

# Distribution of the epiphytic organisms on *Posidonia australis* and *P. sinuosa*, two seagrasses with differing leaf morphology

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**ABSTRACT:** The distribution of epiphytic algae and sessile invertebrates on the leaves of the seagrasses *Posidonia australis* Hooker f. and *P. sinuosa* Cambridge and Kuo is not random. Epiphyte load on the leaves of both species increases with increasing distance away from the basal meristem. There are approximately 3 times as many epiphytic algal species as invertebrate species, and many of these epiphytes grow at distinct locations on the leaves. Epiphytic invertebrates were found primarily on the basal sections of the leaves, whereas algae were most abundant near the leaf apex. Distribution of epiphyte load across the leaf surface was also non-random, with initial settlement of epiphyte propagules occurring at the margins of the leaves. The structure of the epiphytic community is strongly correlated with leaf age, with a greater abundance of epiphytic species occurring on the older leaves. It is clear that leaf morphology also plays a significant role in the distribution of the epiphytes. There is no apparent difference in the epiphytic community between the sides of the flat *P. australis* leaf whereas, in *P. sinuosa*, the concave side of the curved leaf supports a more diverse epiphytic community than the convex side. Similar patterns in the distribution of epiphytic organisms were observed on artificial seagrass leaves, indicating that, although a temporal component is involved, epiphyte distribution is influenced mainly by the relative position upon the leaf surface as well as leaf morphology, which affects the water flow pattern over the leaf.

**KEY WORDS:** Algae · Invertebrates · Artificial leaves · Water flow

## INTRODUCTION

The seagrasses *Posidonia australis* Hooker f. and *P. sinuosa* Cambridge and Kuo are widely distributed in marine embayments and nearshore areas around the temperate coastline of Australia. *P. australis* occurs from Shark Bay in the north of Western Australia, around the southern coastline, northwards to Port Macquarie in New South Wales, and along the northern coast of Tasmania. *P. sinuosa* has a similar geographic range in Western Australia, but does not extend further east than Kingston in South Australia.

Both *Posidonia* species have long, strap-shaped leaves but are easily distinguished by differences in leaf morphology; *P. sinuosa* has a narrow, 4 to 9 mm wide leaf which is slightly curved in cross section,

whereas the leaves of *P. australis* are 10 to 15 mm wide, are flat in cross section, and are approximately twice as thick as those of *P. sinuosa* (Cambridge & Kuo 1979). These leaves are an excellent substratum for the attachment of a wide variety of algae, sessile invertebrates and various microscopic and macroscopic organisms (Novak 1984, Pansini & Pronzato 1985, Borowitzka & Lethbridge 1989, Kendrick & Burt 1997).

The diversity of epiphytic algae<sup>1</sup> on seagrass leaves can be very great and may comprise a major portion of the species present in a given area (Ballantine & Humm 1975, Harlin 1980, Borowitzka et al. 1990). The epiphytic algal biomass on *Posidonia* and *Amphibolis* is often comparable to that of the seagrasses themselves and the epiphytic component of a seagrass com-

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<sup>1</sup>For the purpose of this paper, an epiphyte is defined as 'any organism that lives upon a plant whether or not a nutritional relationship exists' (Harlin 1980)

munity may contribute significantly to community productivity (e.g. Penhale 1977, Bulthuis & Woelkerling 1983, Borum et al. 1984, Heijs 1984, Mazella & Alberte 1986, Moncreiff et al. 1992). Furthermore, calcareous epiphytes contribute to sediment production, leading to the formation of extensive sediment banks such as those found in Shark Bay, Western Australia, and help to reduce beach erosion (Walker & Woelkerling 1988). Changes in the abundance and composition of epiphytic organisms can also be used as sensitive indicators of water quality (May 1982, Cambridge et al. 1986).

The diversity of epiphytes on seagrasses has been well documented (e.g. Humm 1964, May et al. 1978, Harlin 1980, Heijs 1985a), but much of this literature has concentrated on the taxonomy of these organisms, rather than the pattern of epiphyte distribution or the underlying causes for these patterns (e.g. Cattaneo & Kalff 1979, Horner 1987, Lethbridge et al. 1988, Borowitzka et al. 1990, Kendrick & Burt 1997).

The seagrass leaf is an excellent habitat for epiphytic organisms, especially algae, for several reasons: (1) settlement at the apex of the leaves exposes epiphytic algae to higher light intensities and less sedimentation compared with those growing further down the leaf, and (2) the leaf's physical movement through the water also exposes the epiphytic algae to a much greater nutrient supply and washes away any inhibitory substances (Harlin 1975, Cattaneo & Kalff 1979, Keough 1986, Borowitzka & Lethbridge 1989).

This paper compares the spatial and temporal distribution of epiphytic organisms on the leaves of the seagrasses *Posidonia sinuosa* and *P. australis* with related, but different, leaf morphologies and considers how abiotic factors, such as water flow and irradiance, and biotic factors, such as settlement, recruitment and growth habit, may affect the distribution of the epiphytic organisms observed.

## MATERIALS AND METHODS

This study was carried out near Perth, Western Australia, in Shoalwater Bay, south of Point Peron, about halfway between Bird Island and the mainland (approximately 125°41'27" E, 32°17'36" S). This site has extensive *Posidonia* meadows with monospecific stands of both *P. sinuosa* and *P. australis* growing adjacent to each other at a depth of approximately 1 to 2 m.

For the determination of the spatial and temporal distribution and relative abundance of epiphytic organisms on the leaves, random samples of *Posidonia sinuosa* and *P. australis* were collected from the study site on 15 March (late summer) and on 6 August 1990 (late winter). Leaf clusters of both species were col-

lected by digging around the base of the leaves and pulling out the shoots from below substratum level, so that the leaves remained attached to a small intact piece of rhizome. This kept leaf clusters intact and allowed the relative age of leaves within each cluster to be determined. Material collected from the field was frozen at -20°C until analysis.

**Apico-basal distribution of epiphytic organisms.** For detailed analysis of epiphyte abundance and distribution on the seagrass leaves, 20 leaf clusters of each species were selected at random and the leaves in each cluster classified according to age. The shortest, and therefore youngest, leaf was designated Leaf 1, and the other leaves were numbered sequentially. Each cluster generally had 2 or 3 leaves. The leaves were cut from the shoot at the point of emergence at the top of the leaf sheath and divided into 3 equal divisions representing the apical, middle and basal sections of the leaf.

Each side of the leaf was analysed separately. The 2 sides of *Posidonia sinuosa* were easily distinguished as one is concave and the other is convex. The flat leaf of *P. australis* was marked to ensure that all leaves were examined in the same orientation. Epiphytic organisms discernable under the dissecting microscope were identified as far as possible (complete identification was sometimes impossible due to the immaturity of the epiphyte) and recorded along with a measure of their abundance. Due to taxonomic difficulties with the very small Bryozoa and sponges, these were not identified to genus level. Reference specimens are held in the Murdoch University herbarium (MURU).

Algal epiphyte abundance was estimated as percent cover, since most of the algae were too small for accurate dry weight measurements. The percent cover of the algal epiphytes was recorded according to the following scale: 0 (absent), 1 (<5%), 2 (5–20%), 3 (20–50%), 4 (50–80%) or 5 (>80%) cover.

The epiphytic fauna occurred as distinct individuals and, in most cases, was quantified simply by counting the number of individuals present. The abundance of hydrozoans was obtained by counting the number of erect colonies emerging from the stolon, while bryozoans, which often covered larger sections of the leaf surface, were quantified in the same manner as the algae (Borowitzka et al. 1990).

The results were examined by chi square analysis (Kershaw 1973) and by a 2-way indicator species classification (TWINSPAN), a divisive hierarchical 2-way indicator species analysis (Hill 1979).

Microscopic epiphytes were examined semi-quantitatively by scanning electron microscopy (SEM). For SEM 5 mm sections of the apical, middle and basal parts of a leaf were fixed in 3% glutaraldehyde in seawater for 1 h and then dehydrated through a graded

series of ethanol for 15 min at each step before being transferred into 100% amyl acetate. After critical point drying, the samples were mounted on aluminium stubs and sputter coated with gold before examination in the SEM.

**Across-leaf distribution of epiphytic organisms.** To determine the distribution of epiphytic organisms across the leaf surface from margin to margin, a piece of a clear plastic marked in 1 mm intervals was laid across the leaf surface at right angles to the leaf margin and the percent cover of epiphytic organisms within each millimetre section was estimated to the nearest 25% under a dissecting microscope. Five leaves from each species were randomly selected and 3 replicate analyses were performed on each side of each section of the leaves.

**Artificial seagrass leaves.** Artificial seagrass leaves modelling both *Posidonia* species were constructed and deployed in the natural seagrass meadow to determine the time course of settlement, recruitment and subsequent growth phases of the epiphytic organisms in relation to the life span of the seagrass leaves. Artificial leaves modelling *P. australis* were made from 12 mm wide, green, rough-surfaced plastic flagging tape (Horner 1987, Lethbridge et al. 1988). A second model was made by cutting 10 mm wide strips from thin tinted PVC sheets. To model the curved leaves of *P. sinuosa*, a PVC garden soaker hose was cut into 35 cm long sections, and each of these was then cut longitudinally into six 8 mm wide, 1 mm thick strips. These artificial leaves were a little more strongly curved and stiffer than the natural leaves. A second model of *P. sinuosa* leaves was made using the PVC sheets, creating a curve in the plastic by bending it around the heating element of a plastic bag sealer.

One hundred artificial leaves of each type were attached to a rectangular 50 × 100 cm epoxy-coated steel frame, to which a 20 × 20 mm plastic mesh had been attached. Each type of artificial leaf was attached to the plastic mesh in clusters of 2 leaves, with the leaves arranged at an average density of 715 leaves m<sup>-2</sup> (similar to the field density). The frame containing the artificial seagrasses was placed in a shallow bed of *Posidonia sinuosa* at the Bird Island study site at approximately 1.0 m depth on 12 June 1990. After 45 d, the artificial leaves were harvested and analysed in the same manner as the natural leaves.

**Leaf orientation and curvature.** The *in situ* orientation of the leaves of the 2 species in relation to the substrate was measured using a protractor which had a spirit level glued along the horizontal base line. A length of string with a table tennis ball threaded onto the end was attached to the point of origin of the protractor so that when the protractor was held level under water the string would be oriented along the line

of 90°. The range of bending of each species of seagrass could thus be determined.

The degree of leaf curvature of *Posidonia sinuosa* was also determined by cutting free-hand transverse sections of the leaf at 5 cm intervals up the length of the leaf. These leaf sections were then stood on their cut surfaces and photocopied. Using a dissecting microscope, curvature of these sections was determined by drawing a line from one leaf margin to the other, determining the mid point of this line and measuring the perpendicular distance from this point to the concave surface of the leaf.

**Water flow.** The pattern of water flow over individual leaves of both *Posidonia* species was examined in the laboratory using a 1.5 m long, 25 × 40 cm Perspex recirculating flume. Water was circulated around the flume at a velocity of approximately 3.5 cm s<sup>-1</sup>. Flow patterns over the leaves were visualised by the use of red food dye dissolved in seawater which was released just above the surface of the leaf at a constant and controlled rate. Movement and dispersion of the dye was analysed over both sides of the leaf of both species.

In the field, fluorescein dye was used to establish differences in the movement of water over *Posidonia* meadows. Release of dye over and within the meadows was monitored visually and by underwater video which allowed water flow patterns to be determined.

## RESULTS

### Epiphyte distribution

During this study a total of 28 species of epiphytic algae and 8 species of epiphytic invertebrates (other than molluscs) were found on the leaves of *Posidonia australis*, while 37 epiphytic algal and 11 invertebrate species were found on the leaves of *P. sinuosa*. The distribution of epiphytic organisms on the seagrass leaves was not random.

The epiphytic organisms on the *Posidonia* leaves showed clear apico-basal zonation. The majority of the epiphytes, in particular the algae, were found on the apical portion of the leaves (Tables 1 to 4), which also had a higher total percent cover (see Fig. 3). This trend was evident throughout the year, although it was less obvious during winter when the number of species of epiphytic algae declined by almost 50%. The number of species of epiphytic invertebrates remained comparatively constant throughout this study. Hydrozoans were most abundant on the leaves of *P. australis*, with *Plumularia compressa* found on all leaves, with the highest abundance at the base of the leaves. *Plumularia nodosa* was found only in the winter samples and

Table 1. *Posidonia australis*. Distribution and abundance of epiphytic algae and invertebrates on the apical, middle and basal sections of leaves collected on 15 March 1990. Data is the average of the leaves from 20 leaf clusters. Abundances of algae are given on the following scale: 1 (<5%), 2 (5–20%), 3 (20–50%), 4 (50–80%), 5 (>80%) cover. Bryozoans are quantified in the same way as algae, whereas invertebrate abundances are given as either number of individuals per leaf section or, in the case of hydrozoans, as the number of erect colonies emerging from the stolon. %: percentage of leaves the epiphytic species was observed on; a: abaxial side of leaf; b: adaxial side of leaf

	Leaf 1						Leaf 2						Leaf 3								
	%	Apex		Middle		Base		%	Apex		Middle		Base		%	Apex		Middle		Base	
		a	b	a	b	a	b		a	b	a	b	a	b		a	b	a	b	a	b
ALGAE																					
<i>Fosliella-Pneophyllum</i>	29	1	1	1	1			95	2	2	2	2	1	1	100	5	5	3	3	1	1
<i>Centroceras clavulatum</i>	29	1		1				30	1	1	1	1	1	1	40	1	1	1	1	1	1
<i>Laurencia filiformis</i>	0							45	1	1	1	1		1	90	1	1	1	1	1	1
<i>Ceramium puberulum</i>	0							45	1	1	1	1	1	1	85	1	1	1	1	1	1
<i>Entocladia</i> sp.	0							30	1	2	1	1	1		70	2	2	1	1	1	1
<i>Jania</i> sp.	0							20	1	1	1	1			70	1	1	1	1		1
<i>Polycerea nigrescens</i>	0							35	1	1	1	1			65	1	1	1	1		
<i>Sphacelaria rigidula</i>	0							10	1			1			60	1	1	1	1	1	1
<i>Ceramium isogonum</i>	0							15			1	1			50	1	1	1	1		
<i>Champia zostericola</i>	0							15	1	1					45	1	1	1	1		
<i>Giffordia sandriana</i>	0							5	1						40	1	1		2		
<i>Ceramium shepherdii</i>	0							10	1						35	1	1	1	1		
<i>Mychodea gracilaria</i>	0							10		1		1			35	1	1	1			
<i>Johannesbaptista pellucida</i>	0							5		1					35			1	1	1	
<i>Audouinella</i> sp.	0							5			1				30	1	1	1	1		
<i>Chondria</i> sp.	0							0							30	1	1	1			
<i>Laurencia cruciata</i>	0							0							30	1	1	1			
<i>Polysiphonia</i> sp.	0							0							25	1	1	1			1
<i>Calothrix</i> sp.	0							0							20						1
<i>Cladophora</i> sp.	0							15	1		1				10	1	1				
<i>Dasya</i> sp.	0							0							10	1		1			
<i>Antithamnion verticale</i>	0							0							5			1			
<i>Metagoniolithon chara</i>	0							0							5	1					
<i>Enteromorpha</i> sp.	0							5				1			0						
INVERTEBRATES																					
<i>Spirorbis</i> sp.	71	2	3	1	1	1		100	5	15	10	7	6	2	100	15	8	9	10	6	6
<i>Plumularia compressa</i>	43	4	2	1		6		50	7	12	9	11	10	15	70	8	6	13	12	11	22
Foraminiferan 1								40	1	1	2	1	2	2	60	2	1	1	1	2	2
Bryozoan 1								25	1	1	2	1		1	60	1	1	1	1	1	1
Bryozoan 2								15	1	1					50	1		1	1	1	1
Foraminiferan 2								10					1	1	30		2	1	1	1	1
Porifera 1															15	1	1	1	1		1

was also concentrated on the basal sections of the leaves.

The number of epiphytic species and their relative cover varied significantly between the apical, middle and basal sections in the March samples, whereas during winter (August), only the apical and basal sections differed significantly ( $\chi^2$  test,  $p > 0.05$ ). At no stage during the study was any significant difference detected between the 2 sides of the leaves of *Posidonia australis*. In contrast, a highly significant difference ( $\chi^2$  test,  $p > 0.01$ ) was found in the number and distribution of epiphytic organisms between the 2 sides of the leaves of *P. sinuosa* in late summer; however, there was no difference during winter. More species of epiphytic algae and invertebrates were encountered on the concave leaf surface (33 algal and 10 invertebrate species) than

on the convex surface (25 algal and 9 invertebrate species) (Tables 3 & 4).

A number of the algal species recorded on *Posidonia sinuosa* occurred only on the concave side of the leaf. These included *Antithamnion verticale* (Harvey) J. Agardh, 2 species of *Crouania*, *Cladophora* sp. 2, *Herposiphonia* sp., *Jania* sp., *Polysiphonia* sp. 2, *Spyridia filamentosa* (Wulfen) Harvey, *Ulva australis* Areschoug., *Hincksia* sp., and the colonial diatom *Licmophora* sp. (Tables 3 & 4). Invertebrate epiphytes found only on the concave leaf surface were Porifera 1 and *Plumularia compressa* Bale (Tables 3 & 4). Far fewer species were restricted to the convex surface. These were the red algae *Laurencia cruciata* Harvey, *Ceramium isogonum* Harvey and *Chondria* sp., of which only a single plant of each species was recorded.

Table 2. *Posidonia australis*. Average distribution and abundance of epiphytic algae and invertebrates on the apical, middle and basal sections of leaves collected on 6 August 1990. Data is the average of the leaves from 20 leaf clusters. See Table 1 for details regarding abundance scale, quantification methods and %, a and b

	Leaf 1						Leaf 2						Leaf 3						
	%	Apex a b	Middle a b	Base a b	%	Apex a b	Middle a b	Base a b	%	Apex a b	Middle a b	Base a b	%	Apex a b	Middle a b	Base a b			
<b>ALGAE</b>																			
<i>Fosliella-Pneophyllum</i>	0				95	2	3	2	2	2			100	5	5	4	4	2	2
<i>Ceramium puberulum</i>	0				25	1	1	1					80	1	1	1	1	1	1
<i>Entocladia</i> sp.	0				0								90	2	2	1	2	1	
<i>Polycerea nigrescens</i>	0				0								55	1	1	1	1		
<i>Cladosiphon filum</i>	0				0								50	1	1	1	1		
<i>Giffordia sandriana</i>	0				0								20	1		1			
<i>Ulva australis</i>	0				0								15	1	1				
<i>Dasya</i> sp.	0				0								10	1	1				
<i>Laurencia filiformis</i>	0				0								10	1					1
<i>Sphacelaria rigidula</i>	0				0								10	1	1				
<i>Antithamnion verticale</i>	0				0								5						1
<i>Centroceras clavulatum</i>	0				0								5						
<i>Enteromorpha</i> sp.	0				0								5	1					
<b>INVERTEBRATES</b>																			
<i>Plumularia compressa</i>	100	5		4	60	24	26	39	21	49	13		85	20	12	16	35	31	59
<i>Spirorbis</i> sp.	0				65	2	4	2	2	3	2		90	3	4	2	5	2	6
Foraminiferan 1	0				55	2	2	1	2	4	1		80	1	1	2	2	2	3
Porifera 1	0				5					1			5						1
Bryozoan 1	0				0								25	1	1		1		
<i>Plumularia nodosa</i>	0				0								25				38	34	66

A single compound ascidian was also found on the convex side of a *P. sinuosa* leaf. In general, most algal epiphytes growing on the convex surface were small turf-forming species.

Of the species common to both sides of the leaf of *Posidonia sinuosa*, variation in distribution and abundance was apparent for certain species (Tables 3 & 4). *Audouinella* sp., *Calothrix* sp., *Dasya* sp., *Giffordia sandriana* (Zanardini in Kützing) Hamel and Porifera 2 were found on the middle and apical sections of the concave surface, but only on the apical section of the convex surface. Similarly, *Ceramium shepherdii* Womersley, *Cladophora* sp. 1 and *Mychodea gracilaria* (Sonder) Kraft were found along the entire length of the concave surface of the leaf, but only occurred on the middle and apical sections of the convex leaf surface. On the other hand, *Centroceras clavulatum* (C. Agardh) Montagne and *Polysiphonia* sp. 1 were observed on all sections on both sides of the leaf, but were more abundant on the concave side of the leaf. On both seagrasses the encrusting coralline algae *Fosliella cymodoceae* (Foslie) Jones and Woelkerling and *Pneophyllum caulerpae* (Foslie) Jones and Woelkerling were the most common algae, occurring along the entire length of almost all leaves examined. The cover of encrusting coralline algae increased towards the apex of the leaf, at times reaching 100% cover. Inter-

estingly, SEM examination of the leaves showed that on the older leaves of *P. sinuosa* germination disks of *F. cymodoceae* and *P. caulerpae* were common on the convex surface of the leaf, whereas only mature thalli of these algae were observed on the concave side of the leaf. Other widely distributed algal species along the leaf surfaces were *C. clavulatum*, *Laurencia filiformis* (C. Agardh) Mertens, *Sphacelaria rigidula* Kützing, *Ceramium puberulum* Sonder, and an encrusting green alga, *Entocladia* sp. (Tables 1 to 4).

Other algae had a more limited distribution, being restricted to certain areas of the leaf. Many of the larger algae, including *Audouinella* sp., *Ceramium isogonum* Harvey, *Champia zostericola* (Harvey) Reedman and Womersley, *Cladophora* sp. 1, *Cladosiphon filum* (Harvey) Kylin, *Giffordia sandriana*, *Mychodea gracilaria* (Sonder) Kraft, *Polycerea nigrescens* (Harvey ex Kützing) Kylin and *Ulva australis* Areschoug were found commonly on the middle and apical sections of the leaf of *Posidonia australis* but never on the basal section of this species (Tables 1 & 2).

The epiphytic invertebrates *Spirorbis* sp., Bryozoan 2 (= *Thairopora mamillaris*?) and Foraminiferan 1 were found on the leaves of both seagrass species on all sections. In *Posidonia australis* the hydroid *Plumularia compressa* and another bryozoan (Bryozoan 1 = *Lichenopora* sp.) were also found on all parts of the

Table 3. *Posidonia sinuosa*. Distribution and abundance of epiphytic algae and invertebrates on the apical, middle and basal sections of leaves collected on 15 March 1990. Data is the average of the leaves from 20 leaf clusters. c: concave side of leaf; v: convex side of leaf. See Table 1 for details regarding abundance scale, quantification methods and %

	%	Leaf 1						%	Leaf 2						%	Leaf 3					
		Apex		Middle		Base			Apex		Middle		Base			Apex		Middle		Base	
		c	v	c	v	c	v		c	v	c	v	c	v		c	v	c	v	c	v
ALGAE																					
<i>Fosliella-Pneophyllum</i>	57	2	1	1	1			83	2	1	1	1	1	1	100	5	4	3	2	1	1
<i>Sphacelaria rigidula</i>	43			1	1			67	1	1	1	1	1	1	100	1	1	1	1	1	1
Chaetomorpaceae	29	1						50	2	1	1	1			65	2	2	1	1		
<i>Centroceras clavulatum</i>	14	1						56	1	1	1		1		100	1	1	1	1	1	1
<i>Laurencia filiformis</i>	14			1				50	1	1	1		1		95	1	1	1	1	1	1
<i>Cladophora</i> sp.1	0							39	1	1	1				85	1	1	1	2	1	
<i>Polysiphonia</i> sp.1	0							39	1		1			1	45	1	1	1	1	1	1
<i>Giffordia sandriana</i>	0							33	1	1					75	1	1	1	1		
<i>Polycerea nigrescens</i>	0							28	1	1	1	1			35	1	1	1	1		
<i>Ceramium puberulum</i>	0							22	1	1					80	1	1	1	1		1
<i>Ceramium shepherdii</i>	0							22	1	1	1				55	1	1	1	1	1	1
<i>Dasya</i> sp.	0							11	1						25	1	1				
<i>Champia zostericola</i>	0							6		1					80	1	1	1	1		
<i>Mychodea gracilaria</i>	0							6	1						70	1	1	1	1	1	1
<i>Calothrix</i> sp.	0							6			1				35	1	1	1			
<i>Johannesbaptista</i>	0							6	1						35	1	1	1	1		
<i>pellucida</i>																					
<i>Enteromorpha</i> sp.	0							6	1						20			1			1
<i>Crouania</i> sp.2	0							6			1				0						
<i>Jania</i> sp.	0							2	1						75	1		1			
<i>Laurencia cruciata</i>	0							0							30				1		
<i>Audouinella</i> sp.	0							0							25	1	1	1			
<i>Cladophora</i> sp.2	0							0							15	1					
<i>Hincksia</i> sp.	0							0							15			1			1
<i>Polysiphonia</i> sp.3	0							0							15	1	1		1		
<i>Polysiphonia</i> sp.2	0							0							10			1			1
<i>Antithamnion verticale</i>	0							0							5						1
<i>Ceramium isogonum</i>	0							0							5		2				
<i>Chondria</i> sp.	0							0							5		1				
<i>Crouania</i> sp.1	0							0							5			1			
<i>Herposiphonia</i> sp.	0							0							5	1					
<i>Licmorpha</i> sp.	0							0							5	1					
<i>Plocamium mertensii</i>	0							0							5			1			
<i>Spyridia filamentosa</i>	0							0							5	1					
INVERTEBRATES																					
<i>Spirorbis</i> sp.	71	5	3	4	2	3	2	100	14	7	9	4	5	2	100	31	10	31	7	11	3
Foraminiferan 1	43	4	1	1				61	3	2	1	1	1	2	80	3	3	3	2	5	2
Bryozoan 1	14				1			33	1	1	1				55	1	1	1	1		
Porifera 2	0							28	1						70	1	1	1			
Bryozoan 2	0							22		1	1	1			45	1	1	1	1	1	1
Foraminiferan 2	0							22			1		2	1	45	1	1	2	1	2	1
Porifera 1	0							11	1		1				50	1		1		1	
Compound ascidian	0							0							5				2		
<i>Plumularia compressa</i>	0							0							5	2					

leaf, whereas they had a much more restricted distribution on *P. sinuosa*. On the other hand, a sponge, Porifera 1, which was found growing over the whole length of the concave leaf surface of *P. sinuosa*, grew only on the basal and middle sections of *P. australis* (Tables 3 & 4).

Analysis of the youngest leaves in each leaf cluster showed that the encrusting coralline algae *Centro-*

*ceros clavulatum* and foraminiferans were the earliest colonisers of the leaves. SEM also showed the presence of the diatom *Cocconeis* sp. In *Posidonia australis*, *Ceramium puberulum*, the hydrozoans and *Spirorbis* sp. were also early colonisers, whereas in *P. sinuosa* they were only found on the older leaves.

The most obvious seasonal difference between late summer and late winter was the overall reduction in

Table 4. *Posidonia sinuosa*. Distribution and abundance of epiphytic algae and invertebrates on the apical, middle and basal sections of leaves collected on 6 August 1990. Data is the average of the leaves from 20 leaf clusters. See Tables 1 & 3 for details regarding abundance scale, quantification methods and %, c and v

	%	Leaf 1						%	Leaf 2						%	Leaf 3					
		Apex		Middle		Base			Apex		Middle		Base			Apex		Middle		Base	
		c	v	c	v	c	v		c	v	c	v	c	v		c	v	c	v	c	v
ALGAE																					
<i>Fosliella-Pneophyllum</i>	88	3	3	2	1	1	1	100	5	5	4	4	2	2							
<i>Ceramium puberulum</i>	0							65	1	1	1	1									
<i>Entocladia</i> sp.	0							55	1	2	2	2									
<i>Cladosiphon filum</i>	0							50	1	1		1									
<i>Laurencia filiformis</i>	0							40	1	1	1		1								
<i>Polycerea nigrescens</i>	0							30	1	1		1									
<i>Giffordia sandriana</i>	0							25	1	1											
<i>Antithamnion verticale</i>	0							15				1									
<i>Cladophora</i> sp.2	0							15	1												
<i>Sphacelaria rigidula</i>	0							15	1			1									
<i>Centroceras clavulatum</i>	0							10				1									
<i>Enteromorpha</i> sp.	0							5				1									
<i>Ulva australis</i>	0							5	1												
INVERTEBRATES																					
<i>Spirorbis</i> sp.	88	3	2	2	6	2		100	36	3	58	1	17								
Foraminiferan 1	75	1	1	1	1	4	2	85	3	1	6	3	5	2							
Bryozoan 1	25	1	1					60	1	1	1	1	1								
<i>Plumularia compressa</i>	25	3	10	8	25	16	24	25	6		36		47	5							
<i>Campanularia australis</i>	12				5			10			84		115	12							
Porifera 1	0							40	1		1		1								
<i>Pycnotheca producta</i>	0							5	28		115	53	122	117							

algal species number. The number of algal species present in winter was about half that of the late summer sample. In contrast, there was little change in the number of invertebrate species between the seasons (compare Tables 1 & 3 with Tables 2 & 4 respectively).

The epiphyte distribution was further analysed by a TWINSPAN, which also indicated that the oldest leaves differed because of their high epiphyte load and that there were also distinct seasonal differences in the epiphyte communities (Figs. 1 & 2). The classification showed that the epiphytic communities on the 2 sides of the leaf of *Posidonia australis* were similar (Fig. 1), whereas the epiphyte communities on the 2 sides of the leaves of *P. sinuosa* were different, especially in summer (Fig. 2).

#### Across-leaf distribution of epiphytes

An analysis of the distribution and cover of epiphytic organisms across the leaf showed that the percent cover was highest at the margins and least at the centre (Fig. 3). In *Posidonia australis* there was no difference between the 2 sides of the leaf (Fig. 3a,b), whereas in *P. sinuosa* the margin to centre difference was less pronounced on the convex leaf surface than the concave leaf surface (Fig. 3c,d). In *P. sinuosa*, this

leaf edge to centre difference was much more pronounced on the older leaves, especially at the leaf apex.

Analysis of both the natural and artificial leaves indicated that initial settlement of epiphytic propagules occurred near the leaf margins, with further colonisation proceeding inwards, eventually covering most of the leaf surface on older leaves. This general pattern of across-leaf epiphyte distribution was the same for leaves of all ages, except that in the older leaves the epiphyte cover at the centre of the leaf eventually reached 100%.

#### Artificial seagrass leaves

Although the total number of epiphytic species was much reduced on the artificial leaves compared with the natural leaves, a pattern of zonation of epiphytic organisms similar to that found on natural leaves of *Posidonia australis* could already be observed on the artificial leaves made from plastic flagging tape after 45 d (Table 5A). The encrusting coralline algae *Fosliella cymodoceae* and *Pneophyllum caulerpae*, and the green alga *Entocladia* sp. were observed along the entire length of both sides of the artificial leaves, often covering over half the leaf surface. The blue-green

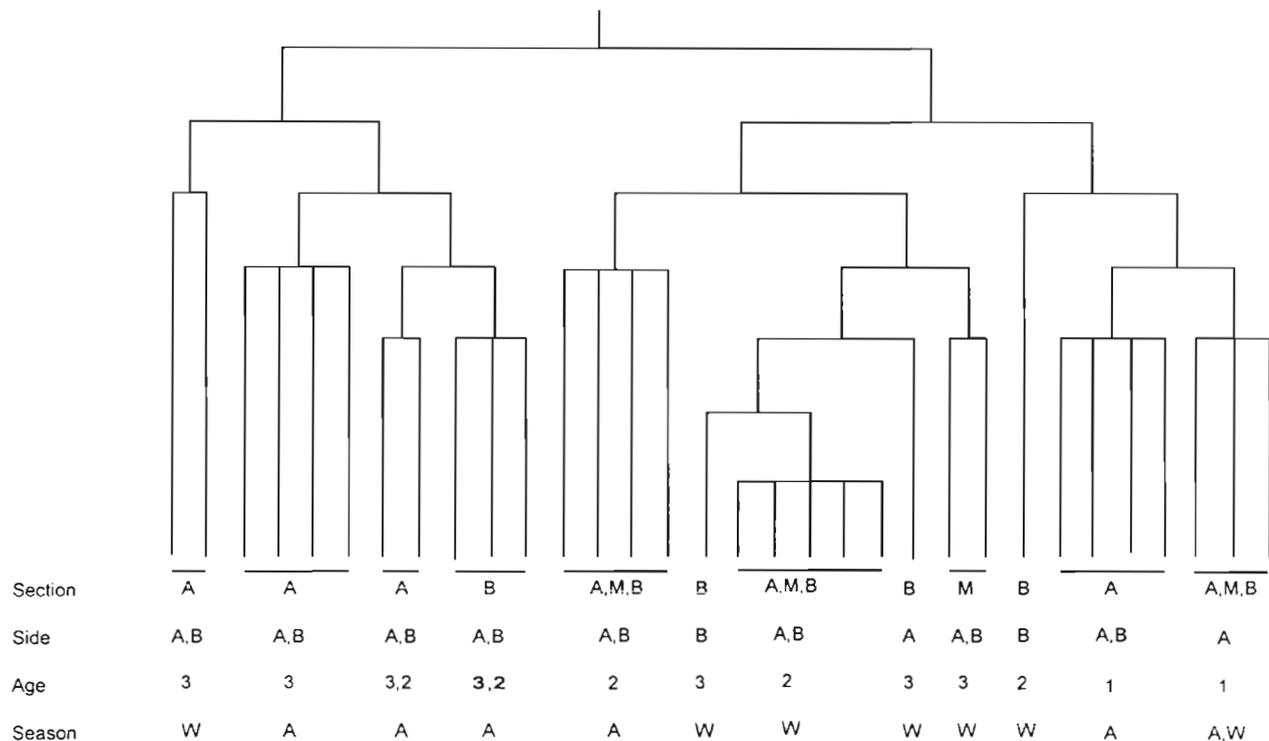


Fig. 1. *Posidonia australis*. TWINSpan classification of leaves based on the organisms present. Dendrogram shows linkages only and the vertical axis does not imply any particular degree of similarity. Section: A = apex, M = middle, B = base of leaf; Side: A = abaxial leaf side, B = adaxial leaf side; Age: 1 = youngest leaf in cluster, 3 = oldest leaf in cluster; Season: A = late summer (March), W = winter (August)

alga *Calothrix* sp. and the algae *Cladosiphon filum*, *Sphacelaria rigidula* and *Ulva australis* were occasionally found on the apical portions of the artificial leaves but only as single plants. *Spirorbis* sp. was the only invertebrate observed, and it was largely restricted to the basal sections of the leaves (Table 5A).

In contrast, the artificial leaves made from the PVC sheet modelling *Posidonia australis*, showed an opposite trend in the distribution of epiphyte load, with most of the 13 species observed only on the basal sections of the leaves (Table 5B). Again, the encrusting coralline algae *Fosliella cymodoceae* and *Pneophyllum caulerpae* as well as the prostrate green alga *Entocladia* sp. were common along the entire length of all the leaves examined, but were most abundant on the basal sections. *Calothrix* sp., *Ceramium puberulum* and a protozoan, Foraminiferan 1, were found on both sides of the leaves but restricted to the basal sections (Table 5B). All other larger algae and invertebrate species on these artificial leaves were found as single individuals on only 1 side of the basal section of 1 leaf and were not considered indicative of the sample. No significant difference ( $\chi^2$  test) in the numbers of epiphytic organisms was found between any of the leaf sections or between the sides of the leaves.

Both types of artificial *Posidonia sinuosa* leaves also tended to have an opposite distribution of epiphytic organisms from the natural leaves, with most of the epiphyte load on the basal sections rather than at the apex (compare Tables 3 & 4 with Table 6). Artificial *P. sinuosa* leaves made from PVC sheets displayed a slightly more widespread distribution of epiphytic organisms in comparison with the artificial leaves of *P. australis* made from the same material. In total, 10 species of epiphytic organisms were identified on these artificial *P. sinuosa* leaves; all of these were algae. The encrusting coralline algae *Entocladia* sp., *Cladosiphon filum* and *Ceramium puberulum* grew along the entire length of the artificial leaves, whereas all other algal species were found mainly on the basal section of the leaves and on the concave surface (Table 6A).  $\chi^2$  analysis indicated no significant difference ( $p > 0.05$ ) in epiphyte distribution between any of the leaf sections or between the sides of the leaves.

Nine epiphytic algal and 2 invertebrate species were found on the artificial leaves of *Posidonia sinuosa* made from PVC hosing (Table 6B). A clear distinction in the distribution of epiphytic organisms was noted between the 2 sides of this leaf. *Fosliella cymodoceae* and *Pneophyllum caulerpae* and *Entocladia* sp. were recorded along the length of both sides, but were pre-

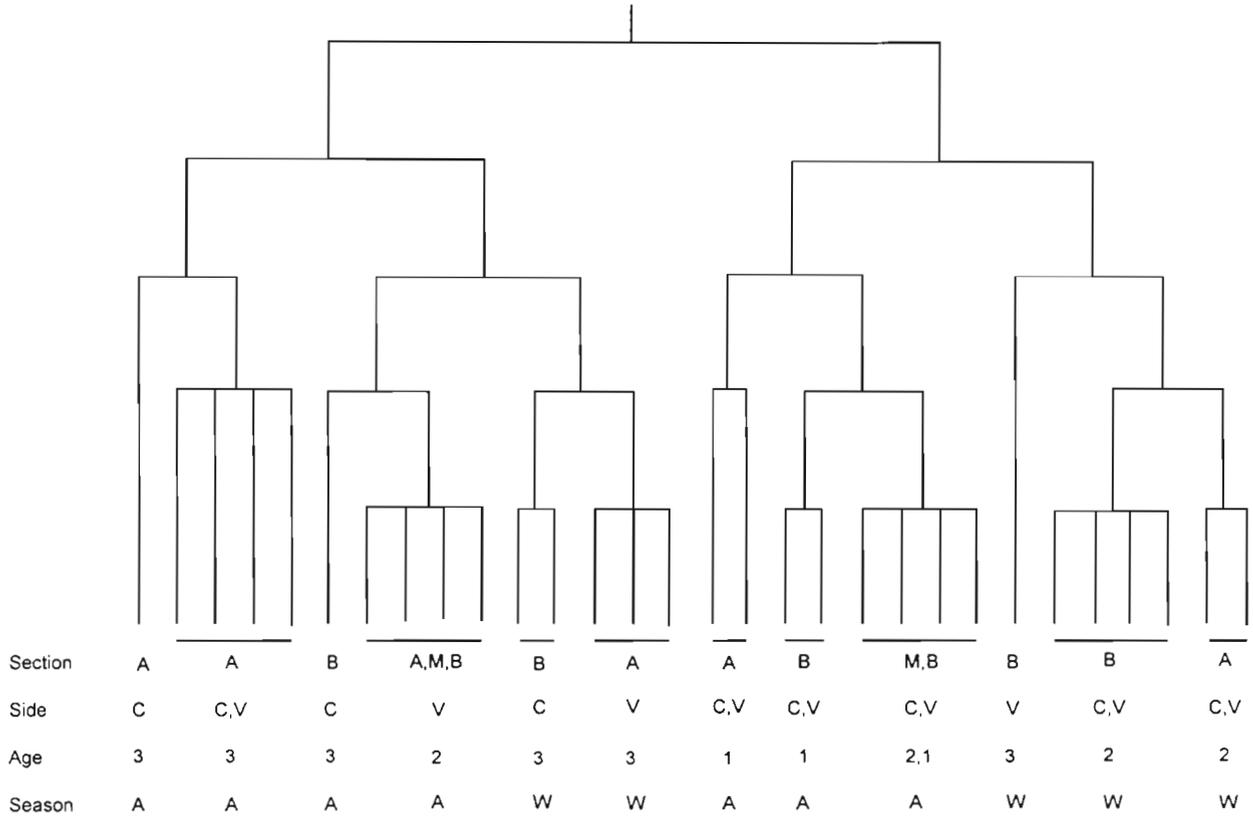


Fig. 2. *Posidonia sinuosa*. TWINSpan classification of leaves based on the organisms present. Dendrogram shows linkages only and the vertical axis does not imply any particular degree of similarity. Section: A = apex, M = middle, B = base of leaf; Side: C = concave leaf side, V = convex leaf side; Age: 1 = youngest leaf in cluster, 3 = oldest leaf in cluster; Season: A = late summer (March), W = winter (August)

sent only as minute colonies on the convex surface. All other algal species grew only on the concave surface and were usually restricted to the basal sections of the leaves (Table 6). *Spirorbis* sp. was found only on the concave surface, primarily on the leaf apex, with a single individual also found on a basal segment. A single Foraminiferan 1 individual was found on the basal section, on the convex side of 1 leaf (Table 6).  $\chi^2$  analysis showed no significant difference in the numbers of epiphytic organisms on the leaf segments or between the sides of the leaves; however, the sides of the leaves were classified into different groups by TWINSpan.

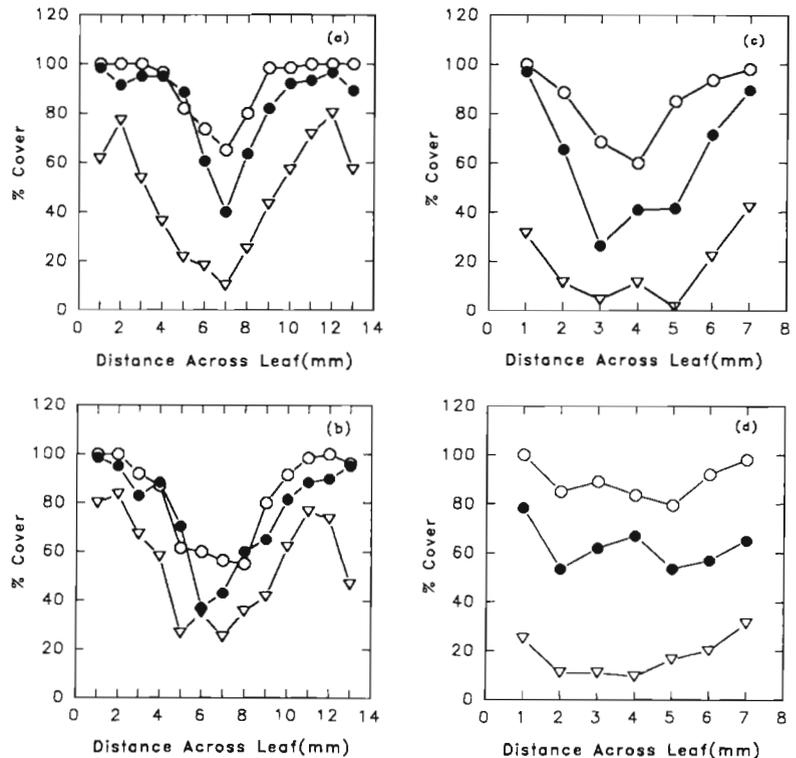


Fig. 3. *Posidonia australis*, *P. sinuosa*. Percent cover of epiphytic organisms across the leaves collected in March (late summer). (a) *P. australis*, abaxial side of leaf; (b) *P. australis*, adaxial side of leaf; (c) *P. sinuosa*, concave side of leaf; (d) *P. sinuosa*, convex side of leaf. (O) Apex of leaf; (●) middle of leaf; (▽) base of leaf

Table 5. Distribution and abundance of epiphytic organisms on artificial leaves modelling *Posidonia australis* after 45 d exposure (see Table 1 for details regarding abundance scale, quantification methods and %). Data is the average from 20 leaves. (A) Leaves made from flagging tape; (B) leaves made from PVC sheet. a, b: different sides of the leaves

	%	Apex		Middle		Base	
		a	b	a	b	a	b
<b>(A)</b>							
ALGAE							
<i>Fosliella-Pneophyllum</i>	100	1	1	1	1	2	2
<i>Entocladia</i> sp.	100	2	2	2	1	1	1
<i>Cladosiphon filum</i>	28	1	1				
<i>Sphacelaria rigidula</i>	8	1	1				
<i>Ulva australis</i>	8	1	1				
<i>Calothrix</i> sp.	5			1	1		
INVERTEBRATES							
<i>Spirorbis</i> sp.	15			1		1	2
<b>(B)</b>							
ALGAE							
<i>Fosliella-Pneophyllum</i>	100	1	1	3	3	5	4
<i>Entocladia</i> sp.	100	1	2	2	2	1	1
<i>Ceramium puberulum</i>	10					1	1
<i>Calothrix</i> sp.	2			1	1		
<i>Centroceras clavulatum</i>	2					1	
<i>Ceramium shepherdii</i>	2					1	
<i>Jania</i> sp.	2					1	
<i>Mychodea gracilaria</i>	2					1	
<i>Polysiphonia</i> sp.1	2					1	
INVERTEBRATES							
Foraminiferan 1	15					1	2
Porifera 1	2					1	
<i>Spirorbis</i> sp.	2					1	

### In situ leaf orientation and water flow

The leaf bases of both species of seagrass in the field are predominantly oriented along a NE-SW direction, which corresponds to the prevailing direction of water flow at this site. The way in which the seagrass leaves lie in the water column differs between the species. In still waters, *Posidonia australis* leaves tend to stand upright in the water column, curving over only at the leaf apex, whereas *P. sinuosa* leaves bend over at a lower point so that the leaves lie closer to the sediment. The leaves of *P. australis* emerge from the sediment at an angle of approximately 70° and bend less abruptly at the tip, whereas the leaves of *P. sinuosa* emerge at an angle of 40 to 50°. The across-leaf curvature of *P. sinuosa* leaves varies between leaves, but increases with increasing distance from the basal meristem (Fig. 4).

Examination of the movement and dispersion of dye over individual leaves of *Posidonia australis* in the laboratory flow tank showed that, at low current speeds of

approximately 3.5 cm s<sup>-1</sup>, water initially pools on the surface of the leaf before travelling only 1 to 2 cm along its length and then lifting off. Both sides of the leaf show the same flow pattern. This pattern of dispersion indicates that the leaf surface is exposed to a large volume of water. The 2 sides of the *P. sinuosa* leaves, on the other hand, showed different patterns of dispersion. On the concave surface of the leaf, the dye was effectively channelled along the entire length of the leaf, whereas on the convex side of the leaf the pattern of dispersion was similar to that observed with *P. australis* leaves, i.e. the dye was initially carried a short distance along the length of the leaf before either lifting off the surface or being deflected off the sides.

Examination of the dispersion of fluorescein dye over a *Posidonia australis* meadow revealed that there is little exchange between the water above and within the seagrass meadow; dye released within the meadow tended to stay within the leaf canopy for some time. In a *P. sinuosa* meadow, however, dye released within the leaf canopy had a tendency to leave the canopy rapidly and disperse out over the seagrass bed and up into the water column.

Table 6. Distribution and abundance of epiphytic organisms on artificial leaves modelling *Posidonia sinuosa* after 45 d exposure (see Table 1 for details regarding abundance scale, quantification methods and %). (A) Leaves made from PVC sheet; (B) leaves made from plastic hosing. c: concave side of leaf,; v: convex side of leaf

	%	Apex		Middle		Base	
		c	v	c	v	c	v
<b>(A)</b>							
ALGAE							
<i>Fosliella-Pneophyllum</i>	100	2	1	3	2	3	2
<i>Entocladia</i> sp.	100	3	1	3	1	2	1
<i>Ceramium puberulum</i>	41	1	1		1	1	1
<i>Cladosiphon filum</i>	26	1	1	1	1	1	
<i>Laurencia filiformis</i>	18	1				1	1
<i>Centroceras clavulatum</i>	9	1				1	
<i>Ceramium shepherdii</i>	9					1	1
<i>Jania</i> sp.	5					1	
<i>Polysiphonia</i> sp.1	5					1	
<b>(B)</b>							
ALGAE							
<i>Fosliella-Pneophyllum</i>	100	3	1	3	1	2	1
<i>Entocladia</i> sp.	60	1	1	1	1	1	1
<i>Laurencia filiformis</i>	10	1		1		1	
<i>Cladosiphon filum</i>	5	1				1	
<i>Ceramium shepherdii</i>	5			1			
<i>Antithamnion verticillat<sup>o</sup></i>	2					1	
<i>Sphacelaria rigidula</i>	2					1	
<i>Ceramium puberulum</i>	2			1			
INVERTEBRATES							
<i>Spirorbis</i> sp.	10	1				1	
Foraminiferan 1	2						2

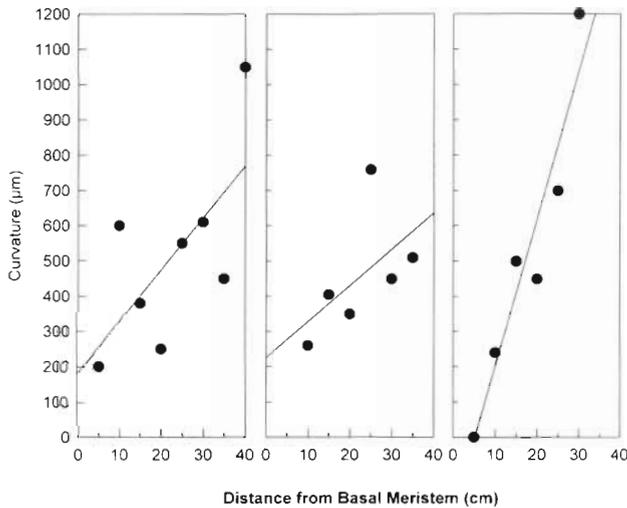


Fig. 4. *Posidonia sinuosa*. Gradient in cross-leaf curvature along the length of 3 randomly selected leaves

## DISCUSSION

Observed changes in epiphyte species composition and abundance on leaves of the seagrasses *Posidonia australis* and *P. sinuosa* clearly indicate non-random spatial and temporal distribution of the epiphytic organisms. Both species had a greater abundance and a higher diversity of epiphytic organisms on the oldest leaf in the cluster and on the oldest section (apex) of all leaves examined. Many of the epiphytes are also more abundant on specific locations on the leaves; generally, epiphytic algae were more abundant near the leaf apex, whereas epiphytic invertebrates were more abundant near the leaf base. Similar trends in epiphyte distribution have been observed for *Posidonia* spp. by Horner (1987) and for *Amphibolis griffithsii* by Borowitzka et al. (1990).

With the exception of isolated occurrences of the coralline alga *Metagoniolithon chara* (Lamarck) Ducker, all the epiphytic algae and invertebrates found on *Posidonia australis* were also present on *P. sinuosa*. However, during March, a greater diversity of epiphytic algae and invertebrates was found on the leaves of *P. sinuosa*. It is likely that this is due to the greater surface area available for colonisation on the longer *P. sinuosa* leaves, as well as the more complex morphology of these leaves. The fact that *P. sinuosa* leaves have a longer life (Cambridge 1996) may also be a contributing factor.

Studies of the natural and artificial leaves showed that the encrusting coralline algae of the *Fosliella-Pneophyllum* complex are the primary leaf colonisers on both *Posidonia* species, and that they occur on all but the newly emergent leaf sections. This has also been observed on many other seagrass species such as

*Amphibolis antarctica* (Labillardiere) Sonder and Ascherson ex Ascherson (Bramwell & Woelkerling 1984), *A. griffithii* (J.M. Black) den Hartog (Borowitzka et al. 1990), and *Thalassia testudinum* Banks ex König (Humm 1964). Among the invertebrates, the hydrozoan *Plumularia compressa*, Foraminiferan 1, and the polychaete *Spirorbis* sp. were the initial colonisers, although these organisms were much less abundant on the artificial leaves. These results confirm that, at least in the early stages of colonisation, seagrass leaves act as a 'neutral' substratum for the attachment of epiphytic organisms. The observations of Harlin (1973), Cattaneo & Kalff (1979), Horner (1987) and Lethbridge et al. (1988), who compared epiphyte growth and distribution on natural and morphologically similar artificial substrata, support this finding. These authors also showed that continued exposure of artificial substrata to epiphyte propagules ultimately results in nearly identical patterns of epiphyte distribution to those occurring on the natural substrata within a time period equivalent to that of the average lifespan of the macrophyte host, therefore indicating that the apico-basal distribution of epiphytes is not due to any inherent properties of the seagrass leaf such as the production of antifouling compounds.

The outcome of selective settlement of larvae as well as different degrees of mortality on specific areas of the leaf surface may have had an effect on the pattern of distribution of epiphytic organisms observed in this study (Keough 1986, Mazella & Russo 1989, Kaehler & Hughes 1992). Many species of encrusting coralline algae (Melobesiaceae) are able to establish themselves where conditions are not favourable for most other species. It has been proposed that these rapidly growing species modify the seagrass leaf surface, creating more suitable substrata for other epiphytic algae (Ballantine 1979, Harlin 1980, Breitburg 1984). However, in this study most epiphytes were observed to attach directly onto the leaf epidermis and not the coralline algae. Thus, it seems unlikely that the crustose coralline algae had a strong influence on subsequent settlement and recruitment. Generally, the initial colonisers were still present in the older portions of the leaf, but they became less important in terms of relative abundance and dominance. Similar observations have been made on the seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson (Heijs 1985b) and algal hosts (Ballantine 1979).

The progressive increases in the mean percentage cover and species diversity of the epiphytic algae as the leaves age has also been reported for *Posidonia oceanica* (L.) Delile (Van der Ben 1971, Borum 1987), *Phyllospadix torreyi* Watson (Willcocks 1982), *Zostera marina* L. (Jacobs et al. 1983), *Heterozostera tasmanica* (Martens ex Ascherson) den Hartog (Bulthuis &

Woelkerling 1983), *Amphibolis antarctica* (Bramwell & Woelkerling 1984), *A. griffithii* (Borowitzka et al. 1990) and *Thalassia hemprichii* (Heijs 1985a). The time available for the accumulation of biomass is also regarded as an important factor in the establishment of zonation of epiphytic organisms on macrophyte hosts (e.g. Ballantine 1979, Borum 1987, Mazella & Russo 1989). Significant differences in the species richness and coverage of epiphytic organisms on *Posidonia* leaves of different ages provide circumstantial evidence to support this hypothesis. However, studies using artificial seagrass leaves exposed for the same time suggest that relative position along the leaf is more important than the time available for biomass accumulation (Harlin 1973, Horner 1987, Borowitzka et al. 1990). Horner (1987) suggests that observed gradients in the distribution of epiphytic organisms are not a result of leaf growth or the time available for colonisation, but rather that they are due to gradients in physical factors which affect the growth rate of settled individuals.

Light, nutrients and current flow are the major environmental variables that universally affect seagrasses and their epiphyte communities (Short 1987, Borowitzka & Lethbridge 1989). Competition for light plays an important role in structuring marine communities (e.g. Sand-Jensen 1977, Reed & Foster 1984, Borum 1987), and there is circumstantial evidence to indicate that light is a primary factor influencing algal recruitment and growth. Epiphytic algae are exposed advantageously to light and nutrients and are less subject to sedimentation at the leaf apices as the leaves move back and forth with the current (Keough 1986, Borowitzka et al. 1990). Self shading, reported to exceed 90% by some workers (Borum & Wium-Andersen 1980, Borum et al. 1984), also affects algal growth toward the leaf base more than competition for space by sessile animals (Sand-Jensen 1977, Borum 1987). On the other hand, nutrient exchange is increased through enhanced water movement near the leaf apex (Harlin 1975, Fonseca et al. 1982, Fonseca & Kenworthy 1987, Horner 1987). This may explain why larger fleshy algae such as *Ceramium* spp., *Champia zostericola*, *Laurencia* spp. and *Mychodea gracilaria* were commonly found on the middle and apical sections of the leaves but rarely on the base.

By comparison, sessile, filter-feeding, epiphytic invertebrates were more abundant on the basal portions of the leaves, presumably as a result of these organisms being less able to compete for settlement space, as well as being outcompeted during the recruitment phase by rapidly growing epiphytic algae in regions of high light (Fletcher & Day 1983, Borowitzka & Lethbridge 1989). Lashing of the distal portions of the leaves and abrasion from adjacent leaves,

as well as predation by mobile epiphytic organisms such as gastropods, are also detrimental to juvenile communities and to delicate and weakly attached organisms (Fletcher & Day 1983, Keough 1986, Mazella & Russo 1989). It is likely that these factors affect sensitive species, such as hydroids, restricting them to the basal regions of the seagrass leaves.

The across-leaf distribution of epiphytic organisms on both natural and artificial *Posidonia* leaves clearly indicates that epiphyte propagules initially settle at the leaf margins. Similar results showing a higher cover of epiphytes on leaf margins have been obtained for *P. oceanica* (Van der Ben 1971), *Zostera marina* (Harlin 1975, Jacobs et al. 1983) and *Thalassia hemprichii* (Heijs 1985a). Furthermore, Harlin (1980) reported that epiphytes on *Z. marina* growing in calm waters tended to concentrate near the margin of the leaf, while in stronger currents the face of the leaf was more heavily colonised.

The results with artificial seagrass leaves presented here show similar across-leaf distribution patterns and indicate water flow patterns over the leaf edges are important in determining epiphyte distribution. As water moves around obstacles, turbulent eddies are formed near the edges, reducing water velocity relative to laminar flow regions (Foster 1975). This reduction in velocity may initially enhance spore and larval settlement, while increased circulation due to turbulence results in enhanced nutrient renewal and waste removal rates which could increase the growth of the plants.

One interesting result of the present study is the observation that epiphyte distribution differs between the 2 sides of *Posidonia sinuosa* leaves. Since the epidermis and cuticle of *Posidonia* leaves are identical in structure on both surfaces (Cambridge & Kuo 1979, Novak 1984), observed differences must be related to other factors, such as variation in water flow patterns or light. Water flowing over the *P. sinuosa* leaf surface remains longer in contact with the concave leaf surface than the convex surface, so that epiphyte propagules have more time to become attached. Luttenton & Rada (1986) have also proposed that, under conditions of increased turbulence, immigrating propagules may be prevented from successfully attaching to a substratum. Turbulence may either limit or inhibit contact between propagules and substrata, thus preventing the formation of an adhesive bond by the cell or propagule. Reduced light at the concave surface may also be a contributing factor. In still water *P. sinuosa* leaves tend to lay so that the convex surfaces of the leaves face upwards, and this implies that the net irradiance received by the concave surfaces of the leaves would be less than that received by the convex surfaces.

The distribution of epiphytic organisms on the strongly curved artificial leaves made from PVC hos-

ing confirmed that leaf curvature strongly influences epiphyte settlement, recruitment and growth. Although no significant differences in species number between the 2 sides of these 'leaves' were found, a markedly greater number of epiphytic algae settled on the concave surface. The artificial seagrasses also illustrate the importance of substratum texture. The PVC leaf models had a very smooth surface compared to the flagging tape, and on the former the epiphytic organisms could not attach successfully at the tips, where water velocity is greatest. Thus the artificial leaves of flagging tape with its rough surface showed the same apico-basal distribution of epiphytic organisms as the seagrass (see also Horner 1987 and Lethbridge et al. 1988 for similar observations), whereas the smooth PVC artificial leaves had a higher number of epiphytic organisms near the base. The importance of roughness is also indicated by the observation that more epiphytes occurred along the central axis of the curved PVC leaves, which was slightly roughened in the process of bending these leaves.

Differences in the growth habits of *Posidonia australis* and *P. sinuosa* also provide further insight into why differences in epiphyte species richness and cover occur between the 2 *Posidonia* species. The leaf density in *P. australis* meadows is significantly less than that of *P. sinuosa*. Furthermore, the shorter and thicker leaves of *P. australis* are quite stiff and tend to stand almost upright, bending over only at the distal end of the leaf, whereas the long flexible leaves of *P. sinuosa* characteristically bend over closer to the ground so that the rows of leaves form a dense mat lying almost parallel to the substratum. The dye studies reported here show that the sparse but erect leaf canopy of *P. australis* reduces circulation beneath it to an extent where the dye diffuses slowly around the leaves, but not into the water column above the bed. On the other hand, the more flexible and densely packed leaves of *P. sinuosa* redirect water flow from within the leaf canopy to the canopy surface. Thus it is likely that propagules of epiphytic species are subject to wider dispersion in a meadow of *P. sinuosa* than in a meadow of *P. australis*.

The effects of grazing, especially by molluscs, on the distribution of epiphytes cannot be ignored (Edgar 1990, Kendrick & Burt 1997); however, we observed very few grazing scars on our leaves, suggesting that such grazing is not a major factor affecting the distribution of epiphytes.

While similar patterns of epiphyte distribution along the leaves of both species were found at both sampling times, there were seasonal differences. During autumn (i.e. April to May), massive shedding of *Posidonia* leaves occurs. This generally leaves *P. australis* plants bearing only 1 mature and 1 newly emergent leaf, and

*P. sinuosa* plants with 1 mature leaf only (Horner 1987, Trautman unpubl.). The abscission of these older leaves, which carry the heaviest epiphyte load, leads to a substantial decrease in the abundance and diversity of epiphytic organisms so that only initial colonising species and small individual macroalgae are observed on the remaining 'younger' leaves. Similar seasonal differences were obtained by Kendrick & Burt (1997) on *P. sinuosa*, by Heijs (1985b), May et al. (1978) Jacobs et al. (1983) with other seagrasses, and by Whittick (1983) on the stipe of *Laminaria hyperborea* (Gunn.) Foslie.

During early autumn many species of epiphytic algae present on the leaves of *Posidonia sinuosa* were absent from the leaves of *P. australis*. However, during winter both *Posidonia* species had almost the same range of epiphytic algae, although the overall species numbers were reduced. By contrast, no marked change between seasons was observed in the occurrence of epiphytic invertebrates. Instead, a marked increase in the numbers of erect colonies of hydrozoans was found in winter, possibly due to reduced competition for space between these species and the epiphytic algae.

Increased turbulence resulting from storms over the winter may also remove or damage many erect or weakly attached species with increased lashing of the seagrass leaves. Luttenton & Rada (1986) found that epiphytic communities exposed to increased levels of turbulence, such as that produced by wind-generated waves, resemble those in early stages of colonisation and development.

In summary, the results presented here indicate that physical factors, especially water flow which affect settlement, recruitment and growth, are important causes of the non-random distribution of epiphytes on *Posidonia*, whereas leaf age and the time of the year affect epiphyte abundance and diversity.

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