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Plant–animal associations in two species of seagrasses in Western Australia

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Abstract

Relationships between algal epiphytes and epifaunal invertebrates (amphipods, molluscs and polychaetes) occurring within meadows of the seagrasses *Posidonia sinuosa* and *Amphibolis griffithii* were compared along the south west coast of Western Australia. Although the seagrasses are very different structurally, many species of algal epiphytes and epifaunal grazers were common to both. However, meadows of *Amphibolis* supported a greater number of both algal epiphyte and epifaunal species. The long-lived stems of *Amphibolis* supported a larger biomass of algal epiphytes and grazers than did the leaves of either *Posidonia* or *Amphibolis*. The densities and biomass of epifauna were variable but on a comparison adjusted to the biomass of seagrass, both the density and biomass of the taxonomic groups were similar between seagrass species except that the density of grazing gastropods and the biomass of polychaetes were greater in *Amphibolis* (by 238% and 252%, respectively). Nested analyses of variance (ANOVA) indicated that variations in plant and animal biomass differed at all spatial scales (sites, meadows within sites and replicates) and the pattern was inconsistent amongst biota. However, a significant proportion of the variability occurred between replicate samples. Canonical correlation and multiple regression analyses indicated that associations between algal epiphytes and epifauna were also inconsistent and differed between seagrass species. These patterns highlight the importance of seagrass species and structural complexity in affecting both the epiphytic and grazer community. The importance of spatial scales at which seagrasses and their associated communities are sampled are equally important because of the differing levels of spatial patchiness. © 1998 Elsevier Science B.V.

Keywords: Seagrass; Periphyton; Epiphytes; Epifauna

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1. Introduction

Seagrass meadows are complex communities providing habitat to many different types of plants and animals (McRoy and Helfferich, 1977; Watson et al., 1984; Edgar and Shaw, 1995a). Their role as nursery areas for fish and crustaceans highlights their productivity which is partly due to the production of epiphytic algae and the invertebrates that graze them (Edgar, 1990a). Apart from providing food for larger animals (Edgar and Shaw, 1995b), epifaunal grazers are essential in maintaining healthy meadows by removal of excessive growth of epiphytic algae that reduce light levels below the minimum necessary for seagrass survival (Orth, 1992; Jernakoff et al., 1996).

Seagrass epifaunal research has focussed mainly on studies of the differences in abundance and diversity between invertebrates in seagrass meadows compared with adjacent unvegetated areas (e.g., Hutchings et al., 1991; Edgar and Shaw, 1995a; Fonseca et al., 1996), on trophic flow of material (e.g., Klumpp et al., 1992; Edgar and Shaw, 1995b), and on the impacts of grazing on the seagrasses and their epiphytes (e.g., Neckles et al., 1993; Jernakoff and Nielsen, 1997).

Few studies, however, have examined the associations in the field of mobile epifauna with sources of potential shelter and food due to the difficulty of carrying out such studies in the field (however, see the works of Virnstein and Howard, 1987, Edgar and Robertson, 1992, Scipione et al., 1996, Alcoverro et al., 1997 and Nelson and Waaland, 1997). Even rarer studies are those that jointly compare motile epifauna together with algal epiphytes within structurally different seagrass meadows.

The present paper describes associations between two structurally different types of seagrasses *Posidonia sinuosa* Cambridge and Kuo, and *Amphibolis griffithii* (Black) den Hartog, their algal epiphytes (large erect, and small filamentous epiphytes and periphyton) and epifauna (suspension-feeding amphipods and molluscs, amphipod and gastropod grazers and polychaetes). These associations provide the basis for hypotheses about the role of seagrasses and their algal epiphytes in affecting the distribution and abundance of epifauna. Specific hypotheses that need to be examined include: (1) Are seagrasses or are algal epiphytes the major determinant for epifaunal abundance and biomass? and (2) Do the invertebrates with different modes of feeding (suspension vs. grazing) have different but consistent associations amongst the seagrass and epiphyte groups?

2. Methods

2.1. Study sites

Surveys were carried out between 5–7 October 1993 at three sites within Perth coastal waters off Western Australia (32°19'S and 115°42'E, 32°17.5'S and 115°41'E, 31°48.5'S and 115°43'E). The sites are relatively sheltered by a series of limestone reefs further offshore, although there can be significant wave-surge during stormy weather. At each site, three replicate 20 cm × 20 cm quadrats were sampled in each of three meadows for each of two seagrass species, *P. sinuosa* and *A. griffithii*. The number and

size of quadrats were a compromise between minimising the statistical error between quadrats and the time required to count and identify epifaunal species (in some cases up to 20 h per 20 cm × 20 cm quadrat; Jernakoff and Nielsen, unpublished data).

2.2. Study organisms

The seagrasses formed monospecific meadows at each site. *P. sinuosa* has 1–2 ribbon-shaped leaves per shoot which are 4–11 mm wide and were up to 55 cm long at the study sites. Leaf longevity is between 84 and 168 days (Jernakoff et al., 1996). The mean (\pm SE) density of *Posidonia* leaves was 1480.0 (\pm 162.5) per m². In contrast, *A. griffithii* has a long-lived, erect, lignified stem with small, short-lived leaves (28–40 days; Kirkman, personal communication) arranged in terminal clusters. *Amphibolis* grew to a length of about 38 cm at the study sites and it had a mean density of 367.5 (\pm 42.5) stems per m².

Algal epiphytes grow on the leaves of *Posidonia* (Silberstein et al., 1986) and on both the leaves and stems of *Amphibolis* (Borowitzka et al., 1990). They include a large variety of species and were, for the purposes of the study, divided into large erect epiphytes, small filamentous epiphytes and periphyton on the basis of size.

Many invertebrates are common to species of *Posidonia* and *Amphibolis*, although *Amphibolis* generally has greater species richness and density than *Posidonia* (Sergeev et al., 1988; Edgar, 1992). Invertebrate grazers make up a significant component of the epifauna and the most abundant grazers on both types of seagrasses are molluscs and crustaceans, dominated numerically by amphipods. In the present study, amphipods were subdivided into those that feed primarily by biting and chewing plant material, those that feed by suspension-feeding and caprellid amphipods that use their antennal setae to brush and scrape the seagrass leaves for food (Jernakoff et al., 1996). Although these divisions are based on dominant modes of feeding, it is likely that many species feed by a combination of methods and are not only grazers but detritivores as well, hence the demarcation into the above groups is somewhat arbitrary. Molluscs were divided into those that graze using a radula to remove food and those that feed by suspension-feeding (i.e., bivalves). Polychaete worms were also sampled because they form a significant component of the biomass of epifaunal invertebrates.

2.3. Collection and processing of data

Three-sided square quadrats were haphazardly placed within seagrass meadows and all material within each quadrat was collected by carefully cutting the seagrass just above the substratum and placing the seagrass and attached epiphytes slowly and carefully into plastic bags so that mobile epifauna stayed within the cut seagrass clumps. Some 5% buffered formalin was added to each sample and the contents were left for 24 h prior to washing and sorting.

Posidonia samples were processed by removing the large erect epiphytes from the seagrass leaves. Small filamentous epiphytes were scraped off the leaves into water and then filtered through a 2-mm filter to separate small filamentous algae from the smaller material (periphyton) that passed through the filter. The seagrass and large erect

epiphytes were dried (80°C) for 24 h to provide a biomass in grams dry weight (DW) per quadrat. The ash-free dry weight (AFDW) of the floral material passing through the 2-mm filter was measured to provide the biomass of periphyton.

In the case of *Amphibolis*, measurements consisted of the stem density, stem length, average number of leaf clusters, average number of leaves per cluster, biomass of leaves, stems, leaf large erect epiphytes, leaf small filamentous epiphytes, leaf periphyton, stem large erect epiphytes, stem small filamentous epiphytes and stem periphyton.

Faunal samples were sorted by sieving through a series of sieve sizes (8 mm, 5.6 mm, 4 mm, 2.8 mm, 2 mm, 1.4 mm, 1 mm, 0.71 mm, 0.5 mm) to provide size-related abundance prior to identification in the broad taxonomic groups. Biomass estimates (mg AFDW) were derived from the relationships established by Edgar (1990a,b) between sieve size and biomass for epifauna within seagrasses.

The number and biomass of suspension-feeding and grazing amphipods, caprellid amphipods, suspension-feeding and grazing molluscs and polychaetes were compared with the abundance and biomass of the seagrass species and their algal epiphytes to determine which components (e.g., periphyton, small filamentous epiphytes etc.) and/or habitat (e.g., seagrass and large erect epiphytes) were associated with epifauna. Floral components within *Posidonia* meadows included: leaf number, leaf biomass, large erect and small filamentous epiphyte biomass and the biomass of periphyton. All epiphyte and epifaunal measurements were standardised to a biomass of seagrass leaf. Floral components in *Amphibolis* included the above in addition to the number of leaf clusters and the density and biomass of *Amphibolis* stems. Epiphyte and periphyton biomass and diversity was partitioned according to that growing on either the stems or the leaves.

3. Results

Nested analyses of variance (ANOVA) were used to assess the variability of data between the three sites, three meadows within each site, and the two seagrass species. The 'Sites' and 'Meadows within Sites' factors were considered to be random in the analyses and 'Seagrasses' was a fixed factor. The data were transformed ($\log [x + 1]$ for biomass) where necessary to satisfy assumptions of ANOVA.

In general, the major source of variability (as expressed by the percentage of the total sum of squares in the analyses) was due to that amongst replicates (Fig. 1). However, patterns of variability for particular biota (e.g., amphipod biomass, seagrass leaf biomass, etc.) were inconsistent across the different spatial scales measured.

Because of the large variability between replicates, data from the three meadows at each site were combined to increase the base level of replication from three to nine. General linear model analyses subsequently indicated that in all cases, the variables when considered individually (i.e., leaf density, amphipod abundance, polychaete biomass, etc.) were not significantly different between the three sites. Data from each site were therefore pooled to increase the replication to 27.

ANOVA were used to compare density and biomass of flora and fauna between the two seagrass species and ($\log [x + 1]$) transformations were carried out in some cases to satisfy assumptions of the analysis.

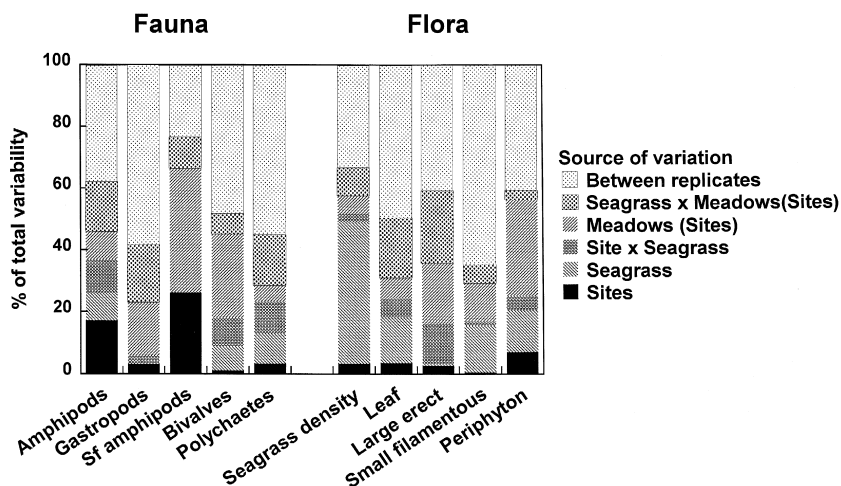


Fig. 1. Levels of variability attributed to the important spatial scales in the nested ANOVA. The analyses were carried out on the biomass of fauna and flora with the exception of seagrass density (leaves for *Posidonia* or stems for *Amphibolis* per m²). Sf amphipods = suspension feeding amphipods, Leaf = seagrass leaf biomass, Large erect = large erect algal epiphytes growing on the seagrasses, Small filamentous = small filamentous algal epiphytes growing on the seagrasses, Periphyton = periphyton growing on the seagrasses.

Two multivariate analyses were used to assess associations between floral and faunal components. Canonical correlation analysis investigated the relationship between the two natural groups of fauna vs. flora. It is possible to interpret general trends with this analysis. Stepwise multiple regressions were used to determine more detailed trends within and between floral and faunal components. The stepwise multiple regressions provide a greater level of detail about the associations than did the canonical correlation analysis. However, each series of multiple regressions for each dependent variable must be considered in isolation from the other series of multiple regressions because otherwise the dependent variable in one series of stepwise multiple regressions may become an independent variable in the other analysis.

3.1. Floral patterns

The mean (\pm SE) density per m² of *Posidonia* shoots (1480.5 ± 162.25) was significantly greater than *Amphibolis* stems (368.5 ± 42.25) (ANOVA: $df = 1,52$; $P < 0.001$). The overall biomass of *Posidonia* leaves was significantly greater than that for *Amphibolis* leaves (ANOVA: $df = 1,52$; $P < 0.01$) although it was approximately equal to the combined weight of the *Amphibolis* stems and leaves (Fig. 2). The biomass of leaves per shoot for *Posidonia* was 0.163 g DW whilst it was 0.398 g DW per stem of *Amphibolis*. Thus, *Amphibolis* stems supported a greater leaf biomass than *Posidonia* shoots.

The biomass of large erect and small filamentous algae on the leaves of *Posidonia* was similar to that on the leaves of *Amphibolis* (Fig. 2). However, the biomass of large

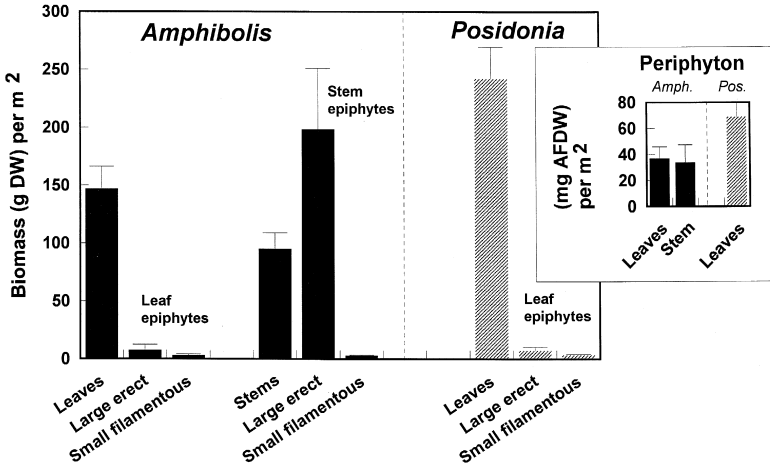


Fig. 2. Mean biomass (\pm SE) of floral material in *A. griffithii* and *P. sinuosa* seagrass meadows. 'Leaves' refer to seagrass leaves, 'Large erect' and 'Small filamentous' refer to algal epiphytes.

erect epiphytes growing on the stems of *Amphibolis* was an order of magnitude larger than the biomass of epiphytes on the leaves (ANOVA: $df = 1,47$; $P = 0.002$).

Overall, *Posidonia* supported a total of 45 different species of epiphytes (35 large erect species and 31 small filamentous species—some occurred both as small filamentous and large erect forms) with a biomass of $0.051 (\pm 0.015 \text{ SE}) \text{ g g}^{-1} \text{ DW } Posidonia$ leaf. In contrast, *Amphibolis* supported 83 epiphyte species (32 large erect species on leaves, 35 small filamentous species on leaves, 45 large erect species on *Amphibolis* stems and 35 small filamentous species on stems) with a biomass of $0.998 (\pm 0.033) \text{ g g}^{-1} \text{ DW}$ of *Amphibolis* stem and leaf.

Although *Posidonia* had approximately half the number of algal epiphyte species compared with *Amphibolis*, similar numbers of species were found on the leaves of *Posidonia* and *Amphibolis* but more species were found on *Amphibolis* stems. Table 1 shows the 10 most dominant large erect and small filamentous species in terms of abundance for *Posidonia* leaves and *Amphibolis* leaves and stems. For both seagrass species, approximately five of the 10 most dominant large erect epiphyte species were common in the small filamentous epiphyte category. Thus, many of the species classed as small filamentous due to their size were germlings of the larger erect species. Four species found on *Amphibolis* leaves were common on the stems, and one species, *Hypnea cervicornis* J. Agardh, was ubiquitous, being found as a small filamentous and large erect epiphyte on both leaves and stems of *Amphibolis*. Only two [*Ceramium monocanthum* J. Agardh and *Laurencia cf. filiformis* (C. Agardh) Montagne] of the 10 most common large erect epiphytes were found on the leaves of both *Posidonia* and *Amphibolis* while five of the 10 small filamentous epiphytes on seagrass leaves were common to both seagrass species. These small filamentous epiphytes were: *Antithamion hanovioides* (Sonder) De Toni, *Dasya* sp. C. Agardh, *Hypnea* sp. F. Lamouroux, *Laurencia cf. filiformis* and *Metagoniolithon stelliferum* (Lamarck) Ducker.

Table 1
The 10 most abundant epiphytes in *P. sinuosa* and *A. griffithii* meadows

	<i>P. sinuosa</i>				<i>A. griffithii</i>						
	Rank	Leaf small filamentous epiphytes	Rank	Leaf large erect epiphytes	Rank	Leaf small filamentous epiphytes	Rank	Stem large erect epiphytes	Rank	Stem small filamentous epiphytes	
<i>Ceramium monacanthum</i>	1.1	<i>Giraudia</i> sp. A	2.2	<i>Herposiphonia secunda</i>	1.3	<i>Herposiphonia secunda</i>	1.5	<i>Hypnea cervicornis</i>	2.3	<i>Dicranema</i> sp. A	2.2
<i>Laurencia</i> cf. <i>filiformis</i>	1.1	<i>Ceramium monacanthum</i>	1.3	<i>Champia zostericola</i>	0.4	<i>Metagoniolithon stelliferum</i>	1.3	<i>Laurencia</i> cf. <i>filiformis</i>	2.0	<i>Metagoniolithon stelliferum</i>	1.3
<i>Enteromorpha</i> sp. A	1.0	<i>Metagoniolithon stelliferum</i>	1.1	<i>Hypnea cervicornis</i>	0.4	<i>Hypnea cervicornis</i>	0.9	<i>Metagoniolithon stelliferum</i>	1.0	<i>Halipylon roseum</i>	1.3
<i>Antithamnion hanovioides</i>	0.9	<i>Helminthora australis</i>	1.0	<i>Metagoniolithon stelliferum</i>	0.4	<i>Halipylon roseum</i>	0.7	<i>Champia zostericola</i>	0.7	<i>Gloiosaction brownii</i>	1.1
<i>Platysiphonia miniata</i>	0.7	<i>Antithamnion hanovioides</i>	1.0	<i>Antithamnion armatum</i>	0.3	<i>Cladophora</i> sp. C	0.5	<i>Dicranema</i> sp. A	0.5	<i>Codotonium</i> sp. A	0.9
<i>Ceramium rubrum</i>	0.6	<i>Enteromorpha</i> sp. A	1.1	<i>Polysiphonia abscondens</i>	0.3	<i>Laurencia</i> cf. <i>filiformis</i>	0.4	<i>Polysiphonia decipiens</i>	0.5	<i>Pterosiphonia</i> cf. <i>pennata</i>	0.7
<i>Helminthora australis</i>	0.6	<i>Dasya</i> sp. F	0.7	<i>Polysiphonia decipiens</i>	0.3	<i>Chondria succulenta</i>	0.4	<i>Cladophora</i> sp. E	0.4	<i>Hypnea cervicornis</i>	0.6
<i>Dasya</i> sp. F	0.5	<i>Ceramium pusillum</i>	0.7	<i>Pterosiphonia pennata</i>	0.3	<i>Dasya</i> sp. A	0.4	<i>Dicranema radicans</i>	0.3	<i>Champia zostericola</i>	0.6
<i>Cladophora</i> sp. D	0.5	<i>Laurencia</i> cf. <i>filiformis</i>	0.6	<i>Ceramium monacanthum</i>	0.3	<i>Antithamnion hanovioides</i>	0.3	<i>Protobactingia australasica</i>	0.3	<i>Dicranema revolutum</i>	0.6
<i>Colpomenia</i> sp. A	0.5	<i>Laurencia forsteri</i>	0.4	<i>Laurencia</i> cf. <i>filiformis</i>	0.2	<i>Dasya</i> sp. D	0.3	<i>Coelonium verticillatum</i>	0.3	<i>Craspedocarpus tenuifolius</i>	0.4

Epiphytes were ranked 1 to 5 (5 being the most abundant) within each quadrat and the ranking is averaged over 27 quadrats.

Although biomass of periphyton on *Posidonia* leaves was significantly greater than that for *Amphibolis* leaves (ANOVA: $df = 1,40$; $P < 0.05$), when adjusted for leaf biomass there was no significant difference (ANOVA: $df = 1,40$; $P = 0.161$). However, *Posidonia* leaves were longer and provided a larger settlement surface. The biomass of periphyton from both the leaves and stems of *Amphibolis* was about the same as that on *Posidonia* leaves (Fig. 2).

3.2. Epifaunal patterns

Data on epifaunal density and biomass were adjusted to the biomass of seagrass (g DW) rather than also to surface area because seagrass leaf surface area and seagrass leaf biomass were highly correlated ($R^2 = 0.997$ for *Posidonia* and 0.996 for *Amphibolis*) and they showed patterns similar to estimates based on a per quadrat measurement. Overall, *Posidonia* supported 20.11 (± 5.57) mg AFDW of epifaunal biomass per gram of seagrass compared to 24.33 (± 4.87) mg AFDW of epifaunal biomass in *Amphibolis*.

The densities of suspension-feeding and grazing amphipods, and polychaetes were an order of magnitude greater than the densities of caprellids and molluscs on both seagrass species (Fig. 3). The biomass of suspension-feeding amphipods in *Posidonia* meadows, in particular, was very variable. The data shown in Fig. 3 are those used in the multiple regression analyses with outlying data for suspension-feeding amphipods from one meadow at one site are removed. When these data are included the density of suspension-feeding amphipods ($\pm SE$) in *Posidonia* is 3442.5 ± 1510.0 and that for *Amphibolis* increases to 2265.0 ± 927.5 . On comparing the density of epifauna in *Posidonia* vs. *Amphibolis* meadows, the only groups that were significantly different from each other were the densities of gastropod grazers (*Amphibolis* > *Posidonia*; ANOVA sqrt ($x + 1$) transform, $df = 1,52$; $P = 0.004$).

The biomass of epifauna is shown in Fig. 4. If the outlier data for suspension-feeding amphipods were included then the biomass in *Posidonia* increased to $1.20 (\pm 0.01)$ mg and in *Amphibolis* the biomass to $1.11 (\pm 0.28)$ g. Of the epifaunal groups, only

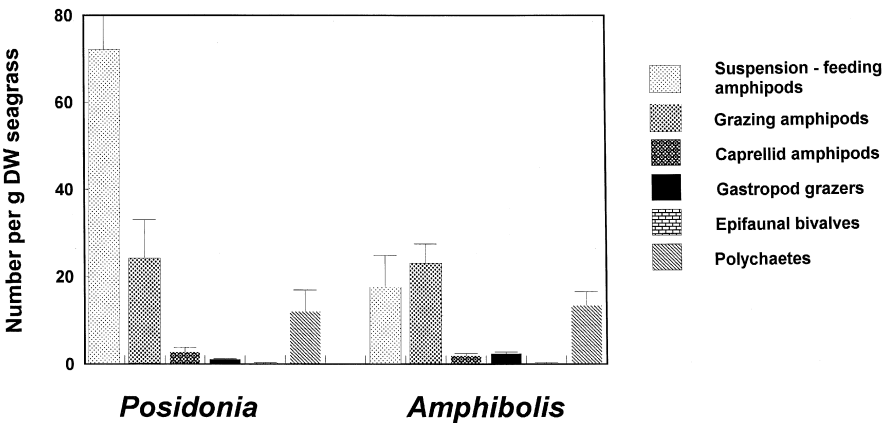


Fig. 3. Mean density ($\pm SE$) of epifauna within *P. sinuosa* and *A. griffithii* seagrass meadows.

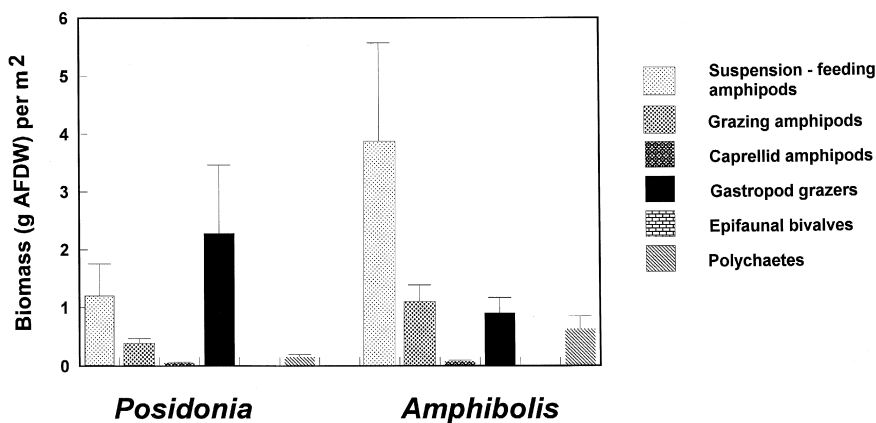


Fig. 4. Mean biomass (\pm SE) of epifauna within *P. sinuosa* and *A. griffithii* seagrass meadows.

polychaetes were significantly different between the two seagrass species (*Amphibolis* > *Posidonia*; ANOVA log ($x + 1$) transform, $df = 1,52$; $P = 0.007$).

The total number of amphipod grazer species recorded in *Posidonia* (25) was approximately half that recorded in *Amphibolis* (40). Six suspension-feeding amphipod species were recorded in *Posidonia*, all of which were also found amongst the nine species in *Amphibolis* meadows. Both caprellid amphipod species were found in both seagrass species. There were 14 and 30 species of gastropod species recorded in *Posidonia* and *Amphibolis*, respectively, and of the five bivalve species found in each of the seagrasses, three were common to both. Polychaete species were not identified and thus it was not possible to say which were unique to *Posidonia* or *Amphibolis*. Eight out of 10 of the most numerous species of amphipod were common to both seagrass species whilst six out 10 were common for molluscs (Table 2).

3.3. Relationships between faunal abundance and biomass

The correlation between numbers and biomass was high for both amphipods and epifaunal bivalves in both *Posidonia* and *Amphibolis* (Table 3), indicating that either abundance or biomass could be used to describe the presence of the fauna. Gastropod numbers and biomass were not as tightly linked although both were significantly correlated for *Posidonia* and *Amphibolis*). In contrast, although polychaete numbers and biomass were correlated, the correlation was higher in *Amphibolis* than in *Posidonia*. All canonical correlation and multiple regression analyses were based on measurements of biomass.

3.4. Relationships amongst fauna and flora

The canonical correlation analysis indicated that there was a high correlation between faunal and floral groups and that the first eigenvalues explained 70% and 71% of the variance for the analyses on *Posidonia* and *Amphibolis* seagrasses, respectively

Table 2

The 10 most dominant amphipod and mollusc species (in terms of average density per 20 cm × 20 cm quadrat) in *P. sinuosa* and *A. griffithii* meadows

<i>P. sinuosa</i>				<i>A. griffithii</i>			
Amphipods	Density	Molluscs	Density	Amphipods	Density	Molluscs	Density
<i>Ampithoe</i> sp. 2 ^a	53.9	Patellid sp. 1	2.5	<i>Cerapus</i> sp. ^b	264.0	<i>Diala</i> sp.	6.0
<i>Hyale media</i> ^a	42.7	<i>Thalotia conica</i>	1.5	<i>Tethygeneia nalgo</i> ^a	84.8	Rissoid sp. 1	3.4
Unidentified sp. 1 ^b	14.9	<i>Ischnochiton</i> sp.	1.4	<i>Paradexamine churinga</i> ^a	24.6	Rissoid sp. 2	2.9
<i>Cerapus</i> sp. ^b	14.3	<i>Diala</i> sp.	1.2	<i>Ampithoe</i> sp. 2 ^a	22.9	Gastropod sp. 7	2.5
<i>Caprella</i> sp. 1 ^c	11.9	<i>Musculus</i> sp	1.0	<i>Caprella</i> sp. 1 ^c	17.7	<i>Microdiscula charopa</i>	1.8
<i>Tethygeneia nalgo</i> ^a	10.7	Bivalve sp. 2	0.9	<i>Paradusa</i> sp. ^a	14.1	Littorinid sp.	1.2
<i>Erichthonius</i> sp. ^b	7.9	<i>Nacule</i> sp. 2	0.2	<i>Erichthonius</i> sp. ^b	14.0	Patellid sp.	1.0
<i>Jassa</i> sp. ^b	7.5	<i>Phasianotrochus irisodontes</i>	0.2	<i>Jassa</i> sp. ^b	9.7	<i>Musculus pavlucciae</i>	0.8
<i>Hyale rubra</i> ^a	7.4	Bivalve sp. 1	0.2	<i>Hyale rubra</i> ^a	9.0	Bivalve sp. 2	0.6
<i>Paradusa</i> sp. ^a	6.0	Rissoid sp. 2	0.2	<i>Gitanopsis</i> sp. ^a	8.3	<i>Phasianotrochus irisodontes</i>	0.6

^aRefers to amphipods with a feeding morphology predominantly suited to biting and chewing.

^bRefers to amphipods with a feeding morphology predominantly suited to suspension-feeding.

^cRefers to amphipods with a feeding morphology predominantly suited to brushing and scraping material.

Note that the densities of suspension-feeding amphipods do not include those of Warnbro Sound, meadow 1.

If the three replicates for this meadow are included then the densities in *Posidonia* of *Jassa* and *Erichthonius* are 727.0 and 59.7, respectively, and in *Amphibolis*, the density of *Cerapus* is 1062.0.

Table 3

Regression of the biomass and density of epifauna in *Posidonia* and *Amphibolis* seagrass meadow

	<i>Posidonia</i>		<i>Amphibolis</i>	
	R^2	P	R^2	P
Amphipod grazers	64.8	< 0.001	88.6	< 0.001
Susp. feed. amphipods	95.9	< 0.001	93.5	< 0.001
Gastropod grazers	29.1	0.004	18.1	0.027
Epifaunal bivalves	95.3	< 0.001	67.6	< 0.001
Polychaetes	13.5	0.065	75.0	< 0.001

Susp. feed. amphipods = suspension feeding amphipods.

The degrees of freedom for the numerator and denominator are 1 and 25, respectively for all regressions.

(Table 4a). Table 4b shows the canonical coefficients for the first eigenvalue and the magnitude of the value (irrespective of sign) indicates the strength of its contribution to the overall association within the faunal or floral group. The faunal components with the highest contribution in *Posidonia* are amphipod grazers and amphipod suspension-feeders whereas floral components that contributed the most were the biomass of small filamentous epiphytes and the density of seagrass leaves. In *Amphibolis*, the two main faunal components are epifaunal bivalves and gastropod grazers while the two major floral components were the biomass of leaves and the biomass of large erect epiphytes growing on the leaves.

The results of the stepwise multiple regression analyses indicated that for both seagrass species, amphipod grazer biomass was very well described by all components in the multiple regression models (Table 5). The biomass of small filamentous epiphytes on leaves accounted for most of the variability in amphipod grazer biomass in *Posidonia* meadows, the biomass of suspension-feeding amphipods accounted for 9% of the variability and all other components, individually, accounted for less than 9%. In contrast, the dominant components in *Amphibolis* meadows were the biomass of *Amphibolis* leaves, and that of amphipod suspension feeders which contributed almost five times more to explaining the variability in amphipod grazer biomass in *Amphibolis* meadows compared to within *Posidonia* meadows.

The biomass of suspension-feeding amphipods was also very well described by all components of the multiple regression models (Table 5). However, the major components that best described the biomass of suspension-feeding amphipods in *Posidonia* were different from those of *Amphibolis*. In *Posidonia* meadows, both the length of leaves and the biomass of large erect epiphytes growing on them accounted for similar levels of variability in describing the biomass of suspension-feeding amphipods. In *Amphibolis* meadows, however, the major components were the presence of amphipod and gastropod grazers, caprellid amphipods and the density of *Amphibolis* stems.

The relationship between caprellid amphipods and other factors was less tight than that of the grazer and suspension-feeding amphipods discussed above (Table 5). In *Posidonia*, the multiple regression explained just over half of the variability in the model. The major animal components were suspension-feeding amphipods and bivalves while the main floral components were the length of leaves and the presence of small

Table 5
Summary of stepwise multiple regressions

Biota	<i>Posidonia</i> meadows	<i>Amphibolis</i> meadows
Amphipod grazers	Small filamentous epiphytes (59.9%), Amph. susp. feeder (9.0%)	Amph. susp. feeders (43.6%), Leaf biomass (40.7%)
Amph. suspension-feeders	Leaf length (26%), Large erect epiphytes (20.4%)	Amphipod grazers (34.5%), Gastropods (17.9%), Caprellids (7.6%), Stem no. (15.0%), Amph. susp. feeders (15.1%)
Caprellid amphipods	Amph. susp. feeders (21.8%)	Amphipod grazers (32.2%), Stem no. (11.5%)
Gastropod grazers	Periphyton (15.9%)	Leaves (35.6%), Stem length (22.4%), Large erect leaf epiphytes (12.9%), Stem no. (12.5%), Amph. susp. feeders (5.0%)
Epifaunal bivalves	Amph. susp. feeders (89.4%)	Leaves (36.4%), Polychaetes (27.9%), Stems (9.5%), Leaf no.
Polychaetes	Epifaunal bivalves (40.5%)	Large erect leaf epiphytes (64.4%)
Leaf periphyton	NIL	N/A
Leaf small filamentous epiphytes	Amphipod grazers (44.3%) Amph. susp. Feeders (22.3%), Leaf no. (18.2%)	Gastropods (60.1%), Amph. susp. feeders (9.4%), Stem no. (9.4%)
Leaf large erect epiphytes	Leaf length (15.5%)	Large erect stem epiphytes (57.4%)
Stem periphyton	N/A	N/A
Stem small filamentous epiphytes	N/A	Leaves (45.7%)
Stem large erect epiphytes	N/A	Amphipod grazers (61.5%), Large erect leaf epiphytes (25.9%)

Components of variation that are significant ($P < 0.05$) are listed with their respective contributions (in parentheses) to the multiple regressions.

The units of all components are in biomass unless specifically stated in the table.

Amph. susp. feeder = amphipod suspension feeders.

N/A = not applicable.

Table 4

(a) Canonical correlates and eigenvalues from the canonical correlation analyses of faunal and floral components in *Posidonia* and *Amphibolis* seagrass meadows

<i>Posidonia</i>		<i>Amphibolis</i>	
Canonical correlation	Eigenvalue	Canonical correlation	Eigenvalue
0.8648	1 2.9676	0.9897	1 48.0060
0.6434	2 0.7065	0.9667	2 14.2742
0.4866	3 0.3102	0.8569	3 2.7624
0.3890	4 0.1783	0.8047	4 1.8374
0.2126	5 0.0473	0.6768	5 0.8454
0.1336	6 0.0182	0.3471	6 0.1370

(b) Canonical coefficients for faunal and floral variables in the canonical correlation analyses of faunal and floral components in *Posidonia* and *Amphibolis* seagrass meadows

<i>Posidonia</i>			
Faunal variable	Canonical coefficient for 1st faunal eigenvalue	Floral value	Canonical coefficient for 1st floral eigenvalue
Amphipod grazers	1.0792	Leaf number	-0.3838
Amph. suspension-feeders	-0.8621	Leaf length	-0.0328
Caprellid amphipods	0.0387	Leaf biomass	-0.0343
Gastropod grazers	-0.0715	Large erect epiphytes	0.0735
Epifaunal bivalves	0.3423	Small filamentous epiphytes	1.0409
Polychaetes	-0.1156	Periphyton	0.1843
<i>Amphibolis</i>			
Amphipod grazers	0.0576	Stem number	-0.2243
Amph. suspension-feeders	0.0760	Stem length	-0.1460
Caprellid amphipods	0.0510	Leaf cluster number	0.0458
Gastropod grazers	0.3643	Leaf number	-0.1546
Epifaunal bivalves	0.5597	Leaf biomass	0.7252
Polychaetes	0.0888	Stem biomass	-0.1473
		Leaf large erect epiphytes	0.3676
		Leaf small filamentous epiphytes	-0.0934
		Stem large erect epiphytes	0.1231
		Stem small filamentous epiphytes	0.0304

filamentous epiphytes. In *Amphibolis* meadows, the main faunal components were grazing and suspension-feeding amphipods while the main floral components were the density of stems and the biomass of large erect leaf epiphytes.

While the biomass of gastropod grazers was poorly described in *Posidonia* meadows by the factors in the present study, the multiple regression fit in *Amphibolis* meadows was very good (Table 5). The main factors explaining the variability in predicting the biomass of gastropod grazers were all floral. The biomass of *Amphibolis* leaves was the most significant followed by the length and density of stems and the biomass of large erect leaf epiphytes.

Although epifaunal bivalves showed good fits with their respective multiple regressions (Table 5), factors contributing to these fits differed between seagrass species. In *Posidonia*, a single major factor used to describe bivalve biomass was the biomass of amphipod suspension feeders. In *Amphibolis*, the major factors were the biomass of *Amphibolis* leaves, the biomass of polychaetes and the biomass of *Amphibolis* stems.

In *Posidonia* meadows, the model describing the biomass of polychaetes was to a large degree determined by the biomass of bivalves (Table 5). In *Amphibolis*, the multiple regression was much tighter, however only one factor explained more than 9% of the variability (the biomass of large erect leaf epiphytes).

The biomass of algal epiphytes, like that of the epifaunal invertebrates, exhibited similar disparity between the seagrass species in the main factors accounting for the variability in the multiple regressions (Table 5). In *Posidonia*, the major factors accounting for the variation in small filamentous epiphyte biomass on leaves were amphipod grazers and suspension feeders. The density of leaves was also a significant factor in the analysis. In *Amphibolis* meadows, however, the major factors were gastropods, amphipod suspension feeders and the density of *Amphibolis* stems.

The biomass of large erect leaf epiphytes was better described by the multiple regression model in *Amphibolis* meadows compared to that in *Posidonia* (Table 5). In both cases, there was only a single significant variable ($P < 0.05$) in the regression. In *Posidonia* meadows, the length of leaves was the most important factor whereas in *Amphibolis* it was the biomass of large erect leaf epiphytes.

There was no significant multiple regression of the biomass of periphyton in *Posidonia*, and it was not possible to carry out a multiple regression of periphyton on *Amphibolis* leaves because of too many missing data.

Significant regressions were apparent in *Amphibolis* stems (Table 5). The biomass of *Amphibolis* leaves accounted for a large component of the variability in the biomass of small filamentous epiphytes on stems while the biomass of amphipod grazers and large erect leaf epiphytes accounted to a large degree for the biomass of large erect epiphytes on the stems.

4. Discussion

The biomass of epifauna and epiphytes were patchy at spatial scales ranging from metres between quadrats to kilometres between sites. The lack of consistency in patterns

of variation within and between epifauna and algal epiphytes highlights the difficulty of setting statistically appropriate spatial scales that accommodate all of the organisms under investigation. Similar challenges exist in other marine systems, e.g., see the work of Morrisey et al. (1992).

The density and biomass of *Posidonia* and *Amphibolis* showed similar levels of patchiness compared with their algal epiphytes and epifauna. *Posidonia* and *Amphibolis* seagrasses are structurally very different from each other. *Posidonia* leaves are generally uniform above the seabed whereas the thin stemmed *Amphibolis* forms a dense canopy of leaf clusters (Borowitzka et al., 1990). Leaf longevity times differ between the species and *Amphibolis* has a long-lived stem as well. Thus, differences in the abundance and composition of epiphytes and fauna may be reflective of the structural and longevity of above ground parts of the different seagrass species. However, an alternative hypothesis is that differences in epiphytes and epifauna may be due to a response to differences in the chemical structure of the seagrass species. Evidence against this hypothesis comes from the studies of Silberstein et al. (1986). They found that the suites of epiphytes growing on natural and artificial *Posidonia* were similar and thus species-specific differences in chemical structure were not important in influencing the algal epiphyte community.

Differences in the composition and biomass of algal epiphytes were apparent between the seagrass species. *Amphibolis* supported a richer diversity of epiphytes than *Posidonia* and many species found on *Posidonia* also occurred on *Amphibolis*. While half of the 10 most dominant small filamentous epiphytes were found on both seagrass species, only two out of 10 large erect epiphytes were common to both seagrasses. The very large biomass of large erect epiphytes on *Amphibolis* stems is due to the fact that the stems, unlike the leaves, are very long lived, and although there has been no research on how long they last, it is believed to be several years (Kirkman, personal communication). The stems also provide a settlement surface for periphyton that had a biomass similar to that growing on the *Amphibolis* leaves and the combined biomass was similar to that on *Posidonia* leaves. Thus, although *Amphibolis* stems are different structurally from the leaves they nevertheless provide a settlement site for a significant proportion of the larger epiphytes and periphyton that grow on *Amphibolis*.

The number of amphipod and mollusc species, like the algal epiphytes, was much greater in *Amphibolis* meadows than in *Posidonia* and there was substantial overlap in species. Although the higher diversity in *Amphibolis* may be due to its more structurally complex canopy, we have no data to support (or refute) this hypothesis. Given that both suspension-feeding and grazing amphipods and molluscs were dominant in both *Amphibolis* and *Posidonia*, it appears that both seagrass types were equally favourable for the two feeding strategies. The fact that one particular meadow and one site supported such high densities of suspension-feeding amphipods for both seagrass species (up to 240,125 and 232,400 per m² for *Posidonia* and *Amphibolis* respectively) suggests that other factors not apparent from our study are also important in affecting the distribution and abundance of epifauna. Such factors might include stochastic settlement processes, as well as physical environmental factors (Keough, 1983; Jernakoff et al., 1996).

The relationships between seagrass, epiphytes and epifauna were complex and differed between seagrass species and the invertebrates being considered. It is important

to note that the correlations reported from the analyses are just associations and do not imply causality. Both amphipod and gastropod grazers appeared to be correlated more with potential food (epiphytes and periphyton) on *Posidonia*. Nielsen and Jernakoff (in press) demonstrated that both types of grazers did not eat *Posidonia* leaves and it is unlikely that they would eat *Amphibolis* leaves. Thus, strong correlation with *Amphibolis* leaves suggests that physical structure is probably the important component.

Factors related to epifaunal suspension-feeders also varied between faunal types and seagrass species. In *Posidonia*, amphipods were more associated with leaves and large erect epiphytes whereas in *Amphibolis*, they were more associated with the other invertebrates. In contrast, epifaunal bivalves in *Posidonia* were highly associated with amphipod suspension feeders whereas in *Amphibolis*, the biomass of leaves and polychaetes were more important. Similarly, the differences in factors related to polychaetes were just as varied.

Associations between epiphytes and other factors were just as varied as for epifauna. The major factor correlated with small filamentous epiphytes on *Posidonia* leaves was the biomass of amphipod grazers whereas it was gastropod grazers in *Amphibolis*. More large erect epiphytes were found on longer leaves in *Posidonia* whereas the biomass of large erect stem epiphytes was the major correlate in *Amphibolis* meadows. Stem large erect epiphytes appeared to be strongly related the biomass of amphipod grazers.

The results of the present study indicate that although there appears to be similar patterns of algal epiphytes and epifaunal invertebrates within the different seagrass species, the actual processes contributing to those patterns, as evidenced by the associations within and between fauna and flora, vary. The seagrasses provide the primary habitat and algal epiphytes have varying degrees of importance depending upon the seagrass species and the epifaunal group under consideration. Both seagrass habitats support diverse and complex communities of attached biota. The habitats appear to be equally suitable for both grazing and suspension-feeding invertebrates and the variability in factors associated within feeding modes (in both amphipods and molluscs) is just as great as between feeding modes between seagrass habitats.

In contrast to *Posidonia*, *Amphibolis* provides a more structurally complex habitat that supports a greater number of species of both algal epiphytes and motile invertebrate grazers. The greater biomass of large erect epiphytes growing on the longer-lived stems also provides both a source of food and shelter for invertebrate grazers which are not present within *Posidonia* meadows. These patterns highlight the importance of seagrass species and structural complexity in affecting both the epiphytic and grazer community. The importance of spatial scales at which seagrasses and their associated communities are sampled are equally important because of their differing levels of spatial patchiness.

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