

**The effects of a warm spring on phytoplankton and zooplankton population
dynamics in small eutrophic lakes in the Canadian prairies: Implications of a
changing climate**

Presented by

Alain Dupuis

A Thesis submitted to the Faculty of Graduate Studies of the
University of Manitoba
in partial fulfillment of the requirements of the degree of

Master of Science

Department of Biological Sciences

University of Manitoba

Winnipeg, Manitoba, Canada

Copyright © by Alain Dupuis

THE UNIVERSITY OF MANITOBA
FACULTY OF GRADUATE STUDIES

COPYRIGHT PERMISSION

**The effects of a warm spring on phytoplankton and zooplankton population
Dynamics in small eutrophic lakes in Canadian prairies: Implications of a
changing climate**

BY

Alain Dupuis

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree**

MASTER OF SCIENCE

Alain Dupuis © 2007

**Permission has been granted to the University of Manitoba Libraries to lend a copy of this
thesis/practicum, to Library and Archives Canada (LAC) to lend a copy of this thesis/practicum,
and to LAC's agent (UMI/ProQuest) to microfilm, sell copies and to publish an abstract of this
thesis/practicum.**

**This reproduction or copy of this thesis has been made available by authority of the copyright
owner solely for the purpose of private study and research, and may only be reproduced and copied
as permitted by copyright laws or with express written authorization from the copyright owner.**

Abstract

Climate projections predict warming trends for the Canadian prairies. This study investigated effects of warmer spring temperatures on phytoplankton-zooplankton populations in small eutrophic lakes. A two-year study of three eutrophic lakes with contrasting spring weather conditions, i.e., 2005 – a ‘normal’ spring and 2006 – a warm spring (+2°C), demonstrated that warmer water temperatures were associated with increased total phytoplankton and relative cyanobacteria biomass and a shift in zooplankton dominance from daphniids to rotifers. Zooplankton hatching experiments and computer simulations tested the hypothesis that a warm spring differently affected daphniid and rotifer emergence from resting eggs. Experimental conditions mimicking an earlier spring (shorter photoperiod) resulted in fewer daphniid but not rotifer hatchlings, and computer simulations indicated that these changes in hatching success could be responsible for shifts from daphniid- to rotifer-dominated systems. Overall, a warm spring negatively affected daphniid populations, indirectly by increasing cyanobacteria prevalence and directly by decreasing hatching success.

Acknowledgements

This research project would not have been possible without the guidance and support provided by my supervisor, Dr. Brenda Hann. I thank her for giving me the opportunity to conduct this research and to explore other important avenues in graduate education such as teaching and presenting at conferences. I thank my committee members, Dr. Michael Paterson and Dr. Mark Abrahams, for their insightful comments and challenges. Several other individuals and organizations provided invaluable expertise and assistance to the project. Dr. Gary Crow and Dr. Darren Gillis provided me with statistical help. Hedy Kling was key in teaching me phytoplankton taxonomy and counting methods. Doug Watkinson and his crew were essential in providing equipment and expertise for collecting data for bathymetry of the Fort Whyte Lakes. I thank Fort Whyte Alive for allowing me to utilize their lakes for this research. This research was funded by: NSERC Postgraduate Scholarship to Alain Dupuis, NSERC Discovery Grant to Dr. Brenda Hann, University of Manitoba Graduate Fellowship to Alain Dupuis, DFO Stewartship-In-Action Grant to Fort Whyte Alive and Fish Futures, Inc to Alain Dupuis. Finally, I thank Lynn Frazer for her continued support, my family for believing in me and so many others that helped in small but significant ways.

Table of contents

Abstract.....	ii
Acknowledgements	iii
Table of contents	iv
List of Tables	vii
List of Figures.....	ix
Chapter 1: Climate change and Canadian prairie lakes.....	1
Water resources in the Canadian prairies.....	2
Climate warming and variability in the Canadian prairies.....	3
Prairie lakes face physical and chemical changes.....	5
Biological changes within the Canadian prairie lakes.....	7
Biological variability: Can we predict change?	10
Climate change research approaches.....	11
Focus of this study.....	12
Literature cited	15
Chapter 2: Consequences of a warm spring for cyanobacteria and daphniid-rotifer populations in small eutrophic lakes in the Canadian prairies.	21
Introduction.....	22
Methods.....	25
<i>Study site</i>	25
<i>Data collection</i>	26
<i>Data processing</i>	27
<i>Data analysis</i>	30
Results	31
<i>Fort Whyte lakes biology</i>	31

<i>Limnological change between 2005 and 2006</i>	32
<i>Relationships between water temperature and phytoplankton</i>	35
<i>Alternative factors regulating cyanobacteria</i>	36
<i>Relationships between water temperature and daphniids</i>	37
Discussion	37
<i>Water temperature and phytoplankton</i>	37
<i>Alternative factors driving cyanobacteria dominance.....</i>	39
<i>Water temperature and daphniids</i>	40
<i>Cyanobacteria and daphniids</i>	41
<i>Shifts in zooplankton body size</i>	43
<i>Zooplanktivory</i>	45
<i>Daphniid-phytoplankton mismatch.....</i>	46
<i>Conceptual summary model.....</i>	48
Literature cited	69
 Chapter 3: Effects of an earlier spring on daphniid and rotifer emergence and population development.	80
Introduction.....	81
Methods.....	84
<i>Laboratory experiment</i>	84
Hatching experiment design	84
Sediment collection and experimental procedure	85
Data analysis	87
<i>Computer simulation modelling.....</i>	88
Zooplankton population development	88
Temperate lake zooplankton hatching dynamics.....	92
Model assumptions	93
Model scenarios	94
Model parameterization	94
Sensitivity analysis	98

Results	99
<i>Hatching dynamics</i>	<i>99</i>
<i>Predator-prey population models</i>	<i>102</i>
Discussion	104
<i>Effects of climate change on daphniid emergence and population development ...</i>	<i>104</i>
<i>Patterns of emergence</i>	<i>105</i>
<i>Effects of environmental cues on emergence</i>	<i>107</i>
<i>Effect of differential hatching response on zooplankton population development .</i>	<i>110</i>
<i>Limitations of model</i>	<i>112</i>
<i>Study implications – extension to the match/mismatch hypothesis.....</i>	<i>113</i>
<i>Conclusions.....</i>	<i>115</i>
Literature cited	137
Chapter 4: Research summary and future directions.....	148
Research summary	149
<i>Research highlights.....</i>	<i>149</i>
<i>Implications of warming for the Fort Whyte lakes – some conclusions</i>	<i>152</i>
Future directions and research.....	154
Literature cited	156

List of Tables

Table 2. 1. Morphological and chemical characteristics of the Fort Whyte lakes. Chemistry data reported as mean (\pm SD) values of May–August in 2005 and 2006.	51
Table 2. 2. Results of simple linear regressions testing for monthly linear relationships between chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$), total phytoplankton biovolume ($\text{mm}^3 \text{ m}^{-3}$), % filamentous cyanobacteria, % inedible phytoplankton and degree-days ($^{\circ}\text{C d}$) in the Fort Whyte lakes 2, 3 and 4 in the years 2005 and 2006. For all models $n=6$ (3 lakes x 2 years).....	52
Table 2. 3. Results of RM-ANOVA testing for differences between 2005 and 2006 monthly means for chemistry (TDN, TDP and TDN:TDP) and water column stability (Schmidt stability index). $N = 6$. Significant results ($P < 0.05$) are indicated in bold.	53
Table 2. 4. Results of simple linear regressions testing for monthly linear relationships between daphniids (individuals L^{-1}) and % filamentous cyanobacteria and % inedible phytoplankton in the Fort Whyte lakes 2, 3 and 4 in the years 2005 and 2006. For all models $n=6$ (3 lakes x 2 years).....	54
Table 3. 1. Two-predator and two-prey model parameters abbreviations, value, units, description and source.	117
Table 3. 2. Total number of zooplankton hatchlings during experiments after (a) 33 days (<i>Keratella spp.</i> , <i>Synchaeta pectinata</i> and <i>Daphnia ambigua</i>) and (b) 45 days (<i>D. parvula</i> , <i>D. pulicaria</i> , <i>Bosmina longirostris</i> , <i>Diaphanosoma sp.</i>). Note that 45 day experiment was only carried out in the 12°C chamber.	118
Table 3. 3. Results of a three-factor ANOVA testing for the effects of temperature, photoperiod, light intensity and their interactions on <i>Keratella spp.</i> hatchling abundance during an incubation period of 33 days.	119
Table 3. 4. Results of three-factor ANOVA testing for the effects of temperature, photoperiod, light intensity and their interactions on <i>Synchaeta pectinata</i> hatchling abundance during an incubation period of 33 days.	120

Table 3. 5. Results of a three-factor ANOVA testing for the effects of temperature, photoperiod, light intensity and their interactions on <i>Daphnia ambigua</i> hatchling abundance during an incubation period of 33 days.	121
Table 3. 6. Results of two-factor ANOVA testing for the effects of photoperiod, light intensity and their interactions on <i>Daphnia parvula</i> hatchling abundance during a 45 day incubation period at 12°C.....	122
Table 3. 7. Results of two-factor ANOVA testing for the effects of photoperiod, light intensity and their interactions on <i>Diaphanosoma sp.</i> hatchling abundance during a 45 day incubation period at 12°C.....	123
Table 3. 8. Sensitivity analysis of selected model parameters for the 12°C simulation experiment with zooplankton hatching dynamics derived at (a) 13 hour and (b) 16 hour photoperiods. Comparison of base model results with $\pm 5\%$ deviations in parameter values for daphniid and rotifer maximum and cyanobacteria end-point biomasses (mg C L^{-1}) of a 60-day simulation. Model parameters and values are defined in Table 3.1. Values indicated in bold are those that produced shifts in dominant zooplankton groups compared to base model results.	124

List of Figures

Figure 2. 1. Bathymetric map of the Fort Whyte lakes 2, 3 and 4 in Winnipeg, MB.....	55
Figure 2. 2. Contour plots of temperature profiles (°C) from May to Mid-August at the Fort Whyte lakes 2 (a, b), 3 (c, d) and 4 (e, f) during the years 2005 and 2006.....	56
Figure 2. 3. Two-year comparison (2005 and 2006) of physico-chemical dynamics from May to August in Lakes 2, 3 and 4.....	57
Figure 2. 4. Two-year comparison (2005 and 2006) of chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$) dynamics from May to August in Lakes 2, 3 and 4.....	58
Figure 2. 5. Two-year (2005 and 2006) comparison of phytoplankton biovolume estimates ($\text{mm}^3 \text{L}^{-1}$) from May to August in Lakes 2, 3 and 4. Phytoplankton are classified by cell size except for filamentous cyanobacteria.....	59
Figure 2. 6. Two-year (2005 and 2006) comparison of relative abundances of dominant filamentous cyanobacteria genus (<i>Aphanizomenon spp.</i> , <i>Planktothrix spp.</i> , <i>Anabaena spp.</i> and <i>Limnothrix sp.</i>) from biovolume estimate from May to August in Lakes 2, 3 and 4. A star indicates no filamentous cyanobacteria in sample.....	60
Figure 2. 7. Two-year comparison (2005 and 2006) of mean zooplankton population dynamics from May to August in Lakes 2, 3 and 4.....	61
Figure 2. 8. Two-year (2005 and 2006) comparison of mean <i>Daphnia pulicaria</i> , <i>D. ambigua</i> and <i>D. parvula</i> population dynamics from May to August in Lakes 2, 3 and 4.....	62
Figure 2. 9. <i>Chaoborus flavicans</i> (III and IV instars L^{-1}) population dynamics for Lakes 2 and 4 in 2005 and 2006 as estimated from daytime collections of the epilimnion...	63
Figure 2. 10. Monthly relationships between degree-days (°C d) and phytoplankton biomass estimated as chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$) for May (a), June (b) and July (c) with the 95% confidence interval (dashed lines).....	64
Figure 2. 11. Monthly relationships between degree-days (°C d) and phytoplankton biomass estimated as biovolume ($\text{mm}^3 \text{m}^{-3}$) for May (a), June (b) and July (c) with the 95% confidence interval (dashed lines).....	65
Figure 2. 12. Monthly relationships between degree-days (°C d) and % filamentous cyanobacteria for July (a) and August (b) with the 95% confidence interval (dashed lines).....	66

- Figure 2. 13. Monthly relationships between % filamentous cyanobacteria and daphniid abundance (ind. L⁻¹) for June (a) and July (b) with the 95% confidence interval (dashed lines). 67
- Figure 2. 14. Conceptual model describing plankton population dynamics in a small eutrophic lake during two scenarios, (a) late warming and (b) an early warming. Edible algae (dotted line), filamentous cyanobacteria (vertical lines), rotifers (dashed lines) and daphniids (solid line, transparent white filling) are presented during early spring, late spring and summer. See discussion for further explanations. 68
- Figure 3. 1. Schematic representation of a two-predator (daphniid and rotifer) and two-prey (edible algae and filamentous cyanobacteria) model. The two predators and two prey are outlined in bold. Arrows represent both positive and negative relationships between components. Emergence cues, temperature and photoperiod, affect both daphniid (a) and rotifer (b) hatching dynamics. Zooplankton hatchlings develop into adults at a given rate (c) and (d). Adult zooplankton have natural mortality rates (e) and (f) but rotifers also succumb to daphniid direct/indirect interference (g). Adult daphniids graze both filamentous cyanobacteria (h) and edible algae (j), while adult rotifers graze only edible algae (i). Population growth of zooplankton is dependent of prey availability, represented by the two-way arrows (h), (i) and (j). Un-grazed algae diffuses into both algal groups (k) and (l). Population growth of algae is both density- (m and n) and temperature-dependent (o and p). 125
- Figure 3. 2. Cumulative mean number of *Keratella spp.* hatchlings \pm 1 SE (n = 5) over time (33 days) incubated at three temperatures, 6°C (a), 9°C (b) and 12°C (c), at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values). 126
- Figure 3. 3. Cumulative mean number of *Synchaeta pectinata* hatchlings \pm 1 SE (n = 5) over time (33 days) incubated at three temperatures, 6°C (a), 9°C (b) and 12°C (c), at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values). 127
- Figure 3. 4. Cumulative mean number of *Daphnia ambigua* hatchlings \pm 1 SE (n = 5) over time (33 days) incubated at three temperatures, 6°C (a), 9°C (b) and 12°C (c), at two

photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values).	128
Figure 3. 5. Cumulative mean number of <i>Daphnia parvula</i> (a) and <i>Diaphanosoma sp.</i> (b) hatchlings ± 1 SE (n = 5) over time (45 days) incubated at 12°C, at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values).	129
Figure 3. 6. Cumulative mean number of <i>Daphnia pulicaria</i> (a) and <i>Bosmina longirostris</i> (b) hatchlings ± 1 SE (n = 5) over time (45 days) incubated at 12°C, at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values).	130
Figure 3. 7. Interaction plots of mean <i>Keratella spp.</i> (a, b), <i>Synchaeta pectinata</i> (c, d), and <i>Daphnia ambigua</i> (e, f) hatchling abundance ± 1 SE (n = 5) of two factors, temperature (6°C, 9°C, 12°C) and photoperiod (13hr, 16hr). Results for both, low and high light intensities are shown.	131
Figure 3. 8. Interaction plots of mean <i>Daphnia parvula</i> (a) and <i>Diaphanosoma sp.</i> (b) hatchling abundance ± 1 SE (n = 5) of two factors, light intensity (low, high) and photoperiod (13 and 16 hours) at an incubation temperature of 12°C.	132
Figure 3. 9. Ephippium of (a) <i>Daphnia ambigua/parvula</i> and (b) <i>Daphnia pulicaria</i> . Solid black line measures 1 mm. Note difference in pigmentation.	133
Figure 3. 10. Mean time to zooplankton hatching (days) ± 1 SE (n = 5) for resting eggs incubated at 6°C (a), 9°C (b) and 12°C (c) under combinations of two photoperiods (13 and 16 hours) and two light intensities (high and low, see text for values).	134
Figure 3. 11. Simulation results in biomass (mg C L ⁻¹) for a two predator (daphniids and rotifers) and two prey (edible algae and filamentous cyanobacteria) model under different zooplankton hatching conditions, i.e., three temperatures (6, 9 and 12 °C) and two photoperiods (13 and 16 hrs).	135
Figure 3. 12. Diagram representing overlap between predator (solid line) and prey (dashed line) populations over time in (a) a high matching scenario and (b) a low matching scenario caused by low predator abundance. Vertical lines show degree of overlap in predator-prey interactions. In (b), only predator abundance is different, i.e., timing of peak abundances remains constant in both scenarios (dotted lines).	136

Chapter 1: Climate change and Canadian prairie lakes.

Water resources in the Canadian prairies

Water bodies in the Canadian prairies are facing a number of environmental threats that often act in synergy. Particularly over the past century, growing urban populations and intensifying rural land-use have caused increasing concern for our lakes and rivers. In the western provinces, from Manitoba to Alberta, lakes and rivers in the prairies have been subjected to multiple stressors from anthropogenic sources. Nutrient inputs, particularly those from sewage, livestock operations, and fertilizer applications, have led to significant eutrophication of prairie water-bodies (Quinlan et al. 2002). In years with droughts, common in the prairies, irrigation practices compromise water quantity and in-stream flow needs for many fishes. Contaminants, such as mercury, enter food webs and motivate fisheries officials to recommend consumption guidelines. Non-native species introductions, such as Common Carp (*Cyprinus carpio*) a hundred years ago (Stewart and Watkinson 2004), have caused restructuring of many food webs. Physical aspects of lakes and rivers have been altered, usually motivated by political and/or economic reasons. In some cases, water-bodies previously disconnected for hundreds of years have been merged, e.g., Devils Lake linkage to the Sheyenne River in North Dakota, USA (Aronow 1957).

Climate change has recently become an important public issue. A growing consensus among scientists suggests that climate change is linked to human activities. The International Panel on Climate Change report (IPCC 2007) states that increasing greenhouse gas concentrations over the last 50 years from anthropogenic sources have very likely caused warming global temperatures. In fact, some scientists have suggested that climate change, acting directly, but also synergistically with other human stresses,

has led to “[a]n impending water crisis in Canada’s western prairie provinces” (Schindler and Donahue 2006). The purpose of this introduction is to discuss the implications of climate change on, primarily, Canadian prairie water-bodies. A comprehensive review of climate change effects for lakes is well beyond the scope of this paper and has been the subject of many reviews (Schindler et al. 1990; De Stasio et al. 1996; Magnuson et al. 1997; Schindler 1997, 2001; Blenckner 2005; Mooij et al. 2005). Instead, important aspects of climate warming and variability on Canadian prairie lakes are presented. In conclusion, the overall goals and scope of the research project are highlighted within the context of its potential contribution to furthering our understanding of climate change impacts on plankton dynamics in prairie water-bodies.

Climate warming and variability in the Canadian prairies

In the Canadian prairies, current and future climate change has serious consequences for air temperature, water availability and inter-annual weather predictability. Historical datasets from across the Canadian prairies over the past 80 to 114 years show that air temperatures have increased by 1 to 4°C, with the greatest changes observed since 1970 (Schindler and Donahue 2006). Over the same period of time, a 14 to 24% reduction in precipitation has been accentuated by increasing evaporative losses. As a result, drought frequency and severity have increased in some parts of the prairies (Tebaldi et al. 2006), sometimes causing economic strain approaching that experienced during the mid-1930s. In addition, in some parts of the prairies, summer river flows are currently 20 to 84% lower than they were during the early 1900s (Schindler and Donahue 2006). Cumulatively, rising air temperatures and intensified agricultural practices have caused decreasing water flows owing to shrinking

glaciers in the Canadian Rockies, increased evaporative losses, and greater irrigation demands (Hoppe 2003). In many prairie rivers, dependence on glacier water is substantial. For instance, the Saskatchewan River system receives 87% of its volume from the spring glacier melt in the Rockies (Schindler 2001).

Recent advances in computer modeling and more comprehensive datasets have enabled scientists to forecast climate changes with a greater level of certainty. Regional climate models (RCMs), downscaled from third generation global circulation models (GCMs), predict transient changes in climate as greenhouse gas concentrations increase. In any given study, several RCMs are employed and predictions are assessed in conjunction with their agreement with historical patterns of change. On average, in the Canadian prairies, RCMs for 2040-60 predict an increase of 2.5 to 5.6°C in air temperature and an increase of 3 to 36% in precipitation (Shepherd and McGinn 2003). Seasonal timing of increased precipitation, however, is critical for meeting our water needs. Generally, annual precipitation will increase in Alberta while southern parts of Saskatchewan and Manitoba could experience decreasing summer precipitation (Shepherd and McGinn 2003). For the eastern Prairie Provinces, this could have important ramifications, as water needs are likely to be greatest during summer months. Increased temperatures would also affect evaporative losses. For example, at the Experimental Lakes Area, Ontario, an increase from 14 to 16°C resulted in a 30% increase in evaporation rates (Schindler 2001). Across the prairies, this could result in a net loss in the water balance.

Climate change is consistent with warming temperatures but also increasing inter-annual variability. Recently, new advances have been made to characterize future

occurrences of extreme events (IPCC 2007). For some parts of the Canadian prairies, indicators of climate extremes such as heat waves, dry days, warm nights, and precipitation intensity are expected to increase in magnitude (Tebaldi et al. 2006). Also, analysis of historical data suggests that increased inter-annual variability in precipitation events has already occurred as a result of climate change (Shepherd and McGinn 2003; Wulder et al. 2007). From 1978-2002, snow cover across central Canada became increasingly variable, particularly in the Canadian prairies (Wulder et al. 2007). In the prairies, changes in winter precipitation would have direct implications for soil water recharge but also the magnitude of spring runoff to water bodies. Furthermore, inter-annual fluctuations in climate will likely have important implications for aquatic ecosystems. This is especially pertinent in lakes where changes in weather phenomena have a strong effect on plankton dynamics (George and Hewitt 2006).

Prairie lakes face physical and chemical changes

Climate change will have several implications for physical and chemical aspects of lakes across the prairies. Lakes with small volumes and shallow morphologies, typical of many Canadian prairie lakes, are particularly sensitive to climate change. In these water-bodies, water temperature closely correlates with ambient air temperature given their high surface area to volume ratios (Carpenter et al. 1992). As a result, smaller heat capacities of small shallow lakes compared to deep lakes leads to their weaker abilities to dampen environmental changes (Adrian et al. 1999).

The effects of climate change on lakes in the Canadian prairies will depend on seasonal timing of warming. For example, weather conditions in spring have strong effects on physical aspects of small lakes. In these small water bodies, a warming trend in

spring is typically correlated with earlier melting of ice and snow. Since the mid-1960s, ice-off and peak spring runoff has advanced by 2 and 2.5 days, respectively, per 1°C increase in March air temperatures in small Minnesota lakes (USA) (Johnson and Stefan 2006). This tight coupling of ambient weather conditions with physical aspects in small lakes will also have important consequences for aquatic organisms. For example, in European lakes, an earlier clear-water phase in shallow lakes was correlated with warming April temperatures but not winter temperatures as was found for deep lakes (Gerten and Adrian 2000).

For lakes in the prairies, symptoms of climate change will likely resemble those of eutrophication (Mooij et al. 2005). Increased evaporation and decreased summer water flows could lead to lower water levels and longer retention times in lakes even with increased precipitation. As a result, under these conditions, nutrient concentrations will increase and chemical ions will have longer to react, thus enhancing phytoplankton productivity (Schindler 2001). In shallow eutrophic lakes this could lead to decreased water transparency (Mooij et al. 2005).

In small lakes, climate change could also lead to greater internal nutrient loading. In shallow polymictic lakes, an earlier ice-off and a longer open-water season may intensify internal loading by increasing the time of sediment resuspension (Niemistö and Horppila 2007). In contrast, lakes that are deep enough to stratify could experience earlier and shallower thermocline development with climate warming (De Stasio et al. 1996) decreasing nutrient fluxes from the sediments. Moreover, increased nutrient availability could also occur as a result of temperature-dependent microbial activity in the sediments. This was shown in a mesocosm experiment where warmer water temperatures produced

increased phosphorus concentrations (McKee et al. 2003) suggesting that climate change could further compound cultural eutrophication problems in the Canadian prairies.

Biological changes within the Canadian prairie lakes

Predicting biological responses to climate change is difficult and few generalities can be made. In an investigation across ecosystems, Parmesan (2006) found that over half of the species investigated have shown changes in distributions and/or phenologies. For example, in north temperate lakes, environmental fluctuations are important seasonal indicators for many organisms. In these lakes, a warming spring has led to advancing phytoplankton and, in some cases, zooplankton phenologies (Gerten and Adrian 2000). In Canadian prairie lakes, abundance of phytoplankton should generally increase as a result of positive physiological responses to temperature and increased nutrient availability (as discussed above). Recently, climate change researchers have begun combining regional climate models with ecological simulation models. One such model developed to investigate climate change in shallow eutrophic lakes in the UK suggested that climate change might not increase annual phytoplankton biomass (Elliott et al. 2005). These models, however predicted increased spring phytoplankton biomass, largely as a result of greater cyanobacteria productivity. Several other studies also suggest that cyanobacteria may become more important at warmer water temperatures (Robarts and Zohary 1987).

Blenckner (2005) stressed the importance of including landscape features such as geographical position, catchment characteristics and lake morphometry when assessing climate-induced change in lakes. For example, in Lake 239 at the Experimental Lakes Area, NW Ontario, effects of catchment disturbance (a forest fire) and a warming trend likely combined to cause greater phytoplankton abundance (Schindler et al. 1990). In

Lake 239, forest fires and declining runoff led to decreased inputs of allochthonous dissolved organic carbon (DOC), deepening the photic zone and allowing greater algal productivity. Landscape features typical of many Canadian prairie lakes, such as nutrient-rich soils and shallow morphometry, suggest that phytoplankton will likely bloom earlier, increase in total biomass, and shift composition towards greater proportions of cyanobacteria with climate change.

Climate change will potentially affect zooplankton in several ways. In some cases, zooplankton, such as *Daphnia* and rotifers, have shown advancement of their spring phenologies with spring warming (Gerten and Adrian 2000). In contrast, other studies have shown that spring population development of *Daphnia* has remained relatively static in time over the years despite an earlier diatom bloom (George and Taylor 1995; Winder and Schindler 2004). In some systems, increasing phytoplankton biomass could lead to greater zooplankton biomass in situations where food quality is maintained (Straile 2000). However, under conditions of increased nutrient concentrations and water temperatures, cyanobacteria can become an important component of plankton biomass. In fact, several authors have observed that increasing relative cyanobacteria biomass has led to shifts towards smaller daphniid species, e.g., from *D. galeata* to *D. cucullata* (Adrian and Deneke 1996; DeMott et al. 2001).

When assessing impacts of climate change on biological systems, timing of change needs further consideration. In the Canadian prairies, many zooplankton survive long harsh winters (>4 months) by entering diapause. For zooplankton, warming could cause changes in this life-history trait. For example, in a small temperate lake, a fall warming caused *Epischura lacustris* resting eggs to hatch prematurely and *Daphnia*

catawba to switch from sexual to asexual reproduction (Chen and Folt 1996). Overall, this could potentially decrease fall production of over-wintering resting eggs and lead to important reductions in recruitment for spring populations.

Warmer summer water temperatures could also impact zooplankton populations and their interactions with phytoplankton. In mesocosm experiments, increasing water temperatures from 18 to 25°C resulted in *Daphnia* population instability and on several occasions, extinctions (Beisner et al. 1997). *Daphnia*-algal interactions were directly affected as differential temperature-dependent responses in *Daphnia* and algal growth rates produced longer time-lags between trophic levels, but also indirectly by increasing proportions of cyanobacteria. In summary, responses of zooplankton populations to climate change will likely vary depending on species-level characteristics, changes in zooplankton-algal interactions, but also timing of warming and its effects on zooplankton life-histories.

Implications of climate change for fish will likely result from both direct and indirect effects of warming. Changes that occur at lower trophic levels could have important ramifications especially for young-of-year fish in early summer. In Lake Washington, USA, juvenile sockeye salmon (*Oncorhynchus nerka*) switch to feeding on *Daphnia* in spring. However, recent climate variability has caused negative changes in daphniid over-wintering and spring populations, thus forcing juvenile salmon to rely on less profitable prey (Hampton et al. 2006). Similar changes in predator-prey interactions could threaten many economically important recreational and commercial fisheries found in the Canadian prairies, e.g., Walleye in Lake Winnipeg.

Climate change has also allowed range expansion of aquatic organisms. In the Laurentian Great Lakes, recent invasions of non-native species from the Ponto-Caspian regions by ballast water discharge from container ships may have been facilitated by a warming climate (Schindler 2001). Schindler (2001) argues that warm-water Eurasian species, such as zebra mussels (*Dreissena polymorpha*) and large predatory cladocerans (*Bythotrephes longimanus*), could out-compete native cold-water species with climate change. In the Canadian prairies, potential human and/or natural dispersal of these species could have important repercussions for fisheries such as in Lake Winnipeg.

Warming could also have direct implications for native fish distributions. Fish species with narrow temperature tolerances are most at risk. Opposite effects will likely be seen for cold and warm stenothermic fishes. Model simulations predict that Brook Trout (*Salvelinus fontinalis*), a cold-water species, could lose nearly 50% of their range by the year 2050 (Chu et al. 2005). Moreover, other fishes predicted to benefit from warmer temperatures, e.g., Walleye (*Sander vitreus*) and Smallmouth Bass (*Micropterus dolomieu*) (Chu et al. 2005) may not experience range expansion if intensified land-use practices, eutrophication, and contaminant concentrations continue to degrade suitable fish habitat.

Biological variability: Can we predict change?

Overall, responses of biological systems to climate change could be variable and complex. In the boreal forest, current observations of climate change responses such as forest fires, insect infestations, treeline expansion and forest composition show agreement with predicted scenarios (Soja et al. 2007). In many cases, Soja et al. (2007) also show that changes have occurred more quickly than anticipated suggesting rapid non-linear

responses rather than progressive changes. In lakes, studies concerning effects of climate warming suggest that outcomes will often be complicated by other factors. For example, mesocosm warming experiments at the Experimental Lakes Area, NW Ontario, suggested that epilithic phytoplankton photosynthetic activity increased but responses in total biomass and species composition varied with substrate-type and successional history (Baulch et al. 2005). Therefore, climate warming will directly affect organism physiologies, but other factors such as basin geochemical composition and disturbance history can considerably complicate patterns of ecological change (Baulch et al. 2005).

Biologically, not all Canadian prairie lakes are likely to respond in a similar way. Studies in northern Wisconsin, USA, suggest that within geographic regions, coherent response to inter-annual weather variability are high for physical and chemical parameters but low for biological ones (Magnuson et al. 1990). Magnuson et al. (1990) suggest that lake heterogeneity produced highly variable biological responses to regional climate. A parallel example comes from the agricultural industry where, crop diversification has been touted as a means for minimizing risks due to climatic variability (Bradshaw et al. 2004). In these systems, climate change could reduce yield in some but not all crop types. Similarly, diversity of lake-type across the prairies could mean that some lakes will be more affected than others. As a result, more research should be conducted to better identify and mitigate potential changes between different lake-types.

Climate change research approaches

Recent climate change research has utilized several methods for investigating potential and current biological implications of climate warming and variability. Long-term datasets are the most useful to detect impacts of climate change in many

ecosystems; however, other mechanistic short-term approaches have greatly improved our understanding of potential ecological responses (Parmesan 2006). For example, experimental manipulations in the field and in the laboratory, as well as basic physiological experiments, have enabled researchers to link ecological change directly to warming conditions. This can be particularly useful as, in some cases, correlations between long-term datasets of climate and biological variation must be interpreted with caution. Several researchers utilized climate indices derived from ocean-atmosphere dynamics (North Atlantic Oscillation and El Niño Southern Oscillation) to correlate with biological variability (e.g., Gerten and Adrian 2000). However, there is some evidence that climate change has influenced ocean and atmospheric circulations and, as a result, it is uncertain how past responses in biological responses reflect future climate change implications (Parmesan 2006). Recently, some researchers have combined regional climate models with ecological models (e.g., Elliott et al. 2005). Modeling of this type can be useful in terms of predicting future changes but also to highlight mechanisms driving patterns in ecosystems. In the latter case, this further motivates research into identified mechanisms of importance.

Focus of this study

This study focuses on the implications of climate change in small eutrophic lakes in the Canadian prairies. A recent review of the world's lakes suggested that small water-bodies (<100 ha) such as lakes, ponds, impoundments, reservoirs and farm dugouts predominate by surface area (Downing et al. 2006). In addition, Downing et al. (2006) suggested that rates of material processing (e.g., carbon, nitrogen, phosphorus cycling) are several times greater in these small water-bodies. This underlines the need for

research on these systems in terms of responses to climate change. A suite of small eutrophic prairie lakes is the Fort Whyte lakes (49° 49.020' N, 97° 13.440' W) located in Winnipeg, Manitoba. These are man-made eutrophic lakes ranging in size from 5 to 15 ha (Frazer et al. 2005). These lakes have high water retention times owing to the lack of inflows and outflows. The Fort Whyte lakes are intermediate between shallow and deep lakes with mean depths of approximately 4.5 to 5.0 m. Harsh winters are typical of Winnipeg's climate with average daily temperatures ranging from -13.6 to -17.8°C from December to February (Environment Canada 2004) and >4 months of ice-cover. As a result, winterkills of fish are sometimes recorded in these lakes and spring zooplankton population development likely depends on emergence from the resting egg-bank (few to no over-wintering *Daphnia* and rotifers). For a more thorough description of the Fort Whyte lakes see Chapter 2.

The overall goals of this study were to investigate the effects of spring warming on plankton dynamics in small eutrophic lakes. Three approaches to study biological responses of climate change were utilized: (1) Chapter 2: An observational approach was used to compare two open-water seasons with contrasting spring weather conditions. A warmer spring was recorded in 2006 compared to 2005 at the Fort Whyte lakes. Since no major changes in water chemistry were recorded inter-annually, changes in thermal regimes were directly and indirectly linked to changes in phytoplankton and zooplankton abundance and composition. (2) Chapter 3: An experimental approach was used to investigate implications of a warm spring on cladoceran and rotifer hatching dynamics from resting eggs. As earlier warming is associated with a shorter photoperiod (photoperiod is independent of climate), factors tested reflected potential changes in

temperature and photoperiod combinations. (3) Chapter 3: An ecological modeling approach was used to investigate how changes in zooplankton hatching dynamics with an earlier spring could affect spring population development. Temperature-dependent models are developed to simulate a two predator (*Daphnia* and rotifers) and two prey (edible algae and cyanobacteria) system in a small eutrophic lake.

Literature cited

- Adrian, R. and R. Deneke. 1996. Possible impact of mild winters on zooplankton succession in eutrophic lakes of the Atlantic European area. *Freshw. Biol.* 36: 757-770.
- Adrian, R., N. Walz, T. Hintze, S. Hoeg and R. Rusche. 1999. Effects of ice duration on plankton succession during spring in a shallow polymictic lake. *Freshw. Biol.* 41: 621-632.
- Aronow, S. 1957. On the postglacial history of the Devils Lake region, North Dakota. *J. Geol.* 65: 410-427.
- Baulch, H. M. and D. W. Schindler. 2005. Effects of warming on benthic communities in a boreal lake: Implications of climate change. *Limnol. Oceanogr.* 50: 1377-1392.
- Beisner, B. E., E. McCauley and F. J. Wrona. 1997. The influence of temperature and food chain length on plankton predator-prey dynamics. *Can. J. Fish. Aquat. Sci.* 54: 586-595.
- Blenckner, T. 2005. A conceptual model of climate-related effects on lake ecosystems. *Hydrobiologia* 533: 1-14.
- Bradshaw, B., H. Dolan and B. Smit. 2004. Farm-level adaptation to climatic variability and change: Crop diversification in the Canadian prairies. *Climate Change* 67: 119-141.
- Carpenter, S. R., S. G. Fisher, N. B. Grimm, J. F. Kitchell. 1992. Global change and freshwater ecosystems. *Ann. Rev. Ecol. Syst.* 23: 119-139.
- Chen, C. Y. and C. L. Folt. 1996. Consequences of fall warming for zooplankton overwintering success. *Limnol. Oceanogr.* 41: 1077-1086.

- Chu, C., N. E. Mandrak and C. K. Minns. 2005. Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. *Diversity Distrib.* 11: 299-310.
- DeMott, W. R., R. D. Gulati and E. Van Donk. 2001. *Daphnia* food limitation in three hypereutrophic Dutch lakes: Evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria. *Limnol. Oceanogr.* 46: 2054-2060.
- DeStasio, B. T., D. K. Hill, J. M. Kleinhans, N. P. Nibbelink and J. J. Magnuson. 1996. Potential effects of global climate change on small north-temperate lakes: Physics, fish, and plankton. *Limnol. Oceanogr.* 41: 1136-1149.
- Downing, J. A., Y. T. Prairie, J. J. Cole, C. M. Duarte, L. J. Tranvik, R. G. Striegl, W. H. McDowell, P. Kortelainen, N. F. Caraco, J. M. Melack, J. J. Middelburg. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* 51: 2388-2397.
- Elliott, J. A., S. J. Thackeray, C. Huntingford and R. G. Jones. 2005. Combining a regional climate model with a phytoplankton community model to predict future changes in phytoplankton in lakes. *Freshw. Biol.* 50: 1404-1411.
- Environment Canada. 2004. Canadian climate normals 1971-2000, Winnipeg Int'l A [online]. Available from <http://climate.weatheroffice.ec.gc.ca/index.html> [accessed on October 05, 2007].
- Frazer, L., A. Dupuis and B. Hann. 2005. Characteristics of the spring clear-water phase and its variability in shallow prairie lakes. Poster presentation *In* 25th International Symposium of the North American Lake Management Society. 9-11 November 2005. Madison, WI, USA.

- George, D. G. and A. H. Taylor. 1995. UK lake plankton and the Gulf Stream. *Nature* 378: 139.
- George, D. G. and D. P. Hewitt. 2006. The impact of year-to-year changes in the weather on the dynamics of *Daphnia* in a thermally stratified lake. *Aquat. Ecol.* 40: 33-47.
- Gerten, D. and R. Adrian. 2000. Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. *Limnol. Oceanogr.* 45: 1058-1066.
- Hampton, S. E., P. Romare and D. E. Seiler. 2006. Environmentally controlled *Daphnia* spring increase with implications for sockeye salmon fry in Lake Washington, USA. *J. Plankton Res.* 28: 399-406.
- Hoppe, T. 2003. Report on "The Potential for Irrigation Expansion in Western Canada" [online]. Available from <http://www.agr.ca/pfra/pub/irrexpan.htm#10> [accessed on November 2, 2007].
- IPCC. 2007. Summary for policymakers. *In* Climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Johnson, S. L. and H. G. Stefan. 2006. Indicators of climate warming in Minnesota: lake ice covers and snowmelt runoff. *Climate Change* 75: 421-453.
- Magnuson, J. J., B. J. Benson and T. K. Kratz. 1990. Temporal coherence in the limnology of a suite of lakes in Wisconsin, U.S.A. *Freshw. Biol.* 23: 145-159.

- Magnuson, J. J., K. E. Webster, R. A. Assel, C. J. Bowser, P. J. Dillon, J. G. Eaton, H. E. Evans, E. J. Fee, R. I. Hall, L. R. Mortsch, D. W. Schindler and F. H. Quinn. 1997. Potential effects of climate changes on aquatic systems: Laurentian great lakes and Precambrian shield region. *Hydrol. Process.* 11: 825-871.
- McKee, D., D. Atkinson, S. E. Collings, J. W. Eaton, A. B. Gill, I. Harvey, K. Hatton, T. Heyes, D. Wilson and B. Moss. 2003. Response of freshwater microcosm communities to nutrients, fish, and elevated temperature during winter and summer. *Limnol. Oceanogr.* 48: 707-722.
- Mooij, W. M., S. Hülsmann, L. N. De Senerpont Domis, B. A. Nolet, P. L. E. Bodelier, P. C. M. Boers, L. Miguel Dionisio Pires, H. J. Gons, B. W. Ibelings, R. Noordhuis, R. Portielje, K. Wolfstein and E. H. R. R. Lammens. 2005. The impact of climate change on lakes in the Netherlands: a review. *Aquat. Ecol.* 39: 381-400.
- Niemistö, J. P. and J. Horppila. 2007. The contribution of ice cover to sediment resuspension in a shallow temperate lake: possible effects of climate change on internal nutrient loading. *J. Environ. Qual.* 36: 1318-1323.
- Parnesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37: 637-669.
- Quinlan, R., P. R. Leavitt, A. S. Dixit, R. I. Hall and J. P. Smol. 2002. Landscape effects of climate, agriculture, and urbanization on benthic invertebrate communities of Canadian prairie lakes. *Limnol. Oceanogr.* 47: 378-391.

- Robarts, R. D. and T. Zohary. 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. *N. Z. J. Mar. Freshw. Res.* 21: 391-399.
- Schindler, D. W., K. G. Beaty, E. J. Fee, D. R. Cruikshank, E. R. DeBruyn, D. L. Findlay, G. A. Linsey, J. A. Shearer, M. P. Stainton and M. A. Turner. 1990. Effects of climatic warming on lakes of the central boreal forest. *Science* 250: 967-970.
- Schindler, D. W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. *Hydrol. Process.* 11: 1043-1067.
- Schindler, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Can. J. Fish. Aquat. Sci.* 58: 18-29.
- Schindler, D. W. and W. F. Donahue. 2006. An impending water crisis in Canada's western prairie provinces. *Proc. Natl. Acad. Sci. U.S.A.* 103: 7210-7216.
- Shepherd, A. and S. M. McGinn. 2003. Assessment of climate change on the Canadian prairies from downscaled GCM data. *Atmos.-Ocean* 41: 301-316.
- Soja, A. J., N. M. Tchebakova, N. H. F. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Parfenova, F. S. Chapin and P. W. Stackhouse. 2007. Climate-induced boreal forest change: Predictions versus current observations. *Global Planet. Change* 56: 275-296.
- Stewart, K. and D. Watkinson. 2004. *Freshwater fishes of Manitoba*. University of Manitoba Press, Winnipeg, MB.

- Straile, D. 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. *Oecologia* 122: 44-50.
- Tebaldi, C., K. Hayhoe, J. M. Arblaster and G. A. Meehl. 2006. Going to the extremes: An intercomparison of model-simulated historical and future changes in extreme events. *Climate Change* 79: 185-211.
- Winder, M. and D.E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85: 2100-2106.
- Wulder, M. A., T. A. Nelson, C. Derksen and D. Seemann. 2007. Snow cover variability across central Canada (1978-2002) derived from satellite passive microwave data. *Climate Change* 82: 113-130.

**Chapter 2: Consequences of a warm spring for cyanobacteria and daphniid-
rotifer populations in small eutrophic lakes in the Canadian prairies.**

Introduction

Temperature is an important determinant of many physiological rates regulating processes from growth to reproduction. Increasingly, warming air temperatures and changing climatic conditions have been linked to population variability, with several terrestrial (plants, Cleland et al. 2007; birds, Torti and Dunn 2005), marine (plankton, Edwards and Richardson 2004) and freshwater (plankton, George and Taylor 1995; Straile 2000; Winder and Schindler 2004) examples. In considering biological implications of warming, the seasonal period at which change is to occur may affect the magnitude of impact on freshwater food webs. Small shallow lakes, in contrast to deep water-bodies, for example, are especially susceptible to warmer temperatures. During early spring, lakes with small volume to surface area ratios quickly respond to changing weather (Adrian et al. 1999, Gerten and Adrian 2000) with water temperatures closely matching those of ambient air (Carpenter et al. 1992). A recent survey of the world's lakes has shown that small water-bodies ($< 1 \text{ km}^2$) dominate by surface area (Downing et al. 2006). Thus, strong responses of small lakes to weather fluctuations combined with their spatial dominance suggest that a changing climate may have broad-ranging consequences for freshwater systems.

Understanding of the direct and indirect effects of increased spring water temperatures will be crucial in determining the impacts of future climate change on zooplankton-phytoplankton interactions in small eutrophic water-bodies commonly found in north-central parts of North America. In spring, under conditions of non-limiting light and nutrients, and prior to the onset of zooplanktivory by young-of-year fish, representations of the planktonic food webs of small eutrophic lakes can be simplified to

two-trophic-level systems composed of phytoplankton and zooplankton. Control of phytoplankton is largely a result of top-down interactions such as grazing by daphniids, which often lead to a clear-water phase (Sommer et al. 1986). In lakes, physical responses to climatic variations are often regionally coherent; however, biological responses remain highly variable and predictions apply to a narrow range of lake types (Magnuson et al. 1990; Mooij et al. 2005). As a result, further study is needed to consider possible effects a warmer spring may have on phytoplankton and zooplankton abundance and species composition in these small eutrophic lakes.

Long-term studies on shallow eutrophic lakes have shown correlations of spring water temperatures with changes in the dynamics of phytoplankton and zooplankton (Adrian et al. 1999; Gerten and Adrian 2000; Benndorf et al. 2001). For example, in Müggelsee, Germany, a shallow eutrophic lake, warmer water temperatures in late April and early May caused an earlier onset of the spring daphniid peak and the clear-water phase (Gerten and Adrian 2000). Further, George and Hewitt (2006) demonstrated that inter-annual weather variations, in temperature and wind speed, not only correlated with daphniid abundance but this was also governed through change in food quality, i.e., an increased abundance of filamentous cyanobacteria. As increased water temperatures have led to longer periods of dominance of cyanobacteria in some eutrophic lakes, further research is needed to elucidate what impact this might have on zooplankton populations, particularly at the species level (Adrian and Deneke 1996). Few studies have investigated impacts of warming on small grazers such as rotifers that may be important food-web components in years when larger daphniids are lacking (Tirok and Gaedke 2006).

Alternative stable state theory suggests that within a range of nutrient concentrations shallow lakes can exist in a clear or a turbid water state (Scheffer et al. 1993). Forcing mechanisms, typically a trophic cascade, have been associated with a switch in the system leading to changes in competitive outcomes between macrophyte and phytoplankton. Some studies have shown that water temperature can play an important role in facilitating a switch in alternative stable states in shallow lakes (McKee et al. 2003; Hargeby et al. 2004). Thus, climate warming could also lead to rapid switches between states particularly if food-web components respond differently to a changing climate.

In some instances, correlations using long-term datasets to relate climate warming to changes in plankton phenologies have been confounded with other factors such as changes in nutrient fluxes or management practices (Scheffer et al. 2001; Jeppesen et al. 2003; Scheffer et al. 2003; Van Donk et al. 2003). Short-term monitoring of abiotic and biotic factors relevant to planktonic populations could be useful to investigate potential effects of climate warming and variability on planktonic populations. This is particularly relevant as increased inter-annual variability with climate change (Tebaldi et al. 2006) suggests that some consequences of climate change could become apparent at relatively short timeframes.

This case study explores the implications of a warm spring on plankton dynamics in small eutrophic lakes in the Canadian prairies. A representative suite of these eutrophic lakes, the Fort Whyte lakes in Winnipeg, Manitoba, Canada, was surveyed over two open-water seasons (2005-06). Over the course of the survey, the implications of a warmer spring in 2006 (+2°C increase over April-May) relative to that experienced in

2005 were investigated in terms of changes in plankton dynamics. The objectives of this study are: (1) to examine implications of a warmer spring on phytoplankton abundance and composition and to relate this to changes in daphniid and rotifer population dynamics, and (2) to discuss these results as they relate to potential climate change implications for small north-temperate eutrophic lakes.

Methods

Study site

The Fort Whyte lakes (49° 49.020' N, 97° 13.440' W) situated in Winnipeg, MB are a set of five man-made lakes, constructed at twenty-year intervals starting in 1920 (see details in Loadman 1980). They are presently used as an environmental education centre (www.fortwhyte.org). For the purpose of this study, Lakes 2, 3 and 4 were selected as suitable models for small eutrophic lakes representative of many prairie water-bodies such as small lakes, large ponds, impoundments and dugouts. The Fort Whyte Lakes 2, 3 and 4 can be characterized as small prairie lakes with small surface areas (5.2 to 14.9 ha) and intermediate mean depths (4.5 to 5.0 m) (Table 2.1, Figure 2.1). Surrounding the lakes, land use includes a mixed-grass bison pasture, deciduous forest, agricultural fields, industrial sites and residential neighbourhoods.

Although Lakes 2, 3 and 4 are interconnected via narrow channels, they show important differences in morphometry and nutrient concentrations. Lake 2 is the smallest with an area of 5.2 ha and a volume of $23.4 \times 10^4 \text{ m}^3$, while Lake 3 is intermediate with a surface area of 9.4 ha and a volume of $43.5 \times 10^4 \text{ m}^3$ (Table 2.1). Lake 4 is the largest, with a surface area of 14.9 ha and a volume of $74.1 \times 10^4 \text{ m}^3$ (Table 2.1). As a result of

the range in surface area, mixis of the lakes varies from dimictic in Lake 2 to polymictic in Lake 4.

Chemically, all three lakes are eutrophic with mean May to August (2005-06) nutrient concentrations ranging from lowest in Lake 2 (TN, 1302.39 $\mu\text{g L}^{-1}$; TP, 106.61 $\mu\text{g L}^{-1}$), intermediate in Lake 3 (TN, 2076.00 $\mu\text{g L}^{-1}$; TP, 172.50 $\mu\text{g L}^{-1}$) and highest in Lake 4 (TN, 2475.57 $\mu\text{g L}^{-1}$; TP, 218.00 $\mu\text{g L}^{-1}$) (Table 2.1). Inflows to the lakes are restricted to spring runoff draining from adjacent agricultural fields. Nutrient loading is greatest in Lake 4 as a consequence of its larger shoreline length, inflow from a primary treatment lagoon (on-site education centre) and its use as a staging site by a large number of migrating Canada geese in the fall. The lakes have no outflows and, therefore, presumably have long residence times. In terms of buffering capacity, the Fort Whyte lakes are high in alkalinity (approx. 4500 $\mu\text{eq L}^{-1}$) (Table 2.1).

Data collection

A sampling station was established at the deepest point of each lake (Figure 2.1). From May to August, all three lakes were sampled weekly in 2005 and twice weekly in 2006, weather permitting. On each sampling date, water transparencies were measured with a Secchi disc and temperature profiles were collected at one-meter intervals with a YSI multi-probe meter (Model 55). Water chemistry samples were taken from just below the surface and analyzed for dissolved and suspended nitrogen (N) and phosphorus (P) as well as chlorophyll *a* (chl*a*). Chemistry analyses were completed in the Water Analysis lab at the Freshwater Institute (DFO) in Winnipeg, MB using standard methods detailed in Stainton et al. (1977).

Phytoplankton samples were collected just below the surface using glass scintillation vials (20 ml) and were preserved with Lugol's solution and stored in the dark. On each sampling date, integrated zooplankton samples were taken through the epilimnion to the surface using a 25 cm diameter Wisconsin zooplankton net with a 73 μm mesh size at similar periods during the day, i.e., between 9:00 and 11:00 am. Zooplankton samples were preserved with 95% ethanol. Epilimnion depth was selected based on temperature/oxygen profiles or, when isothermal, a three-meter integrated depth was sampled.

Data processing

In 2005, bathymetric maps of the Fort Whyte lakes were updated (Figure 2.1). A combination acoustic sounder and GPS unit was used to record transects of lake depths at geographic locations (equipment and expertise provided by Doug Watkinson, Freshwater Institute, DFO, Winnipeg, MB). Data were processed and bathymetric maps were constructed in ArcGIS based on kriging estimations to interpolate between data points.

Water-column stabilities were calculated for each sampling date in 2005 and 2006 using the Schmidt stability index (S). S (g cm^{-1}) describes the amount of work required to mix the entire water column to a uniform temperature and hence density (Robertson and Imberger 1994).

$$S = A_o^{-1} \sum (z - z^*) (\rho_z - \rho^*) A_z \Delta z$$

$$\rho^* = V^{-1} \sum (V_z \cdot \rho_z)$$

where A_z is the lake area (m^2) and ρ_z is the density (g cm^{-3}), both at depth z (m). z^* represents the depth where the mean density is found, and ρ^* is that density. V represents volume (m^3). One-meter depth intervals (Δz) were used for the calculations.

A measure of cumulative daily temperatures, degree-days (DD , $^{\circ}\text{C d}$) was estimated for each day during the open-water season (May to August) above a given threshold temperature (T_{Th}) (Neuheimer and Taggart 2007). Within an appropriate physiological range, ectotherm growth and development is temperature-dependent. Therefore, degree-days can be used to relate temperature to organism developmental time. Degree-days are calculated using the formula:

$$DD(n) = \sum (T_i - T_{Th}) \cdot \Delta d, \quad T_i \geq T_{Th}$$

Relevant threshold temperature (T_{Th}) is given as 4°C , found during isothermal conditions following ice-off. At ice-off, it is assumed that phytoplankton can develop without limitation by light or nutrients. T_i is the mean daily temperature and Δd is a day.

Average daily epilimnetic (0 to 3 m) water temperatures were estimated based on linear interpolations of local air temperatures on measured water temperatures for each lake. A dynamic linear model was used to estimate daily epilimnetic temperatures (Kjellman et al. 2003):

$$WT_t = a + WT_{t-1} + b * (AT_{t-1} - WT_{t-1})$$

Water temperatures (WT_t) were estimated based on air temperatures (AT_t) recorded at time t from a nearby Environment Canada weather station (Richardson International Airport, 49° 55.200' N, 97° 13.800' W). Minimum sum of squares between measured and estimated water temperature were used to estimate parameters a and b . Linear regressions were performed relating predicted values to observed values to determine the suitability of the model in estimating daily epilimnetic temperatures. As a result, the dynamic model gave reasonably good estimates of daily epilimnetic temperatures (linear regressions: Lake 2, observed = $(-2.532 \times 10^{-7}) + 1.000(\text{predicted})$, $F_{1,43} = 55.757$, $P < 0.001$, $r^2 = 0.565$; Lake 3, observed = $(-2.162 \times 10^{-7}) + 1.000(\text{predicted})$, $F_{1,43} = 38.523$, $P < 0.001$, $r^2 = 0.571$; Lake 4, observed = $(-2.057 \times 10^{-8}) + 1.000(\text{predicted})$, $F_{1,43} = 77.949$, $P < 0.001$, $r^2 = 0.644$).

Zooplankton were identified to species using taxonomic keys developed by Hebert (1995) for *Daphnia* and Pennak (1989) for other cladocerans and copepods. Rotifers were only counted as a group; however, identification of dominant species followed Chengalath et al. (1971). For zooplankton, two subsamples of 5 ml were enumerated for each sampling date and extrapolated to total volume sampled. In some cases, subsampled volume was decreased to 2.5 ml when high densities of cyanobacteria filaments obscured visibility. A 2.5 ml subsample volume did not change sample variances compared to samples where 5 ml were counted. Phytoplankton divisions, chlorophyta, chromophyta and cryptophyta, were classified by cell size based on longest linear dimensions. Filamentous cyanobacteria were identified to genus based on Findlay and Kling (1979). Phytoplankton cell counts were done using the Utermöhl inverted-microscope technique. For phytoplankton, a single subsample was counted. Biovolumes

were estimated by approximating cell dimensions to nearest geometrical shapes (Rott 1981).

Data analysis

Statistical analyses are separated into two parts: (1) assessment of factors driving a shift towards cyanobacteria dominance, and (2) the effects of temperature on plankton abundance and composition.

Possible factors leading to cyanobacteria dominance were tested using repeated-measures analysis of variance (RM-ANOVA) with Year as main effect and Lake as random effect. Factors tested were water column stabilities, nutrient concentration (both TDN and TDP) and TDN:TDP ratios. Dissolved forms of nitrogen and phosphorus were selected for analysis because they were assumed to be more readily available for assimilation over the short-term (within a month) in comparison to suspended forms. Monthly means (May to August) for each factor were used to test for difference between years, 2005 and 2006.

Relationships between water temperature and plankton abundance and composition were investigated using the metric, degree-days (*DD*, °C d). Degree-day was related to phytoplankton abundance (*chl a* and biovolume estimates), to relative cyanobacteria biovolume estimates, and to daphniid abundance. These relationships were examined by dividing the field season into monthly intervals (May, June, July, and August). Lake-years were used as independent data points for the analysis (3 lakes x 2 years = 6 data points). Mean monthly values of biological parameters were regressed by end of month values of degree-days, since degree-day values are cumulative measures of temperature over time. In addition, simple linear regressions were used to investigate

indirect effects of water temperature on daphniid abundance by relating a measure of food quality, %cyanobacteria, to daphniid abundance. Normality and homogeneity of residuals were verified using a Shapiro-Wilk's test for normality and visual checks of residuals by predicted values plots for homogeneity. Chlorophyll *a* and total phytoplankton biovolume was log-transformed to ensure normality and homogeneity of its residuals. All statistical tests were performed in SAS 9.1.2.

Results

Fort Whyte lakes biology

In spring, the lakes were dominated by small species of phytoplankton: chlorophyta (*Chlamydomonas* sp.), chromophyta (*Cryptomonas* sp.), and briefly with diatoms. In summer, filamentous cyanobacteria, primarily *Aphanizomenon* sp., *Planktothrix* sp. and *Anabaena* sp. dominated the phytoplankton community. The pelagic zooplankton species assemblage was composed of rotifers dominated by *Keratella quadrata*, *Keratella cochlearis* and *Brachionus* sp., calanoid copepods dominated by *Skistodiaptomus oregonensis*, cyclopoid copepods dominated by *Diacyclops thomasi* and other small cladocerans such as *Diaphanosoma* sp. and *Bosmina longirostris*. Also, three species of daphniids were found: *Daphnia pulicaria*, *D. ambigua*, and *D. parvula*. The dominant large invertebrate predators were larval stages of *Chaoborus flavicans*. Detailed patterns of zooplankton seasonality for the Fort Whyte lakes are described in Frazer (2006). Complete assemblage and abundance of planktivorous fish is unknown. Minnow trap catches suggests that Fathead minnows (*Pimephales promelas*) are the dominant planktivores. Also, angling records from the on-site education centre show populations of

Northern pike (*Esox lucius*), Yellow perch (*Perca flavescens*), Walleye (*Sander vitreus*) and Common Carp (*Cyprinus carpio carpio*) exist in the lakes.

Limnological change between 2005 and 2006

Two field seasons from May to mid-August (2005 and 2006) at the Fort Whyte lakes showed very different patterns in water temperatures, water transparencies, phytoplankton and zooplankton populations. Ice-off in both years, however, occurred on April 14. Spring conditions in 2006 can generally be characterized as ‘warmer than average’. Over the months of April and May, air temperatures remained on average 2°C higher in 2006 compared to 2005 (data not shown). As a result, spring thermal profiles and water temperatures were altered substantially (Figures 2.2a-f). In Lake 2, a dimictic lake, stratification occurred earlier in 2006, beginning in late April. In this lake, warmer spring air temperatures increased temperatures in the epilimnion by 2°C but not in the hypolimnion. Earlier stratification in 2006 caused the hypolimnion to remain cooler at only 6°C during spring, two degrees colder when compared with 2005 (Figures 2.2a, b). In contrast, during spring in the more polymictic Lakes 3 and 4, the entire water-columns warmed by approximately 2°C in 2006 compared to 2005. Also, in 2006, earlier warming led to shallower epilimnion depths in Lakes 2 and 3 and stronger stratification patterns in Lake 4.

Water transparency in the Fort Whyte lakes measured by Secchi disc decreased substantially from 2005 to 2006 (Figures 2.3a, b, c). The largest changes in transparency were measured in Lake 2 where mean Secchi depth decreased from an open-water mean of 2.9 ± 0.3 m (\pm SE) in 2005 to 0.6 ± 0.01 m (\pm SE) in 2006 (Figure 2.3a). In addition, a spring clear-water phase, characterized by a spring maximum in Secchi transparency

occurred only in 2005. In 2006, water transparency did not vary substantially over the entire field season.

Water column stability, measured as the Schmidt stability index (S , g cm^{-1}), was largely similar between years with the exception of two strong stability events separated by de-stratification occurring during the summer of 2005 (Figure 2.3d, e, f). During spring turnover, water column stability was low (nearly 0) across Lakes 2, 3 and 4. In summer, water column stability is greatest in Lake 2 ($\sim 100 \text{ g cm}^{-1}$) and lowest in Lake 4 ($\sim 50 \text{ g cm}^{-1}$) (Figure 2.3d, f).

Spring dissolved nutrient concentrations were generally similar between 2005 and 2006. In spring in all lakes, total dissolved nitrogen (TDN) concentrations were greatest reaching approximately $1000 \mu\text{g L}^{-1}$ in Lake 2, $1500 \mu\text{g L}^{-1}$ in Lake 3 and $2000 \mu\text{g L}^{-1}$ in Lake 4 (Figures 2.3g, h, i). During a short period in 2005 (days 150–200), TDN concentrations in Lakes 3 and 4 were greater than those observed in 2006. Spring concentrations of total dissolved phosphorus (TDP) varied from $25\text{--}50 \mu\text{g L}^{-1}$ for Lake 3 and 4 (Figures 2.3k, l). In contrast, in 2005, early spring TDP concentrations in Lake 2 were 3.3x greater than those in 2006 with initial values of $112 \mu\text{g L}^{-1}$ (2005) compared to $34 \mu\text{g L}^{-1}$ (2006) (Figure 2.3j). Later, between days 150–200, concentrations of TDP were greater in 2005 in all three lakes. TDN:TDP ratios show similar patterns between years (Figures 2.3m, n, o). Largest differences between years were found in Lake 2 where open-water means of TDN:TDP ratios were lower in 2005 at 10 compared to 25 in 2006.

Phytoplankton abundance and species composition changed markedly between field seasons. Both measures of phytoplankton biomass, chlorophyll a ($\mu\text{g L}^{-1}$) and biovolume estimates ($\text{mm}^3 \text{ L}^{-1}$), indicate large increases in 2006 (Figures 2.4 and 2.5).

Across Lakes 2, 3 and 4, mean chlorophyll *a* concentrations ranged from 24.0 – 58.3 µg L⁻¹ in 2005 compared to 38.3 – 93.5 µg L⁻¹ in 2006 (Figures 2.4a, b, c). As a result, decreased water transparency was directly associated with increases in phytoplankton biomass (linear regressions: Lake 2, Secchi = 4.957 – 2.660(logchl_a), $F_{1,21} = 57.902$, $P < 0.001$, $r^2 = 0.734$; Lake 3, Secchi = 4.206 – 1.955(logchl_a), $F_{1,14} = 28.854$, $P < 0.001$, $r^2 = 0.673$; Lake 4, Secchi = 3.901 – 1.695(logchl_a), $F_{1,21} = 19.303$, $P < 0.001$, $r^2 = 0.479$).

Phytoplankton succession in both years followed patterns typical of eutrophic lakes (Sommers et al. 1986), generally shifting from small to large and filamentous algal species (Figures 2.5a-f). The most important change in phytoplankton succession was an increase in the relative biomass of filamentous cyanobacteria in 2006. Proportional cyanobacteria biomass changed substantially from maximum open-water values of 28.2%, 46.7% and 90.9% in 2005, increasing to 77.7%, 90.1%, 95.0% in 2006, for Lakes 2, 3 and 4, respectively (Figures 2.5a-f). In addition, phytoplankton succession progressed earlier in 2006. By mid-May in 2006, cyanobacteria already represented 11 – 15% of the total phytoplankton biomass. In comparison, in 2005, cyanobacteria accounted for only 0.2 – 3% of the mid-May phytoplankton biomass (Figures 2.5a-f). Interestingly, increased total and relative cyanobacteria biomass were also associated with shifts in dominant taxa. In 2005, *Aphanizomenon spp.* was the primary taxon occupying the lakes followed by a shift in 2006 to *Anabaena spp.* and *Planktothrix spp.*, especially during the months of June – August (Figures 2.6a-f).

Two major changes were observed in zooplankton communities between years. (1) In 2006, daphniid populations decreased to virtual absence with the exception of a short-lived peak in Lake 4 (Figures 2.7a, b, c and 2.8). In 2005, two distinct peaks of both

Daphnia pulicaria and *D. ambigua* occurred in all three lakes. In contrast, *D. parvula* were observed almost exclusively in 2006 but at very low densities in Lakes 2 and 3 (Figures 2.8a-f). (2) In 2006, rotifer populations increased to very high values in all lakes with a maximum of 15,000 individuals per litre in Lake 2 (Figures 2.7d, e, f). Other constituents of the zooplankton community demonstrated less consistent changes in population dynamics, particularly during spring, and thus were not the focus of this study. Cyclopoid copepods, dominated by *Diacyclops thomasi*, showed spring peaks in 2005 but not in 2006 except for Lake 4 (Figures 2.7g, h, i). Calanoid copepods, dominated by *Skistodiaptomus oregonensis*, increased in density in 2006, beginning in summer (Figures 2.7j, k, l). Small cladocerans, such as *Bosmina longirostris* and *Diaphanosoma sp.*, showed increases during turbid conditions in 2006 (Figures 2.7 m, n, o). Also, zooplankton predators, instars III and IV of *Chaoborus flavicans*, peaked in summer except for Lake 2 in 2006 (Figures 2.9a, b). For the purpose of this study, both daphniids and rotifer population dynamics were further investigated as they showed major inter-annual shifts during spring.

Relationships between water temperature and phytoplankton

Response of plankton abundance and composition to changes in water temperature, observed from 2005 to 2006, was investigated using simple linear regression models with degree-days as an explanatory variable. In all models, in 2006, warmer water temperatures led to greater degree-day values and phytoplankton abundance compared to 2005 (Figures 2.10 and 2.11). Strong relationships were found between water temperature and phytoplankton abundance and composition. Both measures of phytoplankton biomass, i.e., chlorophyll *a* and biovolume estimates, significantly increased with

temperature during the months of May to July (Table 2.2, Figures 2.10 and 2.11).

Degree-days ($^{\circ}\text{C d}$) explained 81 – 85% of the variability in chlorophyll *a* but slightly less for total biovolumes at 67 – 82% for the months of May to July.

Warmer water temperatures in 2006, indicated by degree-days, were associated with greater relative cyanobacteria biomass in all lakes compared to 2005 (Figure 2.12). Relative filamentous cyanobacteria biomass (%cyanobacteria) significantly increased with temperature in both July and August (Table 2.2). Relative cyanobacteria biomass increased quickly with degree-days, increasing by 30 and 23% in June and July, respectively, for each 100 degree-days (Table 2.2, Figure 2.12). Degree-day explains 96% of the variation in %cyanobacteria in July. In contrast, the relationship is slightly weaker in August ($r^2 = 0.76$).

Alternative factors regulating cyanobacteria

Repeated measures analysis of variance (RM-ANOVA) was conducted to test for difference in nutrient concentrations and water-column stability between 2005 and 2006. Mean monthly nutrient concentrations were not significantly different between years at the Fort Whyte lakes (Table 2.3). Thus, from 2005 to 2006 no important influx of nutrients occurred that was common to all three lakes at the same time. Nitrogen to phosphorus ratios are important predictors of cyanobacteria dominance (Schindler 1977; Smith 1983). Between years, only July and August showed significant differences (Table 2.3). In both cases, however, lowest TDN:TDP ratio was observed in 2005 (Figure 2.3m, n, o).

Similarly, water-column stability can potentially disrupt dominance of buoyancy-controlling cyanobacteria (Reynolds and Walsby 1975). Schmidt stability index

(S , g cm⁻¹) did not vary much among years, despite of the increased epilimnetic water temperatures in 2006 (Table 2.3, Figure 2.3d, e, f). Schmidt stability index reflects the amount of energy required to fully mix the water column to an equal density and depends primarily on air temperatures and wind speeds. In spring of 2006, water-column stabilities did not increase as smaller epilimnion volumes offset the warmer temperatures.

Relationships between water temperature and daphniids

Daphniid abundance was indirectly related to water temperature. Monthly linear regressions between degree-days and daphniid abundance were not significant ($P > 0.05$, data not shown). However, negative relationships between relative cyanobacteria biomass and daphniid abundance were significant for June and July (Table 2.4, Figure 2.13). In 2006, lower daphniid abundance was associated with higher filamentous biomass compared to 2005 (Figure 2.13). Relative biomass of filamentous cyanobacteria, an indicator of food quality, more severely affected daphniid abundance during June (slope = 0.475) compared to July (slope = 0.188) (Table 2.4, Figure 2.13). Percent cyanobacteria explained most of the variation in daphniid abundance in both June ($r^2 = 0.66$) and July ($r^2 = 0.71$).

Discussion

Water temperature and phytoplankton

Water temperature is an important factor regulating phytoplankton physiological rates (Rhee and Gotham 1981). In 2006, a warm spring at the Fort Whyte lakes was correlated with increased total phytoplankton and relative cyanobacteria biomass. This is consistent with long-term (>30 years) patterns observed in several North American and

European lakes where a warming climate has been linked to earlier phytoplankton blooms (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Winder and Schindler 2004), increased total biomass (Schindler et al. 1990) and, in eutrophic lakes, dominance of cyanobacteria (Adrian and Deneke 1996). In nutrient-rich systems, empirical and experimental results suggest that increasing water temperatures are directly linked to changes in phytoplankton species composition, showing an increasing proportion of cyanobacteria taxa (Zhang and Prepas 1996; De Senerpont Domis et al. 2007a). In fact, in some years, warming temperatures have now led to year-round cyanobacteria dominance (Adrian and Deneke 1996).

At the Fort Whyte lakes, higher temperatures in June-August were also associated with shifts in the dominant cyanobacteria taxa, from *Aphanizomenon* in 2005 to *Anabaena* and *Planktothrix* in 2006. This may be attributed to differences in competitive abilities among species under different environmental conditions. At the Fort Whyte lakes, indirect effects of warmer water temperatures in 2006 may have been more important than direct effects. In 2006, decreased water transparency, not increased water temperature, may have facilitated dominance of *Planktothrix* over *Aphanizomenon*. Direct effects of increased temperature did not drive a taxonomical shift as *A. flos-aquae* growth rates are greater than those of *P. agardhii* and *P. redekei* over a range of temperatures (6-15°C) without light limitation (Gibson 1985). However, under conditions of lowered light intensities, several laboratory experiments suggested greater photosynthetic efficiency and growth rates in *P. agardhii* relative to *A. flos-aquae* (Foy et al. 1976; Foy and Gibson 1982) resulting in superiority of the former in low-light environments. Importantly, these shifts in cyanobacteria species could have negative

implications especially when replacement taxa produce toxins and/or are of poorer nutritional quality for zooplankton.

Alternative factors driving cyanobacteria dominance

Shifts toward cyanobacteria dominance have generally been explained by an interplay of factors favouring growth of cyanobacteria over other phytoplankton taxa. Some of these factors include: high nitrogen and phosphorus concentrations (Downing et al. 2001), low N:P ratios (Schindler 1977; Smith 1983), high water column stability (Reynolds and Walsby 1975), zooplankton grazing (Sommer et al. 1986; Lampert et al. 1986) and high water temperature (Robarts and Zohary 1987). These hypotheses were examined as potential candidates to explain a major shift toward cyanobacteria dominance at the Fort Whyte lakes in 2006. In this study, water temperature was hypothesized to be the most important driver for the shift to cyanobacteria dominance because data supporting alternative hypotheses, i.e., water column stability, nutrient concentrations and N:P ratios generally did not change significantly between years.

Dramatic reduction and virtual loss of large cladoceran grazers from the Fort Whyte lakes in 2006 demonstrates that shifting to cyanobacteria can occur even without grazing by large zooplankton species. In some cases, large cladocerans can graze some filamentous cyanobacteria but, ultimately, grazing on other algal taxa generally leads to shifts in phytoplankton composition (Sommer et al. 1986; Epp 1996). High densities of rotifers that replaced daphniid populations in 2006 potentially exerted sufficient grazing pressure on small-celled phytoplankton taxa to affect a shift to cyanobacteria. In the absence of large cladocerans, ciliates and rotifers can dominate the zooplankton community in both deep oligotrophic (Lake Constance, Germany; Tirok and Gaedke

2006) and shallow eutrophic (Lake Võrtsjärv, Estonia; Agasild et al. 2007) lakes. Under conditions of low daphniid abundance, heavy grazing by micro-zooplankton can impact phytoplankton succession by causing the onset of the clear-water phase (Tirok and Gaedke 2006).

Water temperature and daphniids

Unexpectedly, increased phytoplankton biomass was not paralleled by increased daphniid biomass as a consequence of warmer conditions in 2006 at the Fort Whyte lakes. Relationships between water temperature and daphniid abundance were insignificant; however, low populations in 2006 may suggest the presence of some negative temperature effect on daphniid population growth. This is contrary to some studies linking climate warming to changes in plankton timing and abundance. In European lakes, warming temperatures indicated by the North Atlantic Oscillation (NAO) were associated with an earlier peak of both phytoplankton and *Daphnia* (Straile 2002). In some cases, higher water temperatures were also linked to higher daphniid biomass (Straile 2000). At the Fort Whyte lakes, daphniid food quality in 2006, expressed as relative filamentous cyanobacteria, deteriorated with increasing temperatures and was negatively related to daphniid abundance for the months of June and July. In spring of 2006, lower food quality caused by an earlier succession towards filamentous cyanobacteria with warmer conditions, may have had negative consequences for daphniid growth and reproduction. In support of this argument, June showed the steepest negative relationship between relative cyanobacteria and daphniid abundance, indicating greater importance of food quality early in the season. Similarly, in Lake Washington, percent blue-green algae negatively affected *Daphnia* fecundity beginning in June (Scheuerell et

al. 2002). In both Lake Washington and the Fort Whyte lakes, percent cyanobacteria in May likely has an important impact on daphniid fecundity and abundance although this is subject to a time-lagged response and is carried over to the month of June.

Cyanobacteria and daphniids

At the Fort Whyte lakes, several mechanisms associated with increased cyanobacteria filaments may explain the decrease in daphniid abundance in 2006. For daphniids, cyanobacteria have been proposed to be poor quality food due to nutritional inadequacy, decreased manageability with filamentous and colonial morphologies, and inhibitory effects on grazing by toxic substances (Porter and Orcutt 1980; Holm et al. 1983; DeMott 1999). This field study, however, cannot disentangle the several possible mechanisms. At the Fort Whyte lakes, in June, low daphniid abundance (≤ 10 individuals L^{-1}) occurred at a threshold value of 20.5% relative filamentous cyanobacteria. Since this value is estimated with a high degree of variability, interpretation requires caution. Gliwicz (1990) observed that *D. pulicaria* juvenile growth can be maintained at approximately 0.2 day^{-1} when fed a diet consisting of 20% *Aphanizomenon flos-aquae* (0.1 mg C L^{-1}) and 80% *Scenedesmus* (0.5 mg C L^{-1}). In these experiments, growth of *D. pulicaria* ceased only at a high relative abundance of 89% *Aphanizomenon* (4 mg C L^{-1}). Gliwicz (1990) suggested that high filament concentration likely produced a food limitation effect by decreasing assimilation and increasing respiration rates. Therefore, these results suggest that conditions at the Fort Whyte lakes never attained threshold values of no growth for daphniids. A food limitation effect alone may not completely explain lower daphniid populations in 2006.

An alternative explanation may come from toxin production linked to several species of cyanobacteria. One major implication of warmer conditions in 2006 at the Fort Whyte lakes was an important shift in dominant cyanobacteria from *Aphanizomenon* to potentially more toxic taxa such as *Planktothrix*. Few studies have tested the impact of *Planktothrix* on grazers such as daphniids generally opting to focus on the genus *Microcystis* (Oberhaus et al. 2007). *Planktothrix agardhii*, a dominant species in the Fort Whyte lakes, and *P. rubescens* can produce strong chemical defences such as microcystin-LR (Sano and Kaya 1998; Blom et al. 2001). Across studies, daphniid responses to toxic strains of *Planktothrix* show declines in feeding rates while effects on survivorship varies compared to controls (Kurmayer and Jüttner 1999; Oberhaus et al. 2007).

Comparison of these studies with the Fort Whyte lakes, however, is questionable. In the Fort Whyte lakes, toxins were analysed in 2006 and ranged from maximum values of 0.45 and 6.21 $\mu\text{g L}^{-1}$ equivalents of microcystin-LR in Lake 2 and Lake 4, respectively (Dr. Brian Kotak, AlgalTox International, Pine Falls, MB, unpublished data). In comparison, toxicity effects on daphniids reported by both Kurmayer and Jüttner (1999) and Oberhaus et al. (2007) were determined when exposed to toxin concentrations several orders of magnitude greater ranging from 329 to 9400 $\mu\text{g L}^{-1}$ equivalents of microcystin-LR.

Generally, comparisons with these studies suggest that more daphniids should have been present in the Fort Whyte lakes in 2006. One possible explanation is that daphniid clones at the Fort Whyte lakes may lack adaptation to grazing toxic cyanobacteria. Toxin production by cyanobacteria can impart important negative effects

on daphniids; however, this is not equivalent for all clones (Gilbert 1990; Hairston et al. 2001; Sarnelle and Wilson 2005; Wilson and Hay 2007). Regime shifts in lakes towards toxin-producing cyanobacteria strains may cause some short-term impacts on daphniid populations but in the long-term, strong selective pressures could allow local adaptation of daphniid populations to toxic cyanobacteria (Hairston et al. 2001; Sarnelle and Wilson 2005). Exposure of zooplankton grazers to inter-annual shifts in cyanobacteria taxa may become increasingly common, as climate change is associated with increasing occurrences of extreme weather variations (Meehl et al. 2000; Tebaldi et al. 2006). Inter-annual weather variations may reduce the ability of daphniids to adapt to poorer food quality if changing environmental conditions promotes unpredictable shifts between cyanobacteria taxa at short timescales.

Shifts in zooplankton body size

Long-term studies of climate related impacts on plankton show a trend towards smaller daphniid species. In Heiligensee, Germany, *D. cucullata* replaced the larger *D. galeata* as a warming temperature trend increased the relative abundance of filamentous cyanobacteria (Adrian and Deneke 1996). Similarly, at the Fort Whyte lakes, increased water temperature and filamentous cyanobacteria in 2006 were associated with low abundance of small-bodied *D. parvula* compared to high abundances of large-bodied *Daphnia pulicaria* and small-bodied *D. ambigua* in 2005. The presence of filamentous cyanobacteria is often associated with smaller species of daphniid, i.e., <1 mm body length (DeMott et al. 2001; Ghadouani et al. 2003). Laboratory experiments have shown that larger-sized daphniids are more negatively affected by the presence of cyanobacterial filaments than smaller-sized ones causing interference with feeding appendages, high

rejection rates, lowered filtering rates and decreased reproduction (Webster and Peters 1978; Fulton III and Paerl 1987; DeMott et al. 2001). In general, smaller daphniids are less susceptible to feeding interference due to their narrower carapace gapes. As a result, in the presence of filamentous cyanobacteria, the threshold food abundance where growth and reproduction can occur is lowest for small daphniids (Gliwicz and Lampert 1990). Even though total food abundance at the Fort Whyte lakes was higher in 2006, part of the explanation may be that poorer food quality caused some food limitation effect for the larger *D. pulicaria*. However, it is unclear at this point why *D. parvula*, similar in size to *D. ambigua*, was essentially the only daphniid species present in 2006. It is possible that mechanical and/or toxicity effects induced by the presence of filamentous cyanobacteria can impart differential responses between similarly sized daphniid species (DeMott et al. 2001).

Alternatively, changes in spring environmental conditions may differentially affect daphniid species, potentially disrupting spring population development. For example, in Lake Oneida, USA, variations in temperature and photoperiod cues consistent with conditions of an earlier ice-out date were suggested to have induced emergence of *D. pulicaria* but not of *D. galeata mendotae* (Cáceres 1998; Cáceres and Schwalbach 2001). At the Fort Whyte lakes, earlier warming and/or lower light intensities due to higher algal biomass in 2006 may have disrupted dormancy termination, causing failure of *D. pulicaria* and *D. ambigua* but not *D. parvula* to terminate dormancy and recolonize the water-column.

Abundance of rotifers increased substantially as an indirect result of shifts in phytoplankton species composition. Daphniid population development may have been

suppressed by the presence of filamentous cyanobacteria but rotifers did not appear to follow suit, attaining high populations in 2006. Experiments have shown that in the presence of endotoxin-producing *Anabaena affinis*, population growth rates significantly decreased in several daphniid species including *Daphnia ambigua*, *D. pulex* and *D. galeata mendotae* but remained unchanging for rotifer species *Keratella cochlearis*, *K. testudo*, *K. crassa* and *Synchaeta pectinata* (Gilbert 1990). In contrast, a meta-analysis tested cyanobacterial toxicity and morphological effects on cladocerans and rotifers and showed no overall difference in population growth between both groups (Wilson et al. 2006). These conflicting results suggest difficulty in generalizing zooplankton response to cyanobacteria. In other words, species-level differences may lead to differential responses in cladocerans and rotifers in the presence of cyanobacteria. Additionally, the present study provides empirical evidence that high daphniid abundance in 2005 can suppress rotifer populations in nature. Daphniids can cause important interference of rotifers by exploiting similar food sources and by ingesting and damaging rotifers directly (MacIsaac and Gilbert 1991). Thus, at the Fort Whyte lakes a shift to rotifer dominance in 2006 may have been facilitated by a combination of relatively unaffected growth rates in the presence of cyanobacteria and competitive release from daphniids.

Zooplanktivory

Zooplanktivory by young-of-year fish and invertebrates, such as larval stages of *Chaoborus*, can be important factors in regulating zooplankton populations. Water temperature is an important determinant of planktivorous fish development to larval sizes capable of feeding on large cladocerans (Hansson et al. 2007). It is likely that an earlier onset of spring in 2006 at the Fort Whyte lakes led to earlier planktivory pressure,

although fish populations and foraging was not examined in this study. In Bautzen reservoir, Germany, increased May water temperatures led to earlier and increased daphniid consumptive mortality during the spring clear-water phase by both *Leptodora kindti* and young-of-year percids (Wagner and Benndorf 2007). In Bautzen reservoir, this led to lower *Daphnia galeata* abundance at the end of the clear-water phase. In contrast, evidence suggests that planktivory does not prevent the development of the spring population peak in daphniids and the resulting clear-water phase (Rudstam et al. 1993; Mehner and Thiel 1999; Benndorf et al. 2001; Hansson et al. 2007). Therefore, at the Fort Whyte lakes, the absence of a spring daphniid peak in 2006 suggests that there were other factors more important than fish planktivory in controlling daphniid abundance.

Under some conditions, high populations of zooplanktivorous invertebrates, such as larval *Chaoborus*, can cause important fluctuations in zooplankton populations and community. Experimental addition of high densities (2.5 ind. L⁻¹) of predatory III and IV instars of *Chaoborus* larvae produced declines of small cladocerans (*Ceriodaphnia* and *Bosmina*) and rotifers, while large cladocerans (*Daphnia*) were seemingly unaffected (Lynch 1979). In the Fort Whyte lakes, however, daytime sampling may have been inadequate to quantitatively measure vertically migrating populations of *Chaoborus*. Nonetheless, this study suggests that *Chaoborus flavicans* predation did not change consistently between 2005 and 2006 and thus could not be attributed to changes in zooplankton populations.

Daphniid-phytoplankton mismatch

Warmer spring temperatures could potentially drive temporal mismatches between daphniids and higher quality phytoplankton. This could be one possible

explanation for the observed zooplankton-phytoplankton dynamics at the Fort Whyte lakes. Inter-annual variation in weather conditions may have caused an earlier phytoplankton succession to cyanobacteria relative to the spring daphniid population development. In European lakes, however, long-term data suggest that climate warming has led to an advancement of both edible algae and daphniid spring peaks causing an earlier appearance of the clear-water phase (Scheffer 2001; Straile 2002). In contrast, two deep lakes, Lake Washington, USA (Winder and Schindler 2004) and Lake Windermere, UK (George and Taylor 1995) have shown temporal mismatches between daphniids and diatom spring peaks in response to climate warming. Winder and Schindler (2004) hypothesized that earlier warming causes variations in temperature-photoperiod hatching cues and negatively affected timing of emergence and redevelopment of daphniid populations in relation to an earlier diatom bloom. An important caveat of this hypothesis is the necessity of a strong benthic-pelagic coupling for population redevelopment from resting eggs. Recently, however, Hampton et al. (2006) found that *Daphnia pulicaria* over-wintered in Lake Washington and suggested that winter survivorship, not emergence from resting eggs, explained timing of *D. pulicaria* but not *D. thorata* in spring. These results suggest that not all *Daphnia* species respond similarly to climate change. At the Fort Whyte lakes, winter sampling (Loadman 1980; present author February 2007), suggested that daphniids do not over-winter and that recolonization of daphniids may be dependent on emergence from resting eggs. Also, De Senerpont Domis et al. (2007b) suggested that shallower depths and higher latitudes often characterize lakes without over-wintering daphniids. For daphniids, several studies suggest that both temperature and photoperiod are important environmental cues for emergence (Gyllström

and Hansson 2004). As photoperiod is invariant with climate change, timing of daphniid spring populations could remain temporally static if photoperiod is a strong cue for termination of dormancy. An earlier warming in 2006 at the Fort Whyte lakes might have caused such a decoupling of water temperature and photoperiod cues causing delayed emergence of daphniids relative to earlier phytoplankton development in the spring.

In concert with this hypothesis, cooler hypolimnetic temperatures owing to earlier stratification, as shown in the dimictic Lake 2 in 2006, lengthens development time of diapausing daphniids further disrupting daphniid-phytoplankton interactions. Climate change has the potential to produce cooler hypolimnion temperatures in dimictic lakes by causing earlier stratification, a stronger density gradient and, thus, reduced mixing potential with warmer surface water (DeStasio et al. 1996; Jankowski et al. 2006). In many temperate lakes, however, climate change has produced small increases of hypolimnetic temperatures (1°C per 100 years in European lakes) compared with much more substantial surface warming (Arhonditsis et al. 2004; Dokulil et al. 2006). In terms of impacts on hatching dynamics, lake morphometry and spatial distribution of resting eggs may control zooplankton sensitivity to changes in hypolimnetic temperatures with climate change. In summary, lakes that strongly depend on emergence in the spring for population redevelopment and/or the bulk of viable resting eggs reside below the thermocline could anticipate the strongest negative response in zooplankton emergence to a warming climate.

Conceptual summary model

Conceptually, Figure 2.14 summarizes the potential impacts of a warm spring on phytoplankton-zooplankton interactions in small north-temperate eutrophic lakes with a

strong benthic-pelagic coupling in terms of population redevelopment in the spring from the resting egg bank. The model describes two situations, a late warming and an earlier warming scenario, representing the years 2005 and 2006 at the Fort Whyte lakes, respectively. Both scenarios can be compartmentalized into early spring, late spring and summer and their dynamics can be described as follows:

- *Early spring*: Earlier warming produced earlier and greater phytoplankton bloom relative to a later warming scenario. With earlier warming, populations of small grazers, such as rotifers, peak earlier responding strongly to a temperature cue for emergence. In the case of daphniids, earlier warming does not produce an advancement of the spring timing as response is more strongly linked to the coupling of temperature and photoperiod cues in the spring.
- *Late spring*: Dominance of cyanobacteria is, in part, linked to high water temperature and occurs sooner in the earlier warming scenario. Earlier phytoplankton blooms likely decrease availability of some nutrients such as nitrogen and so N-fixing cyanobacteria can become competitively dominant. Also, in the earlier warming scenario, the replacement of large grazers with high abundances of small grazers can efficiently graze small-sized phytoplankton species, promoting a shift to cyanobacteria dominance. Inter-annual changes in environmental conditions (e.g., light, temperature) can cause shifts in dominance between cyanobacteria taxa, in some cases favouring toxin-producers over others. Potentially, with earlier warming, both an earlier shift to cyanobacteria and shifts to toxin producing taxa negatively affected daphniid hatchling

survivorship and population growth, disrupting matching of daphniids with high quality phytoplankton.

- *Summer*: An earlier warming scenario was associated with low abundance of large grazers, such as daphniids, decreasing potential for top-down mediated control of large phytoplankton taxa and thus produced conditions of high phytoplankton biomass and low water transparency.

Table 2. 1. Morphological and chemical characteristics of the Fort Whyte lakes.
Chemistry data reported as mean (\pm SD) values of May–August in 2005 and 2006.

Parameter	Lake 2	Lake 3	Lake 4
Morphometry			
Surface area (ha)	5.18	9.38	14.91
Total volume ($\times 10^4 \text{ m}^3$)	23.45	43.47	74.14
Mean depth (m)	4.5	4.6	5.0
Maximum depth (m)	8.4	7.5	8.3
Chemistry			
Chlorophyll <i>a</i> (\pm SD) ($\mu\text{g L}^{-1}$)	30.87 (22.39)	54.32 (39.47)	84.88 (50.79)
Total nitrogen (\pm SD) (mg L^{-1})	1.30 (0.32)	2.08 (0.72)	2.48 (0.66)
Total phosphorus (\pm SD) ($\mu\text{g L}^{-1}$)	106.61 (36.30)	172.50 (65.23)	218.00 (76.46)
Alkalinity (\pm SD) ($\mu\text{eq L}^{-1}$)	4768.75 (171.67)	4393.75 (226.96)	4488.75 (185.51)

Table 2. 2. Results of simple linear regressions testing for monthly linear relationships between chlorophyll *a* ($\mu\text{g L}^{-1}$), total phytoplankton biovolume ($\text{mm}^3 \text{m}^{-3}$), % filamentous cyanobacteria, % inedible phytoplankton and degree-days ($^{\circ}\text{C d}$) in the Fort Whyte lakes 2, 3 and 4 in the years 2005 and 2006. For all models $n=6$ (3 lakes x 2 years).

	Regression equation	r^2	$F_{1,4}$	P
Chlorophyll <i>a</i>				
May	$\log_{10}(\text{chl}a) = -1.790 + 0.007DD$	0.851	22.92	0.009
June	$\log_{10}(\text{chl}a) = -2.828 + 0.005DD$	0.806	16.56	0.015
July	$\log_{10}(\text{chl}a) = -3.656 + 0.004DD$	0.834	20.13	0.011
August		0.054	0.23	0.657
Total phytoplankton biovolume				
May	$\log_{10}(\text{biovolume}) = 1.060 + 0.005DD$	0.674	8.25	0.045
June	$\log_{10}(\text{biovolume}) = -0.067 + 0.004DD$	0.818	18.02	0.013
July	$\log_{10}(\text{biovolume}) = -1.506 + 0.004DD$	0.722	10.39	0.032
August		0.357	2.22	0.211
% filamentous cyanobacteria				
May		0.356	2.21	0.211
June		0.443	3.18	0.149
July	$\% \text{cyano} = -356.786 + 0.302DD$	0.956	86.03	<0.001
August	$\% \text{cyano} = -368.749 + 0.227DD$	0.754	12.29	0.025

Table 2. 3. Results of RM-ANOVA testing for differences between 2005 and 2006 monthly means for chemistry (TDN, TDP and TDN:TDP) and water column stability (Schmidt stability index). N = 6. Significant results ($P < 0.05$) are indicated in bold.

	Type I SS	F_1	P
Water chemistry: H_0 = 2005 and 2006 values are the same			
May			
TDN	63413.893	5.06	0.153
TDP	1029.660	0.81	0.463
TDN:TDP	1.130	0.01	0.917
June			
TDN	599294.010	4.36	0.172
TDP	5236.260	16.50	0.056
TDN:TDP	29.119	0.49	0.557
July			
TDN	2360.167	0.12	0.766
TDP	2851.440	3.39	0.207
TDN:TDP	329.727	161.37	0.006
August			
TDN	14504.167	1.16	0.394
TDP	3927.042	5.04	0.154
TDN:TDP	376.887	147.05	0.007
Water-column stability (S, gcm^{-1}): H_0 = 2005 and 2006 values are the same			
May			
Schmidt index	3.542	0.05	0.842
June			
Schmidt index	537.091	8.25	0.103
July			
Schmidt index	2.693	0.01	0.919
August			
Schmidt index	31.289	0.14	0.745

Table 2. 4. Results of simple linear regressions testing for monthly linear relationships between daphniids (individuals L^{-1}) and % filamentous cyanobacteria and % inedible phytoplankton in the Fort Whyte lakes 2, 3 and 4 in the years 2005 and 2006. For all models $n=6$ (3 lakes x 2 years).

	Regression equation	r^2	$F_{1,4}$	P
Model: daphniids = $a + b(\%cyano)$				
May		0.070	0.30	0.611
June	daphniids = $19.745 - 0.475\%cyano$	0.663	7.87	0.049
July	daphniids = $17.332 - 0.188\%cyano$	0.712	9.89	0.035
August		0.351	2.17	0.215

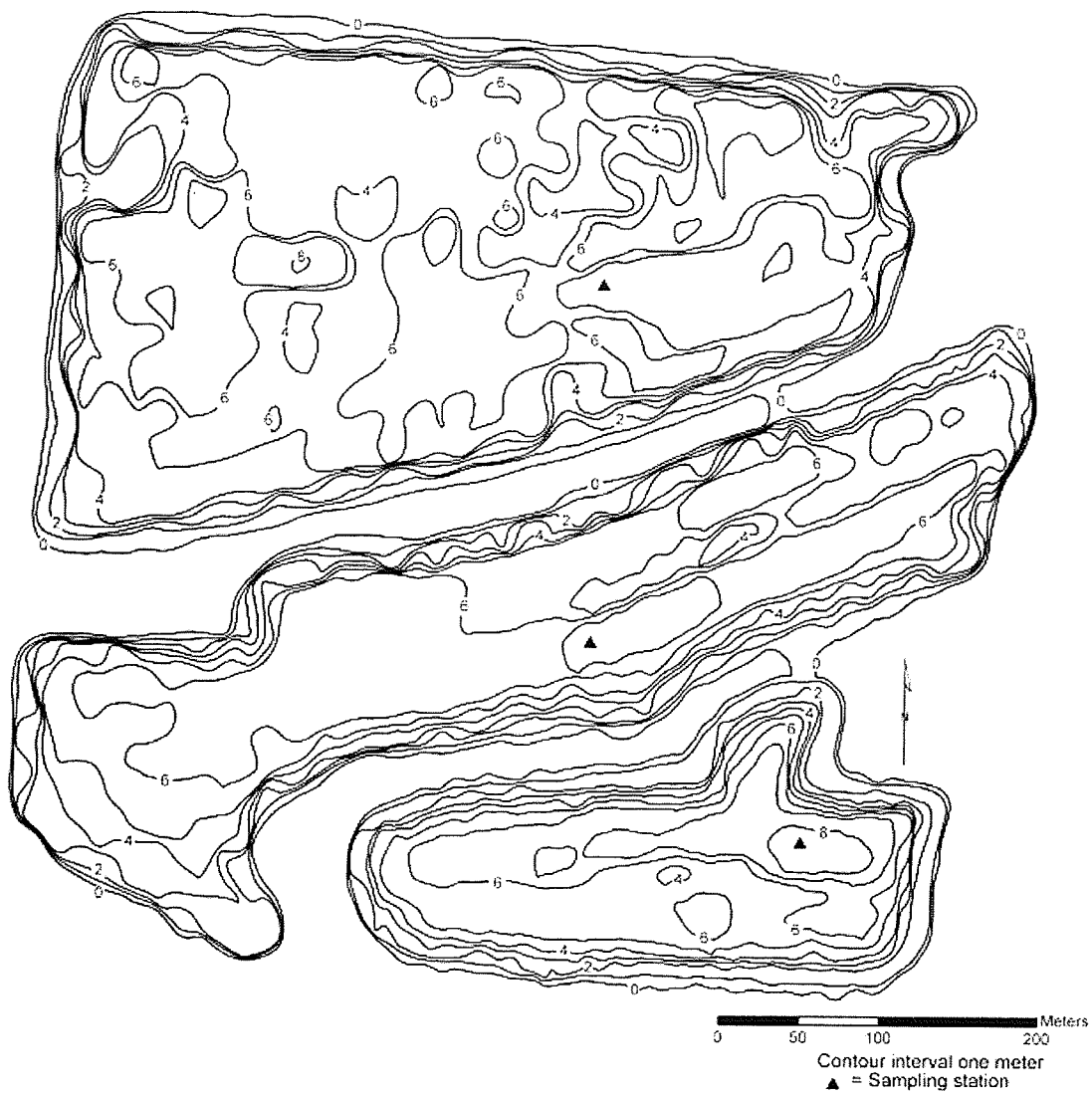


Figure 2. 1. Bathymetric map of the Fort Whyte lakes 2, 3 and 4 in Winnipeg, MB.

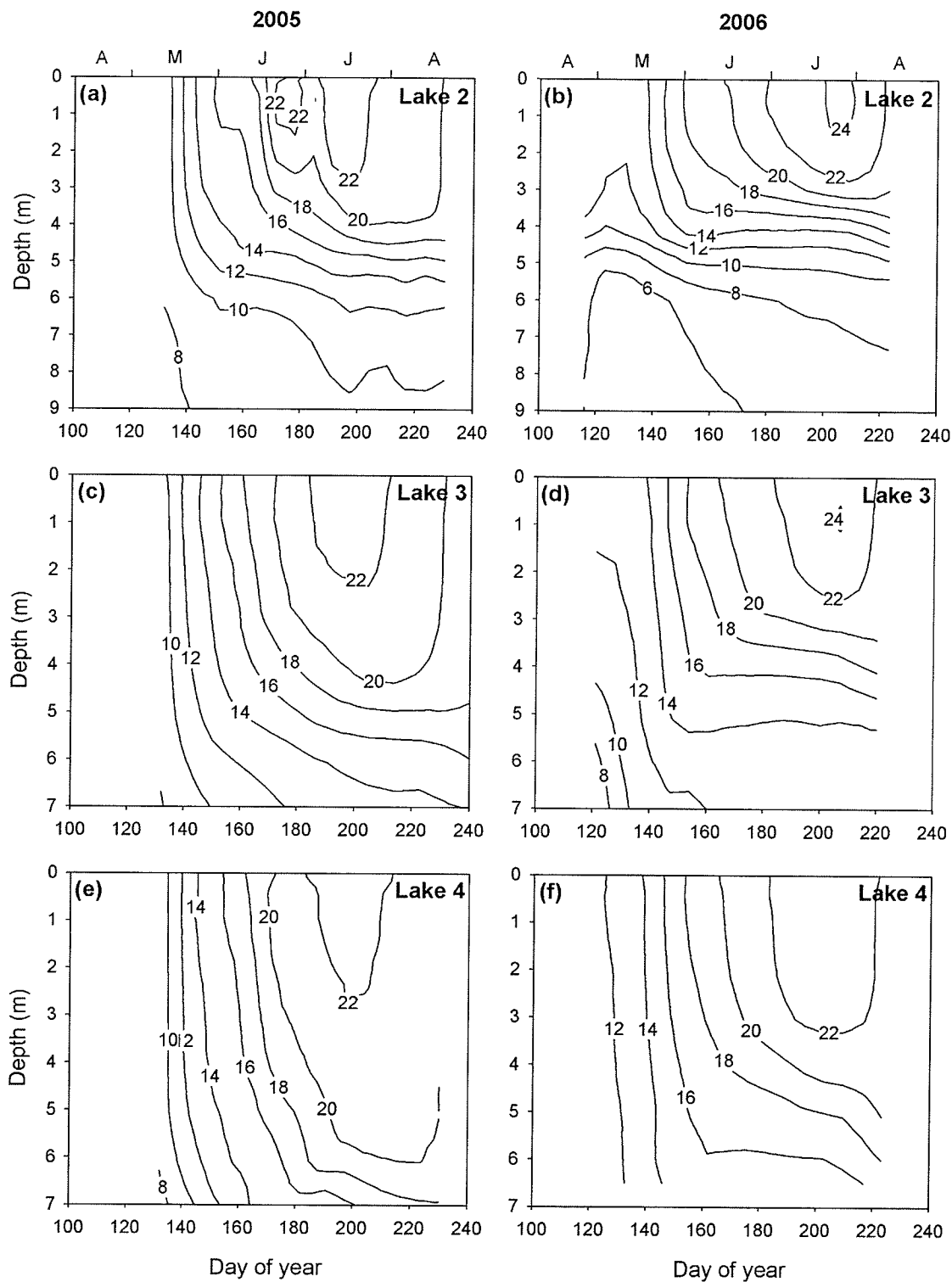


Figure 2. 2. Contour plots of temperature profiles ($^{\circ}\text{C}$) from May to Mid-August at the Fort Whyte lakes 2 (a, b), 3 (c, d) and 4 (e, f) during the years 2005 and 2006.

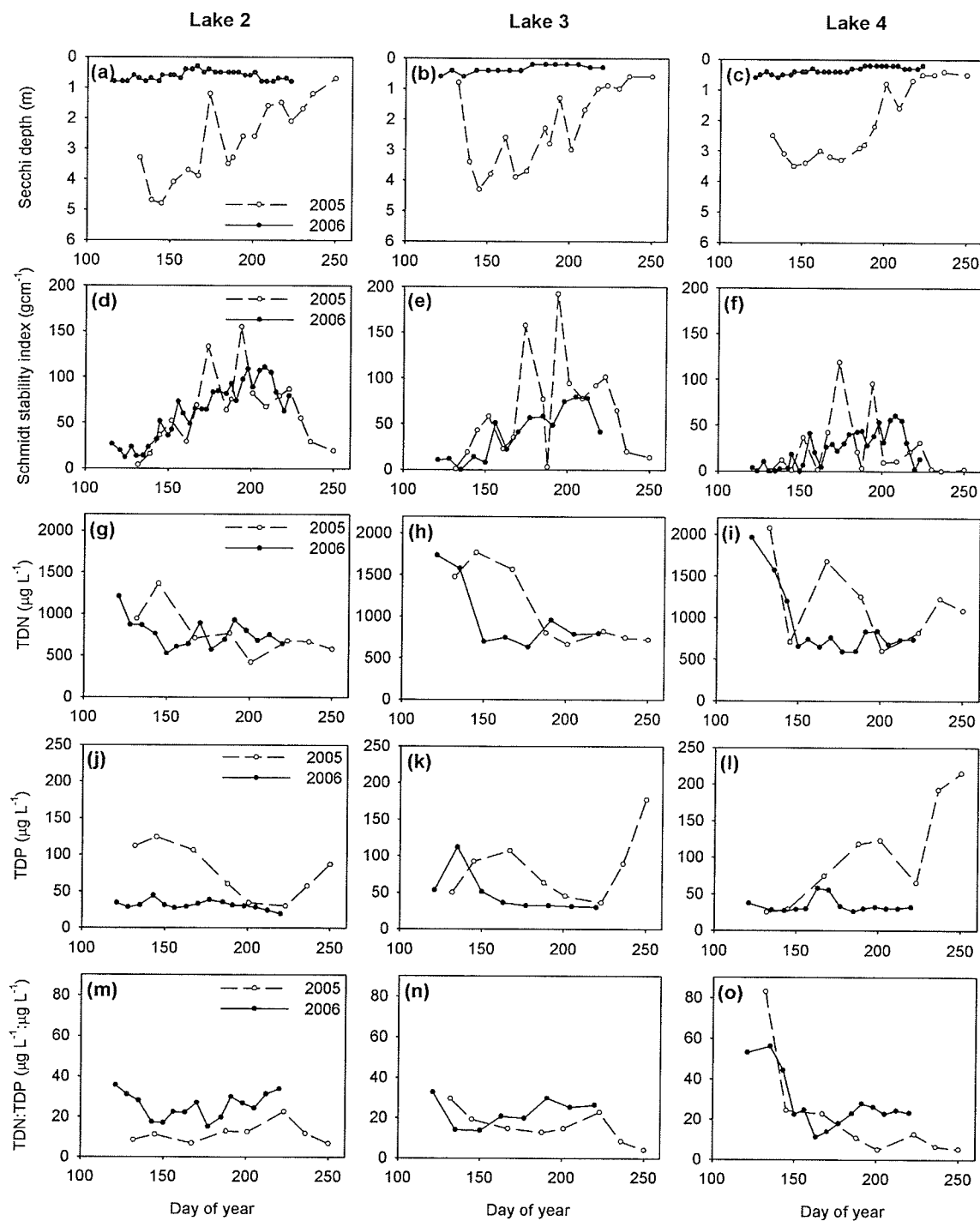


Figure 2. 3. Two-year comparison (2005 and 2006) of physico-chemical dynamics from May to August in Lakes 2, 3 and 4.

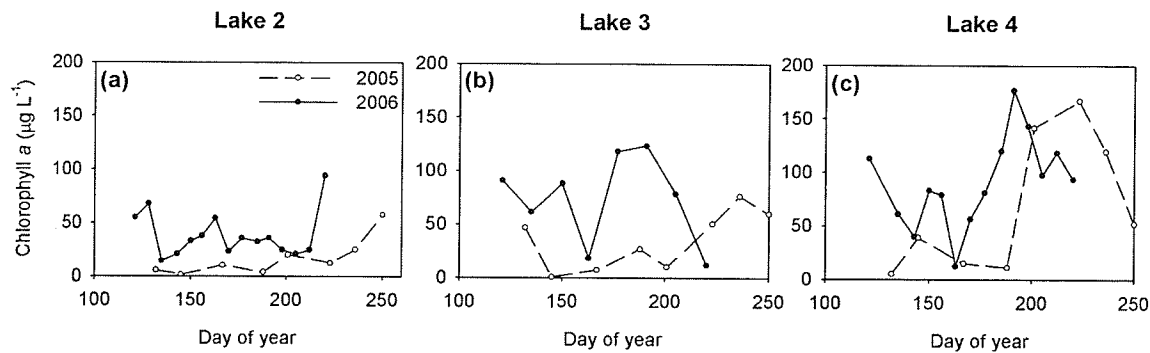


Figure 2. 4. Two-year comparison (2005 and 2006) of chlorophyll *a* ($\mu\text{g L}^{-1}$) dynamics from May to August in Lakes 2, 3 and 4.

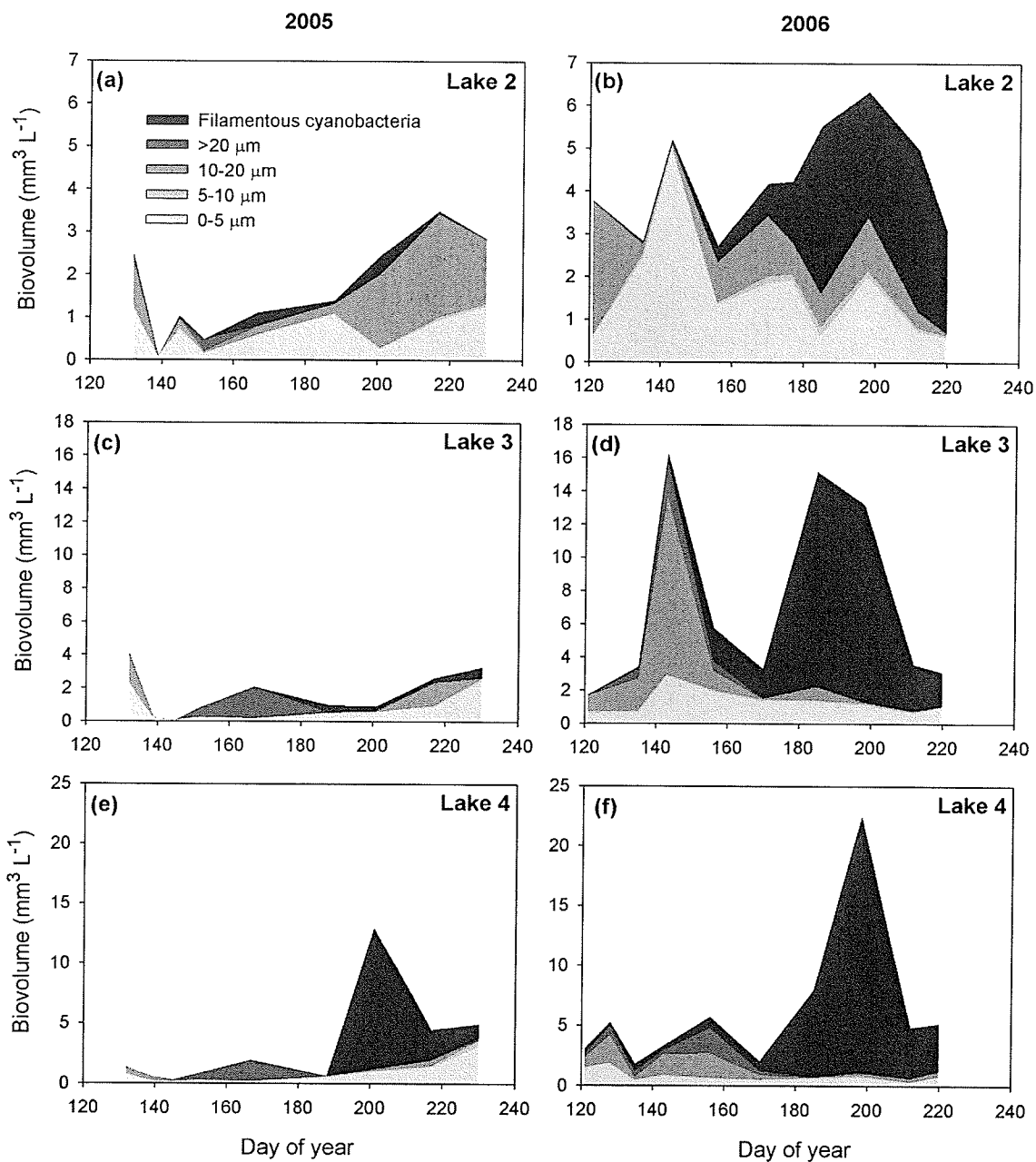


Figure 2. 5. Two-year (2005 and 2006) comparison of phytoplankton biovolume estimates (mm³ L⁻¹) from May to August in Lakes 2, 3 and 4. Phytoplankton are classified by cell size except for filamentous cyanobacteria.

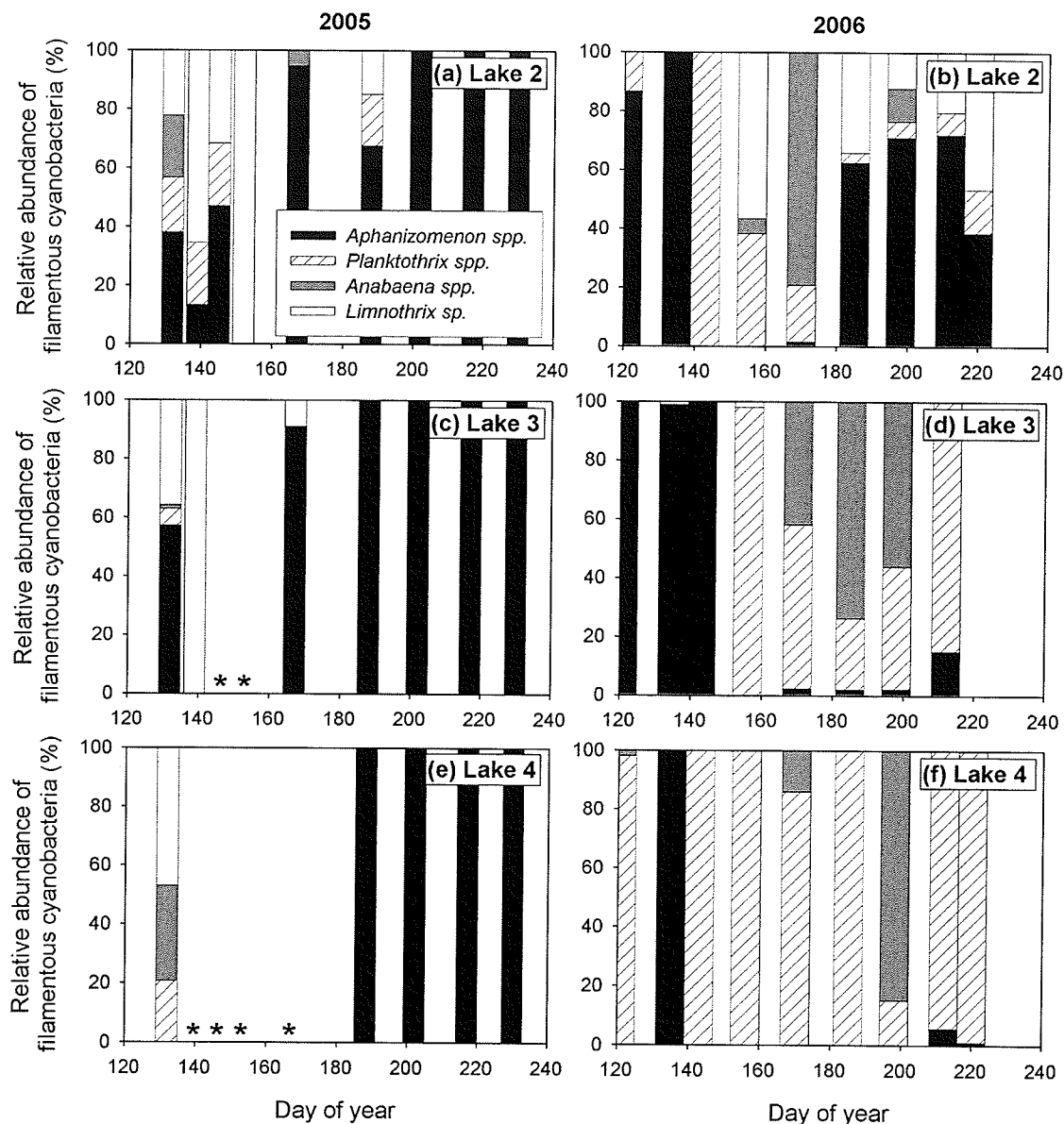


Figure 2. 6. Two-year (2005 and 2006) comparison of relative abundances of dominant filamentous cyanobacteria genus (*Aphanizomenon* spp., *Planktothrix* spp., *Anabaena* spp. and *Limnathrix* sp.) from biovolume estimate from May to August in Lakes 2, 3 and 4. A star indicates no filamentous cyanobacteria in sample.

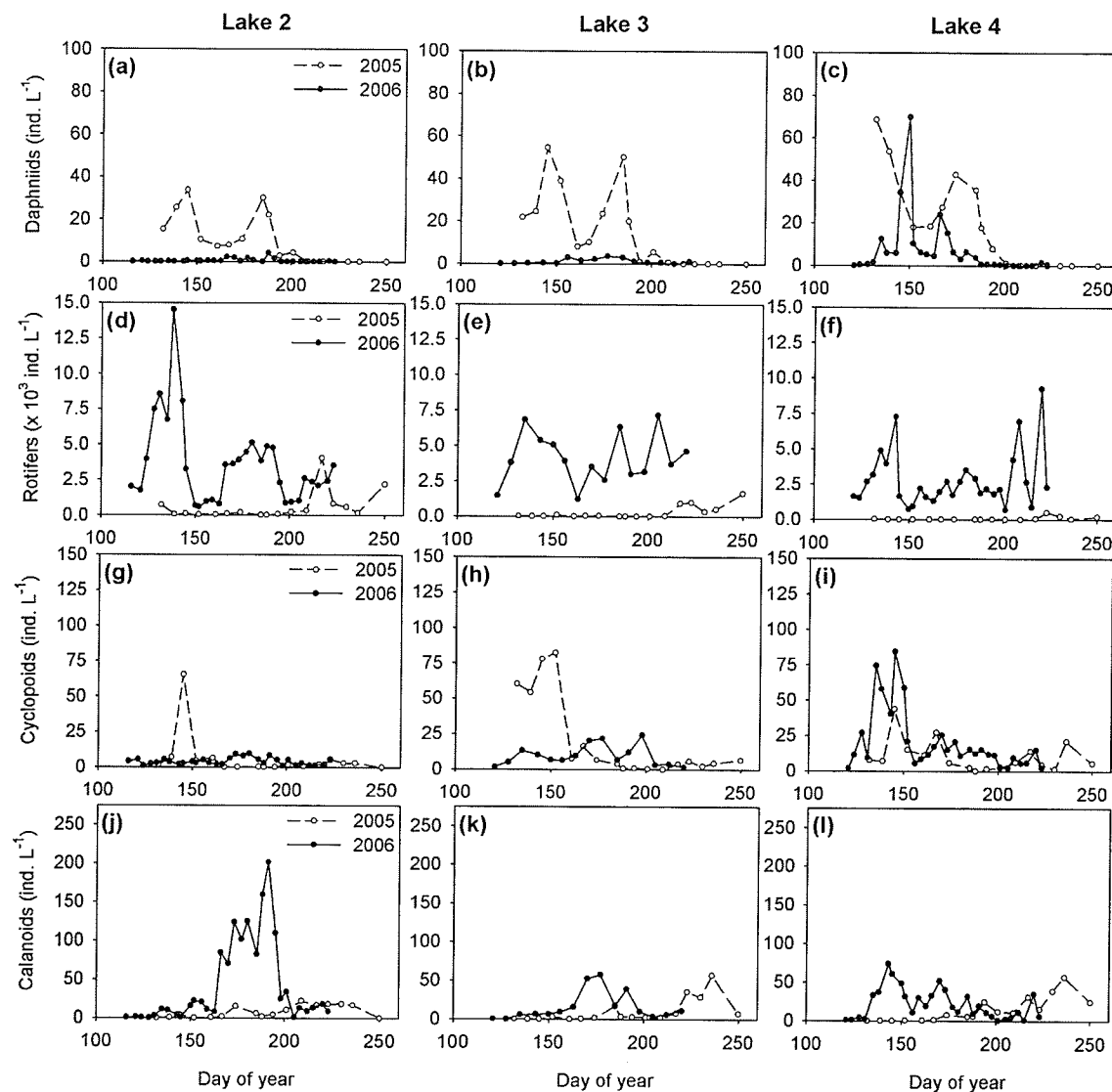


Figure 2. 7. Two-year comparison (2005 and 2006) of mean zooplankton population dynamics from May to August in Lakes 2, 3 and 4.

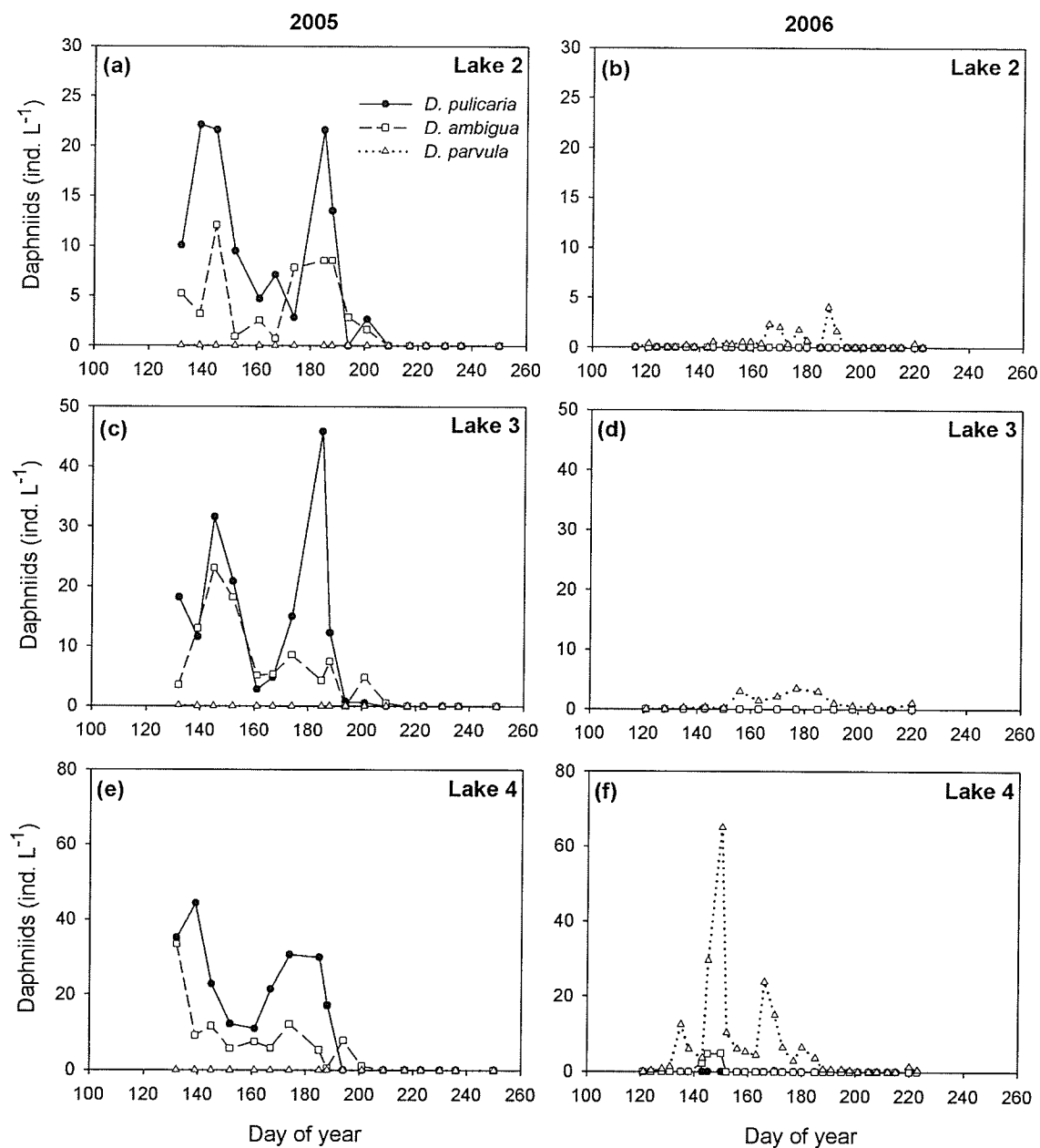


Figure 2. 8. Two-year (2005 and 2006) comparison of mean *Daphnia pulicaria*, *D. ambigua* and *D. parvula* population dynamics from May to August in Lakes 2, 3 and 4.

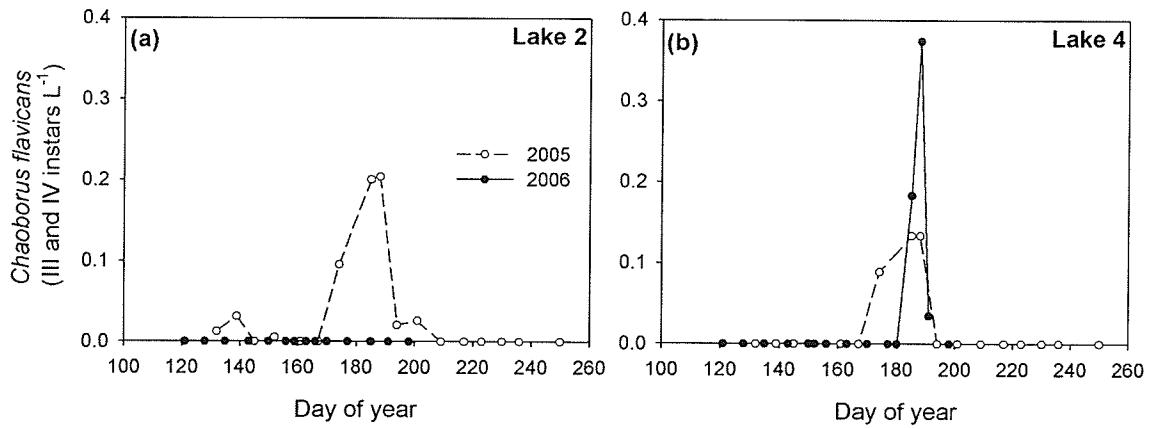


Figure 2. 9. *Chaoborus flavicans* (III and IV instars L^{-1}) population dynamics for Lakes 2 and 4 in 2005 and 2006 as estimated from daytime collections of the epilimnion.

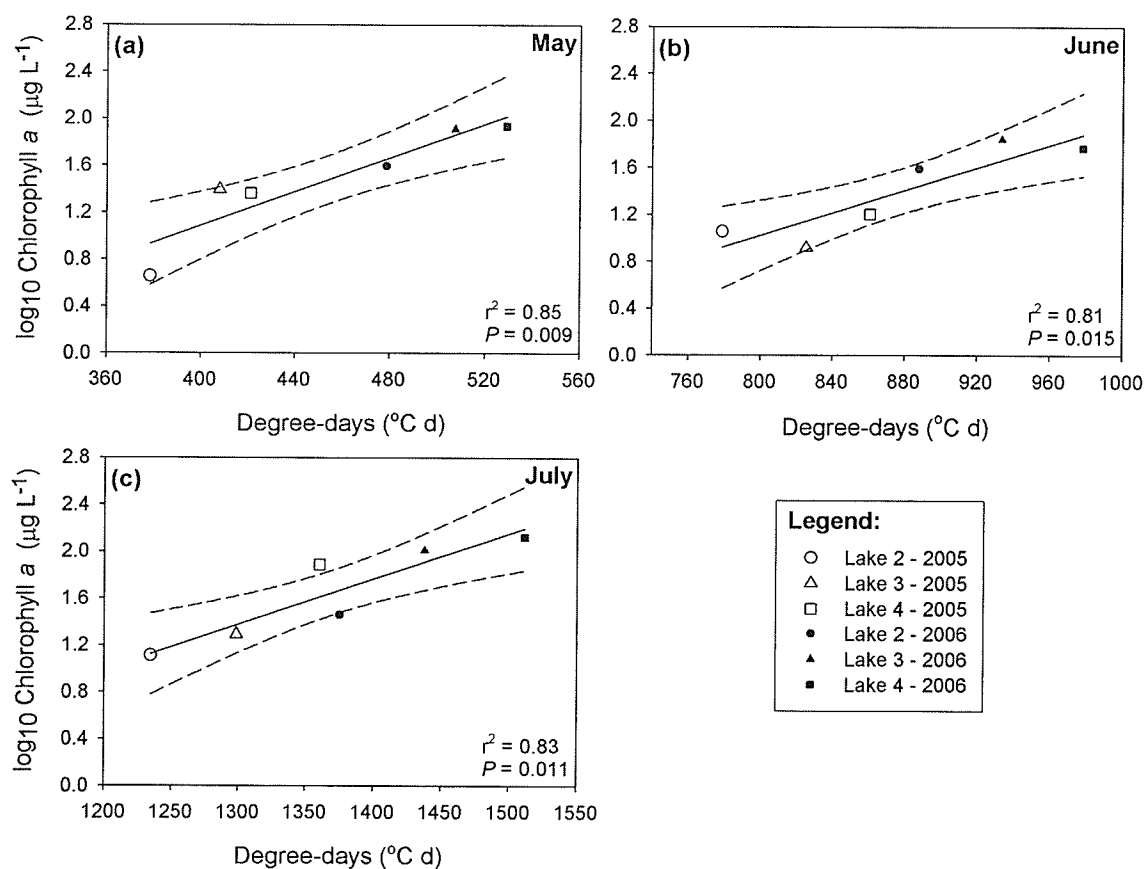


Figure 2. 10. Monthly relationships between degree-days ($^{\circ}\text{C d}$) and phytoplankton biomass estimated as chlorophyll *a* ($\mu\text{g L}^{-1}$) for May (a), June (b) and July (c) with the 95% confidence interval (dashed lines).

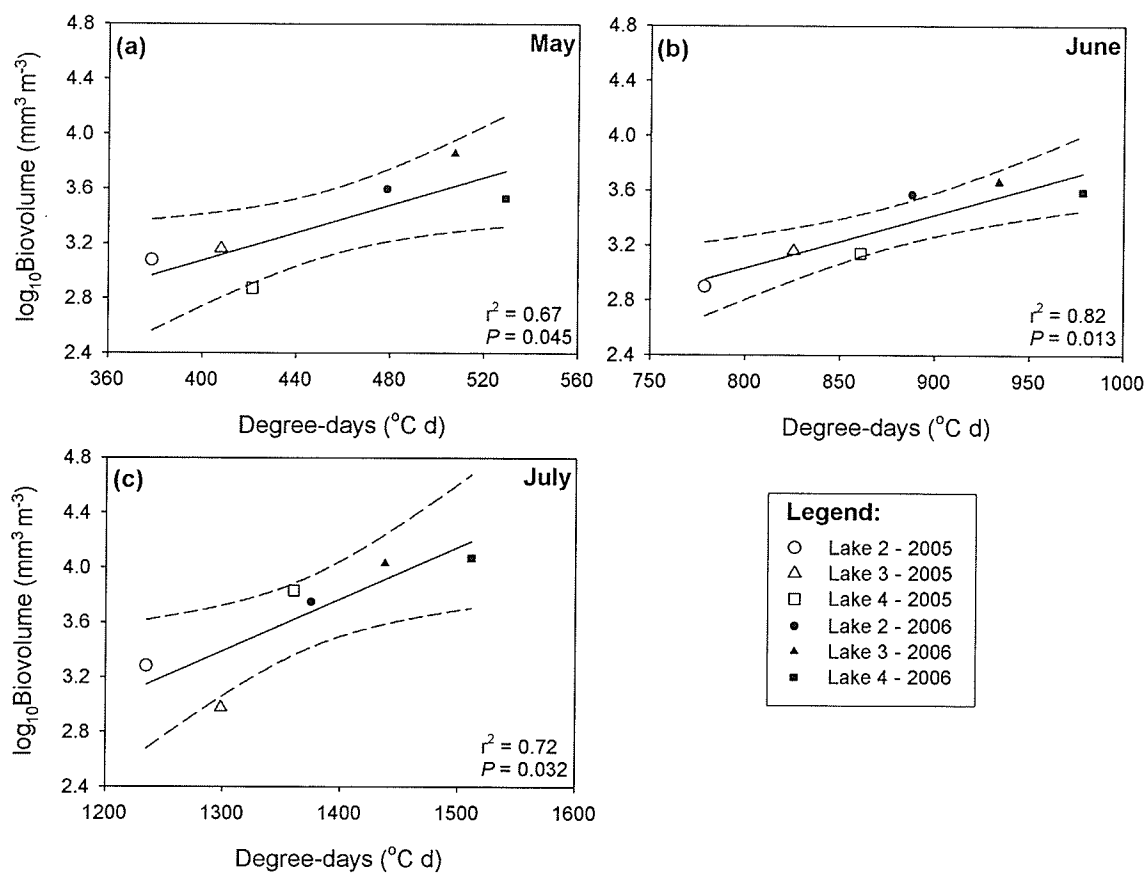


Figure 2. 11. Monthly relationships between degree-days ($^{\circ}\text{C d}$) and phytoplankton biomass estimated as biovolume ($\text{mm}^3 \text{m}^{-3}$) for May (a), June (b) and July (c) with the 95% confidence interval (dashed lines).

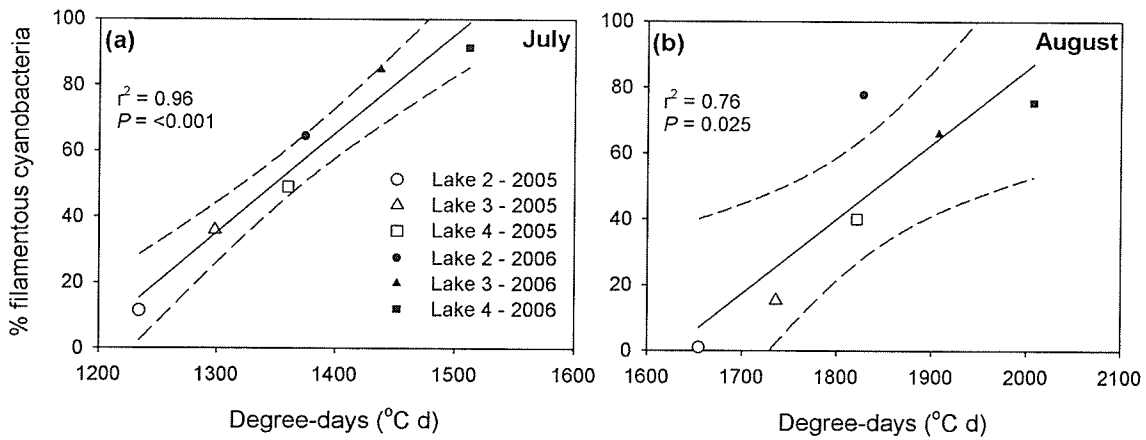


Figure 2. 12. Monthly relationships between degree-days (°C d) and % filamentous cyanobacteria for July (a) and August (b) with the 95% confidence interval (dashed lines).

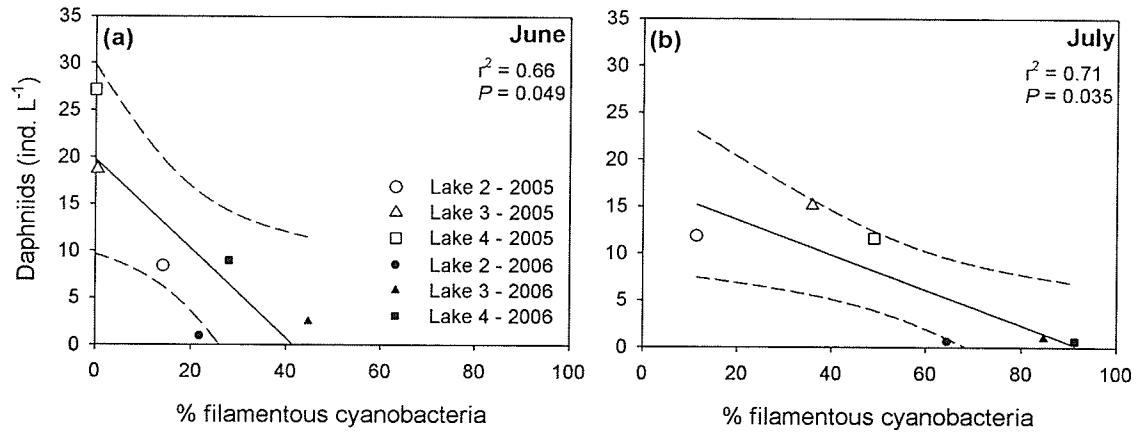


Figure 2. 13. Monthly relationships between % filamentous cyanobacteria and daphniid abundance (ind. L⁻¹) for June (a) and July (b) with the 95% confidence interval (dashed lines).

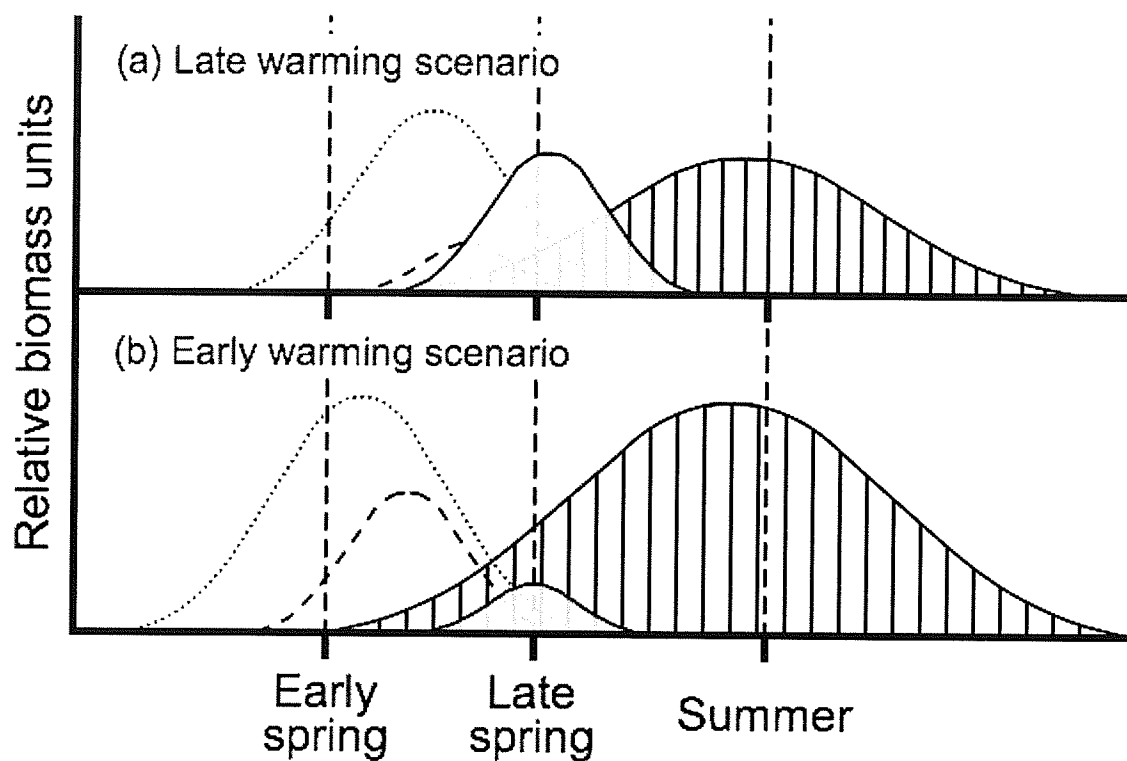


Figure 2. 14. Conceptual model describing plankton population dynamics in a small eutrophic lake during two scenarios, (a) late warming and (b) an early warming. Edible algae (dotted line), filamentous cyanobacteria (vertical lines), rotifers (dashed lines) and daphniids (solid line, transparent white filling) are presented during early spring, late spring and summer. See discussion for further explanations.

Literature cited

- Adrian, R. and R. Deneke. 1996. Possible impact of mild winters on zooplankton succession in eutrophic lakes of the Atlantic European area. *Freshw. Biol.* 36: 757-770.
- Adrian, R., N. Walz, T. Hintze, S. Hoeg and R. Rusche. 1999. Effects of ice duration on plankton succession during spring in a shallow polymictic lake. *Freshw. Biol.* 41: 621-632.
- Agasild, H., P. Zingel, I. Tonno, J. Haberman and T. Noges. 2007. Contribution of different zooplankton groups in grazing on phytoplankton in shallow eutrophic Lake Võrtsjärv (Estonia). *Hydrobiologia* 584: 167-177.
- Arhonditsis, G. B., M. T. Brett, C. L. DeGasperi and D. E. Schindler. 2004. Effects of climatic variability on the thermal properties of Lake Washington. *Limnol. Oceanogr.* 49: 256-270.
- Benndorf, J., J. Kranich, T. Mehner and A. Wagner. 2001. Temperature impact on the midsummer decline of *Daphnia galeata*: an analysis of long-term data from the biomanipulated Bautzen Reservoir (Germany). *Freshw. Biol.* 46: 199-211.
- Blom, J. F., J. A. Robinson and F. Jüttner. 2001. High grazer toxicity of [D-Asp³, (E)-Dhb⁷] microcystin-RR of *Planktothrix rubescens* as compared to different microcystins. *Toxicon* 39: 1923-1932.
- Cáceres, C. E. 1998. Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology* 79: 1699-1710.
- Cáceres, C.E. and M.S. Schwalbach. 2001. How well do laboratory experiments explain field patterns of zooplankton emergence? *Freshw. Biol.* 46: 1179-1189.

- Carpenter, S. R., S. G. Fisher, N. B. Grimm, J. F. Kitchell. 1992. Global change and freshwater ecosystems. *Ann. Rev. Ecol. Syst.* 23: 119-139.
- Chengalath, R., C. H. Fernando and M. G. George. 1971. The planktonic rotifera of Ontario with keys to genera and species. University of Waterloo, Biological Series, No. 2.
- Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. *Trends Ecol. Evol.* 22: 357-365.
- De Senerpont Domis, L. N., W. M. Mooij and J. Huisman. 2007a. Climate-induced shifts in an experimental phytoplankton community: a mechanistic approach. *Hydrobiologia* 584: 403-413.
- De Senerpont Domis, L. N., W. M. Mooij, S. Hülsmann, E. H. Van Nes and M. Scheffer. 2007b. Can overwintering versus diapausing strategy in *Daphnia* determine match-mismatch events in zooplankton-algae interactions? *Oecologia* 150: 682-698.
- DeMott, W. R. 1999. Foraging strategies and growth inhibition in five daphnids feeding on mixtures of a toxic cyanobacterium and a green alga. *Freshw. Biol.* 42: 263-274.
- DeMott, W. R., R. D. Gulati and E. Van Donk. 2001. *Daphnia* food limitation in three hypereutrophic Dutch lakes: Evidence for exclusion of large-bodied species by interfering filaments of cyanobacteria. *Limnol. Oceanogr.* 46: 2054-2060.
- DeStasio, B. T., D. K. Hill, J. M. Kleinhans, N. P. Nibbelink and J. J. Magnuson. 1996. Potential effects of global climate change on small north-temperate lakes: Physics, fish, and plankton. *Limnol. Oceanogr.* 41: 1136-1149.

- Dokulil, M. T., A. Jagsch, G. D. George, O. Anneville, T. Jankowski, B. Wahl, B. Lenhart, T. Blenckner and K. Teubner. 2006. Twenty years of spatially coherent deepwater warming in lakes across Europe related to the North Atlantic Oscillation. *Limnol. Oceanogr.* 51: 2787-2793.
- Downing, J. A., S. B. Watson and E. McCauley. 2001. Predicting cyanobacteria dominance in lakes. *Can. J. Fish. Aquat. Sci.* 58: 1905-1908.
- Downing, J. A., Y. T. Prairie, J. J. Cole, C. M. Duarte, L. J. Tranvik, R. G. Striegl, W. H. McDowell, P. Kortelainen, N. F. Caraco, J. M. Melack, J. J. Middelburg. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* 51: 2388-2397.
- Edwards, M. and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430: 881- 884.
- Epp, G. T. 1996. Grazing on filamentous cyanobacteria by *Daphnia pulicaria*. *Limnol. Oceanogr.* 41: 560-567.
- Findlay, D. L. and H. J. Kling. 1979. A species list and pictorial reference to the phytoplankton of central and northern Canada. Fish. Mar. Serv. Manuscr. Rep. Can. No. 1503.
- Foy, R. H., C. E. Gibson and R. V. Smith. 1976. The influence of daylength, light intensity and temperature on the growth rates of planktonic blue-green algae. *Br. Phycol. J.* 11: 151-163.
- Foy, R. H. and C. E. Gibson. 1982. Photosynthetic characteristics of planktonic blue-green algae: The response of twenty strains grown under high and low light. *Br. Phycol. J.* 17: 169-182.

- Frazer, L. V. 2006. The importance of pelagic zooplankton-phytoplankton interactions in determining the length of the clear-water phase in shallow prairie lakes. Honours Thesis, University of Manitoba, Winnipeg, MB.
- Fulton III, R. S. and H. W. Paerl. 1987. Effects of colonial morphology on zooplankton utilization of algal resources during blue-green algal (*Microcystis aeruginosa*) blooms. *Limnol. Oceanogr.* 32: 634-644.
- George, D. G. and A. H. Taylor. 1995. UK lake plankton and the Gulf Stream. *Nature* 378: 139.
- George, D. G. and D. P. Hewitt. 2006. The impact of year-to-year changes in the weather on the dynamics of *Daphnia* in a thermally stratified lake. *Aquat. Ecol.* 40: 33-47.
- Gerten, D. and R. Adrian. 2000. Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. *Limnol. Oceanogr.* 45: 1058-1066.
- Ghadouani, A., B. Pinel-Alloul and E. E. Prepas. 2003. Effects of experimentally induced cyanobacterial blooms on crustacean zooplankton communities. *Freshw. Biol.* 48: 363-381.
- Gibson, C. E. 1985. Growth rate, maintenance energy and pigmentation of planktonic cyanophyta during one-hour light:dark cycles. *Br. Phycol. J.* 20: 155-161.
- Gilbert, J. J. 1990. Differential effects of *Anabaena affinis* on cladocerans and rotifers: Mechanisms and implications. *Ecology* 71: 1727-1740.
- Gliwicz, Z. M. 1990. Why do cladocerans fail to control algal blooms? *Hydrobiologia* 200/201: 83-97.

- Gliwicz, Z. M. and W. Lampert. 1990. Food thresholds in *Daphnia* species in the absence and presence of blue-green filaments. *Ecology* 71: 691-702.
- Gyllström, M. and L-A. Hansson. 2004. Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. *Aquat. Sci.* 66: 274-295.
- Hairston, N. G., C. L. Holtmeier, W. Lampert, L. J. Weider, D. M. Post, J. M. Fischer, C. E. Cáceres, J. A. Fox and U. Gaedke. 2001. Natural selection for grazer resistance to toxic cyanobacteria: Evolution of phenotypic plasticity? *Evolution* 55: 2203-2214.
- Hampton, S. E., P. Romare and D. E. Seiler. 2006. Environmentally controlled *Daphnia* spring increase with implications for sockeye salmon fry in Lake Washington, USA. *J. Plankton Res.* 28: 399-406.
- Hansson, L-A., A. Nicolle, J. Brodersen, P. Romare, P. A. Nilsson, C. Brönmark and C. Skov. 2007. Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. *Limnol. Oceanogr.* 52: 696-706.
- Hargeby, A., I. Blindow and L-A. Hansson. 2004. Shifts between clear and turbid states in a shallow lake: multi-causal stress from climate, nutrients and biotic interactions. *Arch. Hydrobiol.* 161: 433-454.
- Hebert, P.D.N. 1995. The *Daphnia* of North America: An Illustrated Fauna. C.D.
- Holm, N. P., G. G. Ganf and J. Shapiro. 1983. Feeding and assimilation rates of *Daphnia pulex* fed *Aphanizomenon flos-aquae*. *Limnol. Oceanogr.* 28: 677-687.
- Jankowski, T., D. M. Livingstone, H. Bührer, R. Forster and P. Niederhauser. 2006. Consequences of the 2003 European heat wave for lake temperature profiles,

thermal stability, and hypolimnetic oxygen depletion: Implications for a warmer world. *Limnol. Oceanogr.* 51: 815-819.

Jeppesen, E., M. Sondergaard and J. P. Jensen. 2003. Climatic warming and regime shifts in lake food webs – some comments. *Limnol. Oceanogr.* 48: 1346-1349.

Kjellman, J., J. Lappalainen, L. Urho and R. Hudd. 2003. Early determination of perch and pikeperch recruitment in the northern Baltic Sea. *Hydrobiologia* 495: 181-191.

Kurmayer, R. and F. Jüttner. 1999. Strategies for the co-existence of zooplankton with the toxic cyanobacterium *Planktothrix rubescens* in Lake Zürich. *J. Plankton Res.* 21: 659-683.

Lampert, W., W. Fleckner, H. Rai and B. E. Taylor. 1986. Phytoplankton control by grazing zooplankton: A study on the spring clear-water phase. *Limnol. Oceanogr.* 31: 478-490.

Loadman, N.L. 1980. A comparison of the crustacean zooplankton populations of four man-made lakes in southern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, MB.

Lynch, M. 1979. Predation, competition, and zooplankton community structure: An experimental study. *Limnol. Oceanogr.* 24: 253-272.

MacIsaac, H. J. and J. J. Gilbert. 1991. Discrimination between exploitative and interference competition between cladocera and *Keratella cochlearis*. *Ecology* 72: 924-937.

Magnuson, J. J., B. J. Benson and T. K. Kratz. 1990. Temporal coherence in the limnology of a suite of lakes in Wisconsin, U.S.A. *Freshw. Biol.* 23: 145-159.

- McKee, D., D. Atkinson, S. E. Collings, J. W. Eaton, A. B. Gill, I. Harvey, K. Hatton, T. Heyes, D. Wilson and B. Moss. 2003. Response of freshwater microcosm communities to nutrients, fish, and elevated temperature during winter and summer. *Limnol. Oceanogr.* 48: 707-722.
- Meehl, G.A., F. Zwiers, J. Evans, T. Knutson, L. Mearns and P. Whetton. 2000. Trends in extreme weather and climate events: issues related to modeling extremes in projections of future climate change. *Bul. Am. Meteor. Soc.* 81: 427-436.
- Mehner, T. and R. Thiel. 1999. A review of predation impact by 0+ fish on zooplankton in fresh and brackish waters of the temperate northern hemisphere. *Environ. Biol. Fish.* 56: 169-181.
- Mooij, W. M., S. Hülsmann, L. N. De Senerpont Domis, B. A. Nolet, P. L. E. Bodelier, P. C. M. Boers, L. Miguel Dionisio Pires, H. J. Gons, B. W. Ibelings, R. Noordhuis, R. Portielje, K. Wolfstein and E. H. R. R. Lammens. 2005. The impact of climate change on lakes in the Netherlands: a review. *Aquat. Ecol.* 39: 381-400.
- Neuheimer, A.B. and C.T. Taggart. 2007. The growing degree-day and fish size-at-age: the overlooked metric. *Can. J. Fish. Aquat. Sci.* 64: 375-385.
- Oberhaus, L., M. Gélinas, B. Pinel-Alloul, A. Ghadouani and J-F. Humbert. 2007. Grazing of two toxic *Planktothrix* species by *Daphnia pulicaria*: potential for bloom control and transfer of microcystins. *J. Plankton Res.* 29: 827-838.
- Pennak, R.W. 1989. Fresh-water invertebrates of the United States: Protozoa to Mollusca. 3rd ed. John Wiley & Sons Inc, New York, USA.

- Porter, K. G. and J. D. Orcutt. 1980. Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of green and blue-green algae for *Daphnia*., p. 268-281. In W. C. Kerfoot [ed.], Evolution and ecology of zooplankton communities. University Press of New England, London, UK.
- Reynolds, C. S. and A. E. Walsby. 1975. Water blooms. Biol. Rev. 50: 437-481.
- Rhee, G-Y. and I. J. Gotham. 1981. The effects of environmental factors on phytoplankton growth: Temperature and the interactions of temperature with nutrient limitation. Limnol. Oceanogr. 26: 635-648.
- Robarts, R. D. and T. Zohary. 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. N. Z. J. Mar. Freshw. Res. 21: 391-399.
- Robertson, D. M. and J. Imberger. 1994. Lake number, a quantitative indicator of mixing used to estimate changes in dissolved oxygen. Int. Rev. ges. Hydrobiol. 79: 159-176.
- Rott, E. 1981. Some results from phytoplankton counting intercalibrations. Schweiz. Z. Hydrol. 43: 34-62.
- Rudstam, L. G., R. C. Lathrop and S. R. Carpenter. 1993. The rise and fall of a dominant planktivore: Direct and indirect effects on zooplankton. Ecology 74: 303-319.
- Sano, T. and K. Kaya. 1998. Two new (E)-2-amino-2-butenic acid (Dhb)-containing microcystins isolated from *Oscillatoria agardhii*. Tetrahedron 54: 463-470.
- Sarnelle, O. and A. E. Wilson. 2005. Local adaptation of *Daphnia pulex* to toxic cyanobacteria. Limnol Oceanogr. 50: 1565-1570.

- Scheffer, M., S. H. Hosper, M-L. Meijer, B. Moss and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8: 275-279.
- Scheffer, M., D. Straile, E.H. van Nes and H. Hosper. 2001. Climatic warming causes regime shifts in lake food webs. *Limnol. Oceanogr.* 46: 1780-1783.
- Scheffer, M., D. Straile, E. H. van Nes and H. Hosper. 2003. Climatic effects on regime shifts in lakes: A reply. *Limnol. Oceanogr.* 48: 1353-1356.
- Scheuerell, M. D., D. E. Schindler, A. H. Litt and W. T. Edmondson. 2002. Environmental and algal forcing of *Daphnia* production dynamics. *Limnol. Oceanogr.* 47: 1477-1485.
- Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. *Science* 195: 260-262.
- Schindler, D. W., K. G. Beaty, E. J. Fee, D. R. Cruikshank, E. R. DeBruyn, D. L. Findlay, G. A. Linsey, J. A. Shearer, M. P. Stainton and M. A. Turner. 1990. Effects of climatic warming on lakes of the central boreal forest. *Science* 250: 967-970.
- Smith, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221: 669-671.
- Sommer, U., Z. M. Gliwicz, W. Lampert and A. Duncan. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* 106: 433-471.
- Stainton, M. P., M. J. Capel and F. A. J. Armstrong. 1977. The chemical analysis of fresh water. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. No. 25.

- Straile, D. 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. *Oecologia* 122: 44-50.
- Straile, D. 2002. North Atlantic Oscillation synchronizes food-web interactions in central European lakes. *Proc. R. Soc. Lond. B* 269: 391-395.
- Tebaldi, C., K. Hayhoe, J. M. Arblaster and G. A. Meehl. 2006. Going to the extremes: An intercomparison of model-simulated historical and future changes in extreme events. *Climate Change* 79: 185-211.
- Tirok, K. and U. Gaedke. 2006. Spring weather determines the relative importance of ciliates, rotifers and crustaceans for the initiation of the clear-water phase in a large, deep lake. *J. Plankton Res.* 28: 361-373.
- Torti, V. M. and P. O. Dunn. 2005. Variable effects of climate change on six species of North American birds. *Oecologia* 145: 486-495.
- Van Donk, E., L. Santamaria and W. M. Mooij. 2003. Climate warming causes regime shifts in lake food webs: A reassessment. *Limnol. Oceanogr.* 48: 1350-1353.
- Wagner, A. and J. Benndorf. 2007. Climate-driven warming during spring destabilises a *Daphnia* population: a mechanistic food web approach. *Oecologia* 151: 1432-1939.
- Webster, K. E. and R. H. Peters. 1978. Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. *Limnol. Oceanogr.* 23: 1238-1245.
- Weyhenmeyer, G.A., T. Blenckner and K. Pettersson. 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. *Limnol. Oceanogr.* 44: 1788-1792.

- Wilson, A. E. and M. E. Hay. 2007. A direct test of cyanobacterial chemical defense: Variable effects of microcystin-treated food on two *Daphnia pulicaria* clones. *Limnol. Oceanogr.* 52: 1467-1479.
- Wilson, A. E., O. Sarnelle and A. R. Tillmanns. 2006. Effects of cyanobacterial toxicity and morphology on the population growth of freshwater zooplankton: Meta-analyses of laboratory experiments. *Limnol. Oceanogr.* 51: 1915-1924.
- Winder, M. and D.E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85: 2100-2106.
- Zhang, Y. and E. E. Prepas. 1996. Regulation of the dominance of planktonic diatoms and cyanobacteria in four eutrophic hardwater lakes by nutrients, water column stability, and temperature. *Can. J. Fish. Aquat. Sci.* 53: 621-633.

**Chapter 3: Effects of an earlier spring on daphniid and rotifer emergence and
population development.**

Introduction

In north-temperate regions, there are current and projected increases in ambient air temperature and extreme weather events such as hot days, heat waves, and heavy precipitation events (Christensen et al. 2007). Biological effects of climate change have already been documented in several ecosystems (Walther et al. 2002). In particular, climate variations may result in alterations in trophic-level interactions. In some cases, climate change has led to decreasing matching between predator and prey populations including in bird-insect (Thomas et al. 2001), fish-daphniid (Hampton et al. 2006) and zooplankton-phytoplankton (Edwards and Richardson 2004; Winder and Schindler 2004) systems. These mismatches can sometimes occur when predator and prey respond differently to climate variations. Furthermore, climate change research suggests that in northern parts of North America, warming will continue to be greatest during winter months (Christensen et al. 2007). More research is needed to understand implications of climate change during early parts of the year. This is particularly important as in north-temperate regions most organisms have reproductive cycles tightly coupled to spring conditions. In lakes, several authors have linked spring weather variations to changes in plankton population dynamics (Tirok and Gaedke 2006). Less is known about how spring weather variations might influence benthic-pelagic linkages, such as colonization of the water-column by zooplankton emerging from resting eggs in the sediments.

In many lakes, spring development of zooplankton populations can strongly depend on emerging individuals from the egg-bank. Dormancy in zooplankton is an important life-strategy to avoid poor conditions such as cool temperatures and low food quantity during ice-covered conditions (Gyllström and Hansson 2004). Inter-annually, the

importance of a dormancy life-strategy can also fluctuate, becoming increasingly critical in years with low abundances of over-wintering adult zooplankton (Cáceres 1998).

Dormancy in cladocerans and rotifers is accomplished by resting eggs buried in the sediments. In north-temperate lakes, cues in spring trigger emergence of most species of daphniids and rotifers (Wolf and Carvalho 1989; Cáceres 1998; Hairston et al. 2000; Gyllström 2004). It is unclear how climate variations during this key period of time could affect patterns of zooplankton emergence.

Climate change could have important consequences for zooplankton populations by affecting environmental cues triggering spring dormancy termination. In general, seasonal cues most important for zooplankton dormancy termination are temperature and photoperiod (Gyllström and Hansson 2004). This would be especially critical for some zooplankton species/populations that rely on both temperature and photoperiod cues to trigger dormancy control (e.g., *Daphnia pulex*, Stross 1971; *Diaptomus sanguineus*, Hairston and Kearns 1995). In fact, some temporal mismatches in synchronization between zooplankton and phytoplankton populations in spring have been attributed to variations in temperature and photoperiod cues (Edwards and Richardson 2004; Winder and Schindler 2004). In Lake Washington, Winder and Schindler (2004) suggested that daphniids and diatoms might respond to separate seasonal cues. Thus, earlier spring warming over the past 30 years was linked to an earlier diatom bloom while timing of the daphniid spring peak remained relatively unchanging, responding more strongly to a photoperiod cue. Recently, however, further studies on Lake Washington suggested that over-wintering survivorship and species-level differences in life-history strategies also contributes to the timing and abundance of daphniids in the spring (Hampton et al. 2006).

Impacts of climate change will likely depend on the strength of the benthic-pelagic link in terms of population development in spring. In most cases, the abundance of over-wintering zooplankton will determine the importance of emerging individuals. Recently, an analysis of daphniid life-history strategies in European lakes showed that lake depth was the most important factor in determining the presence of over-wintering populations (De Senerpont Domis et al. 2007). These authors showed that *Daphnia* adopted a diapausing life-strategy in shallower lakes and suggested that shallow depth affected populations by decreasing available refuge. Regional climate is probably another important factor affecting the probability of over-wintering zooplankton. At similar latitudes, European and Canadian prairie lakes are subjected to strongly contrasting winter conditions. Comparatively, Canadian prairie lakes experience much harsher winter conditions with ice-cover for up to 5 months while Danish lakes experience <2 weeks (Jackson et al. 2007). Longer winters and thicker ice-cover likely leads to higher proportions of diapausing zooplankton in Canadian prairie lakes.

To date, only a few hatching experiments have applied ecologically relevant environmental conditions to diapause termination (Cáceres and Schwalbach 2001). Most experiments have been conducted to maximize hatching for community studies by using artificial conditions such as 24-hour photoperiod and ephippia decapsulation (Pancella and Stross 1963; Carvalho and Wolf 1989; Vandekerkhove et al. 2005). Therefore, more focused experimentation is needed to assess the implications of climate change on spring zooplankton hatching success. During spring, climate change will have direct effects on water temperature but not photoperiod length. As a result, combinations of temperature and photoperiod cues experienced by resting eggs in lakes will change accordingly. In

addition, the effects of climate change in lakes will likely resemble symptoms of eutrophication (Mooij et al. 2005). In some lakes, higher water temperatures and evaporative rates have led to increasing nutrient concentrations and primary productivity (Schindler et al. 1990) potentially leading to decreasing light penetration. In some zooplankton, both light and photoperiodic stimuli are needed for dormancy termination (Stross 1971), so it is unclear how lowered light intensity would affect zooplankton emergence. Furthermore, as some lakes strongly rely on spring zooplankton emergence for population development, climate change could potentially alter zooplankton community structure and synchronization of some grazers with edible phytoplankton. Therefore, the objectives of this study are twofold: (1) To determine daphniid and rotifer hatching responses from resting eggs to variations in temperature-photoperiod cues but also light intensity. (2) To determine how potential changes in zooplankton emergence dynamics may affect zooplankton population development and community structure in lakes with strong benthic-pelagic linkages.

Methods

Laboratory experiment

Hatching experiment design

A factorial experimental design was used to test the effects of temperature, photoperiod and light intensity on hatchling abundance and timing of hatching of zooplankton resting eggs. In the present study, levels chosen for each factor were selected to reflect potential climatic changes in north-temperate lakes. Three levels of temperature (6 °C, 9 °C, and 12 °C), two photoperiods (13L:11D and 16L:8D) and two levels of light

intensity ($20 \mu E m^{-2} sec^{-1}$ and $35 \mu E m^{-2} sec^{-1}$) were selected for the experiment. The experiment consisted of five replicates per combination (12) making 60 experimental units in total.

Sediment collection and experimental procedure

An Ekman sampler was used to collect sediment samples from three lake depths (2 m, 3 m and 4 m) at Fort Whyte Lake 2, Winnipeg, Manitoba ($49^{\circ} 49.020' N$, $97^{\circ} 13.440' W$) on October 26, 2006. These are a set of representative eutrophic prairie lakes described in more detail in Chapter 1. From each sampling site, the top three centimetres of sediments were collected with the assumption that this represented the most active 'egg-bank' (Cáceres and Hairston 1998). Sediments were transferred to large plastic containers wrapped in aluminium foil to minimize exposure to light. Sediments were then transported in coolers to the lab where they were stored for four and half months at $4^{\circ}C$ in the dark simulating winter conditions in the bottom sediments (Cáceres and Schwalbach 2001; Vandekerckhove et al. 2005).

After the dormancy period, sediments from the three depths were pooled and thoroughly stirred to ensure homogeneity of resting eggs. Three large environment chambers were used for this experiment. Environment chambers were set at one of three constant temperatures ($6^{\circ}C$, $9^{\circ}C$, or $12^{\circ}C$). In order to enhance the level of realism of the experiment, resting eggs were not isolated from the sediments.

Initially, a small subset of sediments (15 ml) was collected for a single direct count of daphniid ephippia density. Sediments were sifted through incrementally smaller mesh sizes (1000 to $140 \mu m$) until ephippia were readily isolated using a dissection microscope and forceps. Densities in the sediments were determined to be 3520 ephippia

per L of sediments for small *Daphnia* (*D. ambigua* and *D. parvula*) and 680 ephippia per L of sediments for the larger species, *D. pulicaria*. These direct counts reflect potentially viable ephippia assessed on the basis of greenish colouration of resting eggs (C. E. Cáceres [2007], U. of Illinois, pers. comm.). Initial rotifer resting egg densities were not estimated. Ephippia density enumerations were used to ensure appropriately high number of viable resting eggs per experimental unit (>100 resting eggs).

Each experimental unit consisted of 125 ml of sediments placed in a polypropylene container (11.5 cm x 11.5 cm x 5 cm) giving a sediment depth of approximately 1 cm. Each experimental unit received 100 ml of a nutrient medium (COMBO; Kilham et al. 1998) and was covered with a transparent plastic film to minimize evaporative losses. COMBO was utilized because of its suitability for both zooplankton and phytoplankton growth and maintenance. Half of the 60 units were then covered with a 1.22 mm mesh (low light intensity; $20 \mu E m^{-2} sec^{-1}$). The other half was left without mesh to produce the high light intensity treatment ($35 \mu E m^{-2} sec^{-1}$). Twenty units (10 with no mesh, 10 with mesh) were randomly placed under a set of white fluorescent lights in each environment chamber. Timers controlled light to produce a 16-hour photoperiod in each chamber. A 13-hour photoperiod was controlled by manually placing dark boxes over 10 experimental units in each chamber at the appropriate time.

Incubation was carried out for 33 days. The length of the experiment was chosen to reflect duration of the transition from spring to early summer. This was assumed to represent a reasonable timeframe in which reestablishment of the pelagic zone by emerging daphniids and rotifers is most critical (Wolf and Carvalho 1989; Cáceres 1998; Hairston et al. 2000; Gyllström 2004). Every third day, the nutrient medium above the

sediment surface of each experimental unit was carefully siphoned and collected for enumeration of hatchlings. Sampling was conducted during dark period under a red incandescent light bulb to facilitate manipulations without disrupting light regimes. Fresh nutrient medium was then poured in each experimental unit followed by a thorough stirring of the sediments. Stirring of the sediments was conducted to simulate spring mixing conditions. In the field, mixing of the sediments is likely an important factor for hatching by exposing resting eggs in the surficial sediments to the appropriate environmental cues (Gilbert and Schröder 2004). Both cladoceran and rotifer hatchlings were counted using a dissection microscope. *Daphnia* hatchlings were isolated, placed in 100 ml of COMBO medium and fed *Scenedesmus* sp. (≈ 100 cells per ml) until species identification was possible. *Daphnia* identification was based on Hebert (1995). Dead hatchlings were assigned to corresponding species that were identified from adults. Dominant rotifers, i.e., *Keratella* spp. and *Synchaeta pectinata*, were counted and identified based on Chengalath et al. (1971) and Obertegger et al. (2006). For *Keratella*, two dominant species were *K. quadrata* and *K. cochlearis*. In addition, the 12°C chamber was maintained for an extended period of time (45 days) in order to hatch zooplankton species with longer time and higher temperature requirements.

Data analysis

Two response variables, total abundance of hatchlings and mean time to hatching were measured for each experimental unit. Hatching success was assessed based on total abundance of hatchlings in each replicate at the end of the incubation period. Initial counts of ephippia density were not used to calculate hatching success since assessing egg viability based on colouration is not completely reliable. Further, resting eggs were

not isolated, thus it is difficult to determine precisely how many resting eggs are subjected to appropriate cues during the experiment. The number of days needed for the average hatchling of a given taxon to hatch was calculated using the following equation (Vandekerkhove et al. 2004):

$$\text{Mean time of hatch} = \frac{\sum \text{time} \times \text{number of hatchlings}}{\text{total number of hatchlings}}$$

Three-factor analyses of variance (ANOVA) were carried out to test the effects of temperature, photoperiod and light intensity and their interactions on total hatchling abundance and timing of hatching. Prior to analyses, normality and homogeneity of residuals were verified using Shapiro-Wilk's test for normality and visual checks of residuals by predicted values plots for homogeneity. Hatchling abundance was log-transformed to normalize variance of the residuals. All statistical tests were performed in SAS 9.1.3.

Computer simulation modelling

Zooplankton population development

Computer simulation models were developed to determine the effects of possible changes in daphniid and rotifer hatching dynamics as a result of variations of temperature and photoperiod cues. Studies suggest that not all zooplankton will respond the same way to an earlier warming (Winder and Schindler 2004). In the present study, two-prey and two-predator population models tested the effects of an earlier spring relative to a later spring on daphniid and rotifer competitive outcomes in lakes dependent on emergence

from diapausing eggs for spring population development. Experimental emergence results for daphniids and rotifers subjected to combinations of temperature and photoperiod cues (described above) were used in the model to describe spring hatching dynamics in a small north-temperate eutrophic lake.

The two-predator and two-prey model used for this research is an extension of classical predator-prey models. The model developed was based on simple Lotka-Volterra predator-prey models where prey population growth is density-dependent and predator population growth varies as a function of available resources, i.e., prey. Similar models have been developed for plankton dynamics (Kretzschmar et al. 1993; Scheffer et al. 1997). These models are meant to be approximations of the actual population dynamics enabling a better understanding of mechanisms driving field observations. In the present paper, STELLA 7.0.3 was used to develop the model.

The model is similar to that developed in Kretzschmar et al. (1993) for two competing algae groups and a single predator, daphniids. The model is extended to include a second predator, rotifers. This set of four differential equations describes a two-predator and two-prey system:

$$\begin{aligned}\frac{dE}{dt} &= r_1 E \left(1 - \frac{E}{K_1} - \alpha \frac{C}{K_1} \right) - D \left(\frac{g_1 E}{1 + g_1 h_1 E + g_2 h_2 C} \right) - R \left(\frac{g_3 E}{1 + g_3 h_3 E} \right) + d(K_1 - E) \\ \frac{dC}{dt} &= r_2 C \left(1 - \frac{C}{K_2} - \beta \frac{E}{K_2} \right) - D \left(\frac{g_2 C}{1 + g_2 h_2 C + g_1 h_1 E} \right) + d(K_2 - C) \\ \frac{dD}{dt} &= D \left(\frac{e_1 g_1 E + e_2 g_2 C}{1 + g_1 h_1 E + g_2 h_2 C} \right) - m_1 D \\ \frac{dR}{dt} &= R \left(\frac{e_3 g_3 E}{1 + g_3 h_3 E} \right) - m_2 R - m_3 D\end{aligned}$$

In the above equations, the prey are two groups of phytoplankton, edible algae (E) and inedible algae (C) and the predators are two groups of zooplankton, rotifers (R) and daphniids (D). Phytoplankton classification is based solely on cell morphology where edible algae represent smaller cell sizes ($<50\text{ }\mu\text{m}$) and inedible algae represent larger cell sizes ($>50\text{ }\mu\text{m}$) as well as filamentous forms. This definition of phytoplankton groups is based on the general inability of daphniids to consume larger prey items (Burns 1968). Functionally, edible algae (E) represent green algae, such as chlorophyta, and inedible algae (C) represent filamentous cyanobacteria, such as *Planktothrix* and *Aphanizomenon*. Both phytoplankton groups differ in their abilities to grow at sub-optimal temperatures, with cyanobacteria typically dominating at higher water temperatures (Robarts and Zohary 1987). Also, interspecific competition between algal groups is included with the competition coefficients α and β . Phytoplankton population growth is density-dependent describing a logistic increase towards the carrying capacity (K). The carrying capacity implicitly describes the trophic status of the lake. Therefore, by increasing the carrying capacity, one increases the nutrient concentrations in the model allowing greater algal biomass to develop.

Phytoplankton population mortality depends on grazer density and consumption rates. Consumption rates are a function of attack rates, or grazing rates (g) and handling times (h). To increase the realism of the model, algae continuously enters the population (d) to prevent complete extinction of an algal group. This is representative of a heterogeneous environment where lake depth and mixing dynamics allow some algal biomass to escape grazing until a later time (Scheffer and Rinaldi 2000).

The two predators in the model, rotifers and daphniids, are assumed to graze primarily on phytoplankton. Zooplankton grazers are able to feed on other food sources such as bacteria (Porter et al. 1983); however, this is not included in the model. The predator *Daphnia* follows a Holling type II functional response (DeMott 1982; Porter et al. 1982). Therefore, attack rates increase with food concentration until the predators are satiated and the attack rates reach a plateau. In this model, rotifers are assumed to follow a similar functional response. Predator population growth depends on predator density (D or R), attack rates (g), net assimilation efficiencies (e), handling times (h) and prey density (E or C). Both predators have different attack rates, largely as a result of body size differences. Net assimilation efficiency (e) is defined as the conversion efficiency of food into young, after correcting for respiratory losses. In this model, only daphniids are able to feed on filamentous cyanobacteria at reduced attack rate and assimilation efficiency as compared with edible algae. Edibility of the two algae groups is, therefore, indirectly modelled via the predators' differential attack rates and assimilation efficiency for the two algal groups. To simplify the model, daphniids are assumed not to preferentially select one algal group over another. This is not entirely accurate as some species of daphniids are able to avoid feeding on certain strains of cyanobacteria (Epp 1996). Handling times (h) are considered to be the time needed for the mouthparts to manipulate food (McCauley et al. 1988).

Predator mortality rates (m_1 and m_2) include both natural and zooplanktivorous-derived mortality that has not been explicitly modelled. In this model, an explicit representation of zooplankton predators was not included as it was assumed to contribute little to short term cycles of plankton (McCauley and Murdoch 1987; McCauley et al.

1988). Generation times are generally much longer for zooplanktivores, such as fish, and thus their populations cannot respond to increases in their prey at a reasonably short time interval, i.e., within a season. In addition, springtime zooplanktivory is generally low until sufficient warming occurs in early summer. As a result, zooplanktivorous fish do not prevent formation of the clear-water phase but can cause the decline and suppression of zooplankton populations in summer (Rudstam et al. 1993; Mehner and Thiel 1999; Hansson et al. 2007). Therefore, it is assumed here that not explicitly including zooplanktivores into the model is realistic, at least for the springtime zooplankton dynamics. In addition to natural mortality, rotifer death rate also increases with increasing daphniid density via direct and indirect interference (Burns and Gilbert 1986). This is included in the rotifer mortality parameter (m_3).

Temperate lake zooplankton hatching dynamics

The model developed assumes no over-wintering populations of both rotifers and daphniids, typical in many shallow north-temperate lakes (De Senerpont Domis et al. 2007). Hence, in the spring following ice-off, zooplankton emergence from resting eggs in the bottom sediments allows repopulation of the water-column. In order to include appropriate emergence dynamics, results from the zooplankton hatching experiments were included in the model.

The following are the two differential equations with extensions to include hatching dynamics for daphniids (a) and rotifers (b) as a function of time (t) derived from the hatching experiment:

$$\frac{dD}{dt} = (a_i + D) \left(\frac{e_1 g_1 E + e_2 g_2 C}{1 + g_1 h_1 E + g_2 h_2 C} \right) - m_1 D$$

$$\frac{dR}{dt} = (b_i + R) \left(\frac{e_3 g_3 E}{1 + g_3 h_3 E} \right) - m_2 R - m_3 D$$

Each time step is a day, represented here as (t). A schematic representation of the full model is presented in Figure 3.1. Also, a full summary of parameter definitions can be found in Table 3.1.

Model assumptions

In this simple model, certain assumptions have been made in order to simplify the predator-prey interactions. (1) Zooplankton hatchlings are assumed to impose no grazing pressure on phytoplankton. This is not entirely accurate; however, the very low numbers of hatchlings have minimal grazing impact on phytoplankton populations and only on the smallest cells. (2) Interspecific competition between algal groups due to light limitation has not been included in the model. In phytoplankton, under conditions of no nutrient-limitation but low light, cyanobacteria can typically outcompete other algal taxa (Mur et al. 1977; Huisman et al. 1999). Other authors have included competition for light in models and offer a more thorough mechanistic investigation into the potential control of cyanobacteria (Gragani et al. 1999). (3) In an effort to maintain simplicity, temperature in the model is assumed to remain constant over time. Obviously, this is not realistic as water temperature is strongly correlated with increases in ambient air temperature in the spring.

Model scenarios

Scenarios explored with the model correspond to environmental conditions used in the hatching experiment. In this study, temperatures were selected to represent a range of possible spring water temperatures under global warming scenarios. Photoperiods were selected to reflect possible daylight hours under conditions of earlier ice-off caused by increased spring air temperatures (Schindler et al. 1990). This was tested as temperature-photoperiod interactions act as important emergence cues for many zooplankton dormancy stages (Gyllström and Hansson 2004). Therefore, in order to explore potential climate change implications for plankton population dynamics, all combinations of the three temperatures (6, 9 and 12°C) and two photoperiods (13 and 16 hour photoperiods) were examined, giving six different scenarios. Furthermore, as physiological rates in ectotherms are temperature-dependent, all relevant parameter values in the model were estimated for three temperatures 6, 9 and 12°C. In these scenarios, early spring warming corresponds to a 13-hour photoperiod while later spring warming corresponds to a 16-hour photoperiod. Also, model scenarios were restricted to only spring plankton dynamics, therefore, 60 days was selected as the representative springtime period with a starting point at ice-off.

Model parameterization

Most parameters in the model were estimated from independent sources in the literature. Initial values and algal carrying capacities were estimated from field data collected from the Fort Whyte lakes, Winnipeg, Manitoba. Zooplankton hatching dynamics are derived from controlled laboratory experiments described above. This two-predator and two-prey model is presented in mg C L^{-1} . Therefore, conversions of the

relevant data were made to ensure appropriate parameter units. Biological rates dependent on temperature were estimated using published relationships between relevant rates and temperature. In some cases, when no publications were found, biological rates were indirectly estimated using a Q_{10} approach assuming most biological rates double with a 10°C increase in temperature. A summary of the parameter estimates and sources can be found in Table 3.1.

Phytoplankton parameters were estimated based on relationships between growth rate and temperature for edible algae and for filamentous cyanobacteria. Both algal group growth rates (r , d⁻¹) were estimated from relationships established at sub-optimal temperatures ranging from 5 to 20°C without nutrient limitation (*Asterionella formosa* and *Scenedesmus* sp.; Rhee and Gotham 1981 and *Planktothrix redekei*, *P. agardhii* and *Aphanizomenon flos-aquae*; Gibson 1985). Both edible algae (E) and filamentous cyanobacteria (C) carrying capacities (K , mg C L⁻¹) were estimated from spring and mid-summer maxima, respectively, observed at the Fort Whyte lakes. Initial values at ice-off for both algal groups were estimated based on the earliest sampling date at the Fort Whyte lakes (May 1, 2006). When using field data, phytoplankton biovolumes (mm³ L⁻¹) were converted into carbon using a carbon:volume ratio of 0.12 for eutrophic lakes (Reiman et al. 1989).

Zooplankton parameters are estimated based on a 1.50 mm daphniid (functionally representing a large *Daphnia ambigua*, *D. parvula* or a small *D. pulicaria*) and a 0.17 mm rotifer (functionally representing *Keratella* sp.). These were selected as they represented the dominant zooplankton taxa and sizes in the Fort Whyte lakes. The selection of zooplankton size is important as most biological rates are estimated using

relationships based on body length. Conversions of zooplankton biomass to carbon weight were estimated using simple regressions for daphniids (Berberovic 1990) and published values for rotifers (Telesh et al. 1998). Estimated values were 6.75×10^{-3} mg C per 1.50 mm daphniid and 5.80×10^{-5} mg C per 0.17 mm rotifer. For daphniids, body length (mm) was converted into biomass (μg dry wt) using regressions reported in Lynch et al. (1986). Attack rates ($\text{g, L mg C}^{-1} \text{ d}^{-1}$) in the model are assumed to be equivalent to filtering rates (McCauley et al. 1988). Filtering rates are defined as the volume of water filtered for a given food biomass per individual per unit of time. Filtering rates of daphniids decrease when fed filamentous cyanobacteria as they narrow their carapace gape and increase their rejection rates (McCauley et al. 1988; Kretzschmar et al. 1993). Estimates of daphniid filtering rates fed cyanobacteria were determined from published studies using *Planktothrix* and *Aphanizomenon*. Filtering and assimilation rates for daphniids were also shown to vary as a function of temperature (see references in Table 3.1). For rotifers, few papers were found relating biological rates with temperature. Therefore, rotifer filtering and assimilation rates at temperatures 6, 9 and 12°C were estimated using a Q_{10} approach with a coefficient of 2 using spring values from a single field study (Lair and Ali 1990). Handling times (h , d) for daphniids and rotifers were indirectly estimated by calculating the inverse of the ingestion maximum (I_{max} , mg C $\text{ind.}^{-1} \text{ d}^{-1}$) (McCauley et al. 1988), also estimated using a Q_{10} approach (see sources in Table 3.1). Furthermore, as an approximation, daphniid handling times for both edible and filamentous cyanobacteria are assumed to be the same (McCauley et al. 1988 and references herein).

Zooplankton mortality parameters (m_1 and m_2 , d^{-1}) are based on published values measured at low temperatures (daphniids, Prepas and Rigler 1978; and rotifers, Olsen et al. 1993). Rotifer mortality induced by direct and indirect interference by daphniids (m_3 , d^{-1}) was derived from relationships established between *Keratella sp.* killed per day and daphniid body length (Burns and Gilbert 1986).

Zooplankton initial values, i.e., at ice-off, were assumed to be zero. Timing of appearance of zooplankton in the water-column was derived using controlled hatching experiments. Daphniid hatchlings correspond to *D. ambigua* and rotifer hatchlings are pooled numbers of *Keratella spp.* and *Synchaeta pectinata*. Hatching data were converted from individuals m^{-2} to individuals L^{-1} based on hatching occurring in a shallow polymictic lake. Therefore, a lake with morphometric features similar to Lake 4 at the Fort Whyte lakes, i.e., a volume of 7.41×10^8 L and a bottom-sediment surface area of 8.06×10^5 m^2 . A polymictic system was selected since the model did not include spatial extensions to account for thermal stratification. From the experiment, numbers of hatchlings per square meter of sediments was calculated and extrapolated to a theoretical number of hatchlings in Lake 4 given its bottom-sediment surface area. Total number of hatchlings per litre was then calculated by dividing with total Lake 4 litres. Number of hatchlings per litre was then converted to mg C per litre.

Additionally, differential post-embryonic developmental times between species were also included in the daphniid and rotifer hatching dynamics. Inclusion of hatchlings to the population was delayed by τ_1 for daphniids and τ_2 for rotifers where τ is an empirically derived number of days for post-embryonic development to adults at a given temperature (Gillooly 2000). These were included to increase realism of the model as

developmental times depend on species size and water temperature. The equations used for a 1.50 mm daphniid (τ_1 , d) and a 0.17 mm rotifer (τ_2 , d) are the following:

$$\tau_1 = 192.26/x$$

$$\tau_2 = 62.15/x$$

Temperatures (x , °C) used in the calculations correspond to those of the hatching experiment. In this model, differential response in temperature-dependent development is only applied to hatchlings derived from resting eggs. Once included in the classic Lotka-Volterra model, population dynamics of adult zooplankton are assumed to represent a reasonable approximation without further inclusion of time delays.

Sensitivity analysis

A sensitivity analysis of the model was performed to assess how variations in parameter values can alter the final outcome of three model components, rotifers, daphniids and cyanobacteria. This was conducted on selected model parameters that were estimated with an uncertain level of accuracy and were expected to have the most influence on model behaviour. Parameters tested were those related to predators, daphniids and rotifers, and included attack rates, assimilation rates, handling times and post-embryonic developmental times (Table 3.1). Sensitivity analysis was performed in STELLA 7.0.3 using the Sensi specs tool. The analysis compared the base model (values in Table 3.1) with $\pm 5\%$ deviations in parameter values for daphniid and rotifer maximum and cyanobacteria end-point biomasses (mg C L^{-1}) over a 60-day simulation.

Results

Hatching dynamics

After exposure to environmental cues, emergence began immediately for *Keratella* spp. and several days later for *Synchaeta pectinata* and *Daphnia ambigua* (Figures 3.2, 3.3, 3.4). Emergence of *Keratella* spp. and *Daphnia ambigua* from resting eggs continued throughout the 33-day incubation period at all temperatures tested (Figures 3.2, 3.4). At incubation temperatures of 9 and 12°C, hatching of *Synchaeta pectinata* resting eggs had generally ceased after 24 and 21 days, respectively (Figures 3.3b, c). Other cladocerans, *D. parvula*, *D. pulicaria*, *Bosmina longirostris* and *Diaphanosoma* sp., appreciably hatched only in the 12°C treatment, when incubated for a longer period of time, i.e., a 45-day period. Presumably these taxa have higher temperature requirements or, alternatively, other environmental conditions in the laboratory such as lighting did not satisfy developmental needs. Small cladocerans such as *D. parvula* and *Bosmina longirostris* required over 20 days of incubation to begin emerging (Figures 3.5a, 3.6b). In contrast, the largest cladoceran that emerged from the sediments, *D. pulicaria*, began hatching in the 12°C treatment after only three days when subjected to high light intensity and a 16-hour photoperiod (Figure 3.6a). *Daphnia pulicaria* and *Bosmina longirostris* were excluded from further statistical analyses as total number of hatchlings was low (14 and 47, respectively) and variability among treatments was high. Numerically, during the experiment, *D. ambigua* was the dominant cladoceran hatching while *Keratella* spp. and *Synchaeta pectinata* were the dominant rotifers (Table 3.2).

A three-factor analysis of variance (ANOVA) suggested that environmental cues (temperature, photoperiod and light intensity) differently affected rotifer and daphniid hatching abundance and timing. As expected, temperature had a significant main effect on hatching abundance for all zooplankton (Tables 3.3-3.7). In general, few resting eggs were able to develop into neonates when incubated at 6°C (Figures 3.7, 3.8). Moderate success was documented only for *Keratella* spp. rotifers. Hatchling abundance was greater at incubation temperatures of 9 and 12°C for all zooplankton.

Effects of photoperiod differed between rotifers and cladocerans. Photoperiod had a significant main effect on cladocerans, *Diaphanosoma* sp., *D. ambigua* and *D. parvula* (Tables 3.5, 3.6, 3.7). In general, cladoceran hatchling abundance was significantly greater when resting eggs were exposed to a 16-hour photoperiod, especially when incubated at 12°C (Figures 3.7e, f and 3.8a, b). Most striking difference was found in *D. ambigua* at a high light intensity where mean hatchling abundance was 44.4 (\pm 3.7) and 82.4 (\pm 10.7) for 13 hour and 16 hour photoperiods, respectively (Figure 3.7e, f). Comparatively, *D. parvula* abundance was significantly affected by a 16-hour photoperiod but the magnitude of difference was greatest at the low light intensity treatment (Figure 3.8a). Finally, for *Diaphanosoma* sp., more hatchlings were documented at a 16-hour photoperiod, although mean hatchling abundance values remained low at only 1.8 (\pm 0.7) and 1.4 (\pm 0.7) at low and high light intensities, respectively, after a 45-day period (Figure 3.8b). In contrast, variation in photoperiod alone did not significantly affect rotifer hatchling abundance.

Light intensity had a significant main effect on *Synchaeta pectinata* hatchling abundance (Table 3.4). Interestingly, a high light intensity decreased *Synchaeta pectinata*

hatchling abundance (Figure 3.7c, d). In addition, qualitatively, low light intensity may have negatively affected emergence success of *Daphnia pulicaria*. At 12°C, incubation at low light intensity delayed *D. pulicaria* emergence relative to incubation at high light intensity at a 16-hour photoperiod (Figure 3.6a). A light intensity effect for *D. pulicaria* was suspected because of its substantially darker ephippia pigmentation compared to *D. ambigua/parvula* (Figure 3.9).

A significant temperature x photoperiod interaction effect was shown for the rotifer *Keratella spp.* hatchling abundance (Table 3.3). In general, for *Keratella spp.*, increasing temperatures produces greater hatchling abundance. This pattern is reversed, however, at 12°C at a 16-hour photoperiod (Figure 3.7a, b). Also, a significant three-way interaction (temperature x photoperiod x light intensity) was shown for *Synchaeta pectinata* (Table 3.4). Only a 16-hour photoperiod caused substantial hatchling abundance discrepancies between high and low light intensities (Figure 3.7c, d).

In comparison to hatchling abundance, timing of hatching showed parallel responses to the experimental factors tested (Tables 3.3, 3.4, 3.5). However, within zooplankton groups, magnitudes of difference for mean time to hatch between 9 and 12°C were generally small (<2 days), regardless of light regime (Figure 3.10). Largest difference in timing was found when comparing with the 6°C treatment. Mean time to hatch at 6°C took on average 2.3 and 4.7 days longer for *Keratella spp.* and *D. ambigua* compared to the 9°C treatment (Figure 3.10). A 16-hour photoperiod decreased mean time to hatch for *D. ambigua* but this had little effect on rotifers. For *Synchaeta pectinata*, high light intensity negatively affected timing of hatching from the sediments.

Predator-prey population models

Model simulations were performed for 60 days mimicking the spring period following ice-off (Figure 3.11). Both phytoplankton groups showed differing population dynamics with warming temperatures and with increasing zooplankton abundance. Edible algae always attained carrying capacity prior to cyanobacteria, reflecting higher growth rates of smaller sized cells at sub-optimal water temperatures (Figure 3.11). Warming water temperatures allowed earlier development of edible algae to maximum biomass requiring 8.5 days at 12°C compared to 24.8 days at 6°C (Figure 3.11). In contrast, the cyanobacteria early peak required a longer development time than edible algae, requiring 35 days at 12°C and longer than 60 days at 6°C. Also, in all simulation experiments, dominance of cyanobacteria occurred only when daphniids or rotifers grazed edible algae. Overall, these patterns suggest that both temperature and grazing are important factors inducing cyanobacteria dominance in the model.

Early spring warming scenarios reflect conditions when warming occurs at a 13-hour photoperiod (Figures 3.11a, c, e). At the lowest temperature (6°C), zooplankton were absent over the 60 day period due to the long developmental time requirements for embryonic and post-embryonic zooplankton at low water temperatures. Zooplankton were present in low numbers only towards the end of the 9°C scenario and this was reflected by a slight decrease in edible algae and dominance of cyanobacteria beginning on day 45. Rotifer biomass peaked at 0.068 mg C L⁻¹ while daphniids were fewer at 0.016 mg C L⁻¹. In the 12°C scenario (Figure 3.11e), rotifers are the dominant zooplankton attaining a maximum of 0.276 mg C L⁻¹ compared to 0.167 mg C L⁻¹ for daphniids. Earlier development of grazers led to an earlier dominance of cyanobacteria

occurring at 30.25 days. Also, end-point cyanobacteria biomass (at day 60) was high at $0.683 \text{ mg C L}^{-1}$ due to low daphniid abundance in this scenario.

Late spring warming scenarios correspond to warming simulations at the 16-hour photoperiod (Figures 3.11b, d, f). Both 6 and 9°C scenarios show similar population dynamics compared to the early spring warming scenario (Figures 3.11b, d). Again, at 6°C no zooplankton are present and low numbers are observed only at the end of the 9°C scenario. In contrast with the early warming scenario at 12°C , the later warming scenario produced substantial differences in zooplankton population dynamics (Figure 3.11f). Model results for a 16-hour photoperiod at 12°C produced a dominance of daphniids over rotifers. Here, daphniid maximum biomass is over 10x greater than that of rotifers, attaining $0.508 \text{ mg C daphniids L}^{-1}$ compared to $0.054 \text{ mg C rotifers L}^{-1}$. As a direct result of the increased daphniid biomass, end-point cyanobacteria biomass was lowered to $0.589 \text{ mg C L}^{-1}$.

A sensitivity analysis was conducted to determine the importance of varying the parameter values on the overall pattern in population dynamics. As patterns in zooplankton population development were of primary interest in this study, only scenarios run at 12°C were tested. For predators, sensitivity of parameter variations was assessed based on its effect on outcomes in overall dominance. The sensitivity analysis shows that small variations ($\pm 5\%$) in predator parameters in the model generally had no effect on the overall competitive outcomes (Table 3.8). Therefore, this suggests that simulation results produced by the model are robust. Of all parameters tested, only two anomalies occurred, i.e., produced an opposite result of that determined with base model parameters. At the 13-hour photoperiod scenario, a 5% decrease in rotifer assimilation

efficiency and a 5% increase in rotifer handling time produced dominance of daphniids over rotifers while the reverse was predicted in the base model (Table 3.8a). In addition, the effect of parameter variations on end-point cyanobacteria biomass was also recorded. In general, variations that produced greater numbers of daphniids had a negative impact on cyanobacteria biomass (Table 3.8).

Discussion

Effects of climate change on daphniid emergence and population development

In spring, climate change could produce decreased success in daphniid emergence from resting eggs and consequently affect population development in the water-column. Zooplankton emergence experiments produced spring hatching dynamics similar to those of shallow polymictic lakes. Results from these hatching experiments suggest that under conditions of warmer temperatures and shorter photoperiod, mimicking earlier spring warming with climate change, fewer *Daphnia ambigua* emerge from the sediments while rotifers *Keratella spp.* and *Synchaeta pectinata* remain largely impervious to effects of photoperiod length. These differential hatching responses of daphniids and rotifers to an earlier spring are especially critical for lakes where population development is dependent on spring emergence. Simulation models suggest that, in these lakes, a decreased abundance of emerging daphniid biomass alters zooplankton competitive interactions and causes shifts from daphniid- to rotifer-dominated systems. As a result, an earlier spring could produce a decreasing degree of overlap between daphniids and edible algae spring populations.

Patterns of emergence

In this study, zooplankton emergence from sediments continued for longer compared to experiments using isolated resting eggs. Comparisons with other published zooplankton emergence experiments are difficult to make as most experimenters isolate resting eggs prior to incubation either by direct collection from mictic females (Pourriot et al. 1980) or by a sugar-flotation technique (Vandekerkhove et al. 2005). Also, time required for emergence to occur depends on experimental conditions but also species. For rotifers, May (1987) incubated sediments in the laboratory and showed that most rotifer species, including *Keratella cochlearis* and *Synchaeta spp.*, ceased emerging after 30 days when exposed to temperatures of 10 and 15°C. In her experiments, with 5°C incubations, rotifers continued hatching well beyond the 30-day period. For daphniids incubated at 12°C, experiments using isolated ephippia resulted in most resting eggs hatching after only 10 days (Carvalho and Wolf 1989). The present study suggests that resting eggs incubated within the sediments can require a longer period of time to hatch. Over the 33-day period of incubation, *Synchaeta pectinata* was the only zooplankton that ceased to emerge at temperatures of 9 and 12°C.

Patterns of emergence from resting eggs effectively establish the starting conditions for zooplankton population development in spring in shallow temperate lakes. In nature, resuspension of the sediments is likely required to subject resting eggs to appropriate cues for hatching to occur (Hairston and Kearns 2002; Gilbert and Schröder 2004). The present study and that by Cáceres and Schwalbach (2001) intermittently mixed the experimental units every third day over the course of the experiment to mimic the action of mixing in lakes. Thus, in these conditions, hatching could potentially

continue for a relatively long period of time (> 33 days) as new resting eggs are regularly exposed to hatching cues. This situation is likely most similar to shallow lakes where mixing continues for longer in the spring compared to deeper stratifying lakes. Studies using *in situ* emergence traps show that most rotifer and daphniid species hatch during spring coincident with turnover (Wolf and Carvalho 1989; Cáceres 1998; Hairston et al. 2000; Gyllström 2004). Therefore, experimental results from this study likely reflect patterns of zooplankton emergence found in shallow polymictic lakes with longer sediment resuspension in spring.

Number of hatchlings recorded in the present study is likely linked to initial densities of resting eggs in the sediments collected. Other cladoceran species such as *D. parvula*, *D. pulicaria*, *Bosmina longirostris*, *Diaphanosoma* sp. emerged in low numbers. Densities of *Daphnia pulicaria* and *Daphnia ambigua/parvula* ephippia were 2.0×10^4 and 1.1×10^5 ephippia m^{-2} , respectively, in sediment depths from 0 to 3 cm. Comparatively, this is within the range reported for other lakes with *Daphnia* from 1.3×10^3 to 1.6×10^5 ephippia m^{-2} with highest densities found at the deepest locations (Carvalho and Wolf 1989; Cáceres 1998). Methods used to enumerate resting eggs could not differentiate between *D. ambigua* and *D. parvula* but emergence experiment results suggest that the majority of resting eggs contained in the sediments probably belonged to the former species. Low cumulative numbers of hatchlings from some species (e.g., *D. pulicaria*) probably also reflect low hatching success. For *D. pulicaria*, an initial count of ephippia suggested that each experimental unit contained approximately 75 ‘viable’ ephippia, or 150 resting eggs. Therefore, hatching success of *D. pulicaria* in our experiment never exceeded 1% when incubated at 12°C after a 45-day incubation period.

Other studies hatching *D. pulicaria* resting eggs reported greater success rates (ranging from 6 to 50%) but comparison is questionable as these studies isolated eggs prior to incubation (Cáceres and Tessier 2003). In addition, assessment of hatching success is potentially problematic due to the difficulty of identifying ‘viable’ ephippia. In rotifers, Garcia-Rogers et al. (2006) found that over 50% of eggs deemed ‘viable’ did not hatch under a range of environmental cues.

In the present study, it is possible that few *D. pulicaria* hatchlings were observed as a result of inappropriate hatching cues. Environmental cues are the primary driver of hatching success (Cáceres and Tessier 2003). Within species of daphniids, optimal environmental cues stimulating emergence also vary regionally (Schwartz and Hebert 1987). For example, in *D. pulex*, greatest hatching success rate was produced at lower temperatures (7°C) for arctic clones while higher temperatures (14-21°C) were required for temperate clones. The existence of narrow optimal ranges in environmental cues suggests that even small variations in temperature-photoperiod cues could alter overall zooplankton emergence success. Ecologically, this could have significant implications, especially in lakes where emergence plays a strong role in zooplankton population development in spring.

Effects of environmental cues on emergence

This study demonstrates that early warming could negatively impact cladocerans but not rotifer hatching dynamics in north-temperate lakes. A review by Gyllström and Hansson (2004), suggests that daphniids and rotifers might depend on different cues to initiate termination of dormancy. In general, a single seasonal indicator, a temperature cue, is required in rotifers while some daphniid species respond to both a temperature and

a photoperiodic control to terminate dormancy (Stross 1966). The utility of temperature as a hatching cue is not surprising as it affects most biological rates and is directly linked to embryonic developmental times in zooplankton (Gillooly 2000). In the present study, temperature had a significant effect on all zooplankton hatchling abundance.

As summarized in Gyllström and Hansson (2004), our experiments confirmed that photoperiod was also a significant factor contributing to dormancy termination of several cladocerans including *Diaphanosoma sp.*, *D. ambigua* and *D. parvula* but this was most pronounced in treatments of 12°C. Meanwhile, our study and those by Pourriot et al. (1980) showed that rotifer emergence is generally not affected by changes in photoperiod. For cladocerans, Vandekerkhove et al. (2005) found that both temperature (10 to 25°C) and photoperiod (16 and 24 hours) cues were important determinants of cladoceran hatchling abundance (dominated by daphniids) for lakes in Denmark but not for lakes situated in Belgium/Netherlands, nor Spain. Hence, these authors suggested that photoperiod might be a more reliable cue for dormancy termination in north-temperate lakes where fluctuations in daylight hours are larger between seasons. Our study reinforces this hypothesis and further underlines the sensitivity of some daphniid populations to relatively small variations in photoperiod, i.e., 13 and 16 hours compared 16 and 24 hours in Vandekerkhove et al. (2005).

Variations in temperature-photoperiod cues primarily impact hatchling abundance not timing of emergence. Similar to hatchling abundance responses, temperature and photoperiod main effects were significant for mean time to hatch for daphniids while only temperature affected rotifers. However, the magnitude of effects of temperature and photoperiod on mean time to hatch was relatively unimportant, i.e., within a zooplankton

group this varied by less than 2 days at 9 and 12°C regardless of photoperiod or light intensity. In summary, the present study demonstrates that small variations in photoperiod can cause important decreases in *D. ambigua* but not in *Keratella* spp., nor *Synchaeta pectinata*. This is especially pertinent as climate warming simulations predict warmer springs in north-temperate regions of North America (Christensen et al. 2007) conducive to conditions of shorter photoperiods and warmer water temperatures in lakes.

Changes in light intensity could also potentially impact zooplankton emergence in natural systems. In zooplankton, only a handful of studies have investigated the effect of light intensity on dormancy termination (*Pleuroxus denticulatus*, Shan 1970; *Artemia* sp., Vanhaecke et al. 1981; *Brachionus plicatilis*, Hagiwara et al. 1995). The present study shows a significant effect of light intensity for only the rotifer *S. pectinata*. Here, unexpectedly, a low light intensity produced increased *S. pectinata* hatchling abundance. In early spring, *S. pectinata* can sometimes represent 80% of the total rotifer community in lakes (Stemberger and Gilbert 1985). Therefore, in lakes, this adaptation could further contribute to higher rotifer abundance under low light intensities, e.g., under ice or during turbid conditions when phytoplankton abundance increases.

In daphniids, the effects of light and photoperiod are believed to be involved in separate responses, with the latter required to initiate photosensitivity of the embryo (Stross 1966, 1971). During the open-water season in lakes, two factors can limit light reaching embryos. First, the level of ephippium pigmentation, encasing the resting eggs, is highly variable in some species, e.g., *D. pulicaria* (Gerrish and Cáceres 2003) and second, there may be diminished water transparency often as a result of increased algal biomass. For *D. pulicaria*, the present study suggests that darker ephippium pigmentation

of that species relative to *D. ambigua* might have led to its low hatchling abundance. Supporting this hypothesis, although not statistically significant, *D. pulicaria* hatched substantially later under conditions of low light intensity compared to high light intensity and a 16-hour photoperiod. This could imply the presence of some maternal effect in triggering dormancy termination in daphniids. In fact, other studies have suggested both environmental and genetic control have effects on emergence but it remains unclear what factor is most important in natural systems (Pfrender and Deng 1998; Cáceres and Tessier 2003)

Effect of differential hatching response on zooplankton population development

Simulation models were developed to explore the potential disruption of early spring warming on zooplankton population development. This is particularly relevant to lakes where spring population development strongly depends on the resting egg-bank, but also inter-annually as emerging zooplankton can contribute substantially to pelagic populations in years where winter survivorship of adult zooplankton is low (Cáceres 1998; Hampton et al. 2006). In the models, zooplankton population development within 60 days is substantial only at temperatures of 12°C. At low temperatures (6 and 9°C), a longer period is required. Thus, only simulations at 12°C will be further considered in detail, where a 16-hour photoperiod corresponds to a late spring scenario (Figure 3.11f) and a 13-hour photoperiod corresponds to an early spring scenario (13-hour photoperiod) (Figure 3.11e).

Overall, models developed in this study imply that differential responses in daphniid and rotifer development times to variations in temperature-photoperiod cues are the primary mechanism involved in altering zooplankton population development. As a

result, early spring warming could produce shifts from daphniid- to rotifer-dominated systems and reduce top-down control of filamentous cyanobacteria. In addition, this suggests that spring competition among various groups of predators, e.g., daphniids and rotifers, can depend on which predator has the greatest emerging biomass from the sediments. Similarly, in long-term studies of Lake Washington, earlier warming caused mismatching to occur between daphniids and edible algae while rotifer populations continued to develop in synchrony with spring peaks of edible algae (Winder and Schindler 2004). Our simulation models support Winder and Schindler's (2004) hypothesis that earlier warming can negatively affect daphniid population development in populations that require an appropriate photoperiod length to trigger spring emergence.

Other studies also suggest that climate change could most severely affect daphniid-phytoplankton interactions in lakes where spring population development depends solely on a small inoculum of resting eggs (De Senerpont Domis et al. 2007). In these studies, modelling results suggested that warming (+6°C) caused a mismatch between daphniid population development and high quality algae in the spring resulting in the absence of the clear-water phase. Our model results expand those of De Senerpont Domis et al. (2007) as we suggest these diminished inocula of emerging daphniids are more likely to occur as a result of earlier warming/shorter photoperiod. In summary, model results suggest that some lakes with strong dependence on resting eggs for population development could show decreasing probability of a clear-water phase, an increasing proportion of smaller grazers, and increasing filamentous cyanobacteria.

Limitations of the model

Simple plankton models are approximations of reality and can help elucidate underlying mechanisms driving the observed patterns. Several parameters in the model were estimated directly from published research; however, in some cases, only indirect estimates could be made. This is especially true of temperature-dependent responses in rotifers, as few studies were found. Sensitivity analysis conducted in this study demonstrated that for models run at 12°C, scenarios were largely robust to small changes ($\pm 5\%$) in biological parameters. In a few cases, final outcomes were altered. For example, small changes in rotifer feeding parameters, assimilation efficiency and handling time, reversed competition outcomes, suggesting that inter-specific differences in rotifer biological rates could produce different results. Thus, this simple model should be interpreted with caution and underlines the need for more basic research on temperature effects on biological rates in aquatic organisms.

Furthermore, the simple model developed in this study did not consider other biotic and abiotic factors important to plankton dynamics. Physical aspects such as mixing depth and light penetration were not included in the model. With climate change, these factors will likely play an important role in phytoplankton abundance and composition (Berger et al. 2007; Tirok and Gaedke 2007). It is also unclear which populations of daphniids are more susceptible to an earlier warming trend. For example, in contrast to this study, several climate change studies on European lakes suggest that an earlier warming does not decrease the importance of daphniids (Straile 2000, 2002). In some of these lakes, spring development of daphniid populations may depend primarily on overwintering adults. This might also imply that in lakes dependent on diapause

termination for spring population development, genotypic diversity could allow adaptation of daphniid populations to an advancing spring and changing environmental cues. Similarly, deteriorating food quality over a period of 20 years in Lake Constance led to a rapid evolution in resistance of *Daphnia galeata* (Hairston et al. 1999). In this case, selection led to shifts in daphniid genotypes to those able to cope with cyanobacteria. Therefore, adaptive responses in daphniid populations in lakes with high daphniid genotypic diversity in the egg-bank could potentially adapt to earlier spring warming. Evolutionary adaptation might explain some discrepancies between some North American and European studies linking climate change to plankton dynamics (Straile 2000; Winder and Schindler 2004).

Study implications – extension to the match/mismatch hypothesis

This study presents evidence that overlap between predator and prey populations can be disrupted by variable responses in predator emergence to environmental conditions. As suggested by the match-mismatch hypothesis, the level of overlap between predator and prey determines the predator's growth, survival and reproduction (Cushing 1969). Originally developed for fisheries sciences, the match-mismatch hypothesis has been used to explain inter-annual variability in predator populations. Recently, several studies have attributed climate change to temporal and spatial mismatches in marine (Edwards and Richardson 2004) and freshwater systems (Winder and Schindler 2004). Temporally, climate change can lead to mismatching when predator and prey utilize different environmental cues, e.g., temperature and photoperiod (Durant et al. 2007). As photoperiod is independent of climate change, rising spring temperatures can cause a disconnection between predator and prey populations when one also relies on a

photoperiod cue (Edwards and Richardson 2004; Winder and Schindler 2004). In lakes, climate change could also potentially cause spatial mismatches by altering vertical temperature gradients in water and thus the distribution and overlap of predator and prey (De Stasio et al. 1996; Helland et al. 2007). Furthermore, food quantity, not only availability, can directly affect the level of overlap between predator and prey populations (Durant et al. 2005). Change in both predator or prey abundance can either increase or decrease the effects of the match-mismatch hypothesis. For example, Durant et al. (2005) argued that in marine-terrestrial systems, herring abundance was more important than degree of mismatch in explaining puffin chick survival.

Extending this conceptual framework, our study suggests that predator abundance can also influence the match-mismatch hypothesis. As proposed by Durant et al. (2005), the degree of overlap between predator and prey diminishes when predator abundance is low (Figure 3.12). Model results presented in this study provide evidence that low daphniid emergence, as a result of a shorter photoperiod during an early spring, can disrupt the degree of matching with high quality edible algae. An important caveat in these results is the presence of some other factor able to drive a decline in edible algae. In the daphniid-edible algae model presented in this study, high abundance of another predator, i.e., rotifers, over-grazed edible algae and effectively out-competed the sparse daphniid population. In other lake systems, a decline in edible algae can also occur as a result of its high sedimentation rates following stratification. In the literature, similar examples of daphniid-edible algae match-mismatch disruptions have been documented. In Lake Constance, for example, years with low mixing intensity were linked to an early phytoplankton bloom and high abundance of small grazers (Tirok and Gaedke 2006). In

contrast, lower water temperatures during these years delayed development of larger grazers, i.e., daphniids, while high grazing pressure from ciliates and rotifers promoted a shift to more inedible algae. Therefore, similar to the present study, spring environmental conditions determined daphniid abundance and disrupted matching with the spring development of edible phytoplankton.

Conclusions

In conclusion, resting-eggs incubated within the sediments continued hatching for longer than in other published laboratory or field observations. Intermittent mixing of sediments during the experiment probably promoted continued emergence throughout the 33-day incubation period. Low resting egg densities and inappropriate emergence cues were associated with low abundance of some zooplankton hatchlings. Variations in important seasonal cues for termination of dormancy in zooplankton caused differential responses in daphniids and rotifers emergence from resting eggs. While both temperature and photoperiod cues were important for *Daphnia ambigua*, only temperature had a significant effect on *Keratella spp.* hatchling abundance. Conditions simulating an early spring, i.e., a shorter photoperiod, produced a nearly 50% reduction in daphniid hatchling abundance but this only at a temperature of 12°C. As proposed, light intensity can also have important effects on zooplankton hatching response. Low light intensity was related to higher *Synchaeta pectinata* hatchling abundance and to low *Daphnia pulicaria* emergence. Population development models suggested that differential hatching response in daphniids and rotifers to variations in temperature-photoperiod cues results in contrasting outcomes in zooplankton dominance. A late spring produced dominance of daphniids and some control of cyanobacteria while an early spring caused dominance of

rotifers, lowered daphniid biomass and high cyanobacteria biomass. As a result of low daphniid emerging biomass, the degree of matching between daphniids and edible algae can be disrupted when a competing predator drives a decline in food abundance. In summary, this study suggests that an early spring warming due to climate change could cause degradation of some north-temperate lakes with strong dependence of the resting egg-bank for population development in spring. An early warming could drive a shift from daphniid- to rotifer-dominated systems and thus less control of filamentous cyanobacteria blooms.

Table 3. 1. Two-predator and two-prey model parameters abbreviations, value, units, description and source.

Parameter	Value (6°C)	Value (9°C)	Value (12°C)	Units	Description	Source
E_0	0.1	0.1	0.1	mg C L ⁻¹	Initial edible algae biomass	1
C_0	0.001	0.001	0.001	mg C L ⁻¹	Initial cyanobacteria biomass	1
D_0	0	0	0	mg C L ⁻¹	Initial daphniid biomass	1
R_0	0	0	0	mg C L ⁻¹	Initial rotifer biomass	1
r_1	0.23	0.47	0.70	d ⁻¹	Max. edible algae growth rate	2
r_2	0.12	0.25	0.37	d ⁻¹	Max. cyanobacteria growth rate	3
K_1	0.7	0.7	0.7	mg C L ⁻¹	Edible algae carrying capacity	1
K_2	0.7	0.7	0.7	mg C L ⁻¹	Cyanobacteria carrying capacity	1
d	0.01	0.01	0.01	—	Diffusion rate from un-grazed parts	—
α, β	0.1	0.1	0.1	—	Competition coefficients	—
g_1	0.370	0.696	1.185	L mg C ⁻¹ d ⁻¹	Daphniid edible algae grazing rate	4
g_2	0.037	0.070	0.119	L mg C ⁻¹ d ⁻¹	Daphniid cyanobacteria grazing rate	5
g_3	3.657	4.503	5.544	L mg C ⁻¹ d ⁻¹	Rotifer edible algae grazing rate	6
h_1	0.909	0.738	0.600	d	Daphniid edible algae handling time	7
h_2	0.909	0.738	0.600	d	Daphniid cyanobacteria handling time	7
h_3	1.427	1.159	0.941	d	Rotifer edible algae handling time	8
e_1	0.240	0.264	0.569	—	Daphniid assimilation efficiency when grazing edible algae	9
e_2	0.036	0.040	0.084	—	Daphniid assimilation efficiency when grazing cyanobacteria	10
e_3	0.211	0.260	0.320	—	Rotifer assimilation efficiency when grazing edible algae	11
m_1	0.10	0.10	0.10	d ⁻¹	Daphniid mortality rates	12
m_2	0.04	0.04	0.04	d ⁻¹	Rotifer natural mortality	13
m_3	0.03	0.03	0.03	d ⁻¹	Rotifer mortality induced by daphniid interference	14
a_i	exp.	exp.	exp.	mg C L ⁻¹	Daphniid hatching dynamics	15
b_i	exp.	exp.	exp.	mg C L ⁻¹	Rotifer hatching dynamics	15
τ_1	32.04	21.36	16.02	d	Daphniid post-embryonic development time	16
τ_2	10.36	6.91	5.18	d	Rotifer post-embryonic development time	16

Sources: (1) Fort Whyte lakes, Winnipeg, Manitoba (2) Rhee and Gotham 1981, (3) Gibson 1985, (4) Mourelatos and Lacroix 1990, (5) estimated based on 90% reduction in rates when fed filamentous cyanobacteria compared to edible algae; Holm et al. 1983, (6) based on Q_{10} approach (coeff. = 2) derived from filtering rates at 22°C; Lair and Ali 1990, (7) estimated from the inverse of I_{max} corrected for temperature using the Q_{10} approach (coeff. = 2); Lynch et al. 1986, (8) same as in (7) but with values reported for rotifers in Hansen et al. 1997, (9) assimilation rates from Lampert 1977a and corrected for respiration with values from Lampert 1977b, (10) estimated based on 85% reduction in rates when fed filamentous cyanobacteria compared to edible algae; Lampert 1977a, (11) based on Q_{10} approach (coeff. = 2) derived from assimilation rates in spring; Lair and Ali 1990, (12) spring (May-June) values reported in Prepas and Rigler 1978, (13) values reported from 5 to 18°C in Olsen et al. 1993, (14) Burns and Gilbert 1986, (15) Results from controlled laboratory experiment by author, (16) Gillooly 2000.

Table 3. 2.Total number of zooplankton hatchlings during experiments after (a) 33 days (*Keratella spp.*, *Synchaeta pectinata* and *Daphnia ambigua*) and (b) 45 days (*D. parvula*, *D. pulicaria*, *Bosmina longirostris*, *Diaphanosoma sp.*). Note that 45 day experiment was only carried out in the 12°C chamber.

Zooplankton	Total number of hatchlings
(a) 33 day incubation	
<i>Keratella spp.</i>	2541
<i>Synchaeta pectinata</i>	3022
<i>Daphnia ambigua</i>	2725
(b) 45 day incubation (only 12°C chamber)	
<i>Daphnia parvula</i>	47
<i>Daphnia pulicaria</i>	8
<i>Bosmina longirostris</i>	23
<i>Diaphanosoma sp.</i>	18

Table 3. 3. Results of a three-factor ANOVA testing for the effects of temperature, photoperiod, light intensity and their interactions on *Keratella spp.* hatchling abundance during an incubation period of 33 days.

	d.f.	Type I SS	F	P
Hatchling abundance (log)				
Temperature	2	0.936	69.15	<0.0001
Photoperiod	1	0.003	0.48	0.494
Light intensity	1	0.003	0.47	0.498
Temp. x Photo.	2	0.059	4.39	0.018
Temp. x Light int.	2	0.0004	0.03	0.968
Photo. x Light int.	1	0.004	0.59	0.447
Temp. x Photo. x Light int.	2	0.0006	0.05	0.955
Mean time to hatch				
Temperature	2	52.519	6.64	0.003
Photoperiod	1	0.266	0.07	0.797
Light intensity	1	12.758	3.22	0.079
Temp. x Photo.	2	2.690	0.34	0.714
Temp. x Light int.	2	4.508	0.57	0.570
Photo. x Light int.	1	0.000	0.00	1.000
Temp. x Photo. x Light int.	2	5.067	0.64	0.532

Table 3. 4. Results of three-factor ANOVA testing for the effects of temperature, photoperiod, light intensity and their interactions on *Synchaeta pectinata* hatchling abundance during an incubation period of 33 days.

	d.f.	Type I SS	F	P
Hatchling abundance (log)				
Temperature	2	6.103	126.50	<0.0001
Photoperiod	1	0.004	0.16	0.690
Light intensity	1	0.309	12.80	<0.001
Temp. x Photo.	2	0.072	1.50	0.234
Temp. x Light int.	2	0.029	0.59	0.556
Photo. x Light int.	1	0.0006	0.03	0.871
Temp. x Photo. x Light int.	2	0.183	3.79	0.030
Mean time to hatch				
Temperature	2	544.834	82.17	<0.0001
Photoperiod	1	9.804	2.96	0.092
Light intensity	1	19.913	6.01	0.018
Temp. x Photo.	2	20.760	3.13	0.053
Temp. x Light int.	2	6.230	0.94	0.398
Photo. x Light int.	1	11.831	3.57	0.065
Temp. x Photo. x Light int.	2	23.809	3.59	0.035

Table 3. 5. Results of a three-factor ANOVA testing for the effects of temperature, photoperiod, light intensity and their interactions on *Daphnia ambigua* hatchling abundance during an incubation period of 33 days.

	d.f.	Type I SS	F	P
Hatchling abundance (log)				
Temperature	2	10.621	242.49	<0.0001
Photoperiod	1	0.182	8.33	0.006
Light intensity	1	0.059	2.68	0.108
Temp. x Photo.	2	0.089	2.04	0.142
Temp. x Light int.	2	0.052	1.18	0.315
Photo. x Light int.	1	0.0008	0.04	0.846
Temp. x Photo. x Light int.	2	0.007	0.16	0.853
Mean time to hatch				
Temperature	2	406.843	78.10	<0.0001
Photoperiod	1	33.411	12.83	0.0008
Light intensity	1	9.859	3.79	0.058
Temp. x Photo.	2	12.244	2.35	0.106
Temp. x Light int.	2	11.087	2.13	0.130
Photo. x Light int.	1	3.276	1.26	0.268
Temp. x Photo. x Light int.	2	2.554	0.49	0.616

Table 3. 6. Results of two-factor ANOVA testing for the effects of photoperiod, light intensity and their interactions on *Daphnia parvula* hatchling abundance during a 45 day incubation period at 12°C.

	d.f.	Type I SS	<i>F</i>	<i>P</i>
Hatchling abundance (log)				
Photoperiod	1	0.583	18.03	<0.001
Light intensity	1	0.014	0.43	0.522
Photo. x Light int.	1	0.009	0.28	0.602

Table 3. 7. Results of two-factor ANOVA testing for the effects of photoperiod, light intensity and their interactions on *Diaphanosoma sp.* hatchling abundance during a 45 day incubation period at 12°C.

	d.f.	Type I SS	<i>F</i>	<i>P</i>
Hatchling abundance (log)				
Photoperiod	1	0.408	8.80	0.009
Light intensity	1	0.001	0.03	0.876
Photo. x Light int.	1	0.055	1.19	0.291

Table 3. 8. Sensitivity analysis of selected model parameters for the 12°C simulation experiment with zooplankton hatching dynamics derived at (a) 13 hour and (b) 16 hour photoperiods. Comparison of base model results with $\pm 5\%$ deviations in parameter values for daphniid and rotifer maximum and cyanobacteria end-point biomasses (mg C L^{-1}) of a 60-day simulation. Model parameters and values are defined in Table 3.1. Values indicated in bold are those that produced shifts in dominant zooplankton groups compared to base model results.

(a) 13 hour photoperiod		Attack rate						Assimilation efficiency						Handling time				Developmental time			
		g_1		g_2		g_3		e_1		e_2		e_3		h_1		h_3		d_1		d_2	
Maximum	Base model	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%
Daphniids	0.17	0.14	0.19	0.17	0.17	0.19	0.15	0.13	0.21	0.17	0.17	0.26	0.12	0.18	0.16	0.12	0.23	0.20	0.14	0.16	0.18
Rotifers	0.28	0.30	0.25	0.28	0.28	0.26	0.29	0.30	0.25	0.28	0.28	0.18	0.33	0.27	0.28	0.31	0.22	0.25	0.30	0.28	0.27
End-point																					
Cyanobacteria	0.68	0.69	0.68	0.68	0.68	0.68	0.69	0.69	0.68	0.68	0.68	0.66	0.69	0.68	0.68	0.69	0.67	0.68	0.69	0.68	0.68

(b) 16 hour photoperiod		Attack rate						Assimilation efficiency						Handling time				Developmental time			
		g_1		g_2		g_3		e_1		e_2		e_3		h_1		h_3		d_1		d_2	
Maximum	Base model	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%	-5%	+5%
Daphniids	0.51	0.36	0.54	0.51	0.51	0.56	0.36	0.32	0.58	0.50	0.51	0.58	0.26	0.53	0.43	0.27	0.58	0.58	0.32	0.39	0.55
Rotifers	0.05	0.10	0.04	0.05	0.05	0.04	0.09	0.12	0.04	0.05	0.05	0.02	0.21	0.05	0.07	0.18	0.02	0.03	0.13	0.07	0.04
End-point																					
Cyanobacteria	0.59	0.63	0.58	0.59	0.58	0.58	0.63	0.64	0.58	0.59	0.59	0.58	0.67	0.58	0.60	0.67	0.58	0.58	0.65	0.61	0.58

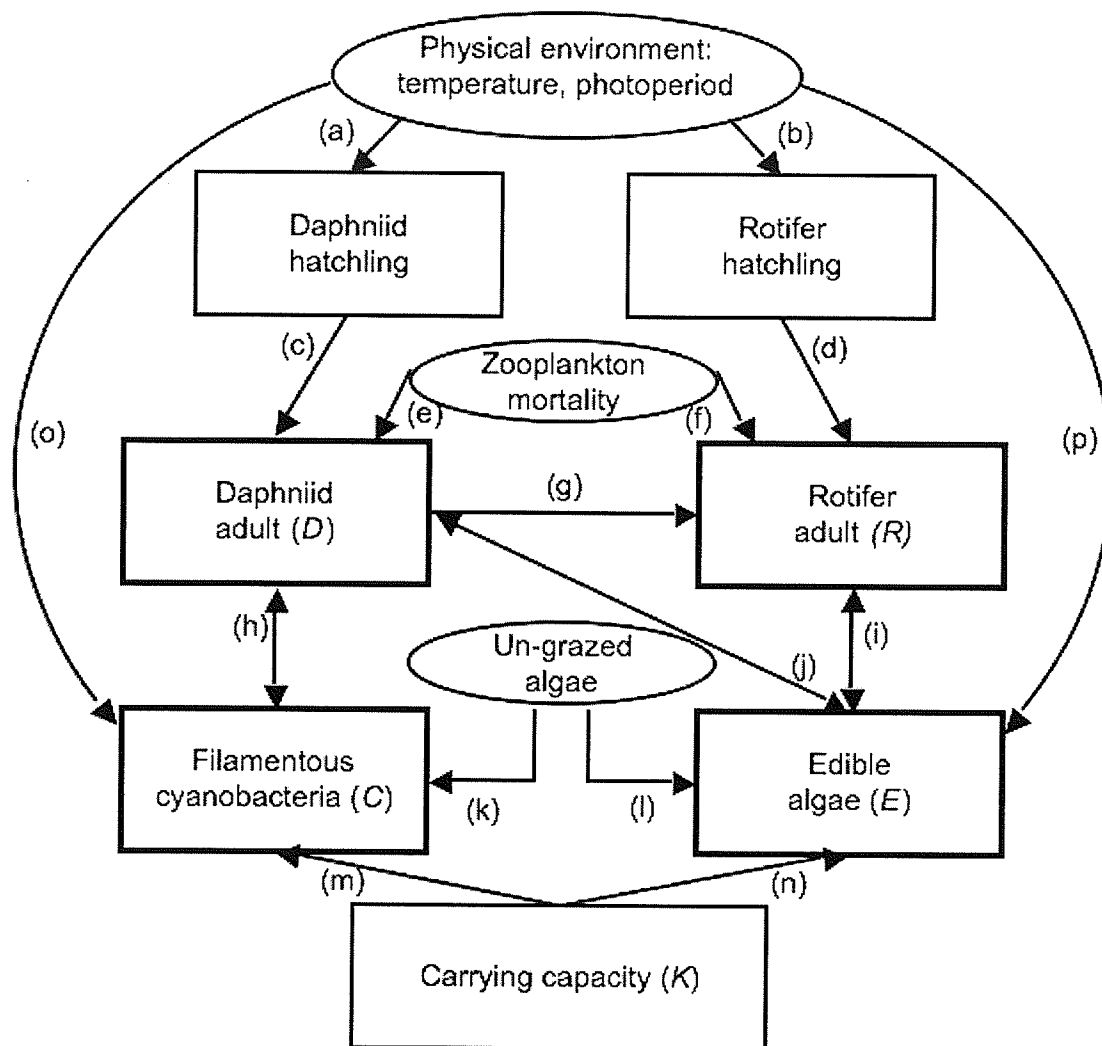


Figure 3. 1. Schematic representation of a two-predator (daphniid and rotifer) and two-prey (edible algae and filamentous cyanobacteria) model. The two predators and two prey are outlined in bold. Arrows represent both positive and negative relationships between components. Emergence cues, temperature and photoperiod, affect both daphniid (a) and rotifer (b) hatching dynamics. Zooplankton hatchlings develop into adults at a given rate (c) and (d). Adult zooplankton have natural mortality rates (e) and (f) but rotifers also succumb to daphniid direct/indirect interference (g). Adult daphniids graze both filamentous cyanobacteria (h) and edible algae (j), while adult rotifers graze only edible algae (i). Population growth of zooplankton is dependent of prey availability, represented by the two-way arrows (h), (i) and (j). Un-grazed algae diffuses into both algal groups (k) and (l). Population growth of algae is both density- (m and n) and temperature-dependent (o and p).

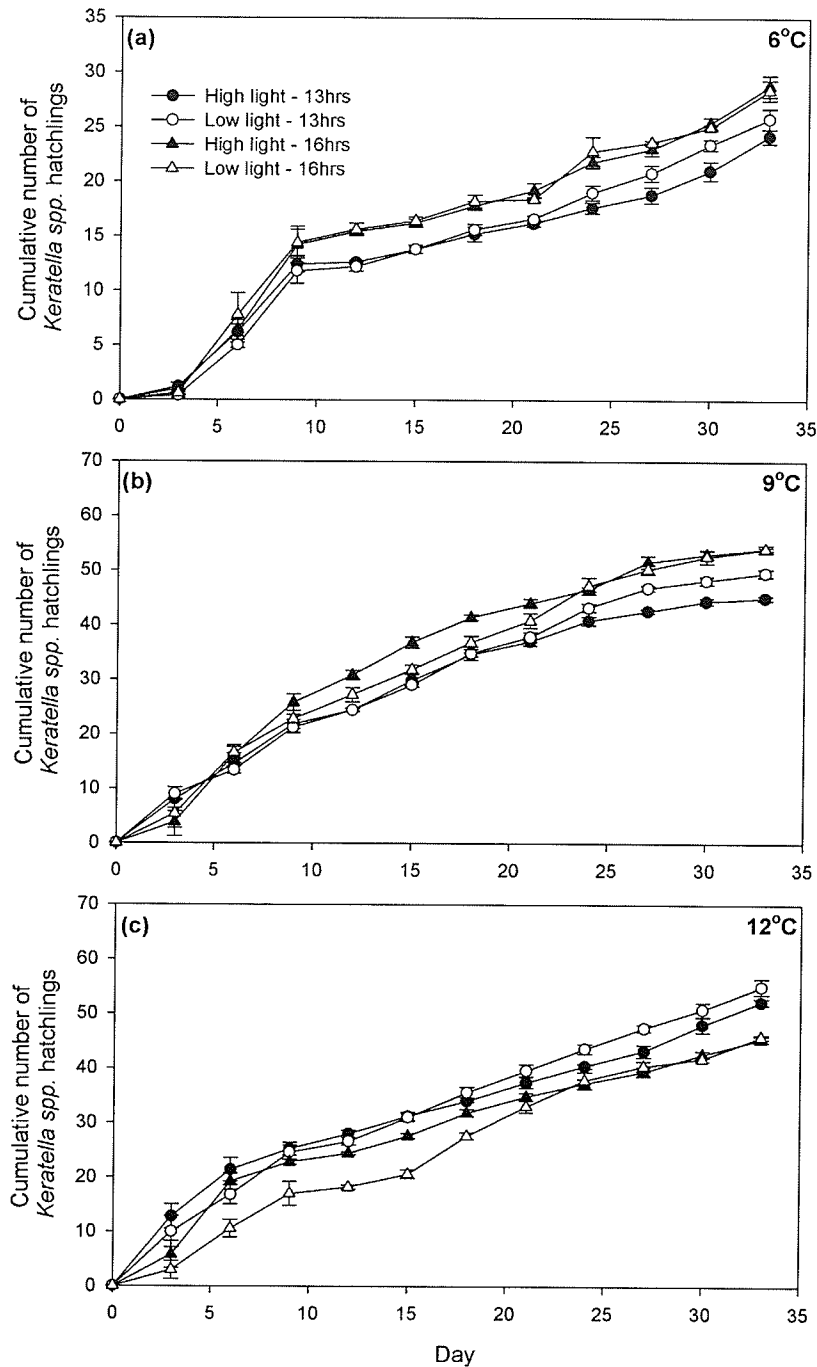


Figure 3. 2. Cumulative mean number of *Keratella* spp. hatchlings \pm 1 SE ($n = 5$) over time (33 days) incubated at three temperatures, 6°C (a), 9°C (b) and 12°C (c), at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values).

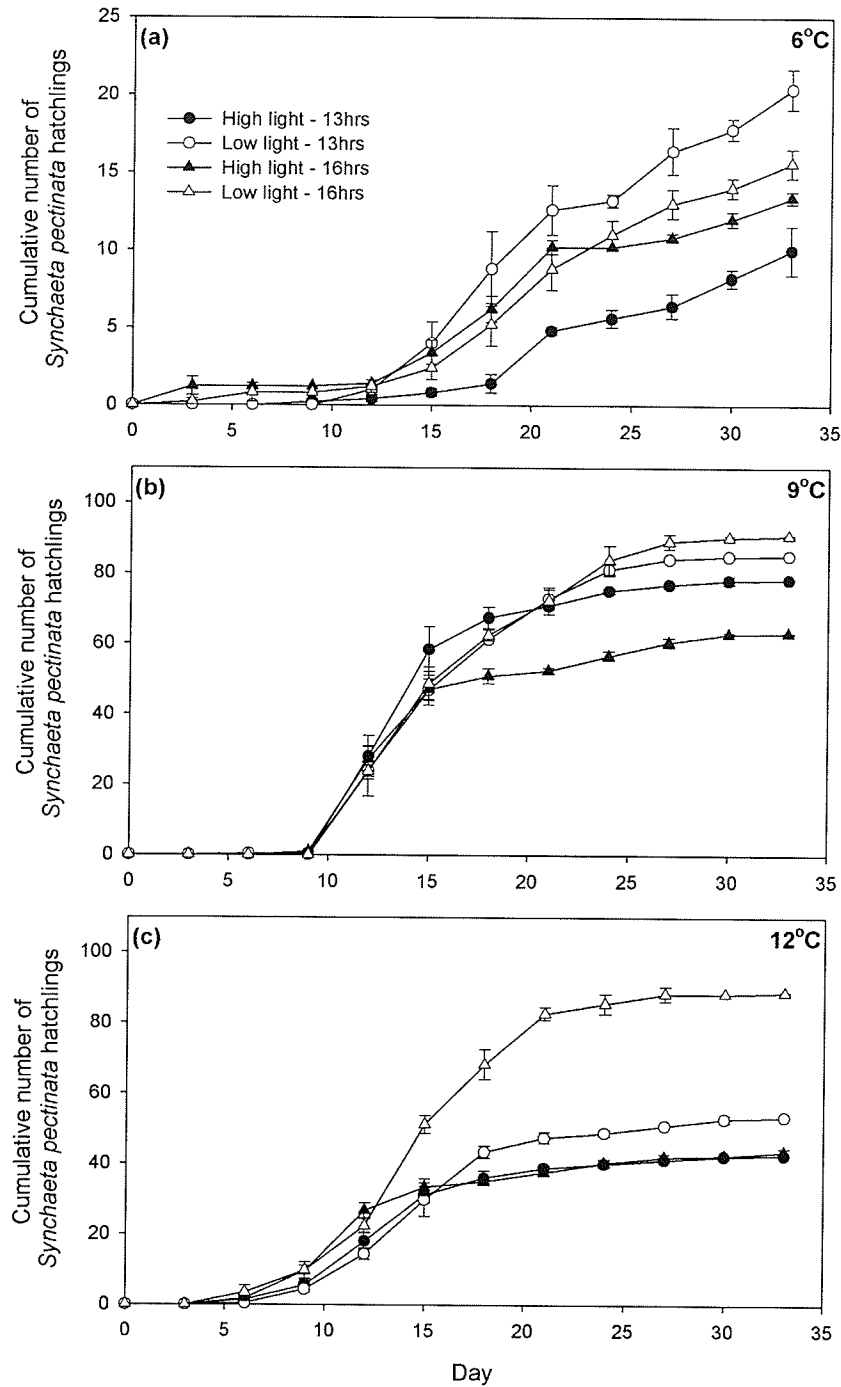


Figure 3. 3. Cumulative mean number of *Synchaeta pectinata* hatchlings ± 1 SE (n = 5) over time (33 days) incubated at three temperatures, 6°C (a), 9°C (b) and 12°C (c), at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values).

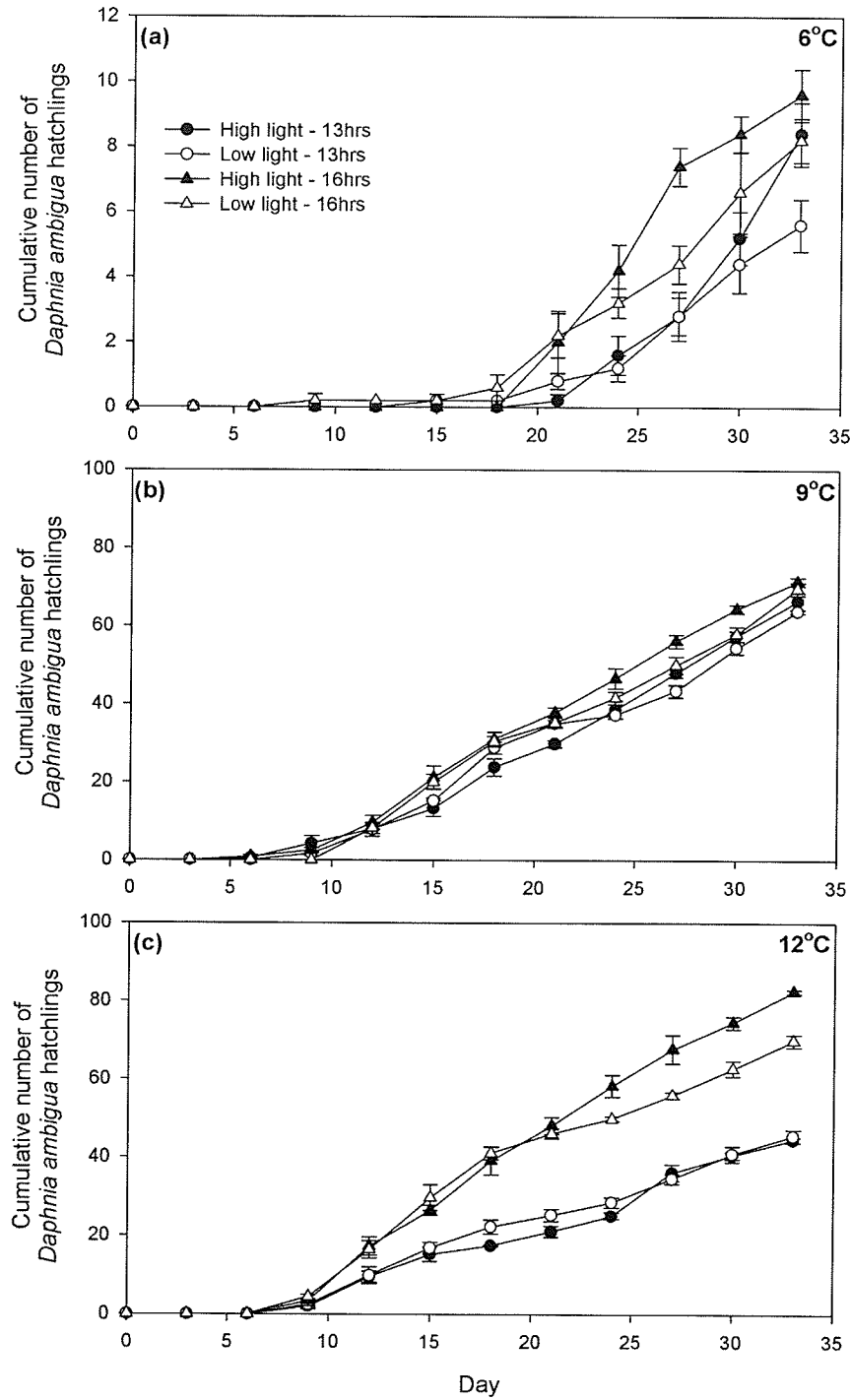


Figure 3. 4. Cumulative mean number of *Daphnia ambigua* hatchlings ± 1 SE (n = 5) over time (33 days) incubated at three temperatures, 6°C (a), 9°C (b) and 12°C (c), at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values).

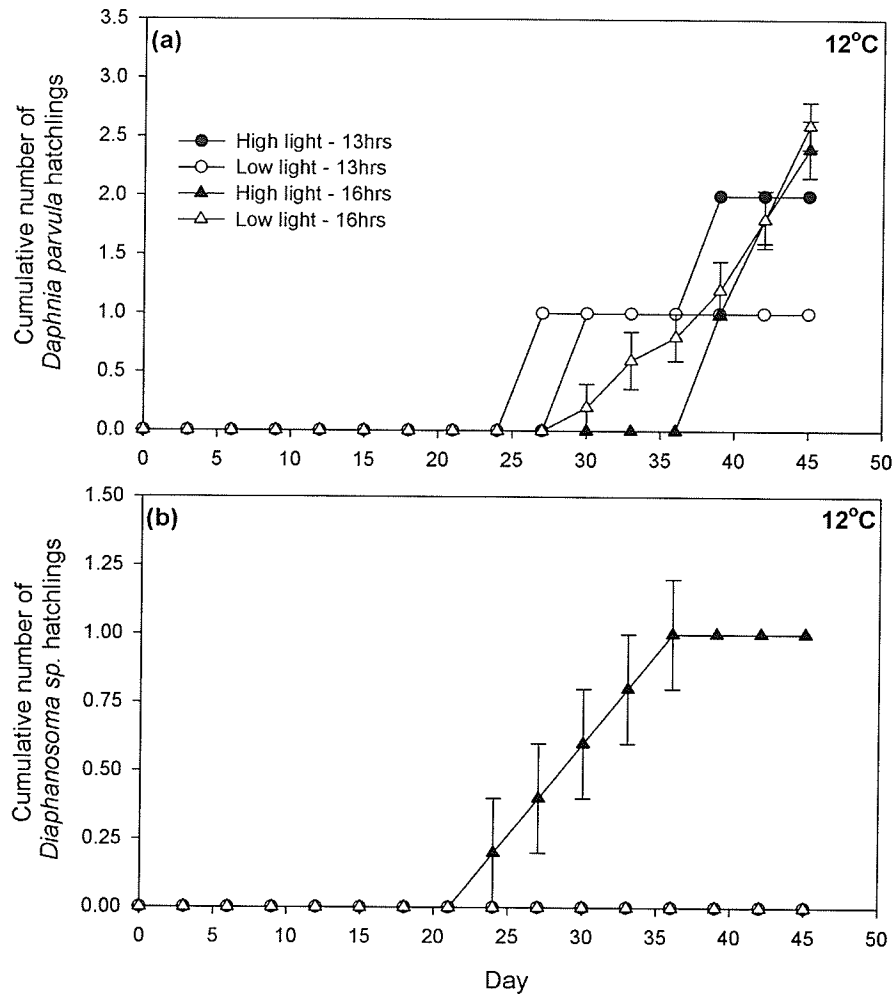


Figure 3. 5. Cumulative mean number of *Daphnia parvula* (a) and *Diaphanosoma* sp. (b) hatchlings \pm 1 SE ($n = 5$) over time (45 days) incubated at 12°C, at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values).

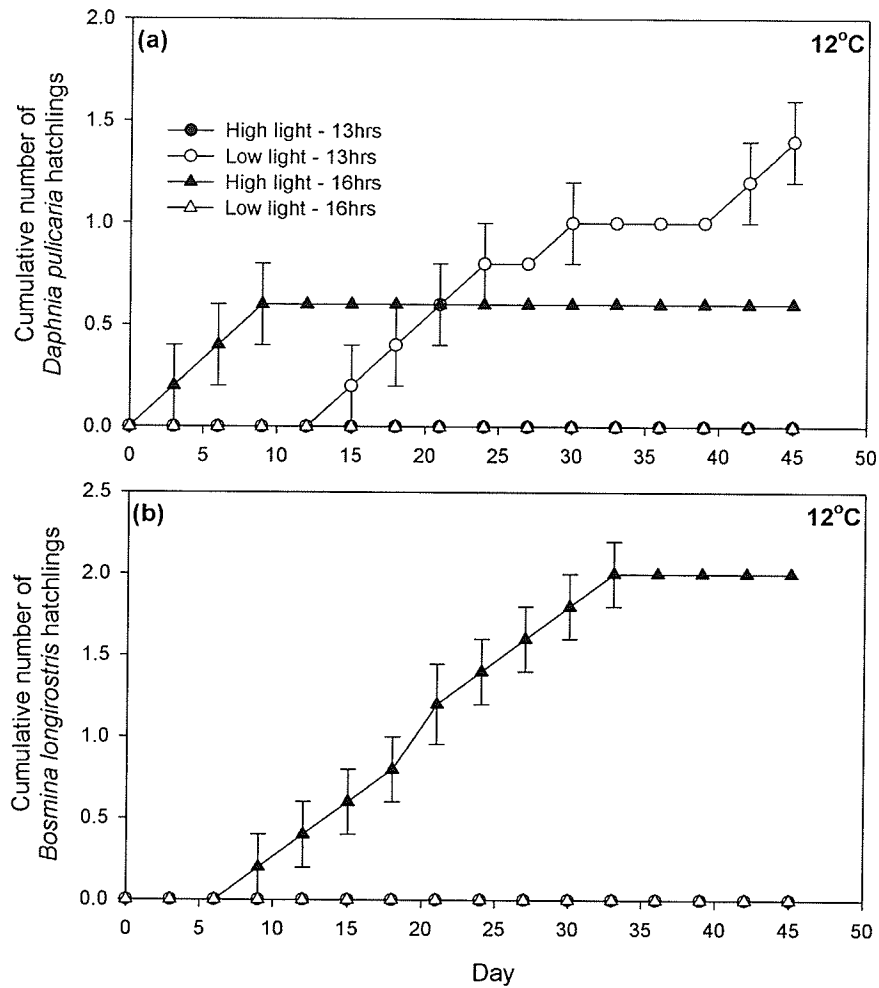


Figure 3. 6. Cumulative mean number of *Daphnia pulicaria* (a) and *Bosmina longirostris* (b) hatchlings \pm 1 SE ($n = 5$) over time (45 days) incubated at 12°C, at two photoperiods (13hrs; circle and 16hrs; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see text for exact values).

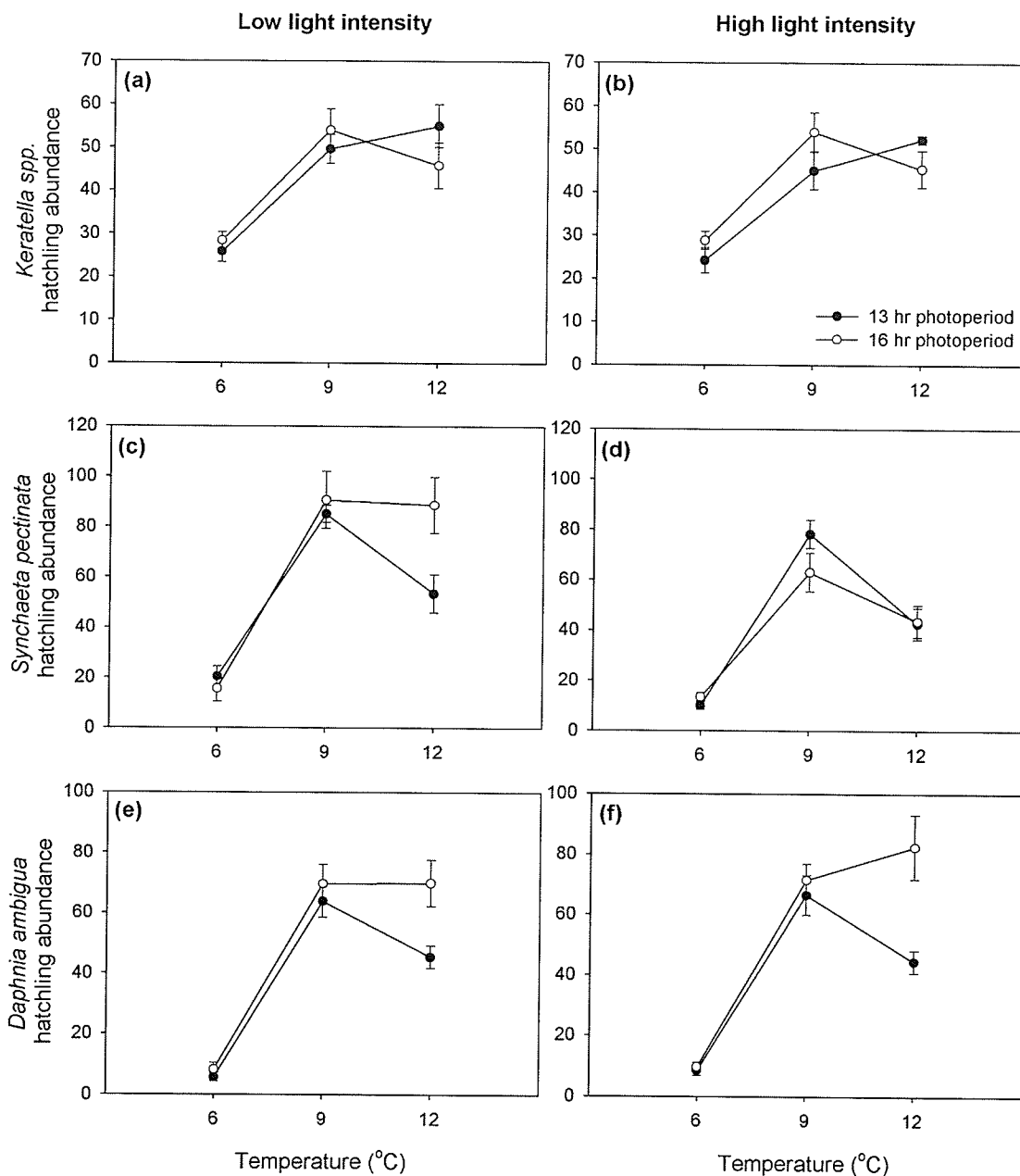


Figure 3. 7. Interaction plots of mean *Keratella* spp. (a, b), *Synchaeta pectinata* (c, d), and *Daphnia ambigua* (e, f) hatchling abundance \pm 1 SE (n = 5) of two factors, temperature (6°C, 9°C, 12°C) and photoperiod (13hr, 16hr). Results for both, low and high light intensities are shown.

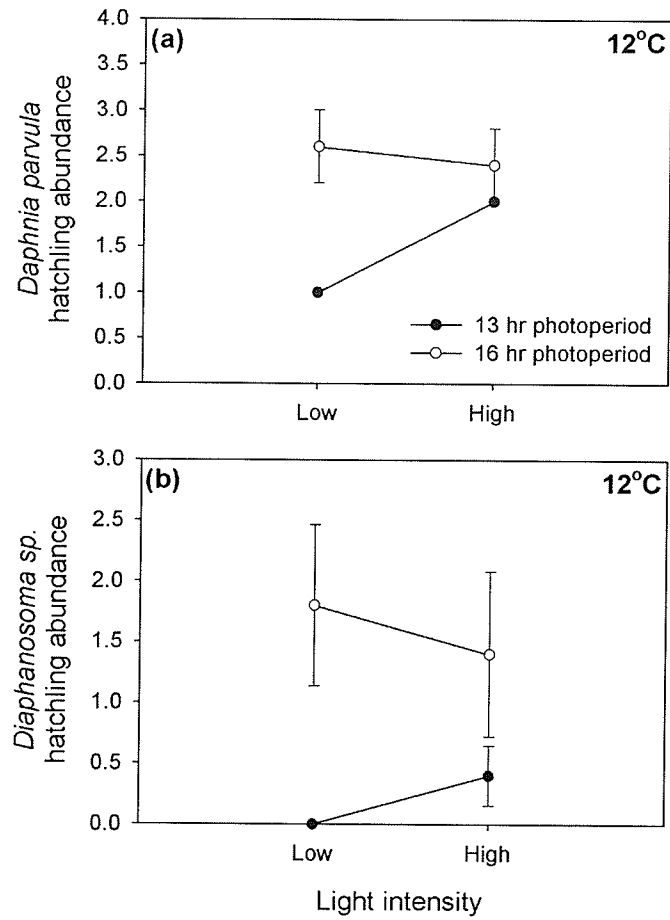


Figure 3. 8. Interaction plots of mean *Daphnia parvula* (a) and *Diaphanosoma sp.* (b) hatching abundance \pm 1 SE (n = 5) of two factors, light intensity (low, high) and photoperiod (13 and 16 hours) at an incubation temperature of 12°C.

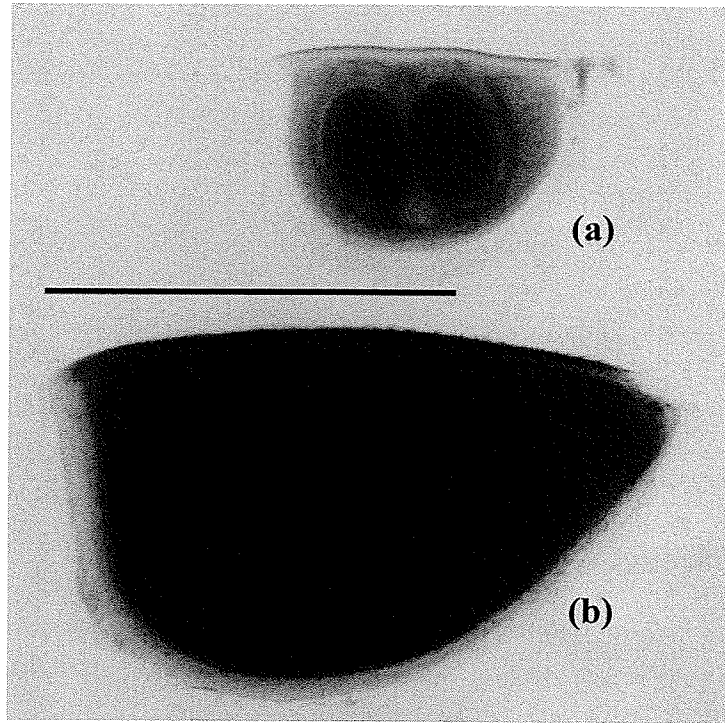


Figure 3. 9. Ephippium of (a) *Daphnia ambigua/parvula* and (b) *Daphnia pulicaria*. Solid black line measures 1 mm. Note difference in pigmentation.

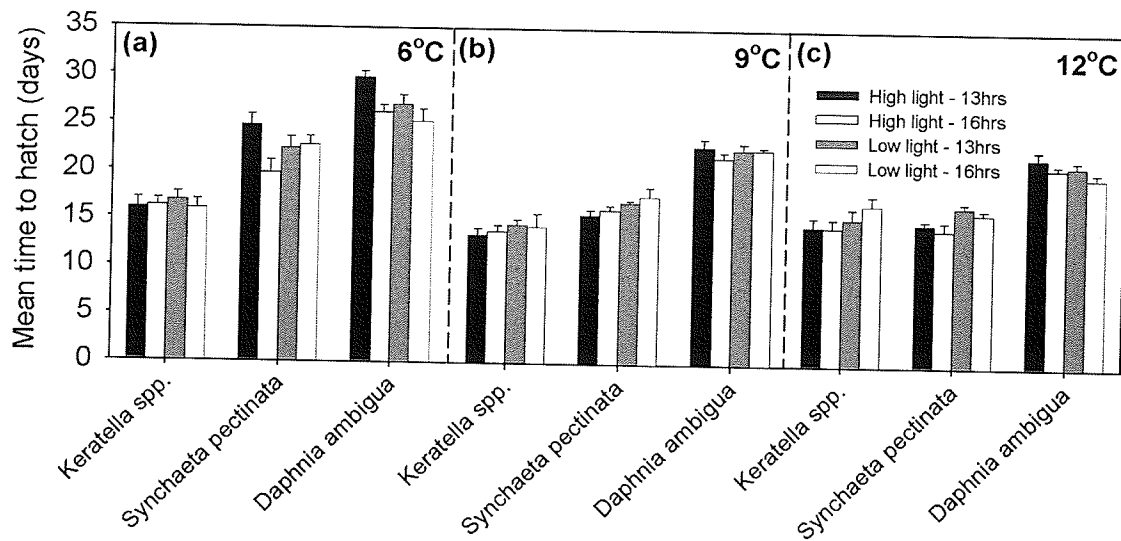


Figure 3. 10. Mean time to zooplankton hatching (days) \pm 1 SE (n = 5) for resting eggs incubated at 6°C (a), 9°C (b) and 12°C (c) under combinations of two photoperiods (13 and 16 hours) and two light intensities (high and low, see text for values).

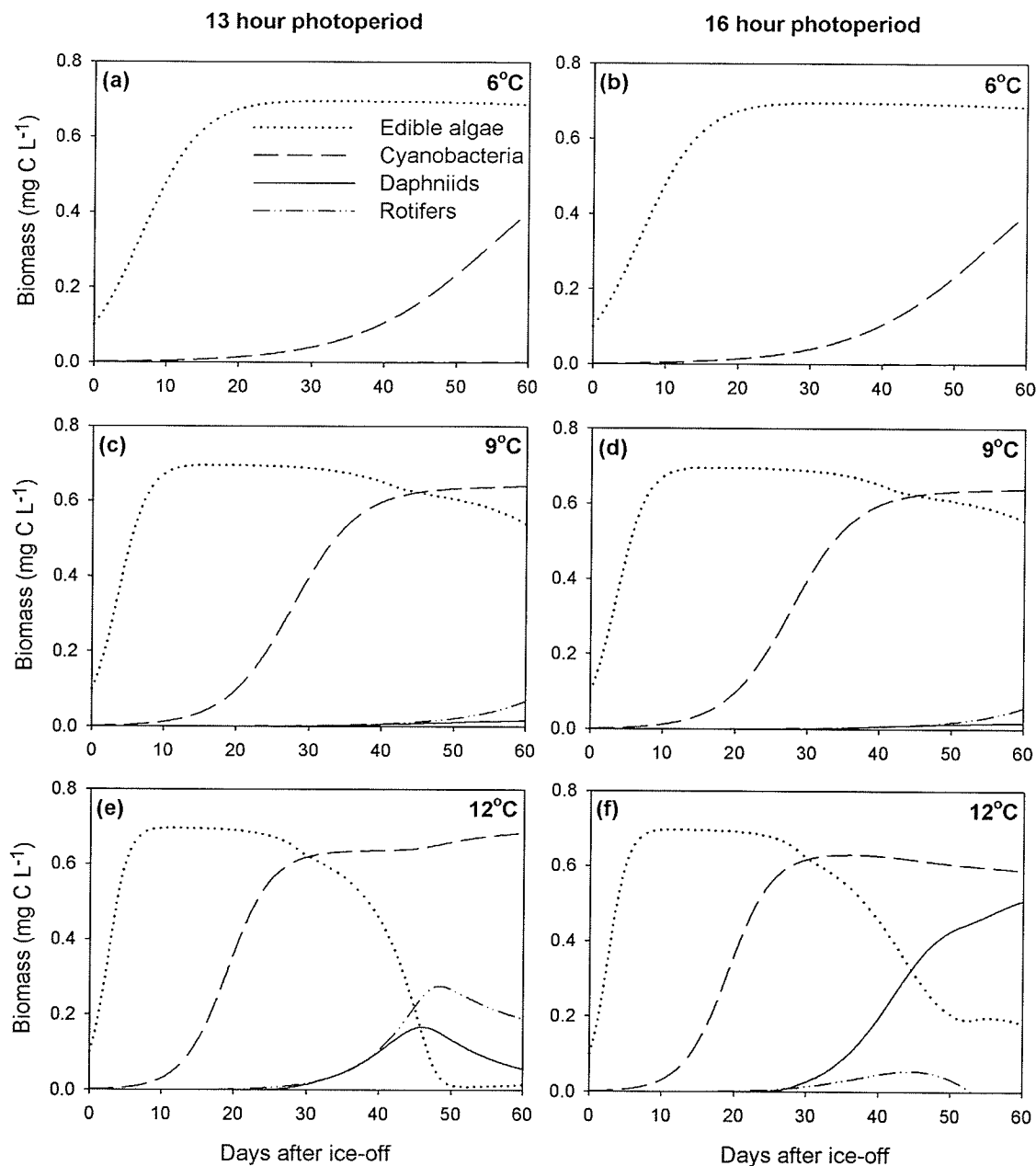


Figure 3. 11. Simulation results in biomass (mg C L⁻¹) for a two predator (daphniids and rotifers) and two prey (edible algae and filamentous cyanobacteria) model under different zooplankton hatching conditions, i.e., three temperatures (6, 9 and 12 °C) and two photoperiods (13 and 16 hrs).

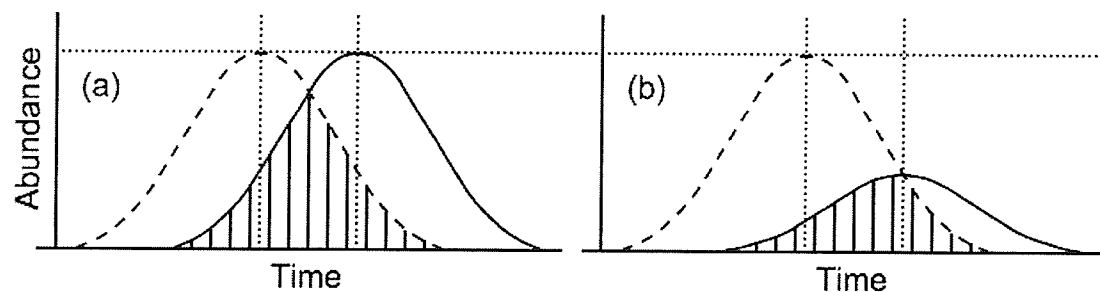


Figure 3. 12. Diagram representing overlap between predator (solid line) and prey (dashed line) populations over time in (a) a high matching scenario and (b) a low matching scenario caused by low predator abundance. Vertical lines show degree of overlap in predator-prey interactions. In (b), only predator abundance is different, i.e., timing of peak abundances remains constant in both scenarios (dotted lines).

Literature cited

- Berberovic, R. 1990. Elemental composition of two coexisting *Daphnia* species during the seasonal course of population development in Lake Constance. *Oecologia* 84: 340-350.
- Berger, S. A., S. Diehl, H. Stibor, G. Trommer, M. Ruhenstroth, A. Wild, A. Weigert, C. G. Jäger and M. Striebel. 2007. Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton. *Oecologia* 150: 643-654.
- Burns, C. W. 1968. The relationship between body size of filterfeeding cladocera and the maximum size of particle ingested. *Limnol. Oceanogr.* 13: 675-678.
- Burns, C. W. and J. J. Gilbert. 1986. Effects of daphnid size and density on interference between *Daphnia* and *Keratella cochlearis*. *Limnol. Oceanogr.* 31: 848-858.
- Cáceres, C. E. 1998. Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology* 79: 1699-1710.
- Cáceres, C. E. and N. G. Hairston. 1998. Benthic-pelagic coupling in planktonic crustaceans: the role of the benthos. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 52: 163-174.
- Cáceres, C.E. and M.S. Schwalbach. 2001. How well do laboratory experiments explain field patterns of zooplankton emergence? *Freshw. Biol.* 46: 1179-1189.
- Cáceres, C. E. and A. J. Tessier. 2003. How long to rest: The ecology of optimal dormancy and environmental constraint. *Ecology* 84: 1189-1198.

- Carvalho, G. R. and H. G. Wolf. 1989. Resting eggs of lake-*Daphnia* I. Distribution, abundance and hatching of eggs collected from various depths in lake sediments. *Freshw. Biol.* 22: 459-470.
- Chengalath, R., C. H. Fernando and M. G. George. 1971. The planktonic rotifera of Ontario with keys to genera and species. University of Waterloo, Biological Series, No. 2.
- Christensen, J.H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R.K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C.G. Menéndez, J. Räisänen, A. Rinke, A. Sarr and P. Whetton, 2007: Regional Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Cushing, D. H. 1969. The regularity of the spawning season of some fishes. *J. Cons. Int. Explor. Mer.* 33: 81-92.
- De Senerpont Domis, L. N., W. M. Mooij, S. Hülsmann, E. H. Van Nes and M. Scheffer. 2007. Can overwintering versus diapausing strategy in *Daphnia* determine match-mismatch events in zooplankton-algae interactions? *Oecologia* 150: 682-698.
- De Stasio, B. T., D. K. Hill, J. M. Kleinhans, N. P. Nibbelink and J. J. Magnuson. 1996. Potential effects of global climate change on small north-temperate lakes: Physics, fish, and plankton. *Limnol. Oceanogr.* 41: 1136-1149.

- DeMott, W. R. 1982. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. *Limnol. Oceanogr.* 27: 518-527.
- Durant, J. M., D. O. Hjermann, T. Anker-Nilssen, G. Beaugrand, A. Mysterud, N. Pettorelli and N. C. Stenseth. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol. Lett.* 8: 952-958.
- Durant, J. M., D. O. Hjermann, G. Ottersen and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.* 33: 271-283.
- Edwards, M. and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430: 881- 884.
- Epp, G. T. 1996. Grazing on filamentous cyanobacteria by *Daphnia pulicaria*. *Limnol. Oceanogr.* 41: 560-567.
- García-Roger, E. M., M. J. Carmona and M. Serra. 2006. Hatching and viability of rotifer diapausing eggs collected from pond sediments. *Freshw. Biol.* 51: 1351-1358.
- Gerrish, G. A. and C. E. Cáceres. 2003. Genetic versus environmental influence on pigment variation in the ephippia of *Daphnia pulicaria*. *Freshw. Biol.* 48: 1971-1982.
- Gibson, C. E. 1985. Growth rate, maintenance energy and pigmentation of planktonic cyanophyta during one-hour light : dark cycles. *Br. Phycol. J.* 20: 155-161.
- Gilbert J. J. and T. Schröder. 2004. Rotifers from diapausing, fertilized eggs: Unique features and emergence. *Limnol. Oceanogr.* 49: 1341-1354.
- Gillooly, J. F. 2000. Effect of body size and temperature on generation time in zooplankton. *J. Plankton Res.* 22: 241-251.

- Gragnani, A., M. Scheffer and S. Rinaldi. 1999. Top-down control of cyanobacteria: a theoretical analysis. *Am. Nat.* 153: 59-72.
- Gyllström, M. 2004. Induction and termination of diapause in a freshwater zooplankton community. *Arch. Hydrobiol.* 161: 81-97.
- Gyllström, M. and L-A. Hansson. 2004. Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. *Aquat. Sci.* 66: 274-295.
- Hagiwara, A., N. Hoshi, F. Kawahara, K. Tominaga and K. Hirayama. 1995. Resting eggs of the marine rotifer *Brachionus plicatilis* Müller: development, and effect of irradiation on hatching. *Hydrobiologia* 313/314: 223-229.
- Hairston, N. G. and C. M. Kearns. 1995. The interaction of photoperiod and temperature in diapause timing: a copepod example. *Biol. Bull.* 189: 42-48.
- Hairston, N. G., W. Lampert, C. E. Cáceres, C. L. Holtmeier, L. J. Weider, U. Gaedke, J. M. Fischer, J. A. Fox and D. M. Post. 1999. Rapid evolution revealed by dormant eggs. *Nature* 401: 446.
- Hairston, N. G., A-M. Hansen and W. R. Schaffner. 2000. The effect of diapause emergence on the seasonal dynamics of a zooplankton assemblage. *Freshw. Biol.* 45: 133-145.
- Hairston, N. G. and C. M. Kearns. 2002. Temporal dispersal: Ecological and evolutionary aspects of zooplankton egg banks and the role of sediment mixing. *Integ. Comp. Biol.* 42: 481-491.

- Hampton, S. E., P. Romare and D. E. Seiler. 2006. Environmentally controlled *Daphnia* spring increase with implications for sockeye salmon fry in Lake Washington, USA. J. Plankton Res. 28: 399-406.
- Hansen, J., P. K. Bjornsen and B. W. Hansen. 1997. Zooplankton grazing and growth: scaling within the 2-2,000- μ m body size range. Limnol. Oceanogr. 42: 687-704.
- Hansson, L.-A., A. Nicolle, J. Brodersen, P. Romare, P. A. Nilsson, C. Brönmark and C. Skov. 2007. Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. Limnol. Oceanogr. 52: 696-706.
- Hebert, P.D.N. 1995. The *Daphnia* of North America: An Illustrated Fauna. C.D.
- Helland, I. P., J. Freyhof, P. Kasprzak and T. Mehner. 2007. Temperature sensitivity of vertical distributions of zooplankton and planktivorous fish in a stratified lake. Oecologia 151: 322-330.
- Holm, N. P., G. G. Ganf and J. Shapiro. 1983. Feeding and assimilation rates of *Daphnia pulex* fed *Aphanizomenon flos-aquae*. Limnol. Oceanogr. 28: 677-687.
- Huisman, J., R. R. Jonker, C. Zonneveld and F. J. Weissing. 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. Ecology 80: 211-222.
- Jackson, L. J., T. L. Lauridsen, M. Sondergaard and E. Jeppesen. 2007. A comparison of shallow Danish and Canadian lakes and implications of climate change. Freshw. Biol. 52: 1782-1792.
- Kilham, S. S., D. A. Kreeger, S. G. Lynn, C. E. Goulden and L. Herrera. 1998. COMBO: a defined freshwater culture medium for algae and zooplankton. Hydrobiologia 377: 147-159.

- Kretzschmar, M., R. M. Nisbet and E. McCauley. 1993. A predator-prey model for zooplankton grazing on competing algal populations. *Theor. Popul. Biol.* 44: 32-66.
- Lair, N. and H. O. Ali. 1990. Grazing and assimilation rates of natural populations of planktonic rotifers *Keratella cochlearis*, *Keratella quadrata* and *Kellicottia longispina* in a eutrophic lake (Aydat, France). *Hydrobiologia* 194: 119-131.
- Lampert, W. 1977a. Studies on the carbon balance of *Daphnia pulex* DE GEER as related to environmental conditions. II. The dependence of carbon assimilation on animal size, temperature, food concentration and diet species. *Arch. Hydrobiol. Suppl.* 48: 310-335.
- Lampert, W. 1977b. Studies on the carbon balance of *Daphnia pulex* DE GEER as related to environmental conditions. III. Production and production efficiency. *Arch. Hydrobiol. Suppl.* 48: 336-360.
- Lynch, M., L. J. Weider and W. Lampert. 1986. Measurement of the carbon balance in *Daphnia*. *Limnol. Oceanogr.* 31: 17-33.
- May, L. 1987. Effect of incubation temperature on the hatching of rotifer resting eggs collected from sediments. *Hydrobiologia* 147: 335-338.
- McCauley, E. and W. W. Murdoch. 1987. Cyclic and stable populations: plankton as paradigm. *Am. Nat.* 129: 97-121.
- McCauley, E., W. W. Murdoch and S. Watson. 1988. Simple models and variation in plankton densities among lakes. *Am. Nat.* 132: 383-403.

- Mehner, T. and R. Thiel. 1999. A review of predation impact by 0+ fish on zooplankton in fresh and brackish waters of the temperate northern hemisphere. *Environ. Biol. Fish.* 56: 169-181.
- Mooij, W. M., S. Hülsmann, L. N. De Senerpont Domis, B. A. Nolet, P. L. E. Bodelier, P. C. M. Boers, L. Miguel Dionisio Pires, H. J. Gons, B. W. Ibelings, R. Noordhuis, R. Portielje, K. Wolfstein and E. H. R. R. Lammens. 2005. The impact of climate change on lakes in the Netherlands: a review. *Aquat. Ecol.* 39: 381-400.
- Mourelatos, S. and G. Lacroix. 1990. *In situ* filtering rates of cladocera: effect of body length, temperature, and food concentration. *Limnol. Oceanogr.* 35: 1101-1111.
- Mur, L. R., H. J. Gons and L. Van Liere. 1977. Some experiments on the competition between green algae and blue-green bacteria in light-limited environments. *FEMS Microbiol. Lett.* 1: 335-338.
- Obertegger, U., M. G. Braioni, G. Arrighetti and G. Flaim. 2006. Trophi morphology and its usefulness for identification of formalin-preserved species of *Synchaeta* Ehrenberg, 1832 (Rotifera: Monogononta: Synchaetidae). *Zool. Anz.* 245: 109-120.
- Olsen, Y., K. I. Reitan and O. Vadstein. 1993. Dependence of temperature on loss rates of rotifers, lipids, and $\omega 3$ fatty acids in starved *Brachionus plicatilis* cultures. *Hydrobiologia* 255/256: 13-20.
- Pancella, J. R. and R. G. Stross. 1963. Light induced hatching of *Daphnia* resting eggs. *Chesap. Sc.* 4: 135-140.

- Pfrender, M. E. and H-W. Deng. 1998. Environmental and genetic control of diapause termination in *Daphnia*. Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 52: 237-251.
- Porter, K. G., J. Gerritsen and J. D. Orcutt. 1982. The effect of food concentration on swimming patterns, feeding behavior, ingestion, assimilation, and respiration by *Daphnia*. Limnol. Oceanogr. 27: 935-949.
- Porter, K. G., Y. S. Feig and E. F. Vetter. 1983. Morphology, flow regimes, and filtering rates of *Daphnia*, *Ceriodaphnia*, and *Bosmina* fed natural bacteria. Oecologia 58: 156-163.
- Pourriot, R., C. Rougier and D. Benest. 1980. Hatching of *Brachionus rubens* O. F. Muller resting eggs (rotifers). Hydrobiologia 73: 51-54.
- Prepas, E. and F. H. Rigler. 1978. The enigma of *Daphnia* death rates. Limnol. Oceanogr. 23: 970-988.
- Reiman, B., P. Simonson and L. Stensgaard. 1989. The carbon and chlorophyll content of phytoplankton from various nutrient regimes. J. Plankton Res. 11: 1037-1045.
- Rhee G-Y. and I. J. Gotham. 1981. The effects of environmental factors on phytoplankton growth: temperature and the interactions of temperature with nutrient limitation. Limnol. Oceanogr. 26: 635-648.
- Robarts, R. D. and T. Zohary. 1987. Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. N. Z. J. Mar. Freshw. Res. 21: 391-399.
- Rudstam, L. G., R. C. Lathrop and S. R. Carpenter. 1993. The rise and fall of a dominant planktivore: Direct and indirect effects on zooplankton. Ecology 74: 303-319.

- Scheffer, M. and S. Rinaldi. 2000. Minimal models of top-down control of phytoplankton. *Freshw. Biol.* 45: 265-283.
- Scheffer, M., S. Rinaldi, A. Gragnani, L. R. Mur and E. H. Van Nes. 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. *Ecology* 78: 272-282.
- Schindler, D. W., K. G. Beaty, E. J. Fee, D. R. Cruikshank, E. R. DeBruyn, D. L. Findlay, G. A. Linsey, J. A. Shearer, M. P. Stainton and M. A. Turner. 1990. Effects of climatic warming on lakes of the central boreal forest. *Science* 250: 967-970.
- Schwartz, S. S. and P. D. N. Hebert. 1987. Methods for the activation of the resting eggs of *Daphnia*. *Freshw. Biol.* 17: 373-379.
- Shan, R. K-C. 1970. Influence of light on hatching resting eggs of chydorids (cladocera). *Int. Revue ges. Hydrobiol.* 55: 295-302.
- Stemberger, R. S. and J. J. Gilbert. 1985. Body size, food concentration, and population growth in planktonic rotifers. *Ecology* 66: 1151-1159.
- Straile, D. 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. *Oecologia* 122: 44-50.
- Straile, D. 2002. North Atlantic Oscillation synchronizes food-web interactions in central European lakes. *Proc. R. Soc. Lond. B* 269: 391-395.
- Stross, R. G. 1966. Light and temperature requirements for diapause development and release in *Daphnia*. *Ecology* 47: 368-374.
- Stross, R. G. 1971. Photoperiod control of diapause in *Daphnia*. IV. Light and CO₂-sensitive phases within the cycle of activation. *Biol. Bull.* 140: 137-155.

- Telesh, I. V., M. Rahkola and M. Viljanen. 1998. Carbon content of some freshwater rotifers. *Hydrobiologia* 387/388: 355-360.
- Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts and J. R. Speakman. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 291: 2598-2600.
- Tirok, K. and U. Gaedke. 2006. Spring weather determines the relative importance of ciliates, rotifers and crustaceans for the initiation of the clear-water phase in a large, deep lake. *J. Plankton Res.* 28: 361-373.
- Tirok, K. and U. Gaedke. 2007. The effect of irradiance, vertical mixing and temperature on spring phytoplankton dynamics under climate change: long-term observation and model analysis. *Oecologia* 150: 625-642.
- Vandekerkhove, J., B. Niessen, S. Declerck, E. Jeppesen, J. M. Conde-Porcuna, L. Brendonck and L. De Meester. 2004. Hatching rate and hatching success with and without isolation of zooplankton resting stages. *Hydrobiologia* 526: 235-241.
- Vandekerkhove, J., S. Declerck, L. Brendonck, J. M. Conde-Porcuna, E. Jeppesen and L. De Meester. 2005. Hatching of cladoceran resting eggs: temperature and photoperiod. *Freshw. Biol.* 50: 96-104.
- Vanhaecke, P., A. Cooreman and P. Sorgeloos. 1981. International study on *Artemia*. XV. Effect of light intensity on hatching rate of *Artemia* cysts from different geographical origin. *Mar. Ecol. Prog. Ser.* 5: 111-114.
- Walther, G-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J-M. Fromentin, O. Hoegh-Guldberg and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.

Winder, M. and D.E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85: 2100-2106.

Wolf, H. G. and G. R. Carvalho. 1989. Resting eggs of lake-*Daphnia* II. *In situ* observations on the hatching of eggs and their contribution to population and community structure. *Freshw. Biol.* 22: 471-478.

Chapter 4: Research summary and future directions.

Research summary

This research aimed to study the implications of a warmer spring on zooplankton-phytoplankton interactions in small eutrophic prairie lakes. The model system, the Fort Whyte lakes located in Winnipeg, Manitoba, Canada was used to represent small eutrophic lakes found in the Canadian prairies. Field observations over two open-water seasons with contrasting weather conditions, i.e., a ‘normal’ spring in 2005 and a warm spring in 2006, provided some insights into potential implications of climate change on zooplankton and phytoplankton abundance and composition (Chapter 2). Furthermore, laboratory experiments investigated the responses of daphniid and rotifer hatching dynamics from resting eggs to advancing spring warming conditions predicted by climate change (Chapter 3). In these experiments, a factorial design was used to determine the effects of variations in temperature, photoperiod and light intensity as environmental cues terminating zooplankton dormancy in spring. Finally, this research also investigated the implications of potential changes in hatching dynamics, following variations in hatching cues, on zooplankton spring population development using predator-prey simulation models (Chapter 3). The following discussion serves to highlight the findings of this research and to provide a link between experimental and theoretical research with observations of the Fort Whyte lakes. Also, future research directions are suggested.

Research highlights

Implications of a warm spring for plankton abundance and composition – Chapter 2:

- Unchanged nutrient conditions and water column stability allowed reasonable association of a warm spring in 2006 with a deterioration of water quality indicators in the Fort Whyte lakes, e.g., an increase in rotifers, total phytoplankton

biomass and relative cyanobacteria biomass but a decrease in daphniids and water transparency.

- For phytoplankton, greater warming in spring led to an earlier bloom, higher total biomass, and greater dominance by cyanobacteria, all leading to a low water transparency. Furthermore, a shift in cyanobacteria taxa was likely promoted by inter-specific competitive abilities under light-limited conditions.
- For daphniids, greater spring warming was indirectly related to abundance and composition changes via increased proportions of cyanobacteria biomass. This study suggests that an earlier bloom of cyanobacteria in 2006 may have inhibited daphniid population development. Filamentous morphology, nutritional inadequacy and toxicity factors alone, however, did not sufficiently explain the lower than expected population size. It is possible that the daphniid decline was also associated with an inability to adapt to a shift in toxin-producing cyanobacteria.
- Conditions of increased relative cyanobacteria biomass apparently favoured smaller zooplankton species. Increasing importance in cyanobacteria filaments (2006) was associated with the small-sized *Daphnia parvula* and high abundance of rotifers.
- Warmer spring temperatures and decreased water transparency in 2006 may have impaired daphniid emergence delaying its population development relative to edible phytoplankton.

Implications of a warm spring for zooplankton emergence from resting eggs – Chapter 3:

- Intermittent mixing of sediments in laboratory experiments likely caused conditions of prolonged zooplankton emergence compared to published field observations. This suggests that spring turnover is probably an important trigger for dormancy termination.
- Variations in temperature-photoperiod cues caused differential responses in daphniid and rotifer emergence dynamics. *Daphnia ambigua* hatchling abundance decreased by 50% when incubated at conditions mimicking early spring (12°C + 13-hour photoperiod) compared to a later spring (12°C + 16-hour photoperiod). In contrast, photoperiod did not have a significant effect on rotifer (*Keratella spp.* and *Synchaeta pectinata*) hatchling abundance. This study suggests that, compared to rotifers, daphniid emergence dynamics is more sensitive to climate change.
- Decreased light intensity enhanced hatchling abundance of *Synchaeta pectinata* and might be associated with low *Daphnia pulicaria* hatching success. This suggests that conditions of eutrophication, compounded by climate change, could cause important changes in zooplankton emergence dynamics via reductions in water transparency.

Implications of a warm spring for zooplankton population development – Chapter 3:

- Models developed suggest that early warming (12°C + 13-hour photoperiod) produces a shift in spring zooplankton size structure, from daphniid to rotifer dominance. These patterns are primarily driven by differential zooplankton development times with variations in temperature-photoperiod cues.

- Sensitivity analysis shows that models are largely robust, as most variations in predator parameters do not change overall patterns. Only two changes in rotifer feeding parameters produced reversed outcomes.
- Model results demonstrate that climate change can lead to disruptions in the match-mismatch hypothesis by affecting zooplankton emergence dynamics. As a result of decreased predator recruitment (daphniids) relative to its prey (edible algae), the degree of the predator-prey overlap declines. This can occur when compensatory grazing by another grazer, i.e., rotifers, drives a decline in prey (edible algae).

Implications of warming for the Fort Whyte lakes – some conclusions

A warm spring in 2006 may have caused a daphniid-edible phytoplankton mismatch at the Fort Whyte lakes. Similarly proposed for Lake Washington (Winder and Schindler 2004), daphniids may have responded strongly to a photoperiod cue while phytoplankton and rotifers developed relatively earlier in response to a shift in temperature cue. In the Fort Whyte lakes, direct evidence of a predator-prey mismatch remains elusive, as is the case for most field studies (Durant et al. 2007). In Chapter 3, hatching experiments and theoretical modelling results support the possibility of a daphniid-edible phytoplankton mismatch at the Fort Whyte lakes in 2006. These results suggest that variations in temperature-photoperiod cues can have important implications for daphniid but not rotifer hatchling abundance. Moreover, theoretical models developed in this study suggest that these differential daphniid and rotifer hatching responses can substantially alter competitive outcomes between the predators.

Of course, the importance of changes in zooplankton hatching responses will depend on its importance for population development in spring. Some lakes could remain unaffected in situations where over-wintering populations drive population increases in spring. The range of lakes to which this study applies is difficult to assess without proper implementation of a winter sampling regime including direct measures of zooplankton emergence. For the Fort Whyte lakes, few sources of information are available. Winter sampling by Loadman (1980) (biweekly samples) and the present author (single sample in 2007, not shown) shows that adult daphniids and rotifers are absent, at least for those years. Furthermore, the importance of zooplankton emergence might fluctuate between years. For example, in Lake Oneida, NY, a comparable small eutrophic lake, daphniid emergence greatly contributed to spring population development in some, but not all, years when over-wintering populations were low (Cáceres 1998), suggesting that mismatches between predator and prey might also depend on inter-annual over-wintering survivorship in daphniids (Hampton et al. 2006).

It is difficult to predict what impact climate change could have on the occurrence of daphniid-phytoplankton mismatches in lakes. In the long-term, mismatches could become less frequent if climate in the Canadian prairies continue to warm creating conditions of milder winters and shorter ice-covered seasons. This could have direct implications on daphniid over-wintering survivorship and lessen the importance of emerging individuals on population development. In addition, evolutionary processes should also be considered. For example, in Lake Constance, daphniids adapted to increasing cyanobacteria biomass over a relatively short period of time, i.e., 20 years (Hairston et al. 1999).

Ultimately, greater variability predicted with climate change could very well become increasingly associated to inter-annual fluctuations in plankton populations in small eutrophic lakes. More variable winter and spring temperatures could hamper the ability of daphniid populations to adapt to changing conditions. As a result, in the future, aquatic scientists and the public should expect quicker and more unpredictable changes to occur in lakes. Similar to behaviour stipulated by shallow lake alternative state equilibria theory (Scheffer et al. 1993), small eutrophic lakes in the Canadian prairies could see increasing fluctuations in water quantity and quality among years. More than ever, prediction of water quality in lakes could become a science of probability, not unlike that of meteorology.

Future directions and research

- Can early warming really lead to shifts in zooplankton species composition? *In-situ* mesocosms experiments could corroborate results from the present study's simulation models (Chapter 3). Population development responses in zooplankton could be tested by artificially varying water temperature at a range of photoperiods, i.e., different starting dates in the spring. There have been few investigations of temperature effects on trophic interactions (Beisner et al. 1997). Mesocosm experiments could help determine the possibility of predator-prey mismatching in temperate lakes.
- Can daphniids adapt to an earlier warming? Hatching experiments, over several generations, could be conducted to determine if early warming produces shifts in dominant clones. Some organisms have shown adaptation to an earlier spring. For example, a pitcher plant mosquito has evolved, over the past 24 years, to use a

shorter photoperiod to enter winter diapause as a response to a longer growing season with climate change (Bradshaw and Holzapfel 2001). Daphniids could be ideal model organisms owing to their short generation times.

- What are the factors associated with daphniid over-wintering success in temperate North-American lakes? Presence/absence of over-wintering daphniids could depend on factors such as latitude, longitude, ice-cover depth and season, oxygen, food-web structure, lake depth, snow cover. This research could be useful in determining which lakes are most susceptible to disruptions in zooplankton emergence dynamics. Only a single study, a literature review, has investigated the occurrence of over-wintering daphniids in European lakes (De Senerpont Domis et al. 2007).
- What are the species-specific relationships between temperature and biological rates in aquatic organisms? More basic research is needed to improve the growing field of theoretical ecological modelling. For many aquatic organisms, such as rotifers, the effects of increased temperature on biological rates such as filtration and assimilation rates have yet to be studied.

Literature cited

- Beisner, B. E., E. McCauley and F. J. Wrona. 1997. The influence of temperature and food chain length on plankton predator-prey dynamics. *Can. J. Fish. Aquat. Sci.* 54: 586-595.
- Bradshaw, W. E. and C. M. Holzapfel. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci. USA* 98: 14509-14511.
- Cáceres, C. E. 1998. Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. *Ecology* 79: 1699-1710.
- De Senerpont Domis, L. N., W. M. Mooij, S. Hülsmann, E. H. Van Nes and M. Scheffer. 2007. Can overwintering versus diapausing strategy in *Daphnia* determine match-mismatch events in zooplankton-algae interactions? *Oecologia* 150: 682-698.
- Durant, J. M., D. O. Hjermann, G. Ottersen and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Clim. Res.* 33: 271-283.
- Hairston, N. G., W. Lampert, C. E. Cáceres, C. L. Holtmeier, L. J. Weider, U. Gaedke, J. M. Fischer, J. A. Fox and D. M. Post. 1999. Rapid evolution revealed by dormant eggs. *Nature* 401: 446.
- Hampton, S. E., P. Romare and D. E. Seiler. 2006. Environmentally controlled *Daphnia* spring increase with implications for sockeye salmon fry in Lake Washington, USA. *J. Plankton Res.* 28: 399-406.
- Loadman, N.L. 1980. A comparison of the crustacean zooplankton populations of four man-made lakes in southern Manitoba. M.Sc. Thesis, University of Manitoba, Winnipeg, MB.

- Scheffer, M., S. H. Hosper, M-L. Meijer, B. Moss and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8: 275-279.
- Winder, M. and D.E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology* 85: 2100-2106.