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Climate change, diapause termination and zooplankton population dynamics: an experimental and modelling approach

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SUMMARY

1. Earlier spring warming as predicted for climate change will alter combinations of water temperature and photoperiod that act as emergence cues for zooplankton resting stages. As a result, water temperature cue thresholds will be experienced at shorter photoperiods, a variable independent of weather variations. Also, light intensity, another potentially important cue for zooplankton emergence, could decrease in many lakes if symptoms of climate change resemble those of eutrophication.
2. We designed a laboratory experiment to test the effects of three factors, temperature (6, 9 and 12 °C), photoperiod (13L : 11D and 16L : 8D) and light intensity (20 and 35 μE m^{-2} s^{-1}) on hatchling abundance and timing of hatching of daphniids (*Daphnia ambigua*) and rotifers (*Keratella* spp. and *Synchaeta pectinata*) from resting eggs. Further, we investigated the implications of potential changes in hatching dynamics, following variations in hatching cues, on zooplankton spring population development using predator–prey simulation models.
3. For hatchling abundance and timing of hatching, photoperiod had a significant effect for *D. ambigua* but not rotifers. *Daphnia ambigua* hatchling abundance decreased by 50% when incubated at conditions mimicking early spring (12 °C + 13-h photoperiod) compared to a later spring (12 °C + 16-h photoperiod). Light intensity has a significant effect only for *S. pectinata*, producing greater hatchling abundance at lower light intensity.
4. Simulation models suggest that in contrast to a later spring, an early warming produces a shift in spring zooplankton community composition, from daphniid to rotifer dominance. These patterns are primarily driven by differential zooplankton emergence response with variations in temperature–photoperiod cues.
5. Overall, our laboratory experiments and simulation models suggest that lakes with strong dependence on the 'resting egg-bank', characteristic of many shallow north-temperate lakes or in years with low winter survivorship of adult zooplankton, may be most susceptible to climate change. Further, fewer large grazers such as daphniids with an earlier spring may result in less control of cyanobacterial blooms in eutrophic lakes.

Keywords: climate change, emergence, photoperiod, resting eggs, temperature

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.*,

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2007). Climate variations have already been documented to disrupt matching between predator and prey populations including bird–insect (Thomas *et al*., 2001), fish–daphniid (Hampton, Romare & Seiler, 2006) and zooplankton–phytoplankton (Edwards & Richardson, 2004; Winder & Schindler, 2004) dynamics. 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 in north-temperate regions where most organisms have phenologies tightly coupled to spring conditions. In lakes, several authors have linked spring weather variations to changes in plankton population dynamics (Tirok & 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.

Climate change may have important consequences for zooplankton populations by affecting important environmental cues triggering spring dormancy termination. In north-temperate lakes, resting eggs from most species of daphniids and rotifers are released from diapause during spring (Wolf & Carvalho, 1989; Cáceres, 1998; Hairston, Hansen & Schaffner, 2000; Gyllström, 2004). Changes in spring warming may be especially critical for zooplankton that rely on both temperature and photoperiod cues to terminate dormancy (e.g. *Daphnia pulex* Stross, 1971; *Diaptomus sanguineus* Hairston & Kearns, 1995). Some mismatches between zooplankton and phytoplankton populations in spring have already been attributed to variations in temperature and photoperiod cues (Edwards & Richardson, 2004; Winder & Schindler, 2004). In Lake Washington, Winder & Schindler (2004) suggested that daphniids and diatoms responded to different seasonal cues. They observed that 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.

The contribution of the emerging individuals from the egg bank to initiate spring population development is most critical in lakes where few zooplankton over-winter. Lake depth was the most important factor in determining the presence of over-wintering populations in European lakes, with shallow lakes more likely to rely on emerging *Daphnia* for the spring population peak (De Senerpont Domis *et al*., 2007). Regional climate is probably another important factor affecting the probability of over-wintering zooplankton. Longer winters and thicker ice-cover likely lead to higher frequency of zooplankton populations being initiated in spring from the egg bank of diapausing eggs in Canadian prairie lakes.

Few experiments investigating cues that stimulate diapause termination have applied ecologically relevant environmental conditions (Cáceres & Schwalbach, 2001). Most experiments have been conducted to maximize hatching for community studies by using artificial conditions such as 24-h photoperiod and ephippial decapsulation (Pancella & Stross, 1963; Carvalho & 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 warming 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 probably 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 lowered light intensity could negatively affect zooplankton emergence. Furthermore, as some lakes strongly rely exclusively on zooplankton emergence from a resting egg-bank for spring population initiation, climate change could potentially alter zooplankton community structure and synchronization of some grazers with edible phytoplankton. Therefore, the objectives of this study are twofold: (i) a laboratory experiment was designed to determine daphniid and rotifer hatching success from resting eggs in response to variation in temperature–photoperiod cues as well as light intensity; (ii) simulation models were used to determine how potential changes in zooplankton emergence dynamics might affect zooplankton

population development, community structure and phytoplankton in lakes with strong benthic–pelagic linkages.

Methods

Hatching experiment

A factorial experiment was designed to test the effects of temperature, photoperiod and light intensity on hatchling abundance and timing of hatching of zooplankton resting eggs. Levels of each factor reflected different climate change scenarios in north-temperate lakes. Three levels of temperature (6, 9 and 12 °C), two photoperiods (13L : 11D and 16L : 8D) and two levels of light intensity (20 and 35 μE m^{-2} s^{-1}) were selected for the experiment. The experiment consisted of five replicates per combination (12), making 60 experimental units in total.

Sediment samples were collected on October 26, 2006 using an Ekman sampler from three lake depths (2, 3 and 4 m) at Fort Whyte Lake 2 in Winnipeg, Manitoba, Canada (49°49.020′N, 97°13.440′W), a small (5.2 ha) nutrient-rich lake. From each sampling site, the top 3 cm of sediments were collected, assuming that this represented the most viable 'egg-bank' (Cáceres & 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 °C in the dark, simulating winter conditions in the bottom sediments (Cáceres & Schwalbach, 2001; Vandekerkhove *et al*., 2005). After the dormancy period, sediments from the three depths were pooled and stirred thoroughly to ensure a well-mixed distribution of resting eggs from sources. Three large environment chambers were used for this experiment (Coldstream Products Corp., Winnipeg, MB, Canada). Environment chambers were set at one of three constant temperatures (6, 9 or 12 °C). In order to enhance the level of realism of the experiment, resting eggs were not isolated from the sediments.

Initially, a small subsample of sediments (15 mL) was collected for a single direct count of daphniid ephippia density. Sediments were sifted through incrementally smaller mesh sizes (1000–140 μm) until ephippia were readily isolated using a dissection microscope and forceps. Densities in the sediments were determined to be 3520 ephippia per litre of sediments for small *Daphnia* (ephippium *c.* 0.7 mm) and 680 ephippia per litre of sediments for larger *Daphnia* (ephippium *c.* 1.6 mm). These direct counts reflect potentially viable ephippia assessed on the basis of greenish colouration of resting eggs (C. E. Cáceres, unpubl. data). 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 ($11.5 \times 11.5 \times 5$ 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 (Glad Cling Wrap, Glad Products Co., Oakland, CA, U.S.A.) to minimize evaporative losses. COMBO was used 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 screen (low light intensity: 20 μE m^{-2} s^{-1}). The other half was left without mesh to produce the high light intensity treatment (35 μE m^{-2} s^{-1}). Light intensities were measured with a LI-185B light meter (LI-COR Inc., Lincoln, NE, U.S.A.) and values provided are those after passing through the transparent plastic film. Twenty units (10 with no mesh, 10 with mesh) were randomly placed under a set of cool white fluorescent lights (Philips F32T8, Royal Philips Electronics Inc., Amsterdam, The Netherlands) in each environment chamber. Timers controlled light to produce a 16-h photoperiod in each chamber. A 13-h 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 recolonization of the pelagic zone by emerging daphniids and rotifers is most critical (Wolf & 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 off and collected for enumeration of hatchlings. Sampling was conducted during the dark period under a red incandescent light bulb to facilitate manipulations

without disrupting light regimes. Fresh nutrient medium was then poured into each experimental unit followed by a thorough stirring of the sediments. Stirring of the sediments was conducted to simulate spring mixing conditions. 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. (*c.* 100 cells mL^{-1}) until species identification was confirmed. *Daphnia ambigua* Scourfield 1947 identification was based on Hebert (1995). Dead hatchlings were assigned to corresponding species that were identified from adults. Dominant rotifers, i.e. *Keratella* spp. [*K. quadrata* (Müller 1786) and *K. cochlearis* (Gosse 1851)] and *Synchaeta pectinata* Ehrenberg 1832, were counted and identified based on Chengalath, Fernando & George (1971) and Obertegger *et al.* (2006).

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. 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):

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

Three-factor analysis of variance (ANOVA) was used to test the effects of temperature, photoperiod and light intensity and their interactions on total hatchling abundance and timing of hatching. Normality and homogeneity of residuals were verified using Shapiro–Wilk's test and visual checks of residuals respectively. Hatchling abundance was log-transformed to normalize variance of the residuals. All statistical tests were performed in SAS 9.1.3 (SAS Institute Inc., Cary, NC, U.S.A.).

Population model

A model approach was used to test the potential implications of changing daphniid and rotifer emergence dynamics, measured in our hatching experiments (as described above), on population development. The applicability of the model was targeted for eutrophic waterbodies commonly found in the Canadian prairies. In these systems, zooplankton grazers typically co-exist with high biomasses of two functional groups of phytoplankton, i.e. edible algae and largely inedible cyanobacteria. Our model, therefore, included these two phytoplankton populations. In addition, initiation of populations of the two grazers, i.e. daphniids and rotifers, were directly derived from results of our hatching experiments to simulate spring population development in lakes dependent on the 'resting egg bank'. The model developed in the present study is similar to that developed by Kretzschmar, Nisbet & McCauley (1993) and De Senerpont Domis *et al.* (2007) for two competing algae groups and a single predator, i.e. daphniids. The model is extended to include a second predator, i.e. rotifers.

Four differential equations describe the two-predator and two-prey system:

$$\frac{dE}{dt} = r_1 E\left(1 - \frac{E}{K_1} - \alpha\frac{C}{K_1}\right) - D\left(\frac{g_1 E}{1 + g_1 h_1 E + g_2 h_2 C}\right) - R\left(\frac{g_3 E}{1 + g_3 h_3 E}\right) + d(K_1 - E)$$

$$\frac{dC}{dt} = r_2 C\left(1 - \frac{C}{K_2} - \beta\frac{E}{K_2}\right) - D\left(\frac{g_2 C}{1 + g_2 h_2 C + g_1 h_1 E}\right) + d(K_2 - C)$$

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

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

where predators are two groups of zooplankton: D, *Daphnia* and R, a rotifer such as *Keratella* sp. Prey comprise two groups of phytoplankton: E, a green algae (e.g. chlorophyta) and C, less edible algae, such as filamentous cyanobacteria (e.g. *Planktothrix* or *Aphanizomenon*). Parameters of the model are described in Table 1. Where possible, parameter estimates were chosen to reflect a 1.5 mm daphniid (e.g. *D. ambigua*) and a 0.17 mm rotifer (e.g. *Keratella* sp.).

In the model, *Daphnia* and rotifers graze on algae using a Holling type II functional response (DeMott, 1982; Porter, Gerritsen & Orcutt, 1982). Only daphniids are able to feed on filamentous cyanobacteria at reduced attack rate (g) and assimilation efficiency (e) as compared with edible algae. Predator mortality rates (m_1 and m_2) include both natural and zooplanktivorous-derived mortality. An explicit representation of predation by fish was not included as it was

Table 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	day^{-1}	Max. edible algae growth rate	2
r_2	0.12	0.25	0.37	day^{-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} day^{-1}	Daphniid edible algae grazing rate	4
g_2	0.037	0.070	0.119	L mg C^{-1} day^{-1}	Daphniid cyanobacteria grazing rate	5
g_3	3.657	4.503	5.544	L mg C^{-1} day^{-1}	Rotifer edible algae grazing rate	6
h_1	0.909	0.738	0.600	day	Daphniid edible algae handling time	7
h_2	0.909	0.738	0.600	day	Daphniid cyanobacteria handling time	7
h_3	1.427	1.159	0.941	day	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	day^{-1}	Daphniid mortality rates	12
m_2	0.04	0.04	0.04	day^{-1}	Rotifer natural mortality	13
m_3	0.03	0.03	0.03	day^{-1}	Rotifer mortality induced by daphniid interference	14
a_t	exp.	exp.	exp.	mg C L^{-1}	Daphniid hatching dynamics	15
b_t	exp.	exp.	exp.	mg C L^{-1}	Rotifer hatching dynamics	15
τ_1	32.04	21.36	16.02	day	Daphniid post-embryonic development time	16
τ_2	10.36	6.91	5.18	day	Rotifer post-embryonic development time	16

Sources: (1) Fort Whyte lakes, Winnipeg, Manitoba; (2) Rhee & Gotham, 1981; (3) Gibson, 1985; (4) Mourelatos & 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 & 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 & Ali, 1990; (12) spring (May–June) values reported in Prepas & Rigler, 1978; (13) values reported from 5 to 18 °C in Olsen *et al*., 1993; (14) Burns & Gilbert, 1986; (15) Results from controlled laboratory experiment by author, (16) Gillooly, 2000.

assumed to contribute little to short-term cycles of plankton (McCauley & Murdoch, 1987; McCauley, Murdoch & Watson, 1988). In addition, rotifer death rates also increase with daphniid density via direct and indirect interference (Burns & Gilbert, 1986), (m_3).

We assume that the plankton populations begin the season with no over-wintering populations, which is typical in many shallow north-temperate lakes (De Senerpont Domis *et al*., 2007). Hatching dynamics for daphniids (a) and rotifers (b) as a function of time (t) were derived from our hatching experiments. In our model, Daphniid hatchlings correspond to the experimental results for *D. ambigua,* and rotifer hatchlings use the pooled results for *Keratella* spp. and *S. pectinata*. Hatching data were converted from individuals m^{-2} to individuals L^{-1} by assuming that hatching occurred in a shallow polymictic lake with a volume of 7.40×10^8 L and a bottom-sediment surface area of 8.00×10^5 m^{-2} (similar to the source lake).

Different post-embryonic developmental times between species were also included in the daphniid and rotifer hatching dynamics. Inclusion of hatchlings into 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). The equations used for a 1.50 mm daphniid (τ_1, days) and a 0.17 mm rotifer (τ_2, days) 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, different temperature-dependent development is applied only 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 developmental time delays.

Scenarios explored with the model correspond to environmental conditions used in the hatching experiment including all combinations of the three temperatures (6, 9 and 12 °C) and two photoperiods (13- and 16-h photoperiods), giving six different scenarios. As physiological rates in ectotherms are temperature-dependent, all relevant parameter values in the model were adjusted for the three temperature scenarios based on published research (Table 1). When no publications were available, biological rates were indirectly estimated using a Q_{10} approach assuming most biological rates double with a 10 °C increase in temperature (Schindler, 1968). In our scenarios, 'early spring conditions' corresponds to a 13-h photoperiod while 'late spring conditions' corresponds to a 16-h photoperiod. Model scenarios were restricted to spring plankton dynamics during the first 60 days of plankton development following ice-off. In the present paper, STELLA 7.0.3 (Isee Systems Inc., Lebanon, NH, U.S.A.) was used for all model simulations.

A sensitivity analysis of the model was performed to assess how variations in parameter values affected the final outcome of three model components, rotifers, daphniids and cyanobacteria. This was conducted for model parameters that were estimated with the greatest uncertainty and were expected to have the most influence on model behaviour. Parameters tested included attack rates, assimilation rates, handling times and post-embryonic developmental times. The analysis compared the base parameter values (Table 1) with ±10% deviations in parameter values for daphniid and rotifer maximum and cyanobacteria end-point biomasses over a 60-day simulation.

Results

Hatching experiments

Numerically, *D. ambigua* (2725 ind.) was the dominant cladoceran hatching from sediments, while *Keratella* spp. (2541 ind.) and *S. pectinata* (3022 ind.) were the dominant rotifers. Other zooplankton species emerged only in low abundances [*Daphnia pulicaria* Forbes 1893, emend. Hrbácek 1959: 8 ind., *Daphnia parvula* Fordyce 1901: 47 ind., *Diaphanosoma* sp. Fischer 1850: 18 ind. and *Bosmina longirostris* (Müller 1785): 23 ind.] and primarily in the 12 °C treatment. As a result, only results for *D. ambigua*, *Keratella* spp., *S. pectinata*, are considered in further analyses below.

After exposure to environmental cues, emergence began immediately for *Keratella* spp. and several days later for *S. pectinata* and *D. ambigua* (Figs 1–3). Emergence of *Keratella* spp. and *D. ambigua* from resting eggs continued throughout the 33-day incubation period at all temperatures tested (Figs 1 & 3). At incubation temperatures of 9 and 12 °C, hatching of *S. pectinata* resting eggs had generally ceased after 24 and 21 days, respectively (Fig. 2b,c).

A three-factor ANOVA suggested that the manipulated environmental cues (temperature, photoperiod and light intensity) differently affected rotifer and daphniid hatching abundance. As expected, temperature had a significant main effect on hatching abundance for *D.* ambigua, *Kereatella* spp. and *S. pectinata* (Table 2). In general, few resting eggs were able to develop into neonates when incubated at 6 °C (Fig. 4) and hatchling abundance was greater at incubation temperatures of 9 and 12 °C for all zooplankton. The effects of changes in light regimes, i.e. photoperiod and light intensity, on hatchling abundance differed among rotifers and daphniids. *Daphnia ambigua* hatchling abundance was significantly greater when resting eggs were exposed to a 16-h photoperiod, especially when incubated at 12 °C (Table 2; Fig. 4e,f). The most striking difference was found for *D. ambigua* at a high light intensity where mean hatchling abundance was 44.4 (±3.7) and 82.4 (±10.7) for 13 and 16-h photoperiods, respectively (Fig. 4e,f). In contrast, variation in photoperiod alone did not significantly affect rotifer hatchling abundance. Light intensity had a significant main effect on *S. pectinata* hatchling abundance (Table 2). Interestingly, high light intensity decreased *S. pectinata* hatchling abundance (Fig. 4c,d).

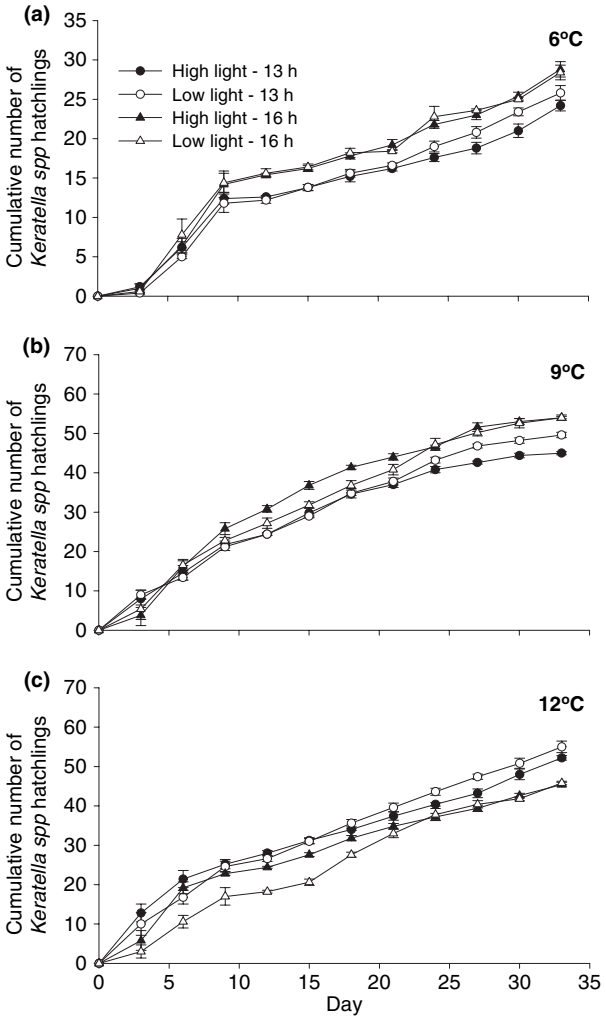

Fig. 1 Cumulative mean number of *Keratella* spp. hatchlings ±1 SE (n = 5) over time (33 days) incubated at three temperatures, 6 °C (a), 9 °C (b) and 12 °C (c), at two photoperiods (13 h; circle and 16 h; triangle) and at two light intensities (high light; filled symbol and low light; open symbol, see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

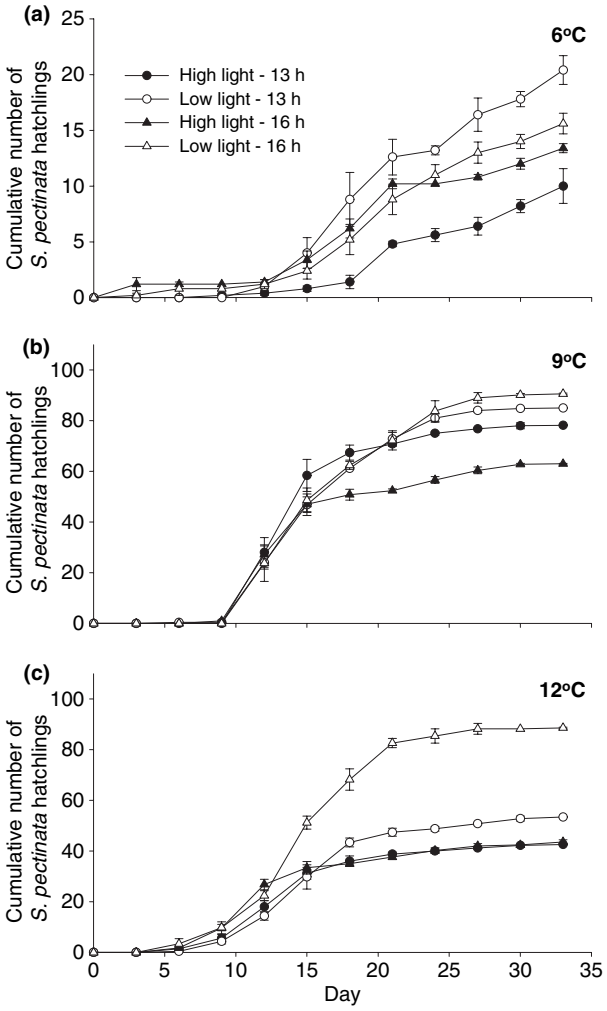

Fig. 2 Cumulative mean number of *Synchaeta pectinata* hatchlings ±1 SE (n = 5) over time (33 days) incubated at three temperatures, 6 °C (a), 9 °C (b) and 12 °C (c), at two photoperiods (13 h; circle and 16 h; triangle) and at two light intensities (high light; filled symbol and low light; open symbol,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

A significant temperature × photoperiod interaction effect was shown for the rotifer *Keratella* spp. hatchling abundance (Table 2). In general, for *Keratella* spp., increasing temperatures produced greater hatchling abundance. This pattern was reversed, however, at 12 °C at a 16-h photoperiod (Fig. 4a,b). Also, a significant three-way interaction (temperature × photoperiod × light intensity) was shown for *S. pectinata* (Table 2). Only a 16-h photoperiod caused substantial hatchling abundance discrepancies between high and low light intensities (Fig. 4c,d).

In comparison, timing of hatching showed similar response to the experimental factors tested (Table 2). However, within zooplankton groups, the magnitude of differences in mean time to hatch between 9 and 12 °C was generally small (<2 days), regardless of light regime (Fig. 5). The largest differences in timing were found in comparison 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 (Fig. 5). A 16-h photoperiod decreased mean time to hatch for *D. ambigua* but this had little effect on rotifers. For *S. pectinata*, high light intensity negatively affected timing of hatching from the sediments.

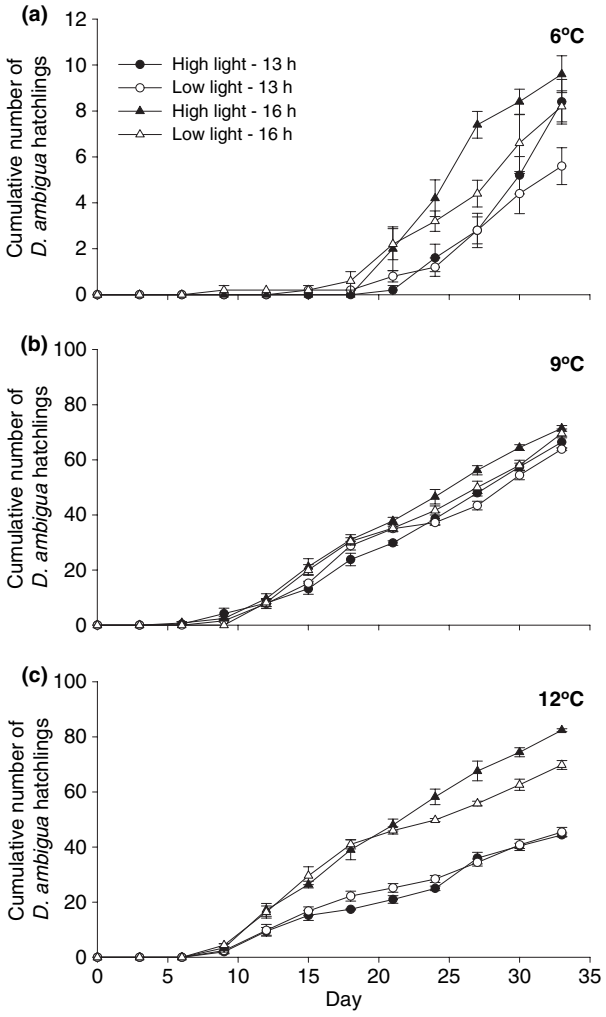

Fig. 3 Cumulative mean number of *Daphnia ambigua* hatchlings ±1 SE (n = 5) over time (33 days) incubated at three temperatures, 6 °C (a), 9 °C (b) and 12 °C (c), at two photoperiods (13 h; circle and 16 h; triangle) and at two light intensities (high light; filled symbol and low light; open symbol,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

Predator–prey population models

Model simulations were used to explore whether the observed variations in hatching dynamics might affect final zooplankton and phytoplankton population dynamics in shallow north temperate lakes experiencing different warming conditions (Fig. 6).

Early spring warming scenarios reflect conditions when warming occurs at a 13-h photoperiod (Fig 6-a,c,e). At the lowest temperatures (6 and 9 °C), model zooplankton populations were absent or very low in density over the 60-day period due to the long time requirements for embryonic and post-embryonic development at low water temperatures. In the 12 °C scenario (Fig. 6e), rotifers were the dominant zooplankton attaining a maximum of 0.276 mg C L^{-1} compared to 0.167 mg C L^{-1} for daphniids. Changes in emergence dynamics allowed rotifers to outcompete daphniids for the edible food resource.

Late spring warming scenarios correspond to warming simulations at the 16-h photoperiod (Fig. 6b,d,f). Both 6 and 9 °C scenarios show similar population dynamics compared to the early spring warming scenario (Fig. 6b,d). Again, at 6 °C model zooplankton were not present and low numbers were 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 (Fig. 6f). Model results for a 16-h photoperiod at 12 °C reversed competitive outcomes between daphniids and rotifers. Here, daphniid maximum biomass was over 10× greater than that of rotifers, attaining 0.508 mg C daphniids L^{-1} compared to 0.054 mg C rotifers L^{-1}.

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 (Fig. 6). Cyanobacteria biomass dominated over edible algae only when populations of daphniids or rotifers exploited edible algae. In the early spring scenario (13-h phototperiod + 12 °C, i.e. Fig. 6e), end-point cyanobacteria remained highest (0.683 mg C L^{-1}) as a result of rotifer dominance. In comparison, increased daphniid biomass in the late spring scenario (16-h photoperiod + 12 °C, i.e. Fig. 6f) lowered cyanobacteria biomass to 0.589 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. The sensitivity analysis shows that small variations (±10%) in predator parameters in the model generally had no effect on the overall competitive outcomes (Dupuis, 2008). Therefore, this suggests that simulation results were robust.

Table 2 Results of a three-factor ANOVA testing for the effects of temperature, photoperiod, light intensity and their interactions on *Keratella* spp., *Synchaeta pectinata* and *Daphnia ambigua* hatchling abundance during an incubation period of 33 days

		Keratella spp.	*S. pectinata*	*D. ambigua*
	d.f.	*F*	*F*	*F*
Hatchling abundance (log)				
Temperature	2	69.15***	126.50***	242.49***
Photoperiod	1	0.48	0.16	8.33**
Light intensity	1	0.47	12.80***	2.68
Temp. × photo.	2	4.39*	1.50	2.04
Temp. × light int.	2	0.03	0.59	1.18
Photo. × light int.	1	0.59	0.03	0.04
Temp. × photo. × light int.	2	0.05	3.79*	0.16
Mean time to hatch				
Temperature	2	6.64**	82.17***	78.10***
Photoperiod	1	0.07	2.96	12.83***
Light intensity	1	3.22	6.01*	3.79
Temp. × photo.	2	0.34	3.13	2.35
Temp. × light int.	2	0.57	0.94	2.13
Photo. × light int.	1	0.00	3.57	1.26
Temp. × photo. × light int.	2	0.64	3.59*	0.49

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Discussion

Effects of climate change on zooplankton emergence and population development

Results from the hatching experiments show that under conditions of warmer temperatures and shorter photoperiod, mimicking earlier spring warming with climate change, fewer *D. ambigua* emerge from the sediments while rotifers *Keratella* spp. and *S. pectinata* are less affected. Hence, climate change could produce decreased success in daphniid emergence from resting eggs and consequently delay population development in the water-column. Our study confirms that even small variations in temperature–photoperiod cues could alter overall zooplankton emergence success. Ecologically, in lakes where spring emergence from diapausing eggs plays a strong role in zooplankton population development, modelling results from this study demonstrate how this could alter zooplankton community composition from large grazers such as daphniids to smaller ones such as rotifers.

Patterns of emergence

Emergence from resting eggs helps establish the starting conditions for zooplankton population development in spring in shallow temperate lakes. In this study, zooplankton emergence from sediments continued for a longer time compared to experiments using isolated resting eggs (e.g. Pourriot, Rougier & Benest, 1980; Vandekerkhove *et al.*, 2005). In nature, resuspension of the sediments is likely required to subject resting eggs to appropriate cues for hatching to occur (Hairston & Kearns, 2002; Gilbert & Schröder, 2004). Our study and that of Cáceres & 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 & 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.

Effects of environmental cues on emergence

Our study demonstrates that early warming could negatively impact daphniid but not rotifer hatching dynamics in north-temperate lakes. Gyllström & Hansson (2004) suggest that daphniids and rotifers might depend on different cues to terminate dormancy. In general, a single seasonal indicator, a temperature cue, is required by rotifers while some daphniid species respond to both a temperature and a photoperiodic control (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 our study, temperature had a significant effect on all zooplankton hatchling abundance.

Similar to other studies testing factors affecting release of diapause in *Daphnia* (Gyllström &

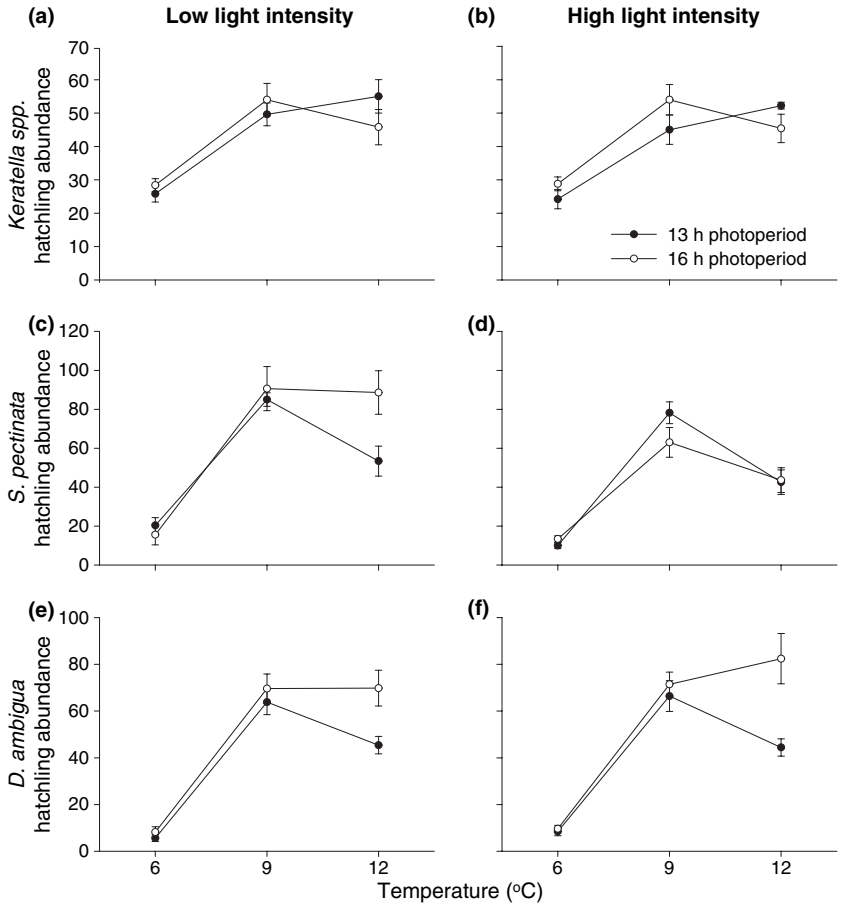

Fig. 4 Interaction plots of mean cumulative totals for *Keratella* spp. (a,b), *Synchaeta pectinata* (c,d) and *Daphnia ambigua* (e,f) hatchling abundance ±1 SE (n = 5) for two factors, temperature (6, 9 and 12 °C) and photoperiod (13 and 16 h). Results for both, low and high light intensities are shown.

Hansson, 2004), our experiments confirm that photoperiod is also a significant factor contributing to dormancy termination in *D. ambigua* but this was most pronounced in treatments of 12 °C. In contrast, 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 (10–25 °C) and photoperiod (16 and 24 h) 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 observation and further underlines the sensitivity of some daphniid populations to relatively small variations in photoperiod, i.e. 13- and 16-h day-lengths compared 16 and 24 h in Vandekerkhove *et al.* (2005).

Variations in temperature–photoperiod cues primarily impact hatchling abundance not timing of emergence. 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 fewer than 2 days at 9 and 12 °C regardless of photoperiod or light intensity.

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, Cooreman & Sorgeloos, 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,

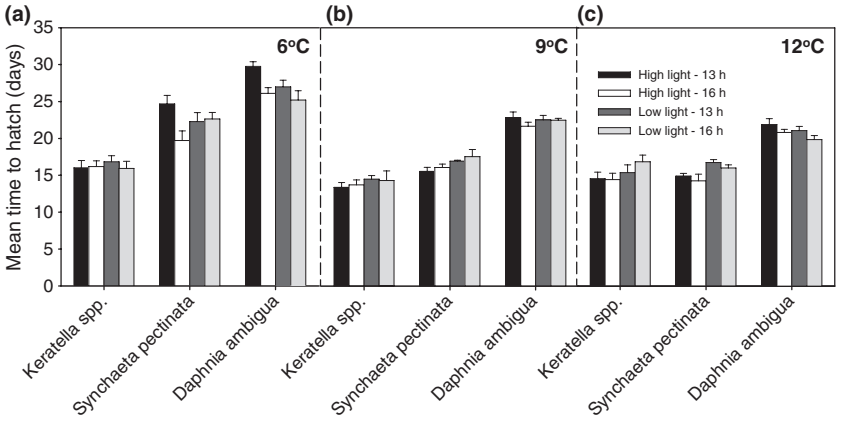

Fig. 5 Mean time to zooplankton hatching (days) ±1 SE (n = 5) for resting eggs incubated at 6 °C (a), 9 °C (b) and 12 °C (c) under combinations of two photoperiods (13 and 16 h) and two light intensities (high and low, see text for values).

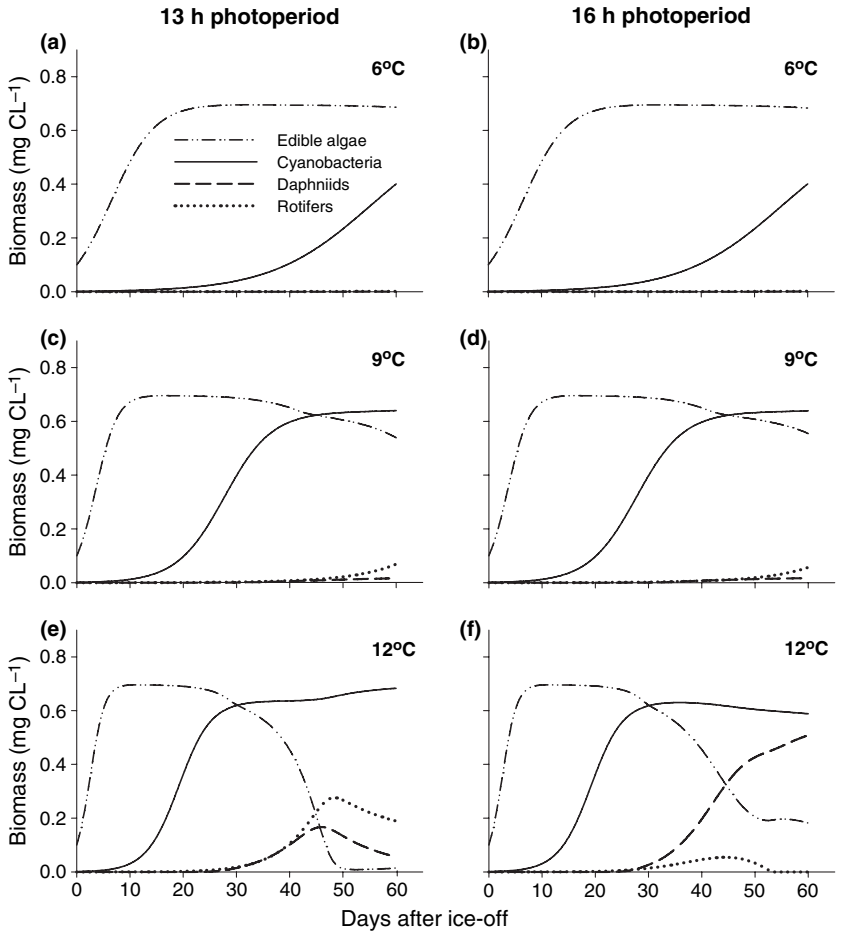

Fig. 6 Simulation results in biomass (mg C L^{-1}) for a two predator (daphniids and rotifers) and two prey (edible algae and filamentous cyanobacteria) model under different zooplankton hatching conditions, i.e. three temperatures (6, 9 and 12 °C) and two photoperiods (13 and 16 h).

S. pectinata can sometimes represent 80% of the total rotifer community in lakes (Stemberger & 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.

Effect of differential hatching response on zooplankton populations

Simulation models were developed to explore the potential disruption of early spring warming on zooplankton population dynamics. This is particularly

relevant in 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 our models, zooplankton population development within 60 days was substantial only at temperatures of 12 °C. At low temperatures (6 and 9 °C), a longer period was required.

Overall, the simulations at 12 °C imply that differential responses in daphniid and rotifer emergence and development times to variations in temperature–photoperiod cues are a potentially critical mechanism 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 grazers, e.g. daphniids and rotifers, can depend on which grazer has the greatest emerging biomass from the sediments. Similarly, in long-term studies of Lake Washington, earlier warming caused mismatching to occur between populations of daphniids and edible algae while rotifer populations continued to develop in synchrony with spring peaks of edible algae (Winder & Schindler, 2004). Our simulation models support Winder & 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 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). Simulation models by these authors showed that when few daphniids emerge from the sediments, warming (+6 °C) causes 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 and a shorter photoperiod. In summary, model results suggest that some lakes with strong dependence on resting eggs for population development could show a decreasing probability of a clear-water phase, an increasing proportion of smaller grazers, and increasing biomass of filamentous cyanobacteria.

Limitations of the model

Simple plankton models are approximations of reality and can help to elucidate underlying mechanisms driving the observed patterns. To maintain simplicity, our models were run at constant temperatures and photoperiods over the 60-day simulations. We were primarily interested in gaining an understanding of effects on fixed environmental conditions (temperature and light regimes). In addition, 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. Future studies should include more direct measurements of temperature effects on organisms and should consider seasonal change to better simulate real systems.

Furthermore, our model did not consider other biotic and abiotic factors important to plankton dynamics, e.g. physical aspects such as mixing depth and light penetration. With climate change, these factors will likely play an important role in phytoplankton abundance and composition (Berger *et al*., 2007; Tirok & Gaedke, 2007). It is also unclear which populations of daphniids are more susceptible to an earlier warming trend. For example, 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 over-wintering 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. Evolutionary adaptation might explain some discrepancies between some North American and European studies linking climate change to plankton dynamics (Straile, 2000; Winder & Schindler, 2004).

In conclusion, 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 *D. 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 *S. pectinata* hatchling abundance.

Resting-eggs incubated within the sediments continued hatching for longer than in other published laboratory experiments. Intermittent mixing of sediments during the experiment probably promoted continued emergence throughout the 33-day incubation period. Thus, our experiments simulate conditions of prolonged sediment mixing in spring found in shallow polymictic lakes.

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, our 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.

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