BOREAL ENVIRONMENT RESEARCH 19 (suppl. A): 112–123 © 2014
ISSN 1239-6095 (print) ISSN 1797-2469 (online) Helsinki 21 March 2014

Population dynamics and growth of perch in a small, humic lake over a 20-year period — importance of abiotic and biotic factors

Martti Rask[1)]*, Samuli Sairanen[1)], Sami Vesala[1)], Lauri Arvola[2)], Satu Estlander[3)] and Mikko Olin[3)]

[1)] *Finnish Game and Fisheries Research Institute, Evo Fisheries Research Station, Rahtijärventie 291, FI-16970 Evo, Finland (*corresponding author's e-mail: martti.rask@rktl.fi)*
[2)] *Lammi biological Station, University of Helsinki, Pääjärventie 320, FI-16900 Lammi, Finland*
[3)] *Department of Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland*

Received 29 Nov. 2012, final version received 4 Sep. 2013, accepted 4 Sep. 2013

Rask, M., Sairanen, S., Vesala, S., Arvola, L., Estlander, S. & Olin, M. 2014: Population dynamics and growth of perch in a small, humic lake over a 20-year period — importance of abiotic and biotic factors. *Boreal Env. Res.* 19 (suppl. A): 112–123.

Population dynamics and growth of perch (*Perca fluviatilis*) were studied over a 20-year period in a small, humic, boreal lake (Valkea-Kotinen). The annual estimated total population size of perch (> 8 cm, total length) varied from 2700–13 400 and the biomass from 16.1–44.2 kg ha^{-1}. Strong year-classes were born at four-year intervals between 1991 and 2003. A decreasing trend was recorded in the growth of 1- and 2-year-old perch, whereas a slight increase appeared in the yearly growth of 4- and 5-year-old fish. Our view is that the decrease in the early growth was caused by negative effects of increased organic carbon loads on water colour and hence on light conditions and the general productivity of the plankton community. These changes outweighed the expected positive effect of increasing temperature for young perch but not for the older fish.

Introduction

The European perch (*Perca fluviatilis*) is a widely distributed fish species in boreal waters. Apart from the subarctic lakes of Lapland, it is the most common species in Finnish lakes (Tonn *et al*. 1990, Tammi *et al*. 2003, Rask *et al*. 2010). The presence of perch in almost all the lakes of southern and central Finland is related to its wide environmental tolerance: the life cycle of perch can be completed in small acidic ponds (Nyberg *et al*. 1995, Tammi *et al*. 2004, Posch *et al*. 2012) as well as in larger lakes of widely different trophic state (Olin *et al*. 2002, Tammi *et al*. 2003). The wide environmental tolerance is complemented by its ecological flexibility; perch is a generalist carnivore feeder, usually shifting during its life span from zooplankton to zoobenthos and later to fish (Allen 1935, Persson 1994, Horppila *et al*. 2000). As it is a visual feeder, light conditions are of importance, low light causing decreased feeding efficiency (Bergman 1988, Estlander *et al*. 2012) and dominance of roach (*Rutilus rutilus*) over perch in competition for zooplankton food in the turbid water of eutrophic lakes (Persson 1983, Olin *et al*. 2002)

Editor in charge of this article: Outi Heikinheimo

or in highly humic lakes (Estlander *et al*. 2010, Olin *et al*. 2010).

Significant environmental trends were recorded in a small, humic Lake Valkea-Kotinen during 1990–2009. Decreasing acidifying deposition resulted in lower SO_4 concentrations and in associated increases in pH (from 5.0 to 5.5) and alkalinity (from 5 to 20 μeq l^{-1}) of water (Vuorenmaa *et al*. 2014). The effects of climate change, predicted to increase the temperature and shorten the ice-covered period of the lake (Saloranta *et al*. 2009), have already been recorded (Lehtovaara *et al*. 2014, Jylhä *et al*. 2014). The increase in organic carbon load, apparently due to the afore-mentioned factors (Monteith *et al*. 2007, Futter *et al*. 2009, Arvola *et al*. 2010), caused brownification of the water, from 100 to close to 200 mg Pt l^{-1}. Such brownification may affect energy and carbon sources and processes within the food webs (Salonen *et al*. 1992, Kankaala *et al*. 2006, Jones *et al*. 2008) and result in a higher proportion of bacterial production via the microbial loop as compared with algal production (Ask *et al*. 2009, Karlsson *et al*. 2009). This may in turn affect food availability to higher trophic levels, i.e., zooplankton (Brett *et al*. 2009) and fish (Estlander *et al*. 2012).

In lakes recovering from acidification, increased reproductive success of perch is expected to lead to increasing population density, and decreasing growth as well as mean size of fish due to food competition (Nyberg *et al*. 1995). However, Ohlberger *et al*. (2011) predicted that increasing temperature, coupled with increasing intraspecific competition, may also result in dominance of younger and smaller perch, which was recorded in some Danish lakes (Jeppesen *et al*. 2012). On the other hand, perch is a warm-water species, and hence is predicted to benefit from warmer waters being a consequence of climatic change (Lappalainen and Lehtonen 1997, Jeppesen *et al*. 2012).

In the present study, we related the changes in perch population dynamics and growth to the environmental trends recorded in the lake during the 20-year study period to compare the impact of each stressor on perch. Both environmental and biological factors were included to evaluate their relative importance.

Material and methods

Small (0.042 km^2), mesotrophic, shallow (maximum depth 6.5 m, mean depth 2.5 m), brown-water Lake Valkea-Kotinen is located in a small headwater catchment (0.22 km^2) in a remote protected forest area in southern Finland. It is affected by pollution from airborne sources only (for details *see* Ukonmaanaho *et al*. 1998, Ruoho-Airola *et al*. 2014). During the growing season, steep thermal and oxygen stratification is typical for the lake, resulting in ca. 2-m thick warm and oxygenated epilimnion, and a cold and anoxic hypolimnion (Forsius *et al*. 2010) restricting the suitable habitat for perch in the lake. The littoral habitat is narrow due to poor light penetration and steep shores, and consists mainly of floating leaved vegetation (*Nuphar lutea*) and aquatic mosses.

Perch and pike (*Esox lucius*) are the only fish species in the lake. The size and structure of the perch population have been monitored since 1991 (Rask *et al*. 1998). Annual population estimates of perch were obtained from two-week continuous marking and recapturing in May without fish removal (Schnabel estimate, Krebs 1989). The fish were caught by wire traps with a 1 cm^2 mesh retaining perch ≥ 8 cm long, which corresponds to ≥ 2 years of age, and targeting the spawning population. Altogether 34 731 perch were captured during the 20-year study period. The fish were measured to the nearest 1 cm (total length) for length distribution evaluation, after which they were fin-clipped and released. Pelvic fins were clipped, one of the two fins each year, to ensure correct interpretation of cuts from consecutive years. Marking and recapturing was done during spawning, some 2–3 weeks after ice-out. The mean number of marked fish varied from year to year between 950 and 4100 resulting in recaptures of 111–811 marked perch. The aim was for the 95% confidence limits to be less than ±20% of the population estimate, and this was achieved in most years. A population estimate for 1990 (to be used in multivariate analysis) was derived from the 1991 value by using an estimate for annual mortality rate (M = 0.6; Thorpe 1977). Annual perch biomass was calculated as follows: first, based on the size distribution of the fish caught in the test fishing, the number of fish

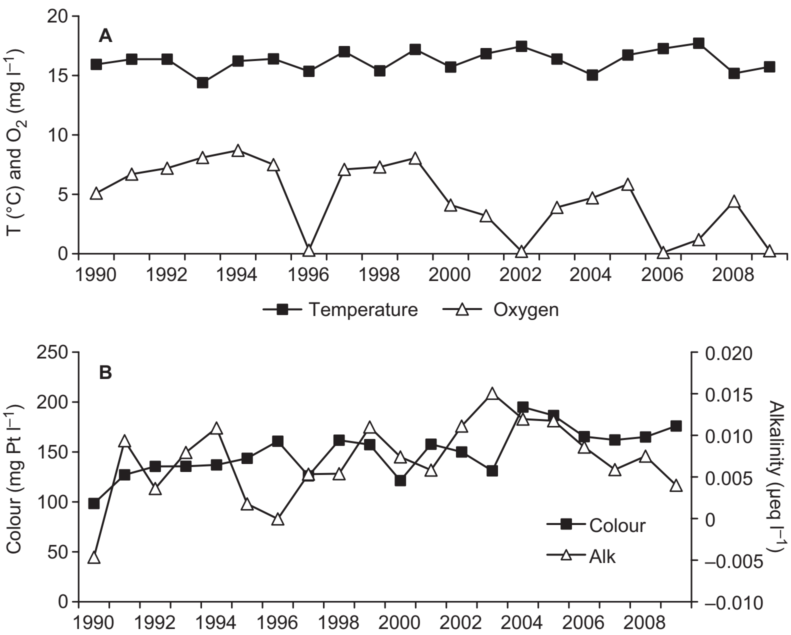

Fig. 1. (**A**) Mean water temperature (1 m depth, June–September) and oxygen concentration (2 m depth, week 33) and (**B**) mean alkalinity and water colour (1 m, June–September) in Lake Valkea-Kotinen during 1990–2009.

belonging to each size class in the whole population was estimated; second, biomass of each size class was estimated using the mean weight of perch from each length group (cm), calculated from the perch sampled for age and growth determination (n = 1266); these results were then summed to give the total biomass. Corresponding data for pike are not available.

Samples for age determination (50–100 perch per year) were taken from the last recapture catch. In some years additional samples were obtained from late summer gill-net sampling (NORDIC survey nets, CEN 2005). Each fish was measured to the nearest mm (total length) and weighed to the nearest g, and opercular bones were used to determine age and to back-calculate growth according to the Monastyrsky procedure (Raitaniemi *et al*. 1988). Relative year-class strength was determined using the Svärdson-Kempe method (Kempe 1962).

Water-quality (Fig. 1) and season-length (the number of days with water temperature at 1 m depth > 15 °C) data were obtained from the database of the Lammi Biological Station (University of Helsinki). Water-quality data are presented in more detail by Vuorenmaa *et al*. (2014). Data on primary production of phytoplankton and chlorophyll *a* (Fig. 2, *see* Arvola *et al*. 2014) and data on main zooplankton groups and *Chaoborus* larvae (Fig. 2, *see* Lehtovaara *et al*. 2014) are from the plankton database of the Lammi Biological Station (University of Helsinki).

A non-parametric Mann-Kendall test (Z-statistics; *see* Hipel and McLeod 2005) was used for long-term monotonic (i.e. increasing or decreasing) trend analyses of the perch population and growth parameters. No assumption of normality is required by the test, hence the non-transformed original data were used. To analyse the joint effects of abiotic and biotic factors (later called environmental variables) on the perch population and its growth parameters, expressed as annual length increment, a redundancy analysis (RDA, Canoco 4.51 (ter Braak & Šmilauer 2002) was applied since the gradient lengths of biotic variables were rather short, 3–4 SD units. All variables were standardized as follows: $(x_i - x)\mathrm{SD}^{-1}$. A Monte-Carlo permutation test (1000 permutations) was used to test the significances of the single variables and the RDA axes. As the measurements of a given variable were related to each other (sampled in successive years from the same lake), a time series option was used as a permutation restriction. The perch variables in the RDA analysis included seven variables that

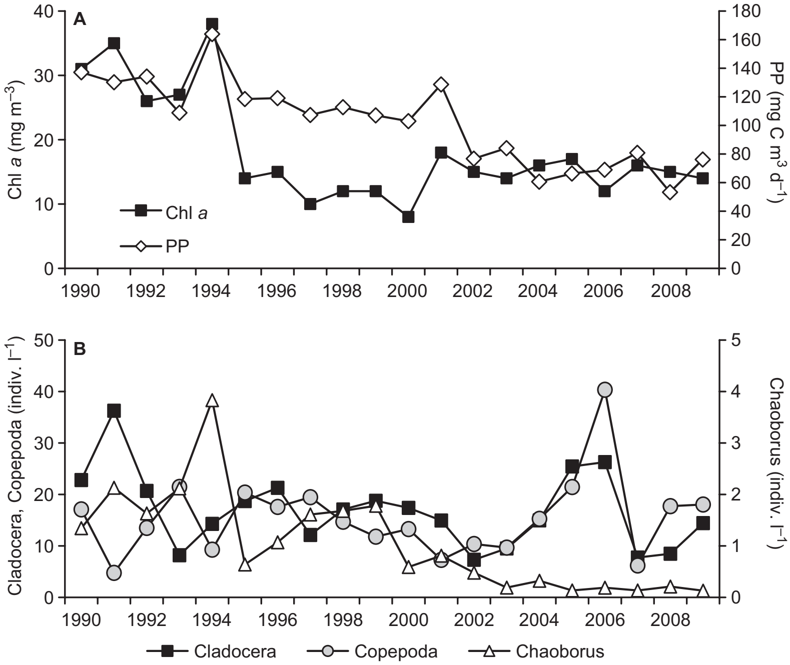

Fig. 2. (**A**) Primary production of phytoplankton (PP, 0–1 m, June–August) and mean chlorophyll a concentration (Chl *a*, 0–1 m, June–August) and (**B**) mean density of cladocerans, copepods and *Chaoborus* larvae (0–5 m, June–August) in Lake Valkea-Kotinen during 1990–2009.

were assumed to respond to environmental variables on a yearly basis: size of population, relative year-class strength and the length increments of 1–5-year-old perch in each year. The environmental variables were first selected in order to avoid high (> 0.8) between-variable correlation causing multicollinearity, and secondly based on maximum extra fit. The eight environmental variables entered in the RDA analysis included five water quality parameters (alkalinity, water colour, oxygen concentration at 2 m depth, total phosphorus (P_{tot}) and water temperature at 1 m depth), season length, and two biological parameters (primary production of phytoplankton and cladoceran zooplankton density).

Results

The perch population

The size of the perch population (individuals of > 8 cm in total length) varied between 2400 and 13 400 (570–3190 perch ha^{-1}) and the biomass between 16.1 and 44.2 kg ha^{-1} with no significant trends during the 20-year monitoring period (Fig. 3 and Table 1). The population size peaked in 1998 and the biomass in 1997, both due to the recruitment into the spawning population of the 1995 year-class, the strongest recorded during the study period.

During the first half of the study period, a four-year interval was apparent in the occurrence of strong year classes, which were born in 1991, 1995, 1999 and 2003 (Fig. 4). The year class 1991 formed the most abundant length group during 1993–1996 (Fig. 5), until the strongest year class 1995 appeared as numerous perch of size 8 and 9 cm in 1997. In 2001, 9 and 10 cm perch of the strong year class 1999 appeared as most abundant. During the latter part of the monitoring period there was less variability in the strength of year classes than in the 1990s but no significant trend was recorded (Table 1). Correspondingly, after 2003 the variation in size structure of the perch population stabilised with a dominance of small individuals (≤ 10 cm in total length; Fig. 5). This resulted in a significant negative trend in the mean length and weight of perch (Table 1).

The growth of perch

The growth of perch in Lake Valkea-Kotinen

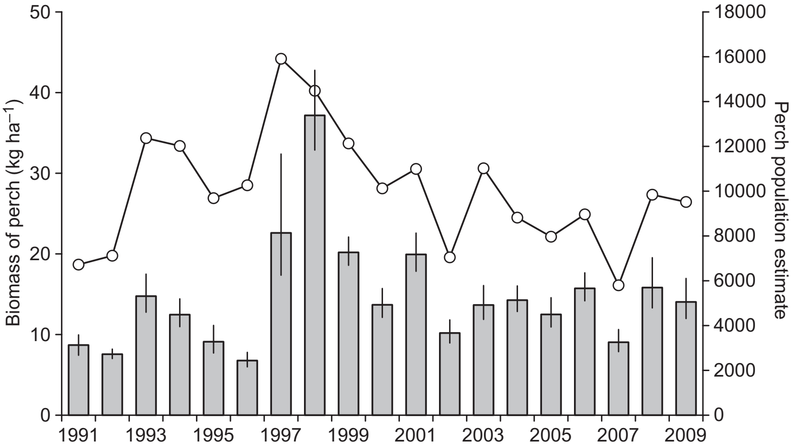

Fig. 3. Estimates (±95% confidence limits) of perch biomass (circles) and population size (bars) for Lake Valkea-Kotinen during 1991–2009.

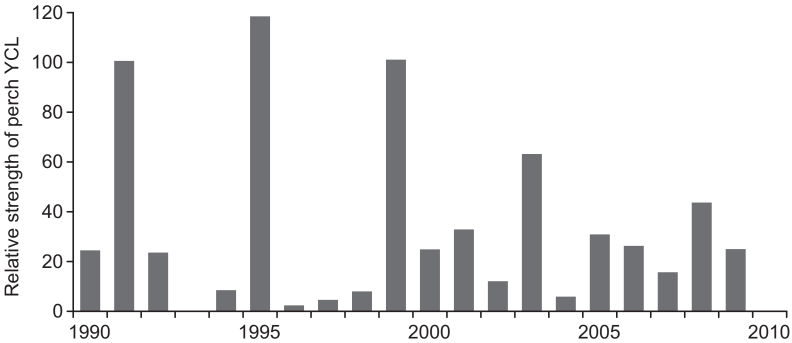

Fig. 4. The relative year-class strength of perch in Lake Valkea-Kotinen during 1990–2009.

was fairly slow as the total length of 15 cm has usually not been exceeded before the fish reached the age of five or six years (Fig. 6). During the study period, a significant decreasing trend in perch growth was recorded in their first summer and slowing growth also during the 2nd and 3rd summers. In contrast, in 4- and 5-year-old perch the trend was slightly positive (Table 1 and Fig. 7), although the back-calculated length of 5-year-old perch in 1990 was close to the

Table 1. Mann-Kendall statistics for trends in perch population variables and growth in Lake Valkea-Kotinen during 1990-2009. Significance of Z values are as follows: $p < 0.1$ when $|Z| > 1.563$, $p < 0.05$ when $|Z| > 1.862$, $p < 0.01$ when $|Z| > 2.447$.

Perch variable	Range	*Z*	*p*
Population size	2400–13400	0.91	ns
Biomass of perch (kg ha^{-1})	16.1–44.2	–0.616	ns
Density of perch > 15 cm (indiv. ha^{-1})	82–487	–1.19	ns
Relative year–class strength	8–355	–0.681	ns
Mean length of perch (mm)	101–155	–2.239	< 0.05
Mean weight of perch (g)	13–50	–2.029	< 0.05
1st year growth (mm)	48.8–63.3	–3.439	< 0.01
2nd year growth (mm)	24.5–45.8	–1.752	< 0.1
3rd year growth (mm)	16.7–29.6	–1.849	< 0.1
4th year growth (mm)	14.5–26.9	1.428	ns
5th year growth (mm)	8.5–24.5	1.622	< 0.1

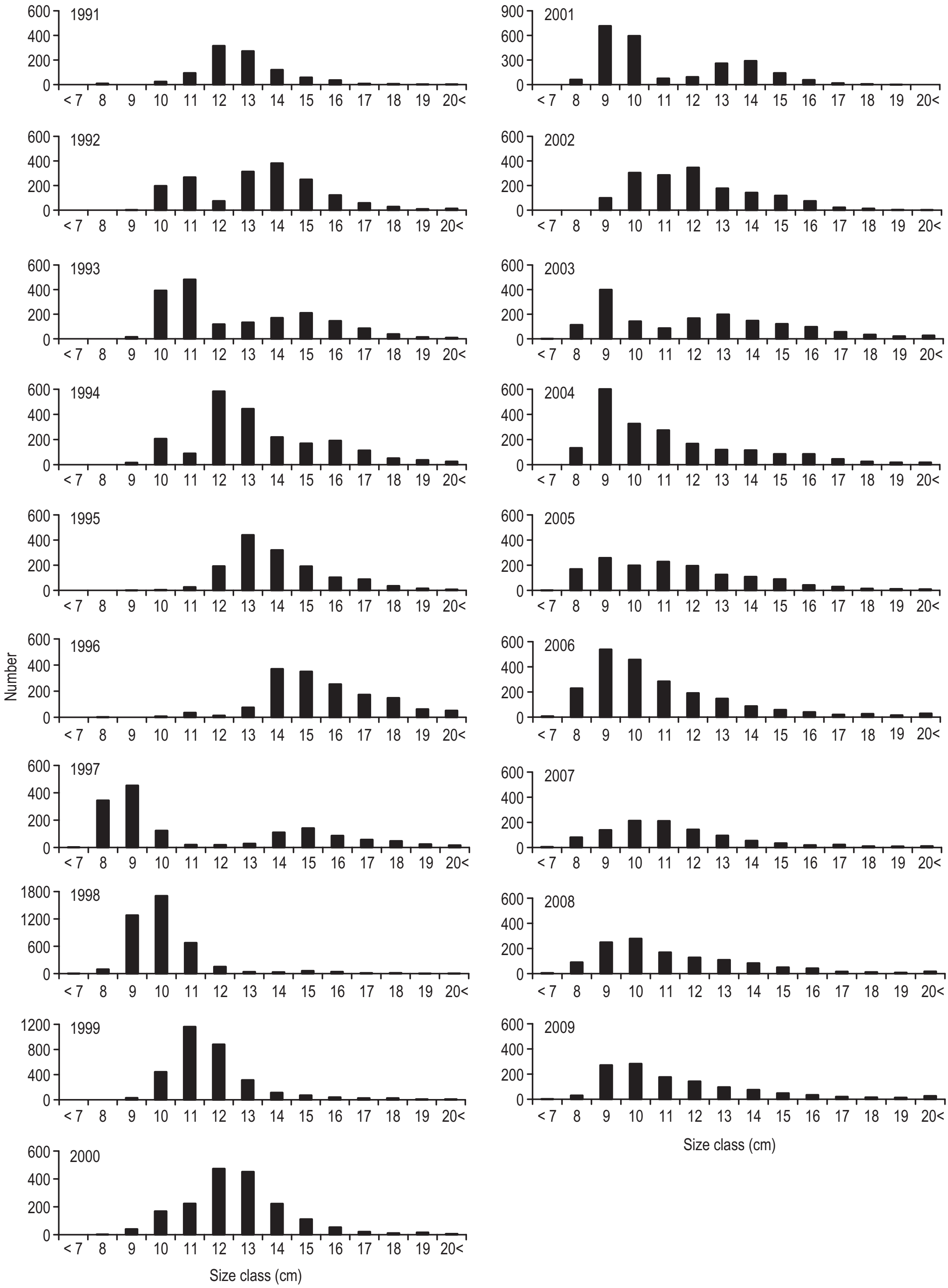

Fig. 5. The length frequency distribution of perch in Lake Valkea-Kotinen during 1991–2009.

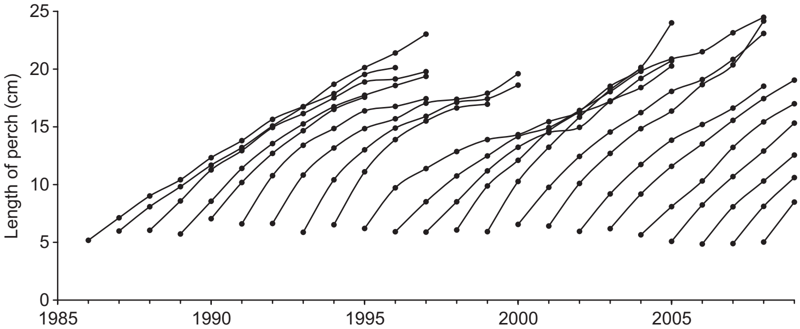

Fig. 6. Back calculated growth of perch from year-classes 1985-2007 (n = 1266, 5–245 per year-class).

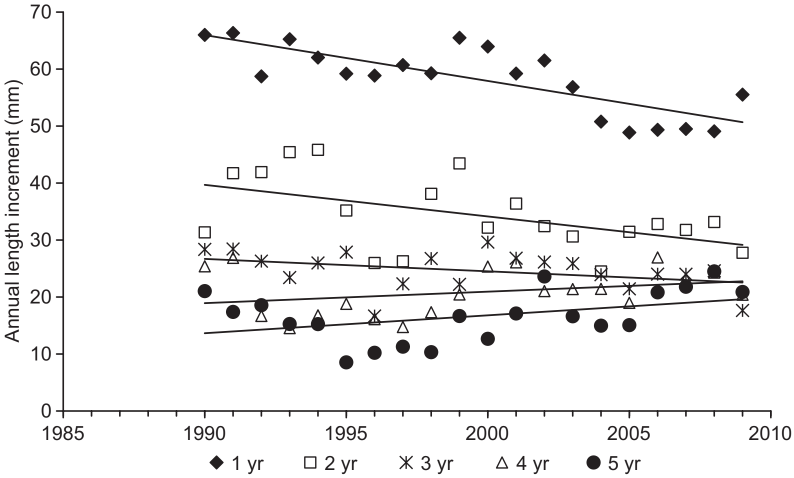

Fig. 7. The trends in annual length increment of perch at age 1–5 years in Lake Valkea-Kotinen during 1990–2009.

records of the last research years indicating that no actual trend existed. Nevertheless, the length at age 5 decreased until the last half of the 1990s, showing slowest growth during the years of highest population size and thus suggesting density-dependent decrease of growth in those years.

Effects of environmental and biological factors

The RDA analysis of the perch and environmental variables suggested that environmental variables had a rather weak effect on the year-class strength or population size, but a relatively strong and varying effect on the growth in different age classes (Table 2 and Fig. 8). The relationships between perch variables, and between perch variables and environmental variables were statistically significant (p = 0.022 in both cases; Table 2). However when the environmental variables were considered separately in the RDA analysis, only oxygen concentration had a significant effect (p = 0.033) on the matrix of perch variables. The first RDA axis explained 26% of the variation in the perch variables and 51% of the variation in the relationships between perch variables and environment variables.

On the first RDA axis, water colour had a strong positive score, and primary production and oxygen concentration had high negative scores indicating the gradient of low productivity, limited oxygenated layer and poor light conditions. Growth in the youngest age groups was strongly negatively affected by these variables; this indicates that during the first years perch growth was positively dependent on primary production and oxygen conditions and negatively dependent on water colour. In contrast, in older perch (age 4 and 5) this relation was positive which suggests a lower dependence of larger fish on pelagic food resources and on light conditions. Furthermore, the relative abundance of small perch increased during the study period providing a better prey-fish resource for large perch. Year class strength and population size were only weakly related to the first RDA axis. The brownification trend of the lake with decreasing oxygen concentration and primary production can also be seen in the RDA analysis, as the later years mostly have higher scores in the first RDA axis than the earlier ones.

The second RDA axis explained 16% of the variation in the perch variables and 24% of the variation in the perch and environment relationship (Table 2). On this axis, water colour had a high negative score, and P_{tot}, water temperature and cladoceran density positive scores indicating the gradient of good light, high food resources and warm water. All the perch variables except population size were positively related on this axis, especially growth of 3–5-year perch. This suggests that growth in older age groups is more dependent on good light conditions and warm water than that in young age groups.

Discussion

Perch population

The perch population and biomass estimates from Lake Valkea-Kotinen are in line with those from other studies of similar lakes in the Evo area (Rask 1983, Lappalainen *et al*. 1988, Horppila *et al*. 2010). The 20-year data from Lake Valkea-Kotinen revealed that the size of the perch population and the occurrence of strong year classes were only weakly associated with the environmental and biological factors considered, and were regulated more through intraspecific processes. This was seen in the weak associations of population density and year-class strength with the axes of the RDA analysis. The lake had never acidified to critical levels for perch reproduction in humic waters (*see* Henriksen *et al*. 1989), as shown by the occurrence of strong year-classes of perch during the "acidification years" of the 1990s, before the onset of pronounced chemical recovery of the lake around the year 2000 (Vuorenmaa *et al*. 2014). Perch is a warm-water species that is predicted to benefit from the warming of waters caused by climate change (Lappalainen and Lehtonen 1997, Jeppesen *et al*. 2012). However, in the case of Lake Valkea-Kotinen, this was seen neither in the occurrence of strong year-classes nor in the positive responses of early growth of perch (*see* Jeppesen *et al*. 2012).

In the first half of the monitoring period, the fluctuation of the perch population size followed the occurrence of strong year-classes that were born at a 4-year intervals until the early 2000s. This kind of pattern has often been recorded in small perch-dominated lakes where larger cannibalistic perch can prevent the recruitment of YOY fish until the density of large individuals is small enough to enable the development of a new strong year-class (Alm 1952, Persson *et al*. 2000). In the latter part of the monitoring period, since the early years of the 2000s, no really strong or weak year-classes occurred and the population was dominated by small individuals. The decreased average size of perch is in line

Table 2. Results of the RDA analysis of perch variables, and of environmental variables during 20 years of monitoring in Lake Valkea-Kotinen. Axes 1 and 2 are the first two RDA axes.

Variable	Axis 1	Axis 2	All
Perch variables			
5 yr. length increment	0.5975	0.3818	
4 yr. length increment	0.5737	0.5322	
Size of population	–0.1583	–0.2489	
Year class strength	–0.1941	0.3051	
3 yr. length increment	–0.2003	0.5918	
2 yr. length increment	–0.6430	0.2875	
1 yr. length increment	–0.7747	0.2713	
Environmental variables			
Water colour	0.5106	–0.5987	
Temperature	0.2018	0.3433	
Alkalinity	0.0791	0.1237	
Number of days when water T > 15 °C	–0.0186	–0.2287	
Total phosphorus	–0.1150	0.5547	
Cladoceran density	–0.1261	0.3472	
Primary production	–0.7632	0.2868	
Oxygen concentration	–0.7863	0.1325	
F	3.8150		2.008
p	0.0220		0.022
Variance explained (%)			
Perch variables	25.75	15.58	54.38
Perch–environment relation	51.29	23.73	91.64

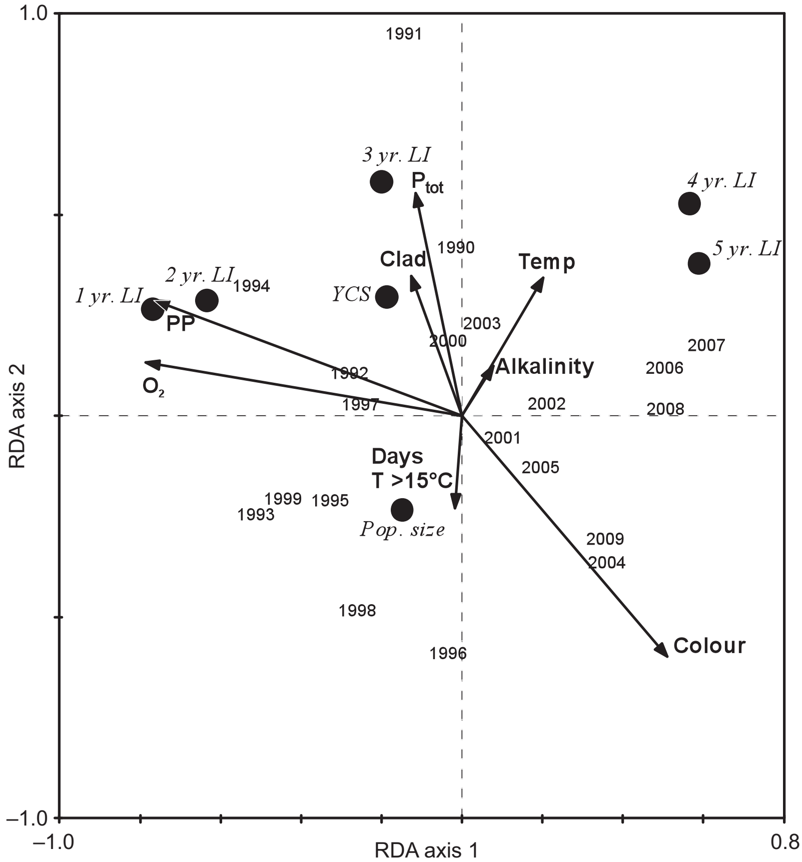

Fig. 8. Biplot of the redundancy analysis for perch variables and environmental variables. Pop. size = size of perch population, YCS = relative year-class-strength of perch, 1 yr. LI = first year length increment etc., Colour = water colour, Temp = water temperature, P_{tot} = total phosphorus, O_2 = oxygen concentration, Days T > 15 °C = number of days with water temperature (1 m) > 15 °C, PP = primary production of phytoplankton, Clad = cladoceran density. Scores for the sampling years (1990–2009) are also shown.

with the observations from Denmark (Jeppesen *et al*. 2012), related to improved recruitment of fish due to higher spring temperatures and increasing survival of fish during winter due to shorter ice-cover period. Moreover, it has been predicted, by using a physiologically structured consumer-resource model that increasing water temperature, connected with enhanced intraspecific competition, may result in dominance of younger and smaller perch (Ohlberger *et al*. 2011).

One possible explanation for decreased mean size of perch might be reduced predation pressure from pike, although due to the lack of long-term pike data this cannot be ascertained. However, other studies from similar lakes have suggested that the intensity of pike predation can affect the perch population structure (Olin *et al*. 2010). Predation by pike decreases the perch population density and the intraspecific food competition among perch thus contributing to faster growth and larger mean size of perch (Rask 1983, Persson *et al*. 1996, Olin *et al*. 2010). On the other hand, dark coloured lake water may reduce the feeding efficiency of pike (Horppila *et al*. 2010).

Growth of perch

The main environmental factor affecting the early growth of perch in Lake Valkea-Kotinen appeared to be the organic carbon load, resulting in darker water, and decreased light. Overall, the limiting effect of worsening light conditions would outweigh the expected positive effect of increasing temperature on the growth of young perch (Jeppesen *et al*. 2012). It is possible that the decrease in the early growth of perch was — at least partly — a direct response to the deterioration of the light conditions as perch is a visually-oriented fish species and active especially at dawn and dusk (Helfman 1979, Rask 1986). Recent field and experimental studies showed the harmful effects of poor light conditions on the ability of perch to compete for food with roach and on the feeding efficiency of perch that may result in slower growth (Estlander *et al.* 2010, 2012).

However, a more important factor causing the decreased early growth of perch is a general decrease in the biological production of the lake, also related to the increased water colour. In Lake Valkea-Kotinen, there was a significant decreasing trend in the primary production (Arvola *et al.* 2014) and also in the densities of important food items for small perch, such as cladoceran zooplankton and *Chaoborus* larvae (Lehtovaara *et al.* 2014). A significant positive association between the primary production of phytoplankton and the early growth of perch, as indicated in the RDA analysis, suggests that the decrease in general productivity of the lake affected the perch growth via zooplankton as zooplankton is the primary food source of perch fry: first ciliates, rotifers and copepod naupli (Siefert 1972, Guma'a 1978, Zingel *et al.* 2012), followed by various crustaceans. The RDA analysis also emphasized the importance of oxygen, suggesting that the decreasing volume of the oxygenated habitat may affect the early growth of perch. The reduction of water volume suitable for perch can lead to increased intraspecific competition. At the same time, perch are forced to use the uppermost and warmer water layer which increases metabolism and the need for energy. The decreased early growth of perch may also be linked to the changes in the population structure, as it has been suggested that slow growth of plankton-feeding perch, especially slow second-summer growth, can lead to delay or inhibition of the later ontogenetic shift from benthivory to piscivory in perch populations (Heibo *et al.* 2005, Estlander *et al.* 2012).

The main reason for the slow growth of perch in Lake Valkea-Kotinen was presumably intraspecific food competition, as there were no competing fish species present. Although the growth was not as slow as in some other humic lakes without pike predation (Rask 1983, Lappalainen *et al.* 1988), it was far below the growth of perch recorded in the more productive and diverse ecosystems of larger lakes (Sarvala and Helminen 1996, Ruuhijärvi *et al.* 2010) or in oligotrophic lakes with low population density (Raitaniemi *et al.* 1988). The slight positive trend in the growth of larger perch, those of age groups of 4 and 5 years, indicates their different trophic position and better food resources or higher feeding efficiency as compared with the small planktivorous perch. The positive relation of older perch (age 4 and 5) to the first RDA axis suggests a lower dependence of larger fish on pelagic food resources and on light conditions, as they mainly consume littoral macroinvertebrates and small fish (Rask *et al.* 1998, Estlander *et al.* 2010). It appears that reduced light conditions have not affected the growth of older perch, although no data are available concerning possible changes in the benthic or littoral production of the lake during the study period. Additionally, as the average size of perch decreased during the monitoring period, there is more intrinsic prey of suitable size for older perch which might partly explain their improved growth.

In conclusion, the results of our 20-year study indicate that the population dynamics of perch is mainly regulated by intraspecific processes, whereas the changes in growth were more closely related to the trends in environmental factors. The decrease in the early growth of perch was most clearly related to the increase in water colour and subsequent decrease in general productivity of the lake, including decrease in food resource production for small perch and subsequent intraspecific food competition. These changes outweighed the expected positive effect of increasing temperature for young but not for the older perch.

Acknowledgements: We express our thanks to the many people from Evo Fisheries Research Station of the Finnish Game and Fisheries Research Institute, Lammi Biological Station of the University of Helsinki, Finnish Environment Institute, and other institutions for contributing to the long-term monitoring in the Valkea-Kotinen area. Roger Jones kindly checked the language of the manuscript.

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