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Factors influencing *Gonyostomum semen* blooms in a small boreal reservoir lake

D.L. Findlay[1,*], M.J. Paterson[1], L.L. Hendzel[1] & H.J. Kling[2]
[1]*Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, Canada R3T 2N6*
[2]*Algal Taxonomy and Ecology Inc., 31 Laval Dr., Winnipeg, Manitoba, Canada R3T 2X6*
*(*Author for correspondence: Tel.: +1-204-983-5193, Fax: +1-204-984-2404, E-mail: findlayd@dfo-mpo.gc.ca)*

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Abstract

Blooms of the nuisance alga *Gonyostomum semen* occurred in Lake 979 (Experimental Lakes Area), a small brown-water lake, that was subjected to several years of an experimental flooding regime. During periods of flooding, blooms of *G. semen* developed when light decreased below 100 μmol m^{-2} s^{-1} and total phosphorous concentrations increased to >30 μg l^{-1}. *Gonyostomum semen* biomass was significantly correlated with total P and DOC concentrations. In addition, *G. semen* abundance increased at times when *Daphnia rosea* had rapidly declined to <10 animals l^{-1}. *Daphnia* egg ratios suggest that declines in *Daphnia* abundance were the result of shifts in mortality and not causally linked to changes in *G. semen* densities. The results observed in Lake 979 were supported by a laboratory experiment where the appearance of *G. semen* from Lake 979 sediment was stimulated by altering chemical and biological variables. The stimulation of *G. semen* blooms appears to be dependant on multiple variables rather than a single variable.

Introduction

Reports of *Gonyostomum semen* (Ehrenberg) Diesing blooms in small humic lakes and water storage reservoirs have increased over the past two decades, with a tendency towards a wider distribution of the alga in non-humic lakes (Cronberg et al., 1988; Eloranta & Räike, 1995; Salonen & Rosenberg, 2000; Reynolds et al., 2002; Salonen et al., 2002). *G. semen* is a nuisance algae species and has the potential to cause minor skin irritation for bathers (Cronberg et al., 1988; Hongve et al., 1988). Like many invasive species *G. semen* is capable of total dominance of an algal assemblage, shifting a lake into steady-state equilibrium (Sommer et al., 1993). Several hypotheses have been advanced concerning factors favoring the dominance of *G. semen*, including light, pH, nutrients, and changes in food web structure. Eloranta & Räike (1995) concluded the main factor influencing *G. semen* was their ability to migrate through the water column to adjust for light conditions. They postulated that *G. semen* avoided higher levels of radiation with 75–95 μmol m^{-2} s^{-1} being the limiting range. Similarly, Salonen & Rosenberg (2000) and Salonen et al. (2002) postulated that the diel vertical migration ability of *G. semen* gave it a competitive advantage over other algal species. Cronberg et al. (1988) concluded that decreased pH coupled with increased phosphorus, enhanced the abundance of *G. semen.* Hansson (1996) reported that the presence of *Gonyostomum* was negatively related to densities of *Daphnia*.

Blooms of *G. semen* regularly occurred after impoundment of an experimentally flooded reservoir (L979) at the Experimental Lakes Area in northwestern Ontario. The reservoir was created to study the effects of mercury cycling and production of greenhouse gases. The food web was intensively studied to determine the pathways of the contaminants (Paterson et al., 1997, 1998). Several biological, chemical and physical variables that have been related to the increased abundance of *Gonyostomum* were measured in Lake 979. Using this data set, we test the hypothesis that light levels, nutrients and food web structure or a combination of these variables influenced *G. semen* blooms in Lake 979.

Site description

Lake 979 is a small brown-water lake situated in the Experimental Lakes Area (ELA 49°38′ N, 93°43′ W) and is surrounded by a peatland. A dam was constructed at the outflow and from July through to the end of September in 1993 and from late May through September of each year since 1994 the water level has been raised 1.3 m increasing the maximum depth from 1.2 to 2.5 m and increasing the surface area from 2.4 to 16 ha (Table 1). The lake level was lowered at the end of each season to simulate a water regime similar to northern hydroelectric reservoirs where water volumes are drawn down during the winter months (Paterson et al., 1997).

Methods

Phytoplankton and bacteria sampling and analysis

Lake 979 was sampled for phytoplankton, water chemistry, and physical parameters such as light and temperature every 2–4 weeks from May to October from 1992 to 1997. Water samples were obtained from the centre buoy station using an integrating sampler (Shearer, 1978).

A 125 ml aliquot of lake water was fixed in Lugol's solution for identification and counting of phytoplankton. Ten-milliliters aliquots of preserved sample were gravity settled for 24 h. Counts were performed on an inverted microscope at magnifications of 125×, 400×, and 1200× with phase contrast illumination. Cells were enumerated using the Utermöhl technique as modified by Nauwerck (1963). Live net samples, taken with a 10 μm mesh net, were examined occasionally to aid in species identification. Cell counts were converted to wet weight biomass by approximating cell volume. Estimates of cell volume for each species were obtained by measurements of up to 50 cells of an individual species and applying the geometric formula best fitted to the shape of the cell (Vollenweider, 1968; Rott, 1981). A specific gravity of 1 was assumed for cellular mass.

For bacterial enumeration, 2 ml aliquots were stained using the DAPI technique (Porter & Feig, 1980) with a final stain concentration of 1.0 μg ml^{-1}. Within 3 weeks of sampling, samples were filtered onto a prestained 0.2 μm polycarbonate membrane filter and examined using epifluorescence microscopy. Cell counts were converted to biomass by measuring 50 individual bacteria cells and applying the geometric formula best fitted to the shape of the cell. Measurements were performed using a micro-metered eyepiece. Measurements done with the eyepiece were randomly checked with measurement performed on the electron microscope.

Zooplankton sampling and analysis

Zooplankton were sampled every 7–14 days during the ice-free season at five randomly located stations (Paterson et al., 1997). Samples were obtained using a 7-cm diameter wire-reinforced plastic tube that collected an integrated sample from the entire water column. Samples were sieved through a 53-μm net, narcotized with methanol (Gannon & Gannon, 1975), and preserved with sugar-formalin (3% final concentration). A minimum total of 300 crustacean zooplankton were counted and identified to species. A minimum of

Table 1. Morphological characteristics for Lake 979 pre- and during flooding

	Pre-flooding 1992	Flooding 1993–1997
Maximum depth (m)	1.2	2.5
Surface area (m^2)	24 000	160 000
Volume (m^3)	16 500	165 000
Water residence time (days)	0.5	>10

100 specimens of each common taxa were measured for each sampling date and lengths were converted to biomass using regression equations in Malley et al. (1989) and McCauley (1984).

Water chemistry sampling and analysis

Dissolved and suspended fractions of carbon (C), nitrogen (N) and phosphorus (P) and pH were routinely measured every 2 weeks for Lake 979. Totals of C, N and P were obtained by summing the fractions. Analytical methods used are described by Stainton et al. (1977).

Alkaline phosphatase, an exo-enzyme which most algae produce at very low ambient phosphorus concentrations allowing them to hydrolyze phosphorus from organic molecules, was measured fluorometrically as described by Healey & Hendzel (1979) bi-weekly from 1993 to 1995. Geraldes & Boavida (2003) have shown that alkaline phosphatase activity and consequently orthophosphate regeneration are little affected by differences in pH, temperature, conductivity and water color making it a robust measure across a wide gradient of lake types.

Design and sampling of sediment experiment

In November 2003, a laboratory experiment was conducted to stimulate the appearance of *G. semen* from Lake 979 sediments by altering selected chemical and biological variables in static containers. Surface sediments from Lake 979 were obtained using an Ekman dredge, along with 25 l of lake water from the center station. Sediment and water samples were kept in the dark and at 4 °C and shipped back to the laboratory. Two hundred milliliters subsamples of Lake 979 sediment were placed in 1 l glass jars. The remaining volume was carefully filled with Lake 979 water, filtered through a 30 μm Nitex mesh net to remove

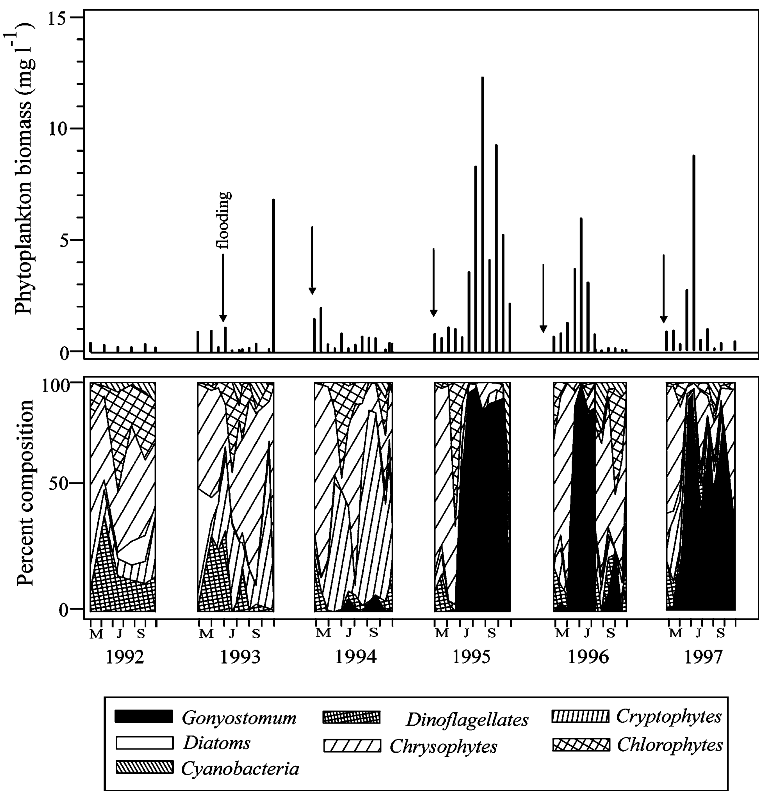

Figure 1. Seasonal phytoplankton biomass (upper panel) and accumulative percent composition by major taxonomic groups (lower panel) for L979 (1992–1997).

any existing *Gonyostomum* and *Daphnia*. The experimental design consisted of three replicated treatments and three replicated controls. Treatments included increasing P to 20, 50, and 50 μg l^{-1} plus six *Daphnia pulex*. P was added as a single pulse of KH_2PO_4-P on day 0. The *D. pulex* were animals that were maintained in culture from original isolates from Lake 110 at ELA. Initial pH was 5.6 with total P and DOC concentrations of 14 μg l^{-1} and 1640 μM l^{-1} respectively. The cultures were subjected to 12 h of light at 80–100 μmol m^{-2}s^{-1} and 12 h dark.

The experiment ran for 17 days with samples taken on days 0 (prior to additions), 5, 8, 12, and 17. *Gonyostomum* biomass was estimated microscopically using the Utermöhl technique as described earlier. DOC, pH, suspended P and total dissolved P were measured on days 0, 8 and 17.

Results

Lake 979

In its pre-manipulated state (1992) Lake 979 had a phytoplankton assemblage co-dominated seasonally by chlorophytes, chrysophytes and dinoflagellates with biomass averaging 0.3 mg l^{-1} (Fig. 1). *Gonyostomum semen* was not present at this time. Bacterial biomass averaged 0.14 mg l^{-1} (Fig. 2a). Total P and DOC averaged 7 μg l^{-1} and 750 μM l^{-1} respectively, while pH values ranged from 6.4 to 6.9 (Fig. 3). In addition the water column from the lake surface to the sediments was well illuminated (Fig. 4). The zooplankton community was dominated by *Bosmina longirostris*, *Polyphemus pediculus*, and cyclopoid copepods (Paterson et al., 1997). *Daphnia galeata mendotae* and *D. rosea* were present in low numbers.

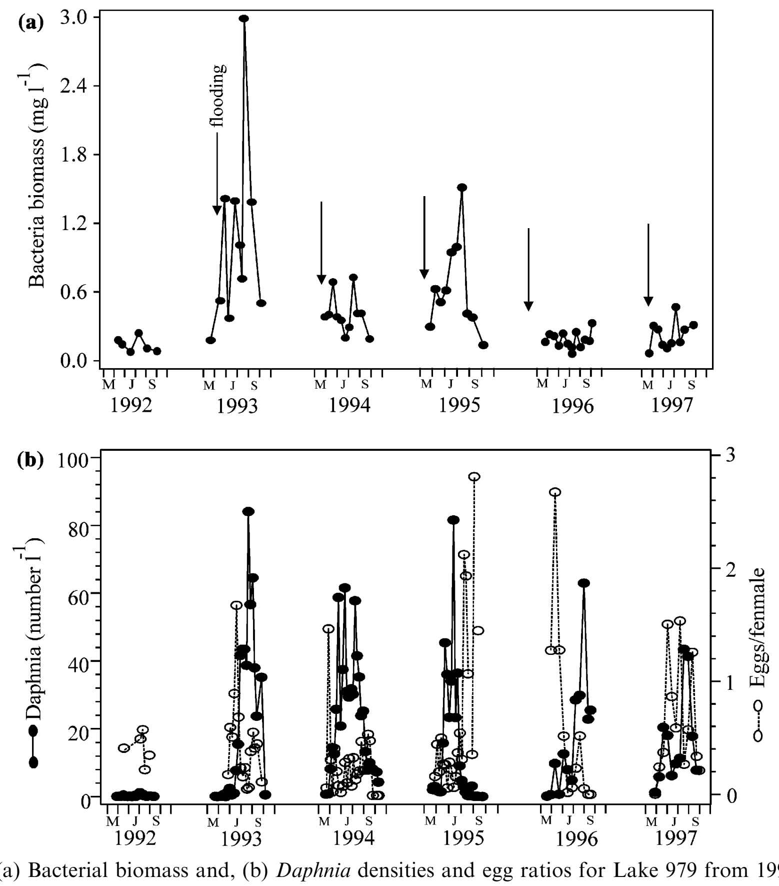

Figure 2. (a) Bacterial biomass and, (b) *Daphnia* densities and egg ratios for Lake 979 from 1992 to 1997.

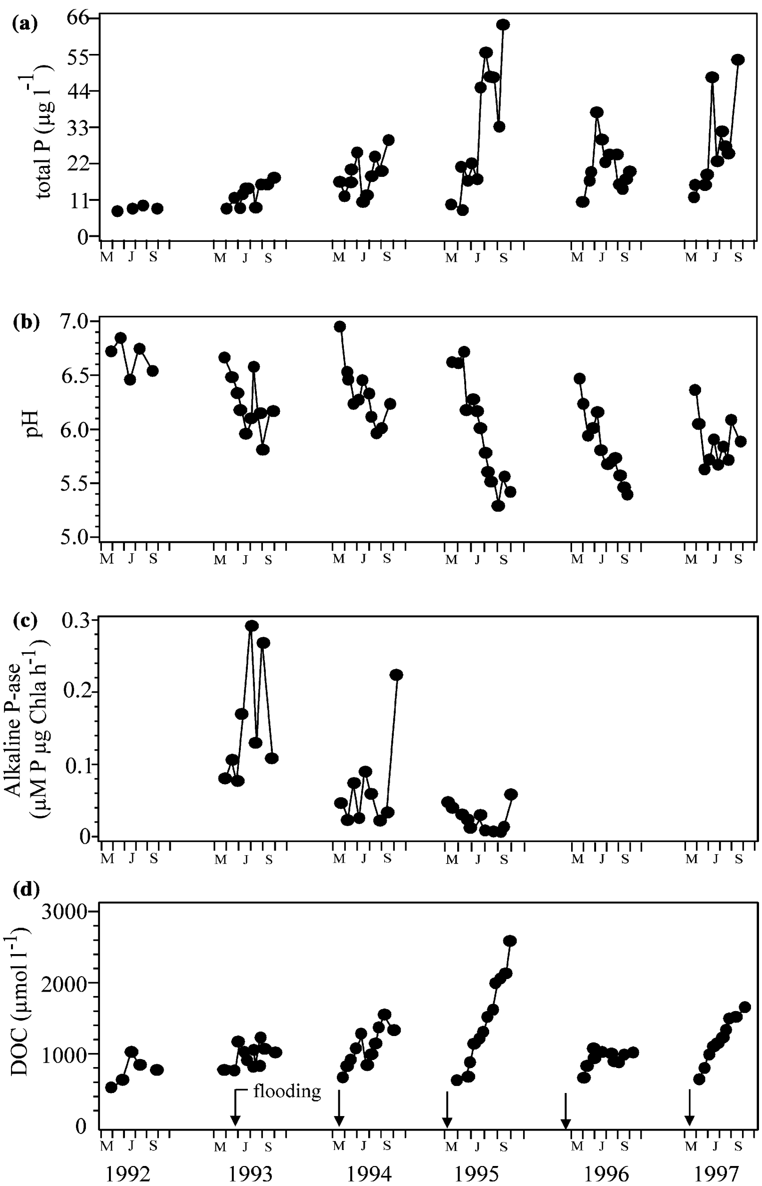

Figure 3. Chemical variables in Lake 979 from 1992 to 1997: (a) total phosphorus, (b) pH, (c) Alkaline phosphatase, and (d) DOC.

In 1993 and 1994, algal biomass in Lake 979 increased immediately after flooding then decreased for the remainder of the seasons (Fig. 1). The decrease in algal biomass was associated with increased grazing pressure from increased abundances of *Daphnia rosea* (Fig. 5a) and increased competition between bacteria and phytoplankton. Bacterial biomass increased by 21× in 1993 and remained elevated throughout the entire period of experimental flooding (Fig. 2a) as compared to pre-flooding (1992). During the 1994 summer, *Gonyostomum semen* was detected in very low concentrations (Figs 1 and 5a). At this time pH had decreased to < 6.0, *D. rosea* abundance had decreased, and total P had increased to 22–28 $\mu g\ l^{-1}$ (Figs 3 and 5a). In addition, DOC had increased to 1540 $\mu M\ l^{-1}$ (44%) causing available surface light in the water column to decrease to <100 $\mu mol\ m^{-2}\ s^{-1}$ below 0.75 m (Fig. 4). Alkaline phosphatase enzyme activity was elevated in

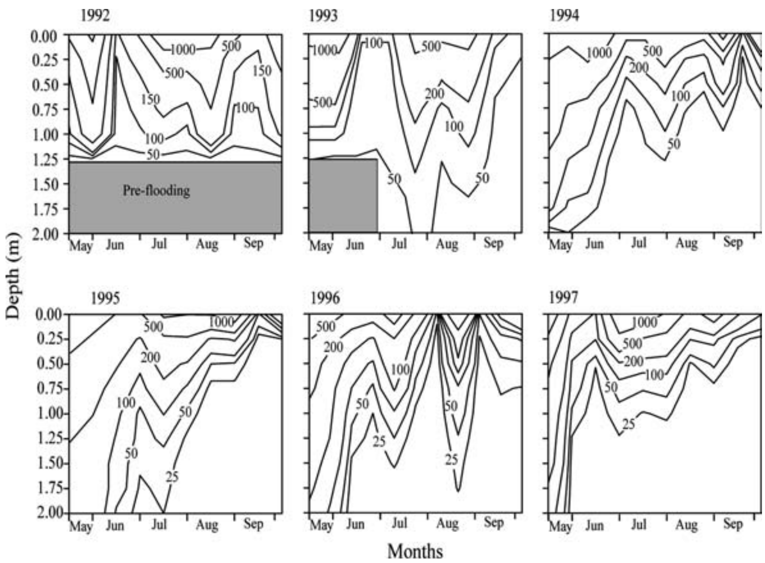

Figure 4. Isopleths plot of seasonal light profiles (μmol m^{-2} s^{-1}) for Lake 979 from 1992 to 1997. The shaded area in 1992 and 1993 signifies the lake bottom prior to initial flooding.

1993 and 1994 indicating that the algal community was extremely P limited (Fig. 3c).

During the 1995–1997 flooding seasons in L979, large blooms of *Gonyostomum semen* occurred (Figs 1 and 5a). Summer maxima occurred in late July and early August and at times attained values >12.6 mg l^{-1} (Fig. 5a) representing between 70 and 95% of the total phytoplankton biomass (Fig. 1). Throughout the 1995–1997 seasons, DOC increased on average from 25 to 96% of preflooding estimates (Fig. 3d) causing pH to decrease below 6.0 (Fig. 3b) and reducing light. During the 1995–1997 *G. semen* blooms, available surface light below 0.5 m was <100 μmol m^{-2} s^{-1} (Fig. 4).

Gonyostomum biomass was significantly correlated with total P (Fig. 6a) with the highest *Gonyostomum* biomasses occurring when total P values were >30 μg l^{-1}. Alkaline phosphatase activity measured in 1995 indicated that the algal assemblage in Lake 979 was less P limited than in previous years (Fig. 3c)

In addition to the observed chemical changes, *G. semen* blooms were negatively correlated with *Daphnia* abundances ($r^2 = 0.37$, $p = 0.001$). *G. semen* was virtually absent when *D. rosea* concentrations were >10 animals l^{-1} (Fig. 5b). *Daphnia* egg production rates were inversely related to changes in *Daphnia* abundance (Fig. 2b) and were significantly positively correlated with *Gonyostomum* biomass ($r^2 = 0.43$, $p = 0.015$). In addition, increases in *G. semen* in 1996–1997 coincided with significant decrease in bacteria biomass (Fig. 2a).

Sediment experiment

During the course of the sediment experiment *Gonyostomum* appeared in all treatments and the controls, but at varying concentrations (Fig. 7). A repeated measures ANOVA indicated that the three treatments differed significantly from the controls (P 20 μg l^{-1} $p = 0.0001$; 50 μg l^{-1} $p \leq 0.0001$ and 50 μg l^{-1} + *Daphnia*, $p \leq 0.0001$). Of the three treatments P 50 μg l^{-1} attained the highest maximum biomass of *G. semen* (0.55 mg l^{-1}), which was 10 times higher than concentrations in the other treatments and controls (Fig. 7). Over the duration of the experiment pH was 5.6 and DOC declined from 1640 to 1460 μM l^{-1}.

Discussion

It's been well documented that major shifts in algal assemblages occur during different types of perturbations, whether they are natural or anthropogenic, and these assemblages often reach steady-state equilibrium as described by Sommer

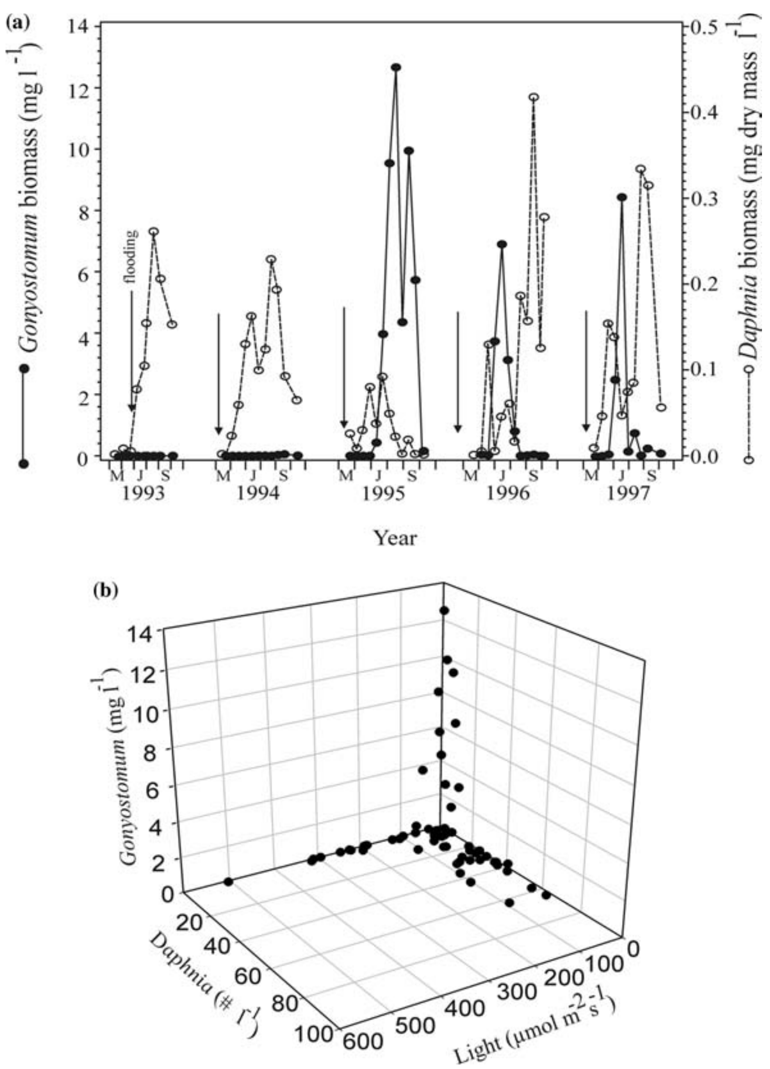

Figure 5. (a) Time-series of *G. semen* and *Daphnia sp.* biomasses for Lake 979 from 1993 to 1997 and, (b) relationship between *G. semen* (mg l^{-1}), *Daphnia* (numbers l^{-1}), and light (μmol m^{-2} s^{-1}) for Lake 979.

et al. (1993). In systems that have been eutrophied, cyanobacteria typically dominate with the N:P ratio being a determining factor for the type of species present (Smith, 1983; Findlay et al., 1994). During extreme acidification (pH < 5.0) dinoflagellates have been documented to dominate because of their ability to vertical migrate (Schindler et al., 1991; Findlay et al., 1999). In small humic lakes and water storage reservoirs *Gonyostomum* has become increasing more abundant. Physical, chemical and biological factors have been hypothesized to induce the onset of *Gonyostomum* blooms (Cronberg et al., 1988; Eloranta & Räike, 1995; Hansson, 1996; Salonen & Rosenberg, 2000; Salonen et al., 2002). In many cases habitat coupled with species tolerances and sensitivity can be factors that determine algal assemblages. Reynolds et al. (2002) classified systems based on these elements, denoting small humic lakes dominated by *Gonyostomum* as alphanumeric coda Q.

G. semen is mixotrophic (Jiang & Heath, 1993) and capable of vertically migrating throughout the water column. Eloranta & Räike (1995) concluded the main factor influencing *G. semen* was their ability to migrate through the water column to adjust for light conditions. They postulated that

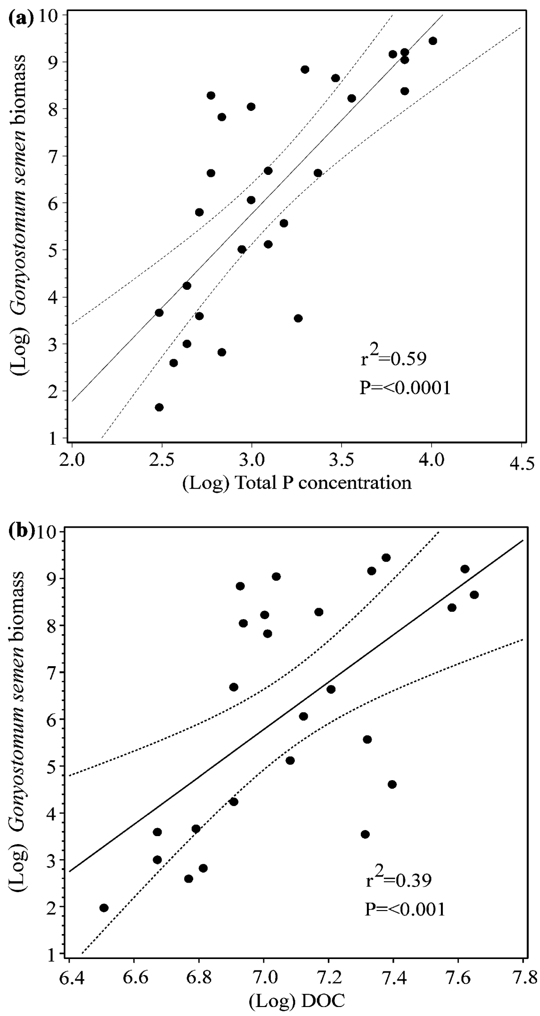

Figure 6. Log–log linear regressions of *G. semen* biomass and (a) total P concentrations and (b) DOC, for Lake 979 from 1992 to 1997.

G. semen avoided higher levels of radiation, with 75–95 μmol m^{-2} s^{-1} being the limiting range. Our results from Lake 979 support the hypothesis that *G. semen* thrives in low light environments below 100 μmol m^{-2} s^{-1}. However, there were also several other factors that contributed to the magnitude of the *G. semen* blooms in Lake 979.

Cronberg et al. (1988) concluded that increased *Gonyostomum* abundance coincided in lakes with high P concentrations and decreased pH as related to acidic deposition in many Scandinavian lakes. Salonen & Rosenberg (2000) postulated that *G. semen* vertically migrated into anoxic and light limited zones of lakes giving them a competitive advantage over other algae because it allows them to acquire essential nutrients by consumption of DOC and bacteria as an alternative source of C (Buchanan 1982). They suggest that vertical migration of *Gonyostomum* was associated with depletion of soluble reactive phosphorus from bottom waters. The results from Lake 979 support the hypothesis that elevated P concentrations coupled with low light influence the growth of *G. semen*. In Lake 979 *G. semen* increased in abundance when total P > 30 μg l^{-1} and pH was <6.0. This was further supported by our laboratory experiment where *G. semen* increased 21× over the control under conditions of low light and increased P > 30 μg l^{-1} at pH 5.6. In Lake 979 *G. semen* biomass was not correlated with pH, because pH was driven by DOC concentrations, which suggests that DOC maybe a driving variable. In our lab experiment *Gonyostomum* biomass decreased as DOC decreased but there was no change in pH observed. The appearance of *Gonyostomum* has been documented occurring over a pH range of 4.4–7.7 (Rosén, 1981; Eloranta & Räike, 1995). pH may have indirectly influenced the presence of *G. semen* in Lake 979 because this species can tolerate lower pH giving it a competitive advantage over many other algae.

Hansson (1996) reported in the presence of *Daphnia*, *G. semen* disappeared from the water column taking refuge in the sediment. He postulated that *G. semen* use the detection of chemicals released by *Daphnia* as an avoidance mechanism from grazers. In our experiment, the addition of *Daphnia* to treatment containers impaired *G. semen* biomass compared to containers with no *Daphnia*. In Lake 979, *Gonyostomum* blooms occurred at times when total P, DOC, and light were at optimum levels and *Daphnia* abundance was low. In general, *Gonyostomum* was absent when the number of *Daphnia* exceeded 10 animals l^{-1}, which supports Hansson's hypothesis. *Daphnia* egg ratios were inversely related to changes in *Daphnia* abundance in Lake 979 and egg ratios often remained high during periods of high *G. semen* densities. Because cladoceran egg ratios are an indicator of *per-capita* food availability, this suggests that declines in *Daphnia* abundance were the result of shifts in mortality, most likely due to increased grazing pressure by *Chaoborus*, and not causally linked to changes in *G. semen* densities.

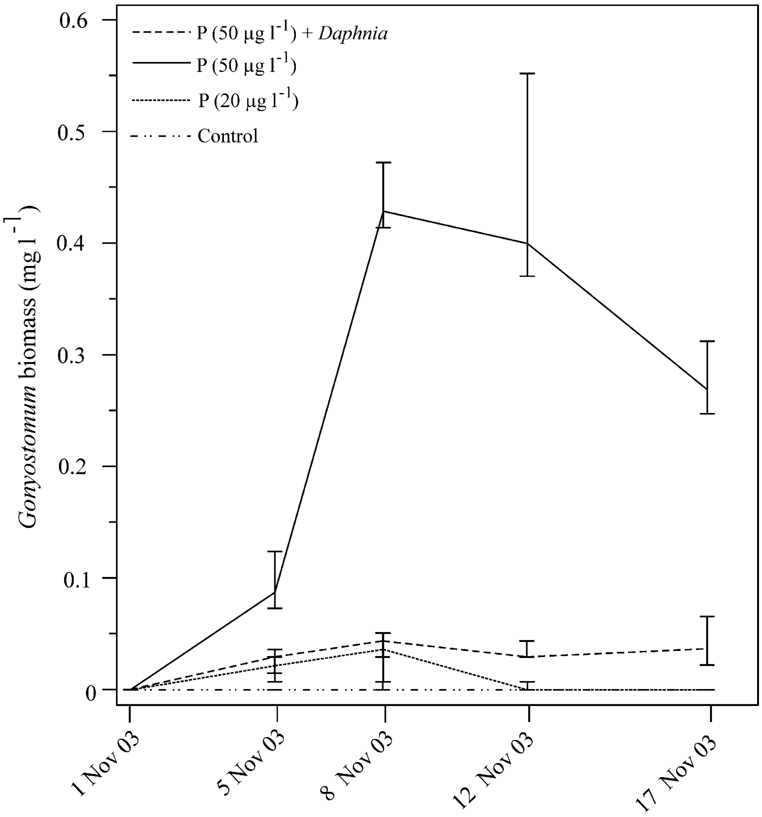

Figure 7. Time-series of *Gonyostomum* biomass in a controlled experiment from Lake 979, with addition of P and *Daphnia*.

Lakes that are dominated/codominated by one to three species for periods of 1 to 2 weeks are considered as being at steady-state equilibrium (Sommer et al., 1993). Since these systems usually have extreme conditions only a few species may be tolerant (Nixdorf et al., 2003; Padisák et al., 2003; Stoyneva, 2003). In a study of 80 assemblages by Padisák et al. (2003) they found only 21% to be at steady-state equilibrium. During the *G. semen* blooms, Lake 979 typified an alphanumeric coda Q system (Reynolds et al., 2002) and the algal assemblage met the criteria of steady-state equilibrium (Sommer et al., 1993). However, dominance by *G. semen* occurred only when *Daphnia* were not present which, provided a condition for *G. semen* to predominated by competition.

Conclusion

In Lake 979 *Gonyostomum* abundance was influenced by multiple variables that created a favorable environment that allowed this species to proliferate. Increased concentrations of DOC caused low light levels. Changes in the light regime coupled with increased total P concentrations and reduced *Daphnia* abundance allowed *G. Semen* to increase in abundance in Lake 979.

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