

Project KESKALA: Studies on Ecologically Sustainable Fishing

Roach (*Rutilus rutilus*) populations respond to varying environment by altering size structure and growth rate

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Received 30 May 2016, final version received 30 Nov. 2016, accepted 30 Nov. 2016

Olin M., Rask M., Estlander S., Horppila J., Nurminen L., Tiainen J., Vinni M. & Lehtonen H. 2017: Roach (*Rutilus rutilus*) populations respond to varying environment by altering size structure and growth rate. *Boreal Env. Res.* 22: 119–136.

To better understand the environmental factors and biological interactions affecting roach abundance and population structure in oligo-mesotrophic lakes, we explored roach population parameters in 24 small forest lakes in southern Finland. In those lakes, roach abundance was only little affected by the abiotic and biotic variables such as lake characteristics, water transparency, nutrient concentrations, pH or related variables, predation and competition. This was probably due to the generalist characteristics of the roach as it is adaptive to a wide variety of environments. Instead, the population structure and age-specific growth of the roach were strongly affected by various environmental variables. The growth rate was negatively related to water colour, calcium and nutrient concentration and roach abundance, and positively related to perch abundance and lake size. The growth patterns and relatively stable abundance showed flexibility in adaptation to different environmental conditions. Our results indicate that the ongoing environmental changes, recovery from acidification and brownification may notably affect the structure and production of roach populations, and may alter the role of the roach in lake ecosystems.

Introduction

Various kinds of waters throughout Europe and western Eurasia are inhabited by the roach (*Rutilus rutilus*) (see e.g. www.fishbase.org). The roach is an omnivore and generalist capable of consuming many types of food material including plants (Vinni *et al.* 2000, Estlander *et al.* 2010), inhabiting different habitats from open water to underwater vegetation (Pekcan-Hekim *et al.* 2010), and preying in low light environments (Persson 1987). As a result, the roach can adapt to rather challenging environmental

conditions. In small boreal forest lakes with high water colour, the roach is often one of the dominant fish species (Tonn *et al.* 1990, Tammi *et al.* 2004, Rask *et al.* 2010). This might be due to limited structural complexity (narrow littoral zone) and low-light conditions favouring roach over perch (Diehl 1988, Bean and Winfield 1995, Estlander *et al.* 2012). However, reproduction of the roach is very sensitive to acidification, and therefore roach can be absent or very scarce in lakes with low pH (Rask *et al.* 2000). The roach benefits from eutrophication and often forms high densities in eutrophic lakes

(Jeppesen *et al.* 2000, Olin *et al.* 2002). The roach can also promote circulations of nutrients from sediments enhancing the internal nutrient load and eutrophication (Horppila and Kairesalo 1992). Therefore, large biomass of the roach and other cyprinids are removed in biomanipulation projects throughout Europe (Bernes *et al.* 2015). On the other hand, the roach is a valued target species in recreational fishing throughout Europe (Craig 2015) and generally used for human consumption in some parts of Europe (Winfield and Nelson 1991).

The roach is one of the main prey items for many piscivores, such as the pike (*Esox lucius*), the pikeperch (*Sander lucioperca*) and the perch (*Perca fluviatilis*) (Eklöv and Persson 1995, Estlander *et al.* 2010, Ranåker *et al.* 2012). The biomass and size distribution of the roach may be regulated by pelagic predatory fish, such as the pikeperch, as the roach as a relatively slender cyprinid is vulnerable to predation and reaches size refuge at relatively old age (Lammens *et al.* 1992). However in highly eutrophic lakes, the effective reproduction of the roach may override the consumption by piscivores (Olin *et al.* 2002, Mehner *et al.* 2005).

The roach can directly and indirectly impact other species in aquatic ecosystems. It is a superior competitor over juvenile perch especially in monotonous, low-light, eutrophicated environments and can depress perch populations (Persson 1990a, 1990b). Interspecific competition between perch and roach is documented to be asymmetric (Persson 1987), as small perch do not have significant competitive effects on roach populations but competition by roach can suppress the growth of small perch. The roach may outcompete other cyprinids, such as the bream (*Abramis brama*) if not reduced by piscivores (Lammens *et al.* 1992). The introduced roach stocks are related to declines in *Coregonus* spp. populations in Europe (Langeland & Nøst 1994, Harrod *et al.* 2002). Because of the aforementioned detrimental effects on other species, the roach has been defined as a 'potential pest' or even 'high risk species' when introduced outside its original distribution (Kottelat and Freyhof 2007, Almeida *et al.* 2013).

The roach is one of the European fish species that is assumed to benefit from global change,

increasing water temperature (Winder & Schindler 2004), turbidity (Mooij *et al.* 2005) and water colour (i.e. brownification, Evans *et al.* 2005) in boreal freshwaters. Thus, the latitudinal distribution of the roach is forecasted to widen with warming climate (Lehtonen 1996, Tarkan and Vilizzi 2015). Also, the growth rate of the roach is expected to increase in higher latitudes due to warming, but this depends also on biological factors (Tarkan and Vilizzi 2015). The competition–predation relationship between roach and perch is regulated by water temperature (Persson 1986) and water colour (Estlander *et al.* 2012, Nurminen *et al.* 2014) which are expected to increase and this likely favours roach over perch. However, Linløkken *et al.* 2010 found that in low water temperatures (4–8 °C) the swimming activity and prey capture rate of the perch decreased much faster than of the roach, indicating that if the period of cold water is shortened it may favour perch growth. In addition, the deteriorating optical conditions may hinder prey detection and eventually piscivore abundance and therefore reduce predation pressure on roach (Ranåker *et al.* 2012). However, lake-specific abiotic and biotic factors ultimately determine the development of a roach population and its effect on the ecosystem on local scale (Tarkan and Vilizzi 2015). Thus, it is important to deepen the understanding of environmental factors affecting roach population parameters. The competitive effect of the roach on the perch has been widely studied (Persson 1986, Nurminen *et al.* 2014), but less is known about the effect of the perch on the roach (Tammi *et al.* 2004) though supposed to be weak (Persson 1987). Furthermore, the negative impacts of roach on perch populations have mainly been observed in eutrophicated lakes (Persson *et al.* 1991, Olin *et al.* 2002). Less is known on the interspecific interaction in oligo-mesotrophic lakes where roach usually occur and can be more abundant than perch (Olin *et al.* 2010). Additionally, more information is needed on the effect of the large piscivore, the pike, on the interspecific interaction when all three species coexist (Tonn *et al.* 1990). The roach is suggested to be more vulnerable to pike predation than the perch (Bean and Winfield 1995), and the predation threat by the pike is claimed to have a stronger

negative effect on the feeding activity of roach than that of perch (Nurminen *et al.* 2014).

In this study, we explored the effects of different abiotic gradients and biological interactions, such as predation and intra- and interspecific competition, on roach population parameters in 24 small forest lakes. Small lakes with low number of fish species were selected to better detect the interactions between the roach, perch and pike. The lakes had a wide range of water colour (oligohumic to polyhumic), and a moderate range of trophic status (oligotrophic to eutrophic) and pH (slightly acidic to neutral). Based on the previous studies, we hypothesized that (1) low transparency (low Secchi depth or high water colour) and high nutrient concentration would increase roach abundance and decrease the growth rate, mean weight and the proportion of large individuals, whereas (2) low pH (and pH-related variables: calcium concentration, alkalinity and conductivity) would result in decreased density and increased growth, mean weight and the share of large individuals in roach populations. Due to intraspecific competition (3) roach mean weight, share of small individuals and growth should be low where roach density is high whereas (4) high piscivore abundance (pike and large perch) would reduce roach density, and lead to increased growth rate, mean weight and share of large individuals. If predation is not effective enough to reduce roach density, (5) predation threat can reduce roach growth due to decreased feeding activity. Because of asymmetric competition, (6) the competitive effect of small perch on roach growth is assumed to be low. However, if roach is more vulnerable (mortality and feeding activity) to pike predation, (7) the competitive effect of the perch on roach growth can be higher in lakes with high pike abundance as compared with lakes with low pike abundance. Potential effects of forecasted trends related to global climate change, i.e. increase in turbidity and brownification, are also discussed.

Material and methods

Study lakes

The study included 24 lakes inhabited by roach,

perch and pike and situated in forested areas in southern Finland. The areas and maximum depths of the lakes ranged between 1 and 95 ha, and 3 and 16 m, respectively (Table 1). Most of the lakes ($n = 18$) were low alkalinity lakes ($< 20 \text{ mg l}^{-1} \text{ CaCO}_3$, i.e. $< 0.2 \text{ mmol l}^{-1}$, WFD) but only one lake (Majalampi) had alkalinity lower than the critical limit (0.02 mmol l^{-1}) or pH lower than 5.5 to disrupt the reproduction of the roach (Rask *et al.* 2000, Linløkken and Hesthagen 2011). In this lake set, the large lakes tended to have lower calcium concentration (Ca) than the small lakes (Pearson's correlation on ln-transformed data: $r = -0.582$, $p = 0.003$). Some of the lakes ($n = 14$) had previously been acidified, but recovered later (Tammi *et al.* 2004). More than half of the lakes ($n = 13$) were polyhumic (water colour $> 90 \text{ mg l}^{-1} \text{ Pt}$, according to Pilke *et al.* 2002), and one third ($n = 8$) of the lakes were oligohumic (water colour $< 30 \text{ mg l}^{-1} \text{ Pt}$). Half of the lakes were oligotrophic (total phosphorus, $P_{\text{tot}} < 12 \mu\text{g l}^{-1}$), one fourth were mesotrophic ($P_{\text{tot}} 12\text{--}24 \mu\text{g l}^{-1}$) and one fourth eutrophic ($P_{\text{tot}} > 24 \mu\text{g l}^{-1}$). Nutrient concentrations (P_{tot} and total nitrogen, N_{tot}) and chlorophyll *a* (chl *a*) were negatively correlated with lake area (P_{tot} : $r = -0.414$, $p = 0.016$; N_{tot} : $r = -0.545$, $p = 0.013$; chl *a*: $r = -0.412$, $p = 0.041$) but strongly positively correlated with water colour (P_{tot} : $r = 0.785$, $p < 0.001$; N_{tot} : $r = 0.934$, $p < 0.001$; chl *a*: $r = 0.816$, $p < 0.001$).

Fish sampling

We sampled the fish communities with Nordic multimesh gillnets (Olin *et al.* 2016) in the years 2001, 2002, 2003, 2005 or 2006, one to three times in July–August with a soak time of ca. 12 h (overnight). For comparability, we included only bottom gillnets in 1.5–5 m water in the data set of this study, and the lake-specific total fishing effort (number of gillnets) ranged from three to 15 gillnets (Table 2). The catch of each gillnet was sorted to species, counted and weighed. The total length (TL) of all individuals was measured (1 cm size classes). Number per unit effort (NPUE, individuals per gillnet night), biomass per unit effort (BPUE, g per gillnet night), mean weight (g) and percentages of the size classes $\leq 10 \text{ cm}$, 11–17 cm and $\geq 18 \text{ cm}$ were

calculated for roach. The three size classes were defined based on the prey they mainly consume (Estlander *et al.* 2010): the smallest roach utilize mainly zooplankton, mid-sized individuals prey on zooplankton, macroinvertebrates and plants, whereas the largest size class mainly consumed plants and macroinvertebrates. The smallest size class can also be regarded as an index of successful reproduction (Tammi *et al.* 2004). For perch, NPUEs of small (< 15 cm) and large (≥ 15 cm) individuals were calculated separately, because these two size classes were supposed to have different effects on the roach. According to Estlander *et al.* (2010), ≥ 15 cm individuals have high potential for piscivory and smaller individuals have similar diet as that of

the roach. Gillnets did not give reliable CPUE estimates for the pike, and the three-level pike abundance index based on a few mark–recapture experiments, catch by angling, and the present and some previous observations from gillnetting was estimated as described in Olin *et al.* (2010).

The age and growth data were collected from the Nordic gillnet samples of 20 lakes, and the number of age-identified roach per lake ranged between 6 and 120 (total $n = 805$). The length of age-identified roach individuals were measured to the nearest 1 mm and weighed to the nearest 1 g. The growth at different ages was determined from scales, and the ageing was verified from cleithral bones by 1–2 experienced readers. The scales were taken from the area between the

Table 1. Lake characteristics. pH, alkalinity, colour, conductivity, Ca, P_{tot} and N_{tot} are mean values from 1997 to 2005 of October (autumn turnover) and March–April (winter stagnation) samples in surface water. Chlorophyll *a* and the Secchi depth were measured July–August in the fish sampling year. Lakes are in the order of increasing area.

Lake	Number	Area (ha)	Max. depth (m)	Catchment (km ²)	pH	Alkalinity (mmol l ⁻¹)	Colour (mg Pt l ⁻¹)	Conductivity (mS m ⁻¹)	Ca (mg l ⁻¹)	P _{tot} (μg l ⁻¹)	N _{tot} (μg l ⁻¹)	Chl <i>a</i> (μg l ⁻¹)	Secchi depth (m)
Syrjäanalunen	12	0.9	8	0.28	6.41	0.22	11	50.09	5.2	7	333	3	2.3
Huhmari	6	1.6	8	0.21	6.20	0.20	177	53.48	6.2	37	591	9	1.5
Särkijärvi	13	1.8	3	0.33	6.37	0.20	158	52.94	5.8	37	587	9	1.6
Haukijärvi	3	2.1	8.5	4.96	6.19	0.14	286	52.66	5.8	20	564	6	0.8
Iso Mustajärvi	7	2.5	6	0.31	6.30	0.18	195	39.92	5.3	25	681	8	1.5
Majajärvi	9	3.4	11	1.13	5.75	0.08	318	42.07	4.7	17	703	6	0.7
Halsjärvi*	2	4.4	6	0.48	6.41	0.20	157	53.67	6.2	8	413	5	1.3
Hautajärvi*	4	5.3	12	1.85	5.97	0.11	314	40.70	4.7	55	790	12	0.7
Hokajärvi	5	8.4	6	2.28	6.26	0.14	126	46.86	4.3	11	443	3	1.5
Majalampi	19	11	5	4.00	5.40	0.01	150	25.00	1.8	16	470	6	1.0
Haarajärvi	1	13.8	12.5	0.59	6.18	0.11	146	36.71	4.0	18	487	5	1.2
Vähä-Melkutin	23	14	14.7	4.68	7.30	0.38	5	57.00	6.1	4	79	1	7.0
Pitkäniemenjärvi*	10	14.4	12	2.17	6.28	0.13	213	44.73	4.8	20	584	7	1.0
Vääriä	24	16	9	0.94	7.00	0.24	22	48.00	4.9	12	350	4	4.5
Iso Ruuhijärvi	8	16.6	6	1.43	5.96	0.08	335	39.75	4.5	54	908	14	0.6
Melalampi	20	25	9.1	2.56	5.95	0.05	84	17.00	1.4	10	320	2	2.9
Savijärvi*	11	25.7	13	1.96	6.08	0.10	247	40.38	4.5	27	674	14	1.2
Ali-Myllä	14	31	14.8	18.20	7.00	0.34	40	58.00	6.1	7	230	2	0.7
Vitsjön1	22	31	11.7	0.88	6.40	0.06	25	38.00	2.2	6	320	4	4.6
Kattilajärvi	18	34	9.2	2.00	6.00	0.03	25	27.00	2.0	5	280	2	3.0
Kankaantakunen	17	43	11	1.74	6.00	0.05	80	28.00	2.1	8	350	6	1.7
Iso-Melkutin	16	62	15.7	6.94	7.40	0.38	5	56.00	5.9	4	120	2	8.2
Iso Hietajärvi	15	83	8.6	4.64	7.00	0.10	15	17.00	1.4	6	240	2	4.1
Saarijärvi	21	95.2	13	5.22	6.50	0.03	15	35.00	2.3	9	240	2	3.9

* roach growth data not available.

Table 2. Roach NPUE and BPUE (number and g gillnet⁻¹ 12 h⁻¹) and mean weight of the Nordic gillnet catches, and NPUE of other fish species and the pike abundance index in the study lakes. Year = the test fishing year, Effort = number of gillnet nights, Perch S_NPUE = NPUE of small (< 15 cm) perch, Perch L_NPUE = NPUE of large (> 15 cm) perch, Hybrids = roach × bream hybrids, Total = total NPUE of all species, Pike index: 1 = low, 2 = medium, 3 = high abundance index; x = present but not caught in gillnets, – = never observed; Occurrence = number of lakes where the species is present. The lakes are in the order of decreasing roach NPUE.

Lake	Year	Effort	Roach NPUE	Roach BPUE	Roach MW	Perch S_NPUE	Perch L_NPUE	Pike NPUE	Ruffe NPUE	Burbot NPUE	Bream NPUE	Bleak NPUE	Eel NPUE	Pikeperch NPUE	Tench NPUE	Whitefish NPUE	Hybrids NPUE	Asp NPUE	Rudd NPUE	Vendace NPUE	Total NPUE	Pike Index
Särkijärvi	2002	5	64.4	1094	17.0	17.4	0.2	0.4	–	–	2.0	–	–	–	–	–	–	–	–	–	84.4	2
Iso Mustajärvi	2006	4	52.0	722	13.9	10.3	1.0	0.3	–	–	–	–	–	–	–	–	–	–	–	–	63.5	2
Haukijärvi	2006	3	43.7	819	18.7	10.3	1.0	x	–	–	1.0	0.3	–	–	–	–	–	–	–	–	56.3	2
Haarajärvi	2006	15	38.9	372	9.6	14.8	1.1	0.2	–	x	–	–	–	–	x	–	–	–	–	x	55.1	3
Halsjärvi	2006	4	29.8	331	11.1	12.8	0.8	x	–	x	0.3	0.3	–	–	–	–	–	–	–	–	43.8	1
Syrjänaalunen	2002	5	25.2	765	30.4	3.4	0.6	0.2	–	–	–	–	–	–	–	–	–	–	–	–	29.4	2
Melalampi	2001	5	20.6	874	42.4	28.8	14.2	0.2	–	–	–	–	–	–	–	–	–	–	–	–	63.8	3
Hokajärvi	2006	12	18.3	420	23.0	9.3	1.8	0.2	x	x	0.6	0.1	x	–	–	x	–	–	–	–	30.3	2
Iso Hietajärvi	2001	5	17.4	604	34.7	20.6	21.0	0.2	0.4	–	–	–	–	–	–	–	–	–	–	–	59.6	2
Huhmari	2002	5	13.0	178	13.7	10.6	0.2	x	–	–	–	–	–	–	–	–	–	–	–	–	23.8	1
Kattilajärvi	2001	5	12.8	464	36.2	40.4	1.6	x	1.4	–	–	–	–	–	–	–	–	–	–	–	56.2	1
Ali-Mylly	2002	5	12.6	218	17.3	6.0	0.2	x	0.8	–	–	0.2	–	–	–	–	–	–	–	–	19.8	1
Vähä-Melkutin	2001	5	11.8	702	59.5	34.4	2.8	x	1.0	–	–	–	–	–	–	–	–	1.0	–	–	51.0	1
Vitsjön1	2001	5	11.2	612	54.6	23.8	5.2	0.4	2.4	–	–	–	–	–	–	–	–	–	–	–	43.0	3
Savijärvi	2003	11	10.4	142	13.7	12.5	2.5	0.1	x	x	0.1	x	x	0.3	–	–	–	–	–	–	25.8	2
Pitkänienjärvi	2005	15	8.8	114	13.0	2.5	2.1	0.5	1.5	x	0.5	0.3	x	0.2	x	–	–	0.1	–	–	16.5	2
Väärä	2001	5	8.6	83	9.6	14.4	0.6	x	1.2	–	–	–	–	–	–	–	–	–	–	–	24.8	1
Majajärvi	2006	6	8.5	147	17.3	3.2	1.0	0.2	–	x	–	–	–	–	x	–	–	–	–	–	12.8	3
Hautajärvi	2005	6	8.2	202	24.8	1.5	1.2	0.7	–	x	–	–	x	–	–	–	–	–	–	–	11.5	3
Iso-Melkutin	2002	5	7.6	432	56.8	11.1	2.1	x	4.0	–	–	–	–	–	–	–	–	–	–	–	24.8	1
Iso Ruuhijärvi	2005	12	7.4	296	39.9	14.2	1.6	x	–	x	0.9	–	–	–	–	–	0.6	–	–	–	24.7	3
Saarjärvi	2001	5	7.4	434	58.6	34.4	2.2	x	2.4	–	–	–	–	–	–	0.2	–	–	–	–	46.6	1
Majalampi	2001	5	2.8	350	125.0	11.6	6.2	x	–	–	–	–	–	–	–	–	–	–	–	–	20.6	1
Kankaantakunen	2001	5	1.2	46	38.2	13.2	2.2	x	–	–	–	–	–	–	–	–	–	–	–	–	16.6	1
Occurrence			24	24	24	24	24	24	11	9	7	6	4	2	2	2	2	1	1	1		

lateral line and the pelvic fin, and the annual increments were measured from the focus to the posterior edge along the anteroposterior axis (see Horppila and Nyberg 1999 for detailed methods). In cleithra, the annuli were measured from the origin to the posterior edge. The growth of each individual was back-calculated by the Fraser-Lee equation (Fraser 1916, Lee 1920). Weight for the average TL at each age was calculated with the lake-specific length–weight relationship by using the age data. The growth rate (G) was then calculated as: $G_t = \ln(W_{t+1} W_t^{-1})$, where W_t is weight at age t .

Statistical analyses

To detect between-lake differences in back-calculated lengths, repeated measures ANOVA with standard variance components as covariance structure including lake and roach individual as the fixed variables, and back-calculated age as the repeated measure, was applied to age groups 1–6 years as older roach were not observed in all lakes. The effects of single environmental variables on roach population variables were analysed with a general linear model (GLM) on ln or arcsine (percentages) transformed data. The analysis of roach growth rates included age (1–6 years) as categorical variable, otherwise variables were continuous. To test for possible age-specific response, the interaction term “age × environmental factor” was also included in the models.

Redundancy analysis (RDA) was used to analyse simultaneously the effects of the perch, pike and other environmental factors on roach population variables. RDA was chosen as a multivariate analysis method, because the gradient lengths of biotic variables expressed in SD units were rather short (between 3 and 4) suggesting linear rather than unimodal relationships between species and environmental variables. The values of the abiotic variables were average values of 2–5 years (except chl a and Secchi depth, see Table 1). To avoid multicollinearity, the environmental variables N_{tot} , chl a , alkalinity and Ca were excluded due to their high correlations ($r > 0.8$) with other variables. The data set including roach BPUE, NPUE, mean weight

and the percentages of the three size classes as the species variables (24 lakes), and the data set including roach growth rates from age 1–6 years as the species variables (20 lakes) were analysed separately because age data were not available from all the lakes. All the variables were standardized [$(x_i - \bar{x})z^{-1}$, where x_i = observation, \bar{x} = mean of observation and z = SD] before analyses. The environmental variables were included in the analyses based on maximum extra fit. In the analysis of the larger lake set with the six species variables (roach BPUE, NPUE, mean weight and the percentages of the three size classes), the environmental variables included in the final model were lake area, NPUE of small (< 15 cm) perch, P_{tot} , Secchi depth, conductivity, water colour, catchment area, NPUE of large (≥ 15 cm) perch, maximum depth, pike index and pH. In RDA of the growth data (growth rate of 1–6 years roach), the initial set of environmental variables included the same selection as in the previous RDA model added with roach NPUE to estimate the effect of intraspecific competition in roach populations. The environmental variables included in the final model were water colour, roach NPUE, NPUE of small (< 15 cm) perch, P_{tot} , pH, pike index, NPUE of large (≥ 15 cm) perch, conductivity, catchment area, maximum depth and lake area. A Monte-Carlo permutation test (999 permutations) was used to test the significance of the RDA axes. For RDA we used the software package CANOCO 4.51 (ter Braak & Šmilauer 2002).

Results

Besides roach, perch and pike that inhabited all of the study lakes, the ruffe (*Gymnocephalus cernua*) was present in almost half of the lakes, and the burbot (*Lota lota*), the bream, the bleak (*Alburnus alburnus*) and the eel (*Anguilla anguilla*) occurred in 17%–38% of the lakes (Table 2). Other fish species (pikeperch, tench *Tinca tinca*, whitefish *Coregonus lavaretus*, asp *Aspius aspius*, rudd *Scardinius erythrophthalmus* and vendace *Coregonus albula*) and roach × bream hybrids were present in only one or two lakes. The share of the roach in gillnet number catches ranged between 7% and 86%, and it was

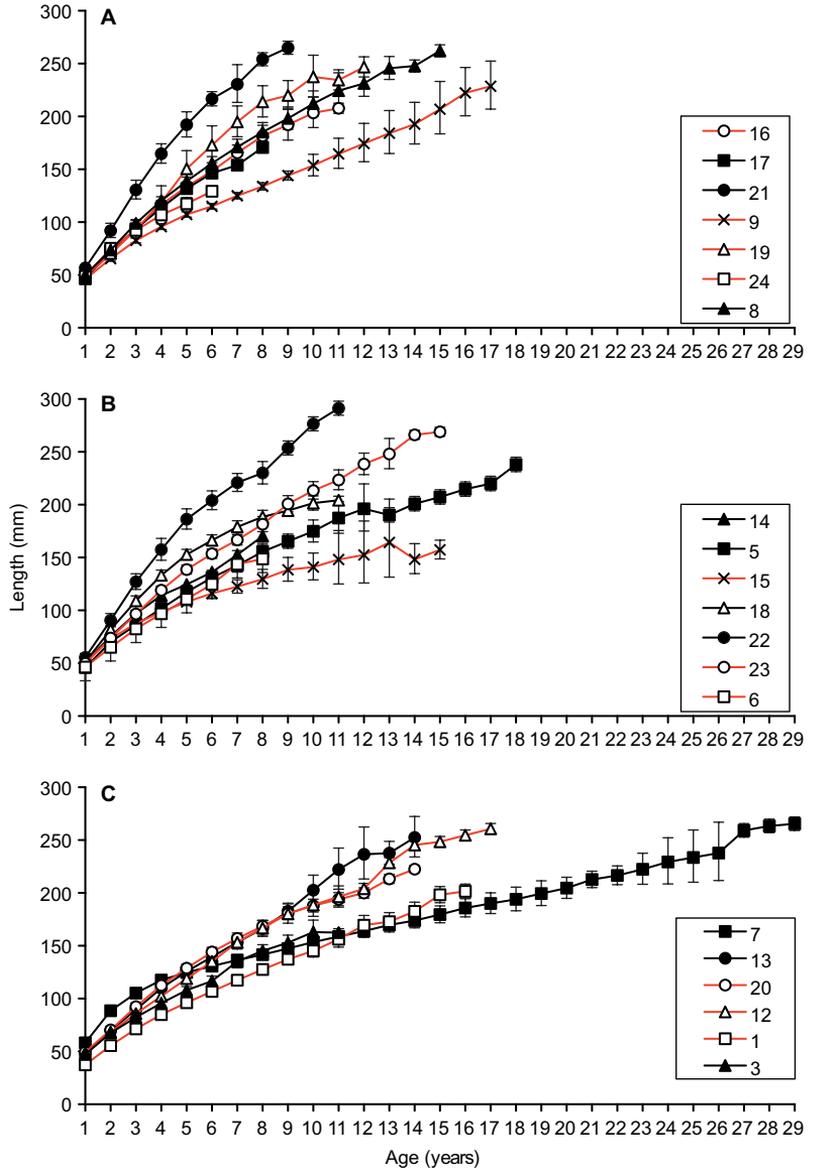


Fig. 1. Growth of roach in the 20 study lakes in southern Finland based on back-calculated length observations (with 95% confidence intervals). Due to the density-dependent growth, lakes are grouped according to different roach abundance (measured as gillnet NPUE indiv. gillnet⁻¹): (A) roach NPUE < 10, (B) roach NPUE 10–20, (C) roach NPUE > 20. Numbers in the figure legends indicate lakes (see Table 1).

the most abundant catch species in half of the lakes ($n = 12$). The roach and perch composed clearly the largest part of the fish abundance in terms of gillnet NPUE (81%–100%) and likely were the dominant species in fish communities.

Roach NPUE, BPUE and mean weight (arithmetic means) in the gillnet catches ranged between 1 and 64 indiv. gillnet⁻¹, 46–1094 g gillnet⁻¹ and 10–125 g, respectively. On average, growth of the roach in the study lakes was slow (Fig. 1), but the variation was high, and significant among-lake differences were detected

(Table 3). Based on back-calculated growth analyses, average TL (and range) of 1-, 3- and

Table 3. *F* statistics of repeated measures ANOVA for back-calculated lengths of roach in 20 lakes (age groups 1–7 years).

Source	d.f.	<i>F</i>	<i>p</i> <
Lake	19	188.18	0.001
Age	6	3954.73	0.001
Lake × age	113	8.44	0.001

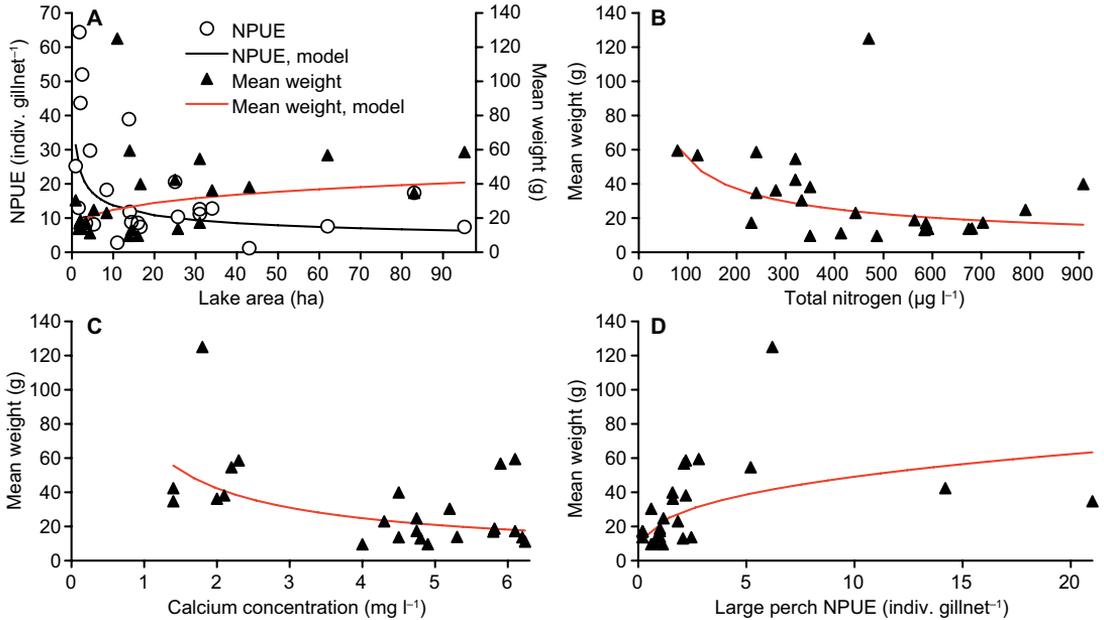


Fig. 2. Roach NPUE and mean weight in relation to most significant single independent variables in 24 small forest lakes. (A) Roach NPUE and mean weight in relation to lake area, (B) mean weight in relation to total nitrogen concentration, (C) mean weight in relation to calcium concentration, and (D) mean weight in relation to large (≥ 15 cm) perch NPUE. Lines represent modelled values (see Table 4).

6-year-old roach in the study lakes were 49 (37–57), 94 (71–130) and 143 (107–213) mm, respectively. The oldest observed roach were 20–29 years old from Iso Ruuhijärvi, otherwise the maximum observed age ranged from 6 to 18 years.

Of the factors that we hypothesized to affect roach abundance (water transparency, nutrient concentrations, pH or related variables, predation), none affected roach NPUE or BPUE significantly. Instead, the mean weight and size structure of the roach populations responded significantly to various environmental variables (Fig. 2 and Table 4). As expected, Ca, one of the pH related variables, had a negative effect on mean weight and the percentage of large individuals and a positive effect on the percentage of small individuals. As also assumed, mean weight and the share of large individuals decreased with roach NPUE but increased with NPUE of large perch indicating density-dependence in growth. Furthermore, NPUE of small perch had a positive effect on the share of the largest roach size class. Expectedly, the percentage of the smallest size class was positively and the largest size

class negatively related to low water transparency (high water colour) and P_{tot} . Additionally, as not hypothesized, roach NPUE was negatively related to lake area. Lake area also had a negative effect on the percentage of the smallest roach size class and a positive effect on mean weight and the percentage of the largest size class.

The growth of roach appeared to be regulated by various environmental factors but there were no significant differences among the responses of different age groups (the interaction terms “age \times environmental factor” had $p > 0.05$). We expected the growth rate to be lowest in the highest roach densities, and this was supported by a negative relation between the age-specific growth rates of roach and roach NPUE (Fig. 3A and Table 5). We assumed no effect of small perch on roach growth, but the NPUE of small perch was positively related with the growth rate of roach (Fig. 3B and Table 5). We expected high predator density to increase roach growth rate, and supposedly NPUE of large perch positively affected the growth rate of roach (Fig. 3C and Table 5). The pike abundance index

affected the growth rate of the roach (Fig. 3D, GLM: $F_{7,112} = 2017.97$, $p < 0.001$) which was the lowest where the pike abundance index was the highest (Tukey: pike index 1 vs. 2, $p = 0.006$, pike index 1 vs. 3, $p = 0.205$). This may indicate decreased feeding activity under predation threat. NPUE of small perch did not have a significant effect on roach growth when included in the previous model. Expectedly, the growth rate of roach increased with decreasing Ca (Fig. 3E). Water colour and lake area had a positive effect and P_{tot} negative effect on the growth rate of the roach (Fig. 3F–H).

In RDA with the species variables NPUE, BPUE, mean weight and the percentage of the three size classes of roach, the first RDA axis explained 33.5% of the variation in species relations and 49.5% of the variations in species–environment relation (Table 6 and Fig. 4). Of the effects of single environmental variables on the roach variable matrix, lake area, NPUE of small perch and lake depth were significant ($p = 0.022$, 0.046 and 0.048, respectively). Lake area, NPUE of small perch and pH were selected first in the RDA model based on maximum extra fit indicating the highest explanatory power of these single variables. Based on the axis scores, the first axis indicated a gradient of high nutrient concentra-

tion, water colour and conductivity, and low perch abundance, lake area and water clarity. The share of large roach individuals, mean weight and roach BPUE had low scores on this axis, suggesting that the roach biomass and average size of individuals was greater in less eutrophic and larger lakes with high water clarity and perch abundance. The share of small roach had a high positive score and also roach NPUE had a positive score on this axis, indicating that high nutrient concentration and water colour had a positive effect on the density of small roach especially in smaller lakes with low abundance of small perch. The second axis explained 20.2% of the variation in species data and 29.7% of the variations in species–environment relation. Lake depth and area had strong positive scores on this axis and pH, conductivity and pike index had negative scores. We interpret the axis as environmental gradient of low pH and pike predation and high lake size. Both roach BPUE and NPUE were negatively related to this axis, indicating lower roach abundance in more acidic, larger and deeper lakes with low pike predation pressure. The mean weight of roach was positively related to this axis, suggesting that the average size of roach increased with low pH and pike predation pressure especially in larger lakes. Interestingly, the

Table 4. GLM models including NPUE, mean weight, and the share of ≤ 10 cm and ≥ 18 cm roach as dependent variables, and the single independent variables with the highest explanatory power. MW = mean weight.

Dependent variable	Independent variable	Intercept	SE	Slope	SE	r^2	$F_{1,22}$	p
ln(roach NPUE)	ln(lake area)	3.410	0.345	-0.344	0.125	0.257	7.601	0.012
ln(mean weight) (g)	ln(lake area)	2.702	0.277	0.221	0.100	0.181	4.852	0.038
	ln(Ca)	4.276	0.343	-0.768	0.239	0.319	10.319	0.004
	ln(large perch NPUE)	3.102	0.123	0.344	0.100	0.348	11.733	0.002
	ln(roach NPUE)	4.214	0.385	-0.378	0.142	0.244	7.117	0.014
arcsine ≤ 10 cm%	ln(lake area)	0.819	0.142	-0.122	0.051	0.204	5.623	0.027
	ln(colour)	0.052	0.226	0.110	0.051	0.176	4.700	0.041
	ln(Ca)	0.118	0.196	0.300	0.136	0.180	4.815	0.039
	ln(P_{tot})	-0.007	0.230	0.206	0.086	0.207	5.729	0.026
	ln(roach NPUE)	-0.007	0.197	0.206	0.073	0.267	8.001	0.010
arcsine ≥ 18 cm%	ln(lake area)	0.047	0.126	0.114	0.046	0.220	6.208	0.021
	ln(colour)	0.895	0.184	-0.133	0.041	0.322	10.453	0.004
	ln(Ca)	0.862	0.151	-0.398	0.105	0.394	14.326	0.001
	ln P_{tot}	0.884	0.196	-0.217	0.073	0.287	8.849	0.007
	ln(small perch NPUE)	-0.085	0.188	0.169	0.073	0.195	5.330	0.031
	ln(large perch NPUE)	0.258	0.056	0.165	0.046	0.367	12.768	0.002
	ln(roach NPUE)	0.709	0.188	-0.149	0.069	0.175	4.652	0.042

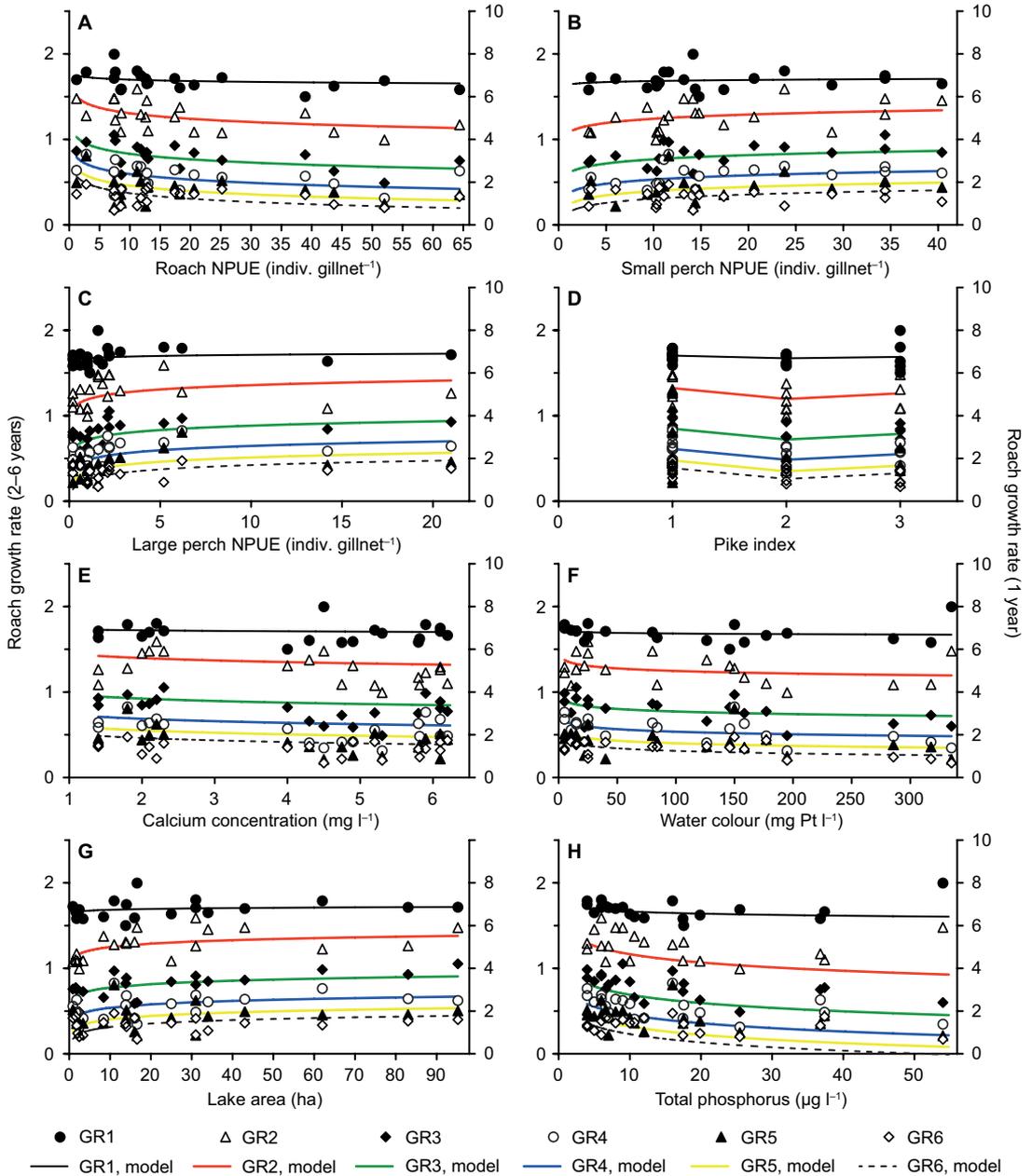


Fig. 3. Average growth rate (GR) of roach age groups 1–6 years in 20 small forest lakes in relation to most significant single environmental variables: (A) roach NPUE, (B) small (< 15 cm) perch NPUE, (C) large (≥ 15 cm) perch NPUE, (D) pike index, (E) calcium concentration, (F) water colour, (G) lake area, and (H) total phosphorus concentration. Lines represent modelled values (general linear models, see Table 5).

share of small roach was not negatively related to this axis, whereas the share of mid-sized roach was strongly negatively affected.

In RDA of growth data, single environmental variables water colour ($p = 0.011$) and con-

ductivity ($p = 0.014$) had significant effects on the roach variable matrix. Water colour, roach NPUE and the NPUE of small perch were the single variables selected first in this RDA and had the greatest explanatory power. The first

Table 5. General linear models including growth rate of roach in ages 1–6 years as dependent variable and the single independent variables with the highest explanatory power. The interaction term “age × environmental factor” was not significant ($p > 0.05$). Estimate = 0.000 is the result of the overparametrized model used by PROC MIXED in SAS.

Independent variable	Estimate	SE	<i>t</i>	<i>p</i>	<i>r</i> ²	Model <i>F</i> _{6,113}	Model <i>p</i> <
Intercept	0.181	0.062	2.920	0.004			
ln(lake area)	0.058	0.016	3.680	0.000	0.992	2486.990	0.001
Age 1	6.426	0.065	99.000	< 0.001			
Age 2	0.935	0.065	14.410	< 0.001			
Age 3	0.461	0.065	7.100	< 0.001			
Age 4	0.224	0.065	3.460	0.001			
Age 5	0.089	0.065	1.370	0.173			
Age 6	0.000						
Intercept	0.510	0.076	6.680	< 0.001			
ln(colour)	-0.043	0.015	-2.920	0.004	0.992	2386.930	0.001
Age 1	6.426	0.066	97.000	< 0.001			
Age 2	0.935	0.066	14.120	< 0.001			
Age 3	0.461	0.066	6.960	< 0.001			
Age 4	0.224	0.066	3.390	0.001			
Age 5	0.089	0.066	1.350	0.181			
Age 6	0.000						
Intercept	0.510	0.086	5.910	< 0.001			
ln(Ca)	-0.069	0.028	-2.440	0.016	0.992	2336.080	0.001
Age 1	6.426	0.067	95.970	< 0.001			
Age 2	0.935	0.067	13.970	< 0.001			
Age 3	0.461	0.067	6.880	< 0.001			
Age 4	0.224	0.067	3.350	0.001			
Age 5	0.089	0.067	1.330	0.186			
Age 6	0.000						
Intercept	0.552	0.090	6.160	< 0.001			
ln(<i>P</i> _{tot})	-0.140	0.049	-2.860	0.005	0.992	2380.330	0.001
Age 1	6.426	0.066	96.870	< 0.001			
Age 2	0.935	0.066	14.100	< 0.001			
Age 3	0.461	0.066	6.950	< 0.001			
Age 4	0.224	0.066	3.380	0.001			
Age 5	0.089	0.066	1.340	0.182			
Age 6	0.000						
Intercept	0.143	0.097	1.470	0.144			
ln(small perch NPUE)	0.071	0.032	2.250	0.026	0.992	2318.850	0.001
Age 1	6.426	0.067	95.620	< 0.001			
Age 2	0.935	0.067	13.920	< 0.001			
Age 3	0.461	0.067	6.860	< 0.001			
Age 4	0.224	0.067	3.340	0.001			
Age 5	0.089	0.067	1.330	0.188			
Age 6	0.000						
Intercept	0.255	0.054	4.730	< 0.001			
ln(large perch NPUE)	0.073	0.025	2.940	0.004	0.992	2389.120	0.001
Age 1	6.426	0.066	97.040	< 0.001			
Age 2	0.935	0.066	14.120	< 0.001			
Age 3	0.461	0.066	6.960	< 0.001			
Age 4	0.224	0.066	3.390	0.001			
Age 5	0.089	0.066	1.350	0.181			
Age 6	0.000						
Intercept	0.585	0.076	7.740	< 0.001			
ln(roach_CPUE)	-0.093	0.022	-4.140	< 0.001	0.993	2557.770	0.001
Age 1	6.426	0.064	100.390	< 0.001			
Age 2	0.935	0.064	14.610	< 0.001			
Age 3	0.461	0.064	7.200	< 0.001			
Age 4	0.224	0.064	3.500	0.001			
Age 5	0.089	0.064	1.390	0.167			
Age 6	0.000						

axis indicated diverse environmental gradient of low humic and nutrient concentration and large lake area with high perch abundance and low pike and roach abundances (Table 7 and Fig. 5). The axis explained 38.1% of the species data and 61.5% of the species–environment relations. The growth rate of 3–6 years had high positive scores on this axis, suggesting that the high growth rate of older roach is accelerated by clear water and adequate lake area. The abundance of large perch had a positive effect on the growth rate of 3–6 years roach whereas pike abundance had a negative effect. However, the first year growth of roach was not strongly affected by the aforementioned environmental conditions. The second axis explained 11.6% of species relations and 18.7% of species–environment relations. The axis was interpreted as the environmental

gradient of low roach abundance, large lake area and high small perch abundance. The growth of 1–2 years roach was strongly positively affected by this gradient, suggesting that these age classes are most vulnerable to intraspecific competition. In both axes small perch abundance was positively related to growth of all roach age groups, indicating that perch doesn't have apparent competition effect on roach in the environmental conditions the study lakes covered.

Discussion

We found roach abundance to be relatively unaffected by the abiotic and biotic parameters of the study lakes. As a generalist, the roach can adapt to varying conditions (Winfield and Nelson 1991), and the environmental gradients in the lakes were not wide enough to induce strong responses in roach abundance. Lake area was the

Table 6. Results of RDA of roach population variables, and biotic and environmental variables in 24 small lakes. Axis 1–2 are the first two RDA axes. Proportion of ≥ 18 , 11–17, and ≤ 10 cm = percentage of the corresponding roach length classes in the gillnet data, BPUE = biomass per unit effort in gillnet data, NPUE = number per unit effort in gillnet data, Perch_S = small (< 15 cm) perch and Perch_L = large (≥ 15 cm) perch.

Variable	Axis 1	Axis 2	All
Roach population variables			
Proportion of ≥ 18 cm	-0.8049	0.2523	
Mean weight	-0.6658	0.3528	
BPUE	-0.4097	-0.6180	
Proportion of 11–17 cm	-0.2133	-0.4508	
NPUE	0.2107	-0.6067	
Proportion of ≤ 10 cm	0.8136	0.2659	
Environmental variables			
Perch_S NPUE	-0.5537	-0.0643	
Lake area	-0.5312	0.3164	
Secchi depth	-0.5153	-0.0330	
Perch_L NPUE	-0.3666	0.0642	
Catchment area	-0.2302	0.0321	
Lake depth	-0.0514	0.4557	
pH	0.0191	-0.3243	
Pike index	0.2198	-0.1945	
Conductivity	0.4254	-0.2803	
Water colour	0.4831	0.0901	
Total phosphorus	0.5342	0.1559	
<i>F</i>	6.049		2.305
<i>p</i>	0.049		0.005
Variance explained (%)			
Species data	33.5	20.2	67.3
Species–environment relation	49.5	29.7	99.1

Table 7. Results of RDA of growth rates (GR) of 1–6-year roach, and biotic and environmental variables in 20 small lakes. Axes 1–2 are the first two RDA axes. NPUE = number per unit effort in gillnet data, Perch_S = small (< 15 cm) perch and Perch_L = large (≥ 15 cm) perch.

Variable	Axis 1	Axis 2	All
Roach growth variables			
GR 1 year	0.2090	0.3832	
GR 2 years	0.3785	0.5730	
GR 3 years	0.7719	0.2329	
GR 4 years	0.7192	-0.1632	
GR 5 years	0.7475	-0.3255	
GR 6 years	0.6534	-0.1775	
Environmental variables			
Perch_S NPUE	0.4945	0.4766	
Area	0.4596	0.5691	
Perch_L NPUE	0.3009	0.0340	
pH	0.0317	0.0329	
Conductivity	-0.2407	-0.1430	
Roach NPUE	-0.3934	-0.5946	
Pike index	-0.4056	0.1177	
Total phosphorus	-0.5394	0.0997	
Water colour	-0.6863	-0.0848	
<i>F</i>	6.154		1.808
<i>p</i>	0.029		0.035
Variance explained (%)			
Species data	38.1	11.6	59.3
Species–environment relation	61.5	18.7	95.8

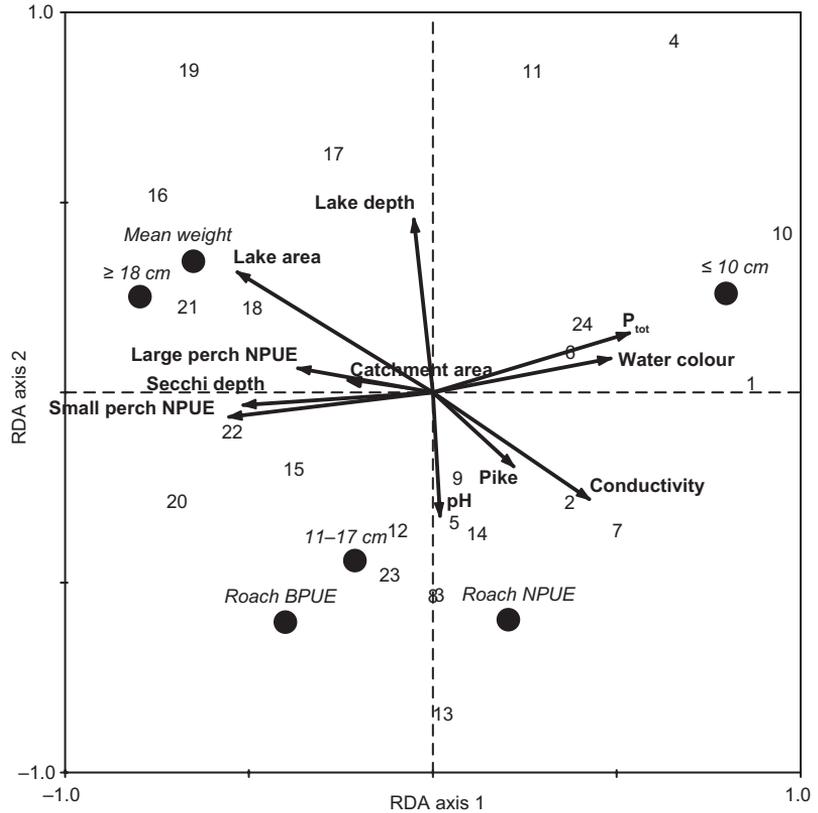


Fig. 4. Biplot of the redundancy analysis (RDA) for biotic and environmental variables, and roach population variables from gillnet data in 24 forest lakes in southern Finland. The numbers in the figure indicate lakes (see Table 1); ≤ 10 cm, 11–17 cm and ≥ 18 cm refer to the corresponding percentages of these size classes in the gillnet catch.

only single variable that had a significant effect on roach abundance which was lower in the larger lakes. This may be due to the overall lower productivity in the larger lakes, as lake area was negatively correlated with nutrient concentration and chlorophyll *a*. Additionally, the lower calcium concentration in the larger lakes, some of which (Kattilajärvi, Saarijärvi, Vitsjön) have a documented acidification (and recovery) history (Tolonen *et al.* 1986), including negative effects on roach populations (Tammi *et al.* 2004, Rask *et al.* 2014), may have contributed to the lower roach abundance. The mean weight and growth rate of the roach were positively dependent on lake size, suggesting that the lower abundance of the roach in large lakes is a real phenomenon and not related to varying gillnet catchability (Olin *et al.* 2016). We did not find the expected response, that low transparency would favour the roach over perch (Estlander *et al.* 2012) and therefore increase roach abundance. This was probably because water clarity was linked to other, more important variables such as calcium concentra-

tion and lake area overriding the expected relation.

Based on earlier studies, we expected roach abundance to be positively dependent on nutrient concentration (Jeppesen *et al.* 2000, Olin *et al.* 2002). RDA revealed a positive effect of P_{tot} concentration on the abundance of small roach. However, the total roach abundance was not positively affected by trophic status. In this study, the lakes that had the highest P_{tot} also had the highest water colour. This might have decreased the general productivity due to light limitation (Keskitalo & Eloranta 1999), resulting in lower roach abundance than expected. Furthermore, we did not have highly eutrophic or hypertrophic study lakes that are documented to have a very high roach abundance (Jeppesen *et al.* 2000, Olin *et al.* 2002).

Unlike abundance, the population structure of the roach expressed as mean weight and percentage of size classes and age-specific growth rate were strongly affected by different abiotic and biotic variables as indicated by the diverse envi-

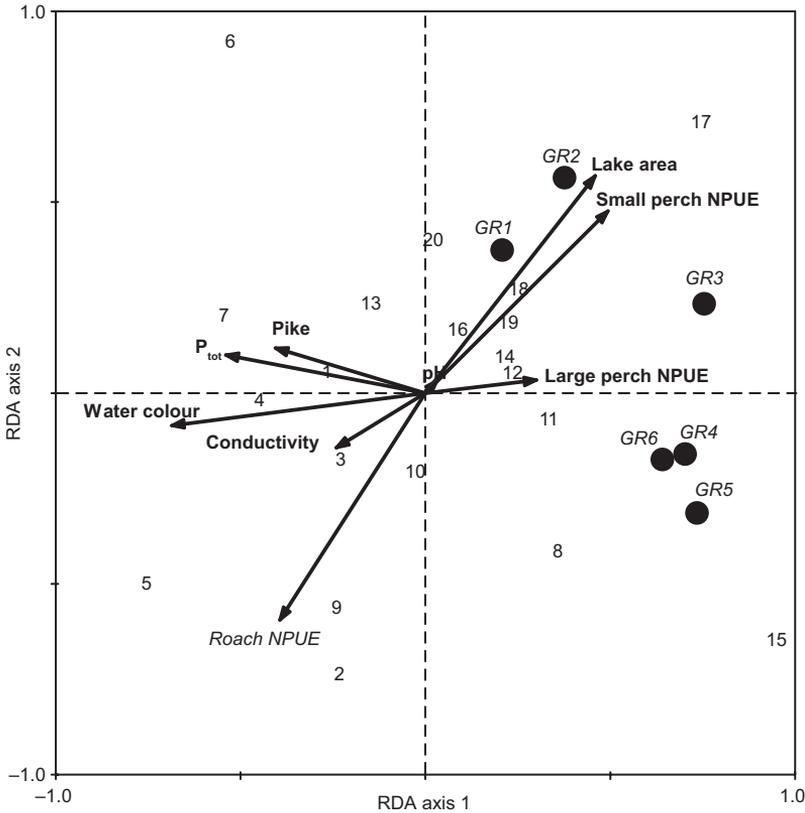


Fig. 5. Biplot of the redundancy analysis for biotic and environmental variables, and growth rates of 1–6 years roach (GR1–GR6) from gillnet data in 20 forest lakes in southern Finland. The numbers in the figure indicate lakes (see Table 1).

ronmental gradients in RDA. The roach growth patterns seem to be flexible, reflecting ability to adapt to different conditions and explaining the relatively stable biomass and abundance in our comparatively diverse set of study lakes. Different age groups responded similarly to single environmental variables but multivariate RDA revealed differences between the age groups. The observed positive relation between water clarity and growth rate of older roach might be due to the fact that plant material, which is more abundant in clearer lakes, is an important food item for these age groups (Estlander *et al.* 2009, 2010, Olin *et al.* 2010). Another possible reason for the higher growth rate may be the lack of intraspecific competition in low alkalinity lakes (Rask *et al.* 2014).

Predator abundance affected the growth of roach age groups differently. We assumed that high piscivore abundance would increase the growth rate of roach because of decreased intraspecific competition, but this was found only when considering the effect of large perch

on growth of older roach age groups. As perch prey on relatively small roach (Jacobsen *et al.* 2002), the reason for the positive relation between large perch and the growth rate of older roach might be that perch reduce the intraspecific competition in roach populations. However, the growth rate of older roach seemed to be quite unaffected by the overall roach abundance. Another explanation is that other environmental factors promote a large average size in both species. In humic lakes, the growth rate of both species is low, decreasing the average size and number of large individuals as compared with clearer lakes (Estlander *et al.* 2010, Olin *et al.* 2010). Unexpectedly, pike abundance had a negative effect on the growth rate of roach especially in older age groups. Pike should target larger prey than perch, and the age groups 3–6 years (average size range 49–143 mm) all are vulnerable to pike predation (Nilsson and Brönmark 2000). It seems that pike predation was not effective enough to reduce the density of older roach but may have altered their behaviour. The

predation threat by pike may have decreased the feeding activity of older roach and forced them to forage in poorer habitats or for shorter time thereby reducing their growth rate (Brabrand & Faafeng 1993, Nurminen *et al.* 2014). Additionally, according to our results pike predation does not have a notable effect on interspecific competition, as the effect of perch abundance on roach growth rate was not affected by pike abundance. It may be that the competitive effect of roach on perch is so strong that it overrides the balancing effect of predation pressure or threat by pike. Perch and roach were usually found in same gillnets, indicating use of same habitat and interspecific competition for resources. It has to be noted, however, that the pike index we used is very rough, and the results have to be interpreted with caution.

We assumed that small perch would not have a strong effect on roach population parameters but we found a clear positive relationship between small perch abundance and roach growth rate. This indicates that small perch and roach favour similar environments but the roach is not affected by perch competition. We found earlier in partly the same study lakes that the growth rate of small perch and roach abundance were negatively correlated (Olin *et al.* 2010). These findings are congruent with the earlier observations of “asymmetric competition” between perch and roach, where competition by roach decrease the growth of perch but perch has no effect on roach (Persson 1987). In this study, some of the lakes had clear water that should favour the perch over roach (Diehl 1988) but the perch did not have a competitive effect on the roach probably because perch was not especially abundant in these lakes. As the overlap in diets of these species is not pronounced (Estlander *et al.* 2010), the density of one species has to be much higher than that of the other to induce competitive effects (Persson 1983).

Intraspecific competition appears to be one of the main factors affecting the growth rate of roach, and as we expected, the mean weight and growth rate of roach were lowest where roach abundance index was highest. Our results also indicate that the youngest age groups were most strongly affected by intraspecific competition. This is logical as the youngest age groups have

the narrowest diet spectra, almost solely zooplankton, whereas older roach are capable to use also other food items, including macroinvertebrates and detritus if zooplankton resource is scarce (Estlander *et al.* 2010).

Acidification is reported to have decreased in Finland but it is suggested that it still affects roach populations and also the recovering perch population might hinder the recovery of the roach (Tammi *et al.* 2004). We did not find a relationship between low pH (or related variables) and roach abundance, and the relation between roach and perch abundance was positive. In all the study lakes, pH values seemed to be sufficient to enable roach reproduction. Also, water colour i.e. the high concentration of humic substances in the lakes with the lowest pH might relieve the toxic effects of e.g. aluminium (Henriksen *et al.* 1989). If roach reproduction is disrupted by acidification, roach abundance can be negatively related to perch abundance (Linløkken and Hesthagen 2011). However, Ca concentration was strongly negatively correlated with the roach mean weight and growth rate, indicating higher average size and growth in low alkalinity lakes. It still might be that the roach populations have not fully recovered in the low alkalinity lakes as evidenced by moderate stock size, fast growth rate and high average size, even though roach abundance was not directly dependent on pH (or related variables). In addition, RDA suggested no negative effect of low pH on the percentage of small roach, but a strong negative effect on the share of mid-sized roach. This might be due to the previous acidification in some of the study lakes that prevented roach reproduction still in the late 1990s but not anymore. Thus large and small roach occur in these lakes, but the imprint of the previous acidification can still be seen in the low abundance of mid-sized roach.

Based on this study, the ongoing environmental changes, recovery from acidification, global climate change, and the related brownification should not immediately and directly affect roach abundance in aquatic ecosystems. However, the effects on the structure and production of roach populations appear more imminent, and these changes may alter the functioning of roach populations in lake ecosystems through changes

in resource use and energy fluxes (Olin et al. 2006). Furthermore, it is likely that the changes will have rapid, direct effects on interspecific interactions with other species, e.g. perch and pike (Estlander et al. 2012, Ranåker et al. 2012, Nurminen et al. 2014). In elevated temperature, roach swim faster and feed more actively than perch (Persson 1986), and the forecasted increase in water temperatures can lead to higher competitive effect of the roach on perch. In the long run the changes in the competition–predation relationships and the ongoing environmental changes may strongly affect roach abundance.

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