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The interactions of abiotic and biotic factors influencing perch *Perca fluviatilis* and roach *Rutilus rutilus* populations in small acidified boreal lakes

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Four small, acidified boreal lakes, all sustaining populations of perch *Perca fluviatilis*, roach *Rutilus rutilus* and pike *Esox lucius*, were studied in four successive years. Three lakes were moderately acidified (mean pH of 5.61–5.83), while the fourth was more acidic (mean pH of 5.16) and had a sparse population of *R. rutilus*. *Perca fluviatilis* density was higher in this lake (1004 ha⁻¹) than in the other three (355–717 ha⁻¹), where *R. rutilus* dominated in terms of numbers (981–2185 ha⁻¹). Large, potentially predatory, *P. fluviatilis* were most abundant in the lake with clearest water, and these seemed to have a negative effect on *P. fluviatilis* density. *Perca fluviatilis* mean mass was negatively correlated with *R. rutilus* biomass and was highest in the most acidic lake with the sparse *R. rutilus* and the highest *P. fluviatilis* density. *Perca fluviatilis* mass correlated positively with pH in two lakes (with the highest fish biomass), suggesting that low pH affected *P. fluviatilis* mass negatively. *Perca fluviatilis* growth correlated positively with summer (July to August) air temperature in the lake with sparse *R. rutilus*, thus differing from *P. fluviatilis* and *R. rutilus* growth in the other three lakes. The mean age of *P. fluviatilis* was generally lower than that of *R. rutilus* and was lowest in the two lakes with the highest fish biomass, indicating that adult mortality was affected by density-induced factors.

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INTRODUCTION

Acidification accompanied by low pH and elevated concentrations of inorganic aluminium (Al-i) impoverishes fish populations (Driscoll *et al.*, 1980; Rosseland *et al.*, 1980). In Fennoscandian waters, several thousand fish populations have become extinct due to water quality degradation during recent decades (Tammi *et al.*, 2003). Perch *Perca fluviatilis* L. 1758 and roach *Rutilus rutilus* (L. 1758) are widespread and often abundant species in boreal Fennoscandian lakes, where their relative abundance and ecological relationships are likely to be affected by acidification (Tammi *et al.*,

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2003). Evidence of the effects of acidification on fish populations takes two different forms; recruitment failure or high adult mortality. Recruitment failure, due to high mortality during early life stages, results in the dominance of older individuals (Muniz & Leivestad, 1980; Rosseland *et al.*, 1980; Muniz, 1990), while high adult mortality results in fish populations that lack old individuals (Cleveland *et al.*, 1991; Hesthagen *et al.*, 1992). Low pH may also affect fish growth negatively (Linløkken *et al.*, 2008).

Inter or intraspecific competition due to resource limitation causing slow growth is often referred to as stunting and has been documented in several studies of both *P. fluviatilis* (Alm, 1946; LeCren, 1958; Rask, 1983; Ridgway & Chapleau, 1994) and *R. rutilus* (Burrough & Kennedy, 1979; Linfield, 1980). Recruitment failure or high adult mortality due to acidification leads to reduced density, which may in turn result in increased growth and mass (Rask, 1983; Raitaniemi *et al.*, 1988). In both *P. fluviatilis* and *R. rutilus*, recruitment failure is the most visible response to acidification, and while the lower limit (during incubation) of *P. fluviatilis* recruitment is around pH 5.0 and Al concentrations of $60 \mu\text{g l}^{-1}$ (Milbrink & Johansson, 1975; Runn *et al.*, 1977; Rask *et al.*, 1995; Hesthagen *et al.*, 2001), *R. rutilus* recruitment fails at $\text{pH} \leq 5.5$ (Milbrink & Johansson, 1975; Keinänen *et al.*, 2000). Acidification may thus reduce or even remove *R. rutilus* in lakes in which *P. fluviatilis* still persist (Tammi *et al.*, 2003; Linløkken *et al.*, 2008; Olin *et al.*, 2010).

In the interspecific relationship between these two species, *R. rutilus* usually dominate in terms of both numbers and biomass in eutrophic waters (Svärdson, 1977; Persson *et al.*, 1991; Olin *et al.*, 2002). This dominance has been explained by a greater ability to utilize available resources, as evidenced by their feeding on detritus (Niederholzer & Hofer, 1980; Rask, 1989; Horppila *et al.*, 2000), and being a more effective zooplanktivore (Lessmark, 1984; Persson, 1987), especially in highly coloured water (Estlander *et al.*, 2010). Reduced competition due to biomass removal of these species has been shown to increase feeding niche widths for both species (Syväranta & Jones, 2008) and to increase growth (Linløkken & Seeland, 1996).

Perca fluviatilis growth has also been found to be positively correlated with air and water temperature (LeCren, 1958; Neuman, 1976; Tolonen *et al.*, 2003). Growth in *R. rutilus* has also been shown to correlate with water temperature in a subalpine lake in Switzerland, where *R. rutilus* and whitefish *Coregonus lavaretus* (L. 1758) dominate, and populations of other cyprinids and *P. fluviatilis* are sparse (Müller & Meng, 1986). To summarize, density, species composition, pH and temperature are all factors that can affect fish growth, and pH may also affect growth indirectly through its effects on recruitment and mortality.

This study was performed in four small acidified boreal lakes, with somewhat different water qualities, all harbouring *P. fluviatilis*, *R. rutilus* and pike *Esox lucius* L. 1758. Effects of environmental factors, and a biotic factor, abundance of predators, on density of *P. fluviatilis* and *R. rutilus* were explored, as well as effects of these factors on *P. fluviatilis* and *R. rutilus* growth. It was hypothesized that the environmental factors affect the abundance, size and age structure of *P. fluviatilis* and *R. rutilus* differently due to differences in tolerance of acidity. A reduction or extinction of the species that is more vulnerable to acidification might benefit the tolerant species if competition exists.

TABLE I. Physical characters of the survey lakes in south-eastern Norway

	Urstjern	Langtjern	Veslevatn	Smedstadtjern
Area (ha)	15.5	10.7	21.0	11.8
Altitude (m a.s.l.)	246	246	254	164
Mean depth (m)	4.9	5.1	7.3	13.9
Area of lake <5 m deep (%)	50	55	45	20
Maximum depth (m)	12	12	16	28
Secchi depth (m)	1.8	2.8–3.0	2.5	3.8
Catchment area (km ²)	13.0	0.93	5.2	1.13
Retention time (years)	0.12	1.2	0.6	2.9

MATERIALS AND METHODS

STUDY AREA

The study lakes are situated between 164 and 254 m a.s.l. in south-eastern Norway (60° 9'–11' N; 12° 10'–12' E), in a coniferous forest area on moraines with patches of rocks, boulders and bogland. They are all small lakes of between 10.7 and 21.0 ha in area, and three of them are relatively shallow; 12–16 m deep, while one (Smedstadtjern) is deeper, with a maximum depth of 28 m (Table I).

SAMPLING

The study was carried out in four successive years, from 1998 to 2001. Fishes were sampled on four occasions from May to September at depths of 0–5 and >5 m each year. The survey used two types of benthic nets; multimesh Nordic survey nets (30 m × 1.5 m) with mesh-sizes of 5.0, 6.5, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0 and 55.0 mm (Appelberg *et al.*, 1995), and single-mesh nets (25 m × 1.5 m) with mesh sizes of 10.0, 12.5, 16.5, 19.5 and 24.0 mm. The annual fishing effort with benthic nets was three to six Nordic nets and two single-mesh series at <5 m depth, and three Nordic nets and one single-mesh series at >5 m, except for the omission of Smedstadtjern in 2001 (due to limited resources). Pelagic multimesh Nordic survey nets (4 m deep and 30 m long) were used in all lakes in August 2000 to compare species composition in benthic and pelagic habitats. The nets were hauled between 0800 and 1000 hours, and catch per unit effort (CPUE) was calculated as number of fishes caught 100 m⁻² net area during one night of sampling. All fishes caught in gillnets were weighed to the nearest 0.1 g and measured to nearest 1 mm from the tip of the snout to the posterior end of the caudal fin in its natural position (L_T). All *P. fluviatilis* were sexed, but this was difficult in *R. rutilus* after spawning, so sexes were pooled. Otoliths of both species were collected for age determination, and opercular bones were also taken from *P. fluviatilis* and scales from *R. rutilus*. Water samples were taken in spring and autumn and on two occasions during the summer at 0.5 m depth, >20 m from shore and stored in 0.5 l PVC bottles at 4°C until they were analysed for pH, alkalinity, conductivity, Al, calcium and water colour. In August, water temperature and oxygen were recorded by means of a Hydrolab Multiparameter Water Quality Monitoring Instrument (Hydrolab Corporation; <http://www.hydrolab.com/>), at depths of 1, 3, 5, 7 and 10 m in three lakes, and in the deepest lake (Smedstadtjern) also at 15, 20 and 26 m depth.

Population estimates were obtained by means of mark–recapture experiments. *Perca fluviatilis* were caught in wire traps with mesh-size 12.5 mm during the spawning season (second and third week of May) from 1998 to 2001, while *R. rutilus* were caught by angling (hook size 12, barbless) in June to early July from 1998 to 2000. Only small *P. fluviatilis* ($L_T \leq 20$ cm) were trapped and marked, while large specimens ($L_T > 20$ cm) were only caught in the gill-nets. Marking was done by fin-clipping (pelvic fins). The fins regenerated during the first summer, but could be detected the following year by their ruptured fin rays. Left fins were

clipped the first year, and right fins were clipped the following year, while the left pelvic fins were clipped again in the third year. Recapture was done by gillnetting in June to September.

CALCULATIONS AND ANALYSIS

Population sizes (N) were estimated according to Petersen's adjusted mark-recapture method (Ricker, 1975): $N = (H + 1)(C + 1)(R + 1)^{-1}$, where H is number of fish marked, C is number of fish (≥ 3 years) captured during gillnetting following the marking and R is number of recaptures. To avoid biased population estimates, it has been recommended that $HC > 4N$ (Robson & Regier, 1964), a condition that was always met in the study. Biomass was calculated from mean values of density and masses (of annual means) in the total gillnet catches of ≥ 3 year-old specimens of both species in each lake. Age determination of both *P. fluviatilis* and *R. rutilus* was based on otoliths, which were burned and annuli read on the cross-section (Christensen, 1964; Beamish & McFarlane, 2000; Peltonen *et al.*, 2002).

Growth analyses were based on fishes caught in May and June, *i.e.* before the growth season, except for large *P. fluviatilis*, which were pooled for all periods and lakes, due to the low numbers taken. Backcalculation of growth rates was based on opercula in *P. fluviatilis* (LeCren, 1947) and scales in *R. rutilus* (Horppila & Nyberg, 1999). Growth was described as the annual mean of age-specific growth rates (G_x), calculated as the natural logarithm of the relationship between individual mass at age x (M_x) and the backcalculated mass at age $x - 1$ (M_{x-1}): $G_x = \ln(M_x M_{x-1}^{-1})$. For large *P. fluviatilis*, means of age-specific M_x and G_x were based on backcalculation for all previous years of each specimen.

STATISTICS

The effects of environmental factors [littoral fraction (F_L)], (p_H) and water colour (C_W) and fraction of large *P. fluviatilis* (L_P) on density of *P. fluviatilis* (D_P) and *R. rutilus* (D_R) were explored by means of linear models, using the R-programme (<http://cran.uib.no/>; Crawley, 2007): $D = a + bx + e$, where a and b were the coefficients under estimation, x was added as F_L , p_H , C_W one by one, and e is the error, which was assumed to be normally distributed. Effects of the same environmental factors, as well as the density and biomass of *P. fluviatilis* and *R. rutilus* (D_P , B_P , D_R and B_R , respectively), on total mean mass (M) of each species were explored similarly with M_P and M_R as response variables: $M = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + e$, where β_i were the coefficients to be estimated, and the predictors x_i are p_H , C_W , L_P , D_P , B_P , D_R and B_R , added stepwise by forward selection; at each step, each variable that was not already in the model was tested for inclusion in the model, and the most significant ($P < 0.05\%$) of these variables was added to the model, step by step (Blanchet *et al.*, 2008). With only four lakes, a maximum of two predictors was fitted into one model. The best model was chosen as the one that gave the lowest AIC value (Crawley, 2007).

Mean age (A) of *P. fluviatilis* (A_P) and *R. rutilus* (A_R) were compared between lakes and years by ANOVA, with $\ln(A)$ as response variable and lake, year, the lake \times year interaction, and for *P. fluviatilis*, also sex, as fixed factors. Mass (M_P , M_R) and growth (G_P , G_R) were compared by ANCOVA (Crawley, 2007) with $\ln(M)$ and $\ln(G)$, respectively, as response variables and lake, year, sex (for *P. fluviatilis*) as fixed factors and A as covariate (continuous). Ln transformations were used to ensure linearity, and Tukey's significant difference test (Tukey HSD; Crawley, 2007) was performed for pair-wise comparison of lakes and years. The analysis were based on age-specific M and G of age groups 2–5 years, averaged for each lake and year (groups of fewer than five specimens were omitted) in order to avoid pseudoreplication. Significant variations between years were further explored for each lake by fitting linear models to A , p_H and air temperature means (T_i , $i = \text{June, July, August, June to August and July to August means}$). Air temperatures were based on measurements at the Vinger Meteorological Station, located 5 to 10 km from the study lakes: $\ln(Y) = \beta_0 + \beta_1 A + \beta_2 F + \beta_3 p_H + \beta_4 T_i + e$, where Y is M and G , F (female) is a categorical predictor, and the others are continuous, added stepwise by forward selection. When a multiple model was found the best, the coefficient of explanation (R^2) and AIC (AIC multiple) were compared to those of the best model with only one predictor (r^2 and AIC simple).

TABLE II. Some water quality variables from the study lakes in south-eastern Norway given as mean \pm 95% c.i.

Variable	Urstjern		Langtjern		Veslevatn	Smedstadtjern
	1997–2001	1997–1999	2000–01*	1997–2001	1997–2000	1997–2000
pH	5.16 \pm 0.32	5.72 \pm 0.38	6.09 \pm 0.13	5.61 \pm 0.29	5.83 \pm 0.25	
Alkalinity ($\mu\text{ekv l}^{-1}$)	22 \pm 15	53 \pm 22	65 \pm 21	36 \pm 18	50 \pm 16	
Conductivity (mS m^{-1})	2.3 \pm 0.2	2.6 \pm 0.4	2.4 \pm 0.3	2.6 \pm 0.2	2.8 \pm 0.5	
Inorganic Al ($\mu\text{g l}^{-1}$)	50 \pm 27	11 \pm 6	8 \pm 10	11 \pm 9	7 \pm 6	
Ca (mg l^{-1})	1.2 \pm 0.2	1.6 \pm 0.2	2.0 \pm 0.4	1.6 \pm 0.2	1.8 \pm 0.2	
Colour (mg Pt l^{-1})	101 \pm 37	70 \pm 25	65 \pm 14	73 \pm 16	28 \pm 9	

*Four tonnes limestone powder added in March 2000 and 4.5 t in September 2000.

RESULTS

ENVIRONMENTAL FACTORS

The lakes were moderately acidified, with mean values of pH and concentrations of Al ranging from 5.16 to 5.83 and from 7 to 50 $\mu\text{g l}^{-1}$, respectively (Table II). Temporal variations in pH and Al showed that pH dropped and Al increased in spring (Fig. 1). In the most acidic lake (Urstjern), pH was significantly lower than in the other lakes (ANOVA and Tukey HSD, to all three lakes $P < 0.001$), seldom exceeding 5.5, while Al frequently exceeded 50 $\mu\text{g l}^{-1}$. In the least acidic lake (Smedstadtjern), pH never dropped < 5.5 . One lake (Langtjern) was limed by adding 4 t limestone powder in spring and 4.5 t in autumn 2000, after which mean pH rose significantly (t -test, d.f. = 17, $P < 0.001$) from 5.72 to 6.09.

The lakes displayed low productivity with conductivities ranging from 2.3 to 2.8 mS m^{-1} , and calcium concentrations ranging from 1.2 to 2.0 mg l^{-1} . Three of the lakes were relatively humic, with a water colour of 70–101 mg Pt l^{-1} . The least acidic and deepest lake (Smedstadtjern) was an exception, with a water colour of only 28 Pt l^{-1} .

Water temperature, measured at a depth of 0.5 m (at 0800–1000 hours) correlated positively with air temperature at the Vinger Meteorological Station; for Urstjern ($r^2_{\text{adj}} = 0.47$, d.f. = 14, $P < 0.01$), Langtjern ($r^2_{\text{adj}} = 0.63$, d.f. = 14, $P < 0.01$), Veslevatn ($r^2_{\text{adj}} = 0.38$, d.f. = 12, $P < 0.01$) and Smedstadtjern ($r^2_{\text{adj}} = 0.52$, d.f. = 14, $P < 0.01$). Summer temperature ranged from 14 to 25°C in the epilimnion, and the metalimnion occurred at 4–7 m depth (Fig. 2). Oxygen was depleted ($< 6 \text{ mg l}^{-1}$) at 0–5 m depth below the metalimnion, except in the deepest lake (Smedstadtjern), where oxygen concentration was $> 6 \text{ mg l}^{-1}$ down to 20 m.

SPATIAL DISTRIBUTION

Benthic Nordic multimesh gillnets caught *P. fluviatilis* and *R. rutilus* at depths of 0–5 m, *i.e.* mainly in the epibenthic zone (Fig. 3), but caught no fishes at greater depth. *Rutilus rutilus* outnumbered *P. fluviatilis* in the benthic catches in two lakes (Langtjern and Veslevatn), while in the most acidic lake (Urstjern), only 11 *R. rutilus* were caught, comprising 1.4% of the benthic catches. Catches in pelagic nets at

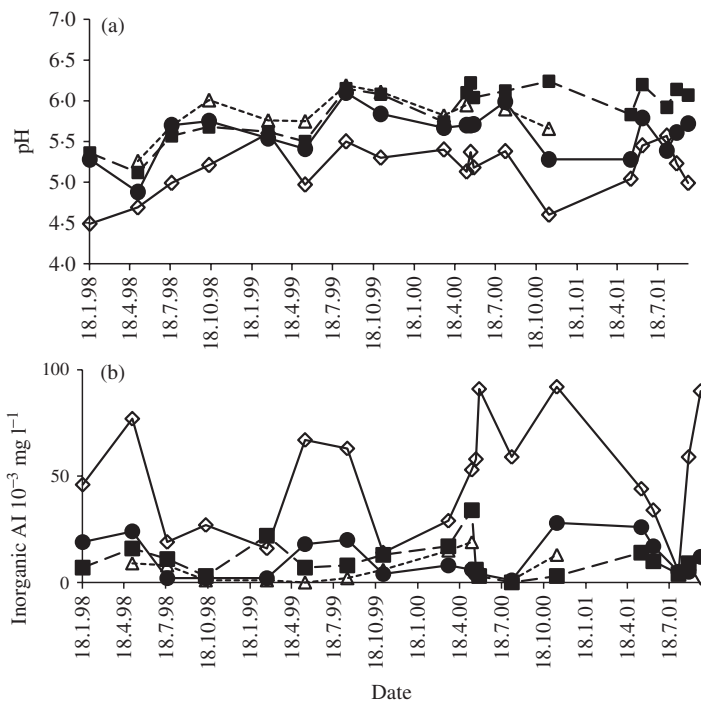


FIG. 1. Variation in (a) pH and (b) concentration of inorganic Al in the four study lakes (\diamond -, Urstjern; \blacksquare -, Langtjern; \bullet -, Veslevatn; \triangle -, Smedstادتjern) in south-eastern Norway during the study period.

0–4 m depth in August 2000 showed that *R. rutilus* were predominant, and pelagic catches of *P. fluviatilis* were low even in the lake with low catches of *R. rutilus*. Pelagic nets at 4–8 m caught no fishes. In addition to *P. fluviatilis* and *R. rutilus*, three to six *E. lucius* were caught in benthic nets in each lake.

DENSITY AND MASS VARIATION BETWEEN LAKES

The *P. fluviatilis* populations consisted of both small (≤ 20 cm, of which $>98\%$ had $L_T < 17$ cm) and large ($L_T > 20$ cm, presumably predatory) specimens. The mean densities of small *P. fluviatilis* and *R. rutilus* aged ≥ 3 years ranged from 355 to 1004 and from 14 to 2185 specimens ha^{-1} , respectively (Table III). In the most acidic lake (Urstjern), *R. rutilus* abundance was calculated on the basis of mean *P. fluviatilis* density (1004 ha^{-1} ; Table III) and fraction of *R. rutilus* in the benthic gillnet catches, $1004(1.4\% R. rutilus/98.6\% P. fluviatilis) \text{ha}^{-1}$, as it was not possible to catch sufficient *R. rutilus* for marking. Density estimates of each species and lake were not significantly different between years as the annual estimates were within each other's 95% C.I., and thus further analyses were based on lake-wise means. Fishing mortality of the small *P. fluviatilis* and *R. rutilus* due to the sampling comprised 154–731 *P. fluviatilis* and 161–1204 *R. rutilus* annually in each lake, *i.e.* $\leq 4.7\%$ of the estimated stocks. The fishing mortality due to other kinds of exploitation was negligible in all lakes.

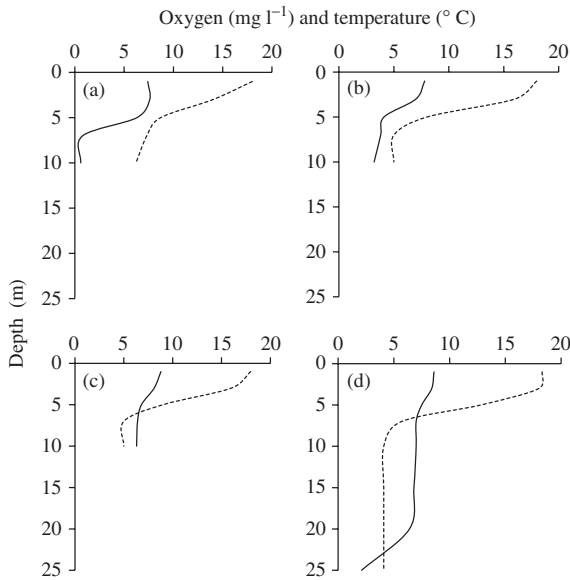


FIG. 2. Vertical distribution of oxygen concentration (—) and temperature (....) in mid-August 2000 in (a) Urstjern, (b) Langtjern, (c) Veslevatn and (d) Smedstadtjern in south-eastern Norway.

A total of 28 large *P. fluviatilis* were caught, all of them in benthic gillnets, and all females. The fraction by mass (of total *P. fluviatilis* catches) of large *P. fluviatilis* (L_P) varied widely between lakes and was lowest in the lake with the sparse *R. rutilus*

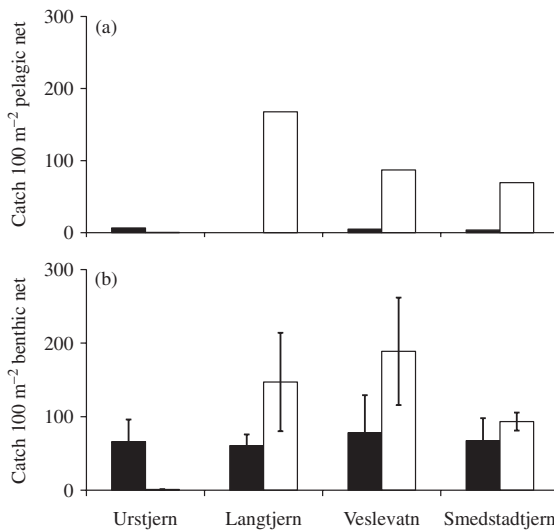


FIG. 3. Number of *Perca fluviatilis* (■) and *Rutilus rutilus* (□) (a) caught per unit effort in pelagic nets in August 2000 and (b) mean \pm s.e. number caught per unit effort in the benthic nets in June to August 1998 to 2000 in the study lakes in south-eastern Norway.

TABLE III. Annual and mean population density (number ha⁻¹) estimates ($\pm 95\%$ c.i.) and mean biomass (kg ha⁻¹) of *Perca fluviatilis* and *Rutilus rutilus* in the study lakes in south-eastern Norway

	Year	Lake		
		Urstjern	Langtjern	Veslevatn
<i>P. fluviatilis</i>	1998	—	724 (432–2225)	898 (481–6750)
	1999	930 (620–1863)	502 (374–759)	764 (560–1201)
	2000	1064 (734–1938)	550 (380–990)	626 (403–1399)
	2001	1017 (636–2542)	748 (514–1369)	575 (377–1211)
	Mean	1004 (927–1081)	631 (510–752)	716 (573–858)
	Biomass	33 (31–36)	15 (12–18)	13 (11–16)
<i>R. rutilus</i>	1998	—	1 428 (775–2634)	2 160 (1045–4477)
	1999	—	1 555 (995–2431)	1 147 (725–1814)
	2000	—	1 185 (825–1702)	1 645 (997–2717)
	Mean	14*	1389 (1177–1602)	2185 (1560–2810)
	Biomass	0.7	28 (24–32)	43 (31–55)
				357 (254–598)
				440 (328–670)
				269 (183–505)
				—
				355 (259–452)
				8 (6–10)
				865 (505–1482)
				1 147 (725–1814)
				931 (397–2196)
				981 (814–1148)
				33 (27–38)

—, no data.

*Estimate based on *P. fluviatilis* density and *R. rutilus* fraction in gillnet catches.

TABLE IV. Two linear models with *Perca fluviatilis* density (D_P) as response variable and fraction of large *P. fluviatilis* (L_P), and water colour (C_W) as predictor variables, a model with L_P as response variable with water colour as predictor and models with mean mass of *P. fluviatilis* and *Rutilus rutilus* (M_P and M_R , respectively) as response variables and *R. rutilus* biomass (B_R), ln transformed *P. fluviatilis* biomass (B_P) and fraction of littoral zone (F_L) as predictor variables (values in parentheses are \pm s.e.). Only significant ($P < 0.05$) models are given

Model parameters (\pm s.e.)	r^2	d.f.	P	AIC
$D_P = -10.4 (\pm 1.0)L_P + 1007.5 (\pm 38.9)$	0.98	2	<0.01	44.1
$D_P = 8.8 (\pm 1.1)C_W + 79.4 (\pm 80.4)$	0.97	2	<0.05	47.0
$L_P = -0.84 (\pm 0.11)C_W + 88.59 (\pm 8.36)$	0.96	2	<0.05	28.9
$M_P = -0.35 (\pm 0.03)B_R + 33.47 (\pm 0.93)$	0.98	2	<0.01	16.8
$M_R = 1.71 (\pm 0.06) \ln B_P - 0.75 (\pm 0.05) \ln F_L + 33.82 (\pm 1.68)$	0.99	2	<0.05	13.9

($n = 3$, Urstjern) with 3% of the total *P. fluviatilis* catches, rising to 23% ($n = 7$, Veslevatn), 37% ($n = 8$, Langtjern) and 64% ($n = 10$, Smedstادتjern). L_P correlated negatively with water colour (Table IV). D_P (small specimens) correlated negatively with L_P and positively with C_W (Table IV), and L_P as predictor gave the best-fit (lowest AIC) model for D_P , while for D_R , no significant model was found. Total mean M_P was negatively related to B_R (Table IV; $F_{1,2} = 126.2$, $P < 0.01$), and M_R was significantly positively correlated with $\ln B_P$ ($F_{1,1} = 153.3$, $P < 0.05$) and barely non-significantly negatively correlated to $\ln F_L$ ($F_{1,1} = 113.5$, $P > 0.05$).

MEAN AGE BY SPECIES, LAKE AND YEAR

Mean A_P (small specimens) ranged from 3.13 to 4.76 years (Table V), and $\ln A_P$ was significantly different between lakes (ANOVA, $F_{3,1144} = 34.87$, $P < 0.001$), between years ($F_{3,1144} = 2.62$, $P < 0.05$) and between sexes ($F_{1,1144} = 6.7$, $P < 0.01$, females grew older). The lake \times year interaction was significant ($F_{8,1144} = 6.39$, $P < 0.001$), reflecting the fact that the annual variation differed between lakes. In the pooled samples of large *P. fluviatilis*, age ranged from 5 to 21 years, with a mean \pm s.e. of 9.8 ± 0.7 years. The mean A_P was highest in the two lakes with lowest total fish density and biomass (Urstjern and Smedstادتjern), and the lowest and highest pH, respectively. Multiple comparisons (Tukey HSD) revealed that $\ln A_P$ was significantly higher in Urstjern and Smedstادتjern than in Langtjern (both $P < 0.001$) and Veslevatn (both $P < 0.001$), while there was no significant difference between Langtjern-Veslevatn ($P > 0.05$), nor between Urstjern-Smedstادتjern ($P > 0.05$).

In the clear-water lake, with the highest L_P (Smedstادتjern 1998), $\ln A_P$ was lower in 2000 than in 1998 and 1999 (Tukey, both $P < 0.05$), due to an increased proportion of 2 and 3 year-old specimens (Fig. 4). No differences between years were found in the other lakes, however (Tukey HSD, $P > 0.05$).

Mean A_R ranged from 4.67 to 7.71 years and was significantly higher than mean A_P (t -test, d.f. = 2203, $P < 0.001$). $\ln A_R$ was significantly different between years ($F_{3,740} = 4.43$, $P < 0.01$) but not between lakes ($P > 0.05$). The lake \times year

TABLE V. Mean age of *Perca fluviatilis* and *Rutilus rutilus* from the four study lakes in south-eastern Norway during the four study years

Lake	Year	<i>Perca fluviatilis</i>			<i>Rutilus rutilus</i>		
		Mean age (years)	<i>n</i>	S.E.	Mean age (years)	<i>n</i>	S.E.
Urstjern	1998	4.30	84	0.17	5.00	2	1.57
	1999	4.03	181	0.21	5.00	2	2.22
	2000	3.87	85	0.24	7.71	7	1.78
	2001	3.89	71	0.25	6.00	1	2.72
Langtjern	1998	3.13	102	0.17	5.85	96	0.27
	1999	3.40	84	0.25	6.23	83	0.39
	2000	3.68	71	0.26	6.30	40	0.53
	2001	3.43	96	0.24	4.67	51	0.45
Veslevatn	1998	3.17	109	0.13	6.18	83	0.28
	1999	3.16	54	0.23	6.17	50	0.48
	2000	2.91	176	0.17	6.23	91	0.38
	2001	2.86	104	0.19	5.91	115	0.36
Smedstadtjern	1998	4.53	73	0.22	7.21	38	0.53
	1999	4.76	87	0.29	5.92	36	0.70
	2000	3.59	75	0.30	5.58	85	0.61

n, number of specimens in the sample.

interaction was significant ($F_{8,740} = 2.39$, $P < 0.05$), reflecting the fact that annual variation was different between lakes, which was due to a drop in mean A_R from 1998 to 2000 in the clear-water lake (Smedstadtjern) caused by an increased proportion of 2 year-old *R. rutilus* (Tukey HSD, $P < 0.01$) in 2000 (as for *P. fluviatilis*; Fig. 4).

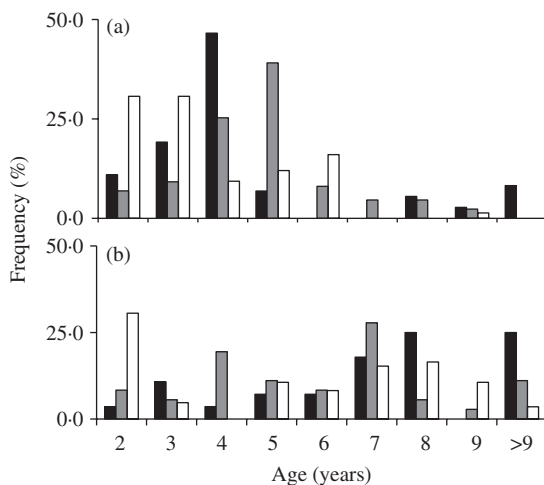


FIG. 4. Age structure in annual samples of (a) *Perca fluviatilis* and (b) *Rutilus rutilus* from the lake with highest abundance of large *P. fluviatilis* (Smedstadtjern) in 1998 (■), 1999 (■) and 2000 (□). Number of specimens in the samples are given in Table V.

MASS AND GROWTH VARIATION BETWEEN YEARS

$\ln M_P$ was significantly affected by A (ANCOVA, $F_{1,91} = 250.7$, $P < 0.001$) and differed significantly between sexes ($F_{1,91} = 26.7$, $P < 0.001$), between lakes ($F_{3,91} = 25.1$, $P < 0.001$) and between years ($F_{3,91} = 19.4$, $P < 0.001$). The lake \times year interaction was significant ($F_{8,91} = 3.3$, $P < 0.01$), reflecting the fact that annual variation was different between lakes. A explained most of variation in $\ln M_P$ in all lakes ($r^2 = 0.48\text{--}0.85$, $F_{1,18-27} = 32\text{--}192$, $P < 0.05$), and females were larger on average than males in all lakes ($r^2 = 0.02\text{--}0.16$, $F_{1,20} = 5.08\text{--}9.98$, $P < 0.05$), except in one lake (Veslevatn), where the difference between the sexes was insignificant ($P > 0.05$; Table VI). In two lakes, p_H had a positive effect on $\ln M_P$, explaining 11 and 20% of variation (Langtjern $r^2 = 0.11$, $F_{1,20} = 15.3$, $P < 0.001$, Veslevatn $r^2 = 0.20$, $F_{1,20} = 12.5$, $P < 0.001$).

$\ln G_P$ was negatively affected by A (ANCOVA; $F_{1,88} = 550.9$, $P < 0.001$) and differed significantly between sexes ($F_{1,88} = 6.3$, $P < 0.05$), and between lakes ($F_{3,88} = 4.3$, $P < 0.01$) and years ($F_{3,88} = 7.0$, $P < 0.001$). The lake \times year interaction was significant ($F_{8,88} = 2.1$, $P < 0.05$), reflecting the fact that the annual variation was different between lakes. Analysis of each lake separately revealed that $\ln G_P$ was significantly different between years in the lake with a sparse *R. rutilus* population (Urstjern, $F_{3,25} = 10.8$, $P < 0.001$), different from the other lakes ($P > 0.05$), and the linear models revealed that it was positively correlated with mean air temperature in July ($r^2 = 0.06$, $F_{1,27} = 14.7$, $P < 0.05$), August ($r^2 = 0.09$, $F_{1,27} = 29.9$, $P < 0.01$) and July to August ($r^2 = 0.08$, $F_{1,27} = 24.4$, $P < 0.01$) and negatively affected by A ($r^2 = 0.71$, $F_{1,27} = 278\text{--}342$, $P < 0.001$) in all three models (August and July air temperature intercorrelated; $r^2 = 0.89$, d.f. = 27, $P < 0.001$). The three models had the same coefficient for A (-0.41) while the coefficient for $T_{\text{Jul-Aug}}$ differed slightly from those for T_{Jul} and T_{Aug} (0.08 compared with 0.07) and the intercepts varied from -0.14 to -0.25 . August air temperature gave the second lowest AIC and the highest coefficient of explanation. $\ln G_P$ in the other lakes was negatively affected by A , but not significantly affected by p_H or air temperature in any period tested for ($P > 0.05$). The model for mass of large *P. fluviatilis* ($\ln M_{LP}$) was similar to that of the small conspecifics, but the model of growth $\ln G_{LP}$, had a shallower slope for large than that for small specimens (-0.13 compared to -0.41 to -0.52) reflecting that large specimens grew faster as adults than the small ones. Mean G at $A = 5$, when all were mature, is according to the models $0.24\text{--}0.28$ for the small, and more than twice as high (0.66) for L_P .

$\ln M_R$ was also significantly affected by A (ANCOVA, $F_{1,29} = 106.77$, $P < 0.001$) and significantly different between lakes ($F_{2,29} = 9.18$, $P < 0.001$), but not between years ($P > 0.05$). $\ln G_R$ was significantly affected only by A ($F_{1,29} = 106.77$, $P < 0.001$), not by lake or year, and there was thus no significant effect of p_H or air temperature, either on $\ln M_R$ or on $\ln G_R$ in any of the lakes ($P > 0.05$).

DISCUSSION

Perca fluviatilis and *R. rutilus* were both abundant in the epibenthic zone, and *R. rutilus* was also abundant in epilimnion in the pelagic habitat. *Rutilus rutilus* may display a more pelagic life style than *P. fluviatilis* (Bergman, 1990; Järvalt *et al.*, 2005; Prchalova *et al.*, 2008) and thus have more space available than *P. fluviatilis*.

TABLE VI. Linear models for mass (M) and growth (G) of *Perca fluviatilis* (P), large *P. fluviatilis* (L_p) pooled for all lakes, and *Rutilus rutilus* (R) with age (A), sex (female, F), pH (P_H) and mean air temperature in July (T_{Jul}), August (T_{Aug}) and July to August ($T_{Jul-Aug}$) as predictors (values in parentheses are \pm s.e.). Only significant models are given as are r^2 for simple and R^2 for multiple regressions

Lake	Model	R^2/r^2	d.f.	P	AIC
Urstjern	$\ln M_P = 0.43 (\pm 0.03) A + 0.16 (\pm 0.07) F + 1.46 (\pm 0.13)$	0.85/0.84	22	<0.001	-9.7/-6.6
Langtjern	$\ln M_P = 0.38 \pm 0.04 \cdot A + 0.25 (\pm 0.08) F + 0.59 (\pm 0.15) p_H - 1.97 (\pm 0.91)$	0.86/0.68	20	<0.001	-5.0/14.0
Veslevatn	$\ln M_P = 0.23 \pm 0.04 \cdot A + 0.98 (\pm 0.28) p_H - 3.99 (\pm 1.65)$	0.65/0.46	19	<0.001	1.6/12.1
Smedstadjern	$\ln M_P = 0.21 (\pm 0.06) A + 0.28 (\pm 0.12) F + 1.98 (\pm 0.22)$	0.73/0.30	18	<0.01	14.2/17.4
Pooled	$\ln M_{L_p} = 0.42 (\pm 0.04) A + 1.48 (\pm 0.34)$	0.91	9	<0.001	17.9
Urstjern	$\ln G_P = -0.41 (\pm 0.05) A + 0.07 (\pm 0.03) T_{Jul} - 0.22 (\pm 0.47)$	0.74/0.70	22	<0.001	5.1/14.5
	$\ln G_P = -0.41 (\pm 0.04) A + 0.07 (\pm 0.02) T_{Aug} - 0.14 (\pm 0.33)$	0.78/0.70	22	<0.001	5.5/14.5
	$\ln G_P = -0.41 (\pm 0.04) A + 0.08 (\pm 0.02) T_{Jul-Aug} - 0.25 (\pm 0.39)$	0.77/0.70	22	<0.001	7.3/14.5
Langtjern	$\ln G_P = -0.50 (\pm 0.05) A + 1.07 (\pm 0.19)$	0.77	20	<0.001	16.0
Veslevatn	$\ln G_P = -0.52 (\pm 0.06) A + 1.26 (\pm 0.19)$	0.78	23	<0.001	13.8
Smedstadjern	$\ln G_P = -0.50 (\pm 0.05) A + 1.21 (\pm 0.18)$	0.82	21	<0.001	7.3
Pooled	$\ln G_{L_p} = -0.13 (\pm 0.03) A + 0.24 (\pm 0.19)$	0.66	9	<0.01	8.0
Langtjern	$\ln M_R = 0.30 (\pm 0.04) A + 0.99 (\pm 0.17)$	0.83	7	<0.01	-10.1
Veslevatn	$\ln M_R = 0.30 (\pm 0.05) A + 1.08 (\pm 0.24)$	0.69	7	<0.01	1.5
Smedstadjern	$\ln M_R = 0.37 (\pm 0.06) A + 1.04 (\pm 0.29)$	0.76	7	<0.01	2.5
Langtjern	$\ln G_R = -0.46 (\pm 0.05) A + 1.07 (\pm 0.19)$	0.87	7	<0.01	-2.4
Veslevatn	$\ln G_R = -0.37 (\pm 0.05) A + 1.34 (\pm 0.23)$	0.79	7	<0.001	-0.3
Smedstadjern	$\ln G_R = -0.46 (\pm 0.06) A + 1.69 (\pm 0.29)$	0.83	7	<0.001	2.7

The vertical distribution corresponds to other studies on *P. fluviatilis* (Craig, 1977; Linløkken, 1988; Järvalt *et al.*, 2005). Järvalt *et al.* (2005) explained this as being due to an oxygen deficit below the metalimnion. The lower oxygen tolerance threshold is 5 mg l^{-1} for both *P. fluviatilis* (Flogbe & Kestemont, 2003) and *R. rutilus* (Seagar *et al.*, 2000), and in three of the study lakes this threshold was in the lower metalimnion (4–7 m depth), while in the deepest lake, the oxygen concentration was 6 mg l^{-1} down to 20 m depth. As the vertical distribution of both species was similar in all lakes, it was probably restricted by the temperature gradient and availability of food.

The sparse *R. rutilus* in the most acidic lake, combined with its age structure (all ≥ 5 years), suggested recruitment failure, which agrees with the lower limit of reproduction at $\text{pH} = 5.5$, reported from experimental studies (Milbrink & Johansson, 1975; Keinänen *et al.*, 2000). *Perca fluviatilis*, on the other hand, can reproduce in water with $\text{pH} \leq 5.0$ (Degerman *et al.*, 1992; Hesthagen *et al.*, 2001) and was about to lose its competitors in this lake.

The *P. fluviatilis* population density correlated negatively with the abundance of large conspecifics, suggesting that density was affected by predation. Ten large *P. fluviatilis*, representing 1.1 kg ha^{-1} (*i.e.* *c.* 10% of the estimated biomass of small specimens), were removed from the clear-water lake during the first season (1998), and these probably comprised a large proportion of the large *P. fluviatilis*, as no such individuals were caught during the rest of the study in this lake. Strong year classes of both *P. fluviatilis* and *R. rutilus* occurred in 1998 and of *P. fluviatilis* in 1997 as well, suggesting predatory control of recruitment prior to the sampling. The clear water combined with a narrow littoral zone with macro-vegetation cover in this lake benefits the visual predator *P. fluviatilis* (Jeppesen *et al.*, 2000) and renders small *P. fluviatilis* and *R. rutilus* more vulnerable to predation (Eklöv & Persson, 1995, 1996). Old *P. fluviatilis* are shown to suppress recruitment until mortality reduces the number of old specimens (Alm, 1946; Persson *et al.*, 2000), and Sumari (1971) and Persson (1997) found a negative effect of large *P. fluviatilis* on *P. fluviatilis* density by analysing data from the same 32 Finnish lakes using different methods.

Perca fluviatilis size was correlated negatively with *R. rutilus* biomass, and both density and mass of *P. fluviatilis* were highest in the lake with the sparse *R. rutilus* population, suggesting that *P. fluviatilis* size was more affected by *R. rutilus* than by conspecific population density and pH in these lakes, as Olin *et al.* (2010) concluded in a study of 18 small boreal lakes in Finland. This may be an effect of interspecific competition as small *P. fluviatilis* and *R. rutilus* in sympatric populations have been shown to compete for food (Bergman, 1990; Persson & Greenberg, 1990; Persson *et al.*, 1999). Moreover, *R. rutilus* affects *P. fluviatilis* size negatively at age 1 and 2 years (Linløkken *et al.*, 2008; Horppila *et al.*, 2010) as *R. rutilus* is the more efficient plankton feeder of the two, especially in humic water (Estlander *et al.*, 2010). The negative correlation between *R. rutilus* mean mass and the width of the littoral zone indicated that a more ample pelagic habitat may benefit *R. rutilus* in sympatry with *P. fluviatilis*, but based on only three lakes with viable *R. rutilus* this should be considered as no more than a possibility.

The generally low *P. fluviatilis* mean age reflected high adult mortality, especially in the two lakes with the highest fish biomass, and this was probably due to intra- and interspecific competition for resources. Heibo & Vøllestad (2002) found even lower mean ages of *P. fluviatilis* in two lakes with $\text{pH} > 6.0$ that contained three and five fish species in addition to *P. fluviatilis*, and it was suggested that this was

due to interspecific interactions. The *P. fluviatilis* mean age was relatively high in the lake with the sparse *R. rutilus*, despite having the lowest pH (Urstjern). Thus, although pH and AI may affect mortality, it was not the main factor in this lake, and liming of one of the lakes with lowest *P. fluviatilis* mean age did not affect the mean age significantly. The L_P grew older and showed less stagnation in growth than the small conspecifics, which suggested that they switched to piscivory and avoided competition from both small conspecifics and small *R. rutilus*, improving both survival and growth.

The positive effect of pH on *P. fluviatilis* mass in the two lakes with highest fish biomass nevertheless suggested a negative effect from low pH. Acidified water has been shown to cause physiological changes like reduced concentrations of sodium and chloride ions in blood plasma of fishes (Muniz & Leivestad, 1980; Holopainen & Oikari, 1992; Harvey & Jackson, 1995), and low pH and high levels of AI may reduce fish growth due to increased energy demands (Neville, 1985; Leino & McCormick, 1993; Morgan *et al.*, 2000), so low pH may reinforce the effect of density-induced competition for food.

The positive effect of air temperature (correlating with water temperature) on *P. fluviatilis* growth in the lake with the sparse *R. rutilus*, compared to no temperature, growth effect in either *P. fluviatilis* or *R. rutilus* in the other lakes, suggested that interspecific interactions masked the effects of temperature. A positive correlation between *P. fluviatilis* growth and summer air and water temperature has been found in other locations in the temperate zone, none of them with abundant *R. rutilus* (LeCren, 1958; Neuman, 1976; Tolonen *et al.*, 2003). Populations in sympatry narrow their niches down to their realized niches, due to interspecific interactions, and the effects of environmental factors such as temperature may be less significant than in allopatric populations, which occupy their fundamental niches (Begon *et al.*, 1996). This is in accordance with the conclusions of Holmgren & Appelberg (2001) from a study based on 22 lakes in Sweden.

The most obvious effect of acidification in these lakes was the sparse population of *R. rutilus* with a lack of young individuals in the lake with lowest pH. The larger *P. fluviatilis* in this lake, in spite of having the highest conspecific density and lowest pH, as well as the negative correlation between *P. fluviatilis* mass and *R. rutilus* density in all the lakes, suggested that abundant *R. rutilus* had a negative effect on *P. fluviatilis* growth. The positive correlation between *P. fluviatilis* mass and pH in two of the lakes indicated, however, that acidity might also affect *P. fluviatilis* growth, although less significantly than the presence of *R. rutilus*. The low mean age of *P. fluviatilis* in the lakes with the highest fish biomass also suggested the effect of density-dependent factors, which was most pronounced in the sympatric populations. As body size is related to food selection and availability, the coexistence of smaller sized *P. fluviatilis* with abundant *R. rutilus* indicated that *P. fluviatilis* niche had been narrowed as a result of interspecific interactions. The temperature-related growth of *P. fluviatilis* in the lake with sparse *R. rutilus*, which differed from the other populations, suggested that interspecific interactions with *R. rutilus* masked the effect of temperature.

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