

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

III. Minimum light requirements

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

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R. J. Masini, J. S Burt and C. J. Simpson

Department of Environmental Protection
Perth, Western Australia, 6000.

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Abstract

Photosynthetically active radiation (PAR) reaching the seagrass canopy was monitored at the maximum depth limits of two *Posidonia sinuosa* meadows (12 m and 15 m) over an annual cycle and used, in conjunction with data on epiphyte shading, to quantify the minimum PAR requirements for meadow survival. *Posidonia sinuosa* plants require an annual average of approximately 5% of the PAR immediately below the water surface (surface PAR) to reach the leaf epidermis for long-term survival. A meadow with moderate epiphyte loadings (1 mg cm⁻² of seagrass leaf) would require an annual average of approximately 10% of surface PAR at the canopy level for longterm survival. Relationships between water column vertical light attenuation coefficient, epiphyte biomass and maximum depth of seagrass survival are presented. These predictive relationships are consistent with past and current seagrass depth distributions in south-west Western Australia and provide a basis for the design and interpretation of water quality monitoring programmes. The results of this study highlight the effect of even small increases in light attenuation coefficient, or epiphyte biomass, on the depth distribution of the ecologically important meadow-forming seagrasses such as *P. sinuosa*.

1. Introduction

Light availability is generally regarded as one of the primary factors controlling the maximum depth limits of seagrasses (Backman and Barilotti, 1976; Dennison and Alberte, 1985; Dennison, 1987; Hillman *et al.* 1989; Duarte, 1991) and submerged freshwater angiosperms (Spence, 1981; Cambers and Kalff, 1985; Dale, 1986). Light is more rapidly attenuated in water than in air (Kirk, 1983) and for an aquatic plant to survive at a given water depth, it must receive sufficient photosynthetically active radiation (PAR; 400-700 nm waveband) to ensure that photosynthetic production is greater than, or equal to, its growth and respiratory requirements over an annual cycle (Sand-Jensen and Madsen, 1991; Masini *et al.* 1995). At a given water depth, PAR availability at the epidermis of the seagrass leaf is dependant on the water clarity and the biomass of epiphytic material coating the leaves (Silberstein *et al.* 1986). The corollary is that for a given water clarity and biomass of epiphytes, the amount of light available for seagrass photosynthesis and growth diminishes with depth. Therefore seagrasses will grow at greater depths in clear waters and with low epiphyte biomass compared to turbid waters and with high epiphytic loads.

Seagrass genera such as *Posidonia*, which have well-developed energy storage structures, are extremely resilient to short-term severe shading (Neverauskas, 1988; Gordon *et al.* 1995), but their low photosynthesis to respiration ratios make them particularly vulnerable to chronic reductions in light, especially near their maximum depth limits (Masini *et al.* 1995). In the sheltered embayments of Cockburn Sound and Princess Royal Harbour, nutrient-induced elevations in the biomass of phytoplankton and epiphytes during the 1970s and 1980s led to chronic light reduction and losses of about 80-90% of the original seagrass meadow area (Cambridge *et al.* 1986; Simpson and Masini, 1990). Once *Posidonia* meadows are lost, there is no evidence to suggest that re-establishment will occur within decades (Clarke and Kirkman, 1989).

Relationships between the vertical light attenuation coefficient and the concentration of phytoplankton and suspended organic and inorganic matter in the water column, and between epiphyte biomass and light reduction, have been derived in parallel studies (Burt *et al.* 1995 a, b). This information, coupled with knowledge of the minimum PAR requirements of seagrasses could provide the basis of an 'early warning' system to detect conditions that may lead to deleterious changes in ecosystem health and allow pre-emptive management action to be taken before serious or irreversible damage occurs.

The Perth Southern Metropolitan Coastal Waters Study (SMCWS) was initiated in 1991 in response to population growth and changing patterns of usage in the area and a gradual deterioration in water quality detected through long-term monitoring of Cockburn Sound. The primary objective of the SMCWS is to understand the environmental consequences of waste discharges to these waters, and this information will be used to develop an integrated management strategy for Cockburn Sound, Warnbro Sound and Sepia Depression consistent with maintaining the long-term health of the marine communities in these waters (Simpson *et al.* 1993).

This present study is a component of the SMCWS and was conducted to determine the minimum *in-situ* light requirements of *Posidonia sinuosa* seagrass meadows in Perth's coastal waters. This involved measuring the PAR regime at the local depth limits of two *P. sinuosa* meadows (12 m and 15 m) over an annual cycle. Shading caused by the epiphytes over the annual cycle was calculated and applied to the PAR reaching the canopy to estimate the PAR regime at the epidermis of the leaf.

2. Methods

2.1 Study area

The study was conducted at two sites on the slopes of Success Bank, a shallow (< 5 m) sill located between the Owen Anchorage basin (~12 m) to the south and Gage Roads (~20 m) to the north (Figure 1a). Success Bank is covered with extensive *Posidonia/Amphibolis* seagrass meadows. Site 1 was 15 m deep on the relatively exposed northwest side of Success Bank. By contrast, site 2 was 12 m deep on the relatively sheltered southeast side of Success Bank. Both sites were located at the local depth limit of a *P. sinuosa* meadow (Figure 1b).

2.2 Data collection

Photosynthetically active radiation and water temperature

Light and temperature metering systems were deployed at the two study sites for a total of 198 days during periods centred around the solstices and equinoxes between August 1992 and June 1993. Photosynthetically active radiation (PAR, 400-700 nm waveband) was measured using an underwater quantum light sensor (Li-cor, LI-192S) and recorded as 20-minute integrated values. Water temperature was measured with either a 100 ohm platinum temperature sensor (± 0.05 °C) or a semi-conductor temperature sensor (± 0.1 °C) and recorded as an instantaneous value at the beginning of each 20-minute PAR-measuring period. Data were integrated, recorded and stored using either multi-channel data loggers (Mcillwraith Instrumentation Pty., Ltd., Australia) or single channel integrating data recorders (Wesdata Pty. Ltd., Australia, model 924a).

The metering systems were fixed to metal stakes so that the light sensors were oriented vertically and protruded just above the height of the seagrass canopy (0.5 m above the seabed). All light sensors were calibrated ($\pm 5\%$) prior to the initial deployment and at 3 month intervals during the study. The light sensors were cleaned at 5 to 7 day intervals during each deployment to ensure the PAR data were unaffected by algal shading. This cleaning regime was established on the basis of a field trial at site 2 during February 1992 when algal-fouling rates were high (Authors' personal observations).

2.3 Data analysis

Light regimes

Data from the deployments were grouped into four seasons: *winter* (June 1 - August 31), *spring* (September 1 - November 30), *summer* (December 1 - February 28) and *autumn* (March 1 - May 31).

Twenty-minute integrated values of global radiation ($W\ m^{-2}$) measured at Hope Valley, approximately 2 km inland and 5-10 km south of the study sites, were converted to PAR ($\mu mol\ m^{-2}\ s^{-1}$) immediately below the water surface (ie. depth = 0 m; $Z_{(0)}$), by applying a factor of 2.15 (Masini and van Senden, 1995), and expressed as daily averages. PAR at the seagrass canopy level was expressed as a percentage of PAR at $Z_{(0)}$.

To calculate the PAR striking the leaf surface it was necessary to account for shading by epiphytes growing on the seagrass leaves. Epiphyte and periphyton species composition and biomass were regularly sampled during the period of this study at the two study sites by Burt *et al.* (1995b) and their data were used to estimate epiphyte biomass and to calculate the associated light reduction for each site and season. PAR at the leaf surface for each period was calculated by applying the

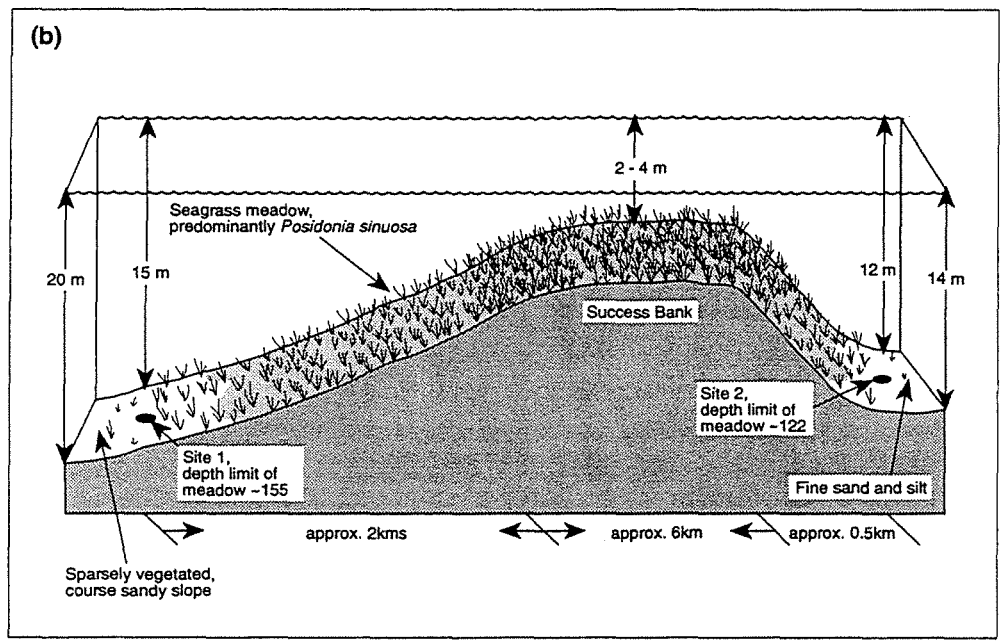
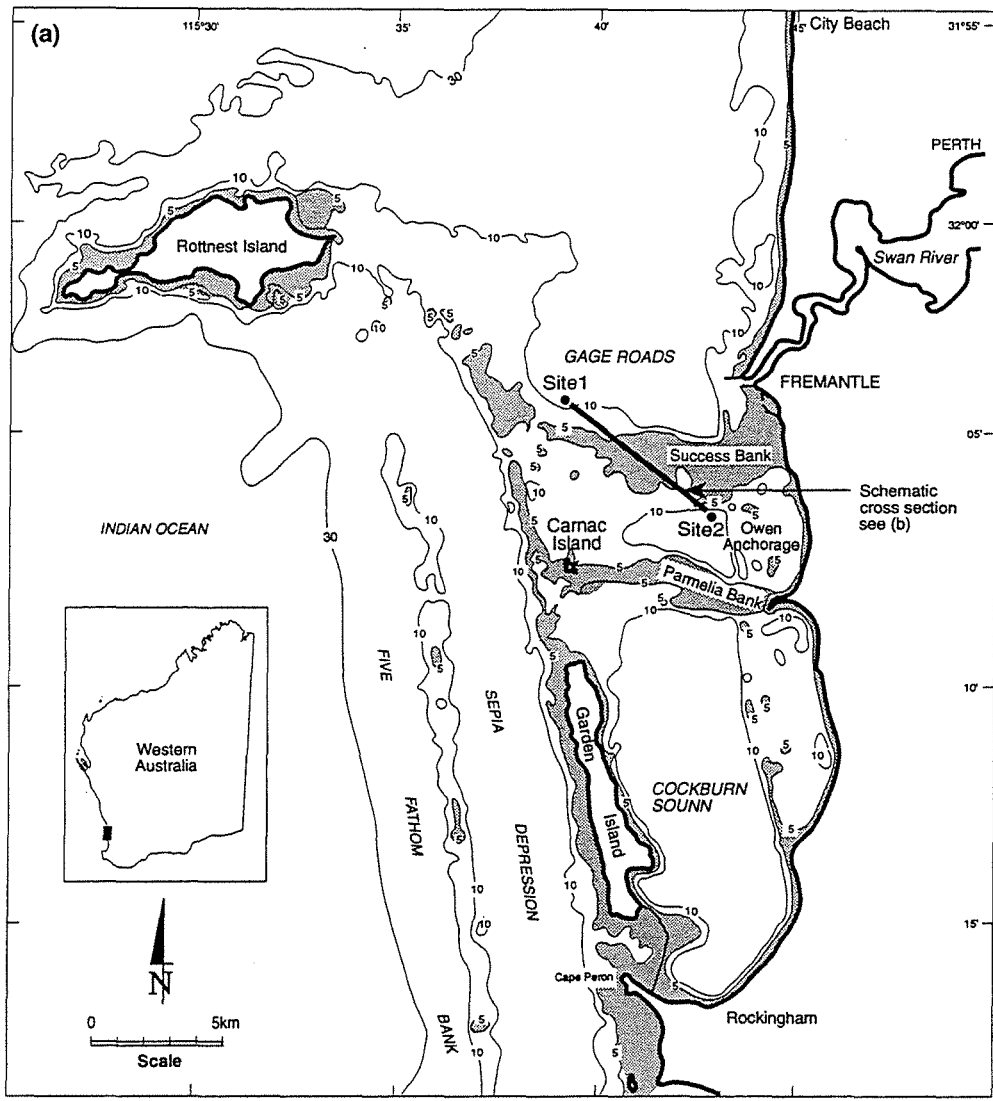


Figure 1. Location map (a) and schematic of Success Bank (b) showing seagrass distribution, water depth, sediment type and site locations for seagrass minimum light requirement studies.

appropriate epiphyte-related shading factor for that season to the measured PAR at the canopy level and expressed as a percentage of PAR at $Z_{(0)}$.

Hours of saturating PAR

The PAR required to reach the onset of light saturation of photosynthesis (I_k ; where the initial slope intersects the maximum photosynthetic rate) and to actually saturate photosynthesis (I_{sat}) are important photometabolic parameters used to help describe the photosynthetic response of plants to light (Bulthuis, 1983; Masini *et al.* 1995). Values for these parameters have been determined for *P. sinuosa* from the study sites, using oxygen flux measurements in the laboratory, and are significantly lower than at sites nearer the mid-point of this species' depth distribution in local waters (Masini and Manning, 1996). These parameters are temperature dependent in *P. sinuosa* (Masini *et al.* 1995) and have been incorporated into a seagrass growth simulation model (SEAGRS; Masini and van Senden, 1995). The time in hours between sunrise and sunset is termed the photoperiod (H) and the portion of the photoperiod that PAR is above a metabolically-critical light intensity has been denoted by a subscript to the value H (after Dennison and Alberte, 1985). The SEAGRS model was used to take the effects of water temperature into account when calculating the average number of hours per day that PAR was above I_k (H_k) or I_{sat} (H_{sat}), for *P. sinuosa* at each site during each season. The initial settings for the SEAGRS model are based on values for I_k at 18 °C and for the H_k and H_{sat} determinations described here I_k was set at $39.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ and I_{sat} was three times the I_k (ie. $117.3 \mu\text{mol m}^{-2} \text{s}^{-1}$). Daily averages of measured water temperature data were used when available, but when measured data were missing, a calibrated cosine function (Masini and van Senden, 1995) was used to predict daily water temperatures for input to the model. Diel variations in water temperature were not included.

The PAR data measured at the canopy level at each site were converted to PAR at the leaf epidermis by applying the appropriate epiphyte biomass-related shading factor as determined above. The resultant timeseries of 20 minute integrated values of PAR, and average daily water temperatures, were input to the SEAGRS model and H_k and H_{sat} calculated for each day. These data were expressed as averages for sites and seasons.

2.4 Inter-annual variability

To provide a measure of the representativeness of the light regime during the period of this study, monthly averages of mean daily global radiation recorded at the Perth Airport meteorological station for each month of the study were compared with long-term (18-19 year) averages (Bureau of Meteorology).

3. Results

3.1 Light regimes

Photosynthetically active radiation at $Z_{(0)}$, at the seagrass meadow canopy and the leaf epidermis during the study period are presented graphically in Figure 2 for sites 1 and 2. Average daily PAR at $Z_{(0)}$ was identical at the two sites (calculated from global radiation data) and ranged from about $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ in June/July to $850 \mu\text{mol m}^{-2} \text{s}^{-1}$ in December/January. Average daily PAR regimes recorded at the seagrass canopy were about an order of magnitude less than at the surface and were different at the two sites due to differences in depth and water clarity.

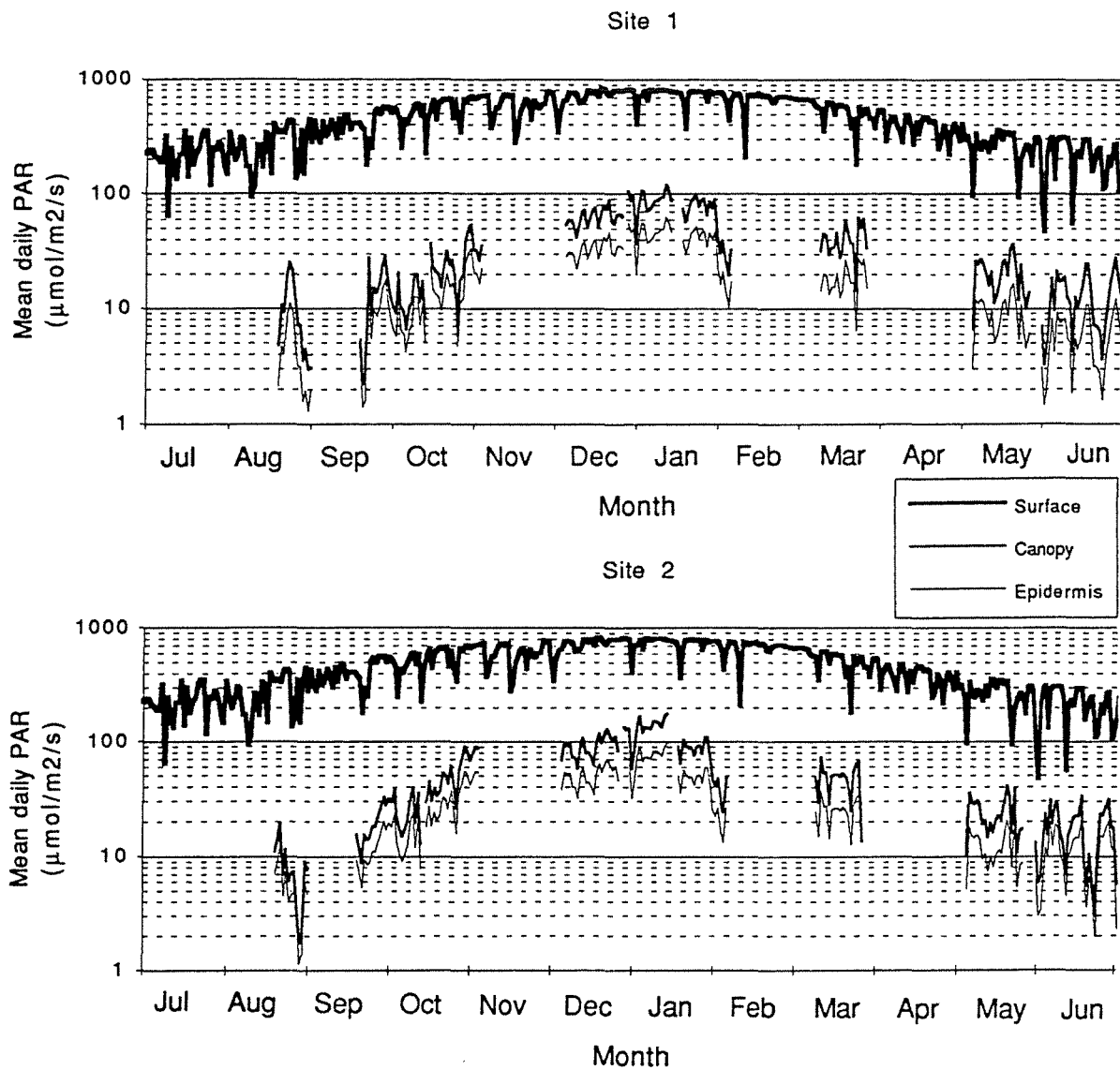


Figure 2. Mean daily photosynthetically active radiation (PAR) at two sites located at the local depth limits of *Posidonia sinuosa* seagrass meadows. 'Surface' is PAR immediately below the water surface and was derived from global radiation recorded at Hope Valley approximately 5 km from the study area. 'Canopy' is PAR recorded *in-situ*, immediately above the seagrass canopy. 'Epidermis' is PAR striking the epidermal layer of the leaf and was derived from 'canopy' data by incorporating shading due to epiphytes. Site 1 is 15 m deep, site 2 is 12 m deep.

The average amount of PAR reaching the level of the seagrass canopy at a depth of 12 m at site 2 was 9.0% of PAR at $Z_{(0)}$ over the annual cycle and was highest in summer and lowest in winter (Table 1). The seagrass canopy at site 1 at a depth of 15 m received 6.7% of PAR at $Z_{(0)}$ over the annual cycle, with a maximum in summer and minimum in spring.

The mean annual epiphytic biomass at site 1 was higher than at site 2 and reduced PAR by an average of 49% compared with 42% at the inshore site (Table 2). When shading by epiphytes is taken into account, the amount of PAR reaching the epidermis of the seagrass leaf is lower than that reaching the canopy (Figure 2) and averaged 3.4% and 5.1% of PAR at $Z_{(0)}$ at sites 1 and 2 respectively (Table 1). The effects of shading by epiphytes is clearly evident in the December/January data when PAR availability at the epidermis was about half of that at the top of the canopy at both sites (Figure 3).

The proportion of PAR reaching the epidermis to that at the canopy was not constant over the study period and differed between sites due to seasonal and between-site differences in epiphyte biomass (Table 2). The greatest inter-site differences in the degree of shading by epiphytes occurred during winter when epiphyte biomass reduced PAR by 56% at site 1 compared to 35% at site 2 (Burt *et al.* 1995b). This difference is seen most clearly in a comparison of data from the two sites during June 1993 (Figure 3).

Table 1. Photosynthetically active radiation (PAR) at the seagrass canopy and the leaf epidermis expressed as a percentage of PAR immediately below the water surface, and the hours per day that PAR was sufficient to reach the point of onset of light saturation of photosynthesis (H_k) and to actually saturate photosynthesis (H_{sat}). Sites were at the local depth limit of a *Posidonia sinuosa* meadow, and locations are shown in Figure 1. Data are presented as annual averages and means of data within four seasons: *winter* (June 1 - August 31), *spring* (September 1 - November 30), *summer* (December 1 - February 28) and *autumn* (March 1 - May 31). n = number of data days. Standard errors are in parentheses.

Site and depth	Season	n	PAR at canopy (% of PAR below water surface; depth = 0 m)	PAR at epidermis	H_k	H_{sat} (hours d ⁻¹)
<i>site 1 (15 m)</i>						
	winter	40	5.7 (0.5)	2.6 (0.2)	0.4 (0.2)	0 (0)
	spring	45	3.7 (0.3)	2.3 (0.2)	2.7 (0.4)	0 (0)
	summer	58	9.6 (0.4)	5.1 (0.2)	8.2 (0.2)	2.5 (0.3)
	autumn	45	7.6 (0.4)	3.4 (0.2)	2.8 (0.4)	0 (0)
	annual average		6.7	3.4	3.5	0.6
<i>site 2 (12 m)</i>						
	winter	40	6.6 (0.7)	4.3 (0.4)	2.0 (0.4)	0 (0)
	spring	45	6.7 (0.4)	4.1 (0.3)	5.2 (0.4)	1.0 (0.3)
	summer	58	13.2 (0.5)	7.3 (0.3)	9.3 (0.2)	4.8 (0.3)
	autumn	45	9.4 (0.5)	4.8 (0.3)	3.9 (0.4)	0.2 (0.1)
	annual average		9.0	5.1	5.1	1.5
<i>mean of sites 1 and 2</i>						
	winter		6.2	3.5	1.2	0
	spring		5.2	3.2	4.0	0.5
	summer		11.4	6.2	8.8	3.7
	autumn		8.5	4.1	3.4	0.1
	annual average		7.8	4.3	4.4	1.1

Table 2. Epiphyte biomass expressed as total dry weight per cm² of seagrass leaf and the associated light reduction predicted using an empirically-based relationship between periphyton biomass and PAR reduction. (data are from Burt *et al.* 1995).

Season	site 1		site 2	
	Epiphyte biomass (mg cm ⁻² leaf)	PAR reduction (%)	Epiphyte biomass (mg cm ⁻² leaf)	PAR reduction (%)
winter	1.93	56	0.57	35
spring	0.67	37	0.74	39
summer	1.15	47	1.02	45
autumn	1.80	55	1.29	49
annual average	1.4	49	0.9	42

3.2 Hours of saturating PAR

Photoperiod at the latitude of the study area (32°S) ranged from about 9.9 hours in winter to 14.1 hours in summer. Mean photoperiods, which determine the maximum possible H_k and H_{sat} periods for each season were 10.2 h in winter, 12.5 hours in spring, 13.8 hours in summer and 11.5 hours in autumn.

At site 2, sufficient PAR was available at the epidermis to allow the onset of light saturation (H_k) for 5.1 hours per day on average over the annual cycle and ranged from 9.3 hours during summer to 2.0 hours during winter. At site 1, the annual average H_k was 3.5 hours per day and seasonal averages ranged from 8.2 hours during summer to 0.4 hours during winter. Seasonal changes in H_k at the two sites were more closely related to photoperiod than to water temperature (Figure 4).

On average during the winter period, there was in-sufficient PAR at the leaf epidermis to actually saturate photosynthesis (i.e. $H_{sat}=0$) at either site. At the offshore site, photosynthesis was only fully light-saturated during summer (2.5 hours per day), and at the inshore site H_{sat} was ≤ 1 hour during spring and autumn and 4.7 hours during summer. On the basis of H_{sat} data averaged for both sites, potential photosynthetic production in *P. sinuosa* was highest during summer and lowest during winter (Table 1).

3.3 Inter-annual variability

Monthly averages of mean daily global radiation during the 1992/93 study period were about 6.6% higher during summer, and about 6% lower during late winter/early spring, than the long-term averages (Figure 5). The root mean square (rms) difference between monthly averages during the study period compared with long-term averages was 1.1 MJ m⁻² or 4.9%. The mean (± 1 standard error) difference between monthly averages during the study period compared with long-term averages was 0.41 ± 0.34 MJ m⁻² or $1.1 \pm 1.56\%$.

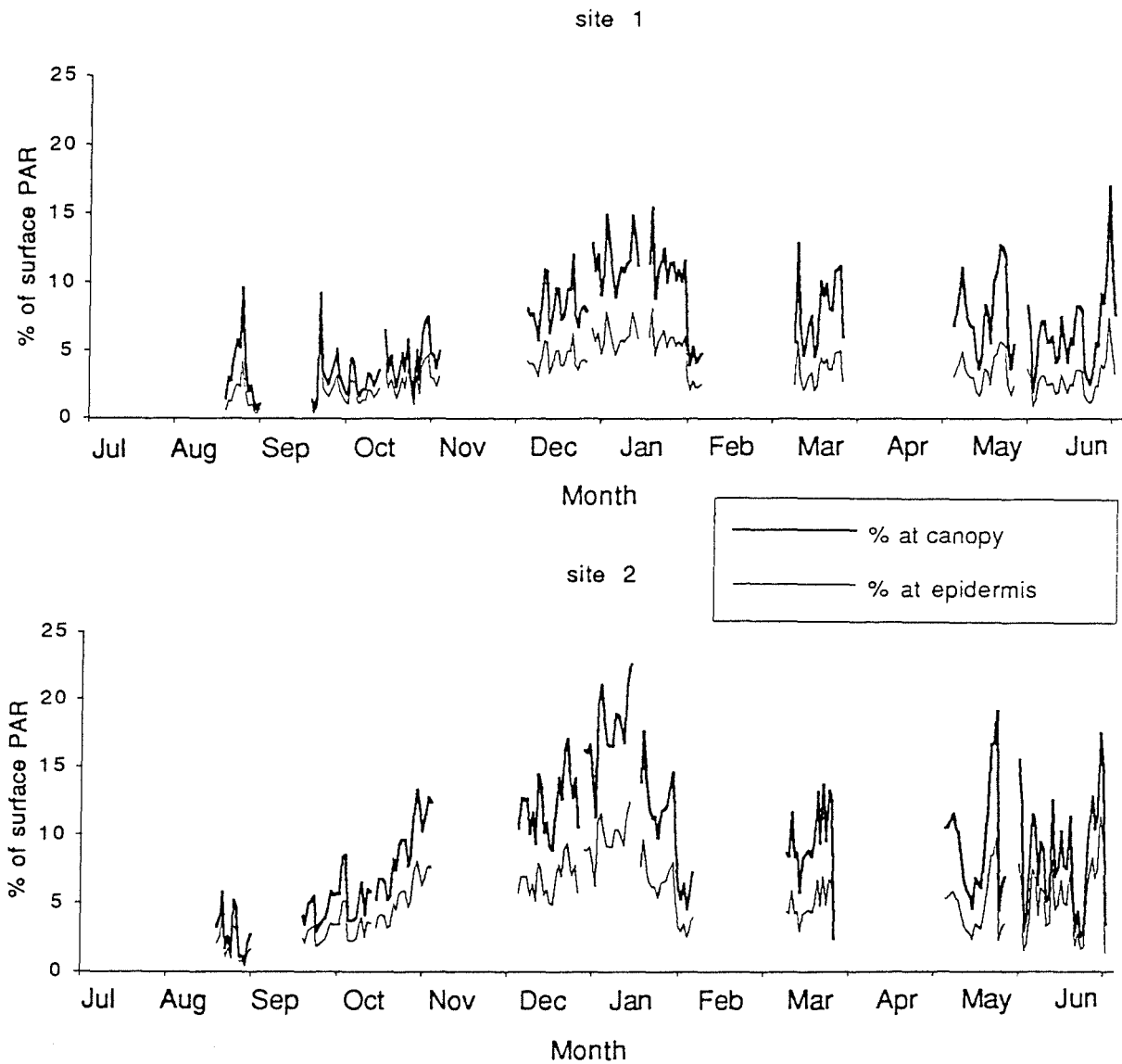


Figure 3. Average daily photosynthetically active radiation (PAR) reaching the canopy and epidermis of *Posidonia sinuosa* at the local maximum depth limit of two meadows. PAR is expressed as a percentage of PAR immediately below the water surface. Site 1 is 15 m deep, site 2 is 12 m deep.

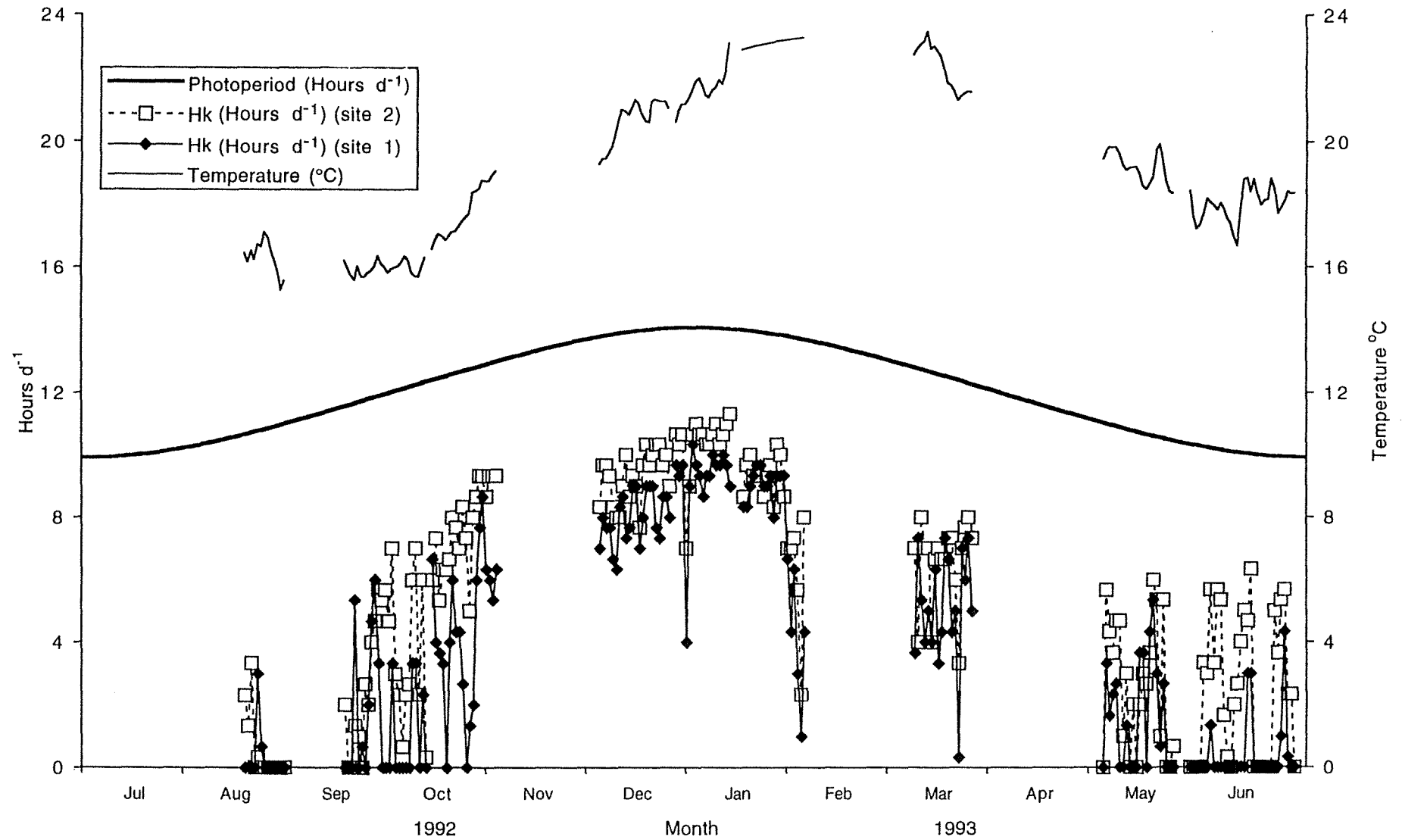


Figure 4. Water temperature, photoperiod and *Posidonia sinuosa* H_k periods at two sites located at the local maximum depth limit of meadow development. Water temperature data shown were measured at site 1, except for the late summer period which were predicted using a fitted cosine function (see Masini and van Senden (1995) for details).

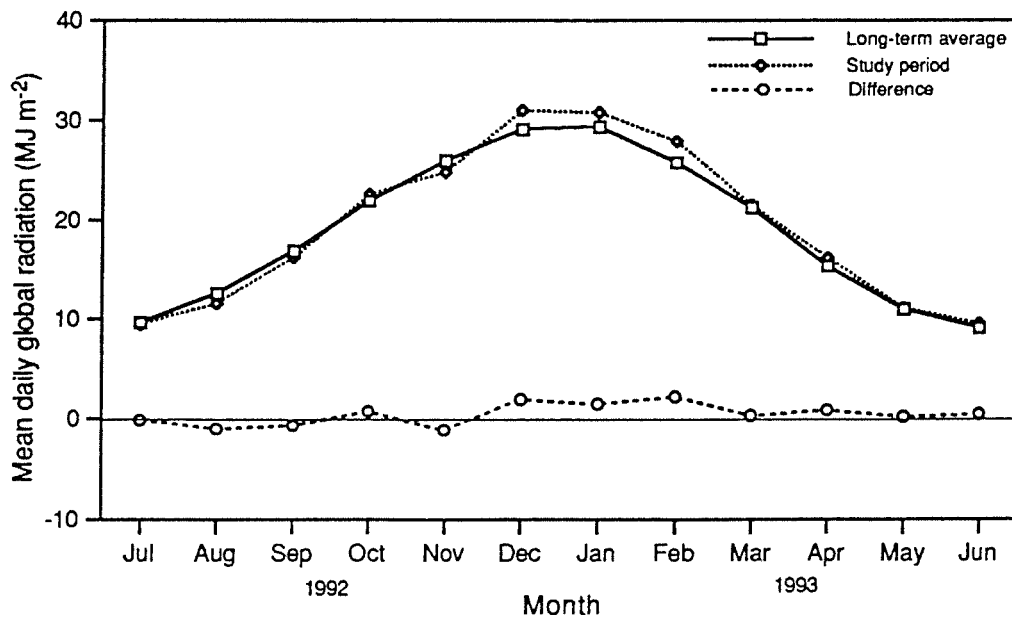


Figure 5. Mean daily global radiation measured at Perth Airport for each month of the study, long-term (18-19 years) averages, and the differences between them.

4. Discussion

The minimum light requirements of *P. sinuosa* were 7.8% and 4.3% of PAR at $Z_{(0)}$, at the canopy and at the epidermis respectively, based on an average of the two study sites (Table 2). Water column light attenuation was monitored during the study period at both sites by Burt *et al.* (1995a), and they concluded that the average water clarity and seasonal trends in light attenuation coefficients at the two sites were 'typical' of the general area, based on comparisons with available data. Mean daily global radiation during the study period was generally within about 6% of 18-year averages when expressed on an average monthly basis and less than 2% different over the annual cycle. The study period was therefore generally representative of longterm conditions in the study area and on this basis the minimum PAR requirements reported here can be considered typical for this species in local waters.

Posidonia which is a 'climax' meadow forming seagrass has morphological characteristics which allow carbohydrate to be stored and accessed when photosynthetic production is insufficient to meet metabolic requirements. These energy reserves allow *Posidonia* to withstand acute shading for substantial periods (months) and recover when the imposed shading is removed (Gordon *et al.* 1995). However, the respiratory burden of the non-photosynthetic parts of the plant produces low net photosynthesis to respiration ratios and makes this genus particularly susceptible to chronic light reduction as long-term survival depends on maintaining a positive energy balance over an annual cycle (Masini *et al.* 1995). Energy reserves can only be produced when photosynthetic production exceeds respiratory demands and this occurs when photosynthetic rates are high and close to saturation for substantial parts of the day. Seasonal differences in daylength, water clarity

and PAR intensity will strongly influence the number of hours of a given day that PAR is sufficient to saturate photosynthesis. Seasonal changes in water temperatures must also be considered as less PAR is required to saturate photosynthesis at low temperatures, due to lower respiration rates, than at high temperatures (Masini *et al.* 1995).

Dennison (1986), in a study of *Zostera marina* conducted near Woods Hole on the northeast coast of the USA (~ 40.5° N), found seasonal patterns of H_k and photoperiod (H) to be offset (ie. maximum H_k in spring; maximum H in summer) and attributed the deviation to the effects of water temperature on photosynthetic responses to light. In the present study the seasonal pattern in H_k period of *P. sinuosa* was related more to photoperiod than to water temperature (Figure 4). The different responses found in the two studies may be related more to seasonal ranges in temperature than to inter-specific differences in P-I response. In Dennison's study, water temperatures ranged seasonally between 0 and 20 °C, whereas in the present study water temperatures ranged between 15.3 and 23.5 °C. The I_k of *P. sinuosa* is significantly affected by water temperature between the range 13 to 18°C but not between 18 and 23°C (Masini *et al.* 1995; Masini and Manning, 1995), so for most of the year temperature has little effect on the PAR level required to saturate photosynthesis in local waters.

Mean water temperatures decrease by about 0.5 °C per degree of latitude (Pearce, 1986) and there are no intrinsic differences in the P-I responses of latitudinally distant populations of *P. sinuosa* in Western Australian waters (Masini and Manning, 1996). So on the lower south coast of Western Australia (~35°S) water temperatures will be about 1.5 °C lower than near Perth and based on temperature alone, the minimum light requirements of *P. sinuosa* at this latitude will be slightly lower during the winter months, but this is likely to be offset to some degree by the shorter photoperiod (9.6 hours at 35°S) and H_{sat} periods are likely to be similar to those in local waters. This supports the view that there are no latitudinal effects on the minimum light requirements of perennial seagrasses, as latitude affects the seasonality of the light regime rather than the annual average, and survival of perennial species is presumably related to a year-round integration of environmental factors (Dennison, 1987), and the maintenance of a positive energy budget over the annual cycle (Masini *et al.* 1995). These findings suggest that the average minimum light requirements of *P. sinuosa* established for Perth waters are generally applicable across the geographic range of this species in Western Australia.

Simulation modelling of seagrass growth, using summer, autumn and winter PAR data from the canopy level at site 2, indicated that plants within the meadow were in a positive carbon balance during summer and a negative carbon balance during winter (Masini and van Senden, 1995). Measurements of seagrass growth[^] at site 2 during the simulation period (Masini, 1994) showed that leaf extension was occurring during winter 1993, when the simulations indicated that the plants were in a carbon deficit. In contrast, measured growth rates during summer were lower than predicted from the simulation modelling. These results provide further indirect evidence that seasonal storage and re-translocation of carbohydrates are required for long-term survival. The average global radiation during the summer period of this study was about 7% higher than the longterm average, so the H_{sat} periods for summer may be slightly above the minimum requirement for that season but nonetheless the data indicate that summer is the period when photosynthetic production and energy storage is likely to be greatest. These findings suggest that reductions in PAR availability, such as by phytoplankton or epiphytic algal blooms, during summer when reserves are being created have the greatest likelihood of upsetting the annual energy balance and jeopardising long-term survival.

[^] plants were kept relatively free of epiphytes by rubbing leaves at regular (2-6 day) intervals.

Seagrass shoot density and biomass decrease with increasing water depth from the depth of maximum biomass to the limit of meadow development (West, 1990; Duarte, 1991). Isolated seedlings may survive in the short-term at greater depths than the limit of meadow development, but will not persist in the long-term when energy reserves contained in the endosperm are depleted and the seedlings become solely reliant on photosynthesis to meet their energy requirements (Dennison, 1987). The sites used in this study were located at the local maximum depth limits of meadow formation where the above-ground dry weight biomass of the meadows ranged from about 12 g m⁻² during winter to 25 g m⁻² during summer; approximately 5% of the biomass of a typical meadow growing under optimal conditions (Hillman *et al.* 1989). At these depths, the plants exhibited photometabolic and morphological differences to plants from shallower depths; the I_k was lower, the leaves were shorter and thinner and the specific leaf area was higher (Masini and Manning, 1996). These characteristics are considered to be 'adaptation' rather than 'acclimation' to low light conditions and as such the light requirements determined for these plants should be considered absolute minima for this species.

Given these considerations, a more conservative estimate of the minimum light requirements of *P. sinuosa* with moderate epiphytic loadings (1 mg dry weight cm⁻² seagrass leaf; 45% PAR reduction) would be $\geq 10\%$ of $Z_{(0)}$ PAR at the canopy and $\geq 5\%$ at the epidermis of the seagrass leaf. The minimum irradiance at the canopy is lower than reported for *Zostera marina* and *Thalassia testudinum*, and for seagrasses in general (Table 3), derived from analysis of the depth distributions of 31 marine angiosperm species world-wide (Duarte, 1991). These studies of light availability and seagrass colonisation depths do not explicitly consider the degree of epiphyte shading, which is clearly an important determinant of the amount of PAR striking the epidermis and hence the amount available for photosynthesis. Logarithmic plots of maximum colonisation depth and light attenuation coefficients are linearly related (Duarte, 1991), and therefore the results of this study, coupled with the epiphyte biomass:shading relationships of Burt *et al.* (1995), allow simple relationships between water column light attenuation and maximum colonisation depths to be determined for a range of epiphyte loads.

Table 3. Relationships between water column attenuation coefficient (AC; log₁₀ base) and maximum colonisation depth ($Z_{(c)}$) of three species of seagrass, and a generic relationship applying to all seagrass species. Photosynthetically active radiation (PAR) at the maximum colonisation depth is expressed as a percentage of PAR immediately below the water surface and also as a percentage of solar radiation above the water surface. Attenuation coefficients (log₁₀ based) were calculated from extinction coefficients (natural logarithm based) by applying a factor of 0.4343.

Species	Maximum colonisation depth (m)	PAR at $Z_{(c)}$ (% of PAR just below water surface)	PAR at $Z_{(c)}$ (% of solar radiation above the water surface)	Sampling location and characteristics	Reference
<i>Zostera marina</i>	$Z_{(c)} = 0.70 / AC$	19.8	8.5	USA northeast coastal waters	Dennison, 1987
"	$Z_{(c)} = 0.66 / AC$	21.6	9.3	Danish estuaries	Neilsen <i>et al.</i> 1989
<i>Thalassia testudinum</i>	$Z_{(c)} = 0.59 / AC$	25.7	11.0	Puerto Rican coastal waters	Vincente and Rivera, 1982
<i>Posidonia sinuosa</i>	$Z_{(c)} = 1.105 / AC$	7.8	3.4	Perth, WA (low epiphyte biomass)	this study
"	$Z_{(c)} = 1.0 / AC$	10.0	4.3	Perth, WA (mod. epiphyte biomass)	this study
"	$Z_{(c)} = 0.862 / AC$	13.7	5.9	Perth, WA (high epiphyte biomass)	this study
All species	$Z_{(c)} = 0.81 / AC$	15.6	6.7	worldwide	Duarte, 1991

With a moderate epiphytic load, the depth limit can be approximated as $D = 1/AC$ where D is the maximum depth limit in metres and AC is the light attenuation coefficient expressed on a \log_{10} basis. With low epiphytic loads (0.4 mg cm^{-2} ; 30% PAR reduction) the relationship becomes $D = 1.105/AC$ and under high loads (2.5 mg cm^{-2} ; 60% PAR reduction) it is $D = 0.862/AC$. These relationships are included in Table 3, and are presented graphically in Figure 6 to highlight the effect of even small increases in attenuation coefficient on the depth of seagrass survival, especially in clear waters. The ecological impact of chronic reductions in light availability will be most pronounced when a large proportion of seagrass cover in an area is near the lower depth limit. This scenario has been documented for *Zostera* in Apponagansett Bay and Waquoit Bay in Massachusetts USA (Costa *et al.* 1992) and for *Posidonia* on the eastern margin of Cockburn Sound (Cambridge and McComb, 1984).

The light availability:depth distribution relationships derived here from *in-situ* measurements are very similar to relationships derived from computer simulation modelling using laboratory-derived metabolic data (Masini and van Senden, 1995), and are in general agreement with literature derived *P. sinuosa* depth distributions shown in Figure 6 and outlined below. The changes in seagrass depth distribution that have occurred in Cockburn Sound (Cambridge and McComb, 1984), and the present depth distributions in Owen Anchorage/Gage Roads (where the *in-situ* relationships were derived) and Warnbro Sound (Kirkman and Walker, 1989) provide support for these relationships. The light attenuation coefficient in Cockburn Sound during the late 1970s was 0.13 m^{-1} (Cary *et al.* 1995a) and these conditions are thought to have existed when the seagrass banks on the 9 m sill on the eastern margin of Cockburn Sound were lost during the early 1970s (Cambridge and McComb, 1984). From the relationships in Figure 6, a light attenuation coefficient of 0.13 m^{-1} would only allow *P. sinuosa* to survive to a depth of about 7.7 m under the moderate epiphytic loading category. There is evidence to indicate that epiphytic loads were substantially higher than this and at times probably exceeded the high load category described here (Silberstein *et al.* 1986). On the basis of this relationship, seagrass with high epiphytic loads could have only survived to a maximum depth of 6.6 m. The current annual average light attenuation coefficient of Cockburn Sound is approximately 0.11 m^{-1} (Cary *et al.* 1995b) which, applying the moderate epiphytic load category would only allow seagrass survival to a depth of 9.1 m. The light attenuation coefficient of Warnbro Sound was about 0.09 m^{-1} in the late 1970s and has remained relatively stable over the past 15-20 years according to available data (Cary *et al.* 1995b). With moderate epiphyte loads, this light attenuation coefficient would allow *P. sinuosa* to survive to a depth of 11.1 m, which is similar to its actual depth distribution in the Sound (Kirkman and Walker, 1989). The light attenuation coefficient of Warnbro Sound is thought to be similar to that of Cockburn Sound pre-industrialisation, and accordingly, *P. sinuosa* would have theoretically existed at a depth of about 11 m, which is consistent with historical records for Cockburn Sound (Anon., 1979).

In Princess Royal Harbour on the southwest coast of Western Australia, the maximum depth of *P. sinuosa* survival regressed to about 5 m when the light attenuation coefficient was about 0.16 m^{-1} and epiphyte loads were high as a result of eutrophication (Simpson and Masini, 1990); under these conditions the maximum depth of survival is predicted to be 5.4 m. *Posidonia* spp. has been recorded from a depth of 27 m in the clear, offshore waters of Geographe Bay situated to the south of Perth (Cambridge, 1980) and according to the relationships in Figure 6, the light attenuation coefficient of these waters would need to be approximately 0.041 m^{-1} to support *P. sinuosa* with low epiphytic loads. The offshore waters in the mid-shelf region off Perth have a mean attenuation coefficient of 0.039 m^{-1} (Cary *et al.* 1995b) and are likely to be of similar clarity to offshore waters of Geographe Bay, providing further support for the relationship outlined previously.

These findings suggest that the minimum light requirements of *P. sinuosa* described by the relationship shown in Figure 6 are generally applicable across the depth and geographic range of this species.

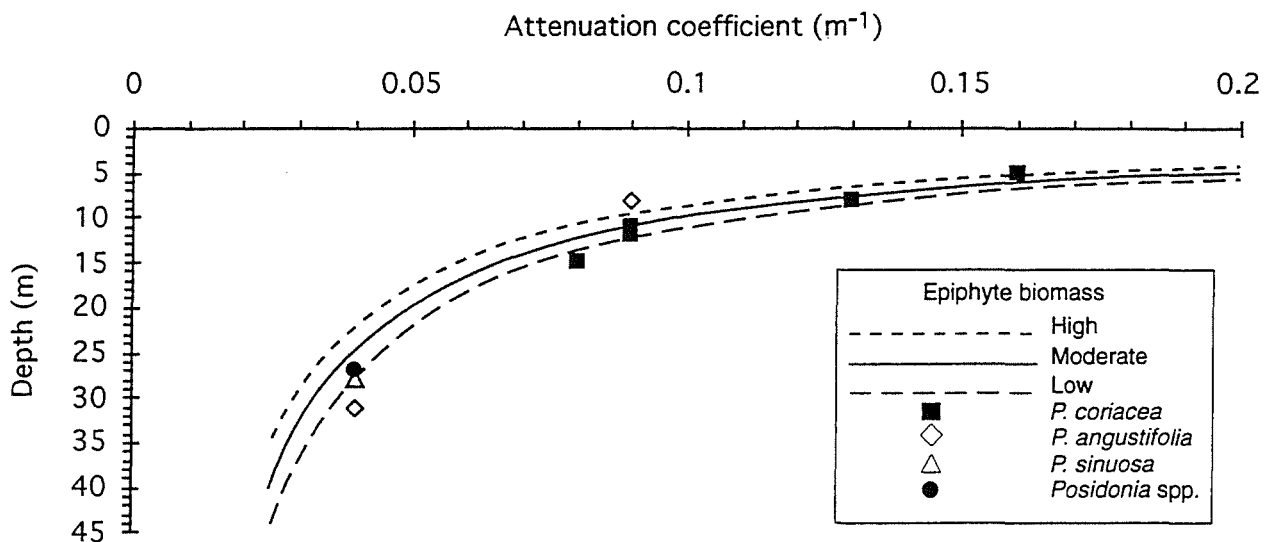


Figure 6. The relationship between depth of seagrass survival and water column light attenuation for three levels of epiphyte biomass levels. Low, moderate and high epiphyte biomass categories represent 0.4, 1.0 and 2.5 mg total dry weight per cm² of seagrass leaf, respectively. Past and present seagrass depth distributions and water clarity are plotted for comparison (see text for details).

Data for two other *Posidonia* species are also shown in Figure 6, and although limited, these data suggest that the relationship may hold for *P. coriacea* but is less useful for *P. angustifolia*. Although not shown in this figure, data for *P. oceanica* (a northern hemisphere species; in Duarte, 1991) suggest it has a different light attenuation:colonization depth relationship to those described here for *P. sinuosa*.

5. Conclusions

Posidonia sinuosa meadows with moderate epiphyte loadings require an annual average of approximately 10% of incident PAR at the canopy level to survive in the long-term. This equates to approximately 5% of surface irradiance at the epidermis of the leaf. The relationship between maximum depth of seagrass survival, epiphyte loading and water column vertical light attenuation coefficient is consistent with past and current seagrass depth distributions in south-west Western Australia and is an important interpretative tool for evaluating the results of water quality monitoring programmes. The results of this study highlight the effect of even small increases in light attenuation coefficient on the depth distribution of the ecologically important meadow-forming seagrasses such as *P. sinuosa*.

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