PRIMARY RESEARCH PAPER

Differential sensitivity of planktonic trophic levels to extreme summer temperatures in boreal lakes

**Megan M. MacLennan · Shelley E. Arnott ·
Angela L. Strecker**

Abstract The stress–size hypothesis predicts that smaller organisms will be less sensitive to stress. Consequently, climate warming is expected to favour smaller taxa from lower trophic levels and smaller individuals within populations. To test these hypotheses, we surveyed zooplankton communities in 20 boreal lakes in Killarney Provincial Park, Canada during 2005 (an anomalously warm summer) and 2006 (a normal summer). Higher trophic levels had larger responses to warm temperatures supporting the stress–size hypothesis; however, rather than imposing negative effects, higher density and biomass were observed under warmer temperatures. As a result, larger taxa from higher trophic levels were disproportionately favoured with warming, precluding an expected shift towards smaller species. Proportionately greater increases in metabolic rates of larger organisms or altered biotic interactions (e.g. predation and competition) are possible explanations for shifts in biomass distribution. Warmer temperatures also favoured smaller individuals of the two most common species, in agreement with the stress–size hypothesis. Despite this, these populations had higher biomass in the warm summer. Therefore, reduced adult survivorship may have triggered these species to invest in reproduction over growth. Hence, warmer epilimnions, higher zooplankton biomass and smaller individuals within zooplankton populations may function as sensitive indicators of climate warming in boreal lakes.

M. M. MacLennan · S. E. Arnott · A. L. Strecker
Department of Biology, Queen's University, Kingston,
ON K7L 3N6, Canada

Present Address:
M. M. MacLennan (✉)
Department of Biological Sciences, University of Alberta,
Edmonton, AB T6G 2E9, Canada
e-mail: mmmaclen@ualberta.ca

Present Address:
A. L. Strecker
Department of Environmental Science and Management,
Portland State University, PO Box 751, Portland, OR
97207, USA

Introduction

Climate change is restructuring communities in complex ways. There is a need to identify patterns characterizing warming responses and the mechanisms and processes underlying these changes to effectively predict and ameliorate impacts. We are currently limited by an incomplete understanding of how direct physiological effects of temperature are

mediated by indirect effects on species interactions. To date, many studies have focused on thermal responses of single species or simplified, constructed communities. Whilst this research provides a good foundation for understanding warming effects, consideration of species interactions in natural communities will be necessary for a comprehensive understanding of warming effects (Walther, 2007, 2010; Gilman et al., 2010; Montoya & Raffaelli, 2010; Woodward et al., 2010).

One general pattern that seems to structure responses to increased temperature is the differential sensitivity of larger organisms. This phenomenon may represent a specific case of the size–stress hypothesis, which predicts that stress, in general, favours smaller organisms (Odum, 1985) and has been demonstrated to hold for metal contamination (Cattaneo et al., 1998) and acidification stress (Vinebrooke et al., 2003). A recent meta-analysis showed that warming can induce a shift towards a smaller size-structure in a community of aquatic organisms by favouring smaller taxa and smaller individuals within populations (Daufresne et al., 2009). Similarly, sensitivity to warming tends to increase with trophic rank, which may be partly because of its tight coupling to body size (Woodward et al., 2005). For example, warmed communities of aquatic microbes resulted in the disproportionate loss of species from upper trophic levels and therefore shifted communities in favour of lower trophic levels (Petchey et al., 1999). In grassland communities, the amount of temporal variance in species abundance explained by climatic factors increased with trophic rank (Voigt et al., 2003, 2007). Larger organisms from higher trophic levels may be more sensitive to stress as a result of their relatively low diversity and functional redundancy or their low dispersal rates (Shurin et al., 2009), both of which reduce the probability that a tolerant species will be present, thereby reducing the potential for compensatory dynamics (Vinebrooke et al., 2003). Slower growth rates and longer reproductive cycles may also contribute to the susceptibility of larger organisms by restricting the rate of evolutionary adaptation to stress (Vinebrooke et al., 2003).

The greater sensitivity of larger organisms to warming may be particularly pronounced in ectothermic organisms because of the fundamental link between temperature and metabolic rate. As a result, temperature-induced changes to metabolism may be the underlying mechanism driving warming

responses. Metabolic rates of ectotherms tend to increase with temperature up to a thermal optimum resulting in higher rates of development, reproduction and feeding (Moore et al., 1996). These physiological changes will govern direct warming effects dependent on species-specific ranges of thermal tolerance. It has been proposed that the greater sensitivity of larger organisms to warming is a result of proportionately greater increases in metabolic costs (Moore et al., 1996). Consequently, systematic differences in thermal tolerances across size fractions and trophic levels may be primarily responsible for warming-induced changes in species interactions (Voigt et al., 2003). In turn, altered species interactions (e.g. changes in food availability) can feedback to modify direct effects. Ultimately, the combination of direct physiological effects and species interactions will structure community responses to warming stress.

Laboratory experiments have provided evidence that warming favours smaller organisms in simplified communities and under controlled conditions but these designs fail to capture the complexities of dynamics in natural communities. It is unclear if this trend would hold in a natural setting, although a recent meta-analysis found that smaller fish were favoured with warming in French rivers (Daufresne et al., 2009). Therefore, our goal was to determine if sensitivity to warming increases with trophic rank and body size in a natural system or if altered biotic interactions caused by warming, such as changes in algal food availability resulting from the greater complexity of a natural community, would obscure this pattern. Specifically, we hypothesized that warming would have the greatest detrimental effects on large omnivores and carnivores, which were classified in the same functional group, followed by large herbivores and then small herbivores, shifting communities towards smaller taxa. We also expected that warming would favour smaller individuals within populations.

Our survey-based design involved analysing interannual differences in zooplankton communities across 20 boreal lakes in Killarney Provincial Park, Ontario, Canada to determine the influence of an anomalously warm, dry summer in 2005 relative to the summer of 2006, which had seasonal temperatures and precipitation similar to the average for the past 50 years. A doubling of CO_2 is predicted to result in temperature increases of 3–4°C in the Killarney Park region

(Mortsch & Quinn, 1996), and trends in the Palmer Drought Severity Index show a consistent drying of the boreal region of Canada since 1900 (Dai et al., 2004). Boreal lakes in this area are considered to be particularly sensitive to warming because they tend to track atmospheric temperature changes (Schindler et al., 1996). Previously, long-term datasets have been used to correlate temporal warming patterns with biological trends in one or two lakes in the region (Schindler et al., 1996). Whilst this approach has the advantage of a large temporal scale (i.e. 20 years), its limited spatial scale restricts the generalization of results. By examining thermal responses of multiple lakes within a region that have inherently variable physical, chemical and biological properties, we hope to extend the generality of our observed warming trends beyond those of single-lake studies.

Methods

Study lakes

Killarney Provincial Park (hereafter Killarney Park) is a wilderness area located near Sudbury, Ontario, Canada, a region characterized by many lakes. The study area was selected because it has a diverse assemblage of lakes that have a wide range of physical and chemical properties but are all located in the same geographic region and experience a similar climate (Snucins & Gunn, 2000); sampled lakes were selected to represent this variation (Table 1). With the exception of Tyson Lake, a large lake located just outside of Killarney Park, sampled lakes were relatively small (surface area range 6.5–406.3 ha) and located within Killarney Park limits. There are currently no mining or forestry industries within Killarney Park, and all sampled lakes have minimal development in their catchments (Gunn et al., 2001).

Data collection

Samples were collected from each of the 20 Killarney Park lakes between July 11th and August 9th in 2005 and between July 23rd and July 26th in 2006, such that no 2006 sample was taken more than two weeks apart from the 2005 sample date for a lake. All lakes were sampled for zooplankton once each year with a single vertical net tow from 3 m off the lake bottom at the

maximum depth station to the surface to ensure zooplankton species characteristic of different vertical strata would be represented. A net with a mesh size of 80 µm and a mouth diameter of 25 cm was used. Zooplankton samples were preserved in 5.5% buffered sugar-formalin. Water temperature was measured at 1-m intervals from the surface of the lake down to 30-m depth using a YSI Model 95 dissolved oxygen and temperature meter (YSI Incorporated, Yellow Springs, OH) and samples for water chemistry and chlorophyll *a* were collected using an integrated tube sampler (2.5-cm inner diameter) from 0- to 5-m depth. Water chemistry samples were analysed following Ontario Ministry of the Environment (2003) protocols. Water for chlorophyll *a* analysis was divided into three subsamples and filtered through Pall[TM] Ultipor glass filters (1.2-µm pore size), which were then frozen and kept in darkness for later analysis. Chlorophyll *a* samples were extracted in methanol for 24 h in the dark in a refrigerator before analysing with a TD 700 Fluorometer (Turner Designs, Sunnyvale, California, USA). Water temperature profiles and water chemistry were not collected for Fish, Gem and Howry lakes in 2006, and these lakes were excluded from the analysis of interannual changes in lake thermal structure and water chemistry. Nellie and Tyson lakes were excluded from the analysis of interannual changes in chlorophyll *a* concentration as samples were not collected for these lakes. Data collected daily from Environment Canada Sudbury Meteorological Station (www.climate.weatheroffice.gc.ca) were used to determine minimum, maximum and mean air temperatures as well as mean precipitation for the past 50 years and the summers of 2005 and 2006.

Interannual changes in lake thermal structure

Measured temperature–depth profiles were used to compare the thermal structures of lakes between 2005 and 2006 sample dates. Epilimnetic depth was defined as the depth from the surface at which a greater than 1°C change per metre was observed. Thermocline depth was defined as the depth at which the greatest rate of temperature change occurred. Hypolimnetic depth was defined as the depth at which a less than 1°C change per metre was observed below the thermocline. The depth interval below the epilimnion over which a 10°C drop in temperature occurred was defined as the G_{10} (Snucins & Gunn, 2000). Only lakes that were

Table 1 Chemical, physical and biological characteristics of study lakes in Killarney Provincial Park measured in 2005

Lake	pH	DOC (mg/l)	Ca (mg/l)	Total P (µg/l)	Total N (µg/l)	Surface area (ha)	Maximum depth (m)	Fish	*Bytho*
Acid	5.3	1.6	1.1	2.6	**107**	19.6	29.0	A	A
A.Y. Jackson	6.3	3.3	1.4	6.1	270	**6.5**	9.8	P	A
David	5.5	1.4	1.1	3.1	214	406.3	24.4	P	A
Fish	6.5	4.4	1.9	6.1	190	115.4	8.5	P	A
Freeland	5.7	3.4	1.6	7.2	242	47.7	**3.5**	P	A
Gail	**4.6**	0.5	**0.6**	2.8	254	20.9	16.8	A	A
Gem	6.8	**5.2**	2.5	8.1	N/A	30.7	19.2	P	A
Great Mountain	6.0	2.6	1.4	**12.9**	262	198.3	37.5	P	A
Helen	7.1	3.4	2.6	3.6	178	82.6	41.2	P	P
Howry	6.9	4.8	2.7	7.2	**592**	118.1	27.5	P	A
Ishmael	7.0	4.0	2.8	4.8	254	72.8	19.8	P	A
Kakakise	6.8	3.0	2.4	2.6	388	112.6	30.5	P	P
Little Mountain	5.2	**0.1**	1.3	1.8	372	23.6	25.0	A	A
Low	**7.8**	3.3	**8.8**	6.6	199	33.8	28.4	P	P
Lumsden	5.6	1.2	1.1	3.3	136	23.8	21.8	A	A
Nellie	4.7	0.5	1.3	**1.2**	360	260.5	**54.9**	A	A
Norway	5.7	1.0	1.3	1.7	176	63.3	33.6	P	A
Partridge	6.2	2.0	1.8	2.6	180	11.0	16.9	P	A
Terry	5.8	4.5	1.4	8.8	309	11.5	8.0	P	A
Tyson	5.8	3.6	1.7	7.1	247	**1087.9**	41.5	P	A

To demonstrate the wide range of variation in these properties, bold values indicate the maximum and minimum values for each variable

DOC dissolved organic carbon; *Ca* calcium; *Total P* total phosphorus; *Total N* total nitrogen; *Fish* presence (P) or absence (A) of fish, *Bytho* presence (P) or absence (A) of *Bythotrephes longimanus*

stratified in both 2005 and 2006 were analysed for changes in thermocline depth, hypolimnetic depth and G_{10}.

Interannual changes in zooplankton assemblages

A minimum of 250 crustacean zooplankton specimens from each sample were morphologically identified using a compound microscope. Sub-samples were taken and counted in their entirety, but after 40–50 adult individuals from a taxon were counted, they were no longer counted in subsequent samples to allow for increased sensitivity for detecting rare species without compromising abundance calculations. Mature Copepoda and Cladocera were identified to species where possible and otherwise classified to genus. In order to assign species to trophic ranks, the analysis included only mature zooplankton for which

it is possible to attain this resolution of taxonomic classification. The lengths of the first 15 specimens of each taxon were measured and used to derive dry-weight biomass estimates using published length–weight regressions (McCauley, 1984; Culver et al., 1985; Lawrence et al., 1987; Yan & Mackie, 1987). Mean weighted length of a zooplankton community was calculated as the product of the mean length of a zooplankton taxa and its proportional relative abundance, summed across all taxa. Zooplankton were grouped by trophic and size classifications following the functional traits defined in Barnett et al. (2007). We refer to these trophic and size classifications henceforth as functional groups for simplicity. Two functional groups were represented by fewer than three species so these groups were amalgamated with the most closely related functional group. The resulting three functional groups were small herbivores,

large herbivores and omnivores/carnivores, an order that corresponds to both increasing average body size and increasing trophic rank.

Statistical analysis

Two-tailed paired *t* tests were used to determine if there were significant interannual differences in water chemistry, lake thermal structure, mean adult zooplankton lengths and chlorophyll *a* concentration (SPSS, version 18.0.0). Analysis of variance (ANOVA) was used to test the hypothesis that warming responses differed across sizes and trophic levels of zooplankton, indicated by a significant interaction between year effects and functional groups. ANOVAs were performed on adult zooplankton biomass, density and taxonomic richness and included lake identity as a random variable. Data for a given functional group within a lake were only included if zooplankton from that functional group were detected in at least one sampling year; otherwise it was assumed that organisms from that functional group did not reside within that particular lake. Post-hoc analyses of significant interactions were not possible due to the inclusion of lake identity as a random variable. Therefore, when a significant interaction was found, two-tailed paired *t* tests were used to determine if the dependent variable differed between years for each functional group. Separate ANOVAs were performed for lakes with and without fish present and for lakes with and without the invasive invertebrate *Bythotrephes longimanus* to test if these factors influenced the results (Table 1). Responses amongst these different lake categories were similar and therefore, we present only the results including all lakes to maximize power. All variables were screened before analysis for equal variances and normality and $\log(x + 1)$-transformed where required.

Results

Interannual differences in air temperature and precipitation

Environment Canada records from Sudbury indicate that 2005 had the highest mean June temperature (19.6°C) and the second lowest mean June precipitation (27.0 mm) over the past 50 years. In contrast, the mean temperature (17.3°C) and precipitation (63.0 mm) in June 2006 were much closer to climatic norms for this month (namely, 16.2°C and 77.8 mm). Temperatures in June and July in 2005 also reached a higher maximum (34.6 vs. 31.6°C) and had a warmer minimum (6.7 vs. 4.0°C) than 2006, representing a shift in temperature range by approximately 3°C.

Interannual differences in abiotic lake conditions

There were no significant differences in any water chemistry variables between 2005 and 2006 including pH ($t = 0.04$, $P = 0.97$), dissolved organic carbon ($t = 0.66$, $P = 0.52$), calcium ($t = 0.61$, $P = 0.55$), total phosphorus ($t = 1.20$, $P = 0.25$) and total nitrogen ($t = 1.69$, $P = 0.11$) (df = 16 for all tests). Chlorophyll *a* concentration also did not differ between years ($t = 0.62$, $P = 0.55$, df = 17). Mean epilimnetic temperatures were significantly higher in the warmer summer, 2005 (24.2°C), relative to 2006 (23.4°C) ($t = 3.84$, $P = 0.01$, df = 16). The G_{10} (the depth interval below the epilimnion over which a 10°C drop in temperature occurred) was larger by 0.6 m in 2005 relative to 2006 (4.7 vs. 4.1 m), indicating a weaker metalimnetic gradient. Although this difference was not statistically significant at this sample size ($t = 2.09$, $P = 0.06$, df = 15), the magnitude of change was large enough to potentially be biologically relevant. There were no significant interannual differences in epilimnetic depth ($t = 0.84$, $P = 0.42$, df = 15), thermocline depth ($t = 1.02$, $P = 0.33$, df = 14), or hypolimnetic depth ($t = 0.27$, $P = 0.79$, df = 13).

Interannual differences in zooplankton communities

A total of 36 crustacean zooplankton taxa were detected in the 20 sampled lakes in 2005 and 2006 with species richness ranging from 2 to 13 taxa/lake and averaging seven taxa/lake (Table 2). The omnivorous calanoid *Leptodiaptomus minutus* was the most common species followed by the generally carnivorous cyclopoid *Diacyclops thomasi*. *L. minutus* was present in all 20 lakes comprising, on average, 34.0% of zooplankton community abundance and *D. thomasi* was present in 13 lakes comprising, on average, 12% of zooplankton community abundance.

Table 2 List of species identified as adult individuals sampled from the study lakes in Killarney Provincial Park and their functional group classification

Species	Functional group	Number of Lakes		Mean biomass (μg/l)	
		2005	2006	2005	2006
Acantholeberis spp.	SH	0	1		0.10
Acroperus spp.	SH	2	2	0.01	1.28
Alona spp.	SH	3	1	3.64	0.29
Bosmina spp.	SH	16	15	8.75	6.96
Chydorus spp.	SH	5	5	0.03	0.40
Cyclops vernalis	OC	1	0	1.85	
Daphnia ambigua	LH	1	3	1.12	0.94
Daphnia catawba	LH	3	1	0.92	0.28
Daphnia dubia	LH	0	2		2.12
Daphnia longiremis	LH	0	2		1.17
Daphnia mendotae	LH	8	2	5.92	3.56
Daphnia parvula	LH	2	0	2.49	
Daphnia pulex/pulicaria	LH	1	0	5.18	
Daphnia retrocurva	LH	1	0	2.17	
Daphnia spp.	LH	2	8	<0.01	2.18
Diacyclops thomasi	OC	13	10	10.38	4.72
Diaphanosoma birgei	LH	13	12	10.56	8.35
Epischura lacustris	OC	4	2	5.46	0.56
Eubosmina longispina	SH	2	4	8.55	0.84
Eubosmina tubicen	SH	6	10	4.14	4.59
Holopedium gibberum	LH	14	14	10.49	3.33
Leptodiaptomus ashlandi	SH	0	2		0.18
Leptodiaptomus minutus	OC	20	20	22.76	11.77
Leptodiaptomus sicilis	SH	1	0	0.77	
Latona spp.	LH	0	1		0.06
Mesocyclops edax	OC	11	10	4.48	1.67
Ophryoxus spp.	SH	0	2		0.75
Orthocyclops modestus	OC	1	0	0.14	
Polyphemus pediculus	OC	3	2	0.34	0.24
Skistodiaptomus oregonensis	OC	5	4	1.93	1.75
Skistodiaptomus reighardi	OC	0	1		61.50
Senecella calanoides	OC	1	1	2.88	0.81
Tropocyclops extensus	SH	9	7	1.25	2.04

The number of lakes in which a species was detected and, when present, the mean species biomass in a lake is given for each sample year

SH small herbivore; *LH* large herbivore; *OC* omnivore/carnivore

Adult zooplankton biomass was significantly higher in the warm year compared to the normal year ($F_{1,20} = 4.36$, $P = 0.05$), but interannual differences depended on functional group (Year × Functional group interaction: $F_{2,31} = 3.35$, $P = 0.05$). Whilst the biomass of small herbivores was relatively unchanged between years, the biomass of both large herbivores and omnivores/carnivores more than doubled in the warm year (Small herbivores: $t = 0.60$, $P = 0.56$, df = 19; Large herbivores: $t = 2.64$, $P = 0.02$, df = 17; Omnivores/Carnivores: $t = 2.18$, $P = 0.04$, df = 19; Fig. 1). Similar to biomass, interannual changes in density depended on functional group (Year × Functional group interaction: $F_{2,31} = 5.06$, $P = 0.01$) with omnivores/carnivores showing the largest density increase in the warm year, followed by large herbivores, and finally small herbivores, which showed relatively little difference between years (Small herbivores: $t = 0.48$, $P = 0.64$, df = 19; Large herbivores: $t = 2.05$, $P = 0.06$, df = 17; Omnivores/Carnivores: $t = 2.55$, $P = 0.02$, df = 19; Fig. 2).
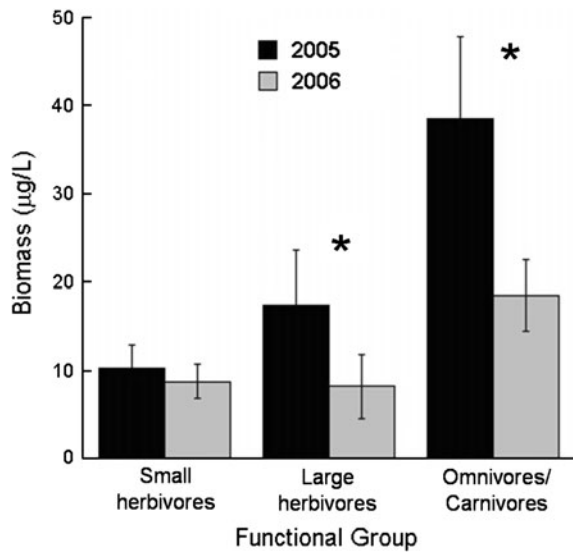
Fig. 1 Interannual differences in adult zooplankton biomass (µg/l) by functional group based on a survey of 20 boreal lakes in Killarney Provincial Park, Ontario comparing the effect of an anomalously warm summer in 2005 (*black*) to an average summer in 2006 (*grey*). *Bars* indicate ±1 standard error and *asterisks* indicate significant differences based on a paired *t* test at $P < 0.05$
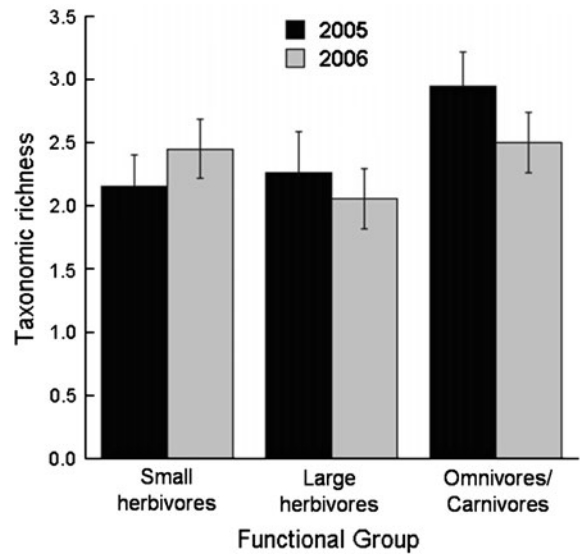

Fig. 3 Interannual differences in adult zooplankton taxonomic richness by functional group based on a survey of 20 boreal lakes in Killarney Provincial Park, Ontario comparing the effect of an anomalously warm summer in 2005 (*black*) to an average summer in 2006 (*grey*). *Bars* indicate ±1 standard error and *asterisks* indicate significant differences based on a paired *t* test at $P < 0.05$
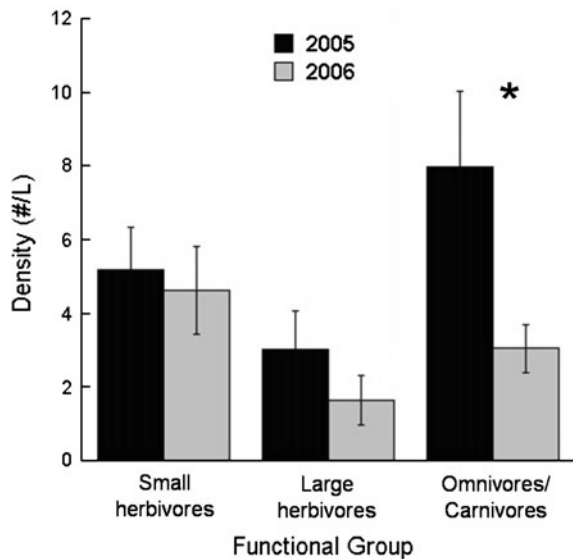

Fig. 2 Interannual differences in adult zooplankton density (#/l) by functional group based on a survey of 20 boreal lakes in Killarney Provincial Park, Ontario comparing the effect of an anomalously warm summer in 2005 (*black*) to an average summer in 2006 (*grey*). *Bars* indicate ± 1 standard error and *asterisks* indicate significant differences based on a paired *t* test at $P < 0.05$

Warmer temperatures did not affect taxonomic richness of zooplankton communities ($F_{1,20} = 0.62$, $P = 0.44$). Although there was no significant interactive effect (Year × Functional group interaction: $F_{2,31} = 2.96$, $P = 0.07$), the response of zooplankton taxonomic richness to warmer temperatures in 2005 showed similar trends to density and biomass responses. Warmer temperatures in 2005 were associated with higher taxonomic richness for omnivores/carnivores and, to a lesser extent, large herbivores compared to 2006, whereas the taxonomic richness of small herbivores was lower in 2005 compared to 2006 (Fig. 3).

There was no evidence for a wide-spread shift towards smaller bodied taxa with warming as zooplankton body size at the community level did not significantly differ between years ($t = 0.69$, $P = 0.52$, df = 19; Fig. 4a). At the population level, however, there were shifts towards smaller individuals in the warm year for the two most common species. The omnivore, *Leptodiaptomus minutus,* and the carnivore, *Diacyclops thomasi*, had significantly smaller mean body sizes in 2005 compared to 2006 (*L. minutus*: $t = 2.42$, $P = 0.03$, df = 19; *D. thomasi*: $t = 3.93$, $P < 0.01$, df = 9; Fig. 4b, c). Despite reduced

Fig. 4 Interannual differences in adult zooplankton body size (mm) based on a survey of 20 boreal lakes in Killarney Provincial Park, Ontario comparing the effect of an anomalously warm summer in 2005 to an average summer in 2006 for (a) the whole-lake community ($n = 20$ lakes), (b) *Leptodiaptomus minutus* ($n = 20$), (c) *Diacyclops thomasi* ($n = 10$), (d) *Bosmina* spp. ($n = 14$), (e) *Holopedium gibberum* ($n = 13$) and (f) *Diaphanosoma birgei* ($n = 10$). *Bars* indicate ± 1 standard error and *asterisks* indicate significant differences based on a paired *t* test at $P < 0.05$
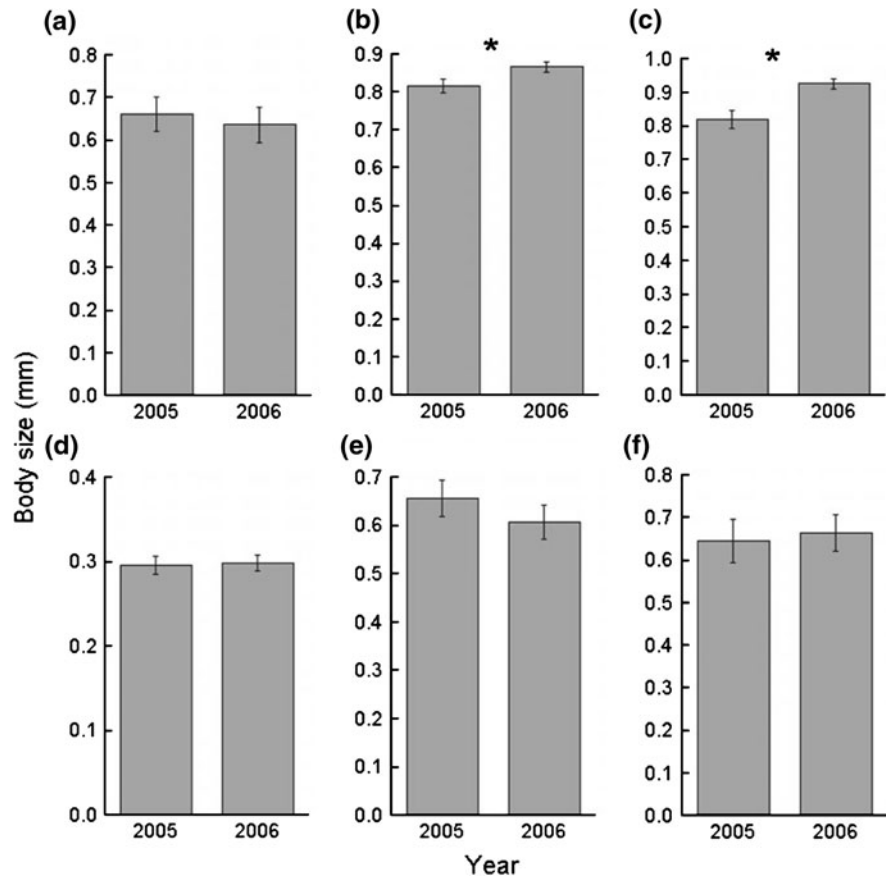
individual body size of these species, these populations had higher biomass in the warm year (*L. minutus*: $t = 2.42$, $P = 0.03$, df $= 19$; *D. thomasi*: $t = 3.21$, $P < 0.01$, df $= 12$; Table 2). On the other hand, there were no significant interannual differences in body size for the small herbivore, *Bosmina* spp., or for the large herbivores *Holopedium gibberum* and *Diaphanosoma birgei* (*Bosmina* spp: $t = 0.25$, $P = 0.81$, df $= 13$; *H. gibberum*: $t = 0.27$, $P = 0.79$, df $= 12$; *D. birgei*: $t = 1.50$, $P = 0.17$, df $= 9$; Fig. 4d–f), and the biomass of these populations did not differ between years (*Bosmina* spp: $t = 1.01$, $P = 0.33$, df $= 16$; *H. gibberum*: $t = 2.00$, $P = 0.07$, df $= 14$; *D. birgei*: $t = 1.07$, $P = 0.30$, df $= 14$; Table 2).

Discussion

The stress–size hypothesis predicts that smaller organisms will be less sensitive to stress (Odum, 1985). Consequently, climate warming is expected to

favour smaller taxa from lower trophic levels and smaller individuals within populations. Our findings show that higher trophic levels had larger responses to anomalously warm summer temperatures supporting the hypothesis that sensitivity to stress increases with trophic rank. However, rather than imposing negative effects that typically characterize stressors, warmer temperatures were associated with increases in biomass that were primarily the result of higher densities. The greater sensitivity of larger taxa from higher trophic levels caused them to be disproportionately favoured with warming, precluding an expected shift towards smaller species. At the population level, warming favoured smaller individuals of the two most common species, in agreement with predictions of the stress–size hypothesis. Despite smaller individuals, the biomass of these populations was higher in the warm year.

Interannual changes in the zooplankton community were most likely attributable to warmer summer temperatures. Epilimnetic temperatures tend to track

interannual variations in air temperatures (Livingstone & Lotter, 1998), and this was the only environmental variable (physical or chemical) that was significantly different between study years. There was a trend towards weaker metalimnetic gradients but we are unable to definitively link this trend to warmer summer temperatures because changes in the strength of this gradient may be caused by the rate of spring heating rather than the overall mean temperature (Snucins & Gunn, 2000). Despite unusually low precipitation in the warmer summer, there was no evidence of effects associated with drier conditions on the lake systems, namely, lower dissolved organic carbon levels from reduced transport from catchments (Schindler et al., 1996; Gunn et al., 2001) or drought-induced acidification (Arnott et al., 2001). Therefore, our results suggest that direct increases in epilimnetic water temperature will be the most immediate effect of warming on lake thermal structure. As such, epilimnetic temperature may be a useful indicator for monitoring climate warming (Adrian et al., 2009).

Our results support the finding that higher trophic rank is linked to greater change in biomass in response to stress (Voigt et al., 2003; Hogsden et al., 2009), implying that the particular susceptibility of higher trophic levels to stress is due to inherently lower stability. Although several mechanisms have been proposed to explain why the magnitude of stress responses tend to increase with trophic rank (e.g. lower diversity, lower dispersal rates, longer reproductive cycles), these explanations are only applicable to negative stressor effects and cannot account for why larger organisms from higher trophic levels were more positively affected by warming in our study. One possibility for this unexpected result is warming directly accelerated metabolic rates to increase growth, reproduction and foraging: it has been suggested that discrepancies in warming responses across trophic levels are due to proportionately greater increases in metabolic rates of larger organisms (Moore et al., 1996). For example, as temperatures rise, *Bosmina* spp. (the most common small herbivore found in the Killarney Park lakes surveyed) increases its filtering rate remarkably little compared to other zooplankton species, which may have led to a competitive disadvantage (Mourelatos & Lacroix, 1990). In 2005, a shift towards larger herbivores and predators may have occurred because temperature-dependent increases in development and reproductive

rates for these functional groups would have been relatively greater than for smaller herbivores, leading to disproportionate increases in population growth rates across trophic levels.

Metabolic demands will also be proportionately greater for larger organisms but can be compensated for by increasing consumption rates, given food resources are not limiting (Moore et al., 1996). As a result, increased predation rates may also have limited the population growth of small herbivores in the warm year. Similarly, increased predator metabolic rates at higher temperatures strengthened top-down effects in old-field food webs (Barton et al., 2009) and pitcher plant communities (Hoekman, 2010). Conversely, algal food availability likely did not limit population growth of small herbivores in our study because epilimnetic chlorophyll *a* levels were not different between years. Therefore, our results support the finding that the strengths of bottom-up effects are relatively unaffected by warming (Barton et al., 2009; Hoekman, 2010). However, if the trend towards weaker metalimnetic gradients is indeed a consequence of warming, then the feeding efficiency of herbivores that rely on the accumulation of phytoplankton at steep metalimnetic gradients (i.e. the deep chlorophyll maxima) may be compromised (Barbiero & McNair, 1996; Snucins & Gunn, 2000; Francis et al., 2011). Although we did not quantify chlorophyll below the epilimnion, we would expect the weaker metalimnetic gradient in the warm year to, if anything, reduce the concentration of the deep chlorophyll maxima, which would have resulted in lower abundance and biomass of herbivores and omnivores. In contrast, we observed higher biomass of large herbivores and omnivores/carnivores in the warm year, suggesting that the deep chlorophyll maxima did not influence zooplankton responses. Clearly biotic interactions play a crucial role in structuring thermal responses in natural communities but an incomplete understanding of these species-mediated warming effects limits our ability to accurately predict the effects of climate warming. Therefore, it is necessary to determine the underlying mechanisms driving change, and our results suggest that metabolic theory may provide a solid basis for the development of a unifying framework (Brown et al., 2004; Woodward et al., 2010). Whilst species-level responses provide a useful starting point for climate change research, there is an increasing realization that investigators will need

to shift their focus to incorporate species interactions to realistically understand the complexities of warming responses in a natural environments (Walther, 2007, 2010; Gilman et al., 2010; Montoya & Raffaelli, 2010; Woodward et al., 2010).

In contrast to community-level responses, effects of warming at the population level were consistent with predictions of the size–stress hypothesis for the omnivore, *Leptodiaptomus minutus* and the carnivore, *Diacyclops thomasi*, which both had significantly smaller individuals in the warm year (Daufresne et al., 2009). Proportionately greater increases in energy requirements are needed to sustain larger individuals of the same species at higher temperatures (Woodward et al., 2010). Therefore, smaller individuals may have been favoured in the warmer year because they were less likely to experience energy deficits than their larger conspecific competitors. Alternatively, if warmer conditions stimulated higher predation rates by larger copepods, macroinvertebrate predators, or fish, then reduced adult survivorship may have triggered these species to invest more highly in reproduction over growth (Stibor, 1992). This explanation could account for both the reduced size at maturity of individuals as well as the higher biomass of these populations in the warm year. Other explanations to account for reduced adult body size of these species are possible, and the underlying mechanism will, however, need to be experimentally tested. On the other hand, there were no significant interannual differences in body size or population biomass for the small herbivore, *Bosmina* spp., or the large herbivores, *Holopedium gibberum* and *Diaphanosoma* spp., consistent with the trend that organisms from lower trophic levels are less sensitive to stress. As a result of their inherently smaller size, herbivores may be less likely to experience energy deficits with warming and may be less affected if warming leads to higher predation intensity.

With a survey-based approach, our study was able to capture the realism of complex responses to extreme summer temperatures in natural communities (Woodward et al., 2010). Similar studies on warming impacts in natural communities are often restricted to one or two lakes (Gerten & Adrian, 2000; Hampton et al., 2008). Despite findings that suggest lake morphology and trophic state may be important drivers of warming responses (Anneville et al., 2010), the trends we observed were consistent across 20 lakes with a range

of physical, biological and chemical characteristics, thereby strengthening the generality of our results. An inherent trade-off of natural experiments, however, is that opportunities to conduct them are restricted by the occurrence of extreme natural phenomenon, which limited the temporal scale of our study to comparisons between two summers. However, Olden et al. (2006) demonstrated that single year estimates of zooplankton community composition in temperate lakes can be adequate if the lakes span a broad environmental gradient. In addition, our observation of higher zooplankton biomass in the warm summer is consistent with climate warming predictions for boreal lakes (Magnuson et al., 1997; Keller, 2007). Nevertheless, higher zooplankton biomass with warming has not been a universal finding. In contrast to boreal systems, experimental studies on alpine lakes showed that warming reduced zooplankton biomass (Strecker et al., 2004; Holzapfel & Vinebrooke, 2005). One explanation for this discrepancy could be differences in the magnitude of warming. Experimentally manipulated increases of 3.6°C (Strecker et al., 2004) and 7°C (Holzapfel & Vinebrooke, 2005) were much larger than the mean June temperature difference of 2.3°C between 2005 and 2006 in our study. Several studies have shown that moderate warming stimulates zooplankton metabolic rates, which could increase biomass production, whereas trade-offs associated with chronic or extreme warming tend to impair production (Burns, 1969; Herzig, 1983; Moore et al., 1996; Chen & Folt, 2002). For example, the most common species, *Leptodiaptomus minutus*, tolerates a broad range of temperatures and therefore may have benefited from moderate warming in 2005 (Carter et al., 1980). Also, community responses to climate warming can reverse trajectories when examined over many years (Suttle et al., 2007). Whilst we observed only positive effects of higher temperatures on zooplankton communities, it is likely that larger temperature increases will exceed the thermal limits of zooplankton species, in particular those of cool-water species (Moore et al., 1996). Higher trophic levels are more likely to face extinction in warmed communities (Petchey et al., 1999), which could reverse the disproportionate positive effects of warming on the biomass of predators and large herbivores. Therefore, the effects that we observed may represent only a transitional stage in longer-term effects of climate warming if increases in temperature greatly exceed the

interannual temperature difference of 2.3°C in this study as they are expected to.

It is possible that changes in the densities, biomasses and mean lengths of zooplankton functional groups and species observed in the warmer summer were a consequence of altered seasonal succession caused by extreme temperatures (Gerten & Adrian, 2000). In particular, the timing of an extreme heat event in relation to the clear water phase can alter the sensitivity of zooplankton species to a warming stressor (Huber et al., 2010). Warming can also lead to temporal asynchrony in spring phytoplankton peaks and maximal zooplankton reproduction (Winder & Schindler, 2004). Although we do not have ice-off dates for our study lakes, ice-off for Ramsey Lake, which is located nearby in Sudbury and experiences a similar climate, was on April 21 in 2005 and April 19 in 2006 (Bill Keller, unpublished). Similar ice-off timing suggests that the start of spring succession for the zooplankton communities did not differ between years and that the observed interannual differences would have accumulated later in the season. Furthermore, a survey of five nearby boreal lakes showed that warmer spring temperatures in April and May 2003 did not lead to differences in spring or summer (July–August) zooplankton biomass for any functional group relative to cooler spring temperatures in 2002 (Shelley Arnott, unpublished), suggesting that spring temperatures likely do not influence summer zooplankton communities in these lakes. Therefore, extreme summer temperatures in 2005 are the strongest explanation for interannual differences in zooplankton communities and any interannual differences in phenology were likely minor.

Freshwater ecosystems are considered to be effective sentinels for climate warming because they respond rapidly to temperature increases with measurable effects (Adrian et al., 2009). The results of our study based on a survey of 20 boreal lakes indicate that warmer epilimnetic temperatures, higher zooplankton biomass and smaller body lengths of individuals within zooplankton populations may function as sensitive indicators for monitoring climate warming effects in boreal lakes. Moreover, we provide evidence that changes in aggregate community measures such as species richness will likely be preceded by subtler changes in zooplankton communities, such as biomass distribution across trophic levels and size classes. In this context, shifts in biomass distribution favouring higher trophic levels and larger organisms could be explained by temperature-dependent physiological effects if warming caused proportionately greater increases in metabolic rates of larger organisms. However, the greater sensitivity of higher trophic levels to warming could also have been a consequence of altered biotic interactions, such as competition and predation, with warming, further underscoring the value of investigating warming effects in natural communities. Indeed, a strong priority has been placed on community and ecosystem-level studies, emphasizing that predicting climate warming responses will be limited by our understanding of how warming alters species interactions (Walther, 2007, 2010; Gilman et al., 2010; Montoya & Raffaelli, 2010; Woodward et al., 2010). Our next challenge will be to isolate and identify mechanisms driving warming effects, including direct physiological responses and altered biotic interactions, and to integrate these findings in a coherent framework to better predict and ameliorate effects of climate warming.

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