

Biotic and abiotic effects on cohort size distributions in fish

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Intraspecific variation in body size is common in animals and plants. Body size affects trophic interactions like foraging ability and vulnerability to predation, which in turn affect individual fitness as well as population stability and extinction risk. Experimental and theoretical work has shown that the size distribution of individuals within cohorts is strongly influenced by intraspecific competition for resources, often leading to skewed frequency distributions. However, little is known about the effects of environmental factors such as climate and eutrophication on the cohort size-structure of natural populations. We use a long-term time series of scientific monitoring of a freshwater fish (European perch *Perca fluviatilis*) to investigate the effects of density dependence, predation, nutrient availability, climate and the timing of spawning on the cohort size distributions. We find that the mean length of the fish is best predicted by the extrinsic factors phosphorus concentration and summer temperature, and the densities of the different age-classes, whereas the skewness of the length distribution is best predicted by phosphorus concentration, summer temperature, abundance of small fish, and the timing of spawning. Higher nutrient levels, temperatures and densities of small fish increase food availability and thus reduce competition, which is reflected in increased mean length and decreased skewness. The timing of spawning affects skewness presumably through changes in the initial size variation of the cohort and the length of the first growth season. Our results indicate that higher temperatures increase the mean length and decrease skewness due to the concurrent eutrophication of the lake. The study thereby highlights the potential impact of human-induced environmental change on the size structure of fish populations. More studies are needed to understand better the complex mechanisms through which these factors alter the intensity of intraspecific competition in fish communities.

Body size is one of the most important traits determining individual performance and life history (Peters 1983, Calder 1984). Intraspecific size variation affects ecological interactions such as competition and predation (Persson and De Roos 2007), population stability and extinction risk through density dependence (Maret and Collins 1994, Grimm and Uchmanski 2002, Pfister and Stevens 2002), as well as food-web structure and evolutionary processes (Blackburn and Gaston 1994, Loeuille and Loreau 2005). Considerable size variation is commonly found within populations due to age structure and genetic variation, and because individuals experience different environmental conditions (Lomnicki 1988, Persson and De Roos 2007). Size differences between age-cohorts can have stabilizing or destabilizing effects on population dynamics, while size variation among individuals within the same cohort generally stabilizes population dynamics (Lindström and Kokko 2002).

Differences in size among similar-aged individuals of a population (cohorts) have been related to intrinsic factors such as initial size variation at birth and extrinsic factors related to interactions between individuals and the environment (Huston and DeAngelis 1987, DeAngelis et al.

1993, Pfister and Stevens 2002, Huss et al. 2007). Despite increasing interest in the role of the environment in generating size differentiation (Peacor and Pfister 2006), little is known about environmental impacts on cohort size distributions in natural populations. This is of particular interest with respect to global change, because climate affects consumer body sizes, population dynamics and community structure through various temporal and spatial processes (Stenseth et al. 2002, Jeppesen et al. 2010, Rogers et al. 2011). Temperature may influence cohort size distributions by altering 1) the competitive interactions between individuals through changes in energy demand/supply (Ohlberger et al. 2011a), 2) rates of size-dependent survival, or 3) the initial size variation at birth through shifts in the timing of the reproductive season (Johnson and Evans 1991). Similarly to climate, eutrophication may affect the size distribution through changes in food supply (Teixeira-de Mello et al. 2009, Davis et al. 2010).

Body sizes of individuals within a cohort are often not normally distributed, but instead show negatively or positively skewed frequency distributions (Uchmanski 1985, Latto 1992). Size distributions are thus more accurately

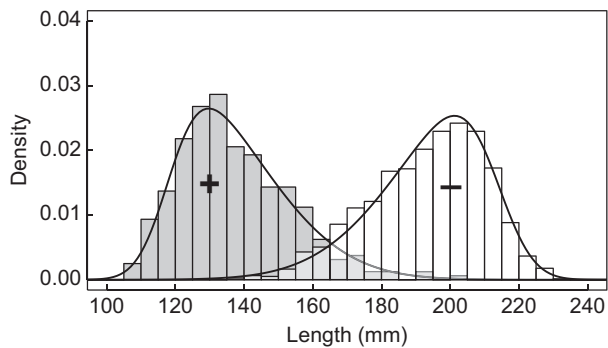


Figure 1. Illustration of the skewness concept exemplified using two observed size distributions of 3-year-old male perch in the Windermere south basin. Solid lines represent the fitted multivariate skew-normal distributions. The two distributions are characterized by different degrees of skewness (5.1, -7.0), but similar coefficients of variation (0.12, 0.09). Positively skewed (+) distributions with a higher frequency of small individuals are expected in high competition environments, whereas negatively skewed ($-$) distributions with a higher frequency of large individuals are expected in low competition environments (see text).

characterized when considering the third moment or skewness of the distribution, instead of using the mean and variance alone, also referred to as size dispersion (Bowker 1995), which implicitly assumes that sizes are normally distributed. For example, the frequency distributions shown in Fig. 1 have very similar variances but clearly different degrees of skewness. Such skewed size distributions may affect ecological processes at the population and community level, for instance through size-dependence in fecundity, food consumption or susceptibility to predation. It is thus important to understand how biotic and abiotic factors affect the mean and variance as well as the shape of cohort size distributions in natural populations.

Stochastic and mechanistic growth models suggest that cohort size distributions are positively skewed (higher frequency of small individuals) when food conditions are poor and population density is high, and symmetrical or negatively skewed (higher frequency of large individuals) when food is not limiting (Uchmanski 1985). Such models generally predict skewed frequency distributions of age-cohorts for populations with density-dependent growth. This has been demonstrated by experimental studies for several animal and plant species (Weiner 1985, Latto 1992, Ziemba and Collins 1999, Peacor and Pfister 2006). Accordingly, measures of skewness have been used to make inferences about resource competition and growth in past and present environments (Benjamin and Hardwick 1986). Nevertheless, simple growth models may be inadequate to predict size distributions in the wild as they ignore features of real populations like size-dependent mortality, migration or complex environmental impacts. Assessments of the effects of environmental conditions on skewness in animal size distributions are scarce (but see Lekve et al. 2002), because they require long time series to detect environmental forcing as well as many individuals per cohort in order to obtain reliable estimates of skewness.

Here, we explore the impacts of biotic and abiotic factors on size distributions of perch *Perca fluviatilis*, a

widely distributed and commercially important freshwater fish. Using a time series from long-term scientific monitoring of perch in the temperate lake of Windermere (UK), we determine skewness of cohort size distributions throughout the time series and model how skewness, mean and variance of the distributions depend on environmental conditions during cohort growth. Windermere, a glacial valley lake in the English Lake District, is divided into a north and south basin by shallows and islands (Le Cren 2001). Perch, the most abundant fish species in the lake, is preyed upon by the top predator pike *Esox lucius*, but is not exploited by removal fisheries. In Windermere, mean annual water temperatures have risen during the last three decades (Winfield et al. 2008) and nutrient levels have increased from the early 1950s to the early 1990s with a more than 10-fold increase in phosphorus and presumably increased bottom-up fuelling of the food-web (Parker and Maberly 2000). In 1976 and during the following years, a disease outbreak in the form of a perch-specific pathogen induced a massive mortality among perch (Bucke et al. 1979), which resulted in a major demographic and life history change in the population (Edeline et al. 2008, Ohlberger et al. 2011b, c).

Building on this knowledge about the various extrinsic impacts on Windermere perch and the importance of resource competition and cannibalism in this population (Le Cren 1992, Ohlberger et al. 2011c), we modelled the mean, variance and skewness in cohort size distributions of 3-year-old perch considering the following explanatory variables: the abundance of the different perch age-classes to test for effects of intraspecific competition (age 3) and cannibalism (ages 2 and 4+); the abundance of pike to test for potential effects of interspecific competition (age 3) and predation (age 4+); the summer surface temperature and the phosphorus concentration in the lake as a proxy for food availability to test for direct and indirect effects on perch growth; the winter North Atlantic Oscillation (NAO) index in the year of birth to test for potential effects of longer-term climate variability; the winter temperature in the first year of life to test for size-specific winter survival, the timing of spawning of the parental cohort to test for indirect effects on progeny size distribution; and the absence or presence of the pathogen to test for interaction effects with other biotic and abiotic variables.

Material and methods

Sampling

Windermere (54°22'N, 2°56'W) comprises a mesotrophic north basin (area 8.1 km², maximum depth 64 m) and a eutrophic south basin (area 6.7 km², maximum depth 44 m). The scientific sampling of perch started in 1943 and continues today with very little changes in gear type and fishing methods. Perch trapping takes place for six weeks on the spawning grounds with traps that are unselective for perch of 90–300 mm total length (Le Cren et al. 1977). Due to the trapping being on the spawning grounds, the catch contains disproportionately high numbers of mature compared to immature fish as well as males compared

to females. Each individual fish is measured for total length, sexed by internal examination and for a subsample of the fish the left opercular bone is removed for age determination.

Biotic and abiotic variables

We used perch abundances of the ages 2, 3, and 4–6 (PE_{age_n}), that is, the subsequent cohort (age 2), the cohort under consideration (age 3), and the preceding cohorts (ages 4–6), thereby testing for the potential effects of cannibalism, competition and predation between age-classes. We further used pike densities of age 3 and ages 4–8 (PI_{age_n}), thereby testing for the potential effects of competition and predation. Pike and perch population abundances were taken from a recent estimation of age-specific population numbers fitted to the long-term time series of catch and effort data from Windermere (Langangen et al. 2011). Environmental variables were taken from the long-term scientific monitoring of Windermere (Parker and Maberly 2000, Le Cren 2001). The phosphorus concentration (P_{year_m}), measured as mean concentration of soluble reactive phosphorus during the first four weeks of the year, and the average summer temperature (ST_{year_m}), measured from July to September, were tested for all lag-effects within a cohort lifetime (e.g. a $year_1$ effect of the environmental variables in our model refers to the 1st year of life). Phosphorus was used as a proxy for food availability, because phosphorus is known to be a limiting factor of phytoplankton and thus zooplankton growth (Urabe et al. 1997, Makino et al. 2002). We used the NAO index of the winter before a cohort was born (NAO_{year_0}) to represent effects of large-scale climate variability on the spawning and early life-stages of the fish (a positive NAO is indicative of warm and wet winters in northern Europe). The average temperature of the first winter (WT_{year_1}), measured from January to March, was used to capture potential effects of size-selective winter survival (Johnson and Evans 1991, Heermann et al. 2009). The timing of spawning of the parental cohort (SP_{year_0}), measured as the week by which 50% of that year's spawner catch had been recorded, was tested because size variation at birth is known to be an important determinant of size variation later in life (Hopper et al. 1996). We further used the absence or presence of the disease (D) and basin (B) as explanatory factors. An overview of all covariates is given in Table 1.

Statistical analyses

We first log-transformed the population estimates of perch and pike, because population numbers were not normally distributed, and centred the continuous predictors. We then tested for collinearity between explanatory variables (in both models, see below) using variance inflation factor (VIF) analysis, in which we iteratively removed covariates from the analysis and re-run the algorithm until all VIF values were lower than 5. We used this cut-off, because strongly correlated covariates were not removed using a threshold of 10 (Montgomery and Peck 1992, Zuur et al. 2010). Based on the VIF analysis, abundances of pike (age 3 and 4+) and the phosphorus concentration in the 2nd

Table 1. Summary of explanatory variables and factors used in the models.

Variable	Term	Description
Time	Y	year
Biotic	PE_{age_n}	perch abundance of the cohort of age n
	PI_{age_n}	pike abundance of the cohort of age n
	SP_{year_0}	week by which 50% of parental spawners had been caught
Abiotic	P_{year_m}	phosphorus concentration in year m of the cohort lifetime
	ST_{year_m}	summer temperature in year m of the cohort lifetime
	WT_{year_1}	winter temperature in the first year of the cohort lifetime
	NAO_{year_0}	NAO index of the winter before a cohort was born
Factor	B	north (n) and south (s) basin
	D	absence (0) or presence (1) of the disease

year were not considered in the model selection (pairwise correlations between variables 0.6–0.9). We tested for interactions among the continuous variables and the extra nominal factors (disease, basin) using conditional plots to identify candidate interaction terms for the models. Model selection was based on significances of parameter estimates using a threshold level of 0.05. Statistical analyses were performed in R (ver. 2.12.2, R Development Core Team).

Mean and variance model

We used linear mixed effects models (LME, Pinheiro and Bates 2000) to simultaneously model changes in the mean and variance in length of all 3-year-old male perch for which length data were available ($n = 25\,471$). Assumption of normality in the distribution of lengths was not violated for the full data set of all individuals over the entire time period. Random effects accounted for the lack of independence of the individual length data within each year. The model was constructed starting with the full model including all explanatory variables and factors. We tested for random effects by comparing the linear model to the same model including random intercepts using a likelihood ratio test between nested models based on a chi-squared distribution. The model was fitted using restricted maximum likelihood (REML) parameter estimation. We then compared different variance structures based on the full model and selected the best variance structure based on the likelihood ratio test. The tested variance structures included the explanatory variables and their interactions with disease and basin according to exponential or power relationships. We subsequently excluded non-significant fixed effects from the model, one at a time, based on the p -values of the parameter estimates. The different fixed effects models were fitted using maximum likelihood (ML) parameter estimation. The model selection was also performed using the BIC, which yielded results that were consistent with the likelihood ratio test. We used the Bayesian information criterion (BIC), because it is more restrictive on increasing model parameter numbers compared to the Akaike information criterion (Schwarz 1978). In order to detect possible nonlinear effects of the covariates, we fit a generalized additive mixed model (GAMM, Wood 2006)

with smoothers (natural cubic splines with three knots) on the previously selected fixed effects. The GAMM model included the random effects and variance structure selected using the LME framework. We limited the number of knots to three to reflect plausible biological responses of mean length to any given covariate. The LME and GAMM were fit using the R packages 'nlme' (ver. 3.1-102, Pinheiro and Bates 2000) and 'mcgv' (ver. 1.7-6, Wood 2006), respectively. The time series for the mean, variance, and skewness are presented in Fig. 2.

Skewness model

The skewness (S) of the length distributions in each year

was estimated according to: $S = \frac{\frac{1}{n} \sum_{i=1}^n (x_i - \bar{x})^3}{\left(\frac{1}{n} \sum_{i=1}^n (x_i - \bar{x})^2\right)^{\frac{3}{2}}}$, where

x_i with $i = 1 \dots n$ denote the sample of n observations (in our case the length measures of a given cohort in a given year), and \bar{x} is the sample mean. It follows from this definition that a normal distribution has a skewness value of 0. The length distributions were tested for normality using the D'Agostino normality test (D'Agostino et al. 1990). We estimated the skewness of size distributions for all cohorts with more than 50 individuals in our dataset, because this minimum sample size is commonly adopted in large-sample normality tests (Sokal and Rohlf 1995). Therefore, we focused on 3-year-old males to model skewness in perch size distributions, which are the most abundant age-sex category in the catch data. Since the north and south basins

of the lake have distinct perch populations (Kipling and Le Cren 1984, Bodaly et al. 1989), we estimated skewness in the two basins independently and pooled these data for our model selection. The number of years for which skewness could be estimated was 32 in the south and 24 in the north basin ($n = 56$). Figure 1 shows two examples of size distributions of 3-year-old male perch from the time series. We tested for correlations between the estimated skewness, mean length and variation in length for each year. Pair-wise correlations were calculated using a correction for autocorrelated time series data where autocorrelation in the variables is accounted for by adjusting the degrees of freedom (according to the modified Chelton method as described by Pyper and Peterman 1998). Variation in length was calculated as the ratio of standard deviation in length to mean length (the coefficient of variation, CV). We used a multiple linear regression approach to model the skewness in the perch length distributions. Because of the low number of skewness data points, we performed a forward model selection by starting with the simplest model using a single explanatory variable that explained most of the variation in the data and subsequently increasing model complexity by adding one variable at a time. In each step, all explanatory variables were tested and only the one with the strongest additional BIC support was retained in the model until none of the remaining variables decreased the BIC value by more than 2. With the final model we tested whether any of the included variables could be removed without increasing the BIC value by more than 2. Once the optimal model was identified, we validated the model by testing for normality and homogeneity in the residuals and for temporal autocorrelation.

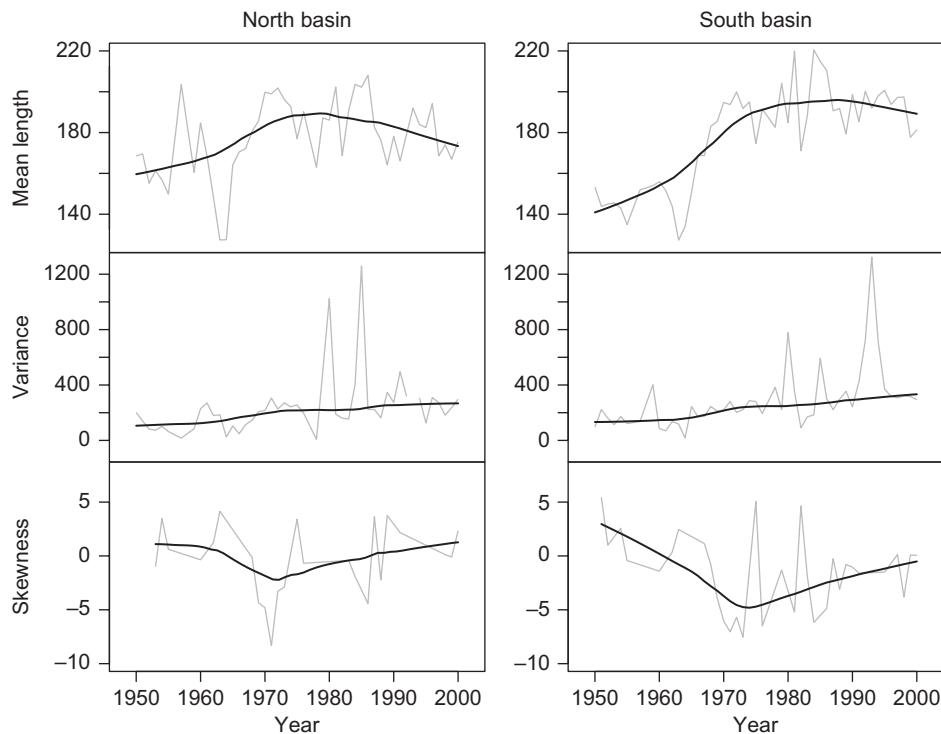


Figure 2. Time series of length data for 3-year-old perch in Windermere. Shown are the time series for mean length (top), variance in length (centre) and estimated skewness (bottom) for the north (left) and south (right) basins. Smoothed lines illustrate trends in the time series and were fitted using loess smoother with a smoothing parameter of 0.5 (span).

Results

Mean and variance

The selected mixed effects model of the mean and variance in length included the densities of perch (PE) in the different perch age-classes (2, 3, 4+), summer temperature (ST), phosphorus concentration (P), and year (Y) as continuous variables, the disease (D) and basin (B) as factors, and the interaction terms between year, basin and disease as follows:

$$L_{i,y} = \beta_0 + \beta_1 D + \beta_2 B + \beta_3 Y + \beta_4 PE_{age_2} + \beta_5 PE_{age_3} + \beta_6 PE_{age_{4+}} + \beta_7 ST_{year_s} + \beta_8 P_{year_1} + \beta_9 D \times B + \beta_{10} Y \times B + \beta_{11} Y \times D + b_y + \epsilon_{i,y},$$

where $L_{i,y}$ is the length of an individual (i) in a given year (y), β s are coefficients of the fixed effects, b_y is the random year group effect that is assumed to be normally distributed ($\sim N(0, \sigma_b^2)$), and $\epsilon_{i,y}$ is the normally distributed error term ($\sim N(0, \sigma^2)$). However, the variance in residual lengths ($\epsilon_{i,y}$) was further modeled as an exponential function of year and depending on the absence or presence of the disease: $\text{var}(\epsilon_{i,y}) = \sigma^2 e^{2\delta_D Y}$. The mean length of 3-year-old perch was found to increase with summer temperature, phosphorus concentration, and the number of young perch (age 2), but decrease with the number of older perch (ages 3 and 4+). The time series of mean summer temperature and the phosphorus content of the two basins are shown in Fig. 3. A temperature rise of 1°C, an increase in phosphorus of 1 mg m⁻³, and a 100% increase in 2-year-old perch increases the mean length of an individual by 5.8, 0.6 and 2.4 mm, respectively (Table 2). In contrast, a 100% increase in 3 and 4+ year old perch decreases the mean length by 1.3 and 2.9 mm, respectively. Furthermore, the disease decreased the mean length of the fish, especially in the north basin where the disease effect has been stronger than in the south basin. The year effect was positive in absence of the disease, and negative when the disease was present. The negative year effect after the disease outbreak was slightly weaker in the south compared to the north basin (Table 2). Furthermore, the variance in length increased over time, with a stronger increase per year before (1.94 mm) compared to after (0.88 mm) the disease outbreak. No apparent structure was present in the random intercepts of the selected model. Further details of the selected model are given in the Supplementary Material Appendix A1 Fig. A1. The generalized additive mixed model as shown in Fig. 4 illustrates the effects of the explanatory variables selected using the LME. The GAMM results justify the use of the linear modelling approach with a basin-specific year effect that switches from positive to negative around the year of the disease outbreak (1976). The goodness of fit of this model was 42% (adjusted $r^2 = 0.42$).

Skewness

In years for which skewness was estimated, the lengths were neither predominantly normally (~46%) nor non-normally (~54%) distributed. We found that the most optimal model describes the skewness (S) of size distributions in age-cohorts of perch as a function of the phosphorus

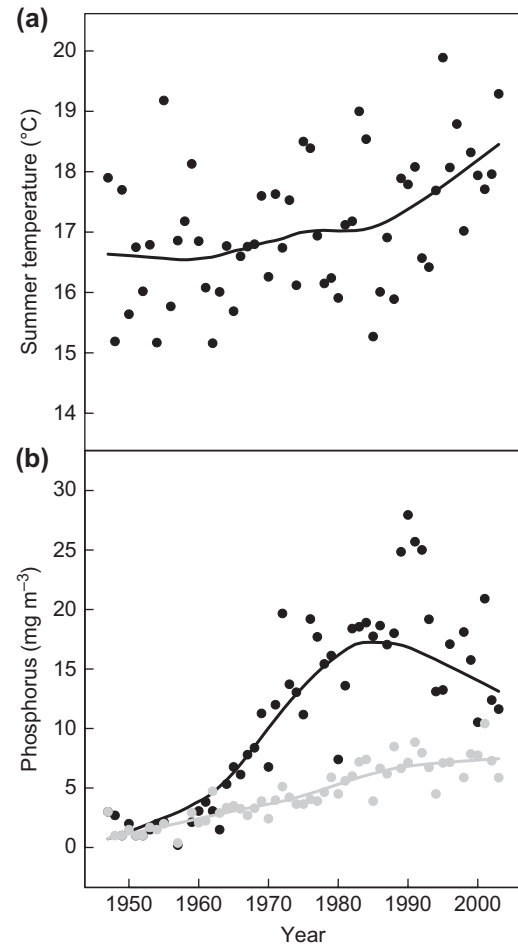


Figure 3. Time series of the two environmental variables included in the mean length and variance as well as the skewness model for (a) average summer temperature, and (b) phosphorus concentration (mean concentration of soluble reactive phosphorus during the first 4 weeks of the year). Temperature was measured in the shallows between the basins, whereas phosphorus was recorded separately for the north basin (grey) and south basin (black). Smoothed lines indicate trends in the time series and were fitted using loess smoother with a smoothing parameter of 0.5 (span).

concentration (P_{year_3}) and the average summer temperature (ST_{year_3}) of the previous year, as well as the time of spawning of the parental cohort (SP_{year_0}) and the density of the subsequent cohort (PE_{age_y}): $S_y = \beta_0 + \beta_1 P_{year_3} + \beta_2 SP_{year_0} + \beta_3 PE_{age_2} + \beta_4 ST_{year_3} + \epsilon_y$, where β s are the regression coefficients and ϵ_y is an error term. All four selected variables had statistically significant effects ($p < 0.05$) and the goodness of fit was 48% (adjusted $r^2 = 0.48$). Furthermore, none of the interaction effects with disease or basin were supported (Table 3). The skewness of the size distribution was found to decrease with increasing phosphorus levels, increasing summer temperature, a later spawning season and higher abundances of the age 2 cohort (Table 3). A temperature rise of 1°C, a one week earlier peak of spawning, an increase in phosphorus by 1 mg m⁻³, and a 100% increase in perch age 2 density decrease skewness by 1.27, 2.08, 0.13 and 0.81 units, respectively. The model partial effects and residuals of the final model variables are presented in Fig. 5. Details of

Table 2. Restricted maximum likelihood parameter estimates for the best linear mixed effects model of mean and variance in length (response centered) of 3-year-old perch ($n=25471$). Given are estimates, approximate upper and lower 95% confidence intervals (CI), and the statistical significances. Random effects represent year-specific intercepts ($n=46$). For explanations see Table 1.

Component	Lower CI	Estimate	Upper CI	t-value	p-value
Fixed effects					
Intercept	3.00	11.44	19.88	2.66	0.0079
B_S	-6.52	-5.02	-3.52	-6.57	<0.0001
D_1	-31.06	-15.86	-0.67	-2.11	0.0411
Y	0.65	1.25	1.85	4.23	0.0001
PE_{age_2}	1.67	2.40	3.14	6.42	<0.0001
PE_{age_3}	-2.14	-1.31	-0.47	-3.07	0.0022
$PE_{age_{4+}}$	-3.75	-2.97	-2.19	-7.44	<0.0001
ST_{year_3}	2.27	5.89	9.52	3.28	0.0021
P_{year_1}	0.42	0.57	0.71	7.72	<0.0001
$D_1 \times B_S$	7.79	10.06	12.33	8.68	<0.0001
$Y \times B_S$	0.29	0.38	0.48	7.92	<0.0001
$Y \times D_1$	-3.16	-2.21	-1.25	-4.64	<0.0001
Random effects*					
σ_b	8.99	11.33	14.28		
$\sigma(\epsilon_{i,y})$	15.36	15.57	15.78		
Variance function**					
δ_0	0.0081	0.0098	0.0116		
δ_1	0.0029	0.0044	0.0058		

*Presented are the standard deviations of the random effects. **The error variance was an exponential function of year depending on the absence (δ_0) or presence (δ_1) of the disease.

the selected model are given in the Supplementary Material Appendix A1 Fig. A2. The pair-wise correlation analysis showed that skewness was not correlated to the coefficient of variation in length ($r^2 = 0.001$, $p = 0.867$), and only marginally correlated to mean length ($r^2 = 0.1$, $p = 0.083$), as suggested by the time series plots presented in Fig. 2.

Discussion

We found that the extrinsic factors summer temperature and winter phosphorus concentration as well as the abundances of the different perch age-classes best predicted the mean length of the perch cohorts. Warm temperatures, eutrophication, and high abundances of small fish increased mean length, suggesting an increase in food availability and perch growth rates. On the other hand, higher densities of similar-aged and older fish decreased the mean length, indicating negative density dependence in perch growth at this level. In line with these results, skewness in the cohort size distributions decreased with increasing summer temperature, phosphorus content and the abundance of small fish, which supports the conclusion that these factors released perch from competition through increasing food supply. The spawning timing, which determines the length of the first growing season and the match/mismatch between perch and its prey, had a significant effect on skewness, but not on the mean length. These results indicate that intraspecific competition is the major process determining cohort length dynamics in perch, which is strongly influenced by environmental conditions such as nutrient concentrations and temperature, both of which increase mean length and decrease skewness.

The significant year effect in interaction with the disease suggests a potential evolutionary change in perch growth rate, considering that most of the ecological factors that are expected to affect the temporal trends in growth were accounted for in this study. The trend towards faster growth before and slower growth after the disease outbreak is in line with previous studies suggesting such an evolutionary response in Windermere perch (Edeline et al. 2008). The results also correspond to previous observations that the disease effect was stronger in the north compared to the south basin (Bucke et al. 1979, Edeline et al. 2008). The variance structure was best modeled using the year effect in interaction with disease. However, as expected much of the within-year variation in individual lengths could not be predicted based on the extrinsic factors considered here, which suggests that much of this variation is caused by intrinsic factors such as differences in genetics, behaviour, and maternal effects, or plasticity in response to some omitted environmental factor.

We found that increasing levels of phosphorus increased the mean length and decreased skewness in perch cohorts. Phosphorus is known to increase the growth rate of zooplankton, for instance in daphnids (Urabe et al. 1997, Makino et al. 2002), one of the main prey organisms of young perch in Windermere (Guma'a 1978). Published data on the plankton community in Windermere have also demonstrated a clear link between the numbers of *Daphnia* and the abundance of edible algae in the lake (George et al. 1990) and suggest that the progressive enrichment of the lake was the most important factor explaining the increase in zooplankton abundance from the 1960s to the 1990s.

The positive effect of increasing summer temperatures on the mean length of perch and the corresponding decrease in skewness are most likely mediated through a longer growing season, higher perch growth rates and an increase in food supply. Higher temperatures, at least within the range observed in Windermere, are known to increase the growth rate of daphnids (Mitchell et al. 2004). The positive effect on food availability seems to be more important than the indirect effects on recruitment and survival, which instead would be expected to result in higher population density and thus stronger competition (Le Cren et al. 1977, Craig et al. 1979, Winfield et al. 1998, Paxton et al. 2004). The fact that winter temperature in the first year of life did not have a significant effect on either mean length or skewness supports the conclusion. Higher average summer temperatures are further associated with a longer growing season and hence a higher growth potential, as Windermere perch will grow at temperatures above 14°C (Le Cren et al. 1977). Nevertheless, higher temperatures may have opposing effects on consumer populations because temperature usually increases resource growth rates, but at the same time leads to higher energy demands due to increasing metabolic costs and thus higher resource depletion. The latter effect can lead to severe consequences for size-dependent competition and survival and may result in resource limitation at high temperatures (Ohlberger et al. 2011a). However, a simultaneously increasing nutrient input into the lake may lead to a strong enough increase in energy supply thereby preventing food shortage. In this case, higher

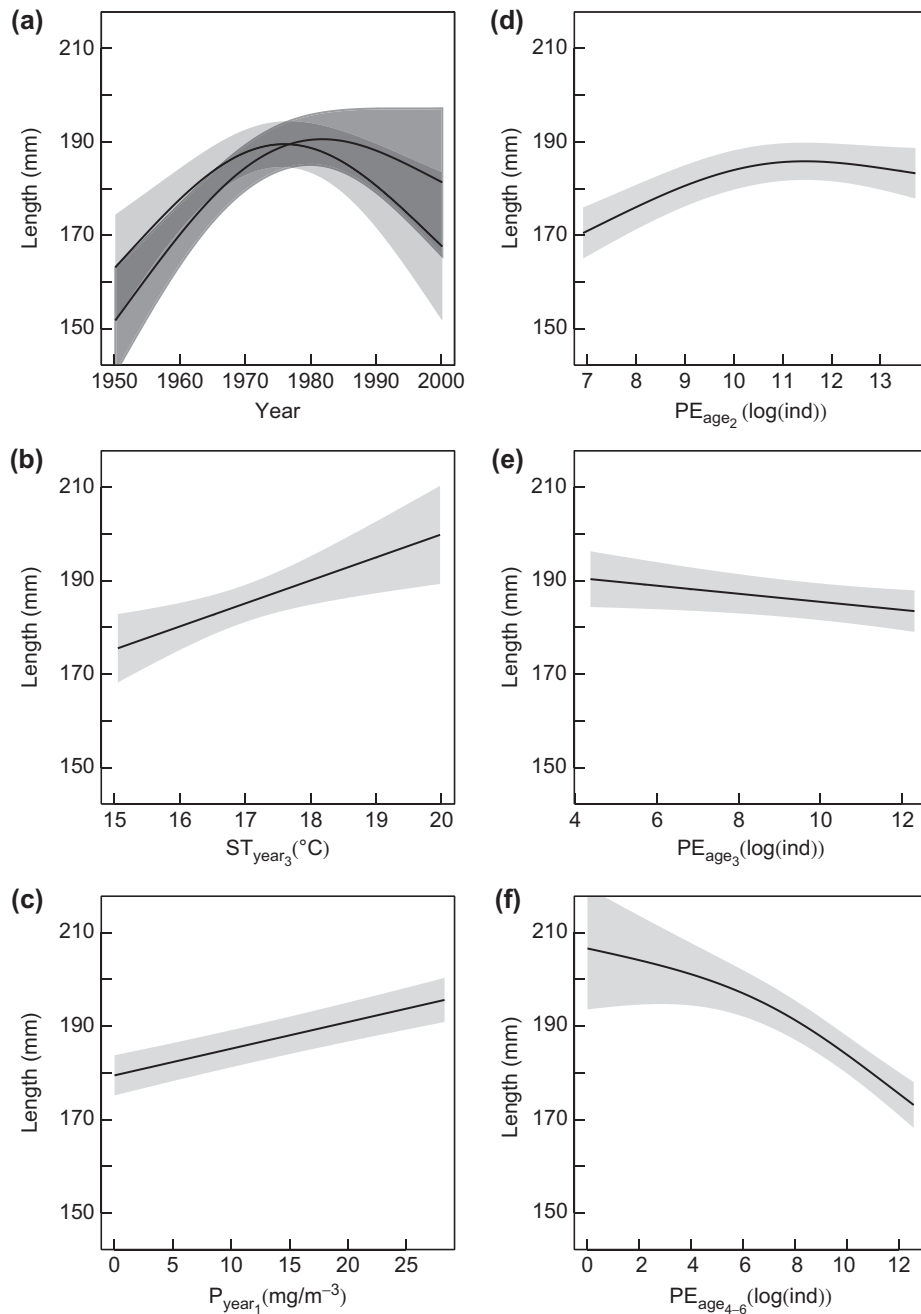


Figure 4. Results of the generalized additive mixed model (GAMM) for the mean and variance in length of 3-year-old perch. The selected covariates (based on the LME model) were year (a), summer temperature (b), phosphorus concentration (c), and the abundances of 2-year-old (d), 3-year-old (e) and 4–6-year-old (f) perch. The year effect is shown for the north (light grey) and south (dark grey) basins, suggesting an interaction between year and disease. For all other covariates the model suggests linear relationships.

Table 3. Parameter estimates for the best linear model of skewness in the length distributions of 3-year-old perch. Given are parameter estimates, upper and lower 95% confidence intervals (CI), and statistical significances ($n = 56$, $k = 6$, $r^2 = 0.48$). For explanations see Table 1.

Effect	Lower CI	Estimate	Upper CI	t-value	p-value
Intercept	-1.72	-1.04	-0.35	-3.04	0.0037
ST_{year_3}	-1.98	-1.27	-0.56	-3.59	0.0007
SP_{year_0}	-2.86	-2.08	-1.31	-5.39	<0.0001
P_{year_3}	-0.25	-0.13	-0.02	-2.35	0.0229
PE_{age_2}	-1.14	-0.81	-0.21	-2.72	0.0089

temperatures are expected to result in higher growth rates, an effect that is reflected in the increase in mean length and the decrease in skewness in perch cohorts. This suggests that increasing temperatures and nutrient levels have interdependent effects on the size structure of fish populations. This reasoning is supported by earlier studies suggesting that climate warming may induce changes similar to those produced by eutrophication and that these two processes of human-induced change may act synergistically on fish communities (Teixeira-de Mello et al. 2009). These conclusions may apply to a broad range of organisms with

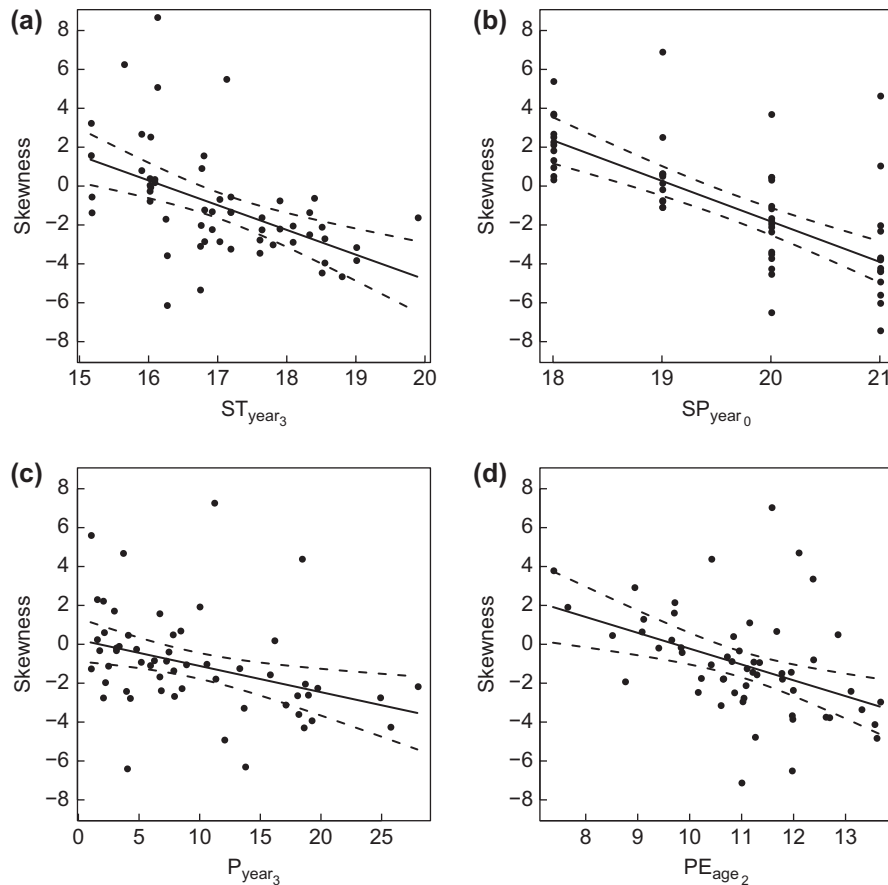


Figure 5. Partial effects for skewness of the size distributions of the 3-year-old perch. Shown are the model fits (solid lines) with 95% confidence bands (dashed lines) for the additive effects of (a) average summer temperature of the previous year (ST_{year_3}), (b) timing of spawning (50% of spawners caught) (SP_{year_0}), (c) phosphorus concentration of the previous year (P_{year_3}), and (d) density of the age 2 cohort (PE_{age_2}).

density-dependent growth within the range of temperatures that enhance individual growth.

Besides abiotic factors that affect the abundance and productivity of lower trophic levels, food availability in perch is also determined by densities of smaller fish, particularly perch fry, as this species is known to cannibalize its own young (Le Cren 1992). Cannibalism can have pronounced effects on individual growth patterns and population dynamics due to the surplus energy gain by cannibals (Persson et al. 2004). The abundance of smaller fish may affect the cohort size distribution in two opposing ways, by either serving as a food resource or by decreasing the availability of the common prey through exploitative competition. Our results show that high densities of 2-year old fish increase the mean length and decrease skewness, which suggests that cannibalism is an important food source for perch. On the other hand, cohort abundance had a negative effect on the mean length, thereby demonstrating density dependence in perch growth. The negative effect of similar-aged and older fish on the mean length was not detected in the skewness model, suggesting that these effects were too weak to be detected based on yearly skewness estimates. Such negative density dependence effects on cohort size distributions are common to age-structured populations in which individuals experience intraspecific competition.

Differences in size among individuals strongly depend on the initial size variation early in development. Besides intrinsic effects such as genetic variation or maternal effects (Wilbur and Collins 1973), slight differences in age result in initial size variation (Hopper et al. 1996). This variation depends on the timing and length of the spawning season and thus the hatching period (Huston and DeAngelis 1987, Borcharding et al. 2010). Our results show that the timing of spawning of the parental cohort influences the shape of the size distribution later in life. Later spawning results in size distributions with higher frequencies of large fish. This observation may have several explanations. First, later spawning is associated with a longer spawning season in perch, which may favour individuals that hatch early, in terms of both competition for zooplankton and intra-cohort cannibalism. Second, later spawning decreases the length of the first growth season, which may shift the size distribution towards larger fish due to higher winter mortality among small perch (Johnson and Evans 1991, Heermann et al. 2009). Third, earlier spawning may imply stronger competition as an effect of a mismatch between perch and its food (Borcharding et al. 2010), which has recently occurred in Windermere due to different phenological responses to climate change (Thackeray et al. 2010).

It has to be noted that other factors than those tested in our model may have altered the size distribution of perch cohorts indirectly. We do not account for behavioural changes such as diet shifts from feeding on zooplankton to feeding on macro-invertebrates (McCormack 1970, Craig 1978) and we do not consider the abundance of other planktivorous fish species in the lake such as roach *Rutilus rutilus* or Arctic charr *Salvelinus alpinus*. In particular, competition from roach, which have been increasing markedly in numbers since the 1990s in Windermere, may have a significant indirect effect on the perch sizes through changes in resource availability (Byström et al. 1998, Winfield et al. 2008). Finally, size-dependent predation can have a structuring impact on prey size distributions (De Roos and Persson 2002).

However, predation effects on size distributions of single cohorts may not be expected considering that pike feed on different parts of the cohort size spectrum at different times during the prey life cycle. Predation was not included in our model due to the strong inter-variable correlations, particularly between pike numbers and phosphorus concentration.

Our correlation analysis showed that skewness is weakly correlated to the mean and not correlated to the variance in length. This suggests that information about the shape of size distributions should be considered in ecological studies at the population level, complementary to the mean size. As an example, the reproductive output of a cohort in a given year will depend on the shape of the size distribution if maturation is size-dependent (e.g. perch: Treasurer 1981, Ohlberger et al. 2011b). Consequently, assessments of recruitment or reproductive output for management purposes that are based on mean size can lead to misinterpretation, depending on the actual distribution of sizes. Furthermore, size structure can be of particular importance in exploited populations, because the percentage of harvestable individuals may not be reliably predictable based on the mean size alone.

In conclusion, we show that cohort size distributions are strongly determined by environmental conditions, namely the availability of nutrients and summer temperature, as well as density-dependent interactions between age-classes. These findings indicate that increasing temperatures and nutrient levels may have synergistic effects on fish size distributions by simultaneously increasing energy supply and growth rates. This highlights the potential impact climate warming and eutrophication may have on the size structure of natural populations. Our results further suggest that the shape of size distributions should be considered in ecological studies, as it may comprise useful information that is not reflected in the mean and variance.

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Supplementary material (available online as Appendix O19858 at <www.oikosoffice.lu.se/appendix>). Appendix A1 (Fig. A1, A2).