

**Changes to the structure and productivity of a
Posidonia sinuosa seagrass meadow in Princess
Royal Harbour, Western Australia, during and after
imposed shading**

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D M Gordon, S C Chase, K A Grey, and C J Simpson

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Abstract

Incident light available to a meadow of the seagrass *Posidonia sinuosa* Cambridge et Kuo in Princess Royal Harbour, Western Australia, was reduced by 80-99% using shadecloth deployed continuously *in situ* for 148 days, starting in summer (January 1989). Shading reduced the density of leaf-bearing shoots, leaf density, leaf length, primary productivity and the leaf production per shoot. Leaf width was unaffected by shading. Recovery of the meadow was assessed from differences in the above variables among control and shaded seagrass plots, measured on different occasions over 245 days after the shadecloth was removed. Shoot densities and primary productivity did not recover fully from shading, being significantly lower than controls at the end of the study. Longer periods of shading produced further reduction in shoot density and in primary productivity; shoot density and primary productivity of seagrasses shaded for 307 days were each about one tenth that of unshaded seagrasses. Primary productivity of seagrasses shaded for 393 days was less than one tenth that of unshaded seagrasses.

The effects of imposed shading on the structure and productivity of the meadow persisted for several months after removal of the shadecloth. The findings suggest that chronic reduction in available light to levels imposed in this study would lead to collapse of the meadow within two years.

Acknowledgements

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1. Introduction

The decline and loss of seagrass beds in Western Australia have been reported in investigations since the early 1970s, notably in the Cockburn Sound Environmental Study (Department of Conservation and Environment (DCE), 1979). This decline has been largely attributed to a reduction in light available to the leaf canopy, either through attenuation of light caused by phytoplankton blooms in the water overlying or shading of the canopy as a result of excessive growth of epiphytic and algae responding to nutrient enrichment of the water from land-based sources (Cambridge and McComb, 1984; Cambridge *et al.*, 1986; Silberstein *et al.*, 1986).

Similar problems have become evident more recently in other locations in Western Australia, for example in Princess Royal and Oyster Harbours, near Albany on the south coast, where there is now clear evidence of the diminution of the once extensive seagrass meadows associated with eutrophication and reduced water quality resulting from input of nutrients in industrial and urban discharges (Bastyan, 1986; Mills, 1987; Simpson & Masini, 1990; Wells *et al.*, 1991).

Eutrophication of the Harbour is now clearly expressed in excess growth of macroalgae, particularly the free-living green macroalga *Cladophora prolifera*. A similar free-living alga of this genus has been a nuisance in waterways elsewhere in Western Australia under the influence of eutrophication (McComb *et al.*, 1981; Gordon and McComb, 1989). Macroalgae are now evident in most of the seagrass meadows in the Harbour, where they are believed to have deleterious effects on seagrasses through their contribution to reducing the light available for photosynthesis.

The changes which occur to seagrass meadows during and after light reduction, and the rapidity with which the plants respond to light manipulation in the field have not been widely studied on Western Australian seagrasses. *In situ* manipulation of the light available to beds of the seagrass *Zostera marina* L. have been undertaken in the USA using shade screens to modify the light climate (e.g. Backman and Barilotti, 1976; Dennison and Alberte, 1982, Dennison and Alberte, 1985). Similar approaches have also been used in eastern Australia to examine the effectiveness of controlling growth of the seagrass *Heterozostera tasmanica* Martens ex Aschers. (Bulthuis, 1983; Bulthuis, 1984) and to examine the response of a *Posidonia sinuosa* meadow to *in situ* shading (Neverauskas, 1988).

The aim of the present study was to measure changes in selected structural features and in primary productivity of a meadow of *Posidonia sinuosa* Cambridge et Kuo in Princess Royal Harbour, Western Australia during and after imposed shading to provide insight into the plants' responses to large and persistent reductions in light imposed under field conditions.

The study also provided the opportunity to obtain preliminary measurements of the starch and sugar content of live rhizomes collected from both shaded and unshaded seagrass plots during the course of the study to evaluate whether these compounds changed markedly during and after shading.

2. Materials and methods

2.1 Description of the study site

The study was conducted in Princess Royal Harbour, a protected coastal embayment, which, with adjacent Oyster Harbour, provides a natural harbour at Albany (Figure 1). Princess Royal Harbour once supported extensive seagrass beds, which now show major symptoms of deterioration. Three species of seagrass dominate the flora and form mixed or monospecific meadows: *Posidonia sinuosa* Cambridge et Kuo, *Posidonia australis* Hook. f. and *Amphibolis antarctica* (Labill.) Sonder et Aschers. Princess Royal Harbour has no significant river-derived input of nutrients in winter and maintains salinity close to that of seawater throughout the year. It has a history of several decades of input of pollutants, including nitrogen and phosphorus derived from rural and urban sources, and effluents discharged by industries located on its northern shore (Mills, 1987).

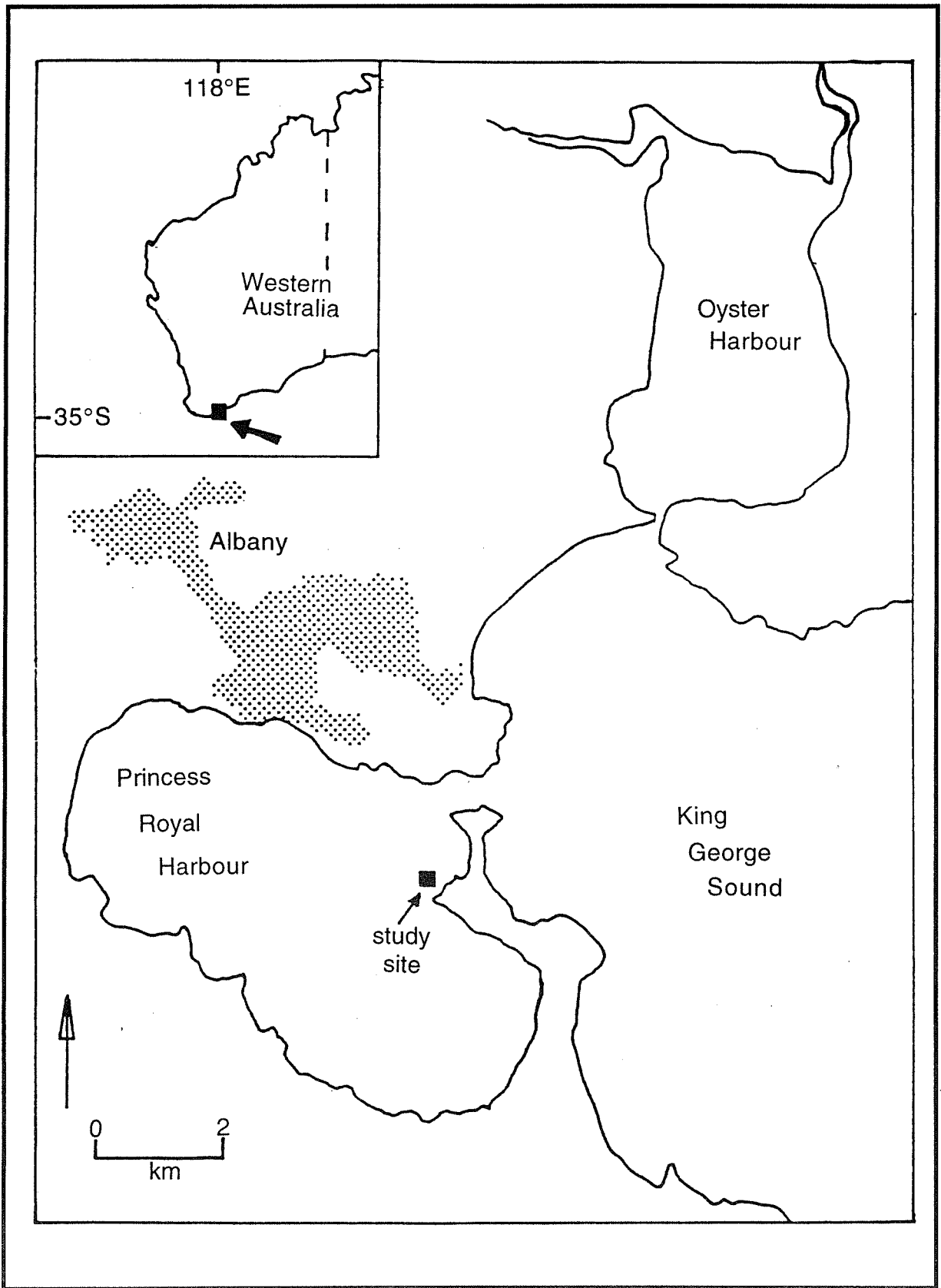


Figure 1: Map showing location of study site in Princess Royal Harbour, Oyster Harbour and the Town of Albany; Inset: Map of Western Australia showing location of Albany.

The study site is in shallow water (3-4 m) and 50 m offshore (Figure 1). It consists of a monospecific meadow of *P. sinuosa* which, at the time of the study, supported low populations of free-living macroalgae compared with seagrass meadows elsewhere in the Harbour.

2.2 Design of shading experiments

The experiments were run in two parts: a shading period, in which shade cloth was deployed over the seagrasses for 148 days, from mid January 1989 until mid June 1989, followed by a recovery period of 245 days, starting from mid June 1989 and finishing in early February 1990.

Sixteen 4.1 m² plots (2.3 m x 1.8 m) were selected at random within a 50 m x 50 m area of the *Posidonia* meadow and each was isolated from the surrounding meadow by sawing through the rhizome and root mat to a uniform depth (0.5 m) along the perimeter of each plot. Four replicates for each of three treatments plus a control were then assigned to the plots. Shade cloth (Sarlon Industries, Western Australia) was then attached to open mesh steel frames (mesh spacing 300 mm x 300 mm) and the frames placed horizontally, about 0.5 m above the seafloor.

The manufacturer's specifications for the degree of shade provided by the shade cloth (50%, 70% and 92%) were confirmed from *in situ* measurements of photosynthetically active radiation (PAR) at the time the shade cloth was first deployed. Subsequent fouling of the cloth by marine organisms made regular cleaning necessary. Light readings taken on several occasions before and after cleaning indicated that fouling increased shade specifications from the original values to values of 80%, 88% and 99%, respectively, within a few days. The higher values are used here to describe the different shade condition used in these experiments as they are a more realistic measure of the shading produced by the screens *in situ*.

The plots given 80% and 99% shade were shaded for 148 days before the recovery period began. Plots given 88% shade were shaded for longer periods to examine effects of more prolonged shading on their structure and productivity. To do this, one half of each of the four replicate plots given 88% shade was shaded for 307 consecutive days from the start of the study then exposed to natural light for the remainder of the study; the other half of each plot was shaded for the entire 393 days of the study.

The leaf canopies of control plots and those shaded to 80% and 99% were clipped back, at points just above the insertion of the leaf blade in the sheath, on day 148 of the study, when the shade cloth was removed from the 80% and 99% shaded plots. This procedure was adopted to provide uniform conditions in all plots at the start of the recovery period; the control plots had considerably greater leaf densities than any of the shaded plots by that stage of the study. Recovery of structural features of the meadow was measured in the 80% and 99% plots, 34, 96, 159 and 245 days after the shade cloth was removed and compared with changes occurring in the control plots over corresponding times. Primary productivity was measured on five occasions during the study: over the first 14 days, days 14-42 and days 76-104 of the shade period and over days 96-127 and 245-280 of the recovery period.

2.3 Measuring structural components

The following structural components of the seagrass meadows were recorded: mean leaf density, mean live shoot density, mean leaf length and mean leaf width. A 0.25 m x 0.25 m quadrat was used to delineate the sampling area within each plot on each sampling occasion. On each occasion, seagrass samples were removed from the meadow by SCUBA divers, placed in a plastic bag and returned to the laboratory for counting.

2.4 Measuring primary productivity

Productivity was measured using a leaf punching technique (Kirkman and Reid, 1979). A 0.25 m x 0.25 m quadrat was placed on the seagrass bed inside each of the 16 plots and small holes (approximately 1 mm diameter) were punched in the leaf blades of approximately 30 shoots in the quadrat using modified surgical scissors. Primary productivity was expressed as increase in leaf dry weight, and as area of new leaf material produced per square metre per day ($\text{g m}^{-2} \text{d}^{-1}$ and $\text{cm}^2 \text{m}^{-2} \text{d}^{-1}$). Mean leaf production per shoot ($\text{mg shoot}^{-1} \text{day}^{-1}$) was computed from the mean dry weight of new leaf material produced from 10-20 shoots obtained from the seagrass samples removed for productivity measurements.

2.5 Statistics

Between and within differences among means were identified using one-way ANOVA and Mann-Whitney U tests.

2.6 Measuring *in situ* light and water temperature

Instantaneous PAR was measured using an underwater light sensor (LiCor, Nebraska, USA). Continuous PAR and seawater temperature were measured using a submersible data logger (McIllwraith Instrumentation Pty Ltd, Tas.). The apparatus was attached to the side of the shadecloth screens at the same height above the seagrass meadow as the shadecloth. Data were recorded at 15 minute intervals continuously over discrete periods: 36 days in summer, 49 days in early winter, 30 days in late spring and 35 days in the early summer (Figure 2).

The mean incident light values reaching the light sensor during the periods of measurement ranged from 250 to about 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These light values were attenuated by the shadecloth and by self shading of the leaf canopy of the seagrass beds. Thus shadecloth providing 80% light reduction reduced light to between 50 and 120 $\mu\text{mol m}^{-2} \text{s}^{-1}$ under the shade screens. Similarly plots shaded to 88% had incident light reduced to only 30 to 72 $\mu\text{mol m}^{-2} \text{s}^{-1}$ while those shaded to 99% received only 3 to 6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ of incident light under the shade screens. Indirect light was not precluded from entering the shaded plots from the sides of the screens. This introduced a small edge effect. Sampling therefore excluded those seagrasses present inside a 20 cm wide zone around the inside edge of each plot.

Water temperature varied from a mean of 21 °C at the start of the study in January 1989, to 15°C in August 1989, before rising again over subsequent months (Figure 2).

2.7 Rhizome starch and sugar content

Rhizome samples were removed from seagrass plots given 0, 80% and 99% shade at the start of shading, after 104 and after 148 days of shading and during recovery, 182, 245 and 275 days after the start of the study. At that time rhizome samples were also obtained from plots given 88% shade for 307 and 393 days. All samples were frozen within 24 hours of sampling, and sorted to dead and 'live' material. The 'live' material was then dried (70 °C) and assayed for sugar and starch. Soluble sugars were extracted using a methanol-chloroform-water method (Crossland *et al.*, 1980) and assayed spectrophotometrically using the p-hydroxybenzoic acid hydrazide method of Blakeney and Mutton (1981) using glucose standards. Starch was assayed using the anthrone method (Southgate, 1976).

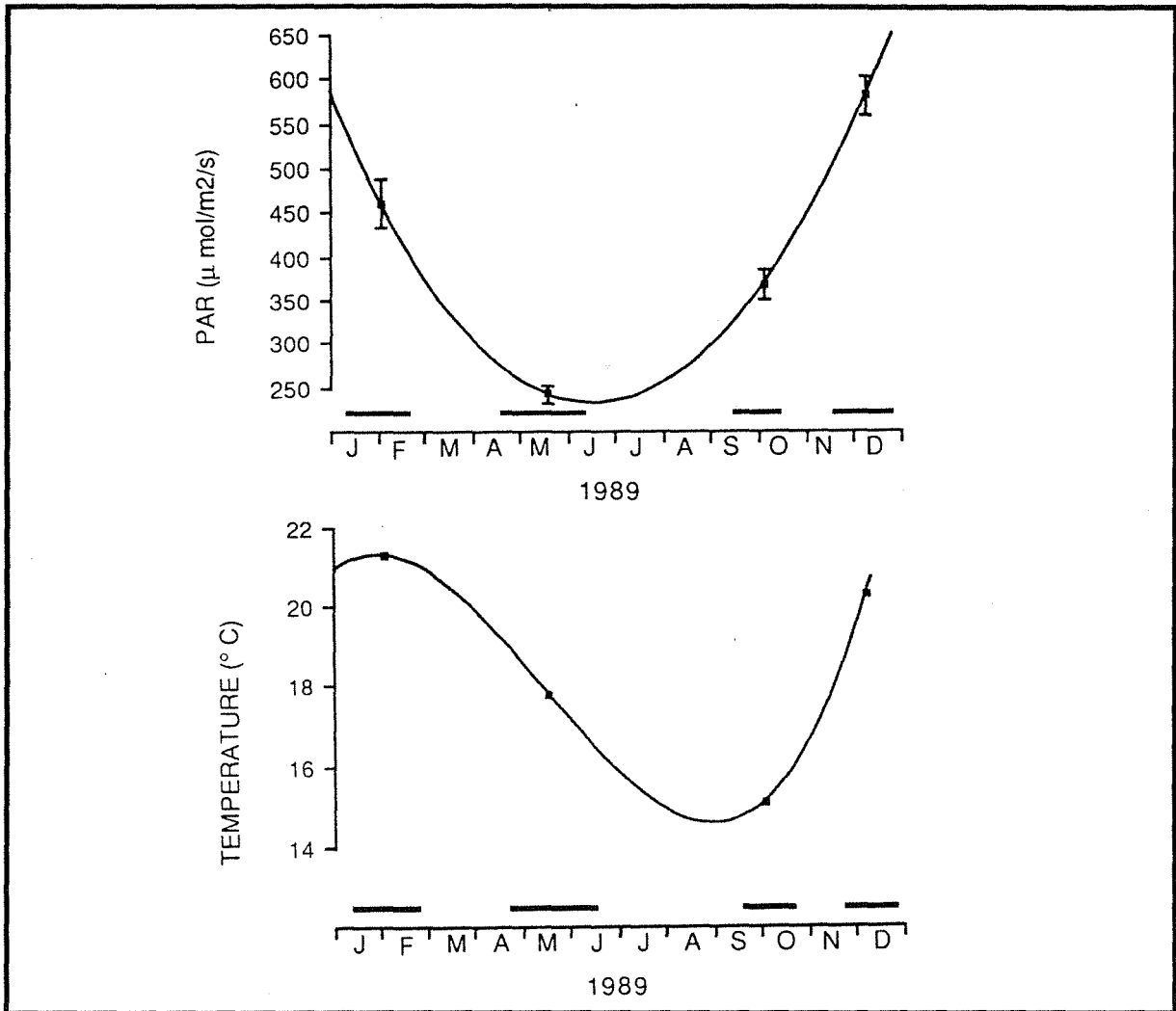


Figure 2: Seasonal variation in photosynthetically active radiation (PAR) and seawater temperature recorded at the study site. Data points for PAR are the mean and standard error of the daily means of daylight PAR for periods ranging from 37 to 48 days. Individual PAR measurements are integrated values for 15 minute sampling intervals. Temperatures are the mean of instantaneous values measured every 15 minutes for each sampling period. Standard errors for mean temperatures are not included as these are less than 0.01. Data were recorded for a total of 150 days.

3. Results

3.1 Changes to the seagrass meadow during shading

Changes in leaf and shoot density, leaf length and leaf width of shaded and unshaded seagrasses in the control, 80% and 99% plots are shown in Figures 4 and 5. Corresponding responses of the seagrasses in the 88% shaded plots (not presented) were found to be intermediate between those of seagrasses given 80% and 99% shade.

Leaf to shoot ratio

The mean leaf to shoot ratio of shaded and unshaded seagrasses was similar during the study, with shaded seagrasses having slightly lower ratios during shading and slightly higher ratios after shading (Figure 3). The mean values varied from around 2.5 in summer to just above 1.0 in winter.

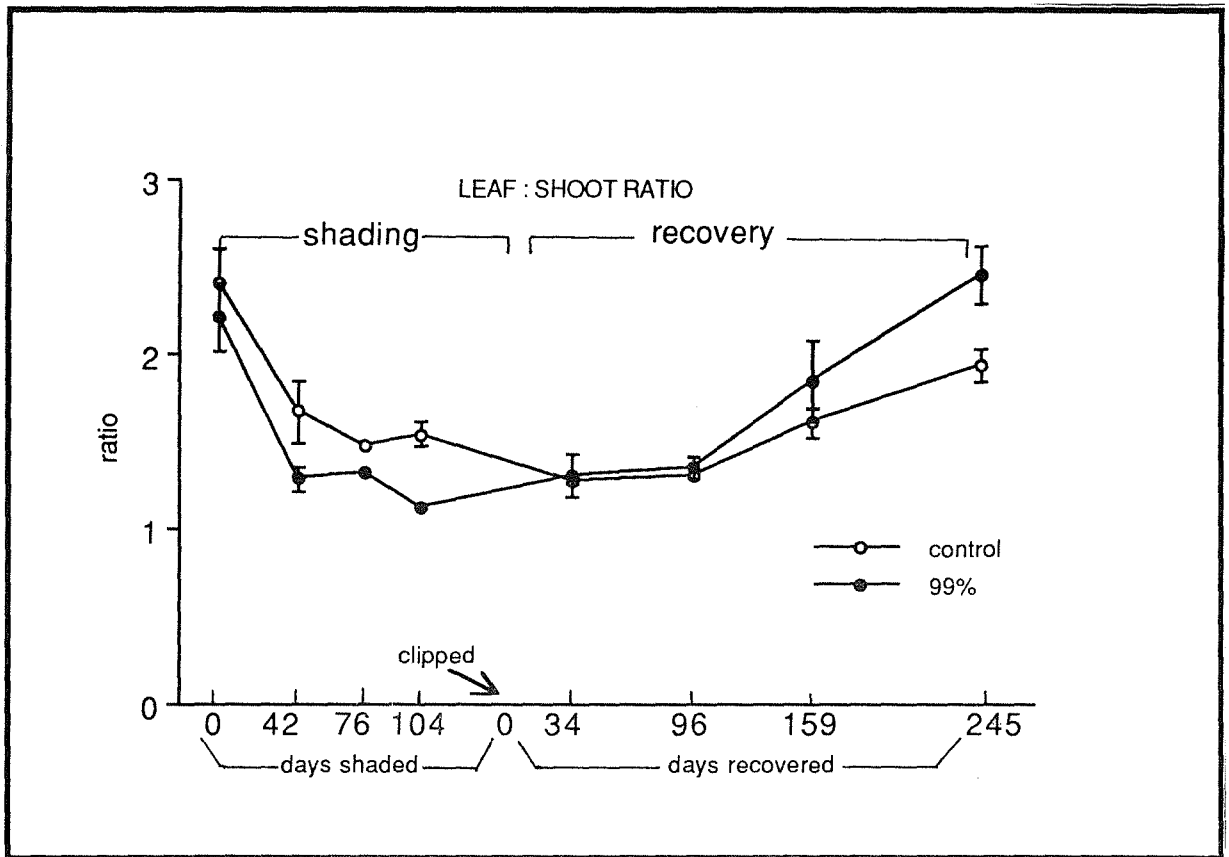


Figure 3: Changes in the leaf to shoot ratio of *Posidonia sinuosa* during the study, January 1989 to February 1990.

Leaf density

Shading caused noticeable thinning of the leaf canopy (Figure 4a). After 104 days, the differences in mean leaf density among unshaded and shaded plots were significant, with seagrasses given 80% and 99% shade decreasing to 48% and 39%, respectively, that of the controls.

Leafy shoot density

Like leaf density, the mean density of leafy shoots was reduced by shading soon after shading commenced (Figure 4b). The differences between mean shoot densities of control and shaded plots were significant when measured after 104 days of shading. At that time mean shoot densities in the plots given 80% and 99% shade were reduced to 62% and 52%, respectively, that of the control plots.

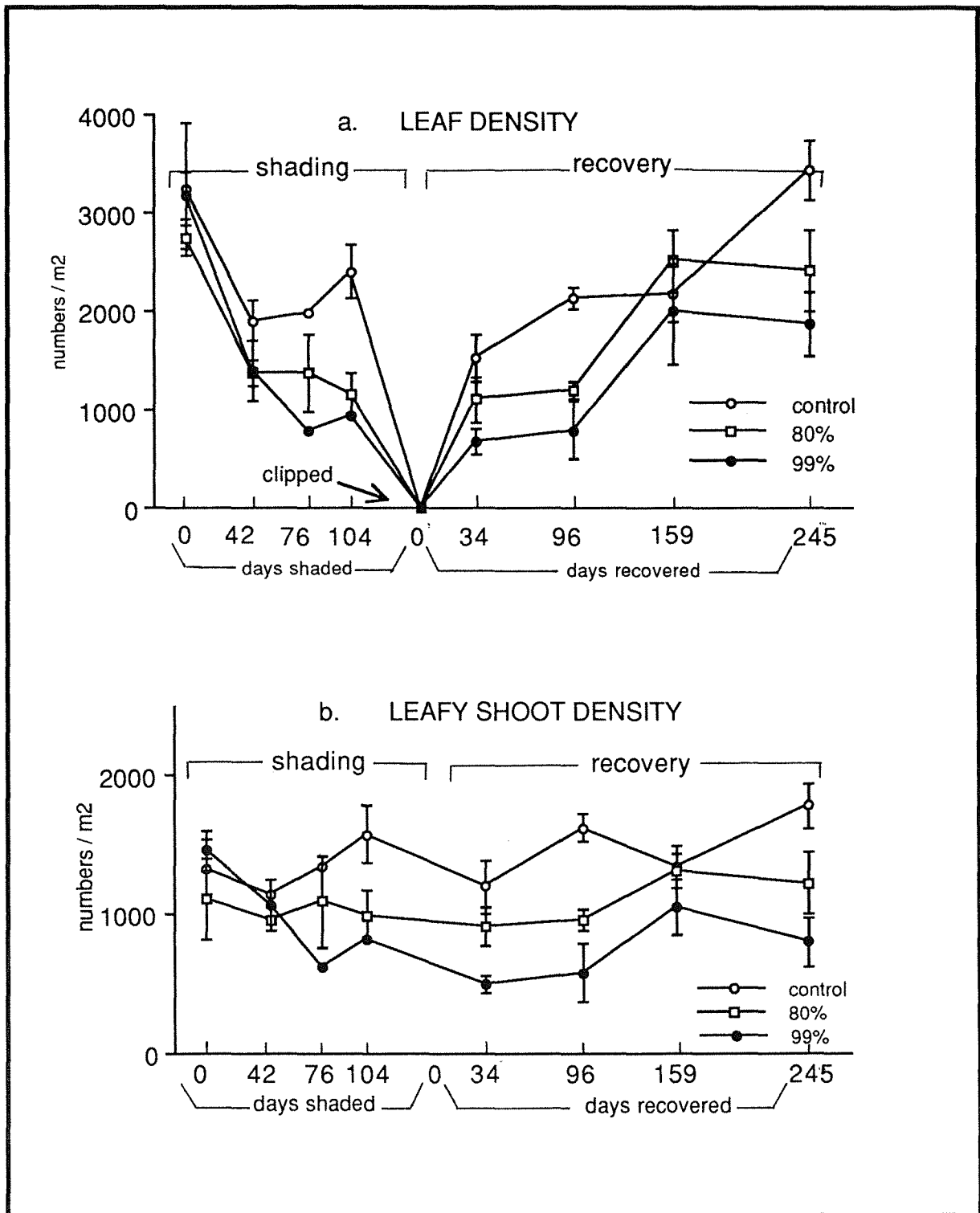


Figure 4: (a) mean live leaf density (number m^{-2}) and (b) mean leafy shoot density (number m^{-2}) of *Posidonia sinuosa* at the study site in Princess Royal Harbour, Western Australia. Data shown are for seagrasses given no shade, 80% shade and 99% shade continuously for 148 days, starting from January 1989. Recovery was monitored for 245 days starting from June 1989, following clipping back of the leaf canopy in all plots and removal of shade cloth on day 148 (= day 0 of the recovery period). Each point shown is the mean (and standard error) of four replicate plots.

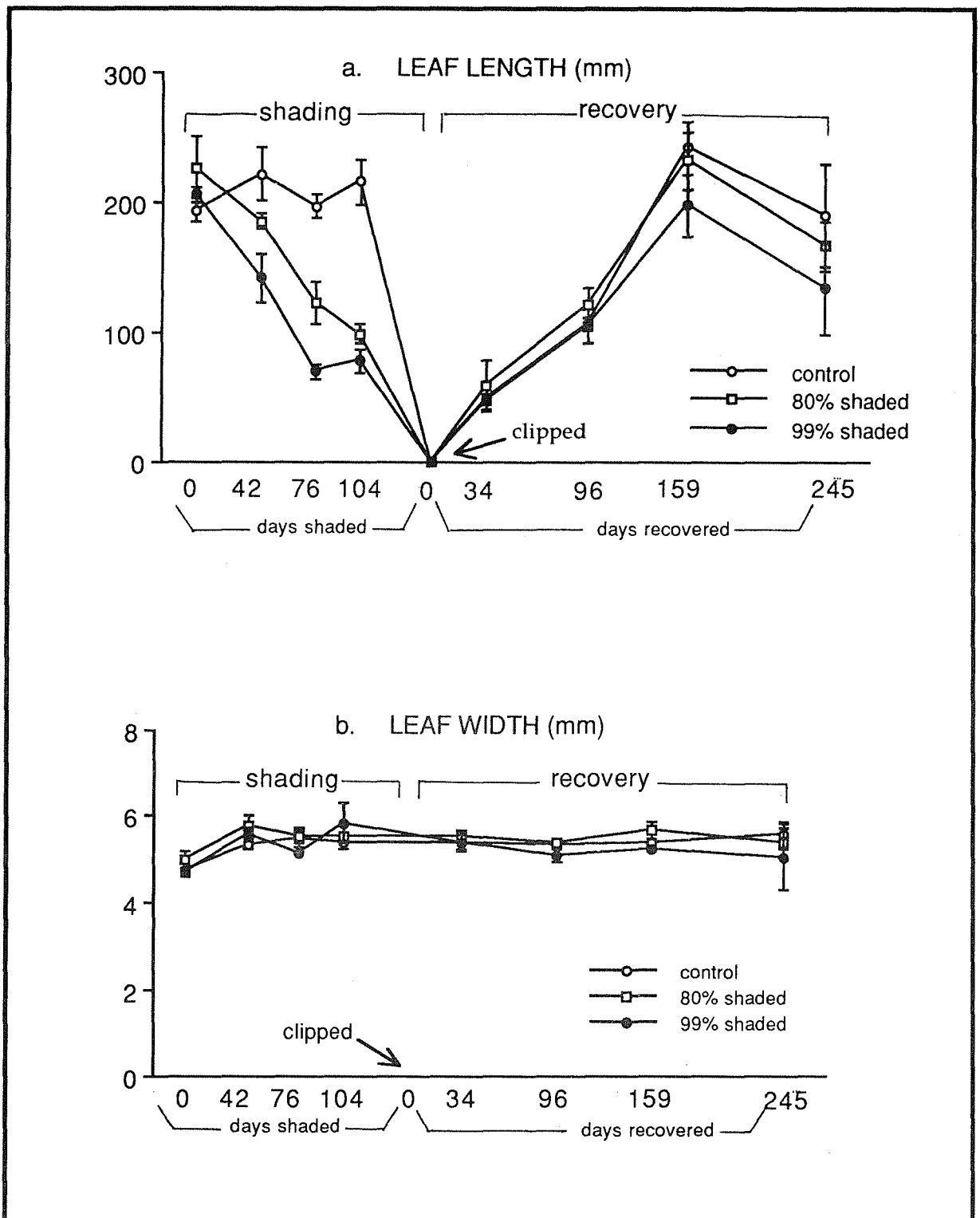


Figure 5: (a) mean leaf length (mm) and (b) mean leaf width (mm) of *Posidonia sinuosa* at the study site in Princess Royal Harbour, Western Australia. Data are shown for seagrasses given no shade, 80% shade and 99% shade continuously for 148 days, starting from January 1989. Recovery was monitored for 245 days starting from June 1989, following clipping back of the leaf canopy in all plots and removal of shade cloth on day 148 (= day 0 of the recovery period). Each point shown is the mean (and standard error) of four replicate plots.

Leaf length and leaf width

Shading markedly reduced the mean length of leaves but had no noticeable effect on the mean width of leaves (Figure 5). The mean leaf length of shaded seagrasses measured 42 days after shading commenced was significantly different to that of the controls for the remainder of the shading period.

3.2 Recovery of the seagrass meadow after shading

The extent of recovery of mean leaf densities, live shoots, leaf length and leaf width following removal of the shade cloth and clipping back of any remaining leaves in each plot is shown in Figures 4 and 5.

Leaf density

Within 34 days of the shade cloth being removed, seagrasses previously shaded to 80% and 99% had mean leaf densities 72% and 44%, respectively, that of the corresponding unshaded plots (Figure 4a). By the end of the study, 245 days after the shade cloth was removed, seagrasses previously given 80% and 99% shading had significantly lower mean leaf densities than controls, 70% and 54%, respectively, that of unshaded plots at that time (Figure 4a).

Leafy shoot density

Leafy shoot numbers in previously shaded seagrass plots remained low and significantly different from those of unshaded plots for most of the recovery period (Figure 4b). For example, 96 days after the shade cloth was removed, mean leafy shoot densities of seagrasses given 80% and 99% shade were 58% and 35%, respectively, that of unshaded seagrasses. At the conclusion of the study, 245 days after the shade cloth had been removed, differences in mean shoot density between control and shaded plots were still significant, being 45% to 69% less than that of the controls.

Leaf length

Recovery of leaf lengths in leaf-bearing shoots after shading was high, with no significant difference between previously shaded seagrasses and their controls at different times during the period of recovery (Figure 5).

3.3 Effects of shading on primary productivity

The effects of shading on primary productivity are shown in Table 1. Mean productivity ($\text{g m}^{-2} \text{d}^{-1}$) of shaded seagrasses was reduced to between 65 and 74% that of controls over the first 14 days of shading. It was reduced to 37-77% of the controls over days 14-42, and to 20-38% of controls over days 76-104.

The corresponding reduction in mean leaf production per shoot during shading is shown in Table 2. Over the first 14 days mean leaf production per shoot in shaded plots decreased to 65-89% of controls and was reduced to 41-53% of controls over days 76-104.

3.4 Recovery of primary productivity

Recovery of primary productivity after shading was assessed from differences in mean productivity values among control and shaded plots measured on the two occasions during the recovery period. Primary productivity of shaded seagrasses did not fully recover over the time of the study, with seagrasses previously given 80% and 99% shade for 148 days declining to 39-62% of controls over days 96-127 of the recovery period and 43-74% of controls at the end of the study (Table 1).

Mean leaf production per shoot recovered well in those shoots which were active following shading. By the end of the study the values were not significantly different between unshaded and previously shaded seagrasses (Table 2).

Table 1. Primary productivity of the seagrass *Posidonia sinuosa* from Princess Royal Harbour, Albany, subjected to different reductions in incident light (shading) of the leaf canopy. Figures show leaf productivity expressed as (a) leaf dry matter: g m⁻² d⁻¹ and (b) as leaf area: cm² m⁻² day⁻¹, during shading and following removal of the shade cloth (recovery). Figures shown are means and standard errors (in parentheses) of four replicates of each treatment.

		Shading			Recovery	
		Days shaded			Days after shade cloth removed	
% light reduction		1-14 Jan - Feb	14-42 ¹ Feb - Mar	76-104 Apr - May	96-127 Sept - Oct	245-280 ² Feb - Mar
0	a	1.25 (0.09)	1.07	1.07 (0.12)	1.28 (0.07)	0.89 (0.29)
	b	194 (14)	148	151 (7)	193 (17)	217 (12)
80	a	0.93 (0.19)	0.50	0.41 (0.02)	0.79 (0.07)	0.66 (0.08)
	b	122 (13)	91	61 (10)	116 (6)	134 (11)
88 ³	a	0.81 (0.08)	0.82	0.22 (0.03)	ND	0.10 (0.02)
	b	125 (8)	126	30 (4)		23 (3)
88 ⁴	a	ND	ND	ND	ND	0.07 (0.03)
	b					19 (3)
99	a	0.88 (0.25)	0.4	0.23 (0.02)	0.50 (0.07)	0.38 (0.14)
	b	127 (11)	75	39 (4)	86 (6)	74 (26)

ND: no data

1: one sample per treatment only;

2: calculated using shoot density data for day 245;

3: seagrasses shaded continuously for 307 days then recovered for 86 days before measurements taken;

4: seagrasses shaded continuously for 393 days with no recovery period before measurements taken; shoot density for plots shaded for 307 days used to measure productivity.

Table 2. Mean production of new leaf material per shoot per day; mg shoot⁻¹day⁻¹) of the seagrass *Posidonia sinuosa* in Princess Royal Harbour, Western Australia, given different degrees of shading. Each figure is the mean and standard error (in parentheses) for 10 - 20 shoots per plot; four replicate plots per treatment; ¹= one sample per treatment only.

	Shading			Recovery	
	Days shaded			Days after shade cloth removed	
% light reduction	1-14 Jan - Feb	14-42 ¹ Feb - Mar	76-104 Apr - May	96-127 Sept - Oct	245-280 Feb - Mar
0	0.97 (0.07)	0.89	0.73 (0.08)	0.82 (0.05)	0.50 (0.16)
80	0.86 (0.18)	0.50	0.39 (0.02)	0.76 (0.07)	0.54 (0.06)
88	0.70 (0.07)	0.63	0.30 (0.05)	ND	0.54 (0.11)
99	0.63 (0.17)	0.33	0.32 (0.03)	0.73 (0.11)	0.48 (0.18)

3.5 Rhizome starch and sugar content

The starch and soluble sugar content of live rhizomes was 2.1-6.7% of dry weight for sugars and 3.3-11.8% of dry weight for starch (Figure 6). Both compounds varied seasonally. The rhizome starch content was greatest in July (day 182) and was least in November (day 307). In contrast, sugar content of rhizomes was least in July and greatest in November for both unshaded and shaded seagrasses.

Both the starch and sugar content did not differ markedly between shaded and unshaded plots on a given sampling date. The most marked change occurred in all plots following clipping of the leaf canopy (day 148), with starch content increased and sugar content decreased in samples measured some 6 weeks after clipping (day 182; Figure 6).

The starch and sugar content of rhizomes at the end of the study are shown along with corresponding values for mean shoot density and primary productivity at that time in Table 3. By the end of the study, both the starch and the sugar content of rhizomes of seagrasses shaded for 307 and 393 days were considerably lower (up to 49% lower for starch and up to 53% lower for sugars) than those of unshaded seagrasses.

3.6 Relationship between duration of imposed shading, shoot density and primary productivity at the conclusion of the study

There was a strong negative relationship between the duration of shading imposed and primary productivity ($r^2=0.89$; $n=5$; Table 3) and between duration of shading and final shoot density ($r^2=0.93$; $n=4$; Table 3) at the end of the study. At that time, seagrasses which were shaded for longest had the lowest productivity, lowest numbers of leafy shoots and the lowest starch and sugar content in live rhizomes (Table 3).

Table 3. Mean shoot density, mean primary productivity and the starch and sugar content of rhizomes from unshaded and shaded plots in the *Posidonia sinuosa* meadow at the study site in Princess Royal Harbour, Western Australia, measured at the conclusion of the study. Values shown in parentheses are standard errors of the mean for four replicates per treatment.

Reduction of incident light (%)	Duration shaded (days)	Recovery time elapsed (days)	Mean shoot density (number m ⁻²)	Rhizome non-structural carbohydrate content		Primary productivity	
				Starch (mg g ⁻¹)	Sugar (mg g ⁻¹)	(g m ⁻² d ⁻¹)	(mg shoot ⁻¹ d ⁻¹)
0	0	0	1784 (163)	51 (12)	36 (9)	0.89 (0.29)	0.50 (0.16)
80	148	245	1224 (226)	63 (14)	23 (9)	0.66 (0.08)	0.54 (0.06)
99	148	245	796 (179)	54 (12)	23 (5)	0.38 (0.14)	0.48 (0.18)
88	307	86	184 (112)	36 (4)	21 (3)	0.10 (0.02)	0.54 (0.11)
88	393	0	ND	26 (3)	17 (3)	0.07 (0.03) ¹	0.38 (0.14)

ND: no data

¹ calculated using shoot density in plots given 88% shade for 307 days.

4. Discussion

4.1 Effects of shading on the seagrass meadow

The results indicate that shading had deleterious effects on the structure and productivity of the meadow that persisted long after return to natural light conditions.

Reductions in leaf and shoot density, and in leaf length during shading have been observed in a similar study, in which *Posidonia sinuosa* was given 50% shade for up to 12 months (Neverauskas, 1988). In that study there was no change in shoot density over the first six months of shading but a noticeable decrease in leaf density, attributed to a gradual reduction in numbers of leaves per shoot. The onset of changes in leaf and shoot density in the present study was more rapid, presumably because of the higher shade levels imposed. Canopy thinning was mostly the result of a reduction in numbers of leafy shoots, although shading probably also caused some increase in leaf abscission since the mean leaf to shoot ratios were lower in shaded plots than in corresponding controls during shading.

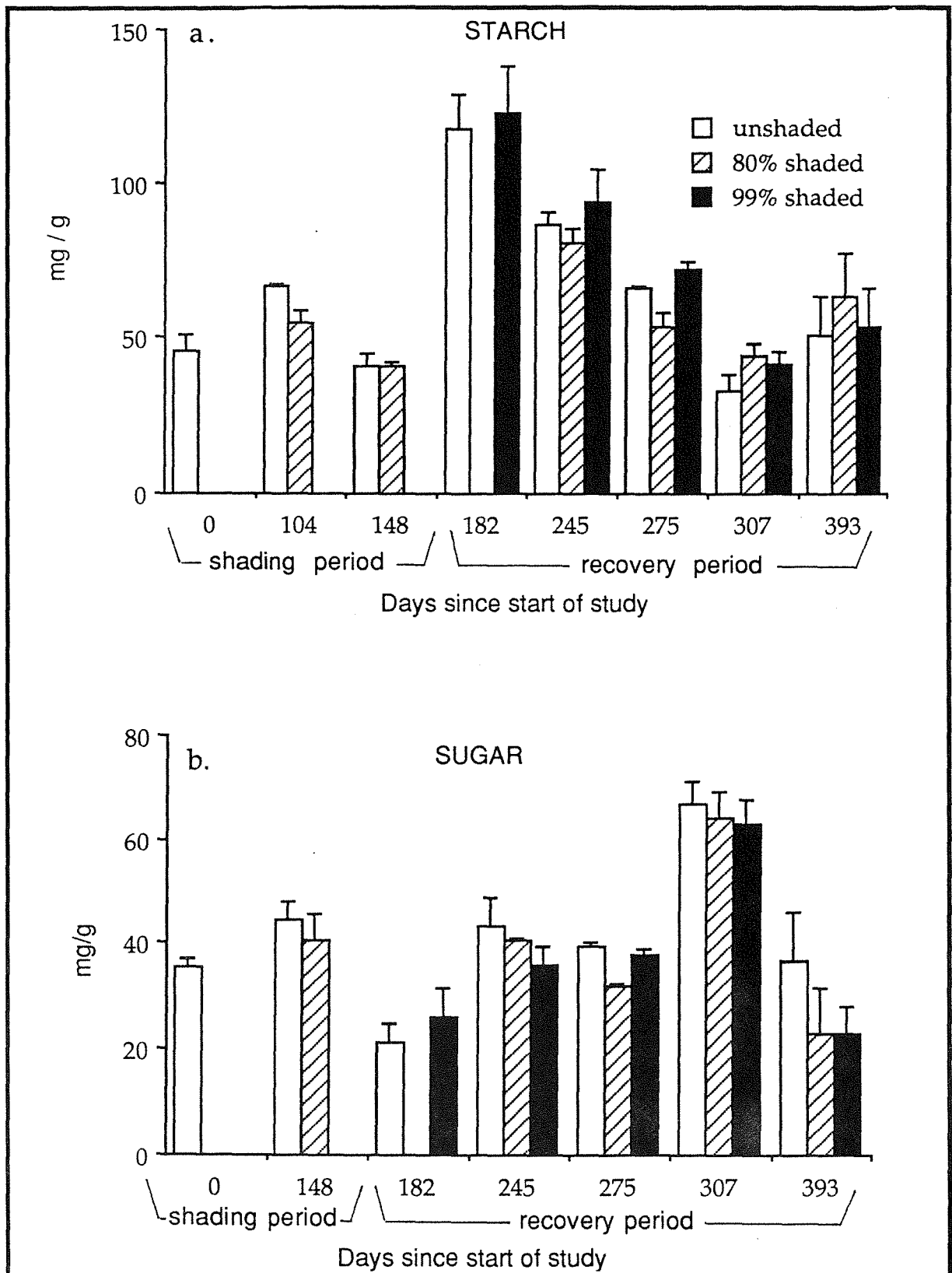


Figure 6: (a) starch and (b) sugar content (mg g^{-1}) of rhizomes of *Posidonia sinuosa* removed from shaded and unshaded seagrass plots during the course of the study. Data shown are means \pm s.e. of 4 replicate plots for seagrasses given no shade, 80% shade and 99% shade during periods of shading and recovery.

The ability of some shoots to produce new leaf material rapidly after severe shading suggests that they were not markedly impaired by shading. However, the overall inability of the meadow to re-establish active shoots at numbers similar to those of the controls, even after several months return to natural light conditions, provides convincing evidence that shading resulted in long-term, possibly permanent, damage to the meadow. We report here only changes in numbers of leafy shoots, regardless of their age or condition, which was not known and therefore have no data to confirm whether the canopy which returned after shading did so through recovery of pre-existing shoots, growth from new shoots, or both.

Longer periods of shading appear to have been even more damaging to the seagrass meadow. For example, the nearly complete loss of primary productivity after 393 days of shading and the markedly reduced leafy shoot numbers in plots shaded for 307 days (Table 3) suggests that the meadow would collapse within about two years if faced with chronic reduction in available light equivalent to the levels of shade imposed here.

4.2 Rhizome starch and sugar content

Starch and soluble sugar compounds appear to be readily translocated and converted in seagrasses (Abel and Drew, 1989) and probably play a role in regulating response to stress such as that created by imposed light reduction. The preliminary data on rhizome starch and sugar contents from the present study are too few and general to permit any close relationships to be drawn between changes in the concentrations of starches and sugars in the rhizome and the observed changes in leafy shoot density during and after shading. There was a noticeable difference in the starch and sugar content of rhizomes in all plots a few weeks after clipping of the leaf canopy, however, which may reflect some influence of this canopy removal on movement of the compounds in the rhizome.

In retrospect, the practice of clipping leaves in order to create uniform conditions at the start of the recovery period in plots which have differing leaf densities after shading might be usefully investigated for its effect on the degree of recovery observed. Studies on other seagrasses suggest that the plants do respond to such manipulations. For example, partial defoliation of shoots of *Thalassia testudinum* resulted in higher growth rates in remaining intact leaves on the shoots compared with similar-aged leaves of non-defoliated shoots (Tomasko and Dawes, 1989). Other experiments with the same seagrass suggest that clipping of leaves above the level of the sheath mobilises soluble carbohydrates, which support blade regeneration after defoliation (Dawes and Lawrence, 1979) and that experimental recropping of leaves can lead to a gradual decrease in leaf weight and depletion of storage reserves of soluble carbohydrate in the rhizome (Greenway, 1974).

4.3 Response to reduced light

Those seagrasses given 99% shade had incident light reduced to values well below the light compensation point reported for *P. sinuosa* collected from the study area ($22 \mu\text{mol m}^{-2} \text{s}^{-1}$ for a uniform light field at 18°C ; Masini *et al.*, 1990). Self-shading would possibly have further reduced available light to lower parts of the leaf canopy. The effects of self-shading on the lower canopy would have decreased as the meadow thinned during shading. However, decreases in leaf production per shoot continued as shading progressed, indicating that the plants did not respond to these reductions in self-shading. This result may be partly due to the severe shade levels imposed, although, in this regard it is interesting to note that P vs I curves obtained in laboratory studies with this species have shown that the light saturation and light compensation points are similar in plants from shallow (2 m) and deeper (4 m) sites in Princess Royal Harbour (Masini *et al.*, 1990).

5. Conclusion

Leaf and shoot densities, primary productivity and leaf production per shoot of the *Posidonia sinuosa* meadow were all reduced by 80-99% shade, imposed *in situ* over 148 days. The effects of shading on shoot density and on primary productivity were more pronounced where the shade period was extended to 393 days. The effects of shading persisted for several months after removal of the shade cloth, suggesting the shading caused long-term damage to the seagrass meadow. The findings support the hypothesis that chronic light reduction, such as that produced by excessive growth of free-living nuisance macroalgae within seagrass beds, poses a real threat to seagrass survival because conditions are created which reduce the opportunity for the meadow to initiate recovery.

Further shade studies on *Posidonia sinuosa* could usefully investigate how storage compounds move between underground and above-ground components of the meadow during and after imposed shading and how such movement affects the degree of recovery observed, and whether the meadow which returns after shading does so through re-activation of old shoots or the growth of new shoots.

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