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Role of temperature in growth, feeding, and vertical distribution of the mixotrophic chrysophyte *Dinobryon*

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ABSTRACT: *Dinobryon* spp. are common components of the phytoplankton in temperate lakes. While these chrysophytes link bacterial carbon as well as primary production to the larger food web, few studies have examined their vertical distribution over a season. Data were collected over a 2.5 yr period in mesotrophic Lake Lacawac in eastern Pennsylvania (USA) to examine water column attributes relating to seasonality of the mixotrophic alga *D. cylindricum*, and specifically to address a hypothesis that abundance and vertical distribution in the genus are associated with temperature. This information was used to guide laboratory experiments examining temperature and light effects on growth, feeding, and vertical migration of cultured *Dinobryon*. Data from Lake Lacawac and the literature indicated that high abundances of *Dinobryon* were associated with a narrow range of temperature (9–18°C) relative to temperatures where they were present (3–26°C). High abundances of several species of *Dynobryon* were associated with this temperature range, and occurred from late winter to late spring, depending on latitude and depth in the water column. Although high *Dinobryon* abundances were not tied directly to levels of photosynthetically active radiation in Lake Lacawac, a UV-exclusion experiment in a nearby oligotrophic lake indicated a temperature-dependent negative effect of UV radiation. UV may limit the occurrence of *Dinobryon* populations in surface waters of clear oligotrophic lakes. Laboratory experiments showed that both light and temperature affected growth and feeding rates of *Dinobryon,* and that maximum feeding and growth rates occurred within the temperature range where high *Dinobryon* abundances were observed in field studies.

KEY WORDS: Phytoplankton · Lake bloom · Succession · Ultraviolet radiation · Seasonality

INTRODUCTION

Chrysophytes in the genus *Dinobryon* are a common and often numerically important component of the phytoplankton in temperate lakes (Ostrofsky & Duthie 1975, Lehman 1976, Siver & Chock 1986, Bird & Kalff 1987, Hitchman & Jones 2000, Watson et al. 2001, Tadonléké et al. 2002, Kamjunke et al. 2007). With a potential to temporarily dominate phytoplankton biomass, they play several key roles in these systems. For example, *Dinobryon* species are mixotrophic — combining phagotrophy with phototrophy — and in Lac Cromwell, Quebec (Canada), they were shown to ingest more bacteria than did crustaceans, rotifers, and ciliates combined (Bird & Kalff 1986). Likewise, in Lake Oglethorpe, Georgia (USA), *Dinobryon*, along with other mixotrophs, were frequently the dominant bactivores (Sanders et al. 1989). *Dinobryon* are consumed by copepods and small *Daphnia*, and can be a major food of large-bodied cladoceran zooplankton (Tappa 1965, Sanders & Porter 1990, Sommer et al.

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2003). Thus, *Dinobryon* spp. link bacterial carbon as well as primary production to the larger food web. In addition, *Dinobryon* spp. can cause water treatment problems (Watson et al. 2001, Satchwill et al. 2007).

Seasonality in the genus is well known and has been attributed to a variety of factors including light, potassium toxicity, iron availability, predation, and an inability to compete with other phytoplankton during periods of high nutrient concentrations (Lehman 1976, Siver & Chock 1986, Dokulil & Skolaut 1991, Veen 1991). The degree to which mixotrophy is related to the vertical and seasonal distribution of *Dinobryon* is uncertain, but the ability to incorporate limiting nutrients via ingestion of bacteria may well contribute to its commonness in oligotrophic systems and to its ability to reach peak abundances at depths where attenuation has reduced light to very low levels (Siver & Chock 1986, Eloranta 1989, Veen 1991, Caron et al. 1993, Kamjunke et al. 2007).

None of the factors proposed to affect the seasonal distribution of *Dinobryon* are mutually exclusive, but an overall importance of temperature is suggested by peak seasonal abundances recorded during late winter in semi-tropical climate, spring in temperate, and summer in colder climates (e.g. Flint 1938, Siver & Chock 1986, Eloranta 1989, Sanders et al. 1989). Furthermore, thermotaxic responses in *Dinobryon* were observed in laboratory experiments. *D. sertularia* responded with slowed swimming and increased turning at 'preferred' temperatures in horizontal temperature gradients (Clegg et al. 2003), and *Dinobryon* sp. migrated to depths with an intermediate temperature range in a vertical gradient in which light and nutrients were constant (Heinze & Sanders 2009). Nevertheless, the role of temperature in the vertical/depth distribution of the genus in lakes is essentially unexplored. In the present study, field data collected from a mesotrophic lake over approximately 2.5 yr, data from the literature, and a series of laboratory experiments were combined to examine how physical attributes of the water column related to the seasonality of *Dinobryon*, and specifically to address the hypothesis that high abundance and vertical distribution are associated with temperature and light.

MATERIALS AND METHODS

Field site and sampling

Lake Lacawac (41° 22.9′ N, 75° 17.5′ W; maximum depth [z_{max}] = 12 m) is a mesotrophic ice-scour glacial lake located in the Pocono Mountains of northeastern Pennsylvania, USA. The 21 ha lake and its watershed remain undeveloped and are protected by the Lacawac Sanctuary Foundation. It is a softwater, slightly acidic lake with little buffering capacity, and total dissolved phosphorus is typically <5 µg l^{-1} in the photic zone (R. E. Moeller & C. E. Williamson unpubl. data). The phytoplankton community is seasonally dominated by chrysophycean algae, including *Dinobryon* (Siver & Chock 1986).

Water was collected at 1 m intervals from the surface to 11 m using a Van Dorn sampler. Sampling spanned the period from April 2005 to September 2007 (Table 1), with collections at a single station in the deepest part of the lake until March 2007 when 3 additional stations were added along a cross-lake transect. These additional stations were sampled at 1, 3, 6, and 9 m depths. For plankton enumeration, 125 ml subsamples from each depth were fixed with Lugol's iodine (3% final concentration).

Secchi disk depth was determined at each station, and temperature and oxygen concentrations were measured using a YSI model 58 meter. Light attenu-

Table 1. Secchi disk depths, mean water temperatures, and maximum *Dinobryon cylindricum* abundances in Lake Lacawac, Pennsylvania, USA

Date	Light attenuation (k, m^{-1})	Secchi disk depth (m)	Depth of max. *Dinobryon* abund. (m)	Max. *Dinobryon* abund. (no. ml^{-1})	Temp. at max. *Dinobryon* abund. (°C)
9 Apr 2005	0.61	2.8	3	2	6.5
13 May 2005	0.63	2.7	4	1677	11.2
13 Jun 2005	0.65	2.6	4	4284	14.6
11 Jul 2005	–	–	9	122	5.8
2 Aug 2005	0.85	2.0	4	11	19.1
1 Oct 2005	0.57	3.0	1	37	17.7
3 Nov 2005	0.68	2.5	4	18	9.1
21 Jan 2006	–	–	1	70	2.9
22 Feb 2006	0.77	2.2	1	395	4.1
23 Mar 2006	0.85	2.0	7	450	3.0
20 Apr 2006	0.65	2.6	1	4608	13.7
13 May 2006	0.68	2.5	1	4488	18.2
22 Jun 2006	0.74	2.3	6	373	9.3
17 Jul 2006	0.74	2.3	4	40	15.8
23 Mar 2007	0.57	3.0	5	2	4.2
13 Apr 2007	0.52	3.3	10	95	4.7
5 May 2007	0.40	4.3	1	6	14.5
22 Jun 2007	0.38	4.5	2	42	22.8
20 Jul 2007	0.40	4.3	5	81	16.3

ation (k; m^{-1}) was estimated from Secchi measurements (1.7/Secchi depth) for all dates sampled, and was compared to light measured at depth using a BIC profiling radiometer (Biospherical Instruments) on May 13, 2005. Data on hourly and daily photosynthetically active radiation (PAR) insolation at Lake Lacawac (Hargreaves 2007) was used with attenuation calculations from Secchi readings to determine light levels at depth for peak *Dinobryon* abundances.

Microscopic enumeration

For field experiments, fixed samples were concentrated by settling in 100 ml graduated cylinders for ≥24 h, after which 90 ml were removed by aspiration; the exact volume of the remaining sample was measured to determine a concentration factor. *Dinobryon* were enumerated in a subsample from transects covering 20 to 100% of a Sedgewick-Rafter chamber at 250× magnification. For laboratory experiments (below), the concentrating step was eliminated.

Response to UVR exposure and temperature

Ultraviolet radiation (UVR) and temperature were experimentally manipulated over a 10 d period beginning on 10 April 2006 in Lake Giles, an oligotrophic system approximately 16 km due east of Lake Lacawac. Although UVR is unlikely to have large effects on *Dinobryon* in Lake Lacawac due to strong absorption of UVR in the top few centimeters, the data are included here for their relevance to vertical distribution and interaction with temperature across lake systems. An integrated sample (0 to 3 m) was passed through a 60 µm screen to remove zooplankton, placed in UV-transparent 3.8 l Bitran® S-series bags (Com-Pac International), and maintained in temperature-controlled incubators on the lake shore in natural sunlight. Replicates were incubated under either UV-transparent (OP-4) or UV-blocking (OP-2) Acrylite® (Evonik Industries). In one set of incubations, the samples were maintained at the initial lake temperature (5.5°C), while for a second set, the temperature was gradually raised 10°C from ambient lake temperature over a 3 d period and samples incubated for a further 7 d at the elevated temperature. *Dinobryon*, and for this experiment other phytoplankton, were enumerated as described above. For comparative purposes, algal abundances were converted to biovolume using dimensions of representative cells matched to geometric shapes (Olenina et al. 2006).

Culture conditions for laboratory experiments

The *Dinobryon* sp. used in all laboratory experiments was obtained from the University of Toronto Culture Collection (UTCC no. 392; UTCC is now the Canadian Phycological Culture Centre). This strain from UTCC originated from the University of Texas Culture Collection (UTEX strain no. 2267). Cells were maintained under a 12:12 h light:dark cycle at 18°C in DY-IV medium (Sanders et al. 2001). Light was supplied by Cool-White fluorescent lamps (PAR: 25–67 µM m^{-2} s^{-1}).

Temperature effects on growth and feeding: laboratory experiments

Experiments were performed in a walk-in cold room (13°C) with 3 replicates per treatment, and temperature was maintained in insulated water baths using Jäger model 3602 submersible heaters (Eheim). Culture flasks with 100 ml of *Dinobryon* culture in dilute (20%) DY-IV medium at 18°C were immersed in the water baths held at 13°, 15°, 17°, 19°, and 21°C without acclimation. Cool-White fluorescent lamps provided constant illumination at 67 µM m^{-2} s^{-1}. Light intensity was measured using Biospherical Instruments model QSL-100 Quantum Irradiance. *Dinobryon* were sampled daily, preserved with Lugol's iodine, and enumerated as above.

A second series of temperature experiments was performed to examine whether gradual temperature shifts (2°C d^{-1}) had similar effects as the acute shift, and to determine rates of bacterivory at different temperatures and light levels. These experiments were run under continuous light in a temperature-controlled incubator (Precision). Two light treatments were used for each temperature, with PAR irradiance of 25 and 67 µM m^{-2} s^{-1}. Treatments had 3 and 5 replicates at the low and high irradiance, respectively.

After acclimation, feeding experiments used subsamples from each temperature–light treatment during mid-exponential growth. Fluorescent polycarbonate microspheres (0.6 µm, Polysciences) were added at ~20% bacterial abundance. Subsamples were fixed immediately after particle addition (T0) and at 30 min using a Lugol's / formaldehyde / $Na_2S_2O_3$ method to prevent egestion (Sherr & Sherr 1993). Ingested microspheres were counted using

epifluorescence on a Zeiss Axiovert microscope, and rates of bacterivory were determined from the ratio of added microspheres to bacterial abundance (Sanders et al. 1989). Preliminary experiments indicated linear uptake by *Dinobryon* for >30 min.

Synthesis and data analysis

Data on vertical distribution of *Dinobryon* and temperature changes with depth in Lake Lacawac were combined with similar data from the literature (Flint 1938, Bird & Kalff 1987, Hitchman & Jones 2000, Kamjunke et al. 2007, R. W. Sanders unpubl. data) to examine patterns across geographical distance and lake type. Abundances were converted to a percentage of maximum observed for each study for comparison. Statistical analyses, including ANOVA, Pearson 2-way chi-squared, and Spearman's rho tests, were performed using SPSS 15.0. For Pearson 2-way chi-squared test, data were grouped into 3 equal temperature ranges: 0°–9.2°, 9.3°–18.3°, and 18.4°–27.5°C. The corresponding groups for abundance were 0, 1–350, and 351–4750 cells ml^{-1}, corresponding to absence, moderate abundances, and bloom condition. The 350 cells ml^{-1} boundary level was chosen because abundances rarely exceeded that number except at times that a bloom occurred at some depth. Contour plots were generated using MATLAB (Mathworks).

RESULTS

Environmental variables and seasonal distribution of *Dinobryon* in Lake Lacawac

Lake Lacawac had strong temperature stratification in summer, cooling and mixing through autumn and winter, with subsequent spring warming of surface waters as daily insolation increased (Fig. 1A). Minimum and maximum incident daily PAR during the study period were 0.5 and 62.8 M m^{-2} d^{-1} on 4 December and 23 June 2005, respectively (Fig. 2). Light attenuation for PAR calculated from Secchi depth and the BIC radiometer in Lake Lacawac had good agreement (0.630 and 0.610, respectively, in May 2005), suggesting that the Secchi depth was an adequate indicator of light attenuation. Subsequent comparisons between the Secchi and a LI-COR LI-250A meter with LI-193 quantum sensor also showed good agreement (S. B. DeVaul unpubl. data). The BIC radiometer also measured penetration of UV-A (380 nm) and UV-B (305 nm) radiation. The depths of 1% of surface irradiance for PAR, UV-A, and UV-B in May 2005 were 4.4, 0.75, and 0.23 m, respectively. Light attenuation showed no clear seasonal pattern during the study, but was distinctly lower in 2007 than in the previous 2 yr (Table 1), indicating increased water clarity at the end of the study period.

During the 29 mo sampling period, *Dinobryon cylindricum* showed late spring population peaks,

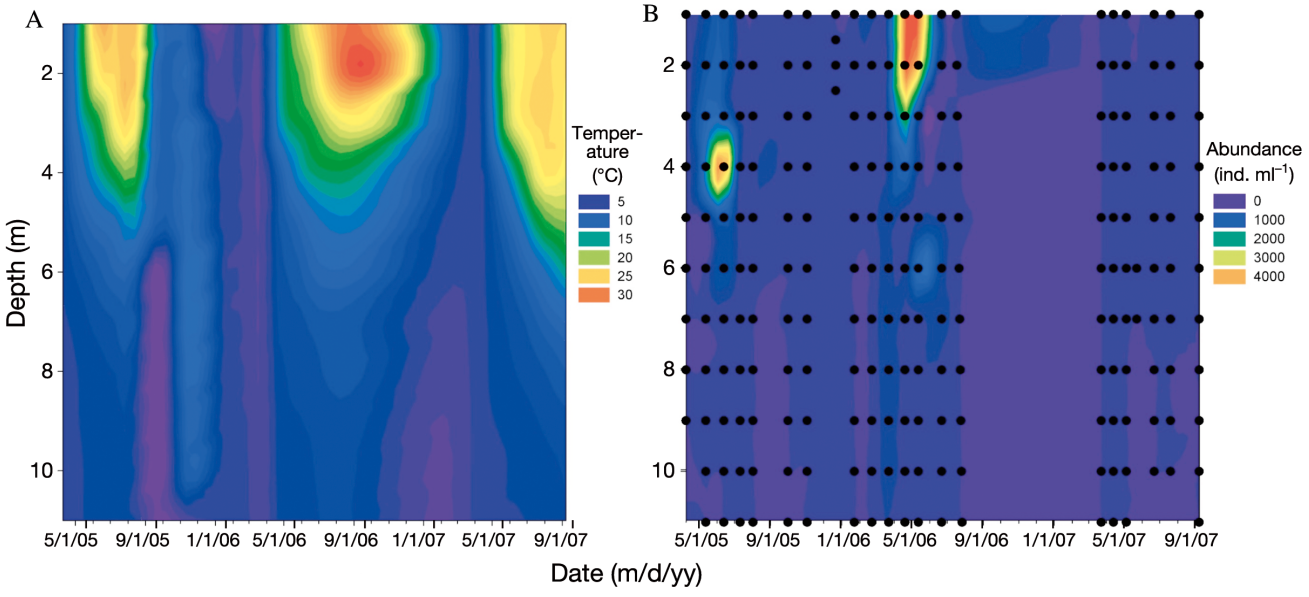

Fig. 1. Contour plots of (A) temperature and (B) *Dinobryon* spp. abundance/distribution in Lake Lacawac, Pennsylvania, USA, from May 2005 through September 2007. Black dots indicate dates and depths of sampling. The color keys for both panels represent a continuum from 0 (magenta) to the highest number recorded (bright orange). Note that for the purpose of constructing a continuum, periods not sampled were represented as zeros

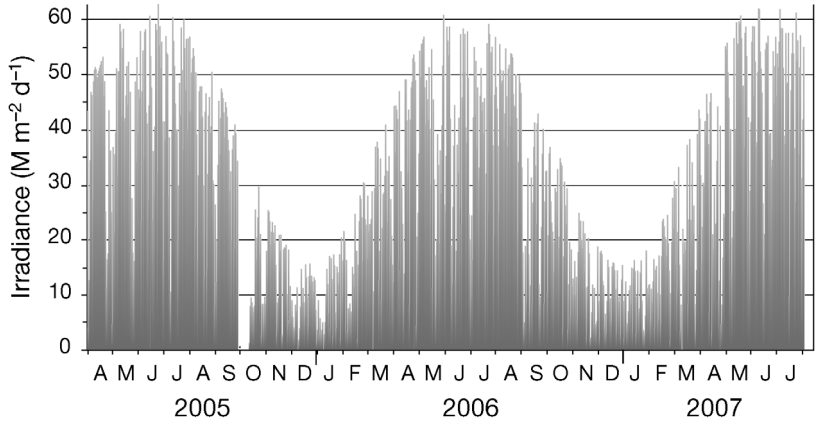

Fig. 2. Summed daily photosynthetically active radiation (PAR) irradiance during the study period plotted from weather station data collected at Lake Lacawac (Hargreaves 2007).

but abundances were close to the level of detection during much of the sampling period (Table 1). Occasional occurences of *D. bavaricum*, also close to the level of detection, were noted. Maximum annual abundances of *D. cylindricum* occurred at a depth of 4 m in June 2005 (4284 cells ml^{-1}) and in a broader water stratum between 1 and 3 m in April 2006 (~4600 cells ml^{-1}) near the onset of stratification (Fig. 1). In spring of 2007, the *Dinobryon* population increased relative to winter abundances, but populations as large as those in the previous 2 yr were not observed (Fig. 1, Table 1).

On the days of maximum *Dinobryon* sp. abundance in 2005 and 2006, the daily surface irradiance was similar, 60.6 and 52.3 M m^{-2} d^{-1} (Fig. 2), as was the average PAR for the week prior to these abundance peaks (43.7 and 42.3 M m^{-2} d^{-1}; Hargreaves 2007). However, the depths of maximum *Dinobryon* abundance (4 and 1 m, respectively, Table 1), and light intensities at those depths at the time of sampling (144 and 868 µM m^{-2} s^{-1}), were considerably different. Conversely, temperatures at those depths were between 13° and 15°C. In 2006, high abundances observed in April were maintained through May at the same depth, although the water warmed to 18°C (Table 1) and average surface irradiance for the week prior to sampling in May 2006 was only 39.2 M m^{-2} d^{-1}. In both 2005 and 2006, *Dinobryon* were virtually absent from the epilimnion once the water reached 20°C.

Dinobryon abundance was not normally distributed, and a non-parametric Spearman's rho indicated a negative correlation between temperature and *Dinobryon* for time periods when the alga was present ($p < 0.009$). However, plotting *Dinobryon* abundance versus temperature for all dates and depths where the species was observed indicated that the highest abundances were recorded at intermediate temperatures (between 13° and 18°C; Fig. 3). The hypothesis that highest abundances (blooms) were found within an intermediate temperature range was tested with a 2-way chi-squared test of temperature to *Dinobryon* cells ml^{-1} for all the samples in the Lake Lacawac study. The null hypothesis of no relationship between the abundance values at different temperature ranges was rejected ($p < 0.001$, 2-sided); the highest abundances occurred significantly more frequently (nearly 3 times greater than predicted) when temperatures were within the range of 9.3° to 18.3°C (Table 2). Over the whole period of observation, abundances over 1000 *Dinobryon* ml^{-1} were observed only at temperatures between 11° and 18.2°C

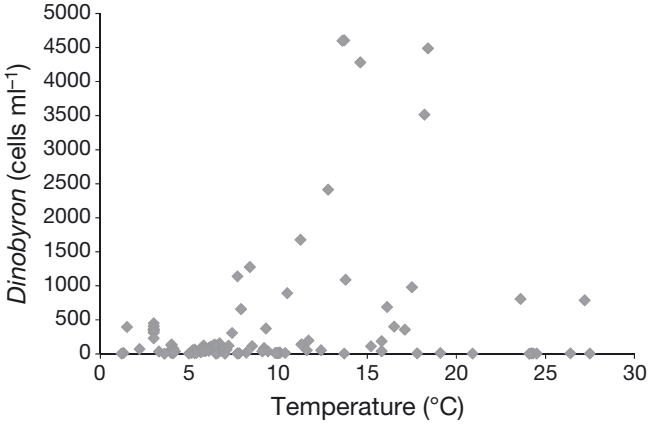

Fig. 3. *Dinobryon cylindricum*. Abundance versus temperature for all samples (dates and depths) when *Dinobryon* were present in the water column

Table 2. Two-way chi-squared test for temperature range and *Dinobryon cylindricum* abundances from all sampling dates and depths at Lake Lacawac. Pearson chi-squared = 22.722, 4 df. Occurrences were significantly higher or lower than expected (*$p < 0.001$) only in the temperature range of 9.3 to 18.2°C

Dinobryon abundance (cells ml^{-1})		Temperature range (°C) 0–9.2	9.3–18.2	18.3–27.5
0	Expected	50.5	14.5	8
	Actual	52	15	6
>0 to 358	Expected	96.9	27.8	15.4
	Actual	103	19*	18
359 to 4700	Expected	16.6	4.8	2.6
	Actual	9	13*	2

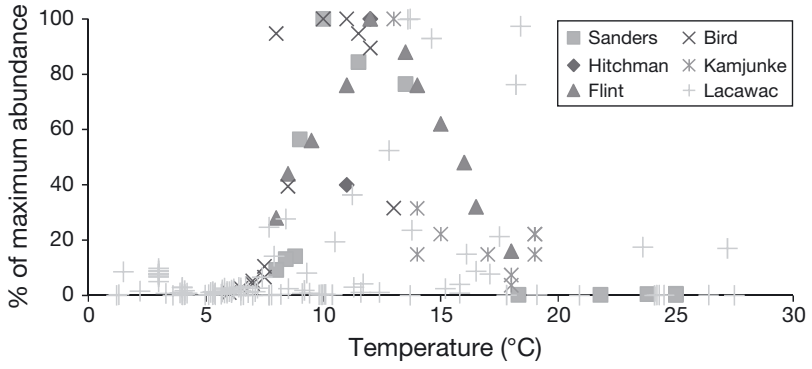

Fig. 4. *Dinobryon* spp. Abundance versus temperature for studies in several lakes. For each study, abundance data were converted to percent of the maximum for the entire observation period. All depths, including samples where *Dinobryon* were not present, were included. Data are from this study (Lacawac), Lake Oglethorpe, Georgia, USA (R. W. Sanders unpubl. data), and the literature (Flint 1938, Bird & Kalff 1987, Hitchman & Jones 2000, Kamjunke et al. 2007)

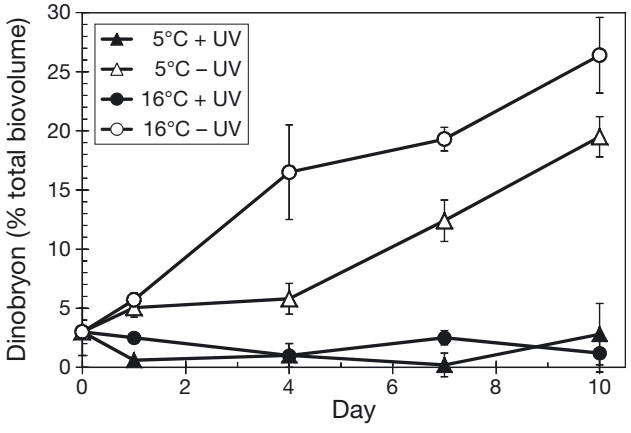

Fig. 5. *Dinobryon cylindricum*. *Dinobryon* as a percentage of total algal biovolume (mean ± SE) determined over time in a temperature shift and UV protection experiment

(Fig. 1, Table 1). When data on *Dinobryon* abundance and temperature at depth for several lakes were combined, the pattern observed in Lake Lacawac remained (Fig. 4). Most of the population during a given study was found at depths where water temperature was between 7° and 17°C, further suggesting a 'preferred' intermediate range of temperature in the vertical (and seasonal) distribution of *Dinobryon*.

Dinobryon responses to natural UVR and changing temperature

UVR attenuates rapidly in the water column of Lake Lacawac (see above), but can penetrate to considerable depth in clear lakes. When UV wavelengths were blocked, *Dinobryon* incubated at the surface of oligotrophic Lake Giles had growth rates of 0.18 and 0.24 d^{-1} over 10 d when kept at 5.5°C or warmed to 16°C, respectively. *Dinobryon* population biovolume increased from <5% of total phytoplankton biovolume to approximately 15 and 25% at the cold and warm temperatures, respectively (Fig. 5). In the presence of full spectrum sunlight, *Dinobryon* abundance declined rapidly, from 50 to 4–12 cells ml^{-1} and remained low to undetectable in all replicates. A 2-way ANOVA showed strong negative correlation of UVR and population growth for *Dinobryon* ($p < 0.001$). The total biovolume of phytoplankton also declined in the treatments exposed to UVR, reflecting the generally negative effect of natural surface levels of UV on the whole phytoplankton community, and not solely on *Dinobryon*.

Temperature, growth, and feeding in the laboratory

Under high light (67 µM m^{-2} s^{-1}) with no acclimation to temperature, *Dinobryon* sp. population growth rates (~0.21 d^{-1}) were similar to acclimated at ≤17°C; growth was slower at 19°C and negative at ≥21°C (Fig. 6a). With a 5 d acclimation period to temperature and high light, growth rate increased (0.15 to 0.31 d^{-1}) as incubation temperature increased from 4° to 16°C, and was lowest at 20°C (Fig. 6b). With acclimation and lower light (25 µM m^{-2} s^{-1}), growth followed the same trend as at higher light levels except at about half the rate for temperatures between 4° and 16°C; population size declined slightly at 20°C (Fig. 6c). Bacterivory by *Dinobryon* during these experiments was significantly greater in low light than in high light, and occurred at a significantly greater rate at 12°C than at higher or lower temperatures for both light levels (Fig. 7). Minimum feeding rates were recorded in high light at the extremes of the temperature range tested.

DISCUSSION

Like other photosynthetic plankton, *Dinobryon* increase in abundance as day length, light intensity,

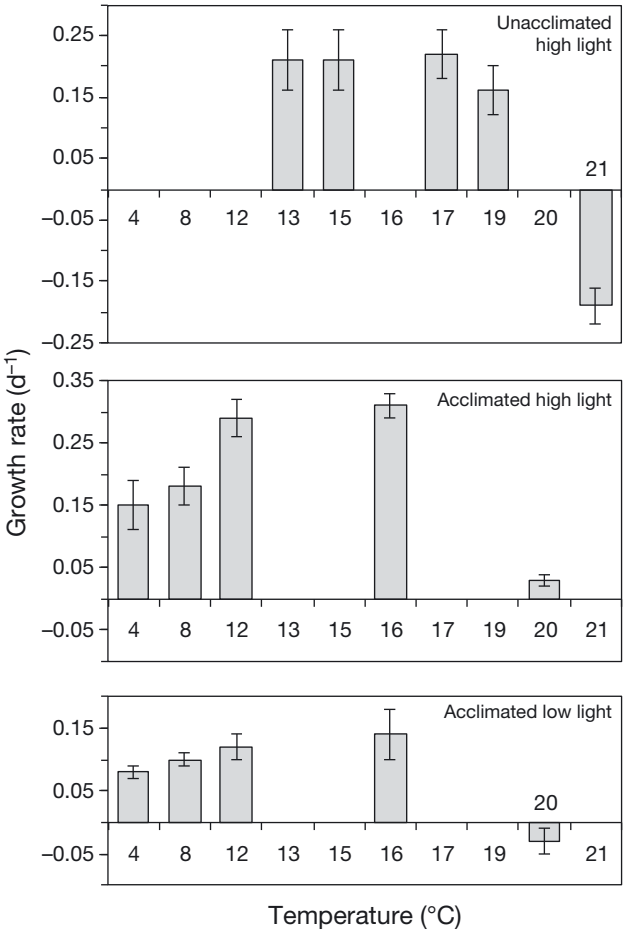

Fig. 6. *Dinobryon* sp. Growth rates (mean ± SE) at different temperatures, acclimation periods, and irradiances

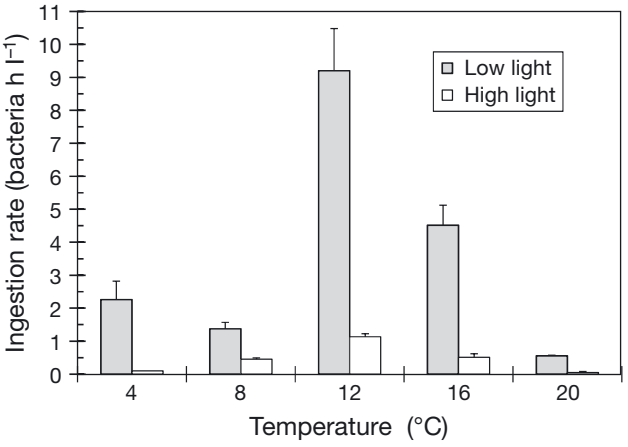

Fig. 7. *Dinobryon* sp. Rates of bacterivory at different temperatures and light intensities (±SE). Shaded and white bars are experiments run with photosynthetically active radiation (PAR) light intensities of 25 and 67 µM m^{-2} s^{-1}, respectively

and surface temperatures increase in the spring (Fig. 1; Siver & Chock 1986, Eloranta 1989). Several non-exclusive environmental factors, including nutrients, light, and predation, have been linked to the seasonal dominance and decline of the genus (Lehman 1976, Siver & Chock 1986, Dokulil & Skolaut 1991, Veen 1991), but factors affecting vertical population peaks have received less attention. Using field and laboratory experiments, coupled with an examination of literature data, this study supports the premise that light and temperature interact to delimit a spatial (depth) / temporal niche where *Dinobryon* will bloom.

As mixotrophs, *Dinobryon* are not dependent on photosynthesis as their sole source of carbon, but laboratory evidence suggests that they are obligate phototrophs that cannot survive long periods in the dark (Caron et al. 1993). During periods of high abundance, the photic zone depth (1% of surface irradiance) in Lake Lacawac was approximately 4.5 m; below 5 m, plankton would experience nearly complete darkness. *Dinobryon* were rarely found below 4 m in our study, suggesting that attenuation of PAR did set a maximum depth limit to their vertical distribution in this lake. However, no statistically significant relationship was noted for photic zone depth and *Dinobryon* abundance, and PAR did not appear to be the single critical component driving vertical distribution in the water column of Lake Lacawac.

Temperature was predictive of high abundances of *Dinobryon* in Lake Lacawac (Table 2). The 2 main seasonal peaks of *Dinobryon* abundance observed during our study occurred during late spring in 2005 and 2006, but with maximum abundances at different depths (Fig. 1, Table 1). Light intensities at those depths were 144 and 868 µM m^{-2} s^{-1} at the time of sampling in 2005 and 2006, respectively, while temperatures were 14.6° and 13.6°C, and overall PAR fluxes during the week prior to each bloom were similar. Furthermore, *Dinobryon* are active swimmers and will migrate in response to temperature in the absence of light and nutrient gradients (Clegg et al. 2003, Heinze & Sanders 2009). *Dinobryon* has a broad range of temperature in which it survives (Table 1). Eloranta (1989) reported abundances for 8 species of *Dinobryon* from hundreds of Finnish lakes over many years and found that all 8 species were present at temperatures ranging from <1° to 22°C. However, the high growth rates that lead to blooms of *Dinobryon* are less likely when temperatures are at the extremes of this range. Butterwick et al. (2005) found that *D. divergens* had maximum growth at an intermediate temperature (17°C) when light and nutrients were not limiting, which agrees with our observations of maximum growth and grazing at an

intermediate temperature for *Dinobryon* sp. (Fig. 6). The trend for maximum abundance at intermediate temperatures observed in Lake Lacawac was also evident in 5 other lakes (Fig. 4). These data were collected in lakes with maximum depths ranging from 8 to >250 m that were distributed in the US, Canada, Europe, and New Zealand, and with different species of *Dinobryon* dominating. Together, these observations strongly support the inference that temperature has an important role in the occurrence of *Dinobryon* blooms and in structuring their vertical distribution.

It is unlikely that the UV component of the solar spectrum contributed much to inhibition of *Dinobryon* in Lake Lacawac because it attenuates rapidly there (Williamson et al. 2001). However, UVR may constrain *Dinobryon* to deeper water in oligotrophic lakes (such as Lake Giles) that are more transparent to UVR. Depending on temperature, *Dinobryon* may have a competitive advantage at the subsurface light levels in oligotrophic lakes; when UVR was blocked, *Dinobryon* populations increased in both absolute and relative abundance to other phytoplankton (Fig. 5). *Dinobryon* were more competitive at 16°C, which is within the temperature range of maximum growth (Fig. 6b).

The lack of a *Dinobryon* bloom in Lake Lacawac during 2007 (Fig. 1, Table 1) was unexpected. Sampling was temporarily suspended during winter that year and an early bloom could have been missed. However, such early blooms have not been previously observed. Berninger et al. (1992) observed bacterivory by *Dinobryon* in Lake Lacawac during late February, but abundance of total mixotrophs (including *Dinobryon*, but dominated by other nanoflagellates) was only between 400 and 1100 cells ml^{-1}. Siver & Chock (1986) reported a bloom in Lake Lacawac in March 1981, but relatively high abundances (>1000 ml^{-1}) were still present the following month. Likewise, for the blooms in 2005 and 2006, abundances >1000 ml^{-1} were observed on at least 2 dates (Table 1), indicating that monthly sampling intervals should have given an indication of a February or early March bloom. The integrated daily PAR averaged over the week prior to the March 2007 sampling date was also low (27.8 versus 42–44 M m^{-1} d^{-1} prior to blooms in 2005 and 2006). Thus it seems unlikely that there was an early, unobserved bloom. Average air temperature during the week prior to blooms in 2007 was approximately 10°C cooler than in 2005 and 2006 (Hargreaves 2007) as were water temperatures (Table 1), and average daily irradiance was considerably lower (Fig. 2). We speculate that cooler temperatures and reduced insolation in March and April 2007 inhibited the initiation of a bloom that year.

Our experiments, and others, show that temperature affects growth and feeding rates in *Dinobryon* as in many other protists (Caron et al. 1986, Bird & Kalff 1987, Jones & Rees 1994, Weisse et al. 2002). Field data indicate that highest abundances of *Dinobryon* are often found at temperatures between 9 and 18°C (Fig. 4), and the tendency of *Dinobryon* to migrate to an intermediate temperature when light and nutrient levels were constant (Clegg et al. 2003, Heinze & Sanders 2009) suggests that there may be a directed movement toward temperatures where growth rates are high. Nutrient concentrations were not reported for the studies plotted in Fig. 4; however, *Dinobryon*, like many chrysophytes, are considered good competitors at low nutrient levels, and can gain nutrients from bacterivory, so migration to depths in search of high nutrient levels seems unlikely. It is more likely that high nutrient levels would put *Dinobryon* at a competitive disadvantage (Sandgren 1988). Thus, while light, nutrients, and predation likely affect the distribution of *Dinobryon*, the field and laboratory data strongly suggest that temperature plays a major role driving depth and seasonal distribution of *Dinobryon* species.

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