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Species richness, spatial distribution and colonisation pattern of algal and invertebrate epiphytes on the seagrass *Amphibolis griffithii*

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ABSTRACT: The distribution of epiphytic algae and sessile invertebrates on the seagrass *Amphibolis griffithii* is not random. The number of epiphyte species increases with increasing seagrass height and there are approximately twice as many epiphytic algal species as invertebrate species. Epiphytes growing on the stems have a clear apico-basal distribution, with algae such as *Haliptilon roseum, Laurencia filiformis* and *Hypnea* spp. most abundant on the upper 30 % of the seagrass stem, while the bryozoan *Celleporina* sp. and the hydrozoan *Thyroscyphus marginatus* are most abundant near the base of the stem. Other species of algae and invertebrates have intermediate distributions. Epiphyte biomass increases with seagrass height and the bulk occurs on the uppermost 20 cm of the tallest plants. This is mainly due to 1 or 2 algal species. Recruitment of epiphytes also follows a distinct pattern related to plant size (age), with species such as the crustose coralline algae rapidly colonising the leaves and stems of new seagrass plants. Other very early colonisers are the bryozoans *Pyripora polita* and *Electra flagellum* on the stems, and the hydrozoan *Plumularia compressa* and the bryozoan *Thairopora mamillaris* on the leaves.

INTRODUCTION

Stands of the seagrass *Amphibolis antarctica* (Labillardiere) Sonder *et* Ascherson *ex* Ascherson and *A. Griffithii* (J. M. Black) Den Hartog (Potamogetonales, Cymodoceaceae) are very common in the shallow waters of southern and southwestern Australia (Kirkman & Walker 1989). *A. antarctica* occurs from Carnarvon, Western Australia (24°55′S) to Wilson's Promontory, Victoria (39°00′S), whereas *A. griffithii* has a more restricted distribution from Kalbarri, Western Australia (27°40′S) to Victor Harbour, South Australia (35°30′S) (Ducker et al. 1977, Borowitzka pers. obs.). Unlike most other seagrasses, *Amphibolis* species have lignified, long-lived, upright stems and these stems, as well as the terminal leaf clusters, provide excellent substrata for many large epiphytic algae and invertebrates.

As first reported by Harvey (1847, 1855), the epiphytic biota of *Amphibolis* spp. are very diverse. Ducker et al. (1977) recorded 116 epiphytic algae and 20 species of invertebrates epiphytic on *Amphibolis*, and noted that their species list was undoubtedly not comprehensive. *Amphibolis* is a major habitat for many of these species, but most are also found on adjacent algae or grow epilithically; only a few algae (*Dicranema revolutum* (C. Ag.) J. Ag., *D. cincinnalis* Kraft and *Metagoniolithon stelliferum* (Lamarck) Weber van Bosse), and invertebrates (*Stenochiton cymodocealis* and *Campanularia tincta*) grow exclusively, or almost exclusively, on *Amphibolis*. The turnover and biomass production of the epiphytic biota contributes significantly to the primary production of the *Amphibolis* ecosystem (Ducker et al. 1977), and thus to the highly productive shallow coastal ecosystems of southern and southwestern Australia. The epiphytes are also an important food resource and habitat for many fish, the western rock-lobster *Panulirus cygnus* and many other invertebrates (Joll & Phillips 1984, Nichols et al. 1985, Howard et al. 1989, Klumpp et al. 1989).

Aside from their importance as food and shelter, *Amphibolis* and its epiphytes also provide a 'natural' model for the study of settlement, recruitment and competition between sessile marine algae and invertebrates. The rather constant morphology of *Amphibolis* stems and leaves over its geographical range make it particularly suitable for studies of this type.

This paper describes the spatial distribution of epiphytes on the seagrass, and the influence of plant

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size and age on the pattern of colonisation and species richness of the epiphytic biota, and provides base-line data for further studies of the temporal and spatial dynamics of the epiphytic populations.

MATERIALS AND METHODS

Stand of *Amphibolis griffithii* were sampled between July and November 1983 at 3 sites in Western Australia; one adjacent to Penguin Island near Fremantle (ca 115°41′ E, 32°19′ S), one at Seven Mile beach near Dongara (ca 114°55′ E, 29°22′ S) and one at Two People's Bay, near Albany (ca 117°54′ E, 35°02′ S). Up to eight 0.25 m^2 quadrats were placed in a predetermined pattern around a randomly selected point in a homogeneous bed of *A. griffithii* at about 2 to 3 m depth. All plants within each quadrat were cut off just above the substratum with scissors and transported to the laboratory where they were either preserved in 6 % (v/v) neutralised formalin in seawater, or frozen at −20 °C until analysis.

Reference samples of all algal species collected are housed in the Murdoch University herbarium (MURU).

Epiphyte diversity and patterns of colonisation. ***Epiphyte diversity:*** In order to assess the diversity of epiphytes on *Amphibolis griffithii* plants of different size, seagrasses from quadrats collected at Penguin Island and Seven Mile Beach in September 1983 and at Two People's Bay in November 1983 were sorted into 10 cm height-interval size classes. Ten plants from each size class were taken at random from each quadrat and their stems and leaves separated for analysis. The number of species of epiphytic algae and sessile invertebrates associated with the stems and leaves were then plotted against the height of each *A. griffithii* plant.

Patterns of colonisation: An insight into the pattern of colonisation of stems and leaves by species occurring in samples from the above collections was obtained by examining the taxa present on all plants in each quadrat. Presence and absence data for each species were then plotted against the heights of the plants in the samples.

Biomass of stems, leaves and epiphytes versus plant height. After inspection of the 10 plants in each size class used to determine epiphyte diversity, all macroscopic epiphytic species, except encrusting coralline algae, were removed with jeweller's forceps. The number of branches on each plant was counted, and the dry weight of the cleaned stems and leaves determined.

All algae from each plant, other than encrusting coralline algae, were separated into species for dry weight determinations. The encrusting coralline algae and small epiphytic invertebrates did not permit meaningful dry weight measurements and were recorded only as present or absent.

The number of branches, and dry weights of stems, leaves and macroalgal epiphytes for plants in each size class were plotted as scattergrams against plant height.

Epiphyte distribution on stems and leaves. The distribution of epiphytic organisms on the stems and leaves was analysed in detail using the November 1983 samples from Penguin Island. Distribution patterns of the algae were based upon 30 randomly selected *Amphibolis* stems, whereas for the less numerous invertebrates 60 stems were employed. After removing the leaves for separate analysis, each of the stems was cut into 10 equal portions, i.e. into percentiles.

Macroalgae were removed from each percentile division, sorted into species, and their wet weight recorded to the nearest 0.1 g. Blotted wet weights were used because the quantities of many algal species associated with each percentile division were frequently too small to yield more accurate dry weight measurements. Macroalgae present on the leaves were also assessed from their blotted wet weight.

The different growth habits and phenology of other epiphytic organisms required different methods of analysis. Thus, the area covered by encrusting coralline algae and bryozoan colonies ensheathing the stems were assesseds visually and scored on a 0 (absent) to 20 (total cover) scale. Quantitative data on the stem hydroids [*Stereotheca elongata* (Lamouroux), *Aglaophenia plumosa* Bale, *Thyroscyphus marginatus* (Bale)] were obtained by counting the number of fans or erect colonies associated with each percentile division.

The predominant hydroids (e.g. *Plumularia compressa*) and encrusting bryozoans (e.g. *Thairopora mamillaris*) on the leaves were quantified by counting the number of leaves per plant that possessed colonies of these species. Small, discrete colonies (e.g. the bryozoan, *Lichenopora* sp.) and non-colonial organisms (e.g. *Spirorbis* sp.) were counted individually.

RESULTS

Epiphyte diversity and patterns of colonisation

To date, we have recorded over 150 species of multicellular algae and over 40 species of sessile invertebrates that grow epiphytically on *Amphibolis griffithii* at the 3 study sites. Only a small number of these species were routinely observed on individual plants because the majority of epiphytes were patchily distributed between plants and between sites.

The number of species of epiphytic algae at all 3 sites

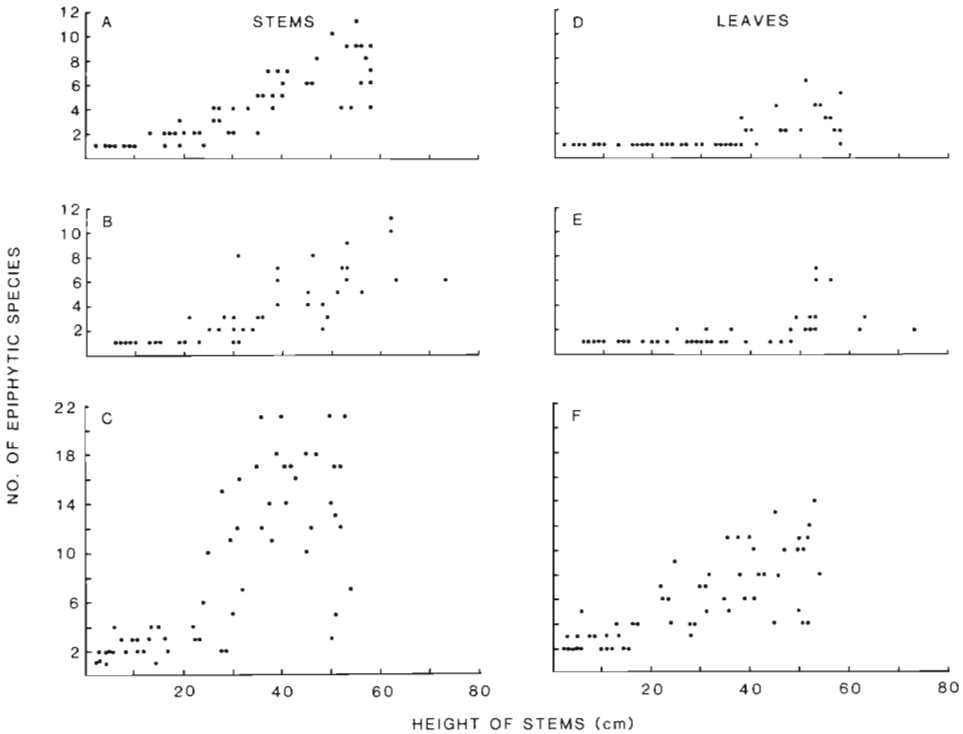

Fig. 1. Numbers of species of algae epiphytic on plants of *Amphibolis griffithii* of different height. (A, D) Seven Mile Beach site, September 1983; (B, E) Penguin Island site September 1983; (C, F) Two People's Bay site, November 1983

Table 1. Number of species of epiphytic organisms on *Amphibolis griffithsii* stems and leaves in 0.25 m^2 quadrats (Penguin Island, November 1983)

Quadrat no.	Numbers of species					
	Stems		Leaves		Total	
	Inverts.	Algae	Inverts.	Algae	Inverts.	Algae
1	8	38	3	25	11	42
3	11	29	3	20	13	38
4	10	34	2	18	12	36
5	8	36	2	19	10	41
8	12	39	3	24	15	47

(Fig. 1, Table 1) exceeded the number of species of epiphytic sessile invertebrates (Fig. 2, Table 1), and more epiphytic species were associated with the seagrass stems than with the leaves. There were up to twice as many epiphytic algal species on stems compared to the leaves, whereas the number of epiphytic invertebrate taxa showed little difference between these substrata (Table 1, Fig. 2) except in November when the overall diversity increased markedly, especially on the stems. Few species of epiphytes, especially invertebrates, were common to both stems and leaves.

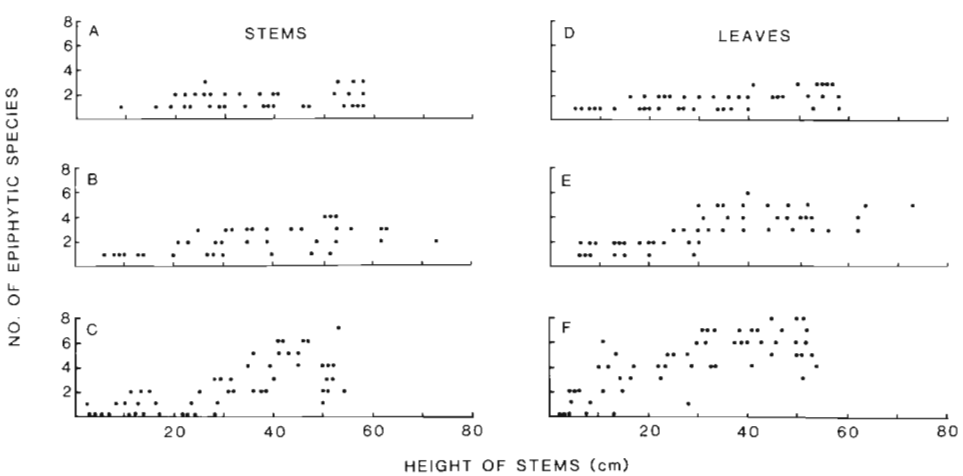

Fig. 2. Numbers of species of sessile invertebrates epiphytic on plants of *Amphibolis griffithii* of different height. (A, D) Seven Mile Beach site; (B, E) Penguin Island site; (C, F) Two People's Bay site. Same quadrats as for Fig.1

There was a clear relationship between the number of epiphytic species recorded at each site and the heights of the *Amphibolis griffithii* plants (Figs. 1 and 2). Thus, the maximum diversity of epiphytic algae was recorded on plants whose height was within 10 to 20 cm of the tallest individuals in the stand. Epiphytic invertebrates, however, approached or reached their maximum diversity on smaller plants. A reduced number of epiphytic algal species occurred on both the stems and leaves of the tallest *Amphibolis* plants in the quadrats (Figs. 1 and 2).

Since plant height is a function of plant age, the pattern of recruitment of epiphytic organisms can be observed by plotting the presence or absence of individual species in the samples against plant height (Fig. 3). The initial colonisers observed on the stems and leaves of 2 to 4 cm tall plants were mainly *Fosliella cymodoceae* (Foslie) Jones & Woelkerling, *F. cruciata* Bressan, and *Pneophyllum caulerpae* (Foslie) Jones & Woelkerling. Almost simultaneously, the bryozoans *Pyripora polita* (Hincks) and *Electra flagellum* (MacGillivray) were recruited on the stems, and the hydrozoan *Plumularia compressa* and the bryozoan *Thairopora mamillaris* appeared on the leaves. Various sponges were also found at times on the stems and leaves of small plants. Older *Amphibolis griffithii* plants that exceeded a height of ca 15 cm were further colonised by other algae such as *Dicranema revolutum, D. cincinnalis, Hypnea* spp., *Gloiosaccion brownii* Harvey and *Rhodymenia australis* Sonder, as well as by the bryozoan *Adeonellopsis portmarina* (Maplestone). The polychaete *Spirorbis* sp., the bryozoan *Lichenopora* sp., and the red alga *Ceramium puberbulum* Sonder occurred on the leaves of these plants. Taller seagrasses (> 30 cm) were further colonised by numerous other species of algae and invertebrates, with *Laurencia filiformis* and the coralline algae *Haliptilon roseum* and *Metagoniolithon stelliferum* almost always occuring (Fig. 3).

There is clearly some seasonality in species diversity, with a clear increase in epiphyte species number in early summer (November) samples compared to the winter and spring samples (Table 2). Most of the additional species were very patchily distributed among the quadrats, and the increase in invertebrates was mainly due to sponges.

Biomass of stems, leaves and epiphytes versus plant height

The relationships betwen these variables were determined from September 1983 samples from Penguin Island and are shown in Fig. 3. Similar results were also obtained at the other 2 sites.

As the *Amphibolis griffithii* plants increased in height the stems became more branched (Fig. 4A), and their dry weight increased progressively (Fig. 4B). Since *A. griffithii* stems and branches are remarkably uniform in diameter along their whole length, their dry weight is essentially a linear index of stem surface area. Taller plants therefore possessed a larger stem and branch surface area for colonisation by epiphytic organisms.

The dry weight of the leaves is also an index of the surface area available for epiphytic colonisation. In our samples leaf dry weight was more variable than stem dry weight, but also increased with increasing plant height (Fig. 4C). This is due to the fact that each branch is normally terminated by a leaf cluster, and these leaf

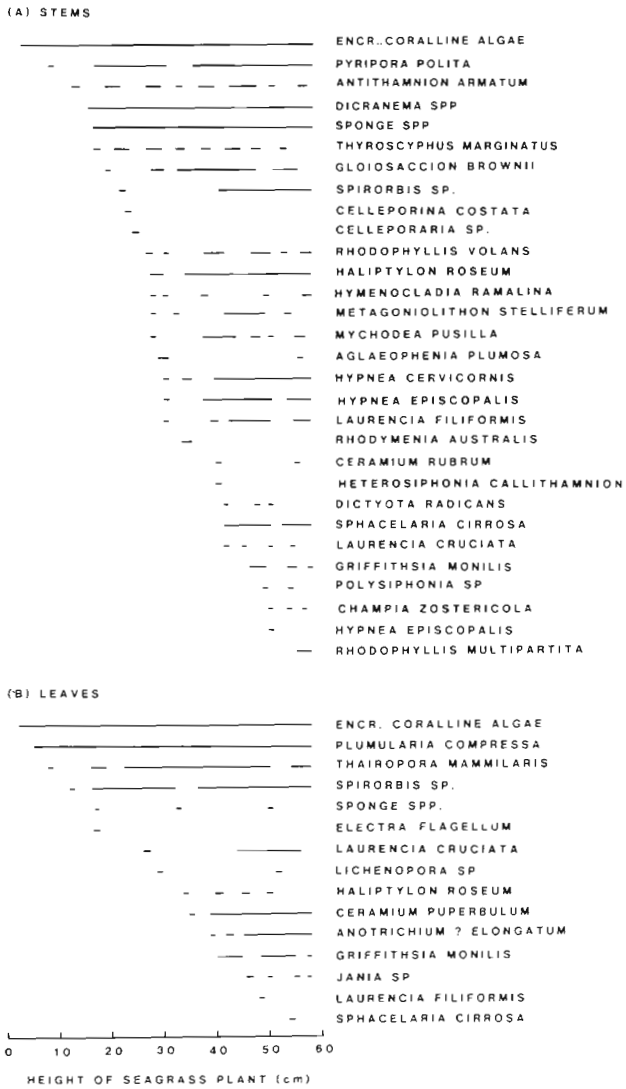

Fig. 3. Distribution of epiphytic organisms on (A) stems and (B) leaves of *Amphibolis griffithii* plants of different height. Data pooled from 150 plants from Penguin Island (September 1983). Species of crustose coralline algae have been combined

Table 2. Total algal species per 0.25 m^2 quadrat

Site	Month	Mean±SE	Range	No. quadrats
Dongara	Sep	18.25±1.75	15–21	8
Penguin Isl.	Jul	23.17±2.48	19–26	6
Penguin Isl.	Nov	40.80±4.21	36–47	5

clusters are of fairly uniform size. The linear regression equation between branch number and leaf weight, calculated for 150 stems collected at Seven Mile Beach, in September 1983 was

$$\text{Leaf dry wt} = -0.152 + 0.158 \text{ Branch no.}$$

with a correlation coefficient of 0.8114. The reduction in leaf dry weight observed in the tallest plants (Fig. 4C) was due to the loss of some terminal leaf clusters from these plants, presumably due to the higher drag that the tallest plants are exposed to.

The biomass of the epiphytic algae was not correlated with the number of taxa on each plant (compare Figs. 1B, 1E and 4D), nor directly related to the increasing height of the seagrass (Fig. 4D). The biomass of the epiphytic algae remained fairly low and constant with increasing seagrass height until the *Amphibolis griffithii* plant reached a size within 10 to 20 cm of the maximum height of the seagrass stand (Fig. 4D). Once this size was reached, there was a sudden and very pronounced increase in epiphytic algal biomass. The biomass of the epiphytic algae on the talles plants often equalled that of the seagrass itself, and more than 80 % of the total algal biomass was restricted to the apical 40 % of the stems.

The increase in epiphyte biomass on these taller stems was due to the proliferation of only 1 or 2 species of algae on each stem. Major contributions to the algal biomass varied between quadrats and sites but were usually made by *Laurencia filiformis, Haliptilon roseum, Hypnea* spp., *Dicranema* spp. and *Metagonio-*

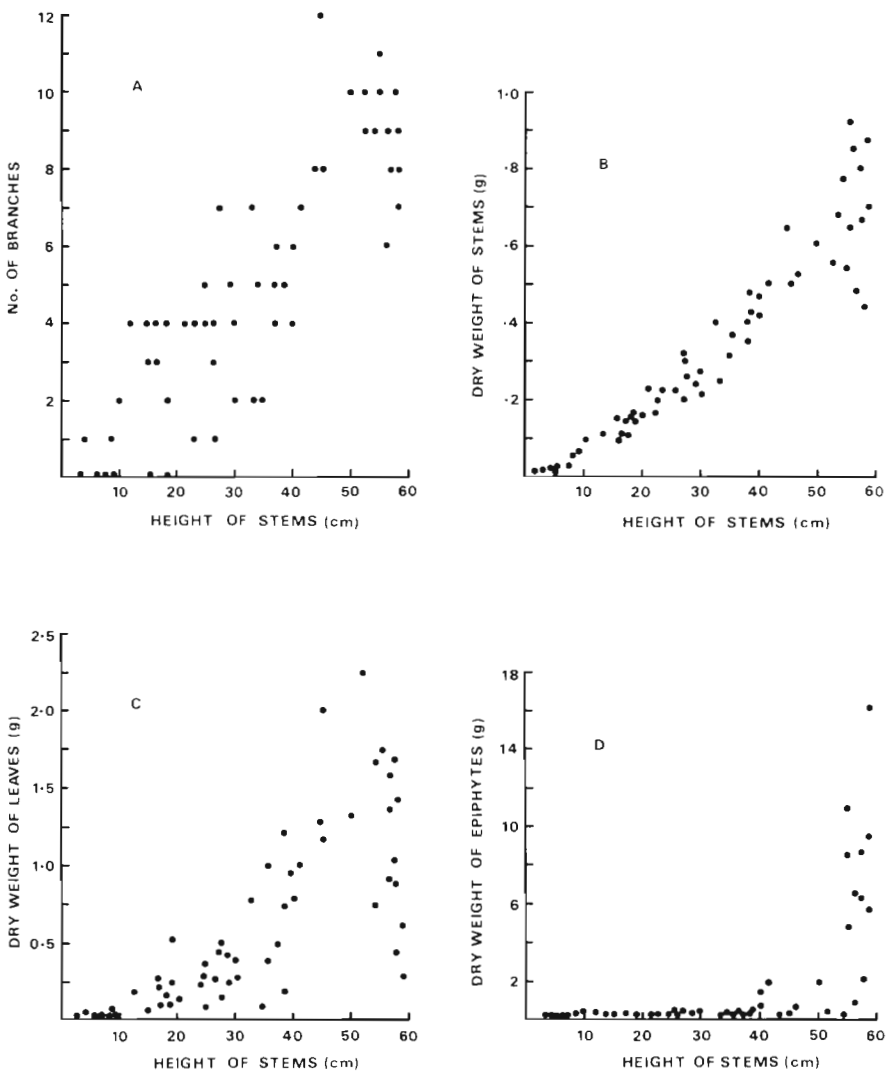

Fig. 4. *Amphibolis griffithii*. (A) Numbers of branches per plant with increasing height of seagrass; (B) dry weight of stems of different height; (C) dry weight of leaves from stems of different height; (D) total dry weight of epiphytic algae on individual plants of increasing height. All samples from Penguin Island site, September 1983

Table 3. Distribution of mean biomass among algal species epiphytic on *Amphibolis griffithsii* at Penguin Island (November 1983), in four 0.25 m^2 quadrats. (N.B. Crustose coralline algae are not listed since their dry weight could not be determined accurately)

Species	Mean dry wt ± SE	Range	
Metagoniolithon stelliferum	7.395 ± 4.399	(3.218 – 13.538)	
Laurencia filiformis	5.855 ± 3.175	(1.649 – 9.048)	
Plocamium mertensii	0.789 ± 1.344	(0.011 – 2.797)	
Haliptilon roseum	0.700 ± 0.083	(0.589 – 0.786)	
Hymenocladia ramalina	0.614 ± 0.382	(0.224 – 0.964)	
Hypnea cervicornis	0.401 ± 0.441	(0.064 – 1.049)	
Heterosiphonia callithamnion	0.366 ± 0.239	(0.206 – 0.723)	
Dicranema revolutum	0.165 ± 0.097	(0.057 – 0.287)	
Rhodymenia australis	0.162 ± 0.083	(0.043 – 0.230)	
Dictyota radicans	0.124 ± 0.209	(0.011 – 0.438)	
Gloiosaccion brownii	0.109 ± 0.124	(0.031 – 0.292)	
Dasyclonium incisum	0.093 ± 0.074	(0.018 – 0.193)	
Haloplegma preissi	0.082 ± 0.036	(0.048 – 0.130)	
Polysiphonia amphibolis/Polysiphonia forfex	0.056 ± 0.035	(0.015 – 0.098)	
Champia zostericola	0.029 ± 0.156	(0.015 – 0.051)	
Chaetomorpha sp.	0.022 ± 0.028	(0.001 – 0.064)	
Craspaedocarpus tenuifolius	0.022	(0.009 – 0.064)	[3][a]
Mychodea marginifera	0.017	(0.009 – 0.058)	[2]
Mycodea australis	0.009	(0.040 – 0.309)	[2]
Bryopsis plumosa	0.006	(0.001 – 0.015)	[3]
Ulva rigida	0.006	(0.001 – 0.015)	[3]
Bornetia binderiana	0.006	(0.009 – 0.015)	[2]
Griffithsia monilis	0.004		[1]
Lenormandia spectabilis	0.004		[1]
Antithamnion armatum	0.004		[1]
Ceramialean alga	0.004		[1]
Codium sp.	0.002		[1]

[a] No. of quadrats in which this species occurred. Otherwise, species occurred in all 4 quadrats

lithon stelliferum (Table 3). In the sample illustrated in Fig. 4D, the increase in dry weight of the epiphytes growing on *Amphibolis griffithii* plants greater than 50 cm high was mainly due to *H. roseum*. Thus, much of the dry weight was $CaCO_3$ since the organic content of this alga is only ca 40 % of total dry weight as determined by ashing at 650 °C.

Epiphyte distribution on stems and leaves

The different epiphytic species clearly recruit successfully to different parts of the *Amphibolis griffithii* plant. Detailed analyses of the stems and leaves were therefore undertaken in order to quantify this differential recruitment.

Stems

Individual algal species sampled at Penguin Island in November 1983 varied in their distribution on the seagrass stems (Fig. 5). Although most abundant in the mid-region, the encrusting coralline alga *Fosliella cymodocaeae* regularly occurred along the whole length of the stem. Other algal species exhibited a more restricted distribution. Thus, the branched, fleshy algae such as *Laurencia filiformis, Hypnea* spp. and *Polysiphonia* spp. occurred mainly on the upper 30 % of the stem (Fig. 5) whereas *Rhodophyllis multipartita, Haliptilon roseum* and *Champia zostericola* sp. were most abundant just below this level (Fig. 5). Other common red algae such as *Dicranema* spp. and *Gloiosaccion brownii* occurred over a wider region of the stem, but were still most abundant on its upper half.

The most common sessile invertebrates on the stems of *Amphibolis griffithii* were 3 colonial hydroids *(Aglaophenia plumosa, Stereotheca elongata* and *Thyrosyphus marginatus)* and 2 bryozoans *(Electra flagellum* MacGillivray, and *Pyripora polita). A. plumosa* and *S. elongata* are both characterised by creeping stolons that give rise to erect, symmetrical and fan-shaped colonies from which the polyps emerge. Both species occurred within all percentile divisions of the stems amongst and between tufts of macroalgae. They were usually more common in the mid-stem region (Fig. 6). *T marginatus* was the least common of the stem-dwelling hydroids and exhibited a marked predeliction for the basal parts of the stem (Fig. 6). When 2 or more hydroid species inhabited the same stem, they were

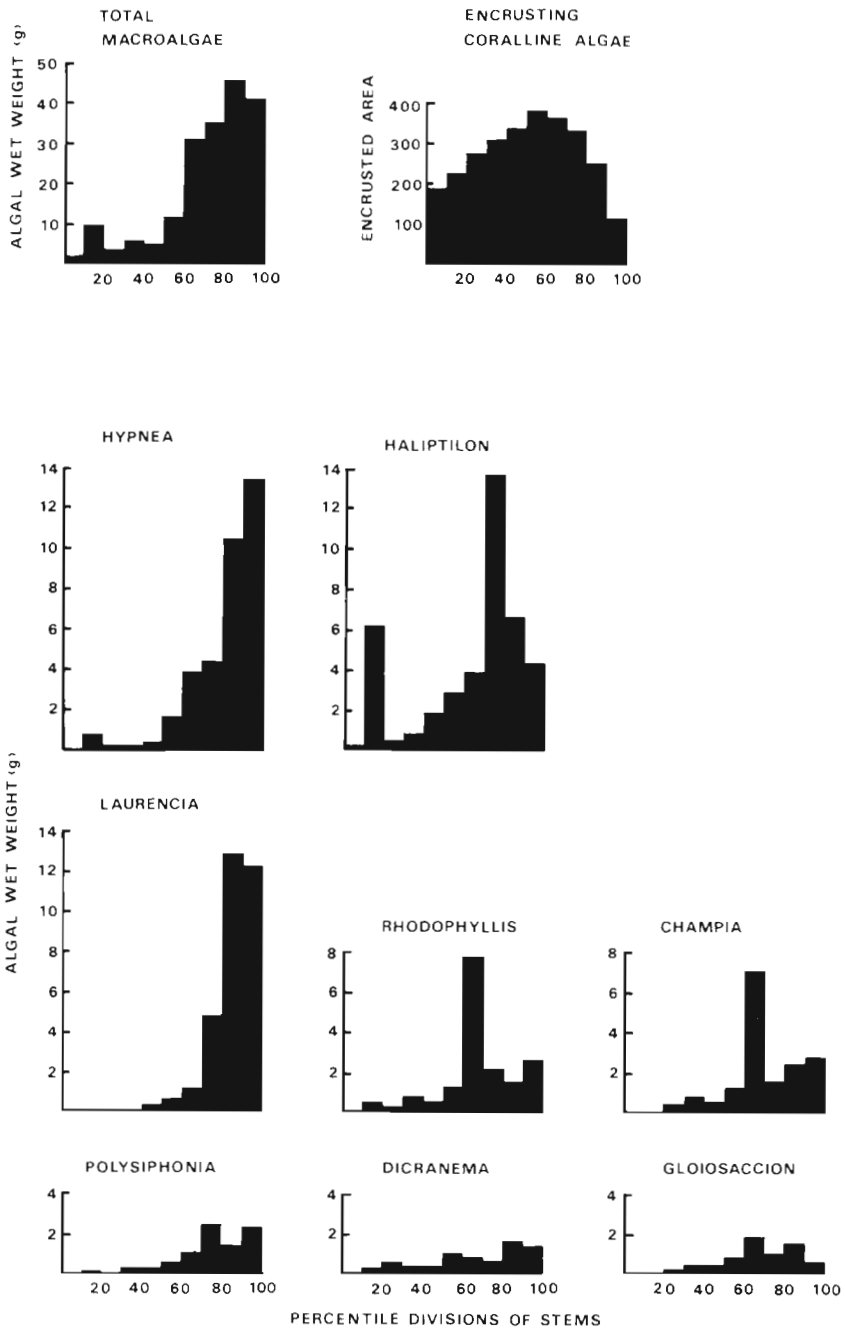

Fig. 5. Distribution of the most common epiphytic algae on 30 stems of *Amphibolis griffithii* (Penguin Island, November 1983) separated into percentile divisions expressed as relative cover (crustose coralline algae) or on a wet weight basis (other species). Species are *Hypnea musciformis, Haliptilon roseum, Laurencia filiformis, Rhodophyllis multipartita, Champia viridis, Polysiphonia* sp., *Discranema revolutum, D. cincinnalis* and *Gloiosaccion brownii*

usually located within different percentile divisions and rarely overlapped (Fig. 6).

The bryozoans *Electra flagellum* and *Pyripora polita* are superficially similar in appearance, but the skeleton of *E. flagellum* is less calcified and apparently much more flexible than that of *P. polita*. This may account for the wider distribution of *E. flagellum* on the upper divisions of the seagrass stem (Fig. 7), where water motion and flexing of the stem are much greater. Although considerably rarer, 4 other bryozoans were associated with *Amphibolis griffithii* stems. *Adeonellopsis portmarina* (Maplestone) formed foliose and highly calcified colonies that projected laterally from the basal region of the stems, and *Celleporaria* sp., with its distinctive calcereous and spiral architecture, also colonised stems close to the level of the substratum. By contrast, *Celleporaria costata* formed irregularly-shaped and calcified colonies that were frequently associated with junction regions between the main and lateral stem branches. The remaining bryozoan, *Elezerina blainvilli*, exhibited a characteristic 3-dimensional branching pattern so that its holdfast regions often formed extensive cross-linkages between stems, leaves and epiphytic macroalgae. Sponges and asci-

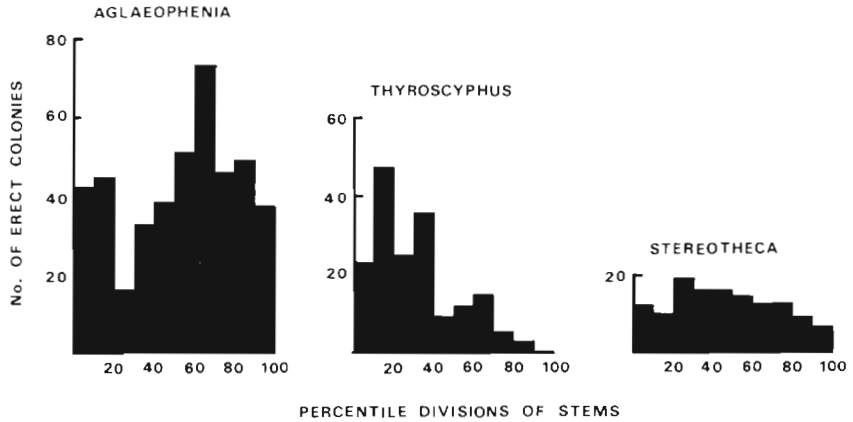

Fig. 6. Distribution of the common epiphytic hydrozoans on the same stem sample as Fig. 4, expressed as the number of erect colonies. Species are *Aglaeophenia plumosa, Thyroscyphus marginatus* and *Stereotheca elongata*

dians also occurred at various points along *Amphibolis* stems but were uncommon.

Leaves

By comparison with the *Amphibolis griffithii* stems, the epiphytic flora and fauna of the leaves are impoverished. Examination of more than 800 individual leaves in this study showed that while most bore the encrusting coralline algae *Fosliella cymodocea* and *Pneophyllum caulerpae*, the area of coverage was very variable. Young (terminal) leaves were generally devoid of any epiphytes, while the area covered by the encrusting coralline algae increased progressively with leaf size (age) and was greater in the lower (older) leaves of a leaf cluster. Area estimates indicated an average of 24.4 % coverage by encrusting coralline algae for all leaves examined in the November 1983 samples from Penguin Island.

Other common epiphytic algae on the leaves were *Bornetia binderiana* (Sonder) Zanardini, *Ceramium puberbulum* and *Heterosiphonia callithamnion*. *B. binderiana* was attached to the leaf by a small holdfast whereas *H. callithamnion* formed a thin mat over all the leaf surface. *Ulva rigida* and *Bryopsis* spp. were occasionally present, and *Laurencia cruciata* developed as small tufts at the junction between adjacent leaves.

The major sessile epiphytic invertebrates associated with the leaves were the hydroids *Plumularia compressa, P. nodosa, Campanularia australis, Amphisbetia minima* and *Pycnotheca producta*, and the bryozoan *Thairopora mamillaris*. The hydroids, most commonly *P. compressa* and *P. nodosa*, were present on one or both faces of 51.7 % of all leaves examined, and they appeared to colonise the leaves as a series of stolons parallel to the leaf axis in advance of the encrusting coralline algae. *T. mamillaris* formed thin membraneous colonies on the clasping leaf bases and at the inner margins of the individual leaves. Approximately 12 % of leaves or leaf bases were colonised by this bryozoan. Other sessile invertebrates occasionally associated with the leaf blades included the polychaete *Spirorbis* sp. and a small coral-like bryozoan, *Lichenopora* sp.

DISCUSSION

Amphibolis spp. provide a habitat for a greater diversity and larger biomass of epiphytic organisms than any other species of seagrass (Borowitzka & Lethbridge 1989). The large number of species epiphytic upon

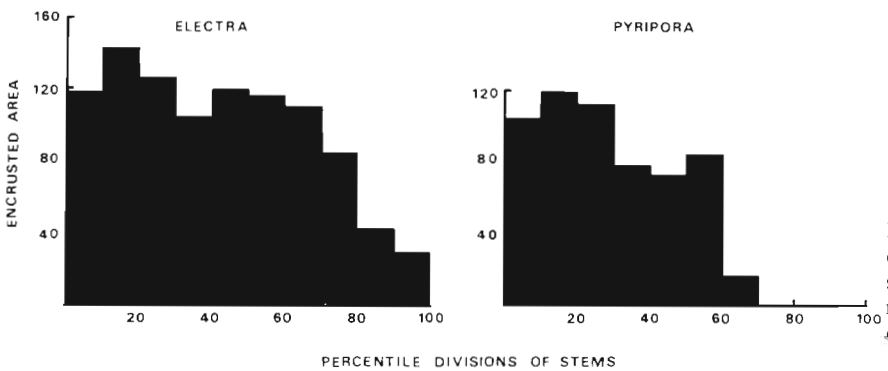

Fig. 7. Distribution of the common epiphytic bryozoans on the same stem samples as Fig. 4, expressed in the same relative cover units used for the crustose coralline algae. Species are *Electra flagellum* and *Pyripora polita*

Amphibolis is probably related to 2 main factors: (1) the coincidence in the distribution of this seagrass genus with one of the world's richest algal floras (Ducker et al. 1977, Womersley 1981); and (2) the morphology of the host plant.

The relatively uniform diameter of the perennial stems and branches contrasts with the terminal clusters of flat leaves which have a turnover period on the order of 3 to 4 mo (Walker 1985). The stems and leaves therefore provide structurally and temporally different habitats for colonisation by epiphytes. Furthermore, the lignified stems survive for several years unlike the leaves of most seagrass species (Borowitzka & Lethbridge 1989), thus providing a more stable substratum for epiphyte colonization.

As might be anticipated from the different morphologies of these habitats, most of the epiphytes observed on *Amphibolis* show a distinct preference for either the stems or the leaves of the seagrass. Thus, epiphytes such as *Dicranema revolutum, D. cincinnalis, Hymenocladia ramalina, Hypnea* spp., *Stereotheca elongata, Thyroscyphus marginatus, Electra flagellum* and *Pyripora polita* are almost exclusively restricted to the stems, whereas *Bryopsis plumosa, Ulva rigida, Ceramium puberbulum, Plumularia compressa* and *Thairopora mamillaris* are confined to the leaves. A few species, such as *Laurencia filiformis, Bornetia binderiana* and *Metagoniolithon stelliferum*, colonise both stems and leaves.

Superimposed upon these gross differences in habitat, there is a finer pattern of distribution with various epiphytes exhibiting preferences for certain positions on the stems and the leaves. For example, *Bryopsis plumosa* plants are usually found only on the leaf tips, whereas *Ceramium puberbulum* is most common at the base of the leaves near the leaf junctions. Similarly, there is a distinct apico-basal organisation of the stem epiphytes as shown in Figs. 5 to 7.

Although the long-term species diversity on the stems and the leaves may be similar (cf. Ducker et al. 1977), the stem supports a greater diversity of species than the leaves on any individual *Amphibolis griffithii* plant. This is presumably a result of the longer life of the stems compared to the leaves, and may also be due to the fact that the stem provides a more diverse habitat (Borowitzka & Lethbridge 1989). The stems pass from a region of low water-motion and lower irradiance near the substratum, to a high irradiance, high water-motion environment at the seagrass apex. Although insufficient data are available to isolate the relative effects of light and water-motion on epiphyte settlement, recruitment and growth, there is circumstantial evidence to indicate that light is the primary factor influencing algal recruitment and growth. The epiphytic algae dominate the upper portions of the plant where light intensity is highest, and where an effectively greater supply of nutrients is available to the algae through enhanced water movement. Thus the algae may outcompete the sessile epiphytic invertebrates by their more rapid growth in these higher light regions. On the other hand, the filter-feeding epiphytic invertebrates grow well at the base of the stems where there may be less competition with algae due to the lower light environment, and presumably also reduced predation. Foster (1975) reached similar conclusions in his study of algal community development in a *Macrocystis pyrifera* forest. A similar pattern of distribution of epiphytes has also been observed on artificial *Amphibolis*-like plants by Lethbridge et al. (1988).

Clearly, the distribution of epiphytic organisms is not random, and this is in keeping with previous observations on the epiphytes of other seagrasses (e.g. Kerneis 1960, Kita & Harada 1962, van der Ben 1971, Willcocks 1982, Heijs 1985) and the distribution of algae on artificial seagrasses (Tanaka et al. 1984, Horner 1987, Lethbridge et al. 1988).

Although the distribution of epiphytes on *Amphibolis* plants appears to be strongly influenced by physical factors as has also been observed for *Posidonia* epiphytes (Horner 1987) and epiphytes on the brown kelp *Nereocystis luetkeana* (Markham 1969), the non-random pattern of recruitment observed in this study may have 2 further causes: (1) the outcome of selective settlement of larvae, spores or propagules; and (2) different degrees of mortality in various areas of the habitat (Underwood 1979, Keogh & Downes 1982).

At least some of the site preferences observed in this study may result from selective settlement as a number of the epiphytes are exclusively confined to either the stems or the leaves of the seagrass. Although our data do not provide information on the settlement phase, they do describe some features of the subsequent recruitment of epiphytic organisms.

The crustose coralline algae are the primary colonisers of both the leaves and stems of *Amphibolis griffithii*, as is also the case for other seagrass species (e.g. van den Ende & Haage 1963, Humm 1964, Bramwell & Woelkerling 1984). The hydrozoans *Plumularia compressa* and *P. nodosa* and the bryozoans *Thairopora mamillaris, Pyripora polita* and *Electra flagellum* also recruit rapidly on newly available leaves and stems. Together with the crustose coralline algae, these invertebrates are usually observed on all but the youngest plants. The crustose coralline algae seem to act, at least in part, as pioneer plants, possibly providing a suitable substratum for other epiphytes. For example, the geniculate coralline alga *Metagoniolithon stelliferum* has been reported to settle and grow only on these coralline algae (Ducker 1979, Ducker & Knox 1984). However, more recent studies by

Christidis (pers. comm.) show that *M. stelliferum* will settle on coralline algal-free artificial seagrass.

Since most epiphytes on *Amphibolis griffithii* showed distinct site preferences, the presence of crustose coralline algae is unlikely to promote successful recruitment of most of the epiphytic species. Indeed, surface texture of the substratum is important for numerous species, and many bryozoans prefer to settle upon smooth surfaces (Ryland 1976). On *A. griffithii*, the bryozoans *Electra flagellum* and *Pyripora polita* are very early colonisers of the smooth lower stem of young plants, often in advance of the encrusting coralline algae. Similarly, *Thairopora mamillaris* is common on the smooth leaf bases, and *Lichenopora* sp. appears to settle preferentially on younger leaves which are not conspicuously covered with encrusting coralline algae. The seagrass itself may therefore act primarily as an inert substratum that is physically suitable for epiphyte growth. The observations of Harlin (1973), Sozka (1975), Catteno & Kalff (1979) and Lethbridge et al. (1988), who compared epiphyte growth on natural vegetation with artificial substrata of similar morphology, support this contention.

The potential impact of grazing animals such as amphipods, gastropods and fish on epiphyte recruitment must not, however, be overlooked. *Amphibolis griffithii* and its associated epiphytic flora support a large community of such individuals, and these may feed upon epiphytic unicellular algae such as diatoms, the sporelings of macrophytic algae, and members of the sessile invertebrate fauna (Bell et al. 1978, Kitting 1984, Morgan & Kitting 1984). The importance of particularly micro-grazers on the distribution of the macroflora and fauna has only recently been recognised (e.g. Underwood 1979, Watzin 1983) and needs to be closely examined before conclusions about the primary factors controlling epiphyte recruitment can be established.

If epiphytes are too abundant on the leaves, seagrass photosynthesis in inhibited (Sand-Jensen 1977, Borum & Wimm-Anderson 1980, Bulthuis & Woelkerling 1983) and this may eventually lead to death of the seagrass (Ott 1980, Silberstein et al. 1986). At the epiphyte loads observed in this study, this may not be a significant problem for *Amphibolis griffithii* as its relatively short-lived leaves are regularly shed together with their adherent epiphytes. This strategy is analagous to the epidermis-shedding which occurs in some algae such as *Haliptilon roseum* (Borowitzka & Vesk 1978) and *Ascophyllum nodosum* (Filion-Myklebust & Norton 1981). On the other hand, the strong, long-lived and essentially non-photosynthetic stems of *A. griffithii* appear to be able to support the epiphyte burdens reported in this study without damage. It is also important to recognise that a relatively dense mass of epiphytic algae acts to reduce water motion within the seagrass bed, thus decreasing erosion of the sediments below the seagrasses. This may, in part, account for the fact that *A. griffithii* tends to grow in more turbulent areas than other seagrasses such as *Posidonia* spp. (Cambridge 1975, Shepherd & Womersley 1981).

Our observations, and those of Ducker et al. (1977) and Kendrick et al. (1988), also show that the species composition and abundance of the epiphytic organisms growing on *Amphibolis* spp. vary greatly with season and with habitat. This variation does not, however, affect the generality of the observations reported in this paper which provides the basis for further studies of seasonal and spatial variation in *Amphibolis* epiphytes.

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