Received: 27 May 2020 | Accepted: 28 December 2020

DOI: 10.1111/1365-2435.13752

RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Cascading effects of algal warming in a freshwater community

Michelle Tseng[1] | Carla M. Di Filippo[2] | Madeline Fung[1] | Jihyun O. Kim[1] | Ian P. Forster[3] | Yilin Zhou[1]

[1]Departments of Botany and Zoology, University of British Columbia, Vancouver, BC, Canada

[2]Department of Botany, University of British Columbia, Vancouver, BC, Canada

[3]Fisheries and Oceans Canada, Vancouver, BC, Canada

Correspondence
Michelle Tseng
Email: mtseng@zoology.ubc.ca

Funding information
Canada Foundation for Innovation; Natural Sciences and Engineering Research Council of Canada; University of British Columbia Work-Learn Program

Handling Editor: Angélica Gonzalez

Abstract

1. Research on the effects of climate warming on ecological communities has focused on how temperature affects resource quantity. However, resource quality is also affected by warming, and changes in resource quality can have meaningful effects on the productivity of higher trophic levels.
2. Aquatic communities in particular experience temperature-mediated shifts in resource quality because the nutritional value of algae is highly sensitive to temperature. For example, the production of healthful omega-3 polyunsaturated fatty acids (n-3 PUFA) by algae often decreases with warming.
3. Decreased levels of some algal PUFAs with warming have led to the hypothesis that global warming should lead to an overall decrease in productivity in aquatic communities. However, this hypothesis: (a) potentially oversimplifies the relationship between algal PUFAs and temperature, and (b) assumes that the nutritional requirements of consumers are not affected by temperature. Here, we test these assumptions using a freshwater community (*Scenedesmus* algae, *Daphnia* zooplankton, *Chaoborus* insects).
4. Warming temperatures increased total algal PUFAs, but decreased algal cell size, resulting in no net effect of temperature on PUFA per algal cell. In contrast, quantities of algal neutral lipids decreased with warming. At the consumer level, *Daphnia* fed 12°C-reared algae maintained higher population sizes than those fed 20°C or 28°C-reared algae. However, the effect of algal food type diminished as *Daphnia* rearing temperature increased. The indirect effects of cold-reared algae on the growth rate of *Chaoborus* predators were minor.
5. These data highlight the importance of investigating the effects of temperature on both resource quality and on the nutritional needs of consumers. Our results suggest that at warmer temperatures, consumer nutritional requirements may be reduced. We caution against broad claims that the negative relationship between some algal PUFAs and temperature should result in overall declines in aquatic productivity with ongoing climate warming.

KEYWORDS

algae, consumer, *Daphnia*, fatty acids, predator, resource, *Scenedesmus*, temperature

Carla M. Di Filippo, Madeline Fung and Jihyun O. Kim authors contributed equally to the manuscript.

1 | INTRODUCTION

Much progress has been made in our understanding of how organisms are responding to temperature increases. For example, we have clear evidence of species ranges shifting polewards and to higher elevations (Hickling et al., 2005; Parmesan, 2006). Phenologically, both plants and insects are starting their life cycles earlier in the year (CaraDonna et al., 2018; Hovel et al., 2017; Poloczanska et al., 2013; Visser & Both, 2005; Winder & Schindler, 2004) and morphologically, whole populations of insects have decreased in body size in response to warming climate (CaraDonna et al., 2018; Tseng et al., 2018). We also now know that interactions between species, such as those between resources and consumers, can accelerate or dampen population responses to warming (Alexander et al., 2015; Jiang & Morin, 2004; Osmond et al., 2017). For example, responses of *Daphnia* to warming are magnified when they are reared in the presence of predators (Tseng, Bernhardt, et al., 2019; Tseng & O'Connor, 2015).

Despite these many advances in our understanding of how ecological communities respond to warming, most of the data and theory on this topic have focused on how the quantities of individuals or populations change with warming (Rosenblatt & Schmitz, 2016). However, there is an increasing number of studies showing that warming affects organism quality as well as quantity, and that shifts in resource quality can have cascading effects on higher trophic levels (Hixson & Arts, 2016; Rosenblatt & Schmitz, 2016). Aquatic ecosystems in particular are likely to exhibit multi-trophic effects of changing resource quality because phytoplankton and macroalgae quality are highly sensitive to warming (Finkel et al., 2010), and because these organisms are the foundation of aquatic communities. Algae often produce lower levels of polyunsaturated fatty acids (hereafter PUFAs) when grown in warmer temperatures (Breuer et al., 2013; Fuschino et al., 2011; Piepho et al., 2012; Sikora et al., 2014). Zooplankton and other ectotherms that are fed diets deficient in the key PUFAs such as the omega-3 PUFAs EPA (eicosapentaenoic acid) and DHA (docosahexaenoic acid) exhibit reduced growth and reproduction (Becker & Boersma, 2003; Brett & Muller-Navarra, 1997; Martin-Creuzburg et al., 2012). Finally, the ratio of omega-6 to omega-3 PUFAs (abbreviated hereafter as n-6 and n-3) also affects consumer health; lower values of this ratio are associated with health benefits (e.g. growth rate, survival) in a wide range of taxa (Hintze et al., 2011; Orlando et al., 2020; Upadhaya et al., 2019; Wijekoon et al., 2015).

The negative relationship between the quantities of some algal PUFAs and elevated temperature, and the positive relationship between healthful PUFAs and general consumer fitness, have led to the prediction that warmer waters will lead to a decrease in secondary productivity in aquatic systems (Hixson & Arts, 2016). However, whether or not this prediction is broadly applicable depends on the robustness of two key assumptions. The first is that the quantities of key algal PUFAs should decrease with warming. While it is widely documented that algae make more PUFAs at colder temperatures to maintain the fluidity of cell membranes (Hazel, 1995), what is often overlooked is that algal PUFAs are also found in several different structures throughout the cell. Algal PUFAs are typically bundled with lipids, and the three major classes of algal lipids are phospholipids, glycolipids and neutral lipids (Kumari et al., 2013). Glycolipids are primarily found in photosynthetic membranes (e.g. thylakoid membranes), while phospholipids are the main components of cell membranes (Wang et al., 2019; Zhu et al., 1997). Algal neutral lipids are primarily comprised of triacylglycerols (TAGs). TAGs contain a glycerol backbone attached to three fatty acids (FAs) and they serve as storage products and energy reservoirs (Breuer et al., 2014; Kumari et al., 2013). In many algal species the majority of the FAs are packaged as TAGs (Breuer et al., 2014; Henderson & Mackinlay, 1989; Wang et al., 2019), and there is some evidence that unlike the PUFAs found in cell membranes, TAG production increases at higher temperatures (Breuer et al., 2013; Zhu et al., 1997). Finally, although healthful n-3 PUFAs are thought to be mostly associated with cell membranes, they also can be stored in TAGs (Guschina & Harwood, 2009; Kumari et al., 2013). Thus, increased temperature could decrease the PUFAs (n-3 and others) found in phospholipid cell membranes, but also increase TAG-bound PUFAs.

The second assumption is that the nutritive value of algal PUFAs for the next trophic level is independent of the environmental conditions. This assumption is not valid if the benefits of algal PUFAs to consumers are reduced at warmer temperatures. This situation could occur if one of the main functions of algal-based PUFAs is to maintain membrane fluidity in consumers. At warmer temperatures, cell membranes (in consumers) may not need additional PUFAs to stay fluid (Hazel, 1995) and thus elevated algal-PUFAs may not be required. A laboratory experiment using the zooplankton *Daphnia magna* and algae *Chlamydomonas klinobasis* found that temperature-mediated shifts in algal fatty acid profiles explained some variation in *Daphnia* somatic growth, but that *Daphnia* rearing temperature also affected their responses to algal fatty acids (von Elert & Fink, 2018).

Here, we use laboratory experiments to test both of these key assumptions: (a) that algal PUFA production decreases with warming, and (b) that the nutritive value of high-PUFA algae is independent of the environmental temperature of the consumer. We use the aquatic community consisting of the algae *Scenedesmus obliquus* (Chlorococcales: Scenedesmaceae, Kützing, 1833; also known as *Tetradesmus obliquus*, *Acutodesmus obliquus*), the zooplankton *Daphnia pulex* (Cladocera: Daphniidae, Leydig 1860) and the zooplankton predator *Chaoborus americanus* (Diptera: Chaoboridae, De Haan 1849). We test the predictions that (1) *Scenedesmus* produces higher levels of PUFAs at colder rearing temperatures, and (2) cold-reared *Scenedesmus* sustain higher population sizes of *Daphnia*, irrespective of *Daphnia* rearing temperature. We also examine whether any shifts in fatty acids are attributable to temperature-mediated changes in algal cell size and morphology. *Scenedesmus* cell size decreases with warming (Chen et al., 2011; Tseng, Yangel, et al., 2019) and thus decreases in algal fatty acids at warmer temperatures may be explained by

shifts in cell size/morphology. Finally, we investigate the effects of temperature on resource–consumer interactions at higher trophic levels by testing the prediction that (3) *Chaoborus* predators fed cold-reared *Daphnia* (themselves fed cold-reared algae) will experience higher growth rates than *Chaoborus* fed warm reared *Daphnia*/algae, irrespective of *Chaoborus* rearing temperature. This careful characterization of how temperature-mediated changes in resource quality cascade through a simple aquatic community is the first step towards a more general understanding of how the overall productivity of aquatic communities may change in response to ongoing warming.

2 | MATERIALS AND METHODS

Scenedesmus are one of the most common genera of freshwater algae, and they grow as single cells or colonies (Lürling, 2003). The zooplankton *D. pulex* are filter feeders, are found in lakes and ponds worldwide, and can reproduce parthenogenically or sexually (Ebert, 2005). *Daphnia* and *Scenedesmus* coexist in lakes and ponds and they are commonly used in laboratory settings to investigate consumer–resource interactions (Lürling & Van Donk, 1996; Martin-Creuzburg et al., 2012; Tseng, Yangel, et al., 2019). *Chaoborus americanus* are a voracious predator of *Daphnia* sp. in nature (Spitze, 1991). They take approximately 1 year to develop from egg to adult (Fedorenko & Swift, 1972). *Chaoborus* adults live only a few days before dying and do not feed prior to ovipositing (Cressa & Lewis, 1986; Moore, 1986).

Scenedesmus obliquus were obtained from the Canadian Phycological Culture Centre (CPCC5) in December 2018 and propagated in COMBO media at 12°C in the lab. (Kilham et al., 1998). Prior to the start of the experiment, thousands of *D. pulex* and hundreds of third-instar *Chaoborus americanus* were collected using hand nets from the experimental ponds facility at the University of British Columbia (Vancouver campus) and maintained in COMBO media at 8°C. *Chaoborus* developmental stage was estimated as third instar based on published studies of *Chaoborus* instar lengths (Carter & Kwik, 1977; Fedorenko & Swift, 1972). *Daphnia* were housed in 20L bins at and fed laboratory cultures of *Scenedesmus* algae ad libitum until the start of the experiment. *Chaoborus* were housed individually in 250-mL glass beakers and were fed wild-caught *Daphnia* until the start of the experiment.

Prior to the start of this experiment we conducted and analysed a similar (but with fewer replicates and a shorter duration) experiment to examine the effect of algal rearing temperature on *Daphnia* population size and *Chaoborus* growth rate. The results of this smaller experiment suggested that algal rearing temperature had cascading effects in this aquatic community. To confirm this result, we repeated the experiment with more replicates and ran it for 11 weeks instead of 7. Because the longer experiment essentially subsumes the first experiment, we report the results of longer experiment here, and report the results and statistical analyses from the shorter experiment in Supporting Information Appendix A.

2.1 | *Scenedesmus* temperature treatments

We grew *Scenedesmus* at three temperatures: 12, 20 and 28°C. We chose these temperatures because they fall within the range of temperatures experienced by this species in nature, and in laboratory settings *Scenedesmus* growth rate at these temperatures is sufficient to maintain 100+ replicate populations of *Daphnia* (Supporting Information Appendix A). Additionally, previous experiments using similar temperatures have shown clear effects of temperature on *Scenedesmus* fatty acid profiles (Breuer et al., 2013; Xin et al., 2011). This temperature range thus allows for comparisons between this experiment and existing literature. Temperature control was achieved using Panasonic MIR-254 incubators (two incubators per temperature treatment). There were eight replicate algal cultures per treatment, and algae were grown in 1 L glass media bottles filled with 950-ml COMBO media. Light intensity was 400 μmol m^{-2} s^{-1} (24W LED, SunBlaster Horticultural Lighting). Filtered (0.3-μm Whatman HEPA-VENT) air was bubbled into each culture bottle at a rate of approximately 0.005 SLPM. All algal cultures were manually agitated daily, and diluted by 50% once per week.

2.2 | *Scenedesmus* density, cell size and growth rate quantification

Three times per week we imaged and quantified algal cultures using an imaging flow cytometer (FlowCam 8400, Fluid Imaging Technologies). We used the 20× objective and FOV50 flow cell, and a flow rate of 0.3 ml/min. We imaged 5,000 cells per run and manually sorted single cells from colonies. Summary statistics for culture density and cell size for single cells, colonies and for the whole culture were generated using Visual Spreadsheet (Version 4.16, Fluid Imaging Technologies). Mean cell density was approximately 1.1×10^6 per/ml. We calculated *Scenedesmus* growth rate at log phase as: ('density 2 days after dilution' – 'density before dilution')/2 days. We used the FlowCam's Equivalent Spherical Diameter (ESD) as the measure of cell size (Kydd et al., 2018). Growth rate of algal cultures was assessed at five time points throughout the experiment.

2.3 | *Scenedesmus* fatty acid and neutral lipid quantification

We examined the effect of temperature on *Scenedesmus* PUFA production. We also quantified *Scenedesmus* neutral lipids to better understand how temperature affects the distribution of PUFAs in the algal cell. There were eight replicates per temperature.

Gas chromatography (GC) analysis of fatty acid methyl esters (FAMEs) was performed at week 8 of the experiment. A 70-ml sample of each replicate culture bottle was filtered onto a 25 mm glass microfiber filter (GE Healthcare Life Sciences Whatman). To each sample, 2 ml of 3 M methanolic HCL (Sigma-Aldrich) and 0.5ml of hexane

(Sigma-Aldrich) were added before overnight incubation at 80°C. To the cooled sample, 2 ml of 0.9% saline and 1.5 ml of hexane was added and the mixture was vortexed. After separation, the upper solvent layer was transferred to a 2-ml vial and analysed using a GC (Scion Instruments Canada). Hydrogen gas was used as a carrier through a 50-m column (Agilent J&W CP-Sil 88 for FAME) and the sample was detected using a flame ionization detector. Peak identification used known standards (mostly GLc455 and GLc37, NuChek Prep Inc.). Fatty acid quantification was based on the relative peak area between individual fatty acids and the internal standard (C19:0, 0.5 mg/sample).

Algal neutral lipids were assessed by staining live cells with BODIPY 505/515 at week 7.5 (4,4-Difluoro-1,3,5,7-Tetramethyl-4-Bora-3a,4a-Diaza-s-Indacene, Thermo Fisher Scientific). A stock solution of 100 μg/ml was prepared by dissolving BODIPY in ethanol (Cabanelas et al., 2015; Chung et al., 2018). The algal culture was diluted 1:100 using distilled water and stained with 5 μg/ml BODIPY for 10 min (Brennan et al., 2012; Cirulis et al., 2012). Fluorescence of stained *Scenedesmus* cells was quantified using a CytoFLEX LX flow cytometer (Beckman Coulter). BODIPY (530/30) and chlorophyll (680/30) fluorescence were measured. Cells were gated on forward and side scatter. Cell size measurements were obtained for each sample using the FlowCam (as above).

2.4 | *Daphnia* treatments

Daphnia were reared in 750-ml glass jars in COMBO media. Jars were seeded with 30 *Daphnia*. *Daphnia* were reared at the same temperatures as algae: 12, 20, 28°C and fed one of three algae types: algae reared at 12°C, 20°C or 28°C. Hereafter we refer to these food treatment levels as A12, A20 and A28. There were nine total *Daphnia* × food type treatments and 20 replicate jars per treatment, for a total of 180 replicate *Daphnia* populations. The density of algae used for feeding was standardized so that all *Daphnia* jars across the three food type treatments received the same density of algae. Algal densities varied slightly week to week and the average cells per ml per feeding was 1×10^6. Algal density was quantified using the FlowCam. Previous studies have shown that *Daphnia* reared at these densities and food levels are not food-limited and thus we expect negligible density-related effects across the three food-type treatments (Supporting Information Appendix A, Tseng, Bernhardt, et al., 2019; Tseng & O'Connor, 2015).

Daphnia populations were maintained for 11 weeks and population size was censused monthly. To count *Daphnia*, all contents of each replicate jar were poured out and individual *Daphnia* were counted and transferred back into the same jar using a 3-ml pipette. Fifty percent of the COMBO media was replaced every 2 weeks.

2.5 | *Chaoborus* treatments

Chaoborus larvae were reared in individual 250-ml beakers in COMBO media. *Chaoborus* were reared at either 12°C or 20°C, and three times per week for 6 weeks were fed one of two types of *Daphnia*: *Daphnia* reared at 12°C and fed A12 (hereafter A12D12), or *Daphnia* that were reared at 20°C and fed A20 (hereafter A20D20). Pilot studies done in the lab have shown that *Chaoborus* have low survival when reared at 28°C and thus we limited the *Chaoborus* rearing temperatures to 12 and 20°C. Similar to the effect of temperature on algal fatty acids, we assumed that A12D12 *Daphnia* would contain more healthful fats compared to A20D20 *Daphnia*. The goal of these *Daphnia-Chaoborus* feeding combinations was to examine whether the effects of *Daphnia* diet type depended on *Chaoborus* rearing temperature.

There were 30 replicates per treatment. Each *Chaoborus* larva was fed two *Daphnia* per feeding, three times per week (six *Daphnia* per week). This feeding rate was based on results from a previous laboratory experiment (Supporting Information Appendix A). The *Daphnia* used for feedings were reared in the same conditions as the experimental *Daphnia*, but we created separate replicate *Daphnia* populations to act as '*Chaoborus* feeder' populations. Larvae were photographed before and after the experiment. individual *Chaoborus* were placed on a Neubauer counting slide and photographed using a dissecting microscope (Zeiss Stemi 508) with an attached camera (Zeiss Axiocam 105). We measured head capsule length as a proxy for body size (Sæther, 1970). This trait was measured using a measuring tool in Zeiss Zen 2.3. Any larvae that died in the first 2 weeks of the experiment were replaced. We calculated *Chaoborus* relative growth rate as: (final head capsule length − initial head capsule length)/initial head capsule length (mm)). We measured *Chaoborus* individual growth rate and not population size (as we did for *Daphnia*) because *Chaoborus* have a 1-year generation time.

2.6 | Statistical analyses

To examine whether temperature affected algal growth rates, we used linear mixed-effects models from the R package lmerTest (Kuznetsova et al., 2017) with 'date' included as a random factor and 'temperature' included as a fixed factor. Cell size and colony number can change rapidly in the first few weeks of culture growth (Lürling & Van Donk, 1999) and thus we analysed data on cell size and percent colonies from week 4 to week 8. These data were taken on 15 different days and were also analysed using linear mixed-effects models with 'date' included as a random factor and temperature included as a fixed factor. We used ANOVA to investigate the effect of temperature on total PUFA per cell size, per ml algal culture and per total cell, and on the ratio of n-6 to n-3 fatty acids. The list of fatty acids included in each of these categories is available in Supplementary Table S1. Finally, we used ANOVA to analyse whether temperature had a significant effect on total neutral lipids per cell size (μm), as measured in RFU (relative fluorescence units), and on total neutral lipids per mL.

We used ANOVA to examine whether algal food type and *Daphnia* rearing temperature had significant effects on *Daphnia* population size at week 11 of the experiment, and on population size averaged across all census days. To calculate mean population size

across all sampling dates, we first averaged the population size of each jar across all dates, and then took the average of the replicate jars per treatment.

We used ANOVA to examine whether algal/*Daphnia* rearing temperature explained variation in *Chaoborus* relative growth rates. For all analyses, we examined whether the data met the assumptions of linear models. We used the 'plot' function in R to visualize the relationship between residuals and fitted values and to examine Q-Q plots (Whitlock & Schluter, 2009). We also used Levene's test to test for homoscedasticity of group variances. All data met the assumptions of linear models. All statistical analyses were conducted in R version 3.6.2 (R Core Team, 2019).

3 | RESULTS

3.1 | *Scenedesmus* growth rate and morphology

Algal growth rate after dilution (log phase) was 0.245 cells per day on average, and there was no effect of temperature on growth rate ($F_{2,8} = 0.46$, $p = 0.65$; Figure 1a). Average *Scenedesmus* cell size was larger in cultures grown at 12°C versus those grown at 20°C/28°C ($F_{2,28} = 146.7$, $p < 0.0001$; Figure 1b). This result was likely driven by a greater proportion of the culture being comprised of colonies rather than single cells at 12°C versus 20/28°C ($F_{2,28} = 117.4$, $p < 0.0001$; Figure 1c).

3.2 | *Scenedesmus* PUFA and neutral lipids

Scenedesmus made more total PUFA per cell size, or per mL, in the 28°C treatment versus 12°C or 20°C (per cell size: $F_{2,21} = 6$, $p = 0.009$; Figure 2a; per ml: $F_{2,21} = 3.5$, $p = 0.048$; Figure S1a). At the whole cell level, there was no difference in the total PUFA produced among the three temperature treatments ($F_{2,21} = 1.15$, $p = 0.34$; Figure 2b). *Scenedesmus* grown at 12°C produced more neutral lipids per cell size or per mL compared to those grown at 20°C or 28°C (per cell size: $F_{2,21} = 23.05$, $p < 0.0001$; Figure 2c; per ml $F_{2,21} = 5.2$, $p = 0.014$, Figure S1b). The ratio of n-6 to n-3 fatty acids was lower at 12°C versus 20°C or 28°C but this pattern was not statistically significant at the $p = 0.05$ level ($F_{2,20} = 2.44$, $p = 0.11$, Figure 2d).

3.3 | *Daphnia* population size

At the end of the 11-week experiment, *Daphnia* population size was highest in the 12°C treatment ($F_{2,134} = 184$, $p < 0.0001$). There was also a significant algal food type × temperature interaction ($F_{4,134} = 6.11$, $p = 0.0002$), and a significant main effect of algal food type ($F_{2,134} = 13.3$, $p < 0.0001$). From Figure 3a, it appears that the effect of algal food type on *Daphnia* population size diminishes as *Daphnia* rearing temperature increases from 12°C to 28°C. At the 12°C rearing temperature, *Daphnia* that were fed A12 had the highest population size, followed by those fed A20 or A28. To confirm this pattern, we conducted a separate ANOVA for the 12°C *Daphnia* rearing temperature treatment and found a significant food type effect ($F_{2,44} = 13.09$, $p < 0.0001$). Tukey's HSD tests showed significant differences in population size between the A12 versus A20 treatments ($p < 0.0001$), and between the A12 versus A28 treatments ($p = 0.003$).

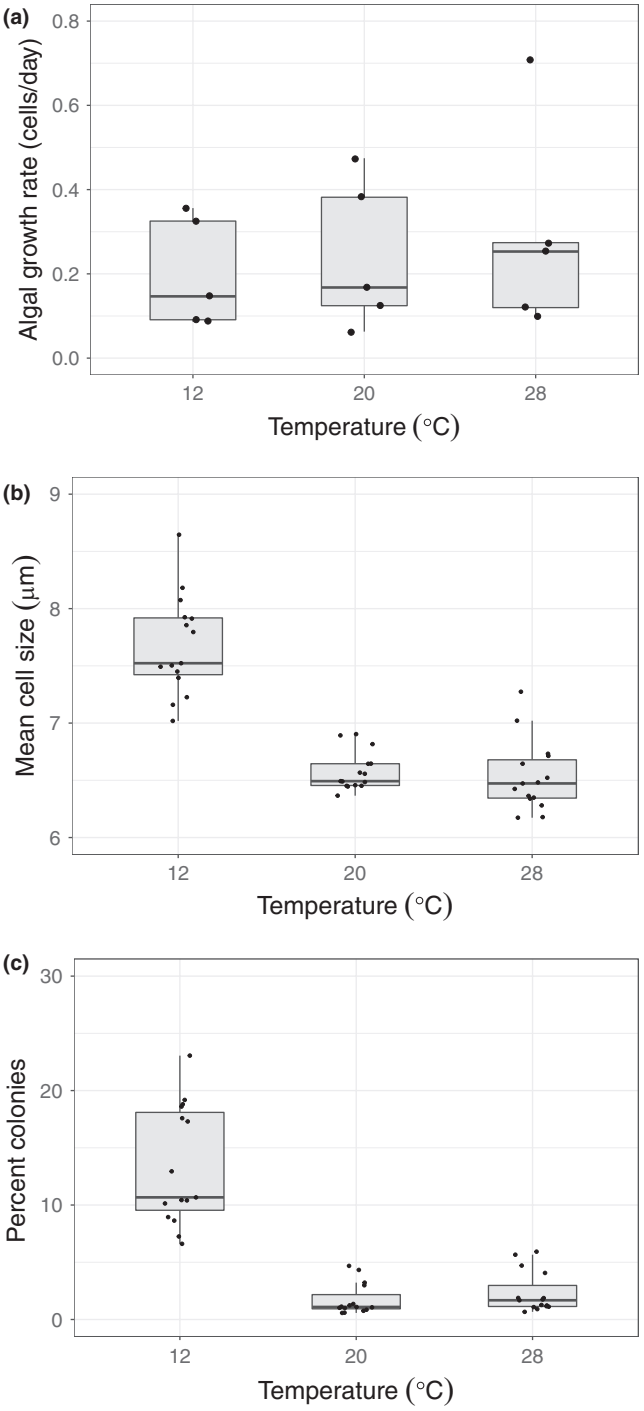

FIGURE 1 The effect of temperature on algal (a) growth rate at log phase (cells per day), (b) mean cell size (single cells and colonies averaged together) and (c) percentage colonies

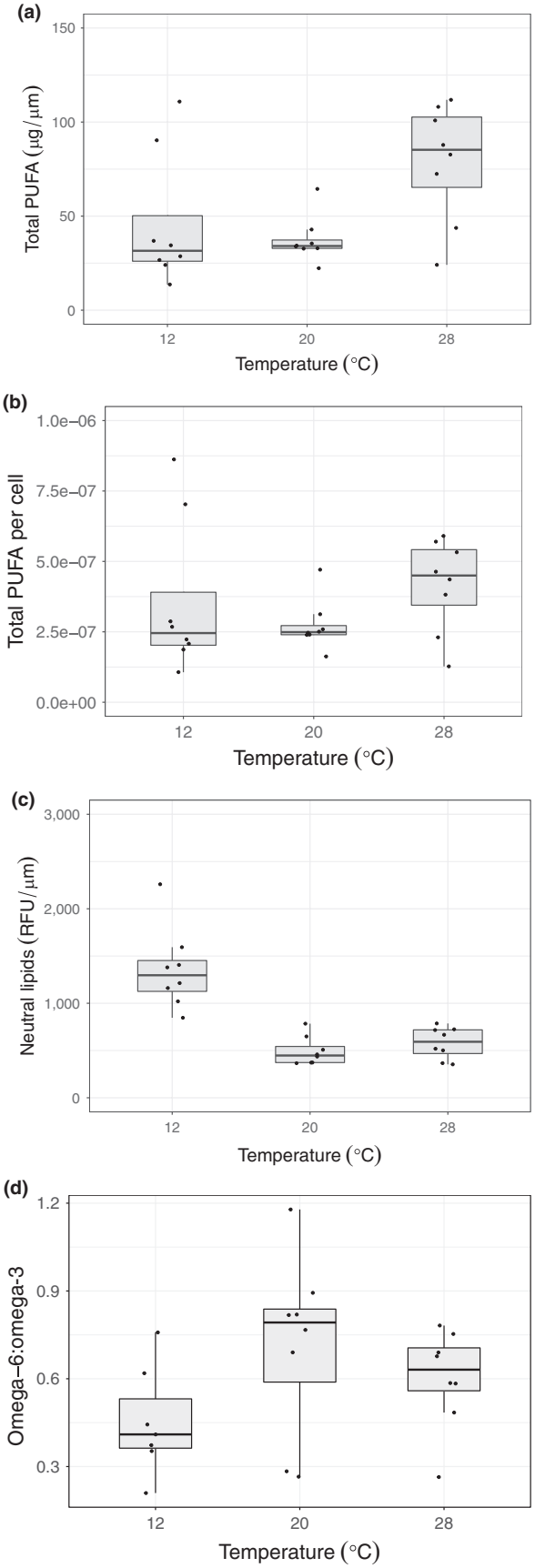

FIGURE 2 The effect of temperature on *Scenedesmus obliquus* (a) total PUFA per cell size, (b) total PUFA per cell, (c) total neutral lipids per cell size and (d) Omega-6:Omega-3 fatty acid ratio

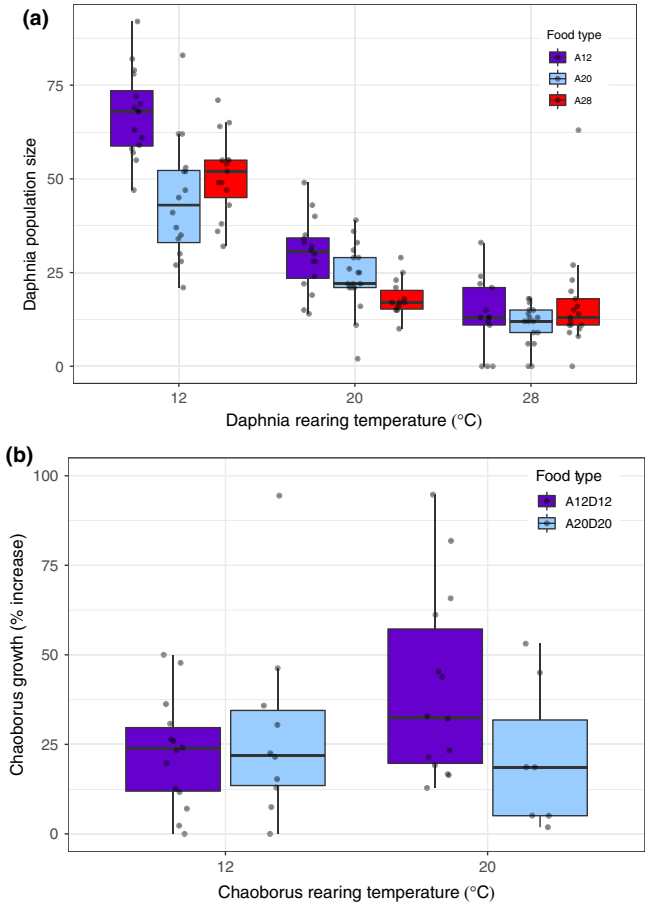

FIGURE 3 (a) The effect of *Daphnia* rearing temperature and diet type on *Daphnia* population size at the end of the experiment (week 11). *Daphnia* were fed algae that were grown at 12°C, 20°C or 28°C (A12, A20, A28 respectively). (b) The effect of rearing temperature and diet type on *Chaoborus* growth ((final head capsule length − initial head capsule length)/initial head capsule length)). *Chaoborus* were fed one of two diet types: A12D12 (*Daphnia* reared at 12°C and fed algae reared at 12°C); A20D20 (*Daphnia* reared at 20°C and fed algae reared at 20°C)

The effect of algal food type was less pronounced in the 20°C *Daphnia* rearing temperature than in the 12°C rearing temperature (Figure 3a). *Daphnia* fed A12 food still had higher population sizes than those fed A20 or A28 but Tukey's HSD tests showed significant differences only between the A12 versus A28 ($p = 0.001$) treatments. Finally, when *Daphnia* were reared at 28°C, there was no effect of algal food type on population size (ANOVA on just 28°C *Daphnia*: $F_{2,44} = 1.2$, $p = 0.3$). The pattern of attenuating effects of food type with increased *Daphnia* rearing temperature was also observed when the data from all of the *Daphnia* census dates were analysed together (Figure S2).

3.4 | *Chaoborus* growth rate

The effect of *Daphnia* food type on *Chaoborus* growth differed slightly but not significantly among the two *Chaoborus* rearing temperatures

(food type × rearing temperature: $F_{1,59} = 7.57$, $p = 0.07$; Figure 3b). At the 12°C rearing temperature, growth did not differ between *Chaoborus* fed A12D12 *Daphnia* and those fed A20D20 *Daphnia*. At the 20°C rearing temperature, *Chaoborus* fed A12D12 *Daphnia* showed slightly higher growth than those fed A20D20 *Daphnia*.

4 | DISCUSSION

The overall goal of this study was to test the prediction that increases in environmental temperature should be correlated with decreases in secondary or tertiary productivity in aquatic communities, and that this decrease is mediated through a reduction in the availability of certain algal-based fatty acids. We tested two underlying assumptions: (a) algal PUFA production decreases with warming, and (b) the nutritional value of algae is independent of the environmental temperature of the consumer. Overall, algal PUFA per unit cell size increased with warming, but because algal cells were smaller at warmer temperatures, the overall PUFA content per cell did not vary among the three rearing temperatures. Additionally, the benefit of consuming cold-reared algae was most pronounced at the coldest *Daphnia* rearing temperature. The effects of algal diet type were dampened at warmer *Daphnia* growing temperatures. Together these results suggest that warming may reduce the nutritional needs of zooplankton (Malzahn et al., 2016), and therefore that warming-mediated changes in resource quality may not lead to lower secondary or tertiary productivity in aquatic systems. We discuss these results in greater detail below.

Despite equal PUFA content at the whole-cell level, *Daphnia* fed 12°C-reared algae maintained higher population sizes compared to *Daphnia* fed 20°C or 28°C-reared algae. This result suggests that 12°C-reared algae were a higher-quality food item. A commonly used metric of resource quality is the ratio of n-6 to n-3 fatty acids, with lower ratios indicative of higher food quality (Simopoulos, 2002). *Scenedesmus* exhibited slightly lower n-6 to n-3 fatty acid ratios when grown at 12°C, matching results from other studies (Fuschino et al., 2011; Roleda et al., 2013; Sikora et al., 2014; von Elert & Fink, 2018), but this pattern was not statistically significant. This result suggests that temperature did not have strong effects on n-6 to n-3 ratios in *Scenedesmus* in this experiment. Algae did produce higher quantities of neutral lipids when grown at 12°C and thus it is possible that the higher overall fat content was beneficial for *Daphnia* reared at 12°C. It is also possible that temperature affected *Scenedesmus* quality in ways that were not quantified here.

It is unclear why the benefits of 12°C-reared algae declined as *Daphnia* environmental temperature increased. We speculated in the Introduction that if the main role of high-PUFA diets is help consumers maintain membrane fluidity in cold environments (Hazel, 1995), organisms growing in warm aquatic environments may not require high-PUFA diets. Future studies that quantify the types of algal PUFAs incorporated into *Daphnia* cells at multiple rearing temperatures, or that include analyses of other nutrients such as nitrogen and phosphorous, can further pinpoint relationships between temperature, algal quality and *Daphnia* population size. A study that examined the effect of food quality (*Scenedesmus* algae vs. *Cryptomonas* algae) on zooplankton growth and reproduction also found that as *Daphnia* temperature increased, the effect of food quality decreased (Masclaux et al., 2009). Similarly, food quality effects were strongest at lowest temperatures and declined with warming in the copepod *Acartia tonsa* (Malzahn et al., 2016). Together these data suggest that either zooplankton do not require high-quality diets at warmer temperatures, or perhaps that when temperatures are warmer, zooplankton are able to least partially make up for lower food quality, perhaps by spending more time foraging.

4.1 | Warming results in the reconfiguration of algal PUFAs

The putative belief is that many algal PUFAs should decrease with warming (Fuschino et al., 2011; Hixson & Arts, 2016; Sikora et al., 2014), but this idea is based mainly on our understanding of how the PUFAs associated with cell membranes change with temperature. At the warmest rearing temperature (28°C), *Scenedesmus* produced high levels of PUFAs and low levels neutral lipids per cell size, suggesting that at this temperature, most PUFAs were associated with non-neutral (polar) lipids, such as phospholipids or glycolipids. These results are consistent with a study showing a decrease in *Scenedesmus* neutral lipid content above 20°C (Xin et al., 2011). Our data for *Scenedesmus* neutral lipids are also similar to studies showing that increased quantities of neutral lipids/TAGs with elevated temperature typically occur under nitrogen limitation, but not when nitrogen is abundant, as it was here (Rukminasari, 2013; Xia et al., 2016).

At 20°C and 28°C, *Scenedesmus* PUFA contained a relatively high content of n-6 PUFAs. Higher levels of n-6 PUFAs at warmer temperatures were also observed in a detailed study of *Scenedesmus* lipids (Fuschino et al., 2011), and this pattern is linked to the responses of algal photosynthetic membranes to elevated temperature. Specifically, MGDG (monogalactosyldiacylglycerol) is a glycolipid that is abundant in the thylakoid membranes of plants and algae (Boudière et al., 2014; Du et al., 2018). MGDG is the most abundant polar lipid in *Scenedesmus*, and both MGDG levels and the n-6 PUFA content of MGDG increased when *Scenedesmus* was grown at 28°C (Fuschino et al., 2011). These data suggest that the relative increase in n-6 PUFAs seen here was likely driven by the remodelling of MGDG glycolipids in photosynthetic membranes.

4.2 | Relative effects of algal rearing temperature on *Daphnia* populations and *Chaoborus* growth

This study demonstrated that temperature-mediated changes in algal quality have meaningful effects on *Daphnia* population size, but also that *Daphnia* rearing temperature explained a larger fraction of variation in *Daphnia* population size, compared to that

explained by algal rearing temperature. In short, the direct effects of temperature on *Daphnia* population growth were stronger than the indirect effects of temperature on resource quality. A study examining the effects of simulated heat waves on green peach aphids also found that the direct effects of temperature on aphid population dynamics were more prominent than the indirect effects of temperature via changes in plant (*Capiscum anuum*) quality (Gillespie et al., 2012). Together, these results suggest that the direct effects of warming play a large role in determining the outcome of warming on ecological communities. However, much more data are needed to better understand the complex relationships between temperature and resource quality (Cross et al., 2015; Rosenblatt & Schmitz, 2016).

Finally, we observed mild effects of food type on *Chaoborus* growth. This result suggests that experimental changes in algal nutrients have mostly disappeared by the time these nutrients have been processed through *Daphnia*. They also suggest that *Daphnia* reared at 12°C versus 20°C may not be nutritionally very different to *Chaoborus*. Previous studies have shown that *Daphnia* fatty acid profiles mimic those of their diet, and also that *Daphnia* can synthesize a small fraction of PUFA de novo (Gladyshev et al., 2016; Nova et al., 2019). *Chaoborus americanus* have a 1-year life cycle and they remain in larval form from late summer to the following spring (Fedorenko & Swift, 1972). It is possible that a longer assay may have resulted in stronger effects of diet type.

5 | CONCLUSIONS

We have demonstrated that warming reduced the nutritional value of *Scenedesmus* algae, and also that warmer temperatures may reduce the nutritional requirements of consumers. Although our experiments were conducted on a simple aquatic community, the three species used here are widely distributed and highly abundant worldwide. Additionally, given that algae form the base of aquatic communities, we believe our results are important for understanding population dynamics and productivity of primary consumers. Overall, we echo the idea that documenting the effects of temperature on both resource quality and quantity will improve our general understanding of how continued climate warming will affect the productivity of resources and consumers (Rosenblatt & Schmitz, 2016). However, given the complexities of how algal fats respond to elevated temperatures, we caution against broad claims of general decreases in aquatic ecosystem productivity with warming.

ACKNOWLEDGEMENTS

We thank the Associate Editor and three anonymous reviewers at Functional Ecology for their thorough review of this study and K. Marshall for helpful comments. Flow cytometry was conducted at the University of British Columbia ubcFLOW facility, with considerable assistance from A. Johnson. Funding for the infrastructure used in this study was provided by the Canada Foundation for Innovation John R. Evans Leaders Fund to M. Tseng. C.M.D.F. was supported by an NSERC-CGS M, M.F. was supported by an NSERC-USRA, and Y.Z. was supported by the University of British Columbia Work-Learn Program. The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

M.T., C.M.D.F., M.F. and J.O.K. developed the experiment; M.T., C.M.D.F., M.F., J.O.K. and Y.Z. conducted the experiment; I.P.F. quantified fatty acids; M.T. wrote the manuscript with edits from C.M.D.F., M.F., J.O.K., I.P.F. and Y.Z.

DATA AVAILABILITY STATEMENT

All raw data used to generate the results presented in this study have been deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.z8w9ghxb6 (Tseng et al., 2021).

ORCID

Michelle Tseng https://orcid.org/0000-0002-4306-507X
Carla M. Di Filippo https://orcid.org/0000-0003-0045-8057
Jihyun O. Kim https://orcid.org/0000-0003-2207-840X
Ian P. Forster https://orcid.org/0000-0002-4256-4432
Yilin Zhou https://orcid.org/0000-0001-6460-2033

REFERENCES

Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, *525*(7570), 515–518. https://doi.org/10.1038/nature14952

Becker, C., & Boersma, M. (2003). Resource quality effects on the life hsitories of Daphnia. *Limnology and Oceanography*, *48*(2), 700–706.

Boudière, L., Michaud, M., Petroutsos, D., Rébeillé, F., Falconet, D., Bastien, O., Roy, S., Finazzi, G., Rolland, N., Jouhet, J., Block, M. A., & Maréchal, E. (2014). Glycerolipids in photosynthesis: Composition, synthesis and trafficking. *Biochimica et Biophysica Acta - Bioenergetics*, *1837*(4), 470–480. https://doi.org/10.1016/j.bbabio.2013.09.007

Brennan, L., Blanco Fernández, A., Mostaert, A. S., & Owende, P. (2012). Enhancement of BODIPY 505/515 lipid fluorescence method for applications in biofuel-directed microalgae production. *Journal of Microbiological Methods*, *90*(2), 137–143. https://doi.org/10.1016/j.mimet.2012.03.020

Brett, M. T., & Muller-Navarra, D. C. (1997). The role of highly unsaturated fatty acids in aquatic food web processes. *Freshwater Biology*, *38*(3), 483–499. https://doi.org/10.1046/j.1365-2427.1997.00220.x

Breuer, G., de Jaeger, L., Artus, V. P. G., Martens, D. E., Springer, J., Draaisma, R. B., Eggink, G., Wijffels, R. H., & Lamers, P. P. (2014). Superior triacylglycerol (TAG) accumulation in starchless mutants of *Scenedesmus obliquus*: (II) evaluation of TAG yield and productivity in controlled photobioreactors. *Biotechnology for Biofuels*, *7*(1), 1–11. https://doi.org/10.1186/1754-6834-7-70

Breuer, G., Lamers, P. P., Martens, D. E., Draaisma, R. B., & Wijffels, R. H. (2013). Effect of light intensity, pH, and temperature on triacylglycerol (TAG) accumulation induced by nitrogen starvation in *Scenedesmus obliquus*. *Bioresource Technology*, *143*, 1–9. https://doi.org/10.1016/j.biortech.2013.05.105

Cabanelas, I. T. D., van der Zwart, M., Kleinegris, D. M. M., Barbosa, M. J., & Wijffels, R. H. (2015). Rapid method to screen and sort lipid accumulating microalgae. *Bioresource Technology*, *184*, 47–52. https://doi.org/10.1016/j.biortech.2014.10.057

CaraDonna, P. J., Cunningham, J. L., & Iler, A. M. (2018). Experimental warming in the field delays phenology and reduces body mass, fat

content and survival: Implications for the persistence of a pollinator under climate change. *Functional Ecology*, *32*(10), 2345–2356. https://doi.org/10.1111/1365-2435.13151

Carter, J. C. H., & Kwik, J. K. (1977). Instar Succession, vertical distribution, and interspecific competition among four species of *Chaoborus*. *Journal of the Fisheries Research Board of Canada*, *34*(1), 113–118. https://doi.org/10.1139/f77-013

Chen, M., Li, J., Dai, X., Sun, Y., & Chen, F. (2011). Effect of phosphorus and temperature on chlorophyll a contents and cell sizes of *Scenedesmus obliquus* and *Microcystis aeruginosa*. *Limnology*, *12*(2), 187–192. https://doi.org/10.1007/s10201-010-0336-y

Chung, T. Y., Kuo, C. Y., Lin, W. J., Wang, W. L., & Chou, J. Y. (2018). Indole-3-acetic-acid-induced phenotypic plasticity in *Desmodesmus algae*. *Scientific Reports*, *8*(1), 1–13. https://doi.org/10.1038/s41598-018-28627-z

Cirulis, J. T., Strasser, B. C., Scott, J. A., & Ross, G. M. (2012). Optimization of staining conditions for microalgae with three lipophilic dyes to reduce precipitation and fluorescence variability. *Cytometry Part A*, *81A*(7), 618–626. https://doi.org/10.1002/cyto.a.22066

Cressa, C., & Lewis, W. M. (1986). Ecological energetics of Chaoborus in a tropical lake. *Oecologia*, *70*(3), 326–331. https://doi.org/10.1007/BF00379492

Cross, W. F., Hood, J. M., Benstead, J. P., Huryn, A. D., & Nelson, D. (2015). Interactions between temperature and nutrients across levels of ecological organization. *Global Change Biology*, *21*(3), 1025–1040. https://doi.org/10.1111/gcb.12809

Du, Z.-Y., Lucker, B. F., Zienkiewicz, K., Miller, T. E., Zienkiewicz, A., Sears, B. B., Kramer, D. M., & Benning, C. (2018). Galactoglycerolipid lipase PGD1 is involved in thylakoid membrane remodeling in response to adverse environmental conditions in chlamydomonas. *The Plant Cell*, *30*(2), 447–465. https://doi.org/10.1105/tpc.17.00446

Ebert, D. (2005). Ecology, epidemiology and evolution of parasitism in Daphnia. *Evolution*, *3*. https://doi.org/10.1108/02634501111102760

Fedorenko, A. Y., & Swift, C. (1972). Biology of *Chaoborus americanus* and *Chaoborus trivittatus* in Eunice Lake, British Columbia. *Limnology and Oceanography*, *17*(5), 721–730.

Finkel, Z. V., Beardall, J., Flynn, K. J., Quigg, A., Rees, T. A. V., & Raven, J. A. (2010). Phytoplankton in a changing world: Cell size and elemental stoichiometry. *Journal of Plankton Research*, *32*(1), 119–137. https://doi.org/10.1093/plankt/fbp098

Fuschino, J. R., Guschina, I. A., Dobson, G., Yan, N. D., Harwood, J. L., & Arts, M. T. (2011). Rising water temperatures alter lipid dynamics and reduce n-3 essential fatty acid concentrations in *Scenedesmus obliquus* (chlorophyta). *Journal of Phycology*, *47*(4), 763–774. https://doi.org/10.1111/j.1529-8817.2011.01024.x

Gillespie, D. R., Nasreen, A., Moffat, C. E., Clarke, P., & Roitberg, B. D. (2012). Effects of simulated heat waves on an experimental community of pepper plants, green peach aphids and two parasitoid species. *Oikos*, *121*(1), 149–159. https://doi.org/10.1111/j.1600-0706.2011.19512.x

Gladyshev, M. I., Makhutova, O. N., Kravchuk, E. S., Anishchenko, O. V., & Sushchik, N. N. (2016). Stable isotope fractionation of fatty acids of Daphnia fed laboratory cultures of microalgae. *Limnologica*, *56*, 23–29. https://doi.org/10.1016/j.limno.2015.12.001

Guschina, I. A., & Harwood, J. L. (2009). Algal lipids and effect of the environment on their biochemistry. In M. T. Arts, M. T. Brett, & M. J. Kainz (Eds.), *Lipids in aquatic ecosystems* (pp. 1–24). Springer.

Hazel, J. R. (1995). Thermal adaptation in biological membranes: Is homeoviscous adaptation the explanation? *Annual Review of Physiology*, *57*, 19–42. https://doi.org/10.1146/annurev.ph.57.030195.000315

Henderson, R. J., & Mackinlay, E. E. (1989). Effect of temperature on lipid composition of the marine cryptomonad Choomonas salina. *Phytochemistry*, *28*(11), 2943–2948.

Hickling, R., Roy, D. B., Hill, J. K., & Thomas, C. D. (2005). A northward shift of range margins in British Odonata. *Global Change Biology*, *11*(3), 502–506. https://doi.org/10.1111/j.1365-2486.2005.00904.x

Hintze, K. J., Gowen, B., Hagloch, J., & Ward, R. (2011). Concentration and ratio of dietary omega 6 (n6) and omega 3 (n3) polyunsaturated fatty acids (PUFA) influences mortality in C57BL/6J mice infected with Punta Toro virus (PTV). FASEB JOURNAL, 25. 9650 ROCKVILLE PIKE, BETHESDA, MD 20814–3998 USA: FEDERATION AMER SOC EXP BIOL.

Hixson, S. M., & Arts, M. T. (2016). Climate warming is predicted to reduce omega-3, long-chain, polyunsaturated fatty acid production in phytoplankton. *Global Change Biology*, *22*(8), 2744–2755. https://doi.org/10.1111/gcb.13295

Hovel, R. A., Carlson, S. M., & Quinn, T. P. (2017). Climate change alters the reproductive phenology and investment of a lacustrine fish, the three-spine stickleback. *Global Change Biology*, *23*(6), 2308–2320. https://doi.org/10.1111/gcb.13531

Jiang, L., & Morin, P. J. (2004). Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. *Journal of Animal Ecology*, *73*(73), 569–576. https://doi.org/10.1111/j.0021-8790.2004.00830.x

Kilham, S. S., Kreeger, D. A., Lynn, S. G., Goulden, C. E., & Herrera, L. (1998). COMBO: A defined freshwater culture medium for algae and zooplankton. *Hydrobiologia*, *377*, 147–159. https://doi.org/10.1023/A:1003231628456

Kumari, P., Kumar, M., Reddy, C. R. K., & Jha, B. (2013). Algal lipids, fatty acids and sterols. In H. Domínguez (Ed.), *Functional Ingredients from Algae for Foods and Nutraceuticals* (pp. 87–135). Woodhead Publishing Limited.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26.

Kydd, J., Rajakaruna, H., Briski, E., & Bailey, S. (2018). Examination of a high resolution laser optical plankton counter and FlowCAM for measuring plankton concentration and size. *Journal of Sea Research*, *133*, 2–10. https://doi.org/10.1016/j.seares.2017.01.003

Lürling, M. (2003). Phenotypic plasticity in the green algae Desmodesmus and Scenedesmus with special reference to the induction of defensive morphology. *Annales de Limnologie - International Journal of Limnology*, *39*(2), 85–101. https://doi.org/10.1051/limn/2003014

Lürling, M., & Van Donk, E. (1996). Zooplankton-induced unicell-colony transformation in *Scenedesmus acutus* and its effect on growth of herbivore Daphnia. *Oecologia*, *108*(3), 432–437. https://doi.org/10.1007/BF00333718

Lürling, M., & Van Donk, E. (1999). Grazer-induced colony formation in *Scenedesmus acutus* (Chlorophyceae): Ecomorph expression at different temperatures. *Journal of Phycology*, *35*(6), 1120–1126. https://doi.org/10.1046/j.1529-8817.1999.3561120.x

Malzahn, A. M., Doerfler, D., & Boersma, M. (2016). Junk food gets healthier when it's warm. *Limnology and Oceanography*, *61*(5), 1677–1685. https://doi.org/10.1002/lno.10330

Martin-Creuzburg, D., Wacker, A., Ziese, C., & Kainz, M. J. (2012). Dietary lipid quality affects temperature-mediated reaction norms of a freshwater key herbivore. *Oecologia*, *168*(4), 901–912. https://doi.org/10.1007/s00442-011-2155-1

Masclaux, H., Bec, A., Kainz, M. J., Desvilettes, C., Jouve, L., & Bourdier, G. (2009). Combined effects of food quality and temperature on somatic growth and reproduction of two freshwater cladocerans. *Limnology and Oceanography*, *54*(4), 1323–1332. https://doi.org/10.4319/lo.2009.54.4.1323

Moore, M. V. (1986). Method for culturing the phantom midge, Chaoborus (Diptera: Chaoboridae), in the laboratory. *Aquaculture*, *56*(3–4), 307–316. https://doi.org/10.1016/0044-8486(86)90345-5

Nova, C. C., Bozelli, R. L., Spitzy, A., & Müller-Navarra, D. (2019). Living in a browning environment: Effects on Daphnia's growth and fatty acid pattern. *Limnology and Oceanography*, *64*(1), 18–31. https://doi.org/10.1002/lno.11016

Orlando, T. M., Fontes, T. V., Paulino, R. R., Solis Murgas, L. D., Fernando Lopez-Olmeda, J., & Rosa, P. V. (2020). Effects of the dietary linoleic acid to linolenic acid ratio for Nile tilapia (*Oreochromis niloticus*) breeding females. *Aquaculture*, *516*, https://doi.org/10.1016/j.aquaculture.2019.734625

Osmond, M. M., Otto, S. P., Klausmeier, C. A., Station, K. B., Otto, S. P., & Klausmeier, C. A. (2017). When predators help prey adapt and persist in a changing environment. *The American Naturalist*, *190*(1), 83–98. https://doi.org/10.1086/691778

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Piepho, M., Arts, M. T., & Wacker, A. (2012). Species-specific variation in fatty acid concentrations of four phytoplankton species: Does phosphorus supply influence the effect of light intensity or temperature? *Journal of Phycology*, *48*(1), 64–73. https://doi.org/10.1111/j.1529-8817.2011.01103.x

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*(10), 919–925. https://doi.org/10.1038/nclimate1958

R Core Team. (2019). *R: A language and environment for statistical computing*. R foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Roleda, M. Y., Slocombe, S. P., Leakey, R. J. G., Day, J. G., Bell, E. M., & Stanley, M. S. (2013). Effects of temperature and nutrient regimes on biomass and lipid production by six oleaginous microalgae in batch culture employing a two-phase cultivation strategy. *Bioresource Technology*, *129*, 439–449. https://doi.org/10.1016/j.biortech.2012.11.043

Rosenblatt, A. E., & Schmitz, O. J. (2016). Climate change, nutrition, and bottom-up and top-down food web processes. *Trends in Ecology & Evolution*, *31*(12), 965–975. https://doi.org/10.1016/j.tree.2016.09.009

Rukminasari, N. (2013). Effect of temperature and nutrient limitation on the growth and lipid content of three selected microalgae (*Dunaliella tertiolecta*, *Nannochloropsis* sp. and *Scenedesmus* sp.) for Biodiesel Production. *International Journal of Marine Science*, *3*(17), 135–144. https://doi.org/10.5376/ijms.2013.03.0017

Sæther, O. A. (1970). Nearctic and paleartic Chaoborus (Diptera, Chaoboridae). *Bulletin of the Fisheries Research Board of Canada*, *174*, 1–58.

Sikora, A. B., Dawidowicz, P., & Von Elert, E. (2014). Daphnia fed algal food grown at elevated temperature have reduced fitness. *Journal of Limnology*, *73*(3), 421–427. https://doi.org/10.4081/jlimnol.2014.898

Simopoulos, A. P. (2002). The importance of the ratio of omega-6/omega-3 essential fatty acids. *Biomedicine and Pharmacotherapy*, *56*(8), 365–379. https://doi.org/10.1016/S0753-3322(02)00253-6

Spitze, K. (1991). Chaoborus predation and life-history evolution in *Daphnia pulex*: Temporal pattern of population diversity, fitness, and mean life history. *Source Evolution*, *458280*(1), 82–92.Retrieved from http://www.jstor.org

Tseng, M., Bernhardt, J. R., & Chila, A. E. (2019). Species interactions mediate thermal evolution. *Evolutionary Applications*, *12*(7), 1463–1474. https://doi.org/10.1111/eva.12805

Tseng, M., Di Filippo, C., Fung, M., Kim, J., Forster, I., & Zhou, Y. (2021). Data from: Cascading effects of algal warming in a freshwater community. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.z8w9ghxb6

Tseng, M., Kaur, K. M., Soleimani Pari, S., Sarai, K., Chan, D., Yao, C. H., Porto, P., Toor, A., Toor, H. S., & Fograscher, K. (2018). Decreases in beetle body size linked to climate change and warming temperatures. *Journal of Animal Ecology*, *87*, 647–659. https://doi.org/10.1111/1365-2656.12789

Tseng, M., & O'Connor, M. I. (2015). Predators modify the evolutionary response of prey to temperature change. *Biology Letters*, *11*(12), 20150798. https://doi.org/10.1098/rsbl.2015.0798

Tseng, M., Yangel, E., & Zhou, Y. (2019). Herbivory alters thermal responses of algae. *Journal of Plankton Research*, *41*(5), 641–649. https://doi.org/10.1093/plankt/fbz043

Upadhaya, S. D., Yang, J., Lee, K. Y., & Kim, I. H. (2019). Effects of changing omega-6 to omega-3 fatty acid ratios in corn-soybean meal-based diet on performance, serum lipid profile and colostrum and milk composition of sows and performance of piglets. *Animal Production Science*, *59*(7), 1235–1243. https://doi.org/10.1071/AN17090

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2561–2569. https://doi.org/10.1098/rspb.2005.3356

von Elert, E., & Fink, P. (2018). Global warming: Testing for direct and indirect effects of temperature at the interface of primary producers and herbivores is required. *Frontiers in Ecology and Evolution*, *6*, 1–10. https://doi.org/10.3389/fevo.2018.00087

Wang, S., Sirbu, D., Thomsen, L., Kuhnert, N., Ullrich, M. S., & Thomsen, C. (2019). Comparative lipidomic studies of *Scenedesmus* sp. (Chlorophyceae) and *Cylindrotheca closterium* (Bacillariophyceae) reveal their differences in lipid production under nitrogen starvation. *Journal of Phycology*, *1257*, 1246–1257. https://doi.org/10.1111/jpy.12887

Whitlock, M. C., & Schluter, D. (2009). *The analysis of biological data* (1st. ed.). Roberts and Company.

Wijekoon, M. P. A., Parrish, C. C., & Mansour, A. (2015). Effect of dietary substitution of fish oil with flaxseed or sunflower oil on muscle fatty acid composition in juvenile steelhead trout (*Oncorhynchus mykiss*) reared at varying temperatures (Reprinted). *Aquaculture*, *447*, 108–115. https://doi.org/10.1016/j.aquaculture.2015.06.022

Winder, M., & Schindler, D. E. (2004). Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, *85*(8), 2100–2106. https://doi.org/10.1890/04-0151

Xia, L., Song, S., & Hu, C. (2016). High temperature enhances lipid accumulation in nitrogen-deprived *Scenedesmus obtusus* XJ-15. *Journal of Applied Phycology*, *28*(2), 831–837. https://doi.org/10.1007/s10811-015-0636-z

Xin, L., Hong-ying, H., & Yu-ping, Z. (2011). Growth and lipid accumulation properties of a freshwater microalga *Scenedesmus* sp. under different cultivation temperature. *Bioresource Technology*, *102*(3), 3098–3102. https://doi.org/10.1016/j.biortech.2010.10.055

Zhu, C. J., Lee, Y. K., & Chao, T. M. (1997). Effects of temperature and growth phase on lipid and biochemical composition of Isochrysis galbana TK1. *Journal of Applied Phycology*, *9*(5), 451–457. https://doi.org/10.1023/A:1007973319348

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Tseng M, Di Filippo CM, Fung M, Kim JO, Forster IP, Zhou Y. Cascading effects of algal warming in a freshwater community. *Funct Ecol*. 2021;00:1–10. https://doi.org/10.1111/1365-2435.13752