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EFFECT OF GROWTH AND LIGHT/DARK CYCLES ON DIATOM LIPID CONTENT AND COMPOSITION[1]

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ABSTRACT

Total extractable lipid (TEL) and lipid composition were studied throughout the growth cycle in three freshwater diatoms—Cyclotella meneghiniana *Kütz.*, Melosira varians *C. A. Ag., and* Stephanodiscus binderanus *(Kütz.) Krieg.—under three light regimes (16:8 h LD, 20:4 h LD, and 12:12 h LD) at 20° C. Two of the diatoms demonstrated strong daylength preferences for growth;* C. meneghiniana *grew best under long-day (20:4-h LD) conditions, whereas* S. binderanus *grew best under short-day (12:12-h LD) conditions. The lipid composition of the diatoms was similar throughout the growth cycle. Aged (2-month-old) cells were high in total lipid and triacylglycerols. Before the onset of active growth and during the early part of active growth, there was a reduction in total neutral lipids, primarily triacylglycerols, and an increase in all polar lipids, including chlorophyll* a, *acetone-mobile polar lipids, and phospholipids. While cell numbers were still increasing, triacylglycerols increased and polar lipids decreased to levels near those found in aged cultures. Results suggest that increased triacylglycerol content of freshwater diatoms is not necessarily indicative of senescent populations.*

Key index words: Bacillariophyceae; Cyclotella meneghiniana; *daylength; growth; light cycle; lipids;* Melosira varians; Stephanodiscus binderanus

Interest in phytoplankton lipid content and composition has increased dramatically in the past decade. Much of this renewed interest is prompted by studies in applied phycology in areas such as aquaculture, the nutritional quality of foods fed to cultured animals, and alternative energy sources (e.g. Ben-Amotz et al. 1985, Volkman 1989, Volkman et al. 1989).

Diatoms appear to be particularly satisfactory foods for many animals (Volkman et al. 1989, Ahlgren et al. 1990). This is due, most likely, to both the high concentration of total fatty acids and lipids (e.g. 4.2–27.8% fatty acids by dry weight and 10.2–38.8% lipid by dry weight) and the high amounts of eicosapentaenoic acid [20:5(n−3)]. Many marine animals have an absolute dietary requirement for this polyunsaturated fatty acid and are unable to synthesize it from linolenic acid (Kanazawa et al. 1979, Waldock and Holland 1984). Eicosapentaenoic acid is present in diatoms, whereas linolenic acid is virtually absent.

The importance of environmental variables such as light, nutrients, and temperature on the fatty acid composition of diatoms has been studied extensively (Ackman et al. 1964, Kates and Volcani 1966, Pugh 1971, DeMort et al. 1972, Opute 1974c, Orcutt and Patterson 1975, Fisher and Schwarzenbach 1978, Ben-Amotz et al. 1985, Amblard and Bourdier 1988, Mortensen et al. 1988, Roessler 1988, Sicko-Goad et al. 1988, Siron et al. 1989, Volkman 1989, Volkman et al. 1989, Thompson et al. 1990). Fewer studies have been conducted on lipid class composition of diatoms (Kates and Volcani 1966, Opute 1974a, b, Orcutt and Patterson 1975, Ben-Amotz et al. 1985, Palmisano et al. 1988, Volkman et al. 1989). As Volkman et al. (1989) pointed out, few studies, especially those dealing with nutritional aspects relevant to aquaculture, use defined culture conditions or harvest algae at a specified stage of growth.

Many of the studies cited above and those summarized in a recent review by Cobelas (1989) are concerned with increases in lipid production and alteration of fatty acid composition under nutrient deficient conditions, particularly nitrogen deficiency. Diel studies on lipid metabolism in diatoms are more common, because lipids and fatty acids are oxidized when cells require energy, as in the dark or when division occurs (Anderson and Sweeney 1977, Fisher and Schwarzenbach 1978, Shifrin and Chisholm 1981, Amblard and Bourdier 1988).

Recent studies in our laboratory (Sicko-Goad et al. 1988, 1989a–d) suggested that there was a diel periodicity in lipid content and fatty acid composition in *Cyclotella meneghiniana.* Furthermore, this periodicity appeared to be responsible for altering the effects of lipophilic toxicants. That is, when cells rich in 16:0 and 16:1 fatty acids (presumably from triacylglycerols; Roessler 1988) were exposed to chlorinated benzenes, toxicity affects were delayed until the quantity of these fatty acids was reduced. Conversely, cells lower in these fatty acids, when exposed to the chlorinated benzenes, experienced more changes in measured cellular constituents; these changes were evident as early as 2 h after exposure to the toxicant. We hypothesized that timing of the initial exposure to lipophilic toxicants might be critical, and this timing effect might be related to either total lipid in the cell or lipid composition.

Continuing these studies, we performed a series of experiments to determine total lipid content and

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lipid class composition relative to changes in the light/dark cycle, temperature, and those changes occurring in a diel cycle. Changes in lipid content and composition as a function of growth stage and light/dark cycle are presented here.

MATERIALS AND METHODS

Cyclotella meneghiniana Kütz. clone CyOH2 was obtained from Dr. S. S. Kilham of the Department of Biological Sciences at the University of Michigan. *Melosira varians* C. A. Ag. (isolated from Lake Michigan) was obtained from Dr. H. Vanderplug of the Great Lakes Environmental Research Lab, NOAA (Ann Arbor, Michigan). *Stephanodiscus binderanus* (Kütz.) Krieg. was isolated by Dr. E. Theriot (Philadelphia Academy of Sciences) from a small inland lake near Ann Arbor. Cultures were maintained in WC medium (Guillard 1975) on a rotary shaker table in a growth chamber set at 20° C on an alternating 16:8-h LD cycle at 50 $\mu E \cdot m^{-2} \cdot s^{-1}$. Cells were subcultured weekly to larger volume flasks to increase cell densities for experiments.

For growth curve studies, aged algal cultures approximately 2 months old were acclimated for a period of 2 weeks at the temperature and light regime at which the experiment was to be conducted to ensure that observed changes in cell composition did not result from temperature or light shock. For growth curve determinations, algae were allowed to settle from stock cultures and approximately 100 mL of concentrated cells were reinoculated into 6-L flasks containing fresh growth medium (day 0) and placed in a growth chamber at 20° C set at one of the following light/dark regimes: 16:8 h, 20:4 h, and 12:12 h LD.

Aliquots from thoroughly mixed 6-L flasks were withdrawn 2–3 times weekly for a period of approximately 6 weeks, depending on the growth. Between 75 and 200 mL were withdrawn per sample. All samples were taken in duplicate, filtered onto pre-washed and preweighed Gelman A/E glass fiber filters, air-dried, then dried in a vacuum oven at 60° C for 24 h. Filters were reweighed to determine dry weight and frozen for subsequent lipid extraction. Concurrent with dry weight analyses, smaller volumes of culture medium (9 mL) were withdrawn and placed in a tube containing paraformaldehyde and glutaraldehyde at final concentrations of 1% in 0.05 M sodium cacodylate buffer at pH 7.2. Cell counts were performed on these samples with either a hemocytometer or plankton counting cell to determine cell densities. Counts reported are averages of four replicates.

For lipid analysis, frozen filters were placed in pre-extracted thimbles and extracted with chloroform/methanol (2:1 v/v) for at least 12 h in a micro-Soxhlet (Orcutt and Patterson 1975). The extract was concentrated, redissolved in chloroform, washed with water in a separatory funnel, dried under a nitrogen stream in a preweighed Teflon-lined screw cap amber vial, and weighed for total gravimetric lipid. Samples were flushed with nitrogen and frozen for lipid class analyses.

Samples were unfrozen and redissolved in methylene chloride to concentrations of 20–50 μg lipid in spotting volumes of 10–20 μL for lipid class analysis. The extracts were spotted with Hamilton syringes onto cleaned and blank-scanned silica coated chromarods (type SIII). Rods were held in a frame and developed, then scanned in an Iatroscan Mark IV TLC-FID (RSS Inc., Costa Mesa, California) system using the development scheme of Parrish (1986). The development was three staged:

1. The rods were developed in 50 mL of a solution of hexane, diethyl ether, and formic acid (98:2:0.5) for 30 min and conditioned for 5 min, followed by redevelopment in the same solvent system for 25 min. Rods were then partially scanned for hydrocarbons, wax/sterol esters, and ketones. β-carotene migrates with hydrocarbons. Wax and sterol esters co-elute in this system.

2. Rods were then reconditioned and developed in 50 mL of a solution of hexane, diethyl ether, and formic acid (80:20:0.1) for 50 min. Rods were scanned for triacylglycerols, free fatty acids, alcohols, and sterols. Because triacylglycerols and free fatty acids are difficult to separate if the load on the chromarod is greater than 10 μg, the area of the split peak has been combined into one class labelled TG/FFA. Diacylglycerols have an Rf value near that of sterols. No diacylglycerol peaks were observed in any samples.

3. The third development consisted of two 15-min developments in 100% acetone, followed by two 10-min developments in dichloromethane, methanol, and water (5:4:1). Rods were then scanned for chlorophyll *a*, acetone-mobile polar lipids (AMPL), and a class containing phospholipids and acetone-immobile polar lipids. During the last scan, an FTID detector was also used for the additional detection of N in chl *a* and phospholipids. The AMPL fraction may contain monoglycerides and glycolipids. Chlorophyll data from the TLC–FTID method were compared with standard fluorometric measurements from two experiments. The data were in agreement within one standard error of the TLC–FTID method.

Quantitative determinations of lipid class composition are based on dose–response calibration equations generated by analysis of a wide range of concentrations of standards for each lipid class (Parrish and Ackman 1985). Standards were obtained from Sigma at a purity of >99% for lipid class composition studies and are listed in Table 1. All lipid class composition determinations were run in duplicate. Thus, data reported are averages of four replicates for each time determination.

TABLE 1. *Standards used for calibration of chromarods.*

Lipid class	Abbrev.	Standards
Aliphatic hydrocarbons	HC	Nonadecane
Wax and sterol esters	WE/SE	Palmitic acid stearyl ester (stearyl palmitate)
Ethyl ketone	KET	3-hexadecanone
Triacylglycerol	TG	Tripalmitin (glyceryl tripalmitate)
Free fatty acids	FFA	Palmitic acid (hexadecanoic acid)
Free alcohol	ALC	Cetyl alcohol (hexadecanol)
Free sterol	ST	Cholesterol (5(6)-cholesten-3-ol)
Phospholipids	PL	L-α-phosphatidylcholine, diheptadecanoyl
Chlorophyll	Chl *a*	Chlorophyll *a*

RESULTS

Growth and Total Extractable Lipid (TEL)

Melosira varians. Three light/dark regimes were utilized in growth experiments. These were 12:12, 16:8, and 20:4 h LD. The inocula of aged cultures were all high in lipid content, ranging from ca. 20 to 50% of total dry weight (Figs. 1–3). *Melosira varians* either grew modestly or at best maintained cell numbers under all three regimes at 20° C (Fig. 1). However, growth was best under the 12:12-h LD regime (Fig. 1A). With the apparent onset of cell division, there was a concomitant decrease in total extractable lipid (TEL). This occurred at day 14 under the 12:12-h regime (Fig. 1A), at day 9 under the 16:8-h regime (Fig. 1B), and at day 4 under the 20:4-h LD regime (Fig. 1C). Under all regimes, the reduction in TEL was ca. 50% during this period.

Stephanodiscus binderanus. Acclimation of *S. binderanus* cultures to a 20:4-h LD regime resulted in

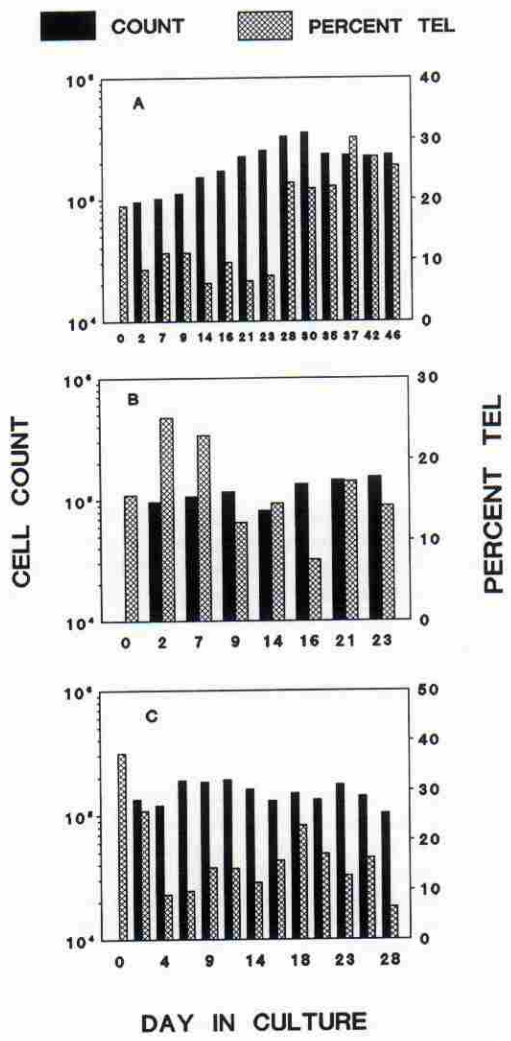

FIG. 1. *Melosira varians.* Cell count and total extractable lipid (TEL; percentage of dry weight) as a function of day in culture. A) 12:12 h LD. B) 16:8 h LD. C) 20:4 h LD.

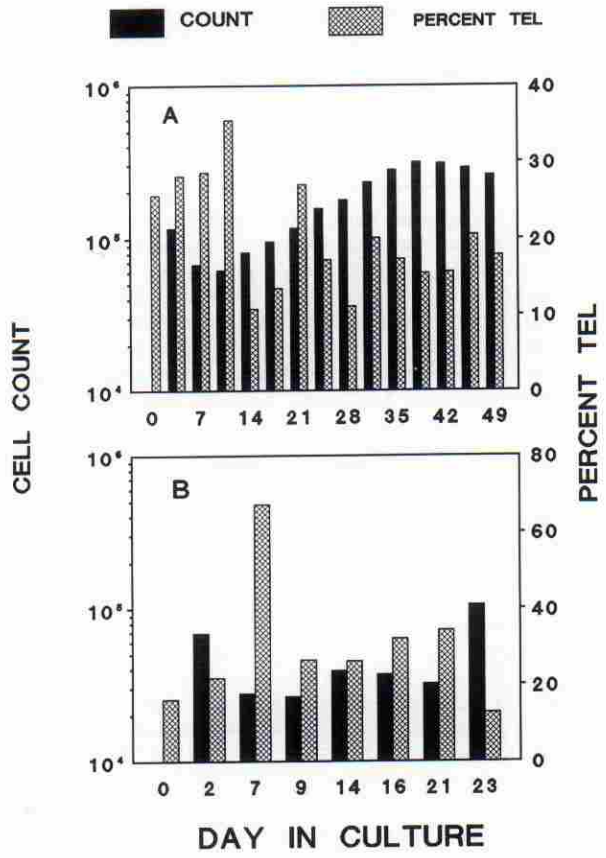

FIG. 2. *Stephanodiscus binderanus.* Cell count and total extractable lipid (TEL; percentage of dry weight) as a function of day in culture. A) 12:12 h LD. B) 16:8 h LD.

the death of the culture. Repeated attempts to culture this organism under the long-day regime failed, even when actively growing cultures in fresh medium were used as inocula. Consequently, data are presented only for the 12:12-h and 16:8-h LD regimes (Fig. 2). Like *M. varians, S. binderanus* grew best under the 12:12-h LD regime at 20° C with sustained growth over a 3-week period, and at best maintained cell numbers or grew slightly under 16:8 h LD. The increase in cell numbers beginning on day 23 of the 12:12-h LD regime was accompanied by a large decrease in TEL (Fig. 2A).

Cyclotella meneghiniana. Acclimation of *C. meneghiniana* to the 12:12-h LD regime resulted in the death of the culture. Repeated attempts to culture this organism from a variety of actively growing stock cultures failed. Thus, data are presented for only the two longer-day light/dark regimes (Fig. 3). In terms of growth, *C. meneghiniana* demonstrated a strong preference for the 20:4-h LD growth conditions (Fig. 3B). Growth was sustained over a 3-week period, beginning approximately 2 weeks after transfer of the aged cultures. Concomitant with the increase in cell numbers starting at day 14, there was a reduction in TEL of over 50%. This reduction in TEL was sustained through day 28. A similar reduction was observed when cells were grown under 16:8 h LD, and this also occurred at day 14. However, smaller increases in cell numbers were observed (Fig. 3A).

Lipid Class Composition with Growth

Melosira varians. Detailed lipid class composition data for *M. varians* as a function of growth condition and day in culture are presented in Table 2. The numbers reported for each class are the percentages of the total lipid weight. The lipid composition of the aged cultures (day 0) was characterized by a high percentage of triacylglycerols (>70%) and a low percentage of polar lipids. The most noticeable difference among the three light regimes is the higher percentage of chlorophyll *a* under the 16:8-h LD regime.

The onset of growth resulted in a noticeably different lipid class composition when compared with other sampling days. Day 14 (12:12 h), day 9 (16:8

h), and day 4 (20:4 h) were characterized by the lowest neutral to polar lipid ratios. This was due to reductions in triacylglycerols and increases in polar lipid fractions, especially chlorophyll *a*. Although increases in cell numbers were maintained under the 12:12-h LD regime at day 30, lipid class composition was very similar to the aged cultures used as inocula. Similarly, day 16 (16:8 h LD) lipid class percent composition resembled the aged inoculum composition, although cell counts were increasing.

Stephanodiscus binderanus. The lipid class percent composition (Table 3) of aged cultures of *S. binderanus* was similar to that of aged cultures of *M. varians* and was characterized by a high percentage of triacylglycerols and a high neutral to polar lipid ratio. The onset of growth, characterized by increases in cell counts and a large reduction in TEL, was characterized by substantial decreases in triacylglycerols and large increases in polar lipids, with a neutral to polar lipid ratio of 1.4, the smallest ratio observed in all experiments. While cell counts continued to increase through day 42 (12:12 h LD; Fig. 2A), lipid composition returned to the composition observed in aged cells, with triacylglycerols increasing to greater than 60% by day 30.

With increased daylength (16:8 h LD), lipid class composition was more variable and there was no sustained growth. Changes occurred between days 2 and 7 (Table 3), and these changes in the ratio of neutral to polar lipids are indicative of synthetic processes. However, no changes were observed in cell numbers to suggest that growth was occurring. Cell counts increased on day 23 after transfer, but growth was not sustained under this light regime and lipid class composition was indicative of senescent cells.

Cyclotella meneghiniana. Lipid class percent composition data for *C. meneghiniana* (Table 4) show that aged cells had similar percent compositions when compared with the other diatoms (cf. Tables 2, 3). The most pronounced changes in lipid class composition under the 16:8-h LD regime occurred between days 2 and 14, when the neutral to polar lipid ratio was reduced by a factor of approximately two. At the onset of growth at day 14, this ratio increased, and the increase was due to both increases in triacylglycerols and reductions in the phospholipid and other acetone-immobile polar lipids (PL). While cell counts were still increasing at days 21 and 23, lipid class percent composition was similar to the aged inoculum.

Similar patterns of lipid class composition were also observed with growth under the 20:4-h LD regime. However, the neutral to polar lipid ratio remained higher for a longer period of time (i.e. 9 days vs. 2 days under 16:8 h LD).

DISCUSSION

One of the most interesting aspects that has emerged from this study of lipid composition is the obvious effect of daylength on the three diatoms studied. At 20° C, *M. varians* and *S. binderanus* demonstrate a short-day preference (12:12 h LD) for growth, whereas *C. meneghiniana* demonstrates a long-day preference (20:4 h LD).

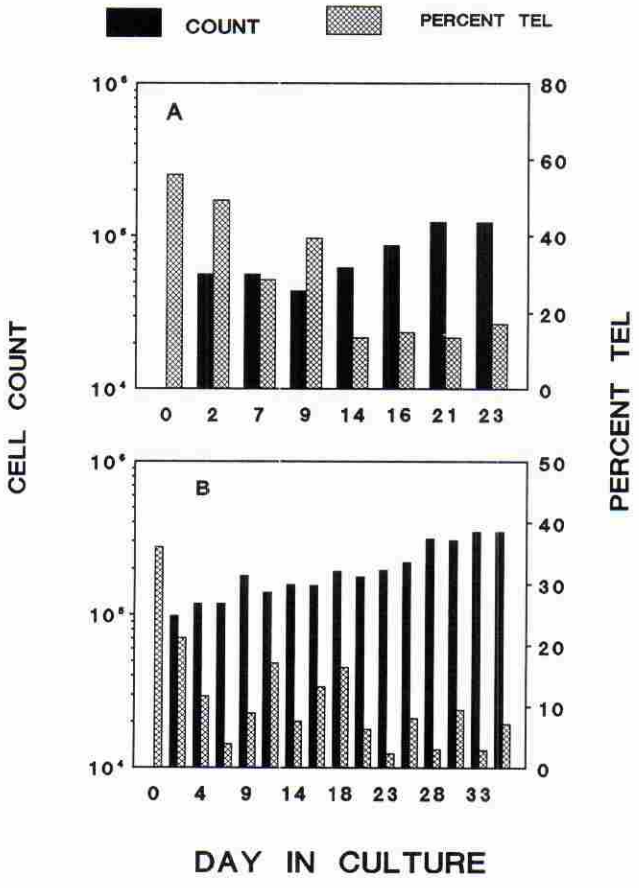

FIG. 3. *Cyclotella meneghiniana.* Cell count and total extractable lipid (TEL; percentage of dry weight) as a function of day in culture. A) 16:8 h LD. B) 20:4 h LD.

The literature contains examples of daylength optima and suggestions that daylength may be crucial in the ecology and distribution of many planktonic species, especially at high latitudes and in polar regions (Castenholz 1964, Eppley and Coatsworth 1966, Durbin 1974, Holt and Smayda 1974, Hickman 1976, Brand and Guillard 1981, Hegseth and Sakshaug 1983, Sakshaug and Andresen 1986, Gibson and Foy 1988, Gilstad and Sakshaug 1990). In temperate climates, especially in lakes, the succession of planktonic populations is most often explained by a variety of physical, biological, and chemical factors (e.g. Amblard 1988) such as light irradiance, temperature, nutrient availability, and grazing. The interplay between light and temperature effects on algal growth was reviewed by Round (1968). This review and the papers cited above suggest that some algal species exhibit daylength preferences, that daylength optima may be related to temperature, and that some widely occurring species may not have daylength optima.

TABLE 2. Melosira varians. *Lipid class percent composition and selected ratios as a function of growth condition and day in culture. Mean (SE). Abbreviations as in Table 1. AMPL = acetone-mobile polar lipids.*

Day in culture	Growth condition	HC	WE/SE	TG/FFA	ALC	ST	Chl *a*	AMPL	PL	Chl *a*/ NEUT	NEUT/ POLAR
0	12:12 h LD, 20° C	1.5 (0.3)	3.8 (1.0)	73.0 (1.9)	0.01 (0.0)	6.9 (0.8)	3.1 (0.5)	4.8 (0.6)	6.8 (1.3)	0.04 (0.01)	5.8 (0.7)
7		1.4 (0.1)	1.3 (0.4)	76.6 (1.5)	0.01 (0.0)	3.6 (0.3)	4.7 (1.3)	4.2 (0.9)	8.4 (1.1)	0.06 (0.02)	4.8 (0.6)
9		1.4 (0.4)	2.2 (0.4)	79.3 (4.4)	0 (0.0)	4.9 (0.8)	1.3 (0.1)	5.6 (1.4)	5.3 (1.5)	0.01 (0.0)	7.2 (2.1)
14		3.6 (1.0)	3.6 (0.4)	63.6 (4.0)	0.4 (0.3)	7.3 (1.1)	5.2 (0.7)	6.1 (1.6)	10.3 (1.6)	0.07 (0.01)	3.6 (0.5)
30		0.5 (0.1)	2.4 (0.6)	82.7 (3.3)	1.0 (1.0)	4.2 (0.8)	2.9 (0.9)	1.9 (0.5)	4.5 (0.9)	0.03 (0.01)	9.9 (2.0)
37		0.4 (0.1)	0.9 (0.04)	83.6 (0.4)	2.0 (1.1)	4.1 (1.1)	2.5 (0.3)	1.9 (0.2)	4.6 (0.5)	0.03 (0.0)	10.1 (0.5)
0	16:8 h LD, 20° C	1.3 (0.1)	2.8 (0.2)	70.4 (1.4)	3.1 (0.1)	4.9 (0.2)	11.5 (1.4)	4.7 (0.3)	1.3 (0.2)	0.14 (0.02)	4.7 (0.4)
2		4.6 (0.9)	5.1 (1.4)	49.5 (6.9)	1.1 (1.1)	6.9 (1.6)	25.8 (2.4)	6.2 (2.3)	0.8 (0.2)	0.38 (0.05)	2.0 (0.3)
7		4.7 (0.3)	5.2 (0.2)	52.1 (5.2)	0 (0.0)	6.8 (0.8)	21.2 (8.8)	6.0 (1.9)	4.0 (1.1)	0.31 (0.1)	2.2 (0.6)
9		3.6 (0.3)	7.5 (0.5)	35.8 (1.1)	1.4 (0.9)	7.7 (0.5)	26.3 (2.6)	13.5 (2.5)	4.2 (1.3)	0.32 (0.08)	2.1 (0.7)
14		1.6 (0.2)	2.9 (0.1)	75.0 (0.8)	1.4 (0.5)	3.7 (0.2)	9.6 (0.3)	5.4 (1.1)	0.5 (0.1)	0.11 (0.01)	5.5 (0.4)
16		1.3 (0.1)	3.5 (0.4)	73.8 (0.8)	0.3 (0.2)	4.0 (0.1)	13.8 (0.5)	2.8 (1.0)	0.6 (0.2)	0.17 (0.01)	4.8 (0.4)
21		0.9 (0.1)	2.2 (0.2)	71.1 (1.9)	2.3 (1.4)	3.9 (0.1)	11.3 (3.3)	7.0 (2.8)	1.3 (0.3)	0.14 (0.04)	4.1 (0.4)
23		1.1 (0.1)	6.1 (1.5)	66.7 (4.5)	3.2 (1.1)	6.2 (0.7)	12.3 (2.0)	3.2 (0.8)	1.4 (0.2)	0.15 (0.03)	4.9 (1.1)
0	20:4 h LD 20° C	0.6 (0.1)	0.7 (0.4)	87.3 (1.0)	0.2 (0.2)	3.7 (0.2)	2.3 (0.4)	1.8 (0.5)	3.4 (0.6)	0.02 (0.0)	12.3 (1.3)
4		3.5 (0.4)	10.0 (2.9)	69.1 (1.1)	0.9 (0.5)	3.9 (0.7)	2.6 (0.9)	3.7 (1.1)	6.3 (1.6)	0.03 (0.01)	6.9 (2.1)
16		0.6 (0.1)	4.2 (1.1)	77.3 (1.5)	0.5 (0.3)	8.3 (0.2)	1.9 (0.4)	3.6 (0.5)	3.6 (0.3)	0.02 (0.0)	10.0 (0.6)
18		0.7 (0.3)	4.3 (1.3)	73.9 (0.7)	3.7 (1.9)	8.1 (0.3)	2.0 (0.9)	3.7 (0.7)	3.6 (0.6)	0.02 (0.01)	9.7 (0.10)
25		0.7 (0.02)	3.0 (0.2)	79.8 (2.1)	0.2 (0.2)	6.7 (0.4)	3.5 (1.4)	1.9 (0.4)	4.2 (0.5)	0.04 (0.02)	9.4 (1.7)

Under our experimental conditions of batch culture with excess nutrients, the three diatoms repeatedly demonstrated daylength preferences. This result is not really surprising in view of the distribution patterns of these diatoms.

Cyclotella meneghiniana has a worldwide distribution and occurs primarily in benthic and littoral communities of lakes and rivers and is entrained in the potamoplankton. It has been characterized as a warmwater taxon in the Laurentian Great Lakes (Stoermer and Ladewski 1976), which is consistent with longer photoperiods.

Melosira varians also has a worldwide distribution and tolerates a broad range of environmental parameters as a littoral taxon of eutrophic waters. Although it grew at all light regimes, it showed a preference for short daylengths. The data of Stoermer and Yang (1969) demonstrate that occurrences of this taxon in the Great Lakes nearshore waters cluster around the vernal and autumnal equinox.

Stephanodiscus binderanus has a moderately high latitude distribution pattern in the Northern Hemisphere, and there is only one report (Cholnoky 1968) of it from the Southern Hemisphere. Stoermer and Ladewski (1976) reported that *S. binderanus* has an apparent temperature preference of 8–9° C, which is consistent with shorter photoperiods in the spring and fall.

Lipid class composition patterns are remarkably consistent when compared with growth patterns. In all three diatoms, the major neutral lipid fraction is triacylglycerol, whereas the predominant polar lipid fraction is usually chlorophyll *a*. In other studies of lipid class composition of phytoplankton using the Iatroscan thin layer chromatography–flame ionization detection method (e.g. Parrish 1987, Parrish

TABLE 3. Stephanodiscus binderanus. *Lipid class percent composition and selected ratios as a function of growth condition and day in culture. Mean (SE). Abbreviations as in Table 1. AMPL = acetone-mobile polar lipids.*

Day in culture	Growth condition	HC	WE/SE	TG/FFA	ALC	ST	Chl *a*	AMPL	PL	Chl *a*/ NEUT	NEUT/ POLAR
0	12:12 h LD, 20° C	1.3 (0.5)	1.4 (0.3)	88.7 (3.0)	0.01 (0.0)	1.1 (0.03)	1.1 (0.4)	3.8 (1.2)	2.6 (0.5)	0.01 (0.01)	12.4 (4.2)
9		4.5 (0.2)	13.4 (0.3)	66.4 (0.6)	0.7 (0.7)	2.6 (0.1)	3.2 (0.02)	4.2 (0.9)	5.0 (1.0)	0.04 (0.0)	7.1 (1.2)
14		3.5 (0.6)	3.2 (0.2)	60.4 (8.0)	1.3 (1.3)	5.2 (0.6)	16.5 (6.2)	2.9 (0.6)	7.0 (1.3)	0.22 (0.1)	2.8 (1.2)
23		2.7 (0.2)	14.1 (1.2)	32.5 (1.3)	4.3 (3.0)	4.2 (0.9)	7.0 (1.3)	13.7 (1.6)	21.4 (4.5)	0.12 (0.01)	1.4 (0.3)
30		1.9 (0.2)	4.3 (0.6)	67.2 (1.2)	1.6 (1.6)	9.5 (1.6)	4.5 (0.6)	3.4 (0.7)	7.7 (1.4)	0.05 (0.01)	5.4 (0.8)
37		1.2 (0.1)	6.5 (1.0)	68.7 (4.1)	0.7 (0.7)	8.8 (1.4)	4.3 (0.8)	3.0 (0.5)	6.8 (1.1)	0.05 (0.01)	6.1 (0.8)
49		1.1 (0.2)	5.0 (1.2)	71.5 (2.5)	2.1 (1.1)	6.3 (0.4)	4.0 (1.0)	2.0 (0.7)	7.9 (1.2)	0.05 (0.01)	6.2 (1.1)
0	16:8 h LD, 20° C	6.8 (0.8)	1.6 (1.0)	63.0 (6.4)	1.0 (1.0)	4.6 (0.5)	9.6 (0.8)	7.6 (2.9)	5.8 (3.1)	0.12 (0.01)	3.3 (0.9)
2		19.7 (4.9)	3.8 (0.3)	46.8 (6.7)	2.4 (1.2)	4.5 (0.4)	14.3 (6.7)	4.7 (3.3)	3.6 (1.7)	0.19 (0.10)	3.4 (0.7)
7		4.9 (1.7)	0.9 (0.6)	71.6 (11.4)	1.0 (0.7)	0.01 (0.0)	14.8 (8.2)	5.1 (2.2)	1.8 (0.6)	0.19 (0.14)	3.6 (4.8)
9		5.2 (0.5)	1.3 (0.3)	77.8 (2.1)	0.6 (0.4)	2.3 (0.8)	4.8 (3.3)	0.7 (0.4)	7.4 (4.8)	0.04 (0.04)	7.3 (0.6)
14		5.4 (3.6)	1.0 (0.5)	77.3 (5.9)	0.7 (0.6)	0.3 (0.2)	12.4 (2.0)	2.1 (0.5)	0.9 (0.3)	0.15 (0.03)	5.4 (0.9)
16		5.6 (2.8)	1.5 (1.0)	76.1 (3.9)	1.4 (1.0)	2.2 (0.5)	9.0 (0.2)	2.2 (0.2)	1.7 (0.4)	0.10 (0.0)	6.8 (0.2)
21		1.5 (0.3)	0.6 (0.1)	88.9 (0.4)	1.9 (0.1)	1.1 (0.4)	4.0 (0.4)	1.4 (0.05)	0.6 (0.2)	0.04 (0.0)	15.8 (1.6)
23		2.6 (0.3)	3.6 (1.0)	76.6 (1.2)	3.2 (0.3)	2.1 (0.1)	6.9 (1.2)	3.7 (1.0)	1.4 (0.5)	0.08 (0.01)	7.4 (0.6)

and Wangersky 1987, Volkman et al. 1989), chlorophyll *a* has been included in either the acetone-mobile polar lipid fraction (AMPL) or polar lipid fraction (AMPL + phospholipid). Consequently, on first examination, some of our polar fractions appear to be lower than previously reported. It is obvious, however, that the data presented here most closely resemble the percent composition of lipid classes reported by Volkman et al. (1989) and Parrish and Wangersky (1990) for *Chaetoceros gracilis*, in which polar and neutral lipids are present in approximately equal percentages in log-phase growth.

Cell division occurred at modest rates in all cultures. Although these long generation times may seem indicative of a culture-induced stress, we feel that these numbers cannot be directly compared with standard growth curves that have been derived under continuous light conditions. Fogg (1966) reported generation times of between 10 and 30 h for five diatoms growing under continuous light. However, he also demonstrated that the relative rates of increase of *Asterionella* under lake conditions corresponded to doubling times of 5–7 d, attributing this difference to light and temperature limitation as well as sinking. The data presented here (Tables 2–4) and other unpublished data suggest that the light/dark regime can indeed result in a stress, as evidenced by triacylglycerol content. However, in cultures where cell numbers increased, triacylglycerol content was lowest prior to the onset of growth (e.g. *M. varians*, day 14; Table 2, Fig. 1).

At the onset of growth in our cultures, the approximate ratio of neutral to polar lipids was 3:2. However, this ratio was not sustained throughout the division period, and cells quickly reverted to a ratio of approximately 4:1 neutral to polar lipids. Many of the studies of lipid composition of diatoms have been conducted under silicon or nitrogen deficiencies, which increase both total lipid and neutral lipid (particularly triacylglycerol) content (Werner 1966, Shifrin and Chisholm 1981, Parrish and Wangersky 1987, 1990, Taguchi et al. 1987, Roessler 1988). These studies might suggest that our cultures are nutrient limited as indicated by the high triacylglycerol content. However, a comparison of total extractable lipid (TEL) on a percent dry weight basis from all three diatoms shows that while growth is occurring, percent TEL ranges between <5 and 20, which is far below the range given for nutrient limitation and is also well below the percentages re-

TABLE 4. Cyclotella meneghiniana. *Lipid class percent composition and selected ratios as a function of growth condition and day in culture. Mean (SE). Abbreviations as in Table 1. AMPL = acetone-mobile polar lipids.*

Day in culture	Growth condition	HC	WE/SE	TG/FFA	ALC	ST	Chl *a*	AMPL	PL	Chl *a*/ NEUT	NEUT/ POLAR
0	16:8 h LD, 20° C	7.1 (3.2)	1.4 (0.5)	74.0 (1.8)	1.0 (0.6)	1.7 (0.4)	12.9 (1.4)	1.2 (0.4)	0.7 (0.2)	0.15 (0.02)	5.8 (1.1)
2		9.8 (2.0)	3.1 (2.7)	51.6 (7.9)	1.1 (0.9)	2.5 (1.2)	26.7 (7.1)	3.6 (0.8)	1.6 (0.2)	0.40 (0.15)	2.1 (1.0)
7		26.1 (1.5)	4.1 (0.8)	30.6 (4.7)	2.4 (0.8)	3.6 (0.3)	29.6 (6.6)	1.6 (0.9)	2.0 (0.7)	0.44 (0.12)	2.0 (0.7)
9		8.3 (1.2)	1.2 (0.8)	58.8 (2.2)	2.2 (1.6)	1.4 (1.0)	19.6 (5.5)	3.2 (0.3)	5.3 (1.6)	0.28 (0.09)	2.5 (0.7)
14		17.7 (6.9)	4.2 (0.6)	55.6 (8.7)	1.9 (0.1)	3.8 (0.1)	15.6 (0.8)	0.7 (0.1)	0.6 (0.2)	0.19 (0.01)	4.9 (0.4)
16		16.8 (7.1)	4.1 (0.8)	56.0 (0.4)	1.9 (0.7)	2.1 (0.3)	16.5 (7.1)	1.2 (0.1)	1.4 (0.4)	0.20 (0.11)	4.3 (2.9)
21		4.4 (1.0)	1.4 (1.2)	70.6 (1.0)	0.8 (0.7)	1.1 (1.0)	15.2 (1.7)	3.1 (0.6)	3.5 (0.5)	0.19 (0.03)	3.6 (0.4)
23		3.5 (0.8)	3.3 (0.4)	73.8 (5.3)	2.6 (0.3)	2.5 (0.8)	8.7 (3.9)	4.1 (1.3)	1.6 (0.6)	0.11 (0.05)	6.0 (1.7)
0	20:4 h LD, 20° C	1.5 (1.0)	0.9 (0.7)	68.8 (8.9)	0.02 (0.01)	6.6 (2.5)	5.8 (2.2)	5.4 (1.3)	10.9 (3.4)	0.07 (0.03)	3.5 (2.1)
2		3.8 (1.7)	1.7 (0.5)	67.4 (15.2)	0.01 (0.01)	4.7 (2.6)	5.6 (2.2)	6.4 (3.3)	10.4 (5.5)	0.06 (0.04)	4.8 (6.5)
9		3.9 (0.03)	5.1 (0.01)	59.5 (2.1)	2.8 (0.1)	8.5 (0.5)	5.1 (0.5)	5.7 (1.8)	9.5 (1.0)	0.06 (0.01)	3.9 (0.8)
16		9.4 (1.7)	5.9 (1.3)	47.0 (2.1)	0.02 (0.0)	6.6 (0.6)	8.2 (0.7)	11.0 (1.4)	11.8 (1.7)	0.11 (0.01)	2.3 (0.2)
18		1.7 (0.1)	8.0 (2.9)	75.6 (2.9)	0.7 (0.3)	2.2 (0.6)	1.6 (0.6)	5.9 (0.5)	4.3 (0.9)	0.02 (0.01)	7.2 (0.6)
21		5.6 (0.7)	20.2 (4.0)	34.0 (2.3)	0.01 (0.0)	9.1 (0.5)	6.9 (0.6)	8.4 (1.2)	15.7 (0.3)	0.11 (0.01)	2.2 (0.1)
23		4.4 (0.1)	10.7 (0.2)	60.6 (1.0)	1.4 (0.1)	4.4 (0.2)	7.9 (0.3)	1.9 (0.3)	8.8 (0.6)	0.09 (0.01)	4.3 (0.3)
25		2.1 (0.6)	5.4 (1.8)	68.7 (4.6)	2.3 (1.9)	5.0 (0.8)	5.7 (0.7)	4.0 (0.9)	6.7 (0.6)	0.06 (0.01)	5.1 (0.4)
30		2.7 (0.3)	4.9 (0.4)	55.7 (2.2)	0.01 (0.0)	11.0 (0.3)	10.1 (1.6)	5.2 (1.0)	10.5 (1.6)	0.16 (0.02)	2.6 (0.5)
35		0.9 (0.3)	11.1 (3.1)	49.7 (8.6)	0.3 (0.3)	11.3 (0.9)	6.3 (1.7)	8.6 (2.7)	11.7 (1.7)	0.07 (0.03)	3.2 (0.9)

ported for a variety of freshwater algae in log-phase growth (Shifrin and Chisholm 1981, Cobelas and Lechado 1989). These data then suggest that freshwater diatoms have a higher triacylglycerol content during growth than some marine species examined (Roessler 1988, Parrish and Wangersky 1990).

Parrish (1987) demonstrated a shift to triacylglycerol production in natural populations of phytoplankton at the end of the spring bloom. Parrish and Wangersky (1990) suggested that production of triacylglycerols can be used as an indicator of physiological stress and further predicted that triacylglycerols would be the major lipids present in batch culture past the period of log-phase growth. Our data demonstrate that triacylglycerol production occurs during growth in batch culture and that this fraction is lowest prior to increases in cell numbers. This reduction in triacylglycerols is accompanied by an increase in polar lipids, particularly phospholipids and AMPL, suggesting much increased metabolic activity prior to the onset of active growth.

These results suggest that care be taken when interpreting lipid analyses for freshwater diatoms, because increased triacylglycerol content is not necessarily indicative of senescent populations.

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ACTIVE GLIDING MOTILITY IN AN ARAPHID MARINE DIATOM, *ARDISSONEA* (FORMERLY *SYNEDRA*) CRYSTALLINA[1]

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ABSTRACT

Active gliding movement over long distances was observed and filmed in the marine pennate diatom Ardissonea (Synedra) crystallina *(Agardh) Kütz. Typical speeds measured ca. 1–2 $\mu m \cdot s^{-1}$. Motion was often smooth and steady; however, discontinuous jerky motions and rolling movements were common. Motion was associated with secretion of twin or, less commonly, single straight trails of mucilage from one end of the cell. In a few instances, reversal in direction was related to cessation of mucilage secretion at one end and commencement at the other. Temporary cessation of movement due to an obstruction was accompanied by a build-up of mucilage at one end of the cell. Mucilage was apparently secreted at two specific sites at each end of the cell and was stained by alcian blue.*

Persistent trails were visible under scanning electron microscopy (SEM). SEM confirmed that cells had no raphes or labiate processes. The apparent site of secretion was a deep groove formed at the junction of the valve and valvocopula (first girdle band) at each end of the cell. Transmission electron microscopy confirmed the presence of mucilage vesicles in the cytoplasm, but these were not in any manner obviously related to secretion nor was any morphological structure associated with secretion. Cells often become epiphytic through secretion of a terminal stipe. Both stipe secretion and movement may involve the same structural differentiation of the frustule.

These results demonstrate a previously unrecorded type of diatom motility. The mechanism involves mucilage secretion and appears similar to that seen, for example, in some other algae such as the desmids (green algae).

Key index words: araphid diatoms; Ardissonea crystallina; *Bacillariophyceae; frustule; motility;* Synedra; *valve*

Certain diatoms have long been known to move actively by a smooth or jerky gliding motion (e.g. Lauterborn 1896). Until recently, motility has been considered the exclusive property of pennate diatoms that possess the raphe. Mechanisms of motility, the subject of considerable speculation (reviewed by Edgar and Pickett-Heaps 1984), are likely to be related to mucilage secretion through the raphe fissure, associated with the activity of bundles of actin filaments (Edgar and Zavortink 1983) lining the cell membrane immediately adjacent to the raphe.

Recently, two centric diatoms—*Odontella* (Pickett-Heaps et al. 1986) and *Actinocyclus* (Medlin et al. 1986)—were reported to display motility. In *Odontella,* movement consisted of continuous small oscillations that were not directed in any apparent fashion; they were presumed to be due to mucilage secretion through the labiate processes. In *Actinocyclus,* movement was more directed, at about 1 $\mu m \cdot s^{-1}$, and involved rotation. There was good indirect evidence that this movement was also brought about by mucilage secretion through the numerous small labiate processes.

This paper reports another type of active gliding motion in diatoms, this time in a pennate that has no detectable labiate processes or raphes. To the best of our knowledge, this activity has not been recorded before.

MATERIALS AND METHODS

A marine *Ardissonea* was isolated from a plankton sample collected by net-tow off Blairgowrie, Port Phillip Bay (Victoria, Aus-

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