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Responses to high irradiance contribute to the decline of the spring diatom maximum

Abstract—The effect of high irradiance was studied with cultures and samples from natural populations of the colonial diatom *Asterionella formosa* Hass. The fluorescence ratio $F_v : F_m$, where F_v is the difference between DCMU-enhanced fluorescence (F_m) and normal, dark-adapted fluorescence (F_0), was used as a relative measure of photosynthetic performance. *A. formosa* grown in batch culture displayed a 70–80% decrease in $F_v : F_m$ during 1 h of exposure to 1,600 μmol quanta m^{-2} s^{-1}. In addition, sinking rate increased from a mean of 0.23 m d^{-1} in controls to 0.43 after high irradiance. *A. formosa* populations were sampled in May, the later stage of the spring abundance maximum in the north basin of Windermere (English Lake District). Diatoms in the upper 1–3 m exhibited low $F_v : F_m$ (0.1–0.2) during near-surface stratification (four of five dates) but no depression of $F_v : F_m$ on the one occasion of sunny weather and strong surface winds. Near-surface cell abundances were also significantly lower during high-irradiance, stratified conditions. The results suggest that high irradiance lowers production rates and increases sedimentation of diatom populations during the later stages of the spring maximum.

The spring phytoplankton maximum or "bloom" is one of the most important seasonal events in temperate waters (Fogg and Thake 1987). Growth is usually dominated by diatoms and controlled by light availability in the surface mixing layer (*see* Neale et al. 1991). Much less is known about what factors cause the decrease in growth rates and eventual decline in the spring diatom populations. Typically, the growth deceleration phase is associated with the setup of stratification, followed by sedimentation from the surface layer (Lund et al. 1963; Smetacek 1985). Under stratified conditions, accumulated biomass will rapidly deplete the surface layer of nutrients, particularly silicate in the case of diatoms, and growth will be slowed by nutrient limitation (Lund 1964). Nutrient-limited diatoms are known to have enhanced sinking rates (Titman and Kilham 1976; Jaworski et al. 1981; Davey 1988) and in marine systems may flocculate to form marine snow (Alldredge and Gotschalk 1989). The end of a diatom-dominated spring bloom can be marked by a very rapid collapse in which there is almost total collapse of the populations in the surface layer over the time scale of days (Alldredge and Gotschalk 1989).

The spring diatom maximum in lakes of the English Lake District has received extensive study (Neale et al. 1991 and references cited therein). Phytoplankton populations have been enumerated on a regular basis since 1945, and Chl *a* measurements have been made since 1964 (Talling and Heaney 1988). Populations of the dominant diatom, *Asterionella formosa* Hass., usually decline rapidly once nutrient depletion occurs (Lund 1964; Neale et al. 1991). Statistical analysis of the spring increase of *A. formosa,* however, has shown that net specific rates of increase fall off in the late-spring stratification period before there is any significant nutrient limitation of growth (Neale et al. 1991). Such a falloff could not be accounted for by sedimentation of nutrient-sufficient cells under stratified conditions. Sinking rates are known to increase, however, in response to adverse environmental conditions (e.g. for *A. formosa*: Jaworski et al. 1981; Davey 1988; Davey and Heaney 1989). The intensity of stratification (e.g. N^2, the square of the Brunt-Väisälä buoyancy frequency) has been correlated with sedimentation of diatom blooms in the English lakes (Reynolds et al. 1982). Other factors that have been considered are grazing, washout by floods, parasitism, and competitive interactions (*see* Lund 1964).

Asterionella formosa is sensitive to high

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irradiance and exposure to near-surface irradiance results in decreases in photosynthetic rates (Belay 1981; Belay and Fogg 1978), although it has not been established whether such effects extend to natural populations that are not confined to incubation bottles (Talling 1955). Use of in vivo fluorescence measurements circumvents the possibility of containment artifacts. Such methods showed the occurrence of in situ photoinhibition in tropical Lake Titicaca when diurnal stratification trapped near-surface phytoplankton populations in high-irradiance conditions (Vincent et al. 1984; Neale and Richerson 1987). The correlation between stratification and depression of DCMU-induced fluorescence has also been shown for temperate freshwaters in summer (Elser and Kimmel 1985; Putt et al. 1987).

In the present work, we examine high-irradiance effects on the in vivo fluorescence and sinking rates of *A. formosa* in relation to conditions during the later stages of the spring diatom abundance maximum in the north basin of Windermere. We present results on the responses of both cultures and natural populations of *A. formosa* to high irradiance.

Asterionella formosa was grown in the medium of Davey (1988) except that Na_2SiO_4 was lowered to 12.5 mg liter^{-1}, and P was added as 36 mg liter^{-1} of $Na_2HPO_4 \cdot 12H_2O$ in a 12 : 12 L/D regime at an irradiance of 40 μmol quanta m^{-2} s^{-1} (4π sensor, Biospherical Instr.) and 20°C. The growth rate is ~30% of maximum at this irradiance (Heaney unpubl.), which is within a factor of 2 of the mean surface-layer irradiance experienced by natural populations of *A. formosa* in Windermere during April and May. Cells were grown in batch cultures and harvested in late log phase (density ~20 × 10^3 cells ml^{-1}). Photoinhibition was induced with a halogen incandescent light source which was filtered through an 8-cm water bath to maintain a temperature of 20°–21°C. The light intensity was 1,600 μmol quanta m^{-2} s^{-1} (SD = 130 μmol quanta m^{-2} s^{-1} over illumination surface). Colony sinking rate was determined with the sucrose gradient method (Davey 1988). Settling of photoinhibited colonies was done in complete darkness for 20–30 min. Colony density was measured by isopyric banding on Percoll continuous gradients; the density of the band was determined with a paraffin/carbon tetrachloride density gradient calibrated with sucrose standards.

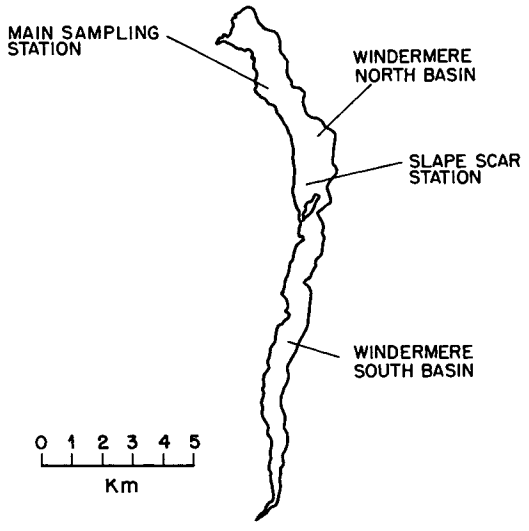

Fig. 1. Sampling stations in the north basin of Windermere. The main sampling station was used for routine measurements of cell abundance, pigments, and nutrient concentrations (7-m sampling tube). The Slape Scar station was used for profiles of near-surface fluorescence, abundance, and water temperature.

Samples were taken of phytoplankton population (>90% *A. formosa*) on several dates in April through June 1988 at two midbasin sites in the north basin of Windermere. The main sample station was near the deepest point of the basin and a second station (Slape Scar station) was located at the southern end of the main deep portion of the basin (Fig. 1). Samples were collected with a peristaltic pump and stored in dark bottles. Temperature (±0.1°C) was measured with a thermistor. During the same period weekly measurements were made of total Chl, dissolved inorganic nutrients, pH, and phytoplankton numerical abundance as described by Talling and Heaney (1988). Total solar irradiance (cal cm^{-2}) incident on the water surface was measured by an integrating thermopile solarimeter (Kipp) on the roof of the Windermere Laboratory of the Institute of Freshwater Ecology; photosynthetically active irradiance (PAR) was estimated as 46% of total (Talling 1971).

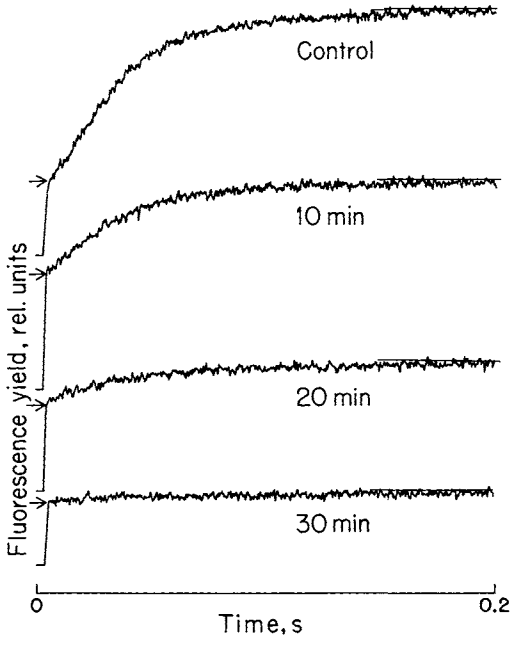

Fig. 2. Fluorescence induction curves of *Asterionella formosa* monitored over 0.2 s of illumination with bright blue light in the presence of DCMU. The F_0 (arrows) and F_m (horizontal lines at ends of curves) relative fluorescence yields are indicated for cells preilluminated for the indicated periods of high irradiance, ~1,600 μmol quanta m^{-2} s^{-1}. Samples were dark adapted for 30 min before measurement.

The steady state in vivo Chl fluorescence was measured with low-level blue excitation (excitation filter, Corning 5-60; emission filter, Corning 2-64; Turner Designs model 10 or Turner Associates 111). Measurements were made in dim room light. An initial fluorescence (F_0) was measured (a subsequent slow upward drift was occasionally noted), 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU) was added to a final concentration of 10 μM, and a second reading (F_m) was taken. The time-course of in vivo fluorescence increase (0–0.2 s) upon high-intensity illumination of *A. formosa* cultures (the fluorescence induction curve) was measured with a specially constructed fluorometer with 1-ms time resolution. Excitation light was provided by a filtered (Corning 5-60) 250-W light source connected to a fiber-optic light guide. Fluorescence was detected with a shielded (Corning 2-64) Hansatech FDP photodiode (Hansatech, Kings Lynn, Norfolk).

The fluorescence characteristics of *A. formosa* cultures during exposure to high irradiance were characterized by each of these two methods. The fluorescence induction curve of *A. formosa* (Fig. 2) shows a typical sigmoidal increase in fluorescence from an initial yield (F_0) to maximal yield (F_m) that is ~2.0–2.5 times higher than F_0 in dark-adapted control cells. The F_0 to F_m increase, the variable fluorescence (F_v), corresponds to the reduction of the primary acceptor of the photosystem 2 (PS2) reaction center, Q_A (Duysens and Sweers 1963). When Q_A reduction occurs, further photochemistry is prevented and the reaction center is closed. The amplitude of F_v, and to a lesser extent F_0, decreased during exposure to high irradiance (Fig. 2). This decline occurs because of the loss of functional PS2 reaction centers, i.e. photoinhibition (*see* Neale 1987). A convenient, nondimensional measure of the loss of photosynthetic performance is the ratio $F_v : F_m$. Decreases in $F_v : F_m$ are directly proportional to photoinhibition-caused decreases in photosynthesis (i.e. quantum yield and maximal electron transport) in both higher plants and algae (e.g. Neale et al. 1989).

When the same culture material was used to measure steady state F_m (presence of DCMU) and steady state F_0 (absence of DCMU), $F_m : F_0$ was also 2.5–2.6. Moreover, the two methods gave essentially equivalent estimates of $F_v : F_m$ during photoinhibition, i.e. a linear regression gave an intercept of 0.0 and slope of 1.0 ($r^2 = 0.997$, $n = 5$). Thus, equivalence exists between fluorescence induction curve parameters and steady state fluorescence, at least for the steady state fluorometers such as the Turner 111 or Turner Designs model 10 used with *A. formosa* (Harris 1980). Subsequently, we report only steady state fluorescence data and interpret variations in steady state $F_v : F_m$ as relative changes in the quantum yield of photosynthesis.

A high-irradiance treatment of 60 min resulted in a decrease in $F_v : F_m$ to 20–30% of the initial value (Fig. 3). This decrease is comparable with reports of decreases in photosynthetic rates of *A. formosa* during exposure to 2,000 μmol quanta m^{-2} s^{-1} (Belay and Fogg 1978). The relative decrease

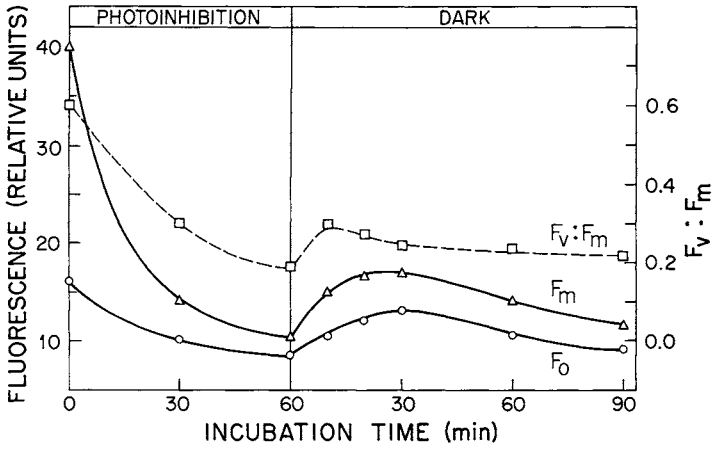

Fig. 3. Steady state in vivo fluorescence of *Asterionella formosa*. Fluorescence was measured both in the absence of DCMU (F_0) and in its presence (F_m) to calculate the fluorescence ratio ($F_v : F_m$) where $F_v = F_0 - F_m$. Photoinhibition—time-course of response to high-irradiance exposure; dark—time-course of response to dark adaptation after 60 min of exposure to high irradiance.

in $F_v : F_m$ is less than that in F_0 or F_m (Fig. 3) (cf. Heaney 1978).

It has been suggested that maintenance of low sinking rates is linked to vigorous metabolic activity (Andersen and Sweeney 1978). This suggestion motivated experiments on the effect of high irradiance on the colony sinking rate of *A. formosa*. Samples taken from cultures maintained in control conditions (nutrient sufficient, low irradiance) had an average sinking rate of 0.23 $\pm$0.09 m d^{-1} (SD, $n = 4$ cultures). A sinking rate of 0.2 m d^{-1} is considered typical of healthy *A. formosa* (e.g. Titman and Kilham 1976; Jaworski et al. 1981; Davey 1988). After 1 h of high-light treatment, the sinking rate was from 1.5 to 3.4 times higher than in controls (Table 1). The average sinking rate of photoinhibited colonies was 0.44$\pm$0.18 m d^{-1} (SD, $n = 5$). The density of control colonies (mean$\pm$SD, 1,145$\pm$30 kg m^{-3}) was not significantly different from that of photoinhibited colonies (mean$\pm$SD, 1,138$\pm$48 kg m^{-3}). The increase in sinking rate was not associated with any change in gross cell morphology or breakup of cell colonies. The sinking rate was faster when photoinhibition was more severe. Log-transformed sinking rate increased and $F_v : F_m$ had $r = -0.88$ ($P < 0.05$, $n = 5$).

Photoinhibition curtails metabolic activity and thus the sinking rate may increase in the same way as when metabolism is limited by nutrient availability (Davey 1988) or low light (Davey and Heaney 1989). The mechanism(s) that change the sinking velocity are unknown, though changes in colony size and density do not appear to be important. Discrepancies between theoretical (Stokes' law) and measured sinking ve-

Table 1. Determination of colony sinking rates for *Asterionella formosa*. Cultures were maintained at 40 μmol quanta m^{-2} s^{-1}, 12 : 12 L/D at 20°C. Sinking rates (m d^{-1}) were determined on controls sampled at midday or after 1 h of exposure at the indicated irradiance (μmol quanta m^{-2} s^{-1}). The $F_v : F_m$ for each experiment is also given; cells were dark adapted for 30 min before the fluorescence determination.

Expt. No.	Irradiance	Treatment $F_v : F_m$	% control $F_v : F_m$	Sinking rate		% increase
				Control	Treatment	
1	1,600	0.24	40	0.35	0.57	167
2	1,600	0.35	60	0.21	0.33	157
3	1,600	0.14	20	0.18	0.62	344
	150	0.57	90		0.23	127
4	1,600	0.26	41	0.15	0.24	160

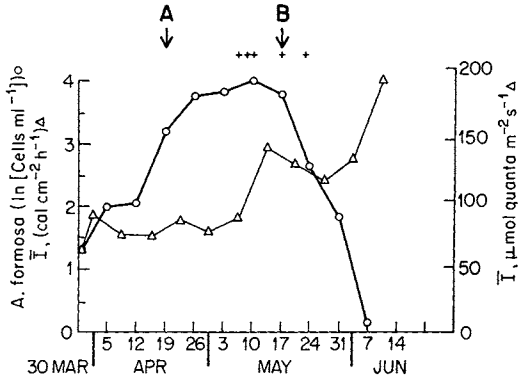

Fig. 4. Abundance of *Asterionella formosa* and mean surface layer irradiance (PAR) for the north basin of Windermere in spring 1988. Arrows indicate (A) setup of the seasonal thermocline at 7 m in the third week in April and (B) depletion of dissolved silicate to <0.05 mg SiO_2 liter^{-1}.

locities have been found in studies of other diatom species (Davey 1988). Due to the rapid response time scale, the increase in sinking rate during photoinhibition may be useful as a model system for studying the response of algal buoyancy to stress.

The results with cultures demonstrated the rapid decrease in $F_v : F_m$ and increase in sinking rate that occurs when *A. formosa* is exposed to high irradiance and provided a basis for interpreting field observations made during the 1988 spring maximum in the north basin of Windermere. The 1988 spring maximum was typical of long-term averages (Neale et al. 1991): the surface-layer (0–7-m sampling tube) abundance of *A. formosa* increased at an average specific rate of 0.19 d^{-1} between weeks 12 and 17 (30 March–26 April) (Fig. 4). Afterward the rate of increase slowed and averaged 0.04 d^{-1} during weeks 17–19. Silicate concentrations remained >0.5 mg liter^{-1} (8.3 μM) until week 19. After 10 May (weeks 20–23) silicate was <0.1 mg liter^{-1} (1.6 μM) and *A. formosa* populations started a dramatic decline. Mean daily surface irradiance increased throughout this period and peaked in June well after the end of the spring bloom (Fig. 4). The surface pH during this period varied between 7.2 and 7.6.

Profiles of in vivo fluorescence were made on five occasions in May. Mean surface irradiance on sampling days ranged from 7.2 to 11 cal cm^{-2} (PAR) h^{-1}, or ~400–650 μmol quanta m^{-2} s^{-1}. Mean irradiance in the surface layer (calculated as described by Neale et al. 1991) ranged between 1.25 and 3 cal cm^{-2} (PAR) h^{-1} (Fig. 4). The long-term average (1964–1988) for weeks 20–23 is 9.33 cal cm^{-2} h^{-1}. Mid- or lower euphotic zone ($z \geq 3$ m) samples typically had $F_v : F_m$ ratios of 0.5–0.6, similar to ratios exhibited by healthy *A. formosa* cultures (*see above*). On four of the five days, the near-surface portion of the populations sampled at this time had significantly depressed $F_v : F_m$, decreasing to ~0.1 (20% of the value in deep samples) (Fig. 5). $F_v : F_m$ was lower in the upper 2–3 m of the 5–5.5-m euphotic zone (1% light depth). After silicate was depleted, $F_v : F_m$ was lower at all depths. Surface populations, however, continued to have lower $F_v : F_m$ relative to deep populations (Fig. 5).

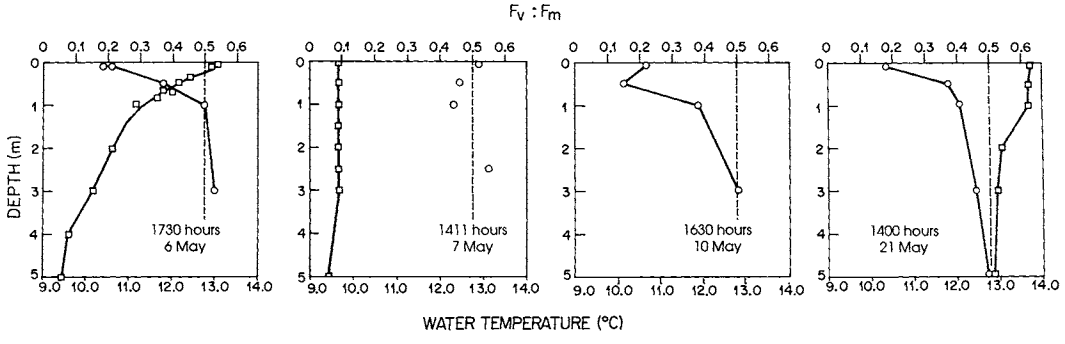

Fig. 5. Profiles of the in vivo fluorescence ratio (○) and temperature (□) in the surface layer of the north basin of Windermere on days before and after surface silicate depletion (*see Fig. 4*). Weather conditions for these dates were morning overcast and afternoon sun on 6 May, fair weather combined with sustained surface winds on 7 May, and both morning and afternoon sun on 10 and 21 May.

The depression of $F_v : F_m$ occurred at times when stratification extended to the surface, resulting in prolonged residence times of near-surface populations at high irradiances (cf. Vincent et al. 1984; Neale and Richerson 1987). On the basis of typical light penetration and midday surface irradiance, the average quantum flux in the upper meter of the water column was 1,400 μmol m^{-2} s^{-1} (assuming 2,000 μmol m^{-2} s^{-1} surface irradiance and 14 μg $liter^{-1}$ Chl, Neale et al. 1991) during this period. Interestingly, $F_v : F_m = 0.1$ was attained after only 1 h of exposure of cultures, whereas field populations may have seen several hours of high irradiance before sampling. This equivalent response is consistent with the notion that after an initial exposure period damage reaches a steady state that is determined by the maximum dose rate (Neale and Richerson 1987; Neale 1987).

A diurnal cycle of near-surface stratification during the day and partial or total overturn associated with wind mixing and nocturnal cooling has already been shown for another nearby basin, Esthwaite Water (Frempong 1983), as well as for other lakes (e.g. Vincent et al. 1984; *see* Neale 1987). The one sampling date when no surface depression of $F_v : F_m$ was observed despite clear skies was when southerly winds (aligned with the basin) persisted through the day and the upper part of the water column was isothermal (Fig. 5, 7 May). These results confirm that both high surface irradiance and surface stratification (e.g. from diurnal thermoclines) is required before significant in situ photoinhibition can occur (Neale 1987).

Profiles of cell abundance on dates when photoinhibition was significant also showed a pronounced surface depletion of cell abundance (Fig. 6). A similar pattern of decrease was exhibited by the dark-adapted in vivo fluorescence (F_0). Note that the decreased surface $F_v : F_m$ is independent of variations in biomass and thus was not caused by cell depletion.

The field studies reported here show that near-surface stratification sufficiently extends residence times of *A. formosa* in high irradiance so that photoinhibition, as assayed by $F_v : F_m$, occurs in situ during the later stages of the spring *A. formosa* maximum in the north basin of Windermere. Chronic in situ photoinhibition will result in decreases in growth rate. The overall impact of high-irradiance damage depends on the rate of recovery, which can be quite slow in *A. formosa* (Belay and Fogg 1978). In addition, high-irradiance-dependent increases of *A. formosa* sinking rate should result in significant depletion of cells from the surface layer. The occurrence of this phenomenon is supported by a strong surface depletion of natural populations of *A. formosa* in the photoinhibition zone. This surface depletion was not apparent during isothermal conditions. A sinking rate enhanced by high irradiance would explain not only the depletion of cells at the surface but

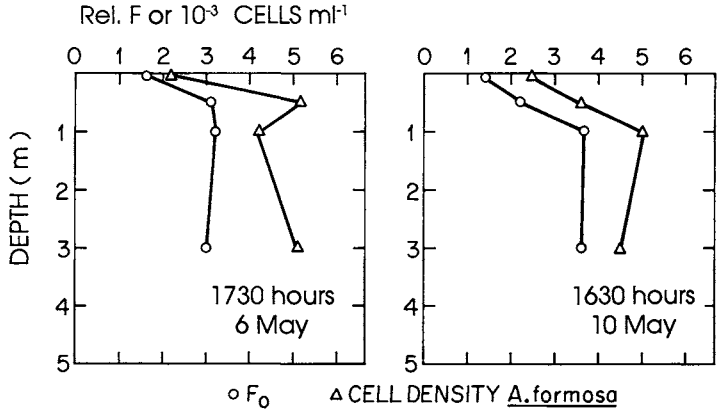

Fig. 6. Depth profiles of cell abundance of *Asterionella formosa* (△) and dark-adapted in vivo fluorescence (○) on days of surface stratification and low near-surface $F_v : F_m$ (*see Fig. 5*).

also the appearance of photoinhibited cells (based on $F_v:F_m$) at depths below where photoinhibiting irradiances occur (i.e. 1 m), for example in the 10 May profile (Fig. 5).

Asterionella formosa does not seem to adapt quickly to high irradiance; the enhanced sinking rates after exposure to high irradiance may be advantageous to escape continued exposure to it under stratified conditions. At the maximal sinking rate observed after photoinhibition in the culture studies (0.6 m d^{-1}), cells sinking for 1 d in Windermere would experience a decrease of ~40% in mean irradiance (Neale et al. 1991). The lowered irradiance would be unlikely to cause further photoinhibition (Belay and Fogg 1978). It has been suggested that increases in sinking rate during adverse conditions, leading to a fairly rapid settling out of diatom populations, may be part of the diatom life strategy (Smetacek 1985). Photoinhibition results from very localized damage to the algal photosynthetic apparatus; the PS2 reaction center is usually the only affected complex (reviewed by Neale 1987). Although protein synthesis is necessary to repair PS2, the rest of the chloroplast and cytosol survives intact. Repair requires light, but the rate of repair is saturated at very low light intensities (Neale 1987). *A. formosa* sinking in response to photoinhibition has a high probability of surviving for an extended period in the metalimnion before remixing into surface waters enables summer regrowth (Heaney and Butterwick 1985) or settling into bottom waters (Heaney et al. 1989; Davey and Heaney 1989).

In several respects photoinhibition and nutrient limitation act in similar ways to mediate the stratification-initiated decline in the spring diatom maximum. Both result in a decrease in growth rate and enhance sedimentation out of the surface layer. Nutrient limitation and photoinhibition can operate independently or may interact. Mass sedimentation of *Fragilaria crotensis* was observed once stratification formed in limnetic enclosures even when high concentrations of silicate were maintained (Reynolds et al. 1982). Reynolds et al. (1982) speculated that photoinhibition may be an important factor in this situation, although pH was high enough (>9) that growth limitation and increased sedimentation could also have been caused by CO_2 depletion (Jaworski et al. 1981). Conversely, *A. formosa* populations were kept at near peak levels in a eutrophic lake (Crose Mere) when unusually stormy spring conditions delayed the development of stratification despite depletion of silicate to very low levels (Reynolds and Reynolds 1985). *A. formosa* cultures in plateau (nutrient depleted) phase can be kept for long periods in low light, but will die rapidly when exposed to high irradiance (Moed 1973). The results of this study show that other factors can work before nutrient limitation, and later together with nutrient limitation, to cause rapid declines in spring diatom populations.

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