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Thalassiosira oceanica and *T. pseudonana*: two different photoadaptational responses

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ABSTRACT: The oceanic centric diatom *Thalassiosira oceanica* (13-1) and the neritic *T. pseudonana* (3H, both formerly *T. pseudonana*) differ in their photoadaptational responses. According to flow cytometric studies with nutrient-saturated cultures in the laboratory at 15 °C, *in vivo* fluorescence and chlorophyll per cell of *T. oceanica* varied negligibly between cultures adapted to 70 and 300 µmol m^{-2} s^{-1}. The cultures decreased in cell density when exposed to outdoor light (2800 µmol m^{-2} s^{-1} at noon), and the still viable subpopulation exhibited a 70 to 75 % lower fluorescence and chlorophyll per cell than the laboratory cultures. In *T. pseudonana* the same photoadaptive parameters were markedly dependent on photon flux. It grew actively albeit at a reduced rate in strong outdoor light, at which *in vivo* fluorescence was reduced by 30 to 60 %. Suppression of fluorescence was reversible and independent of cellular chlorophyll content (which increased somewhat) and was completed within 30 to 40 min. This 'sunglass' effect is apparently a manifestation of a protective mechanism against strong light and should be advantageous for a neritic opportunistic species. Rates of adaptation were within known limits. Neither species grew actively at 17 µmol m^{-2} s^{-1}, at which viable subpopulations retained the photoadaptational characteristics of the inoculum. Thus sudden transfer of algae to marginally low light arrests the photoadaptational response. Decreasing average fluorescence and volume per cell in slowly dying cultures of *T. pseudonana* was solely due to increasing prominence of a subpopulation of cells with abnormally low fluorescence and small volume.

INTRODUCTION

Fluctuations in the light regime of phytoplankton in nature comprise variational patterns on different time scales, ranging from seasonal variations to fluctuations on the scale of seconds to hours (Dera & Olszewski 1967, Legendre 1981, Demers et al. 1986). Phytoplankton respond to such fluctuations by photoadaptation in such a fashion that the accompanying variation in growth rate is usually minimized (Sakshaug & Holm-Hansen 1986). Photoadaptation comprises light-dependent alterations in various physiological processes (Prézelin & Sweeney 1979, Falkowski & Owens 1980, Perry et al. 1981) as well as the overall biochemistry of the cell, particularly pigment content and composition (Steemann Nielsen & Jørgensen 1968, Geider & Platt 1986, Sakshaug & Andresen 1986, Yentsch et al. 1986).

While light-dependent changes in chlorophyll content of the cells may be completed in a matter of hours or a few days (Gallegos et al. 1983, Post et al. 1984), other light-dependent changes, such as fluorescence quenching in strong light and in the ratio between diatoxanthin and diadinoxanthin may be completed within minutes. These rapid changes may be useful indices for vertical mixing (Vincent 1979, Harris 1980, Welschmeyer & Hoepffner 1986).

Photoadaptative strategies are clearly species-specific (Falkowski & Owens 1980). Richardson et al. (1983) have ranked groups of algae according to light preferences suggesting that chlorophytes are in general the most photophilic ones. Some dinoflagellates may, in contrast, prefer the low light near pycnoclines (Tyler & Seliger 1978, Holligan et al. 1984). Rock-pool algae have to tolerate strong sunlight regularly, while some polar species have to tolerate the particularly harsh combination of strong light and near-freezing

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temperatures (Sakshaug 1988). Thus species-specificity in photoadaptive strategy may bear strong relation to the distribution of algal species in time and space.

In the present study we illuminate some of the features mentioned above through experiments with 2 diatom species, *Thalassiosira pseudonana* and *T. oceanica*, which live in neritic and oceanic mid-latitude habitats, respectively. They were earlier regarded as 2 clones of 1 species (Guillard & Ryther 1962). They have been studied by means of flow cytometry: changes in *in vivo* fluorescence, chlorophyll and volume per cell were recorded for cultures exposed briefly to or grown at different photosynthetic photon flux densities (PPFD). We also studied the time-course of adaptation as well as the behavior of cultures at marginally low and marginally high light. The use of flow cytometry made it possible to study the properties of individual cells and to carry out rigorous statistical treatment of data including subpopulations of the cultures.

MATERIAL AND METHODS

Thalassiosira oceanica Hasle and *T. pseudonana* (Hustedt)Hasle and Heimdal (formerly *T. pseudonana* clones 13-1 and 3H, respectively; source: Center for Culture of Marine Phytoplankton at Bigelow Laboratory) were grown at 15 °C in batch cultures made from natural seawater collected at the pier at Bigelow Laboratory. Salinity was 32.5‰. Growth medium was enriched according to the 'f' recipe of Guillard & Ryther (1962) at 1/10 strength (nitrogen source: f/10 nitrate plus f/20 ammonia, total 265 µmol l^{-1}; N/P, atoms, = 36). The cultures were diluted with fresh medium when necessary to keep cell density well below the density which was characteristic at the end of the exponential phase, so as to avoid nutrient limitation. Control cultures were grown in continuous light (cool-white fluorescent tubes) at photosynthetic photon flux densities (PPFDs) of 17,70 and 330 µmol m^{-2} s^{-1} (measured with a QSL-100 photometer with spherical collector, Biospherical Instruments, Inc.) for 8 d, after which they were sampled 3 to 5 times d^{-1} for up to 4 d. Cultures for studies of adaptation rates were grown for 4 to 7 d and were then assumed to be adapted to the PPFD in question. They were then transferred to another of the PPFDs and were sampled 5 to 7 times d^{-1} for up to 3 d. Some of the cultures were transferred to natural light which around noon ranged from 500 (foggy) to 2800 µmol m^{-2} s^{-1} (sunshine). The exceptionally high photon flux in sunshine was partly a result of the high reflectivity of a white tray in which the cultures were placed. Outdoor daylength was about 11 h, and temperature was 11 and 14 °C for *T. pseudonana* and *T. oceanica*, respectively. These cultures were sampled for 2 to 4 d following the day of transfer. Additional experiments in strong light (photoinhibition studies) were carried out in the laboratory by using a 500 W projection bulb (Sylvania) as a light source. It yielded 2300 µmol m^{-2} s^{-1} in the culture chamber.

Per cell *in vivo* fluorescence and cell volume were determined at 4 to 8 h intervals. A FACS Analyzer flow cytometer (Beckton-Dickinson, Mountain View, California) was used to measure cell volume and relative fluorescence from chlorophyll *a* on an individual particle basis (excitation light: 488 nm band of a mercury lamp; collected emission: >650 nm). At least 1000 counts of fluorescence were used to generate each data point along the time course of the experiments (30 s interrogation time). The data represent mean values for the whole counted population unless subpopulations are specified. Cell sorting was done with an EPICS V Flow Cytometer/Sorter (Coulter Electronics, Hialeah, Florida; see Phinney et al. 1987 for details).

Flow cytometer measurements were calibrated against fluorescent beads (Fluorosphere Fullbright) so that fluorescence per cell was on the same relative scale for both species and from day-to-day. Cell volume is given as the spherical equivalent (µm^3) as measured by the flow cytometer. Cell surface area was calculated on basis of the spherical equivalent volume and the assumption of a spherical shape of the cells. This yields a scale for cell surface area which is directly related to volume measurements by the flow cytometer. Chlorophyll *a* (extraction in absolute methanol) was measured with a Turner model 111 fluorometer according to Holm-Hansen et al. (1965). Cell density (cells ml^{-1}) is the number of simultaneous fluorescence and volume counts recorded by the flow cytometer divided by the volume of the sample drawn through the instrument. The latter was measured by pipetting before and after analysis.

Studies of carbon uptake in strong light were carried out by adding 3.7×10^6 Bq (100 µCi) of ^{14}C bicarbonate to 100 ml culture in flint glass bottles. They were exposed to 19 µmol m^{-2} s^{-1} for 30 min, then to 2300 µmol m^{-2} s^{-1} for 1 h, and finally to 19 µmol m^{-2} s^{-1} again. Samples of 1 ml were collected at 2 to 5 min intervals. They were placed in scintillation vials with 0.5 ml 6N HCl and shaken for 1 h. Then 0.5 ml 6N NaOH was added. Scintillation cocktail was added the following day, and the samples were counted in a Beckman scintillation counter after several hours in the dark. Activity was determined by adding an aliquot of the inoculated culture to PEA (phenethylamine), adding fluor and counting. The CO_2 concentration was assumed to be 2 mmol l^{-1}.

The effect of gramicidin D (Sigma Chemical Co.) at 10 µmol l^{-1} concentration on *in vivo* fluorescence was

tested at various times in strong as well as low light. Gramicidin is a ionophore which allows passive, diffusion-limited transport of small molecules through membranes by forming channels through them (Alberts et al. 1983).

RESULTS

The highest growth rate of control cultures of *Thalassiosira pseudonana* and *T. oceanica* was observed at 330 μmol m^{-2} s^{-1} (Table 1). *T. pseudonana* exhibited the higher maximum rate (2.12 *vs* 1.75 doubl. d^{-1}). At 70 μmol m^{-2} s^{-1}, however, control cultures of *T. oceanica* grew faster than control cultures of *T. pseudonana*. When exposed to natural light (up to 2800 μmol m^{-2} s^{-1}), the latter grew at 0.89 doubl. d^{-1}, while *T. oceanica* decreased quickly in cell density (corresponding to −1.2 doubl. d^{-1}). Thus both species were sensitive to the light regime, but *T. pseudonana* was superior at the high end of the PPFD scale, and *T. oceanica* at the lower end.

In *Thalassiosira oceanica, in vivo* fluorescence and chlorophyll per cell exhibited virtually identical values at 70 and 330 μmol m^{-2} s^{-1}, and 70 to 75 % lower values in outdoor light. Even if cell density decreased with time in the latter case (e.g. parts of the population died), the estimates for fluorescence and chlorophyll per cell were highly reproducible. Some abnormal and presumably dying cells were detected by the flow cytometer, but were too few to affect the results significantly. These values may therefore represent a lower limit for *in vivo* fluorescence and chlorophyll of viable cells in strong light. Because cell volume appeared independent of photoadaptational status (Table 1), chlorophyll and fluorescence per unit cell surface largely followed the variational pattern for chlorophyll per cell.

In *Thalassiosira pseudonana* all measured cellular parameters were dependent on the photoadaptational status of the cells (Table 1). *In vivo* fluorescence and chlorophyll per cell were clearly higher in cultures adapted to 70 than to 330 μmol m^{-2} s^{-1}, while cell volume and the ratio between fluorescence and chlorophyll were smaller. Correspondingly, chlorophyll per unit cell surface also varied, but the average value (0.0042 pg μm^{-2}) was virtually identical to that of *T. oceanica* grown in moderate to low light. Surprisingly, chlorophyll per cell of cultures which were exposed to natural light was about 1.6 times higher than at 330 μmol m^{-2} s^{-1}, whereas fluorescence per cell and the ratio between fluorescence and chlorophyll were reduced by 60 and 75 %, respectively, except on one foggy day at which the maximum photon flux was only 500 μmol m^{-2} s^{-1}.

Neither species grew actively at 17 μmol m^{-2} s^{-1}. When *Thalassiosira oceanica* was transferred to this regime from the culture bank (70 μmol m^{-2} s^{-1}), the cells

Table 1. *Thalassiosira oceanica* and *T. pseudonana*. Characteristics of laboratory (control) cultures grown at 17, 70 and 330 μmol m^{-2} s^{-1} and of cultures exposed to outdoor light of up to 2800 μmol m^{-2} s^{-1} on clear days and up to 500 μmol m^{-2} s^{-1} on one foggy day between the clear days. Average values for a number of estimates (n); coefficient of variation of the mean (%) given in parentheses; growth rate (μ) as doublings d^{-1}; *in vivo* chlorophyll fluorescence per cell (FL) in relative units (same for both species); chlorophyll as pg $cell^{-1}$; cell volume as μm^3; ratio between chlorophyll and cell surface area as pg μm^{-2}

PPFD	μ	FL	Chl	Vol	FL/chl	Chl/area
T. oceanica (13-1)						
17*	0	35 (1.3)	0.57 (7.6)	150 (2.0)	61	0.0043
70	1.34 (3.6)	37 (3.6)	0.58 (7.9)	150 (2.1)	64	0.0044
330	1.75 (3.9)	37 (2.2)	0.56 (16)	160 (1.6)	66	0.0040
2800**	−1.2 (8.5)	8.6 (2.5)	0.17 (5.6)	150 (2.2)	50	0.0013
n	3	18	6	18	6	6
T. pseudonana (3H)						
17***	–	–	–	–	–	–
70	0.85 (7.8)	21 (1.4)	0.33 (5.0)	32 (1.5)	64	0.0067
n	3	25	6	25	6	6
330	2.12 (3.5)	14 (1.2)	0.13 (11)	36 (1.6)	110	0.0025
n	3	25	6	25	6	6
500	–	15 (4.5)	0.22 (8.3)	41 (2.9)	68	0.0039
n		4	4	4	4	4
2800	0.89 (8.3)	5.8 (8.8)	0.20 (10)	41 (2.6)	27	0.0037
n	4	10	10	10	10	10

* Cultures may retain characteristics of the inoculum instead of having adapted
** Cultures die, but exhibit reproducible values
*** Two subpopulations appear The viable subpopulation (see text) differs from the inoculum by <10 % in terms of fluorescence and volume per cell

underwent one doubling after which the cell density remained virtually constant (observed for up to 14 d, data not shown). The cells generally retained the same values for fluorescence, chlorophyll and volume as observed for control cultures which were adapted to 70 or 330 μmol m^{-2} s^{-1}. They may therefore have retained the photoadaptational characteristics of the inoculum.

Cultures of *Thalassiosira pseudonana* would also increase somewhat in cell density during the first 2 d after transfer from the culture bank to 17 μmol m^{-2} s^{-1}. Later the cell density decreased slowly (Fig. 1). After a

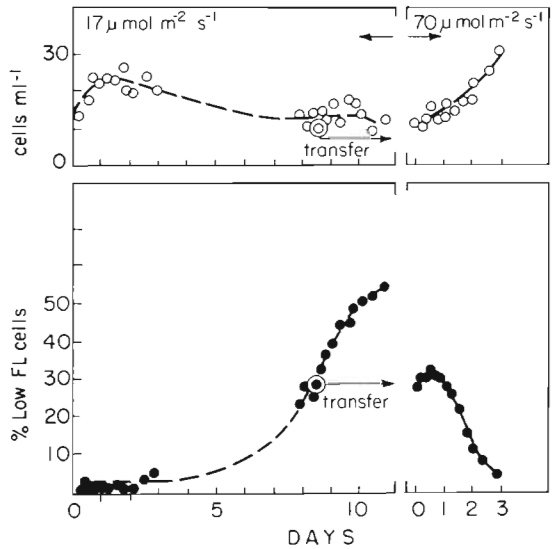

Fig. 1. *Thalassiosira pseudonana*. Time course of cell density and percentage of low-fluorescent cells at 17 μmol m^{-2} s^{-1} and after transfer from 17 to 70 μmol m^{-2} s^{-1}

while this species exhibited a distinct bimodal distribution of cellular fluorescence and volume (Fig. 2). One peak was characterized by low-fluorescent cells with small cell volume. The characteristics of the second peak corresponded to the light regime from which the cells were transferred (Fig. 4A). When the cultures became older, the proportion of small, low-fluorescent cells became larger (Fig. 1 & 3). They may possibly represent a last stage before cells died and decayed beyond flowcytometric recognition. The low-fluorescent cells were recoverable, because healthy cultures grew up from them after they were repeatedly sorted electronically to >99 % purity and brought to optimum light regimes. It is noteworthy that the decrease with time in average cellular fluorescence and chlorophyll in this case (Fig. 3C) was due to changes in the relative number of cells of 2 distinct subpopulations and not due to changes in the characteristics of each subpopulation.

Chlorophyll-dependent changes in *in vivo* fluorescence were notable only when *Thalassiosira oceanica* was transferred to outdoor light and *T. pseudonana*

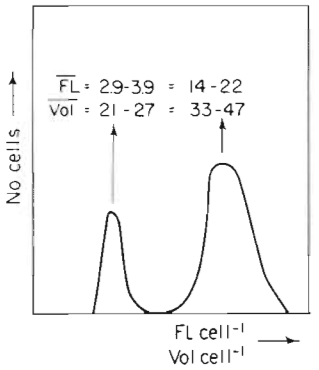

Fig. 2. *Thalassiosira pseudonana*. Schematical illustration of bimodal frequency distribution of fluorescence and volume per cell at 17 μmol m^{-2} s^{-1} (number of cells *vs* fluorescence or volume per cell). Left peak: low-fluorescent cells which disappear in light regimes which allow active growth. Right peak: cells which retain the characteristics of the inoculum. Average fluorescence (relative units) and volume per cell (μm^3) given for each of the 2 subpopulations. Dispersion of measurements around the mean of each peak corresponded to a coefficient of variation of 35 % for fluorescence and 43 % for cell volume

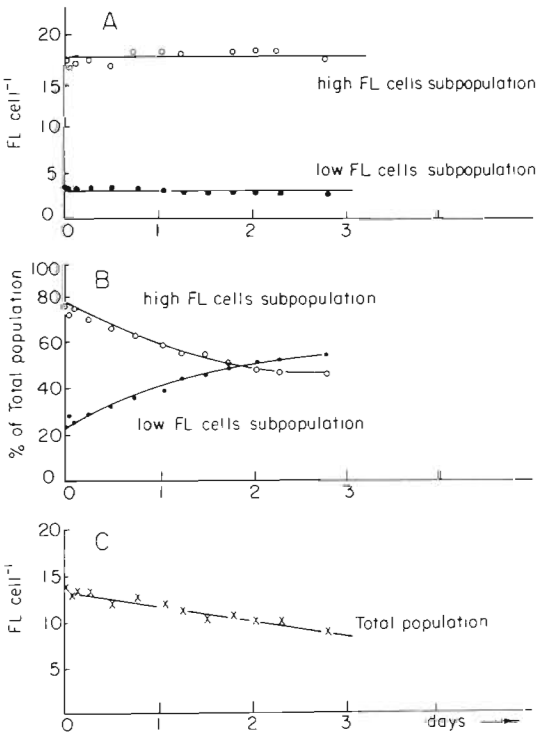

Fig. 3. *Thalassiosira pseudonana*. Time-course of *in vivo* fluorescence per cell (relative units) at 17 μmol m^{-2} s^{-1} (A) Average fluorescence per cell within each subpopulation (cf. Fig. 2); (B) relative frequency of each subpopulation; (C) resulting average fluorescence per cell of total population

from 70 to 330 μmol m^{-2} s^{-1} and vice versa. In the case of *T. oceanica* the transition was already concluded at the first measurement 1.2 d after transfer This corres-

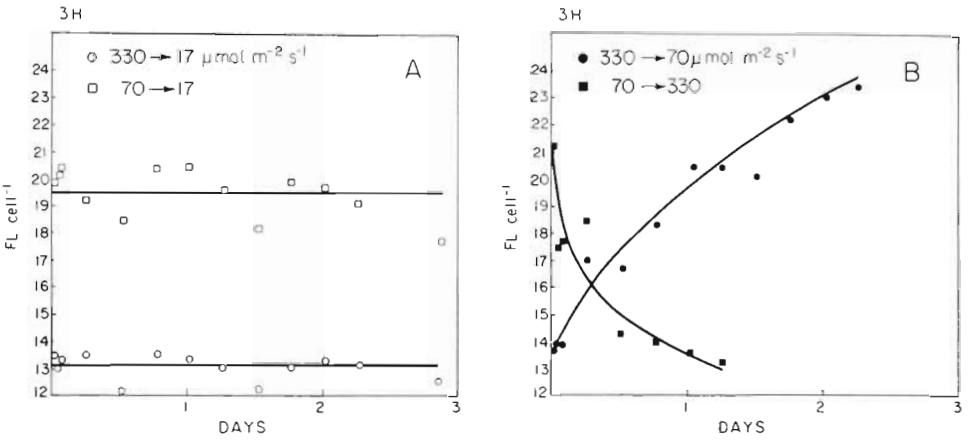

Fig. 4. *Thalassiosira pseudonana*. Time course of *in vivo* fluorescence per cell (relative units). (A) Cultures transferred from 70 and 300 to 17 µmol m^{-2} s^{-1} (data for low-fluorescent population excluded); (B) cultures transferred from 70 to 330 µmol m^{-2} s^{-1} and from 330 to 70 µmol m^{-2} s^{-1}

ponds to a first-order rate constant of at least 0.051 h^{-1}. With *T. pseudonana*, adaptation from light to shade took longer than adaptation the opposite way (Fig. 4B) and yielded first order rate constants of about 0.020 and 0.033 h^{-1}, respectively. This asymmetry was evident also when calculations were based on inverse values (Geider & Platt 1986).

Table 1 indicates that only *Thalassiosira pseudonana* exhibited the marked chlorophyll-independent decrease in cellular fluorescence when cultures were transferred to strong outdoor light. This phenomenon was studied further by transferring cultures of both species in outdoor light from 600 to 800 to 2800 µmol m^{-2} s^{-1} and vice versa (Fig. 5A). Evidently the cellular fluorescence of *T. pseudonana* started dropping after a lag of at most 10 min when cultures were exposed to strong light. The new fluorescence level was 50 to 70 % of the former and stabilized in less than 30 min. When cultures were transferred to low light again, fluorescence increased and reached its original level after 25 to 35 min. Cellular chlorophyll varied negligibly during this experiment, but was at a lower level (0.091 to 0.11 pg) than for outdoor cultures in Table 1, which probably means that the cells still reflected the pigment content typical at 330 µmol m^{-2} s^{-1} after only 1 dark cycle. The fluorescence quenching in strong light was thus again independent of the chlorophyll content of the cells. It is noteworthy that this quenching again was not evident in *T. oceanica* (Fig. 5A).

In a similar transfer experiment in the laboratory (from 19 to 2300 µmol m^{-2} s^{-1} and vice versa), the carbon uptake increased in strong light for both species, but the uptake rate of carbon per unit cell volume for *Thalassiosira oceanica* was only half of that for *T. pseudonana* (Fig. 6). When gramicidin was added to cultures of *T. pseudonana*, the quick decrease in fluorescence, otherwise noted in strong light, was evident at low light (Fig. 5B).

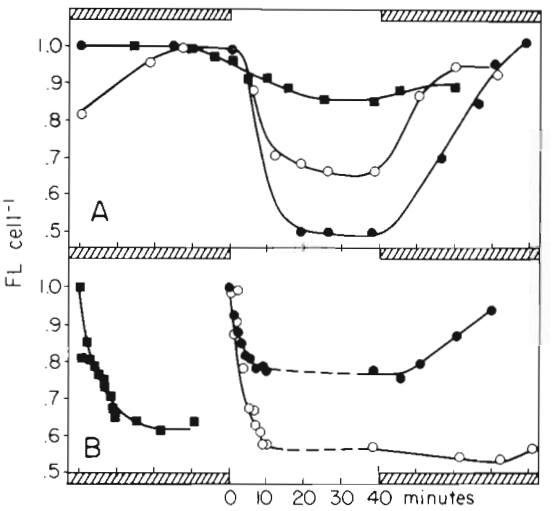

Fig. 5. *Thalassiosira pseudonana and T oceanica*. Short-term changes of *in vivo* fluorescence per cell normalized to the highest observed value in each experiment. (A) *T pseudonana* at 600 (○) or 800 µmol m^{-2} s^{-1} (●) exposed to 2800, and then to 600 or 800 µmol m^{-2} s^{-1} and *T. oceanica* (■) at 800 µmol m^{-2} s^{-1} exposed to 2800 and then to 800 µmol m^{-2} s^{-1} (B) Changes in *in vivo* fluorescence per cell of *T. pseudonana* after addition of gramicidin; (■) cultures at 800 µmol m^{-2} s^{-1}; (○) cultures at 2800 µmol m^{-2} s^{-1} followed by darkness; (●) control (no gramicidin), cultures at 800 µmol m^{-2} s^{-1} followed by darkness. Horizontal bars: period of low light or darkness according to descriptions above

DISCUSSION

The present investigation has shown how 2 species react to variation in PPFD, and it is evident that they respond differently. Photoadaptation obviously involves changes in pigment content as well as fluorescence properties. By means of flow cytometry it has become possible to study the population structure of algal cultures, and this has revealed some peculiar

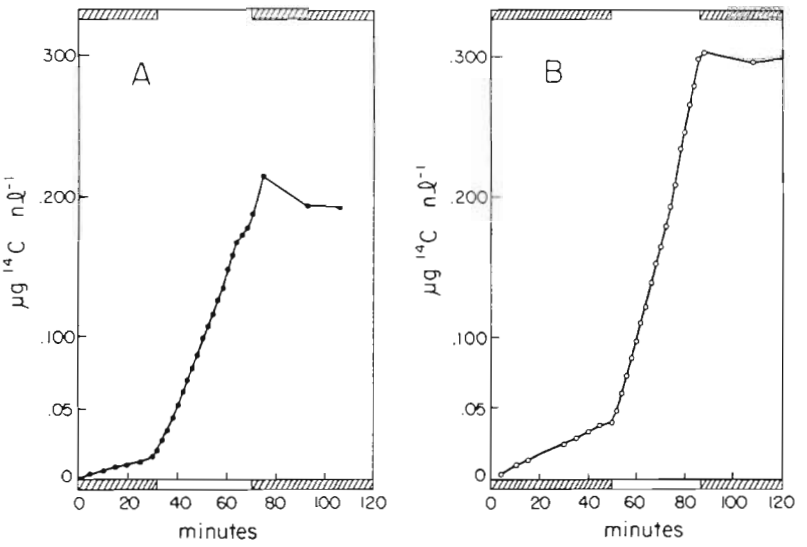

Fig. 6. *Thalassiosira oceanica* (A) and *T. pseudonana* (B). Content of ^{14}C per unit cell volume (µg ^{14}C nl^{-1}) of cultures exposed to 19 (dashed area), then to 2300, and finally to 19 µmol m^{-2} s^{-1} again

phenomena related to zero growth in marginally low light.

The chlorophyll-independent photoadaptive response which is mediated through inverse changes in cellular fluorescence relative to PPFD is of particular interest, because it happens on a scale of minutes, is species-specific, and breaks with the usual pattern in which the ratio between *in vivo* fluorescence and chlorophyll increases somewhat when cells become adapted to a higher PPFD. Considering the active growth of chlorophyll-rich *Thalassiosira pseudonana* in strong light in contrast to the rapid death of *T. oceanica* in strong light in spite of lowered chlorophyll, it is likely that this effect represents a protective mechanism which may diminish, if not fully prevent, damage to the photosynthetic apparatus. The likeness between this effect and the effect of gramicidin, may suggest that the electrochemical gradient across relevant membranes becomes reduced in strong light so that the energy supply to Photosystem II, where fluorescence is generated, becomes reduced. We have no evidence of the details of such a proposed mechanism, but this 'sunglass' effect acts at the time scale of the reversible and PPFD-dependent cycling of the xanthophylls diadinoxanthin and diatoxanthin in diatoms (Hager 1975, Goedheer 1984). These processes may therefore be related in analogy with a suggested relationship between fluorescence quenching and the violaxanthin/zeaxanthin cycle in a variety of higher plants (Demmig & Björkman 1987). HPLC analysis of diadino- and diatoxanthin on corresponding samples for *in vivo* fluorescence quenching demonstrates that *T pseudonana* has a greater amount of the total 2 pigments as compared to *T. oceanica* grown under similar environmental conditions (J. Brown pers. comm.).

The protective nature of the mechanism behind the quenching of fluorescence in strong light and its rapid response is ecologically significant. It provides the algae with a means to respond to rapid changes in irradiance, in addition to the slower response which involves regulation of pigment content and composition. It makes a species flexible in its response to quickly fluctuating and strong light, such as during rapid vertical mixing and on days with variable cloudiness. Not surprisingly, some common 'laboratory weeds' derived from rockpools apparently possess this mechanism (Falkowski pers. comm.). The protective mechanism may also in certain circumstances represent an alternative to the more time-consuming regulation of the amount of cellular chlorophyll. The high chlorophyll content of cells of *Thalassiosira pseudonana* after 1 diurnal cycle in strong outdoor light (Table 1) is an example of this, and probably reflects a compensation for short days (Sakshaug & Andresen 1986). The protective mechanism may thus enable algae to tolerate periods of strong sunlight and at the same time retain the high pigment contents which are necessary to ensure active growth in low light and short days. For *T. oceanica* this mechanism may not be critically important, because PPFDs >1000 µmol m^{-2} s^{-1} are likely only in the upper few meters of a 60 to 100 m euphotic zone in the Sargasso Sea.

The combination of short days and strong light around noon is quite typical in winter at 30 to 45° latitude; at higher latitudes short days are accompanied by low light. Presumably therefore a Trondheimsfjord (63°N) clone (Skel 5) of *Skeletonema costatum* (Grev.) Cleve does not need and does not have this protective mechanism (Sakshaug & Andresen 1986), in contrast to a New England clone of the same species (Falkowski pers. comm.).

It is expected, when the light regime stays constant

for an adequate period, that light-limited phytoplankton will yield a set of values for photoadaptational parameters which is characteristic for the light regime in question. The present investigation demonstrates that such sets may exist and that they also are species-specific. In nature, however, the light regime never stays constant, so adaptation in the above sense would be unlikely Phytoplankton tend, however, to adapt to the higher irradiances they experience (Sakshaug 1988). The reproducible and low cellular content of chlorophyll in outdoor cultures of *Thalassiosira oceanica* may therefore really have reflected both the light regime around noon and the absence of the 'sunglass effect'.

Cultures transferred to marginally low light (17 µmol m^{-2} s^{-1}) did not become adapted in a meaningful sense. Instead, the subpopulation which still remained healthy seemed to carry over the fluorescence and chlorophyll characteristics of the inoculum. Apart from the possibility of adaptation on time-scales much longer than the one employed, which cannot be entirely excluded in the case of *Thalassiosira oceanica*, it seems that sudden transfer to marginally low light or total darkness primarily arrests the photoadaptational response. This is in striking contrast to the gradual adaptations which are brought about in nature by seasonal changes towards winter (Sakshaug & Andresen 1986). Thus 'winter cells' found in nature may differ considerably from cells kept for a time after sudden transfer to darkness (Hargraves & French 1975).

The rate constants presented here for chlorophyll-dependent changes in fluorescence per cell are within the range of 0.017 to 0.062 h^{-1} reported in the literature for changes in chlorophyll per cell (Falkowski 1984). The rates for *Thalassiosira pseudonana* belong to the lower part of this range, and the evidence of asymmetrical photoadaptation, e.g. that adaptation to strong light proceeds faster than adaptation to low light, is noteworthy, because this has also been observed for other algae (Gallegos et al. 1983, Post et al. 1984). The rate for *T. oceanica* belongs to the higher part of this range, which is not unexpected for cultures transferred to very strong light. In this case light was, however, too strong for the alga to cope with through regulation of the cellular content of chlorophyll, and the cultures consequently declined.

In summary, even very closely related species regarded earlier to belong to one and the same species may be very different in their photoadaptation response: *Thalassiosira oceanica* appears inflexible, e.g. its chlorophyll content appears invariable unless it is exposed to inhibitory strong light. Then it decreases rapidly. It does not appear to have the fluorescence quenching mechanism. It should be successful in most of the euphotic zone, but not in the upper few meters. In contrast, *T. pseudonana* may be the epitome of oportunism and flexibility in its photoadaptive strategy. Due to the fluorescence quenching mechanism, it becomes rapidly adapted to sudden changes in PPFD. It should be successful in light regimes consisting of short days and strong light and should tolerate well the rapid changes in light regime brought about by turbulence etc. in near-shore waters.

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