

# Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish

Thomas Mehner, Peter Kasprzak, and Franz Hölker

**Abstract:** Evolutionary hypotheses for diel vertical migrations (DVM) of aquatic animals include foraging opportunity, predator avoidance, and bioenergetics efficiency. Here we test which hypothesis predicts DVM in the small planktivorous coregonids vendace, *Coregonus albula*, and Fontane cisco, *Coregonus fontanae*, in a deep oligotrophic lake. Densities and population depths of young-of-the-year and larger coregonids were determined by hydroacoustics during day and night over 10 consecutive months. Depth distributions of predator-like fishes and zooplankton resources were recorded as well. Furthermore, Secchi depth, water temperature, oxygen concentrations, and pH values were determined at each sampling month. A DVM of the coregonids was observed in all months. Population depths during the night were significantly correlated to water temperatures, oxygen concentrations, and pH values. In contrast, the vertical distributions of predators or resources were not correlated with the coregonid depth distribution. These results do not correspond to the feeding opportunity or predator avoidance hypotheses of DVM, but support in part the bioenergetics efficiency hypothesis. However, the stable migration pattern of fishes over all months despite substantial changes in biotic and abiotic conditions suggests that diel migrations in the coregonids are a genetically fixed behavioral trait to minimize the anticipated potential predation risk in the illuminated water layers during daytime.

**Résumé :** Parmi les hypothèses évolutives évoquées pour expliquer les migrations verticales journalières (« DVM ») des animaux aquatiques, il y a celles des possibilités alimentaires, de l'évitement des prédateurs et de l'efficacité bioénergétique. Nous vérifions laquelle de ces hypothèses permet d'expliquer la DVM des petits corégonidés planctonophages, le corégone blanc, *Coregonus albula*, et le corégone de Fontane, *Coregonus fontanae*, dans un lac oligotrophe profond. Nous avons déterminé par hydroacoustique les densités et les répartitions en profondeur des populations de jeunes de l'année et d'adultes des corégonidés durant le jour et la nuit pendant 10 mois consécutifs. Nous avons aussi précisé les répartitions en profondeur des poissons de type prédateur et des ressources en zooplancton. Nous avons, de plus, mesuré la profondeur de Secchi, la température de l'eau, les concentrations d'oxygène et les valeurs de pH à chaque mois de l'échantillonnage. Les corégonides font des DVM à tous les mois de nos observations. Durant la nuit, les profondeurs choisies par la population sont en corrélation significative avec les températures de l'eau, les concentrations d'oxygène et les valeurs de pH. En revanche, les répartitions verticales des prédateurs et des ressources ne sont pas en corrélation avec la répartition en profondeur des corégonidés. Ces résultats n'appuient pas les hypothèses des possibilités alimentaires, ni de l'évitement des prédateurs de la DVM, mais elles soutiennent en partie celle de l'efficacité énergétique. Cependant, la stabilité des patrons de migration des poissons au cours de l'ensemble des mois d'échantillonnage, malgré les changements importants dans les conditions biotiques et abiotiques, laisse croire que les migrations journalières chez les corégonidés sont des caractéristiques comportementales fixées génétiquement visant à minimiser le risque potentiel de prédation dans les couches d'eau éclairées pendant la journée.

[Traduit par la Rédaction]

## Introduction

Diel vertical migrations (DVM) were reported from a wide range of aquatic animals. The regular DVM pattern is a stay in deep, dark water layers during daytime followed by an ascent and stay in higher water layers during dusk and at night, with the descent back to the deep layers occurring during dawn. DVM are well studied in zooplankton popula-

tions, including *Daphnia*, *Chaoborus*, copepods, and euphausiids (reviewed by Lampert 1993; Hays 2003), and freshwater and marine fish (Rudstam and Magnuson 1985; Huse and Korneliussen 2000; Scheuerell and Schindler 2003). Mechanistic explanations differentiate between proximate and ultimate factors (Pijanowska 1993). There is a broad consensus that in both fish and zooplankton, the rela-

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tive change in illumination strength at dusk and dawn is the proximate factor triggering the onset of the upward and downward migrations, respectively (Hamrin 1986; Ringelberg 1991; Lampert 1993). The ultimate (evolutionary) causes for DVM can be summarized into three hypotheses, namely feeding opportunity, predator avoidance, and bioenergetics efficiency hypotheses (Hays 2003; Scheuerell and Schindler 2003).

The feeding opportunity hypothesis claims that animals follow their prey in space and time to maximize foraging and subsequent growth rates, although empirical evidence in fish is rare (Levy 1990). More often, the avoidance of visual predators by the prey was found to explain the preference of dark habitats during daytime (Clark and Levy 1988; Lampert 1993; Hays 2003). The third hypothesis of bioenergetics efficiency assumes that there is an energetic advantage if animals can feed in the warm, food-rich water layers at night, but digest in the colder, deeper layers during daytime, thus maximizing their growth rate (Bevelhimer and Adams 1993).

A further differentiation can be made with respect to the evocation of migrations. Empirical research has provided evidence that concentrations of kairomones released by planktivorous fish are used by *Daphnia* to evaluate their predation risk (Ringelberg 1991). Consequently, migration is inducible by an increase in predator densities, and an inducible trait reflects the variable phenotypic expression of a single genotype (Pijanowska 1993). In contrast, the coexistence of migrating and nonmigrating *Daphnia* clones was reported as the source of observed variability in DVM patterns (Weider 1984; De Meester et al. 1995). Accordingly, DVM can be considered as a genetically fixed strategy reflecting genetic polymorphism in zooplankton populations. Although this dichotomy between fixed and induced behavioral traits has received some attention in discussing DVM patterns in zooplankton (Pijanowska 1993), no study has formally analyzed whether fish DVM is inducible or genetically fixed. However, a genetical fixation of DVM was not reported in any of the available studies (e.g., Hamrin and Persson 1986; Bevelhimer and Adams 1993; Scheuerell and Schindler 2003).

Here we study DVM patterns of two small coregonid fishes, the European vendace (*Coregonus albula*) and the Fontane cisco (*Coregonus fontanae*), in Lake Stechlin (Germany). These coregonids are primarily zooplanktivorous fishes inhabiting the pelagic area of deep oligo- and mesotrophic lakes (Hamrin 1986; Garcia et al. 2006). A DVM in vendace was reported from a range of lakes (Northcote and Rundberg 1970; Hamrin 1986; Sydänoja et al. 1995). However, no attempt has been made to explore the evolutionarily adaptive value of these regular habitat shifts. Furthermore, it is not known whether the migration patterns in coregonids are genetically fixed or inducible. We used hydroacoustic sampling during day and night over 10 months to cover a wide range of abiotic conditions and resource and predator densities. We explored whether the adaptive value of the DVM in the coregonids can be explained by the feeding opportunity, the predator avoidance, or the bioenergetics efficiency hypotheses. We expected that population depths or migration amplitudes would be modified or even induced or interrupted by the seasonal changes in abiotic and biotic

environments, in line with the assumption that the DVM is a variable phenotypic expression of a single genotype.

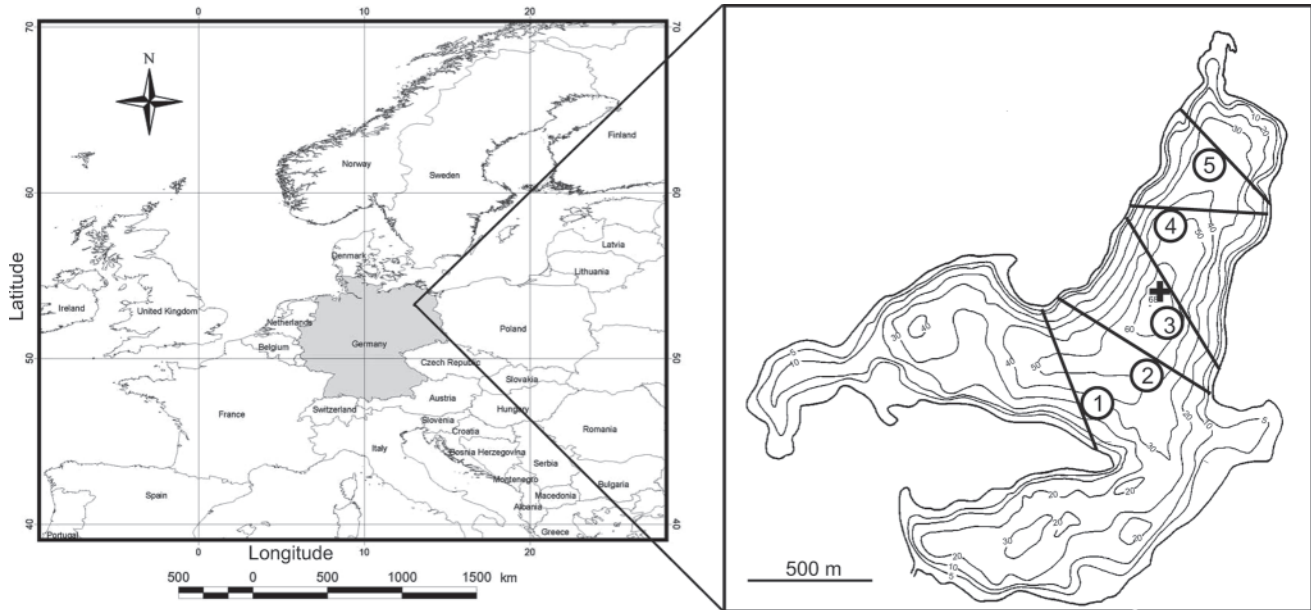
## Materials and methods

The study was conducted in the deep, oligotrophic Lake Stechlin (53°10'N, 13°02'E; 4.3 km<sup>2</sup> surface area), situated approximately 120 km north of Berlin in the Baltic lake district of Germany (Fig. 1). Mean and maximum depths are 22.8 m and 69 m, respectively. A total of 13 fish species has been reported in Lake Stechlin, among which the European vendace and the smaller endemic Fontane cisco dominate the pelagic fish community with about 70% and 30% of total numbers, respectively (Helland et al. 2007). Other fish species that occasionally occur mainly above the thermocline are roach (*Rutilus rutilus*), bleak (*Alburnus alburnus*), and Eurasian perch (*Perca fluviatilis*) (Anwand et al. 2003).

Diel differences in vertical fish distribution were estimated from hydroacoustic recordings. Echosoundings were conducted monthly between March and December 2005 at dates not more than 1 week distant from the full moon (29 March, 18 April, 23 May, 13 June, 18 July, 9 August, 21 September, 17 October, 14 November, 13 December 2005). Ice cover prevented samplings in January and February. A SIMRAD EY-60 split-beam echosounder with 120 kHz operating frequency (7° × 7° circular transducer, type ES 120-7C) was applied. The equipment was calibrated twice that year (February on ice and in September) with a standard copper sphere of 23.0 mm diameter (reference target strength (TS) = -40.4 dB at 1490 m·s<sup>-1</sup> sound speed). However, the measured TS did not deviate by more than 0.1 dB from the reference value. Furthermore, there were no changes in angle sensitivity and little changes in angle offset (shift of -0.04 athwart) or 3 dB beam widths (maximum shift 0.19°, i.e., <3% variability) according to the calibrations. Additional on-axis calibrations were conducted in May and November, and again TS did not deviate by more than 0.1 dB from the reference value. Pulse duration during all surveys was 256 μs, resulting in a sample interval of 0.047 m at a receiver bandwidth of 8.71 kHz. Pulse interval was set to 0.3 s at an approximate boat speed of 6 km·h<sup>-1</sup>. The sound speed was adjusted to average water temperature according to the equation implemented in the SIMRAD software (SIMRAD, Kongsberg, Norway). All surveys consisted of five nonoverlapping cross transects in the central and northern basins of Lake Stechlin (45–65 m deep, 900–1200 m long) with a total length of 5.5 km (about 8000 pings; Fig. 1). To keep all surveys comparable in spatial cover, more transects could not be included because the short nighttime period of full darkness during summer defined the maximum duration of each survey.

Data analysis was performed by the Sonar 5Pro software, version 5.9.5 (Balk and Lindem 2005). Upper echo thresholds for file conversion were set to -80 dB (volumetric backscattering strength,  $S_v$ ) and -75 dB (TS). Single-echo detection (SED) was based on 0.8 to 1.2 relative pulse widths, a one-way beam compensation of 3 dB, and a maximum phase deviation of 0.8. The recorded file of each transect was split into 13 separate 5 m thick depth layers, starting outside of the near-field range of the transducer at 1 m water depth (1–6, 6–11, ..., 61–66 m). These layers

**Fig. 1.** Map of Europe with Germany and location of Lake Stechlin highlighted, and contour map with water depth isolines (10 m range) of Lake Stechlin. The five transects sampled with the echosounder are indicated by lines and numbers; the plus sign (+) represents the location for abiotic and zooplankton sampling.



were separately analyzed to prevent biased estimates of total fish densities due to lack of homogeneity in vertical distribution. Later inspection of the files indicated that the first layer frequently contained numerous echoes from gas bubbles induced by strong winds during the surveys. Accordingly, this layer was excluded, and all results of fish densities and vertical distributions are based on the depth range between 6 and 66 m. The average Sawada index ( $N_v$ ; number of fish per effective reverberation volume) per survey ranged between 0.0008 and 0.016 and thus was below the recommended critical threshold of 0.04 (Sawada et al. 1993), except for the March surveys where it was 0.051 and 0.054 during the daytime and nighttime surveys, respectively. This indicates that the measured TS values were likely not biased by overlapping multiple SEDs.

$S_v$  per depth layer was converted into volumetric densities ( $D_{vol}$ ; individuals·1000 m<sup>-3</sup>) according to the TS frequency distribution of single echoes in 1 dB classes between -60 dB and -30 dB by

$$D_{vol} = \frac{S_v}{\frac{1}{N} \sum_{k=1}^K n_k TS_k} = \frac{10^{S_v/10}}{\frac{1}{N} \sum_{k=1}^K n_k 10^{TS_k/10}}$$

where  $S_v$  and TS are mean volume backscattering strength and target strength (in dB), respectively;  $N$  is the total number of fish;  $K$  is the number of size classes (here 30);  $k$  indicates the  $k$ th size class; and  $n_k$  the number of fish in size class  $k$  (Bodholt (1990), cited in Balk and Lindem (2005)).

During the daytime surveys, however, the number of SEDs per depth layer was <10 in the upper six depth layers down to 36 m. In this case, layer-specific density estimates would have been based on uncertain fish length distributions. To avoid this bias, all SEDs in the 6–36 m depth layers of the five transects per survey were summed, and the

conversion of  $S_v$  into fish densities for the 6–36 m depth layers during daytime was based on these cumulative TS frequency distributions. Total densities per layer were split into values reflecting either small or large coregonids, based on the TS–length regression for vendace

$$TS \text{ (dB)} = 25.5 \log_{10}(\text{total length (cm)}) - 70.9$$

(Mehner 2006). Because the two coregonid species could not be discriminated by the hydroacoustics, the fish size groups were chosen to reflect roughly either young-of-the-year (2.5–8 cm total length, equivalent to a TS of -60 to -48 dB) or juvenile and adult (8–24 cm total length, -48 to -36 dB) vendace and Fontane cisco. The maximum size of the coregonids in Lake Stechlin is about 25 cm, and no other species of that size occur in the pelagic area below the thermocline (Mehner and Schulz 2002; Anwand et al. 2003). Targets with TS in the range of -36 to -30 dB were considered to be potential predators of the coregonids with 25–50 cm total length. According to earlier observations, the only predator in this size range occurring in the upper pelagic layers of Lake Stechlin is perch (Anwand et al. 2003).

The volumetric densities per fish size group were averaged over the 12 water layers to obtain group-specific densities per transect. The average volumetric density per survey was calculated from the five transects, weighted by the ping number per transect. The population depth (PD; in metres) of the fish groups per transect during day or night at each sampling date was calculated as weighted average by

$$PD = \frac{\sum_{i=1}^a \frac{D_i}{\bar{D}} z_i}{a}$$

with  $D_i$  is the density of group in depth layer  $i$ ,  $\bar{D}$  is the average group density over all depth layers,  $z_i$  is the average

depth of sampled layer  $i$ , and  $a$  is the number of depth layers sampled. For each survey, the ping-weighted average of PD from the five transects was calculated.

Simultaneously to the hydroacoustic surveys, zooplankton were sampled with a conical closing plankton net (mesh size 90  $\mu\text{m}$ , opening 0.02  $\text{m}^2$ , length 1.2 m) at a fixed location near the deepest point (69 m) in the central basin of Lake Stechlin (Fig. 1). Triplicate hauls were taken from five water depths (0–10, 10–20, 20–30, 30–40, and 40 m to the bottom). The three hauls per depth layer were subsequently pooled and fixed in sugar–formaldehyde, and species were identified and enumerated in the laboratory from at least three smaller subsamples. Zooplankton were categorized into four groups, namely daphnids (*Daphnia cucullata*, *D. hyalina*), small cladocerans (*Bosmina coregoni*, *Bosmina longirostris*, *Alonella nana*, *Ceriodaphnia quadrangula*, *Acroperus harpae*, *Alona quadrangula*, *Disparalona rostrata*, *Chydorus sphaericus*, *Diaphanosoma brachyurum*, *Pleuroxus uncinatus*, *Polyphemus pediculus*, *Canthocamptus staphylinus*), adult copepods (*Eudiaptomus gracilis*, *Eurytemora lacustris*, *Cyclops strenuus*, *Thermocyclops oithonoides*, *Mesocyclops leukarti*, *Megacyclops viridis*, *Heterocope appendiculata*, *Diacyclops bicuspidatus*), and immature copepods (copepodit and nauplii stages). Group-specific population depths were calculated similar to the procedure described for fish.

Water temperatures were continuously recorded every 30 min by temperature loggers fixed close to the deepest point of the lake at the surface and at 2 m depth intervals down to 20 m, with an additional logger placed nearby at a depth of 30 m. Water temperatures in the same layers were not substantially different between day and night (maximum difference 0.9 °C at the surface during some summer days). Accordingly, daily average temperatures for the lake were calculated from the 48 recordings per day over all 12 depths of measurements. Other abiotic variables (oxygen concentration ( $\text{mg}\cdot\text{L}^{-1}$ ), pH value, and Secchi depth (m)) were determined at 5 m depth intervals close to the deepest point of the lake during routine surveys conducted monthly (October to April) or biweekly (May to September). For oxygen concentrations and pH values, both a vertical average and a gradient (maximum – minimum values over the depth intervals) were calculated per sampling date.

### Statistics

Comparisons of lake-wide fish and zooplankton densities over the diel, seasonal, horizontal, and vertical sampling scales were not the purpose of this study and are described elsewhere based on earlier surveys in Lake Stechlin (Mehner et al. 2005b). Therefore, here only the average densities and population depths of the three fish groups were compared between day and night and over the 10 sampling months. To achieve normal distribution and homoscedasticity, Box–Cox transformations (Sokal and Rohlf 1995) were applied to fish densities and population depths. Natural-log transformation ( $\lambda = 0$ ) resulted in normality (Kolmogorov–Smirnov tests,  $P > 0.087$ ) and homoscedasticity (Brown–Forsythe tests,  $P > 0.81$ ) for volumetric densities, whereas a Box–Cox transformation with  $\lambda = 0.4$  (Rundom BC 1.0, freely available from <http://pjadw.tripod.com/soft.htm>) achieved normality ( $P > 0.16$ ) and homoscedasticity ( $P > 0.23$ ) for population depths. Further-

more, the ping-weighted mean densities and population depths per fish group and month were not serially auto-correlated at lags 1 or 2 (all  $r < 0.48$ ,  $P > 0.09$ ). Densities and population depths could be calculated for both small and large coregonids from all transects sampled (total  $N = 5$  transects  $\times$  10 months  $\times$  2 diel samplings = 100 each). In contrast, echoes from predator-like fishes were missing at 14 transects (4 in April, 5 in May, 2 in June, 1 in July, 2 in August; in total four daytime values, 10 nighttime values) so that the total number of measurements from all three fish groups included was 286. The missing cells were excluded from analyses. For both fish densities and population depths, an univariate three-way analysis of variance (ANOVA) was applied (type III sums of squares to account for nonorthogonal design) by including fish size GROUP (small, large, predators), DIEL (day/night), and MONTH (March to December) as the main effects, and all possible two-way and three-way interactions. If interaction effects were significant, overall statements for main effects were considered to have little meaning (Sokal and Rohlf 1995, p. 336).

Correlations were calculated between the monthly population depths of small or large fish and the abiotic variables water temperature, pH value, oxygen concentration, and Secchi depth. In addition, the experienced water temperature at the population depths and the temperature difference experienced during diel vertical migrations (temperature at nighttime population depth minus hypolimnetic temperature below 30 m depth) were included in correlation analyses. It was assumed that depth distribution of fish was correlated to abiotic variables (in particular the water temperature) if the bioenergetics efficiency hypothesis of DVM applied. Although water temperatures were measured at the dates of hydroacoustic samplings, all other variables were taken from measurements conducted close to the dates of fish samplings (21 March, 9 April, 26 May, 9 June, 26 July, 11 August, 21 September, 19 October, 10 November, 6 December 2005). This temporal deviation most likely did not produce substantial bias because of the rather continuous succession of the abiotic conditions over the sampling period (see Results).

Furthermore, correlations were calculated between population depths of fish and the average population depths of the four zooplankton groups to elucidate whether fish depth distribution corresponded to the depth distribution of zooplankton (feeding opportunity hypothesis). The average population depth of the predator-like fish group was included to test whether population depth of coregonids was negatively correlated to depth of potential predators (predator avoidance hypothesis). Finally, the mean target strength of all echoes reflecting either small or large fish per survey was correlated to the population depths of fish to test whether the seasonal variability in population depth was mainly attributable to changes in average fish size due to recruitment. All variables ( $N = 10$  in each case except for nighttime predator depth where  $N = 9$ ) were normally distributed (Kolmogorov–Smirnov test,  $Z > 1.21$ ,  $P > 0.110$ ) such that Pearson's linear correlation coefficients ( $r$ ) were calculated. We did not correct the significance level from  $\alpha = 0.05$  to a lower, table-wide value by a sequential Bonferroni procedure according to recent discussions that the chance of many weakly signifi-

**Table 1.** Results of univariate three-way analyses of variance (ANOVAs) on natural log transformed volumetric densities (individuals·1000 m<sup>-3</sup>) or Box–Cox transformed ( $\lambda = 0.4$ ) population depths (m) of three size groups of fish from five hydroacoustic transects per survey at Lake Stechlin in 2005 (total  $N = 286$ ).

	Sums of squares	df	<i>F</i>	<i>P</i>
<b>Volumetric density</b>				
Model	1 319.2	58	25.4	<0.0001
Constant	33.5	1	37.4	<0.0001
DIEL	200.1	1	223.5	<0.0001
MONTH	79.5	9	9.86	<0.0001
GROUP	821.9	2	458.8	<0.0001
DIEL × MONTH	22.7	9	2.81	0.004
DIEL × GROUP	53.0	2	29.6	<0.0001
MONTH × GROUP	45.9	18	2.85	<0.0001
DIEL × MONTH × GROUP	41.2	17	2.70	<0.0001
Error	203.3	227		
Corrected total	1 522.6	285		
<b>Population depth</b>				
Model	437.1	58	10.3	<0.0001
Constant	13 205.0	1	18 104.9	<0.0001
DIEL	263.5	1	361.3	<0.0001
MONTH	46.3	9	7.05	<0.0001
GROUP	3.5	2	2.38	0.095
DIEL × MONTH	12.6	9	1.92	0.050
DIEL × GROUP	13.4	2	9.18	<0.0001
MONTH × GROUP	40.9	18	3.11	<0.0001
DIEL × MONTH × GROUP	55.6	17	4.48	<0.0001
Error	165.6	227		
Corrected total	602.7	285		

**Note:** The main effects and their two-way and three-way interactions tested were DIEL (day/night), MONTH (10 months between March and December 2005), and size GROUP of fish (small coregonids, large coregonids, predator-like fishes).

cant correlations being spurious is extremely improbable (Moran 2003).

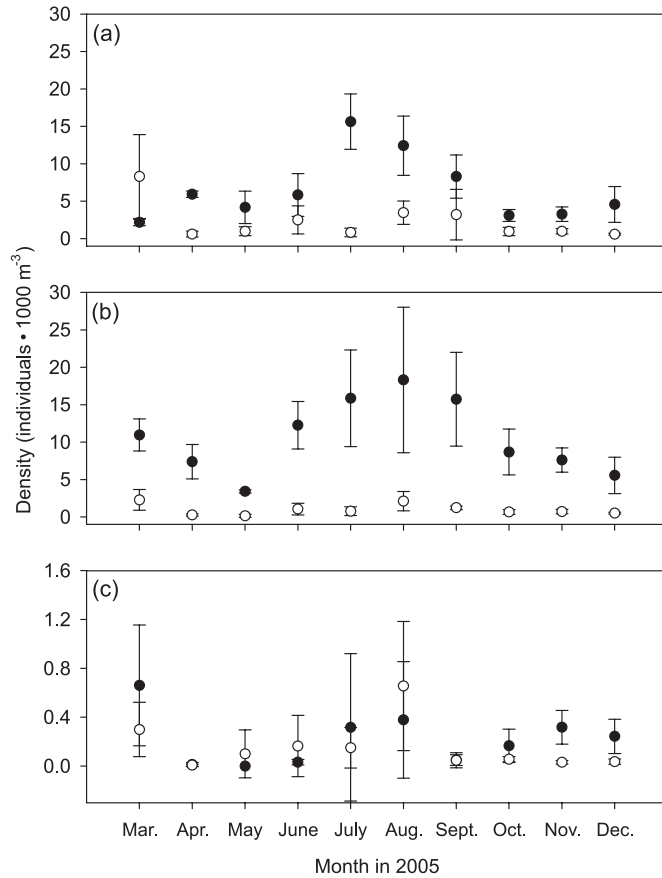
All calculations were performed by SPSS 9.0 (SPSS Inc. 1999).

## Results

Average ping-weighted volumetric densities of the three fish groups substantially varied between day and night and between the 10 sampling months (Fig. 2). Annual average densities were lower for small (6.54 individuals·1000 m<sup>-3</sup>) than for large (10.58 individuals·1000 m<sup>-3</sup>) coregonids at night, whereas the density of predator-like fishes was about 30–50 times lower (0.22 individuals·1000 m<sup>-3</sup>). Total fish density was equivalent to about 693 000 fish·km<sup>-2</sup> if an average depth of the five transects of 40 m is considered. Densities of small and large coregonids during daytime surveys were always lower than during nighttime recordings (Fig. 2). Coregonid densities peaked in July (Fig. 2a, small fish) or August (Fig. 2b, large fish), whereas highest densities of predator-like fishes were found in March (Fig. 2c). All two-way (DIEL × MONTH, DIEL × GROUP, MONTH × GROUP) and three-way (DIEL × MONTH × GROUP) interaction effects were significant in the ANOVA of natural log transformed densities, indicating that the temporal differences between the months and between day and night were variably expressed in the densities of the three fish groups (Table 1).

The ping-weighted average population depths of small or large coregonids showed little variability between the five transects per survey during the night compared with the higher differences between transects found during daytime surveys (Fig. 3). The annual average population depth of small coregonids at night (18.5 m) was slightly lower than that calculated for large coregonids (22.2 m) or predator-like fishes (24.5 m). Nighttime population depths were reduced from March to the summer months (June to August) and were located again deeper from September to November (Figs. 3a, 3b). Population depths during daytime did not follow a regular pattern, but fish were always found deeper during the day than at night. The estimated average diel migration amplitudes were 18.7 m (range 9.2–28.2 m) in small coregonids and 14.3 m (range 7.0–25.9 m) in large coregonids. In predator-like fishes, nighttime population depth was lowest in April and June, but fish moved deeper during the summer (Fig. 3c). In some months, the population depth was found at lower depths during daytime than at night. The annual average migration amplitude of predator-like fishes was 12.4 m (range –5.4 to 31.0 m). In the ANOVA of Box–Cox transformed population depths, the MONTH × GROUP, DIEL × GROUP, and DIEL × MONTH × GROUP interactions were significant, indicating that the differences in population depth between months or day and night were not identical in the three fish groups (Table 1). However, the DIEL × MONTH interaction was only weakly

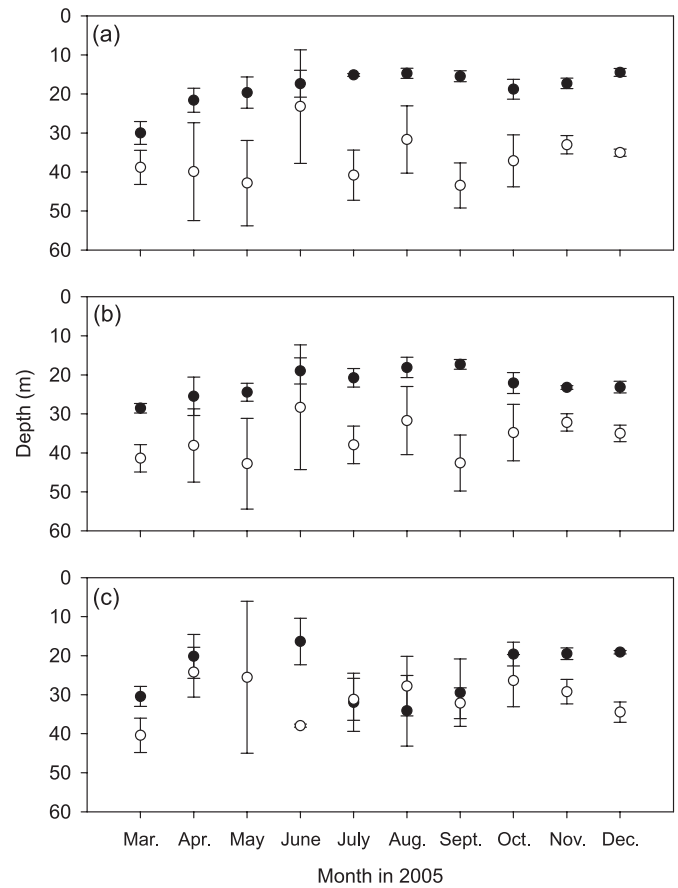
**Fig. 2.** Average volumetric densities (individuals·1000 m<sup>-3</sup> ± standard deviation, SD) of fish in Lake Stechlin, as estimated from five hydroacoustics transects during day (open circles) or night (solid circles) over 10 months in 2005. Fish size groups displayed: (a) small (2.5–8 cm length) and (b) large (8–24 cm length) coregonids and (c) predator-like fishes (24–45 cm length). Predator density was zero during nighttime in May.



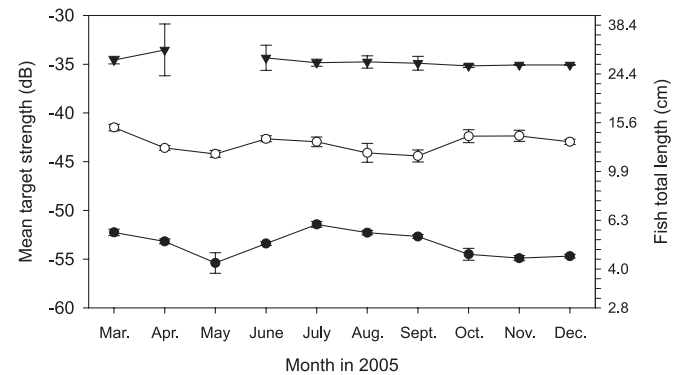
significant ( $P = 0.05$ ). This means that as an overall tendency, the differences in depth distributions between day and night were stable over all sampling months, thus reflecting that the coregonids performed a regular DVM without seasonal interruption. However, because of the continuously substantially lower volumetric densities and the much stronger intertransect variability of both densities and population depths during daytime surveys compared with nighttime surveys, we considered the daytime estimates to be less reliable and focused further correlation calculations exclusively on the nighttime data.

The mean TS per fish group varied little between the five transects per nighttime survey but showed some seasonal fluctuations, presumably owing to variable contributions of newly recruited fish (Fig. 4). In zooplankton, the population depths did not substantially differ between day and night during the majority of the 10 sampling months (Fig. 5). Diel differences in population depths were most pronounced in immature and adult copepods. However, there were no continuous migration patterns because the population depth shifted irregularly upwards or downwards between day and night over the 10 months in all groups. For most of the zooplankton, the diel average population depth shifted upwards

**Fig. 3.** Average population depth (in metres ± standard deviation, SD) of fish in Lake Stechlin, as estimated from five hydroacoustics transects during day (open circles) or night (solid circles) over 10 months in 2005. Fish size groups displayed: (a) small (2.5–8 cm length) and (b) large (8–24 cm length) coregonids and (c) predator-like fishes (24–45 cm length). No data on nighttime depth of predators are available during May.

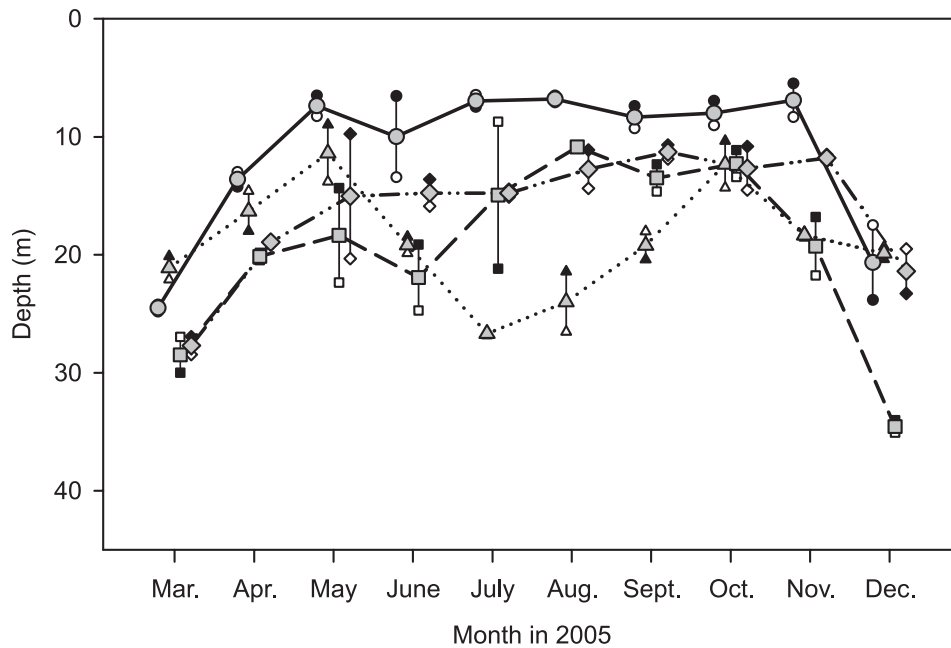


**Fig. 4.** Average target strengths (in dB ± standard deviation, SD) of fish in Lake Stechlin, as estimated from five hydroacoustics transects during day or night over 10 months in 2005. Fish size groups displayed: small (2.5–8 cm length) coregonids, solid circles; large (8–24 cm length) coregonids, open circles; predator-like fishes (24–45 cm length), solid triangles.



in summer and was situated in deeper layers in the early spring and late autumn (Fig. 5). Accordingly, the majority of the zooplankton was always found 10–15 m higher in the

**Fig. 5.** Diel average population depths (m) of four zooplankton groups (*Daphnia* spp., solid line and circles; small cladocerans, dotted line and triangles; adult copepods, dashed line and squares; immature copepods, dashed-dotted line and diamonds) in Lake Stechlin during day or night over 10 months in 2005. The diel migration amplitudes are indicated by the whiskers; open symbols indicate daytime depth, solid symbols indicate nighttime depth. The symbols are slightly staggered along the x axis to improve readability.



water column than the coregonids during daytime, whereas there was a closer spatial overlap during nighttime.

Annual succession of water temperature was highly divergent between surface and hypolimnetic water layers (Fig. 6a). The highest temperature difference between the surface and the 30 m depth was recorded at about 17 °C in July (Fig. 6a). The steepest temperature gradients were always found during the stratification period around the thermocline between water depths of 8 and 14 m. Secchi depth varied between 6.8 and 11.2 m (Fig. 6b). The average oxygen concentration, estimated over the water column, declined over the season and reached its lowest value in December (7.26 mg·L<sup>-1</sup>; Fig. 6c). Simultaneously, the difference between the highest and the lowest concentrations increased such that the vertical oxygen gradient was steepest at the end of the year (Fig. 6c), but low concentrations between 3 and 4 mg·L<sup>-1</sup> were recorded only in depths of more than 60 m between the end of November and December 2005. The average pH values only slightly declined from 8.5 to 7.7 over the year, whereas the differences between maximum and minimum values, indicating a vertical gradient, were a bit higher during summer than in the other periods (Fig. 6d).

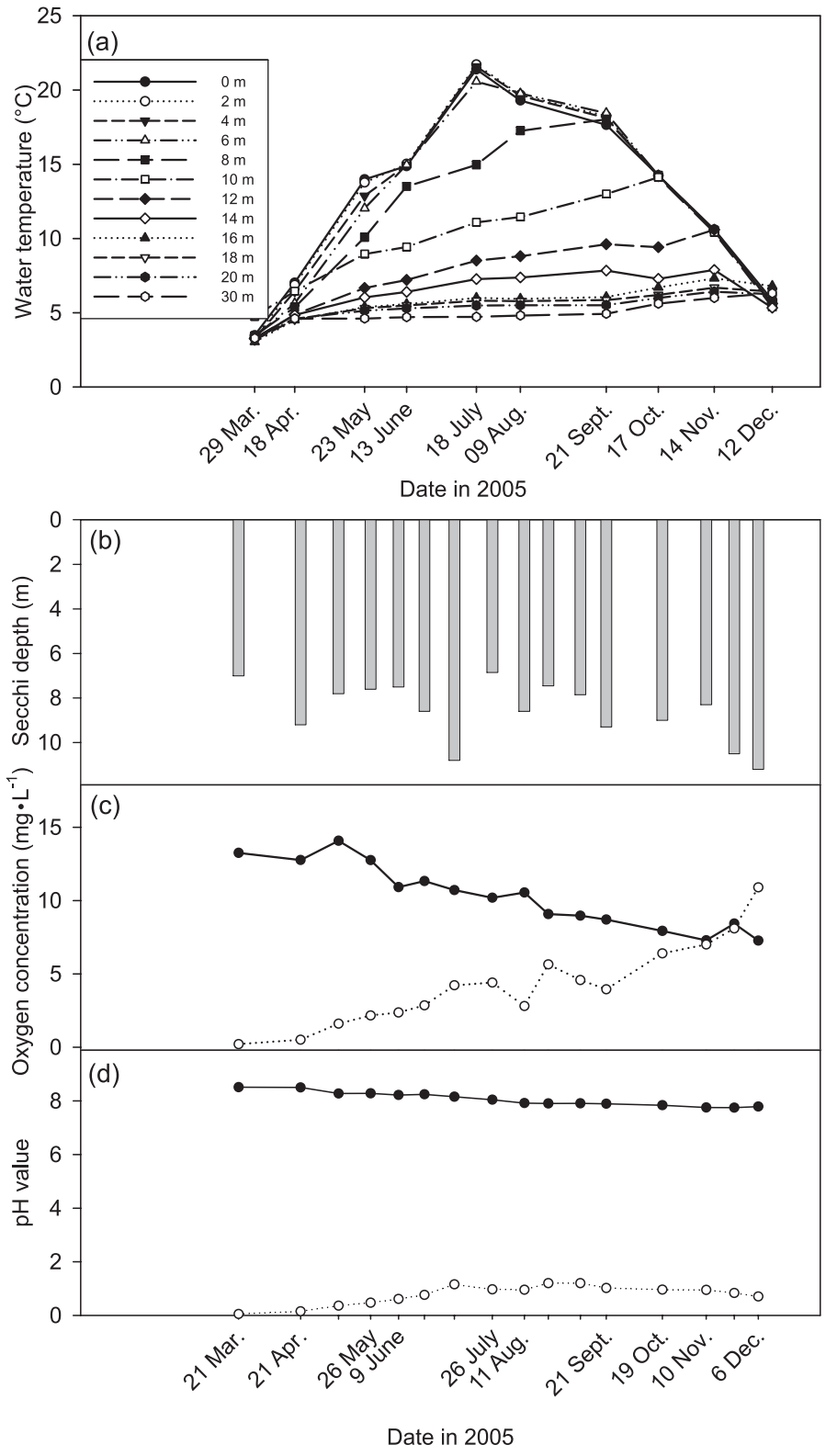
The nighttime population depths of both small and large coregonids were not correlated to population depths of either predators or the four zooplankton groups, except for a weakly significant correlation between depths of large fish and immature copepods (Table 2). Furthermore, the seasonally varying target strengths of fish did not correspond to the nighttime population depths.

However, significant correlations were calculated between some abiotic variables and depths of fishes. In addition to

calculating an average temperature over the full vertical gradient (0–30 m), averages were also calculated over the surface (0–6 m) and over the hypolimnetic layers (16–30 m) according to similar temperature trends in these water layers (Fig. 6a). The four layers in between (8, 10, 12, and 14 m) were tested separately. Population depths of both small and large fish were negatively correlated to temperatures in the surface layer and at 8, 12, and 14 m and to the average temperature over the full depth range (Table 2). Hypolimnetic water temperature corresponded to population depths of small fish only, whereas temperatures at 10 m corresponded to depths of large fish only. In total, the average temperature over 0–30 m best corresponded to population depths of small and large coregonids (average of the two coefficients  $r = -0.805$ ), thus indicating that fish occupied lower water depths during warmer months (Fig. 7). Accordingly, the experienced water temperature at the population depth at night was significantly negatively correlated to population depth for both small and large coregonids. Furthermore, the temperature difference experienced during the migration from daytime to nighttime population depths was negatively correlated to the nighttime depth of large fish (Table 2).

Secchi depths and fish depths were not correlated. However, the population depths of small fish were positively correlated to average oxygen concentrations and pH values and negatively correlated to the difference between maximum and minimum pH values. The latter variable was negatively correlated also to the depth of large fish. It has to be noted, however, that all these variables were similarly strongly correlated to the hypolimnetic water temperature (all  $N = 10$ ; oxygen concentration,  $r = -0.89$ ,  $P = 0.0006$ ; pH,  $r = -0.90$ ,  $P = 0.0003$ ; pH gradient,  $r = 0.80$ ,  $P = 0.005$ ). This indicates

**Fig. 6.** Overview on seasonal succession of abiotic conditions in Lake Stechlin between March and December 2005. Data displayed: (a) water temperature (°C) in 12 depths; (b) transparency, measured as Secchi depth (m); (c) average oxygen concentration (mg·L<sup>-1</sup>) over the full vertical range (solid circles) and vertical gradient in oxygen concentration (maximum – minimum; open circles); and (d) average pH value over the full vertical range (solid circles) and vertical gradient in pH (maximum – minimum; open circles).

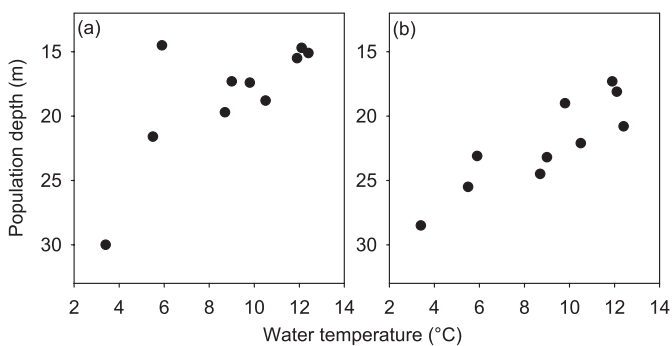


**Table 2.** Overview on linear correlations (Pearson's  $r$ ) between average population depths (m) of small or large coregonids during nighttime hydroacoustic surveys in Lake Stechlin over 10 months in 2005, and target strength of this fish group, population depths of predators and four zooplankton prey groups (m), and 14 abiotic variables ( $N = 10$  in all cases except for predator depth where  $N = 9$ ).

Variables	Population depth (m)	
	Small coregonids	Large coregonids
Target strength (dB)	0.088	0.52
Population depth of predators (m)	0.047	-0.18
Population depth of daphnids (m)	0.50	0.62
Population depth of small cladocerans (m)	-0.22	-0.27
Population depth of adult copepods (m)	0.33	0.56
Population depth of immature copepods (m)	0.58	<b>0.65 *</b>
Average water temperature at 0–30 m (°C)	<b>-0.74 *</b>	<b>-0.87 **</b>
Average water temperature at 0–6 m (°C)	<b>-0.66 *</b>	<b>-0.83 *</b>
Water temperature at 8 m (°C)	<b>-0.66 *</b>	<b>-0.91 ***</b>
Water temperature at 10 m (°C)	-0.53	<b>-0.71 *</b>
Water temperature at 12 m (°C)	<b>-0.68 *</b>	<b>-0.70 *</b>
Water temperature at 14 m (°C)	<b>-0.78 **</b>	<b>-0.79 **</b>
Average water temperature at 16–30 m (°C)	<b>-0.84 **</b>	-0.52
Experienced temperature at population depth (°C)	<b>-0.83 **</b>	<b>-0.64 *</b>
Difference in experienced temperature between day and night	-0.36	<b>-0.83 **</b>
Average oxygen concentration at 0–69 m (mg·L <sup>-1</sup> )	<b>0.65 *</b>	0.44
Gradient in oxygen concentration (maximum – minimum)	-0.60	-0.20
Average pH value at 0–69 m	<b>0.75 *</b>	0.57
Gradient in pH (maximum – minimum)	<b>-0.82 **</b>	<b>-0.79 **</b>
Secchi depth (m)	-0.41	-0.14

**Note:** Significant correlations are given in bold and  $P$  values are indicated by asterisks (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ).

**Fig. 7.** Scatter plots of average water temperature at 0–30 m depth vs. population depth (m) at night of (a) small (2.5–8 cm length) or (b) large (8–24 cm length) coregonids in Lake Stechlin over 10 months in 2005.



that water temperature, oxygen concentration, and pH were strongly coupled in the layers below the thermocline in Lake Stechlin.

## Discussion

Our data show that both small (young-of-the-year) and large (juvenile and adult) coregonids in Lake Stechlin exhibit diel vertical migrations with an average amplitude over all months of about 14–19 m. Size-group specific differences in residence depths and migration amplitudes were relatively low. The overall migration pattern of the coregonids varied little over a full seasonal cycle, irrespective of the docu-

mented changes in population depths of both food resources (zooplankton groups) and potential fish predators. Consequently, from our data there is only weak support for the predator avoidance or feeding opportunity hypotheses in the DVM of coregonids in Lake Stechlin. In contrast, there was a high number of strongly significant negative correlations between water temperatures in several layers and other inter-related abiotic factors on the one hand and average depths of the fish populations at night on the other hand. This modification of nighttime population depths by temperature might support the bioenergetics efficiency hypothesis of DVM. A similar temperature-dependent distribution pattern was found for zooplankton in several deep lakes (Burns and Mitchell 1980; Winder et al. 2003; Thackeray et al. 2006).

The fish densities estimated by hydroacoustics during daytime were continuously lower than the recordings at night. Furthermore, the estimated population depths of the fish groups were highly variable between the five transects per survey during daytime but showed little variability during nighttime surveys. Both patterns are attributable to the differing dispersal of the coregonids between day and night. During daytime, fish aggregate in large schools at water depths below about 40 m. In all areas where the lake is shallower, fish hide directly at the bottom in the “dead zone” such that the strong bottom echo superposes the fish echoes (see Axenrot et al. 2004). During the night, fish ascend into shallower water layers and disperse more evenly. Accordingly, the number of SEDs increases substantially, and the average population depths can be estimated with higher precision. Thus, whereas estimates of fish population depths

during nighttime were reliable, daytime recordings have to be treated with caution, as the calculations of population depth are based only on a limited part of the entire population. A similar improvement in precision of hydroacoustic recordings during the night as compared with daytime surveys has been reported from other studies in which diel migrations of fish were tracked (Appenzeller and Leggett 1992; Axenrot et al. 2004). In contrast, it is highly unlikely that the density differences between day and night were attributable to horizontal migrations out of the study area as earlier analyses revealed little fish density differences between the four main basins of Lake Stechlin (Mehner et al. 2005b).

Methodological difficulties of hydroacoustic recordings may have also influenced the estimates of density and depth distribution of the predator-like fishes. SEDs  $> -36$  dB, i.e., fish bigger than about 25 cm length, were relatively scarce. The relative density of predators in that size range was estimated with 1.27% of total pelagic fish density, based on the annual averages from the nighttime surveys. Perch, a day-active cruising predator (Bergman 1988) reported to feed on vendace (Huusko et al. 1996; Heikinheimo 2001), is present also in Lake Stechlin (Anwand et al. 2003). However, fishing data from Lake Stechlin revealed an only occasional occurrence of perch in the pelagic area. The relative proportion by numbers of perch was 0.8% during a standardized fishing with 13 pelagic gillnets in Lake Stechlin in 2002 (see Mehner et al. 2005a). Regular fishing by gillnets in the pelagic area of Lake Stechlin over 8 months in 2000 caught only 12 perch among the total of 1871 fish (0.6%) (Mehner and Schulz 2002). Several hauls by a pelagic midwater trawl did not catch any perch in 2002 and 2003 (Mehner 2006). Likewise, in a total of 80 hauls with the same trawl in 10–35 m depth completed concurrently with the hydroacoustic estimates in Lake Stechlin during day and night in 2005, no perch was caught at all (Helland et al. 2007). In none of the pelagic fishing surveys was any other piscivorous species caught. Accordingly, it is very likely that the hydroacoustic data overestimated the pelagic predator densities.

One possible reason was found while thoroughly inspecting the hydroacoustic files in which SEDs  $> -36$  dB were found. Predator-like echoes were almost always located within the densest parts of large schools of coregonids. In this case, superimposed echoes from two fish near to each other may have a combined energy more than that coming from one fish, resulting in the indicated target strengths being too high (Simmonds and MacLennan 2005). If all of these suspicious detections of predators were excluded, the predator densities would amount to less than 0.1% of the total densities estimated for the coregonids. More recently, fish-eating birds were considered as a major source of fish mortality (Steinmetz et al. 2003). However, the number of cormorants (*Phalacrocorax* spp.) did not exceed 20 on any of the sampling occasions, and great crested grebes (*Podiceps cristatus*) were likewise not abundant. This overall very low predator density let us conclude that the real risk of being prey in the illuminated layers was not a main factor triggering the occurrence of vendace and Fontane cisco in the dark hypolimnetic layers during daytime. The low risk of encountering predatory fish in the upper water layers was furthermore indicated by the estimated population depths of

predator-like fishes, which were situated outside of the illuminated zone below 25 m during daytime in all months. Accordingly, population depths of predators were not at all correlated to the coregonid population depths.

Feeding opportunity was likewise an inappropriate explanation for the DVM in coregonids. Population depths of zooplankton were seasonally variable but relatively invariant between day and night. This distribution pattern corroborates earlier findings that migration amplitudes of the zooplankton in Lake Stechlin are small (Kasprzak and Schwabe 1987). Levy (1990) argued that DVM in zooplankton might be linked to the presence or absence of diel migrations in coldwater pelagic planktivorous fish. He found that zooplankton distribution was vertically invariant in those lakes in which juvenile sockeye salmon (*Oncorhynchus nerka*) undertook diel vertical migrations. Accordingly, a zooplankton DVM is not expected in Lake Stechlin because of the strong DVM of the coregonids. The zooplankton groups concentrated in water layers above the preferred water depth of the coregonids during daytime, thus preventing strong habitat overlap with and predation mortality by the planktivores. In turn, the feeding opportunities for fish were good only during nighttime when the coregonids had ascended into those layers where zooplankton groups persisted. The following downward migration during dawn is, however, inefficient as only individuals that remained in the upper layers over all the diel cycle would maximize their feeding rates. Therefore, if food availability alone determined the depth distribution of coregonids, then daytime occurrence of fish below the layers where zooplankton occur would be a maladaptive strategy.

The strong correlation between population depths of coregonids during nighttime and the average water temperature seems to support the bioenergetics efficiency hypothesis of DVM. Two contradicting mechanisms, postfeeding and prefeeding thermotaxis, have been described. Larval Bear Lake sculpins (*Cottus extensus*) were found to speed up their postfeeding digestion rate by migrating into warmer water where the higher temperatures allowed the fish to feed and grow three times faster than if they had remained in the cold layers close to the bottom (Wurtsbaugh and Neverman 1988). In contrast, if fish feed intensively in warm, food-rich layers during the night but save energy by migrating to colder water during the day, then their total scope for growth likewise may be higher. Bevelhimer and Adams (1993) modeled the bioenergetics efficiency of DVM in juvenile kokanee salmon (*Oncorhynchus nerka*). They found that when the preferred temperature and optimum prey densities were spatially separated, vertical migrations could result in greater growth compared with no migration. The general rule developed for DVM from the model was to feed where net energy is maximized and then reside when not feeding where energetic costs are minimized and food is digested to the point that consumption during the next feeding period is not limited by the stomach capacity (Bevelhimer and Adams 1993). Recently, a combination of empirical observations and experimental approaches confirmed that adult male dogfish (*Scyliorhinus canicula*) could lower daily energy costs by just over 4% by adopting a “hunt warm – rest cool” strategy (Sims et al. 2006). The gain in efficiency will probably increase with the temperature difference between the two

layers, thus explaining why coregonids shifted their nighttime population depth upwards during warmer months. The experienced temperatures in these depths did not exceed 7.4 °C, which is metabolically not critical for coregonids. Experimental data suggest that adult vendace avoid water temperature above 18 °C, although their lethal temperature is even 23–24 °C (Hamrin 1986). The final temperature preferendum of juvenile vendace is also higher than 7.4 °C and was determined at about 16 °C in summer and 12 °C in winter (Tapaninen et al. 1998).

Bioenergetics explanations of DVM have additionally to consider the costs of the migration itself. Earlier models of DVM have assumed no costs (Clark and Levy 1988), or it was assumed that migration costs are substantial, although reliable estimates were not available (Bevelhimer and Adams 1993). Using a bioenergetics model of buoyancy regulation in adult Atlantic cod (*Gadus morhua*), it was shown that regulation of swimbladder volume during DVM is energetically cheap but slow (Strand et al. 2005). The application of the model to in situ observations of vertical positions of living cod revealed average energy consumption rates of about 0.28 J·kg<sup>-1</sup>·s<sup>-1</sup>, with the additional costs of vertical migrations being about 50% of the standard metabolic rate (Strand et al. 2005, their fig. 7c). If the rate of 0.28 J·kg<sup>-1</sup>·s<sup>-1</sup> is applied to a 10 g vendace, costs of DVM would amount to about 242 J in 24 h, equivalent to about 0.5% of the body energy content of this fish. In a strict sense, the model, which was developed for the physoclist cod, cannot be applied to the physostome vendace. However, the rough estimate shows that costs of DVM are probably relatively low compared with other components of bioenergetics budgets. Accordingly, to make DVM an efficient strategy, the metabolic advantage gained by the migration between the layers with differing temperature can be expected to exceed the pure migration costs.

However, the bioenergetics efficiency hypothesis fails to explain why DVM of coregonids was stable over all sampling seasons. During all those months when the lake is not stratified, the lacking temperature gradient prevents improvements of bioenergetics efficiency by migrations. Lake Stechlin was completely isothermal in March 2005, and temperature differences between surface and bottom were less than 2.5 °C in April and December 2005. Nevertheless, the coregonids also migrated in these months, and no temporal interruption of DVM was observed. Similarly, a vendace DVM was also documented in the shallow Lake Pyhäjärvi (Finland), which did not show thermal stratification during the study period (Sydänoja et al. 1995). Consequently, the water temperature (or the interrelated oxygen concentrations and pH values) obviously modified the migration range but did not induce or stop the migration as such.

The seasonal stability of the migration patterns suggests that the DVM of coregonids in Lake Stechlin is, at least in part, a genetically fixed behavioral strategy. This would distinguish the DVM of the coregonids from other adaptive habitat use patterns described for fish. DVM in juvenile sockeye salmon was considered to be adaptive and inducible as fish matched the antipredation window against predatory salmonids during their ascent and descent in dusk and dawn (Clark and Levy 1988; Scheuerell and Schindler 2003). Re-

cent studies on lake ciscoes (*Coregonus* spp.) in the North American Lake Superior likewise indicated that diel variability in predation risk by siscowet (*Salvelinus namaycush siscowet*), controlled by changing light levels, modified the diel vertical distribution of cisco populations (Hrabik et al. 2006; Jensen et al. 2006). Similarly, horizontal migrations of fish between littoral and pelagic sites in lakes, or timing of ontogenetic habitat shifts, can be highly flexible and inducible by varying diet profitabilities and predator densities (Werner et al. 1983; Byström et al. 2003; Hölker and Mehner 2005). In contrast, a genetically fixed behavior was suggested to explain the early offshore migration of perch larvae (Post and McQueen 1988; Byström et al. 2003), which occurs in almost all perch populations studied irrespective of whether the predation risk in the pelagic area was high or low. In a similar way, DVM in vendace is reported from a wide range of lakes, although mean depths, water temperatures, diet availabilities, and predator densities differ substantially between these locations (Dembinski 1971; Hamrin 1986; Sydänoja et al. 1995).

Recently, the nocturnal feeding of the small benthivorous stone loach (*Barbatula barbatula*) was interpreted as a fixed behavioral strategy (Fischer 2004). The stone loach did not adopt daytime feeding, even when there was no acute daytime predation risk and the fish were severely starving. Fischer (2004) thus suggests that the fish use the anticipated rather than the observed predation risk, a strategy that may have primacy if an animal has imperfect knowledge about its stochastic environment (Bouskila and Blumstein 1992). As a consequence, the animal does not quantitatively weigh mortality versus growth rates to choose the optimal habitat but favors safety over food and frequently maintains predator-avoidance behavior even in the absence of continued threat (Hampton 2004). Accordingly, the stability of the DVM pattern in the coregonids in Lake Stechlin may be interpreted as anticipation of predation risk by visual predators in the illuminated upper water layers during daytime, although the real predation threat was negligible. Blumstein (2006) assumes that in species that have experienced a multiple predator environment in former times, antipredator behavior will persist despite the loss of one or more predator species. He suggests that pleiotropy and (or) linkage seem to be reasonable mechanisms explaining persistence of antipredator behavior. Pleiotropy occurs when a single gene influences multiple phenotypic traits; thus, elements of antipredator behavior may have a function in nonpredatory situations. Linkage means that genes influencing the expression of antipredator behavior do not assort independently. In such cases, the underlying genetic basis of antipredator behavior has, by pleiotropy or linkage, become a functional package.

Accordingly, a heritable basis of the vertical migration behavior in the coregonids should be expected to exist. There is experimental evidence that the average swimming depth in lake whitefish (*Coregonus clupeaformis*) ecotypes is, at least in part, a heritable trait. Rogers et al. (2002) found that the dwarf ecotype preferred the highest position in the water column, whereas the normal-sized ecotype preferred deeper waters. Hybrid crosses showed an intermediate swimming depth, leading to the conclusion that the genetic basis of depth preference consists of an additive component. In

*Daphnia*, the coexistence of genetically different, migrating and nonmigrating clones was reported as a source of observed variability in vertical migration patterns (Weider 1984; De Meester et al. 1995). No such studies are available for fish. However, if one considers that regular short-term changes over temperature or pressure gradients require substantial physiological adaptations (e.g., Stensholt et al. 2002; Speers-Roesch et al. 2004), then it seems to be plausible to assume that vertical migrations have at least a heritable component also in fish.

In conclusion, we suggest that the DVM of coregonids in Lake Stechlin is not an inducible phenotypic trait as has been suggested for most of the zooplankton DVM (Hays 2003). Instead, it seems to be a fixed behavior adapted to minimize the potential predation risk by predators stochastically occurring in the illuminated upper layers, e.g., perch or fish-feeding birds. As long as the net energy gain of this behavioral trait is positive, allowing the fish to grow, there is no selection pressure towards a more efficient strategy. The inefficient DVM of the coregonids in Lake Stechlin is not a disadvantage to fitness as there are no other planktivorous species in the pelagic area that could outcompete the coregonids by staying continuously in the layers where zooplankton concentrate. Levy (1990) speculated that a change in DVM patterns of juvenile kokanee salmon might be created if kokanee has to compete with coexisting three-spined sticklebacks (*Gasterosteus aculeatus*). Therefore, the interdependencies of changed habitat profitabilities due to competition, the DVM patterns in fish, and their genetic fixation need to be explored in more detail.

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## References

- Anwand, K., Valentin, M., and Mehner, T. 2003. Species composition, growth and feeding ecology of fish community in Lake Stechlin — an overview. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **58**: 237–246.
- Appenzeller, A.R., and Leggett, W.C. 1992. Bias in hydroacoustic estimates of fish abundance due to acoustic shadowing: evidence from day–night surveys of vertically migrating fish. *Can. J. Fish. Aquat. Sci.* **49**: 2179–2189.
- Axenrot, T., Didrikas, T., Danielsson, C., and Hansson, S. 2004. Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upward-facing transducer. *ICES J. Mar. Sci.* **61**: 1100–1104.
- Balk, H., and Lindem, T. 2005. Sonar4 and Sonar5-Pro post-processing system manual, version 5.9.5. University of Oslo, Oslo, Norway.
- Bergman, E. 1988. Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. *J. Anim. Ecol.* **57**: 443–453.
- Bevelhimer, M.S., and Adams, S.M. 1993. A bioenergetics analysis of diel vertical migration by kokanee salmon, *Oncorhynchus nerka*. *Can. J. Fish. Aquat. Sci.* **50**: 2336–2349.
- Blumstein, D.T. 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. *Ethology*, **112**: 209–217.
- Bodholt, H. 1990. Fish density derived from echo-integration and in-situ target strength measurements. *ICES Special Paper CM 1990/B:11*.
- Bouskila, A., and Blumstein, D.T. 1992. Rules of thumb for predation hazard assessment — predictions from a dynamic model. *Am. Nat.* **139**: 161–176.
- Burns, C.W., and Mitchell, S.F. 1980. Seasonal succession and vertical distribution of zooplankton in Lake Hayes and Lake Johnson. *N.Z. J. Mar. Freshw. Res.* **14**: 189–204.
- Byström, P., Persson, L., Wahlström, E., and Westman, E. 2003. Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. *J. Anim. Ecol.* **72**: 156–168.
- Clark, C.W., and Levy, D.A. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.* **131**: 271–290.
- Dembinski, W. 1971. Vertical distribution of vendace (*Coregonus albula* L.) and other pelagic fish species in some Polish lakes. *J. Fish Biol.* **3**: 341–357.
- De Meester, L., Weider, L.J., and Tollrian, R. 1995. Alternative antipredator defences and genetic polymorphism in a pelagic predator–prey system. *Nature (London)*, **378**: 483–485.
- Fischer, P. 2004. Nocturnal foraging in the stone loach (*Barbatula barbatula*): fixed or environmentally mediated behavior? *J. Freshw. Ecol.* **19**: 77–85.
- Garcia, X.-F., Diekmann, M., Brämick, U., Lemcke, R., and Mehner, T. 2006. Correlations between type-indicator fish species and lake productivity in German lowland lakes. *J. Fish Biol.* **68**: 1144–1157.
- Hampton, S.E. 2004. Habitat overlap of enemies: temporal patterns and the role of spatial complexity. *Oecologia*, **138**: 475–484.
- Hamrin, S.F. 1986. Vertical distribution and habitat partitioning between different size classes of vendace, *Coregonus albula*, in thermally stratified lakes. *Can. J. Fish. Aquat. Sci.* **43**: 1617–1625.
- Hamrin, S.F., and Persson, L. 1986. Asymmetrical competition between age classes as a factor causing population oscillations in an obligate planktivorous fish species. *Oikos*, **47**: 223–232.
- Hays, G.C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, **503**: 163–170.
- Heikinheimo, O. 2001. Effect of predation on the low-density dynamics of vendace: significance of the functional response. *Can. J. Fish. Aquat. Sci.* **58**: 1909–1923.
- Helland, I.P., Freyhof, J., Kasprzak, P., and Mehner, T. 2007. Temperature sensitivity of vertical distributions of zooplankton and planktivorous fish in a stratified lake. *Oecologia*, **151**(2): 322–330.
- Hölker, F., and Mehner, T. 2005. Simulation of trait-mediated and density-mediated indirect effects of piscivorous predators on a lake food web. *Basic Appl. Ecol.* **6**: 289–300.
- Hrabik, T.R., Jensen, O.P., Martell, S.J.D., Walters, C.J., and Kitchell, J.F. 2006. Diel vertical migration in the Lake Superior pelagic community. I. Changes in vertical migration of

- coregonids in response to varying predation risk. *Can. J. Fish. Aquat. Sci.* **63**: 2286–2295.
- Huse, I., and Korneliussen, R. 2000. Diel variation in acoustic density measurements of overwintering herring (*Clupea harengus* L.). *ICES J. Mar. Sci.* **57**: 903–910.
- Huusko, A., Vuorimies, O., and Sutela, T. 1996. Temperature- and light-mediated predation by perch on vendace larvae. *J. Fish Biol.* **49**: 441–457.
- Jensen, O.P., Hrabik, T.R., Martell, S.J.D., Walters, C.J., and Kitchell, J.F. 2006. Diel vertical migration in the Lake Superior pelagic community. II. Modeling trade-offs at an intermediate trophic level. *Can. J. Fish. Aquat. Sci.* **63**: 2296–2307.
- Kasprzak, P., and Schwabe, W. 1987. Some observations on the diurnal vertical migration of crustacean zooplankton in a stratified oligotrophic clear water lake (Lake Stechlin, GDR). *Limnologica*, **18**: 297–311.
- Lampert, W. 1993. Ultimate causes of diel vertical migration of zooplankton: new evidence for the predator-avoidance hypothesis. *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **39**: 79–88.
- Levy, D.A. 1990. Reciprocal diel vertical migration behaviour in planktivores and zooplankton in British Columbia lakes. *Can. J. Fish. Aquat. Sci.* **47**: 1755–1764.
- Mehner, T. 2006. Prediction of hydroacoustic target strength of vendace (*Coregonus albula*) from concurrent trawl catches. *Fish. Res.* **79**: 162–169.
- Mehner, T., and Schulz, M. 2002. Monthly variability of hydroacoustic fish stock estimates in a deep lake and its correlation to gillnet catches. *J. Fish Biol.* **61**: 1109–1121.
- Mehner, T., Diekmann, M., Brämick, U., and Lemcke, R. 2005a. Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human use intensity. *Freshw. Biol.* **50**: 70–85.
- Mehner, T., Hölker, F., and Kasprzak, P. 2005b. Spatial and temporal heterogeneity of trophic variables in a deep lake as reflected by repeated singular samplings. *Oikos*, **108**: 401–409.
- Moran, M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, **100**: 403–405.
- Northcote, T.G., and Rundberg, H. 1970. Spatial distribution of pelagic fishes in Lambarfjärden (Malaren, Sweden) with particular reference to interaction between *Coregonus albula* and *Osmerus eperlanus*. *Rep. Inst. Freshw. Res. Drottningholm*, **50**: 133–167.
- Pijanowska, J. 1993. Diel vertical migration in zooplankton: fixed or inducible behavior? *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **39**: 89–97.
- Post, J.R., and McQueen, D.J. 1988. Ontogenetic changes in the distribution of larval and juvenile yellow perch (*Perca flavescens*): a response to prey or predators? *Can. J. Fish. Aquat. Sci.* **45**: 1820–1826.
- Ringelberg, J. 1991. A mechanism of predator-mediated induction of diel vertical migration in *Daphnia hyalina*. *J. Plankton Res.* **13**: 83–89.
- Rogers, S.M., Gagnon, V., and Bernatchez, L. 2002. Genetically based phenotype–environment association for swimming behavior in lake whitefish ecotypes (*Coregonus clupeaformis* Mitchill). *Evolution*, **56**: 2322–2329.
- Rudstam, L.G., and Magnuson, J.J. 1985. Predicting the vertical distribution of fish populations: analysis of cisco, *Coregonus artedii*, and yellow perch, *Perca flavescens*. *Can. J. Fish. Aquat. Sci.* **42**: 1178–1188.
- Sawada, K., Furusawa, M., and Williamson, N.J. 1993. Conditions for the precise measurement of fish target strength *in situ*. *J. Mar. Acoustic Soc. Jpn.* **20**: 73–79.
- Scheuerell, M.D., and Schindler, D.E. 2003. Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. *Ecology*, **84**: 1713–1720.
- Simmonds, E.J., and MacLennan, D.N. 2005. Fisheries acoustics: theory and practice. Blackwell, Oxford, UK.
- Sims, D.W., Wearmouth, V.J., Southall, E.J., Hill, J.M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J.D., Nash, J.P., and Morritt, D. 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *J. Anim. Ecol.* **75**: 176–190.
- Sokal, R.R., and Rohlf, F.J. 1995. Biometry. 3rd ed. Freeman, New York.
- Speers-Roesch, B., Lingwood, D., and Stevens, E.D. 2004. Effects of temperature and hydrostatic pressure on routine oxygen uptake of the bloater (*Coregonus hoyi*). *J. Gt. Lakes Res.* **30**: 70–81.
- SPSS Inc. 1999. SPSS 9.0. SPSS Inc., Chicago, Ill.
- Steinmetz, J., Kohler, S.L., and Soluk, D.A. 2003. Birds are overlooked top predators in aquatic food webs. *Ecology*, **84**: 1324–1328.
- Stensholt, B.K., Aglen, A., Mehl, S., and Stensholt, E. 2002. Vertical density distributions of fish: a balance between environmental and physiological limitation. *ICES J. Mar. Sci.* **59**: 679–710.
- Strand, E., Jørgensen, C., and Huse, G. 2005. Modelling buoyancy regulation in fishes with swimbladders: bioenergetics and behaviour. *Ecol. Model.* **185**: 309–327.
- Sydänoja, A., Helminen, H., and Sarvala, J. 1995. Vertical migrations of vendace (*Coregonus albula*) in a thermally unstratified lake (Pyhäjärvi, SW Finland). *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **46**: 277–286.
- Tapaninen, M., Marjomäki, T.J., and Keskinen, T. 1998. The seasonal final temperature preference of immature vendace, *Coregonus albula* (L.). *Arch. Hydrobiol. Spec. Issues Adv. Limnol.* **50**: 131–141.
- Thackeray, S.J., George, D.G., Jones, R.I., and Winfield, I.J. 2006. Statistical quantification of the effect of thermal stratification on patterns of dispersion in a freshwater zooplankton community. *Aquat. Ecol.* **40**: 23–32.
- Weider, L.W. 1984. Spatial heterogeneity of *Daphnia* genotypes: vertical migration and habitat partitioning. *Limnol. Oceanogr.* **29**: 225–235.
- Werner, E.E., Gilliam, J.F., Hall, D.J., and Mittelbach, G.G. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**: 1540–1548.
- Winder, M., Buerge, H.R., and Spaak, P. 2003. Seasonal vertical distribution of phytoplankton and copepod species in a high-mountain lake. *Arch. Hydrobiol.* **158**: 197–213.
- Wurtsbaugh, W.A., and Neverman, D. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. *Nature (London)*, **333**: 846–848.