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The Effect of Light, Temperature and Salinity on Photosynthetic Rates of an Estuarine *Cladophora*

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Abstract

Cladophora occurs throughout the year as free-living, densely-branched spheres in beds on the floor of the Peel Inlet, Western Australia. Short-term experiments on photosynthetic rates with an oxygen electrode show that the plant tolerates wide changes in salinity. Temperatures fall to limiting levels in winter, as do light intensities at the surface of an algal bed. However, even at high light intensities in summer, algae more than 1 cm below the surface of a bed are below the compensation point. Thus light presumably limits rate of dry matter increase in these beds even in summer.

Introduction

Cladophora aff. *albida* (Huds.) Kütz. occurs as a free-living green alga in the Peel Inlet, a large, shallow estuary 80 km south of Perth, Western Australia (Fig. 1). The alga grows as densely-branched, spherical clumps which form loose-lying beds, typically 1–10 cm in depth, though they may reach 40–50 cm in some areas. These are present permanently in some regions. Since about 1966 *Cladophora* has become the predominant benthic alga and has reached nuisance proportions with large masses of decomposing algae covering much of the shoreline at certain times of the year (Cross 1974).

Growth mainly occurs during summer when light and temperature are high but nutrients, and in particular inorganic nitrogen and phosphorus, are low in the water column. The plants are subjected to a wide seasonal range of salinities, from as low as 2‰ in winter to some 50‰ in summer (McComb *et al.* 1980).

Because of the difficulty in unravelling the roles of the major environmental parameters which control growth from field data alone, laboratory studies were initiated with the aim of assessing the effects of light, temperature and salinity on *Cladophora* photosynthesis. The oxygen electrode was used to provide a rapid and sensitive measure of oxygen output (eg. Griffiths *et al.* 1978) and is ideally suited for use with the smaller, free-floating species such as the alga under study here.

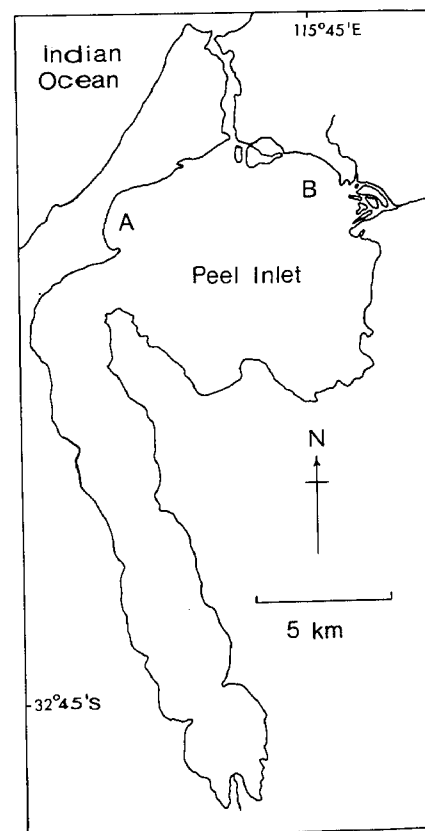


Fig. 1. Peel Inlet, Mandurah, Western Australia showing sites of *Cladophora* beds, (A and B), from which material was collected for this study.

Materials and Methods

Plant material and media

Material was collected from essentially permanent algal beds at two sites in the Inlet (Fig. 1), and placed in either estuary water or artificial seawater supplemented with high levels of inorganic nitrogen and phosphorus (Tab. I). The artificial media were modified from the ASP₁₂ recipe described by Provasoli (1964).

Solutions of different salinities were prepared by partially evaporating estuary water and reconstituting with appropriate additions of distilled, deionised water. These were supplemented with vitamins, trace elements, phosphate-phosphorus at 155 $\mu\text{g l}^{-1}$, nitrate-nitrogen at 310 $\mu\text{g l}^{-1}$ and NaHCO_3 at seawater concentration (200 mg l^{-1}). Artificial seawater solutions of varying salinity were also prepared, by manipulating the concentrations of major salts (Tab. I), while maintaining their ratios. The artificial media were supplemented with phosphate-phosphorus at 250 $\mu\text{g l}^{-1}$ and ammonia + nitrate-nitrogen at 2,500 $\mu\text{g l}^{-1}$.

Cladophora was placed in estuary water of different salinities over the range 10–59‰. Some of those at 10‰ were transferred to solutions at 0.2‰ after 3 days. Oxygen production (see below) was determined after 6 days in a growth cabinet at 25 °C, 12 hr photoperiod at a light intensity of 200 $\mu\text{E m}^{-2}\text{sec}^{-1}$ from a mixture of fluorescent tubes (warm white, Philips) and incandes-

cent bulbs. A similar set was prepared in artificial seawater in the range 2.8 to 60‰, and rates of photosynthesis determined immediately, and again after 19 days in the growth cabinet as described above.

Oxygen production

This was monitored using a Clark-type oxygen electrode (Rank Bros., Bottisham, England) consisting of a platinum cathode and silver anode separated from the stirred reaction chamber by a thin teflon membrane. The concentration of O_2 was recorded on a chart recorder, and rate of O_2 production calculated from the slope of a 5–10 min chart record. The electrode was calibrated with air-saturated medium at the start of each run, and checked for drift frequently. Solubilities of oxygen were calculated using a standard nomogram which allowed for temperature and salinity (Strickland and Parsons 1972). These table values were periodically checked with Winkler O_2 titrations; variation between the two was never more than 10%.

Fragments of *Cladophora* (1–5 mg fresh weight) were introduced into the reaction chamber and equilibrated with 8 ml of medium, which had been previously deoxygenated by bubbling for 2 min with nitrogen containing 0.03% CO_2 .

A quartz-halogen lamp (Philips, 150 W, 15 V) attached to a fibre optic arm (L150B, Schott, Mainz, West Germany) provided a source of cold illumination for the electrode. The working wavelength of the lamp was 400–850 nm. Intensity was varied with the control of the instrument and by mesh screen filters of varying density. Light was measured as photosynthetically-active radiation (PAR) with an underwater light sensor (Licor, Lambda Instrument Company, Nebraska, U.S.A.) placed at the base of a reaction chamber from which the electrode had been removed. The source provided up to 2,150 $\mu\text{E m}^{-2}\text{sec}^{-1}$ quantum flux.

A water jacket surrounding the reaction chamber and fed from a thermostatically-controlled water bath provided temperature regulation.

Field measurements

Field measurements of PAR (using the instrument described above), temperature and salinity (using a Model 602 Hamon Salinity Temperature Bridge, Autolab, Sydney) were monitored on a weekly basis for over a year at the two sites in Figure 1. PAR at the surface of the algal bed at both sites was calculated from the regression obtained from a vertical profile through the water column, and extrapolated to the depth of the bed. Data for site A were collected at about mid-day, and from site B in mid-afternoon.

Tab. I. Modified artificial seawater medium (ASP₁₂) (adapted from Provasoli 1964)

	chemical	amount (g l ⁻¹)
Salt block	NaCl	28.0
	KCl	0.7
	MgSO ₄ ·7H ₂ O	7.0
	MgCl ₂ ·6H ₂ O	4.0
	Ca(asCl)	0.4
Nutrient block	NH ₄ NO ₃	1.430 × 10 ⁻² (= 5,000 $\mu\text{g N l}^{-1}$)
	K ₂ HPO ₄	1.405 × 10 ⁻³ (= 250 $\mu\text{g P l}^{-1}$)
	NaHCO ₃ ^a	0.2
	Na ₂ SiO ₃ ·9H ₂ O	1.5 × 10 ⁻²
Vitamin block	B ₁₂	2 × 10 ⁻⁷
	Biotin	1 × 10 ⁻⁶
	Thiamine – HCl	1 × 10 ⁻⁴
Buffer	TRIS	1.0
Trace metals	P _{II} ^b	10 ml
	S _{II} ^c	10 ml
pH	8.0	
Salinity	33.7‰	

^a Bicarbonate added at levels similar to those indicated from alkalinity measurements from estuary water in Peel Inlet.

^b 1 ml of P_{II} contains: EDTA (Na₂), 1 mg; Fe (asCl), 0.01 mg; B(H₃BO₃), 0.2 mg; Mn (as Cl), 0.04 mg; Zn (as Cl), 5 μg ; Co (as Cl), 1 μg .

^c 1 ml of S_{II} metals contains: Br(as Na), 1 mg; Sr(as Cl), 0.2 mg; Rb(as Cl), 0.02 mg; Li(as Cl), 0.02 mg; Mo(as Na salt), 0.05 mg; I(KI), 1 μg .

Algal bed measurements

The amount of photosynthetically-active radiation which could pass through successively deeper layers of a bed of *Cladophora* was determined. A transparent, Perspex jar, basal area 314 cm², was illuminated from above with a source (500 W Photolita, Philips) which provided 1,800 $\mu\text{E m}^{-2}\text{sec}^{-1}$ over the base of the jar. A quantum sensor was placed beneath the jar, which contained water. Increasing amounts of *Cladophora* were added to form a successively deeper "algal bed", and PAR through the bed was recorded. Twenty readings were taken across the base of the jar at each chosen depth.

Results

Light and temperature

The dependence of photosynthesis on PAR is shown in Figure 2. There are two distinct portions of these curves — a light-dependent phase, where the photosynthetic rate depends on intensity, and a light-independent phase, where light is not limiting. Saturating light levels were reached between 200 and 300 $\mu\text{E m}^{-2}\text{sec}^{-1}$ for both estuary water and artificial seawater. This approximates 15% full sunlight PAR. The compensation point, where net photosynthesis balances dark respiration, occurred at 20 $\mu\text{E m}^{-2}\text{sec}^{-1}$ (approximately 1% full sunlight PAR). There appeared to be no photosynthetic inhibition at high light intensities. However, at intermediate intensities, higher rates were obtained as intensities were increased towards that of full sunlight, when compared

with those obtained when stepwise decreases from high levels were used (Fig. 3). The effect was not observed when plants at low levels (200 $\mu\text{E m}^{-2}\text{sec}^{-1}$) were subjected to short (2 min) exposures to high levels (2,000 $\mu\text{E m}^{-2}\text{sec}^{-1}$) and returned to low levels.

Attenuation of light through the *Cladophora* bed is shown in Figure 4; levels decreased markedly with increasing bed depths, the compensation point, taken as 1% of incident PAR, being reached within 1 cm of the surface. The light intensity at the surface of the *Cladophora* bed, on the floor of the estuary, is given in Figure 5, where saturating light levels are indicated by the broken line. At the surface of the bed PAR is often below compensation in winter, partly because of cloud cover and partly due to the high turbidity of the estuary water when the rivers flow.

Photosynthetic-light curves at different temperatures are shown in Figure 2 for estuary water and artificial seawater. Maximum rates occurred at 32 °C for short exposure times, falling away sharply above 42 °C (Fig. 6). Increasing the exposure time to 30 minutes at each temperature tended to lower the optimum. When *Cladophora* was maintained in enriched artificial seawater at 32 °C the rate fell up to 40% in 8 hours, but had returned to the original rate when tested after 27 hours at 32 °C.

Salinity

The effects of altered salinity on photosynthetic rates are shown in Figure 7 for enriched estuary water and artificial seawater. In both cases there was little effect over the range 10–40‰, though there is some suppression at 0.2‰ and 60‰.

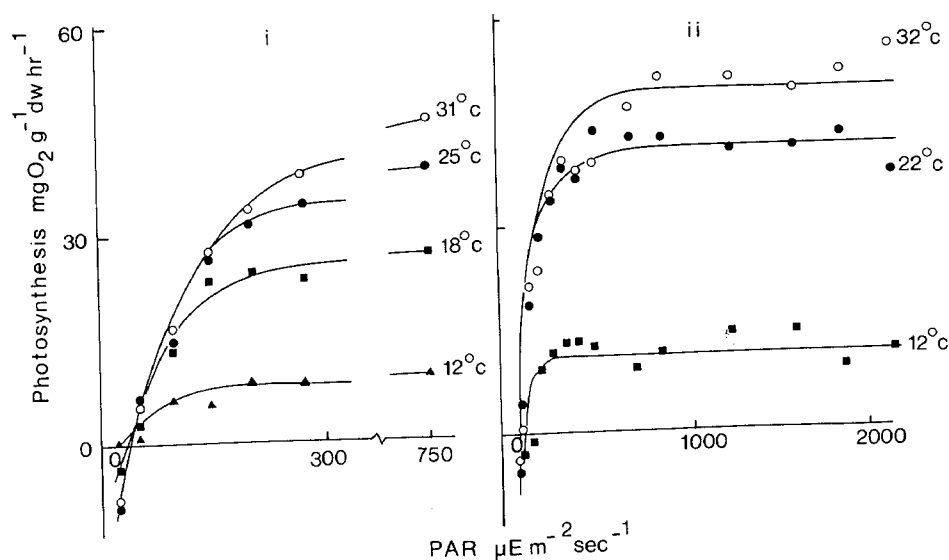


Fig. 2. The dependence of rate of photosynthesis of *Cladophora* on photosynthetically-active radiation (PAR) at different temperatures in (i) estuary water and (ii) artificial seawater media

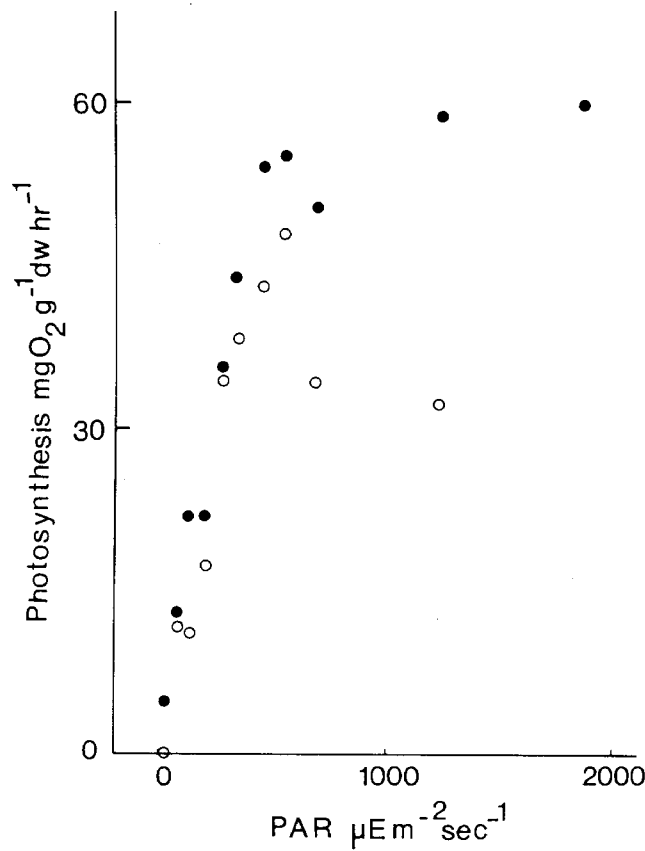


Fig. 3. Rates of photosynthesis of *Cladophora* produced from successively increasing light intensities (closed circles) to saturating levels, followed by subsequent stepwise return to low levels (open circles)

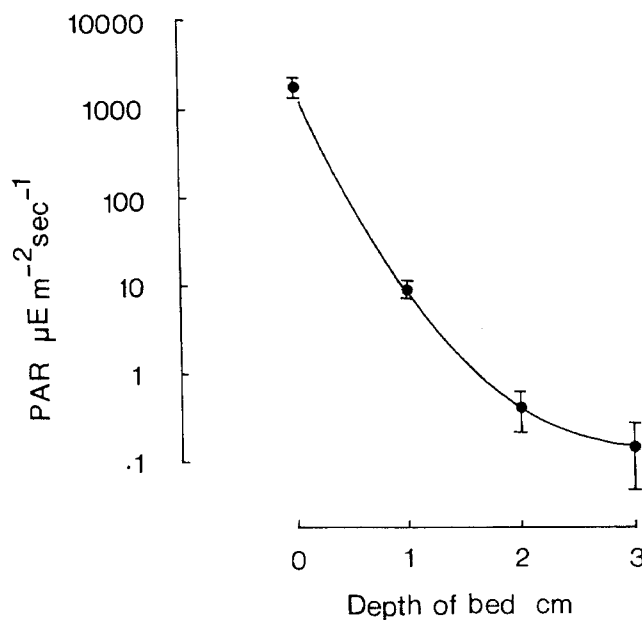


Fig. 4. Attenuation of light as photosynthetically-active radiation (PAR) through different depths of *Cladophora* in an algal bed. Each point is the average of 20 readings along with its standard error.

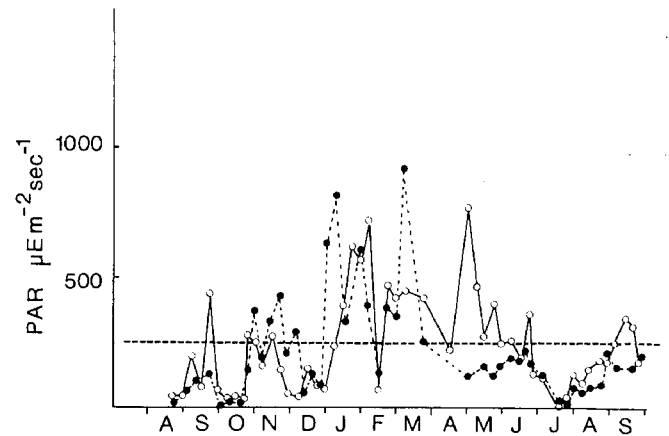


Fig. 5. Photosynthetically-active radiation (PAR) reaching the surface of the *Cladophora* beds at site A (open circle) and site B (closed circle). Data shown are readings taken weekly between August and September 1979. The dashed line represents the level of saturating light ($250 \mu\text{E m}^{-2}\text{sec}^{-1}$ PAR) obtained experimentally for *Cladophora* at 22°C .

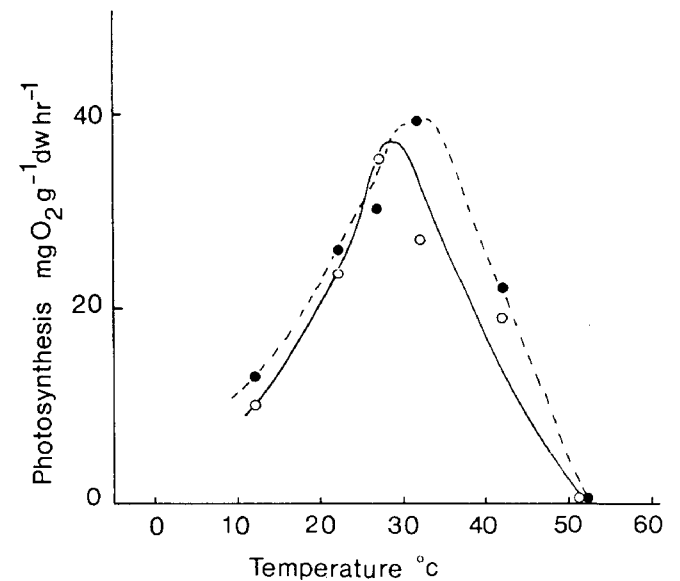


Fig. 6. Rates of photosynthesis of *Cladophora* over a range of temperatures. The algae were subjected to either 5 minutes (closed circles) or 30 minutes (open circles) exposure at each temperature before readings were taken.

Discussion

Light

The level of light saturation for the species in this study, 15% of full sunlight PAR, resembles that reported for *Cladophora glomerata*¹ in the Pamlico River estuary,

¹ Much of the work reported for the genus *Cladophora* has been undertaken with *C. glomerata*. The alga in the Peel Inlet was earlier thought to be *Cladophora* aff. *battersii* (eg. Hornberger and Spear 1980), but more recent work suggests a closer affinity with *C. albida* (Huds.) Kütz. (see van den Hoek 1963). The alga here is clearly distinct from either *C. glomerata* or *C. prolifera*, both of which form large accumulations under eutrophic conditions.

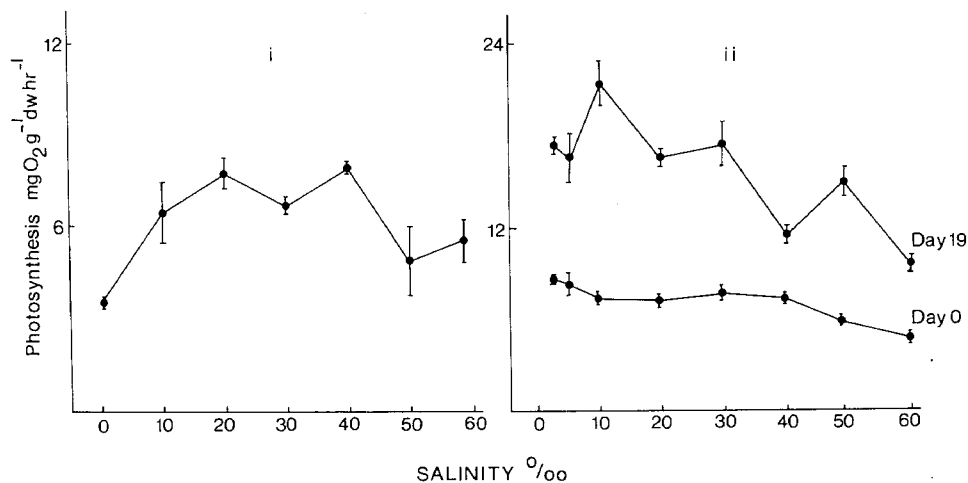


Fig. 7. Rates of photosynthesis of *Cladophora* over a range of salinities in (i) estuary water and (ii) artificial seawater medium. Rates in (ii) are shown at day 0 and after 19 days at their respective salinities. Each point is the average of 3 replicates along with its standard error. Saturating light intensities were used.

North Carolina (Holmes 1976). The light-productivity curves in this study are also similar to that produced for *Cladophora glomerata* growing in the littoral zone of the Baltic Sea (Wallentinus 1978). Wallentinus considered this particular species to require high light intensities and reported a good correlation between productivity and insolation. The data for *C. glomerata* growing in the intertidal zone of the Baltic (King and Schramm 1976) was estimated by us to be light-saturated above 17% full sunlight, assuming full sunlight as $1,160 \text{ Wm}^{-2}$ (Jerlov 1970). Whether *Cladophora* favours low or high light intensities has been the subject of some debate (Adams and Stone 1973, Mantai 1974). Despite the existing discrepancies in saturation levels, which are partially a result of morphological differences, these figures suggest that *Cladophora* species, in general, utilise light at levels fairly typical of submerged aquatic higher plants (Lloyd *et al.* 1977).

Light reaching the estuary floor at the sites of collection in summer ranged from 46 to 798 with an average of $333 \mu\text{Em}^{-2}\text{sec}^{-1}$, while winter values were between 3 and 353 with an average of $140 \mu\text{Em}^{-2}\text{sec}^{-1}$ (Fig. 5). During peak river flow, which occurs in winter, increased turbidity can reduce light at the bed to nearly undetectable levels. Comparing experimentally-obtained saturating light values with these field data suggests that light often limits photosynthesis at the surface of the bed in winter, but not in summer. However, reduction in PAR within the algal bed, through self-shading, is dramatic (Fig. 4); the uppermost 1 cm very efficiently excludes light from lower layers, with over 99% of light being removed at this depth. Net photosynthesis would cease at the compensation depth, just under 1 cm, even if full sunlight reached the surface of the beds. As these are often 10 cm, and up to 40 cm deep, it must be concluded that productivity in the beds is light limited. Indeed, the

lower layers of such a bed are typically decaying. The significance of self-shading to productivity rates has also been shown for a bed of *Cladophora prolifera* in Bermuda, where there is a 90% reduction in productivity below a single layer of the ball-like algae, each sphere being about 3 cm in diameter (Bach and Josselyn 1978). Nevertheless, plants lower in the bed do receive light if wave action produces movement of the algae. Further, oxygen bubbles trapped within individual plants result in their becoming buoyant and drifting away, exposing previously-shaded, underlying layers.

Although there is no photoinhibition at high intensities, lower rates were obtained on return from high to lower light levels. A similar response has been reported for several phytoplankton species by Harris and Lott (1973), who found the effect to be more pronounced the higher the light intensity reached above saturating levels. In our work the effect was not observed after short (2 min) exposures to high levels, suggesting some impairment of photosynthesis by prolonged periods at high light intensity. Prolonged exposures (1 hr) to high light intensity (about 100 Klux; almost $2,000 \mu\text{E m}^{-2}\text{sec}^{-1}$) have been shown to decrease photosynthesis of *Cladophora insignis* (Steemann-Nielsen 1952), resulting in reduced rates on return to low levels (3 Klux; about $60 \mu\text{E m}^{-2}\text{sec}^{-1}$). This effect, put down to photooxidation of the photochemical mechanism, was reversible, with reestablishment to normal rates after a number of hours. Such an effect might be expected to occur with the species in this study following prolonged exposure, but is probably of little ecological significance in the algal beds, in view of the range of intensities shown in Figure 5. However, at shallow sites in summer where intensities can be sometimes well above saturation over much of the day, prolonged periods of high light intensity may well reduce the productivity of the alga.

Temperature

The temperatures used here are within the range encountered in the estuary. Water above the algal bed may reach 27 °C in summer, while shallow, inshore bays can reach 35 °C on a hot day. Winter temperatures are typically between 11 ° and 15 °C (McComb *et al.* 1980).

The high rates observed above 30 °C (Fig. 6) indicate that, for short exposure times at least, *Cladophora* may efficiently photosynthesise in the warmer, inshore areas during summer. Q_{10} measurements of 3.55 between 12 and 22 °C, and 1.19 between 22 and 32 °C indicate a greater sensitivity to temperature change over the lower range. The reduced rates at 12 °C at saturating light levels (Fig. 2) suggest that low water temperatures may contribute significantly to a reduction in photosynthetic activity in winter.

Most reports on limits of temperature tolerance have been related to growth data rather than the shorter-term phenomenon of rate of photosynthesis. The distinction between the two is clear; nevertheless it is interesting to compare our data with those obtained in growth experiments on other *Cladophora* species. Bellis (1968) working with *C. glomerata* reported vigorous growth in culture up to 30 °C, though the alga was killed after 24 hours at 35 °C. Riverine *Cladophora* in temperate habitats appear to survive best between 15 ° and 25 °C, though cell damage occurs above 33 °C (Witton 1967). This contrasts with *Cladophora prolifera* which has been shown to survive 46 °C for up to 2 hours, following a gradual warm-up to this temperature (Vilhelm cited in Gessner 1970).

It is clear from this study that *Cladophora* photosynthesises actively over a wide range of temperatures; however there is some evidence for this range being extended further if more prolonged exposure times were used.

Salinity

Varying the salinity did not markedly affect the photosynthetic rates in either estuary water or artificial seawater over a wide salinity range (Fig. 7). Rates were relatively high in artificial seawater after 19 days due to a gradual response to the high level of available nutrients. A study of the rates of photosynthesis of *Cladophora repens*, growing in the intertidal zone of a mangrove community, showed a similar broad tolerance to salinity variations, between 10 and 40‰ (Dawes *et al.* 1978). This ability to tolerate such a wide range is presumably an adaptive advantage in an environment with strongly fluctuating salinities. Though there was some suppression

at hypersaline levels in the present study, ongoing experiments in the laboratory show *Cladophora* from Peel Inlet can survive at 97‰, but dies after several weeks at 120‰.

General

In summary, these short-term studies strongly suggest that salinity changes between winter and summer are unlikely to be involved in directly controlling algal growth. Winter temperatures potentially reduce photosynthesis to limiting levels in winter. Light intensities at the surface of the bed fall to limiting levels in winter; however, since any material more than 1 cm underneath the surface of the bed is below the compensation point, productivity of the whole bed will also be light-limited in summer.

The Peel-Harvey estuary has been used as an example for the essentially speculative modelling of complex systems, in which Monte Carlo methods have been used to select sets of parameters, including those which might control growth of *Cladophora*, the ranges of which have been chosen largely from the literature (Hornberger and Spear 1980). The data presented here will be useful in providing experimentally-determined inputs of information for such modelling exercises, so reducing the uncertainties which surround at least some of the parameters. It is useful to note that as suggested earlier, our results are similar to those obtained for other *Cladophora* species, at least as far as light is concerned, and so one feels some confidence in the validity of using such models as first approximations where few environmental data are already available. Both the experimental work reported here, and the speculative model of Hornberger and Spear, emphasise the importance of light intensity in understanding the productivity of *Cladophora* beds in the estuary, even though in a more general sense the problem of excessive algal growth is one of eutrophication.

Acknowledgements

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