

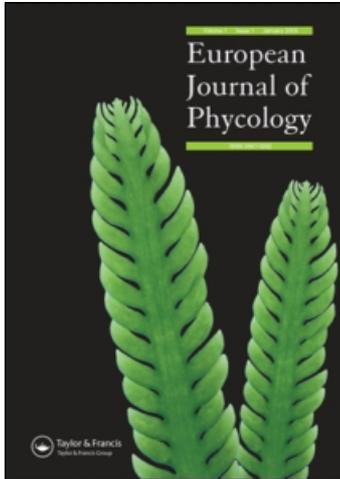
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# Phenology and small-scale distribution of some rhodomelacean red algae on a western Mediterranean rocky shore

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Distribution and phenology of some filamentous species of Rhodomelaceae in the low littoral and shallow sublittoral zones of an exposed, western Mediterranean rocky shore were studied for 1 year. The spatial distribution of many species shows a pronounced small-scale (metres or tens of metres) variability. *Boergeseniella fruticulosa* was most abundant in spring and fertile (tetrasporangia only) in spring and summer. *Polysiphonia flocculosa* was most abundant in spring and summer and reproductive throughout the year. *Polysiphonia opaca* was most abundant in summer and fertile in spring–summer. Maximal vegetative development and reproduction of *Lophosiphonia cristata* were observed in summer; conversely, *Polysiphonia ceramiaeformis* and *Polysiphonia subulata* were best developed and mostly reproductive in winter and spring. *Womersleyella setacea* was the least abundant of the studied species and apparently reproduced only by vegetative growth and fragmentation. The reproductive phenology of the species investigated is generally in agreement with reports for other Mediterranean regions. The life history traits of most species are typical of seaweeds in which environmental factors directly govern the onset of the main activities of the organism by meeting the primary physiological needs ('season responders').

**Key words:** algal turfs, *Boergeseniella*, distribution, *Lophosiphonia*, Mediterranean Sea, phenology, *Polysiphonia*, *Womersleyella*

## Introduction

Species of *Polysiphonia* and similar genera consist of finely branched filaments formed by a central axial filament covered by whorls of periaxial cells (i.e. 'polysiphonous' structure). *Polysiphonia* is one of the largest genera in the Rhodophyta, with few to many species occurring on virtually all coasts of the world (Womersley, 1979), from cold (Kjellman, 1883) to tropical waters (Hollenberg 1968*a, b*). *Polysiphonia* species are among the most common filamentous algae in many intertidal and shallow subtidal ecosystems and some species extend their distribution to deeper waters (Womersley, 1979) and low-salinity habitats (Fralick & Mathieson, 1975).

As a result of the floristic and ecological importance of this algal group, studies on *Polysiphonia* relate mainly to species identification based on morphological features (see Yoon, 1986, and references therein). Although there have been several studies of cytology (Tripodi, 1971, 1974; Kapraun, 1978; Goff & Coleman, 1986, 1990; Oates & Cole, 1989) and reproductive biology (Hommsand & Fredericq, 1990; Kaczmarek & Dowe, 1997), less work has been carried out on other aspects of the biology of this group. Most of the published information for the Mediterranean area dates back to the nineteenth and early twentieth centuries (Preda, 1909, and references therein); the studies of Lauret (1967, 1970) for the Languedoc

littoral are the only relatively recent, available monographs. Other contributions are essentially floristic accounts, sometimes reporting distributional or phenological details, or isolated records (Cormaci *et al.*, 1998).

An important aspect of the biology of Mediterranean Rhodomelaceae for which few detailed data are available is the vegetative and reproductive phenology. In the study of marine ecosystems in which benthic algae are dominant, it is very important to know when the different species grow and reproduce (Kain, 1986). Recruitment of macroalgae may result from regeneration from stolons or holdfasts of previous residents left behind on the rock or from an influx of propagules from plants in adjacent areas (Kain & Norton, 1990). As the nature of the latter inoculum is dependent on seasonal changes in the fertility of local plants, the reproductive phenology of macroalgae is of critical importance for the recolonization of disturbed sites and may determine the kind of assemblage that occupies these areas. For the Mediterranean, phenological observations are available for some regions and some algal groups (Cormaci *et al.*, 1984, and references therein; Soto & Conde, 1989; Boisset, 1992). With a few exceptions, however, these observations are occasional and are not the result of studies specifically designed to elucidate the patterns of growth and reproduction of algal species. In most cases, neither the number of plants on which the observations are based nor the criteria followed in their collection are mentioned; this does not allow an assessment of the reproductive peaks, which can be

determined by the ratio between the number of fertile plants and the total number of plants collected in each season (Kain, 1982; Cormaci *et al.*, 1984). For these reasons, knowledge of the phenology of most Mediterranean macroalgae is still uncertain and not as detailed as for several northern European species (Kain, 1982, 1986; Maggs & Guiry, 1987; Cunningham *et al.*, 1993; Kain & Bates, 1993; Molenaar & Breeman, 1994; Molenaar *et al.*, 1996*a, b*; Molenaar & Breeman, 1997).

Preliminary floristic investigations determined the quantitative abundance and structural importance of species of *Polysiphonia* and similar genera, such as *Boergeseniella*, *Lophosiphonia* and *Womersleyella*, in the benthic algal assemblages of some coastal areas of north-western Italy. A detailed study was conducted from September 1997 to November 1998 to elucidate the spatial and temporal distribution of the most common species.

## Materials and methods

### Study site

The study was carried out between Castel Boccale and Punta Pacchiana (43° 30' N, 10° 20' E), 10 km south of Livorno (north-western Italy); the site is a stretch of rocky shore with a horizontal extent of about 1 km (Fig. 1). The coast consists of sandstone platforms that extend 300 m seaward, to a depth of about -40 m (Airoidi *et al.*, 1996). The shore is exposed to strong wave action and open to winds from the south-east to north-west; the tidal range is very limited (about 20 cm). Sea surface temperatures range from 12–13 °C in February/March to 25 °C in August (US Navy, 1981; Airoidi *et al.*, 1996). During the study period, sea surface temperatures were obtained from

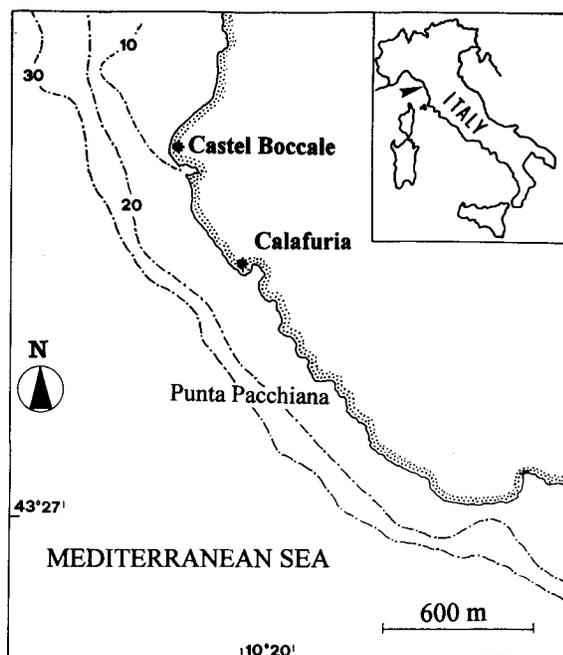


Fig. 1. Location of the study site.

Table 1. Sea surface temperatures in the north-western Mediterranean in the period October 1997–September 1998.

Date	Temperature (°C)
21 October 1997	21.3
25 November 1997	15.6
6 December 1997	14.8
23 January 1998	11.9
10 February 1998	12.2
26 March 1998	13.1
20 April 1998	15.6
12 May 1998	16.8
10 June 1998	23.8
24 July 1998	26
18 August 1998	26.7
12 September 1998	24.5

measurements made at -1 m depth at a site near Punta Bianca (La Spezia, north-western Italy), about 50 km north of the study site. These data were not available during the summer months, so temperature was measured at the study site (-0.5 m depth) by the thermal sensor of a SCUBA watch (Citizen Aqualand) (Table 1). Daylength is longest in June (up to 15.30 h) and shortest in December (about 8.50 h).

Filamentous Rhodomelaceae are most abundant in the lower littoral zone and in the sublittoral fringe. These zones correspond respectively to the mean level of water surface and the shallowest part of the sublittoral; they occupy a belt with a vertical extent of 25–30 cm, starting from immediately beneath the mid-littoral zone (which corresponds to the shore level where the red alga *Rissoella verruculosa* (Bertolini) J. Agardh can be found in winter and spring). At these levels dense turfs, mainly formed by *Boergeseniella*, *Lophosiphonia* and *Polysiphonia*, are the most common algal growth form. These species are usually mixed with other filamentous algae (*Ceramium* spp., *Cladophora* spp., *Dasya hutchinsiae* Harvey, *Herposiphonia secunda* (C. Agardh) Ambronn, *Sphacelaria* spp.) and coarsely branched algae (*Chondria* spp., *Laurencia* spp., *Osmundea ramosissima* (Oeder) Athanasiadis); they also occur as epiphytes on the articulated coralline *Corallina elongata* Ellis *et* Solander. In contrast to the other rhodomelacean species, *Womersleyella setacea* is most common in the sublittoral, occurring from the surface to -40 m depth and forming a dense, almost monospecific turf between -5 and -20 m depth (Airoidi *et al.*, 1995).

### Sampling

The survey was carried out from October 1997 to September 1998. Sampling was performed in the lower littoral and sublittoral fringe; samples were collected by snorkelling. All plant biomass was removed from quadrats (25 or 100 cm<sup>2</sup>) placed on bedrock, in areas where filamentous algae were detectable by eye. Before examination in the laboratory, the material was fixed and stored

**Table 2.** Sampling dates

Autumn	A1	21 October 1997
	A2	17 November 1997
	A3	6 December 1997
Winter	W1	23 January 1998
	W2	10 February 1998
	W3	3 March 1998
Spring	Sp1	20 April 1998
	Sp2	14 May 1998
	Sp3	18 June 1998
Summer	Su1	24 July 1998
	Su2	18 August 1998
	Su3	12 September 1998

in 5% formalin in seawater; voucher specimens are deposited in the Phycological Herbarium, National University of Ireland, Galway (GALW).

Different sampling designs were followed to assess: (1) spatial and temporal distribution of the rhodomelacean species in the algal turfs; (2) seasonal variations in the size of the erect axes; (3) reproductive phenology.

#### *Spatial and temporal distribution*

Three sampling dates were randomly selected for each season (for this study autumn includes October, November and December 1997; winter: January, February and March 1998; spring: April, May and June 1998; summer: July, August and September 1998). In order to achieve a good spread of dates within the seasons, two conventions were followed: (1) for each season the first and last 2 weeks were excluded from sampling; (2) for each season an interval of at least 15 days elapsed between one sampling date and the next (Table 2). For each sampling date, two non-adjacent areas (each corresponding to 20–25 m stretches of coast) were randomly selected within the study site. In each area 15 samples (25 cm<sup>2</sup> quadrats) were randomly collected, in spots occupied by algal turfs; care was taken to collect every sample at least 1 m apart from the others. For each sample, thalli of the species of *Boergeseniella*, *Lophosiphonia* and *Polysiphonia* were sorted in the laboratory and their abundance was expressed as percentage cover. A 5 × 5 cm quadrat was divided into 100 subquadrats and the sum of the subquadrats covered in vertical projection by thalli (or fragments of thalli) of a species was treated as the percentage cover for that species. The data were analysed by a multifactorial ANOVA, where season was a fixed factor, date a random factor nested within season, and area a random factor nested within season and date (Fig. 2). Cochran's test was used to check for homogeneity of variances (Underwood, 1981); logarithmic or arcsine transformations were applied when necessary. Student Newman-Keuls (SNK) tests were used for *a posteriori* multiple comparisons of means. The STATISTICA package was used for all analyses;  $\alpha = 0.05$  was regarded as significant, unless Cochran's value was still significant after

transformation of data; in this case, following Underwood (1997),  $\alpha = 0.01$  was regarded as significant.

#### *Size of the erect axes*

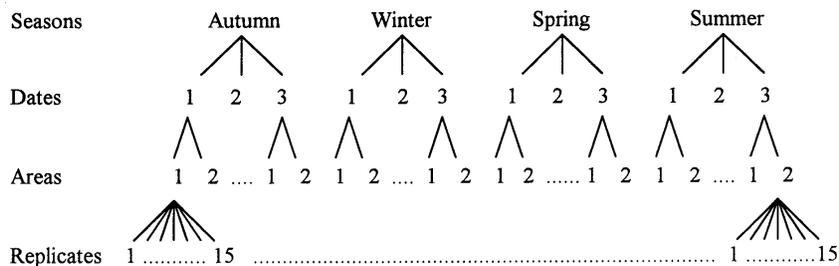
For some species (*Boergeseniella fruticulosa*, *Lophosiphonia cristata* and *Polysiphonia opaca*), the effect of season on the size of the erect axes was examined by a one-way ANOVA; for each season 60 (for *B. fruticulosa* and *P. opaca*) or 50 (for *L. cristata*) erect axes were haphazardly chosen for measurement in the samples used for the spatial and temporal distribution.

#### *Reproductive phenology*

For each species four phases of the life history were considered: non-reproductive thalli; tetrasporangial thalli (bearing mature tetrasporangia); spermatangial thalli (bearing mature spermatangial branches); cystocarpic thalli (females bearing cystocarps with carposporangia; in all species cystocarps were produced very quickly after fertilization, so procarpic, unfertilized female thalli were virtually never observed).

Because of the structure of the algal assemblage, small-scale observations on the distribution of the phases were usually very difficult. Filamentous turfs consist of a large number of species; their thalli form a very compact and dense structure and the individual isolation of every single plant would be, although not impossible, a very time-consuming task. This is true, in particular, for species with erect parts arising from creeping axes (such as *B. fruticulosa*, *L. cristata* and *P. opaca*). We therefore followed a different procedure for *Polysiphonia flocculosa* compared with all the other species. *P. flocculosa* was the only species for which sorting individual plants was a relatively easy and fast job. For this species the spatial and temporal distribution of the life history phases was analysed by ANOVA following the same design and using the same samples of the distributional analysis. In each sample all thalli of *P. flocculosa* were separated and the percentage of thalli in every phase was calculated. In the analysis the life history phase was added as a random factor nested within season, date and area; spermatangial plants and cystocarpic plants were combined together as fertile gametophytes. The statistical treatment was the same as above.

For the other species, the long time necessary to separate all the individuals in a sample did not allow a similar analysis. Thus, for each sampling date, a certain number of thalli of each species was examined. A single thallus of each rhodomelacean species was haphazardly chosen and separated out intact, both in the samples of the distributional analysis and in some additional random samples, which were collected in other areas at the study site (this was done essentially to get a higher number of thalli for the rare species, such as *L. cristata*, *P. ceramiaeformis* and *W. setacea*; even in this case samples were collected at least 1 m apart from each other as, on the basis of previous observations, it was assumed that such a



**Fig. 2.** Sampling design employed to investigate the effect of season, sampling date and area on the distribution of *Boergeseniella*, *Lophosiphonia*, *Polysiphonia* and *Womersleyella*.

**Table 3.** Number of individuals of *Boergeseniella*, *Lophosiphonia*, *Polysiphonia* and *Womersleyella* examined for each sampling date

	A1	A2	A3	W1	W2	W3	Sp1	Sp2	Sp3	Su1	Su2	Su3
<i>Boergeseniella fruticulosa</i>	49	58	72	60	61	57	69	66	46	45	41	32
<i>Lophosiphonia cristata</i>	24	26	22	26	22	12	19	11	9	34	45	38
<i>Polysiphonia ceramiaeformis</i>	18	8	17	17	22	61	22	17	20	7	0	0
<i>Polysiphonia flocculosa</i>	156	244	289	278	287	420	443	373	343	271	306	233
<i>Polysiphonia opaca</i>	60	54	51	66	50	51	62	65	62	37	56	53
<i>Polysiphonia subulata</i>	38	52	94	291	400	450	342	321	169	35	48	54
<i>Womersleyella setacea</i>	16	11	19	18	25	15	18	24	32	22	10	12

See Table 2 for definitions of sampling dates.

distance is sufficient to sample different individuals of the same species). The reproductive condition of the plants was noted and the number of plants examined for each species is reported in Table 3.

**Results**

Seven species were considered: *Boergeseniella fruticulosa*, *Lophosiphonia cristata*, *Polysiphonia flocculosa*, *Polysiphonia opaca*, *Polysiphonia subulata*, *Polysiphonia ceramiaeformis* and *Womersleyella setacea*. Their main morphological features are summarized in Table 4.

*Boergeseniella fruticulosa*

*Boergeseniella fruticulosa* was abundant in the lower littoral and in the sublittoral fringe, where it was one of the most

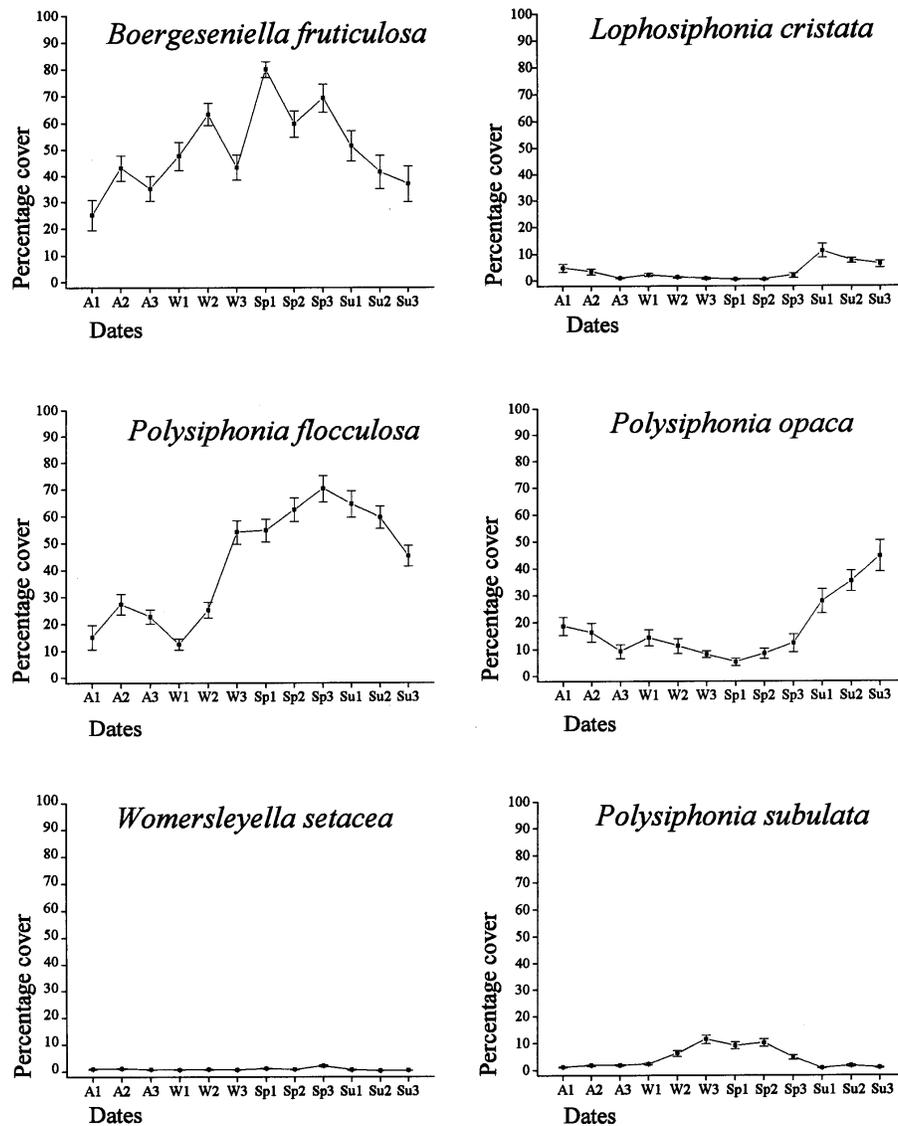
common algae; in some areas it formed almost mono-specific turfs, 0.5–1 cm thick. It was less abundant in the shallow sublittoral, where it was found to 1–1.5 m depth. The species occurred on rock and epiphytically on several algae; in particular, it was frequently found on *Corallina elongata* and *Cystoseira compressa* (Esper) Gerloff et Nizamuddin. Season and area were the most important factors influencing the spatial and temporal distribution of *B. fruticulosa* at the study site (ANOVA, 0.01 < p < 0.05 for season, p < 0.00001 for area); no significant effect of the sampling date was observed. In spring the percentage cover (Fig. 3) and the size of the erect axes (p < 0.00001; Fig. 4) were significantly higher than in the rest of the year. In fact, the tallest plants (up to 3–4 cm) were found on the first and second spring dates.

Tetrasporangia were the only reproductive structures recorded for this species. In autumn and winter only non-

**Table 4.** Main morphological features of the species of Rhodomelaceae

Species	No. of pericentral cells	Presence of cortication	Presence of creeping axes
<i>Boergeseniella fruticulosa</i> (Wulfen) Kylin	10–12	++	++
<i>Lophosiphonia cristata</i> Falkenberg	8–10	–	++
<i>Polysiphonia ceramiaeformis</i> Crouan et Crouan	8–10	–	+
<i>Polysiphonia flocculosa</i> (C. Agardh) Kützing	4	++	–
<i>Polysiphonia opaca</i> (C. Agardh) Moris et De Notaris	18–22	–	++
<i>Polysiphonia subulata</i> (Ducluzeau) J. Agardh	4	+	–
<i>Womersleyella setacea</i> (Hollenberg) R.E. Norris	4	–	++

For cortication and creeping axes: ++, very abundant; +, present but not abundant; –, absent.



**Fig. 3.** Abundance (expressed as percentage cover) of the species of *Boergeseniella*, *Lophosiphonia*, *Polysiphonia* and *Womersleyella* in lower littoral and shallow sublittoral algal turfs at the study site, during the period October 1997–September 1998. Bars indicate standard errors ( $n = 30$ ). See Table 2 for definitions of sampling dates.

reproductive plants were collected (Fig. 5); tetrasporangia occurred in the field only in spring and summer, but tetrasporangial plants represented a low percentage of the population (no more than 20%, as recorded on the first spring date). Moreover, even though detailed observations on the distribution of the reproductive stages were not possible for this species, a clustering of the tetrasporangial plants was apparent; when present, they were usually concentrated in short shore stretches, a few metres long.

#### *Lophosiphonia cristata*

*Lophosiphonia cristata* was most abundant in the sublittoral fringe. It grew on rock and epiphytically on encrusting corallines and it was often associated with *Polysiphonia opaca*. The ANOVA showed a significant effect of season ( $p < 0.001$ ) and area ( $p < 0.01$ ), while the sampling date was not a significant factor. Although its percentage cover

was quite low throughout the year (Fig. 3), this species was significantly more abundant in summer, showing the highest mean cover (11.2%) on the first date. In summer and autumn the size of the erect axes was also significantly higher than in other seasons ( $p < 0.00001$ ; Fig. 4).

Reproduction was associated with the warmest months of the year (Fig. 5); fertile plants were observed only in late spring and in summer. At these times fertile tetrasporophytes were dominant, forming up to 53% of the population on the first summer date. Cystocarpic plants were most abundant on the third spring date and their percentage gradually decreased on the following dates. Spermatangial plants were very rare; overall, only 3 plants bearing mature spermatangial branches were found.

#### *Polysiphonia ceramiaeformis*

Plants belonging to *Polysiphonia ceramiaeformis* were found mixed with other filamentous algae in the low littoral and

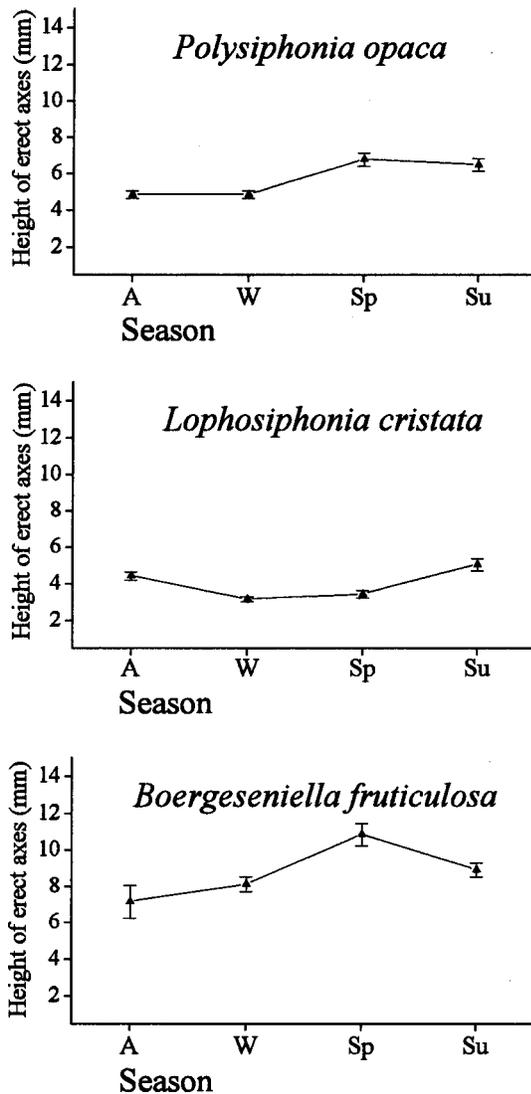


Fig. 4. Seasonal variation in the size of erect axes of *Polysiphonia opaca*, *Lophosiphonia cristata* and *Boergeseniella fruticulosa*. Bars indicate standard errors ( $n = 60$  for *P. opaca* and *B. fruticulosa*,  $n = 50$  for *L. cristata*).

in the sublittoral fringe. At the study site, *P. ceramiaeformis* was one of the least common Rhodomelaceae; its percentage cover was generally low (never more than 8% in a sample). Because of such a low cover, the distribution of this species was relatively uniform in both space and time; no significant differences were found for any of the factors considered. However, thalli of *P. ceramiaeformis* appeared generally more branched and developed in winter and spring. In summer and autumn this species was rare and the few specimens collected were formed by creeping filaments, reduced and devoid of erect axes; on the second and third summer dates no plants of *P. ceramiaeformis* were found. Moreover, reproductive plants were mainly found in winter and spring (Fig. 5). Spermatangia were first observed in late autumn and fertile male plants were collected throughout the winter and the spring, with the highest percentage (25%) on the last winter date. Cystocarpic plants showed a more restricted temporal distribution; cystocarps were found from the second winter date to the second spring date, with the

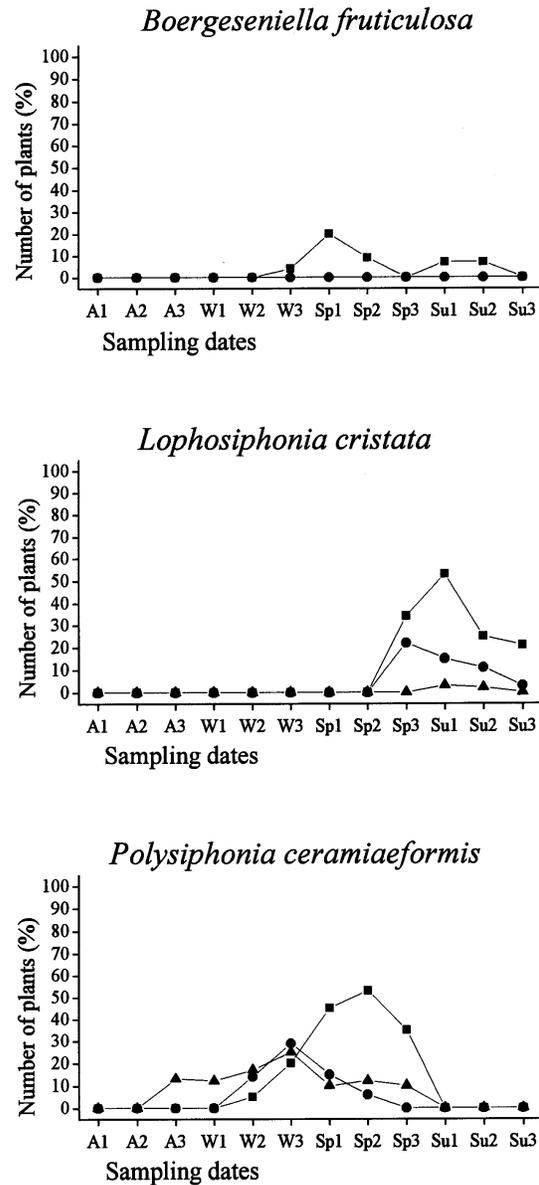


Fig. 5. Reproductive phenology of *Boergeseniella fruticulosa*, *Lophosiphonia cristata* and *Polysiphonia ceramiaeformis*. For each life history stage the percentage of the total of sampled plants is reported. Squares, tetrasporangial plants; circles, cystocarpic plants; triangles, spermatangial plants. See Table 2 for definitions of sampling dates.

maximum on the last winter date as well. A similar pattern was observed for the tetrasporangial plants, but in this case the highest percentage was recorded on the second spring date, when fertile tetrasporophytes were the most abundant phase in the population (54%). *P. ceramiaeformis* was also the only species for which mixed reproductive phases were observed; two plants, collected on the first spring date, bore both spermatangial branches and tetrasporangia.

*Polysiphonia flocculosa*

*Polysiphonia flocculosa* was a common epiphyte of many algae of the lower littoral and sublittoral fringe (*B. fruticulosa*, *Corallina elongata*, *Laurencia* spp. and *Nemalion*

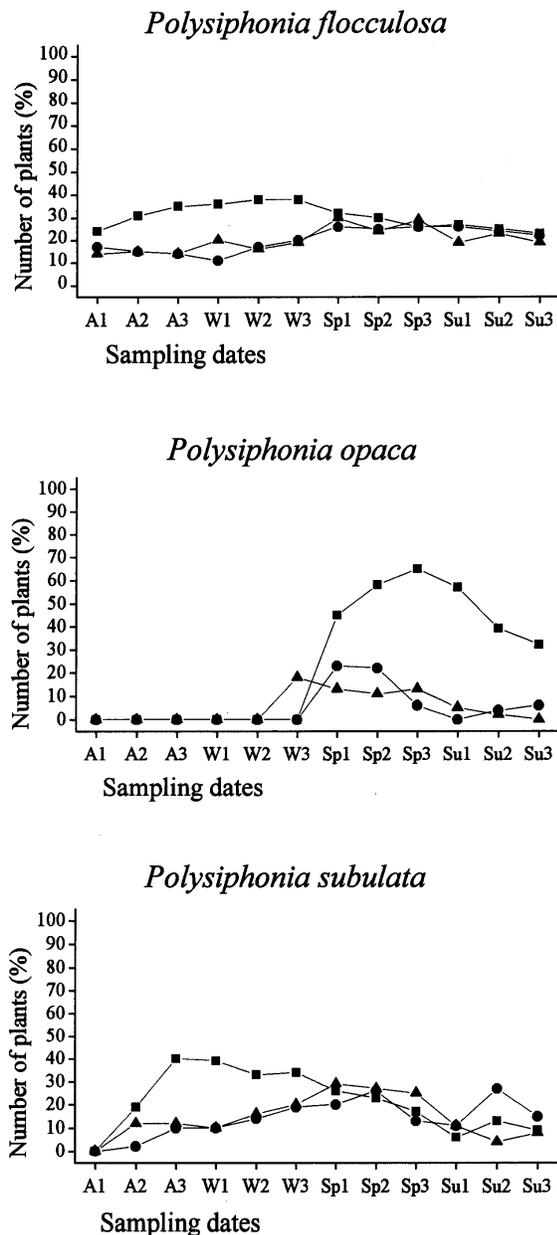


Fig. 6. Reproductive phenology of *Polysiphonia flocculosa*, *Polysiphonia opaca* and *Polysiphonia subulata*. For each life history stage the percentage of the total of sampled plants is reported. Squares, tetrasporangial plants; circles, cystocarpic plants; triangles, spermatangial plants. See Table 2 for definitions of sampling dates.

*heminthoides* (Velley) Batters). *P. flocculosa* was common throughout the annual cycle, but a significantly higher percentage cover was found in spring and summer (Fig. 3); the ANOVA performed on cover data showed a significant effect of all considered factors (season,  $0.01 < p < 0.05$ ; date,  $p < 0.01$ ; area,  $p < 0.01$ ). In the field, fertile gametophytes and tetrasporophytes of *P. flocculosa* were recorded throughout the period of the survey (Fig. 6); in spring and winter the majority of the sampled plants were reproductive (up to 88% in the first spring date), while in autumn the highest percentages of non-reproductive plants were observed (up to 45% on the first date). This is reflected by the results of the ANOVA, which showed a strongly significant effect of the life history phase ( $p <$

$0.000001$ ) on the percentage of fertile plants; however, the distribution of the life history phases was spatially and temporally uniform, as the effects of season, date and area were not significant.

#### *Polysiphonia opaca*

*Polysiphonia opaca* colonized rocky substrata and encrusting corallines, while it was less frequently epiphytic on other algal species. *P. opaca* occurred in the mid- and low littoral, but was usually most abundant in the shallowest part (30–40 cm) of the sublittoral zone, where it formed extensive, thin carpets (mixed with *L. cristata* and other filamentous red algae). The abundance of this species was significantly influenced by season ( $p < 0.001$ ) and area ( $p < 0.00001$ ), while no significant effects of the sampling date were found. The percentage cover was significantly higher in summer than in the other seasons (Fig. 3); erect axes were significantly taller in spring–summer ( $p < 0.00001$ ; Fig. 4). The reproductive period of *P. opaca* started in late winter and continued until the end of the summer (Fig. 6). Male gametophytes became fertile earlier than female gametophytes and tetrasporophytes; plants bearing spermatangial branches were first collected in late winter and, although not abundant, were recorded throughout spring and summer. Plants with cystocarps were most abundant in spring (up to 23% of the population on the first spring date), but were also commonly found in summer. Tetrasporangial plants occurred in the same seasons; in late spring and early summer they were the dominant phase, representing up to 65% of the sampled plants (last spring date).

#### *Womersleyella setacea*

In the sublittoral fringe, plants of *Womersleyella setacea* formed thin, individual filaments, creeping between other algal species. Their cover was very low (Fig. 3) and showed significant variations between sampling dates ( $0.01 < p < 0.05$ ; the highest mean cover, 2.20%, was recorded on the last spring date); for this species season and area were not significant factors. No fertile plants of *W. setacea* were collected.

#### *Polysiphonia subulata*

*Polysiphonia subulata* was a common epiphyte on many algal species. Its distribution was influenced by season ( $p < 0.01$ ) and area ( $p < 0.000001$ ), while the effect of sampling date was not significant. *P. subulata* was most abundant in winter and spring (Fig. 3); in these seasons its cover was significantly higher than in summer and autumn and the species appeared vegetatively well developed. Specimens collected in winter and spring were extensively branched and showed a more or less strong cortication (rarely observable in summer and autumn, when *P. subulata* mainly consisted of decumbent and poorly branched filaments). Throughout the annual cycle the species was

represented in the field by very small plants, rarely exceeding 5–6 mm in length and quickly reaching reproductive maturity (spermatangial branches even occurred on plants just 2 mm tall; tetrasporangia and cystocarps were also repeatedly observed on specimens no more than 4 mm tall). In winter and spring most plants bore reproductive structures (in contrast with summer and autumn, when the population was mainly formed by sterile plants). Spermatangial and cystocarpic plants were collected for almost the whole annual cycle, being most abundant on the first and second spring dates (Fig. 6). Tetrasporangial plants were also found on nearly all sampling dates (the first autumn date being the only exception), but their percentage was generally higher in late autumn and winter.

## Discussion

A strong variability on small spatial scales (metres, or tens of metres) is an important characteristic of the algal assemblages of the rocky shore where the study was carried out; in the low littoral and in the shallow sublittoral the assemblages exhibit a very patchy and irregular distribution and their composition may show substantial variations even over short distances. In the present study this is indicated by the significant effect of the area on the distribution of many rhodomelacean species. The only exceptions are *Polysiphonia ceramiaeformis* and *Womersleyella setacea*; the distribution of these species was relatively uniform, probably because of their general scarcity. A detailed discussion of factors determining this spatial heterogeneity, which would go beyond the scope of the present paper, is reported in other studies performed in the same zone (Benedetti-Cecchi & Cinelli, 1994; Benedetti-Cecchi *et al.*, 1996; Menconi *et al.*, 1999).

For most of the species considered, the spatial variability is accompanied by more or less evident temporal variations on a seasonal scale. In fact, nearly all species of *Boergesenella*, *Lophosiphonia* and *Polysiphonia* show seasonal patterns of abundance in the field, as indicated by the significant effect of the season on their occurrence (and, for *Boergesenella fruticulosa*, *Lophosiphonia cristata* and *Polysiphonia opaca*, by significant seasonal differences in the size of erect axes); *P. ceramiaeformis* and *W. setacea* are exceptions. However, the seasonal patterns vary considerably, with *B. fruticulosa* most abundant in spring, *Polysiphonia flocculosa* in spring and summer, *L. cristata* and *P. opaca* from late spring to early autumn and *P. ceramiaeformis* and *Polysiphonia subulata* in winter and early spring.

Different seasonal patterns are also evident when the reproductive phenology is considered. Two groups of species can be separated: (1) species with a reproductive period extended over the whole annual cycle; (2) species with reproduction concentrated in one or two seasons. The first group consists of *P. flocculosa* and *P. subulata*; the

second one includes *P. ceramiaeformis* (fertile in winter and spring), *L. cristata* (fertile in late spring and summer), *B. fruticulosa* and *P. opaca* (fertile in spring and summer). For all species, reproduction generally coincides with the periods of best vegetative development and highest abundance in the field; the only partial exception is *P. opaca*, for which the reproductive season starts in spring (when the species is not yet as abundant as in summer).

For *W. setacea* no observations on reproductive phenology are possible, because no fertile material was found. Vegetative growth and fragmentation seem to be the only forms of reproduction and the complete absence of gametangia and sporangia is in agreement with previous surveys carried out in the same zone (Airoldi *et al.*, 1995) and other parts of the Mediterranean (Verlaque, 1989; Cormaci *et al.*, 1994; Athanasiadis, 1997); Rindi *et al.* (1999) provide further discussion on this subject.

For the other species, reproduction of different life history phases takes place in the same seasons, but often the time of maximal fertility is not the same for tetrasporophytes and gametophytes. This can be noted in particular for *P. ceramiaeformis* and *P. opaca*: the time of highest abundance of fertile gametophytes, both male and female (late winter–early spring), seems to precede by about 2 months the time of highest abundance of tetrasporangial plants (late spring). In these species male gametophytes become reproductive somewhat earlier than female ones (1.5–2 months before); this phenomenon, not uncommon in the Florideophycidae (e.g., Cunningham *et al.*, 1993; Molenaar & Breeman, 1997), ensures that fertilization occurs as soon as carpogonia have been formed. Even though less marked, similar differences are also observable for *P. flocculosa* and *P. subulata*.

The phenological data presented here allow a comparison with similar observations reported for the same species in other regions of the Mediterranean and northern Europe (at least regions for which more or less detailed observations are available). They also give some clues about the possible environmental factors regulating the vegetative and reproductive phenology, but, from this point of view, care should be exercised in making generalizations, because of the lack of complementary culture observations and of the depth range occupied by the rhodomelacean algae. At the study site these algae mainly occur in the low littoral, where abiotic factors which may be important for macroalgal phenology (such as temperature, hydrodynamism and salinity) undergo much stronger short-term variations than in properly subtidal habitats. In these situations, local factors can be critical and parameters such as sea surface temperature are not necessarily as important as for subtidal species; studies on intertidal seaweeds have shown clear phenological differences even between populations only a few kilometres apart (Breeman & Guiry, 1989).

Nevertheless, at least for some species, there is an apparent correlation between phenology and some environmental parameters. In *L. cristata*, for example, the best vegetative development and reproduction are clearly

associated with the time of highest sea surface temperatures; this species seems to be reproductive only when sea surface temperatures are about 20 °C, or higher. The control by this factor appears to be exerted directly on sporangial and gametangial induction; production of reproductive structures is not size-dependent, because they are produced even by erect axes only a few millimetres tall, present in the field throughout the annual cycle. The small amount of phenological information available for this species agrees with the present data; for the Gulf of Naples and eastern Sicily tetrasporangial plants have been reported only in summer (Cormaci *et al.*, 1984). This kind of phenology is not unexpected for a species widely distributed in tropical regions (Børgesen, 1915–20; Taylor, 1960; Hollenberg, 1968c; Silva *et al.*, 1987). The Mediterranean is probably the northern distribution limit for *L. cristata*, resulting in optimal environmental conditions for only a restricted part of the annual cycle.

Other species, such as *P. ceramiaeformis* and *P. subulata*, find better conditions at the times when sea surface temperature is lowest; these species are endemic to the temperate zone of the north-eastern Atlantic, occurring from the Mediterranean and the Canary Islands northwards to southern England (in the case of *P. ceramiaeformis*; Maggs & Hommersand, 1993) and northern France (in the case of *P. subulata*; Feldmann, 1954). At the study site, *P. ceramiaeformis* is fertile and more developed from January to May; temperatures below 18 °C seem to be most favourable for its growth and reproduction. *P. ceramiaeformis* seems to suffer particularly from high temperatures, as in summer it virtually disappeared. On Languedoc shores (Lauret, 1970), *P. ceramiaeformis* shows a similar phenology; the period of vegetative growth, however, seems to be more prolonged, as it begins to be abundant in January–February and persists for most of summer, declining in August–September. The reproductive period of gametophytes corresponds well with our observations, while tetrasporophytic fertility extends to nearly all year (except November and December; Lauret, 1970). Without the support of culture observations, it is impossible to elucidate the cause of these differences, although the possibility that such prolonged tetrasporophytic persistence is favoured by slightly lower surface temperatures cannot be excluded; in fact the Languedoc littoral borders the Gulf of Lion, an area where the surface temperature is 2–3 °C lower than in the rest of the western Mediterranean (Lüning, 1990). For the British Isles, Maggs & Hommersand (1993) report that populations are apparently ephemeral and occur very sporadically, all collections (including some fertile) having been made in April. Considering the phenology observed in the Mediterranean, it is difficult to see how the phenology of Mediterranean and Atlantic populations could be regulated by a common set of environmental signals; there is no apparent reason why *P. ceramiaeformis* should not be expected even in summer months in the British Isles. In Southern England, however, this species reaches the northern limits of its distribution and its presence is

limited to a narrow range of habitats (Maggs & Hommersand, 1993), where the environmental conditions may not reflect those of the open shore.

The phenology of *P. subulata* is quite similar to that of *P. ceramiaeformis*. At the study site, *P. subulata* is an ephemeral species quickly reaching reproductive maturity and showing the best vegetative development from January to June; in this regard our observations agree with Feldmann's (1942) remarks, reporting that on the Côte des Albères (southern France) this species is abundant and well developed mainly in winter and spring. *P. subulata* seems to show the same reproductive phenology on the shores of north-western Italy and the Languedoc littoral; Lauret (1967) reported that, on shores of the latter region, the species occurs with tetrasporangia, spermatangial branches and cystocarps almost throughout the year. For other Mediterranean (Feldmann, 1942; Cormaci *et al.*, 1984) and north Atlantic regions (Feldmann, 1954), fertile plants are reported for much more limited periods; we believe that this difference is due to the small number and irregularity of collections examined in those studies.

*P. flocculosa* is distributed in the western Mediterranean, Adriatic Sea and Canary Islands (Preda, 1909; Børgesen, 1930). This species is most abundant in spring and summer, but it is reproductive for the whole year; such a reproductive phenology is clearly recurrent in all regions for which data on *P. flocculosa* are available (Lauret, 1970; Gomez Garreta *et al.*, 1982).

On the basis of our observations, *P. opaca* is the only species for which an involvement of the photoperiod in the regulation of reproductive phenology might be possible: reproduction is associated with seasons (spring and summer) characterized by long days (daylength > 12 h). A comparison with other regions shows, however, that this pattern is not general. In the whole Mediterranean area this species is fertile in spring and summer (De Toni, 1924; Feldmann, 1931; Lauret, 1970; Gomez Garreta *et al.*, 1982; Cormaci *et al.*, 1984; Soto & Conde, 1989); but tetrasporangial plants have also been reported in autumn in eastern Sicily (Cormaci *et al.*, 1984) and in winter in the Balearic Islands (Gomez Garreta *et al.*, 1982). For the Languedoc, Lauret (1970) reported fertile tetrasporophytes and gametophytes for most of the year. Probably the reproductive phenology of this species is influenced by factors working on regional (or even smaller) scale; culture observations would be useful to elucidate them. Unfortunately, phenological data for extra-Mediterranean populations of *P. opaca* are too few for a comparison.

Like *W. setacea*, *B. fruticulosa* apparently does not complete a typical *Polysiphonia*-type life history at the study site. Tetrasporangia are the only reproductive structures recorded and the population mainly consists of non-reproductive plants throughout the year, which is unusual. The species is widespread in the Mediterranean, Canary Islands and on Atlantic European shores northwards to the Shetland Islands (Maggs & Hommersand, 1993). Although there are no clear common seasonal patterns, reports of fertile gametophytes and sporophytes

are available for many Mediterranean (De Toni, 1924; Funk, 1955; Gomez Garreta *et al.*, 1982; Cormaci *et al.*, 1984; Soto & Conde, 1989) and north Atlantic localities (Maggs & Hommersand, 1993) where the species occurs. This observation is not easy to explain. One hypothesis is that, in the relatively short shore stretch where the study was performed, *B. fruticulosa* rarely reaches the minimal size necessary for production of gametangia and sporangia. In fact a generally reduced size is a common feature of all rhodomelacean species found at the study site; plants of *B. fruticulosa* are not an exception, rarely exceeding 1.5–2 cm in height, and tetrasporangia were common in the tallest specimens found during the study. We examined tetrasporangial and cystocarpic plants of *B. fruticulosa* from the British Isles and other Mediterranean localities; in every case the size was definitely greater (erect parts up to 6–7 cm tall) than in our plants. Another possibility is that in the field gametophytes are less abundant than sporophytes (as reported, for example, for populations of the British Isles: see Maggs & Hommersand, 1993); thus, although unlikely, the possibility that they were missed in our survey cannot be excluded. Furthermore, spermatangial branches and cystocarps might occur for short periods and rapidly release their products, even though, considering phenological data available for other Mediterranean localities, this seems quite unlikely as well. It is also possible that, at least in some cases, sporogenesis and gametogenesis are stimulated by stress conditions; we have observed several tetrasporangial plants which appeared more or less unpigmented. Whatever the cause of the lack of gametangia may be, vegetative reproduction (mainly growth and extension of creeping parts) appears to have a fundamental role in the persistence of *B. fruticulosa* at the study site; further studies, however, are required.

In conclusion, most rhodomelacean species considered in this study share a number of life history traits (a general association of vegetative growth and both gametangial and sporangial reproduction; more or less identical reproductive seasons in different life history phases; absence of photoperiodic responses; quick release of propagules after fertilization or sporangial induction) that qualify them as seaweeds of type 1 as defined by Lüning & tom Dieck (1989), i.e. algae for which the environmental factors satisfying the primary physiological needs directly govern the onset of the main activities of the organism. This kind of response, also comparable to Kain's (1989) 'season responders' (although this concept is best applied to properly subtidal species), is not unexpected for algae with a relatively simple morphology which, inhabiting the low littoral and the shallow sublittoral, experience in the field more variable and less predictable environmental conditions than subtidal seaweeds. Nevertheless, a certain amount of ecological differentiation is apparent in this group. *P. flocculosa* and *P. subulata*, for example, differ both phenologically and structurally from the other species. They seem to show characteristics typical of ephemeral species, with reproduction and recruitment of new plants

occurring throughout the year. They lack prostrate axes and in the algal turfs are among the most common epiphytic algae. Other species (*B. fruticulosa*, *L. cristata*, *P. opaca*) reproduce in one or a few seasons. These species probably have a higher capacity for vegetative persistence, as juvenile plants were not frequently observed. Their abundant creeping axes ensure that they are the main anchor species in the turf assemblages.

It is interesting that such ecological differences occur between four-siphoned species (*P. flocculosa* and *P. subulata*) and species with more than four siphons (the remainder). As recent studies based on molecular data indicate a clear separation between species with four siphons and those with larger numbers of siphons (L. McIvor & C. Maggs, personal communication), it is not unlikely that this situation reflects a phylogenetic differentiation; however, further studies concerning more rhodomelacean species are necessary to confirm it.

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