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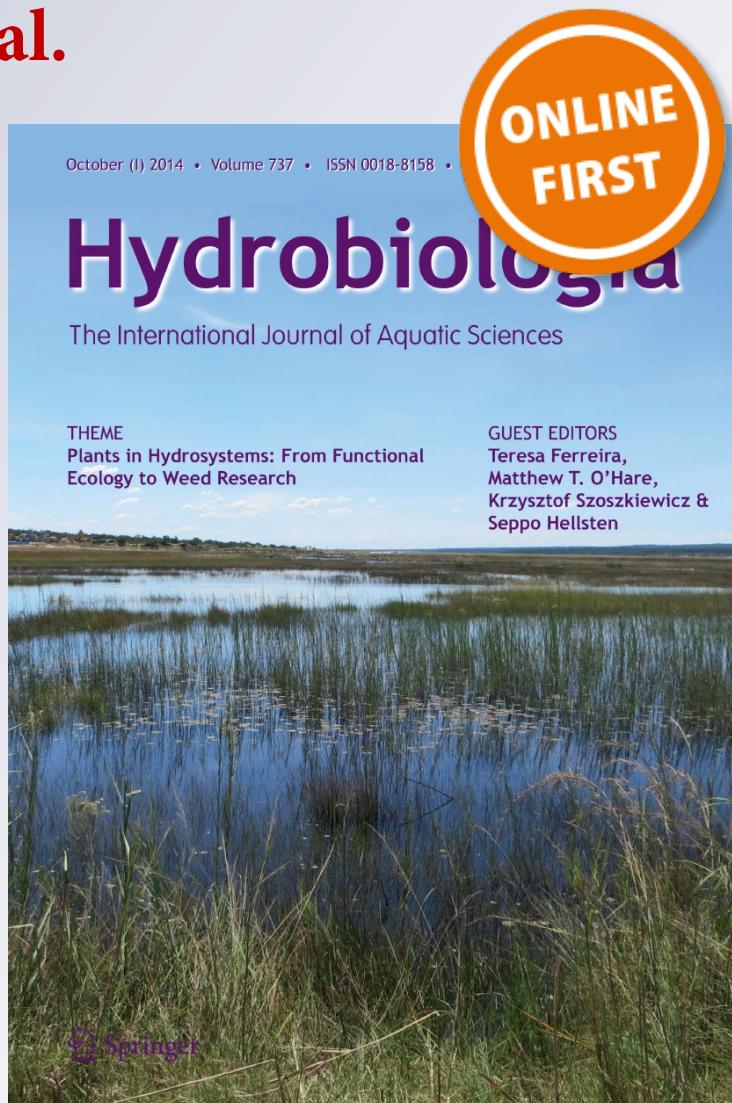
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Temperature effects on body size of freshwater crustacean zooplankton from Greenland to the tropics

Karl E. Havens · Ricardo Motta Pinto-Coelho · Meryem Beklioğlu ·
 Kirsten S. Christoffersen · Erik Jeppesen · Torben L. Lauridsen ·
 Asit Mazumder · Ginette Méthot · Bernadette Pinel Alloul ·
 U. Nihan Tavşanoğlu · Şeyda Erdoğan · Jacobus Vijverberg

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Abstract The body size of zooplankton has many substantive effects on the function of aquatic food webs. A variety of factors may affect size, and earlier studies indicate that water temperature may be a particularly important variable. Here we tested the hypothesis that the body size of cladocerans, calanoids, and cyclopoids declines with increasing water temperature, a response documented in an earlier study that considered only cladoceran zooplankton. We tested the hypothesis by comparing body size data

that were available from prior studies of lakes ranging from 6 to 74° latitude and encompassing a temperature range of 2–30°C. Cladoceran body size declined with temperature, in a marginally significant manner ($P = 0.10$). For cyclopoids, the decline was more significant ($P = 0.05$). In both cases, there was considerably more variation around the regression lines than previously observed; suggesting that other variables such as fish predation played a role in affecting size. Calanoid body size was unrelated to temperature. In contrast with cladocerans and cyclopoids, perhaps calanoid body size is not metabolically constrained by temperature or is differently affected by changes in fish predation occurring with increasing temperature. The unexpected result for calanoids requires further investigation.

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K. E. Havens (✉)
 University of Florida and Florida Sea Grant, Gainesville,
 FL 32608, USA
 e-mail: khavens@ufl.edu

R. M. Pinto-Coelho
 Departamento de Biología General, Universidad Federal
 de Minas Gerais, Belo Horizonte 31270-901, Brazil

M. Beklioğlu · U. N. Tavşanoğlu · Ş. Erdoğan
 Department of Biological Sciences, Middle East
 Technical University, Ankara, Turkey

M. Beklioğlu
 Kemal Kurdaş Ecological Research and Training Stations,
 Lake Eymir, Middle East Technical University, Ankara,
 Turkey

K. S. Christoffersen
 Institute of Biology, Universitetsparken 4, Copenhagen,
 Denmark

E. Jeppesen · T. L. Lauridsen
 Department of Plant Biology, University of Aarhus,
 Nordlandsvej 68, Risskov, Denmark

E. Jeppesen · T. L. Lauridsen
 Sino-Danish Centre for Education and Research, Beijing,
 China

A. Mazumder
 Department of Biology, University of Victoria,
 P.O. Box 3020, Stn. CSC, Victoria, BC V8W 3N5,
 Canada

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Introduction

Body size of zooplankton is a highly important attribute because of the influence it has on bioenergetics in aquatic food webs. Body size affects the manner in which the zooplankton interacts with its resources. Large-bodied zooplankton have higher grazing rates, they graze a wider size range of food items, and, therefore, have greater top-down effects on resources than small-bodied zooplankton (Carpenter & Kitchell, 1988). Likewise, body size affects the availability and antipredator responses of zooplankton to both invertebrate and vertebrate predators (Zaret, 1980; Gélinas et al., 2007), and the relationship between phytoplankton biomass and phosphorus in lakes (Mazumder, 1994a, b and see the review by Meerhoff et al., 2012).

In warm water lakes, the size of zooplankton generally is smaller than of those in cold water lakes. The reasons for this trend have been debated, yet so far, answers are inconclusive. When considered alone and independent of other factors, higher temperature is expected to result in smaller animals because higher temperature shortens generation time (Gillooly, 2000) resulting in smaller adult body size (Geiling & Campbell, 1972; Angilletta & Dunham, 2003). This phenomenon is not restricted to zooplankton. Atkinson (1994) conducted a review and found that >80% of ectothermic species studied in laboratory experiments displayed faster growth and smaller adult size at higher temperatures, and in general, animals in colder climates are larger as adults than conspecifics at colder temperatures (Ashton, 2001).

Larger zooplankton also may be more susceptible to thermal stress at high temperatures (Moore et al.,

1996). However, changes in temperature also can have indirect effects on the food web, and these could be of greater importance than direct effects in determining zooplankton body size. Hart & Bychek (2011) reviewed the factors affecting body size and concluded that 'direct thermal effects on body size are commonly confounded by other environmental factors that are related directly or indirectly to temperature' and that 'predation undoubtedly has an over-riding influence on body size selection.'

One prior study examined the relationship of body size in freshwater cladoceran zooplankton with latitude and temperature (Gillooly & Dodson, 2000) using data from 1,100 lakes between 7° and 78° latitude in North, Central, and South America. The authors found that temperature alone explained over 90% of variation in cladoceran body size. In that study, the authors did not use direct measurements of size. They took species lists from the literature and estimated size based on assumptions including invariant size within species and even distribution of density among species in lakes. This makes our study unique, in being the first to address the relationship between size and temperature with actual measurements of density and biomass of cladocerans, and the first to broaden the assessment to include cyclopoids and calanoids.

We obtained crustacean zooplankton data from published studies conducted in Brazil, Canada (British Columbia and Ontario), Ethiopia, Greenland, Turkey, and the USA (Alaska and Florida). All datasets had direct measurements of density, and biomasses were calculated from body lengths using published and well-accepted allometric methods. We calculated the mean body size (μg dry weight) of cladocerans, calanoids, and cyclopoids in each region, and tested the hypothesis that body size in all three groups declines with temperature across the broad latitudinal gradient of our study lakes.

Methods

Study lakes

We used pre-existing data from lakes representing a wide range of nutrient concentrations, six countries and several climactic regions (Fig. 1; Table 1). Late summer samples were used (August–September in Canada, United States and Turkey, and September in

G. Méthot · B. P. Alloul
Département de Sciences biologiques, Groupe de
Recherche Interuniversitaire en Limnologie, Université de
Montréal, C.P. 6128, Succ. Centre-ville, Montreal, QC,
Canada

J. Vijverberg
Netherlands Institute of Ecology, Droevendaalsesteeg 10,
6708 PB Wageningen, The Netherlands



Fig. 1 Map showing the general locations of lakes included in this paper, in: Alaska, Brazil, British Columbia, Ethiopia, Florida, Ontario, and Turkey

Table 1 Lake regions, latitudes, numbers of lakes, and water temperatures at the time of sampling

Region	Latitude	No. of lakes	Temp (°C)
Greenland	66°–74°N	57	2–16
Alaska	55°–60°N	5	15–17
Ontario	49°N	5	17–19
British Columbia	49°N	4	19
Turkey	38°–42°N	32	9–17
Florida	28°N	6	30
Brazil	19°–21°S	4 (13)*	23–27
Ethiopia	6°–13°N	9	19–26

* Parenthetical value includes multiple sampling sites in two large dendritic reservoirs

Greenland), because only that period of time was sampled in synoptic surveys in Greenland and Turkey

and so that data would be comparable in regard to the time of full development of crustaceans and highest fish predation (Jeppesen et al., 1997). In Ethiopia and Brazil, data were taken from the dry season (November to January in Ethiopia, July–August in Brazil), which also are times of high fish predation (Vijverberg et al., 2014). During the rainy season (July–September) in NE Africa and in South America, short water residence times flush zooplankton from lakes and reservoirs, making it an unsuitable time for studying zooplankton.

Sampling methods

Detailed sampling methods are provided in published papers dealing with other aspects of the plankton: for Greenland (Jeppesen et al., 2001); Ontario, Florida

and Brazil (Pinto-Coelho et al., 2005); British Columbia (Kainz et al., 2004); and Africa (Vijverberg et al., 2014). Therefore, only brief descriptions of methods are provided here.

Sampling methods in all lakes except Turkey collected animals from the entire water column. In Greenland, mid-lake depth-integrated water samples (20–25 l) were taken with a Patalas sampler. Of the pooled sample, a 15–20 l subsample was filtered on a 20 µm filter. In Turkey, a 40 l mid-lake integrated water sample through the entire mixed layer was taken with a KC Denmark Water Sampler (3.5 l), and 20 l was filtered through a 20 µm filter. In Ontario, zooplankton was sampled from the entire water column at the deepest site in the lakes by vertical tows with a 53 µm mesh conical plankton net. In British Columbia and Alaska, vertical tows of a 64-µm mesh conical net were taken from 1 m above the sediments to the surface at the deepest location in the lakes. In Florida, Ethiopia, and Brazil, single vertical tows of the entire water column were done with conical nets with 153, 150, and 90 µm mesh, respectively. In Ethiopia, water column samples were collected from three open-water sites, whereas in Brazil, water column samples were taken from 11 sites in Furnas Reservoir and 2 sites in Ibirité Reservoir (Pinto-Coelho et al., 2005).

Samples from Alaska, Canada, Florida, Ethiopia, and Brazil were preserved in 10% formalin. In Greenland and Turkey, samples were preserved in 4% Lugol's. Crustacean zooplankton was enumerated at 40, 50, or 100× magnification, and 25–50 individuals (where possible) of each species were measured with an ocular micrometer to the nearest 25 µm. Standard allometric equations were used to convert body lengths to biomass (Dumont et al., 1975; McCauley, 1984).

In a large compilation of data from many different regions, it is optimal if sampling methods are identical. In practice this rarely is possible, but the methods used here were comparable and were adequate to collect a representative sample of crustacean zooplankton, as for the most part, only nauplii and rotifers passed through the nets, even in Florida, where the largest mesh size was used (Havens et al., 1996). Here we examined body size only for adults and copepod copepodids, so loss of those smaller animals was not an issue. While chemical preservation can affect the dry weight of zooplankton (Giguere et al., 2011), we

are aware of no literature that examines effects of different chemical preservatives on body lengths, which were used in this study to estimate weight with standard equations.

The average body size (μg dry weight animal $^{-1}$) was determined separately for cladocerans, calanoids, and cyclopoids, and represent means weighted by species densities within each of those groups. Although body lengths (rather than weights) might be more relevant to predators than body size in μg , the authors did not have access to the thousands of raw count sheets where body length measurements were recorded.

Water temperatures were measured in situ and reflect either near-surface temperatures in shallow mixed lakes or the average epilimnetic temperatures in deeper stratified lakes.

Data analysis

We examined graphically the relationship between the body size of cladocerans, calanoids, and cyclopoids and water temperature, and fitted linear regressions to the non-transformed data, using means from each lake region. We did not use data from individual lakes, because the number of data points varied widely among the regions, such that certain lake-rich locations such as Greenland would have largely driven the results. We also did not transform the data because in general, the number of lakes per region was low.

In the 59 lake dataset from Greenland, 29 of the lakes were free of fish. These lakes either freeze solid to the bottom in winter or lack connections to the sea, preventing fish colonization. In order to elucidate the importance of fish predation on mean body size of crustacean zooplankton, we compared body sizes of cladocerans, cyclopoids, and calanoids between the two groups of Greenland lakes: fishless vs. lakes with fish using one-way ANOVA. The raw data were skewed, so they were log-transformed prior to analysis.

We also examined an alternative explanation for body size differences among lake regions; i.e., differences in trophic state. We used linear regression to explore whether there were significant relationships between lake trophic state and the body size of cladocerans and copepods. We used total phosphorus (TP) as a surrogate for trophic state, because it was measured in all of the lakes except for those in

Ethiopia. All statistical analyses were done with SYSTAT 13.

Results

Across all of the lakes, there were 85 species of cladocerans, 18 calanoids, and 27 cyclopoids (Appendix S1). Only five species of cladocerans occurred in more than four lake regions (*Bosmina longirostris*, *Chydorus sphaericus*, *Diaphanosoma brachyurum*, *Holopedium gibberum*, and *Polyphemus pediculus*). No species of calanoids or cyclopoids occurred in more than two regions.

The mean body size of cladocerans declined with increasing temperature (Fig. 2A). The largest mean size was in Greenland at an average water temperature of 12°C, and smaller animals occurred in Florida at 30°C. There was considerable scatter of data around the mean values, and the linear regression explained just 33% of the variability in the data ($P = 0.10$). There were smaller cladocerans in Alaska at 16°C than in Florida at 30°C (one-way ANOVA, $P < 0.05$). Mean body size of cyclopoids also declined with increasing water temperature; there was somewhat less scatter around the means, and a larger amount of overall variation in body size was explained by temperature than was the case for cladocerans (38%, $P = 0.05$). Largest animals were in the cold lakes in Greenland and smallest animals were in the warm-water lakes in Florida (Fig. 2B). In contrast, we found no significant relationship between the mean body size of calanoids and water temperature (Fig. 2C). It was equally likely to find large and small animals in lakes at high and low water temperatures.

Although earlier studies have identified effects of trophic state on zooplankton body size, in particular smaller cladocerans and larger copepods in lakes with higher TP (Jeppesen et al., 2000), in this study body size was not affected by that attribute. There were no significant relationship between body size and TP for any crustacean zooplankton group in the regionally aggregated data (cladocerans: $r^2 = 0.08$, $P > 0.4$; cyclopoids, $r^2 = 0.01$, $P > 0.9$; calanoids, $r^2 = 0.07$, $P > 0.6$).

A closer examination of the Greenland data was done by comparing lakes with fish and without fish. The lakes differed somewhat in trophic state (TP $10 \pm 6 \mu\text{g l}^{-1}$ with fish, $18 \pm 8 \mu\text{g l}^{-1}$ without fish)

and had very similar water temperatures ($12.2 \pm 4^\circ\text{C}$ with fish vs. $11.7 \pm 3^\circ\text{C}$ without fish). The greatest difference between the lakes was in regard to the presence or absence of planktivorous fish. Cladoceran body size was fivefold higher in the fishless lakes ($10.9 \pm 3.1 \mu\text{g}$) than in the lakes with fish ($2.2 \pm 1.3 \mu\text{g}$) (One-way ANOVA, $F = 25.2$, $P < 0.001$). Body size of cyclopoids was significantly higher in the fishless lakes ($6.1 \pm 1.4 \mu\text{g}$) than in the lakes with fish ($4.4 \pm 1.5 \mu\text{g}$) (One-way ANOVA, $F = 5.2$, $P < 0.05$), and body size of calanoids did not significantly differ between lake types ($1.4 \pm 0.2 \mu\text{g}$ in lakes with fish, vs. $1.6 \pm 0.2 \mu\text{g}$ in fishless lakes) (One-way ANOVA, $F = 2.3$, $P = 0.14$).

Discussion

This is the first study to quantify, with actual measurements of density and biomass of zooplankton (from 123 lakes including 85 species), whether or not cladocerans become smaller as one moves southward from the Arctic to the tropics. We observed a declining trend in size that was marginally significant at $P = 0.10$. While the trend was weak, in general it was in agreement with that found in an earlier study (Gillooly & Dodson, 2000). The greater variability of our results is possibly explained by differences in methodology. While we measured species' densities and biomass, Gillooly and Dodson (2000) worked only with species lists, and they assumed that: (1) in any lake, the density of every species is equal; and (2) across all lakes, the size of any given species does not vary. Because we took a more direct approach that did not require such assumptions, our results provide a more realistic picture of what occurs in lakes, where other factors interact with temperature to influence body size.

To illustrate what effect the assumption of invariant species' size can have on the variability of results, we examined the degree of variation in mean body size of dominant cladoceran species between individual lakes, considering two selected regions—one in the subtropics (Florida) and one in the north temperate zone (British Columbia). In Florida, four species accounted for 94% of the total density of cladocerans: *Bosminopsis dietersi*, *Eubosmina tubicen*, *Daphnia lumholtzi*, and *Diaphanosoma brachyurum*. Had we assumed invariant body sizes, it would have markedly

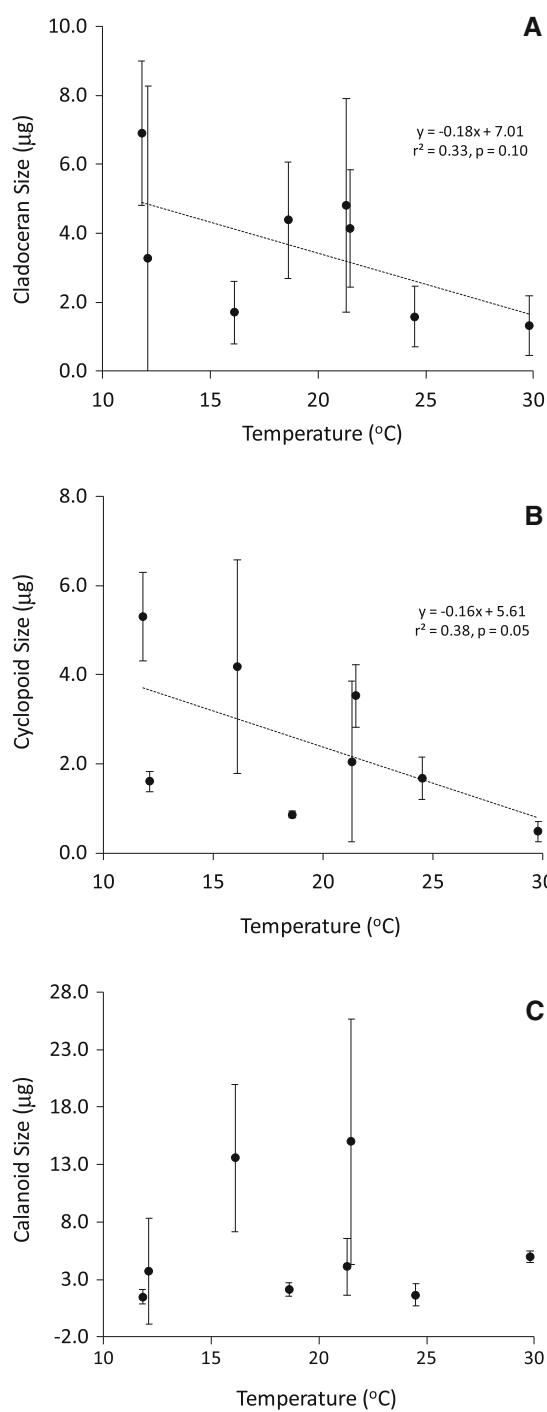


Fig. 2 Relationships between the mean size ($\mu\text{g dry weight animal}^{-1}$) of cladocerans (A), cyclopoids (B), and calanoids (C) and water temperature for the eight lake regions. Data are regional means \pm 95% confidence intervals. Linear regressions are shown where there is significance at $P \leq 0.10$

affected our results, because actual body sizes varied by more than twofold among the lakes. The actual mean sizes (in μg dry weight, averaged by lake) ranged from 0.7 to 1.2 for *B. dietersi*, from 0.4 to 0.8 for *E. tubicen*, from 3.5 to 8.4 for *D. lumholtzi*, and from 0.6 to 1.4 for *D. brachyurum*. In British Columbia, where the mean body size of the cladoceran assemblage was highly variable, four species accounted for 99% of total biomass: *Bosmina longirostris*, *Diaphanosoma brachyurum*, *Holopedium gibberum* and *Daphnia* sp. Again, had we assumed an invariant species' body sizes, it would have considerably affected our results, greatly reducing variation. The actual mean sizes (in μg dry weight, averaged by lake) ranged from 0.8 to 3.7 μg for *B. longirostris*, from 0.8 to 18.9 μg for *D. brachyurum*, from 0.1 to 9.5 μg for *H. gibberum*, and from 0.9 to 11.5 μg for *Daphnia* sp.

There also is evidence, from our study and others, that a viewpoint (e.g., Crisman, 1992) that sub-tropical and tropical lakes contain only small cladocerans is incorrect. Iglesias et al. (2011) found that in warm water lakes in Uruguay (34° latitude), some lakes had small cladocerans while in other lakes they were large and included large *Daphnia*. The difference was due to an absence of visual predation (by zooplanktivorous fish) in the *Daphnia* dominated lakes, not to a difference in water temperature. Further, when fish-free enclosures were placed into the lakes with high fish predation and small cladocerans, large *Daphnia* appeared within 2 weeks, and they only were eliminated when fish were added to the enclosures.

A stronger relationship occurred between body size and temperature in cyclopoids than in cladocerans. This is consistent with a greater relative control of cyclopoids by temperature than by fish predation or resource composition. Because of their escape swimming behaviors, cyclopoids are less sensitive to fish predation than cladocerans, especially when considering large species such as *Daphnia* (Fernando, 1994; Jeppesen et al., 2001). Also, because cyclopoids are omnivorous (Adrian & Frost, 1993) and better at selective particle capture than cladocerans (Richman & Dodson, 1983), they may be less sensitive to changes in phytoplankton composition. Resistance of cyclopoids to increased fish predation is evidenced by results of controlled experimental (e.g., Drenner &

McComas, 1984) and whole-lake studies (Brooks & Dodson, 1965).

An unexpected result in the current study was the finding that body size of calanoid copepods did not vary with water temperature. The literature on calanoid response to temperature also is rife with inconsistent results. Some studies document an inverse relationship between adult body size and temperature (Lonsdale & Levinton, 1985; Atkinson, 1994); others indicate more complex effects that depend on species and resource availability (Lin et al., 2013); and some indicate that no relationship exists. For example, Twombly & Tisch (2000) found that in controlled experiments, temperature had no significant effect on mature adult body size of *Boeckella triarticulata* or *Diaptomus leptopus*, and Escribano & McLaren (1992) found no significant effect of temperature on *Calanus glacialis* size. These findings are in contrast to results from the ocean, where there is a well-established relationship between the size of copepods and temperature. In general, marine cold-water calanoids are large and have large lipid deposits, and warm-water calanoids are small and have small lipid deposits (e.g., Hooff & Peterson, 2006; Lee et al., 2006). In lakes, more is known about fish predation on calanoids (and cyclopoids) than about temperature effects. Catching these animals may be challenging because copepods are fast swimmers and, therefore, have a better chance to escape predation than cladocerans (Drenner & McComas, 1984). Yet this explanation does not address the different response of calanoids and cyclopoids to temperature. More research is needed to discern the underlying cause.

More evidence regarding the importance of fish predation on the zooplankton came from the analysis of Greenland data from lakes with vs. without fish. Cladocerans, the group most affected by fish predation, were much larger in lakes without fish. Cyclopoids, less affected by fish predation, were only slightly smaller in the presence of fish, and calanoids were unaffected. We do not have data from the other regions to make such a comparison because Greenland was the only region where we encountered fishless lakes. However, the results are consistent with the hypothesis that fish predation plays a greater role in regulating body size of cladocerans than copepods. The results also reinforce the importance, for cladocerans in particular, of measuring body size on a lake-

by-lake basis, rather than assuming invariant species' body sizes across all lakes.

It is possible that other factors, such as invertebrate predation, also could influence the observed variation in body size in this study, as generally discussed by Hart & Bychek (2011); however, we have no such data to analyze.

Another factor not considered in this study, which could influence body size estimates, is diel vertical migration. In lakes with planktivorous fish, it is well established that larger zooplankton migrate to deeper water to avoid predation by sight-feeding fish. We do not expect this factor to largely influence our results, because except for Turkey, all samples encompassed the entire water column. It is possible that in Turkish lakes, especially those with a thermocline and fish predation, the body sizes could be underestimated. Lacking information on whether or not migration occurred, we cannot test this hypothesis.

From our results, it is not clear whether the changes in body size with temperature were driven primarily by a change in species composition or by individual species becoming smaller. Daufresne et al. (2009) found that reduced size in warm waters can be attributed to small species replacing larger ones, smaller individuals within a species being favored over larger ones, or a combination of both. In our analysis, very few species occurred over the entire geographic range (Appendix S1), so with just a few exceptions, the changes in body size likely were driven by a change in the taxonomic composition of the communities.

It is well established that temperature affects growth rates and adult size in a wide range of organisms, both from field and laboratory experiments (Atkinson, 1994; Ashton, 2001). Yet it also has been established that temperature can have both direct and indirect effects, the latter being mediated by changes in food web structure, including changes in predation pressure. Here we demonstrated that in lakes over a broad latitudinal gradient, cladocerans displayed a marginally significant decrease in body size with water temperature, as documented in an earlier synoptic study. However, in the present study the variation in body size at any given temperature was higher than previously reported, and that it may be attributed to differences in fish predation. Cyclopoids responded to temperature in a similar manner as cladocerans; however, the degree to which

temperature explained the variation in size was greater and in line with expectations considering the greater ability of cyclopoids to co-exist with fish predators. Calanoid size did not vary with temperature. This lack of covariance suggests that in contrast with cladocerans and cyclopoids, calanoid body size is not metabolically constrained by higher temperatures. This unexpected result requires further investigation.

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