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Overwinter changes in mass and lipid content of *Perca fluviatilis* and *Gymnocephalus cernuus*

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The body condition, lipid reserves and mortality of 0 and 1 year-old perch *Perca fluviatilis* and ruffe *Gymnocephalus cernuus*, sampled during the winter in Lake Constance, Germany, were compared. Length-frequency analyses did not provide evidence for overwinter mortality in either species. The fresh and dry mass of perch as well as their lipid contents decreased during winter, while ruffe were heavier and contained more lipid at the end of the winter. The superior performance of ruffe was mainly attributed to its sensory capabilities, which allowed it to ingest zoobenthos throughout the winter, while the zooplankton feeding of perch was constrained by low light levels. In lakes that undergo a process of re-oligotrophication, this advantage of ruffe over perch may be even more pronounced, since lower food supply during the growth season and thus lower fish lipid content at the start of winter is probably better tolerated by ruffe than by perch.

Key words: lipid content; overwinter; perch; re-oligotrophication; ruffe.

INTRODUCTION

Winter is a critical period for fishes in temperate regions as reduced food availability, short days, low light levels, especially under ice, and low temperatures may lead to reduced food intake or even cessation of feeding. Fishes must then rely on stored energy reserves and low energy density at the start of winter, coupled with a long, cold winter, may decrease the overwinter success of fishes. If their energy reserves are insufficient, fishes will starve to death (Oliver & Holeton, 1979; Henderson *et al.*, 1988; Fullerton *et al.*, 2000; Sogard & Olla, 2000), and smaller fishes generally suffer higher mortality due to metabolic allometries (Post & Evans, 1989; Shuter *et al.*, 1989; Bernard & Fox, 1997). Apart from mortality, there may be sub-lethal effects of harsh winter conditions, which include low condition factor and depletion of lipid reserves. These may lead to increased incidence of disease and risk of predation (Wedemeyer *et al.*, 1976; Miranda & Hubbard, 1994; Tort *et al.*, 1998).

In addition, the condition in which fishes emerge from winter may influence their growth during the following growth season and eventually their reproductive success. Therefore, when two fish species utilize the same habitats during winter and during the growing season, different overwinter performances might

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influence their interactions and, ultimately, their population dynamics. One such species pair is formed by perch *Perca fluviatilis* L., or its American sister species yellow perch *Perca flavescens* (Mitchill), and ruffe *Gymnocephalus cernuus* (L.). They may compete for food resources (Bergman & Greenberg, 1994; Fullerton *et al.*, 1998), and both stay in the profundal zone during winter in large, deep lakes (Schmid, 1999). A comparative analysis of these species overwintering is particularly important in the light of the recent invasion by ruffe of many European and North American lakes (Ogle, 1998; Winfield *et al.*, 1998). Any eventual advantage of ruffe over perch during winter might contribute to the effect of ruffe on native *Perca* populations.

Overwinter mortality of yellow perch is clearly size-dependent, and mortality rates due to starvation can be predicted from initial body size and duration of the winter (Post & Evans, 1989). Death is probably inevitable when body fat falls below a critical level of 2% of total dry mass (Newsome & Leduc, 1975). Yellow perch, however, have evolved adaptations to counteract critical energy depletion during winter. Their routine metabolic rate, for example, is lower than that of white perch *Morone americana* (Gmelin), and thus energy consumption, and hence mortality rates, of yellow perch are much lower than those of white perch (Johnson & Evans, 1991). Yellow perch may also continue feeding during winter and maintain an approximately constant body lipid content (Sullivan, 1986).

No experimental study on overwinter mortality has been conducted for perch. Both *Perca* species are, however, very similar in many physiological attributes (Thorpe, 1977), so results obtained in studies with yellow perch are probably also valid for perch. Radke & Eckmann (1999) analysed length distributions of age-0 year perch and, based on the study of Post & Evans (1989), suggested that overwinter mortality is probably insignificant for perch in temperate central European lakes. Since ruffe are better adapted to low temperature than perch (Bergman, 1987; Henson & Newman, 2000), overwinter mortality should be insignificant for ruffe as well. The aim of this study was to compare body condition, lipid reserves and mortality of perch and ruffe during winter.

MATERIAL AND METHODS

STUDY SITE

Upper Lake Constance (Bodensee-Obersee) is a large (472 km^2), deep (mean depth 101 m), warm-monomictic prealpine lake situated in the northern fringe of the European Alps (47°39′ N; 9°18′ E). With rare exceptions, the lake does not freeze (the last complete freeze-over was in 1963). The lake was originally oligotrophic but underwent pronounced eutrophication during the 20th century. Total phosphorus concentration during winter turnover (TP$_{mix}$) peaked at $>80\,\mu g\,l^{-1}$ around 1980 (Baeuerle & Gaedke, 1998). As a result of sewage treatment, including partial P-removal, however, the lake had returned to an oligotrophic state by the end of the 20th century (TP$_{mix}$ in 2000: $14\,\mu g\,l^{-1}$).

Perch is the second most important fish species (after lake whitefish *Coregonus* sp.) in the lake, both in terms of catch volume and economic importance for professional fishermen. During eutrophication, the proportion of perch in the fishery increased and the proportion of lake whitefish decreased, but this trend has reversed since the 1980s (Eckmann & Roesch, 1998). Ruffe was encountered for the first time in Lake Constance in 1987 and had become the most numerous littoral fish species by 1996 (Roesch &

Schmid, 1996). Concerns arose that ruffe might compete with the native perch, but there is no conclusive evidence so far that ruffe have contributed to the recent decrease in growth and yield of perch (Schmid, 1999). Perch of all age-classes move to depths of 40 to 70 m, where water temperature is between 4 and 6° C (Eckmann & Imbrock, 1996) for overwintering and return to the littoral in spring (Wang & Eckmann, 1994; Imbrock *et al.*, 1996). From preliminary samples it was evident that ruffe used the same overwintering habitat (pers. obs.).

FISH SAMPLING AND PROCESSING

Fish samples were taken on 16 November 1999 and 10 January, 14 February, 13 March and 14 April 2000. They were collected with a bottom trawl, which was deployed at between 60 and 70 m depths and pulled perpendicularly to the shoreline to *c.* 30 m depth. Mesh-size in the codend was 5 mm, so that age-0 year perch and ruffe could be sampled representatively. Sampling took place shortly after sunset, since during daylight catches were much lower. Fishes were stored on ice overnight and processed the next morning.

Perch >200 mm in total length (L_T) were not retained for analysis but, in the case of ruffe, fish of all sizes were processed. Total length was measured to the nearest mm, and fresh mass (M_F) to the nearest 0·1 g. Randomly taken fishes (Table I) were dried for 48 h at 80° C and dry mass (M_D) was measured to 0·1 mg. Dried fishes were individually homogenized in a grinder, and sub-samples of 60 to 90 mg were taken for total lipid determination (a modified procedure from Ahlgren & Merino, 1991). Lipid was extracted by washing a sample for 1 min with 5 ml of a 2 : 1 (v/v) mixture of chloroform and methanol. The sample was filtered using a glassfibre filter and the extract was retrieved in a pre-weighed glass tube. This procedure was repeated with 3 and 2 ml of solvent. Finally, the solvent was evaporated in a water-bath, the tube was dried at 60° C overnight, and the extracted lipid was weighed to the nearest 0·01 mg. Analyses were carried out in duplicate and results were averaged. When per cent lipid contents differed by >2% between the duplicates, a third sub-sample was analysed.

TABLE I. Range of variable values [total length (L_T), fresh mass (M_F), dry mass (M_D) and total lipid content] and numbers of fishes (*n*) that were used in the analysis of overwinter changes (1999–2000) in mass and lipid content of perch and ruffe

		November	January	February	March	April
Perch	L_T (mm)	73–177	66–157	65–158	65–146	68–163
	(*n*)	(751)	(448)	(412)	(328)	(374)
	M_F (g)	3·4–116·0	2·6–38·3	2·3–44·8	2·3–30·0	2·5–43·1
	(*n*)	(751)	(448)	(412)	(328)	(374)
	M_D (g)	0·7–8·0	0·5–10·1	–	0·6–7·0	0·5–6·0
	(*n*)	(120)	(120)		(87)	(113)
	Lipid (mg)	68–1905	–	–	35–1040	35–845
	(*n*)	(118)			(85)	(105)
Ruffe	L_T (mm)	55–122	54–124	57–122	54–117	55–123
	(*n*)	(93)	(171)	(50)	(255)	(254)
	M_F (g)	1·9–25·1	1·8–21·2	2·2–25·9	1·1–23·4	2·1–29·6
	(*n*)	(93)	(171)	(50)	(255)	(254)
	M_D (g)	0·3–5·8	0·3–5·2	–	0·4–6·8	0·5–10·4
	(*n*)	(70)	(104)		(89)	(79)
	Lipid (mg)	21–1088	–	–	–	32–1084
	(*n*)	(68)				(77)

A second sub-sample of fishes was taken randomly from the total catch, and used for the gravimetric determination of stomach contents. Stomachs were dissected and their contents transferred to pre-weighed porcelain dishes. After drying at 80° C for 24 h and cooling in a desiccator, the stomach contents were weighed to 0·01 mg. Relative stomach contents were expressed as a percentage of fish M_F.

STATISTICAL ANALYSES

Empirical quantile-quantile plots (Post & Evans, 1989) were used to test for size-selective mortality. Since the monthly samples contained at least two age-classes of perch (age-0 and age-1 years) and three age-classes of ruffe (age-0 to age-2 years) whose L_T distributions overlapped in some cases, an algorithm was used to separate age-groups (Gayanilo *et al.*, 1996). This procedure was applied to the linear and $\log_{10}$-transformed L_T data of both species. To avoid confusion, fish age was not increased by one on 1 January 2000, so that fishes that had hatched in 1999 are referred to as age-0 years throughout the winter irrespective of the time of sampling.

Regressions between L_T and M_F, M_D and lipid content were tested with ANCOVA with the sampling date as covariate. Relative stomach contents were compared using non-parametric tests, since in most cases the data were not normally distributed. The software package STATeasy (Lozán & Kausch, 1998) was used for all analyses.

RESULTS

In total, 2313 perch and 823 ruffe were caught and all were used for the length-frequency analyses, while sub-samples were analysed for M_F, M_D, lipid content and stomach contents (Tables I and II), excluding perch >200 mm. Perch L_T distributions were separated into two age-classes. In all samples the L_T distributions of age-0 year perch followed a normal distribution while this was not the case for age-1 year perch in the February and March samples. Their L_T distributions could not be modelled by either a normal or a $\log_{10}$-normal distribution (Table III). Quantile-quantile plots of the November and January age-0 year length distributions suggested size-selective mortality of the larger fish. The January *v.* April quantile-quantile plot was ambiguous, suggesting some growth combined with mortality of the larger fish. Neither case provided evidence for size-selective mortality of the smaller individuals.

For ruffe, only the January length distribution could be separated into three age-classes (age-0 year: $68{\cdot}3 \pm 5{\cdot}4$ mm, age-1 years: $84{\cdot}9 \pm 3{\cdot}4$, age-2 years: $102{\cdot}6 \pm 8{\cdot}6$; mean ± S.D.). In all other samples, the numbers of larger ruffe were too low to allow a reliable separation of the overall L_T distribution into different age-classes. Therefore, all ruffe L_T distributions were truncated at 78 mm (the intersection of the January age-0 and age-1 year distributions) and the resulting distributions of the smallest size-class of ruffe were characterized by their median and 1st and 3rd quartile (Table III). Quantile-quantile plots of the age-0 year ruffe thus defined did not indicate size-selective mortality.

The perch lost M_F during winter. The slopes of the $\log_{10}$-transformed L_T-M_F regressions did not differ among the five samples (ANCOVA, d.f. = 2307, $P > 0{\cdot}05$). But intercept values were all significantly different (ANCOVA, d.f. = 2311, $P < 0{\cdot}05$) and decreased from November to April. During 153 days, from 16 November 1999 to 17 April 2000, a perch of a given length lost *c.* 0·1% of its M_F per day. Daily M_F loss was highest at the start of winter (0·17% day^{-1} from 16 November to 10 January) and decreased thereafter (0·1,

TABLE II. Fresh mass (median ± S.E.) and relative stomach content expressed as stomach content dry mass as a percentage of fish fresh mass (median ± S.E.) of perch and ruffe sampled in the winter of 1999–2000 from Upper Lake Constance. Data are presented separately for age-0 year and older fishes. Sample size (the same for fresh mass and relative stomach content in all cases) is given in parentheses. Values in a row with the same superscript are not significantly different at $P = 0{\cdot}05$

		November	January	March	April
Perch age-0 year	Fresh mass (g)	7·0 ± 0·3^{a}	4·5 ± 0·5^{b}	4·8 ± 0·4^{b}	5·2 ± 0·4^{b}
	Relative stomach content (%)	0·084 ± 0·010^{a,b}	0·122 ± 0·010^{a,c}	0·141 ± 0·015^{c}	0·072 ± 0·014^{b}
		(40)	(49)	(40)	(41)
Perch ≥ age-1 year	Fresh mass (g)	23·8 ± 0·8^{a}	18·9 ± 1·0^{b}	–	19·0 ± 0·7^{b}
	Relative stomach content (%)	0·072 ± 0·020^{a}	0·040 ± 0·002^{b}	–	0·054 ± 0·006^{a,b}
		(38)	(46)		(38)
Ruffe age-0 year	Fresh mass (g)	3·5 ± 0·3^{a}	3·8 ± 0·2^{a}	3·8 ± 0·2^{a}	3·7 ± 0·3^{a}
	Relative stomach content (%)	0·187 ± 0·025^{a,b}	0·112 ± 0·013^{a}	0·119 ± 0·019^{a}	0·241 ± 0·025^{b}
		(14)	(43)	(40)	(40)
Ruffe ≥ age-1 year	Fresh mass (g)	13·8 ± 1·8^{a}	15·6 ± 1·1^{a}	–	14·9 ± 0·9^{a}
	Relative stomach content (%)	0·222 ± 0·091^{a}	0·098 ± 0·020^{a}	–	0·179 ± 0·063^{a}
		(9)	(23)		(13)

TABLE III. Total length (L_T) of age-0 and age-1 year perch (mean ± s.d.) and age-0 year ruffe (median, 1st/3rd quartile) sampled on five dates in the winter of 1999–2000 from Upper Lake Constance. Sample sizes are given in parentheses

	November	January	February	March	April
Perch age-0 year L_T (mm)	91·0 ± 9·3 (278)	82·7 ± 7·5 (265)	82·2 ± 6·7 (320)	83·2 ± 7·0 (288)	85·3 ± 8·6 (157)
Perch age-1 year L_T (mm)	138·6 ± 15·6 (440)	125·2 ± 13·6 (183)			130·7 ± 15·7 (217)
Ruffe age-0 year L_T (mm)	67·0, 61/71 (63)	68·0, 65/71 (100)	66·0, 63/69 (39)	67·0, 63/70 (209)	66·0, 63/71 (206)

0·06 and 0·06% day^{-1} from 10 January to 14 February to 13 March to 17 April, respectively). After 153 days perch M_F had dropped to 85% of the November value.

Ruffe, in contrast, gained M_F during winter. As for perch, the slopes of the log$_{10}$-transformed L_T-M_D regressions did not differ (ANCOVA, d.f. = 817, $P > 0·05$) while the intercept values were all significantly different (ANCOVA, d.f. = 821, $P < 0·05$). With the exception of the January sample, intercept values increased from November to April. During 153 days, a ruffe of a given length gained *c.* 0·05% M_F day^{-1} and finally achieved 107% of its November M_F.

Perch also lost M_D during winter. The slopes of the log$_{10}$-transformed L_T-M_D regressions did not differ (ANCOVA, d.f. = 435, $P > 0·05$) while the intercept values did (ANCOVA, d.f. = 438, $P < 0·05$), decreasing from November to April. During 153 days, a perch of a given length lost *c.* 0·18% M_D day^{-1} and finished with 73% of its November M_D. In contrast to the M_F loss, M_D loss increased during winter from 0·15 to 0·16 to 0·33% day^{-1} for the time intervals 16 November to 10 January to 13 March to 17 April, respectively.

Again, ruffe showed the opposite pattern, gaining M_D during winter. The slopes of the L_T-M_D regressions did not differ (ANCOVA, d.f. = 337, $P > 0·05$) while the intercept values did (ANCOVA, d.f. = 340, $P < 0·05$). Only the November value, however, was significantly lower than those of the other samples, which did not differ from each other. Hence, ruffe gained M_D from 16 November to 10 January at an average rate of 0·125% day^{-1}, and then maintained their M_D more or less constant (−0·025% day^{-1} from 10 January to 13 March, +0·07% day^{-1} from 13 March to 17 April). Overall, a ruffe of a given length had 108% of its November M_D after 153 days.

Perch lost lipid during winter. Both the slopes (ANCOVA, d.f. = 304, $P < 0·05$) and intercepts (ANCOVA, d.f. = 306, $P < 0·05$) of the log$_{10}$-lipid and log$_{10}$-L_T regressions were significantly different among the November, March and April samples. The lipid content of a fish of a given length was therefore calculated separately for each sampling date according to the regression for that particular sample. The percentage lipid loss was higher for the larger individuals (Table IV). After 153 days overwintering, a perch of 80 mm L_T retained 36% of its November lipid content while a perch of 120 mm retained only 27%. The percentage lipid loss was 2·4 to 2·8 times higher than the percentage M_D loss for perch from 80 to 140 mm L_T (Table IV). Ruffe, in contrast, gained lipid during

TABLE IV. Dry mass (M_D) and total lipid content of perch of a given total length (L_T) on three dates (16 November, 13 March and 17 April) in the winter of 1999–2000, and M_D and lipid content in April as a percentage of the November values (% of November)

L_T (mm)	November M_D (g)	November lipid content (mg)	March M_D (g)	March lipid content (mg)	April M_D (g)	April lipid content (mg)	April M_D (% of November)	April lipid content (% of November)
80	1·07	156	0·88	65	0·78	56	73	36
100	2·32	383	1·91	168	1·69	118	73	31
120	4·36	799	3·59	366	3·17	218	73	27
140	7·43	1487	6·12	705	5·4	367	73	25

winter. The slopes of the $\log_{10}$-lipid and $\log_{10}$-L_T regressions did not differ between the November and April samples (ANCOVA, d.f. = 142, $P > 0{\cdot}05$) while the intercepts did (ANCOVA, d.f. = 143, $P < 0{\cdot}05$). Ruffe lipid content increased on average by 0·22% day^{-1}, and at the end of winter had reached 133% of the November value. As lipid content of ruffe was only determined at the start and end of the winter, the time course of lipid accumulation could be determined.

The per cent lipid content in November was significantly related to L_T for both ruffe and perch, while in April this was only true for ruffe (Fig. 1). The slopes of the three regressions did not differ (ANCOVA, d.f. = 259, $P > 0{\cdot}05$) while the intercepts did (ANCOVA, d.f. = 261, $P < 0{\cdot}05$). Perch sampled in November had the highest lipid content (16·4% at 90 mm L_T), followed by ruffe sampled in April (14·4% at 90 mm L_T) and ruffe sampled in November (12·0% at 90 mm L_T). For perch sampled in April, the per cent lipid content in dry matter was not related to L_T (ANOVA, d.f. = 104, $P > 0{\cdot}05$). Thus, at the end of the winter, perch of all sizes had a median lipid content of 6·5% with the 1st percentile = 4·4% and the 9th percentile = 11·6%, *i.e.* the per cent lipid content was skewed to low values.

Relative stomach contents of perch (Table II) differed significantly between months for both age-0 year and older fish (Kruskal–Wallis-test; age-0 year:

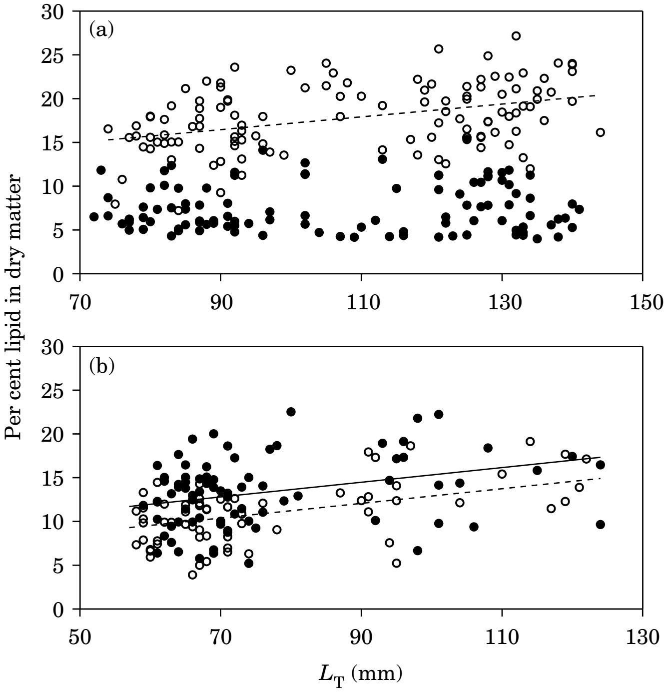

FIG. 1. Percentage lipid content in dry matter and total length of (a) perch ($y = 0{\cdot}07x + 9{\cdot}88$; $n = 118$, $r^2 = 0{\cdot}16$) and (b) ruffe sampled in November 1999 (○, – – –; $y = 0{\cdot}08x + 4{\cdot}52$; $n = 67$, $r^2 = 0{\cdot}28$) and April 2000 (●, ——; $y = 0{\cdot}08x + 6{\cdot}93$; $n = 67$, $r^2 = 0{\cdot}28$) from Lake Constance, Germany. All regressions were significant ($P < 0{\cdot}05$).

d.f. = 3, $P < 0{\cdot}05$; older fish: d.f. = 2, $P < 0{\cdot}05$). The highest values for age-0 year fish were observed in January and March and in November for older fish. In both age-groups, however, fish sampled in November were significantly heavier than those of the other samples (Kruskal–Wallis-test; age-0 year: d.f. = 3, $P < 0{\cdot}05$; older fish: d.f. = 2, $P < 0{\cdot}05$). Relative stomach contents of ruffe (Table II) differed between months for age-0 year fish (Kruskal–Wallis-test; d.f. = 3, $P < 0{\cdot}05$) with higher values in November and April (Nemenyi-test, $P < 0{\cdot}05$). Relative stomach contents for older ruffe did not differ between months (Kruskal–Wallis-test; d.f. = 2, $P > 0{\cdot}05$). Within both age-groups, M_F did not differ with time (Kruskal–Wallis-test; age-0 year: d.f. = 3, $P > 0{\cdot}05$; older fish: d.f. = 2, $P > 0{\cdot}05$). Stomach contents of perch and ruffe were not analysed in detail in this study. From gross inspection of stomachs, however, it was obvious that perch consumed zooplankton almost exclusively while ruffe consumed mainly benthos (chironomid larvae, ostracods, mayfly larvae and turbellarians).

DISCUSSION

Perch did not experience size-selective mortality of smaller individuals during overwintering in the profundal zone of Lake Constance. Yellow perch in Lake St George, Canada (34°57′ N, mean depth 5·7 m) by contrast suffered size-selective mortality (Post & Evans, 1989). In both studies, winter duration (the number of days with mean epilimnetic water temperature $\leq 6^\circ$ C) was nearly identical (153 days in Lake Constance *v.* 154 ± 8 days in Lake St George) and the fishes lived at winter temperatures $<6^\circ$ C in both lakes. Mean ± s.d. fish L_T at the start of winter, however, differed between the two lakes (60·7 ± 4·7 and 71·4 ± 4·1 mm for two cohorts of Lake St George yellow perch *v.* 91·0 ± 9·3 mm for Lake Constance perch). Both yellow perch and perch are very similar in all aspects of their biology (Thorpe, 1977), and thus the model of Post & Evans (1989), which estimates the probability of overwinter starvation mortality as a function of L_T at the start of winter and of winter duration, can be applied to data for perch. For the November sample in the present study, this model estimated a total cohort mortality of only 0·6% after 153 days, while mortality was 76 and 42% for the yellow perch cohorts in Lake St George. Based on the January length distribution of perch in Lake Constance, total cohort mortality after 153 days would be 1·2%. The lack of evidence for size-selective mortality of the Lake Constance perch can therefore be attributed to their larger L_T at the end of the first growing season.

A different explanation for the low mortality rates of overwintering perch has previously been put forward by Radke & Eckmann (1999), who studied perch in a set of small and mainly shallow lakes in northern Germany. They suggested that higher overwinter survival when compared with that of the Lake St George yellow perch was due to food intake by perch during winter. Since these authors did not sample fish for stomach content analyses during winter, their conclusion was not verified. The present study, however, clearly demonstrates that perch ingested food during winter (Table II) even though they were distributed at depths between 40 and 80 m. Even at these depths, light levels in ice-free Lake Constance were obviously sufficient for a visual forager such as perch, while long-lasting and thick ice and snow cover in Canadian lakes set constraints on the foraging ability of yellow perch. It has already been shown by Sullivan (1986) that perch may continue to feed when offered food under simulated winter conditions, and thus maintain their lipid content more or less constant throughout winter. Therefore, feeding during winter can be considered as an additional factor, in addition to large autumn body size, that allowed the Lake Constance perch to overwinter without dying of starvation. For perch in Lough Neagh, feeding during winter is probably even more important as their L_T at the end of the first growing season ranged from 53 to 67 mm (Griffiths & Kirkwood, 1995). When starving, these fish, according to the model of Post & Evans (1989), would suffer even higher mortality than the Lake St George yellow perch, yet there was conflicting evidence for both mortality, following the worst summer, and growth during winter.

Ruffe probably did not experience size-selective mortality during winter either but, unfortunately, the present data did not allow for a rigorous test of size-selective mortality. Quantile-quantile plots of the arbitrarily defined age-0 year length distributions, however, did provide evidence that overwinter mortality is probably as insignificant in ruffe as it is in perch. Additionally, the minimum L_T of the ruffe (55 mm) did not increase from November to April, which further suggests that smaller individuals did not starve to death during winter. Finally, since body condition and lipid reserves of ruffe of all sizes, but not of perch, increased during winter, it is most probable that overwinter mortality in ruffe is even less important than in perch.

Apart from not suffering from starvation mortality during winter, the performance of perch and ruffe was markedly different. Perch lost M_F, M_D and lipid content, while ruffe were heavier at the end of winter and contained more lipid. This might be caused by the different food sources that the two species utilized, mainly zooplankton in the case of perch and mainly zoobenthos (chironomids) in the case of ruffe. Since it is generally accepted that perch and ruffe are potentially strong competitors for food resources (Bergman & Greenberg, 1994; Fullerton *et al.*, 1998) and that ruffe is the superior competitor for zoobenthos (Bergman & Greenberg, 1994), the different food spectra of the two species during winter might result from competition. This is, however, highly unlikely since chironomid biomass did not differ significantly between winter months at 20, 40 and 60 m depth (two-way ANOVA, $P > 0{\cdot}05$, unpubl. data).

An alternative explanation for the use of different food resources by perch and ruffe during winter is based upon the species' sensory capabilities. Perch is a visually oriented forager, and prey consumption decreases strongly with decreasing light intensity (Bergman, 1988). Ruffe on the other hand has a very sensitive lateral line system, particularly in the cephalic region (Disler & Smirnov, 1977; Gray & Best, 1989), which permits them to ingest food even in complete darkness (Bergman, 1988; Janssen, 1997). Ruffe therefore has the potential to consume chironomids in the profundal zone of a deep lake such as Lake Constance during both the day and night. Perch from the winter samples almost never contained chironomids in the digestive tract, which supports the contention that they are far less efficient than ruffe, or perhaps unable, at detecting this type of prey with their lateral line. At the same time, when perch live on, or close to, the bottom (Eckmann & Imbrock, 1996) light intensity during the day was obviously too low for the perch to detect chironomids by vision. With a typical winter attenuation coefficient of $0{\cdot}21\,\text{m}^{-1}$, downwelling light intensity at 60 m depth ranges from 0·3 mlx on overcast days (*c.* 100 lx at the lake surface) to 33 mlx on sunny days (*c.* 10 000 lx at the lake surface). Perch, however, did ingest zooplankton, which might be explained by different optical conditions for feeding in the open water as compared to feeding on the bottom.

The poor overwinter performance of perch, as compared to ruffe, may have profound consequences for their population dynamics. The lipid reserves of the perch were severely depleted by the end of winter, ranging from 36 to 25% of the autumn lipid contents of perch from 80 to 140 mm L_T. For yellow perch, energy density of somatic tissue also declined during winter (Henderson *et al.*, 2000), while in Lough Neagh only small but not larger perch lost lipid overwinter (Griffiths & Kirkwood, 1995). Poor condition and low energy reserves in particular may lead to increased incidence of disease (Wedemeyer *et al.*, 1976). High mortality losses of perch are regularly observed in Lake Constance at the end of the spawning period, which occurs in early May, immediately after the perch have returned from their overwinter habitat to the littoral zone. The severely depleted energy reserves of the perch, together with general spawning stress, may contribute to this elevated postspawning mortality.

Depleted energy stores set constraints on the growth of the perch during the following growing season. While ruffe can for example channel all available energy into somatic growth or reproduction, perch must during the growing season invest part of the available energy in replenishing their energy stores. The lower their lipid content at the end of winter, the more growth will be affected during the following season. Lipid content at the end of winter does not only depend on lipid consumption during winter but also on the amount of lipid deposited during the previous growth season. Lipid deposition depends on food supply during the growth season, which is ultimately controlled by lake production. Thus, the continuing re-oligotrophication of Lake Constance may depress growth rates of perch in two ways: firstly, as a direct consequence of lower food supply during the growing season, and secondly due to the more depleted energy reserves at the end of winter, which must be replenished during the next growing season. If re-oligotrophication continues and food supply decreases further, then ultimately size-selective overwinter mortality may occur due to reduced somatic growth of perch during their first growing season.

The prospects for ruffe populations in lakes of decreasing nutrient content are less obvious. Ruffe abundance generally increases with lake productivity, while ruffe are rare or even completely absent from oligotrophic lakes (Leach *et al.*, 1977; Bergman, 1991). The present data on overwinter performance support previous findings that ruffe are less affected by low temperature and light levels than perch. Additionally, since ruffe is able to grow during winter and even to accumulate lipid, reduced food supply during the growing season should probably be less detrimental for ruffe than perch. As long as food supply during winter remains high enough, so that ruffe can make use of their sensory and physiological capabilities, ruffe populations will probably decline at a slower rate than perch populations during the re-oligotrophication of lakes. When lake re-oligotrophication proceeds further, food supply might become a limiting factor for growth, energy accumulation and reproductive output even for ruffe.

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