed values of biomass were positively correlated to equivalent values of upright density (site 1: $r=0.80$, $p<0.001$; site 2: $r=0.75$, $p<0.001$) (Figure 12). The p-values are relatively low owing to the large number of replicates. The coefficients of determination are around 60% for both sites, indicating that a relatively large proportion (~40%) of the variation in biomass is unexplained by variation in density.

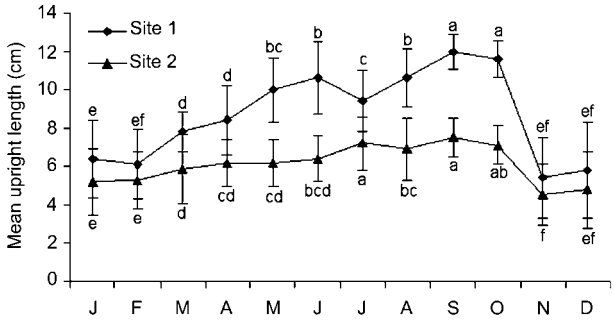


Figure 7 *Pterocladiella capillacea*: mean upright length variation (±SD, n=50) at sites 1 and 2 throughout the year. Significant differences between site×month combinations are indicated by different letters (SNK, $p<0.05$).

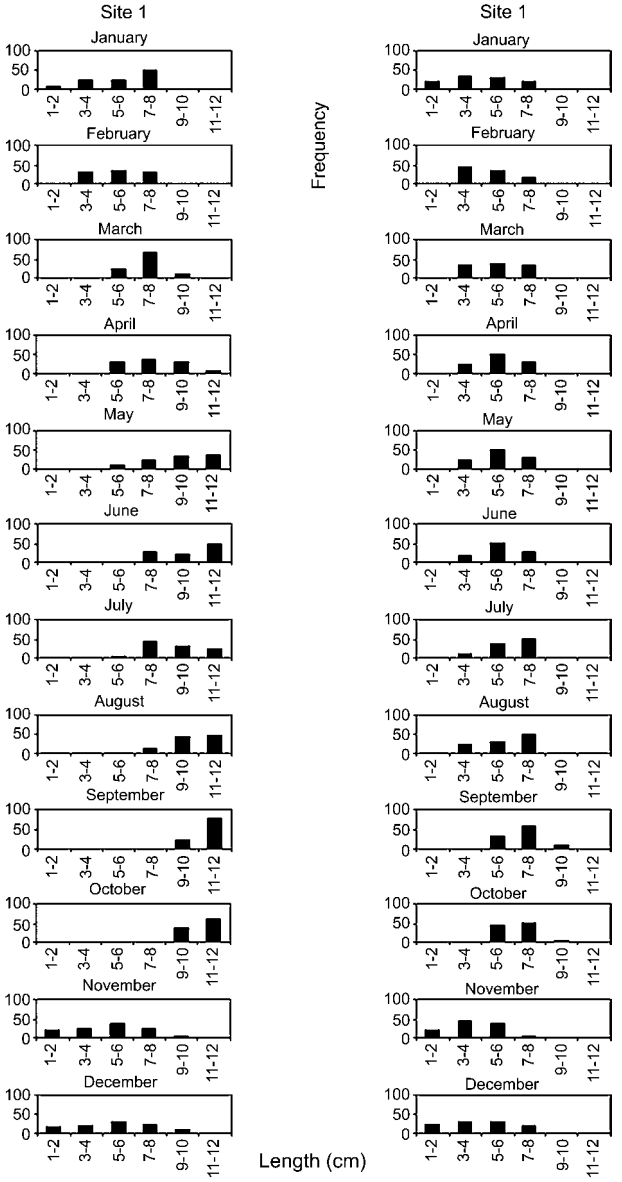


Figure 8 *Pterocladiella capillacea*: size frequency distribution of sites 1 and 2 uprights throughout the year.

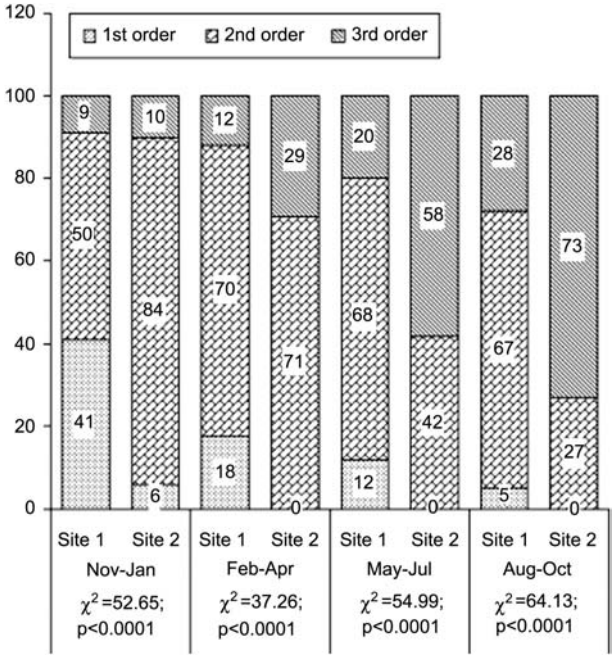


Figure 9 *Pterocladiella capillacea*: percentage frequency occurrence of different branch orders in different seasons for sites 1 and 2 uprights (n=150). χ^2-test values for each seasonal group are reported.

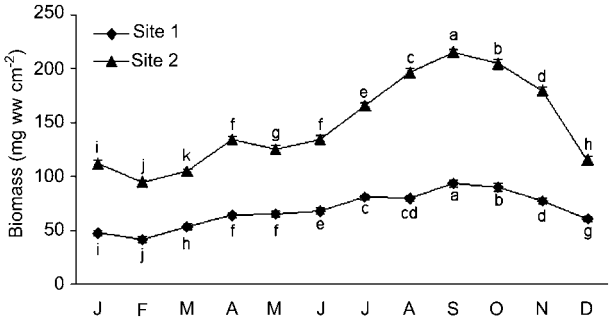


Figure 10 *Pterocladiella capillacea:* mean upright biomass variation (±SD, n=10) at sites 1 and 2 throughout the year. Significant differences between months ($p<0.05$) are indicated by different letters (SNK tests).

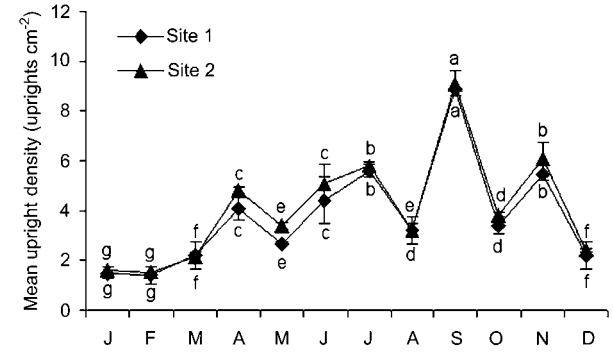


Figure 11 *Pterocladiella capillacea*: mean upright density variation (±SD, n=10) at sites 1 and 2 throughout the year. Significant differences between months ($p<0.05$) are indicated by different letters (SNK tests).

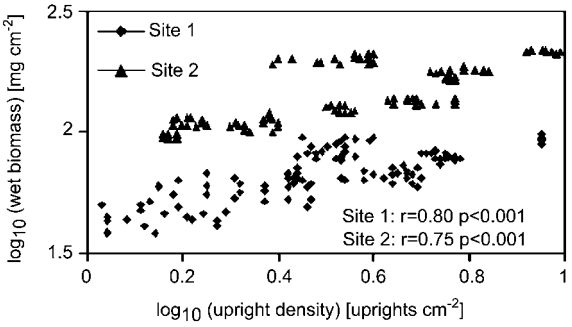


Figure 12 *Pterocladiella capillacea*: relationship between $\log_{10}$ (wet biomass) and $\log_{10}$ (upright density) at sites 1 and 2 (n=120).

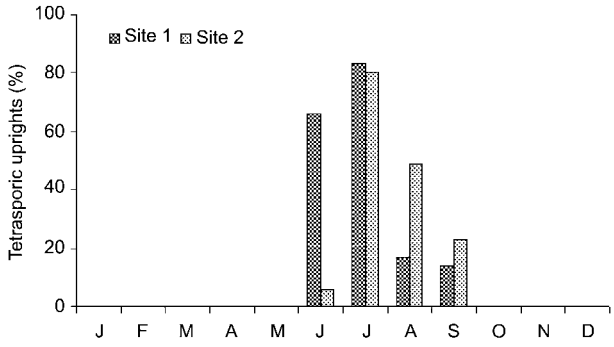


Figure 13 *Pterocladiella capillacea*: percentage occurrence of tetrasporic uprights at sites 1 and 2.

Reproductive phenology

Tetrasporic upright distribution for the two sites was significantly different among months (χ^2=35.68, $p<0.001$). In both sites, tetrasporic uprights were present from June to September, with the highest percentage (83% at site 1 and 80% at site 2) in July (Figure 13). At site 1, tetrasporic uprights were longer (mean length: 14.2 cm vs. 10.7 cm, t= 6.1, $p<0.001$) than sterile uprights. There was no difference in length between tetrasporic and sterile uprights (mean length: 7.1 cm vs. 7.4 cm) at site 2. Tetrasporangia were observed on all order branches and on stichidium-like ramuli directly inserted on the main axis.

Cystocarpic uprights were rather rare (4% at site 1 and 2% at site 2) and were recorded in August only. Therefore, they were not processed and only qualitative observations were made. Cystocarps were found exclusively on second-order branches. Branches bearing cystocarps were regularly spaced 2 mm apart. Development and maturation of cystocarps were acropetal. On the youngest branches, developing cystocarps were usually distal; on mature branches, they occupied an intermediate-proximal position. Branches with two cystocarps in series (aligned along the median line) or cystocarps with two ostioles were rarely observed.

Spermatangial uprights were never observed or not recognized under a stereomicroscope.

Discussion

In the Grotta della Regina, *Pterocladiella capillacea* populations follow a pattern of year-round growth in length. At both the selected sampling sites, very small uprights were present from November; therefore, production of new uprights from creeping axes was not continuous, but limited to late autumn–winter. In spring, uprights continued to grow, as shown by length and branching order increases, reaching their maximum size in late summer. Even though this growth trend was almost the same at the two sites, throughout the year, two stably distinct morphotypes occurred in this population of *P. capillacea*. Site 2 uprights were the well-known bushy, regularly pinnate, pyramidal fronds of the species; moreover, they also regenerated more frequently due to the loss of apical parts. Apex damage likely resulted from exposure to air and direct sunlight, especially during low spring tides. Obviously, the consequent reduction in apical dominance induces the formation of one or more often numerous apex-substitutive branches, strongly modifying branching and size of fronds (Buggeln 1981). The ability to regenerate in response to any injury is a widespread phenomenon in the Gelidiales, and in other red seaweeds; it has been widely studied in *P. capillacea* (Felicini and Arrigoni 1967, Felicini 1970, 1993, Felicini and Perrone 1986). For *P. capillacea* the occurrence of apical dominance had been suggested based on qualitative (Felicini and Perrone 1994) and quantitative (Scrosati 2002) observations. In *P. capillacea*, past regenerations can be easily detected by persistent marks on the thallus (Felicini and Perrone 1994).

Site 1 uprights had a different morphology, viz., longer and narrower main axes, scarce and longer "capillaceous" branches, some of which becoming new prostrate axes in late summer. Secondary formation of stoloniferous axes from upright distal parts has been termed "secondary heterotrichy" by Dixon (1973). According to Dixon (1958), plagiotropic differentiation of thallus in *Pterocladiella capillacea* may occur under unfavorable ecological conditions. In laboratory cultures, such a morphogenetic pattern has been triggered by irradiances lower than 10 μmol photons m^{-2} s^{-1} (Felicini 1970, Felicini and Perrone 1994) and regulated by temperatures higher than 18°C (Felicini et al. 2002), conditions occurring at site 1 in summer. Under constant low light intensity, upright morphogenesis seemed to be controlled by a strong apical dominance, giving them the typical appearance of etiolated plants.

Previous work has shown that in the Gelidiales (as in many other red algae) light intensity interacts synergistically with temperature, water movement and nutrients (Santelices 1991).

Different morphotypes have been also described for *Pterocladia caerulescens* from Hawaii and interpreted as a consequence of season and depth (Santelices 1978a). Slightly distinct morphotypes of *P. capillacea* from Brazil were found along a gradient of water exposure (Oliveira et al. 1996).

Between our collection sites, seawater temperatures and water movements were quite similar; in contrast, daily irradiances were significantly different. Results from

the present study suggest that in the cave light, intensity may be the main physical factor influencing the distinct morphotypes of *Pterocladiella capillacea*.

In the population of *Pterocladiella capillacea* from Grotta della Regina, mean upright densities were comparable between sampling sites, and biomass values were higher at site 2 due to the greater abundance of lateral branching. Biomass at the two sites was higher than that found in Hawaiian and Californian populations of *Pterocladia capillacea*. In Hawaiian populations of *P. capillacea* and *P. caerulescens*, Santelices (1978b) found seasonal cycles of biomass with maxima in December and minima in May. For *P. capillacea* from Baja California, Mexico, the highest biomass values were generally observed in spring and summer and the lowest in autumn and winter (Scrosati and Servière-Zaragoza 2000).

In the Grotta della Regina, the diploid phase of *Pterocladiella capillacea* was the most abundant, though this cannot be proven, as it is impossible in the field to distinguish each individual thallus (genet) due to various factors, such as high frond densities and stolon intermingling. In addition, counts of reproductive fronds may not accurately represent the abundance of a given life-history phase (Servière-Zaragoza and Scrosati 2002), because the haploid and diploid phases cannot be distinguished until mature reproductive organs are evident; at present, there is no quick method for the determination of the life-history phase of vegetative fronds for the Gelidiales, unlike the Gigartinales (Garbary and DeWreede 1988). On the other hand, tetrasporophyte dominance in our population of *P. capillacea* agrees with the observations of many researchers at different latitudes (Oliveira and Sazima 1973, Fralick and Andrade 1981, Neto 2000, Servière-Zaragoza and Scrosati 2002). At our study sites, maximum abundance of tetrasporic uprights occurred at the time of maximum vegetative growth. This would suggest that growth and tetraspore production may be regulated by the same environmental parameters, as was shown for *P. caerulescens* in Hawaii (Santelices 1978a).

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References

Akatsuka, I. 1982. Preliminary observations and literature analysis of morphological variability in some Japanese species of *Gelidium* (Gelidiales, Rhodophyta) and an evaluation of criteria used in their discrimination. *Nova Hedwigia 36*: 759–774.

Buggeln, R.G. 1981. Morphogenesis and growth regulators. *In*: (C.S. Lobban and M.J. Wynne, eds.) *The biology of seaweeds*. Blackwell Scientific Publications, Oxford. pp. 627–660.

Calabrese, G. and G.P. Felicini. 1970. Ricerche sui pigmenti delle alghe rosse. I: analisi qualitativa e quantitativa dei pigmenti di *Pterocladia capillacea* (Gmel.) Born. et Thur. coltivata in presenza di alcune fonti minerali di azoto. *Giornale Bot. Ital. 104*: 81–89.

Dixon, P.S. 1958. The structure and development of the thallus in the British species of *Gelidium* and *Pterocladia*. *Ann. Bot. 22*: 353–368.

Dixon, P.S. 1966. On the form of the thallus in the Florideophyceae. *In*: (E.G. Cutter, A. Allsop, F. Cusick and I.M. Sussex, eds.) *Trends in plant morphogenesis*. Longmans, London. pp. 45–63.

Dixon, P.S. 1973. *Biology of the Rhodophyta*. Oliver and Boyd, Edinburgh. pp. 285.

Doty, M.S. 1971. Measurement of water movement in reference to benthic algal growth. *Bot. Mar. 14*: 32–35.

Felicini, G.P. 1970. Ricerche sulla rigenerazione in coltura di *Pterocladia capillacea*. 2. Influenza della intensità luminosa sulla morfologia del tallo. *Giornale Bot. Ital. 104*: 35–47.

Felicini, G.P. 1992. Colonization of artificial substrata with the agarophyte *Pterocladia capillacea* (Gelidiaceae, Rhodophyta): some basic criteria. *Giornale Bot. Ital. 126*: 738–740.

Felicini, G.P. 1993. La rigenerazione nelle macroalghe: un approccio allo studio della morfogenesi e dei fenomeni di correlazione. *Giornale Bot. Ital. 127*: 823–834.

Felicini, G.P. and O. Arrigoni. 1967. Ricerche sulla rigenerazione in coltura di *Pterocladia capillacea*. *Giornale Bot. Ital. 101*: 199–217.

Felicini, G.P. and C. Perrone. 1972. Sulla formazione di galle nella rigenerazione di *Pterocladia capillacea* (Gmel.) Born. et Thur. in coltura. *Giornale Bot. Ital. 106*: 351–358.

Felicini, G.P. and C. Perrone. 1986. Une étude en lumière polarisée sur le parcours des hyphes dans le thalle de *Pterocladia capillacea*. *Phycologia 25*: 37–46.

Felicini, G.P. and C. Perrone. 1994. *Pterocladia*. *In*: (I. Akatsuka, ed.) *Biology of economic algae*. SPB Acad. Publ. bv, The Hague, Netherlands. pp. 283–344.

Felicini, G.P., A. Bottalico and M. Fanelli. 2002. Morphogenesis in *Pterocladiella capillacea* (Rhodophyta, Gelidiales): bud differentiation in relation to irradiance-temperature combinations. *Plant Biosyst*. *136*: 261–268.

Fralick, R.A. and F. Andrade. 1981. The growth, reproduction, harvesting and management of *Pterocladia pinnata* in the Azores, Portugal. *Proc. Int. Seaweed Symp. 10*: 289–295.

Garbary, D.J. and R.E. DeWreede. 1988. Life history phases in natural populations of Gigartinaceae (Rhodophyta): quantification using resorcinol. *In*: (C.S. Lobban, D.J. Chapman and B.P. Kremer, eds.) *Experimental phycology. A laboratory manual.* Cambridge University Press, Cambridge. pp. 174–178.

Hommersand, M.H. and S. Fredericq. 1996. Vegetative and reproductive development of *Pterocladia capillacea* (Gelidiales, Rhodophyta) from La Jolla, California. *Nova Hedwigia 112*: 147–160.

Lobban, C.S., P.J. Harrison and M.J. Duncan. 1985. *The physiological ecology of seaweeds*. Cambridge University Press, Cambridge. pp. 242.

Millar, A.J.K. and D.W. Freshwater. 2005. Morphology and molecular phylogeny of the marine algal order Gelidiales (Rhodophyta) from New South Wales, including Lord Howe and Norfolk Islands. *Aust. Syst. Bot. 18*: 215–263.

Neto, A.I. 2000. Observations on the biology and ecology of selected macroalgae from the littoral of São Miguel (Azores). *Bot. Mar. 43*: 483–498.

Oliveira, E.C. and I.P. Sazima. 1973. Estudos sobre a biologia de algas agarófitas. 1. Recolonizaçâo, brotamento e fenologia em populaçôes naturais de *Pterocladia capillacea*. *Bol. Zool. Biol. Mar., N.S. 30*: 677–690.

Oliveira, E.C., R.M. Saito, J.F.S. Neto and G.M.C. Garófalo. 1996. Temporal and spatial variation in agar from a population of *Pterocladia capillacea* (Gelidiales, Rhodophyta) from Brazil. *Hydrobiologia 326/327*: 501–504.

Perrone, C., G.P. Felicini and A. Bottalico. 2006. The prostrate system of the Gelidiales: diagnostic and taxonomic importance. *Bot. Mar. 49*: 23–33.

Santelices, B. 1978a. The morphological variation of *Pterocladia caerulescens* (Gelidiales, Rhodophyta) in Hawaii. *Phycologia 17*: 53–59.

Santelices, B. 1978b. Multiple interaction of factors in the distribution of some Hawaiian Gelidiales (Rhodophyta). *Pac. Sci. 32*: 119–147.

Santelices, B. 1990. New and old problems in the taxonomy of the Gelidiales (Rhodophyta). *Hydrobiologia 204/205*: 125–135.

Santelices, B. 1991. Production ecology of *Gelidium*. *Hydrobiologia 221*: 31–44.

Santelices, B. 1998. Taxonomic review of the species of *Pterocladia* (Gelidiales, Rhodophyta). *J. Appl. Phycol. 10*: 237–252.

Santelices, B. and M. Hommersand. 1997. *Pterocladiella*, a new genus in the Gelidiaceae (Gelidiales, Rhodophyta). *Phycologia 36*: 114–119.

Scrosati, R. 2002. Morphological plasticity and apparent loss of apical dominance following the natural loss of the main apex in *Pterocladiella capillacea* (Rhodophyta, Gelidiales) fronds. *Phycologia 41*: 96–98.

Scrosati, R. and E. Servière-Zaragoza. 2000. Ramet dynamics for the clonal seaweed *Pterocladiella capillacea* (Rhodophyta): a comparison with *Chondrus crispus* and with *Mazzaella cornucopiae* (Gigartinales). *J. Phycol. 36*: 1061–1068.

Servière-Zaragoza, E. and R. Scrosati. 2002. Reproductive phenology of *Pterocladiella capillacea* (Rhodophyta: Gelidiales) from Southern Baja California, Mexico. *Pac. Sci. 56*: 285–290.

Shimada, S. and M. Masuda. 2002. Japanese species of *Pterocladiella* Santelices et Hommersand (Rhodophyta, Gelidiales). *In*: (I.A. Abbott and K.J. McDermid, eds.) *Taxonomy of economic seaweeds with reference to some Pacific species.* Vol. 8. California Sea Grant College, La Jolla, CA. pp. 167–181.

Stewart, J.G. 1968. Morphological variation in *Pterocladia pyramidale*. *J. Phycol. 4*: 76–84.

Xia, B.-M., C.K. Tseng and Y.-O. Wang. 2004. Studies on Chinese species of *Gelidiella* and *Pterocladiella* (Gelidiales, Rhodophyta). *Hydrobiologia 512*: 201–207.

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