

Changing climate cues differentially alter zooplankton dormancy dynamics across latitudes

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Summary

1. In seasonal climates, dormancy is a common strategy that structures biodiversity and is necessary for the persistence of many species. Climate change will likely alter dormancy dynamics in zooplankton, the basis of aquatic food webs, by altering two important hatching cues: mean temperatures during the ice-free season, and mean day length when lakes become ice free. Theory suggests that these changes could alter diversity, hatchling abundances and phenology within lakes, and that these responses may diverge across latitudes due to differences in optimal hatching cues and strategies.

2. To examine the role of temperature and day length on hatching dynamics, we collected sediment from 25 lakes across a 1800 km latitudinal gradient and exposed sediment samples to a factorial combination of two photoperiods (12 and 16 h) and two temperatures (8 and 12 °C) representative of historical southern (short photoperiod, warm) and northern (long photoperiod, cool) lake conditions. We tested whether sensitivity to these hatching cues varies by latitudinal origin and differs among taxa.

3. Higher temperatures advanced phenology for all taxa, and these advances were greatest for cladocerans followed by copepods and rotifers. Although phenology differed among taxa, the effect of temperature did not vary with latitude. The latitudinal origin of the egg bank influenced egg abundance and hatchling abundance and diversity, with these latter effects varying with taxa, temperature and photoperiod.

4. Copepod hatchling abundances peaked at mid-latitudes in the high temperature and long photoperiod treatments, whereas hatchling abundances of other zooplankton were greatest at low latitudes and high temperature. The overall diversity of crustacean zooplankton (copepods and cladocerans) also reflected distinct responses of each taxa to our treatments, with the greatest diversity occurring at mid-latitudes (~56 °N) in the shorter photoperiod treatment.

5. Our results demonstrate that hatching cues differ for broad taxonomic groups that vary in developmental and life-history strategies. These differences are predicted to drive latitude-specific shifts in zooplankton emergence with climate change and could alter the base of aquatic food webs.

Key-words: bet hedging, common garden experiment, diapause, dormancy termination, optimal hatching fraction, resurrection ecology, spring warming, temporal dispersal

Introduction

Dormancy is a common strategy that is essential to the persistence of many species in seasonal climates and has the potential to be strongly impacted by climate change (Hance *et al.* 2007; Williams, Henry & Sinclair 2015). Both the onset and termination of dormancy depend on

environmental cues, with many species from diverse taxa responding to climatic conditions such as temperature and precipitation (Vandekerkhove *et al.* 2005; Hance *et al.* 2007; Levine, Mceachern & Cowan 2008). Despite the importance of dormancy for community assembly and ecological dynamics generally (Hairston & Kearns 1995; Ellner *et al.* 1999; McNamara & Houston 2008), there has been relatively little research on the impacts of climate on dormancy dynamics for many taxa, and the work that

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has been done has often been too localized to allow for the general predictions needed when planning for climate change (Hairston 1996; Dupuis & Hann 2009; Angeler 2011).

Zooplankton are numerically and functionally dominant animals that form the basis of aquatic food webs, with taxa performing different roles within lake ecosystems (Barnett, Finlay & Beisner 2007). Although dormancy is a critical part of the annual life cycle of most zooplankton species (Varpe 2012), biogeographic trends in zooplankton dormancy dynamics, and their climatic underpinnings, are not understood. Nonetheless, most zooplankton species are sensitive to environmental cues that alter their hatching dynamics, and as a result may be particularly sensitive to climate change. Shifts in the timing, abundance or diversity of species that hatch as climate cues shift could scale up to impact the functioning and trophic structure of aquatic ecosystems (Winder & Schindler 2004; Woodward, Perkins & Brown 2010; Dossena *et al.* 2012).

In freshwater lakes, climate change is altering cues that terminate zooplankton dormancy by changing the timing of ice-free conditions in spring and average spring temperatures (IPCC 2013). In temperate and polar aquatic ecosystems, water temperature and photoperiod are considered the primary cues for terminating zooplankton dormancy (Stross 1966; Sorgeloos 1973; May 1987; De Stasio 2004). Many zooplankton have long-term dormancy strategies, where some proportion of eggs hatch in a given year and the remainder lay dormant, potentially hatching in subsequent years (Cáceres & Tessier 2003). Despite some overwintering under lake ice (e.g. Vanderploeg *et al.* 1992) most species produce eggs in the fall that hatch somewhat synchronously in the spring as day length and temperature increase (Hairston, Hansen & Schaffner 2000; but see De Stasio 1990), producing a seasonal succession in the taxa that appear (Hutchinson 1967).

A major challenge to predicting the impact of climate change on dormancy dynamics within ecological communities is that hatching rates, or termination of dormancy, are likely to differ across latitudes, even for similar taxa (Posledovich *et al.* 2015). In regions where active individuals fail to reproduce in some years, species are predicted to have lower average hatching rates (Cohen 1966; Levins 1969; Ellner 1985). As a result, the prevalence of dormancy has been shown to increase towards the poles in some taxa, such as plants and insects, because high seasonal variation and short growing seasons have selected for dormancy (Mousseau & Roff 1989; Molina-Montenegro & Naya 2012). This 'temporal dispersal' strategy, referred to as bet hedging in the evolutionary literature (e.g. Venable 2007), and storage in literature on species coexistence (e.g. Chesson 1994), maintains long-term persistence by decreasing the mean and variability of population growth among years (Slatkin 1974; Ellner 1985).

In addition to a gradient in hatching rates across latitudes, strong selection for high latitude species to emerge and reproduce in a short growing season may result in a gradient of sensitivity to the cues that break dormancy (Conover, Duffy & Hice 2009); the importance of fast emergence from dormancy may be reduced in lower latitude regions with longer growing seasons (Masaki 1961). As a result, conditions that are typical of an ideal spring (warm temperatures during a short photoperiod), may elicit higher and faster hatching rates in northern compared with southern lakes. More generally, the interplay among latitude, long-term dormancy and phenology is expected to lead to latitudinal differences in hatching rates and cues that correspond to differences in species' traits (species sorting, e.g. Whittaker 1975) as well as differences among populations of widespread species (local adaptation, e.g. Kawecki & Ebert 2004).

A second challenge to predicting the effects of climate on dormancy lies in determining whether co-occurring taxa have qualitatively similar responses to changing climatic cues. When most species in a community are limited by similar environmental constraints, responses to climatic cues should be similar, as has been seen for some annual plants (Elmendorf & Harrison 2009). However, the major zooplankton taxa have very different rates of development (Gillooly 2000), minimum sizes at which reproduction occurs (Geller 1987; Maier 1994), and reproductive modes and, as a result, rates of reproduction (Allan 1976). These differences may lead to a systematic divergence in responses to the climatic cues that terminate dormancy, with smaller taxa being more responsive to temperature (Winder & Schindler 2004; Adrian, Wilhelm & Gerten 2006). In addition, species that have dormant stages may coexist by specializing on environmental conditions that occur in only some years (via the storage effect; Chesson 1994). Indeed, the sensitivity of zooplankton to hatching cues can differ at several taxonomic levels, from broad zooplankton taxa (copepods, cladocerans and rotifers), to co-occurring species within lakes (e.g. Dupuis & Hann 2009). However, much of the literature on hatching dynamics has focused on subsets of the diversity within a lake by examining a single species or taxon at a time.

Despite the potential for different responses to cues that end dormancy across latitudes and among taxa, aquatic studies have yet to incorporate this complexity into studies of plankton dormancy dynamics to understand the effects of current and changing climatic conditions. Prior research has mainly focussed on assessing dormancy dynamics in a small number of lakes within a region (e.g. Arnott & Yan 2002) or has combined lake samples into regional mixtures (e.g. Vandekerckhove *et al.* 2005), precluding an analysis of latitudinal variation in hatching dynamics.

In this study, we determine how temperature and day length impact dormancy dynamics of freshwater zooplankton that differ in latitudinal origin. We collected sediment containing 'egg banks' from 25 lakes across an

1800 km latitudinal gradient and exposed a subsample of the sediment from each lake to a factorial treatment of high and low temperature crossed with long and short photoperiod. By assessing the effects of temperature and photoperiod on hatching abundance, diversity and phenology within each lake, we were able to test how these climatic cues drive biotic responses of taxa that co-occur across a latitudinal gradient. Based on the ecological and evolutionary factors considered above, we predicted that: (i) at higher latitudes, the density of eggs in the egg bank will increase, while under typical spring conditions the abundance of hatchlings will decrease at higher latitudes because selection for dormancy is higher in northern regions, (ii) high temperatures will advance hatching phenology, and this advance will be greatest for small-bodied taxa, (iii) conditions suggestive of a good, early season (warm temperature and short photoperiod) will generate the greatest abundance of hatchlings in northern lakes, because the ability to capitalize on favourable conditions is essential for persistence in those regions and (iv) conditions typical of a late season (long days coupled with high temperature) will decrease hatchling abundance and diversity, and this effect will be strongest in northern lakes because they typically experience short growing seasons.

Materials and methods

We collected sediment samples from 25 lakes along an 1800 km latitudinal gradient that ranged from southern British Columbia to the mid-latitude Yukon Territory in Canada in July 2011 (Fig. 1). The pelagic zooplankton community of these lakes had been previously characterized in the 1960s and 1970s (Lindsey

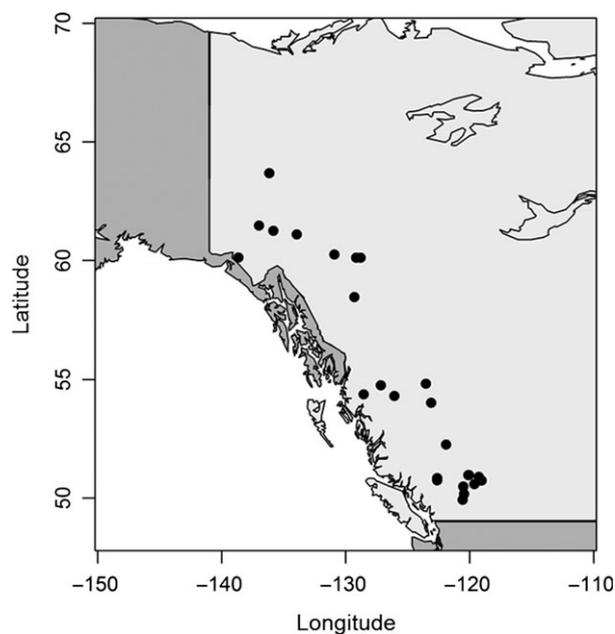


Fig. 1. Map displaying the location of the 25 lakes in western Canada that were sampled for sediment in July 2011.

et al. 1981; Patalas, Patalas & Salki 1994) and were again characterized in 2011 (Jones unpublished). Chemical and physical properties of lakes were also characterized in earlier studies and were used to select lakes that showed no latitudinal patterns in these properties (Fig. S1, Supporting information).

We used a 6" × 6" × 6" Eckman dredge to collect the top 5 cm of the benthos from nearshore areas, from a maximum depth of 20 m if shallower samples could not be collected (two samples per lake which were combined). Most hatching occurs in nearshore environments (De Stasio 1989; but see Hairston, Hansen & Schaffner 2000), which are characterized by higher temperatures and light levels as well as more substantial mixing events (Hairston & Kearns 2002). Eggs that settle in the deeper parts of the lake require mixing events to re-suspend and transport them to the sediment surface in shallower nearshore waters (Kerfoot *et al.* 2004). Previous work investigating egg viability through time has been mixed; some studies show that egg quality declines with age (e.g. Weider *et al.* 1997), while others have found that viability is maintained through time for decades to hundreds of years (e.g. Cousyn & De Meester 1998). Our collection was designed to maximize egg collection by targeting depths where eggs settle but would still be likely to re-suspend through mixing events. Because our sampling was consistent across lakes, and eggs from deeper waters can hatch when incubated under nearshore conditions (Cáceres & Tessier 2003), we expect our results to reflect general trends.

The collected sediment was packaged in black whirlpak bags to eliminate light then stored in the dark at 4 °C in a refrigerator (to simulate the conditions of a lake bottom to maintain dormancy) until the experiments were initiated in 2012. We determined the density of copepod, cladoceran and rotifer eggs using the sugar floatation method on a 100 g subsample of sediment (Marcus 1990). We identified different types of eggs by morphology and counted the eggs of cladocerans (eggs within undamaged, unopened ephippia), rotifers and copepods. Cyclopoid copepods diapause as juveniles (Ferrari & Dahms 2007), therefore, our egg counts of copepods refer to the density of calanoid eggs only.

To mimic spring conditions when the bulk of hatching occurs (Hutchinson 1967; Hairston, Hansen & Schaffner 2000), we compiled thaw dates for our focal lakes using national (Polar Data Catalogue) and international (The National Snow and Ice Data Center) data bases. We determined average ice thaw dates by converting annual thaw dates into Julian dates and taking the average from 1971 to 2000. The average day length and air temperature for that month was recorded to determine appropriate treatments. We were unable to collect this information for all lakes, but had data for lakes across our entire gradient and used typical conditions from northern and southern lakes for our treatments (Table S1).

Our experimental treatments were designed to simulate a nearshore aquatic environment, as the majority of spring hatching occurs in the littoral zone for freshwater crustaceans (Cáceres & Schwalbach 2001; Cáceres & Tessier 2003). Our experiment crossed temperature (two levels; 8 and 12 °C) and light (16 and 12 h), which represent the approximate mean photoperiods and spring temperatures at the northern limit and southern limit, respectively. We conducted the experiment in a growth chamber, by setting up 10 racks that each had a single photoperiod treatment. Within these treatments, we randomized the placement of 20 water baths (each bath was 30" × 22" × 10.5"), with water baths randomly assigned to racks and equally divided between

two temperatures. We then placed egg banks from five lakes inside each bath, with the egg banks housed in their own 7-l aquaria (Fig. S2; Table S2). Thus, the treatment combination was nested in bath and rack, which we account for using a mixed model (below). We used submersible heaters to increase water temperature and water pumps to circulate water within each bath. We enclosed each rack with shade cloth to eliminate surrounding light. After 12 h, lights in the short day treatment would turn off, while the 16-h photoperiod treatment would receive light for an additional 4 h. For each lake, we divided the sediment into four samples of 75 g and randomly assigned each sample to a temperature by light treatment (temperature \times light \times 25 lakes = 100 experimental units; Fig. S2; Table S2). By incorporating the lake as a random effect we were able to account for the lack of independence among treatments (see data analyses section). However, because each lake was exposed to each treatment combination only once, we do not have an estimate of error for each lake within a treatment. The sediment layer was spread evenly to <1 cm thick across the aquarium, such that all eggs were close enough to the sediment surface to experience treatment conditions.

To create a suitable environment for zooplankton, aquaria were filled with four litres of fresh artificial *Daphnia* medium (ADaM) and four phytoplankton species (*Ankistrodesmus* sp., *Chlorella vulgaris*, *Scenedesmus obliquus*, *Pseudokirchneriella subcapitata*; approximately 30×10^6 cells of each species). We replenished the ADaM and phytoplankton every 6–10 days and topped up the mesocosms with dechlorinated water as needed every 3 days.

The experiment ran for 60 days, with zooplankton collected from each aquarium every 3 days. To collect zooplankton, we created polycarbonate (lexan) inserts that were the length of the aquaria and 1 cm deep. The inserts were placed in the bottom of the aquaria prior to the initiation of the experiment. We also created 20- μ m mesh filters that were designed to exactly fit the dimensions of the aquaria. To collect the plankton that hatched, we conducted a single 'sweep' by anchoring the filter on the lexan guide rails at one end of the aquarium, then gently pushing the filter through the water, along the length of the aquarium. This method moderately disturbed the sediment layer, but this layer remained <1 cm deep.

On sampling days, we counted all copepods, cladocerans and rotifers. At the same time, we identified juvenile crustaceans to the family level (cladocerans) or order level (copepods) using a dissecting microscope. We did not identify rotifers; therefore, the analysis and discussion of zooplankton diversity refers to the crustacean community only. Crustacean zooplankton juveniles were individually reared in 50-ml centrifuge tubes. We maintained individuals by transferring them every 3–7 days into fresh ADaM and feeding them approximately 30×10^6 cells of a mixture of the four phytoplankton species previously described every 3 or 4 days. Following the rearing process, we identified the individuals that survived to maturity (65%). The individuals that did not survive to maturity could only be included in the abundance analysis as they were not identified to species or genus.

DATA ANALYSES

We used R statistical software for all analyses (R Core Team, 2014). We tested for a relationship between latitude and the density of dormant eggs (log transformed to account for heteroscedasticity of residuals) using a linear mixed model (lmer function in lme4

package; Bates *et al.* 2014). Taxon, latitude and their interaction were included as fixed factors and lake as a random factor.

In all analyses (egg density, phenology abundance and diversity), we began with the most complex model for fixed effects and dropped higher order terms if they did not significantly improve model fit (using log likelihood ratios based on maximum likelihood) until we arrived at a best fit model. All random effects were kept in models, as these reflected known constraints on sampling (i.e. a random effect for lake as each lake was used in all four treatment combinations) and on experimental design (a random effect for bath nested within rack to account for the nesting structure). We initially explored the effect of number of eggs on emergence dynamics. However, egg number was not a significant predictor of abundance or diversity in any group (all *P* values > 0.20), and we therefore discuss the difference in these responses qualitatively instead of including egg number as a covariate in abundance and diversity analyses.

To test for changes in phenology, we calculated the first hatching day and the time for 50% of individuals to hatch for each taxon (cladocerans, copepods, rotifers) in each lake over the 60 days experiment. We fit linear mixed models with a Gaussian distribution and the same fixed factors and random factors as described previously. A single lake, Watson, was an outlier and drove a 3 way interaction (Tables S3 and S4) so we removed it from all subsequent phenology analyses.

We determined how our treatments affected the number of hatchlings of copepods, cladocerans and rotifers using generalized linear mixed models with a Poisson distribution and a log link function. To account for a nonlinear trend in the hatching rates across the latitudinal gradient, we created a second-order polynomial latitude variable (after centring latitude), which accounted for the curvature in the data. Initial models included latitude, latitude², temperature (8 or 12 °C), day length (16 or 12 h) and taxon (copepod, cladocerans, rotifer), and their interactions as fixed effects. The individual lake was included as a random effect and the experimental water bath nested within the shelf rack was added as an additional random effect. Zooplankton hatching was calculated as the total number of individuals that emerged over the 60 days duration of the experiment. If we detected a significant 4th order interaction (temperature \times photoperiod \times latitude \times taxon interaction), we fit the models separately for each taxon as the scale differed among taxa by orders of magnitude.

To test how seasonal cues impact crustacean hatchling diversity across latitudes, we used a similar statistical approach. The predictor variables for the initial full model contained latitude, latitude², temperature, day length and taxon (copepod or cladoceran), and their interactions as fixed effects, and the same random effects as in the abundance analysis. For our response variable, we developed a 'proportional diversity' measure that counted the number of species that emerged relative to the total number of species found in the lake [based on previous standardized sampling from the lakes (Lindsey *et al.* 1981; Patalas & Salki 1994) and samples that we collected following the same methods in 2011 (Jones unpublished)]. The proportional diversity approach allowed us to account for differences in species richness among the lakes, which also shows a latitudinal trend (Fig. S3). Our resulting data were binomial (hatching species/total species) and analysed using a generalized linear mixed model with a logit link function. As with the hatchling abundance analysis, we fit models separately for each taxon after detecting a significant 4th order interaction.

Results

We found a significant effect of taxon ($F = 11.5$, $P < 0.0001$) and latitude ($F = 7.6$, $P = 0.010$) on the density of zooplankton resting eggs. Contrary to our prediction, the density of eggs declined latitudinally for all taxa (no latitude \times taxon interaction; $F = 0.71$, $P = 0.50$), but each taxon differed in their average egg density at a given latitude (Fig. 2).

PHENOLOGY

Phenology was affected by temperature and latitude. Higher temperatures advanced the first and median hatching day (Fig. 3; Tables S3 and S4) for all taxa. The magnitude of the temperature effect depended on taxon, but not in the way that we expected; the hatching of the smallest taxon, rotifers, advanced the least (Fig. 3). The days to hatch was advanced the most for cladocerans, by approximately 10 days, followed by copepods ~ 5 days and rotifers by ~ 2 days. The patterns were qualitatively similar for the first and median days to hatch, except that rotifers took the longest to reach 50% hatching, likely due to their higher abundances. For the first hatching day, temperature caused the order of emergence among taxa to reverse at 12 °C relative to 8 °C. The time for 50% of individuals to hatch was slightly affected by latitude for copepods ($t = 2.92$, $P = 0.004$) and rotifers ($t = 2.34$, $P = 0.02$) (Table S3). Day length did not impact phenology (all P values > 0.20).

HATCHLING ABUNDANCES

The abundance of hatchlings of each taxon was affected differently by latitude, temperature and photoperiod

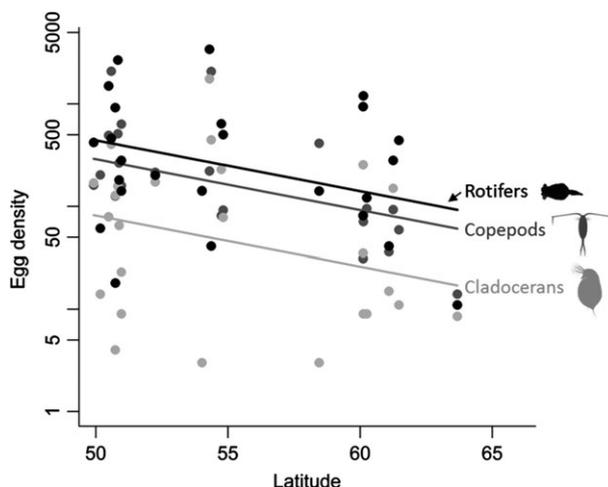


Fig. 2. The relationship between latitude and the egg abundance of cladocerans (light grey), copepods (dark grey) and rotifers (black). Eggs were isolated from 100 g of lake sediment using the sugar flotation method (see methods). Fitted lines indicate when latitude was significant at $P < 0.05$.

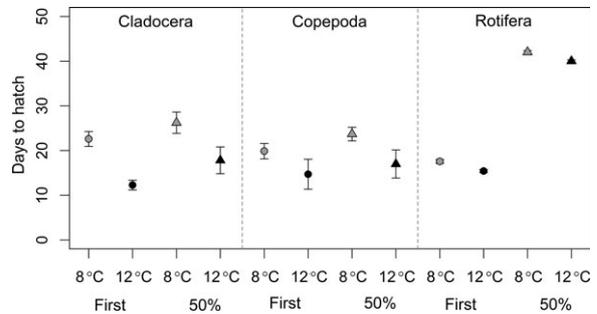


Fig. 3. The effect of temperature (8 °C; grey and 12 °C; black) on the average number of days until the first individual ('First'; circles) and half ('50%'; triangles) of all individuals from each taxon hatch. Error bars represent one standard error of the mean. See Tables S3 and S4 for the model summary.

(temperature \times photoperiod \times latitude \times taxon interaction; $F = 34.30$, $P < 0.001$). The abundance of cladocerans that hatched varied with temperature and day length, but the effects of these cues depended on the latitude of the lake (significant temperature \times photoperiod \times latitude interaction, $\chi^2 = 33.6$, $P < 0.0001$; Fig. 4a,b; Table S5). Warmer conditions and long days caused a greater number of individuals to hatch in low latitude lakes, but not in high latitude lakes (Fig. 4b). In contrast, in the low temperature treatment, latitude and photoperiod had no effect on the abundance of cladocerans that hatched (Fig. 4a).

For copepods, the number of individuals hatching peaked at mid-latitudes ($\sim 56^\circ\text{N}$), with the height of this peak differing by treatment (Fig. 4c,d); higher temperatures and longer days led to more copepods hatching (significant third-order interactions; linear = $\chi^2 = 8.6$, $P = 0.0034$, nonlinear = $\chi^2 = 7.9$, $P = 0.005$; Table S5).

The abundance of rotifers that hatched was greatest at low latitudes (Fig. 4e,f). However, unlike the crustaceans, the greatest abundance of rotifer hatchlings occurred at the higher temperature and shorter photoperiod treatment (Fig. 4f). In particular, the higher temperature caused a large increase in rotifer hatching in the 12-h photoperiod treatment (solid lines in Fig. 4e,f) and caused a more modest increase in the 16-h photoperiod treatment (dashed lines in Fig. 4e,f; significant third-order interaction, $\chi^2 = 131.7$, $P < 0.0001$; Table S5, Supporting information). Together these results provide mixed support for our hypotheses that hatching will be higher at low latitudes and that early spring conditions will increase hatching in northern lakes. Under simulated spring conditions, hatching declined at higher latitudes for copepods and cladocerans, however, caused higher hatching for rotifers.

HATCHLING DIVERSITY

In total, 406 individual crustaceans hatched from the egg banks (9 cladoceran species and 9 copepod species,

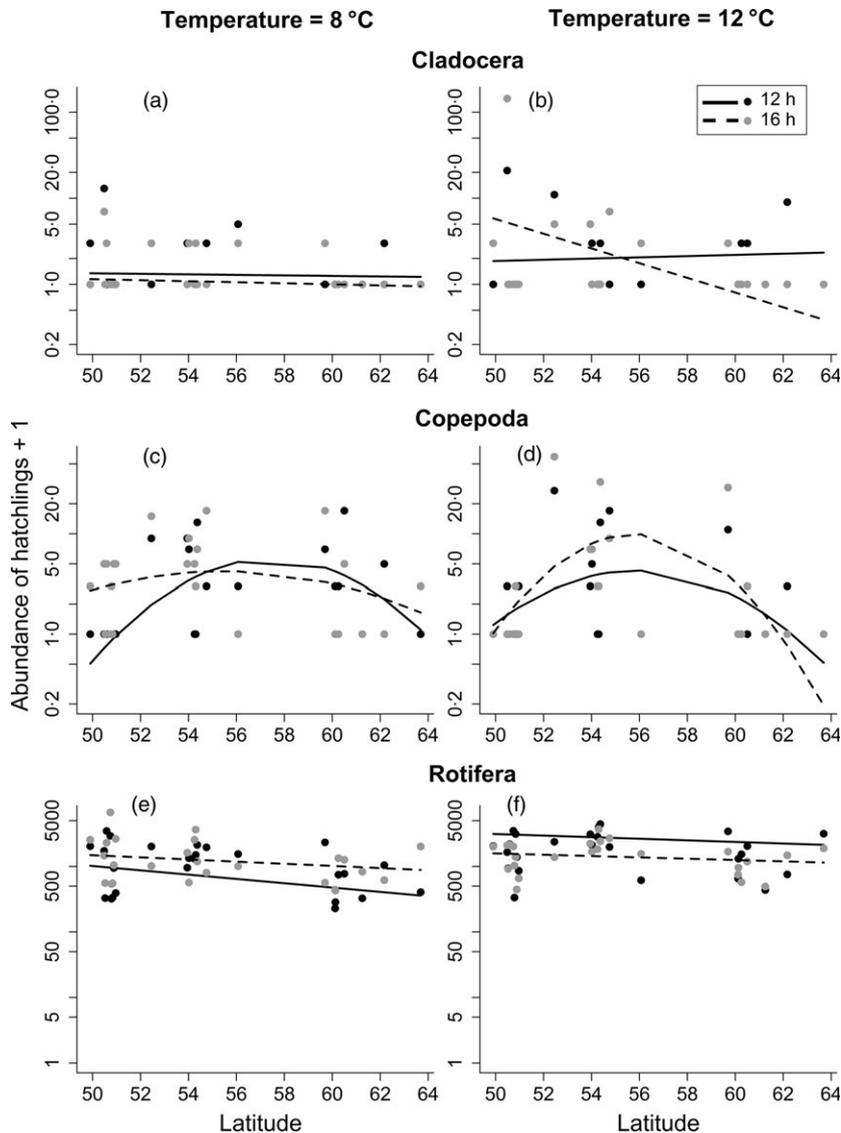


Fig. 4. The effect of temperature and photoperiod on the emergence of (a, b) cladocera individuals, (c, d) copepods individuals and (e, f) rotifera individuals that hatched from 25 lakes across a 1800 km latitudinal gradient in western Canada. Emergence is summed by lake across the 60-days sampling period. Data points are the abundance of hatchlings + 1. Lines are the fitted curves for a general linear mixed model for Poisson distributed data using a log link function. Note that the y-axes are presented on a logarithmic scale.

Table S6) which represent 41% of the species documented in these lakes. Thirty-five per cent of the hatchlings did not survive to adulthood, but survival did not differ between copepods and cladocerans ($\chi^2 = 2.0$, $P = 0.16$). Due to potentially confounding patterns in crustacean diversity with latitude (Fig. S3), we tested for trends in relative diversity by examining the proportion of species present in each lake that emerged – our relative diversity measure therefore calculates the fraction of species in each lake that were both present in the egg bank and responded to our experimental treatments.

The relative diversity of species that emerged differed between cladocerans and copepods, and these diversity responses were distinct from abundance responses for both taxa (temperature \times photoperiod \times latitude \times taxon interaction; $\chi^2 = 5.14$, $P = 0.0233$). When all crustaceans species were considered together, diversity showed a unimodal trend with latitude ($\chi^2 = 5.5$, $P = 0.002$), with the location of the peak in diversity depending on

photoperiod (significant photoperiod \times latitude interaction, $\chi^2 = 9.4$, $P = 0.002$; Table S7; Fig. 5a,b).

Cladoceran diversity responded strongly to photoperiod and latitude, but not temperature (photoperiod \times latitude interaction, $\chi^2 = 5.5$, $P = 0.02$; temperature, $\chi^2 = 2.3$, $P = 0.13$; Fig. 5c,d). In the longer (16-h) photoperiod, the relative diversity of cladoceran species that hatched was the highest at low latitudes, whereas in the shorter photoperiod treatment relative diversity was greatest at high latitudes (Fig. 5c,d).

Copepod diversity varied with temperature and day length, but the effects of these cues depended on the latitude of the lake (significant third-order interactions; linear $\chi^2 = 8.8$, $P = 0.003$, quadratic $\chi^2 = 4.00$, $P = 0.046$; Fig. 5e,f; Table S7). We predicted that conditions typical of a late season (long days coupled with high temperature) would decrease the diversity of the hatching community; however, diversity was highest at mid-latitudes, with 30% or more of species emerging when day length was

short and temperatures were low. Copepod diversity was lower in the warmer temperature treatment, with the maximum peak of approximately 20% of species hatching (Fig. 5f). Interestingly, the treatment that combined long day length and low temperatures had higher copepod diversity in lower latitudes (Fig. 5e).

Discussion

Our study demonstrates that several responses of zooplankton resting eggs to hatching cues change with latitude and that the pattern of this change differs among taxa. Our assessment of the effects of day length and temperature on the phenology, abundance and diversity of zooplankton communities is the first to systematically collect egg banks from across a latitudinal gradient. In doing so, we have shown that cues associated with changing climate can have consistent (phenology) or distinct (abundance, diversity) effects at different latitudes, indicating

that we cannot accurately predict responses to climate change without considering how these factors interact across biologically diverse landscapes.

Contrary to our hypothesis, phenological shifts in response to temperature caused the relative order of the first hatching to reverse for the three taxa (Fig. 3). At 8 °C, phenological patterns were consistent with previous research, with rotifers hatching first and cladocerans hatching last, but rotifers showed a surprising lack of phenological response to temperature, thereby reversing the relative order of first appearance. Our phenology results are partially consistent with field research, which has shown that crustacean zooplankton dominating the water column in early spring (i.e. cladocerans) are more sensitive to temperature than later successional taxa (i.e. copepods) (Adrian, Wilhelm & Gerten 2006). It is, however, inconsistent with a meta-analysis that spanned many species and showed that high temperatures advance phenology, but that species with the smallest egg sizes always tend to

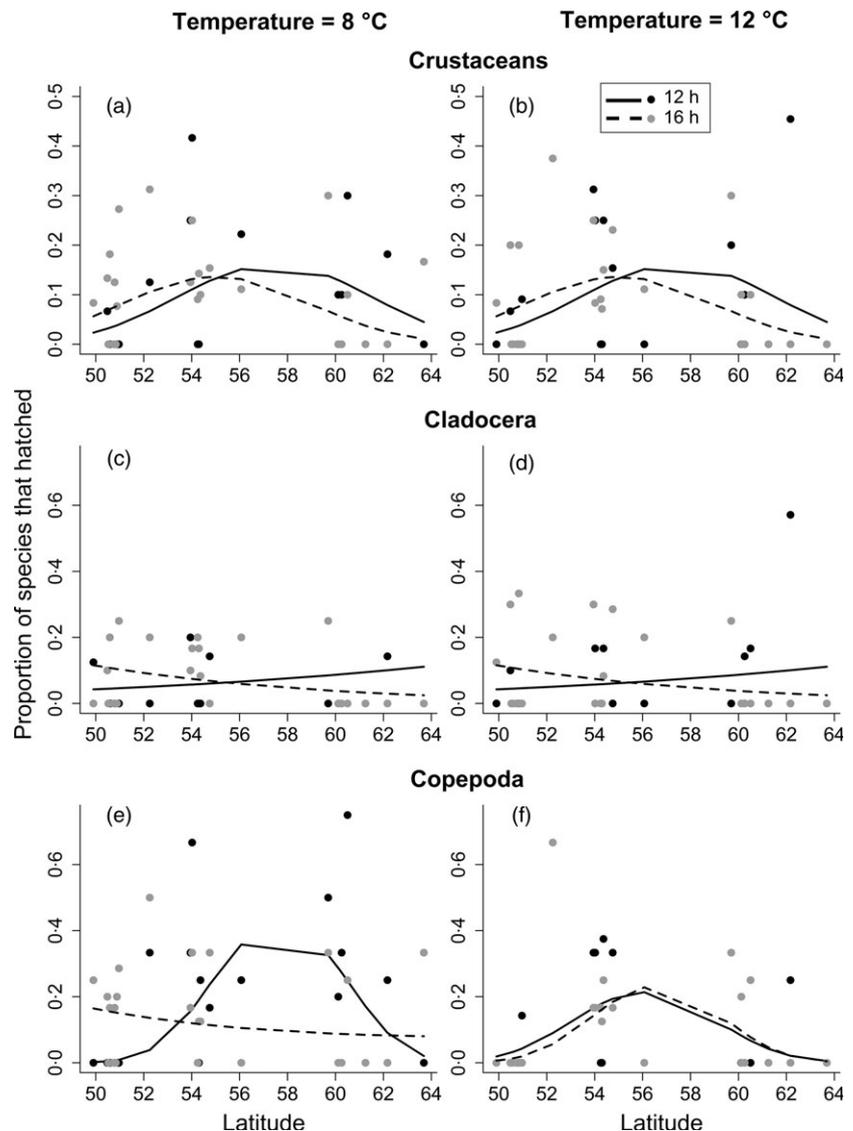


Fig. 5. The effect of temperature and photoperiod on the proportion of the (a, b) total crustacean diversity, (c, d) cladoceran diversity and (e, f) copepod diversity that hatched from 25 lakes across a 1800 km latitudinal gradient in western Canada. Diversity is summed by lake across the 60-days sampling period. Data points are the proportion of species that hatched. Lines are the fitted curves for a general linear mixed model using a logit link function.

emerge first (Gillooly & Dodson 2000). For rotifers, our taxa with the smallest eggs, we clearly did not see this pattern. Similarly, Winder & Schindler (2004) used long-term monitoring of a single lake to show that rotifer populations advanced their phenology over a 40 years period of warmer springs, whereas cladocerans did not. Although we do not have an explanation for the reversal of hatching times observed, our results suggest that elevated spring temperatures have the potential to alter the order that zooplankton hatch in lakes. Given the importance of phenological differences for competitive and successional dynamics, further verification of this trend and its causes are important for aquatic ecology.

Beyond phenological changes, the effect of climate on community composition can be quantified through two general responses: changes in abundance of specific taxa and changes in diversity. Numeric and diversity effects are frequently considered inter-dependent as they are often correlated in nature (via the species-accumulation curve, e.g. Uglund, Gray & Ellingsen 2003), suggesting that higher hatching rates should translate into a greater proportion of the community emerging. However, abundance responses appear to have been influenced by high hatching rates from a subset of species, as our results show that copepods and cladocerans have qualitatively distinct abundance and diversity responses (compare Figs 4 and 5). For example, the higher temperature increased the abundance of cladocerans in the long photoperiod treatment, but did not impact cladoceran diversity. A similar result was found by Preston & Rusak (2010), who showed that temperature effects manifested as a numerical response, having little impact on diversity. However, those authors linked ice-off date with community composition and found that spring warming reduced zooplankton density, while in our study the higher temperature treatment generally increased hatching. Overall, this difference between numeric and diversity responses suggests that the effects of climate change can manifest by favouring a small subset of species and by simultaneously altering the diversity of communities.

The effects of climate cues on zooplankton hatching diversity offers new insights into how climate can differentially structure community dynamics across latitudinal gradients. We expected that hatching rates would be greatest in southern latitudes, where growing seasons are longer and climatic conditions are milder. Surprisingly, the dynamics we observed were more complex and could not have been predicted from a geographically and taxonomically restricted study. In particular, cladoceran diversity was only influenced by photoperiod, with a longer photoperiod increasing diversity at low latitudes, but decreasing diversity at high latitudes (Fig. 5). The reversal of the day length effect at high latitudes is consistent with our hypothesis that northern zooplankton may experience strong selection to emerge and reproduce in a short growing season, causing northern populations to be locally adapted to those conditions (Kawecki & Ebert 2004;

McNamara & Houston 2008). However, when we investigated the hatching dynamics of three common species (copepods: *Diaptomus sicilis* and *Hetercope septentrionalis*; cladoceran: *Ceriodaphnia lacustris*), we did not detect evidence for local adaptation. Instead, differences among populations of widespread species were idiosyncratic (Fig. S4, Supporting information), suggesting that the apparent consistency with our hypothesis was due to species sorting effects. We note, however, that our experiment is not well-suited to testing local adaptation because we have no measure of individual fitness and no control of maternal effects; more targeted tests of local adaptation in plankton from across latitudes would be valuable. Our results, which effectively average the effects of climate cues over species that change along the latitudinal gradient (Patalas, Patalas & Salki 1994), indicate that northern cladoceran communities respond positively to shorter days, as is predicted when growing season is limited (Conover, Duffy & Hice 2009) or shorter day length corresponds with increases in food availability (Cáceres & Schwalbach 2001).

Differential responses of taxa to climate cues also challenge simple models for community change across latitudinal gradients. Space-for-time substitutions, which are often employed where temporal replication is difficult, can be a powerful tool to predict community or population level responses to climate change (Pickett 1989). If experimental temperature responses are correlated with the temperature response across latitude in nature, then a space-for-time substitution would capture how the community will respond to climate change (Dunne *et al.* 2004). Our experiment revealed that numeric and diversity responses of zooplankton to temperature and photoperiod can differ across latitude, suggesting that we may be unable to construct predictions for how temperature will alter community composition based on spatial patterns of temperature responses.

An important question that arises from our study is how our findings can be generalized to different habitats and organisms. Marine plankton, for example, differ from freshwater plankton in that long-term dormancy is less prevalent overall (Hairston & Cáceres 1996), potentially because of the more continuous nature of the marine realm. However, the hatching of marine zooplankton is also influenced by temperature and photoperiod (Uye, Kasahara & Onb 1979; Preziosi & Runge 2014), but more work is needed to understand how these dynamics vary latitudinally. In addition, extrapolating our results to latitudes beyond our sampling sites is challenging due to the complexity of the responses we observed. Future work should extend sampling to determine whether egg banks continue to increase at low latitudes and assess patterns in hatching dynamics. In most cases, we see declines in hatching at the northern extreme of the latitudinal gradient that we sampled, but species persist at (and beyond) these latitudes (Patalas, Patalas & Salki 1994), raising questions about the nature of this latitudinal variation

that should be addressed with more detailed studies within and across species.

Life-history differences among zooplankton are likely candidates for the different responses to light and temperature that we observed and may be generally useful for predicting responses to changing climate cues. Cladocerans are born as miniature adults and are facultatively sexual, reaching reproductive maturity in 5–10 days at 20 °C (Geller 1987). In contrast, copepods are obligately sexual and have a development time of 20–42 days at 20 °C depending on species (Maier 1994). Fast generation times and parthenogenesis cause cladocerans to have higher growth rates than copepods (Allan 1976) and may structure differences in the successional niches of these taxa (Adrian, Wilhelm & Gerten 2006). Growing season lengths declines latitudinally (Environment Canada 2014), and lower temperatures that are characteristic of northern lakes slow development of all zooplankton (Gillooly 2000). This time constraint could be especially acute for copepods because of their comparatively long development times. Moreover, when cladocerans undergo sexual reproduction they have large egg size to adult body size ratios compared to copepods, leading to relatively long development times for the egg stage (Gillooly 2000). This systematic difference between taxa may impose different selection pressures on the initiation of egg development in response to environmental cues. For example, the relatively slow development rates of sexual cladoceran eggs into juveniles may cause cladocerans to be more strongly impacted by longer-term environmental conditions, as may be signalled by day length.

Although we were unable to quantify rotifer diversity in our lakes, we saw that rotifer abundance responded to temperature and that the size of this response depended on day length (Fig. 4). Our results for rotifers supports previous work that used a 40-years time series to show that the abundance of rotifers can increase in response to spring warming (Winder & Schindler 2004). Rotifers play a critical role in lakes by acting as a food source for crustacean zooplankton (copepods and cladocerans) and by facilitating nutrient cycling by consuming bacteria, detritus and algae (Hutchinson 1967; Bogdan & Gilbert 1982; Arndt 1993). The strong, positive effect of short days and high temperature on the abundance of rotifers that hatch raises the possibility that changing climate cues could greatly increase rotifer abundances and thus alter nutrient cycling and the supply of food to higher trophic levels.

Interestingly, the abundance and diversity responses of zooplankton were not related to the density of eggs in lake sediment, which declined latitudinally for all taxa (Fig. 2). This pattern of declining egg density may be due to the negative correlation between season length and latitude, reducing the number of generations per growing season in the north (Corbet, Suhling & Soendgerath 2006). However, in addition to lower voltinism in higher latitudes, the density of eggs in lake sediment is also a consequence of

the accumulation of eggs that are produced but do not hatch the following year. Because of short growing seasons and lower temperatures, we predicted this unhatched fraction to represent a greater proportion of eggs produced at higher latitudes. Egg density is ultimately the product of both processes; the reservoir of eggs declines with latitude because of lower voltinism, but the fraction of these eggs that hatch determine the number that remain in the sediment. Our study suggests that the latter of these two processes is unlikely to account for differences in egg densities, as hatchling densities were not universally higher in northern lakes for any of the taxa studied (Fig. 4).

Our investigation of the effects of temperature and day length on the termination of dormancy is one of the first to choose communities that differ in latitudinal origin. In doing so, we have demonstrated that the sensitivity of zooplankton to temperature and day length can differ across latitude and between co-occurring taxa, a result that would be obscured if we selected communities from the same region. By considering how climatic cues may shift dynamics across latitudes, we were able to provide new insights that suggest changes in dormancy dynamics with spring warming may be an under-appreciated but important consequence of climate change and could lead to zooplankton community shifts that will depend on latitudinal origin.

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.r80d3> (Jones & Gilbert 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Latitudinal changes in six physical and chemical characteristics from the 25 lakes that we collected sediment containing zooplankton egg banks from in July 2011.

Figure S2. Schematic of experimental design.

Figure S3. Relationship between the crustacean zooplankton species richness of our 25 experimental lakes and latitude.

Figure S4. The effect of temperature and day length on the hatching of three zooplankton species that occurred across the latitudinal gradient.

Table S1. Summary of temperature and day length data during ice-off.

Table S2. The treatment allocation and corresponding latitude of the 25 lakes that we collected sediment from.

Table S3. Summary of final models, determining the effects of latitude, temperature and photoperiod on zooplankton median hatching day, after removing non-significant higher-order terms.

Table S4. Summary of final models, determining the effects of latitude, temperature and photoperiod on the number of days until the first individual of each taxon hatched per lake, after removing non-significant higher-order terms.

Table S5. Summary of full models determining the effects of latitude, temperature and photoperiod on zooplankton hatching abundance.

Table S6. The crustacean zooplankton species that hatched from the sediment of 25 lakes in western Canada.

Table S7. Summary of full models, determining the effects of latitude, temperature and photoperiod on zooplankton diversity.