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Photoadaptation in Marine Arctic Diatoms*

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Summary. Photoadaptation in some marine Arctic diatoms has been studied. *Thalassiosira antarctica*, *Nitzschia delicatissima* and *Chaetoceros furcellatus* were grown at −0.5 °C and various irradiances and continuous light. Growth and cellular chlorophyll were followed during transitional phase after the algae had been transferred from one irradiance to another. Adaptation time for cellular chlorophyll was linearly related to the gradient in irradiance, and adaptation to transfer from high to low light was faster than from low to high light. Adaptation time was found to be species dependent, and Arctic diatoms growing at low temperature seemed to adapt as fast as temperate species.

Introduction

Photoadaptation in phytoplankton—the physiological response of cells to changes in ambient light—has been the subject of several studies (Steemann Nielsen and Jørgensen 1968; Jørgensen 1969; Prezelin and Sweeney 1978; Prezelin and Matlick 1980; Falkowski and Owens 1980; Falkowski et al. 1981; Perry et al. 1981; Rivkin et al. 1982; Falkowski 1984; Post et al. 1984, 1985; Geider et al. 1986; Queguiner and Legendre 1986; Clausert and Gostan 1987). Studies of photoadaptation in polar phytoplankton are, however, sparse and have focussed on the photosynthetic response (Platt et al. 1982; Gallegos et al. 1983; Cota 1985; Palmisano and SooHoo 1985; Rochet et al. 1986), and changes in chlorophyll *a* absorbtion- and fluorescence exitation spectra (Neori et al. 1984).

Studies of adaptation rates and time scales for cellular parameters are even less common and have involved only transfer between two light regimes. Information on how the adaptation rate and time course depend on the direction and magnitude of the change in the light regime is scanty, and very little is known about the temperature-dependence of adaptation.

The present investigation presents data for adaptation rates of Arctic marine diatoms grown at low temperature (−0.5 °C), and attempts to establish a relationship between adaptation rates and the magnitude of change in scalar irradiance.

Material and Methods

Three diatom species were used in the experiments: *Thalassiosira antarctica* Comber (clone Tal), *Chaetoceros furcellatus* Bail (clone Cf1) and *Nitzschia delicatissima* Cleve (clone Nd2); all isolated from the Barents Sea by Erik Syvertsen, University of Oslo. The algae were grown in 2 l polycarbonate bottles in natural seawater enriched as the f/2 medium (Guillard and Ryther 1962). Cultures were inoculated with stocks maintained at 120 μmol $m^{-2} s^{-1}$ of scalar irradiance. Both stock cultures and experimental cultures were grown at −0.5 °C in continuous light. After inoculation, the algae were grown at a selected scalar irradiance for 1 to 2 weeks to ensure complete photoadaptation and sufficient cell densities. Exponentially growing cells were then transferred to another irradiance, and growth (based on cell counts and chlorophyll measurements) was monitored until a new exponential phase was established. Cultures were diluted when necessary to avoid nutrient deficiency.

Experimental cultures were transferred from various high to various low irradiances (H→L) and vice versa (L→H). Cell density and chlorophyll *a* concentration were measured several times per day for the first days after transfer; thereafter once per day. Particulate carbon and nitrogen were measured in adapted cultures before and after transfer.

The experiments were carried out in water baths in an open freezer. Temperature in the freezer was kept at −18 °C, and the water baths were heated with thermostats to −0.5 °C, thus keeping the temperature virtually constant (occasional variations were between −0.2° and −0.6 °C). Light was provided from an Osram HQI-T 250W/D dysprosium-halogen lamp or from banks of fluorescent tubes (Philips TL-55 Daylight de Luxe and Osram L 36 W/77 FLUORA plantlight) above the freezer. Light was attenuated by wrapping the bottles in neutral glass fiber net. Scalar irradiance (PAR) was adjusted to 2–450 μmol $m^{-2} s^{-1}$ and was measured inside the bottles with a QSL-100 Quantum Irradiance Meter (Biospherical Instruments). Chlorophyll was measured fluorometrically in a Turner 111 fluorometer (Holm-Hansen et al. 1965) using methanol as extractant. Particulate organic carbon and nitrogen was analysed in a Carlo Erba Elemental Analyzer Model 1104. Cells were counted in a haemocytometer or in a Nagoette counting chamber.

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Results

Thalassiosira antarctica had 2.9 pg chl cell^{-1}, when adapted to 450 μmol m^{-2} s^{-1}, and 20 pg cell^{-1} when adapted to 10 μmol m^{-2} s^{-1}; e.g. a 7-fold increase in chlorophyll. In *Nitzschia delicatissima*, the corresponding increase was only 3-fold (from 0.25 to 0.77 pg cell^{-1}) (Table 1).

The pigment content (average of several experiments) of these two species appeared to be exponentially related to growth irradiance over a wide range (Fig. 1) as has been shown earlier, e.g. Falkowski (1980). The equations for the chl/irradiance relationships were:

T. antarctica

$$\text{chl/chl}_{max} = 1.52 - 0.30 \log I_o \quad r = -0.98 \qquad (1)$$

N. delicatissima

$$\text{chl/chl}_{max} = 1.42 - 0.39 \log I_o \quad r = -0.99 \qquad (2)$$

Chaetoceros furcellatus exhibited, in contrast, insignificant changes in cellular chlorophyll for the same range in irradiance, and the average value was 0.98 pg cell^{-1} (Table 1).

In *T. antarctica* cellular carbon increased 3-fold, in *N. delicatissima* C cell^{-1} was virtually constant, and in *C. furcellatus* C cell^{-1} decreased by one third (Table 1).

The chl/C ratio increased 2-3-fold from 450 to 10 μmol m^{-2} s^{-1}, and both cellular chlorophyll and carbon may alter during light-shade adaptation. The chl/C ratios were exponentially related to irradiance in the same fashion as cellular chlorophyll (Fig. 2). The relationships for the three species can be expressed as follows:

T. antarctica

$$\text{chl/C} = 0.046 - 0.011 \log I_o \quad r = -0.93 \qquad (3)$$

Table 1. Cellular carbon (pg) and chlorophyll (pg) (average of several experiments), and maximum growth rates (div. d^{-1}) for *Thalassiosira antarctica*, *Nitzschia delicatissima* and *Chaetoceros furcellatus* at various irradiances (standard deviation SD expressed as % of biomass 1^{-1})

μmol m^{-2} s^{-1}		10	50–70	110–160	200–300	450
c cell^{-1}	Tal	526	409	523	267	211
(n=2,	Nd2	20	22	34	19	19
SD=5.5%)	Cf1	27	43	54	75	96
chl cell^{-1}	Tal	20.0	12.3	11.2	5.4	2.9
(n=2,	Nd2	0.77	0.55	0.45	0.28	0.25
SD=3.1%)	Cf1	0.96	0.84	1.02	1.12	0.80
μ (div. d^{-1})	Tal	0.47	0.66	0.78	0.49	0.42
(n=6,	Nd2	0.61	0.65	0.73	0.43	0.49
SD=15.5%)	Cf1	0.72	0.75	0.92	0.84	1.00

N. delicatissima

$$\text{chl/C} = 0.055 - 0.016 \log I_o \quad r = -0.92 \qquad (4)$$

C. furcellatus

$$\text{chl/C} = 0.049 - 0.015 \log I_o \quad r = -0.98 \qquad (5)$$

These curves are so similar that it may be justified to present an "average" curve for all three species as follows:

$$\text{chl/C} = 0.049 - 0.014 \log I_o \quad r = -0.91 \qquad (6)$$

Chaetoceros furcellatus exhibited the highest growth rates, maximum 1.0 div. d^{-1} at 450 μmol m^{-2} s^{-1} (Table 1). Variation was small, from 0.72 to 1.00 div. d^{-1}. For the other two species the growth rate varied in a similar fashion. Maximum values were 0.73 and 0.78 div. d^{-1} for *Nitzschia delicatissima* and *Thalassiosira antarctica*, respectively, and photoinhibition was apparent at $I_o > 150$ μmol m^{-2} s^{-1}. All species grew at relatively high

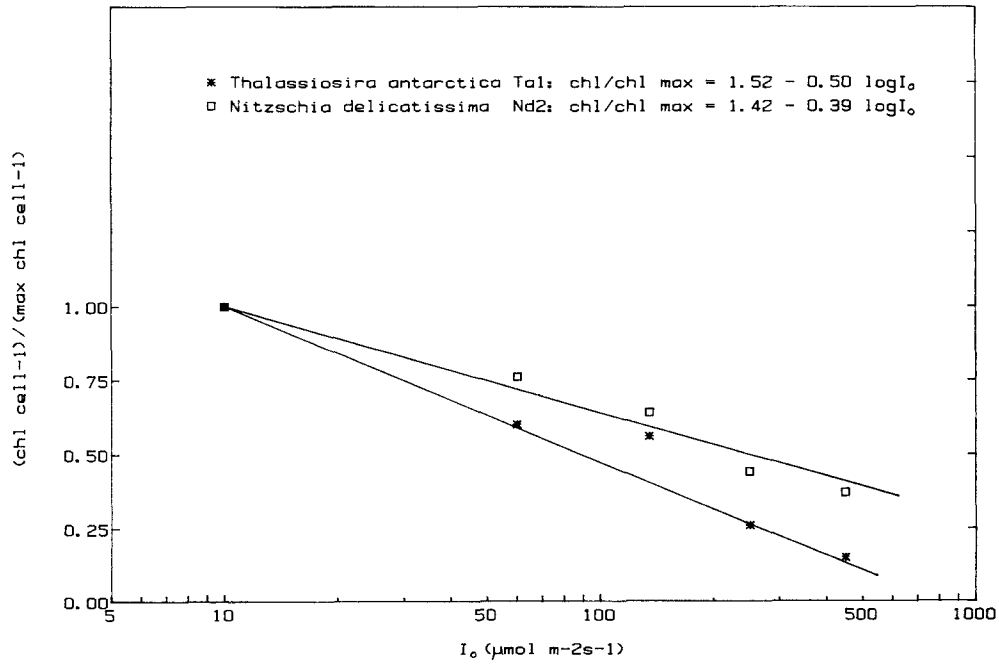

Fig. 1. Relationship between chlorophyll cell^{-1} (pg) (here expressed as chl cell^{-1}/max chl cell^{-1}) and light in *Thalassiosira antarctica* Tal and *Nitzschia delicatissima* Nd2

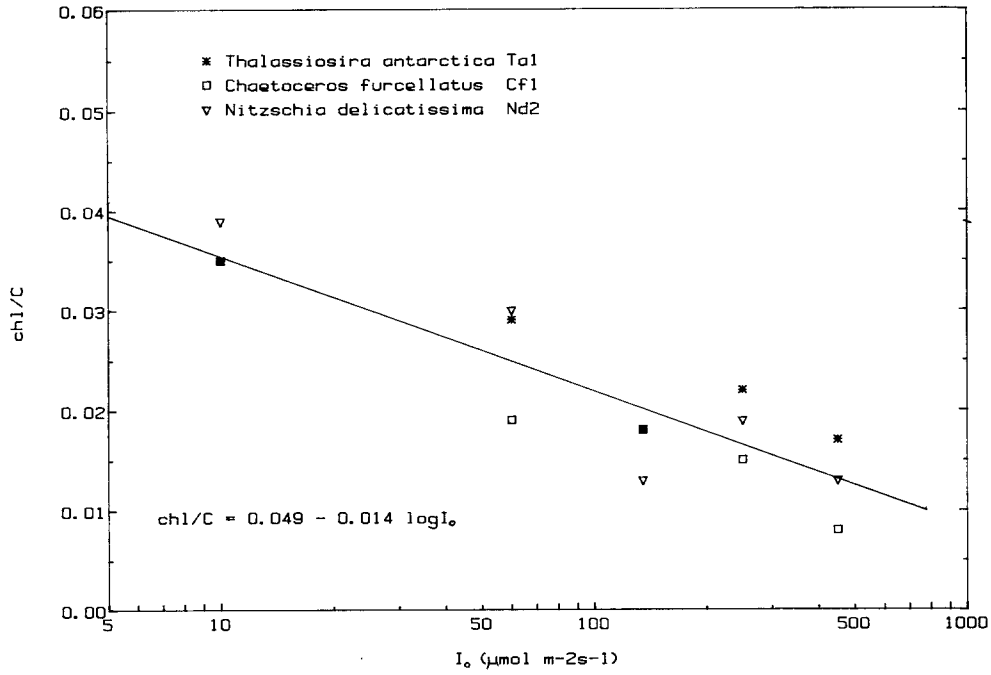

Fig. 2. The effect of light intensity (μmol $m^{-2}s^{-1}$) on the chl/C ratios of photoadapted cells of *Thalassiosira antarctica*, *Chaetoceros furcellatus* and *Nitzschia delicatissima* grown at low temperature and continuous light

rates (>0.45 div. d^{-1}) at low irradiance, (10 μmol $m^{-2}s^{-1}$).

Although there are few data points, it seems that the growth rate/irradiance curves may be described satisfactorily by a logarithmic function below inhibitory irradiances, in analogy with Falkowski (1980) (Fig. 3). For *C. furcellatus* photoinhibition was not observed, whereas the other two species exhibited marked photoinhibition above about 150 μmol $m^{-2}s^{-1}$.

Adaptation Time and Kinetics

The changes in cellular chlorophyll in *T. antarctica* and *N. delicatissima* with time when transferred from one irradiance to another, were analyzed according to first order kinetics as suggested by Falkowski (1980, 1983, 1984):

$$R_t = (R_o - R)e^{-kt} + R \tag{7}$$

giving

$$-kt = \ln\left[\frac{(R_t - R)}{(R_o - R)}\right] \tag{8}$$

where R_t = chl $cell^{-1}$ at time t
R_o = chl $cell^{-1}$ at time zero
R = chl $cell^{-1}$ at infinite time after adaptation
k = rate constant (h^{-1})

The chlorophyll data before, during and after the transition phase were fitted into Eq. 8 and plotted against time to calculate the rate constant k (Fig. 4, Table 2). There was a pronounced variation in k for the two species, from 16.8×10^{-2} to 1.1×10^{-2} for Tal and 14.1×10^{-2} to 1.4×10^{-2} for Nd2. These values are within the ranges reported elsewhere (see e.g. Falkowski 1983; Post et al. 1984 and references therein). It is evident, however, that the adaptation rates are dependent on the difference between the old and the new irradiance. Small differences yield higher rate constants than large differences, whether the direction of change is up or down.

The adaptation time may be expressed as the time required for half of the adaptation (change to a new, stable cellular chlorophyll level) to be completed; that is when

$$R_t = \frac{(R_o + R)}{2} \tag{9}$$

Solving equation (8) with this R_t value for t yields:

$$t_{1/2} = \frac{\ln 2}{k} \tag{10}$$

Adaptation time showed large variations for both species (Table 2). For *Thalassiosira* the adaptation time ($t_{1/2}$) varied from 4.1 to 63.5 h, and for *Nitzschia* the variations were from 4.9 to 49.5 h. Adaptation time, like adaptation rate, is dependent on the magnitude of the change in irradiance. The relationship between $t_{1/2}$ and shifts in irradiance seems to be linear both for up-shifts as well as down-shifts, but the time course is different as exemplified in Fig. 5. Adaptation is faster downshifts than for upshifts. This is evident for both species, but to a lesser extent for *Nitzschia*. It follows that adaptation time is species dependent.

Evidently, adaptation cannot cope with very high shifts in irradiance. None of the species were able to adapt to 10 μmol $m^{-2}s^{-1}$ when transferred from 450 μmol $m^{-2}s^{-1}$. The cells survived for several months,

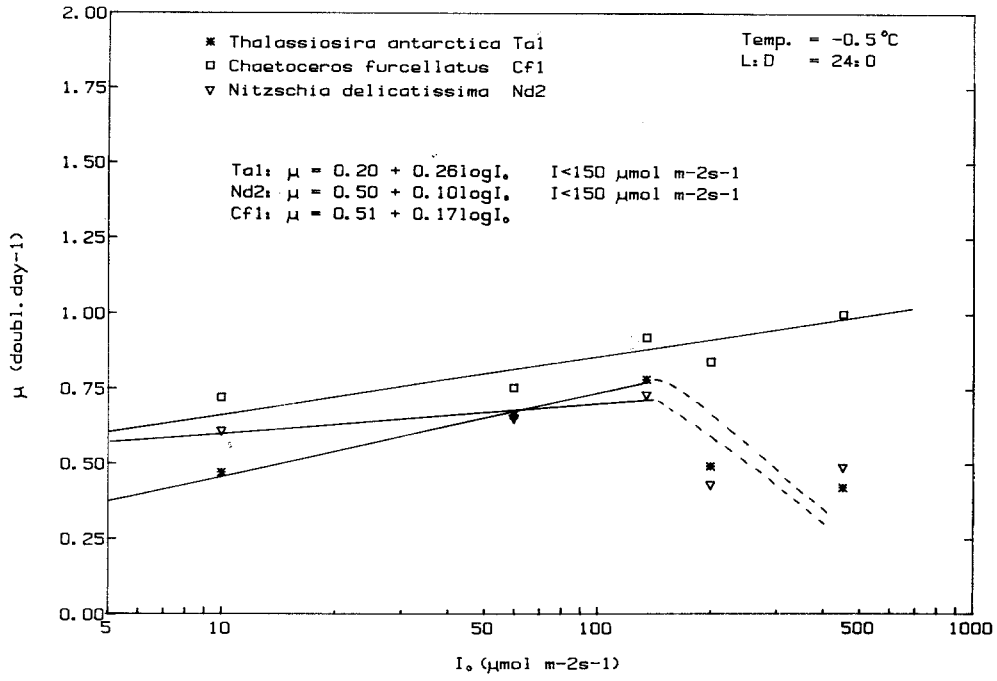

Fig. 3. The relationship between light intensity (μmol $m^{-2} s^{-1}$) and the growth rates (div. d^{-1}) of *Thalassiosira antarctica*, *Chaetoceros furcellatus* and *Nitzschia delicatissima*

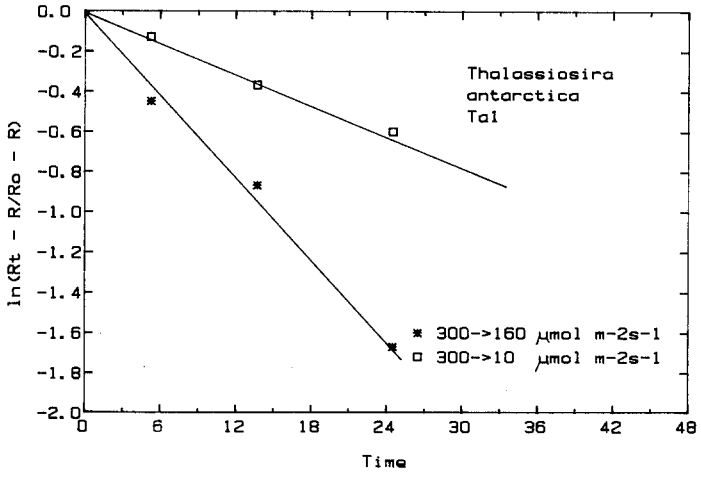

Fig. 4. An example of the time course of changes in the chl $cell^{-1}$ during transition from low to high light for *Thalassiosira antarctica*. R_0 = chl at the start, R_t = chl at time t, R = chl after adaptation

but did not grow (Fig. 6). Cellular chlorophyll increased slowly, but without reaching a stable value. Adaptation at transfer from 10 to 450 μmol $m^{-2} s^{-1}$ was however, completed within 4 days (Tal, Table 2).

The time needed to accomplish a new exponential growth curve after transfer to a new irradiance seemed in general to be shorter than the time required for chlorophyll adaptation. Though, adaptation rate constants have not been calculated for growth rate changes, because the rapid transfer gave too few points for an accurate calculation.

Discussion

Photoadaptation in unicellular algae involves changes in the content of several cellular constituents apart from pigments and at various time scales (Falkowski 1980; Post et al. 1985). Here we have considered some of the slowly responding process (time-scales of hours or days) to changes in light, e.g. cellular chlorophyll, the chl/C ratio and the growth rate.

In *T. antarctica* cellular carbon increased in shade-adapted cells. This is reported for other diatoms as well (Falkowski and Owens 1980; Sakshaug and Andresen 1986; Geider et al. 1986). For *C. furcellatus*, on the other hand, carbon decreased with decreasing irradiance, as in the haptophyte *Hymenomonas* (Claustre and Gostan 1987). Cellular nitrogen varied in accordance with carbon, so that the N/C ratios varied negligibly for either species (Tal: 0.174, Cf1: 0.169 and Nd2: 0.170, atoms).

Despite the species-dependent pattern of variation for cellular carbon, it seems justifiable to assume that the chl/C ratio varies in a similar fashion with light in the three

Table 2. Rate constants (k_{chl}), correlation coefficients (r) and adaptation time scales ($t_{1/2}$) (adaptation half completed) for chl cell^{-1} in *Thalassiosira antarctica* Tal and *Nitzschia delicatissima* Nd2. Transfer both from H→L and L→H irradiances

Interval	$k_{chl}(h^{-1})$		r		$t_{1/2}$	
	Tal	Nd2	Tal	Nd2	Tal	Nd2
H→L						
120–50	16.8×10^{-2}	14.1×10^{-2}	0.98	0.99	4.1	4.9
120–10	11.7×10^{-2}	11.4×10^{-2}	0.99	0.99	5.9	6.1
300–160	6.6×10^{-2}	5.6×10^{-2}	0.99	0.99	10.5	12.4
300–70	4.5×10^{-2}		0.97		15.4	
300–50	4.0×10^{-2}			0.98		17.5
300–10	2.5×10^{-2}	2.8×10^{-2}	0.99	0.96	27.7	24.2
450–200	2.9×10^{-2}	2.1×10^{-2}	0.93	0.99	23.9	33.6
450–50	1.7×10^{-2}	1.4×10^{-2}	0.98	0.82	40.8	49.5
450–50		1.1×10^{-2}		0.96		63.5
450–10	failure	failure				
L→H						
10–60	4.7×10^{-2}	3.9×10^{-2}	0.85	0.99	14.7	17.5
10–110	3.6×10^{-2}	2.8×10^{-2}	0.95	0.93	19.3	24.0
10–200	3.3×10^{-2}		0.79		21.0	
10–450	1.4×10^{-2}		0.90		50.3	
50–200	2.2×10^{-2}	4.4×10^{-2}	0.98	0.85	31.5	15.5
200–450	2.1×10^{-2}	1.6×10^{-2}	0.92	0.98	32.9	44.6

species. The equation expressing this variation (eq. 6) is, however, based on studies in continuous light and is therefore presumably invalid for shorter days, at which the chl/C ratios would be higher for corresponding irradiances (Sakshaug and Andresen 1986).

Equation 6 predicts chl/C ratios from 0.035 to 0.049 for algae growing at irradiances between 10 and 1 μmol m^{-2} s^{-1}. This is somewhat lower than the values of 0.05–0.075 which are typical for strongly shade-adapted diatoms at 20°–25 °C (Geider et al. 1986 and references therein), and for diatoms growing in situ in the Trondheimsfjord (Hegseth and Sakshaug 1983). On the other hand, for *Melosira arctica*, a diatom living below the perennial ice in northern Barents Sea and in the Arctic Sea chl/C ratios of 0.049 have been found in summer (Sakshaug 1985).

Earlier experiments have yielded chlorophyll adaptation rate constants from 0.5 to 8.1×10^{-2} h^{-1} (Falkowski 1983, 1984; Post et al. 1984, 1985) for diatoms growing between 15° and 25 °C. To the best of my knowledge no experiments have been carried out with polar species at low temperatures. According to Jørgensen (1968) temperature may influence the adaptation rate. Falkowski (1983) has compared chlorophyll adaptation rate constants of different temperate species by recalculating the k_{chl} value for different temperatures using a Q_{10} value of 2.0. A further recalculation of the k_{chl} values down to 0 °C reveals that these temperate species yields chlorophyll adaptation rate constants from 0.8 to 1.6×10^{-2} at such low temperatures. The rate constants of the Arctic algae in the present investigation cover a broad range from $1-17\times10^{-2}$ h^{-1}. Temperature in the Barents Sea varies from −1.8° to 8 °C during summer (Loeng 1980) (Arctic or Atlantic waters). Consequently, Arctic algae seem to be at least as effective adapters at their in situ temperatures as temperate species are at theirs, and probably even better than temperate species might be at low temperatures.

The adaptation time for chlorophyll varied between 10 and 125 h for *T. antarctica* and *N. delicatissima*. Both these algae adapted to small changes in light gradients (below 200 μmol m^{-2} s^{-1}) in less than a generation time (30–60 h), which has been observed also for *Skeletonema* (Riper et al. 1979). Transfer across larger light gradients will yield a longer adaptation time (up to 2 generations). Adaptation time appears not to be related to the generation time.

Both for *T. antarctica* and *N. delicatissima*, down-shifts are faster than up-shifts, although the difference is smaller in the latter. Several earlier investigations conclude, however, that there is virtually no difference in adaptation time (Geider and Platt 1986: chl/C and C/chl; Falkowski 1984: chl cell^{-1}), others have found that up-shifts are faster than down-shifts (Post et al. 1984, 1985: chl cell^{-1}; Gallegos et al. 1983: photoinhibition) or the opposite (Falkowski 1984: growth rate; Post et al. 1984, 1985: growth rate). However, all these experiments were carried out for shifts between only two irradiances, and the interval between initial and final irradiance has usually been larger than those in the present investigation. The curves for up-shifts and down-shifts in Fig. 5 are approaching each other as the difference between the initial and final irradiance increases, implying that the difference in adaptation time ($t_{1/2}$) for up-shifts and down-shifts is largest for small differences in irradiance. Given a large enough light gradient, virtually no difference in adaptation rate and time will be found for up- and down-shifts if it is not so big that adaptation does not take place at all.

The ability to adapt is species dependent. Arctic diatoms growing at low temperature are not able to adapt to changes in irradiances as great as temperate species can (Falkowski 1984; Post et al. 1984; Geider and Platt 1986). In the present experiments the algae were able to adapt when transferred from 10 to 450 μmol m^{-2} s^{-1}, but not the other way. All species were, however, able to grow both at 10 and 450 μmol m^{-2} s^{-1}. There must thus exist an upper limit of the light gradient beyond which adaptation does not take place. The nonadapted cells of the low shift did not grow actively, e.g. they altered their cellular chlorophyll content very little so that they exhibited characteristics of light adaptation even after weeks in low light. This has obvious implications for natural phytoplankton communities. Populations which may suddenly be brought from the surface into deep waters may become unable to adapt because of the large gradient in irradiance. The algae may thus become "trapped" in deep waters while still retaining their light-adapted characteristics. Likely examples of such "trapped" populations may be those reported by Sakshaug and Holm-Hansen (1986) from the

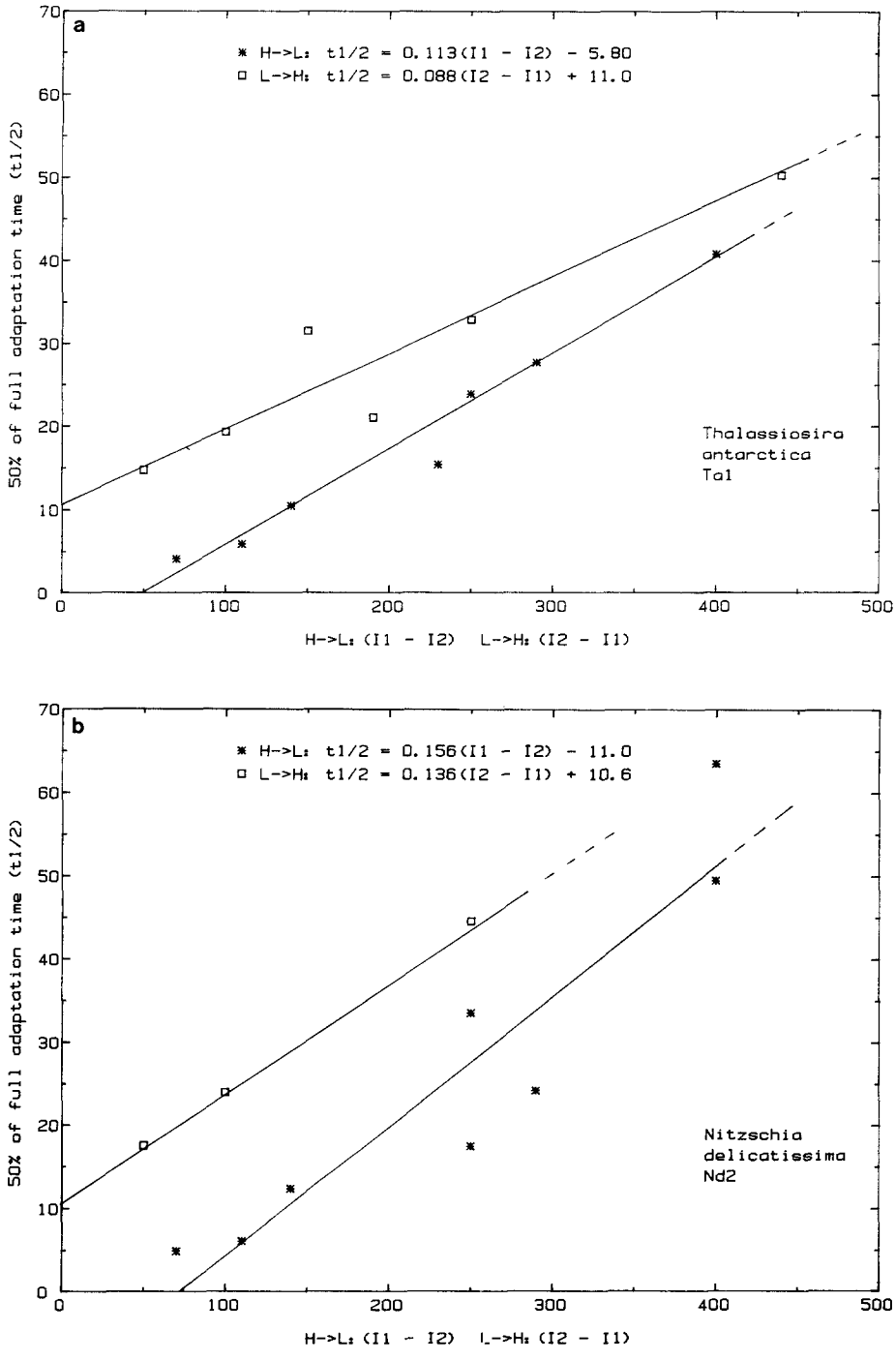

Fig. 5a, b. The relationship between adaptation time ($t_{1/2}$ in hours) for cellular chlorophyll and the magnitude of changes in irradiance from high to low (H→L) and low to high (L→H) light. **a** *Thalassiosira antarctica*, **b** *Nitzschia delicatissima*

Antarctic: at two stations populations with low chl/C ratios at 75 m depth were separated from the upper populations by a layer of phytoplankton with a higher chl/C ratio. If "trapped" populations are brought into upper waters again by vertical mixing, they should resume growth within a few days.

Light-shade adaptation in phytoplankton has been extensively studied and discussed in the context of vertical mixing in the sea (Falkowski 1980, 1983; Slagstad 1982; Gallegos et al. 1983; Lewis et al. 1984). If the time scale of photoadaptation is shorter than the time scale for vertical mixing, phytoplankton in the mixed layer should exhibit different photoadaptational characteristics according to depth. But if the rate of the vertical mixing exceeds the adaptation rate, the phytoplankton populations should be uniformly photoadapted in the mixed layer (Tilzer and Goldman 1978). Knowledge of the time scale of change in a photoadaptive variable may enable vertical mixing rate calculations.

Adaptation kinetics have usually been described by the first order kinetics (Falkowski 1980, 1983), and this formulation seems to be useful in describing the kinetics of photoadaptation for one particular light shift in one given direction. But a descriptive model of the whole concept of

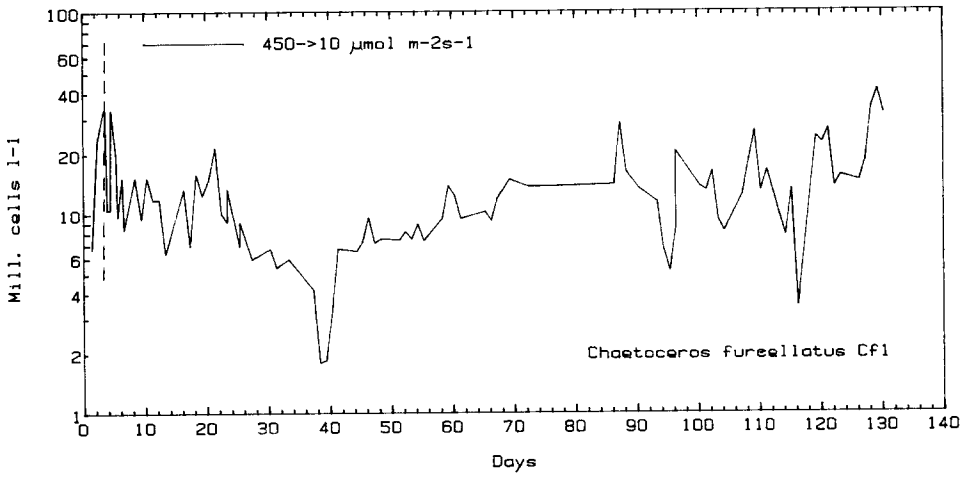

Fig. 6. Growth curve for *Chaetoceros furcellatus* transferred from high to low light (450→10 µmol $m^{-2} s^{-1}$). *Stippled line* transfer time

photoadaptation has to take into consideration the relationship between magnitude of light shifts and adaptation time, as well as the different time courses in up-shifts and down-shifts (Post et al. 1984). The latter will have pronounced influence on the description of phytoplankton in a mixed layer, and on calculations of mixing rate.

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