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Turbidity and reduced light responses of the meadow forming seagrasses Amphibolis and Posidonia, from the Adelaide metropolitan coastline.



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*Turbidity and reduced light responses of the meadow forming seagrasses *Amphibolis* and *Posidonia*, from the Adelaide metropolitan coastline.*

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1. Executive overview

It has been proposed that poor optical quality of the water body may be detrimental to the productivity of seagrasses, and that this may explain the loss of seagrass from the Adelaide metropolitan coast. In order to test this hypothesis, light was continuously recorded by light meters placed at depths of 3, 6, 12 and 18 metres off the coast of Grange. Seagrass beds in this region extend from 5 to 18 m depth.

Calculation of attenuation coefficients indicated that optical water quality was extremely poor in the nearshore region, particularly the 3 m and (to a slightly lesser extent) the 6 metre site. Beyond this, optical water quality improved. This is indicative of plumes of turbidity being entrained in the nearshore region, a feature which is consistent with the water movement modelling conducted as part of the ACWS project.

Despite the poorer water quality, the fact that the nearshore regions are shallower results in a greater amount of light reaching the seafloor at the three metre site on an annual basis than at other sites. This refutes the simple hypothesis that lower light levels in the nearshore region were responsible for seagrass loss, as regions further offshore support seagrass despite lower levels of light.

The higher average levels noted at the inshore sites were the result of only five months of elevated light. During the period June to December, poor optical water quality reduced light at these inshore sites to the same level as those at 18 metres (which should have been far lower because of their greater depth). Reduced light levels were strongly associated with the discharge of land-based inputs to the coastal zone.

The current nearshore light conditions probably do not represent the worst conditions that have been experienced. When the initial losses occurred in these seagrass beds, periodic turbidity events were probably more pronounced because the buffering influence of the Kangaroo Creek reservoir did not exist at this stage. Ameliorating this beneficial effect, however, is the fact that lost seagrass has decreased sediment stability, thereby increasing turbidity.

The hypothesis that seagrass loss in the inshore region is due to a poor light climate is based on the fact that light drives photosynthesis, and if photosynthesis is not adequate to provide enough energy to balance the needs of metabolic processes and growth, then the plant can not survive in the long term. If light were linearly related to productivity, then the demonstration of higher light levels would refute the hypothesis. However, the relationship between productivity and light is complex and non-linear. Therefore, an attempt is made to estimate productivity using a modelling approach to address the possibility that productivity might be limiting despite higher average daily irradiance.

The modelling has demonstrated that greater variability in the light field, as has been measured in the nearshore region in the current study, has a detrimental effect on productivity. Thus, variability of light field, which is a function of the turbidity introduced from land-based sources, may provide an explanation for the disappearance of seagrass from the nearshore region.

To investigate this possibility, the productivity model was parameterised using productivity – irradiance relationships derived from the literature and the irradiance measured from the Adelaide metropolitan coast. This model was able to demonstrate an annual nett productivity which was lower at three metres than at any other depth. Considering that one of those depths represented the deep margin of the bed, a boundary generally considered to represent the point where productivity is barely sufficient for plant maintenance, this supports the hypothesis that the light climate of the nearshore zone may not be suitable for seagrass.

While we cannot determine whether the light climate alone might be the cause of inshore seagrass loss , the possibility cannot be discounted on the basis of this work, and at the very least, this light climate will provide an extra stress on the seagrass.

2. Introduction

Since the 1940's, over 5200 ha of seagrass meadows have been lost from the Adelaide metropolitan coast (Seddon 2002). In particular, major losses of nearshore seagrasses have occurred in the region between Outer Harbour and Seacliff (Westphalen et al. 2005). Degradation and loss of seagrass meadows is a major cause of concern for coastal managers due to the importance of these systems to nearshore productivity, seabed stability, and biodiversity (Clarke 1987; Duarte and Chiscano 1999; Ruiz and Romero 2003). Seagrass losses along the Adelaide coast have previously been linked to the construction of stormwater drains, wastewater discharges, coastal developments, and the re-channelling of the Torrens River to the sea (Westphalen et al. 2005). Nonetheless, the primary causes of seagrass decline are poorly understood for the Adelaide metropolitan coast where seagrass loss has mainly occurred from the shallow inshore margin advancing seaward. Potential causes of seagrass decline along the Adelaide coast include elevated nutrients, toxicants, increased turbidity, and decreased salinity (see Westphalen et al. 2005 for a review). Potential toxicants include heavy metals, pesticides, herbicides, and petrochemicals. Erosion processes have also played a role in ongoing seagrass losses (Clarke 1987, Seddon 2002). Furthermore, Tanner (2005) reported the disappearance of deep-water seagrasses (*Zostera tasmanica*) from lower Gulf St Vincent between the 1970's and 2000/01, postulating that a possible cause of the losses was a long-term increase in turbidity due to coastal inputs from Adelaide.

Almost universally, the causes proposed for seagrass loss have been anthropogenic in nature (see Shepherd et al. 1989; Gabric and Bell 1993; Vermaat et al. 1996; Short and Wyllie-Echeverria 1996). As seagrasses are restricted to the narrow coastal margin, they are also particularly prone to land-based inputs, and therefore, the effects of man (e.g. Vermaat et al. 1996; Livingston et al. 1998; Bearlin 1999) Increased nutrients, decreased salinity, toxicants and decreases in the quantity of light are all likely to be concentrated in the area closest to the coast where rivers, which run through cities and agricultural land, terminate; where stormdrains end; where dredging occurs and where effluent outfalls are found (Phillips and Scholz 1982; Fourqurean et al. 2003). Whilst the rationale is to dilute these effects below the level of harm in the vastness of the sea, currents and weather patterns may resist such a dilution and entrain the effects within a much smaller region closer to the coast (Burt et al. 1995; Pattiaratchi and Jones 2005).

The Adelaide Coastal Waters Study has addressed a number of these potential stressors in an attempt to isolate which causes are likely to be responsible for the loss of seagrass which has occurred off the Adelaide coast since the 1940s. Of these, eutrophication appears to be an important factor, whilst salinity and toxicants have proven unlikely. This particular study represents an investigation of the likelihood that poor light conditions are responsible for seagrass losses in this area.

Light is critical to the survival of all photosynthetic organisms (Shepherd et al. 1989; Perez and Romero 1992; Best et al. 2001). It is the sole energy source of photosynthesis, which fixes carbon dioxide and water into carbohydrates and oxygen (Falkowski and Raven 1997). The accumulation of carbohydrates through photosynthesis represents gross productivity. Nett productivity is calculated by subtracting the continuous metabolic demands of the plant (i.e. respiration) from gross productivity.

Nett productivity may be negative, where the demands of respiration outweigh what can be supplied through photosynthesis i.e. more energy is required than is being supplied. This situation can be supported over a limited timeframe through the accumulation of reserves in times of high light which can be utilised when respiratory demands cannot be otherwise met

(Burke et al. 1996; Alcoverro et al. 2001; Holmer and Bondgaard 2001). The timescale of such a deficit is of critical importance. Over short timeframes, it is not an issue as evidenced by the fact that the natural cycle involves nighttime where respiration continues at approximately the same rate as during the day despite the lack of any light to drive photosynthesis. Over longer timeframes, storage organs such as the root biomass of seagrasses can act as a store of carbohydrates to be called upon during periods where insufficient light is available (Burke et al. 1996; Touchette and Burkeholder 2000; Cabello-Pasini et al. 2002). This has been suggested as a major mechanism for the survival of seagrasses across seasons where light levels would otherwise be too low and also as a mechanism to support survival when sedimentation results in burial (Clarke 1987).

Generally, it is accepted that the offshore (deep) margin of the seagrass bed defines the point where the amount of light received is only just sufficient to allow enough productivity to balance the carbon demands of the plant (Duarte and Chiscano 1999). Any deeper than this, and the consequent decrease in light dictates that productivity is unable to balance these demands. For this reason, a decrease in water clarity (which can be due to either or both of turbidity (suspended solids) and dissolved organic compounds) is likely to result in loss of seagrass in the deeper regions, where the added turbidity pushes light levels below a critical threshold (Duarte 1991). Thus the result of increased turbidity is often felt at the offshore margin of the seagrass bed (See also Masini et al. 1995a for a similar argument about the effect of epiphytes at the deep margin). Adelaide is unusual in that much of the loss of seagrass has occurred from the *nearshore* margin (Westphalen 2005). On first glance, this may seem inconsistent with the effects of decreased water clarity. However, there are two important factors relevant to this situation which need to be considered.

Firstly, it is possible, through the effects of wind and water movement, that the effects of the land-based discharges are entrained in a region close to shore rather than distributed evenly across the range of the seagrass. This could result in a situation where light levels were actually lower in the nearshore region despite the far shallower depth. Aerial photographs would support this hypothesis (see, for example Figure 1). The potential for entrainment due to wind and current driven water movement is addressed in the modeling exercises of Pattiaratchi and Jones (2005), where a clear case is made for this argument.

The second possibility revolves around the fact that light levels only tell half the story. Ultimately, it is not low light which is responsible for the loss of seagrass – it is the low levels of productivity which may be caused by poor light conditions (e.g. Alcoverro et al. 2001). Productivity is determined, not only by the amount of light, but also by the relationship between the level of irradiance and the amount of productivity.

The instantaneous rate of carbon fixation is dependent upon the ambient light. At low light levels, little carbon is assimilated, but as the light increases, this fixation rate increases. However, the relationship is typically asymptotic, with increasing light levels not resulting in as much increase in photosynthesis (i.e. carbon assimilation) when light levels are high (e.g. Cheshire et al. 1995, 1997). The relationship is known as the photosynthesis : irradiance (or “P:I”) curve and is pictorially represented in Figure 7. It can be described relatively accurately with a knowledge of three key parameters: the maximal photosynthetic rate (P_{max}); the dark respiration rate (R_d); and the subsaturating light intensity (I_k). These are collectively known as photokinetic parameters.

Whilst plants can adjust their pigment systems to become more efficient where light levels are low, and it is commonly accepted that deeper plants make more efficient use of the available light, such adjustment has energy costs associated with it and is often slow. Furthermore, such adjustment is not infinitely possible. Thus there are critical limits to light, beyond which a plant is unable to adapt and cannot harvest enough energy to survive.

The shape of the P:I curve often varies across light regimes and species (Masini et al. 1995a; Major and Dunton 2002; Campbell et al. 2003). Typically, plants in deep water environments tend to be far more efficient harvesters of light than those in shallow waters because they need to be in order to achieve positive net productivity (e.g. Titlyanov et al. 1992) with less available light. Conversely, shallow plants actually have a requirement to be relatively inefficient in their harvesting of light because the high light levels would cause photo-damage if they were not “de-tuned” (Lüder et al. 2002; Major and Dunton 2002). This means that despite having higher light levels on the nearshore margin, the inefficiency dictates that productivity is no higher. Furthermore, if that environment is highly variable on short timescales, then slow pigment system adaptation rates would render the plants less productive.



Figure 1: Major discharge of stormwater from the Torrens River into Adelaide's coastal waters on 25 October 2005. Dark region is increased turbidity. Photo: S. Bryars

In the absence of any definitive identification of the length of time across which net negative productivity can be supported, and the large quantity of underground biomass which could assist in maintenance of respiration across extended periods, it seems likely that an annual cycle is an appropriate length of time over which to analyse the net productivity of seagrasses. Importantly, such an extended period takes into account all the major fluctuations operating over the period likely to be of importance to the seagrass. In particular, changes across the course of the day are integrated, as are the seasonal changes associated with the sun angle and cloudiness of the atmosphere. Predictable seasonal changes also influence the average sea-state and the amount of runoff from land-based discharges. All of these changes are integrated by measuring light levels at the level of the seagrass canopy and producing productivity models which operate across an annual cycle. Anything less than that and the results are biased against any part of the annual cycle which has been missed. If that was a high light period, then the output would be likely to underestimate productivity, whilst if a low light period was missed, the productivity would be overestimated.

There are a number of approaches which can be taken to investigate the possibility that poor light climate may be responsible for the loss of seagrass on the Adelaide metropolitan coastline. However, most are plagued by the fact that seagrass loss has not been a rapid process – it has been a chronic decline, and as a result short term approaches to the investigation of stress are likely to be inappropriate, or at best we would be unsure of how much confidence to place on the results when extrapolated to an ecologically appropriate timescale. For instance, the work of Gaetjens (2005), using effective and maximum quantum yield as indicators of the effect of variable light levels is more suited to identifying an acute stress than identifying long term effects. Shading experiments have the effect of reducing the mean light intensity, but a laboratory or mesocosm scale experiment fails to replicate the natural variability in the light climate which may be very relevant to this situation. Shading in the natural environment was impractical as, apart from altering the hydrodynamic environment, it would have required more maintenance time than was available if the experiment was to be sufficiently long term. Thus, we directed energies toward constructing a high quality, intensive dataset across a complete annual cycle. With this data, we can construct models which predict productivity under a variety of scenarios. Within the constraints of this study, it was not possible to characterise the photosynthesis : irradiance relationship of the major species down a depth profile and across the annual seasonal cycle. However, data were available from published sources which could be used to at least construct a simple model which would indicate whether it was possible that light conditions were causing productivity levels which could explain seagrass decline. Furthermore, as more detailed information becomes available on the P:I relationship, we will be able to recalibrate and fine tune the model. It has also provided an excellent long term study of the light climate of the Adelaide coast which stands in its own right as a valuable description of an important feature of the marine environment of the Adelaide metropolitan coast.

With this approach in mind, we aimed to test the general hypothesis that the light climate was worse in the nearshore zone at three metres (from where seagrass beds have been lost) than at other sites further from shore where seagrass has not been lost. This was extended to include variability in the photokinetic parameters of the plants to investigate whether the light conditions could explain the loss of seagrass when depth-specific photokinetic parameters were utilized. There were five specific hypotheses to be tested:

- 1. That there was less photosynthetically active radiation at the nearshore site than further offshore.** This would represent powerful evidence that the light climate may be responsible for productivity levels which were insufficient to support the seagrasses.
- 2. That the light climate was more variable at the nearshore site than further offshore.** On the basis of the fact that plants are known to tune their photosynthetic apparatus (often slowly) to the ambient light conditions, large fluctuations in light may make this a difficult task.
- 3. That reduced light levels are caused by increased land-based runoff.** This hypothesis investigates the likely cause of the light environment experienced by the Adelaide metropolitan coast.
- 4. That variability in light climate (without any change in mean levels) is disadvantageous for seagrasses on the basis of lower productivity.** This puts Hypothesis 2 into the perspective of an effect on the plants. Whilst it does not answer the question of whether these conditions caused seagrass loss, it does indicate whether variability is inherently disadvantageous to seagrasses by way of decreased productivity.

5. That the light climate of the Adelaide metropolitan coast produces conditions which, in the context of reasonable photokinetic parameters, explain the loss of seagrass from the nearshore zone of this region. Using modeling, we investigate whether a scenario can be produced which demonstrates poorer productivity for the nearshore site (which has lost its seagrass beds) than it does for other sites further offshore, yet still allows for lower productivity at the deeper edge (where productivity is marginal) than at intermediate sites (which support dense seagrass beds and are presumably relatively productive).

3. Materials and Methods

3.1. Light Environment

3.1.1. Field Deployment

A series of Odyssey photosynthetically active radiation (PAR) (400-700 nm) cosine type light meters (Dataflow Systems, New Zealand) were deployed off Grange at a range of depths on March 10th 2005, recording average light intensity for each half hour period. Each of these was attached to the top of a star picket with cable ties such that it sat 60 cm above the sand substratum to approximate the canopy height of an *Amphibolis* / *Posidonia* meadow. Meters were located at distances of 0.5, 1, 2.5 and 3.5 km from the shore in depths of 3.5, 6.5, 12.5 and 18.5 m (mean tide level; Figure 2). These are referred to as the 3, 6, 12 and 18 metre sites. The 3 m site was inshore of the nearshore seagrass edge, in the area from which seagrass has been lost. The 6 m site is just within the seagrass zone, and the 18 metre site is just within the seaward (deep) edge of the seagrass zone. The 12 m site was approximately 2/3 of the way to the deeper edge. Meters were retrieved and substituted on an approximately fortnightly basis in order to ensure that light readings were not affected by algal growth on the sensors.

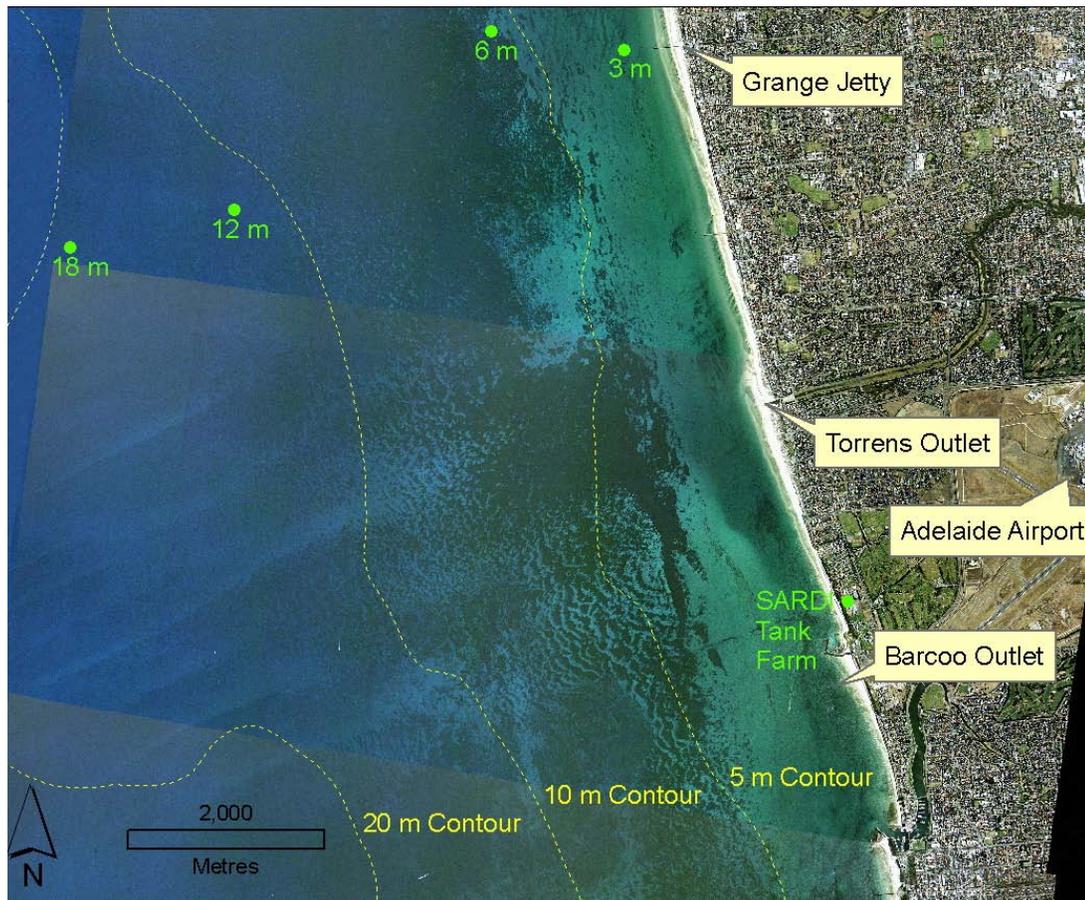


Figure 2: Aerial photograph showing the location of offshore submerged light meters off Grange, the West Beach (SARDI Tank Farm) surface light meter and Adelaide airport, where some values were obtained to replace data missing from the West Beach dataset. Some of the small northern area beyond the 20m depth contour is artificially coloured where no aerial photographs were available.

3.1.2. Calculation of Subsurface Light

Assessing optical water quality requires both a measurement of the light at the seafloor and at the surface in order to calculate how much has been cut out (absorbed) by the water column. The light measurement at the surface has to be just below the surface in order to take into account the fraction of light which is reflected from the sea surface. This is therefore termed a “subsurface” reading. However, subsurface light is difficult to measure in a long term field trial because waves and tidal movement will dictate that a fixed light meter will be submerged part of the time and in air at others. For this reason, subsurface light was calculated by measuring PAR with an Odyssey light meter in air at the SARDI Aquatic Sciences Tank Farm at West Beach and then applying a conversion factor which simulated the amount which would be reflected for any given sun angle.

The conversion factor applied to simulate the effect of reflection from the sea surface is dependent on sun angle, which in turn is dependent upon the latitude of the reading, the day of the year and the time of day. Only a small proportion is reflected unless the angle to the surface of the sea is quite acute (i.e. very early or late in the day). The relationship is demonstrated in Figure 3. Whilst the relationship assumes a flat reflecting surface, it is robust to the effects of waves on the surface (Angstrom 1925 in Kennish 1989).

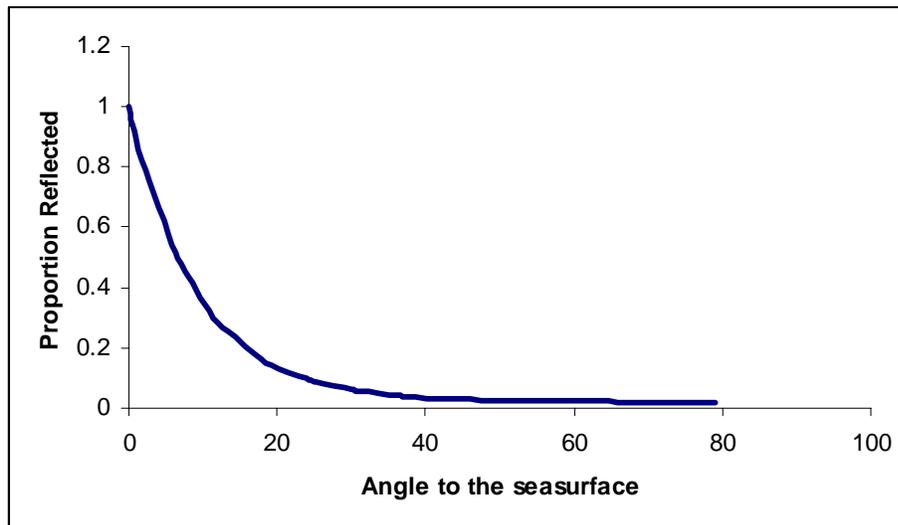


Figure 3: The effect of the angle of the sun on the amount of light reflected at the surface of the sea. Beyond an angle of 20 degrees, the majority of light is transmitted rather than reflected. This graph is derived from the reflectance model described below.

The equations used to determine the light transmitted immediately subsurface are:

1. Subsurface Irradiance = Surface Irradiance x (1 - Reflected Fraction)

2. Reflected Fraction = $\frac{1}{2} \times \left[\frac{\sin^2(i - r)}{\sin^2(i + r)} + \frac{\tan^2(i - r)}{\tan^2(i + r)} \right]$

where; i = angle of incidence and r = angle of refraction and are related by the formula;

$$\sin(i) = 1.3398 \times \sin(r). \quad \text{(from Kennish 1989)}$$

3. Angle of incidence (i) = $\sin^{-1}[\cos(H).\cos(SD).\cos(\text{latitude})+\sin(SD).\sin(\text{latitude})]$ where;
 H (=Hour Angle) = 15° for each hour beyond solar noon and;
 SD (=Solar Declination) = $-23.45^\circ.\cos((360/365).(N+10))$ (N=days since Jan 1)

Equation 1 was used to determine the fraction of light lost to reflection at the sea surface (as opposed to being refracted and transmitted below the surface). Only when the sun angle was very low was there a marked reduction in the amount of light transmitted. This is demonstrated in figures 4 and 5. where the effect of time of day and day of year on transmittance are shown. Generally, after the first three of hours of the day and before the last three, the proportion of light transmitted was relatively high and constant (Figure 4). On a yearly basis, there was a reduction in the proportion of light transmitted toward the middle of the year, and this was more pronounced when the sun was low in the sky because of the time of day (Figure 5).

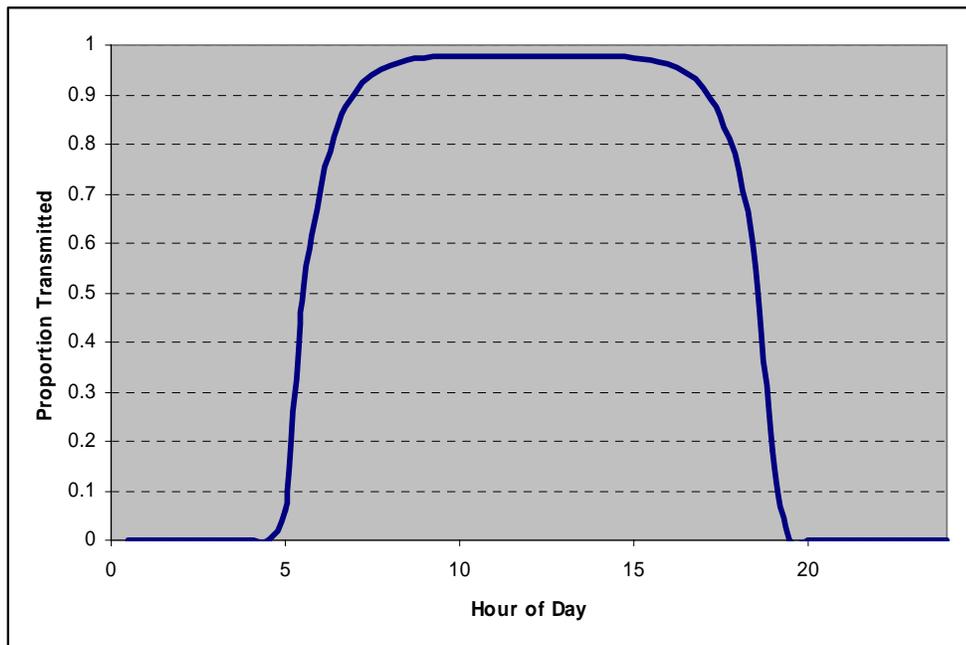


Figure 4: The modelled proportion of light transmitted below the surface of the water as a function of time of day. In this instance, the day demonstrated is January 1st. Other than very early and late hours of daylight, the angle of the sun is such that very little light is reflected and a large and relatively constant proportion of light is transmitted.

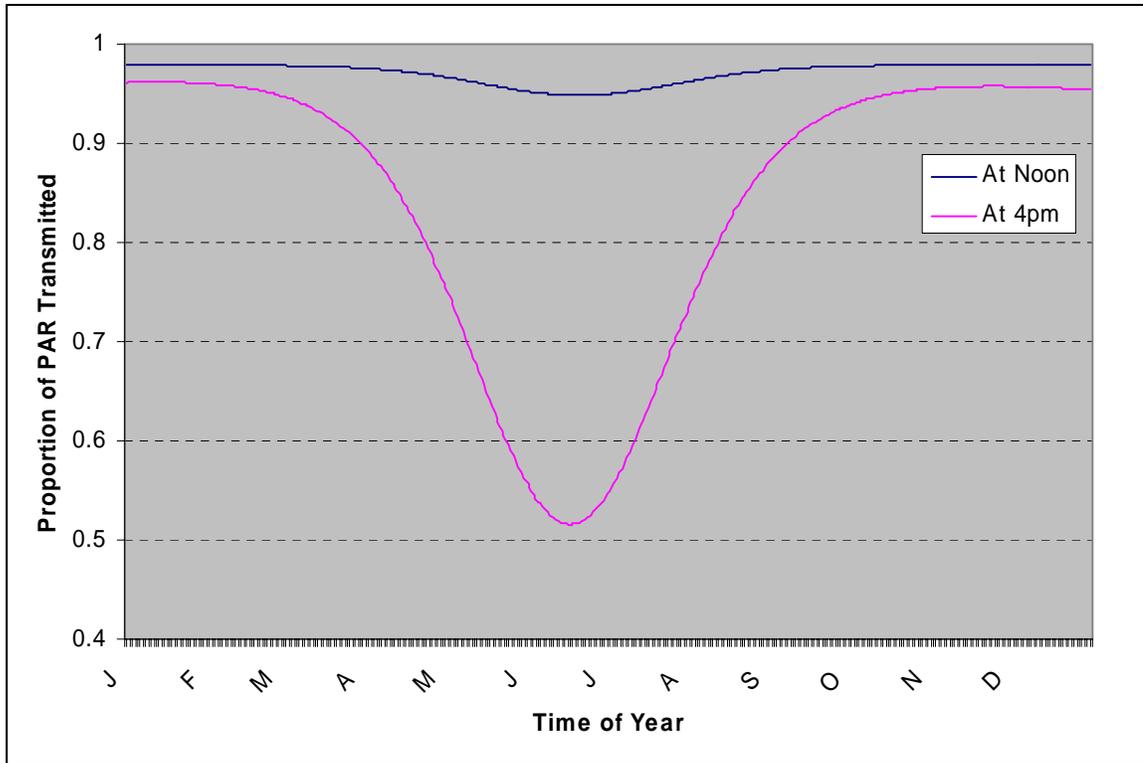


Figure 5: The modelled proportion of light transmitted below the surface of the water as a function of time of year and time of day. There is an increase in the amount of light lost to reflectance toward the middle of the year (winter). This is more evident at 4pm, when the sun angle is already low, than at noon.

3.1.3. Modelling missing data

Submerged Light

On occasion, because of problems with the light logging units, it was necessary to estimate appropriate values. For example, when light loggers were changed over, there was a period of an hour where the data might be dubious as there was a period during this time when both the new and replaced light metres were on deck, receiving full sun. For these periods, the values were modelled using the following formula:

$$\text{Irradiance}_{d,t} = \text{Irradiance}_{d-1,t} \times (\text{Irradiance}_{d,t-1} + \text{Irradiance}_{d,t+1}) / (\text{Irradiance}_{d-1,t-1} + \text{Irradiance}_{d-1,t+1})$$

where d indicates the day in question and d-1 indicates the previous day

t= the time requiring a modelled value; t-1 indicates the previous hour, t+1 the following hour

In essence, this creates a value based on the value at the same time on the previous day modified by the ratio of irradiance on the day in question to the previous day. Calculation of this ratio is based only on the hour either side of the time in question.

Surface Light

Where surface light readings were unavailable (approximately 7% of readings), they were modelled from half hour global insolation data recorded at Adelaide airport by the Bureau of Meteorology. By comparing daily total insolation as recorded by our loggers with that obtained from Adelaide airport over all periods where both were available, it was possible to calculate the ratio between the two for each month. This ratio was then applied to the airport data in order to model half hourly insolation as it would be recorded by our loggers. To check the validity of the approach, a month where data were available from both sources was used to produce a modelled light field. When compared to the actual data, the model produced an excellent fit (Figure 6). The r^2 value (Sum of Squares_{model}/Sum of Squares_{actual}) was 0.98, indicating that 98% of the variation in the real data was explained by the model. On this basis, it was concluded that the modelled data would be appropriate.

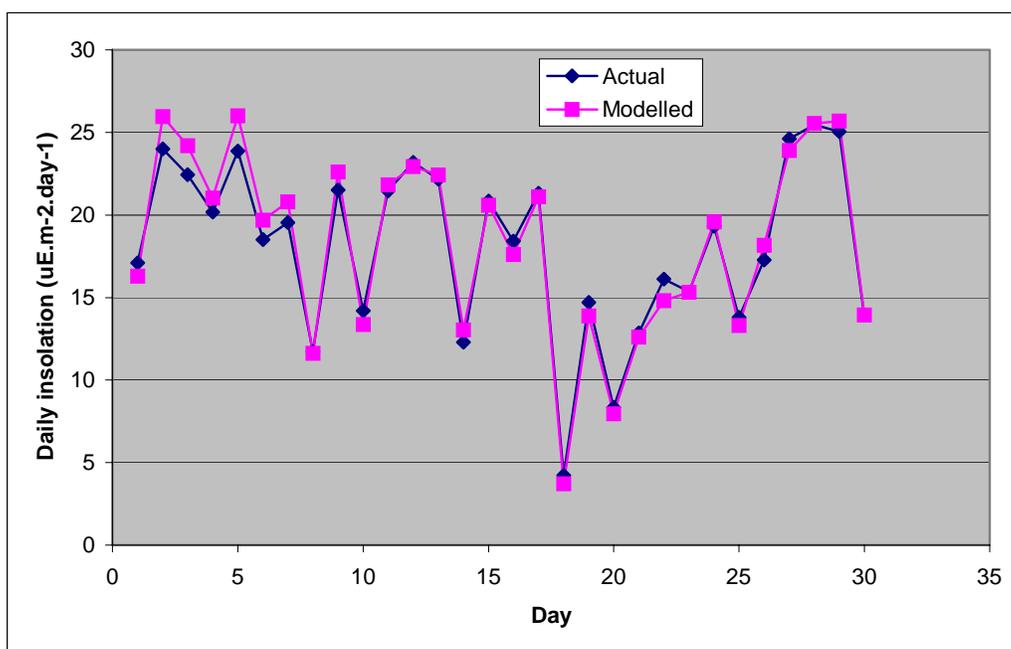


Figure 6: Fit of the modelled data against real data to test whether modelled data were appropriate for use where actual data were not available. r^2 was 0.98, indicating an extremely good fit.

3.1.4. Calculations

Half-hourly readings of average PAR intensity were provided by the loggers. These were summed and multiplied by 1800 to reflect the fact that the reading was expressed in $\mu\text{mol photons m}^{-2}$ per second rather than per half hour. This provided readings for daily PAR dose which were then used to create monthly and yearly averages. In order to calculate the percentage of subsurface light lost to attenuation in the water column, the daily dose was calculated in the same way for the subsurface light (as calculated in section 3.1.2) and compared with the sum for the same day at the depth in question. It was calculated on the basis of the daily totals, rather than half hourly, because the geographic distance between the canopy level underwater meters (at Grange) and the meter measuring subsurface light (at West Beach) meant light conditions may not be comparable on a short timescale. Any short term differences in light should be integrated across the course of the day.

Variability in light field is calculated for each site in each month. In the first instance, this is done by simply calculating a) the range (maximum for month minus minimum for month) and b) the standard deviation of daily irradiances across the month. In recognition of the fact that the variability will naturally be associated with the mean, regardless of any influence of variable optical water quality, a third comparison is made where the standard deviations are calculated on the basis of light fields which have been standardised for the effect of the mean. This was done by calculating the mean daily irradiance for each site in each month, then standardising daily totals by the appropriate mean. Standard deviations for each month and depth were recalculated on the basis of these adjusted daily values.

3.2. Productivity Modelling

This section uses the annual irradiance dataset which has been collected for each site to investigate, in a comparative manner, the effects of certain characteristics of the light field on the productivity of seagrasses. In order to do so, it draws upon an understanding of the relationship between light levels and the productivity of the plant which is relatively incomplete and therefore makes numerous assumptions. Considerations such as seasonal changes in the photophysiology of the plant are not considered, and our understanding of the influence of light levels on these is also not well developed. Furthermore, what understanding we do have is derived from studies elsewhere. For this reason, the conclusions drawn from these modelling studies are therefore necessarily circumscribed by our confidence in these assumptions. This is not to say that we have no confidence in the conclusions, merely that the conclusions must be drawn in terms of comparison of various models (for example comparing productivity at different depths), rather than placing credence on an absolute value demonstrated by a single site and drawing conclusions from that.

The productivity of any photosynthetic organism is dependent upon the level of light which they are subjected to. However, this relationship is a complicated one, demonstrating a linear response at low irradiance levels, but tapering off to an asymptote at higher levels (Figure 7). Additionally, this response is not consistent between species (e.g. Masini et al. 1995a; Masini and Manning 1997; Cummings & Zimmerman 2003), nor within species where differences may occur according to environment; in particular light environment (e.g. Mazella and Alberte 1986; Masini et al. 1995a; Masini and Manning 1997) and temperature (e.g. Perez and Romero 1992; Touchette & Burkholder 2000).

Several mathematical models have been fitted to describe the relationship of productivity to ambient light conditions (Fourqurean and Zieman 1991, Falkowski and Raven 1997). Essentially each represents a line of best fit to describe productivity based on the ambient light and on certain parameters of the plant which describe the maximal productivity (P_{max}), efficiency at sub-saturating light intensities (I_k) and dark respiration (R_d).

For the purposes of our study, Chalker's (1981) model was utilised:

$$P_I = P_{max} \times (1 - e^{\frac{-I}{I_k}}) - R_d$$

where; P_I represents the nett productivity at a given level of illuminance, I ;
 P_{max} represents the gross maximum productivity;
 I_k represents the subsaturating light level and,
 R_d is the dark respiration rate

Chalker's (1981) model has been shown in many studies to provide a good fit to measured P-I data (e.g. Cheshire et al. 1995, 1997).

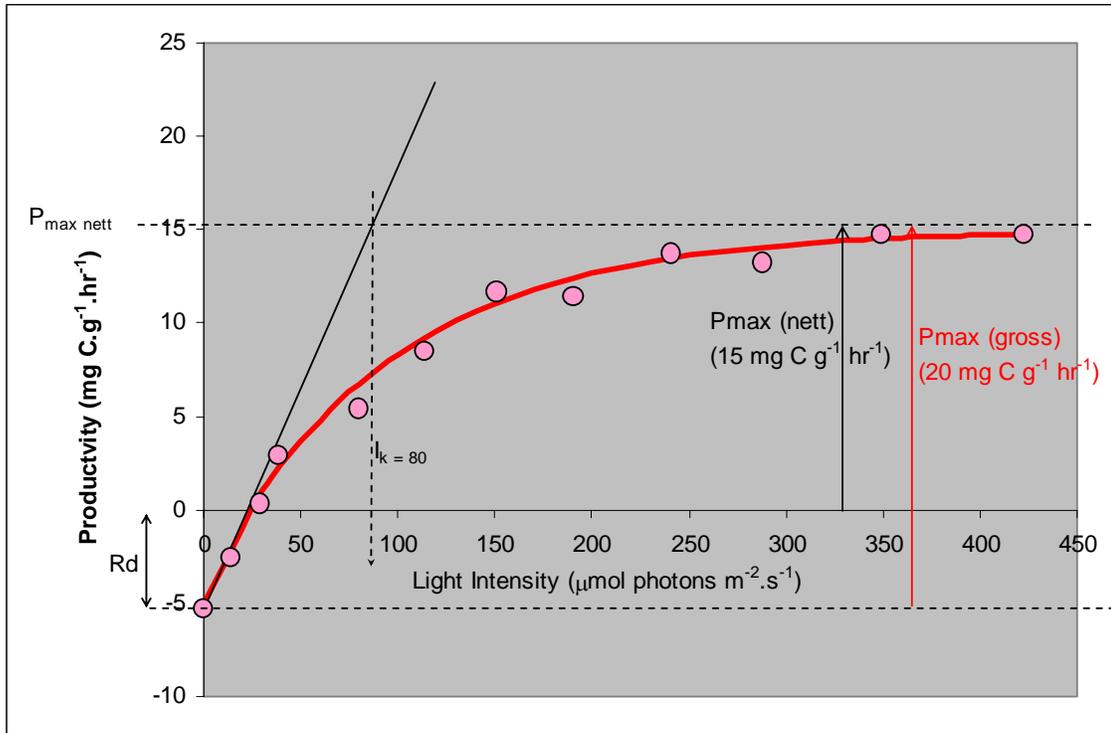


Figure 7: A typical Photosynthesis – Irradiance (P-I) curve showing productivity as a function of light intensity. Nett productivity at any light intensity represents gross productivity minus dark respiration (Rd). P_{max} indicates the maximal productivity achievable and can be expressed either as gross or nett P_{max} . I_K is a measure of the photosynthetic efficiency at sub-saturating light and is determined by extending a line as a tangent to the initial slope of the curve until it intercepts the P_{max} and dropping a line to the x axis. A small I_K value is indicative of a plant that is making efficient use of available light.

Nett productivity was calculated for every half hour on the basis of the above equation and the irradiance (PAR) data collected at 3 m, 6 m, 12 m and 18 m. Estimates of P_{max} , I_K and Rd were made on the basis of a number of scenarios.

It is worth noting that the literature reveals a range of responses in the photosynthetic parameters of seagrasses. Some authors identify a lack of change in P_{max} , Rd and/or I_K with temperature or depth, whilst others are able to demonstrate changes in these parameters which are dependent on the environment.

This productivity model was utilised under a series of different scenarios in order to demonstrate the effects of a range of photokinetic factors and features of the light-field. The entire model was created and run under a Microsoft Excel 2000 spreadsheet environment.

3.2.1. Scenario 1 – Effect of altering photokinetic parameters (sensitivity analysis)

Good understanding of the outputs of a model relies upon an understanding of the reaction of a model to alterations in the parameters used to formulate it. In this instance, there are four parameters which can be changed – maximal gross photosynthetic rate (P_{max}), subsaturating light intensity (I_K), dark respiration rate (Rd) and the actual light regime itself. In order to facilitate this understanding it is necessary to assess the effect of changes of these parameters in isolation -essentially simplifying the system so that only one variable at a time is having an effect.

In keeping with the philosophy of simplification where possible, rather than using the measured stochastic light field, a more standardised version was provided, by measuring the total amount of irradiance for the year at any given site and then allocating equally to each day. Within each day, hourly irradiance was calculated on the basis of a sine curve:

Light at time H = $\text{Sin}(\text{Hour of Day}) \times \text{SiteMultiplier}$

where hour of day was expressed in radians and SiteMultiplier was a constant (for the site) which ensured total daily light under this model was equal to the average total daily irradiance calculated from the real dataset.

The result is an identical irradiance pattern throughout the day for each day which differed only between sites (and then, only in magnitude as the sine curve pattern was constant between sites).

The standard parameters used were obtained from Masini and Manning (1997) for a population of *Amphibolis antarctica* from Western Australia. These were

$$\begin{aligned} \text{Gross maximal productivity } (P_{max}) &= 0.9375 \text{ mg C.g dwt}^{-1} \cdot \text{s}^{-1} \\ \text{Dark respiration } (Rd) &= 0.2775 \text{ mg C.g dwt}^{-1} \cdot \text{s}^{-1} \\ \text{Subsaturating light level } (I_K) &= 32 \text{ } \mu\text{mol.m}^{-2} \cdot \text{s}^{-1} \end{aligned}$$

The model was then run, altering each factor by +/- 20% whilst maintaining the others at a constant level. This is essentially a demonstration of the working of the model rather than a test of any particular hypothesis. It does demonstrate the effects of altering the photokinetic parameters, and acts as a sensitivity analysis.

3.2.2. Scenario 2 - the effect of variable optical water quality

Importantly, each of the sites chosen for this study represents not just a different depth, but also a different distance from shore and therefore from the land-based discharges which originate there. It is therefore important to assess the effect of the differential light penetration (caused by different optical clarity) at varying distances from the shore on the productivity of the seagrasses.

The linear attenuation coefficient (LAC) is a measure of the optical quality of the water. LAC increase is a reflection of greater turbidity, and hence is associated with a smaller fraction of light penetrating to any given depth. This may result in a reduction in productivity. Note that LAC is not dependent on depth, but is an indicator of the quantity of light lost for each metre of water. The potential effect on productivity of such differential turbidity is investigated in this scenario. The hypothesis in this case is that productivity is limited by the lower average daily irradiance *caused by poor optical water quality* (i.e. higher attenuation coefficient). It is important to note that this hypothesis specifically excludes the effect of the naturally lower amount of light which is the effect of deeper water and concentrates on the turbidity of that

water. In this manner, the model tests the effect of increased turbidity by comparing productivity using the measured amount of light with productivity using the amount of light which *would* have been received if the LAC was the same as at the offshore (18 m) site where the influence of turbidity is least.

The method uses a simple productivity model utilising the standardised (sine curve) light field described in Scenario 1 and constant photokinetic parameters across all sites ($P_{max}= 1.0275 \text{ mg C.g dwt}^{-1}.\text{s}^{-1}$, $R_d = 0.21375 \text{ mg C.g dwt}^{-1}.\text{s}^{-1}$, $I_K = 50.4 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ from Masini and Manning 1997). Two models are created which

- 1) reproduce the effect of depth on light field by use of a constant LAC across all sites and
- 2) use the actual LAC measured across the year for each separate site.

These models are compared in terms of their productivity at each site, thereby demonstrating the loss of productivity associated with poorer water quality close to shore.

Model 1

Average daily PAR was calculated for the 18 m site, and the LAC calculated by reference to the light immediately subsurface. A simulated 18 m light field was created using a sine curve and an appropriate constant to ensure that the modelled light field provided the same total amount of light as that which was actually measured:

Light at time H = $\text{Sin}(\text{Hour of Day}) \times \text{SiteMultiplier}$, where hour of day was expressed in radians

In the first model, the SiteMultiplier was 54.6731 (calculated from measurements at the 18 m site).

This was applied to provide light for 12 hours and the remaining 12 hours were dark. This light field pattern was repeated for 365 days to provide an annual budget with the same total as that measured at 18 m in the field. The 12 m, 6 m and 3 m light fields were then created without reference to any field measurements at these sites. Instead they were provided with a light field which mirrored the 18 m field but multiplied by factors which reflected the different depth of water. i.e. they assumed the same LAC as the 18 m site in each case. This essentially simulates a set of sites with identical optical water quality to that at 18 m, differing only in the amount of light removed because of differing depth. The relative levels of PAR under conditions of constant attenuation coefficient are demonstrated in Figure 8. The appropriate amount of light for any given depth (site) and time was calculated using the formula

$$I_D = (I_{18m} / e^{-K \cdot 18}) \cdot e^{-K \cdot D}$$

Where I_D = Light intensity at a given depth, D and I_{18m} is the intensity at 18 m depth

K is the linear attenuation coefficient (LAC).

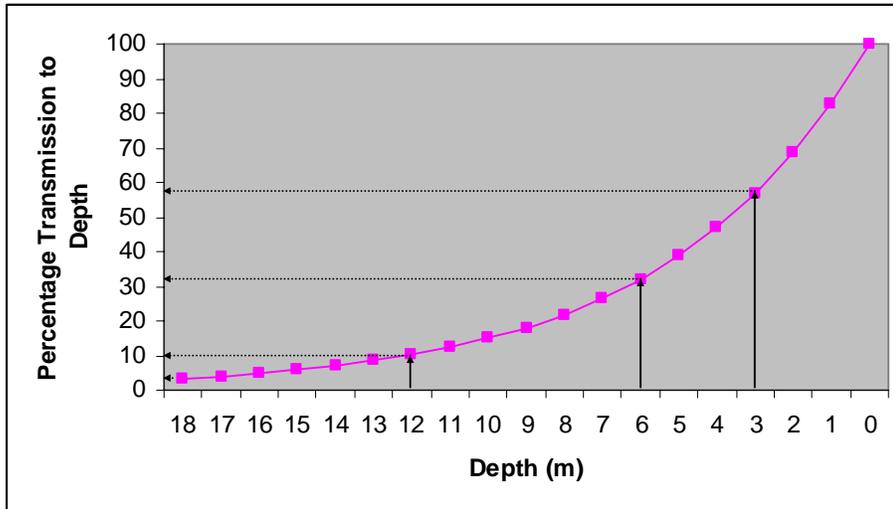


Figure 8: The relationship between depth and percentage transmission of irradiance to the seafloor if constant attenuation coefficient is assumed. Under these conditions it is only the depth of the water which affects transmission. By following the arrows up from the x-axis to the line and then back across to the y-axis, the percentage of subsurface light being transmitted to that depth can be determined. These values provide the ratio of irradiances for Model 1 in Scenario 2.

Model 2

Model 2 differs from Model 1 only in that the attenuation coefficient applied to the standard light environment was that measured from the actual site (calculated on the basis of 12 months of field readings), rather than a single LAC from the 18 m site (as was the case in Model 1). The formulae used were:

$$\text{Light at time H, depth D m} = \text{Sin(Hour of Day)} \times \text{LAC}_D$$

where: LAC_D is the linear attenuation coefficient for the site representing that depth; $\text{LAC}_{18\text{m}} = 54.6731$, $\text{LAC}_{12\text{m}} = 84.7736$, $\text{LAC}_{6\text{m}} = 113.1124$. $\text{LAC}_{3\text{m}} = 132.7975$.

These LAC_D values were calculated based on the relative average daily PAR measured across the course of the year. Note that the $\text{LAC}_{18\text{m}}$ provides a light environment identical to that of Model 1.

Thus any differences we see between the two models represent only the difference caused by changes in attenuation coefficient (and therefore optical water quality) at different distances from shore.

This is a relatively simple model designed to investigate only the effect of optical water clarity. It focuses on the *difference* between the two models, deliberately simplifying the system to investigate the influence of a single factor, rather than providing a complex model where any differences are difficult to attribute to particular factors. Thus, no attempt is made to put any real credence in the absolute values of productivity as the light field is relatively removed from reality (modelled with consistency across the year). The relativity of the models, however, gives important information on the potential impacts of increased turbidity in the nearshore zone.

3.2.3. Scenario 3 - the effect of light field variability on productivity

The natural light field is a variable one, and it has been suggested that the *variability* may be as important as the average in determining the net productivity of the seagrasses. For this reason, a comparison of models is made between the standardised light environment outlined in Scenario 1 and two scenarios of reduced light. The first of these situations models a system where the light field has been simply reduced by 20% at all times. The second situation also involves a 20% reduction in the total irradiance, but achieves this through total blackout of the light on one day in every five. Both of these scenarios demonstrate an equal reduction in light quantity (20%), but the first demonstrates no daily variability, whilst the second exhibits a level which has been demonstrated in the field (in extent, if not frequency). Regardless of its applicability it demonstrates the effect of daily variability. Both are compared to the standardised situation.

3.2.4. Scenario 4 – The application of literature photokinetic parameters

Pragmatic considerations prevented an assessment of the photokinetic parameters of the seagrass species. For this reason, values of P_{max} , I_K and R_d were obtained from the literature and applied to the light data which were collected across a twelve month period to represent the Adelaide metropolitan coast. The data used comes from Masini and Manning (1997) and describes the photokinetic parameters of *Posidonia sinuosa* and *Amphibolis antarctica*.

Masini and Manning (1997) present data which describe the photokinetic parameters of *Posidonia sinuosa* at depths of both 4 m and 12-15 m (the deep edge of the bed). As it is available, these differential photokinetic parameters are applied at the different depths. The 4 m parameters are applied to the 3 m population of this study and the 12 – 15 m parameters are applied to the 12 m population from Adelaide. The 6 m site at Adelaide used mean values weighted according to depth (i.e. it was 1/3 of the way between the 3 m and the 12 m data). In the absence of any measurement of photokinetic parameters beyond 12 – 15 m by Masini and Manning, these values were applied also at the 18 m site rather than attempting to extrapolate beyond the depths actually measured. i.e. interpolation between 3 and 12 m was considered acceptable, but extrapolation beyond this was not.

No data on the effect of depth on the photokinetic parameters of *Amphibolis antarctica* were available, so a single set of parameters (from winter) were applied for this species across the year. These data were sourced from Masini and Manning (1997).

The parameters used are described in Table 1. The model is run for both species, first allowing no change of photokinetic parameters with depth, and then again including the change in parameters detailed by Masini and Manning (1997) for *Posidonia sinuosa* in southwest Western Australia. Where no effect of depth was incorporated, the parameters for the 12 m plants were applied to plants at all depths.

As no data was available with which to characterise the manner in which the photokinetic parameters of *Amphibolis* might change with depth, the changes described above for *Posidonia* were converted to percentages, and then applied to the single depth measurements obtained by Masini and Manning (1997) for *Amphibolis*. It was assumed that the reported data referred to shallow (3 m) water plants and parameters were then calculated for the 6 m, 12 m and 18 m sites. As with the *Posidonia*, the parameters remained constant across the 12 to 18 m range as there is no basis for extrapolation.

Table 1: Photokinetic parameters used in the model to simulate productivity under the measured light regime. The data are taken from Masini and Manning (1997) which details the parameters for two depths (4 m and 12-15 m) at a single point in time (winter) for *Posidonia sinuosa* and provides data for *Amphibolis* at a single depth and point in time. Modification of *Amphibolis* values over depth was achieved by mirroring the changes demonstrated by *Posidonia*. Note that both P_{max} and R_d are expressed as per g of canopy, but the R_d value has been doubled to reflect the fact that Masini and Manning express P_{max} per g of leaf biomass, whilst R_d is reported as per g plant weight (i.e. including underground biomass). Thus the value is doubled on the basis that the general relationship in seagrasses is to balance above and below-ground biomass (Duarte and Chiscano 1999).

Species	Parameter	Depth			
		3 metres	6 metres	12 metres	18 metres
<i>Amphibolis</i>	P_{max} (mg C.gdwt.hr)	0.9375	1.0604	1.3061	1.3061
	I_K ($\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$)	32.0	29.6	24.8	24.8
	R_d (mg C.gdwt.hr)	.2775	0.2926	0.3228	0.3228
<i>Posidonia</i>	P_{max} (mg C.gdwt.hr)	0.7375	0.8342	1.0275	1.0275
	I_K ($\mu\text{mol photons.m}^{-2}.\text{s}^{-1}$)	50.4	46.63	39.1	39.1
	R_d (mg C.gdwt.hr)	0.3675	0.3875	0.4275	0.4275

4. Results

4.1. Light Environment

On average, irradiance levels at the water surface followed a truncated sine curve, but levels were substantially depressed in winter compared with summer levels (Figure 9). The daily values used to create this average were, however, highly variable as a result of atmospheric conditions.

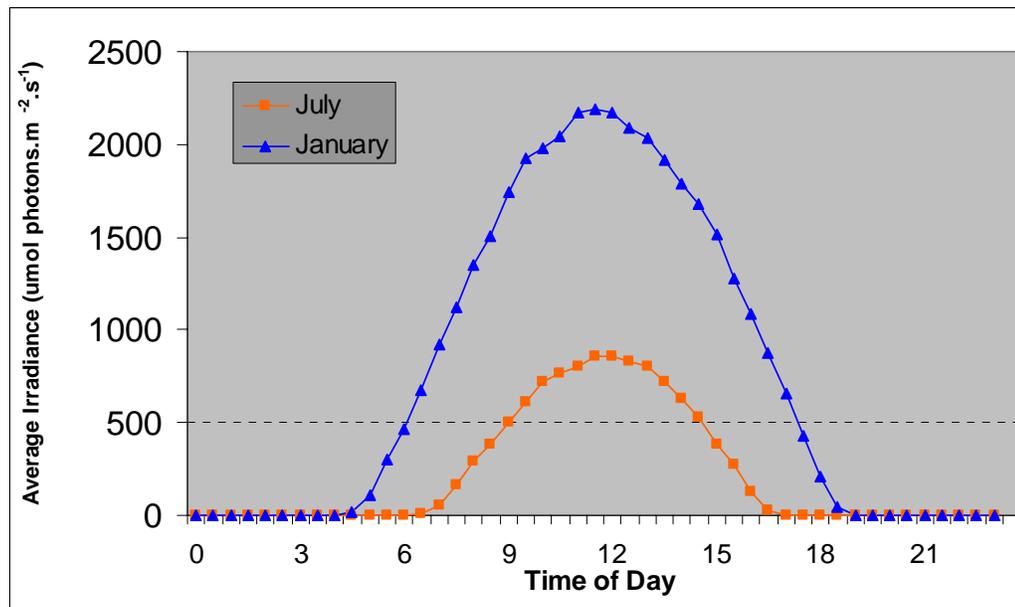


Figure 9: Average irradiance above the water surface in mid-winter (July 2005) and mid-summer (January 2006).

The irradiance reaching the canopy follows a pattern reflected by the depth of the sites (Figure 10). As would be expected, the shallowest site (3 m) experiences the highest total amount of light across the course of the year, followed by the 6 m site, the 12 m site and finally the 18 m site, which was subject to the least irradiance.

Whilst the annual pattern indicates a trend of irradiance decreasing with depth, this was not evident at all times of the year. The 3 and 6 metre sites experienced markedly higher PAR than the deeper sites during the five month period from March to May 2005 and January to March 2006 (Figure 11). However, during the 7 month period, from June until December (inclusive), there was little difference between each of the sites, and indeed, on occasion, slightly higher irradiances were recorded at deeper depths than at the nearshore 3 m site.

It is worthy of note that while canopy level irradiance levels were determined to some degree by the incoming solar irradiance, clearly the turbidity of the water body has an influential modifying influence. It is really only after December that water clarity improves to a point where irradiance at three metres depth reacts to the increasing surface irradiance which has been occurring since June (Figure 11). Indeed, across the period June to December, subsurface irradiance increased from 15.4 to 60.7 mol photons.m⁻².day⁻¹ (an increase of 385%). Across the same period, PAR at the 3 m site increased from 1.13 mol photons.m⁻².day⁻¹ to 2.07 mol photons.m⁻².day⁻¹ (183% increase). Once the water cleared up, in

January, PAR at 3 m increased to 8.3 mol photons.m⁻².day⁻¹ (a 307% increase) despite no increase in surface light (Figure 11). This is an indication of very poor water quality across the period from June to December. The range, from month to month is far greater at 3 m than experienced at the sites deeper and further offshore.

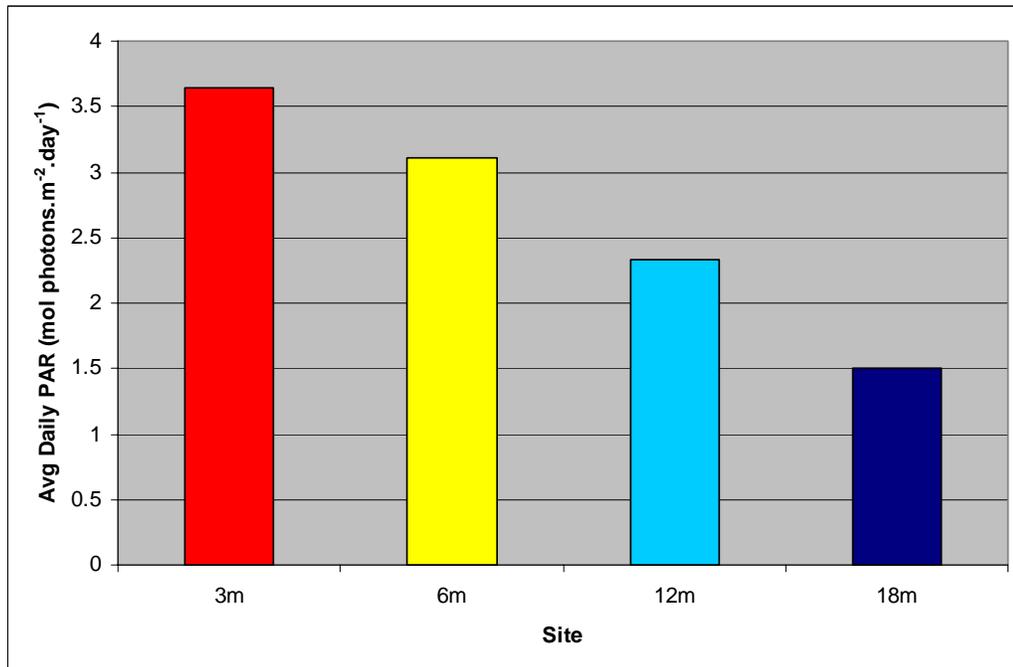


Figure 10: Daily PAR averaged across the annual cycle at 4 depths off Grange. Note that the average daily insolation, calculated across the entire year is greatest at the shallowest depth, and decreases as depth increases. Error bars are not provided as this variability is addressed directly elsewhere (Figures 13 and 14).

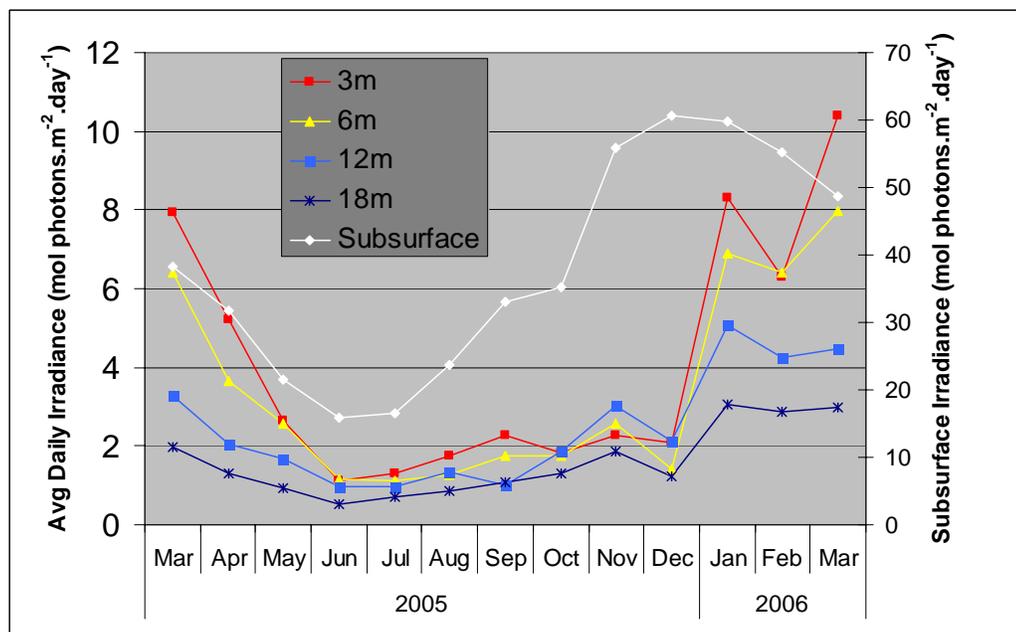


Figure 11: Average daily PAR for each month at each of the sampling locations. Subsurface light is presented on the right hand axis. Whilst the 3 m and 6 m sites were lighter than the

deeper sites in the period January to May, over the period June to December, light in the shallower regions was depressed to a similar level as that found at 18 m.

When the light reaching the canopy at each of the different sites is expressed as a percentage of the surface light, it is clear that it is only in the period January to May that a substantially greater proportion of the surface light is evident at the seafloor of the shallower, more nearshore sites (Figure 12). The proportion of subsurface light reaching the seafloor is far more consistent at the deeper, offshore sites than those close to shore (and the associated land-based inputs). On an annual basis, the 3 and 6 metre sites (9.7% and 8.2% of subsurface light, respectively) demonstrated light environments in excess of the 7.8% required according to DEP (1996) for the survival of *P.sinuosa*. The 12 and 18 metres sites (6.2% and 4% of subsurface light) had light environments well below this level. This was also the general pattern on a seasonal basis; the 3 and 6 metres sites were above the requirement for each season, whilst the 12 and 18 metre sites were below this level.

These findings, in terms of the proportion of subsurface light transmitted to the seafloor, is in keeping with the changes noted in the linear attenuation coefficient (LAC) (Figure 13). LAC is an indication of water clarity, or more specifically, the amount of light which fails to be transmitted across each metre of water. In this way, it is possible to compare optical water quality across a range of sites of different depths. LAC was lowest at the 12 and 18 metre sites and highest at the 3 and 6 m sites. This indicates worse optical water quality at the nearshore sites. In addition to being relatively low, the 12 and 18 metres sites were very similar to one another in terms of LAC. They also varied very little from month to month. In contrast, LAC was extremely high at the nearshore sites, particularly the 3 metre site. It was also extremely variable from month to month.

It is apparent that the water quality is, to a large degree correlated with the amount of outflow from the major land-based discharges – the River Torrens at Henley Beach and the Barcoo Outlet at Glenelg. The six periods of lowest flow are also the six periods of lowest LAC, which indicates the effect of discharge volume on the water clarity of the nearshore regions (Figure 13). However, the relationship is not an entirely simple one, as is indicated by the fact that discharge rates peaked in November, but the attenuation coefficient was greatest in the following month despite a marked decrease in discharge rate in December. It is also necessary to point out that the relationship which is evident between outflow and attenuation coefficient is not a linear one as outflow is expressed on a natural log scale.

In general, there is a relatively rapid response in water quality to events of high flow. Figure 14 demonstrates the relationship between daily flow and light penetration at each of the sites representing different depths. Recovery to higher light levels may take some time after periods of high flow, particularly at the nearshore site, as evidenced by the lack of light present from October 11 to October 15th at the three metre sites despite rising light levels at all the sites further offshore (Figure 14). In contrast, the initial decline is largely synchronous with the flow rates. It is also noteworthy that there is no clear timelag associated with the response of the sites further from shore, at least on a daily timescale.

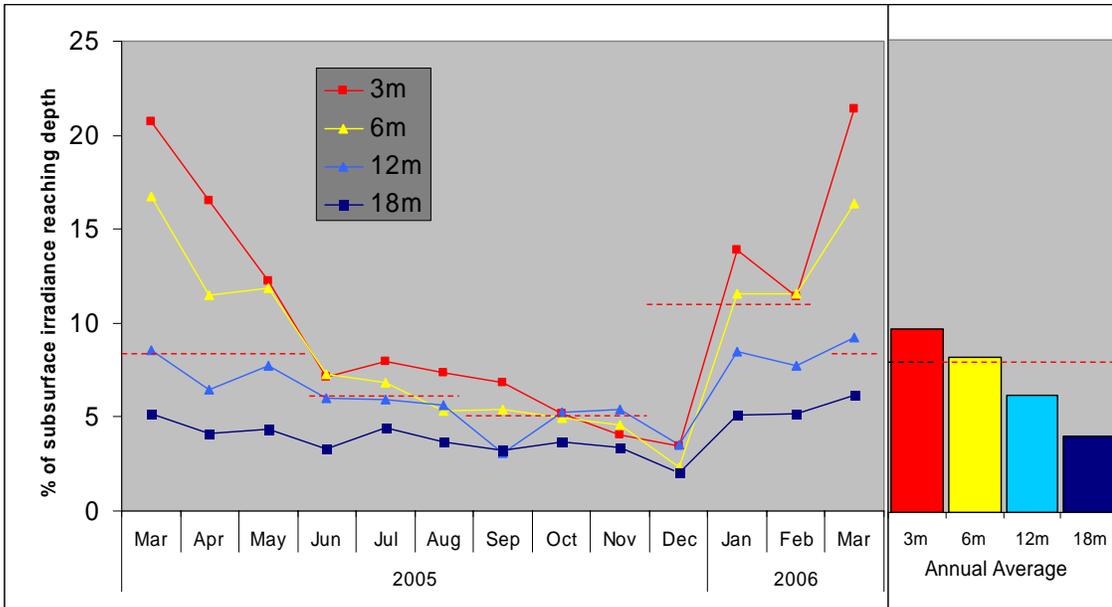


Figure 12: Average percentage of subsurface light reaching the seafloor at the 3, 6, 12 and 18 m sites for each month of the year and as an annual average. This presents the information from Figure 11 in a manner that allows it to be compared with literature values which indicate the percentage of subsurface light required to support seagrass beds. Horizontal dashed red lines indicate the minimum required light levels for *P. sinuosa* in each season and annually according to DEP (1996).

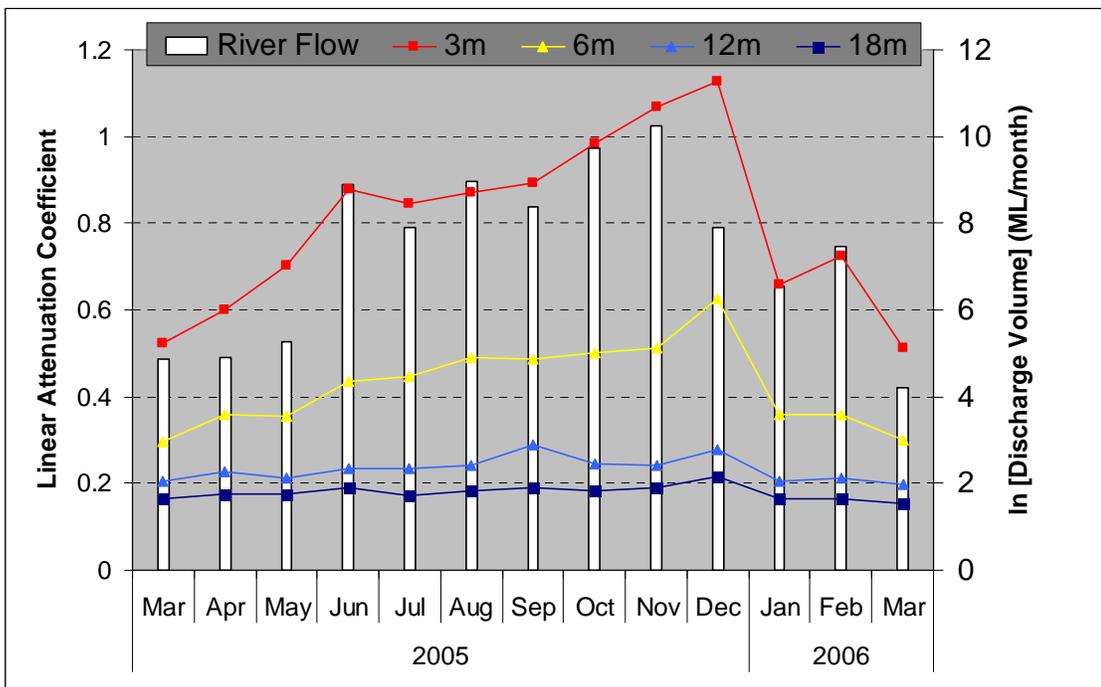


Figure 13: Average linear attenuation coefficients calculated for each month at each site with the combined Barcoo Outlet and Torrens River outflows overlaid. River flow is expressed on a natural log scale. The river flow value for March 2006 is based upon a scaled up estimate of flow from the small dataset available, rather than a full month. The apparent response of attenuation to river flow is most notable in the nearshore (3 m) region and becomes more muted at sites further from the shore.

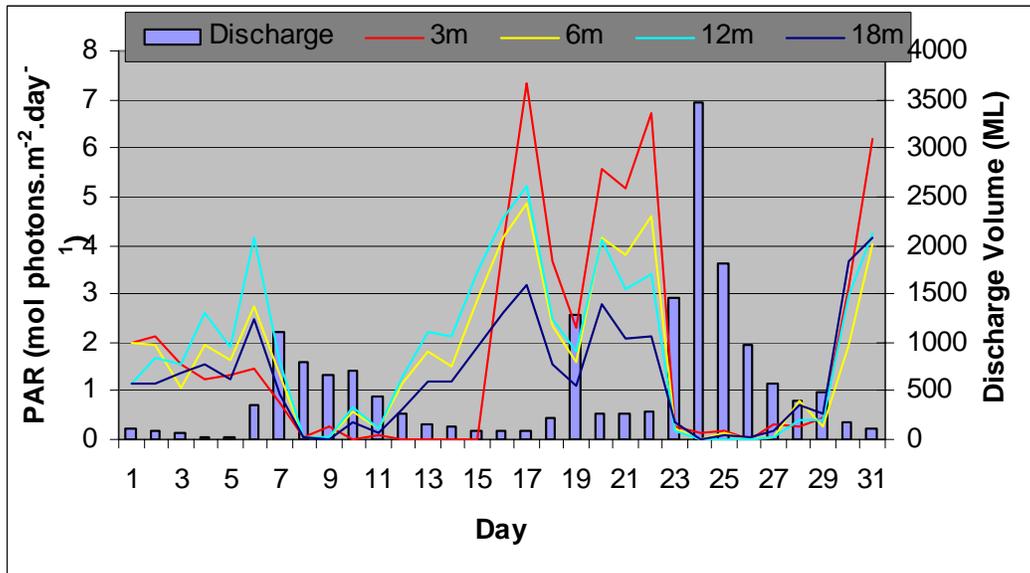


Figure 14: Relationship between discharge volume and irradiance at each site on a daily basis within the month of October. There is a clear effect of periods of high discharge, particularly on the 3 m site. There appears little lag in the onset of this effect, but the period of low light may persist for some time after discharge volumes subside.

Whilst the variability of the light field within each month appears well correlated with the mean light level (Figures 15 and 16), there is a marked increase in variability from June to December which is not as apparent in the mean light levels (Figure 11). In the absence of an effective understanding of the effect of variability of light field on the photokinetic parameters of seagrass, both range and standard deviation are presented (Figures 15 and 16). The general trends are extremely similar. Importantly, the variability is greatest at the shallow, nearshore sites, and least in those sites furthest offshore. It is greatest in summer and least in winter.

In order to identify whether extra variability can be attributed to nearshore sites, it is necessary to negate the influence of the increased mean. The problem is that if water quality remained constant, there would still be apparently greater variability in those sites receiving higher average irradiance. An analysis of the data standardised by the mean of the site and month allows this influence to be removed. It is clear that whilst this extra variability (beyond that of simply higher light levels) is less disparate between sites, it still exists and it is still greater at the nearshore sites than it is further offshore (Figure 17). However, variability is greatest in the winter and spring months, peaking across the period October to December at the 3 and 6 metre sites.

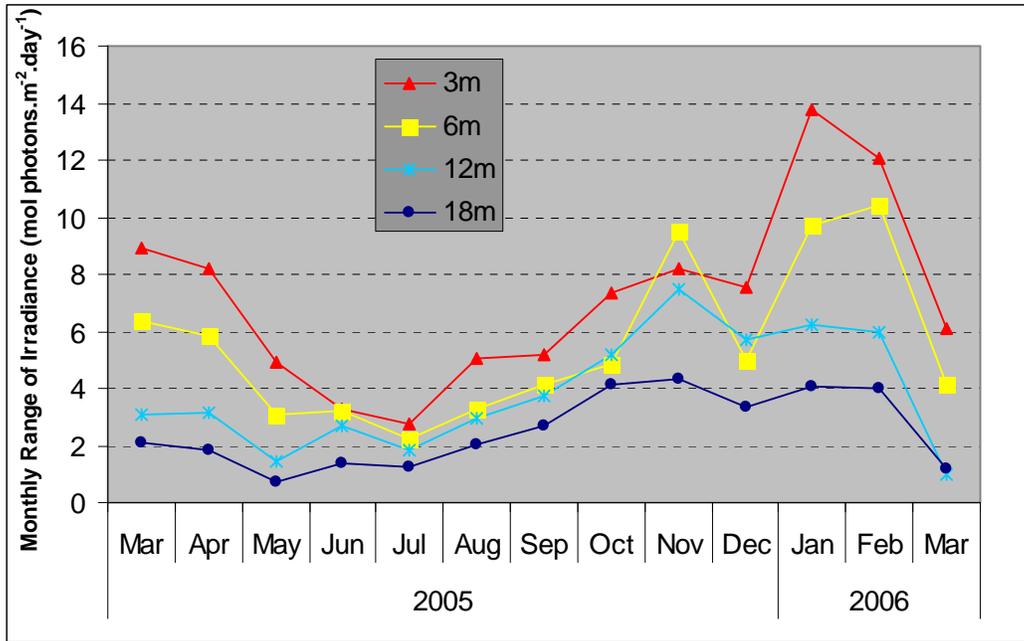


Figure 15: Monthly range of daily PAR totals at each of the different depths. The range of PAR irradiances experienced at each site is greatest in the nearshore region and decreases as distance from the shore increases. This range is greatest in summer and least in winter. Note that the March range in both years is probably artificially low because each of these periods were calculated over considerably fewer days than any other month (20 in 2005 and 11 in 2006). It was not considered appropriate to combine these as they were from periods separated by 12 months.

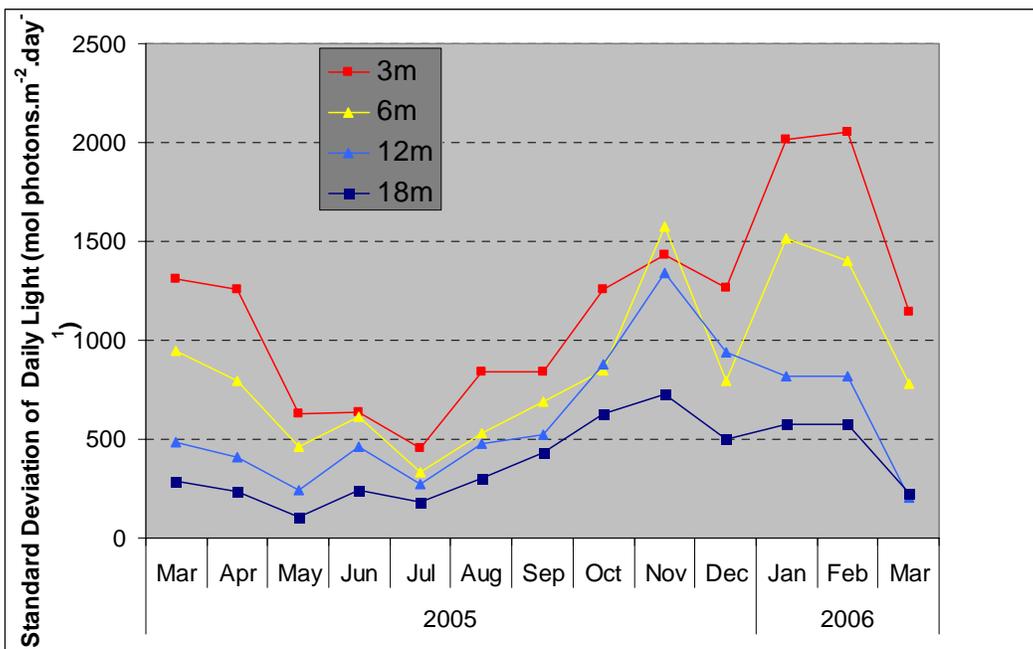


Figure 16: Standard deviation associated with the daily PAR totals within a month at each of the different depths. Standard deviation is greatest in the nearshore region and decreases as distance from the shore increases. It is greatest in summer and least in winter. The March value in both years is probably artificially low for the same reasons as outlined in Figure 15.

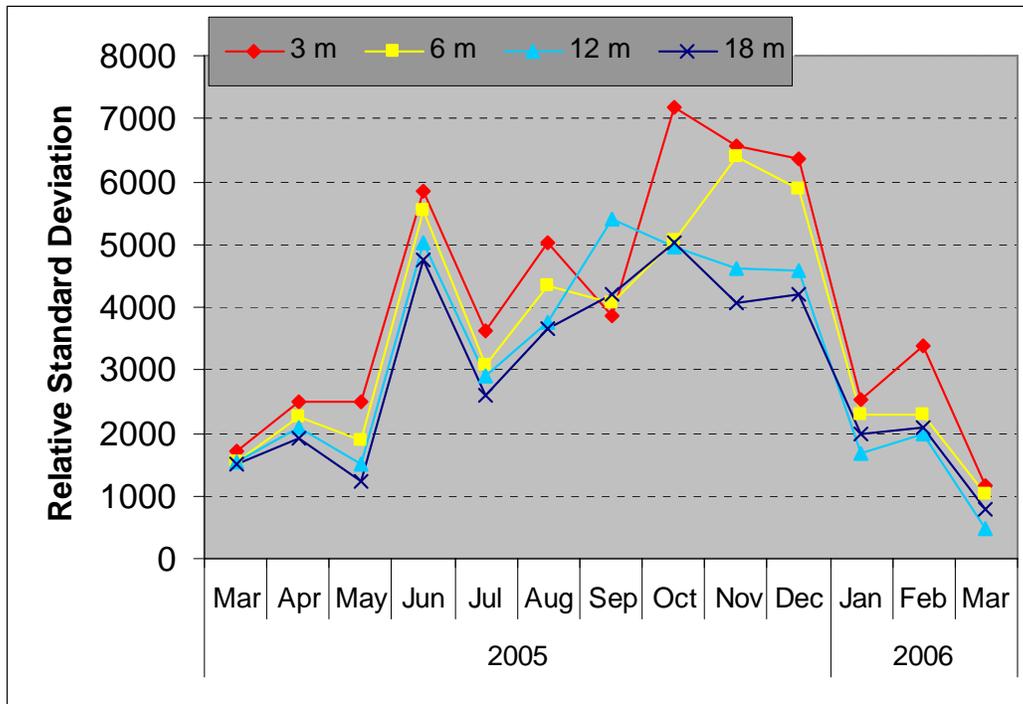


Figure 17: Standard deviation associated with the standardised daily PAR levels. This figure compares the relative variability of PAR after standardization to the mean for month and depth. Whilst removal of the influence of variable mean levels has resulted in greater similarity between depths, there is still a clear trend toward greater variability at the nearshore sites than those further offshore. No units are provided in this instance because the standardization procedure renders the actual figures meaningless except in relative terms to each other.

4.2. Productivity Modelling

4.2.1. Scenario 1 – Effect of altering photokinetic parameters (sensitivity analysis)

By changing one factor at a time, this scenario demonstrates the effect of altering the photosynthetic parameters, P_{max} , I_K and R_d , by a moderate amount (20%). It is designed to provide a gross demonstration of the way the model will react to these changes, and no implication is made that this situation is related to the real-world example.

P_{max} and R_d cause similar additive responses, but they are contrasting in effect. Increasing P_{max} by 20% results in a marked increase in productivity, whilst decreasing it by the same amount has a negative effect of approximately the same magnitude (Figure 18). R_d has a similar effect, but applies in the reverse direction – as R_d increases the productivity decreases (Figure 19).

Whilst changing I_K appears to have the same sort of effect as changing R_d (Figure 20 c.f. 19), (i.e. increasing I_K decreases productivity), it does so in an entirely different manner. In the case of R_d , there is a direct use of accumulated carbon for metabolic purposes. By contrast, an increase in I_K actually decreases the efficiency of the plant in the accumulation of carbon at lower light levels. Thus, whilst the effects of altering P_{max} and R_d are relatively simple, I_K is more complicated in its effects. This is evidenced by the non-linear nature of the relationship demonstrated in Figure 7.

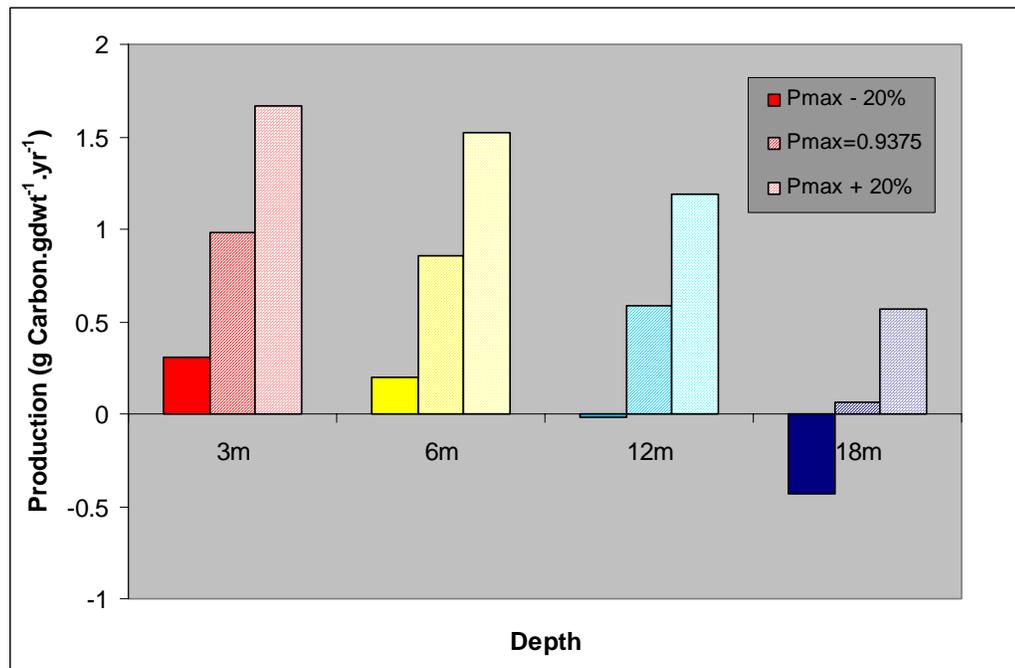


Figure 18: The effect of changing the maximal gross photosynthetic rate. Using the base model described in Scenario 1, and allowing for different attenuation coefficients at different sites (depths), the effect of decreasing (solid bars), and increasing (brickwork bars) P_{max} by 20% is examined. The striped column is the reference and uses a P_{max} of $0.9375 \text{ mg C. g dwt}^{-1} \cdot \text{hr}^{-1}$. R_d is maintained at $0.2775 \text{ mg C. g dwt}^{-1} \cdot \text{hr}^{-1}$ and I_K at $32 \text{ umol. m}^{-2} \text{ s}^{-1}$.

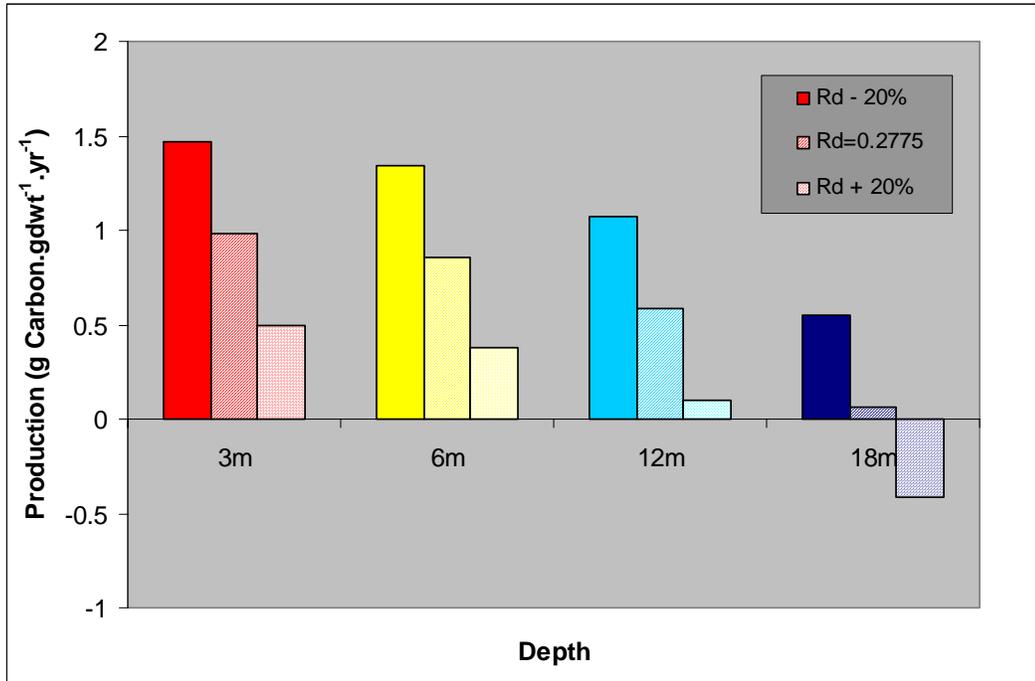


Figure 19: The effect of changing the dark respiration rate. Using the base model described in Scenario 1, and allowing for different attenuation coefficients at different sites (depths), the effect of decreasing (solid bars), and increasing (brickwork bars) R_{max} by 20% is examined. The striped column is the reference and uses a P_{max} of $0.9375 \text{ mg C. g dwt}^{-1}.\text{hr}^{-1}$. R_d is maintained at $0.2775 \text{ mg C. g dwt}^{-1}.\text{hr}^{-1}$ and I_K at $32 \text{ umol.m}^{-2}\text{s}^{-1}$.

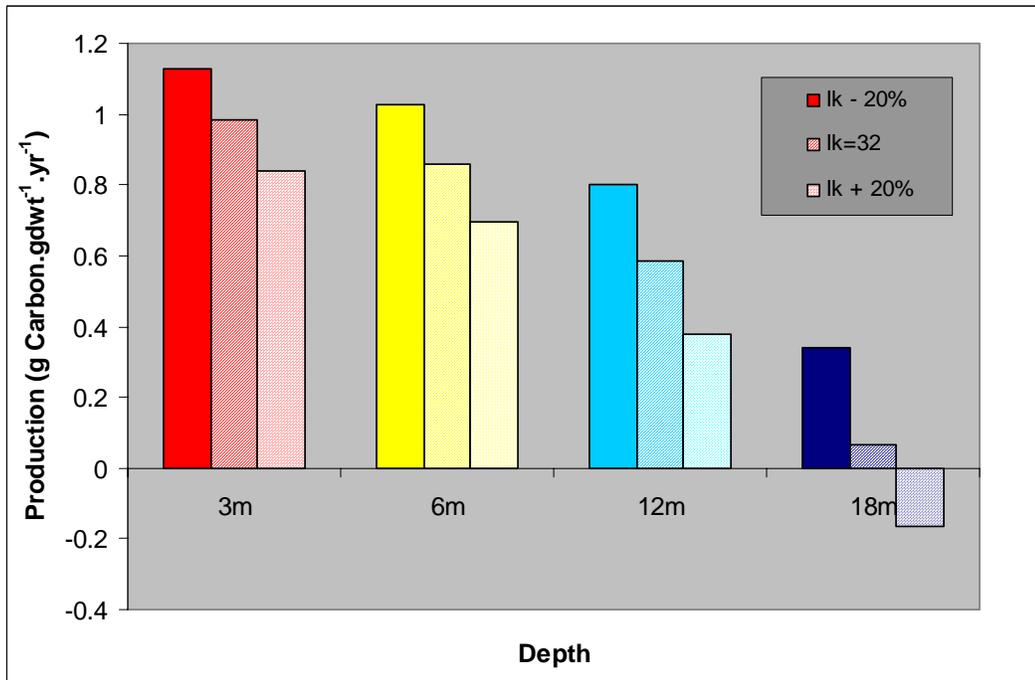


Figure 20: The effect of changing I_K . Using the base model described in Scenario 1, and allowing for different attenuation coefficients at different sites (depths), the effect of decreasing (solid bars), and increasing (brickwork bars) I_K by 20% is examined. The striped column is the reference and uses a P_{max} of $0.9375 \text{ mg C. g dwt}^{-1}.\text{hr}^{-1}$. R_d is maintained at $0.2775 \text{ mg C. g dwt}^{-1}.\text{hr}^{-1}$ and I_K at $32 \text{ umol.m}^{-2}\text{s}^{-1}$.

4.2.2. Scenario 2 - the effect of variable optical water quality

Using this simple model of productivity, it is clear that the more turbid waters close to shore have a marked effect on the amount of light reaching the seagrass (Figure 21). For instance, if the same attenuation coefficient was demonstrated at the 3 m (close inshore) site as was apparent at the 18 m (offshore) site, we would expect to see an average PAR of $22.1 \text{ mol m}^{-2} \cdot \text{day}^{-1}$. Instead, what we see in reality is only $3.6 \text{ mol m}^{-2} \cdot \text{day}^{-1}$. The difference between the two models decreases as distance offshore increases (with the consequent improvement in water clarity).

The difference in productivity is not linearly related to the difference in light levels (Figure 21). There is a substantial decrease in productivity caused by the higher attenuation coefficients found closer to shore (for example, productivity at 3 m was $1.49 \text{ g C.gdwt}^{-1} \cdot \text{yr}^{-1}$ under the constant (18 m) attenuation model, and only $0.98 \text{ g C.gdwt}^{-1} \cdot \text{yr}^{-1}$ under the model using measured attenuation coefficients. This represents a decrease of $0.51 \text{ g C.gdwt}^{-1} \cdot \text{yr}^{-1}$. However, even at 12 m, where the difference in light regime between the models was not nearly as marked, the lost productivity still amounted to $0.52 \text{ g C.gdwt}^{-1} \cdot \text{yr}^{-1}$. Thus, even moderate decreases in water quality can have a marked effect on productivity.

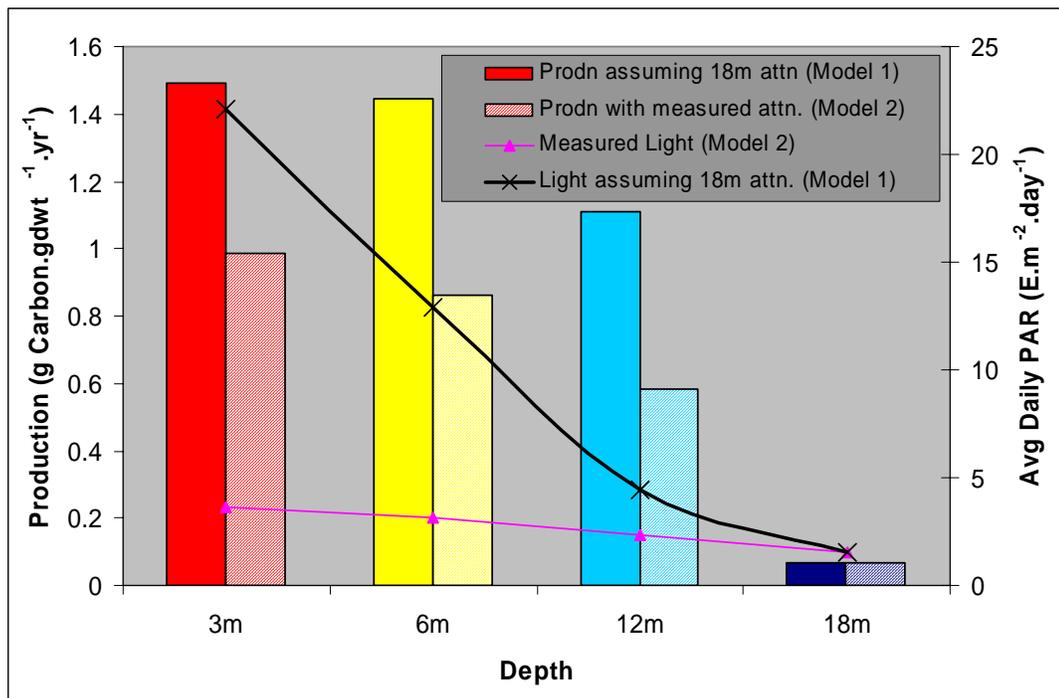


Figure 21: The effect of variable attenuation coefficient on light and productivity. A simple model (see details in methods) to demonstrate the effects of a spatially variable attenuation coefficient on productivity and light.

1. Solid bars represent productivity on the basis of the light at 18 m being extrapolated to other depths under the assumption that the linear attenuation coefficient was the same at all sites as 18 m (Model 1). The black line represents the average daily PAR under this scenario.
2. Striped bars show the productivity when the actual attenuation coefficient from each site was used (Model 2). The pink line represents the average daily PAR under this scenario.

The difference between the scenarios represents the effects of variable attenuation coefficient.

4.2.3. Scenario 3 - the effect of daily light field variability on productivity

This scenario investigated the effects of variability in light climate on productivity. Comparison was made between the productivity achieved under the standard light environment, that achieved under a 20% reduction in total irradiance by a simple multiplication of each light value by 80%, and that where the same reduction was achieved by simulating the original situation with every fifth day being completely dark. It is clear that reducing the light climate causes a substantial reduction in productivity, and equally, that reducing it by simulating light fluctuations across days caused a greater loss than by simulating a simple shading by 20% effect (Figure 22). In both cases, the 18 m site was unable to achieve compensation (nett productivity ≤ 0), but this was particularly the case where fluctuations were introduced.

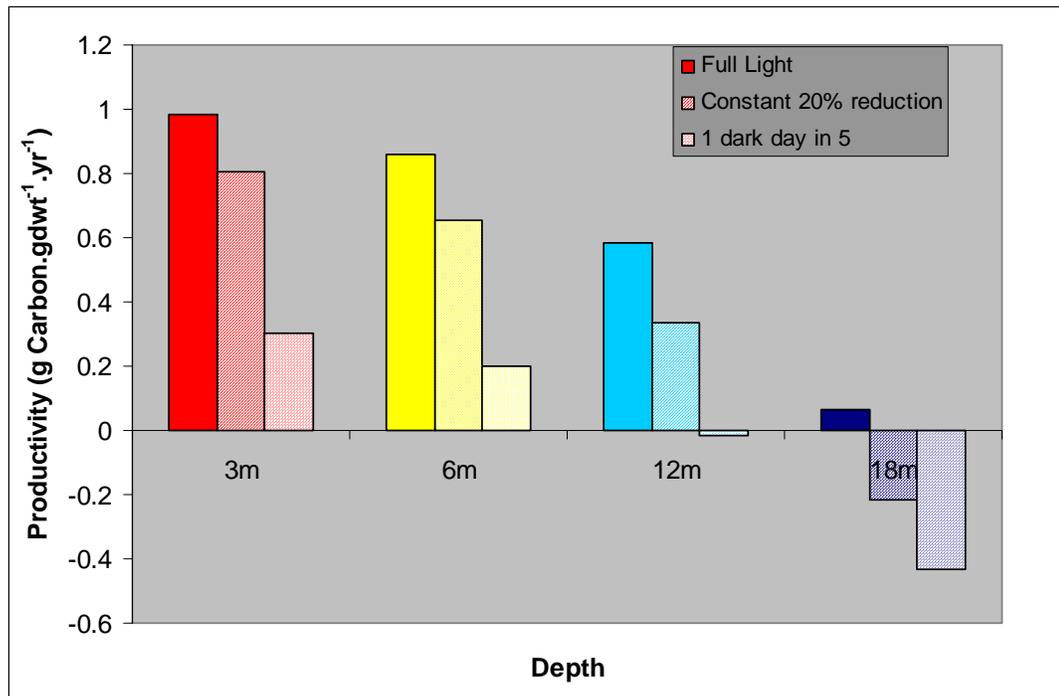


Figure 22: The effects of altering light levels on productivity. Solid columns represent the productivity under the standardised light field described in Scenario 1. Striped columns represent production under a light regime where the incoming light has simply been decreased by 20%. Brickwork columns also represent a decrease of 20% of the recorded total light dose, but it is achieved by alternating between full (standard) light days and (on every fifth day) zero light days. Whilst diminishing the light in a uniform manner does decrease productivity, it is far more detrimental to decrease the light in a fluctuating manner.

4.2.4. Scenario 4 - The application of literature photokinetic parameters

4.2.4.1. No photoacclimation included in model

Using the data supplied for *Amphibolis antarctica* by Masini and Manning (1997), and assuming no photoacclimation with depth (i.e. all photokinetic parameters remain the same across the depth profile), it is evident that productivity in the natural (fluctuating) light field is far lower than that modelled under conditions of a standardised light field, despite the fact that the average daily light dose remained the same (Figure 23). It is also noteworthy that the model indicates that productivity under the measured light conditions is similar at all sites except the 18 m site which is lower. Whilst we would expect the 18 m site to be lower as it is on the deeper edge of the seagrass bed, the three metre site (where seagrasses have been lost) demonstrates no less productivity than the 6 and 12 metre sites which do support seagrass. Thus this model, parameterised as it is, does not provide evidence that light conditions at three metres cause diminished productivity, possibly leading to loss of *A. antarctica*.

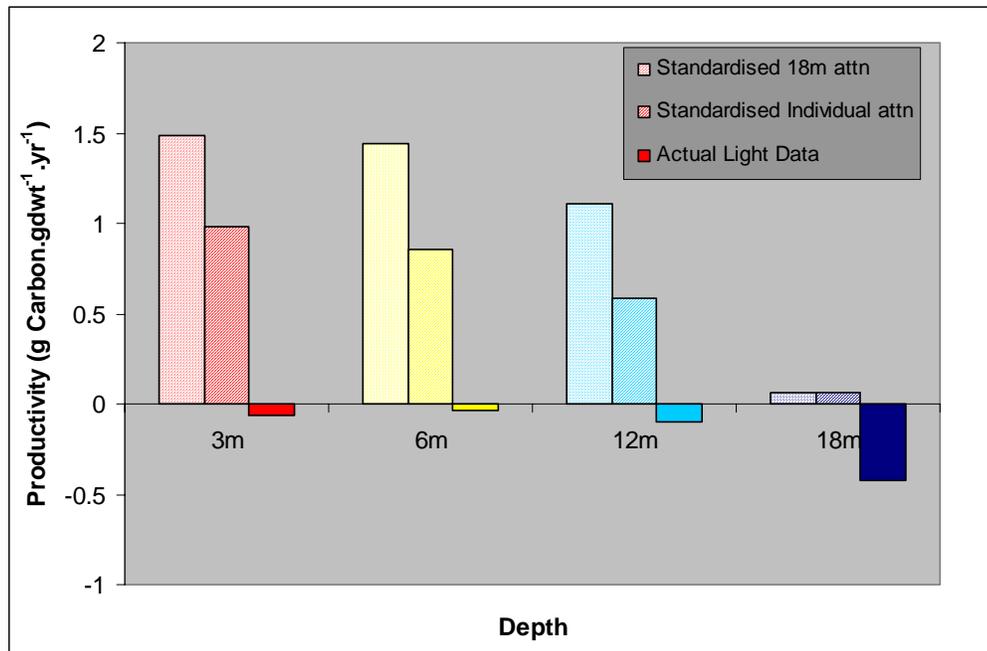


Figure 23: Annual productivity of *Amphibolis antarctica*. Constant I_K , P_{max} and R_d values are maintained across both time and depth. P_{max} of $0.9375 \text{ mg C.g dwt}^{-1}.\text{hr}^{-1}$, an R_d of $0.2775 \text{ mg C.g.dwt}^{-1}.\text{hr}^{-1}$ and an I_K value of $32 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ PAR were assumed, using the data of Masini & Manning 1997 for *A. antarctica* in southern Western Australia. The model is run with the standardised light field assuming 18 m attenuation, with the standardised field using measured attenuation (both of which are consistent between days across the year), and with the actual light data.

The situation for *Posidonia sinuosa*, again using data from Masini and Manning (1997) also fails to provide a scenario which explains seagrass loss in the inshore regions when photokinetic parameters are kept constant across the depth profile (Figure 24). Like *Amphibolis*, *Posidonia* demonstrates far less productivity under the measured, naturally fluctuating light fields than where the light field is standardised. It also demonstrates a situation where nett annual productivity is approximately the same at all sites except 18 m which is lower. Thus the scenario does not demonstrate a situation whereby poorer optical water quality causes productivity at the three metre site to be lower than at deeper sites

further offshore. Furthermore, the fact that all sites demonstrate nett negative productivity is not consistent with the fact that seagrass does exist at the 6, 12 and 18 metre sites.

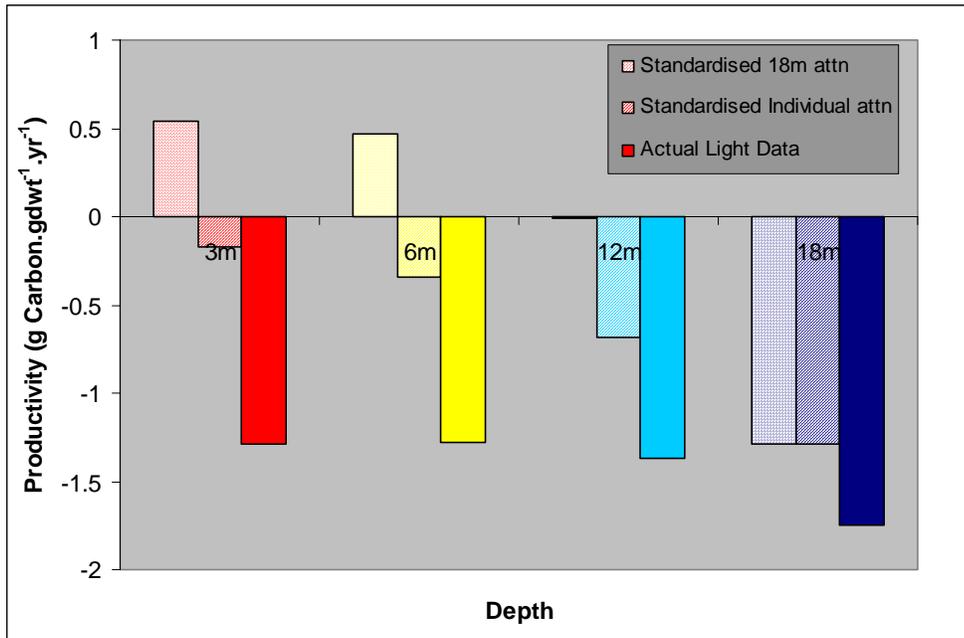


Figure 24: Annual productivity of *Posidonia sinuosa*. Constant I_K , P_{max} and R_d values are maintained across both time and depth. P_{max} of $1.02 \text{ mg C.g dw}^{-1}.\text{hr}^{-1}$, R_d of $0.214 \text{ mg C.g.dwt}^{-1}.\text{hr}^{-1}$ and I_K of $39.1 \text{ } \mu\text{molm}^{-2}.\text{s}^{-1}$ were assumed, simulating values typical of 12 m *Posidonia sinuosa* plants (Masini & Manning 1997). The model uses the standardised light field assuming 18 m attenuation, the standardised field using measured attenuation, and the actual light data. Under this scenario, the 3 metres site did not demonstrate lower productivity than the other sites, regardless of which light field was used.

4.2.4.2. Photoacclimation included in model

Masini and Manning (1997) provide data which describes the photokinetic parameters for *Posidonia sinuosa* plants at both 4, and 12 to 15 metres depth. This allowed a scenario to be developed where changes in photokinetic parameters could be integrated within the model. The model was run using the 4 m parameters to describe the seagrass at the three metre site, and the 12 to 15 metre parameters were applied to our 12 metre site. Our 18 metre site also used the same parameters without any attempt at extrapolation, whilst the 6 metre site used a depth weighted average of the literature values for three metres and those for 12 metres.

Using the depth dependent photokinetic parameters of Masini and Manning (1997) the model demonstrates higher productivity at the three metre site than the 18 metre site when using the normalised light fields with both site-specific and constant 18 m attenuation coefficient (Figure 25). However, when the depth dependent parameters are applied in conjunction with the actual fluctuating light levels, the model indicates a situation where productivity is greatest at 12 metres, but least at the three and 18 metre sites. This description could be somewhat misleading – whilst accurate, in considering relative productivity, it is necessary to remember that under no circumstances was nett productivity ever positive. This indicates a situation where seagrasses would never be able to produce enough to balance respiration and therefore never survive. As seagrass does exist at three of the four sites, this is obviously unrealistic.

If changes in photokinetic parameters with depth are simulated for *Amphibolis*, it is clear that productivity is markedly lower under conditions of natural, fluctuating light than it is when standardised light fields are used. Furthermore, when the real light data are used, *Amphibolis antarctica* demonstrates a far lower productivity at the 3 metre site than at any other depth (Figure 26). In fact at 3 metres, it demonstrates a nett carbon loss across this annual cycle. Next lowest productivity was demonstrated by the 6 and 18 metre sites, which demonstrated marginally positive nett productivity. It is worthy of note that at the three metre site, under conditions of depth-related photokinetic parameters, *Amphibolis* could demonstrate nett negative productivity. However, this only occurred when the actual measured light climate was utilised. Under the more benign standardised light fields, positive nett productivity was achieved, although it was still less productive than the 18 metre site when the site-specific LAC values are used to model productivity. Thus, this represents the application of a reasonable set of photokinetic parameters to the actual light data, resulting in a scenario which sees the three metre site unable to support seagrass, whilst the sites further offshore are more productive.

An assessment of productivity on a monthly basis for each of these sites reveals that the period from June till December (inclusive) is particularly poor in terms of productivity for both *Posidonia* and *Amphibolis* (Figure 27). It is worthy of note that the period from October to December is characterised, for both species, by a substantial increase in productivity at the 12 and 18 metre sites which is not demonstrated by those sites closer to shore. The fact that *Posidonia* displays positive nett productivity in only a single month and for only one site is a further indication that the data provided by Masini and Manning (1997) are not applicable in this situation.

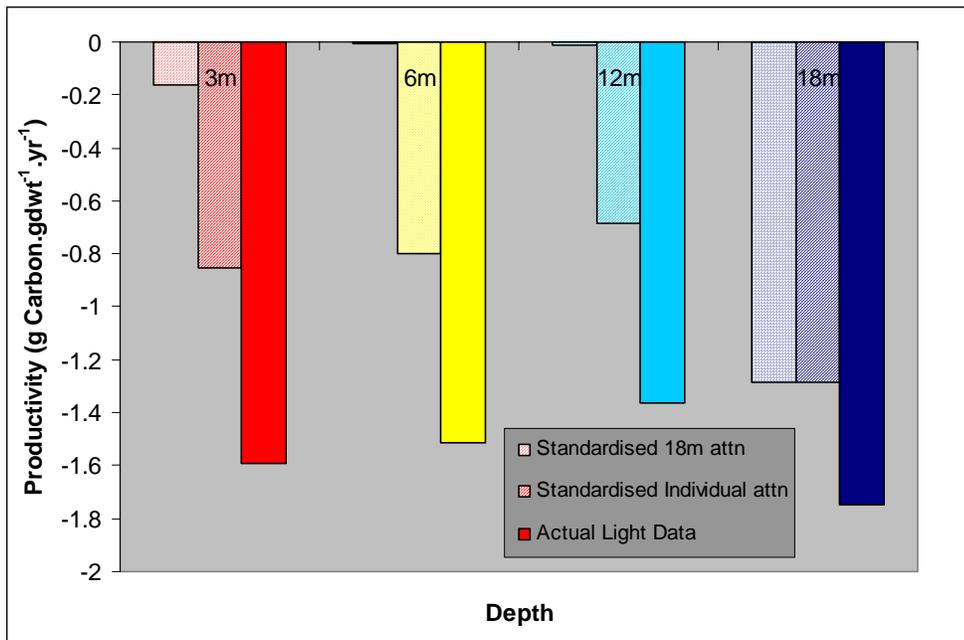


Figure 25: Annual *Posidonia* productivity assuming maintenance of constant I_K , P_{max} and R_d values across time but allowing for changes across the depth profile. Details are provided in Table 1. The model is run with the standardised light field assuming 18 m attenuation (brickwork), with the standardised field using measured attenuation (striped), and with the actual light data (solid bars). The three metre site is less productive than either the 6 or the 12 m sites, under all three light scenarios, but is less productive than the 18 m site.

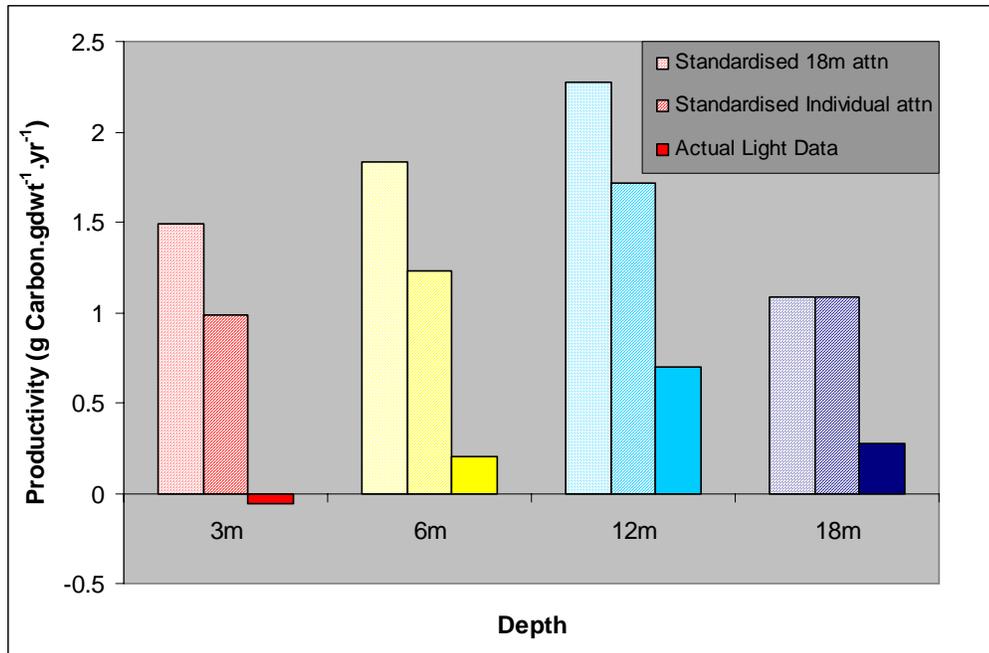


Figure 26: Annual *Amphibolis* productivity assuming maintenance of constant I_K , P_{max} and R_d values across time but allowing for changes across the depth profile. Details are provided in Table 1. The model is run the standardised light field assuming 18 m attenuation (brickwork), with the standardised field using measured attenuation (striped), and with the actual light data (solid bars). The three metre site is less productive than either the 6 or the 12 m sites, under all conditions, and is worse than the 18 m site under all light scenarios except for that which assumed constant LAC across sites.

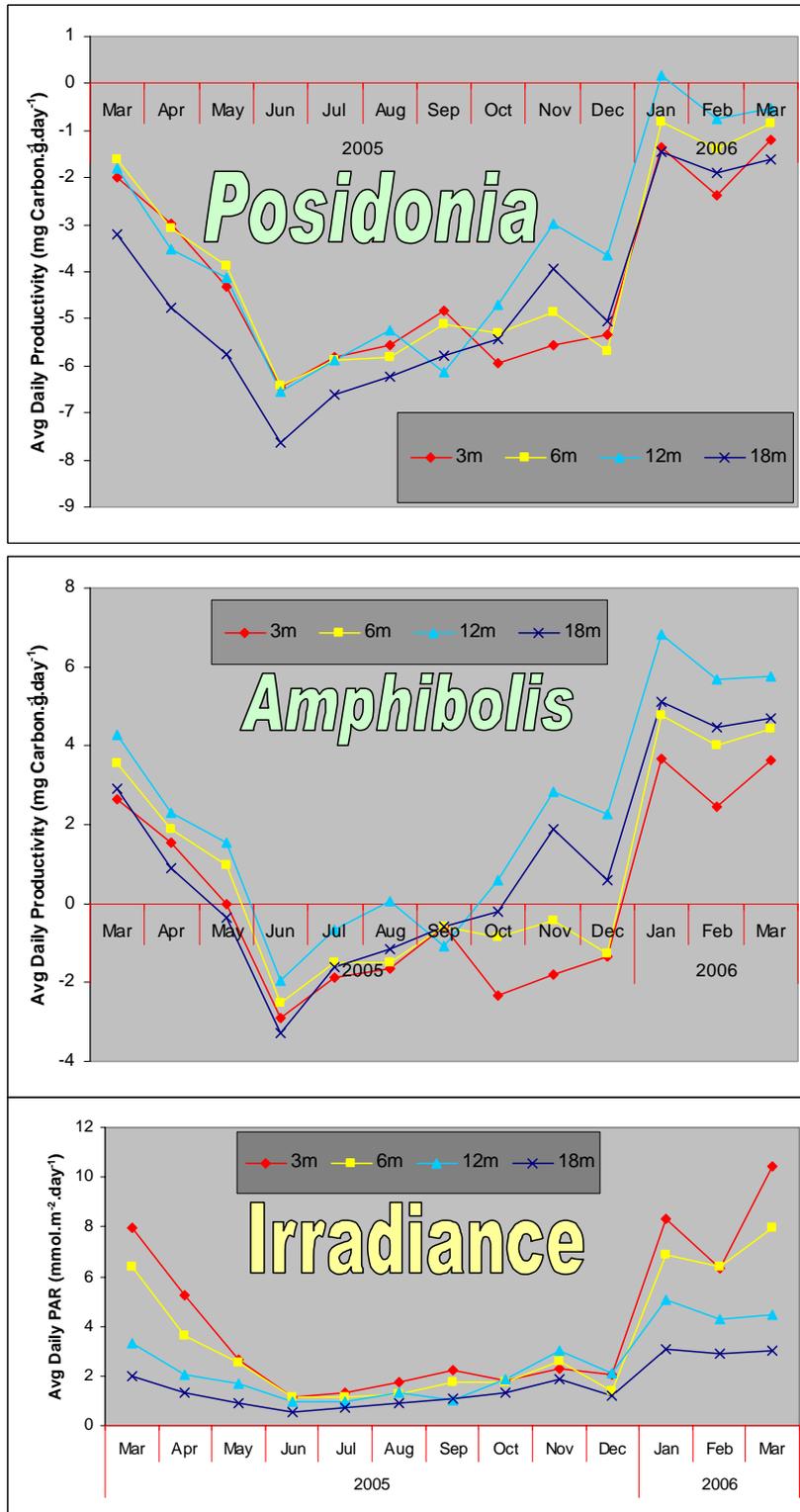


Figure 27: Monthly production across the course of the study for both *Posidonia* and *Amphibolis*, assuming the photosynthetic parameters typical of *Posidonia sinuosa*, and allowing variability with depth. *Amphibolis* photokinetic parameters were, on a proportional basis, varied in the same manner across depth. The irradiance data upon which the output is based are presented in the lower portion of the figure.

5. Discussion

The loss of seagrass from the nearshore region of the Adelaide Metropolitan Coast is unusual as the common pattern is a retreat *toward* the shore from the deeper offshore (e.g. Duarte 1991). The deep margin is generally believed to be defined by the point where there is insufficient light to produce enough photosynthesis to balance respiratory and other demands (Duarte 1991; Fourqurean and Zieman 1991). Thus, increasingly bad water clarity will reduce light at this already critical point and the seagrass will no longer have enough light to support itself at this depth (Duarte 1991). As a result, the offshore margin retreats toward shallower waters where more light is available. This study investigated whether the proximity of land-based inputs of turbidity (stormwater drains, creeks and rivers) and poor mixing characteristics might produce a light environment less favourable in the nearshore area despite the fact that the water column is so much shallower. If this is true, then a case could be mounted that the loss of seagrass from the nearshore region may have been due to poor productivity caused by poor water clarity.

The initial argument investigated the simple question of whether the total amount of light (integrated across an annual period) was less at the three metre nearshore site than it was at sites further offshore which were able to support seagrass beds. It was demonstrated that the total annual light budget at the three metre site was greater than at all other sites (Figure 10), invalidating the hypothesis that the total light budget could have been responsible for the decline of seagrass in this region. It is worth noting, however, that despite achieving a higher total irradiance than sites further offshore, this is due in large part to being so shallow. If the same clarity existed at the 3 m site as the 18 metre site then the three metre site would receive 614% more irradiance than it actually does under its own, more turbid, water column. Thus, whilst we cannot demonstrate a scenario whereby seagrass may have been lost from the nearshore zone because of the absolute amount of irradiance reaching the seafloor, it cannot be denied that the nearshore region of this segment of the Adelaide metropolitan coastline does have poor water clarity.

The linear attenuation coefficient (LAC), which describes water clarity, varies considerably across the course of the year in a way which is relatively consistent, both on short and medium term timescales, with the volume of land-based turbid inputs (Figure 13). Importantly, the three metre site has, by far, the worst water clarity, demonstrating LACs of between 0.51 m^{-1} and 1.13 m^{-1} as an average for a month. In comparison, at the 18 m site, LAC was relatively low and consistent, varying between 0.15 m^{-1} and 0.22 m^{-1} . These attenuation coefficients are similar to those recorded over a far shorter time period by Phillips and Scholz (1982). They recorded levels off the Adelaide coast of 0.4 m^{-1} to 0.5 m^{-1} . However, these readings were taken on relatively calm days. A longer term study, integrating stormier periods, is likely to have produced higher values. Elsewhere, Ruiz and Romero (2001) in a study of the effects of light attenuation utilised a “highly disturbed” site with a LAC of 0.205 m^{-1} . Duarte (1991) presents a comparison of seagrass depth limits with recorded attenuation coefficients. Of 72 recorded attenuation coefficients, only 8 exceeded that recorded in our study at 3 metres (0.82 m^{-1}). Of these eight, only one (in Western Port Bay; Bulthuis 1983) had seagrass beds which extended below a depth of 2.5 m. Thus, the Adelaide population of seagrasses would have to be very unusual to be able to survive at a depth of 3 metres with an attenuation coefficient as low as measured in this study.

The high light attenuation coefficients result in a substantial proportion of the subsurface light being cut out before it reaches the seagrass canopy, where it could otherwise drive productivity. Attenuation of light reduces the incoming light to differing degrees according to time of year. This difference is particularly marked at the nearshore sites. Over the annual cycle, 9.7% of light reaches the canopy at 3 metres, 8.3% at 6 m, 6.1% at 12 m and 4.0% at 18 m. These figures are remarkably low in comparison to findings elsewhere. Duarte (1991)

reports a reasonably consistent average of 11% of surface irradiance must be achieved to support most seagrass species. Similarly, Masini et al. (1995b) found that *Posidonia sinuosa* required 10% of surface irradiance at the level of the canopy, and DEP reported an annual requirement for 7.8% of subsurface light. On this basis, it appears that the seagrasses of the Adelaide metropolitan coast are surviving at considerably lower levels (4%) than have generally been reported.

The annual light budget measured here for a range of depths off the Adelaide coast is an important set of data when considering the impact of light levels on seagrass beds. Comparisons with literature values are useful and indicate a high degree of photosynthetic efficiency, but the significance would be further strengthened by comparable studies in South Australian regions other than the Adelaide metropolitan coast.

There are no historical data to describe water clarity in a manner comparable to the current study. However, the relatively clear relationship between turbidity and land-based inputs allows some insight into conditions in the past. Many authors (e.g. Orth and Moore 1983; Longstaff and Dennison 1999; Ruiz and Romero 2003) have commented on the significant effect of runoff on the turbidity of the receiving body of water. Prior to the 1930s, the Torrens River entered the Port River via a series of wetlands, which would have had the capacity to considerably reduce discharge and silt loading to the sea. However, in 1932, Breakout Creek was constructed which diverted the Torrens River directly to the sea in Holdfast Bay, causing a significant increase in the input of turbid water to the nearshore coastal system. This was reduced with the construction of the Kangaroo Creek reservoir on the River Torrens in 1969 (Wilkinson 2005). Thus it is the period from 1932-1969 which probably represents the worst time for water clarity and consequently seagrass productivity. Present conditions are therefore probably worse than the period prior to 1932 but still more productive than the years between 1932-1969. The added mobilisation of sediment associated with the loss of stabilising seagrass beds remains unquantified, but may be responsible for poorer conditions in more recent times.

Whilst the annual budget is greater at the 3 metre site, this situation is not constant throughout the year. Across the period June to December, there is very little difference in light budget between all sites, a feature correlated with the volume of land-based discharges. The three metre site fails to demonstrate the significantly higher light levels which might otherwise be expected. This has been commented upon previously by Phillips and Scholz (1982) in their surveys of the attenuation coefficients of the waters of Gulf St Vincent. They were surprised that the attenuation coefficient failed to improve in November and December beyond that of June, when runoff was far higher. This similarity across two studies 30 years apart may be an indicator of a biological phenomenon such as phytoplankton blooms occurring consistently in this spring/summer period. As this is a period where it might be expected that non-photosynthetic reserves would be being laid down to buffer against times of low productivity in winter, this timing is of concern. Masini et al. (1990) identify this as a critical period for *Posidonia sinuosa* for this reason. However, it should be noted that the three metre site does not (at least on a monthly basis) experience less light than the 18 metre site, where the light is clearly sufficient to provide for enough productivity to support at least some seagrass.

This extrapolation assumes no adjustment of photokinetic parameters with depth (acclimation effects), a scenario often reported in the literature whereby plants in constant low light conditions optimise their photosynthetic performance for that range of light (Mazzella and Alberte 1986; Perez and Romero 1992; Masini and Manning 1997; Major and Dunton 2002; Campbell et al. 2003). If plants at the 3 metre site have different photokinetic parameters to those elsewhere, then this simple comparison of light levels may not be appropriate, as the relationship between light and productivity becomes variable.

While the subject is a controversial one and the results conflicting, it has been suggested that plants tend to acclimate to the ambient light conditions (Falkowski and Raven 1997; Raven 1994). This essentially is a protection and/ or optimisation response. Highly efficient photosystems may be damaged, when suddenly exposed to a high light environment. Therefore, plants are able to “detune” their photosynthetic apparatus in response to a period of high light (i.e. good optical water quality). However, the response to low light (i.e. increased efficiency at low light levels) is often a slow one, as demonstrated for *Posidonia sinuosa* by Masini and Manning (1997) or may even fail to occur (e.g. Major and Dunton 2000). For this reason, acclimation to high light conditions would be a distinct disadvantage when it is followed by a period of low light intensity. Thus, the *variability* of the light field may be as important as the mean value. In this case, it is clear that the variability is greatest at the three metre site, from where seagrass has been lost. Depending on how the photosystems are acclimated, this may put these plants at a significant disadvantage.

The combination of the shallow depths allowing the possibility of a high degree of light penetration and the drastic reductions caused by the nearshore-entrained periodic turbidity events leads to a far greater monthly range of light conditions in the shallow regions than deeper ones. That this greater variability is due not only to higher potential light conditions, but also a greater influence of turbidity events in shallow waters, is evidenced by the fact that when the daily light doses are standardised by the average daily input for the month at each site, the nearshore sites still demonstrate higher variability. Thus the influence of the entrainment of periodic nearshore turbidity events does increase the variability of the light field, thereby producing conditions less favourable for the seagrass. Interestingly, this is particularly the case across the period September to December, which was identified as a critical growth phase by Masini et al. (1990) when productivity should be strongly positive to produce storage carbohydrate for use in less productive times. However, this period is characterised by a light regime which is both of low intensity and highly variable, and particularly so at the nearshore (three metre) site. Thus, the light regime is likely to represent a significant stressor to seagrass beds in this region.

The light climate is not of itself what directly determines the survival of a seagrass bed. Rather, it is the productivity of the bed which is the direct cause, and light climate is *one* of the factors which affects productivity (Masini et al. 1995a; Touchette and Burkholder 2000). The other important factor to consider here is the relationship between light climate and productivity – a particularly efficient plant may be productive despite low light levels, whilst an inefficient individual may require far higher light levels to be sufficiently productive to survive. Thus, demonstrating a poor light climate, as has been done thus far, does not necessarily implicate low productivity as the cause of seagrass loss. This argument can be strengthened significantly by a productivity model which utilises measured, or at least reasonable, photokinetic parameters and applies these to the measured light field to make predictions regarding the level of productivity. Essentially, this assists in putting some perspective on the measured light climate, and assists in determining whether it is likely to be responsible for productivity levels which might be so low as to result in loss of seagrass beds.

Measurement of the photokinetic parameters of the seagrasses, both across the depth profile and across the annual cycle, would have allowed a far more detailed examination of this question. This would have allowed an incorporation of innate biological rhythms and the seasonal effects of temperature (Pérez and Romero 1992; Masini et al. 1995a; Herzka and Dunton 1997; Alcoverro et al. 2001). However, it was not pragmatic within this project. Therefore, the object of the modelling was to demonstrate, using reasonable parameters defined by literature values, that a scenario could be illustrated which explained seagrass loss.

In simple experimental terms, the hypothesis was that the light climate of the Adelaide metropolitan coast in the nearshore (3 m) region is insufficient to allow enough productivity to support seagrass with depth dependent photokinetic parameters measured for the same species in Western Australia. Support for the hypothesis would consist of a situation which demonstrated productivity estimates in the order $3\text{ m} < 18\text{ m} < (6\text{ m or } 12\text{ m})$. 3 m must be lowest because it is only here that seagrass is absent. The 18 m site must be next lowest as this represents the point at which the seagrass bed peters out on the deep margin, a point generally assumed to be defined by productivity levels being unable to balance respiratory and other demands. Thus productivity here must be higher than the 3 m site, but not as high as the 6 m and 12 m sites. As the 6 m site is only just within nearshore edge of the seagrass bed, it might be reasonably assumed that this site should demonstrate lower net productivity than the 12 m site or even the 18 m site (both the 6 m and 18 m sites are very close to the margins of the bed).

Seagrasses represent a more complicated system to model than many other organisms (Bearlin et al. 1999). In part this is because of the complex interactions of storage carbohydrates and the differential physiological behaviour of the above and below-ground components (Fourqurean and Zieman 1991; Alcoverro et al. 2001). A critical concept here is the fact that the below-ground components (roots and rhizomes) act as storage organs (Masini and van Senden 1995; Touchette and Burkholder 2000; Cabello-Pasini et al. 2002; Fourqurean et al. 2003). This highlights the necessity to use a model which is run on a long enough time scale. It should incorporate periods where productivity debt is balanced by material in below-ground biomass stored during periods of high productivity. It also highlights the need to assess productivity on a basis which includes the respiratory demands of the below-ground biomass (see also Herzka and Dunton 1998; Alcoverro et al. 2001). Our model and light data represent such a long term view.

In addition to investigating support for the hypothesis that the light climate might, through its influence on productivity, be responsible for seagrass loss, this model allowed some general statements to be made regarding aspects of the light climate which may increase or decrease productivity.

With steep decline in seagrass beds around the world (e.g. Brush and Nixon 2002), many authors have attributed loss, at least in part, to poor water clarity (e.g. Peres 1984 in Shepherd et al. 1989; Longstaff and Dennison 1999; Ruiz and Romero 2001, 2003; Zimmerman 2006). An important finding from this study was that, regardless of whether it caused actual seagrass loss, there was a substantial reduction in productivity caused by the increased turbidity entrained within the nearshore region. Using standardised (i.e. sine curve simulated identically for each day) light fields which used light intensity assuming a constant attenuation coefficient (i.e. the turbidity at all sites was constant and equal to that of the 18 m site) productivity was far greater than it was when the actual individual attenuation coefficients were applied to the data. This is an indication of the fact that the poor optical water quality has a substantial deleterious effect on amount of photosynthetically active radiation reaching the canopy and the net productivity of the seagrass.

Furthermore, any reduction in productivity caused by lower average light levels is magnified when day to day fluctuations are included in the model. Figure 22 illustrates that a decrease in productivity, caused by a reduction in light, is made worse when that reduction is achieved by greatly reducing light on a single day rather than reducing it by a smaller amount on every day. This demonstrates the multiplicative problems in the light climate facing the Adelaide metropolitan coast, where land-based inputs becoming entrained in the nearshore zone have reduced light, and done so in a way which fluctuates greatly from day to day.

Major sources of the sediment causing this turbidity are probably storm water inputs, the River Torrens and the Barcoo outlet. Whilst not representing the total land-based

discharges, they are likely to be strongly associated with storm activity, and therefore other inputs such as stormwater drains are likely to be well correlated. However, quantifying the relative magnitude of these has not been investigated as part of this study. It is worth noting that dredging will also add to the sediment load, but is more a process of resuspension than an input to the system. Furthermore, given the repetitiveness of the operation, it will reduce light in a more consistent manner than the massive sporadic turbid inputs which occur during periods of high rainfall, and consequently high river flow. This is not to negate the effect of dredging on light levels, merely to indicate that the effect will tend to be felt in terms of average level of irradiance rather than variability of those levels.

Beyond being able to demonstrate that the low, fluctuating light conditions of Adelaide's nearshore margin are detrimental to the productivity of seagrass beds, parameterising the model with photokinetic parameters has demonstrated that the light conditions may be responsible for loss of seagrass from the shallow waters. However, such a demonstration requires the incorporation of photokinetic parameters which vary with depth, and even then, it is possible to demonstrate scenarios which are either consistent or inconsistent with the hypothesis of productivity-mediated seagrass decline, depending on the specific set of parameters used.

In the absence of a set of photokinetic parameters measured on a seasonal basis and across a range of depths on the Adelaide metropolitan coast, it was necessary to rely on data accumulated from Western Australia (Masini and Manning 1997) and apply this to the light data collected from Grange. Clearly the use of photokinetic parameters from populations outside of the Adelaide region is not ideal. This needs to be kept in mind in considering the confidence with which we can state that seagrass decline in the nearshore region is due to poor light conditions. Because of these limitations, the object of the model was simply to demonstrate whether it was possible to eliminate poor light conditions as the cause of the seagrass decline.

The characterisation of photokinetic parameters provided by Masini and Manning (1997) was utilised because it describes the situation for *Posidonia sinuosa* and *Amphibolis antarctica*, which represent two of the major groups of seagrasses on the Adelaide metropolitan coast. Whilst data exists elsewhere for other species, this was considered most relevant because differences between species are likely to be large. However, application of the parameters from this single paper is likely to represent a relatively crude simplification for a number of reasons. In particular, depth specific data for *Posidonia sinuosa* is collected only in winter, and therefore takes no account of any seasonal or temperature related changes. Furthermore, Masini and Manning (1997) make no attempt to identify depth related changes in the photokinetic parameters of *Amphibolis antarctica*. Whilst this paper, and others do provide information on the effects of temperature on productivity, it was not considered appropriate to structure the model with such effects as they could not be verified for the Adelaide populations, so the additional complexity would produce no further confidence in the conclusions. In the absence of data from Masini and Manning (1997) on the effects of depth on photokinetic parameters of *Amphibolis antarctica*, an assumption has been made that the proportional change is the same as that of *Posidonia*. This is not an unreasonable assumption, but it does remain untested.

Whilst it would have been possible to produce scenarios based on a wide variety of photokinetic parameters, this was not necessary to address the hypothesis which was posed. In the absence of a set of depth related photokinetic characters from the Adelaide coast, there was only a requirement to demonstrate that productivity-mediated seagrass loss was possible. Application of data beyond the set used (which was considered the most appropriate as it dealt with the both *Posidonia sinuosa* and *Amphibolis antarctica* and included changes in depth for *Posidonia*) would simply result in a collection of results, some of which supported the hypothesis and some which did not. The conclusions would be unaltered – it is possible to demonstrate scenarios which are consistent with the hypothesis,

but it is also possible to demonstrate those which do not. Thus we could not rule out the possibility of productivity-mediated loss. Rather than complicate the issue, a single set of data was used to provide this demonstration.

When the attenuation coefficient data obtained in this study is put into the context of the depth limits of other species found elsewhere, it is clear that the seagrasses of the Adelaide metropolitan coast are surviving to a depth which is extremely unusual given the measured light conditions. Duarte (1991) provides a regression which relates the LAC of the water column to the depth limit of the seagrass bed. On the basis of this regression, it is suggested that seagrass could extend to 2.2 m, 4.4 m, 8.5 m and 11.3 m according to the LACs measured at our 3 m, 6 m, 12 m and 18 m sites. i.e. that seagrass should not be found at any of our sites based on the clarity of the water. Given that this is clearly not the case at the 6, 12 and 18 m sites, it is evident that the seagrasses of the Adelaide metropolitan coast are unusually efficient at utilising available light.

Both of the taxa involved in our study, and the two which have been implicated in seagrass loss from the Adelaide coast are morphologically large species. Larger species tend to have higher light requirements because of the large amount of non-photosynthetic biomass involved in respiration (Ruiz and Romero 2001). For this reason they tend to be more sensitive to chronic light reduction (note though that short term light reductions are likely to be better tolerated because of the large stored source of carbohydrate represented by the below-ground biomass). Whilst this general hypothesis is consistent with the finding that these species have disappeared from the metropolitan coast, it is at odds with the apparent efficiency of these populations and their ability to grow deeper than the LAC would suggest.

Modelled annual productivity rates for *Posidonia sinuosa* are clearly an underestimate as nett productivity is uniformly negative when depth adaptation is assumed, and there is therefore little point in making comparison to literature values. *Amphibolis*, however did demonstrate a reasonable scenario so it is worth comparing productivity here with that found in the literature. At best (i.e. at the 12 m site), annual nett production was only 0.7 g C g dwt of leaf¹ yr⁻¹. If this is scaled to represent a square metre (assuming 500 g dwt m⁻² leaf weight), it represents 350 g C m⁻² year⁻¹. Cambridge and Hocking (1997) report productivity in the range of 500-1000g dwt m⁻² yr⁻¹ for *Posidonia sinuosa* but this represents total productivity rather than just carbon, so it would adjust downwards toward 168-336 g C m⁻² yr⁻¹ assuming 33.6% carbon by dryweight (Duarte 1990). Duarte and Chiscano (1999), in a reassessment of the productivity of seagrasses in general, estimate productivity of seagrass communities (on average) at 1012 g dwt m⁻² yr⁻¹, which represents approximately 340 g carbon dwt m⁻² yr⁻¹. Thus modelled productivity for *Amphibolis* in this study appears relatively high. However, it is worth noting that Perez and Romero (1992) in a study of *Cymodocea nodosa* in Spain found their model overestimated productivity by approximately 60% compared with the actual field values, presumably because of factors such as self-shading. Our modelled figures for *Amphibolis* also do not take into account such factors, and therefore are probably also an overestimate. However it can be said that they are in the expected range for seagrasses.

The fact that using the parameters of Masini and Manning (1997) results in apparent negative nett productivity for *Posidonia* in the present study indicates that either the light recorded over this annual cycle is atypical of previous years (and less productive) or, as is more likely, that the parameters measured in the Western Australian populations are not applicable to the seagrasses beds growing off Adelaide. Photoacclimation to the light environment presented by the Adelaide coast is an unknown. Furthermore, in light of the ability of Adelaide seagrasses to survive in light levels which Duarte (1991) indicates are below the level required by most species, it must be acknowledged that these parameters underestimate productivity. This does not imply that the levels of productivity relative to each

other are incorrect, but our conclusions must reflect this uncertainty. Nevertheless it does highlight the urgent need for such photophysiology studies to be carried out on seagrass beds of the Adelaide region.

This study has demonstrated that the nearshore region of the Adelaide metropolitan coast has water clarity characteristics which are detrimental to seagrass species. Highly variable and low light levels are strongly associated with land-based turbid inputs. Productivity modelling has provided a demonstration that these characteristics cause low productivity and may have been responsible for the loss of seagrass beds from this area. Whilst photokinetic studies are required to draw this conclusion with greater confidence, this study has failed to rule out the possibility, and has demonstrated that, at the very least, these conditions represent a serious stressor for seagrass beds in the region. It has also highlighted the need to concentrate research on this dynamic region, where seagrass beds may be continuing to recede seawards, remaining stable, or beginning to revegetate after documented historical losses. Optical water clarity, through its effect on productivity, is likely to be an extremely important variable to consider.

6. Conclusions and further directions

This study began by specifying five specific hypotheses which we aimed to test. We are now in a position to address each of these:

1. That there was less photosynthetically active radiation at the nearshore site than further offshore. Using an extensive dataset which spanned the entire annual cycle, it was demonstrated conclusively that this hypothesis was false. In terms of the average daily dose of PAR, there was greater light at the nearshore site than at sites further offshore. Whilst the optical clarity of the water was significantly worse in the region where seagrass had been lost, the effect of the shorter water column outweighed this, resulting in greater light at the three metre site than any other.

2. That the light climate was more variable at the nearshore site than further offshore. Despite the fact that variability can be described in various ways (e.g. range, standard deviation, standard deviation as a function of mean), all measures indicated a greater variability in the three metre site than at the others.

3. That reduced light levels are caused by increased land-based runoff. Whilst this was not an hypothesis which could be tested by experimentation, there was a clear correlation between discharge volumes of the main land based sources (which we treated as a surrogate for the total land-based discharges) and the optical clarity of the water. This relationship was evident across a medium timescale (i.e. comparison of months) and on a daily timescale. There was no consistent lag evident on a daily scale, indicating rapid mixing of the turbid water to quite some distance from shore. However, the effect was far more muted at sites further offshore, indicating some degree of entrainment and/or relatively rapid settlement of suspended particles from the water column.

4. That variability in light climate (without any change in mean levels) is disadvantageous for seagrasses on the basis of lower productivity. Using our model with a variety of modeled light datasets, it was established that a constant daily light field resulted in greater productivity than a light field which represented the same total amount of light but was delivered in a more variable fashion (ie one dark day in five). Thus, in the absence of any difference in mean light levels, variability in light climate represents a stressor for the plants.

5. That the light climate of the Adelaide metropolitan coast produces conditions which, in the context of reasonable photokinetic parameters, explain the loss of seagrass from the nearshore zone of this region.

There was variable support for this hypothesis, depending on the set of photokinetic parameters utilized. Unless depth dependent changes in photokinetic parameters were utilized, it was not possible to demonstrate, for either *Posidonia* or *Amphibolis*, a scenario consistent with the productivity-induced loss from the nearshore site whilst seagrass beds were maintained further offshore. When depth dependent changes in photokinetic parameters were included, it was possible to demonstrate a scenario whereby seagrass may have been lost because of poor productivity levels. However, confidence in the extrapolation of results from Western Australia is not high because it would indicate that *Posidonia sinuosa* makes a nett productivity loss on an annual cycle at all sites, and therefore should not occur at any depth, which it quite clearly does. Thus, whilst it is possible to demonstrate a situation for *Amphibolis* which shows seagrass loss on the basis of poor productivity, the conclusion must be that the model fails to rule out the possibility, but further work is required to provide strong support. What can be said, however, is that nearshore Adelaide coastal waters represent a poor environment in terms of optical quality, and that these conditions, whilst they may not be solely responsible for seagrass loss in the area, represent a significant stressor, which may, in conjunction with another factor, be responsible for such a loss.

This work has yielded an excellent record of the light climate of the Adelaide coast in the Grange region. In order to strengthen arguments for the effect of this light environment on the loss of seagrass beds, further work should be directed towards identifying the photosynthetic characteristics (P_{\max} , R_d and I_k) of *Posidonia* and *Amphibolis* off the coast of Adelaide. The application of such parameters from Western Australia has proven a useful exercise, but to take this model further requires a knowledge of the characteristics of local populations, both across the course of a year and as they vary across a depth / light profile.

7. References

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