Daphnia control of the spring clear-water phase in six polymictic lakes of varying productivity and size

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Introduction

Phytoplankton biomass and community composition are regulated by interactions between light, nutrients, physical and chemical conditions (e.g., stratification, pH), and biotic mechanisms (e.g., herbivory, competition), although the relative strength of individual regulatory processes varies substantially among seasons, years, and lakes (Vanni & Temte 1990). Often phytoplankton communities exhibit a predictable temporal sequence of change in species abundance and composition (Lampert & Schober 1978), as has been described in detail by the Plankton Ecology Group (Sommer et al. 1986). In particular, development of the spring clear-water phase (CWP) is a characteristic event in the plankton phenology of many dimictic lakes within temperate regions. This sudden transition from turbid to clear water has been attributed to different causes, including elevated grazing by zooplankton (Lampert et al. 1986, Tönnö et al. 2003), reductions in available nutrients during spring (Huppert et al. 2002), reduced turbulence and algal suspension following thermal stratification (Reynolds 1973), and increased suppression of low light adapted vernal taxa (Romo & Miracle 1995). Similarly, it has proven difficult to evaluate whether subsequent collapses of herbivore populations are caused by food depletion and starvation (Shei et al. 1988) or whether intense predation by fish (Luecke et al. 1990) contributes to population crashes. Improved understanding of the controls of plankton succession during CWP development is essential to predict how plankton dynamics might be affected by climate warming in the future.

We measured seasonal changes in algal and invertebrate abundance in 6 lakes for 12 years to quantify the role of herbivory, particularly by Daphnia, in regulating the onset and intensity of the CWP in productive lakes that lack pronounced thermal stratification. Further, we quantified Daphnia gut contents during 2006 to determine whether selective feeding by Daphnia contributed to increased water clarity. Although Daphnia are known to be important controls of CWP development in mesotrophic systems (Elser & Goldman 1990, Jeppesen et al. 2003), the role of these grazers in more productive lakes is controversial and uncertain (Degans & De Meester 2002).

Key words: clear-water phase, Daphnia, pigments, selective grazing

Study site

The Qu’Appelle Valley river basin encompasses 52 000 km² in southern Saskatchewan, Canada, and extends ~400 km from its western headwaters near Lake Diefenbaker to the eastern confluence with the Assiniboine River. The region exhibits a subhumid continental climate and is characterized by short warm summers with an average of 105 frost-free days and cold winters (Hall et al. 1999a). Study lakes are either linked by the Qu’Appelle River (Diefenbaker, Buffalo Pound, Katepwa, and Crooked lakes) or lie on mid-reach tributaries (Last Mountain and Wascana lakes). Primary production and chlorophyll (Chl-a) content increases from mesotrophic Lake Diefenbaker, through more fertile sites (Buffalo Pound and Last Mountain lakes) to highly eutrophic downstream or tributary lakes (Katepwa, Crooked, and Wascana lakes). Because all lakes exhibit low relative depth (<1%; Wetzel 2001) and are polymictic in most years, variation in thermal stratification does not contribute to CWP development.

Methods

Field sampling

All lakes were sampled biweekly from early May until early September during 1995–2006, except Wascana Lake (1996–2006). Zooplankton were collected using a 20-cm diameter, 243-µm mesh conical net towed to the surface from maximum depth and were preserved with an ethanol-sucrose solution. Unique algal carotenoid pigments were extracted from the guts of Daphnia pulex and D. galeata-mendotae by immersing 50–100 individuals into 5 ml of 15% methanolic acetone (Gráham 1997). Secchi depths and temperature profiles were recorded, while water samples for chemical analyses were obtained from pooled Van Dorn casts taken at 1-m depth intervals. Prescreened (243-µm mesh) surface water samples were...
filtered onto prewashed GF/C glass fiber filters and were frozen (−10 °C) until analysis for Chl-a by standard trichromatic methods. Depth-integrated water samples were also used to quantify the abundance and gross composition of phytoplankton communities by high-performance liquid chromatography (HPLC).

**Laboratory analyses**

Zooplankton samples were enumerated to species level, whereas algal abundance and composition in the water column (all years) and *Daphnia* guts (2006 only) were estimated for the main functional groups (e.g., chlorophytes, cyanobacteria, diatoms) using HPLC analysis (Graham 1997, Hall et al. 1999b). Pigment concentrations were quantified using a Hewlett Packard model 1050 or 1100 HPLC system following standard procedures detailed in Leavitt & Hodgson (2001). Biomarker concentrations were estimated for pigments characteristic of total algal abundance (Chl-a), siliceous algae and some dinoflagellates (fucoxanthin), mainly diatoms (diatoxanthin), cryptophytes (alloxanthin), siliceous algae, some dinoflagellates and cryptophytes (diadinoxanthin), chlorophytes (Chl-b), chlorophytes and cyanobacteria (lutein-zeaxanthin), total cyanobacteria (echinenone), colonial cyanobacteria (myxoxanthophyll), and Nostocales cyanobacteria (canthaxanthin) (Hall et al. 1999b).

**Definition of clear-water phase**

Time courses of biweekly Secchi depth, Chl-a concentration, and zooplankton densities were used to define the CWP in each lake. In general, CWP was determined to be the first peak in Secchi depth following ice-out that coincided with low concentrations of trichromatically-measured Chl-a and elevated density of total zooplankton.

**Data analysis**

Spearman correlation coefficients (p) were calculated for individual lakes to quantify the site-specific statistical relationships between densities at different zooplankton groups (total, Cladocera, Copepoda, genus, and species), Secchi depth, and water-column pigment concentrations, including surface water and depth-integrated Chl-a, and carotenoid biomarkers. In addition, we used redundancy analyses (RDA) to quantify the interactions between algae and invertebrates, and to evaluate the degree to which *Daphnia* were responsible for formation of the CWP at the landscape scale.

**Results**

Densities of both total zooplankton and total *Daphnia* (sum of *D. magna*, *D. pulicaria*, *D. galeata-mendotae*,

![Fig. 1. Mean seasonal development of algal taxa as reflected in water column concentrations of biomarker pigments in 6 study lakes during 1995–2006. All time series are standardized to the date of clear-water phase occurrence (zero), with negative numbers representing the biweekly interval before each clear-water phase, and positive values indicating the time interval after the event. All pigment concentrations are in units of nmols pigment L⁻¹ of depth-integrated lake water. Pigments include compounds from siliceous algae (fucoxanthin, diadinoxanthin), diatoms (diatoxanthin), dinoflagellates (fucoxanthin, diadinoxanthin), cryptophytes (alloxanthin, diadinoxanthin), chlorophytes (Chl-b), and cyanobacteria (echinenone).](image-url)
and *D. retrocurva*) were uncorrelated to any measure of algal abundance during the ice-free season for all lakes except Wascana, in which *Daphnia* (mainly *D. magna* and *D. pulicaria*) was negatively correlated to both Chl and carotenoid concentrations ($\rho < -0.503$, $p < 0.005$). However, when analyses were restricted to the central date of the CWP in each lake, total *Daphnia* density was positively correlated to secchi depth ($\rho = 0.188$ to $0.661$, median $\rho = 0.396$) and inversely correlated with surface ($\rho = -0.143$ to $-0.717$, median $\rho = -0.358$) and depth-integrated Chl-$a$ ($\rho = -0.212$ to $-0.697$, median $\rho = -0.495$). Although these correlations were not statistically significant for all lakes ($p > 0.05$), they were stronger and more consistent for *Daphnia* than for any other zooplankton group.

Analysis of mean water-column carotenoid concentrations during the summers of 1995–2006 demonstrated that algal abundance and community composition varied substantially among lakes, with lowest pigment concentration and diversity in mesotrophic Lake Diefenbaker, and progressively greater algal densities and evenness among pigments in downstream lakes (Fig. 1). In most lakes, populations of diatoms (fucoxanthin and diadinoxanthin) were elevated before the CWP, but declined sharply in the weeks leading into the event. These patterns were much less developed for pigments characteristic of summer blooms (e.g., Chl-$b$ from chlorophytes and echinenone from cyanobacteria).

Redundancy analysis confirmed the negative relationship between *Daphnia* density and diatom abundance during CWP (Fig. 2). This canonical analyses explained 96.8% of variance in species-environment relationships on the first (89.1% of variance explained) and second (7.7%) axes. Monte-Carlo permutation tests using forward selection revealed that the mean CWP densities of *Daphnia, Cladocera, Diaphanosoma birgei* and *Leptodiaptomus siciloides* all contributed significantly to the model ($p < 0.05$) and that all canonical axes were significant with $p = 0.006$. The inverse relationship between *Daphnia* density and the water-column concentrations of diatom pigments (diadinoxanthin and fucoxanthin) is striking, whereas the influence of *Daphnia* on the other water column pigments was less pronounced (Fig. 2).

Analysis of *Daphnia* gut contents during 2006 revealed that the intestinal concentrations of fucoxanthin (siliceous algae) increased prior to development of the CWP (Fig. 3). Similarly, maximum gut concentrations of diatom pigments generally occurred on the date of maximum water clarity, although not necessarily minimum total algal abundance. Overall, temporal changes in gut pigment concentrations of fucoxanthin paralleled those recorded in the water-column, with intestinal concentrations lagging water column concentrations by about 2 weeks (Fig. 3C). In contrast, gut contents of Chl-$a$ were uncorrelated to changes in water column Chl-$a$ (Fig. 3B). Although *Daphnia* densities declined in parallel to the
quantity of diatoms in their guts (Fig. 3A vs. 3C), and suggested that starvation contributed to reductions in Daphnia density, this pattern was not repeated in all lakes.

**Discussion**

Prior research suggests that clear-water phases are the result of complex interactions between light, temperature, nutrients, and biotic interactions of plankton and their predators (Sommer et al. 1986). In contrast to those findings, our study suggests that CWP development in prairie lakes is driven mainly by selective grazing of Daphnia on siliceous algae. Because all lakes are polymictic, thermal stratification cannot explain declines in diatom density during CWP development, although receipt of solar energy may contribute to Daphnia population growth during spring (Scheffer et al. 2001). Similarly, because dissolved nutrient concentrations do not vary substantially during the summer in most lakes (Patoine et al. 2006), we infer that the decline in algal abundance was not caused by severe nutrient limitation (Huppert et al. 2002). Instead, parallel but lagged changes in diatom abundance in gut and water-column samples, combined with strong negative correlations between Daphnia density and concentrations of pigments from diatoms, but not other algae (Fig. 2), showed that CWP development arises primarily from preferential grazing on diatoms by Daphnia.

Univariate statistical analysis suggested that zooplankton, including Daphnia, were incapable of regulating total algal abundance throughout the summer, even given the comparatively high grazer densities common in these lakes (10–20 Daphnia L⁻¹; Fig. 3 and unpubl. data). At least part of the reason for this apparent discrepancy is that cycles of species replacement are common in these lakes, with small-bodied Daphnia retrocurva and moderately-sized D. galeata-mendotae replacing early summer populations of larger D. pulicaria. The importance of grazer body size can be inferred from a comparison among lakes: only Wascana Lake exhibited substantial densities of D. magna or D. pulicaria of 5–20 ind. L⁻¹ during summer, and it is the sole site in which winterkill of fish is common (McGowan et al. 2005.) and in which total Daphnia density was inversely correlated with Chl-a concentrations throughout the year. Thus, although we have no direct measure of vertebrate predation in these lakes, we hypothesize that variation in size-selective feeding by fish underlies the differences among lakes in annual patterns of Daphnia-Chl relationships.

Our conclusion that selective feeding by Daphnia on diatoms is responsible for CWP development in polymictic lakes is robust to a wide range in variability of mean annual lake productivity (0.1–12 mg C m⁻³ h⁻¹) and basin volume (0.68–9400 × 10⁶ m³). In contrast, we could not yet determine whether the regular and prolonged drop in Daphnia density following the CWP was the result of resource limitation due to overgrazing on diatoms, or whether other toxic (microcystis), biotic (fish predation), chemical (pH >9.5), or physical (temperature >25 °C) factors may have played a role (Scheffer 1998). However, regardless of the precise mechanism restricting herbivore effect, it is evident that Daphnia mainly affected early summer plankton communities, rather than algal populations later in the year.

**Fig. 3.** Seasonal development of (a) water transparency and Daphnia abundance, (b) Chl-a in Daphnia and water samples, and (c) fucoxanthin (from siliceous algae) in the water column and in Daphnia samples during 2006 in Crooked Lake. Pigments concentrations as nmols pigment L⁻¹ (water) or nmols pigment g⁻¹ lipid free mass of Daphnia (guts).
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