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On the cost of vertical migration: are feeding conditions really worse at greater depths?

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SUMMARY

1. The ultimate explanation for diel vertical migration (DVM) of zooplankton is the avoidance of visual predation in surface waters. Studies on migrating zooplankton have shown that remaining in the cold and food-poor hypolimnion during the day, however, has demographic costs. Higher temperatures and greater food concentrations in the surface waters are thought to be the main reasons why *Daphnia* species move upwards at night.
2. In this study, we investigated the growth condition of daphniids raised on seston taken from different depths from a lake with and without a deep-water chlorophyll maximum.
3. Juvenile growth rates of *Daphnia galeata x hyalina* from the lake without a deep-water chlorophyll maximum were similar for all treatments. After temperature correction, however, growth rates were significantly higher on seston taken from the surface layers.
4. In contrast, in the lake with the deep-water chlorophyll maximum, *D. galeata* growth rates were higher in deeper strata, even after temperature correction. Although this lake had a weak temperature gradient, *D. galeata* left the food-rich strata at night and migrated into the surface food-poor environment. Invertebrate predation and oxygen depletion are probably not the reasons for the nocturnal upward migration into the surface strata. Therefore, we assume that *D. galeata* migrates upwards to take advantage of higher temperatures. Using several temperature–egg-development models, we could not, however, fully explain this behaviour.

Keywords: *Daphnia*, food quality, growth rate, high-mountain lake, vertical migration

Introduction

The pelagic habitat of lakes is characterised by pronounced vertical gradients in light, temperature, resources, competition strength and predation risk (Zaret, 1980; DeMott & Kerfoot, 1982; Geller, 1986). The vertical stratification of these factors strongly affects the vertical distribution of zooplankton. Many zooplankton species avoid the surface layers during daytime, migrating downward to deep layers and returning to surface waters at night (Gliwicz, 1986; Stich, 1989; Ringelberg *et al.*, 1991b). The reaction to relative changes in light intensity (secondary phototaxis) is the primary physiological mechanism underlying this diel vertical migration (DVM) behaviour (Ringelberg, 1999). Changes in DVM behaviour can be induced by chemical cues exuded from potential predators (for a review, see Pijanowska, Weider & Lampert, 1993). The daytime distribution is determined largely by vertical differences in predation risk (i.e. juvenile fish) or by the deleterious effect of ultraviolet radiation (UVR) in surface waters and is often related to zooplankton body size, transparency and pigmentation (Ringelberg, 1999). It is generally accepted that DVM is an adaptive predator avoidance strategy (Lampert, 1993). However, migrating deeper

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into cold and food-poor waters has significant costs (Orcutt & Porter, 1983; Gabriel & Thomas, 1988). These costs are expressed as a reduction in somatic growth and egg production because of reduced temperature and food in the deep daytime refuge, thereby resulting in an overall reduced growth rate (Stich, 1989; Ringelberg *et al*., 1991a; Loose & Dawidowicz, 1994). Hence, migrating species normally trade-off light-dependent mortality risks (i.e. visual hunting fish, UVR) against reduced growth to optimise their fitness (Ringelberg, 1999).

The nocturnal upward migration of zooplankton is usually explained by the higher food quantities and higher temperatures in surface waters (Lampert, 1989). However, little is known about how the quality of the food changes in the water column, and vertical distribution of food resources are seldomly measured in combination with migration patterns (but see Stich & Lampert, 1981; Gliwicz & Pijanowska, 1988; Schöps, 1999). Recent studies have demonstrated that resource availability may not necessarily be worse at greater depths (Williamson *et al*., 1996). This experimental study by Williamson *et al*. (1996) is one of the first to indicate that food availability can in fact be better in deeper layers compared with surface waters. Their study also showed that in many DVM studies, the reduced food effect in the deep-water daytime refuge might have been overestimated. Thus, low temperature, rather than food availability, may be the most important cost for animals that migrate downward and stay in dark daytime refuge, as was earlier suggested by Kerfoot (1985).

Some lakes have deep-water chlorophyll maxima, especially during the summer months (Fee, 1976; Tilzer & Schartz, 1976; Williamson *et al*., 1996). For example, increased algal biomass in deeper strata is typical for alpine lakes and is attributed to higher nutrient availability and reduced solar radiation at depth (Tilzer & Schartz, 1976). These deep-water chlorophyll maxima may be dominated by filamentous cyanobacteria or other low quality foods (Kasprzak *et al*., 2000), and hence chlorophyll or particulate organic carbon (POC) measurements may not be adequate indicators of food availability for zooplankton. Quantitative food measurements do not generally consider edibility, changes in quality (e.g. biochemical composition) or microbial communities that might change with depth (Uehlinger & Bloesch, 1987; Bennett, Sanders & Porter, 1990; Müller-Navarra & Lampert, 1996). The quality of natural seston as food for zooplankton can be highly variable and the importance of mineral and biochemical composition in algae for zooplankton growth is evident from recent studies (Boersma, Schöps & McCauley, 2001; Elser, Hayakawa & Urabe, 2001). An approach to quantify food quality is to raise zooplankton on natural seston and measure life-history traits (Boersma & Vijverberg, 1995; Müller-Navarra & Lampert, 1996).

Given the occurrence of deep-water chlorophyll maxima, we hypothesised that food conditions at depth in lakes with a deep chlorophyll maximum should be much better relative to those at the surface than in those lakes where these deep chlorophyll maxima are absent. This would imply that in lakes with a deep chlorophyll maximum, the effect of temperature as a cost should be more pronounced than in those lakes that do not have higher food levels at depth. Hence, we addressed the question whether the feeding conditions at greater depths are as good as in surface water in a lake with and without a deep-water chlorophyll maximum. *Daphnia* species were raised at a standard temperature on seston collected from different depths. Thus, any changes in life-history traits should be caused by differences in food availability and not temperature. In a lake with a deep-water chlorophyll maximum, we would expect better *Daphnia* growth conditions when raised on water taken from deep strata compared with surface strata. In contrast, in the lake without a deep-water chlorophyll maximum, we expect that growth conditions of the daphniids are better on water taken from the surface layers.

Methods

Field sampling

Two lakes differing in the distribution of algae over depth were sampled. The lake with a deep-water food maximum was the high-mountain lake Oberer Arosasee (Arosa, Switzerland; Winder & Spaak, 2001). The lake without a deep-water food maximum was the lowland lake, Schöhsee (Plön, Germany; Lampert, 1988).

In the Oberer Arosasee, POC and particulate phosphorus (P) samples were taken at six depths (0, 2.5, 5, 7.5, 10 and 12.5 m) every third week during the open water period from May 1998 to October 2000 and once under the ice cover in winter (for analytical method, see Uehlinger *et al.*, 1984). Phytoplankton samples were taken from the six depths from June to August 1998 every third week using a 5-L Schindler trap. In summer 1998, zooplankton was sampled weekly at mid-day and mid-night from three stations around the deepest part of the lake at 2.5-m intervals from 0 to 12.5 m depth using a duo-closing net with 95-µm mesh size (Bürgi, 1983). A total of 300 L per depth stratum was collected; samples per depth stratum were pooled.

In the Schöhsee, vertical profiles of POC and particulate P were measured fortnightly from April until October 1998 from 1, 5 and 12 m depth (for analytical method see Uehlinger *et al.*, 1984). From June until August 1998 phytoplankton samples were taken fortnightly at 1, 5 and 12 m depth. At the same dates, zooplankton was sampled from 1 to 12 m depth at 1-m intervals at mid-day and once in June and July at mid-night using a 23-L Schindler trap.

In both lakes, temperature was recorded from the surface to the bottom at 1-m intervals on each sampling occasion. For phytoplankton identification, 100 mL of lake water from each depth stratum were fixed with Lugol's solution and analysed with the Utermöhl settling technique (Rott, 1981). Biovolumes were estimated from cell dimensions and geometry; cell size and shape distinguished edible from inedible algal cells (Infante, 1973; Porter, 1973; Conover & Mayzaud, 1984). Zooplankton samples were concentrated and preserved in 96% ethanol. At least 100 individuals of adult daphniids (if possible) were counted from each depth.

Growth experiment under natural food conditions

Using *Daphnia* from both lakes, we conducted two growth experiments during the summer (when vertical migration is strongest) in the laboratory with lake seston. For the Oberer Arosasee experiment we used a clone of *Daphnia galeata*, originating from this lake, and for the Schöhsee experiment a *D. galeata x hyalina* clone, originally collected from nearby Lake Plußsee was used. The experiments were carried out in flow-through chambers (170 mL) similar to those described by Lampert, Schmitt & Muck (1988), with a flow rate of 40 mL h^{-1} and constant temperature conditions (Oberer Arosasee 18 °C; Schöhsee 20 °C). Fresh water was collected from the lakes every morning: in the Oberer Arosasee, with a deep-water chlorophyll maximum, at five depths (1.3, 3.8, 6.3, 8.8 and 11.3 m) and in the Schöhsee, without a deep-water chlorophyll maximum, from 1, 5 and 12 m. The water was prefiltered through a 30-µm mesh sieve, to remove larger zooplankton and inedible algae, and used to fill the reservoirs of the flow-through systems. These reservoirs were placed in the dark to avoid photosynthesis, and stirred continuously to prevent sedimentation.

Third brood neonates of mothers acclimated to standard conditions (12 : 12 light : dark photoperiod, 1 mg C L^{-1}, Oberer Arosasee 18 °C, Schöhsee 20 °C) were collected within 12 h after birth. At the start of the experiment, 10 neonates were transferred to each of four preweighed aluminium weighing boats. The boats were dried overnight at 60 °C, cooled in a desiccator and weighed to the nearest 0.1 µg with an ultramicrobalance. This provided the initial dry weight per animal. Five neonates were placed in each flow-through vessel and provided with lake water (seston) from the different depths. In the Oberer Arosasee we used nine replicates per depth and in the Schöhsee three replicates per depth. After 3 days, these animals were removed from the vessels and placed in preweighed aluminium boats, dried and weighed. All animals of a vessel were pooled to reduce measurement errors. Dry weights were converted into somatic growth rates per day using the formula

$$g_j = [\ln(W_3) - \ln(W_0)]/3,$$

where W_0 is the mass of the animals at day zero, W_3 the mass at the end of the experiment and 3 is the duration of an experiment in days. Juvenile growth rate was used as a measure of fitness, as it is strongly correlated to the intrinsic rate of population increase (Lampert & Trubetskova, 1996). Juvenile growth rates were corrected for *in situ* temperatures, using the relation between temperature and developmental time determined by Vijverberg (1980), under the assumption that somatic growth rates scale with temperature in a similar way.

Results

Vertical profiles in the lakes

In the Oberer Arosasee, a distinct thermocline was absent and vertical temperature gradients were weak

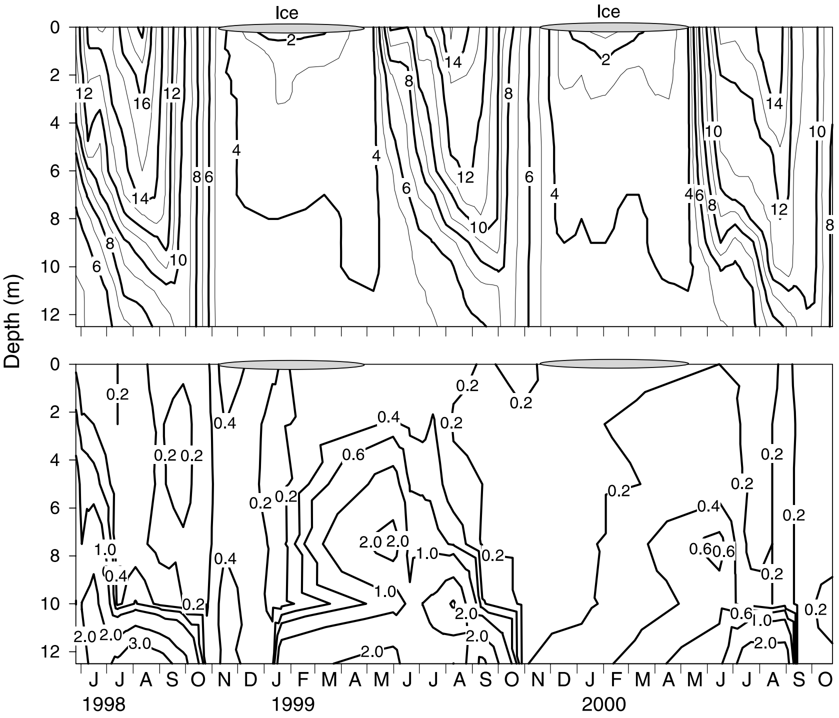

Fig. 1 Isopleth plots of temperature (°C, top panel; POC mg L^{-1}, bottom panel) in the Lake Oberer Arosasee from May 1998 to October 2000.

(Fig. 1); the lake is dimictic with a 6-month period of ice cover. The POC accumulates in deep layers, especially during the summer months (up to 3.6 mg L^{-1}). At this time, concentrations were low in surface waters (~0.2 mg L^{-1}). After the autumn turnover, POC was uniformly distributed throughout the water column (Fig. 1). The Schöhsee is a dimictic lake with a distinct thermocline during the summer months; the upper limit of the thermocline increased from 8 m in May to 10 m in October (Fig. 2). The POC concentrations were similar throughout the water column from April until October 1998 and between 0.7 and 0.4 mg L^{-1} (Fig. 2).

In the Oberer Arosasee, diatoms (mainly *Cyclotella*, *Synedra*) were the dominant phytoplankton species in spring; the summer phytoplankton consisted mainly of chrysophytes (mainly *Cryptomonas* and *Rhodomonas*), dinophytes (mainly *Gymnodinium*) and cyanobacteria (*Microcystis*, *Pseudanabaena*). Diatoms and chrysophytes (divers species) were the most abundant phytoplankton taxa from 0 to 10 m depths (>90%). In the deepest strata, the amount of chlorophytes (*Chlamydomonas*), cryptophytes (*Cryptomonas*, *Rhodomonas*) and cyanobacteria (*Pseudanabaena*) increased (data not shown). Edible and inedible phytoplankton biomass increased with depth during the summer months (Fig. 3). During this period, *D. galeata* stayed in deep layers during the day and moved to the surface waters at night (Fig. 3).

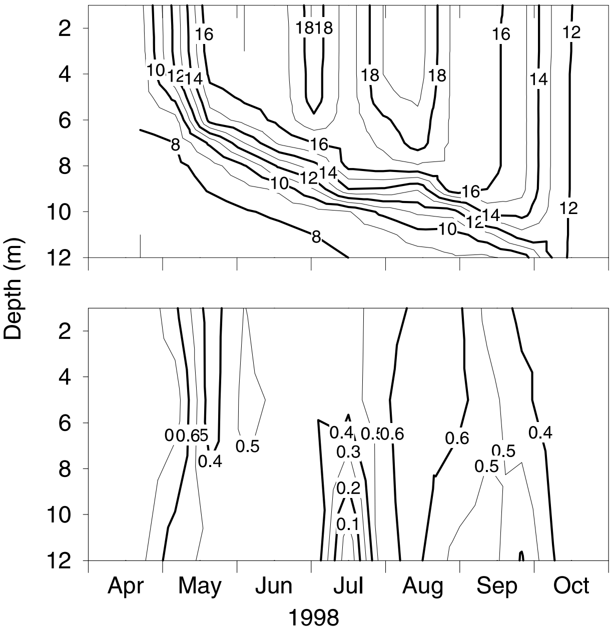

Fig. 2 Isopleth plots of temperature (°C, top panel; POC mg L^{-1}, bottom panel) in the Lake Schöhsee in 1998.

In the Schöhsee, edible phytoplankton biomass peaked slightly at 5 m depth and the inedible fraction increased with depth (Fig. 4). Chrysophytes (mainly

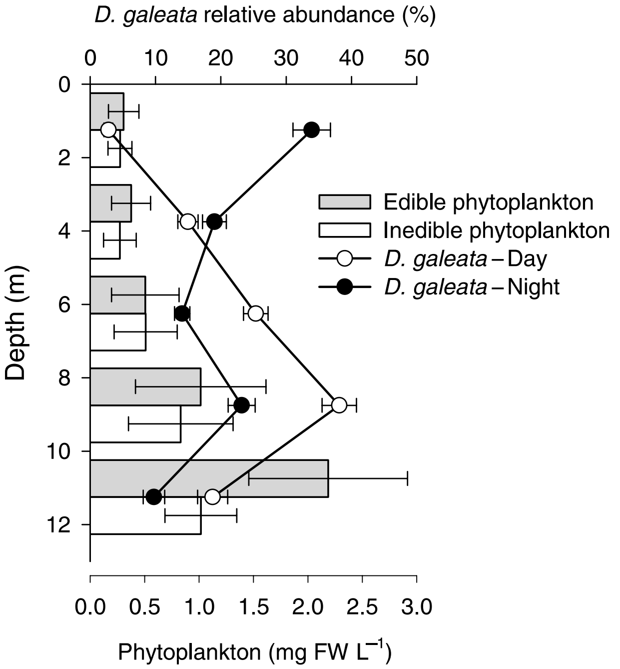

Fig. 3 Vertical distribution of adult *Daphnia galeata* relative abundance (%), and edible and inedible phytoplankton biomass (FW = fresh weight) in the Oberer Arosasee during the summer 1998 (June 23–August 31). Error bars indicate standard errors.

Cryptomonas, *Rhodomonas* and *Chrysochromalium*) and cyanobacteria (mainly *Chlorococcus*, *Aphanocystis* and *Coelospheria*) dominated throughout the water column. During the day, daphniids (mainly *D. galeata x hyalina*) stayed in deeper strata and a part of the population moved upwards at night (Fig. 4).

Juvenile growth experiments

In the Oberer Arosasee, we measured considerable differences in somatic growth rates of *D. galeata* when raised on water taken from different depths under constant temperature (18 °C) for both experiments in July (Fig. 5), and we found a significant depth effect (Table 1). *Daphnia galeata* growth rate increased strongly in the two deepest water layers. At the time of the experiments, there was a weak temperature gradient and oxygen decreased strongly below 10 m depths. The POC concentrations of the seston increased and C : P ratios decreased with depth (Fig. 5). Growth rate was strongly correlated with total POC ($r^2 = 0.83$, $P = 0.003$) and the POC fraction <30 μm ($r^2 = 0.83$; $P = 0.002$) across depth and time.

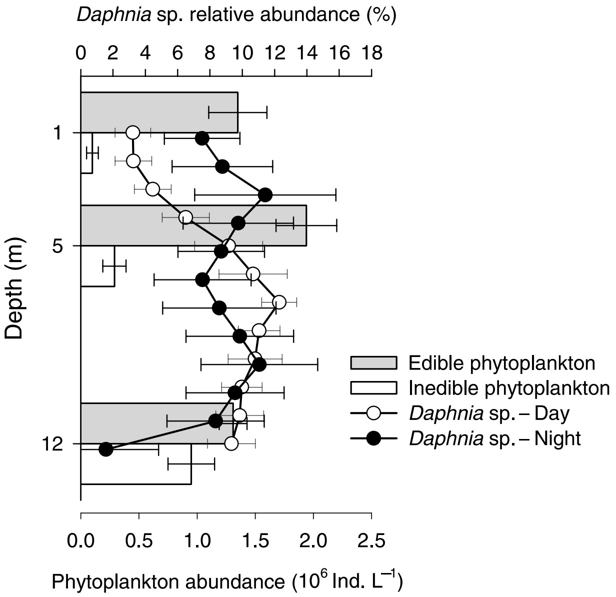

Fig. 4 Vertical distribution of adult *Daphnia* sp. relative abundance (%), and edible and inedible phytoplankton abundance (ind. 10^6 L^{-1}) in the Schöhsee during summer 1998 (June 3–August 26). Error bars indicate standard errors.

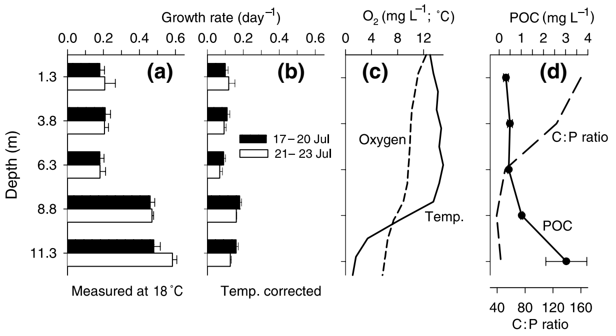

Fig. 5 Growth rates of *Daphnia galeata* cultured at 18 °C on lake seston collected from five different depths in the Oberer Arosasee in two periods in July 2001 (a). Growth rates are corrected for differences in temperature at the different depths in (b). Vertical profiles of temperature and oxygen (c), POC and C : P ratio (d) during the experiments. Error bars indicate standard errors.

After correction for the temperature differences in the different strata, we found a significant depth effect (Table 1). Temperature-corrected growth rates of the daphniids grown on seston from 8.8 and 11.3 m depths were significantly higher than those on seston from the upper depths (Fig. 5).

In the Schöhsee, growth conditions for daphniids were very similar among depths for the two dates in summer; POC values increased slightly at 5 m depth

Table 1 Summary ANOVA table of growth rates of experimental animals (raw and temperature-corrected values) as the dependent variable and date (random) and depth (fixed) as independent factors in the Oberer Arosasee and Schöhsee. Data are from two dates during the summer

	d.f.	MS	d.f. error	MS error	F	*P*
Raw values						
Oberer Arosasee						
Date	1	0.0161	73	0.0085	1.90	0.17
Depth	4	0.4510	73	0.0085	53.25	<0.001
Date × depth	4	0.0072	73	0.0085	0.86	0.50
Schöhsee						
Date	1	0.0001	12	0.0046	0.03	0.88
Depth	2	0.0029	12	0.0046	0.64	0.54
Date × depth	2	0.0001	12	0.0046	0.03	0.97
Temperature-corrected values						
Oberer Arosasee						
Date	1	0.0023	73	0.0022	1.05	0.309
Depth	4	0.028	73	0.0022	12.73	<0.001
Date × depth	4	0.0008	73	0.0022	0.38	0.823
Schöhsee						
Date	1	0.0006	12	0.0014	0.40	0.54
Depth	2	0.0752	12	0.0014	52.53	<0.001
Date × depth	2	0.0001	12	0.0014	0.087	0.92

d.f. – degrees of freedom, MS – mean square.

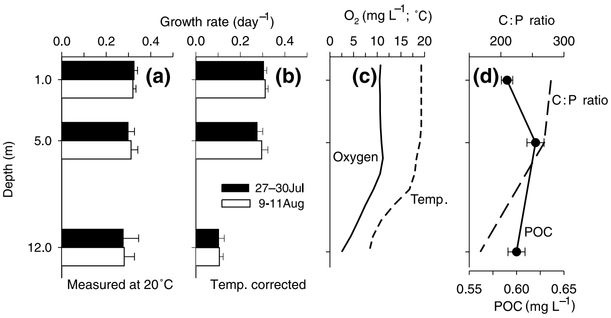

Fig. 6 Growth rates of *Daphnia galeata x hyalina* cultured at 20 °C on lake seston collected from three different depths in the Schöhsee in two time periods in summer 1998 (a). Growth rates are corrected for differences in temperature at the different depths in (b). Vertical profiles of temperature and oxygen (c), POC and C : P ratio (d) during the experiments. Error bars indicate standard errors.

and the C : P ratios decreased with depth (Fig. 6). We measured no significant effect of depth or date on growth rates (Table 1). After temperature correction, the depth effect was significant (Table 1) and temperature-corrected growth rates on seston collected at 12 m depth were significantly lower (Tukey *post hoc* comparison) than at 1 and 5 m (Fig. 6).

Discussion

In this study, we have shown that in summer, juvenile growth rates of *Daphnia* were not necessarily lower when fed seston from deep-water depth strata, both in populations from lakes with and without deep-water chlorophyll maxima. Our results are in agreement with the study of Williamson *et al.* (1996), who also measured higher reproductive rates in the metalimnion compared with the epilimnion in a lake with a deep-water chlorophyll maximum. These experiments provide evidence that in natural situations, growing conditions are not necessarily worsen in deeper strata compared with surface strata. In the Oberer Arosasee, deep-water food maxima were observed every summer over the 3-year study (Fig. 1) and the biomass of both edible and inedible phytoplankton increased with depth (Fig. 3). Growth rates of *D. galeata* were significantly higher in deeper strata compared with surface waters (Fig. 5), suggesting that food conditions in the deeper strata were better than in shallower strata. Quantitative food measurements (i.e. POC) explained a large part of the variation in *D. galeata* growth rate (~83%). In the Schöhsee, without a deep-water food maximum (Figs 2 and 4), growth rates of daphnids were not significantly different between depths (Fig. 6) and growth rates at 12 m were never lower during the growing season at standard temperature (Schöps, 1999). Also in this lake, seasonal changes in POC concentration explained a significant part of the variation in *Daphnia* growth rate (Boersma *et al.*, 2001).

In addition to food quantity, the quality of seston is important in zooplankton production (Urabe *et al.*, 2002). In the Oberer Arosasee and Schöhsee, C : P values of the seston decreased with depth (Figs 5 and 6). Thus, P limitation of *Daphnia* growth was most likely in surface and middle strata in both lakes. But given the relative low seston C : P values, especially in the Oberer Arosasee, the effect of P limitation on *Daphnia* growth rate was probably not very pronounced (Urabe, Clasen & Sterner, 1997). Nevertheless, the increase in food quantity or quality may have led to better or equal growth conditions in the deep-water layers. Although several studies on *Daphnia* reported food-search behaviour of daphniids, with the animals swimming towards the highest densities of algae (Larsson & Kleiven, 1996; Plath, 1999; W. Lampert, unpublished data), we observed that in the field, they did not show this behaviour. If the differences in growth rate were caused by quality differences, this could be explained if daphniids are unable to detect differences in food quality (but see Plath & Boersma, 2001).

The growth experiments were carried out at 18 or 20 °C and not at *in situ* temperatures. By computing the temperature-corrected growth rates, we were able to estimate the effects of the temperature differences in the different strata. Comparisons between raw and temperature-corrected rates showed that temperature indeed played an important role. In the Schöhsee, the temperature gradient was strong, and after temperature correction, growth rates of animals fed seston from shallow depths were higher compared with seston from the deep-water layer (Fig. 6, Table 1). At night, a part of the *Daphnia* population migrated into the warmer surface waters (Fig. 4). In contrast, the Oberer Arosasee had a weak temperature gradient, and after temperature correction, the highest growth rates were still found in the deeper strata. Thus, according to the growth rates calculated on seston from the deeper strata in the Oberer Arosasee, daphniids should stay in deep water both day and night to maximise fitness. However, part of the *D. galeata* population migrated into the surface waters at night in this lake (Fig. 3). This upward migration was observed each summer during the 3-year study (Winder, 2002). This nocturnal upward migration in the Oberer Arosasee contradicts the hypothesis that migration occurs only when increased food levels at the surface make upward migration worthwhile, as suggested by Gliwicz & Pijanowska (1988). These authors showed that in lakes with fish, a weak temperature gradient and a high food concentration in deep waters that *Daphnia* stayed in deep waters both day and night. The upward migration of *D. galeata* at night in the Oberer Arosasee might reflect avoidance of unknown costs of staying in the deep-water refuge. The intriguing question that remains is, what are these costs and why do *D. galeata* move into surface waters at night if growing conditions are more favourable in the deep layers?

First of all, there are two aspects of our methodology, which could contribute to the explanation. First, we removed many of the inedible algae in our growth experiments by filtering the water to remove other zooplankters, hence, inedible algae could not interfere with feeding (Gliwicz, 1990). Especially in the Schöhsee, filamentous cyanobacteria were abundant during the experiment, whereas in the Oberer Arosasee, large-sized diatoms and chlorophytes dominated the inedible taxa. Therefore, it could be that we overestimated growth, especially at depths where the ratio between edible and inedible algae is low, as was the case in the Schöhsee at 12 m depth (Schöps, 1999). Secondly, to correct growth rates measured at laboratory temperatures with the ambient temperatures we used the formula from Vijverberg (1980). However, several temperature functions have been proposed to calculate egg development time of daphniids in relation to temperature, some of them are plotted in Fig. 7 (Bottrell, 1975; Munro & White, 1975; Bottrell *et al*., 1976). Egg development time of *D. galeata* from the Oberer Arosasee measured in a laboratory experiment at 7 and 14 °C (S. Lass, unpublished data) was within the range of the other functions (Fig. 7). If we assume that the growth rates in the different depths need to be at least identical to make it worthwhile for the daphniids to migrate upwards at night, we can compute the temperature correction necessary to achieve this. This function of egg development time with temperature has been added to the ones shown in Fig. 7. It is clear that this function is far outside the range of the other functions. Especially at higher temperature, egg development time should be much faster compared with the other functions. In addition, Q_{10} of the hypothetical function was outside what have been measured in biological systems (Fig. 7 legend; Krogh, 1914). Therefore, it is very unlikely that the exact form of the temperature curve chosen here affected our results.

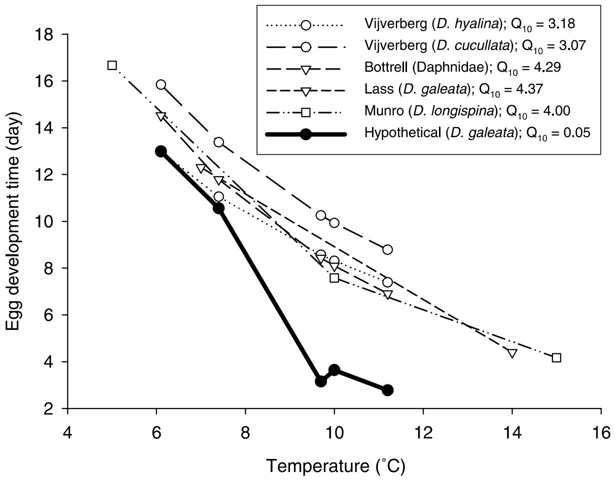

Fig. 7 The duration of egg development at various temperatures for *Daphnia* spp. reported in the literature. Daphnidae (Bottrell *et al*., 1976); *Daphnia galeata* (S. Lass, unpublished data), *Daphnia longispina* (Munro & White, 1975); *Daphnia cucullata* and *Daphnia hyalina* (Vijverberg, 1980). Hypothetical egg development times of *D. galeata* that would give equal growth for the different depth strata for our experiments in the Oberer Arosasee. For each function Q_{10} was calculated between the temperature range of 5 and 15 °C (for formula see Bottrell, 1975).

To achieve equal growth rates in the different depths in the Oberer Arosasee, the temperature difference between the surface and deepest depth should be ~9 °C, with a steep temperature gradient (e.g. ~13 °C in the upper three depth strata and ~4 °C in the deeper strata). In the Oberer Arosasee, the average difference during the summer months between the surface and deepest depth is ~8 °C; however, the gradient is weak (Fig. 1). Nevertheless, the higher temperature in surface waters might be important for the development of eggs in the *D. galeata* population. It could be that the temperature effect is different for juvenile growth rate and egg development. For developing eggs warm water conditions may be very important, thus migration into warmer surface waters might be a useful strategy to maximise fitness in the absence of light-dependent mortality risk, which are in surface waters at night.

Nocturnal migration into warmer water at night after feeding on benthic prey species was observed in larval fish species (Wurtsbaugh & Neverman, 1988). The upward migration promoted digestion, thereby allowing greater feeding and growth and resulted in three times faster growth than if they had remained in the cold hypolimnion. For *Daphnia*, Haney & Hall (1975) observed an increase in filtering rate per individual *Daphnia* up to 10-fold at night in warmer surface waters. In contrast, Lampert & Taylor (1985) report no rhythmic feeding behaviour and no differences in filtration rates per unit biomass between day and night for *Daphnia* in Schöhsee. Grazing experiments in the Oberer Arosasee indicated no difference in the community grazing rate per unit biomass (M. Winder, unpublished data), suggesting that migration patterns can not be explained by diel rhythms in grazing activity. Feeding rates are linked to temperature and also to ambient food concentration (Beisner, McCauley & Wrona, 1997; Plath, 1999); filtration rates decrease at lower temperature and food quantity. Orcutt & Porter (1983) showed that food and temperature have a synergistic effect on *Daphnia* growth, i.e. *Daphnia* responded stronger when food and temperature was increased. Therefore, our temperature-corrected values may have overestimated the growth rates during our experiments, especially for seston from the deep strata of the Oberer Arosasee.

A number of alternative reasons could exist for the observed vertical migration behaviour in the Oberer Arosasee. In the Oberer Arosasee, *Cyclops abyssorum*, the only predaceous zooplankter, may influence to the vertical migration behaviour of *D. galeata*. However, this copepod species also exhibits a nocturnal DVM behaviour with mean day and night depths similar to *D. galeata* (M. Winder, unpublished data). If *D. galeata* migrates to avoid predation from *C. abyssorum*, it should have a different migration behaviour (Ohman, Frost & Cohen, 1983). Avoidance of nocturnally predaceous invertebrates like *Chaoborus* may result in a reverse migration behaviour of the prey species (Neill, 1990); however, induction of DVM by copepods has not yet been observed.

In addition, low oxygen concentrations can restrict the vertical distribution of *Daphnia* (Wright & Shapiro, 1990), although some species can counteract low oxygen concentration to a certain extent by producing haemoglobin (Sell, 1998). In the Oberer Arosasee, an anoxic layer develops below 10 m depth during the summer months. The anoxic area, however, did not prevent the daphniids from inhabiting the 10–12.5 m depth stratum, suggesting that they are highly tolerant to oxygen deficiency. Weider & Lampert (1985) observed that *Daphnia pulex* species were able to regulate oxygen metabolism across a wide range of ambient oxygen concentrations, but below a critical oxygen concentration level of 3.5 mg L^{-1}, filtering and respiration rates in *D. pulex* decreased dramatically. A low oxygen layer may serve as a refuge from fish predation (Hanazato, 1992) in that fish are obligate aerobic animals. However, haemoglobin production requires energy and low oxygen concentrations are unfavourable for reproduction, thus influencing life-history traits such as a reduction in juvenile growth rates (Hanazato, 1995). The oxygen concentration in the Oberer Arosasee can explain, to a certain extent, the migration out of the deeper strata, but not the upward migration above 8 m depth, as above-that-layer oxygen concentrations and saturation were always beyond 8 mg L^{-1} and 85%, respectively, during summer (Fig. 5).

In conclusion, our growth experiments showed that food availability for *Daphnia* in deep waters can be as good as in surface strata in lakes with and without deep-water chlorophyll maxima. Therefore, temperature appears to be the main cost for staying in deep refuge in lakes with a steep temperature gradient. However, also in a lake with a weak temperature gradient but overall low temperatures daphniids migrated upwards at night and may benefit from warmer temperatures to optimise fitness in the absence of light-dependent mortality risks. This indicated that the conditions in surface waters make upward migration worthwhile, even when food quantity and quality is decreasing. The main cause for this phenomenon still needs to be clarified.

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