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# Photoinhibition of photosynthesis on a coral reef

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## ABSTRACT

**Photoinhibition of macroalgae in the epilithic algal community (EAC) of coral reefs was studied using chlorophyll fluorescence techniques at One Tree Island, Great Barrier Reef, Australia. $F_v/F_m$ (variable to maximum fluorescence, darkened samples) of shallow macroalgae declined by 50% on fine summer and winter days, recovering in late afternoon. Within a species, thalli from low-light habitats were more photoinhibited (2 h at 1400 μmol $m^{-2}$ $s^{-1}$) than those from high-light habitats. The sensitivity of *Lobophora variegata* (Phaeophyta) and *Chlorodesmis fastigiata* (Chlorophyta) increased with depth (1 versus 20 m). However, shallow *Halimeda tuna* (Chlorophyta) plants growing between corals were more photoinhibited than those from deep, open areas.**

**Photoinhibition and recovery were depth- and species-specific. Shallow *Lobophora* and *Chlorodesmis* maintained a greater degree of $Q_A$ oxidation during photoinhibition. In deep thalli, reduced effective quantum yield of open photosystem II centres reflected lower proportions and excitation capture efficiencies of open centres. In *Lobophora*, zeaxanthin formation accompanied non-photochemical fluorescence quenching (NPQ), but in *Chlorodesmis* NPQ was limited and no zeaxanthin or antherxanthin formed. Higher photosynthetic efficiency in the lower storey of the EAC may compensate for photoinhibition in the upper storey, thereby reconciling photoinhibition of individual thalli with previous observations of no net inhibition of community productivity.**

*Key-words: Chlorodesmis fastigiata; Halimeda tuna; Padina pymnospora; Lobophora variegata; Laurencia intricata;* chlorophyll fluorescence; coral reef; macroalgae; photoinhibition; photosynthesis.

## INTRODUCTION

Coral reefs, like rainforests, have one of the highest primary productivities of any natural community (reviewed by Hatcher 1988, 1990). The greatest contribution to primary production on a coral reef comes from the epilithic algal community (EAC), the filamentous and thalloid macroalgae which cover the well-grazed limestone substratum (Lewis 1980; Hatcher & Larkum 1983; Larkum, Kennedy & Muller 1988). In addition to contributions of organic matter, the deposition of carbonate by calcareous, reef-building members of the EAC is essential to reef structure and is closely correlated with the productivity of these species (Borowitzka 1977). There is great interest in the effect of environmental change on coral reefs. Reefs are characteristically shallow structures restricted to oligotrophic tropical waters, and subjected to periods of very high insolation. Despite decades of research to determine the amount of primary production attributable to the various algal components of reefs and to identify limits to productivity (Lewis 1980; Larkum 1983; Larkum *et al.* 1988), little is known about the effect of high light on this ecosystem.

Exposure to excessive irradiance can lead to photoinhibition, defined here as reduced photosynthetic efficiency (quantum yield) under high-irradiance conditions (Osmond 1994). Sustained exposure to high light may lead to a reduction in the maximum rate of photosynthesis, potentially affecting plant growth and distribution (Ball *et al.* 1991). The effects of high light on photosynthetic efficiency are usually observed before a reduction in the maximum rate of photosynthesis ($P_{max}$) occurs. Reduced efficiency reflects the balance between two suites of processes (Chow 1994; Osmond 1994): (1) protection, whereby excess energy is dissipated as heat in proportion to the extent of the proton gradient across the thylakoid membrane, and (2) impairment, whereby turnover of key proteins of PSII, notably D1, is altered. This balance may shift depending on the interaction of light with other environmental factors (e.g. temperature; Franklin 1994). The mechanism of photoprotective, non-radiative dissipation of energy by PSII reaction centres (Weis & Berry 1987) and/or by the light-harvesting antenna with a possible contribution from zeaxanthin formation by the xanthophyll cycle (Demmig Adams & Adams 1992) remains controversial (Osmond 1994).

Photoinhibition has been observed in all divisions of macroalgae (e.g. Herbert & Waaland 1988; Nultsch, Pfau & Huppertz 1990; Henley *et al.* 1991a,b). On a diurnal basis, photoinhibition of many intertidal and shallow water species occurs when low tides coincide with solar noon (Huppertz, Hanelt & Nultsch 1990; Henley *et al.* 1991a; Hanelt 1992; Hanelt, Li & Nultsch 1994). As in higher plants, low-light-acclimated thalli are more susceptible to

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photoinhibition than are high-light-acclimated thalli (Herbert & Waaland 1988; Henley *et al.* 1991a,b; Osmond *et al.* 1994). On a seasonal basis, high-light stress may interact with temperature to further reduce efficiency and $P_{max}$ (Henley *et al.* 1992; Franklin 1994). Furthermore, sensitivity to high light has been proposed to influence the depth distribution of species (Herbert & Waaland 1988; Hanelt 1992).

Significantly, field experiments on the EAC of shallow reef environments on the Great Barrier Reef (Klumpp & MacKinnon 1992; A.W.D. Larkum, K. Koop & G. Westphalen, University of Sydney, unpublished results) and in the Caribbean (Carpenter 1985) have indicated no net inhibition of primary production in the daily course of photosynthesis. The dearth of information on the specific high-light responses of reef algae may reflect the difficulty in obtaining detailed and reliable photosynthetic light response curves in these systems (Henley 1993). Alternatively, these algae may be specially adapted to this unique environment. The recent development of portable chlorophyll fluorescence instrumentation facilitates the analysis of photosynthetic regulation under field conditions, and allows these questions to be addressed explicitly. In order to determine whether the macroalgae of coral reefs are susceptible to photoinhibition, a series of field experiments was undertaken on the Great Barrier Reef, using representative green, brown and red algal species. We found that all algae studied did exhibit photoinhibition.

## MATERIALS AND METHODS

### Field site and plant material

Experiments were performed on macroalgae from the reef surrounding One Tree Island (23°31'S, 152°08'E), a coral cay in the Capricorn section of the Great Barrier Reef. One Tree Reef covers ≈19 km$^2$, comprising an extensive patch reef system within an enclosed lagoon. During falling tides, the lagoon is ponded for several hours. Species examined were: *Chlorodesmis fastigiata* (C. Ag.) Ducker, *Halimeda tuna* (Ellis and Sol.) Lamouroux (Chlorophyta, Caulerpales), *Padina pymnospora* (Kutz) Vick, *Lobophora variegata* (Lam.) Womersley (Phaeophyta, Dictyotales) and *Laurencia intricata* Lamouroux (Rhodophyta, Ceramiales). Where possible, specimens of the same species were collected from populations at both 1–2 and 20–22 m (by SCUBA). In shallow water, intact (ungrazed?) *Halimeda* thalli were most often found within crevices in the coral, while small bits of thalli occurred in more open areas. The thalli in crevices were collected for experiments. Due to weather conditions, collection sites were not accessible on a daily basis. Consequently, specimens were held at least overnight, but not more than 3 d before use in short-term experiments. Storage conditions were as follows: for thalli from deep water, constantly flowing seawater, in shade (PFD < 30 $\mu$mol m$^{-2}$ s$^{-1}$, natural light and photoperiod), and for thalli from shallow water, full natural light in shallow water near to the shore. Experiments were performed during the winter (July 1993) and summer (February 1994). The water temperature varied between 20 and 21 °C during the winter experiments and between 26 and 27 °C during the summer experiments, and did not vary significantly within the tidal cycle.

### Diurnal, *in situ* measurements

Comparisons of diurnal changes in photosynthetic efficiency were made on 3–4 samples from populations of macroalgae at similar depths between 1 and 2 m, with new samples being collected for each time point. A similar assessment of changes in photosynthetic efficiency of macroalgae at deeper sites was impossible to perform. Photosynthetic efficiency was determined from measurements of the dark-adapted chlorophyll *a* fluorescence parameters $F_o$, $F_m$ and $F_v = F_m - F_o$. The ratio $F_v/F_m$ is correlated to the quantum yield of photosynthesis (Björkman & Demmig 1987), where a value of $F_v/F_m$ of ≈0·83 corresponds to the maximal quantum yield of an unstressed green plant. Samples were darkened for 10 min in a leaf clip (Hansatech, Ltd, King's Lynn, Norfolk, UK), *in situ* and under water. Just prior to fluorescence measurements, the clip and enclosed sample were cut free of the parent plant and brought on board, where the sample remained wet for the duration of the measurement. Chlorophyll fluorescence was measured with a plant efficiency analyser (Hansatech). Photon flux density (PFD) was measured with a cosine-corrected quantum sensor (LiCor, Lincoln, NE, USA). Tests for the effect of cutting showed no resulting change in fluorescence.

### Short-term photoinhibitory treatments

In order to assess the sensitivity of macroalgae to a brief high-light stress, the dark-adapted chlorophyll fluorescence parameters of 4–5 thalli of each species and depth were measured under similar light conditions. Thalli were selected at dawn from among the stored samples, and had no high-light exposure that day, prior to the start of the experiment. They were placed in 40 cm of water on the natural coral rubble bottom just off shore. $F_v/F_m$ was measured, as described above, at half-hourly intervals for 2 h. At the end of the high-light treatment, the samples were returned to the shade (PFD < 30 $\mu$mol m$^{-2}$ s$^{-1}$) and flowing seawater for an 18–19 h recovery period, including the intervening night. Fluorescence was measured periodically during recovery. Experiments were begun at nearly the same time each morning (1000 h ± 0·5 h), and repeated on 2–3 d. The maximum irradiance during these 2 h experiments was similar (≈1400–1500 $\mu$mol m$^{-2}$ s$^{-1}$) during the two seasons, due to variable cloud cover and storms. Extended sunny periods were rare during these two trips.

### Chlorophyll fluorescence quenching analysis and photosynthetic oxygen evolution

In the summer, additional thalli were collected before and during the short-term photoinhibitory treatments and

recovery periods for simultaneous measurement of modulated chlorophyll fluorescence and photosynthetic $O_2$ evolution (Seaton & Walker 1990). The $O_2$ evolution rate of a 1·5 $cm^2$ sample (or uniform layer of filaments in the case of *Chlorodesmis*) was measured polarographically (chamber DW3; Hansatech) at 25 °C. Modulated chlorophyll fluorescence was recorded using a PAM 101 Chlorophyll Fluorometer/FL 103 additionally equipped with a PAM 102/102FR, PAM 103/Schott KL 1500 electronic flash lamp and a polyfurcated fibre-optic (H. Walz, Effeltrich, Germany). At the end of a 10 min dark period, respiration and $F_o$ were recorded, followed by a 1 s saturating flash to determine $F_m$. An ascending series of actinic irradiances (white light) was then applied, and $O_2$ evolution and modulated fluorescence ($F_s$) were measured at steady state. Immediately following $F_s$ measurement, a saturating flash was delivered to detect $F_m'$, followed by darkening to obtain the $F_o'$ measurement. Unlike our previous measurements of fluorescence in higher plants, we found that application of far-red light appeared to slow re-oxidation of the intersystem electron transport chain in these macroalgae. Consequently, the $F_o'$ value was recorded as in Osmond *et al.* (1993). Flashes were triggered and signals were recorded by an IBM-compatible 386 computer equipped with an analogue-to-digital conversion board (model IF-1, Hansatech). Fluorescence quenching coefficients were calculated according to Schreiber, Bilger & Neubauer (1994), where photochemical quenching was calculated as $q_P = (F_m' - F_s)/(F_m' - F_o')$. It is generally agreed that the photochemical quenching parameter $q_P$ is an estimate of the average reduction state of the pool of primary electron acceptors, $Q_A$, that is, the 'openness' of PSII centres that are active (Schreiber *et al.* 1994). Non-photochemical quenching, thought to be indicative of non-radiative dissipation of energy, was calculated as $q_N = (F_m - F_m')/(F_m - F_o')$, and NPQ = $(F_m - F_m')/F_m'$ in order to account for possible effects of antenna-based quenching and the potential difficulty in determining $F_o'$. There was no qualitative difference in the results obtained using different methods of calculating non-photochemical quenching, and therefore only NPQ data are presented. The effective quantum yield of active PSII centres during illumination, which reflects the combined effect of fewer numbers of open centres and lower excitation capture efficiency of these centres, was calculated according to Genty, Briantais & Baker (1989): $\Phi_{II} = (F_m' - F_s)/F_m'$, where the excitation capture efficiency of open PSII centres was calculated as $F_v'/F_m'$.

## Pigment analyses

After a short-term photoinhibitory treatment performed as above, samples were collected for pigment analysis, particularly analysis of the xanthophyll cycle pigments. Tissue was ground in 100% methanol and dim light in the field, and the entire sample was dried and stored frozen until it could be re-extracted in 85% buffered acetone. After centrifugation, the pellet was washed in 100% buffered acetone. Pooled extracts were analysed by high-performance liquid chromatography, following the method of Gilmore & Yamamoto (1991), using their solvents A and B. Pre-extraction of pigments in methanol was tested in lab-reared *Ulva* sp. and was found to have no effect on the overall extraction efficiency (data not shown). Pigment concentrations were calculated using standards as described in Franklin (1994).

## RESULTS

### Diurnal, *in situ* measurements of $F_v/F_m$

In all cases, photosynthetic efficiency of macroalgae from shallow sites declined in response to daily increasing PFD, and recovered rapidly as PFD declined late in the day. This is illustrated in Fig. 1 where, for three macroalgae, changes in $F_v/F_m$ throughout representative summer and winter days are shown. Measurements were made on at least 2 days during both seasons, and although a similar trend in response was observed each day, the absolute loss of $F_v/F_m$ depended on cloud cover. Only 1 day of measurements was almost completely clear (Fig. 1b). The greatest inhibition of efficiency (50%) was recorded in *Padina* (Fig. 1e,f), which responded quickly to the initial rise in

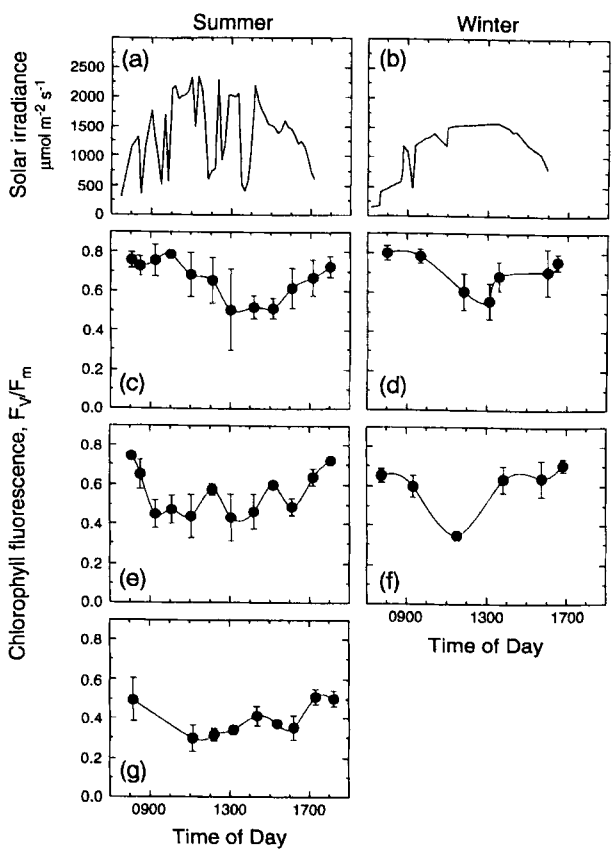


**Figure 1.** Diurnal pattern of photoinhibition in *Chlorodesmis fastigiata* (c,d), *Padina pymnospora* (e,f), and *Laurencia intricata* (g) as a function of daily irradiance at the surface (a,b) during 2 days in the summer (a,c,e) and winter (b,d,f).

PFD and to changing PFD as clouds passed over. In *Chlorodesmis* (Fig. 1c,d), $F_v/F_m$ was maintained at 0·8 until the maximum daily irradiance was reached; then $F_v/F_m$ fell by 40%. In contrast, the photosynthetic efficiency of *Laurencia* (Fig. 1g) declined by 40% by mid-morning. In all species, recovery of $F_v/F_m$ to the value seen at dawn occurred before darkness. On completely overcast days, $F_v/F_m$ remained high (data not shown).

Despite 50% higher maximum PFD on the summer measurement day (Fig. 1a,b), there were no obvious seasonal differences observed in the response of $F_v/F_m$ in *Chlorodesmis* or *Padina*.

## Short-term photoinhibitory treatments

### *$F_v/F_m$ and $F_o$ measurements*

Short-term experiments with a known light treatment allowed us to compare directly the susceptibility to photoinhibition among species growing at shallow (1 m) or deep (20 m) sites. This is illustrated in Fig. 2 for macroalgal species found growing at both 1 and 20 m, or just 1 m. It should be noted that most macroalgae are restricted either to shallow or to deep sites on a coral reef and very few are found from the surface down to 20 m. Irradiance at 20 m was ≈10% of that measured at 1 m (for example: 190 and 1610 $\mu$mol $m^{-2}$ $s^{-1}$, respectively). The short but necessary storage in flowing seawater had no noticeable effect on the initial values of $F_v/F_m$, which were about 0·8 (0·55 for *Laurencia*).

In two of three cases, loss of photosynthetic efficiency was greater for the deeper plants. The $F_v/F_m$ of shallow-grown *Chlorodesmis* declined by 30% (summer) or 40% (winter) from the initial, low-light value (Fig. 2a,b), a loss of efficiency similar to that observed on a diurnal basis in *in situ* populations (Fig. 1c,d). *Chlorodesmis* from 20 m was more severely affected than thalli from 1 m, with $F_v/F_m$ declining by 55% in both seasons. *Lobophora* plants (Fig. 2c,d) from both depths were more severely affected than *Chlorodesmis*, with $F_v/F_m$ declining by 60 and 85% in thalli from 1 and 20 m, respectively. In contrast, *Halimeda* thalli collected from shallow habitats (Fig. 2e) were more sensitive to high light than thalli from deep habitats, with $F_v/F_m$ declining by an additional 10% in thalli from 1 m during each season.

The photosynthetic efficiency of *Padina* and *Laurencia* plants collected from 1 m (Fig. 2g,h) also declined rapidly under these light conditions, to the extent predicted from *in situ* measurements of diurnal photoinhibition (Fig. 1e–g), and to the same degree as that observed in *Lobophora*.

Generally, the time required for $F_v/F_m$ to recover 50% of the total decline observed in 2 h ($t_{1/2}$) (Table 1) reflected the degree of photoinhibition experienced. Slower recovery occurred in those thalli which were more photoinhibited at the end of the 2 h high-light treatment (Fig. 2). The most rapid recovery measured occurred in *Padina*, regardless of season (Table 1).

Seasonal effects were more apparent during recovery from photoinhibition than during its onset (Table 1 & Fig. 2). For example, there was little seasonal difference in the extent of inhibition between the two populations of *Lobophora*, but recovery of $F_v/F_m$ was slower in the summer. In all cases except *Chlorodesmis* collected from 1 m, photoinhibition was somewhat more severe in the summer.

In *Chlorodesmis* from both 1 and 20 m, loss of photosynthetic efficiency during exposure to 1400–1500 $\mu$mol $m^{-2}$ $s^{-1}$ was accompanied by a rise in initial fluorescence, $F_o$ (Fig. 3a,b). The increase varied between 25 and 60%. Initial fluorescence also rose, to a lesser extent, in *Lobophora* from 20 m (Fig. 3d). Whereas the *Chlorodesmis* $F_o$ returned to low-light, pre-stress levels during the recovery period, the 20 m *Lobophora* $F_o$ remained higher during recovery. In contrast, the $F_o$ of 1 m *Lobophora* thalli (Fig. 3c) declined by ≈35% during the light stress, and returned to the pre-stress level during recovery.

## Pulse amplitude modulated fluorescence and oxygen evolution measurements

Analysis of quenching of pulse amplitude modulated chlorophyll fluorescence and $O_2$ evolution permit investigation of photosynthetic processes during illumination. On the basis of the results of the dark-adapted $F_v/F_m$ measurements, we chose two species, *Lobophora* and *Chlorodesmis*, in which to study the processes contributing to lower photosynthetic efficiency during a brief full-sun treatment. These measurements are comparable to the dark-adapted measurements in Figs 2a,c and 3a–d. Initial light response measurements indicated that, in both species, thalli from 20 m were less able to maintain a pool of oxidized $Q_A$ (cf. Figs 4c&h, Figs 5c&h; filled circles), suggesting that 20 m thalli have greater susceptibility to photoinhibition. This was confirmed by measurements of the light dependence of $O_2$ evolution, the effective quantum yield of PSII ($\Phi_{II}$), the reduction status of the $Q_A$ pool ($q_P$), and the excitation capture efficiency ($F_v'/F_m'$) of open centres (Figs 4 & 5). Species-specific responses were also observed.

In *Lobophora* from 1 m, a 2 h exposure to high light (1400 $\mu$mol $m^{-2}$ $s^{-1}$) led to a lower quantum yield of $O_2$ evolution and $\Phi_{II}$ (Fig. 4a,b), but no change in $P_{max}$ or the light response curve of $q_P$ (Fig. 4c). The reduction in $\Phi_{II}$ at low measuring PFD was similar to the 50% reduction in excitation capture efficiency of open centres, $F_v'/F_m'$ (Fig. 4d), and was correlated with the increase in the capacity for non-photochemical quenching, NPQ (Fig. 4e). After 2 h in high light, NPQ was equal to the maximum level observed in controls. In contrast, high-light treatment of *Lobophora* thalli from 20 m led to a greater decline in the quantum yield of $O_2$ evolution (Fig. 4f) and $\Phi_{II}$ (Fig. 4g) than that found in thalli from 1 m. The light response curve of $q_P$ changed after the high-light stress (Fig. 4h), with ≈20% of the $Q_A$ pool being in the reduced state at low light. Although the $F_v'/F_m'$ of control 20 m thalli (Fig. 4i, filled circles) was higher than that of control 1 m thalli (Fig. 4d, filled circles), it declined more during the high-

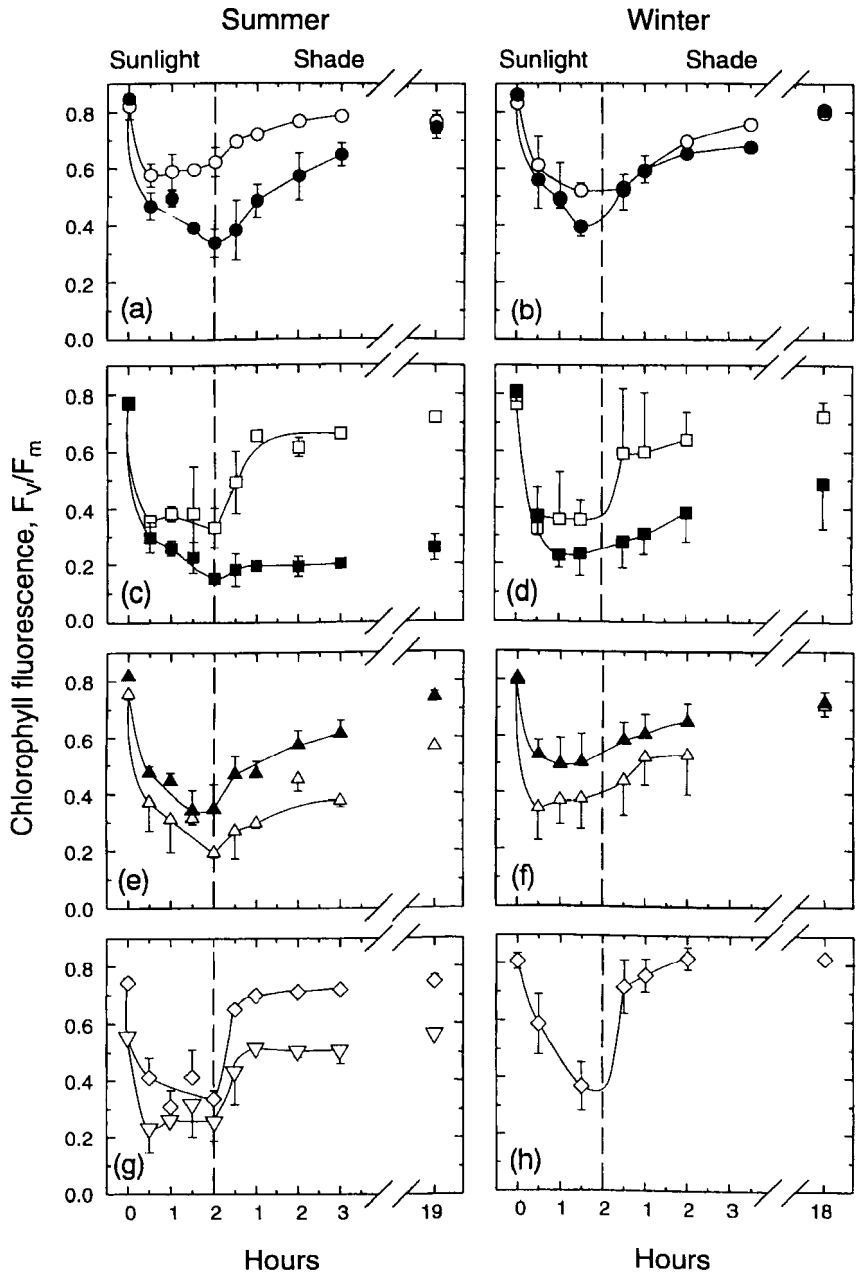


**Figure 2.** Effect of a 2 h sunlight treatment (1400–1500 μmol $m^{-2}$ $s^{-1}$) on $F_v/F_m$ of *Chlorodesmis fastigiata* (a,b), *Lobophora variegata* (c,d), *Halimeda tuna* (e,f), *Padina pymnospora* (g,h; ◇), and *Laurencia intricata* (g; ▽). At the end of 2 h, thalli were placed in the shade for a recovery period. Thalli were collected from 1 m (open symbols) and 20 m (filled symbols) (a–f), and from 1 m (g,h). Experiments were performed in both summer (a,c,e,g) and winter (b,d,f,h) months. Data are means (± SD) for two experiments.

light stress. Control *Lobophora* thalli from 20 m possessed a lower capacity for NPQ (Fig. 4j, filled circles) than did control thalli from 1 m (Fig. 4e, filled circles), and after only 1 h in high light, NPQ increased quickly to above 2·5, corresponding to a 80% reduction in $F_v'/F_m'$ (Fig. 4i). Thus, lower $\Phi_{II}$ in 20 m thalli reflected both fewer open PSII centres and a lower capture efficiency of the remaining open centres.

In *Chlorodesmis* thalli from 1 m, a similar high-light treatment (2·5 h at 1400 μmol $m^{-2}$ $s^{-1}$) led to reductions both in the quantum yield of $O_2$ evolution and in $P_{max}$ (Fig. 5a). While $\Phi_{II}$ (Fig. 5b) and $F_v'/F_m'$ (Fig. 5d) did decline overall with time under high-light stress, they were not particularly reduced at low measuring PFD. As observed for *Lobophora* from shallow water, these changes occurred without change in the light response curve of $q_P$ (Fig. 5c). In comparison, *Chlorodesmis* thalli from 20 m had lower $\Phi_{II}$ (Fig. 5g) and $F_v'/F_m'$ (Fig. 5i) at low PFD after the high-light treatment, and the light response of $Q_A$ reduction changed (Fig. 5h), again with ≈20% of the $Q_A$ pool being in the reduced state at low light. In contrast to *Lobophora*, NPQ in control

**Table 1.** Approximate time required for $F_v/F_m$ to recover 50% ($t_{1/2}$) of the total decline observed in 2 h of high-light treatment. *Projected time; n.o. = 50% recovery not observed

| Species | Collection depth (m) | Season | $t_{1/2}$ (min) |
|---|---|---|---|
| *Chlorodesmis* | 1 | S | 60 |
| | | W | 100 |
| | 20 | S | 130 |
| | | W | 90 |
| *Halimeda* | 1 | S | 470* |
| | | W | 190* |
| | 20 | S | 135 |
| | | W | 85 |
| *Lobophora* | 1 | S | 40 |
| | | W | 30 |
| | 20 | S | n.o. |
| | | W | 1080 |
| *Padina* | 1 | S | 15 |
| | | W | 15 |
| *Laurencia* | 1 | S | 30 |

*Chlorodesmis* thalli from either depth (Fig. 5e,j, filled circles) was not rapidly engaged as PFD increased. However, NPQ did increase with increasing photoinhibition. Also in contrast to *Lobophora*, there was no initial difference in the capture efficiency of open centres or NPQ in *Chlorodesmis* thalli from the two habitats (cf. Figs 5d&i, 5e&j, filled circles).

Consistent with the changes in dark-adapted $F_v/F_m$ measurements for *Chlorodesmis* from 1 m (Fig. 2a), the rate of $O_2$ evolution and $\Phi_{II}$ recovered by about 50% and NPQ relaxed almost to control values within 70 min of returning photoinhibited thalli to low light (Fig. 5, shaded symbols). Thalli from 20 m were much more severely affected than in any previous experiment, and no recovery was observed.

## Xanthophyll cycle measurements

Activity of the xanthophyll cycle was measured in *Lobophora* and *Chlorodesmis* in experiments similar to those above, and begun in the early afternoon when maximum PFD was 1980 $\mu$mol $m^{-2}$ $s^{-1}$, declining over 3 h to 1390 $\mu$mol $m^{-2}$ $s^{-1}$. A rapid and extensive conversion of violaxanthin to zeaxanthin occurred in *Lobophora* col-

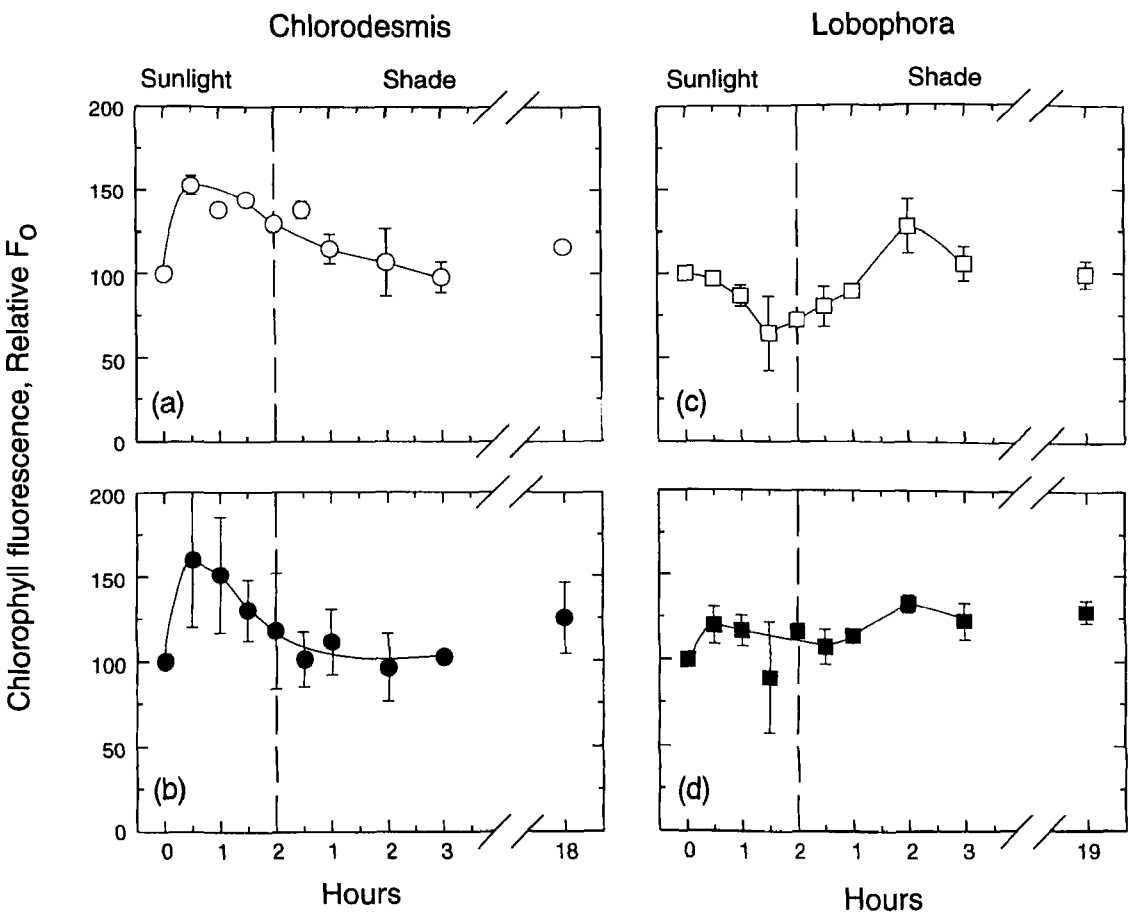


**Figure 3.** Effect of a 2 h sunlight treatment (1400–1500 µmol $m^{-2}$ $s^{-1}$) on $F_o$ of *Chlorodesmis fastigiata* (a,b) and *Lobophora variegata* (c,d) in the summer experiments from Fig. 2. At the end of 2 h, plants were placed in the shade for a recovery period. Plants were collected from 1 m (open symbols) or 20 m (filled symbols). Values are means (± range) of values for two experiments.

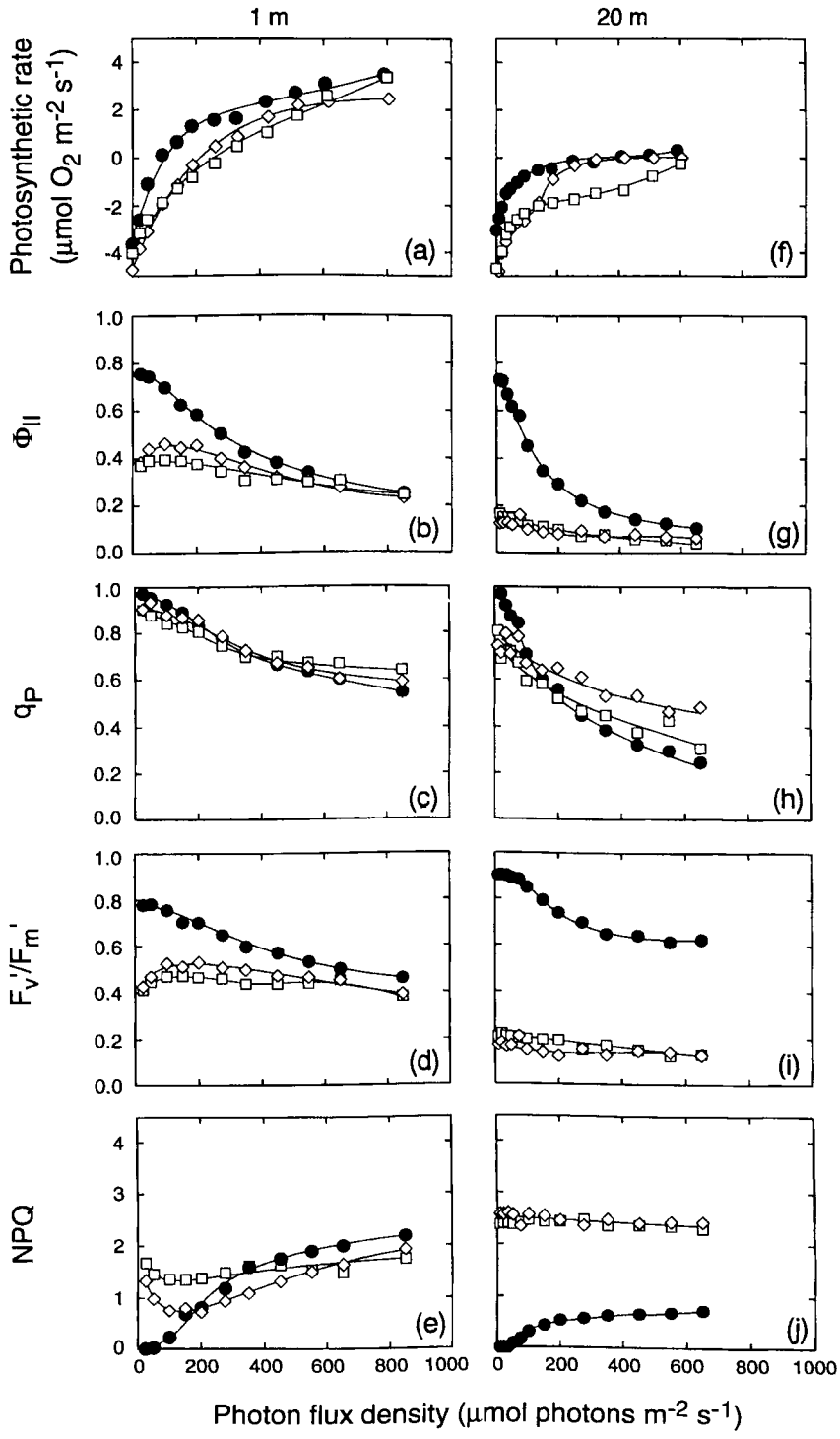


**Figure 4.** Light response curves for photosynthesis (a,f), PSII efficiency, $\Phi_{II}$ (b,g), $q_P$ (c,h), $F_v'/F_m'$ (d,i) and NPQ (e,j) in *Lobophora variegata* during a high-light treatment (1400–1500 µmol $m^{-2}$ $s^{-1}$). Samples were collected at time 0 (control, ●), after 1 h photoinhibition (□) and after 2 h photoinhibition (◇). Thalli, collected in the summer, were from 1 (a,b,c,d,e,) or 20 m (f,g,h,i,j).

lected from 1 m, and to a much lesser extent in 20 m samples (Fig. 6a,c). While both violaxanthin and antheraxanthin were present in *Chlorodesmis* (Fig. 6b,d), it is particularly noteworthy that *no* conversion to zeaxanthin or significant accumulation of antheraxanthin was ever detected.

## DISCUSSION

### Photoinhibitory stress

Given the great importance of macroalgal photosynthesis to coral reef productivity and structure (Hatcher 1988, 1990), it is important to ask whether these algae are sus-

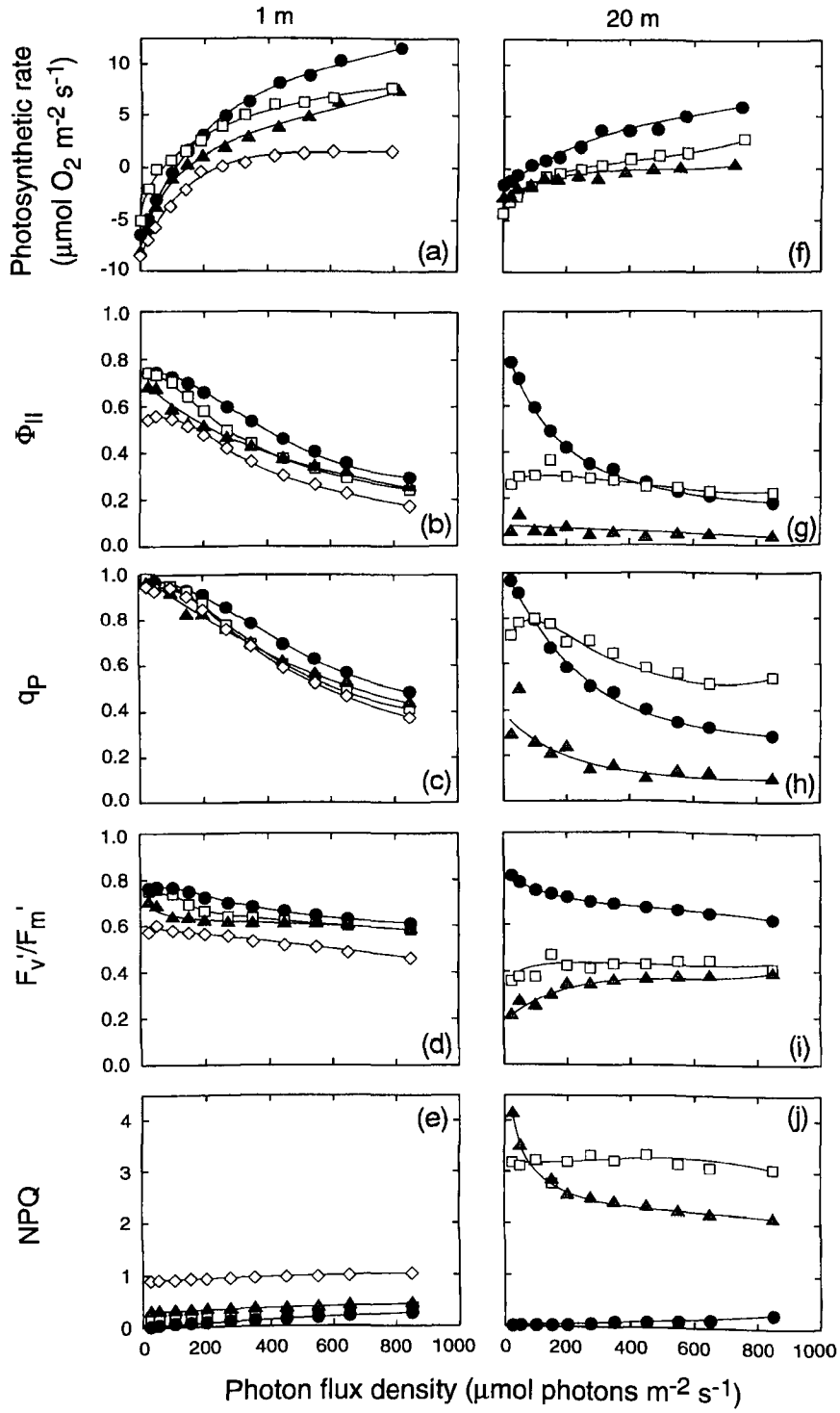


**Figure 5.** Light response curves for photosynthesis (a,f), PSII efficiency, $\Phi_{II}$ (b,g), $q_P$ (c,h), $F_v'/F_m'$ (d,i), and NPQ (e,j) in *Chlorodesmis fastigiata* during a high-light treatment (1400–1500 μmol $m^{-2}$ $s^{-1}$). Samples were collected at time 0 (control, ●), after 1 or 1·5 h photoinhibition (□) and after 2·5 h photoinhibition (◇), as well as after 70 min recovery in low light (▲). Thalli, collected in the summer, were from 1 (a,b,c,d,e,) or 20 m (f,g,h,i,j).

ceptible to photoinhibition, as are other plants and algae, or whether adaptation to this unique environment enables them to remain unaffected by excess light. Reduced photosynthetic efficiency towards midday is a widespread phenomenon in natural plant populations (Baker & Bowyer 1994), and is correlated with the daily pattern of irradiance. In contrast to current thinking, the present results (Fig. 1) indicate that the macroalgae of coral reefs are no different from macroalgae of other habitats in their susceptibility to photoinhibition (e.g. Henley *et al.* 1991a; Hanelt *et al.* 1994). The results presented here show that all shallow specimens measured *in situ* responded to the daily light

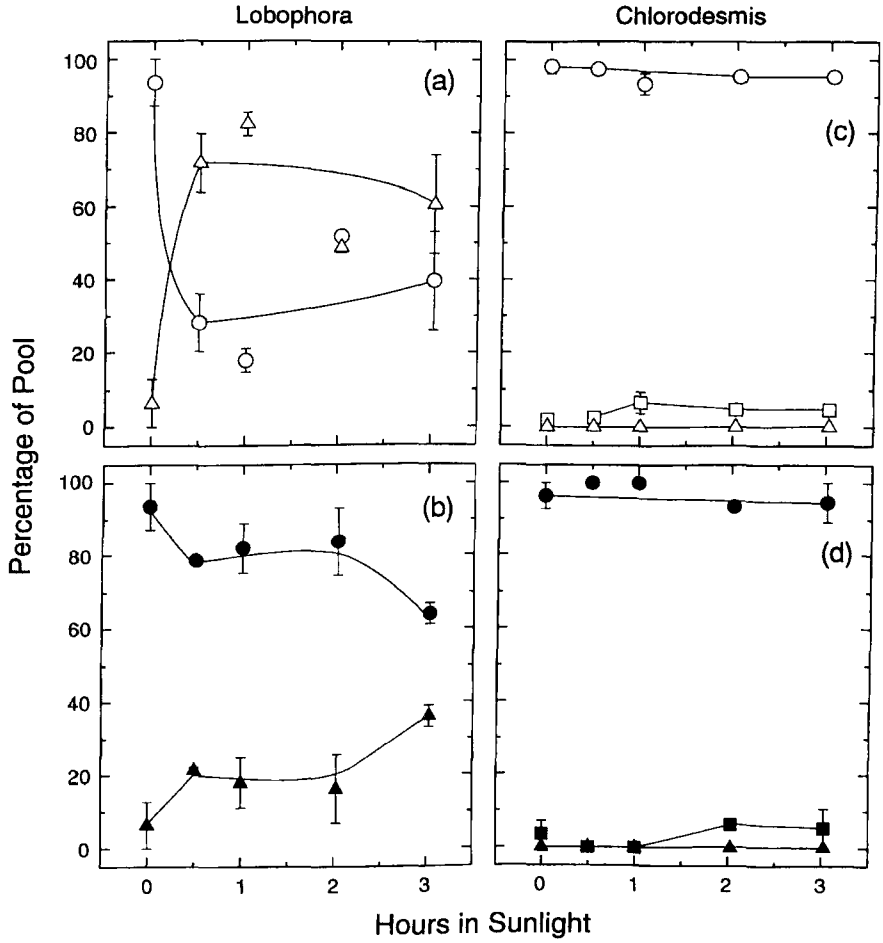


**Figure 6.** Xanthophyll cycle pigments in *Lobophora variegata* (a,b) and *Chlorodesmis fastigiata* (c,d) from 1 (open symbols) or 20 m (filled symbols). Amounts of violaxanthin (○), antheraxanthin (□), and zeaxanthin (△) are expressed as the mean (± SD) percentage of the total xanthophyll cycle pigment pool in two samples, after a period in full sunlight.

flux with an ≈50% reduction of photosynthetic efficiency ($F_v/F_m$) during the middle of the day, followed by complete recovery by late afternoon (Fig. 1). The reduction was similar among species, despite diversity in both thylakoid membrane structure and complement of light harvesting pigments (Lobban, Harrison & Duncan 1985). Henley *et al.* (1991a) found a significant linear correlation between a decline in dark-adapted $F_v/F_m$ and the quantum yield of $O_2$ evolution in high-light-acclimated *Ulva rotundata* during the morning half of the diurnal light cycle. Yet, during the afternoon, only variable fluorescence recovered. Our results for short-term photoinhibitory treatments of *Chlorodesmis* (Fig. 5) indicate that there is recovery of the quantum yield along with $F_v/F_m$ recovery in the afternoon, at least for this alga.

Furthermore, light-acclimation history plays a role in the sensitivity of coral reef macroalgae to high light similar to that observed in higher plants and other macroalgae (cf. Henley *et al.* 1991a; Herbert & Waaland 1988; Chow 1994). Low-light-acclimated macroalgae were more susceptible to photoinhibition than high-light-acclimated thalli of the same species, when subjected to similar irradiance for short periods (Fig. 2). Although $F_v/F_m$ recovery rates in thalli from 20 m varied among species, thalli which were left for longer periods in surface irradiance were dead and bleached within 24 h (data not shown). Whereas sensitivity to photoinhibition increased with increasing depth in the cases of *Chlorodesmis* and *Lobophora*, irradiance microclimate may account for the somewhat surprising difference between *Halimeda* plants collected from 1 and 20 m. In contrast to collections from 20 m, *Halimeda* from 1 m was found in and collected from crevices between corals; crevices too small to accommodate our light meter. While this obviously shaded habitat may provide refuge from herbivory, such a strategy has an inherent potential cost to the macroalga in terms of increasing photoinhibition after removal of shading coral in the summer by storms and cyclones.

## Patterns of photoinhibitory response

Despite the generalized photoinhibition shown by reef macroalgae in this study, the individual pattern of onset and recovery varied with species. This is especially obvi-

ous in a comparison of *Padina* and *Chlorodesmis* (Fig. 1). In the former case, $F_v/F_m$ changed rapidly in a changing light field, whereas in the latter, $F_v/F_m$ remained high until the maximum PFD was reached. These differences suggest that the regulation of the light reactions of photosynthesis under high-light stress, i.e. the balance between protective and damage-related processes which constitute the integrated photoinhibitory response (Osmond 1994), is highly specific.

Comparison of *Lobophora* and *Chlorodesmis* also demonstrates the species-specfic nature of photoinhibition. For thalli of both *Lobophora* and *Chlorodesmis* collected from 1 m, exposure to 1400 $\mu$mol $m^{-2}$ $s^{-1}$ was approximately equivalent to 2 times the irradiance required to saturate photosynthesis. In *Lobophora*, this exposure led to reduced excitation efficiency of open centres, with no change in the proportion of open to closed centres. The level of dark-adapted $F_o$ declined, at the same time that 60% of the xanthophyll cycle pool was converted to zeaxanthin and non-photochemical quenching was rapidly engaged. Recovery of $F_v/F_m$ was rapid in low light. The response of this phaeophycean alga is remarkably similar to that found in a comprehensive study of the model higher plant *Arabidopsis* (Russell *et al.* 1995). In contrast, a similar high-light stress for the chlorophycean alga *Chlorodesmis* led to a smaller reduction in capture efficiency with slow engagement of non-photochemical quenching. There was no xanthophyll cycle conversion detected in this alga, and the level of $F_o$ rose. Yet, the maximum reduction of photosynthetic efficiency was less, and recovery of $F_v/F_m$ was almost as rapid as in *Lobophora* (Table 1).

For thalli collected from 20 m, the light stress treatment represented ≈7 times the irradiance required for light-saturated photosynthesis. The fluorescence responses of *Lobophora* and *Chlorodesmis* from that depth reflected the greater degree of photoinhibitory stress for these low-light acclimated algae, with increased reduction of the $Q_A$ pool, greater loss of excitation capture efficiency and effective quantum yield, and, now in both cases, increased $F_o$.

It was suggested previously that the balance between protection and damage to PSII may be revealed by examination of changes in the dark-adapted $F_o$ level (Osmond 1994). Increases in $F_o$ have been correlated with inhibition of chloroplast protein synthesis during onset of and recovery from photoinhibition in *Ulva rotundata* (Franklin *et al.* 1992), and wheat (Hurry & Huner 1992), and in tranformants of *Chlamydomonas reinhardtii* which were impaired in synthesis of the D1 protein (Heifetz *et al.* 1992). However, high $F_o$ has also been observed during photoinhibition at low temperature, where dissipation of excess energy by inactive PSII centres was proposed (Kirilovsky *et al.* 1990; Setlík *et al.* 1990; Franklin 1994). Decreases in $F_o$ during photoinhibition are believed to indicate dissipation of excess energy within the light-harvesting antenna (Krause 1991), and in some algae are correlated with the formation of zeaxanthin (Franklin *et al.* 1992; Franklin 1994; Uhrmacher, Hanelt, & Nultsch 1995). Analysis of changes in absolute values of fluorescence can be further complicated by the effects of changes in optical properties in intact tissues (e.g. chloroplast movement).

Here, a correlation between $F_o$ quenching, zeaxanthin formation and NPQ was observed in *Lobophora* from 1 m. Operation of the xanthophyll cycle in brown algae was observed previously (Hager 1980), and correlated with declines in $F_v/F_m$ and $F_o$ as a consequence of high-light exposure (Uhrmacher *et al.* 1995). Even less is known about the mechanism by which zeaxanthin is related to protection from photoinhibition in these algae than in higher plants (e.g. Ruban *et al.* 1992; Chow 1994; Owens 1994). However, in *Lobophora* from 20 m, where zeaxanthin formation was reduced, $F_o$ values rose, NPQ was quite high, and recovery of $F_v/F_m$ was much reduced. In terms of $F_o$ changes, zeaxanthin formation and reduced recovery, this response was analogous to that of low-light-acclimated *Ulva*, where the xanthophyll cycle operates slowly, and where damage to PSII centres is believed to precede engagement of non-radiative dissipation (Franklin *et al.* 1992; Osmond *et al.* 1993). From the present results, we cannot conclusively state that damage to PSII has occurred in *Lobophora* from 20 m. Absence of the xanthophyll cycle in *Chlorodesmis* was unexpected, in view of previous results with *Ulva* (Franklin *et al.* 1992; Franklin 1994) and other chlorophyll *b*-containing plants (Demmig-Adams & Adams 1992). However, the increases in non-photochemical quenching and $F_o$ in *Chlorodesmis* were similar to those seen in *Ulva* (Osmond *et al.* 1993) and *Arabidopsis* (G.G.R. Seaton, The Australian National University, unpublished results) when the xanthophyll cycle in these species was inhibited with dithiothreitol. Uncoupling of xanthophyll cycle pigment concentration and zeaxanthin formation from the development of non-photochemical quenching has been demonstrated in higher plants (Hurry & Huner 1992; Hurry *et al.* 1992) subjected to a combination of high-light and cold treatments. These authors have suggested that, under these cold-hardened conditions, PSII centres may be converted into quenching centres, providing another route for energy dissipation. The fact that $F_v/F_m$, $F_v'/F_m'$, $\Phi_{II}$, and $q_P$ of *Chlorodesmis* recovered rather quickly under low light (Fig. 2e) indicates that there was no *long-lasting* damage to PSII centres, but we cannot rule out the possibility of rapid degradation and re-synthesis of the D1 protein, or the accumulation of protective, quenching PSII centres.

Furthermore, *Chlorodesmis* possesses morphological features which may contribute to its successful growth on shallow reef flats. This common filamentous alga occurs in clumps, from near the limit of low tide to at least 20 m. The morphology of the clumps changes with depth, varying from quite dense clumps of short filaments which completely cover 10 $cm^2$ or more of substrate at the surface, to very sparse groups of longer filaments at depths of 20 m or so. Thus, shelf-shading within the dense clumps may protect a significant proportion of the filaments from

excess irradiance. Since *Chlorodesmis* is coenocytic, there is also the potential for chloroplasts to move within the filaments to positions of lower irradiance (Menzel 1985). This strategy would effectively lower the absorption cross-section of the filament as a whole (Falkowski, Greene & Kolber 1994). We did not observe any obvious, large-scale movement of chloroplasts during these short-term experiments, though we cannot rule out accumulation of chloroplasts into many discrete areas within each filament. Hanelt & Nultsch (1991) observed that movement of chromatophores in *Dictyota dichotoma* from a low-intensity arrangement in the morning to a high-intensity arrangement during midday reduced absorption of visible light, and may be viewed as a mechanism by which the thallus is protected from photoinhibition.

### Potential impact of photoinhibition on the EAC

Ögren (1994) and Raven (1994) have discussed photoinhibition in relation to carbon gain and a cost/benefit analysis of resource allocations in individual plants. In extrapolating to the community level, they conclude that photoinhibition may well influence community-level processes, from productivity to species distribution. Since many of the species in the present study are common in the epilithic algal community, our results should apply to some degree to the EAC as a whole. Having confirmed that macroalgae of coral reefs are subject to photoinhibitory stress, under what circumstances, if ever, does lower photosynthetic efficiency have a significant impact on the community as a whole? Although we observed that photoinhibition was somewhat greater in the summer, we were unable to detect a substantial seasonal effect on the extent of photoinhibition in the reef habitat (cf. Henley *et al.*1992). Whereas strong photoinhibition occurred in the winter, the impact of brief periods of high-light stress is potentially less during this season, for at least two reasons. Firstly, our data on diurnal photoinhibition apply to fine day, and such fine days are less frequent in the winter than in the summer. Secondly, the periods of midday high-light stress are shorter in winter (Fig. 1).

It is clear that utilization of protective strategies and the capacity for recovery vary from species to species, and vary with light-acclimation history within a species. It is therefore difficult to make precise estimates of how diurnal photoinhibition affects overall community productivity and structure. Since field experiments on the EAC of shallow reef environments (Carpenter 1985; Klumpp & MacKinnon 1992; W.D. Larkum, K. Koop, & G. Westphalen, University of Syndney, unpublished results) indicate that no net inhibition of primary production occurs in these brightly lit environments, we propose that photoinhibition occurs in algae in the upper storey of the EAC but is compensated for by increased photosynthesis by algae in the lower (shaded) storey. While photoinhibition may not be such an important phenomenon in terms of primary production at the community level, it is still important in terms of the individual macroalga and coralline alga.

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