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Lake thermal structure influences macroinvertebrate predation on crustacean zooplankton

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Changes in lake thermal structure, which are predicted with future climate warming, may alter predator–prey interactions if foraging rates or the spatial overlap of predators and prey depend on thermal conditions. Small Boreal Shield lakes are particularly responsive to weather-induced changes in thermal structure. They are often fishless, with macroinvertebrate predators regulating crustacean zooplankton communities. We performed a mesocosm experiment to examine how thermal structure (stratified and isothermal) influences the predation impact of surface-orienting *Buenoa macrotibialis* and vertically migrating *Chaoborus punctipennis* on crustacean zooplankton. We expected predation from surface-orienting predators to be greatest in stratified conditions when food resources are concentrated near the surface in proximity with predators. Surprisingly, surface predators had no effect on zooplankton abundance, and zooplankton avoided surface predators regardless of thermal habitat structure. In contrast, *Chaoborus* had a strong predation impact and reduced total zooplankton abundance, but only in isothermal conditions. We hypothesize that this predation effect was due to increased predator metabolism, foraging and ingestion rates when migrating through a thermally homogenous warm water column without access to cool bottom waters. These results demonstrate that changes in lake thermal structure may result in strong, unexpected consequences for predator–prey dynamics.

KEYWORDS: thermal stratification; climate warming; *Chaoborus*; notonectid; Boreal Shield; mesocosm

INTRODUCTION

Climate change is expected to alter the timing, strength and depth of thermal stratification in temperate-region lakes (Keller, 2007; Adrian *et al.*, 2009), particularly in small or shallow lakes that are highly responsive to weather-induced changes in thermal structure (Gao and Stefan, 1999; Gerten and Adrian, 2001). Aquatic predator–prey interactions may be altered by changes in lake stratification because feeding and production rates are temperature dependent (Peters, 1984; Rigler and Downing, 1984), habitat choice may depend on temperature (Pangle and Peacor, 2006) and predator–prey interactions depend on both the temporal and spatial overlap of potential prey with predator species (Williamson *et al.*, 1989). Predator–prey interactions in small lakes may be particularly susceptible to altered thermal regime because trophic interactions are

typically intense in small lakes where space, habitat heterogeneity, trophic complexity and thermal refuges are limited (Keller and Conlon, 1994; Moore et al., 1996; Post et al., 2000).

The Boreal Shield Ecozone contains 22% of Canada's freshwater surface area (Urquizo et al., 2000) and is numerically dominated (~50%) by small lakes (<10 ha in size) (Cox, 1978). Thousands of small Shield lakes are fishless, and macroinvertebrates represent the top predators of zooplankton prey (Yan et al., 1991; Wissel et al., 2003; Arnott et al., 2006). Crustacean zooplankton can alter their vertical habitat selection in response to both food resources and invertebrate predators (Leibold, 1990). For example, zooplankton lower their daytime depth distribution to avoid surface-orienting predators such as dytiscids (Arts et al., 1981) and notonectids (Herwig and Schindler, 1996; Gilbert and Hampton, 2001), and migrate at night to limit overlap with vertically migrating Chaoborus (Fedorenko, 1975a).

Predictions for changes in the thermal structure of small north-temperate lakes with future climate warming include increased mixed layer warming which may, depending on transparency (Fee et al., 1996; Snucins and Gunn, 2000), result in weaker thermal stratification, decreased bottom coldwater habitat and periods of isothermal conditions (Schindler et al., 1990; Moore et al., 1996; Schindler, 1997). If thermal conditions become increasingly well-mixed (isothermal), zooplankton may lower their daytime depth distribution to obtain algal food resources at greater depth while avoiding time spent in contact with surface-orienting predators, such as notonectids. Also, since Chaoborus spend time in the cool bottom waters and sediments, loss of stratification may alter their mean exposure temperature, potentially altering metabolic demand and foraging rate. These processes may have implications for crustacean zooplankton community structure with future climate warming.

To date, few studies have directly investigated how climate-related changes in lake thermal habitat may alter the outcomes of spatially dependent predator–prey interactions, and most have focused on fish–zooplankton interactions. For instance, Tessier and Welser (Tessier and Welser, 1991) found that Daphnia benefit from a thermal refuge from fish predation by remaining in the cold bottom water of deep, thermally stratified lakes. Similarly, early onset of spring thermal stratification provides Bythotrephes with a longer duration refuge from fish predation, increasing Bythotrephes abundance and subsequent regulation of Daphnia (Manca and DeMott, 2009). Despite the importance of macroinvertebrate predators in many of the small, shallow lakes that are

abundant throughout the Boreal Shield (e.g. Arnott et al., 2006; Malkin et al., 2006), the influence of thermal structure on macroinvertebrate-zooplankton predation has not been investigated.

We used in situ enclosures to address the following questions: (i) are there differences in the daytime vertical distributions of crustacean zooplankton associated with differences in lake thermal structure?; (ii) do crustacean zooplankton demonstrate predator avoidance behavior dependent on lake thermal structure?; and (iii) does macroinvertebrate predation depend on lake thermal structure?

METHOD

Experimental design

We deployed enclosures in Swan Lake near Sudbury, Ontario (46° 22′ 81° 04′) (Arnott et al., 2001) using a 2×2 factorial experimental design that included two levels of a vertically migrating predator treatment with Chaoborus punctipennis (present, absent), and two levels of a surface-orienting predator treatment with Buenoa macrotibialis (present, absent). Fishless lakes are typically dominated by the large, pigmented, non-migrating species Chaoborus americanus (e.g. Wissel et al., 2003) but can also contain dense populations of the vertically migrating species C. punctipennis (Yan et al., 1985), as was the case for Swan Lake. We conducted two thermal trials of the experiment: stratified and isothermal. Predator treatments were replicated four times within each level of thermal habitat. We conducted thermal habitat trials by incubating enclosures during a stratified (June) and isothermal (August) period in Swan Lake. For each thermal trial, the enclosures were incubated for 15 days, a period long enough to detect the effects of macroinvertebrate predation without thermal structure changing dramatically over the course of the experiment.

The first thermal trial (04–18 June 2007) simulated thermal conditions of a typical year in which a lake is stratified with a warm epilimnion (20.3°C $\pm$ SE 0.3°C) and cooler bottom water (14.9°C $\pm$ SE 0. 1°C) below a thermocline. In contrast, the second thermal trial (23 August 2007–6 September 2007) simulated warm conditions where a lake is isothermal at a temperature of 21.2°C ($\pm$ SE 0.4°C). This latter scenario corresponds to potential thermal conditions with future climate change for small, shallow, moderately clear lakes, where the whole lake is weakly stratified or is warm isothermal, with no thermocline or bottom coldwater habitat (Schindler et al., 1990; Moore et al., 1996; Schindler,

1997). In Swan Lake, the number of days with bottom water temperature exceeding $10°C$ (an index of available cold-water habitat) (Snucins and Gunn, 2000) has increased from 1993 to 2008 (Mann–Kendall non-parametric trend test: $r^2 = 0.41$, $P = 0.008$, Fig. 1). This trend is due to both advanced onset of the isothermal period and the persistence of warming in autumn.

Enclosure deployment and stocking

Enclosures (1 m diameter, 6.5 m length, ~5100 L) were constructed from 5 mm clear cylindrical polyethylene bags (Filmtech Plastic, Brampton, Ontario, Canada) suspended from wooden frames buoyed on Styrofoam® blocks. Enclosures were filled with filtered Swan Lake water using a 2-inch centrifugal water pump with a 50 μm mesh output filter to exclude zooplankton. Enclosures were covered with a 0.25 cm mesh screen to prevent invertebrate colonization and emigration of notonectids, and stocked with zooplankton collected with a 36 cm diameter, 80 μm mesh conical plankton net. Stocking densities aimed to be the long-term mean annual density of the most abundant species (*Leptodiaptomus minutus*) in Swan Lake from 1993 to 2002 (~11.9 individuals L^{-1} ± SD 3.9). Actual stocking densities were within the range of long-term density at $13.8 ± SD 4.5$ and $8.7 ± SD 2.8$ individuals L^{-1} in the stratified and isothermal trials, respectively. Zooplankton were acclimated overnight prior to predator additions.

At the time of this study, monitoring data indicated the Swan Lake zooplankton community had been >99% dominated by calanoid copepods both annually and seasonally for >10 years (W. Keller, unpublished data). Therefore, an assumption of the experimental design was that the relative abundance of crustacean zooplankton species used to stock the enclosures during each incubation period would be consistent. The stratified trial was stocked with Swan Lake zooplankton, however, prior to deployment of the isothermal trial, the crustacean zooplankton community composition of

Fig. 1. Number of days with bottom water temperature exceeding $10°C$ in Swan Lake, 1993–2008 ($r^2 = 41$; $P = 0.008$).

Swan Lake changed unexpectedly. Subsequently, zooplankton for the isothermal trial were collected from nearby Clearwater Lake (<1 km from Swan Lake), where *L. minutus* also dominates the crustacean zooplankton community. Crustacean zooplankton transferred between lakes with similar water chemistry have equal survival success in mesocosm experiments (Derry and Arnott, 2007).

On 03 June 2007, a mixture of III and mostly IV instar *C. punctipennis* larvae was collected 45 min after dark from Swan Lake using a 30 cm diameter, 153 μm mesh conical net towed from 6 m to the surface. To ensure consistent age and size structure of the predator assemblage, *Chaoborus* were stored at $4°C$ in the dark between thermal trials. These are conditions typically experienced by over-wintering III and IV instars (Von Ende, 1982) in which developmental arrest occurs until food and photoperiod synergistically induce the termination of diapause (Bradshaw, 1969). We assumed any potential effects of starvation on stored *Chaoborus* were negligible because starvation effects on *Chaoborus* feeding rate only persist for the first 6–8 h of feeding (Pastorok, 1980). Mites and other conspicuous aquatic macroinvertebrates were excluded from the enclosures. On Day 0 of each experiment, *Chaoborus* were added live to treatment enclosures at the ambient June lake density of 2.75 individuals L^{-1}. The notonectid predator *B. macrotibialis* was collected from Swan Lake on Day 0 of each thermal trial and stocked at a visually determined ambient density of 16 per enclosure (0.003 individuals L^{-1}).

Enclosure sampling

Zooplankton, chlorophyll *a*, water chemistry [dissolved organic carbon (DOC), pH and conductivity], Secchi depth and temperature/dissolved oxygen (DO) profiles were sampled at mid-day on Day 1 and Day 15 of each thermal trial. Temperature/DO profiles were measured at 0.5 m intervals using a YSI model 55 probe (Yellow Springs Institute, Yellow Springs, OH, USA). During each 2-week experiment, HOBOware® Tidbit temperature loggers (www.onsetcomp.com/products/data-loggers) were installed in a control bag and temperature was measured every hour at 1 m intervals. Chemical parameters were sampled with a 1.8 cm diameter, 5 m integrated tube sampler. In addition, Day 1 total chlorophyll *a* samples were collected with an integrated tube sampler from 0 to 5 m. Total chlorophyll *a* was sampled on Day 15 from 0–6 m at 1 m intervals using a Van Dorn sampler.

Day 1 (initial) zooplankton were sampled from each enclosure at 0–6 m with a 7.5 cm diameter, 80 μm mesh conical tow net to verify that starting densities of
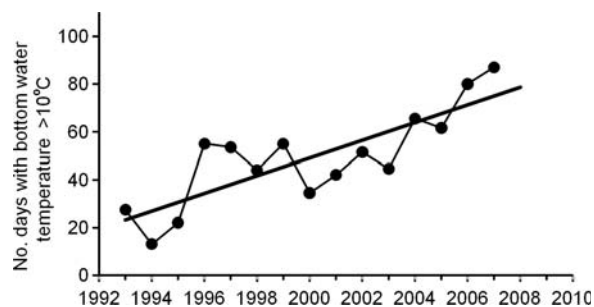
zooplankton were similar among treatments. To assess the effect of predator treatments, zooplankton were sampled on Day 15 (final) with a 12 L, 63 μm mesh Schindler-Patalas trap from 0 to 6 m at 1 m intervals starting near the surface and working towards the bottom of the enclosures. Zooplankton sample collection alternated with discrete total chlorophyll *a* collection at each depth interval to minimize mixing of the water column upon sampling the next strata.

Chemical analyses

Conductivity and pH were measured using a PHM64 Research probe (Bach Simpson Ltd., London, ON, Canada). For total chlorophyll *a* analysis, 500 mL of lake water was filtered through 47 mm diameter Whatman GF/C pore filters and frozen prior to a 24 h extraction in methanol and fluorometric analysis using a TD 700 Fluorometer (Turner Designs, Sunnyvale, CA, USA). DOC samples were processed at the Dorset Environmental Science Centre, Dorset, Ontario, Canada, following standard protocols (Ontario Ministry of the Environment, 2009).

Zooplankton enumeration

Zooplankton were preserved in 5.5% sugared buffered formalin (Haney and Hall, 1974) and enumerated using a Leica MZ 12.5 stereomicroscope (Leica Microsystems, Richmond Hill, Ontario, Canada). A total of $100-150$ individuals from at least two equal fractions were counted per initial (Day 1) sample; sub-samples were generated using a Folsom plankton splitter (Girard and Reid, 1990). Final (Day 15) samples were counted in their entirety. For all samples, adult zooplankton were identified to species. Juvenile copepods were identified to order (Calanoida or Cyclopoida). Immatures, i.e. nauplii and juvenile *Bosmina* (<0.20 mm), were not considered in the experiment because they were not vulnerable to notonectid predation (Cooper, 1983). While nauplii are vulnerable to *Chaoborus* predation (Swift and Forward, 1981), they are typically only consumed by first and second instar larvae and are rarely ingested by IV *C. punctipennis* (Fedorenko, 1975b; Moore, 1988). The number of stocked immatures did not differ between predator treatments ($P > 0.14$ for all treatment combinations).

Statistical analyses

The effect of *Chaoborus* and notonectid predation on mean zooplankton abundance in stratified and isothermal habitats was tested with a 2×2 factorial analysis of variance (ANOVA). A 2×2 ANOVA was also performed on mean abundance-weighted depth calculated as:

$$= \sum \frac{(n_d \cdot d)}{\sum n}$$

where n_d is the number of individuals at a given depth (no. individuals m^{-3}) and d is depth (m). ANOVAs were performed using the statistical package R (R Development Core Team, 2007). ANOVA assumptions were checked using Levene's test and by visually examining histograms, boxplots and residual plots. Abundance data were $\log_{10}(x + 1)$ transformed to achieve homogeneity of variance and normality. During the stratified thermal trial, one *Chaoborus* × notonectid replicate bag developed a hole and this replicate was excluded from the analyses, resulting in an unbalanced design. We did not sample through time to avoid problems with the removal of zooplankton and predators by sampling effort. Instead, we assessed predation effects by comparing control and treatment conditions on Day 15; initial samples were only collected to evaluate starting conditions on Day 0. We analyzed the stratified and isothermal trials separately because a preliminary comparison indicated that initial stocking densities differed between thermal trials ($t = -3.74$, $P < 0.001$). There were no differences in initial stocking densities within or between predator treatments in either thermal trial ($P > 0.21$).

Finally, a 2×2 repeated-measures ANOVA (RM ANOVA) with depth as the repeated measure was used to test for treatment effects on total crustacean zooplankton daytime depth distribution in stratified and isothermal conditions using the statistical package JMP 7.0 (SAS Institute Inc., 2007). The univariate Greenhouse–Geiser adjusted *F*-ratio is reported to avoid problems with satisfying the assumption of sphericity (Quinn and Keough, 2002).

RESULTS

Enclosure conditions

Initial DOC concentration was consistent between thermal trials (*t*-test; $P = 0.11$). Initial pH (range: $5.35-5.65$) and conductivity (range: $42.4-49.0$ μS cm^{-1}) differences between the stratified and isothermal trials were not ecologically relevant to the acid-tolerant (Marmorek and Korman, 1993) zooplankton community, and enclosure values were similar to the natural range in Swan Lake from 1993 to 2007 for both pH

(5.42–5.84) and conductivity (37.91–47.50 μS cm^{-1}). Total chlorophyll *a* concentrations were higher at the start of the predation experiment in the stratified (0.59 + SE 0.01) than in the isothermal trial (0.29 + SE 0.01). As expected, chlorophyll *a* concentrations varied with depth in stratified conditions (RM ANOVA; Stratified Trial: Depth Effect: $F = 2.97$; $P = 0.03$) such that levels were highest at the thermocline. Enclosure communities were 90% dominated by calanoid copepods (*L. minutus*) in the stratified trial, but in the isothermal trial calanoids comprised 45% and cladocerans (*Bosmina* spp.) comprised 50% of the total crustacean zooplankton community. This community is typical of isothermal conditions in that although calanoid copepods dominate the Swan Lake zooplankton community, the relative abundance of small cladocerans increases in years with a longer duration late-summer isothermal period (MacPhee, 2009).

Notonectid survival was 80–82% by the end of each thermal trial. While some *Chaoborus* emergence did occur during each thermal trial, adults were captured in the mesh enclosure covers and there were no apparent differences in adult density between thermal trials based on visual inspection. *Chaoborus* survival was not enumerated but live individuals were captured in 6 m samples during daytime hauls. Predation pressure was assumed to be constant because *C. punctipennis* were never food-limited and survive well in experimental enclosures for periods exceeding 15 days (Arnott and Vanni, 1993).

Treatment effects on mean abundance

Chaoborus reduced zooplankton abundance in isothermal (ANOVA; *Chaoborus* Effect: $F = 29.92$; $P < 0.0001$, Fig. 2), but not in stratified conditions (ANOVA; *Chaoborus* Effect: $F = 1.02$; $P = 0.33$, Fig. 2). Mean final crustacean zooplankton abundance was 20.6 individuals L^{-1} ($\pm$ SE 0.4) across all predator treatments in the stratified trial. However, in isothermal conditions, the presence of *Chaoborus* reduced crustacean zooplankton abundance by 73%, from a mean of 33.5 individuals L^{-1} ($\pm$ SE 1.5) in treatments where *Chaoborus* was absent to a mean of 9.0 individuals L^{-1} ($\pm$ SE 0.5) in the presence of *Chaoborus*. This predation effect did not change when *Chaoborus* co-occurred with notonectids in either the stratified (ANOVA; *Chaoborus* × Notonectid Effect: $F = 1.35$; $P = 0.27$) or isothermal trials (ANOVA; *Chaoborus* × Notonectid Effect: $F = 0.86$; $P = 0.37$), and notonectids did not significantly affect mean crustacean zooplankton abundance in either thermal treatment (ANOVA; Stratified: Notonectid Effect: $F =$

0.01; $P = 0.93$; Isothermal Trial: Notonectid Effect: $F = 0.86$; $P = 0.37$, Fig. 2).

Treatment effects on zooplankton depth distribution

Zooplankton exhibited a narrower range in abundance-weighted depth in treatments containing notonectids (Fig. 3), suggesting some predator avoidance behavior, although the effect was not significant in stratified ($F = 2.07$; $P = 0.18$) or isothermal conditions ($F = 0.25$; $P = 0.63$). In general, zooplankton were evenly distributed throughout the water column, except near the surface where they were less abundant in both thermal trials. Variability in zooplankton daytime depth distribution was greater in stratified than isothermal conditions for all treatments except where both predators were present (Fig. 4). The *Chaoborus* predation effect in the isothermal treatment did not vary with daytime zooplankton depth distribution (ANOVA; Depth × *Chaoborus* Effect: $F = 2.16$, $P = 0.12$).

DISCUSSION

The impact of a ubiquitous vertically migrating aquatic invertebrate predator on crustacean zooplankton prey depended on the thermal characteristics of the water column and was more pronounced under thermal conditions expected with climate change in small, shallow Boreal Shield lakes. *Chaoborus punctipennis* reduced total crustacean zooplankton abundance in an isothermal habitat but had no impact in stratified conditions. Contrary to expectations, crustacean zooplankton did not adjust their daytime depth distribution in response to surface-orienting predators in the two lake thermal structure scenarios. While zooplankton were located deeper in the water column in response to the surface-orienting notonectid predator *Buenoa macrotibialis*, this occurred in both stratified and isothermal conditions. Consequently, notonectids had no significant effect on overall crustacean zooplankton abundance, despite high observed predation impact in shallow enclosures (Hampton *et al.*, 2000). There was no interaction between the effect of *Chaoborus* and notonectids on zooplankton abundance, so they are discussed separately below.

The strong *Chaoborus* predation effect in isothermal conditions may be due to increased frequency of predator–prey encounters in a warm habitat. *Chaoborus* are ambush predators and predation efficiency is related to the frequency of encounter with prey items, which depends in part on prey swimming speed (Swift and
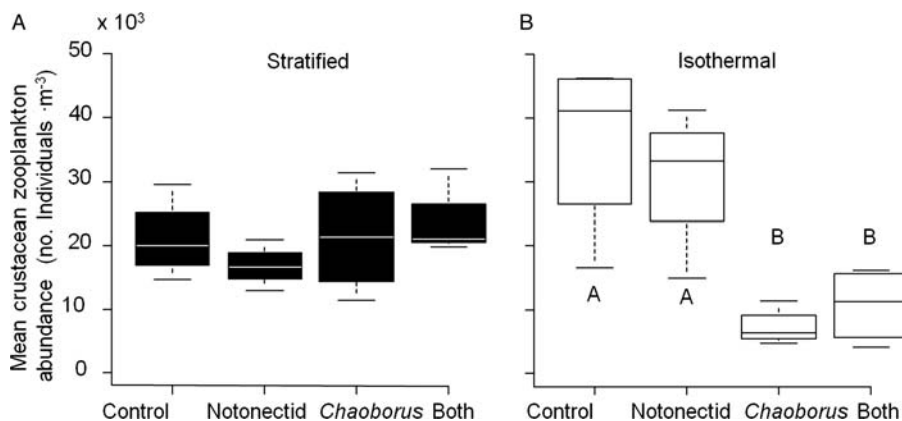
Fig. 2. Boxplots of mean crustacean zooplankton abundance (no. individuals m^{-3}) by predator treatment within the (**A**) stratified (black boxes) and (**B**) isothermal (white boxes) habitat trials. Line represents median, box represents upper and lower (25% and 75%) quartiles, bars represent data range. Note that statistical analyses were performed on $\log(x + 1)$ transformed abundance data. Crustacean zooplankton abundance was significantly lower in treatments containing *Chaoborus* in the isothermal trial (ANOVA; $F = 25.33$, $P < 0.0001$). Different letters indicate significant differences between treatments where *Chaoborus* is present and absent (Tukey's HSD: $P < 0.05$).
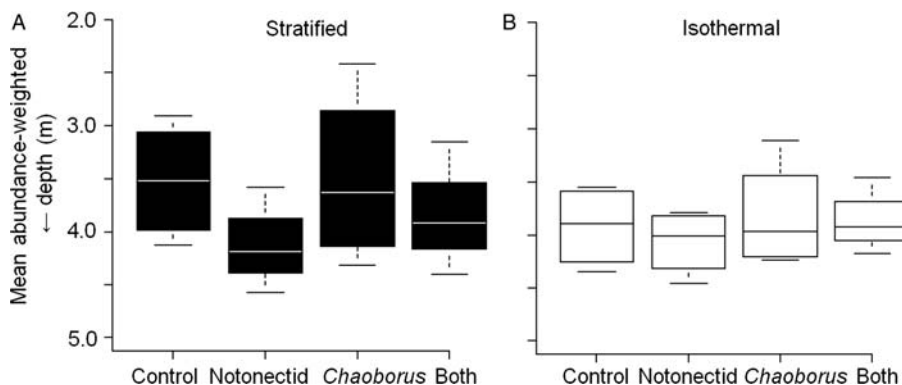

Fig. 3. Mean abundance-weighted depth (m) by predator treatment for the (**A**) stratified (black boxes) and (**B**) isothermal (white boxes) habitat trials. Line represents median, box represents upper and lower (25% and 75%) quartiles, bars represent data range.

Fedorenko, 1975; Pastorok, 1980, 1981; Riessen *et al.*, 1988). Swimming speeds of *Daphnia* (Pastorok, 1980; Spitze, 1985) and *Diaptomus* (Pastorok, 1980) increase with temperature, ultimately resulting in a higher frequency of *Chaoborus* attacks. However, Swift and Fedorenko (Swift and Fedorenko, 1975) only observed a temperature effect on swimming speed for *Polyphemus*, but not for *Bosmina* or *Diaptomus*, the dominant prey species in our experiment. Furthermore, no predation effect was detected in stratified conditions, despite epilimnetic temperatures being comparable to the isothermal water-column temperature (20.3 versus 21.2°C, respectively).

Alternatively, water temperatures experienced by *Chaoborus* throughout their diel migration may have influenced predation impact on zooplankton. *Chaoborus* respiration (Swift, 1976; Sigmon *et al.*, 1978), metabolism (Kajak and Rybak, 1979; Giguère, 1980; Büns

and Ratte, 1991) and digestion rate (Giguère, 1981; Spitze, 1985), the limiting factor in handling time, all increase with temperature. Therefore, as the average temperature experienced by *Chaoborus* increases, attack and ingestion rates concurrently increase to satisfy metabolic demands (Fedorenko, 1975a; Kajak and Rybak, 1979; Croteau *et al.*, 2002).

Survey data from Yan *et al.* (Yan *et al.*, 1991) indicate that mass-specific respiration for IV instar *C. punctipennis* in Swan Lake is almost twice as high when conditions are isothermal than when stratified. Our enclosure study demonstrates that this higher respiration may account for increased predation pressure on crustacean zooplankton prey. In our experiment, migration through stratified water resulted in a decreased mean exposure temperature for *Chaoborus* because of time spent in the cool hypolimnion. Heat content was similar between thermal trials over the 15-day study period such that
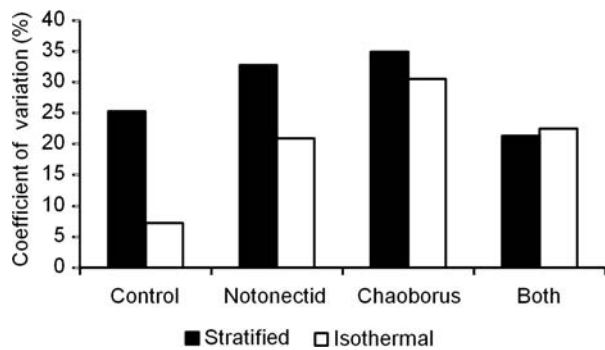
Fig. 4. Coefficient of variation in mean zooplankton abundance between depths.

the stratified trial had a mean whole-water column temperature of 19.5°C compared to 21.2°C in the warm isothermal trial. However, mean bottom water (6 m) temperature was 5.4°C warmer in the isothermal than stratified trial. Exposure to cooler water in the stratified trial may have lowered basal respiration and metabolism, reducing overall *Chaoborus* foraging and ingestion rate. In contrast, with exposure to warm, isothermal conditions, assimilation efficiency decreases, metabolic demand increases and predators spend more time actively foraging, likely resulting in greater predation impact. It is also possible that higher rates of prey consumption in the warmer exposure conditions of the isothermal trial were due to increased *Chaoborus* growth rate. Unfortunately, it was not feasible to measure *Chaoborus* body size at the beginning and the end of the experiment, so we were unable to calculate biomass and evaluate growth rate with our data. Overall, our experiment suggests that among migrating *Chaoborus* populations, those migrating through homogeneous, warm water will have a greater predation impact than those migrating through a thermal gradient with access to a cool water refuge.

It is unlikely that differences in initial prey community structure or chlorophyll concentrations account for the 73% reduction in zooplankton abundance by *Chaoborus* in isothermal conditions. As previously mentioned, prey density does affect encounter frequency with ambush predators such as *Chaoborus*. However, to account for stochastic processes in the prey community over the duration of the experiment, predation effect was always measured relative to a control treatment and not to initial prey densities. Furthermore, differences in prey community composition are negligible because *Chaoborus* forage opportunistically based on encounter frequency with prey when they are not prey-saturated and therefore not limited by prey handling time (Fedorenko, 1975a). In our experiment, *Chaoborus* were never prey-saturated.

Measured saturation densities are >20 copepods L^{-1} for IV *C. americanus* and IV *C. trivittatus* (Fedorenko, 1975a), 90 (<1.0 mm size) prey L^{-1} and 150 *Daphnia* (0.8 mm size) prey L^{-1} for *C. americanus* (Vinyard and Menger, 1980; Spitze, 1985) and >150 small-bodied cladoceran and copepod (<0.8 mm size) prey L^{-1} for Swan Lake *C. punctipennis* (Daly, 2008).

Furthermore, based on Ivlev's Electivity Index (Ei) (Ivlev, 1961), *Chaoborus* did not select for either copepods or cladocerans in the isothermal trial (Welch's non-parametric ANOVA; $F = 0.06$; $P = 0.81$; Ei $= 0.009 \pm$ SE 0.02 for copepods; $-0.001 \pm$ SE 0.02 for cladocerans), and weakly avoided cladocerans in the stratified trial ($F = 19.51$; $P < 0.01$; Ei $= 0.01 \pm$ SE 0.05 for copepods; Ei $= -0.32 \pm$ SE 0.05 for cladocerans), likely because they were not abundant. Additionally, in a separate analysis of a subset of the zooplankton data including only calanoid copepods as prey, *Chaoborus* had a predation impact on total calanoid abundance in isothermal conditions but not in the stratified trial (ANOVA; Thermal $\times$ *Chaoborus* Effect: $P < 0.0001$). Finally, the relative abundance of *Bosmina* sp. in the isothermal trial was consistent between treatments with and without *Chaoborus* (t-test; $P = 0.083$). Given the same *Chaoborus* predation effect on both the entire zooplankton community and for calanoids alone, combined with the lack of prey selection by *Chaoborus*, the change in prey composition between thermal trials does not likely explain the large *Chaoborus* predation effect in the isothermal versus stratified trial.

In contrast to the strong *Chaoborus* predation effect observed in isothermal conditions, notonectids had no predation effect in either stratified or isothermal conditions. Zooplankton daytime depth distribution shifted slightly deeper in the presence of notonectids relative to controls, but, in contrast to expectations, and although algal food resources (as measured by total chlorophyll *a* concentration) differed with depth in stratified conditions, this effect occurred in both thermal habitats. There was greater variability in zooplankton depth distribution in stratified than isothermal conditions, perhaps because food resources were more heterogeneously distributed, or because notonectids are restricted to feeding near the surface, where water temperatures were $1-2°C$ higher in the stratified trial, possibly increasing metabolic demand and predation pressure. Nevertheless, the weak avoidance behavior by zooplankton may have been sufficient to offset notonectid predation.

Crustacean zooplankton migrate downwards during the daytime to limit time spent in contact with surface-orienting aquatic insect predators. Gilbert and Hampton (Gilbert and Hampton, 2001) also observed

downward migration in zooplankton (*Tropocyclops extensus*) in response to *B. macrotibialis*. In shallow pond enclosures, predatory, surface-orienting dytiscid larvae reduced the abundance and deepened the depth distribution of *Daphnia* (Arts *et al.*, 1981). When Herwig and Schindler (Herwig and Schindler, 1996) removed all surface-orienting aquatic insect predators from a shallow treatment pond, *Daphnia* migration strategy was reversed to spend more time higher in the water column during the day in comparison to pre-manipulation patterns and to a reference system. In our study, migration away from surface predators resulted in no detectable notonectid predation impact on crustacean zooplankton abundance. Furthermore, this predator avoidance behavior was independent of lake thermal structure.

Predation by notonectids may have been minimal compared to that of *Chaoborus* because notonectids occur in much lower densities (3 per m^3 *Buenoa* versus 275 per m^3 *Chaoborus*). We stocked the enclosures with natural densities of notonectids for Swan Lake, which are comparable to notonectid densities in other small, fishless lakes. Bendell and McNicol (Bendell and McNicol, 1987) found a mean of 16 *Buenoa* m^{-2} with densities ranging from 0 to 70.8 m^{-2} across 15 small, fishless lakes near Sudbury, Ontario. Although notonectids can regulate zooplankton abundance in very shallow systems where encounter rates are higher (Hampton *et al.*, 2000), it may be that their predation impact on zooplankton in the pelagic zone of deeper stratified lakes is only apparent at higher predator densities.

Overall, our results suggest that changes in lake stratification will not affect the spatial overlap or predation impact of surface-orienting predators with crustacean zooplankton prey in shallow lakes, particularly in systems where surface predators are not abundant. In contrast, the importance of vertically migrating predators in reducing crustacean zooplankton abundance may increase in warm isothermal habitats that are expected to occur in small shallow lakes with future climate change. Changes in the predation regime of small lakes are of broad ecological significance because invertebrate predation appears to be much more important in structuring zooplankton communities in small, shallow lakes than in larger systems with more complex communities (Roff *et al.*, 1981; Keller and Conlon, 1994; Malkin *et al.*, 2006). Also, small lakes (<10 ha) are numerically the most abundant aquatic systems across the Boreal Shield Ecozone and, in fact, globally (Cox, 1978; Downing *et al.*, 2006). Predicting the outcomes of biological interactions under various thermal regimes is a current challenge in global change ecology. This study demonstrates

the potential for strong changes in predator–prey dynamics associated with climate warming. Furthermore, the intensity of these predation effects will vary with the severity of warming and associated changes in lake thermal regime, and may depend not only on increases in surface water temperature, but on integrated whole-lake water temperatures and the spatial distribution of predators and prey.

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