

Morphology and distribution of nongeniculate coralline algae (Corallinaceae, Rhodophyta) on the leaves of the seagrass *Cymodocea nodosa* (Cymodoceaceae)

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Four species of nongeniculate coralline algae (Corallinaceae, Rhodophyta) were identified on leaves of the seagrass *Cymodocea nodosa* (Ucria) Ascherson: three *Fosliella* states of *Hydrolithon* Foslie and one species of *Pneophyllum* Kützing. The species were identified by the morphology of the spore germination disc, the position of the trichocytes and the morphology of the ventral filaments, trichocyte fields, and sporangial and gametangial conceptacles. The distribution of the epiphytes was examined in terms of density, cover and fertility along the old leaves and during a whole annual cycle from a sublittoral meadow at El Médano, Tenerife, Canary Islands. Marked seasonal variations were recorded in density, cover and fertility. In spring density, cover and fertility were low, increasing during summer and reaching maximal peaks in late summer; in autumn cover and fertility decreased but high density persisted; in winter low cover and low fertility were detected, together with high density values. The density of coralline epiphytes along the leaves also showed seasonal variations. Density increased from proximal (younger) to distal (older) segments of the leaf in winter, decreased in summer and was relatively constant in spring and autumn. The percentage cover increased at all seasons, from proximal to distal segments. Although sterile plants were more abundant than fertile ones, the fertility always increased from proximal to distal segments.

INTRODUCTION

Seagrasses support a great diversity of epiphytic organisms, nongeniculate coralline algae often being the most ubiquitous (Harlin 1980; Borowitzka & Lethbridge 1989). Although seagrass epiphytes have been widely studied (e.g. Humm 1964; van der Ben 1969; Ducker *et al.* 1977; Hall & Eiseman 1981; Heijs 1985), members of the Corallinaceae have frequently been treated as one group, due to taxonomic difficulties. Recently more detailed information about the coralline epiphytes on some seagrasses has been published (Bramwell & Woelkerling 1984; Cullinane *et al.* 1985; Harlin *et al.* 1985). These studies have reported dense populations of taxa belonging to *Pneophyllum* Kützing and *Fosliella* Howe. According to Penrose & Chamberlain (1993) *Fosliella* cannot be recognized as a genus distinct from *Hydrolithon* Foslie and these authors proposed that thin plants, traditionally attributed to *Fosliella*, be referred to as the *Fosliella* state of *Hydrolithon*. *Pneophyllum* differs from *Fosliella* state plants of *Hydrolithon* in possessing an eight-celled instead of a four-celled central element in the germination disc and in producing intercalary rather than terminal trichocytes in the ventral filaments (Chamberlain 1983).

Information on the distribution of crustose epiphytes on leaves of *Zostera marina* Linnaeus was published by van den Ende & Haage (1963) from Brittany (France) and by Cullinane *et al.* (1985) from Ireland. Battiato *et al.* (1982), Ballesteros (1987) and Romero (1988) studied the distribution of epiphytes on leaves of *Posidonia oceanica* (Linnaeus) Delile from the Mediterranean Sea. Bramwell & Woelkerling (1984) provided numerical data on the differential distribution of coralline epiphytes and found that the cover, density and relative fertility increased from proximal (youngest) to distal (oldest)

regions of leaves of *Amphibolis antarctica* (Labillardière) Sonder et Ascherson ex Ascherson from south-eastern Australia. However, no attempt has been made to determine the distribution of coralline epiphytes on the seagrass *Cymodocea nodosa* (Ucria) Ascherson.

Cymodocea nodosa forms extensive sublittoral meadows and is the most common seagrass in the Canary Islands (unpublished data, Reyes 1993). This perennial angiosperm has long rhizomes bearing shoots with 2–4 linear leaves, 100–400 mm long by 2–4 mm wide, cut off from a proximal meristem (Reyes & Sansón 1994). Afonso-Carrillo *et al.* (1985) showed that, among the crustose epiphytes growing on the leaves of this seagrass from the Canary Islands, *Hydrolithon farinosum* (Lamouroux) Penrose et Chamberlain (as *Fosliella*), *Pneophyllum fragile* Kützing (as *Fosliella*) and *Melobesia membranacea* (Esper) Lamouroux were present. The present study was designed to determine the extent to which density, cover and fertility in epiphytic corallines may vary along the leaves of *Cymodocea nodosa* throughout the year. It also provided an opportunity to study details of species morphology including species not reported by Afonso-Carrillo *et al.* (1985).

MATERIALS AND METHODS

Shoots of *Cymodocea nodosa* supporting evident epiphytic crustose communities (Fig. 1) were collected at random in meadows at 4–5 m depth in El Médano, Tenerife, Canary Islands (Fig. 2). Samples were collected monthly from December 1987 to November 1988 and preserved in 4% Formalin in sea water. Water temperature during this study ranged from 18.5°C (January–February) to 24.5°C (August–September).



Fig. 1. *Cymodocea nodosa*, showing leaves with nongeniculate coral-line epiphytes.

To ensure standardization and examination of the mature stages of the epiphyte community, the outermost (oldest) leaf of each of 10 randomly selected shoots was chosen. Leaves with abundant filamentous epiphytes were not considered. From each leaf, the distal (oldest), mid and proximal (youngest) segments of 4 cm length were cut out. The percentage cover of each epiphyte species was estimated using a Zeiss binocular microscope. Plants on the segments were then decalcified in P er enyi's solution, stained in 5% aqueous aniline blue for 12 min and mounted in 20% aqueous Karo[®] dextrose (Jones & Woelkerling 1984). Preliminary investigations showed no significant differences in cover and density between abaxial and adaxial surfaces of the leaf (unpublished data, Reyes 1993), thus no distinction was made in this study. For each segment, all individuals were counted at 100–400× magnification with a Zeiss microscope, and the reproductive stage was indicated (sterile, sporangial or gametangial). Frequency data were based on 10 leaves for each month. All data were standardized to areas of 1 cm². Biometric data for each species were obtained from 80 measurements for vegetative cells and 40 for reproductive structures.

The scanning electron microscope was used for a better morphological characterization of the crustose epiphytes and the procedure employed was outlined in Afonso-Carrillo *et al.* (1984). Segments of leaves with coralline epiphytes were

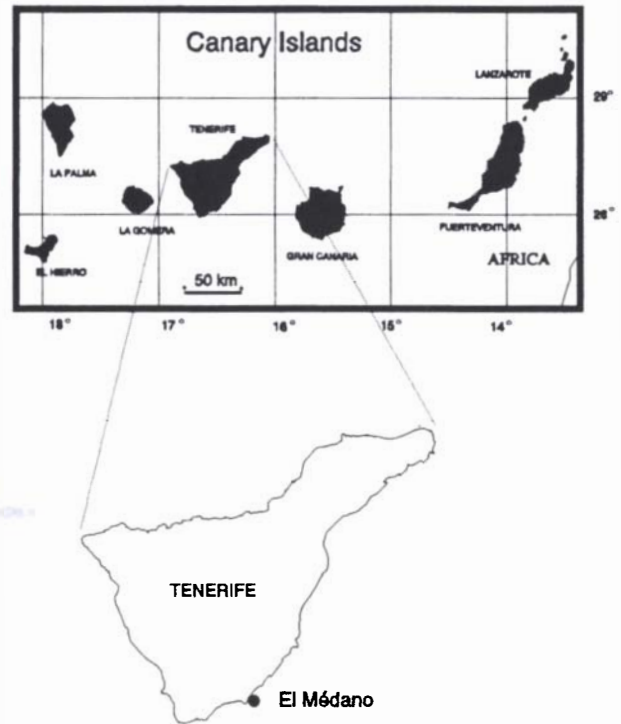


Fig. 2. Sampling site.

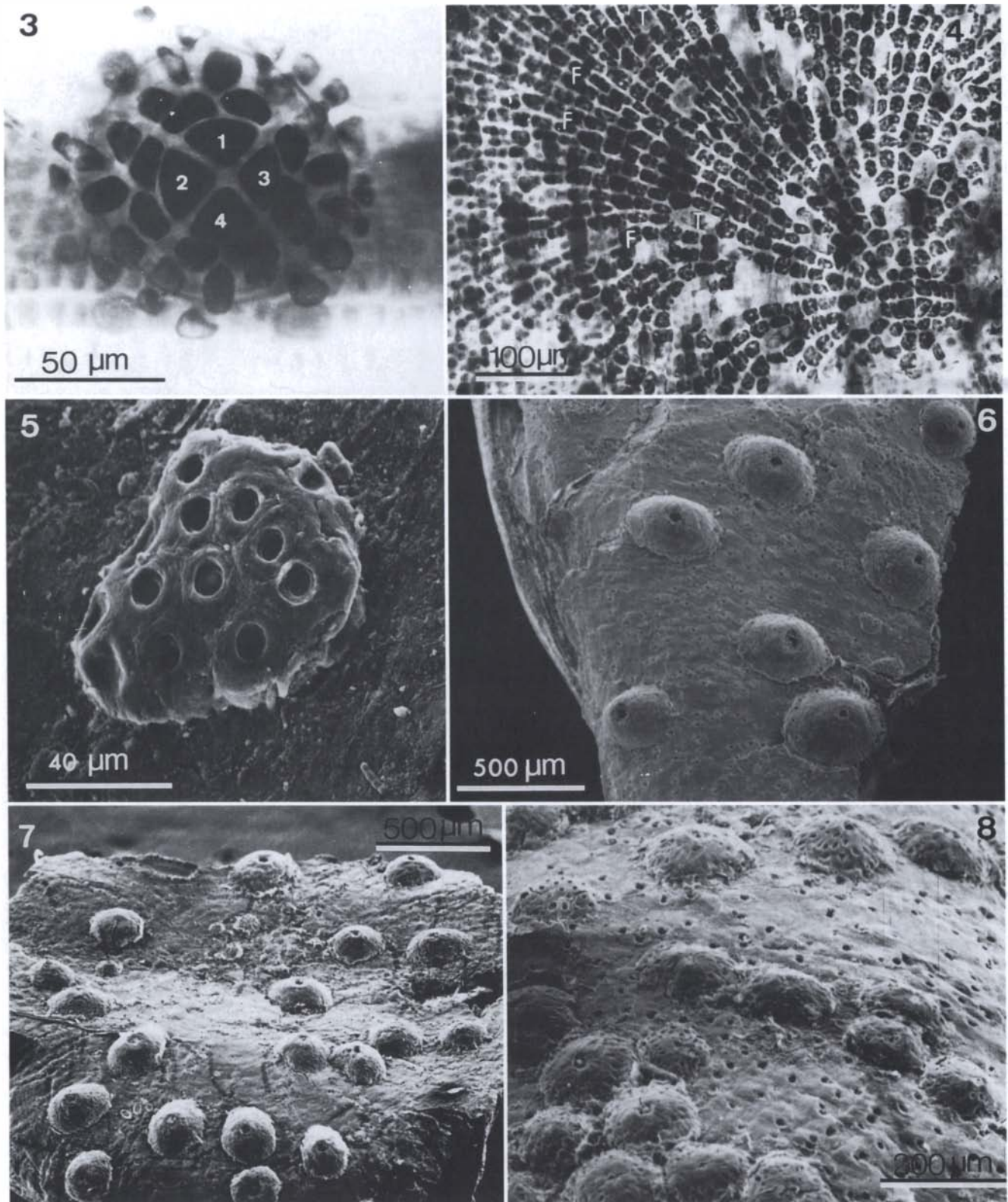
selected and rinsed with distilled water. After air drying, segments were coated with gold and viewed in a Hitachi S-450 Stereoscan Microscope. Nomenclature follows Chamberlain (1994). Voucher specimens have been deposited in TFC (Departamento de Biolog a Vegetal, Universidad de La Laguna).

RESULTS

Species morphology

Crustose epiphytes were identified from the early stages of development by the characteristic pattern of the spore germination disc. Although germination discs are generally evident in both sterile and fertile plants, the following morphological features were also used in species segregation: ventral filaments and position of trichocytes, trichocyte fields and sporangial and gametangial conceptacles. Four species of nongeniculate coralline algae were identified on leaves of *Cymodocea nodosa*. Three were *Fosliella* states of *Hydrolithon* s.l.: *Hydrolithon* sp. (probably a widely distributed undescribed species), *Hydrolithon boreale* (Foslie) Chamberlain and *Hydrolithon cruciatum* (Bressan) Chamberlain. The fourth species was *Pneophyllum fragile*. The species will be described separately below.

Hydrolithon sp. (Figs 3–8) has spore germination discs consisting of a four-celled circular central element consisting of cells that are three-sided in surface view and surrounded by eight cells (Fig. 3). Mature thalli are pseudoparenchymatous and only two cells thick in vegetative regions. The ventral region is composed of a single layer of filaments with radially elongate, subcylindrical cells. The dorsal region consists of a layer of epithallial cells. Cell fusions, scattered



Figs 3–8. Morphology of *Hydrolithon* sp.

Fig. 3. Spore germination disc consisting of a 4-celled central element (1–4) surrounded by 8 cells.

Fig. 4. Surface view of thallus, showing cells of adjacent filaments connected by cell fusions (F) and trichocytes terminating filaments (T).

Fig. 5. Surface view of trichocyte field.

Fig. 6. Surface view of tetrasporangial conceptacles.

Fig. 7. Surface view of carposporangial conceptacles.

Fig. 8. Surface view of spermatangial conceptacles.

trichocytes and protruding suborbicular trichocyte fields are evident in surface views of thalli (Figs 4, 5). Tetrasporangial plants possess prominent uniporate conceptacles in the central regions of thalli (Fig. 6). Gametangial plants are dioecious. Carpogonial/carposporangial conceptacles are hemispherical and irregularly scattered (Fig. 7). Spermatangial conceptacles are slightly convex and frequently arranged in rows (Fig. 8). Dimensions of vegetative cells and reproductive structures are summarized in Table 1.

Hydrolithon boreale (Figs 9–13) has spore germination discs consisting of a four-celled ellipsoidal central element, the cells four-sided in surface view and surrounded by eight (four large and four small) cells (Fig. 9). Filaments of the ventral region are composed of subcubical to subcylindrical cells subtending epithallial cells. Cell fusions, scattered trichocytes and trichocyte fields are present (Fig. 10). Trichocyte fields vary from circular to ellipsoidal in outline and are convex and slightly protruding above the surrounding thallus surface (Fig. 11). Tetrasporangial conceptacles are uniporate, hemispherical and surrounded by a prominent ring of trichocytes (Fig. 12). Gametangial plants are monoecious, with spermatangial and carpogonial/carposporangial conceptacles adjacent to each other (Fig. 13), irregularly scattered on the central portion of thalli. The shape of carpogonial/carposporangial conceptacles is similar to that of the tetrasporangial one. Spermatangial conceptacles are rarely apparent, showing a peripheral ring of epithallial cell traces. Dimensions of vegetative cells and reproductive structures are summarized in Table 1.

Hydrolithon cruciatum (Figs 14–17) possesses spore germination discs consisting of a four-celled ellipsoidal central element, the cells three-sided in surface view and surrounded by eight cells (Fig. 14). The ventral region is composed of a single layer of filaments with subcylindrical cells subtending epithallial cells. Abundant cell fusions, marginal trichocyte rows and trichocyte fields are evident in surface view (Fig. 15). Trichocyte fields are circular in outline, forming prominent

elevations with trichocytes arranged in the flat central region (Fig. 16). Tetrasporangial conceptacles are uniporate and hemispherical. The roof surface is initially similar to the surrounding thallus surface and abundant epithallial concavities are evident only on the top (Fig. 16). Gametangial plants are monoecious, with irregularly scattered spermatangial and carpogonial/carposporangial conceptacles adjacent to each other (Fig. 17). Carpogonial/carposporangial conceptacles are similar in shape to the tetrasporangial one. Spermatangial conceptacles are inconspicuous. Dimensions of vegetative cells and reproductive structures are summarized in Table 1.

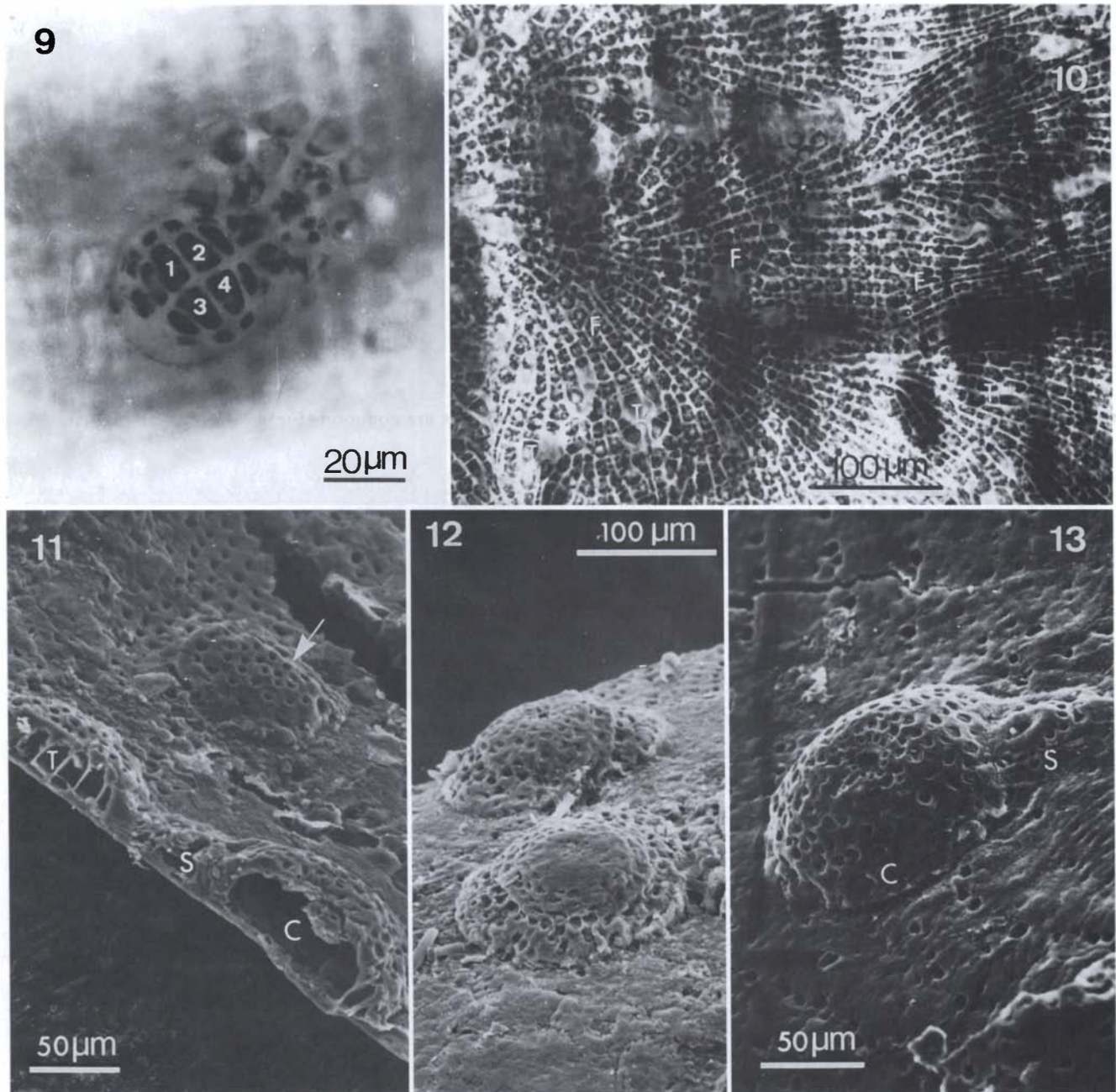
Pneophyllum fragile (Figs 18–21) has spore germination discs of an eight-celled ellipsoidal central element, with subrectangular cells in surface view (Fig. 18). The ventral region is composed of a single layer of subcubical to subcylindrical cells, radially arranged. The dorsal region consists of a layer of epithallial cells. Cell fusions and scattered intercalary trichocytes are common (Fig. 19). Uniporate tetrasporangial conceptacles are flattened, somewhat raised and tending to form 2–3 groups in the central region of the thalli (Fig. 20). Gametangial plants are monoecious. Spermatangial and carpogonial/carposporangial conceptacles are flat, slightly raised and generally adjacent to each other, forming small groups on thalli (Fig. 21). Dimensions of vegetative cells and reproductive structures are summarized in Table 1.

Community structure and composition

The development of the coralline community usually begins on the younger parts of leaves of *Cymodocea nodosa* from spores that settle and divide to produce germination discs and vegetative thalli. Evidence of vegetative thallus fragmentation, as a means of vegetative reproduction, was not observed, and both sterile and fertile individuals commonly have germination discs. During winter (December–March) the structure of the coralline epiphyte community did not

Table 1. Dimensions of vegetative and reproductive structures of nongeniculate corallines on *Cymodocea nodosa* leaves at El Médano, Canary Islands (in μm unless stated)

	<i>Hydrolithon</i> sp.	<i>Hydrolithon boreale</i>	<i>Hydrolithon cruciatum</i>	<i>Pneophyllum fragile</i>
VEGETATIVE STRUCTURES				
Germination disc diameter	67–72	31–33	24–26	40–48
Thallus diameter	Up to 3.5 mm	Up to 2 mm	Up to 1.5 mm	Up to 1 mm
VS thallus depth	Up to 17	Up to 12	Up to 10	Up to 12
Cell length	14–26	7–17	7–17	6–12
Cell width	4–12	4–13	4–12	4–12
VS cell height	9.6–14.4	6–7	7.2–9.6	6–7
Epithallial cell length	7–12(14.4)	2.4–7.2	2.4–4.8	1.2–4.8
Epithallial cell diameter	4–12	2.4–8.4	2.4–7.2	2.4–7.2
VS epithallial cell height	2.4–4.8	1.2–2.4	1.2–2.4	1.2–2.4
Trichocyte type	Terminal	Terminal	Terminal	Intercalary
Trichocyte length	19–41	10–26	8–16	6–15
Trichocyte width	9–22	4–17	4–12	6–12
Trichocyte fields diameter	Up to 100	Up to 120	Up to 72	–
TETRASPORANGIAL CONCEPTACLE				
External diameter	264–384	72–156	96–156	91–151
VS height	139–144	28–48	c. 45	c. 32
CARPOSPORANGIAL CONCEPTACLE				
External diameter	192–312	60–132	72–115	60–108
VS height	91–96	36–48	c. 52	c. 30
SPERMATANGIAL CONCEPTACLE				
External diameter	96–132(156)	24–48	24–36	16–29
VS height	31–36	19–20	c. 21	–



Figs 9–13. Morphology of *Hydrolithon boreale* (Foslie) Chamberlain.

Fig. 9. Spore germination disc consisting of a 4-celled central element (1–4) surrounded by 8 (4 large and 4 small) cells.

Fig. 10. Surface view of thallus showing cells of adjacent filaments connected by cell fusions (F) and trichocytes terminating filaments (T).

Fig. 11. Surface view of a trichocyte field (arrow). Note a trichocyte field (T), spermatangial (S) and carposporangial (C) conceptacles in section.

Fig. 12. Surface view of two tetrasporangial conceptacles, each with a prominent ring of trichocytes.

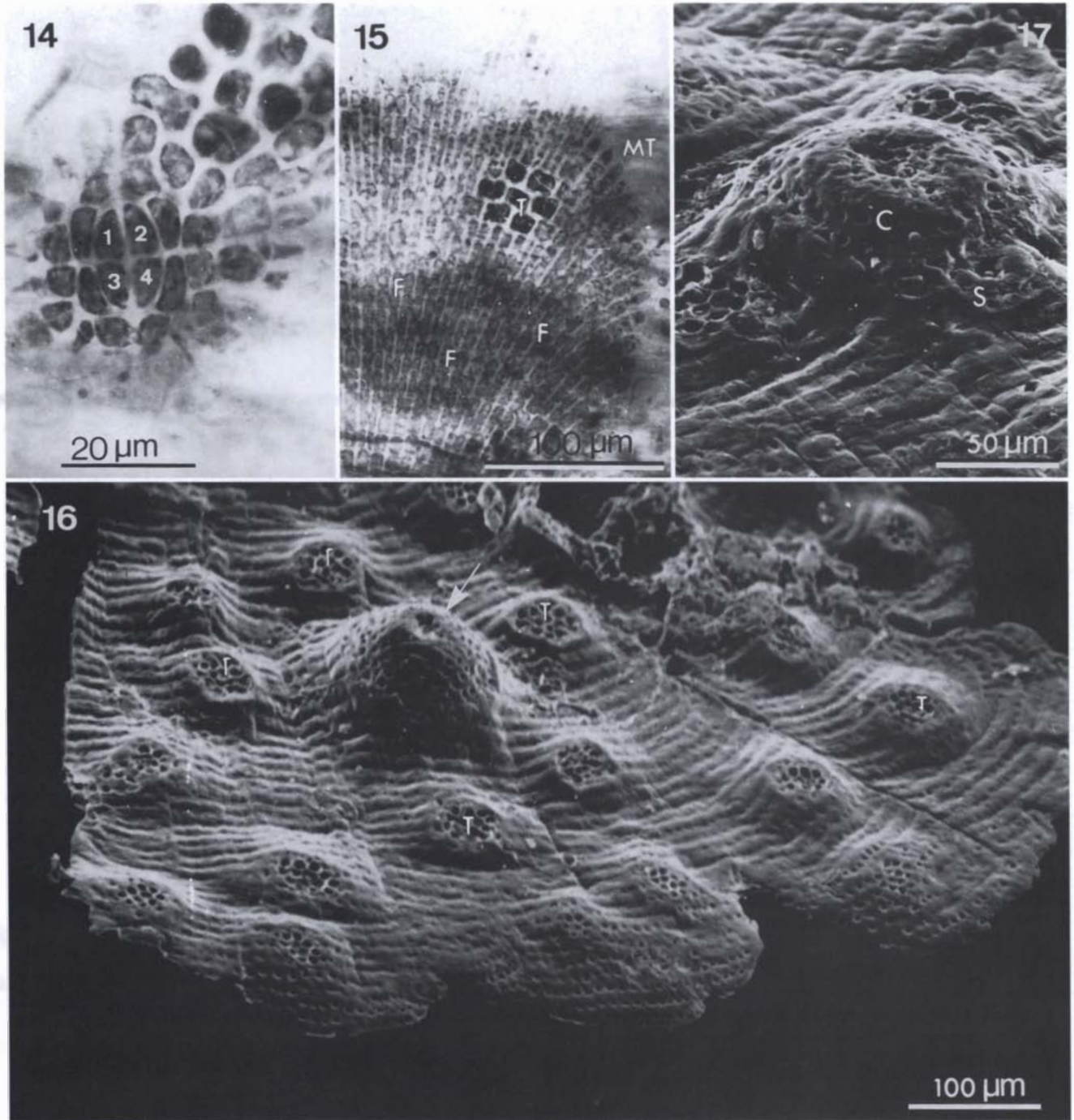
Fig. 13. Surface view of spermatangial (S) and carposporangial (C) conceptacles.

change much but showed an increase in the number of algae from the proximal (youngest) to the distal (oldest) segment of the leaf (Table 2). In spring and early summer (April–July) and autumn (October–November) no marked differences in numbers were observed along the leaf. However, in mid and late summer (August–September) the structure was slightly different, with higher density values on the proximal and mid segments. The overall density of coralline algae increased over the summer (July–September) and decreased between late

winter and early spring. The lowest density values were observed from April to July (Table 2).

As a rule, sterile plants were more abundant than fertile ones and the number of individuals with conceptacles increased from proximal to distal leaf segments (Table 2). The lowest fertility values were observed in late winter and early spring and the number of plants with conceptacles rose over spring and summer, with a maximum in September (Table 2).

In all months, the percentage cover of coralline epiphytes



Figs 14–17. Morphology of *Hydrolithon cruciatum* (Bressan) Chamberlain.

Fig. 14. Spore germination disc consisting of a 4-celled central element (1–4) surrounded by 8 cells.

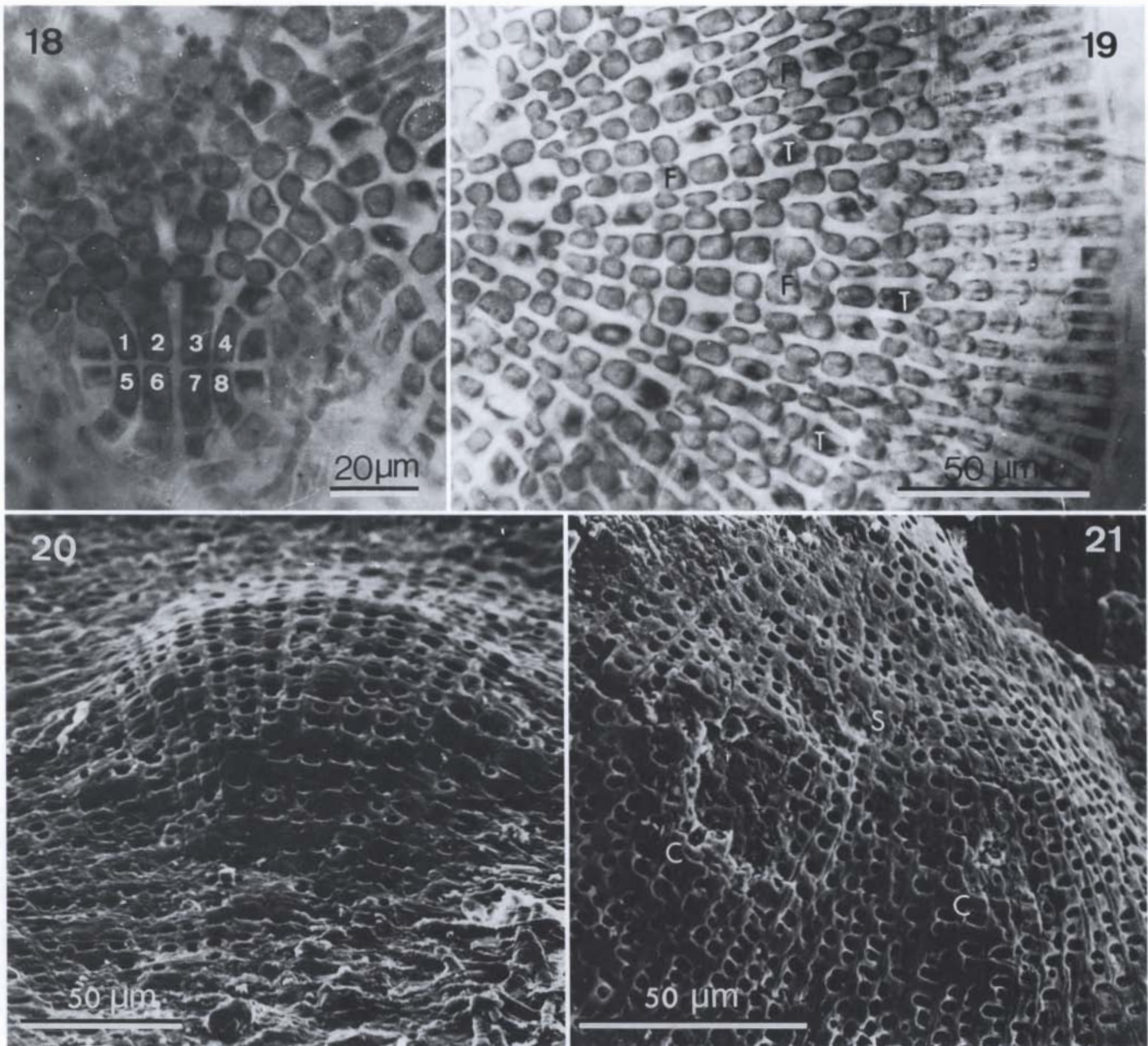
Fig. 15. Surface view of thallus, showing cells of adjacent filaments connected by cell fusions (F), marginal trichocyte rows (MT) and a trichocyte field (T).

Fig. 16. Surface view of a tetrasporangial crust showing a tetrasporangial conceptacle (arrow) and numerous trichocyte fields (T).

Fig. 17. Surface view of spermatangial (S) and carposporangial (C) conceptacles.

increased from proximal to distal segments of the leaf (Table 2). The percentage cover was low on all segments in spring and increased over the summer, reaching a peak in September. Thus there seems to be a correlation between percentage cover and density. However, in autumn and winter, high density values were observed, although with low percentage cover due to the high presence of young sterile plants (Table 2).

The four species of corallines growing on *Cymodocea* leaves were observed throughout the year but their relative abundance in terms of cover and density showed large differences. *Hydrolithon* sp. and *Hydrolithon boreale* were the most abundant species throughout the year on all leaf segments (Table 2). *Hydrolithon cruciatum* and *Pneophyllum fragile* were always relatively insignificant. *Hydrolithon* sp. was the most abundant



Figs 18–21. Morphology of *Pneophyllum fragile* Kützing.

Fig. 18. Spore germination disc consisting of a 8-celled central element (1–8).

Fig. 19. Surface view of thallus, showing cells of adjacent filaments connected by cell fusions (F) and intercalary trichocytes (T).

Fig. 20. Surface view of a tetrasporangial conceptacle.

Fig. 21. Surface view of spermatangial (S) and carposporangial (C) conceptacles.

species from January to October, with a spring peak (March–April) on the three segments of the leaf (Table 2). *Hydrolithon boreale* was the most abundant in late autumn (November–December), again on all leaf segments. The contribution of *Hydrolithon cruciatum* and *Pneophyllum fragile* to the epiphyte community was relatively small; they showed a seasonal peak in autumn (September–November).

Species density and fertility

In most months, the density of *Hydrolithon* sp. was similar on the different leaf segments (Table 3). In March, however,

the density increased markedly from the base to the apex of the leaf, and in August and September the sequences were inverse, with the highest densities on the proximal segment. However, marked differences occurred over the year (Table 3). The lowest densities were observed in May–July and January, and the highest ones occurred in March and September–October. In *Hydrolithon* sp. fertility always increased from the proximal to the distal segment and sporangial, spermatangial and carposporangial conceptacles were observed in all months (Table 3). The percentage of fertile plants was low in spring (March–April), showing peaks in late summer (September–October) and winter (January). Among fertile plants,

Table 2. Numerical data on density, fertility and cover of epiphytic coralline algae on distal, mid and proximal segments of *Cymodocea nodosa* leaves from December 1987 to November 1988 at El Médano, Canary Islands. Data reported as mean number, mean percentage cover and species percentage of individuals (n = 10) per cm² host leaf surface (Standard deviation in brackets)

	DECEMBER	JANUARY	FEBRUARY	MARCH	APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER	OCTOBER	NOVEMBER
Distal segment of the leaf:												
Total no. individuals	94 (21)	75 (15)	73 (35)	75 (12)	27 (3)	23 (6)	29 (12)	27 (10)	44 (10)	69 (26)	62 (15)	59 (24)
Total no. individuals with conceptacles	7 (10)	25 (18)	3 (6)	2 (4)	1 (1)	7 (7)	9 (6)	15 (10)	22 (11)	36 (24)	21 (16)	23 (15)
Total percentage cover	39.5 (20.9)	54.4 (15.7)	24.4 (21.7)	46 (14.9)	20 (10)	26.2 (10.2)	35 (16.6)	46.1 (17.2)	58.8 (20.2)	73 (16.7)	46 (18)	29.6 (8.5)
Total percentage individuals:												
<i>Hydrolithon</i> sp.	18.5	51.7	44.3	86.6	85.2	62.7	55.9	53.9	54.3	54.9	81.6	38.5
<i>Hydrolithon boreale</i>	81.2	46.9	55.3	12.9	14.8	35.7	44.1	45.3	45.3	43.1	16.2	59.8
<i>Hydrolithon cruciatum</i>	0	0.7	0.4	0.5	0	0	0	0.4	0.2	0.6	1.1	1.3
<i>Pneophyllum fragile</i>	0.3	0.7	0	0	0	1.6	0	0.4	0.2	1.4	1.1	0.4
Mid segment of the leaf:												
Total no. individuals	75 (33)	72 (27)	60 (13)	51 (26)	33 (5)	23 (8)	32 (9)	30 (9)	63 (26)	84 (28)	73 (34)	57 (23)
Total no. individuals with conceptacles	4 (6)	17 (21)	1 (2)	<1	<1	9 (8)	3 (3)	10 (9)	21 (18)	31 (21)	8 (14)	23 (17)
Total percentage cover	21.1 (14.6)	33.8 (25.4)	8.3 (11)	12.5 (6.8)	17.5 (11.2)	19.4 (12.2)	19.5 (12.7)	30.5 (12.1)	54.5 (21.7)	50.5 (17.2)	24.5 (15.4)	28 (12.2)
Total percentage individuals:												
<i>Hydrolithon</i> sp.	18.9	48.4	50.2	79.9	76.8	65.8	63.1	63.5	61.4	61.9	79.7	41.5
<i>Hydrolithon boreale</i>	80.5	50.6	48.2	19.5	22.9	32.6	35.7	35.5	37.4	35.8	17.3	56.2
<i>Hydrolithon cruciatum</i>	0.3	0.4	0	0.6	0	0.8	0.6	0.6	0.6	1.3	2.1	1.7
<i>Pneophyllum fragile</i>	0.3	0.6	1.6	0	0.3	0.8	0.6	0.4	0.6	1	0.9	0.6
Proximal segment of the leaf:												
Total no. individuals	48 (38)	70 (21)	48 (38)	9 (12)	29 (24)	15 (8)	22 (12)	14 (8)	68 (42)	88 (19)	60 (35)	56 (26)
Total no. individuals with conceptacles	0	<1	<1	0	0	2 (3)	<1	<1	17 (15)	17 (16)	2 (3)	17 (17)
Total percentage cover	6.7 (8.5)	6.2 (4)	6 (11.4)	0.4 (0.4)	4 (3)	7 (7.5)	4.5 (3.9)	3.8 (1.8)	34.5 (22)	29.5 (23.7)	12.9 (12.9)	18.2 (15.86)
Total percentage individuals:												
<i>Hydrolithon</i> sp.	21.9	55.4	51.6	96.6	78	70.5	78.9	78.9	60.2	69.3	71.1	41.8
<i>Hydrolithon boreale</i>	78.1	44.4	47.9	3.4	21.6	26.7	19.7	19	37.2	27.3	25.7	53.4
<i>Hydrolithon cruciatum</i>	0	0.1	0	0	0	1.4	0.9	1.4	1.3	2.8	0.5	2.8
<i>Pneophyllum fragile</i>	0	0.1	0.5	0	0.4	1.4	0.5	0.7	1.3	0.6	2.7	2

Table 3. Density and fertility of *Hydrolithon* sp. on distal, mid and proximal segments of *Cymodocea nodosa* leaves from December 1987 to November 1988 at El Médano, Canary Islands. Data reported as mean number of individuals (n = 10) per cm² host leaf surface (Standard deviation in brackets)

	DECEMBER	JANUARY	FEBRUARY	MARCH	APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER	OCTOBER	NOVEMBER
Distal segment of the leaf:												
Total no. individuals	17 (9)	39 (16)	33 (24)	65 (11)	23 (1)	14 (3)	16 (5)	14 (4)	24 (11)	38 (12)	50 (10)	23 (11)
Sterile	14 (9)	20 (11)	26 (24)	57 (11)	21 (1)	7 (4)	11 (6)	6 (4)	10 (5)	21 (16)	35 (14)	13 (6)
With sporangial conceptacles	1 (2)	3 (3)	2 (4)	<1	0	1 (1)	1 (1)	3 (2)	5 (3)	6 (3)	3 (4)	3 (2)
With spermatangial conceptacles	2 (2)	10 (9)	4 (4)	6 (4)	2 (1)	4 (1)	2 (1)	3 (2)	6 (3)	8 (5)	9 (5)	4 (3)
With carposporangial conceptacles	<1	6 (4)	1 (2)	2 (2)	0	2 (1)	2 (1)	2 (1)	3 (2)	3 (3)	3 (3)	3 (3)
Percentage fertile individuals	20.3	49.7	21.2	12.8	10 (4)	46.8	33.9	59	58.4	44.5	30	43.8
Mid segment of the leaf:												
Total no. individuals	14 (8)	35 (19)	30 (18)	41 (20)	25 (10)	15 (6)	20 (4)	19 (10)	38 (18)	52 (23)	58 (24)	24 (12)
Sterile	12 (7)	20 (11)	28 (19)	40 (20)	24 (9)	8 (3)	18 (6)	13 (12)	22 (14)	35 (31)	50 (25)	14 (7)
With sporangial conceptacles	<1	1 (1)	<1	0	0	1 (2)	1 (0)	2 (2)	3 (3)	5 (3)	1 (2)	4 (5)
With spermatangial conceptacles	1 (2)	9 (14)	<1	<1	<1	4 (3)	1 (1)	3 (3)	8 (4)	9 (6)	5 (6)	4 (2)
With carposporangial conceptacles	<1	5 (7)	1 (2)	0	0	2 (1)	<1	1 (1)	5 (4)	3 (3)	2 (4)	2 (2)
Percentage fertile individuals	12.6	44.1	5.3	2.2	1.9	45.4	10.8	34.2	42.9	31.9	14.5	42.1
Proximal segment of the leaf:												
Total no. individuals	10 (9)	39 (19)	25 (23)	9 (11)	23 (17)	10 (4)	18 (8)	11 (6)	41 (28)	61 (27)	43 (22)	24 (18)
Sterile	10 (9)	39 (19)	24 (21)	9 (11)	23 (17)	9 (4)	17 (8)	10 (6)	34 (25)	55 (31)	42 (21)	20 (13)
With sporangial conceptacles	0	0	0	0	0	0	0	<1	<1	1 (1)	0	<1
With spermatangial conceptacles	0	<1	<1	0	0	<1	<1	<1	4 (3)	4 (5)	1 (1)	3 (5)
With carposporangial conceptacles	0	0	<1	0	0	<1	0	0	2 (2)	1 (1)	0	<1
Percentage fertile individuals	0	0.5	3.6	0	0	12.6	1.1	2.6	16.6	9.6	2.1	14.8

plants bearing spermatangial conceptacles were the most abundant, with the maximum number of individuals in January and September–October and minimal numbers in spring (April–June). Carposporangial plants were abundant in January and sporangial plants mainly occurred in late summer (August–September).

Except for December, no gradient was observed in the density of *Hydrolithon boreale* plants along the leaf (Table 4). Nevertheless, variations in density were marked over the year. The lowest densities occurred from March to July and the highest one was observed in December. As in *Hydrolithon* sp. the fertility of *Hydrolithon boreale* increased from the proximal to the distal segment of the leaf. In March and April only sterile plants were observed, whereas sporangial and gametangial conceptacles occurred in other months (Table 4). Plants with conceptacles were relatively common from July to January, although no significant peaks of fertility were observed. Among the fertile plants, gametophytes were more common than sporophytes.

Hydrolithon cruciatum and *Pneophyllum fragile* contributed only slightly to the crustose community and insufficient data were obtained on their density and fertility to detect variations along the leaf. However, both species seem to be most abundant in late summer but with density values lower than 3 individuals per cm² leaf surface.

DISCUSSION

Several authors have shown that species of *Hydrolithon* (as *Fosliella*) and *Pneophyllum* are the most common epiphytes on seagrasses in many parts of the world (e.g. Humm 1964; Chamberlain 1977, 1983; Harlin 1980; Bramwell & Woelkerling 1984; Jones & Woelkerling 1984; Harlin *et al.* 1985), and the present investigation has shown that this applies also to the Canary Islands.

Among the *Fosliella* states identified on the leaves of *Cymodocea nodosa* at El Médano, plants referred to in this paper as *Hydrolithon* sp. cannot be attributed to any described species. *Hydrolithon* sp. shows the pattern of spore germination disc illustrated by Harlin *et al.* (1985, fig. 6) for a species of *Fosliella* (reported as *Fosliella* A) from Shark Bay, Western Australia, but cells of *Hydrolithon* sp. from the Canaries are larger. The absence of additional information in the study by Harlin *et al.* (1985) prevents further comparison.

Based on material from El Médano, it seems that *Fosliella* states can be delineated on the basis of differences in the arrangement of cells in the germination discs. Three distinct patterns were found, which remained constant and distinctive along the leaves of *Cymodocea* and over the year. Results from the present study support the hypothesis that differences in the arrangement of cells in the germination disc form a stable character which can be used for species delimitation. Other vegetative features (e.g. morphology of ventral filaments or trichocyte fields) and reproductive features (e.g. morphology of sporangial or gametangial conceptacles) also permit species identification.

The distribution of epiphytes on seagrass leaves is influenced by the relative age of the different segments of the leaves (Harlin 1980; Borowitzka & Lethbridge 1989). In all leaves

Table 4. Density and fertility of *Hydrolithon boreale* on distal, mid and proximal segments of *Cymodocea nodosa* leaves from December 1987 to November 1988 at El Médano, Canary Islands. Data reported as mean number of individuals (n = 10) per cm² host leaf surface (Standard deviation in brackets)

	DECEMBER	JANUARY	FEBRUARY	MARCH	APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER	OCTOBER	NOVEMBER
Distal segment of the leaf:												
Total no. individuals	76 (21)	35 (16)	41 (30)	10 (7)	4 (2)	8 (5)	13 (9)	12 (8)	20 (12)	30 (21)	10 (6)	35 (21)
Sterile	57 (12)	26 (13)	36 (23)	10 (7)	4 (2)	5 (2)	12 (9)	8 (4)	12 (6)	18 (9)	7 (3)	24 (19)
With sporangial conceptacles	5 (4)	1 (2)	3 (5)	0	0	1 (2)	<1	1 (2)	4 (4)	3 (4)	<1	5 (3)
With gametangial conceptacles	14 (14)	9 (11)	3 (5)	0	0	1 (1)	1 (2)	3 (4)	4 (3)	9 (10)	2 (2)	6 (6)
Percentage fertile individuals	24.7	26.4	10.1	0	0	33.7	7.8	31.4	38.1	39.8	32.3	31
Mid segment of the leaf:												
Total no. individuals	60 (37)	36 (21)	29 (11)	10 (15)	8 (6)	8 (4)	12 (5)	11 (6)	23 (14)	30 (18)	13 (8)	32 (16)
Sterile	57 (34)	32 (16)	29 (11)	10 (15)	8 (6)	6 (3)	11 (5)	9 (5)	15 (7)	21 (12)	10 (5)	22 (10)
With sporangial conceptacles	<1	<1	0	0	0	<1	0	1 (1)	4 (4)	1 (1)	<1	4 (5)
With gametangial conceptacles	3 (2)	4 (4)	0	0	0	1 (1)	<1	<1	5 (5)	8 (9)	2 (4)	6 (6)
Percentage fertile individuals	5.1	12.0	0	0	0	24	1.7	13.9	37.6	30.1	20.6	29.9
Proximal segment of the leaf:												
Total no. individuals	38 (32)	31 (19)	23 (25)	<1	6 (7)	4 (4)	4 (4)	3 (3)	25 (22)	24 (13)	16 (16)	30 (23)
Sterile	38 (32)	31 (19)	23 (25)	<1	6 (7)	3 (4)	4 (4)	3 (3)	22 (19)	19 (8)	15 (16)	28 (22)
With sporangial conceptacles	0	0	0	0	0	<1	0	0	1 (1)	<1	0	<1
With gametangial conceptacles	0	0	<1	0	0	<1	0	0	2 (3)	4 (5)	<1	1 (2)
Percentage fertile individuals	0	0	0.05	0	0	10.2	0	0	12.3	20	1.3	6.6

examined, significant increases in epiphyte cover and fertility occurred from proximal to distal segments (Table 2). Bramwell & Woelkerling (1984) found similar results for the distribution of *Hydrolithon* (as *Fosliella*) and *Pneophyllum* plants on leaves of the seagrass *Amphibolis antarctica* collected in March (late summer) in south-eastern Australia. According to Bramwell & Woelkerling (1984), the increases in cover and fertility as well as in the density of epiphytes along the leaves may be partly due to the relatively greater levels of illumination at the distal ends of the leaves and partly to the fact that the distal regions of leaves are the oldest. The seasonal variations may be due to the growth rates and life span of the leaves and the growth rates of the epiphytes.

The total density, cover and fertility of the coralline epiphytes recorded on the leaves of *Cymodocea nodosa* presented marked seasonal variations. In spring the density, cover and fertility were low, increasing during the summer before reaching maxima in late summer. In autumn cover and fertility decreased while density remained high and in winter low cover and low fertility were detected, together with high density values.

The absence of similar studies on the annual distribution of coralline epiphyte communities on leaves of seagrasses prevent further comparisons. However, data on the effects of environmental and biological factors on the epiphytes have been published. According to Adey (1970), temperature and light are major factors affecting the growth rates of both thin crustose epiphyte taxa and thick crustose epilithic taxa of Corallinaceae. Bressan *et al.* (1979) concluded that light is one of the primary factors affecting growth and that *Hydrolithon cruciatum* (as *Fosliella cruciata*) grew more rapidly under diffuse lighting conditions. Bressan & Tomini (1980) concluded that temperature had the greatest effect on the growth of species of *Hydrolithon* (as *Fosliella*) and *Pneophyllum* and that the fastest growth was observed under summer conditions and the slowest growth in winter and spring. Most recently, Jones & Woelkerling (1983) showed that growth and conceptacle production in *Hydrolithon cruciatum* (as *Fosliella*) were affected by light and temperature. The growth rates and conceptacle production in species of *Hydrolithon* and *Pneophyllum* may therefore be higher than in more massive epilithic taxa of nongeniculate Corallinaceae and this may help to explain why taxa of *Hydrolithon* and *Pneophyllum* are able to survive and develop as epiphytes on ephemeral seagrass leaves.

Summer conditions, with high values of light and temperature, may explain why density, cover and fertility of crustose epiphytes on the leaves of *Cymodocea nodosa* at El Médano increased during summer, showing peaks in September. With the decrease in light and temperature in autumn and winter, the cover and fertility of crustose epiphytes also decreased. The high number of individuals that persisted during these months were mainly sterile juvenile plants. This appears to confirm the results of Jones & Woelkerling (1983) on the effects of light and temperature on conceptacle production in *Hydrolithon cruciatum* (as *Fosliella*). However, minimal values in density, cover and fertility of crustose epiphytes observed in spring cannot be explained satisfactorily on the basis of light and temperature variations. According to Borowitzka & Lethbridge (1989), in the seagrasses the life span of the leaves

and the rates of leaf replacement affect epiphyte diversity and biomass. The rates of growth and replacement of leaves regulate the abundance and persistence of the available substratum for crustose epiphytes. Rapid growth and replacement of leaves can reduce competition for space among epiphytes. Seed & O'Connor (1981) provided examples of these processes for invertebrate communities on marine algae and, according to Borowitzka & Lethbridge (1989), similar principles may apply to seagrass epiphytes. In populations of *Cymodocea nodosa* at El Médano the mean life span of leaves is about three months from October to December and about two months from May to July, and leaf growth-rate values observed from April to July doubled or tripled those for October–November (unpublished data, Reyes 1993). These data suggest that the low density, fertility and cover of crustose Corallinaceae observed in early spring may be due to the short life of the substratum, whereas the longer mean life span of leaves in autumn–winter permits a greater development of crustose algae.

Finally, gametangial plants of *Hydrolithon* were more common than sporangial ones (Tables 3, 4). In the dioecious *Hydrolithon* sp. spermatangial plants were more common than carposporangial ones (Table 3). A similar gametangial predominance was reported by Harlin *et al.* (1985) in *Hydrolithon* (as *Fosliella*) from the epiphyte community of *Amphibolis antarctica*. According to Harlin *et al.* (1985) these variations were probably due to a high level of fragmentation in gametangial plants. However, in the coralline epiphyte community of *Cymodocea nodosa* leaves, evidence of vegetative thallus fragmentation as a means of vegetative reproduction was not observed and most fertile individuals had germination discs. The high percentage of plants lacking conceptacles may help to explain the variations in the ratios of gametangial/sporangial plants and spermatangial/carposporangial plants, but further studies are needed to clarify this question.

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