

Daphnia fed algal food grown at elevated temperature have reduced fitness

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ABSTRACT

Lake water temperature is negatively correlated with fatty acids content and P:C ratio in green algae. Hence, elevated temperature may indirectly reduce the fitness of *Daphnia* due to induced decrease in algal food quality. The aim of this study was to test the hypotheses that quality of algal food decreases with increasing temperature of its culture and that large-bodied *Daphnia* are more vulnerable to the temperature-related deterioration of algal food quality than small-bodied ones. Laboratory life-table experiments were performed at 20°C with large-bodied *D. pulicaria* and small-bodied *D. cucullata* fed with the green alga *Scenedesmus obliquus*, that had been grown at temperatures of 16, 24 or 32°C. The somatic growth rates of both species decreased significantly with increasing algal culture temperature and this effect was more pronounced in *D. pulicaria* than in *D. cucullata*. In the former species, age at first reproduction significantly increased and clutch size significantly decreased with increasing temperature of algae growth, while no significant changes in these two parameters were observed in the latter species. The proportion of egg-bearing females decreased with increasing algal culture temperature in both species. The results of this study support the notion that the quality of algal food decreases with increasing water temperature and also suggest that small-bodied *Daphnia* species might be less vulnerable to temperature-related decreases in algal food quality than large-bodied ones.

Key words: Temperature, food quality, *Daphnia*, body size, *Scenedesmus obliquus*, life history.

Received: November 2013. Accepted: March 2014.

INTRODUCTION

Water temperature can strongly affect the quality of the algae used as food by herbivorous zooplankton. Elevated temperature results in an increase in phytoplankton C:P ratio and in a reduction in their polyunsaturated fatty acids (PUFAs) content, thus causing an overall decrease in the nutritional value of the algae (Woods *et al.*, 2003; Fuschino *et al.*, 2011; Makino *et al.*, 2011). In crustaceans, phosphorus is important in the synthesis of biological compounds (*e.g.* DNA, RNA, phospholipids, proteins) and the carapace (reviewed in Elser *et al.*, 1996; Vrede *et al.*, 1999). Moreover, the biochemical composition of green algae (proteins, lipids, fatty acids and vitamins) is related to phosphorus content (Kilham *et al.*, 1997; Lüring and Van Donk, 1997; Weers and Gulati, 1997). The highly unsaturated fatty acids (HUFAs), important in maintaining membrane fluidity, can also be used as energy resources, and some [eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA)] are involved in the regulation of many metabolic processes (Blomquist *et al.*, 1991; Brett and Müller-Navarra, 1997).

Consequently, although elevated water temperature enhances zooplankton metabolic rates (Heinle, 1969), it may indirectly reduce the fitness of herbivorous zooplankton (Makino *et al.*, 2011), which can affect key life history

traits. Deficiency of phosphorus and highly unsaturated fatty acids (HUFAs), in algal food reduces individual and population growth rates, increases the rate of respiration and enhances feeding activity of zooplankton (Sterner and Smith, 1993; von Elert, 2004). It could also reduce clutch size, the number of broods per female and elevate age at first reproduction (Sterner *et al.*, 1993; Weers and Gulati, 1997). Lake water temperature can affect global patterns in the size structure of zooplankton communities. In tropical and subtropical waters, small-bodied zooplankton taxa often predominate, while large species frequently occur in temperate lakes (Gillooly and Dodson, 2000). However, within temperate lakes large-bodied cladocerans tend to retreat during the warm summer period, a phenomenon known as *midsummer decline* (Benndorf *et al.*, 2001). Two non-contradictory hypotheses have been suggested to explain the relationship between zooplankton body size and water temperature: i) increased temperature may intensify size-selective predation, which in turn contributes to the elimination of large-bodied species (Zaret, 1980); and ii) small-bodied species may be physiologically better adapted to higher temperatures (Moore *et al.*, 1996). It is possible that at elevated temperatures, small-bodied species are better competitors because they are less susceptible to the presence of filamentous cyanobacteria (which are more common in tropical than in temperate waters)

than large species (Abrusán, 2004). They might also be less vulnerable to poor food quality. The aim of this study was to test the hypotheses that i) the quality of algal food decreases with increasing temperature of its culture; and ii) that large-bodied *D. pulicaria* is more vulnerable to the temperature-related deterioration of algal food quality than small-bodied *D. cucullata*, by comparing key life history parameters of *Daphnia* fed on green alga *Scenedesmus obliquus* grown at three different temperatures (16, 24, 32°C).

METHODS

Laboratory growth experiments were carried out with three clones of large-bodied *Daphnia* (*D. pulicaria*) and three clones of small-bodied *Daphnia* (*D. cucullata*). The clones of *D. pulicaria* were isolated from Lake Brome and the clones of *D. cucullata* were isolated from Lake Roś, Lake Kociołek and Lake Beldany. Characteristic of lakes are given in Tab. 1. All clones have been maintained in the laboratory for many generations prior to the study. Before the experiment, the mothers from all species and clones were maintained at room temperature (20±0.1°C) in 3-L glass beakers containing lake water (filtered through a 0.45 µm filter) with a summer photoperiod (16:8 h light:dark cycle). Lake water used in experiment came from small eutrophic lake – Szczęśliwice located in Warsaw, Poland and has been filtered through a 1-µm filter and stored in aerated tanks for at least 2 weeks before it was used. The *Daphnia* were fed on the green alga *Scenedesmus obliquus* (strain no. 72, University of Texas Collection Center, Austin, USA) batch-cultured in Bold's basal medium (Borowitzka and Borowitzka, 1988). *Daphnia* neonates (<24-h-old) from the second clutch of the clonal mothers were used to start the experiment. The weight of juveniles of each clone was determined for aliquots of nine individuals (in three samples consisting of three individuals). The experiment was carried out in 200

mL beakers filled with filtered (0.2 µm) lake water enriched with *S. obliquus* cells to a density equivalent to 1 mg organic C L⁻¹. The carbon concentration of the algal cell suspensions was estimated from photometric light extinction at 800 nm using previously established carbon-extinction regressions for cultures grown at 16, 24 or 32°C (Sikora, unpublished data). Three experimental treatments were established, in which the *Daphnia* were fed with algae that had been cultured at 16, 24 or 32°C. For each *Daphnia* clone, three beakers containing 10 to 12 animals were set up. The animals were transferred daily into fresh water with respective food algae. The experiment was run at a constant temperature of 20±0.1°C until the animals released their first clutch of eggs into the brood chambers. Depending on the food treatment, the experiment took from four to seven days. The number of eggs in the brood chamber carried by the *Daphnia* was counted under a dissecting microscope. Each individual was then transferred to a pre-weighed aluminum boat and dried at 60°C for 24 h, and then weighed in on an Orion Cahn C-35 microbalance to the nearest 0.1 µg. Somatic growth rate (g) was calculated according to the formula: $g = (\ln W_t - \ln W_0) * t^{-1}$, where W_0 is dry weight of juveniles, W_t is the weight of the individual at the end of the experiment and t is the duration of the experiment. Age at maturity was defined as the age at which individuals produced their first clutch. Phosphorus content in the algae was determined according to molybdenum blue method (Murphy and Riley, 1962). Fatty acid analysis was performed according to methodology described in von Elert (2002).

Three-way analysis of variance (ANOVA) followed by the Tukey-HSD test for multiple comparisons were used to test the effects of temperature of algal food culture (three-level factor: 16, 24 and 32°C), the species of *Daphnia* (two-level factor: *D. pulicaria* and *D. cucullata*) and the clone (three-level factors nested within the species) on the measured life history parameters. Data for clutch size were log-

Tab. 1. Morphometric and trophic characteristics of the lakes from which *Daphnia* clones were taken.

Lake	Location	Area	Depth	Temperature	Nutrient	Chlorophyll a	Data sources
Brome	Canada (45°14' N, 72°30' W)	14.00 km ²	Mean 5.9 m Max 12.2 m	Epilimnion spring: 10°C Epilimnion summer: 24°C Hypolimnion: 15-17°C	Mesotrophic TP: 19.0 µg L ⁻¹	8.0 µg L ⁻¹	Gélinas <i>et al.</i> , 2007
Roś	Poland (53°40' N, 21°53' E)	18.90 km ²	Mean 8.1 m Max 31.8 m	Epilimnion spring: 6-8°C Epilimnion summer: 22-24°C Hypolimnion: 6°C	Eutrophic TP: 160-790 µg L ⁻¹	12.3 µg L ⁻¹	Jańczak, 1999; Surga, 2007; Brzeziński <i>et al.</i> , 2010
Kociołek	Poland (54°1' N, 22°12' E)	0.15 km ²	Mean 6.5 m Max 13.3 m	Epilimnion spring: 12-16°C Epilimnion summer: 22°C Hypolimnion: 4°C	No data	No data	Jańczak, 1999; Surga, 2007
Beldany	Poland (53°43' N, 21°35' E)	9.41 km ²	Mean 10.0 m Max 46.0 m	Epilimnion spring: 8°C Hypolimnion 4°C	Eutrophic TP: 56.0 µg L ⁻¹	24.7 µg L ⁻¹	Kalinowska, 2013; Kalinowska <i>et al.</i> , 2013

transformed and data for percentage of egg-bearing females were arcsine transformed prior to analysis. The analyses were performed using Statistix 9.0 software.

RESULTS

Increasing temperature of *S. obliquus* culture changed their biochemical composition, significantly decreased total fatty acids (FAs), polyunsaturated fatty acids (PUFAs, especially n-3 PUFA, n-3/n-6 PUFA and phosphorus content of their cells. An increase in amount of SAFA (palmitic acid 16:0 and stearic acid 18:0) with increasing temperature of the *S. obliquus* culture was detected, but this relationship was only significant for palmitic acid (Tab. 2).

Somatic growth rate of both *Daphnia* species decreased with increasing temperature of algal food culture and was significantly lower for *D. cucullata* (significant general effect of Temperature in ANOVA, Tab. 3). Somatic growth rate in *D. pulicaria* decreased with increasing temperature of algal food culture, while in *D. cucullata* it remained constant within 16–24°C range, to decrease significantly only at 32°C as was indicated by a significant Temperature × Species interaction in ANOVA (Tukey-HSD test, $P < 0.05$; Fig. 1a, Tab. 3). The somatic growth rate varied significantly among clones within both *Daphnia* species – significant Clone × Species and Clone × Temperature × Species interaction (Tab. 3). The main variation in somatic growth rates

were observed among *D. cucullata* clones were they were fed on algae grown at 16 and 24°C, while *D. pulicaria* clones varied only in food treatment with algae cultured at 24°C. The effect of temperature of *S. obliquus* culture on age at first reproduction (AFR) varied between the *Daphnia* species (Fig. 1b) as was indicated by a significant Temperature × Species interaction in ANOVA (Tab. 3). The AFR of *D. pulicaria* increased with increase of algal culture temperature, but this was not the case for *D. cucullata* (Tukey-HSD test, $P < 0.05$; Fig. 1b, Tab. 3). AFR did not significantly differ among clones within the two *Daphnia* species (Tab. 3). Similarly, clutch size decreased significantly with increasing algal culture temperature for *D. pulicaria*, but not for *D. cucullata* (Tukey-HSD test, $P < 0.05$; Fig. 1c, Tab. 3), producing a significant Temperature × Species interaction in ANOVA (Tab. 3). Effect of differences between clones in clutch size within the two *Daphnia* species is significant only in interaction Clone × Temperature × Species, because of different response of Clone 3 of *D. pulicaria* in food treatment with algae cultured at 24 and 32°C (Tab. 3). In both *Daphnia* species, the percentage of egg-bearing females decreased with increasing temperature of *S. obliquus* culture (significant general effect of Temperature in ANOVA, Fig. 1d, Tab. 3). The percentage of egg-bearing females varied significantly among clones as was indicated by significant Clone × Species interaction in ANOVA (Tab. 3).

Tab. 2. Biochemical composition of *Scenedesmus obliquus* culture grown at 16, 24 and 32°C.

	<i>S. obliquus</i> culture at 16°C	<i>S. obliquus</i> culture at 24°C	<i>S. obliquus</i> culture at 32°C	F-value	P-value
Fatty acid content ($\mu\text{g} \cdot \text{mg C}^{-1}$)					
14:0	2.01±0.56	1.46±0.03	1.49±0.34	1.76	0.2405
14:1 n-9	1.10±0.06 (A)	1.09±0.01 (A)	0.77±0.06 (B)	43.37	<u>0.0001</u>
16:0	13.03±0.67 (B)	15.21±1.03 (A)	15.00±0.55 (A)	10.53	<u>0.0078</u>
16:1 n-9	2.25±0.12 (A)	1.74±0.13 (B)	0.73±0.02 (C)	285.49	<u>0.0000</u>
18:0	0.20±0.07	0.28±0.01	0.27±0.02	2.74	0.1325
18:1 n-9 c	4.84±0.31 (C)	8.04±0.31 (A)	6.67±0.16 (B)	113.45	<u>0.0000</u>
18:1 n-7	0.49±0.03 (B)	0.82±0.05 (A)	0.37±0.01 (C)	166.16	<u>0.0000</u>
18:2 n-6 c	7.77±0.42 (B)	12.16±0.51 (A)	12.78±0.39 (A)	156.54	<u>0.0000</u>
18:3 n-6	0.20±0.01 (B)	0.59±0.01 (A)	0.59±0.03 (A)	411.96	<u>0.0000</u>
18:3 n-3	38.04±1.82 (A)	30.71±1.30 (B)	19.44±0.83 (C)	178.29	<u>0.0000</u>
18:4 n-3	2.77±0.13 (B)	3.20±0.14 (A)	1.96±0.11 (C)	76.77	<u>0.0000</u>
20:1 n-9	0.07±0.08	0.10±0.14	0.11±0.07	0.21	0.8140
22:0	0.13±0.04 (A)	0.13±0.02 (A)	0.00±0.00 (B)	21.19	<u>0.0011</u>
Total FAs	72.90±3.83 (A)	75.52±3.68 (A)	60.19±1.83 (B)	23.37	<u>0.0008</u>
Total SAFAs	15.37±0.98	17.08±1.10	16.76±0.37	4.27	0.0614
Total MUFAs	8.75±0.56 (B)	11.79±0.64 (A)	8.65±0.29 (B)	32.94	<u>0.0003</u>
Total PUFAs	48.78±2.37 (A)	46.66±1.94 (A)	34.78±1.35 (B)	57.51	<u>0.0000</u>
n-3 PUFA	40.81±1.95 (A)	33.90±1.44 (B)	21.41±0.94 (C)	166.09	<u>0.0000</u>
n-6 PUFA	7.97±0.43 (B)	12.76±0.50 (A)	13.37±0.42 (A)	171.19	<u>0.0000</u>
n-3/n-6 PUFA	5.12±0.06 (A)	2.66±0.01 (B)	1.60±0.02 (C)	6994.99	<u>0.0000</u>
Phosphorus content (mg L^{-1})	6.04±0.06 (AB)	6.61±0.13 (A)	5.86±0.26 (B)	8.04	<u>0.0201</u>

FAs, fatty acids; SAFAs, saturated fatty acids; MUFAs, mono-unsaturated fatty acids; PUFAs, polyunsaturated fatty acids. Letters in bracket indicates homogenous groups between experimental treatments (Tukey-HSD test for multiple comparisons, $P < 0.05$). Data are means±1 SD; significant results of one-way ANOVA are underlined.

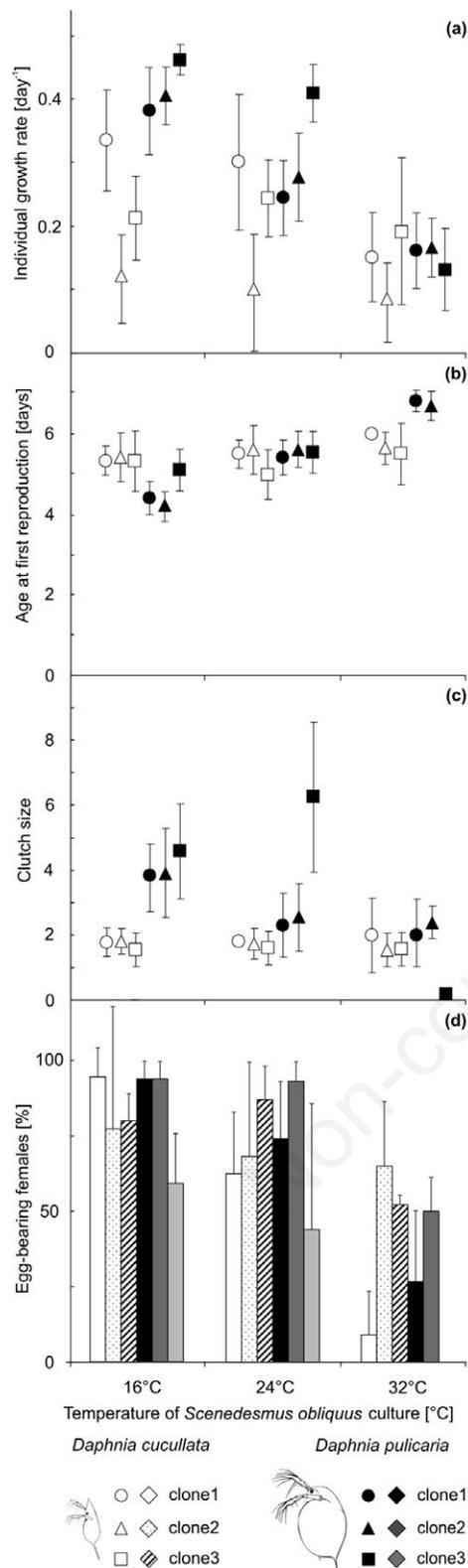


Fig 1. a) Individual growth rates; b) Age at first reproduction; c) Clutch size; d) Percentage of egg-bearing females of *D. cucullata* and *D. pulicaria* fed on *S. obliquus* grown at three temperatures 16, 24 and 32°C. Symbols/bars represent means±SD for three replicates per clones per food treatment.

DISCUSSION

In the present study, a decrease in the quality of the green alga *S. obliquus* with an increase in culture temperature was indicated by the decrease of total fatty acids (FAs), n-3 PUFA (especially α -linolenic acid ALA 18:3 n-3) and phosphorus content in their cells (Tab. 2). This results are in accordance with the previous studies, in which decline of n-3 PUFA, in particular ALA 18:3 n-3 and increase in SAFA (palmitic acid 16:0 and stearic acid 18:0) between *S. obliquus* grown at lower in comparison to higher temperature has been observed (Hodaife *et al.* 2010; Fushino *et al.* 2011). Observed decrease in phosphorus content of *S. obliquus* between warm- and cold-exposure culture are confirmed by other studies – negative correlation between temperature and phosphorus content has been found in *S. obliquus* (Rhee and Gotham, 1981; Makino *et al.*, 2011) and also in others species from different groups (plants, animals, algae, bacteria and yeast; Woods *et al.* 2003). As has been suggested by Park *et al.* (2002) the quality of algae as a food for *Daphnia* decrease due to reduced amount of phosphorus and fatty acids, mainly ALA 18:3 n-3 - precursor for others n-3 PUFA – eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), both being essential components of zooplankton diets. Although increasing temperature enhance, within the suboptimal temperature range, growth rate of algae (Rhee and Gotham, 1981; Lürling and Van Donk, 1999; Hodaifa *et al.*, 2010), it lowers the quality of algal food also due to morphological changes of their cells. With increasing temperature *S. obliquus* cells become smaller, shorter and broader (Margalef, 1954), while the frequency of colony formation increases (Lürling and Van Donk, 1999).

Temperature-related variation in algal quality significantly affected all the studied life history parameters of the large-bodied species, *D. pulicaria*. This effect was weaker in small-bodied species, *D. cucullata*. The somatic growth rate of *D. pulicaria* raised on *S. obliquus* cultured at 16°C (0.44 day⁻¹) was comparable with that reported by DeMott and Pape (2005) for the same species reared on a phosphorus-rich diet (0.41 day⁻¹), while *D. pulicaria* fed with *S. obliquus* cultured at 32°C grew at similar rates that *Daphnia* fed phosphorus-deficient algae (0.15 day⁻¹ compared with 0.1-0.2 day⁻¹). *D. pulicaria* showed a delay of first reproduction and a decrease in clutch size with increasing temperature of algal culture, while none of these parameters varied in *D. cucullata*.

The observed differences in the responses of *D. pulicaria* and *D. cucullata* to variable algal food quality may be explained by many factors. First, as a consequence of different body size, these species probably have different phosphorus demands. Phosphorus content in *Daphnia* is inversely related to body size at maturity (DeMott, 1998; DeMott *et al.*, 2004). Hence, large-bodied species contain

less phosphorus (per unit of biomass) than small-bodied species when fed on P-sufficient algae. Also phosphorus content change in life stage of *Daphnia*; juveniles have more phosphorus than adults (Hessen, 1990). Stoichiometric models proposed by Sterner and Hessen (1994) predict that organisms with higher phosphorus content are more sensitive to phosphorus-limited food. This premise is also supported by the results of other studies (Schultz and Sterner, 1999; Ferrão-Filho *et al.*, 2007). The findings of the present study, that large-bodied *Daphnia* are more sensitive to low quality food than small-bodied ones apparently contradicts the predictions of stoichiometric models. The demand of phosphorus could be species-dependent or could vary between individuals of different body-size within species (DeMott *et al.* 2004). Variability in life-history traits among similar-sized species within *Daphnia longispina* group in response to different environmental conditions (temperature and food concentrations) have been shown by Weider and Wolf (1991) and Spaak and Hoekstra (1995). Sensitivity to phosphorus limitation may also depend on other factors like feeding and respiration rates and digestion efficiency (DeMott and Tessier, 2002; Hall, 2004).

Some authors have suggested that differences in *Da-*

phnia sensitivity to food phosphorus content are not size-dependent, being rather a result of adaptations to local resource conditions (Tessier and Woodruff, 2002). Therefore, the different origin of the two *Daphnia* species examined in the present study is another possible reason for the differences in their responses to food quality. The *D. cucullata* used in the reported experiments came from deep, eutrophic lakes (TP 56-790 $\mu\text{g l}^{-1}$), while the *D. pulicaria* came from shallow, mesotrophic lake (TP 19 $\mu\text{g l}^{-1}$). Thermal characteristic of lakes did not significantly differ (Tab. 1). Because of different trophic status of lakes, one might expect different evolutionary adaptations to cope with low-quality food in the two *Daphnia* species studied here. Species from lakes with phosphorus-deficient resources should be less sensitive to poor food quality and should have a lower phosphorus content (Sterner and Hessen, 1994; DeMott and Pape, 2005). However, results of our experiment are not consistent with this presumption, *i.e.*, *D. cucullata* originating from deep lakes, was less vulnerable to poor food quality than *D. pulicaria*.

The differences between species in response to changes in algal incubation temperature could result from factors other than phosphorus limitation, *e.g.*, from the variable demand for fatty acids or sterols. Some authors

Tab. 3. Results of three-way ANOVA for life history traits: individual growth rate, age at first reproduction, clutch size, and percentage of egg-bearing females of two experimental species: *Daphnia pulicaria* and *Daphnia cucullata*, for three different temperatures of *Scenedesmus obliquus* culture: 16, 24 and 32°C.

Dependent variables	Source of variation	df	SS	MS	F-value	P-value
IGR	Temperature	2	0.27170	0.13585	158.93	<u>0.0000</u>
	Species	1	0.12701	0.12701	148.59	<u>0.0000</u>
	Temperature x species	2	0.07144	0.03572	41.79	<u>0.0000</u>
	Clone x species	4	0.14351	0.03588	41.97	<u>0.0000</u>
	Clone x temperature x species	8	0.08458	0.01057	12.37	<u>0.0000</u>
	Error	35	0.02992	0.00085		<u>0.0000</u>
AFR	Temperature	2	17.2788	8.63939	39.58	<u>0.0000</u>
	Species	1	0.1218	0.12180	0.56	0.4601
	Temperature x species	2	6.0848	3.04240	13.94	<u>0.0000</u>
	Clone x species	4	1.7252	0.43130	1.98	0.1198
	Clone x temperature x species	8	3.2670	0.40837	1.87	0.0966
	Error	35	7.6400	0.21829		
CS	Temperature	2	0.55083	0.27541	27.75	<u>0.0000</u>
	Species	1	0.73831	0.73831	74.39	<u>0.0000</u>
	Temperature x species	2	0.30796	0.15398	15.52	<u>0.0000</u>
	Clone x species	4	0.04889	0.01222	1.23	0.3148
	Clone x temperature x species	8	0.35728	0.06472	6.52	<u>0.0000</u>
	Error	35	2.52100	0.00992		
EBF%	Temperature	2	5.37686	2.68843	19.25	<u>0.0000</u>
	Species	1	0.06219	0.06219	0.45	0.5090
	Temperature x species	2	0.17867	0.08933	0.64	0.5336
	Clone x species	4	1.52179	0.38045	2.72	<u>0.0449</u>
	Clone x temperature x species	8	1.26924	0.15865	1.14	0.3644
	Error	35	4.88844	0.13967		

df, degree of freedom; SS, sum of squares; MS, mean square; IGR, individual growth rate; AFR, age at first reproduction; CS, clutch size; EBF%, percentage of egg-bearing females. Significant results for general effects and interactions are underlined ($P < 0.05$).

suggest that the phosphorus content in algae is more important than the composition of fatty acids (Boersma, 2000; Plath and Boersma, 2001), but other observations and experimental results suggest the opposite patterns (Park *et al.*, 2002). Reduced content of PUFA in algal food cultured at increasing temperature could be the reason for the smaller clutch sizes observed in this study. These components are important in egg production in *Daphnia* (Blomquist *et al.*, 1991; Brett and Müller-Navarra, 1997; Martin-Creuzburg and von Elert, 2009).

Understanding the mechanisms underlying the size-dependent responses of *Daphnia* to algal food quality should help to explain the observed global distribution patterns of zooplankton. The predicted increase in lake water temperature due to climate change is expected to enhance the risk of dietary phosphorus and sterols limitation (Sperfeld and Wacker, 2009; Persson *et al.*, 2011).

CONCLUSIONS

The results of present study suggest that small-bodied *Daphnia* species could be less vulnerable to temperature-related decreases in algal quality than large-bodied species. Further studies are required to understand the body-size-dependent effects of food quality on *Daphnia* performance.

ACKNOWLEDGMENTS

We are grateful to Paweł Koperski for statistical advice and valuable comments on the manuscript and Piotr Maszczyk for his assistance in the laboratory. We also thank two anonymous reviewers, for their valuable comments on an early draft of this manuscript. Financial support by Grant n. N305 134440 from Polish Ministry of Science and Higher Education to P. Dawidowicz.

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