THE ROLE OF HEAT AND DROUGHT DURING OCCASIONAL BLOOMS OF PICOPLANKTON AND NANOPLANKTON IN A LARGE DRINKING WATER RESERVOIR (ALLATOONA LAKE, GEORGIA)

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Abstract. In the late summers of 1993 and 2007, phytoplankton communities in Allatoona Lake shifted from typically diverse assemblages to near monospecific blooms of small cell-size species (a 0.5 X 2 µm cyanobacterium and a 2.5 X 15 µm diatom, respectively). These changes resulted in major increases in the amount of flocculating chemicals used to treat drinking water. Water temperatures in the epilimnion during the late summer in each year were the highest measured in these two decades, and these warmest years were associated with very low inflows into the reservoir. Limited nutrient data also indicate an unusual shift to nitrogen limitation during the 1993 bloom. Literature based on physiological studies suggests that small cells (having relatively less surface areas) may have an advantage when the limiting nutrient shifts and temperatures increase, providing an explanation for these blooms of small cells consistent with the meteorological and limnological changes observed during the blooms.

INTRODUCTION

Over the past few decades, there has been increasing recognition of the importance of ultraplankton (collectively picoplankton ranging from 0.2-2 µm and nanoplankton ranging from 2-20 µm) in freshwaters (e.g. Stockner 1991; Callieri and Stockner 2002). Their ecological significance has been considered to be greater in oligotrophic systems in both freshwater and marine systems (Happey-Wood 1993, Fogg 1995; Callieri and Stockner 2002). Fewer studies have described small autotrophic cells in mesotrophic and eutrophic systems (e.g. Cronberg and Weibull 1981; Bailey-Watts et al. 1968: Wehr 1990; Happey-Wood 1991, Ochs and Rhew 1997; Carrick and Schelske 1997). In contrast to oligotrophic systems, picoplankton occurrence is more temporary and their numerical dominance much greater during peak abundance (Cronberg and Weibull 1981; Bailey-Watts et al. 1968). Unlike typical algal blooms, rapid increases in picoplankton can be associated with times of nutrient scarcity rather than abundance (e.g. Wehr 1990; Weisse and Kenter 1991; Szelag-Wasielewsha 2005).

Major shifts in the phytoplankton communities of Lake Allatoona (Georgia USA), a mesotrophic-eutrophic impoundment, toward near monospecific assemblages of small cell-size species occurred in both the late summers of 1993 and 2007. These blooms significantly affected the treatment of drinking water and have not been noted during any other year over the four decades of water withdrawal from the reservoir. Because smaller cells have less surface area relative to volume, potentially influencing both efficiency of nutrient uptake and sinking rates, this paper investigates changes in nutrient and temperature regimes associated with observed ultraplankton blooms in Lake Allatoona to develop an explanation for the occurrence of such periodic dominance by small cells.

MATERIAL AND METHODS

Allatoona Lake is a 4804-hectare flood control impoundment of the Etowah River located ~50 km northwest of Atlanta, Georgia. Its southern subwatersheds have experienced rapid suburban development over the last three decades. Allatoona Lake is monomictic, ranging from mesotrophic to eutrophic depending on location, and has a mean annual residence time of 3.8 months (U.S. EPA 1998). The two largest arms of the lake (the main Etowah River Arm and the Allatoona Creek Arm to the south) converge at the dam where water depth typically exceeds 40 m from late spring to early fall, after which time lake level is dropped during the winter for flood control. Water is withdrawn for drinking water treatment at the dam and midway up the Allatoona Creek Arm of the reservoir.

Lake Allatoona was sampled bimonthly (April-October) and monthly (November-March) from May

1992 to October 1996 at six sites as part of a U.S. EPA Clean Lakes Phase I Diagnostic and Feasibility Study. Nutrient, chlorophyll, and phytoplankton were analyzed from composited samples taken at four evenly distributed depths through the photic zone. Analyses followed U.S. EPA approved methodology (APHA 1991). Phytoplankton were identified, measured, and quantified over four seasons at eight locations during the first year of the study. Phytoplankton samples were taken sporadically in subsequent years. Algal growth potential tests were performed periodically thoughout the Clean Lakes study.

Vertical distribution of water temperature on the Allatoona Creek Arm at mid-channel across from the 28A channel marker (Station 28A) and near the dam (Station 1E) was monitored in most years subsequent to the study by the Georgia Environmental Protection Division in mid August (2001-2007) and by the author in late August to early Septembers (1999-2001, 2003, 2005, 2007, 2009) prior to breakdown of thermal stratification in late September. Temperature at depths of 1 and 4 m are were chosen for analysis to assess both waters subjected to short-term meteorological changes (1m), and waters less frequently mixed with surface waters, which better reflect meteorological and hydrological influences over the summer season (4m). Because water temperatures are expected to be influenced by previous meteorological and hydrological conditions over the preceding months, late summer water temperatures were compared to air temperature and to hydrological parameters averaged over three summer months. Linear correlation was used to examine the relationship among these parameters over multiple years between 1992 and 2007 for which data are available (n=12 years for all parameter except Etowah River Temperature where n=10). Summer air temperatures for each year are means of daily averages from June to August for the northern portion of Georgia (NOAA 2010); inflows, lake elevation, and residence time are means of daily averages from June to August (U.S. ACE 2010); Etowah River water temperatures are means of bimonthly measurements at Canton Georgia just upstream of Allatoona Lake (USGS 2010).

RESULTS

The most dramatic change in water quality over the five years of the Clean Lakes study occurred in the late summer of 1993. Water samples at several sites along the Allatoona Creek Arm and near the dam on the Etowah River Arm became difficult to filter for both chlorophyll and fecal coliform bacterial analyses, and water transparency was lower than in the other four years of monitoring (U.S. EPA 1998). During this same period, the drinking water treatment facilities drawing water from the lake reported a dramatic increase in the amount of flocculating chemicals used to treat water (Cobb Marietta Water Authority, pers. comm.). Microscopic examination of lake water and of flocculent taken from the drinking water treatment plant revealed a numerical dominance of a small rod shape cell (~0.5 X 2 μm). These cells autofluoresced upon excitation of light at 450 nm indicating the presence of chlorophyll, and, along with their extremely small size and lack of organelles, this suggests the organism to be a cyanobacterium. Densities of these cells in the Allatoona Creek Arm were extremely high (e.g. 132,000 cells/ml at 28A in September 1993, more than an order of magnitude greater than all phytoplankton cells in the previous September). Chlorophyll concentration remained within ranges observed in late summers in the other years of the Clean Lakes study. Ratios of nitrogen to phosphorus were lower throughout the lake in the summer of 1993 (all ratios < 10:1 suggesting nitrogen limitation; n = 22 sites-dates) than in the other years of the study (50 of 72 sites-dates with calculable ratios > 20:1 suggesting phosphorus limitation, and only five sites-dates < 10:1). Both decreased nitrogen levels and increased phosphorus levels contributed to this shift (Figure 1). Algal growth potential tests performed periodically during the first four years of the study also support strongest nitrogen limitation in the late summer of 1993 with nitrogen limitation occurring at eight of the eleven lake sites (nitrogen limitation only occurred at three of the other 41 site-dates tested at other times) (U.S. EPA 1998).

Not until the late summer of 2007 were there similar problems in treating drinking water (Cobb Marietta Water Authority, pers. comm.). Microscopic examination of samples taken at several locations in the Allatoona Arm revealed that a small diatom (2.5 X 15 μm), *Achnanthes minutissima*, dominated phytoplankton assemblages (e.g. during early September 2007 in the Allatoona Creek Arm, *A. minutissima* comprised 99% of a phytoplankton cells and 74% of phytoplankton biomass). While the cell size of this diatom is an order of magnitude larger than the cyanobacterium of 1993, it ranks as the second smallest of 14 diatom species quantified in Lake Allatoona and falls well within the lowest size quartile reported for freshwater diatoms (Litchman et al. 2009). As in 1993, diversity of the phytoplankton community declined dramatically relative to other

years in which phytoplankton were examined (e.g. Shannon-Weiner Diversity Index for September 2007 was 0.10 whereas diversity varied from 1.64 to 2.12 across eight sites in September of 1992).

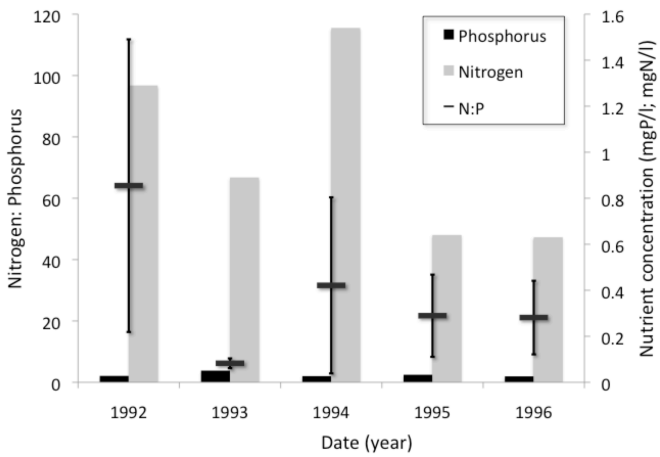

Figure 1. Mean nutrient concentrations (total kjeldahl nitrogen and total phosphorus and ratio between the two (N:P) for summer months over the five years of the Clean Lakes study; n=94 site-dates). Nitrate and nitrate were often below detection limits so by excluding these in from the N:P calculation more site-dates could be considered (nitrate and nitrite were usually a small fraction of TKN so TP:TN co-varied with TP:TKN on dates where nitrate/nitrite is calculable; r=0.99 n=220 site-dates). Vertical lines are +1 standard deviation from mean for N:P.

Late summer, epilimnetic temperatures tended to be higher in the two summers that blooms occurred (1993 and 2007) than in other years over the 15 summers in which measurements were made from 1992 to 2009. While mid-August water temperatures in other years were occasionally higher than the bloom years of 1993 and 2007 (e.g. 1995), only during the bloom years were temperatures consistently high at both sample depths, both sites, and both dates (Figure 2). Mean summer air temperature was hotter in 1993 than any year in these two decades and the third hottest in 2007, while 2007 had the least summer tributary inflow and 1993 the third least inflow. Over all of the years analyzed in this study, summer air temperatures co-varied with lake hydrology (inflow, residence times, and lake levels) indicating that hotter years tend to be drier years (Table 1). Epilimnetic temperatures were positively correlated with summer air temperature and inversely correlated with summer lake elevation. However, hypolimnetic temperatures show opposite trends, where water temperatures in the deepest part of the lake (Station 1E) were coolest in 2007, and bottom temperatures were positively correlated with inflow and inversely with lake levels and residence times. Over the years that temperatures were monitored, hypolimnetic temperatures tended to decline (Figure 3).

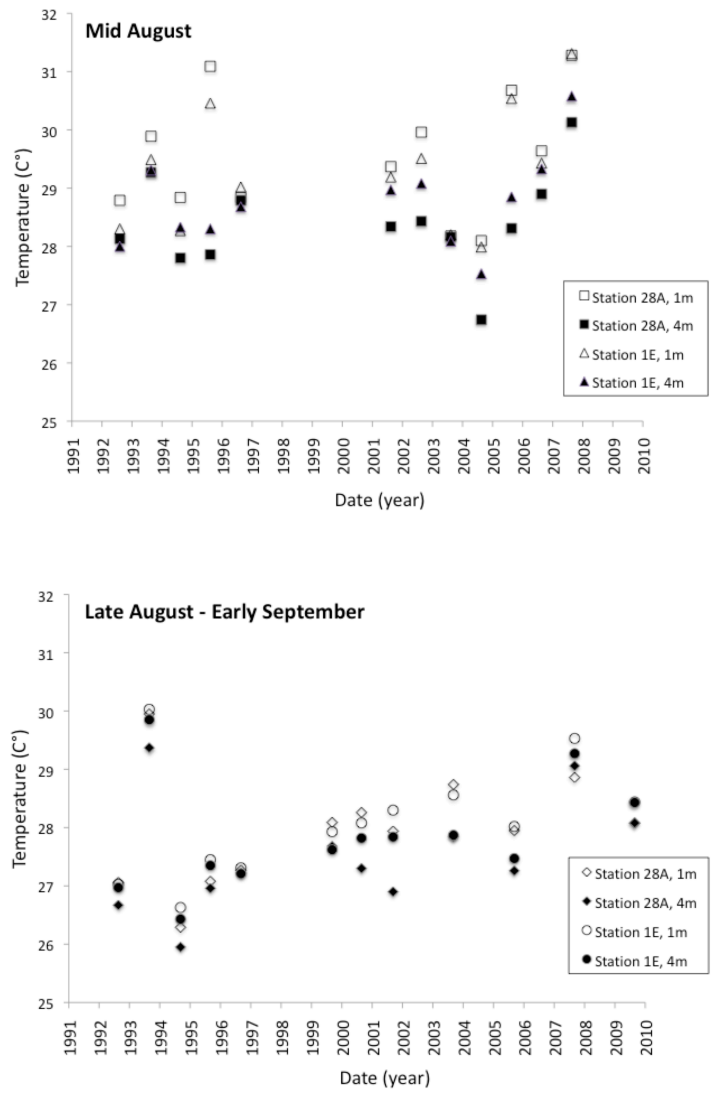

Figure 2. Water temperature over 15 years at two depths (1 m and 4 m) at two stations (Stations 28A and 1 E) and over two time intervals. Tick marks on the horizontal axis indicate the beginning of the labeled year.

Table 1. Correlation r values (product-moment correlation coefficients) among various parameters (P<0.05 indicated by bold font) over multiple years between 1992 and 2007 for which data are available (n=12 years for all parameter except Etowah R. Temperature where n=10). Water temperature measurements are from mid August data; similar relationships among these parameters also occurred for water temperatures measured in the late August - early September data set.

	Water temperature 4m (28A)	Water temperature 4m (1E)	Water temperature 26-30m (1E)	Summer inflows into lake	Summer lake elevation	Etowah R. temperature	Summer residence time	Summer air temperature
Water temperature 4m (28A)	**1.00**							
Water temperature 4m (1E)	**.95**	**1.00**						
Water temperat. 26-30m (1E)	-.56	**-.59**	**1.00**					
Summer inflows into lake	-.37	-.45	**.84**	**1.00**				
Summer lake elevation	**-.58**	**-.67**	**.80**	**.80**	**1.00**			
Etowah R. temperature	.52	**.62**	**-.72**	**-.84**	**-.70**	**1.00**		
Summer residence time	.56	**.66**	**-.87**	**-.80**	**-.85**	**.66**	**1.00**	
Summer air temperature	**.73**	**.75**	-.53	**-.57**	**-.71**	**.65**	**.59**	**1.00**

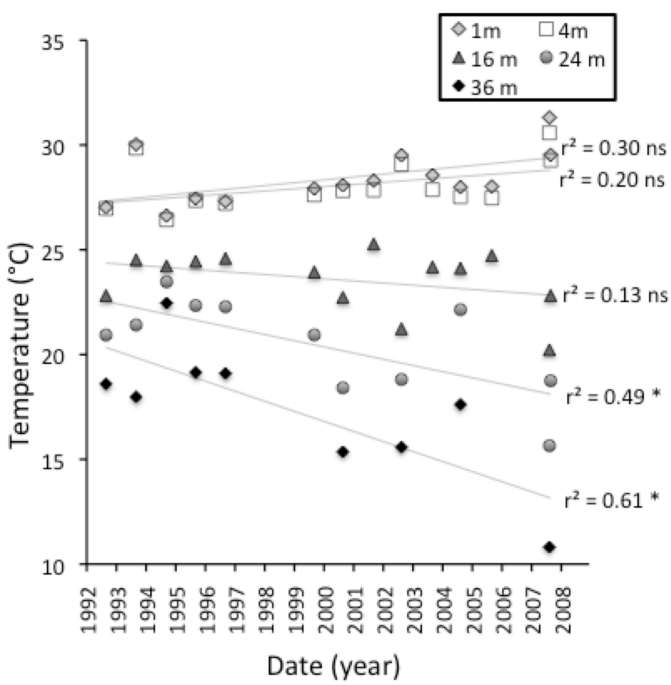

Figure 3. Water temperature at Station 1E at various depths over time for all sample dates.

DISCUSSION

The phytoplankton blooms of 1993 and 2007 have in common numerical dominance of single small-celled species during years of unusually warm epilimnetic waters. While air temperature is expected to influence water temperature, other factors also seem to influence the distribution of heat and nutrients in the reservoir. Though such factors are confounded (Table 1), they tend to favor a shift toward nitrogen limitation. As lake levels drop in drier years, exposed sediments are resuspended by wave action potentially making adsorbed phosphorus available. In Allatoona, resuspension of previously deposited sediments by waves during periods of low lake level explain seasonal increases in turbidity (Dirnberger and Weinberger 2005). Cooler hypolimnetic waters during hot, dry summers may be the result of not only less mixing as surface waters warm, but also longer summer residence times which would retain more of the water that was cooled during the previous winter. Changes in the strength of stratification may in turn

differentially affect the entrainment of phosphorus and nitrogen from the epilimnion. In Lake Tahoe, Winder, et al. (2009) found that N:P ratios were inversely correlated with strength of stratification as reduced mixing limited return of regenerated nitrogen from deeper waters. Another factor that may contribute to a shift toward nitrogen limitation in hot, dry years is a reduction in atmospheric deposition of nitrogen across the watershed. Atmospheric deposition can represent a significant portion of nitrogen loading into a lake (e.g. Morales 2001; Mosello et al. 2001), and lakes in arid regions tend more toward nitrogen limitation (Camacho et al. 2003; Fenn et al. 2003). A similar effect may be occurring in dry years in Allatoona Lake where nitrogen declined in both lake and tributaries during the two driest summers of the Clean Lakes study (whereas phosphorus increases in the lake could not be attributed to phosphorus changes in the tributary loads) (U.S. EPA 1998).

The conditions described above can favor smaller phytoplankton cells in two ways. First, changes in nutrient concentrations appear to alter the competitive advantage between small and large phytoplankton cells (Parson and Takahashi 1973; Lean and White 1983; Suttle and Harrison 1988; Wehr 1993; Ochs and Rhew 1997; Philippart et al 2000; Viličić et al 2007). The competitive advantage of smaller cells in nutrient poor waters has been attributed to greater surface area relative to volume and to improved efficiency of material transport at small scales, increasing the rate of nutrient supply relative to cellular demand (e.g. Fogg 1986; 1995). While low nutrient concentrations can explain the prevelance of smaller cells in oligotrophic water (e.g. Callieri and Stockner 2002), irregular shifts to nitrogen limitation may also explain their episodic dominance in more eutrophic systems. Larger-celled species adapted to phosphorus-limited conditions are out-competed by small cells, while larger-celled species with specific adaptations to more efficiently acquire and store nitrogen (e.g. Collos 1986) would be rare or absent where nitrogen limitation is infrequent, as is typical of temperate freshwaters (Schindler 1977) such as Allatoona Lake.

Second, cell size may also be affected by water temperatures which differentially influence sinking rates of cells from the photic zone in accordance with Stokes' Law (Smayda 1970). Warmer temperatures increase sinking rates, yet smaller cells sink more slowly. In addition, less turbulence associated with stronger stratification may differentially increase loss of larger cells from the photic zone (Ruiz et al. 1996). While Winder et al. (2009) attribute the shift toward smaller diatom species in Lake Tahoe over 24 years to differential sinking due to climate change, it is hard to imagine how size-dependent sinking alone would result in such a dramatic shift to near mono-specific assemblages as observed in Lake Allatoona.

Traditionally, freshwater phytoplankton communities have been noted for their exceptional diversity (Hutchinson 1961). In Allatoona, it appears that dramatic declines in diversity occur because few species are pre-adapted to environmental extremes. Human impacts often increase the magnitude of environmental variations. When nutrient loads were lower in previous decades prior to rapid urbanization of the southern watersheds (U.S. EPA 1998) and nutrient variability was likely less because non-point sources were fewer, blooms were not noted. As eutrophication has proceeded in Allatoona Lake, short-term nitrogen limitation may be becoming more likely (e.g. Downing and McCauley, 1992), occasionally shifting the competitive balance toward those phytoplankton species that are efficient at acquiring nutrients by virtue of their small size. Climate change would as be expected to have a similar effect, forcing greater extremes onto the natural variations in heat and drought (e.g. Wang et al. 2010). In fact, recent studies have attributed shifts in cells size of freshwater phytoplankton to climate change (Christoffersen et al. 2006; Winder et al. 2009). The trend in the vertical heat distribution in Allatoona observed over the years of this study (Figure 3), whether the result of nutrient eutrophication or change in meteorological conditions associated with climate change, suggest that blooms will continue to occur periodically in the lake.

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