

Trade-offs in the vertical distribution of zooplankton: ideal free distribution with costs?

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Zooplankton vertical migratory patterns are a classic example of optimal habitat choice. We hypothesize that zooplankton distribute themselves vertically in the water column according to an ideal free distribution (IFD) with costs such as to optimize their fitness. In lakes with a deep-water chlorophyll maximum, zooplankton are faced with a trade-off, either experiencing high food (high reproductive potential) but low temperature (slow development) in the hypolimnion or high temperature and low food in the epilimnion. Thus, in the absence of fish predation (e.g. at night) they should allocate the time spent in the different habitats according to fitness gain dependent on the temperature gradient and distribution of food. We tested this hypothesis with a *Daphnia hyalina* × *galeata* clone in large indoor columns (Plön Plankton Towers) and with a dynamic energy budget model. In the tower experiments, we simulated a deep-water algal maximum below the thermocline with epilimnetic/hypolimnetic temperature differences of 2, 5 and 10 °C. Experimental data supported the model. We found a significantly larger proportion of daphniids in the hypolimnion when the temperature difference was smaller. Our results are consistent with the concept of IFD with costs originally developed for stream fishes. This concept can be applied to predict the vertical distribution of zooplankton in habitats where fish predation is of minor importance.

Keywords: deep-water chlorophyll maximum; food-temperature trade-off; dynamic energy balance model; ideal free distribution; diel vertical migration; zooplankton

1. INTRODUCTION

The vertical distribution of zooplankton is largely determined by diel vertical migration (DVM). ‘Normal’ migration behaviour is a response to predation of visual hunters in the epilimnion (Lampert 1993), where the cost of hiding in the dark hypolimnion during the daytime is balanced by the benefits of avoiding predation mortality. These costs are assumed to arise from experiencing low food availability and low temperature in deep waters. Different combinations of food, temperature and predation pressure may, thus, cause the large variability in migration patterns observed (Haney 1988). Although recent studies have highlighted the role of predation (e.g. Dini & Carpenter 1991; Ringelberg *et al.* 1991; Loose 1993) as the primary factor controlling migration patterns, the vertical distribution is also influenced by food availability (Huntley & Brooks 1982; Dagg 1985; Johnsen & Jakobsen 1987; Leibold 1990; Dini & Carpenter 1992) and by temperature (Kerfoot 1985; Gliwicz & Pijanowska 1988). Zooplankton evidently exhibit a trade-off in their ability to exploit resources and their susceptibility to fish predation (Leibold 1991).

Most studies on the ultimate causes of DVM that explain the nocturnal ascent of zooplankton to the epilimnion, assume that the epilimnion has both higher temperature and a higher concentration or quality of food for filter feeders. This assumption has been challenged by Williamson *et al.* (1996). Systems with strong temperature gradi-

ents and deep-water chlorophyll maxima (i.e. algal maxima below the thermocline) seem to be common in both freshwater (Fee 1976; Padisak *et al.* 1997; Barbiero & Tuchman 2001; Winder & Spaak 2001) and marine (Cullen 1982) systems, and in these systems DVM patterns for zooplankton are altered (Williamson *et al.* 1996). These studies raise several questions about how predation, food availability and temperature act to determine the vertical distribution of zooplankton.

The vertical distribution of zooplankton in the food gradient can be considered a case of an ideal free distribution (IFD) with costs (Tyler & Gilliam 1995). Larsson (1997) proposed that the distribution of *Daphnia* in a patchy environment may follow the IFD model (Fretwell & Lucas 1970) and tested this hypothesis experimentally using a horizontal food gradient at a constant temperature. He found that *Daphnia* behaviour was consistent with the ‘input matching’ IFD model; individuals used both food concentration and population density in choosing their position in the patch. This model is not suitable to describe the vertical distribution in a lake as more factors than food and population density vary with depth. If the effect of predation is excluded (i.e. for the night situation or a fishless lake), temperature remains as an important factor that changes vertically. It adds environmentally induced costs independent of population density. In this situation, an IFD with costs model as developed by Tyler & Gilliam (1995) may be more appropriate. This model has been tested with fish when the costs associated with food patches were energy requirements to match water currents.

IFD models are usually applied to discrete food patches. In a stratified lake, we can consider epilimnion and hypolimnion as distinct habitats, but it is more realistic to assume continuous vertical gradients for both food

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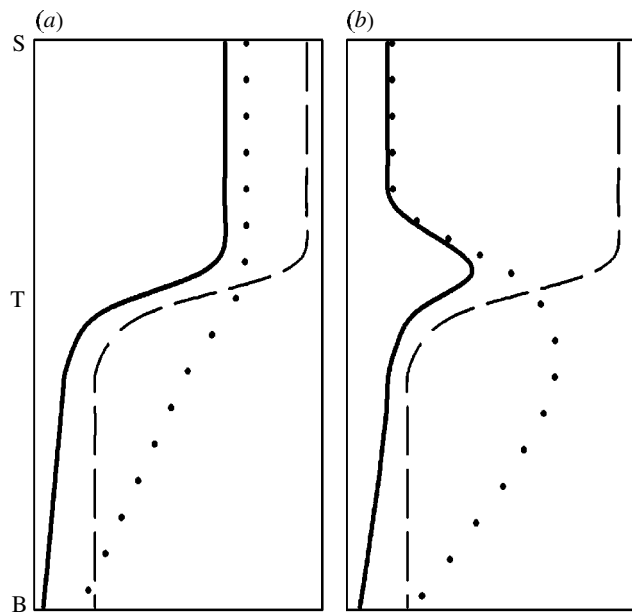


Figure 1. A conceptual model of the fitness distributions (thick line) of *Daphnia* in vertical gradients of temperature (dashed line) and food (dotted line). (a) The situation in a 'normal', stratified lake. Food is distributed in a meta/hypolimnetic algal maximum in (b). Letters on the y-axis denote vertical structure of the water column: S, surface; T, thermocline; B, bottom.

availability and temperature. Although the temperature gradients in stratified lakes may differ considerably in steepness and absolute difference between the two layers the general pattern does not change (i.e. the epilimnion is always warmer). The vertical gradient of food, however, can be much more variable as pointed out by Williamson *et al.* (1996). A simple conceptual model (figure 1) can illustrate the situation. Both food concentration and temperature have a positive effect on the fitness (expressed as instantaneous rate of increase) in a filter feeder. Higher food availability increases clutch sizes (Lampert 1978) and higher temperatures increase the rate of development (Bottrell *et al.* 1976). The product of the relative values of food and temperature, thus, provides a proxy for relative fitness in a particular depth. In case of a 'normal' food gradient, with high food concentrations prevailing in the epilimnion, the fitness profile is as expected; fitness is highest in the epilimnion and drops sharply towards the hypolimnion. However, in case of a deep-water algal maximum the zooplankton experience a trade-off between food and temperature. In the epilimnion, egg production is low but development is fast whereas in the hypolimnion, resources for egg production are high but development is slow. The resulting fitness profile has a maximum in the metalimnion. According to the IFD with costs model, zooplankton should allocate the time spent in different depths according to their fitness profile. Intuitively it is easy to understand that the proportion of time each individual should spend in the hypolimnion will increase if the temperature gradient is shallower, i.e. the costs are lower. A larger proportion of the total population will then be found in the hypolimnion.

To test this model in the field is notoriously difficult, as the temperature profile cannot be manipulated and it

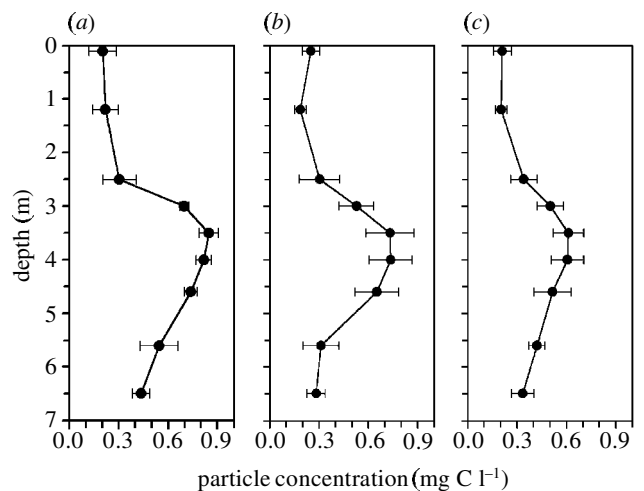


Figure 2. Mean algal distributions in the Plankton Tower experiments at different temperature gradients (epi/hypolimnetic temperatures): (a) 20/10 °C; (b) 20/15 °C; and (c) 20/18 °C. Error bars indicate 1 s.d. of four or five experiments.

will be hard to find situations with different temperature regimes but identical food situations and zooplankton composition. Therefore, we used a large indoor mesocosm system (Plön Plankton Towers) where vertical profiles of food and temperature can be manipulated, and a physiological model of *Daphnia* to estimate fitness profiles. IFD predicts equilibrium conditions depending on resource supply and population feedback. A perfect test of the hypothesis would, thus, require long-term experiments. As such experiments are difficult to perform, we applied an indirect test by experimentally maintaining a fixed environmental gradient and estimating the individual fitness of *Daphnia* in the local environment. We tested the hypothesis that, in the absence of predator threat, *Daphnia* distribute vertically in response to food and temperature conditions and that their distribution corresponds to an IFD with costs.

2. METHODS

(a) *Experimental design*

We ran these experiments in a large indoor mesocosm system, the Plön Plankton Towers. These are basically two vertical stainless steel columns, *ca.* 11.5 m high and 1 m in diameter. They can be filled with filtered water from a nearby mesotrophic lake (Schöhsee) and thermally stratified, manipulated and sampled with a resolution of 50 cm (for details see Lampert & Loose 1992).

We measured the vertical distribution of *Daphnia* in a varying temperature and food gradient by thermally stratifying the columns in four layers of *ca.* 2.80 m each. The upper layer was always set at 20 °C and the two lowest layers to 8 and 6 °C, respectively. The temperature in the second (intermediate) layer was adjusted to either 18 °C (shallow gradient), 15 °C (intermediate gradient) or 10 °C (steep gradient). This resulted in temperature distributions as depicted in figure 3. Algal food was always added to the second layer to produce a deep-water algal maximum. We managed to produce a distinct algal maximum although the steepness of the algal gradient depended on the temperature gradient (figure 2). Hence daphniids had to

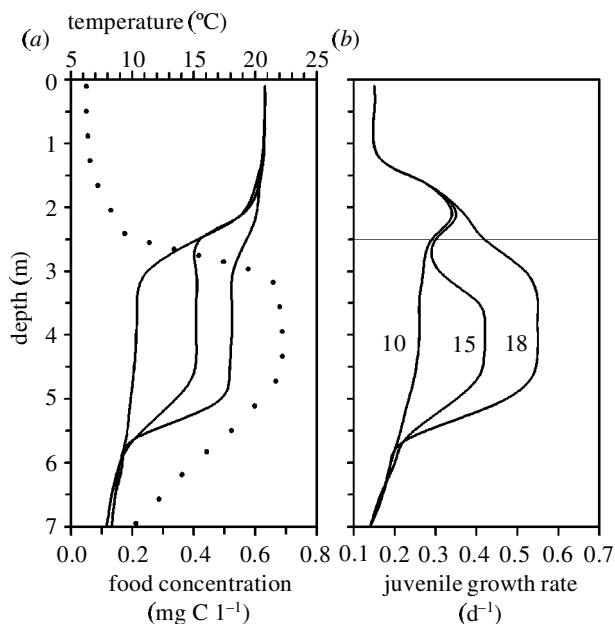


Figure 3. Vertical fitness (g) profiles of *Daphnia* (b) calculated with the *Daphnia* model for the 'ideal' environmental conditions outlined in (a). Numbers indicate hypolimnetic temperatures. The dotted line in (a) represents the algal concentration aimed at in the experiments (not always met). Solid lines are mean temperatures measured in the three experimental set-ups. The horizontal line defines the thermocline.

make a choice between the warm 'epilimnion' devoid of food and the cooler, food-rich 'hypolimnion'.

(b) Organisms

We used a *Daphnia hyalina* × *galeata* clone originally isolated from Lake Constance (Germany) and kept in the laboratory for more than 10 years at ca. 20 °C and dim continuous illumination. This clone is known to react with diel vertical migration to the presence of a chemical signal from fish (Loose 1993). Mass cultures of *Daphnia* were raised in 100 l containers before they were transferred to the towers to start with a sufficient inoculum.

Scenedesmus obliquus (formerly known as *S. acutus* strain SAG 276-3a, algal collection Göttingen) was used as unialgal food. This is our standard algal food for *Daphnia*, which provides good growth. Algae were cultured in 10 l jars in dilute (1 : 4) Z4 medium (Zehnder & Gorham 1960) under continuous light.

(c) Preparation and sampling

To start an experiment, we filled the towers with filtered (nominal pore size 5 µm) hard but nutrient poor ($p < 5 \mu\text{g l}^{-1}$) lake water. The temperature control in the intermediate layer was always set to different temperatures in the two parallel towers. When the temperature gradient was stable, we added a concentrated suspension of *Scenedesmus* cooled to the appropriate temperature through tubing with two outlets at 3.5 m and 4.5 m depth. Beforehand, we measured the light absorption (800 nm) of the algal suspension in a photometer and used a pre-established calibration curve (extinction versus particulate organic carbon) to estimate the amount of algal suspension needed to enrich the second layer (volume ca. 1.7 m³) with 1 mg C l⁻¹ algal biomass. The next day, we added *Daphnia* to the surface layer. The daphniids were then allowed to build up a dense

population, which took about one week to 10 days, depending on the inoculum density. The concentration of algal particles was monitored and adjusted if necessary.

To monitor profiles of algal biomass we withdraw small samples of water (5 ml) through the syringe needles at the sampling ports at every meter, but every half meter in the area of the temperature gradient from 2.5 m to 4.5 m depth. The live samples were transferred to the laboratory immediately and the particle density (volume) was measured by a CASY (Schärfe GmbH) particle counter. As the equivalent spherical diameter of an individual *Scenedesmus* cell is ca. 5.5 µm, we set the limits of the particle counter from 3 to 15 µm equivalent spherical diameter, which covered all size classes of *Scenedesmus* aggregates. The particle volume was converted into particulate organic carbon using a calibration curve.

Daphnia were sampled at nine different depths simultaneously. As zooplankton sampling requires large volumes of water, we used glass traps as described in Lampert & Loose (1992) to sample a volume of 48 l from each depth. Sucrose formalin (Haney & Hall 1973) preserved *Daphnia* samples were transferred to a Bogorov chamber and counted under a dissecting microscope.

(d) Experimental procedure

After the daphniids had established populations sufficiently dense to be sampled, which could be checked visually through the observation windows, their depth distributions were monitored according to a routine programme. The light period was set from 0400 to 1800. At 0800, we measured the first profile of algal biomass and calculated the amount of algae to be added to replenish an algal concentration of 1 mg C l⁻¹ in layer two. The respective amount of concentrated algal suspension was added immediately afterwards. Preliminary measurements had shown that the algae needed several hours to distribute homogeneously, hence we left the towers untouched until 1400 before we measured a new algal profile and sampled zooplankton immediately afterwards at 1430. Algae and zooplankton were resampled at 1700 before the light was switched off at 1800. Finally, zooplankton were sampled after 2 h in the dark at 2000. Immediately afterwards we set the temperature control for layer two to a new value. The next day we adjusted the algal concentration but did not sample zooplankton. The whole sampling programme was repeated on the third day after zooplankton had two light cycles to adjust their vertical distribution to the new temperature conditions. Two days later the cycle was repeated with new temperature conditions assigned at random again. As the towers were set to different temperature conditions each sampling cycle resulted in two temperature combinations. We ran three cycles in April and four cycles in July 1998, which yielded 14 measurements (i.e. five replicates for the 20/18 °C treatment, four for 20/15 °C and five for 20/10 °C), each consisting of two day and one night profile. Although the successive measurements in one tower were done with the same population of *Daphnia* we considered them statistically independent for three reasons: (i) in the 2 days between the measurements the daphniids experienced two light cycles which caused vertical relocations; (ii) food concentration in the second layer was low in the morning before we replenished it, hence daphniids tended to distribute equally in search of food; and (iii) daphniid populations were growing, i.e. offspring were born continuously and there was population turnover.

The absolute numbers of *Daphnia* caught in a vertical profile varied between sampling dates, owing to the growth of the

population, and between day and night, probably owing to difference in the horizontal distribution. Therefore, we integrated the total number of daphniids over the sampled water column and calculated the proportions of the total population contained in the water layers represented by the sampling port (for example, port 5, located at 2.1 m depth, covered the layer from 1.85 m to 2.3 m). This yielded relative depth distributions of the population, and the respective percentages in each depth were used for statistical analysis. According to the temperature profiles depicted in figure 3, we defined the thermocline at 2.5 m depth (at port 6) and calculated the proportions of the *Daphnia* population above and below the thermocline. There were only minute differences between the 1400 and 1700 *Daphnia* distributions; thus we pooled the two measurements to get a single daytime value.

(e) Modelling

We modelled the vertical change in fitness of *Daphnia* with respect to temperature and food in terms of the juvenile growth rate (g_j), which is a good predictor of the instantaneous rate of population growth (r) (Lampert & Trubetskova 1996).

We used a dynamic energy budget model for individual growth (e.g. Gurney *et al.* 1990; McCauley *et al.* 1990; Kooijman 1993; Noonburg *et al.* 1998) based on net production allocation rules (R. M. Nisbet, E. McCauley, W. W. Murdoch, W. S. C. Gurney and S. Wood, unpublished data; E. McCauley, W. Lampert and R. M. Nisbet, unpublished data). Within a moult, an individual of a given length ingests food and respire carbon at a rate determined from energetic scaling functions that relate rates to lengths of individuals. Moult duration is inversely related to energy acquisition rates, and at the moult individuals change length as a function of their net production realized during the previous instar (i.e. the balance between assimilated carbon and carbon expended on maintenance). The translation of carbon weight to length uses a measured length–weight relationship that is not dependent on food or temperature. There are two key features of this dynamic energy budget model (E. McCauley, W. Lampert and R. E. Nisbet, unpublished data). First, it is independently parameterized based on a synthesis of physiological data on *Daphnia* (i.e. food and temperature dependence in ingestion rate, assimilation efficiency, and maintenance rates, or allometric scaling for ingestion, maintenance, length–weight relationships, etc.). All parameters governing in the differential equations are fully specified by independent observations on physiological processes (Muck & Lampert 1980; Urabe & Watanabe 1990, 1991; Boersma & Vijverberg 1994; McCauley *et al.* 1996)—there are no free-fitting parameters. Second, the model predictions have been tested against independent experiments varying food levels and temperature of the environment. The model captured significantly the average growth of different clones of *Daphnia* reared under different combinations of fixed levels of food and temperature.

For the analysis in this paper, we used the dynamic energy budget model to predict g_j under different combinations of food and temperature. To capture g_j , the model has to accurately predict the size at first reproduction (i.e. the change in weight of an individual from birth to first reproduction, which includes the weight of an individual in the first adult instar plus the weight of eggs produced during the first adult instar) and the time to first reproduction. We restricted our analysis to estimating g_j ; we did not predict adult performance nor did we consider food-dependent mortality. We calculated vertical profiles of g_j for two scenarios: (i) to predict the response to aimed food and mean

temperature conditions as depicted in figure 3; and (ii) to calculate the distributions of g_j in the individual experiments and predict the proportion of the total daphniids to be found in the hypolimnion assuming they maximized their growth. The model used is a close match to the experimental set-up and the predictions calculate a proxy of fitness that would be realized for an individual living at a specific depth (i.e. experiencing a fixed level of food at a given temperature) and operating independently of other individuals in the population.

(f) Statistics

To characterize the distribution patterns obtained with different treatments, the 28 percentages at each of the nine ports were subjected to a principal component analysis (PCA). Usually PCA is done on the correlation matrix so that each of the original variables being analysed makes an equal contribution to determining the principal components. However, here we used the covariance matrix so that the results from the ports that showed most variation in percentages would be most influential in the analysis (McGarigal *et al.* 2000, § 2.7.1).

PCA produces linear combinations of the original variables Z_1, Z_2, Z_3 , etc. that are uncorrelated, and therefore in our case represent different aspects of the distribution of daphniids over the nine ports in a tower in terms of contrasts between the percentages at different ports. Furthermore, Z_1 is chosen to represent the maximum amount of the total variation, Z_2 is chosen to represent the maximum amount of the total variation that is not accounted for by Z_1 , Z_3 is chosen to account for the maximum amount of variation that is not accounted for by Z_1 and Z_2 , and so on. Hence the first few principal components can be used to describe the main aspects of the distribution of daphniids.

Following the PCA we chose enough principal components to account for most of the variation in the data (about 95% of the total), and analysed these further to relate them to the experimental factors of the tower used, the temperature regime, and the time of day when an observation was taken. Analysis of variance was used for this purpose, with residual plots to test assumptions. A general linear model was fitted for each of the principal components, with estimation of the main effects (tower, temperature and time) and the two-way interactions between them. This then established which of the experimental factors were significantly related to different aspects of the vertical distribution of daphniids. The PCA and analyses of variance were done using the NCSS statistical package (Hines 2000).

3. RESULTS

(a) Model predictions

We modelled the effect of varying temperature gradients on the vertical fitness profile of *Daphnia* using the juvenile growth rate (g_j) as a proxy (figure 3). The inputs for temperature gradients were mean temperatures measured in the experimental runs with 20 °C in the epilimnion and 10 °C, 15 °C and 18 °C in the hypolimnion, respectively. Thus, the temperatures are empirical values as we could produce them in the tower system. According to the temperature profiles, the thermocline was defined at 2.5 m depth. The food profile was identical in all three model runs, reflecting our aimed values for the experiments.

There is a striking similarity between the model results at 10 °C difference and the conceptual model (figure 1) with arbitrary assumptions. Maximum fitness is predicted

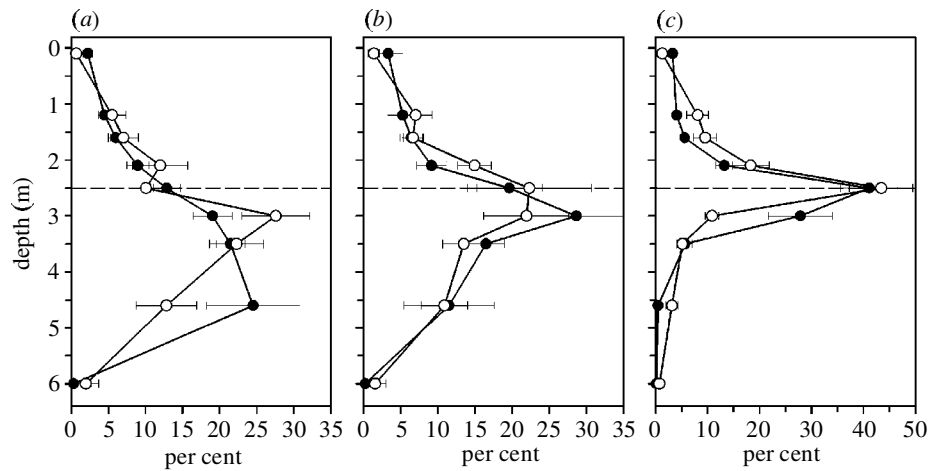


Figure 4. Mean (± 1 s.d., $n = 4$ or 5) proportions of the total population of *Daphnia* in the experiments with different temperature gradients (epilimnetic/hypolimnetic temperatures): (a) 20/18 °C; (b) 20/15 °C; and (c) 20/10 °C. Filled circles, night values; open circles, day values.

Table 1. Eigenvectors for principal components 1–3 (PC1–PC3) and percentage of variation accounted for by the principal components. Reasonably large coefficients are in bold.

sampling port	depth (m)	PC1	PC2	PC3
P1	0.1	−0.018	−0.035	0.006
P3	1.2	−0.000	−0.108	0.316
P4	1.6	0.024	−0.071	0.349
P5	2.1	0.154	0.001	0.570
P6	2.5	0.805	−0.044	−0.463
P7	3.0	−0.200	0.794	−0.190
P8	3.5	−0.373	0.081	−0.264
P10	4.6	−0.386	−0.584	−0.363
P13	6.0	−0.005	−0.034	0.037
per cent variation		60.0	24.8	10.0

just above the thermocline. As expected, the maximum shifts down with warming of the hypolimnion, but the absolute growth rates increase, too. Provided the daphnids distribute according to their relative fitness, we can calculate the proportions of animals residing below the thermocline to 67.8%, 79.1% and 83.5%, respectively.

(b) Tower experiments

Depending on the temperature gradient, *Daphnia* populations in the Plankton Towers showed different vertical distributions in relation to the thermocline (figure 4). As expected, a larger part of the population resided in the hypolimnion when the temperature gradient was shallow. The visual impression is confirmed by the PCA (table 1). About 95% of the variation is explained by three principal components. The first one (PC1) accounts for the largest proportion (60%). PC1 is mainly a contrast between port 6 (2.5 m) and ports 7–10 (3–4.6 m). Port 6 is located at the thermocline (cf. figure 3). Thus PC1 describes the population shift across the thermocline. PC2 is a contrast between ports 7 and 10, i.e. it reflects shifts within the hypolimnion, while PC3 is a contrast between ports 3–5 and ports 6–7, i.e. between epilimnion and hypolimnion.

Table 2. Results of the general linear model ANOVA on principal component PC1 with estimation of the main effects of the factors tower, temperature gradient (temp), time of the day (time), and the two-way interactions between these.

factor	d.f.	<i>F</i>	<i>p</i>
tower	1,18	0.00	0.981
temp	2,18	27.66	<0.001
time	1,18	0.59	0.454
tower × temp	2,18	1.66	0.218
tower × time	1,18	1.19	0.289
temp × time	2,18	0.18	0.839

The ANOVA on PC1 (table 2) shows the temperature difference to be the only significant factor. ‘Tower’ and ‘time of the day’ are not significant and there are no significant interactions. We do not present ANOVAs on PC2 and PC3. For PC2, only the temperature × time interaction is marginally significant ($p = 0.046$). As this is a contrast within the hypolimnion it is not really of interest to the topic. The factors tower ($p = 0.041$) and time ($p = 0.047$) are marginally significant in the ANOVA on

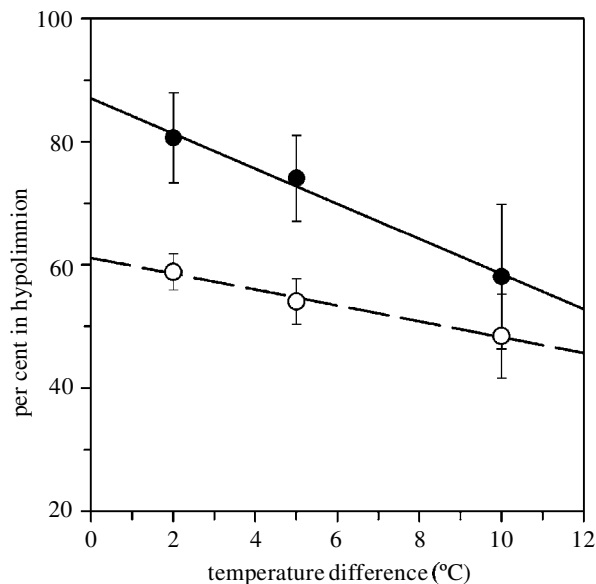


Figure 5. Mean (± 1 s.e.m., $n = 4$ or 5) proportions of the total *Daphnia* population below the thermocline in experiments with increasing temperature difference between epi- and hypolimnion. Filled circles, measured night distributions; open circles, model predictions of g_j for the actual temperature and particle volume values measured in the experiments.

PC3, but this principal component explains only a small portion of the variation (cf. table 1).

(c) Proportions in the hypolimnion

To quantify the shift in population distributions with the increasing temperature difference between the epi- and hypolimnion, we calculated the proportions of the total population dwelling in the hypolimnion (i.e. below 2.5 m). Owing to inhomogeneous variances we could not run an ANOVA for the main effects time and temperature. Using a Kruskal–Wallis ANOVA, only temperature showed a significant effect ($H_{2,90} = 33.40$, $p < 0.0001$). This demonstrates the overwhelming effect of the temperature gradient (figure 5). There is a significant linear regression between temperature difference (ΔT) and measured proportion of daphniids in the hypolimnion (PH_m): $\text{PH}_m = 87.01 - 2.85 \Delta T$ ($n = 14$, $r^2 = 0.590$, $p = 0.001$).

Using measured temperature and food profiles for the individual experiments, we independently modelled vertical profiles of the juvenile growth rate (g_j) for *Daphnia*. Then, as for the predictions in figure 3, we calculated the predicted proportion of daphniids in the food-rich hypolimnion (PH_p). Although the regression of PH_p versus ΔT is significant ($\text{PH}_p = 61.08 - 1.28 \Delta T$, $n = 14$, $r^2 = 0.508$, $p = 0.004$), there is a discrepancy between the model results and the measured proportions (figure 5). The model predicts smaller proportions in the hypolimnion at all temperature gradients and the slope of the regression is lower, i.e. the daphniids react much more strongly to the change in temperature gradient than predicted.

4. DISCUSSION

Faced with the trade-off of either high temperature but low food or low temperature and high food, *Daphnia* dis-

tribute vertically as predicted. The measured distributions (figure 4) resemble the model predictions of fitness (figure 3); hence it is likely that the daphniids allocate their time in the different habitats to maximize fitness.

Our experiments do not test the concept of IFD *sensu stricto* as we decoupled the population feedback on the resource, but they represent snapshots of *Daphnia* behaviour under non-equilibrium conditions. Equilibrium conditions may, in fact, rarely be met in the field. The resource distribution at equilibrium should be equal in all habitats, but consumers should distribute in response to the supply rate. In filter feeders, the feeding rate is related to the food concentration (e.g. Muck & Lampert 1980), hence the constant food gradient (owing to daily replenishment) mimics a constant supply rate, and daphniids can distribute accordingly.

However, our model includes food and temperature, but not density effects, which would be required for an IFD. Although the daphniids were 'free' to choose the depth we do not have direct proof for an IFD as defined by Fretwell & Lucas (1970). To estimate the density effect, one would need an unequal food distribution in a homothermic water column, which is technically not possible in our system. We only have indirect evidence for a weak density effect. Without a temperature gradient and with no density effect, all daphniids should tend to stay where the food is, i.e. in deep waters. Hence no animals should be found near the surface (100% near the maximum food availability). Extrapolating the proportions in the hypolimnion to zero temperature difference in figure 5, however, does not result in 100% but only 87%; i.e. even without a temperature effect 13% would remain in the food-poor surface waters. Although this effect is not strong it may be an indication for the avoidance of competitors. This observation is consistent with the results of Larsson (1997), who studied the distribution of *D. magna* in a horizontal food gradient. In accordance with the IFD model, he found in some experiments flatter distributions of *Daphnia* than expected from the food distribution, but the effect was also weak.

Owing to the temperature–food trade-off, an IFD with Costs (Tyler & Gilliam 1995) is the most probable model to explain our data. The smaller the temperature difference (the lower the costs) the larger was the proportion of the total population residing in the food-rich hypolimnion. The temperature was the only factor that significantly affected the vertical distribution of *Daphnia* (tables 1 and 2). The strongest contrast occurred at the thermocline, indicating that more daphniids crossed the thermocline in a smaller temperature gradient. Low temperature bears demographic disadvantages owing to slow development and lower production. Temperature-related disadvantages have been considered the major cost of DVM (Kerfoot 1985; Dawidowicz & Loose 1992). Experiments in short vertical tubes clearly demonstrated the difference in *Daphnia* response to thermal gradients in the absence of fish (Calaban & Makarewicz 1982; Haney 1993). The proportions are a quantitative estimate of the daphniids residing below the thermocline. As hypothesized, they increase with decreasing temperature difference. The values are slightly lower (58%, 74% and 81%, respectively) than predicted by the model under ideal conditions (figure 3), but the trend is very similar. The

deviation can be explained by our inability to maintain the food conditions in the towers perfectly as intended. However, when we used the *Daphnia* model to calculate vertical profiles of g_i with food and temperature conditions measured in any single experiment, the proportions predicted for the hypolimnion are considerably lower (figure 5). This is a consequence of the vertical distribution of the modelled g_i not mimicking the counted distributions of *Daphnia*. The model overestimated g_i , particularly in the epilimnion and in the deep hypolimnion. This discrepancy is neither a problem of the model parameters nor of the temperature input to the model. It can only be caused by improper input of food. The input considers the quantity of food, but not the quality. Not only was the food quantity higher in the deep-water maximum, but also the quality as these algae were replenished every day. Laboratory growth experiments with epilimnetic particles from a similar experiment (K. Kessler, unpublished results) confirm the differences in food quality. The importance of food quality for *Daphnia* has been frequently stressed in recent years (e.g. DeMott & Müller-Navarra 1997; Boersma *et al.* 2001; Tessier *et al.* 2001). The discrepancy between the model results and the true *Daphnia* distributions suggests that daphniids do not simply distribute to maximize the food input but maximize the net gain.

Our experiments do not provide direct evidence for the mechanisms involved in fitness optimization by individual *Daphnia*. By observing shifts in population distribution it is not possible to decide if the distribution results from individuals staying permanently in different places or from a dynamic movement of all animals allocating a certain proportion of their time to a certain place (Pearre 1979). Following the swimming path of individuals over long distances is impossible in large populations of *Daphnia*. The IFD with costs model would require a dynamic distribution with animals moving between habitats. *Daphnia* have been observed to perform directed movements towards food particles (Haney 1993) on small scales. Even with random movements over distances of 10 m they can find a food patch in the Tower rapidly. If the food concentration is very low they distribute throughout the column, evidently in search of food. After the addition of a localized patch, regardless of which depth, a dense aggregation of daphniids forms in the patch within 2.5 h (Plath 1999). An elegant experiment by Jensen *et al.* (2001) demonstrated that horizontal long-distance movements of *Daphnia* into a food patch occur also in the field. The fact that daphniids reacted to an artificial patch of algae in the lake but not to a patch of clay seems to exclude an optical orientation towards the patch.

These observations support the idea that daphniids swim randomly until they find a food patch and then remain there. What are the mechanisms enabling *Daphnia* not only to be attracted to a food patch over short distances (Jakobsen & Johnsen 1987), but even to position themselves in food environments within some 'optimum' range of food levels (Neary *et al.* 1994)? There is contradictory literature about the role of chemical stimuli. In some experiments (Lauren-Määttä *et al.* 1997; Van Gool & Ringelberg 2001) daphniids were attracted by the odour of edible algae but not of toxic cyanobacteria, whereas in others (Roozen & Lüring 2001) this effect was not found. Entering a food patch, daphniids have been

observed reducing their swimming speed (Larsson & Kleiven 1996) to linger around in regions of high food concentration (Cuddington & McCauley 1994). The change in swimming behaviour can explain the formation of a swarm, but this is only one component modifying the vertical distribution in a deep-algal maximum situation. Daphniids must leave the optimum food conditions for periods of time to maximize the net gain. This is a directed movement following the temperature gradient.

The IFD with costs model (Tyler & Gilliam 1995) seems to be a useful concept for the analysis of vertical distribution of zooplankton, although some of the conditions may have to be relaxed. The costs in a particular lake are represented by gradients in abiotic factors (temperature, oxygen, ultraviolet) as well as mortality (predation). They may apply differently to different species, causing habitat partitioning (Threlkeld 1980; Leibold & Tessier 1997). Predation is a strong modifying factor but only during the day and for conspicuous zooplankton. Dini & Carpenter (1992) support a hierarchical view of vertical migration with presence of fish the primary factor and food availability the second factor. We can predict that fish predation is acting as long as we observe regular patterns of DVM. Only at night will the zooplankton then distribute in an IFD with costs excluding predation effects. In many cases this would not be evident as food and temperature (and thus fitness) are highest near the surface where the zooplankton 'normally' return at night. Unusual distributions of food like deep-water algal maxima provide a means to test this hypothesis in the field. The observations of Williamson *et al.* (1996) are an example as both *Daphnia* and *Diatomus* showed a tendency to migrate upwards at night, but the largest part of the population stayed in the metalimnetic chlorophyll maximum, creating similar distributions as we found in the tower system.

With missing fish predation, zooplankton should dwell in the optimal depths during day and night. A very clear example of this strategy has been reported by Kettle *et al.* (1987) for the small, oligotrophic experimental lakes area Lake 223. As deep-water algal maxima are not so uncommon, careful analyses of the relationship between different zooplankton species and algal distribution in combination with estimates of the food quality in different strata (cf. Threlkeld 1980; Tessier *et al.* 2001) and modelling may lead to an enhanced theory of zooplankton distributions.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.