

**Light and *Posidonia sinuosa* seagrass meadows
in the temperate coastal waters of Western
Australia**

**II. Effect of epiphyte species assemblage and biomass on
attenuating light to the leaf surface**

**A contribution to the Southern Metropolitan Coastal Waters
Study (1991-1994)**

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Light and *Posidonia sinuosa* seagrass meadows in the temperate coastal waters of Western Australia

II. Effect of epiphyte species assemblage and biomass on attenuating light to the leaf surface

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Contents

	Page
Acknowledgments	
Abstract	
1. Introduction	1
2. Materials and methods	3
2.1 Statistical treatment	5
3. Results	6
3.1 Epiphyte assemblages	6
3.2 Epiphyte biomass	7
3.3 Nutrient regime	10
3.4 Periphyton biomass-light reduction relationship	11
4. Discussion	13
4.1 Epiphyte assemblages	13
4.2 Epiphyte biomass	15
4.3 Periphyton biomass-light reduction relationship	16
4.4 Implications for management	16
5. References	17
Tables	
1. Number of macroalgal species on 12 leaves of <i>P. sinuosa</i> during summer and winter, at sites 1 and 2.	6
2. Percent occurrence of epiphyte taxa on 12 leaves of <i>P. sinuosa</i> during summer and winter, at sites 1 and 2.	6
3. Mean epiphyte biomass expressed as either chlorophyll <i>a</i> , total dry weight or the organic, carbonate and refractory components, at sites 1 and 2 during the annual, winter and non-winter periods. Epiphyte biomass expressed as (a) mean with standard errors (in parentheses) and as a percentage of total dry weight, and (b) ranges	8
4. Summary of correlation analyses (r^2) between percent light reduction and log transformed periphyton biomass expressed as either chlorophyll <i>a</i> , total dry weight or the organic, carbonate and refractory components, at sites 1 and 2 during the annual, winter and non-winter periods. All correlations were significant at $p \leq 0.05$, except the refractory component during non-winter, at site 1. n = sample size.	11

Contents

Page

5. Comparisons between the slopes of the periphyton biomass-light reduction relationships between sites and, between seasons at each site, were determined by comparing slopes of linear regressions between log transformed periphyton biomass and percent light reduction, over comparable ranges in biomass values. Significance level; * * $p \leq 0.01$; NSD = not significantly different. 12

Figures

1. Location map of (a) the study sites and (b) schematic of Success Bank showing the distribution of the seagrass meadow, water depth and sediment type at the two sites. 2
2. Apparatus for (a) measuring light transmission through the periphyton assemblage growing on artificial seagrass leaves and (b) detailed cross section of the water bath and light sensor. 4
3. Seasonal variation in epiphyte biomass expressed as (a) chlorophyll *a*, (b) total dry weight, (c) organic matter, (d) calcium carbonate and (e) refractory material at sites 1 (•) and 2 (o). Each point represents the analysis of a combined sample of epiphyte material removed from 15 *P. sinuosa* leaves. 9
4. Composite annual cycle of total inorganic nitrogen concentrations in the bottom waters at sites 1 (n = 44) and 2 (n = 46) derived from data collected between June 1992 and July 1993. 10
5. The relationship between periphyton biomass expressed as total dry weight and light reduction, at sites 1 (squares) and 2 (circles) during the winter (shaded) and non-winter (unshaded) periods. For graphical purposes the standard errors have been omitted but were generally less than 10 % (Burt, 1994). 12
6. The relationship between periphyton biomass and light reduction, at sites 1 (•) and 2 (+) during the non-winter period. Periphyton biomass is expressed as (a) chlorophyll *a*, (b) organic matter or (c) calcium carbonate. For graphical purposes the standard errors have been omitted but were generally less than 10 % (Burt, 1994). 14

Appendices

- I. Occurrence of macroalgal species on 12 leaves of *P. sinuosa* and on 12 artificial seagrass leaves (plastic strips), at sites 1 and 2 during summer and winter. Species occurrence on a seagrass leaf or artificial leaf scores 1.

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Abstract

Algae growing on artificial seagrass (periphyton) were used to examine the relationship between the epiphyte biomass on the leaves of the seagrass *Posidonia sinuosa* and the attenuation of light through this layer. Epiphyte and periphyton biomass and species assemblage were monitored over an annual cycle at two sites considered to be broadly representative of the inshore *protected* and offshore *semi-exposed* zones, the two major zones where seagrass grow in the southern coastal waters of Perth. These data were used to assess the influence of seasonal and site differences in species assemblage on this relationship. Significant logarithmic relationships between percent light reduction and periphyton biomass expressed as either chlorophyll *a*, total dry weight or the organic, carbonate and refractory components were evident at both sites. Periphyton biomass measured as total dry weight provided the only biomass-light reduction relationship with no significant site or seasonal differences. The site and seasonal differences in the relationship for other measures of periphyton biomass were attributed to differences in the species composition of the epiphyte assemblages. At the offshore site, the epiphyte assemblage changed from predominantly filamentous species with relatively high species richness in summer to predominantly coralline species with lower species richness during winter. The epiphyte assemblage at the inshore site was comprised predominantly of filamentous species with similar species richness in summer and winter. Ambient nutrient concentration and differential erosion/abrasion due to wave action appear to be the key factors influencing the composition of epiphyte assemblages on *P. sinuosa* in these waters. Consequently, activities that lead to changes in the nutrient status or wave climate have the potential to alter epiphyte communities and therefore the attenuation of light through this layer and, as a result, the amount of light reaching the seagrass leaf. Furthermore, the logarithmic nature of the epiphyte biomass-light reduction relationship indicates that even relatively small increases in standing crop above background values will be potentially harmful to seagrasses growing at or near their depth distribution.

1. Introduction

The survival of benthic plants in the marine environment is related to the amount of light reaching their leaves (Dennison, 1987; Carter and Rybicki, 1990; Kenworthy and Haurert, 1991; Chesapeake Bay Programme, 1992) and growth occurs where light levels ensure photosynthetic production exceeds respiratory losses (Dennison and Alberte, 1982; Masini *et al.*, 1995b). Light availability to benthic plants is determined by factors attenuating light through the water column (Chesapeake Bay Programme, 1992; Dennison *et al.*, 1993) and by epiphytic algae attached to the leaf surface (Silberstein *et al.*, 1986; Dennison, 1992).

Spatial and temporal changes in epiphyte assemblages are influenced by numerous biological and physical factors such as epifaunal grazing (Steneck 1983; Nielsen and Lethbridge 1989; Steneck *et al.*, 1991), the overall algal diversity in an area (Borowitzka and Lethbridge, 1989), the proximity to sources of algal epiphyte propagules (West, 1990), the availability of light (Cambridge *et al.*, 1986) and water temperature (Heijs, 1985). However changes in species composition and biomass of epiphyte assemblages is a typical response to changing nutrient status and, to a lesser extent, wave energy of the waters over benthic plant communities (May *et al.*, 1978; Cambridge, 1979; Harlin and Thorne-Miller, 1981; Cambridge *et al.*, 1986; Hillman *et al.*, 1991). There are numerous instances in Western Australia where nutrient enrichment of coastal waters has led to an excessive growth of epiphytes attached to seagrass leaves, contributing to a decreased in photosynthesis and subsequent decline of the seagrass communities due to light starvation (eg. Cambridge *et al.*, 1986; Hillman, 1986; Simpson and Masini, 1990). The relationship between the epiphyte assemblage and light reduction through this layer is, therefore, important in understanding the effects of nutrient enrichment on seagrass communities.

Seagrasses, particularly the meadow forming *Posidonia*, are among the most productive and important components of the temperate coastal ecosystems off Western Australia (Kirkman, 1992). The distribution of *Posidonia* meadows is generally restricted to low energy coastal lagoons and embayments with relatively clear, oligotrophic waters (Clarke and Kirkman, 1989). The relatively poor flushing rates of these areas resulting in longer retention times of nutrients in the water column, coupled with low rates of meadow expansion, make *Posidonia* seagrasses particularly vulnerable to the effects of nutrient enrichment (Simpson and Masini, 1990). These seagrasses have morphological and physiological adaptations (eg. rhizomes with soluble carbohydrate reserves) to recover from relatively short periods (weeks-months) of light reduction (Gordon *et al.*, 1994). However chronic reductions in available light will affect seagrasses growing at or near their depth limits, especially species such as *P. sinuosa* that have a low net photosynthesis to respiration ratio (Masini *et al.*, 1995a, b). Extensive meadows of *Posidonia* seagrasses occur in the protected embayments and lagoons of Perth's southern coastal waters.

The primary objective of this study was to examine the relationship between epiphyte biomass on the leaves of the seagrass *Posidonia sinuosa* Cambridge & Kuo and light attenuation through this layer. Epiphyte and periphyton biomass and species assemblage were monitored over an annual cycle at two sites considered to be broadly representative of the inshore *protected* and offshore *semi-exposed* zones, the two major zones where seagrass grows in the southern coastal waters of Perth. These data were used to assess the influence of seasonal and site differences in species assemblage on the biomass-light reduction relationship. A secondary objective was to quantify the epiphyte biomass-light reduction relationship for input to a nutrient-effects ecological model being developed as part of the Southern Metropolitan Coastal Waters Study (1991-1994), by the Western Australian Department of Environmental Protection, with the aim of developing an understanding of the cumulative environmental impacts of waste discharges to Perth's coastal waters (Simpson *et al.*, 1993). Companion studies were also conducted at these sites and examined the physical and biological processes that influence water column light attenuation (Burt *et al.*, 1995a) and quantified the minimum light requirements of *P. sinuosa* (Masini *et al.*, 1995a).

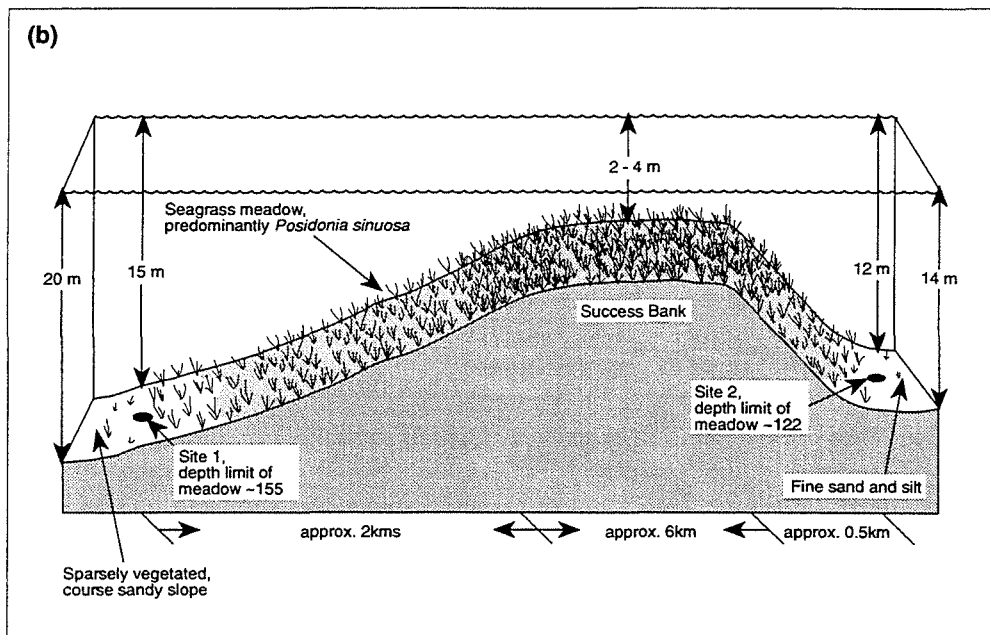
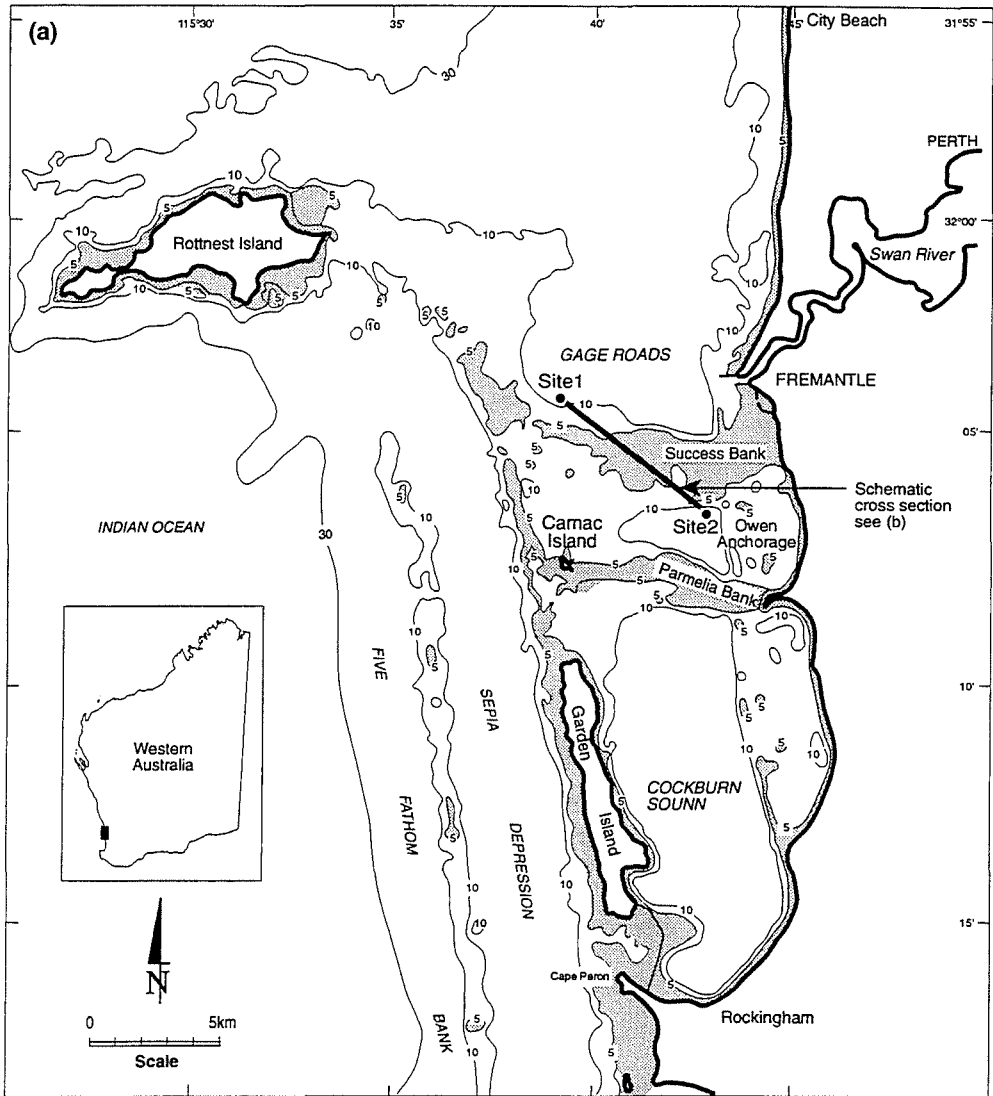


Figure 1. Location map of (a) the study sites and (b) schematic of Success Bank showing the vertical distribution of the seagrass meadow, water depth and sediment type at the two sites.

2. Methods

The study was conducted at two sites on the slopes of Success Bank, a shallow (< 5 m depth) sill located between the Owen Anchorage basin (~ 12 m depth) to the south and Gage Roads (~ 20 m depth) to the north (Fig. 1a). Much of Success Bank is covered with seagrass meadows dominated by *Posidonia* species (LeProvost Environmental Consultants, 1991). *Posidonia sinuosa* dominates the meadows on the slopes of the Bank in the vicinity of the study sites. Site 1 is located in 15 m water depth on the relatively exposed north-west side of Success Bank and is considered to be representative of the offshore *semi-exposed* zone. By contrast site 2, which is situated in 12 m water depth on the south-east side of Success Bank, is relatively sheltered from ocean swells by Success Bank to the north and a chain of reefs and islands to the west and south-west. This site is considered to be representative of the inshore *protected* zone. Both sites were located at the local depth limit of a *P. sinuosa* meadow (Fig. 1b).

The design of the artificial seagrass leaves used in this study was based on the morphometrics and mean shoot densities of *P. sinuosa* growing at both sites in June 1992. To mimic the relatively *long* primary and *shorter* secondary leaves of *P. sinuosa*, 5 mm wide strips of polyurethane plastic (0.9 mm thick) were cut to lengths of 280 mm and 130 mm for site 1 and 380 mm and 200 mm for site 2 and stapled together to form an artificial seagrass shoot. Shoots were stapled to square's (25 cm x 25 cm) of plastic coated steel mesh, termed periphyton collectors, at densities of 256 m⁻² and 184 m⁻² for sites 1 and 2 respectively.

Four periphyton collectors were deployed at both sites on six occasions at intervals of 30 to 40 days between August 1992 and June 1993. The collectors were left *in-situ* for approximately 80 days, the estimated mean age of *P. sinuosa* leaves (Hugh Kirkman, personal communication). Divers deployed the collectors within the seagrass meadow by pegging the base of the collectors to the seabed. The collectors were retrieved in separate plastic bags to minimise abrasion of the periphyton material, refrigerated, and light transmission determined within 24 hours of retrieval from the field.

The apparatus for measuring transmission of photosynthetically active radiation (PAR, 400-700 nm waveband) through the plastic strips consisted of a tungsten filament incandescent light source (Crompton Ltd, Edison screw, 45 mm round pearl lamp 1J, 40 W, 240 V) positioned approximately 150 mm above an integrating quantum light sensor (Li-cor, LI-192S; ± 5 %; Fig. 2a). To determine light transmission a strip was pinned down in a glass bottom cartridge, under approximately 25 mm of seawater, and measurements of light intensity were recorded at regular intervals along the length of the strip by passing the cartridge between the light source and the sensor (Fig. 2b). Ten strips, five *long* and five *short*, were randomly chosen from each periphyton collector and trimmed to equal length. The mean of five light intensity measurements was recorded every 30 mm along the length of a strip and these values were averaged to provide the mean light intensity for a strip. The same procedure was used to measure light intensity through five unused 'control' strips. Light reduction through periphyton assemblages was calculated by subtracting light intensity values from the mean 'control' value and expressed as a percentage.

After the light transmission measurements were completed, each strip was rinsed in distilled water to remove salts, laid flat on a glass slab and both sides scraped with a razor blade to remove the periphyton. Scrapings of the *long* and *short* strips were combined to form an homogeneous slurry. The homogenate was approximately halved, placed in pre-weighed centrifuge tubes, re-weighed and frozen for chlorophyll *a* and dry weight analyses. The remaining strips from each collector were frozen for determination of species composition.

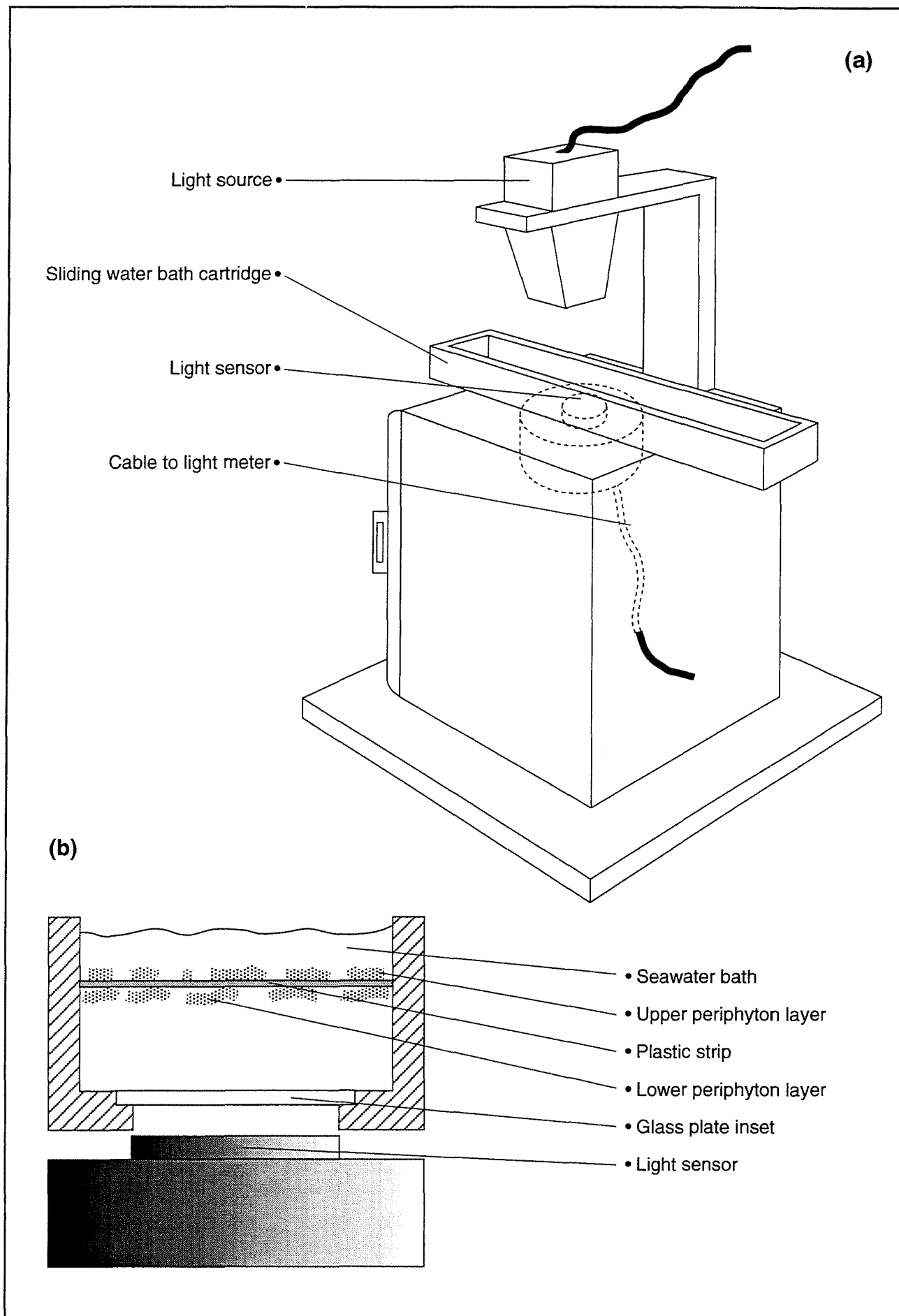


Figure 2. Apparatus for (a) measuring light transmission through the periphyton assemblage growing on artificial seagrass leaves and (b) detailed cross section of the water bath and light sensor.

Approximately 20 seagrass shoots from both sites were harvested on seven occasions at intervals of about 60 days and analysed for epiphyte macroalgal species composition and epiphyte biomass. Fifteen undamaged seagrass leaves were rinsed in distilled water and the epiphytes scraped from the area of living tissue (non-necrotic). The scrapings were bulked, divided into pre-weighed centrifuge tubes, re-weighed and frozen for chlorophyll *a* and dry weight analyses. The mean width, length of living leaf tissue and total length (including necrotic tissue) of each leaf were recorded. The remaining seagrass leaves were fixed in 10% formalin for 24 hours, then frozen for subsequent determination of species composition.

Chlorophyll *a* and phaeophyton concentrations ($\pm 0.06 \mu\text{g l}^{-1}$) were determined using the acetone extraction method (Jeffery and Humphrey, 1975) and applying a phaeophyton correction (Strickland and Parsons, 1972). Total dry weight was determined by drying samples to a constant weight at 105°C and the organic and carbonate fractions determined by subsequent weight losses at 550°C and 1050°C respectively. A correction factor of 2.27 was applied to the carbonate fraction to account for the residual calcium oxide. The 'refractory fraction' (inorganic, non-carbonate material) was calculated by subtracting the organic and calcium carbonate fractions from the total dry weight.

Species richness of the epiphyte and periphyton assemblages in summer and winter were determined by recording the presence of macroalgae species growing on 12 seagrass leaves and 12 plastic strips collected from both sites between (December, 1992 - February, 1993) and between (June, 1993 - July, 1993) respectively. Presence of a species on a leaf or plastic strip scored one and these scores were summed with a maximum score of 12. Species occurrences were summarized as percentage occurrence for the divisions Rhodophyta, Phaeophyta and Cyanophyta and for coralline and non-coralline algae within the Rhodophyta.

Samples of seawater were collected for nutrient analysis at both sites every 5-7 days, during six periods of approximately 42 days between March 1992 and June 1993. Ten-litre samples were collected from approximately 3 m below the water surface and approximately 3 m and 5 m above the seabed at sites 1 and 2 respectively, using a Niskin bottle. Approximately five litres were filtered through a 1.2 μm G/FC millipore filter (Whatman Ltd, England) at a maximum negative pressure of 75 KPa and subsampled for analysis of inorganic nitrogen (ammonia and nitrate-plus-nitrite). In the field, water samples were placed in 150 ml polyethylene bags (*Whirlpak*, Nasco Ltd, Kansas, USA.) and temporarily stored in darkness and on ice. In the laboratory samples were frozen and analysed within one month of collection. Ammonia-nitrogen ($\pm 5 \mu\text{g l}^{-1}$) was measured using the isocyanurate method (Dal Pont *et al.*, 1974). Nitrate+nitrite-nitrogen ($\pm 2 \mu\text{g l}^{-1}$) was determined with a Technicon Autoanalyser II after copper-cadmium reduction (Technicon Industrial Systems, 1972).

2.1 Statistical treatments

Parametric (Student's *t*-test, t_p) and non-parametric (Mann-Whitney U-test) statistical analyses were used to determine if pairs of sample means were significantly different (Snedecor and Cochran, 1967). Differences in the slopes of the periphyton biomass-light reduction relationships between sites and between seasons at each site, were determined by comparing slopes of linear regressions between log transformed periphyton biomass and percent light reduction, over comparable ranges in biomass values (Sokal and Rohlf, 1969). Probabilities of ≤ 0.05 were taken as significant unless stated otherwise

To assess seasonal trends in epiphyte biomass, the study period was divided into four seasons: *winter* (June 1 - August 31), *spring* (September 1 - November 30), *summer* (December 1 - February 28) and *autumn* (March 1 - May 31). Periphyton biomass-light reduction relationships were analysed for *winter* (June 1 - August 31) and *non-winter* (September 1 - May 31) periods.

3. Results

3.1 Epiphyte assemblages

Seasonal comparisons

At site 1 (offshore) a total of 33 taxa of macroalgal epiphytes were observed: 23 Rhodophyta, including 4 taxa of coralline algae, 8 Phaeophyta and 2 Cyanophyta (Appendix I). Species richness of the epiphyte assemblage was higher during summer ($n = 30$) than winter ($n = 7$; Table 1). Of the seven taxa that occurred in winter, four were also found in summer (Appendix I). Coralline Rhodophyta were the most common taxa during summer (89 %) and winter (67 %; Table 2). In comparison, the occurrence of non-coralline Rhodophyta was approximately 20 % during both seasons. Phaeophyta occurrence was higher in summer (21 %) than winter (8 %).

Table 1. Number of macroalgal species on 12 leaves of *P. sinuosa* during summer and winter, at sites 1 and 2.

Family	Summer		Winter	
	Site 1	Site 2	Site 1	Site 2
Rhodophyta	20	8	6	6
• coralline	3	2	2	2
• non-coralline	17	6	4	4
Phaeophyta	8	6	1	4
Cyanophyta	2	1	0	2
<i>Total</i>	30	15	7	12

Table 2. Percent occurrence of epiphyte taxa on 12 leaves of *P. sinuosa* during summer and winter, at sites 1 and 2.

Family	Summer		Winter	
	Site 1 (%)	Site 2 (%)	Site 1 (%)	Site 2 (%)
Rhodophyta	32	42	34	32
• coralline	89	33	67	54
• non-coralline	22	46	19	21
Phaeophyta	21	30	8	13
Cyanophyta	21	100	0	2

At site 2 (inshore) a total of 20 taxa of macroalgal epiphytes were observed: 11 Rhodophyta, including 3 taxa of coralline algae, 7 Phaeophyta and 2 Cyanophyta (Appendix I). Species richness of the epiphyte assemblage was similar between summer ($n = 15$) and winter ($n = 12$; Table 1) and of the 12 taxa that occurred in winter, seven also occurred in summer (Appendix I). Non-coralline Rhodophyta were the most commonly occurring taxa at site 2 during summer 50 % (Table 2). By comparison coralline Rhodophyta and Phaeophyta had similar occurrences of about 30 %. During winter the occurrence of all epiphytic taxa were relatively low except the articulated coralline algae *Fosliella* spp. which occurred on over 95 % of the leaves.

Spatial comparisons

Species richness of the epiphyte assemblage at site 1 was higher than site 2 during summer but lower during winter (Table 1). During summer all but one of the 14 taxa that occurred at site 2 were common to both sites (Appendix I). In contrast during winter only 3 of the 12 taxa that occurred at site 2 were common to both sites and 2 of these taxa were coralline algae. Species of Rhodophyta and Phaeophyta were the main components of the epiphyte assemblages at the two sites during summer (Table 1). During winter, species composition at site 1 was dominated by Rhodophyta, especially coralline algae, in contrast to site 2 where Rhodophyta and Phaeophyta both remained major components of the epiphyte assemblages. The occurrence of Phaeophyta and non-calcareous Rhodophyta species during summer were lower at site 1, however over the same period, the mean occurrence of coralline Rhodophyta was higher (Table 2). During winter the occurrence of non-coralline Rhodophyta species was similar at the two sites, however site 1 continued to have a lower occurrence of Phaeophyta species and a higher occurrence of coralline Rhodophyta species.

3.2 Epiphyte biomass

Seasonal comparisons

Epiphyte biomass was measured as either chlorophyll *a*, total dry weight, or the organic, carbonate and refractory (inorganic, non-carbonate) fractions of the total dry weight. Seasonal changes in epiphyte biomass were compared between winter and non-winter periods to assist with the interpretation of seasonal comparisons between epiphyte biomass-light reduction relationships (Table 3).

At site 1 all estimates of epiphyte biomass were lowest in early-summer and highest in late-autumn (Fig. 3). The distributions of chlorophyll *a*, total dry weight and calcium carbonate had the largest ranges in biomass values over the study period. In comparison the values of organic and refractory material were relatively constant over the same period. The organic content of epiphyte biomass was lower during winter than the non-winter period whereas the carbonate content was higher during winter (Table 3). The refractory content increased between winter and the non-winter period however it remained a relatively minor component of the epiphyte biomass.

At site 2 epiphyte biomass expressed as chlorophyll *a* was lowest in early-summer and highest in late-autumn (Fig. 3). In contrast values of total dry weight and the dry weight fractions were relatively low in late-spring/early-summer, increased and remained relatively high throughout the summer and early-autumn periods, then declined sharply during winter to values similar to spring values. The distributions of chlorophyll *a*, total dry weight and calcium carbonate had the largest ranges in biomass values over the study period. In comparison the values of organic and refractory material were relatively constant throughout the study period. There were no seasonal differences in the composition of epiphyte biomass with similar proportions of organic and carbonate material during winter and non-winter periods (Table 3). The refractory content increased between winter and the non-winter period however it remained a relatively minor component of the epiphyte biomass during the two seasons.

Table 3. Mean epiphyte biomass expressed as either chlorophyll *a*, total dry weight or the organic, carbonate and refractory components, at sites 1 and 2 during the annual, winter and non-winter periods.

Epiphyte biomass expressed as (a) mean with standard errors (in parentheses) and as a percentage of total dry weight, and (b) ranges.

Site	Epiphyte biomass		Annual	%	Winter	%	Non-winter	%	
1	Chlorophyll <i>a</i> ($\mu\text{g cm}^{-2}$)	a	0.87 (0.19)	-	1.35 (0.29)	-	0.67 (0.18)	-	
		b	0.28 - 1.64		1.05 - 1.64		0.28 - 1.19		
	Total Dry weight (mg cm^{-2})	a	1.33 (0.22)	100	1.93 (0.02)	100	1.09 (0.22)	100	
		b	0.61 - 1.9		1.90 - 1.95		0.61 - 1.80		
	Organic matter (mg cm^{-2})	a	0.34 (0.04)	26	0.43 (0.02)	22	0.31 (0.04)	30	
		b	0.23 - 0.45		0.40 - 0.45		0.23 - 0.42		
	Calcium carbonate (mg cm^{-2})	a	0.92 (0.17)	69	1.43 (0.02)	74	0.72 (0.16)	64	
		b	0.31 - 1.45		1.41 - 1.45		0.31 - 1.22		
	Refractory material (mg cm^{-2})	a	0.08 (0.02)	5	0.073 (0.02)	4	0.08 (0.03)	6	
		b	0.04 - 0.16		0.05 - 0.09		0.04 - 0.16		
	2	Chlorophyll <i>a</i> ($\mu\text{g cm}^{-2}$)	a	0.77 (0.09)	-	0.93 (0.26)	-	0.71 (0.09)	-
			b	0.53 - 1.20		0.67 - 1.19		0.53 - 1.05	
Total Dry weight (mg cm^{-2})		a	0.85 (0.11)	100	0.57 (0.17)	100	0.96 (0.11)	100	
		b	0.40 - 1.29		0.40 - 0.74		0.65 - 1.29		
Organic matter (mg cm^{-2})		a	0.28 (0.03)	34	0.20 (0.07)	34	0.32 (0.02)	34	
		b	0.13 - 0.34		0.13 - 0.27		0.28 - 0.37		
Calcium carbonate (mg cm^{-2})		a	0.53 (0.07)	61	0.36 (0.09)	63	0.59 (0.08)	60	
		b	0.26 - 0.80		0.26 - 0.45		0.33 - 0.80		
Refractory material (mg cm^{-2})		a	0.06 (0.02)	5	0.02 (0.01)	3	0.08 (0.02)	6	
		b	0.01 - 0.12		0.01 - 0.03		0.02 - 0.12		

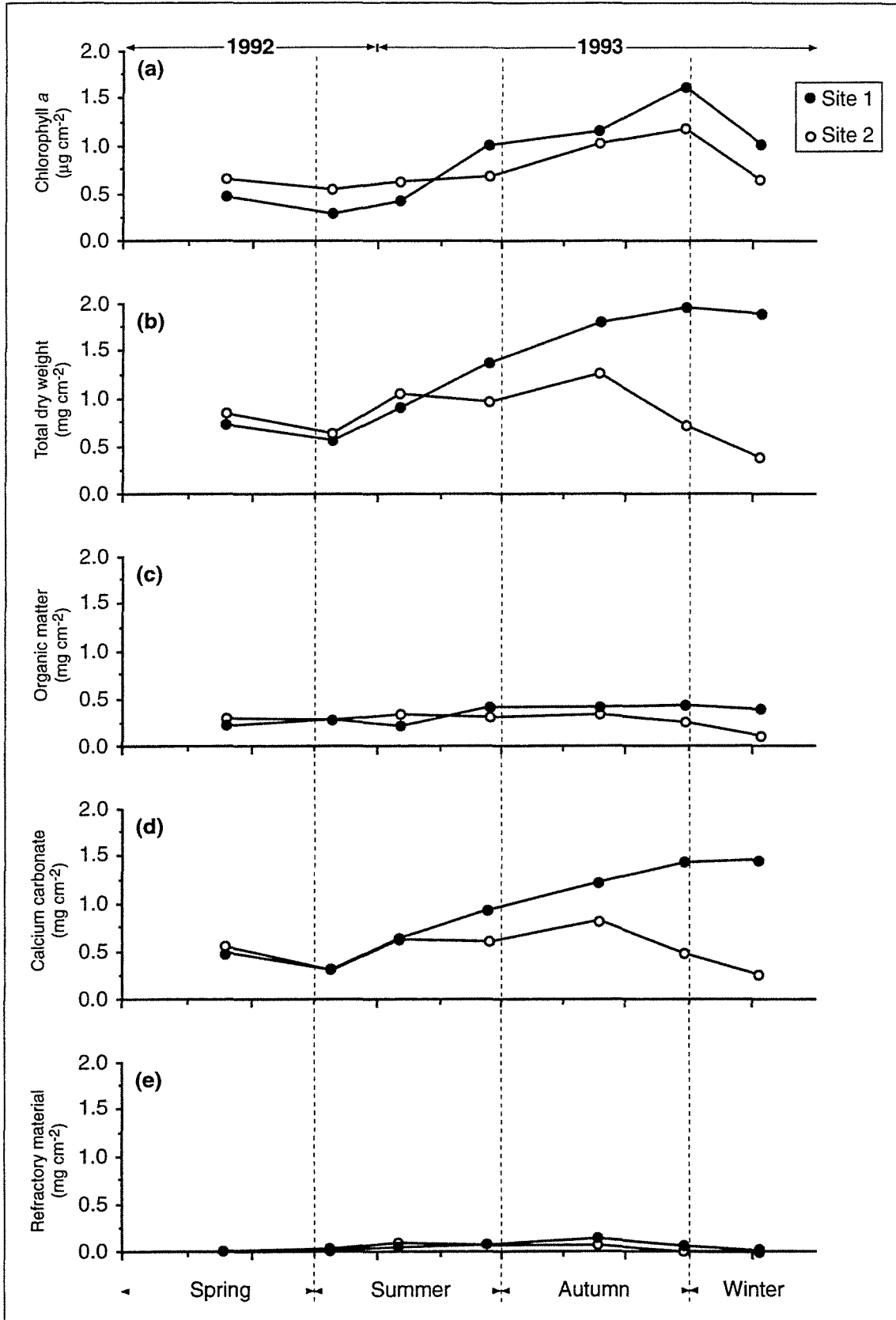


Figure 3. Seasonal variation in epiphyte biomass expressed as (a) chlorophyll *a*, (b) total dry weight (c) organic matter, (d) calcium carbonate and (e) refractory material at sites 1 (●) and 2 (○). Each point represents the analysis of a combined sample of epiphyte material removed from 15 *P. sinuosa* leaves.

Spatial comparisons

The seasonal distributions of epiphyte biomass expressed as total dry weight and calcium carbonate were similar between sites 1 and 2 during late spring/early summer but diverged markedly during autumn and winter (Fig. 3). In contrast values of epiphyte biomass expressed as either chlorophyll *a*, organic or refractory material were similar between the two sites throughout the study period.

During the non-winter period the total dry weight of epiphytes at sites 1 and 2 were similar. In contrast, during winter the total dry weight of epiphytes at site 1 was more than three times higher than site 2 (Table 3). The epiphytic assemblage at site 1 had a lower organic content and a higher carbonate content than site 2 during both the winter and non-winter periods. Differences between the sites in the percentages of organic and carbonate material were greatest during the winter period.

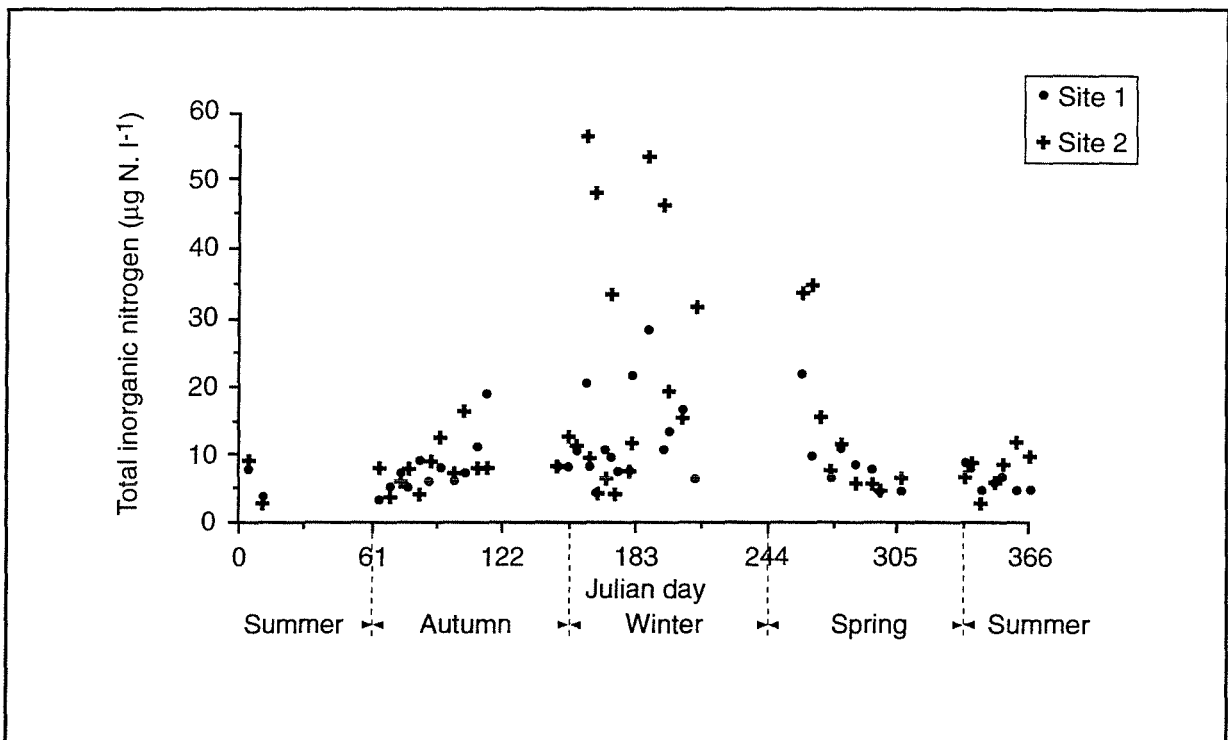


Figure 4. Composite annual cycle of total inorganic nitrogen concentrations in the bottom waters at sites 1 ($n = 44$) and 2 ($n = 46$) derived from data collected between June 1992 and July 1993.

3.3. Nutrient regime

Seasonal comparisons

Seasonal distributions of total inorganic nitrogen (TIN) concentrations in the *bottom* waters at sites 1 and 2 were unimodal with minima in summer and maxima in winter (Fig. 4). Annual concentrations of TIN at site 1 ranged from $3 \mu\text{g l}^{-1}$ to $28 \mu\text{g l}^{-1}$ and at site 2 ranged from $2 \mu\text{g l}^{-1}$ to $56 \mu\text{g l}^{-1}$. The mean concentrations of TIN during the winter and non-winter periods at site 1 were $13 \mu\text{g l}^{-1}$ and $7 \mu\text{g l}^{-1}$ and at site 2 were $24 \mu\text{g l}^{-1}$ and $9 \mu\text{g l}^{-1}$. TIN was significantly higher during winter at site 1 ($t = 2.89$, $p \leq 0.01$, $df = 42$) and site 2 ($t = 3.65$, $p \leq 0.001$, $df = 44$).

Table 4. Summary of correlation analyses (r^2) between percent light reduction and log transformed periphyton biomass expressed as either chlorophyll *a*, total dry weight or the organic, carbonate and refractory components, at sites 1 and 2 during the annual, winter and non-winter periods. All correlations were significant at $p \leq 0.05$, except the refractory component during non-winter, at site 1. n = sample size.

Site	Periphyton biomass	Annual	n	Winter	n	Non-winter	n
1	Chlorophyll <i>a</i>	0.214	56	0.876	16	0.249	40
	Total Dry weight	0.679	56	0.939	16	0.542	40
	Organic component	0.359	56	0.869	16	0.292	40
	Calcium carbonate component	0.583	56	0.908	16	0.340	40
	*Refractory component	0.191	43	0.411	13	0.081	30
2	Chlorophyll <i>a</i>	0.714	48	0.852	14	0.475	34
	Total Dry weight	0.929	48	0.832	14	0.694	34
	Organic component	0.894	48	0.820	14	0.535	34
	Calcium carbonate component	0.904	48	0.760	14	0.624	34
	*Refractory component	0.758	32	0.860	14	0.577	22

* values less than $1\mu\text{g cm}^{-2}$ (limit of detection) were excluded.

Spatial comparisons

The concentration of TIN was significantly lower at site 1 over the annual cycle ($t_p = 2.69$, $p \leq 0.05$, $df = 43$) and during the winter period ($t_p = 2.50$, $p \leq 0.05$, $df = 14$). TIN concentrations were similar at the sites during the non-winter period.

3.4. Periphyton biomass-light reduction relationships

The composition, species richness and relative abundance of the epiphyte and periphyton assemblages were similar at site 1 and site 2 during summer and site 1 during winter (Appendix I). Samples of the winter periphyton assemblage at site 2 were misplaced. However, since the structure of epiphyte and periphyton assemblages were similar during summer at this site and during summer and winter at site 1, it is reasonable to assume that the periphyton assemblage in winter at site 2, was similar to the epiphyte assemblage. A parametric and non-parametric statistical comparison of light intensity values measured through *long* and *short* plastic strips indicated that there were no significant differences at the two sites during the winter and non-winter periods and as a result the data for the different leaf lengths were combined.

Table 5. Comparisons between the slopes of the periphyton biomass-light reduction relationships between sites and, between seasons at each site, were determined by comparing slopes of linear regressions between log transformed periphyton biomass and percent light reduction, over comparable ranges in biomass values. Significance level; * * $p \leq 0.01$; NSD = not significantly different.

	Periphyton biomass				
	Chlorophyll a	Total dry weight	Organic component	Calcium carbonate component	Refractory component
Site 1	**	NSD	NSD	**	**
Winter Vs Non-winter					
Site 2	NSD	NSD	**	NSD	NSD
Winter Vs Non-winter					
Winter	**	NSD	**	**	**
Site 1 Vs Site 2					
Non-winter	NSD	NSD	NSD	NSD	**
Site 1 Vs Site 2					
Annual	NSD	NSD	**	**	**
Site 1 Vs Site 2					

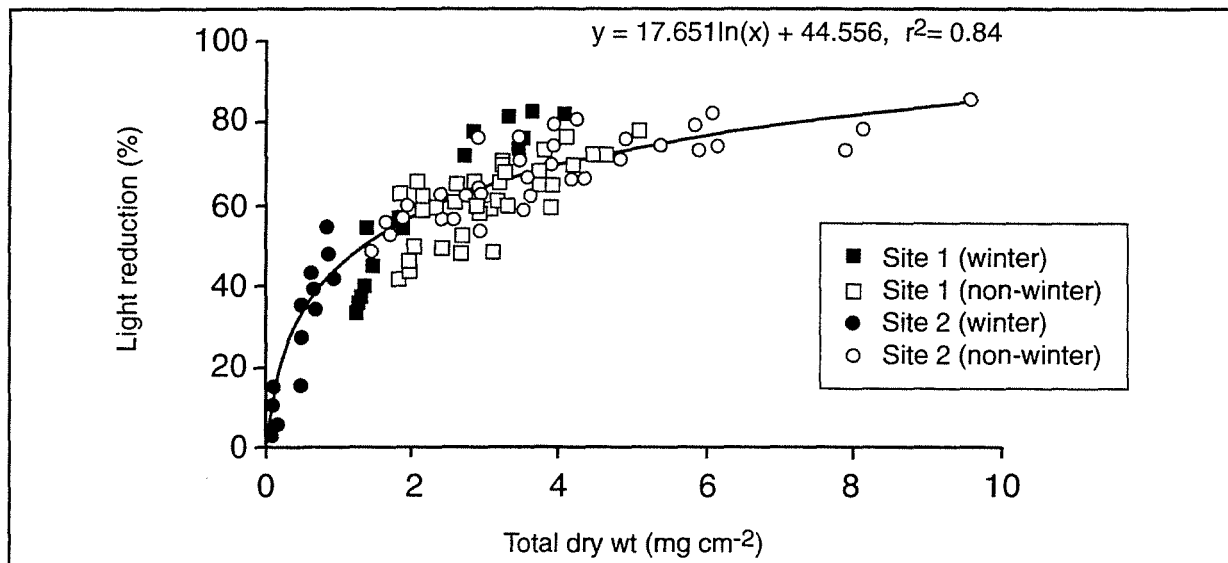


Figure 5. The relationship between periphyton biomass expressed as total dry weight and light reduction, at sites 1 and 2 during the winter and non-winter periods. For graphical purposes the standard errors have been omitted but were generally less than 10 % (Burt, 1994).

The relationship between percentage light reduction and periphyton biomass can be described by a logarithmic function. The slope and intercept of this relationship were determined by applying a simple linear regression to log transformed periphyton biomass values.

Percent light reduction and periphyton biomass expressed as either chlorophyll *a*, total dry weight or the organic, carbonate and refractory fractions were significantly correlated during the winter and non-winter periods at sites 1 and 2, except for the refractory component during the non-winter period at site 1 (Table 4). Correlation coefficients were higher during winter than non-winter at both sites. In winter the fraction of total dry weight with the most significant correlation with percent light reduction occurred when biomass was expressed as calcium carbonate at site 1 and refractory material at site 2, whereas during the non-winter period, the primary correlate at both sites was calcium carbonate.

There were no significant site or seasonal differences between the slopes of the light reduction relationships for periphyton biomass expressed as total dry weight (Table 5) enabling site and seasonal data to be pooled to establish a single relationship for the two study sites (Fig. 5). Site and seasonal differences in the light reduction relationship were found however when periphyton biomass was expressed as either chlorophyll *a*, organic, carbonate or refractory material (Table 5). At site 1, there were significant differences in the relationship between seasons for biomass expressed as chlorophyll *a*, calcium carbonate and refractory material. In contrast, at site 2 the only significant seasonal difference in the light reduction relationship expressed periphyton biomass as organic matter. During winter, there were significant differences in the relationship between sites for all measures of periphyton biomass, except total dry weight. By contrast, during the non-winter period there were no significant sites differences in the light reduction relationship, except for biomass expressed as refractory material. Values of periphyton biomass expressed as either chlorophyll *a*, organic or carbonate material at the two sites could therefore be pooled over the non-winter period to provide a common light-reduction relationship for the two study sites (Fig. 6).

4. Discussion

4.1. Epiphyte assemblages

At the offshore site (site 1) the species composition of the epiphyte assemblage changed from non-coralline dominated during summer to coralline dominated during winter. Epiphyte assemblages with high proportions of coralline algae are considered to be indicative of oligotrophic conditions (May *et al.*, 1978; Harlin and Thorne-Miller, 1981; Hillman *et al.*, 1991). However, ambient concentrations of total inorganic nitrogen in the 'bottom' waters at this site were significantly higher, not lower, during winter than summer suggesting that nutrients were not influencing the seasonal changes in epiphyte assemblage. Previous studies have reported differential erosion of epiphytes by wave action with higher erosion rates for filamentous and erect foliose species compared to 'low profile' encrusting coralline species (Cambridge, 1979; Burt *et al.*, 1995b). Consequently, under conditions of high wave energy coralline algae can become the dominant epiphytic taxa on seagrass leaves (Kendrick, 1991). Wave energy is significantly higher in the study area during winter and is approximately 50 % higher offshore compared to the inshore site (Burt *et al.*, 1995a). Thus the most likely explanation for the seasonal change in the species composition of the offshore assemblage is that higher wave energy during winter removes more filamentous species providing the coralline species with a competitive advantage.

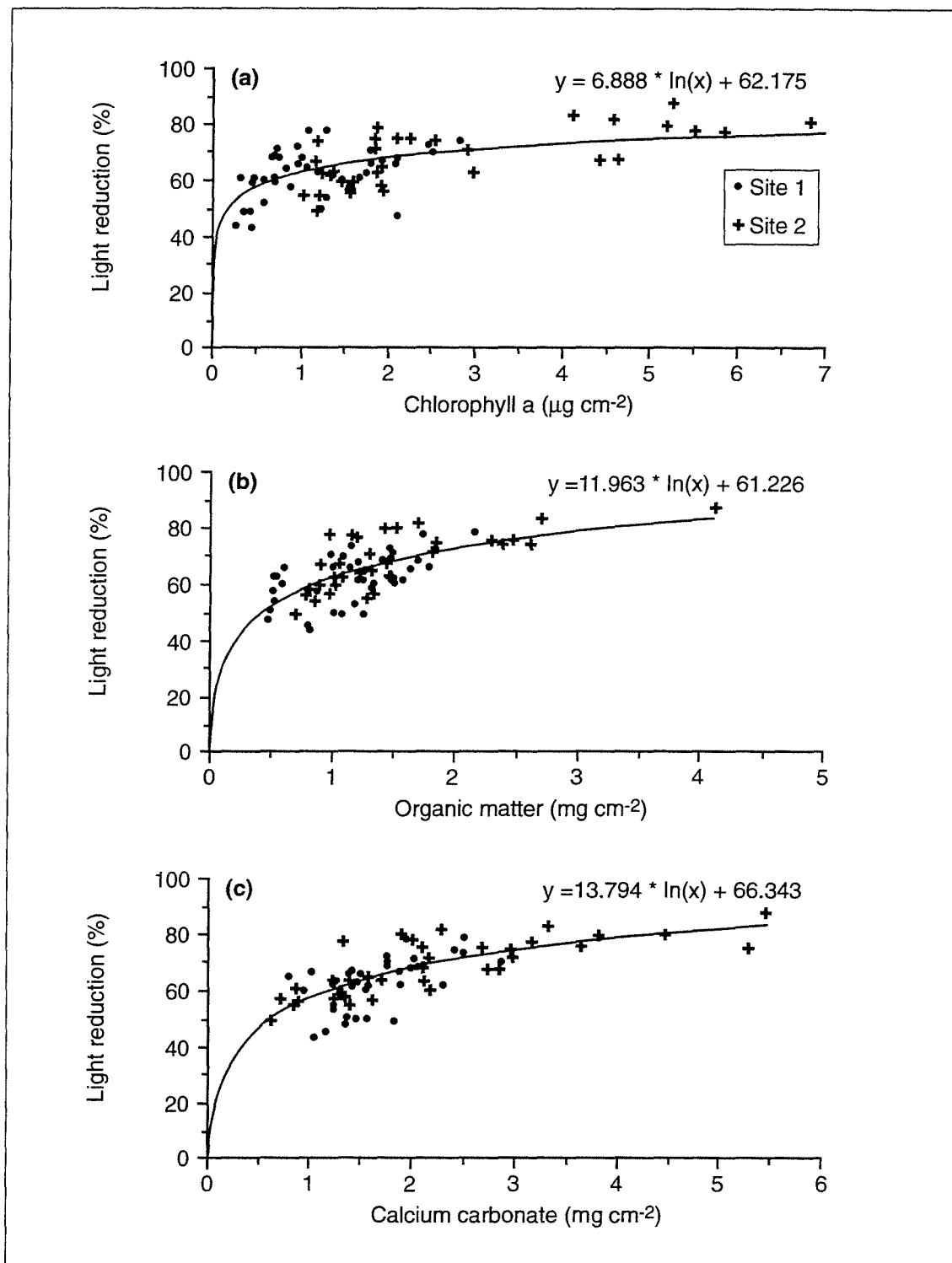


Figure 6. The relationship between periphyton biomass and light reduction, at sites 1 (•) and 2 (+) during non-winter period. Periphyton biomass is expressed as (a) chlorophyll a, (b) organic matter or (c) calcium carbonate. For graphical purposes the standard errors have been omitted but were generally less than 10 % (Burt, 1994).

The epiphyte assemblage at the inshore site (site 2) consisted mainly of filamentous species, with a similar species richness, composition, and species occurrence during summer and winter. Epiphyte assemblages dominated by filamentous species are considered to be characteristic of eutrophic conditions (May *et al.*, 1978; Harlin and Thorne-Miller, 1981; Cambridge *et al.*, 1986; Hillman *et al.*, 1991) suggesting that the species composition of the inshore assemblage is primarily nutrient induced. Previous studies indicate that in general the coastal waters of Perth are oligotrophic and suggest that nitrogen is usually the macro-nutrient limiting plant growth (Pearce, 1991; Simpson *et al.*, 1993; Cary *et al.*, 1995a). The mean concentration of total inorganic nitrogen of 'bottom' waters at the inshore site during most of the year (non-winter) was $9 \mu\text{g l}^{-1}$ and was similar to background concentrations ($6 \mu\text{g l}^{-1}$) in Perth's coastal waters (Cary *et al.*, 1995b). However, during winter at the same site, the mean concentration of total inorganic nitrogen was four times background. These data indicate that the occurrence of elevated nitrogen concentrations at the inshore site is restricted to winter. Ambient nitrogen concentrations however are not considered to be the most useful index of eutrophication in predominantly oligotrophic ecosystems due to the rapid assimilation of available nitrogen by primary producers (Cary *et al.*, 1995a). Under these conditions, the biomass of phytoplankton is considered to be a better indicator of eutrophication than dissolved nutrient concentrations (ANZECC, 1992). The mean concentration of chlorophyll *a* (a measure of phytoplankton biomass) at the inshore site were higher than the offshore site during winter and the non-winter period (Burt *et al.*, 1995a) suggesting that this site is relatively 'eutrophic' throughout the year, and supports the suggestion that the composition of the epiphyte assemblage at the inshore site is primarily nutrient-induced.

Species composition and biomass of epiphyte assemblages are influenced by numerous factors such as the availability of light (Cambridge *et al.*, 1986), water temperature (Heijs, 1985), epifaunal grazing (Steneck 1983; Nielsen and Lethbridge 1989; Steneck *et al.*, 1991), the overall algal diversity in an area (Borowitzka and Lethbridge, 1989) and the proximity to sources of algal epiphyte propagules (West, 1990). However, the results in this study suggest that differential erosion due to wave action and nutrient concentrations in the water column are the key determinants of species composition of epiphyte assemblages growing on *P. sinuosa* in the southern coastal waters of Perth.

4.2. Epiphyte biomass

Seasonal patterns of epiphyte biomass on *Posidonia* seagrasses in temperate coastal waters of Western Australia are generally unimodal with minima in late-summer and maxima in late-winter or early spring, with an annual variation in biomass of four to six-fold (Kirkman, 1981; Silberstein, 1985; Hillman *et al.*, 1991). In the present study, the seasonal changes of epiphyte biomass at the offshore site followed this general pattern however at the inshore site the maximum values of epiphyte biomass are reached by early autumn and then decline sharply during late autumn with minima in mid-winter. This sharp decrease in epiphyte biomass at the inshore site coincided with the occurrence of the first winter storm (Burt *et al.*, 1993). Cambridge (1979) found that strong wave action can 'strip' large quantities of 'loosely' attached filamentous algae from seagrass leaves. In a recent field study in Cockburn Sound Burt *et al.* (1995b) found that over a 26-day deployment the biomass of periphyton on artificial seagrass leaves that were tethered (i.e. protected from abrasion/erosion) was up to 100 times greater than untethered leaves that were allowed to move freely. These results suggest that the discontinuity between the sites in epiphyte biomass is most likely due to higher rates of erosion for the filamentous dominated inshore assemblage compared to the coralline dominated offshore assemblage.

Silberstein *et al.* (1986) found the biomass of epiphytes on *P. australis* seagrass growing in the same area at relatively protected sites was correlated with nutrient concentrations in the water column. However, the results of this study suggest that the biomass of epiphytes on *Posidonia* seagrasses in more exposed locations in Perth's coastal waters is the result of the interaction between the ambient nutrient regime and erosion/abrasion due to wave action.

4.3. Periphyton biomass-light reduction relationships

Comparisons between epiphyte assemblages on seagrass leaves and periphyton assemblages on artificial seagrass showed there were no significant substrate effects on species composition and biomass. This finding is consistent with numerous studies that have used the same technique (Silberstein *et al.*, 1986; Neverauskas, 1987; Horner, 1987; Lethbridge *et al.*, 1988) and allows the relationship derived between periphyton biomass and percent light reduction to be used for epiphyte assemblages.

During the non-winter period, when the species assemblages at the two sites were similar, there were no significant differences in the light reduction relationships between the sites, except when biomass was expressed as refractory (inorganic, non-carbonate) material. In contrast, during winter when coralline species dominated the offshore assemblage and filamentous species dominated the inshore assemblage, there were significant differences in the light reduction relationships between sites for all relative measures of biomass, except total dry weight. These results suggest that differences in species composition of epiphyte assemblages can significantly change the relationship between epiphyte biomass and light attenuation.

A secondary objective of this study was to derive a epiphyte biomass-light reduction relationship for input into a nutrient effects ecological model being developed as part of the SMCWS (Simpson *et al.*, 1993). Most biological and physical relationships used in ecological models need to be generic so they apply over the entire model domain and for the annual cycle. In this study, periphyton biomass expressed as total dry weight was the only biomass-light reduction relationship with no significant site or seasonal differences. This general relationship is very similar to functions derived in the same area by Silberstein *et al.* (1986) for *P. australis* and in Perth's northern coastal waters by Manning (1994) for *P. sinuosa*. Therefore it would be reasonable, in the absence of other site-specific information, to use this relationship to estimate percentage light reduction through the epiphyte layer of *P. sinuosa* throughout Perth's coastal waters.

There were no significant differences in light reduction relationship between the sites during the non-winter period for periphyton expressed as chlorophyll *a*, organic matter and calcium carbonate. The availability of light during the non-winter period is considered to be critical to the production of non-structural carbohydrate energy reserves that are used for growth and survival of *P. sinuosa* seagrasses in winter (Masini *et al.*, 1995a, b). The generic light reduction relationships derived in this study for the non-winter period provide a number of biomass indices that can be used to determine the effect of epiphyte loads on light attenuation during this period. However these relationships should be applied with some caution, due to the absence of data at relatively low biomass values where subtle changes in the slope of the light-reduction relationship may significantly alter the amount of light reaching the seagrass leaf.

4.4. Implications for management

In Perth's coastal waters species composition and biomass of epiphyte assemblages are key factors influencing light attenuation through the epiphytic layer on leaves of *P. sinuosa* seagrasses. The

relative contribution of these factors is the result of the interaction between the ambient nutrient regime and erosion/abrasion due to wave action. Consequently, activities that lead to changes in the nutrient status or wave climate of these waters have the potential to alter the attenuation of light through the epiphyte layer and therefore the amount of light reaching the seagrass leaf.

The relationship between periphyton biomass and percent light reduction indicates that a small increase in epiphyte biomass on the leaves of seagrasses can significantly reduce the light reaching the surface of the leaf. The logarithmic nature of the light reduction relationship means that the relative effect of a given increase in biomass on percent light reduction is higher at relatively low biomass values. For example, in this study periphyton biomass expressed as total dry weight ranged between 0.5 to 2.0 mg cm⁻². An increase of 1.0 mg cm⁻² in epiphyte biomass at the lower end of the range (ie. 0.5 to 1.5 mg cm⁻²) would increase the attenuation of light through the epiphyte layer from 32 % to 52 %. An equivalent 1.0 mg cm⁻² increase at the higher end of the range (ie. 1.5 to 2.5 mg cm⁻²) results in a relatively small increase in light attenuation from 52 % to 61 %. This further illustrates why seagrass meadows growing at their depth limits in clear oligotrophic waters, with relatively low standing crops of epiphytes, are very susceptible to even small increases in the biomass of epiphytes.

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Appendix I

Occurrence of macroalgal species on 12 leaves of *P. sinuosa* and on 12 artificial seagrass leaves, at sites 1 and 2 during summer and winter. Species occurrence on a seagrass leaf or plastic strip scores 1.

SPECIES	Site 1				Site 2			
	Seagrass		Periphyton		Seagrass		Periphyton	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Rhodophyta								
(Coralline)								
Corallinales								
<i>Fosliella</i> spp.	12	12	12	12	7	11	7	-
<i>Haliptylon cuvieri</i>	9	0	8	0	1	0	0	-
<i>Jania</i> sp.	0	4	7	0	0	2	0	-
<i>Metagoniolithon stelliferum</i>	11	0	0	0	0	0	0	-
(Non-coralline)								
Nemaliales								
<i>Helminthora australis</i>	5	0	4	0	0	0	8	-
Gigartinales								
<i>Hypnea</i> sp.	2	0	2	1	0	5	1	-
Rhodymeniales								
<i>Champia zostericola</i>	1	0	1	0	0	0	0	-
Ceramiales								
Ceramiaceae								
<i>Antithamnion verticale</i>	0	2	1	4	0	0	0	-
<i>Callithamnion</i> sp.	0	0	1	0	0	0	0	-
<i>Centroceras clavulatum</i>	1	0	1	0	0	0	0	-
<i>Ceramium australe</i>	1	0	1	0	0	0	0	-
<i>Ceramium cliftonianum</i>	6	0	3	0	4	1	1	-
<i>Ceramium filicinium</i>	0	0	2	0	0	0	0	-
<i>Ceramium monocanthum</i>	1	0	1	0	0	0	0	-
<i>Ceramium shepherdii</i>	2	0	0	0	0	0	0	-
<i>Griffithsia</i> sp.	0	0	1	0	0	0	0	-
<i>Griffithsia teges</i>	0	4	0	0	0	0	0	-
<i>Griffithsia ovalis</i>	3	0	0	0	1	0	0	-
<i>Ptilocladia australis</i>	3	0	0	0	0	0	0	-
<i>Spyridia filamentosa</i>	3	0	0	0	0	0	0	-
<i>Wrangelia</i> sp.	1	0	0	0	0	0	0	-
Rhodomelaceae								
<i>Chondria</i> sp 1	0	0	4	0	0	0	3	-
<i>Herposiphonia pectinella</i>	4	0	0	0	9	0	10	-
<i>Laurencia</i> sp 1	5	0	1	0	12	3	6	-
<i>Polysiphonia</i> sp.	1	0	0	0	0	0	0	-
<i>Polysiphonia decipiens</i>	2	1	2	0	0	1	2	-
<i>Polysiphonia shepherdii</i>	0	0	1	0	4	0	0	-
<i>Polysiphonia scopulorum</i>	4	2	1	0	3	0	1	-
Phaeophyta								
<i>Dictyota furcellata</i>	0	0	0	0	0	0	1	-
<i>Dictyota</i> sp.	4	1	0	0	5	0	1	-
<i>Ectocarpus</i> sp.	3	0	3	0	0	0	1	-
<i>Ectocarpus fasciculatus</i>	0	0	0	0	0	0	3	-
<i>Elachista orbicularis</i>	0	0	10	0	0	0	4	-
<i>Feldmania irregularis</i>	2	0	0	0	1	2	3	-
<i>Giraudia</i> sp.	4	0	7	0	1	0	10	-
<i>Hinksia mitchelliae</i>	1	0	4	0	2	2	9	-
<i>Myrionema strangulans</i>	3	0	0	0	0	1	7	-
<i>Padina</i> sp.	0	0	0	0	0	0	1	-
<i>Ralfsia</i> sp.	0	0	0	0	0	0	3	-
<i>Sphacelaria furcigera</i>	1	0	5	0	6	1	3	-
<i>Sphacelaria rigidula</i>	2	0	0	0	6	0	7	-
<i>Sphacelaria tribuloides</i>	0	0	0	0	0	0	1	-
Cyanophyta								
Blue green branched filament	1	0	1	0	0	0	3	-
Blue green filament	4	0	2	0	12	2	12	-
Blue green coccoid	0	0	0	7	0	1	10	-