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Invasion of a littoral cladoceran *Sida crystallina* into the pelagic zone of Christine Lake, NH and its potential impact on the phytoplankton community

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Abstract

This study evaluated the phytoplankton community and grazing influences of the zooplankton in oligotrophic Christine Lake, NH, by assessing the body size and clearance rates of the three dominant crustaceans: *Sida crystallina* (0.08 individuals L⁻¹), *Daphnia dubia* (0.11 individuals L⁻¹), and *Leptodiptomus sicilis* (2.11 individuals L⁻¹). *Sida crystallina*, typically a littoral cladoceran, was abundant throughout the water column in the open water, and contributed approximately 44% of the grazing in the pelagic zone. Phytoplankton abundance was examined to assess the potential impact *S. crystallina* might have on the phytoplankton in Christine lake. *Aphanocapsa*, the dominant phytoplankton in Christine Lake (relative abundance 68.54%), is a picocyanobacterium capable of forming colonies in the presence of planktonic grazers. Its ability to out-compete other phytoplankton due to differential grazing pressure suggests the appearance of the strong grazer *S. crystallina* may have contributed to the dominance of cyanobacteria in this oligotrophic lake.

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Introduction

Trophic interactions are important in explaining differences in productivity among lakes with similar nutrient levels, but contrasting food webs (Carpenter *et al.* 1985). Oligotrophic lakes, such as Christine Lake, have low nutrients and primary production, well-oxygenated water, and low algal production. A typical lake food web has four trophic levels: piscivores, zooplanktivores, herbivorous zooplankton, and phytoplankton (Carpenter *et al.* 1985). Due to the top-down effects of visual predation in some lakes, small zooplankton species such as copepods, often dominate when piscivores are rare and zooplanktivorous fish are abundant. However, large herbivorous species, such as *Daphnia*, dominate when zooplanktivores are scarce (Vanni *et al.* 1997).

Crustacean zooplankton includes grazers such as *Daphnia* and calanoid copepods,

whereas phytoplankton can be divided by size into four groups: picoplankton too small to be grazed, nanoplankton subject to grazing by all herbivores, edible net phytoplankton grazed only by larger zooplankton, and large (>50 µm) inedible algae (Carpenter *et al.* 1985). The density and composition of a phytoplankton community can be greatly affected by zooplankton grazing. Although nutrient concentrations influence the phytoplankton communities, grazing by zooplankton can also have influential effects on phytoplankton relative abundance and community structure (Vanni 1987).

This study originally set out to examine the biological and chemical characteristics of Christine Lake, as well as the density and composition of the plankton community. However, the appearance of a littoral cladoceran in the pelagic zone of the lake raised questions concerning possible effects of this unusual grazer on the phytoplankton community.

Methods

Study Site – Christine Lake is an oligotrophic lake in Stark, NH with a mean depth of 7.3 m and a maximum depth of approximately 20 m (Fig. 1). The lake has a forested watershed with

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little development, and the surrounding mountains and smooth sandy shore attract wildlife such as loons. Christine Lake is stocked yearly with coldwater salmonids such as brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) (NHFGD 2010).

photosynthetically active radiation (400-700 nm). Measurements were recorded on a Li-Cor Radiometer 1400 at 0.5-m intervals. Light extinction coefficient (k_{ext}) was calculated as the absolute slope of $\ln(I)$ vs. depth (m). Secchi disk depths were measured using a black and white

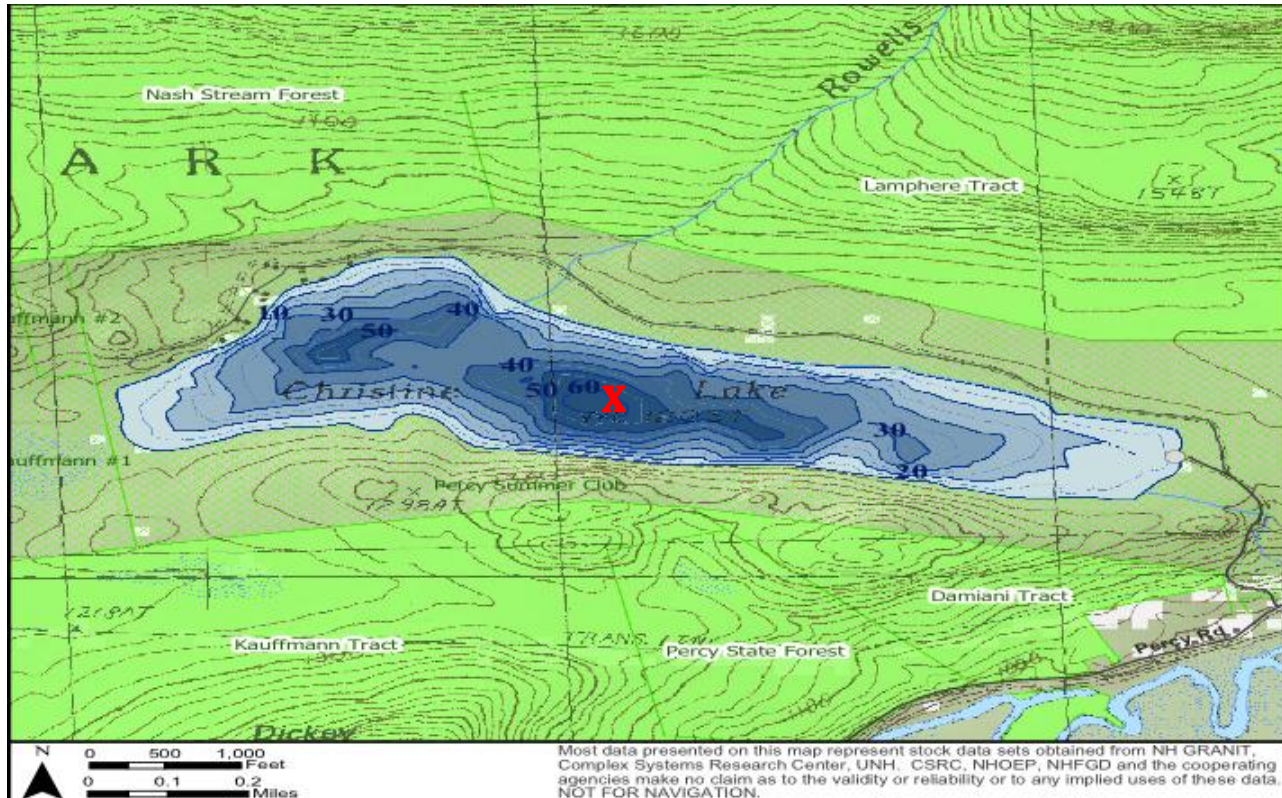


Fig. 1: Topographical map of Christine Lake in Stark, NH (NHFGD 2010) showing the sampling location (X).

Field Methods – A multi-parameter probe (Yellow Springs Instrument 6600 M V2) equipped with a YSI 650 MDS data logger was used to measure the vertical profile of the lake. Parameters included temperature (C), depth (m), dissolved oxygen concentration (mg L^{-1}), turbidity (NTU), chlorophyll *a* ($\mu\text{g L}^{-1}$), phycocyanin concentration (*Microcystis* equivalent cells mL^{-1}), pH, specific conductivity ($\mu\text{S cm}^{-1}$), and oxidation-reduction potential (mV). The probe was slowly lowered at a rate of 0.5 m min^{-1} and data were recorded every 3 s or approximately 2.5-cm depth intervals.

Light intensity (*I*) was measured with an underwater quantum sensor and a sensor for correcting variations in down-dwelling light intensity. Both sensors measured

disk (20-cm diam.), and a viewscope to eliminate surface reflection.

Discrete-depth plankton collections, as well as a live plankton haul were collected. Vertical hauls were made with a 50- μm mesh closing net (20-cm diam.) lowered to discrete depths every 2 m and closed. Each discrete sample was preserved with 4% formalin-sucrose.

Laboratory Methods – Multiparameter data were uploaded from the data logger, exported into Excel, and graphed and analyzed in Sigma Plot 11.0 with SigmaStat for all statistics and graphics.

Plankton were counted and identified for each discrete depth to determine the densities of zooplankton (individuals L^{-1}) and the relative abundance of phytoplankton (%). Body lengths



Fig. 2: The dominant zooplankton found in Christine Lake included *Daphnia dubia* (1.3 mm), *Sida crystallina* (1.7 mm), and *Leptodiptomus sicilis* (0.56 mm). Mean size of all crustacean zooplankton (1.2 mm) led to an estimated high predator-to-panfish ratio (0.73) (Mills *et al.* 1987).

(mm) of the major crustaceans were measured at depths 0-2m, 4-6m, 8-10m, and 10-12m for representation of each layer. *Daphnia* body lengths were measured from the base of the tail spine to the top of the helmet. Similarly, *Sida* body lengths were measured from the top of the head to the bottom of the abdomen. Copepod body lengths were measured from the top of the head to the split of the urosome. The geometric mean was calculated to find the average body length of each adult crustacean so that this measurement could be used to estimate zooplankton clearance rates, which have a power function relationship with body length (Burns 1969).

Filtering (clearance) rates were calculated for *Daphnia dubia*, *Sida crystallina*, and *Leptodiptomus sicilis* using regression model equations below. In order to calculate the grazing pressure of *Daphnia dubia*, the following general log-log equation was used at 20C:

$\log_{10} F = \log_{10} 0.208 + 2.80 \log_{10} L_b$
 where F is filtering rate (mL animal⁻¹ hr⁻¹) and L_b is body length in mm (Burns 1969).

The grazing pressure of *Sida crystallina* was calculated based on the regression equation with a low seston value (S_n = 0.8 mg liter⁻¹ dry wt) because of the oligotrophic status of Christine Lake:

$V_F = (1.139 + 1.166L - 0.104S_n)^4$
 where V_F is filtering rate (mL animal⁻¹ day⁻¹), L is body length in mm, and S_n is suspended particles or seston (mg liter⁻¹ dry wt particulate matter <35µm) (Downing and Peters 1980).

The grazing pressure of *Leptodiptomus sicilis* was assumed based on an average filtering rate (0.15 mL animal⁻¹ hr⁻¹) at 100 percent cultured algae (Richman and Dodson 1983). Hourly filtering rates (mL animal⁻¹ hr⁻¹) were assumed to be constant over a 24-h period and converted (mL animal⁻¹ day⁻¹) to the daily grazing pressure in Christine Lake.

Results

Zooplankton and Phytoplankton Composition – The zooplankton community in Christine Lake was dominated by large crustacean zooplankton including *Daphnia*

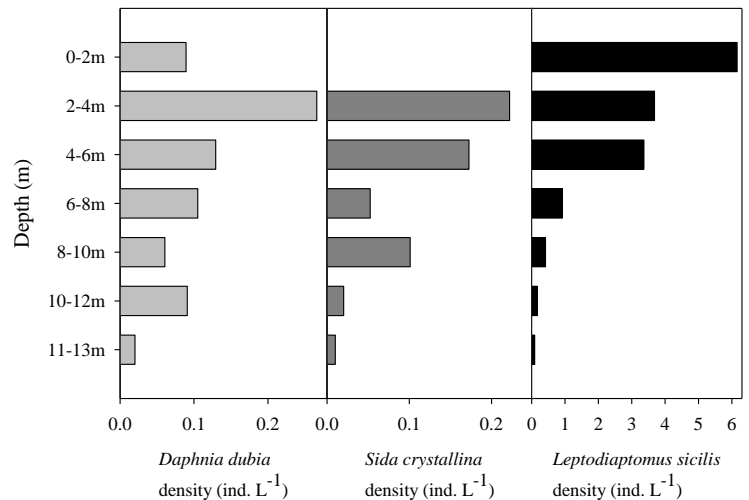


Fig. 3: The density (individuals L⁻¹) of each major crustacean at various depths in Christine Lake. Each species, *Daphnia dubia*, *Sida crystallina*, and *Leptodiptomus sicilis*, thrived at depths 2 to 4 m. The densities at this depth were 0.11 individuals L⁻¹, 0.08 individuals L⁻¹, and 2.11 individuals L⁻¹, respectively.

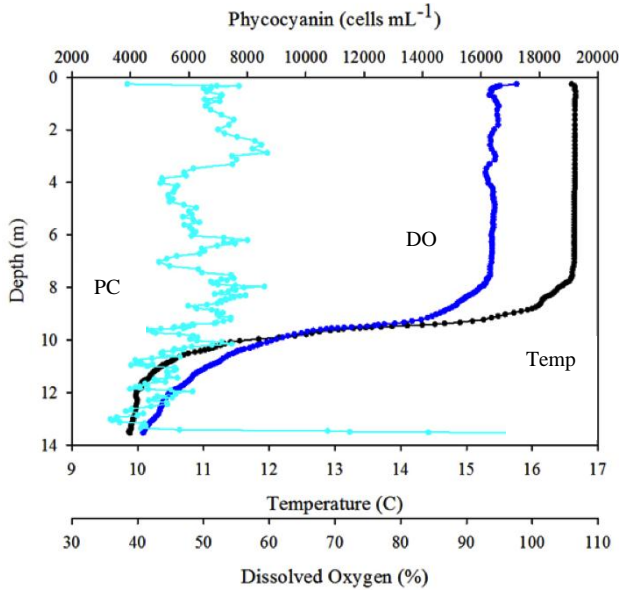


Fig. 4: Temperature (C), dissolved oxygen (%), and phycocyanin (cells mL^{-1}) of Christine Lake. The epilimnion was well mixed from 0 to 8 m where there are also high amounts of dissolved oxygen. Phycocyanin ranged from 4000-9000 cells mL^{-1} throughout the entire water column.

dubia, *Sida crystallina*, and *Leptodiptomus sicilis* (Fig. 2). *Sida crystallina*, typically a littoral species with long, massive swimming antennae, was found in the pelagic zone throughout the water column. This organism was most abundant at 2-4 m (0.22 individuals L^{-1}) (Fig. 3), where there was a constant temperature, high concentration of dissolved oxygen, and a peak in phycocyanin levels (Fig. 4). *S. crystallina* reached densities close to that of *D. dubia* (0.27 individuals L^{-1}) at that same depth. *Leptodiptomus sicilis* dominated the

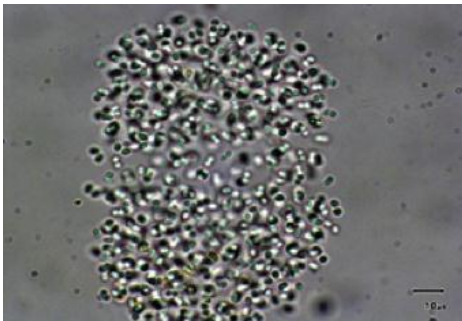


Fig. 5: *Aphanocapsa*, the dominant phytoplankton in Christine Lake, was found in large colonies ($> 50 \mu\text{m}$) throughout the water column. Image taken from the University of New Hampshire PhycoKey.

entire profile, also most abundant at 2-4 m (3.68 individuals L^{-1}) (Fig. 3).

The phytoplankton community was dominated by the cyanobacteria *Aphanocapsa* (68.54%) (Fig. 5). High relative abundances of *Aphanocapsa* occurred throughout the water column, reaching 87% at depths between 6 to 8 m (Fig. 6). This spherical-celled cyanobacteria was found in large colonies ($>50 \mu\text{m}$) at all depths. However, phycocyanin levels decreased to about 4500 cells mL^{-1} at depths where *Aphanocapsa* was most abundant (Fig. 4).

Both plankton communities were best represented throughout the euphotic zone (0-9.5 m), below which the light intensity decreased to $<1\%$ of that at the surface. Light attenuation decreased at a constant rate (avg. $k_{\text{ext}}=0.48$), and average secchi disk depth was $6.9 \pm 0.19 \text{ m}$ (Fig. 7).

Grazing Pressure – Because *Sida crystallina* was found in the pelagic zone, filtering rate and grazing pressure of the dominant crustaceans were calculated at each depth to determine the potential impacts on the phytoplankton community. *S. crystallina* had the highest clearance rate of $84.65 \text{ mL animal}^{-1} \text{ day}^{-1}$, and a mean body length of 1.7 mm. This typical littoral species is much larger in size than *Daphnia dubia* and *Leptodiptomus sicilis*, and has a greater grazing influence on the lake. The grazing pressure at 2-4 m, for instance, was $1.88\% \text{ day}^{-1}$, $0.28\% \text{ day}^{-1}$, and $1.32\% \text{ day}^{-1}$ for

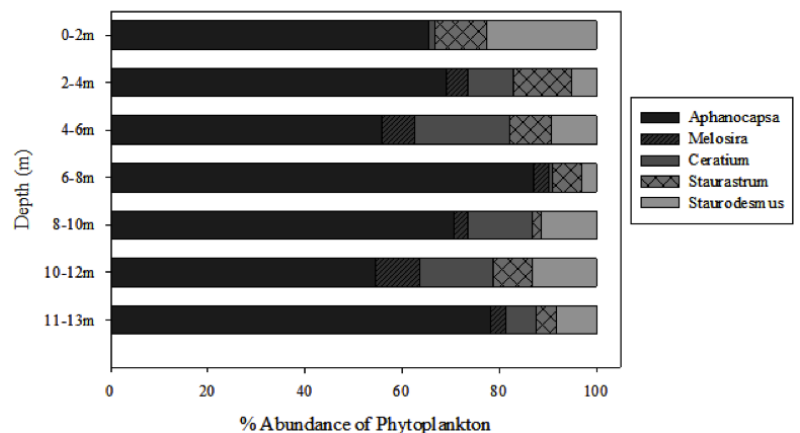


Fig. 6: Relative abundance of phytoplankton (%) at each depth. *Aphanocapsa*, shown in black, was the dominant phytoplankton species in Christine Lake.

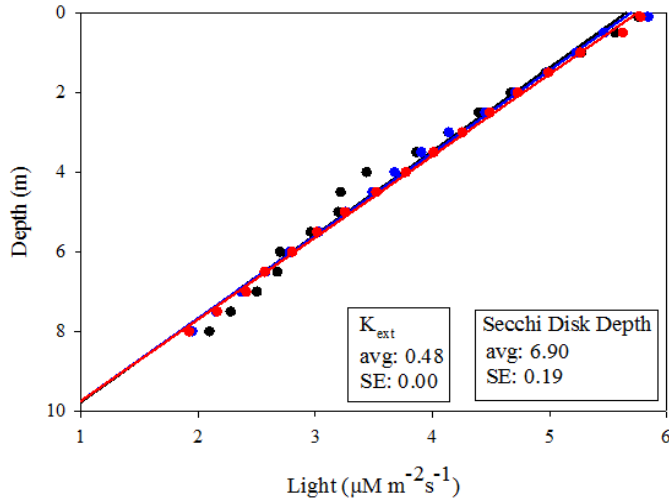


Fig. 7: Light attenuation at Christine Lake decreased at a constant rate throughout the water column. Average secchi disk depth was 6.9 +/- 0.19 m.

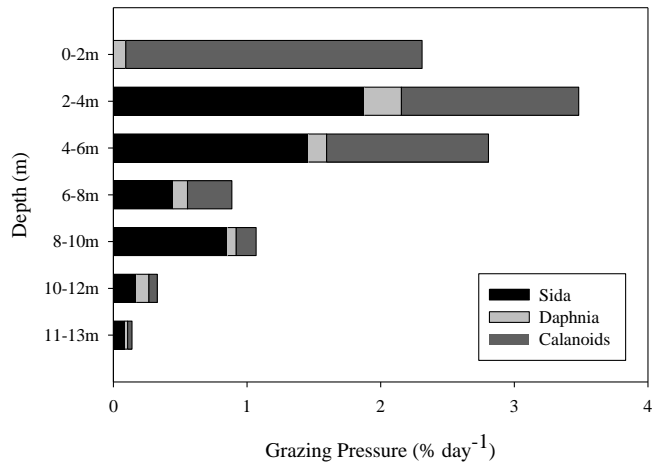


Fig. 8: Calculated grazing pressure from geometric means of body lengths and clearance rates of *Sida crystallina*, *Daphnia dubia*, and *Leptodiptomus sicilis*. The total grazing pressure of the combined crustaceans was highest at depths 2 to 4 m (3.48% per day).

Sida crystallina, *Daphnia dubia*, and *Leptodiptomus sicilis*, respectively.

Daphnia dubia had a clearance rate of 10.44 mL animal⁻¹ day⁻¹, and a mean body length of 1.3 mm. The average estimated grazing pressure of *D. dubia* throughout the entire water column was only 7.2% of the total community grazing pressure, whereas *L. sicilis* contributed 48.4% of the total grazing pressure. The clearance rate of

Leptodiptomus sicilis was 3.60 mL animal⁻¹ day⁻¹, and the mean body length was 0.56 mm.

The overall grazing pressure was highest at 3.4% day⁻¹ between 2-4 m where the three dominant zooplankton grazers were most abundant (Fig. 8).

Discussion

Sida crystallina in the pelagic zone – *Sida crystallina* is a common littoral species encountered mostly on aquatic macrophytes or other submerged objects (Szlauer 1973) where it filter feeds from a fixed position (Fairchild 1981). Positioned behind their head, *S. crystallina* have anchoring organs that secrete gelatinous glue allowing them to attach to solid substrates (Korovchinsky 1992). *Sida crystallina* sense the presence of substrates for reattachment by sight (discrimination between light and dark objects; Fairchild 1981). They tend to feed on small particles such as microscopic algae, fine detritus, and bacteria (Korovchinsky 1992). There have been occasional reports of some littoral species such as *S. crystallina* in the pelagic zone in European lakes (Korovchinsky 1982), however, few studies have reported hypotheses for this phenomenon.

Most reports on *Sida crystallina* in the pelagic zone have observed its appearance on solid objects, rather than free-swimming forms of the species. Fairchild (1981) found that larger individuals (>1.8 mm) had a greater tendency to remain in a fixed position than did smaller individuals (<1.8 mm). Juveniles swam more frequently than adults, and appeared to swim for long periods of time before reattaching (Fairchild 1981). This would not account for *Sida* in Christine Lake, as the population consisted of both adults and immature individuals. Also, there was no evidence suggesting that *Sida crystallina* in Christine Lake had morphological adaptations that aid in swimming. However, two extremes can be considered when talking about the organisms' ability to swim: i) an infrequent and poor swimmer that immediately attaches to the nearest available substrate, or ii) a frequent

swimmer that chooses to remain in the water column for longer periods of time (Fairchild 1981). It is likely that the organisms in Christine Lake are more frequent swimmers, although, this contradicts the idea that *S. crystallina* swim until they find a solid substrate (Fairchild 1981, Korovchinsky 1982).

Szlauer (1973) proposed the movement of *S. crystallina* into the pelagic zone may be caused by water currents from the littoral zone. Such currents may arise from increased rainfall or stream inflow. *Sida* can also be driven into the pelagic zone by wind agitation and the presence of various floating objects at different times of year, such as autumn leaves that fall into the water (Korovchinsky 1982). However, this does not account for free-swimming *Sida crystallina*, as there was no evidence of floating objects at the sampling site in Christine Lake, and *S. crystallina* were caught with a closing net without catching solid substrates (e.g. aquatic macrophytes, debris or leaves).

The appearance of *S. crystallina* in Christine Lake appears to be a new phenomenon, especially since no *Sida* were reported at the same site in Christine Lake in 2004 (Godkin).

Szlauer (1973) found that this species was particularly dense in the epilimnion and upper layer of the metalimnion in the littoral zone. *Sida crystallina* in Christine Lake were most abundant in the epilimnion at depths 2-4 and 4-6 m (0.22 individuals L⁻¹ and 0.17 individuals L⁻¹, respectively), where light and oxygen levels were plentiful. It is possible that competition on littoral macrophytes or increased predation by littoral predators might cause a movement of *S. crystallina* into the pelagic zone. Fairchild (1981) described potential benefits and costs of attachment of *Sida crystallina* to solid substrates such as reduced susceptibility to visual predation and exposure of an attached organism to plant-associated predators.

Plant associated predators (e.g. littoral, planktivorous fish) could play a role in leading *S. crystallina* away from any potential substrate in the littoral zone, making the organisms more susceptible to fish predation in the open water. However, if planktivorous fish are hiding from piscivores in the macrophytes, this would limit

predation on large zooplankton in the pelagic zone. The predator-to-panfish ratio was calculated after Mills *et al.* (1987) to assess the fish community structure in Christine Lake (Fig. 2). The mean size of all crustacean zooplankton (1.2 mm) led to an estimated high predator-to-panfish ratio (0.73), which suggests Christine Lake has a relatively large piscivore population (Mills *et al.* 1987). Lakes dominated by piscivores have few panfish (Mills *et al.* 1987), which feed on zooplankton, particularly littoral and benthic prey (Vanni *et al.* 1997). Thus, it is possible that *S. crystallina* is present in the pelagic zone to avoid predation by planktivorous fish in the littoral zone. Another possible explanation would be that very high populations of *S. crystallina* in the littoral zone may result in a migration to the open water, where the scarcity of planktivorous fish enables *S. crystallina* to survive. Of course, these hypotheses need to be tested by direct observations of fish and zooplankton in the littoral zone of Christine Lake. It would also be useful to conduct laboratory studies to determine whether the Christine Lake *S. crystallina* population has unique morphological or behavioral features that allow it to survive without substrates in the open water.

Aphanocapsa and grazing impacts on the phytoplankton community – *Aphanocapsa* was the dominant phytoplankton in Christine Lake consisting of about 68.5% of the average relative abundance of the net phytoplankton. Most species of *Aphanocapsa* grow amongst the periphyton, phytobenthos and filamentous algae of lakes, usually in clear water (Komárek 1992). *Aphanocapsa* occurs in colonies that may be considered to be autotrophic picoplankton (APP) because they do not form blooms and their individual cells are in the size range of picoplankton (Callieri and Stockner 2002).

Picoplankton ranges in size from 0.2-2 µm (Sieburth *et al.* 1978), and includes prokaryotic (picocyanobacteria) and eukaryotic phototrophs and heterotrophs (Stockner and Shortreed 1991). In oligotrophic lakes, picoplankton is thought to be responsible for most of the productivity (Callieri and Stockner 2002; Stockner 1988).

The APP community, particularly the picocyanobacteria, can play an important role in the microbial food web (Porter *et al.* 1985; Simek *et al.* 1995). If light conditions, grazing impact and competition are favorable, picocyanobacteria can out-compete other larger autotrophic algae (Callieri and Stockner 2000). Because of their small size, the ability to out-compete other phytoplankton is especially noticeable when nutrients are scarce (Callieri and Stockner 2000). Christine Lake may be a good example of this due to its oligotrophic status (mean TP=5.9 ppb), deep euphotic zone (0-9.5 m), and grazing pressure (community grazing pressure=11.02% day⁻¹) from large cladocerans such as *S. crystallina* and *D. dubia* (Fig. 2).

Aphanocapsa in Christine Lake was identified in large colonies (>50 µm) throughout the water column. Klut and Stockner (1991) suggested that the presence of clustered colonies, both loosely and tightly grouped together, may be adaptive in providing protection against grazers. The colonial picoplankton in Christine Lake could reflect the shift in grazers from *D. dubia* and *Eubosmina* in 2004 to *D. dubia* and *S. crystallina* in 2010.

Geller and Müller (1981) found that filtering appendages of 1.5-1.7-mm *Sida crystallina* had a mesh-size of 0.9-2.3 µm at the gnathobasal setae and 2.3-4.2 µm at the distal endite setae. These coarse mesh filter-feeders are found in oligotrophic lakes throughout the year, and are unable to feed on suspended bacterial cells (Geller and Müller 1981). Therefore, *S. crystallina* in Christine Lake grazing on the individual cells of *Aphanocapsa*, may be promoting the colony formation seen throughout the lake.

Based on field data on zooplankton and phytoplankton populations in eight European lakes, phytoplankton densities generally decreased when zooplankton community grazing rates exceeded 80% per day (Lampert 1988). Although community grazing rates in Christine Lake did not exceed 80%, it is possible that the total pressure (11% day⁻¹) of the three dominant grazers in this oligotrophic

lake had impacts on the phytoplankton community structure. *Sida crystallina* contributed 44.4% of the total estimated grazing pressure in Christine Lake and also made up more than half of the grazing pressure at 2-6 m, the depths with the highest community grazing (3.14% day⁻¹) (Fig. 8).

The appearance of *Sida crystallina* in the pelagic zone of Christine Lake, in the absence of any floating substrates, represents a unique observation. The high densities of *Sida* in the plankton community raises the possibility that feeding by this large cladoceran promotes the dominance of cyanobacteria in Christine Lake.

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