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François Massol*†, Patrice David*, Daniel Gerdeaux† and Philippe Jarne*

* Centre d'Écologie Fonctionnelle et Évolutive (CNRS) - UMR 5175, 1919, Route de Mende, 34293 Montpellier cedex 5, France
† Centre Alpin de Recherche sur les Réseaux Trophiques des Écosystèmes Limniques (INRA), 75, avenue de Corzent - BP 511, 74203 Thonon-les-Bains cedex, France

Correspondence: François Massol
Address: Centre d'Écologie Fonctionnelle et Évolutive (CNRS) - UMR 5175, 1919, Route de Mende, 34293 Montpellier cedex 5, France
Email: francois.massol@cefe.cnrs.fr

Summary

A recurrent question in ecology is the influence of environmental factors, particularly nutrients and climatic variables, on community structure and functioning, and their interaction with internal community processes (e.g. competition).
Perialpine lakes have been subject to two main kinds of human-induced changes over the last fifty years: eutrophication - reoligotrophication, represented by lake-specific changes in total phosphorus concentration (TP), and long-term global climatic change, captured by average winter temperature (AWT).
Changes in fish communities (abundance of seven species from fishery data) in 11 Perialpine lakes during 31 years (1970-2000) were investigated in relation to variation in TP and AWT using models incorporating the effects of fish maturation age, and potentially discriminating effects on adult survival and recruitment.
We show that phosphorus concentration affects fish abundance in species-specific ways. These effects are mediated by recruitment rather than by adult survival. Phosphorus effects are probably modulated by interspecific interactions, as increasing TP enhances total community biomass, which in turn is either positively or negatively associated with species abundance depending on species position in trophic chains.
Climatic change has very little effect on fish abundances, which is not consistent with the prediction of larger changes in species near their southern distribution boundary.
We propose several hypotheses to account for those findings, and place our study in the wider framework of community ecology.

Keywords: fishery, foodweb, global warming, oligotrophication, recruitment.

Introduction

Changes in environmental conditions influence community structure, for instance by altering rates of physiological processes (e.g. consumption, maintenance), which may in turn affect ecological interactions (e.g. competition). The impact of environmental changes has been modelled through variation in resource consumption rate among species (Tilman, 1982) or dispersal patterns among communities (Levins & Culver, 1971; Tilman, 1994). Trophic (i.e. resources) and climatic (e.g. temperature) variables are thought to be of primary universal importance, whereas other environmental variables (e.g. pH, oxygen concentration, light) may be crucial in certain communities only. Community stability (Boer, Kooi & Kooijman, 1998; Hulot et al., 2000) and diversity (Ellner, 1996; Tilman, 1982) are theoretically affected by changes in resources. Nutrient concentration may influence species abundances, either through direct resource-dependence (Tilman, 1982), or through indirect food web effects (Hulot et al., 2000; Oksanen et al., 1981; Persson et al., 1992). Growth of aquatic plants and algae, for instance, depends crucially on the concentration of limiting nutrients such as phosphorus (Carpenter et al., 1987; Craft, Vymazal & Richardson, 1995). Climatic effects have also often been invoked to explain changes in species abundances (Blenckner & Hillebrand, 2002; Ottersen et al., 2001). External temperature indeed affects animal metabolism, especially in poikilotherms (Charnov & Gillooly, 2004; Gillooly et al., 2001), with consequences on feeding interactions (Vasseur & McCann, 2005). Moreover, it influences chemical and physical processes, thereby affecting the dynamics of nutrients (e.g. in freshwater ecosystems, Carpenter et al., 1992; Straile, 2002). Intrinsic processes, such as competition, recruitment and predation, also modulate the effect of environmental variables on communities. For instance, competition and maturation result in cyclical dynamics of abundances of adult year-classes (de Roos & Persson, 2003; Persson et al., 1998), while intra-guild predation may destabilise communities and induce alternative demographic stable states (Claessen & de Roos, 2003; Mylius et al., 2001; Persson, de Roos & Bertolo, 2004).

The interplay between resources and climatic variables on community structure will be studied here considering fish species in Perialpine (European) lakes. Over the last decades, some of these lakes have experienced dramatic change in trophic status, with a substantial increase in total phosphorus (TP) concentration (i.e. eutrophication) followed by reoligotrophication, whereas TP remained low in the other studied lakes (Gerdeaux, Anneville & Hefti, 2006). TP variation is known to affect fish communities (Colby et al., 1972; Gaedke, 1999): oligotrophic lakes experience a rise in percids and cyprinids, and a decline in salmonids when TP increases (Persson et al., 1992 and references therein). Meanwhile, minimum and average water temperatures in Perialpine lakes have likely increased due to the effects of global warming. Increasing lake temperature can affect fish communities in the wild (Beamish, 1995), for instance by enhancing the risk of deep water anoxia (de Stasio et al., 1996; Magnuson, Meisner & Hill, 1990; Schertzer & Sawchuk, 1990; Shuter & Post, 1990) by affecting reproduction e.g. in Arctic charr (Gillet, 1991) or roach (Gillet & Quetin, 2006), or by changing the timing of resource peaks (Straile, 2002). As both TP and temperature influence fish life-history traits and the abundance of their preys, these variables are expected to affect the structure of fish communities (e.g. Hill & Magnuson, 1990; Persson et al., 1992; Shuter et al., 1990). For instance, primary productivity is expected to increase with TP (Vadeboncoeur et al., 2003), and thus to affect positively piscivores and omnivores while having no effect on planktivores (Mylius et al., 2001; Oksanen et al., 1981; Persson et al., 1992). However, assessments of modifications in fish communities due to environmental changes have not been evaluated at large geographic scale (e.g. Perialpine lakes) yet.

Here we answer several questions related to dynamics of fish communities in Perialpine lakes. First, is it possible to disentangle and compare the effects of two environmental variables on communities using ecological time series? Second, do environmental variables have more impact on communities through their effect on per capita recruitment than through their effect on adult survival? Third, are the effects of temperature and TP consistent with what we know about the biology of studied species? Fourth, does community biomass mediate indirect effects of environmental variables on species abundances?

These questions were addressed by analyzing fishery yields of seven fish species over 31 years (1970-2000) in 11 Perialpine lakes distributed over 350 km along the North-western Alps (same data as in Gerdeaux *et al.*, 2006).Those data were analyzed using two statistical families of models. Fish abundances obtained from catches were analyzed together with environmental parameters, namely TP concentration in these lakes and the average winter temperature (AWT) in the studied region. We built alternative models to infer the validity of proposed hypotheses.

Material and methods
Study sites and data
Fishing yields and TP were recorded over the 1970-2000 period in 11 Perialpine lakes from the North-western Alps, including the largest lakes of this area. Some characteristics of these lakes are provided in Table 1. All of them are monomictic (i.e. undergo a single phase of water mixing-stratification per year), are located at relatively low altitude, and their surfaces never freeze in winter. TP records (Fig. 1 A) are the mean of TP concentrations (in $\mu g.l^{-1}$) over the whole water column just after winter vertical mixing, a variable commonly used to describe trophic status in lakes (Gerdeaux, 2004). Fishing yields were available for the whole period considered (Fig. 2), while some gaps occurred in the TP time series (Table 1).

We used monthly temperature reconstructions in the European Alps (Casty, 2005; Casty *et al.*, 2005), available online at ftp://ftp.ncdc.noaa.gov/pub/data/paleo/historical/alps/, to obtain the AWT around the 11 studied lakes during the 1970-2000 period. Data are available as monthly air temperature at different latitudes and longitudes. We used ten points of temperature reconstructions, corresponding to coordinates nearest to the studied lakes: 45°25'N/6°25'E (Annecy), 47°25'N/7°25'E (Biel), 45°25'N/5°75'E (Bourget), 46°25'N/7°75'E (Brienz), 47°25'N/9°25'E (Constance and Walenstadt), 46°25'N/6°25'E (Geneva), 46°75'N/8°25'E (Lucerne), 46°75'N/6°75'E (Neuchâtel), 46°25'N/7°25'E (Thun), and 47°25'N/8°25'E (Zurich). The AWT was defined as the temporal average from December to March of the average temperature over these ten points. Using the AWT as an indicator of climatic effects on fish communities is justified for two reasons. First, time series of monthly air temperature are best described using a linear model with a site-independent inter-annual component (Online Appendix S1). Second, the AWT is strongly correlated to the first principal axis of a principal component analysis of the monthly degree-days observed in the littoral waters of Lake Geneva (D. Gerdeaux, unpublished data) over the 1970-2000 period ($R^2 = 0.50$). This principal axis is well correlated with early spring degree-days in littoral waters, which affect the timing of zooplankton peaks, and thus the timing of resource availability for larvae of all lacustrine fish species (Straile, 2002).

Catch data were obtained for seven species: Arctic charr (*Salvelinus alpinus*, salmonid), brown trout (*Salmo trutta*, salmonid), burbot (*Lota lota*, gadid), Eurasian perch (*Perca fluviatilis*, percid), Northern pike (*Esox lucius*, esocid), roach (*Rutilus rutilus*, cyprinid), and whitefish (*Coregonus* sp., salmonid). These species can be considered as belonging to the

same community because they share resources (e.g. zooplankton and benthos), habitat (most reproduce in the littoral area) and predators (e.g., birds and humans), at least during part of their life cycle. Other species occurring in the lakes studied did not account for a significant proportion of fishery yields and will not be considered further. As a measure of species abundance, we used total catch per area per year (B, in kg.ha^{-1}.yr^{-1}). We assumed that fishing effort was constant for each species in each lake, implying that total catch and true abundance were multiplicatively related. The natural logarithm of total catch is thus a function of the logarithm of abundance, plus a constant accounting for capturability, which allows one to assess changes in abundance through changes in log B. Fishery yields and TP values were obtained from the "Fédérations Cantonales de Pêche" in Switzerland and the French "Ministère de l'Agriculture" (Gerdeaux *et al.*, 2006). The AWT was derived as explained above.
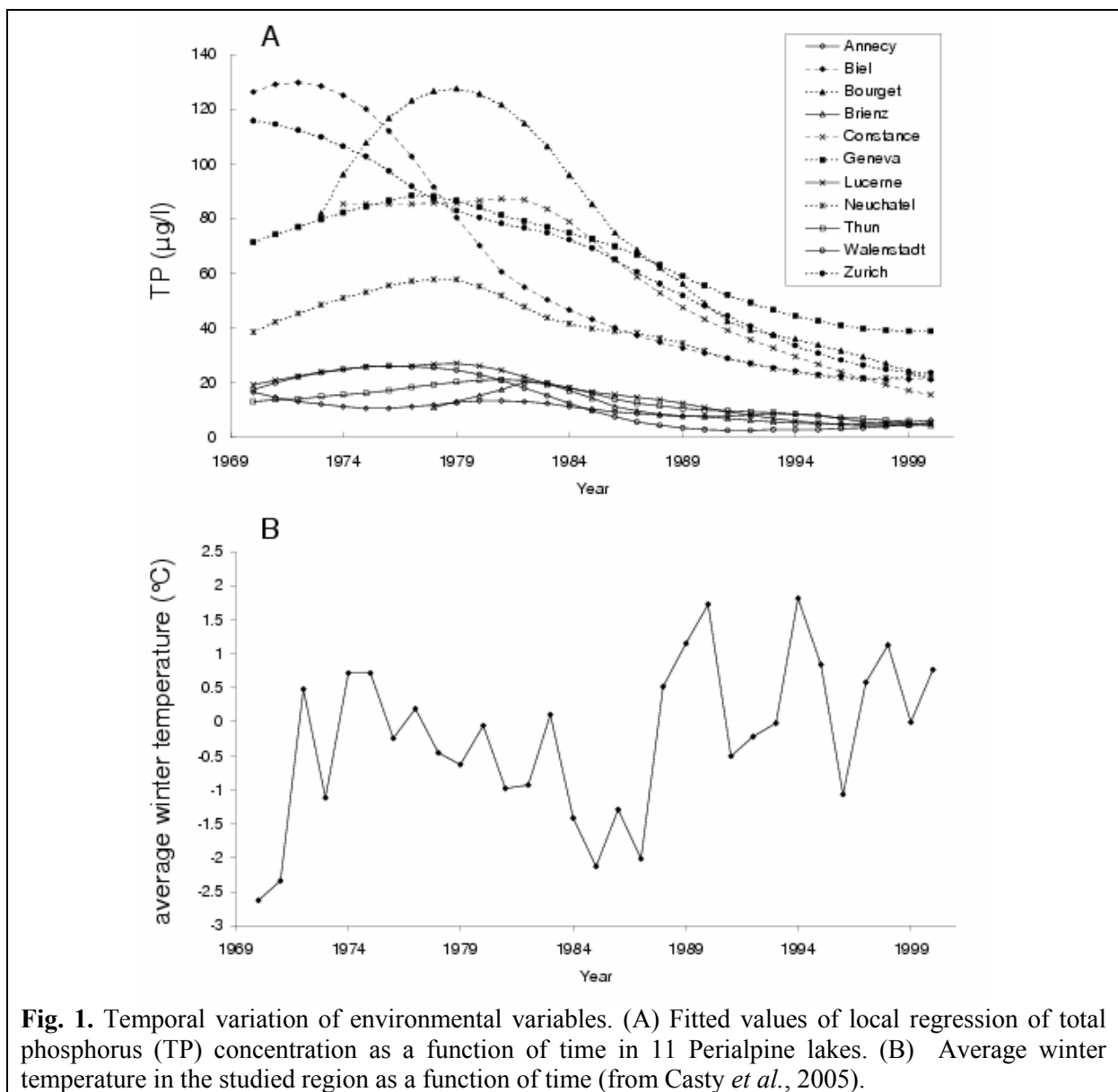
Fig. 1. Temporal variation of environmental variables. (A) Fitted values of local regression of total phosphorus (TP) concentration as a function of time in 11 Perialpine lakes. (B) Average winter temperature in the studied region as a function of time (from Casty *et al.*, 2005).

Table 1. General characteristics of the eleven lakes studied. Residence time refers to the average residence time of water. Total catch and total phosphorus concentration (TP) are given as average ($\pm$ standard deviation) over years. # TP corresponds to the number of years for which TP was available. R^2 refers to the multiple R^2 of TP fit in the loess regression (see text for details).

Lake	Altitude (m)	Max. depth (m)	Aver. depth (m)	Area (km²)	Volume (km³)	Resid. time (year)	Latitude (N)	Longitude (E)	Total catch (kg.ha⁻¹)	TP (µg.l⁻¹)	# TP	R²
Annecy	447	65	41.0	27.6	1.124	3.8	45°5'	6°1'	11.3 ($\pm$ 3.0)	9.4 ($\pm$ 3.5)	21	0.87
Biel	410	74	30.5	39.3	1.240	0.2	47°5'	7°10'	32.5 ($\pm$ 6.2)	60.9 ($\pm$ 41.4)	31	0.99
Bourget	228	145	51.0	42.0	3.600	3.8	45°44'	5°52'	15.5 ($\pm$ 5.5)	62.5 ($\pm$ 34.9)	22	0.98
Brienz	564	261	173.0	29.8	5.170	2.7	46°43'	7°58'	9.0 ($\pm$ 5.3)	10.3 ($\pm$ 5.7)	19	0.88
Constance	400	254	100.0	540.1	49.000	4.3	47°39'	9°19'	32.0 ($\pm$ 10.4)	56.8 ($\pm$ 27.5)	27	0.99
Geneva	372	309	152.1	582.0	89.000	11.4	46°26'	6°33'	16.6 ($\pm$ 5.5)	65.5 ($\pm$ 17.8)	31	0.98
Lucerne	434	214	104.0	114.1	11.800	1.0	47°0'	8°28'	25.6 ($\pm$ 8.8)	16.0 ($\pm$ 8.7)	31	0.93
Neuchatel	429	152	64.2	217.9	13.979	8.2	46°54'	6°51'	18.3 ($\pm$ 6.8)	38.7 ($\pm$ 12.9)	31	0.96
Thun	558	217	135.2	48.4	17.500	1.9	46°41'	7°43'	16.6 ($\pm$ 17.3)	13.6 ($\pm$ 5.2)	11	0.99
Walenstadt	600	145	103.0	24.1	2.521	1.5	47°7'	9°12'	14.3 ($\pm$ 7.2)	12.6 ($\pm$ 9.6)	31	0.97
Zurich	406	136	51.7	85.3	3.800	1.4	47°15'	8°41'	26.8 ($\pm$ 6.7)	66.8 ($\pm$ 31.0)	31	0.99
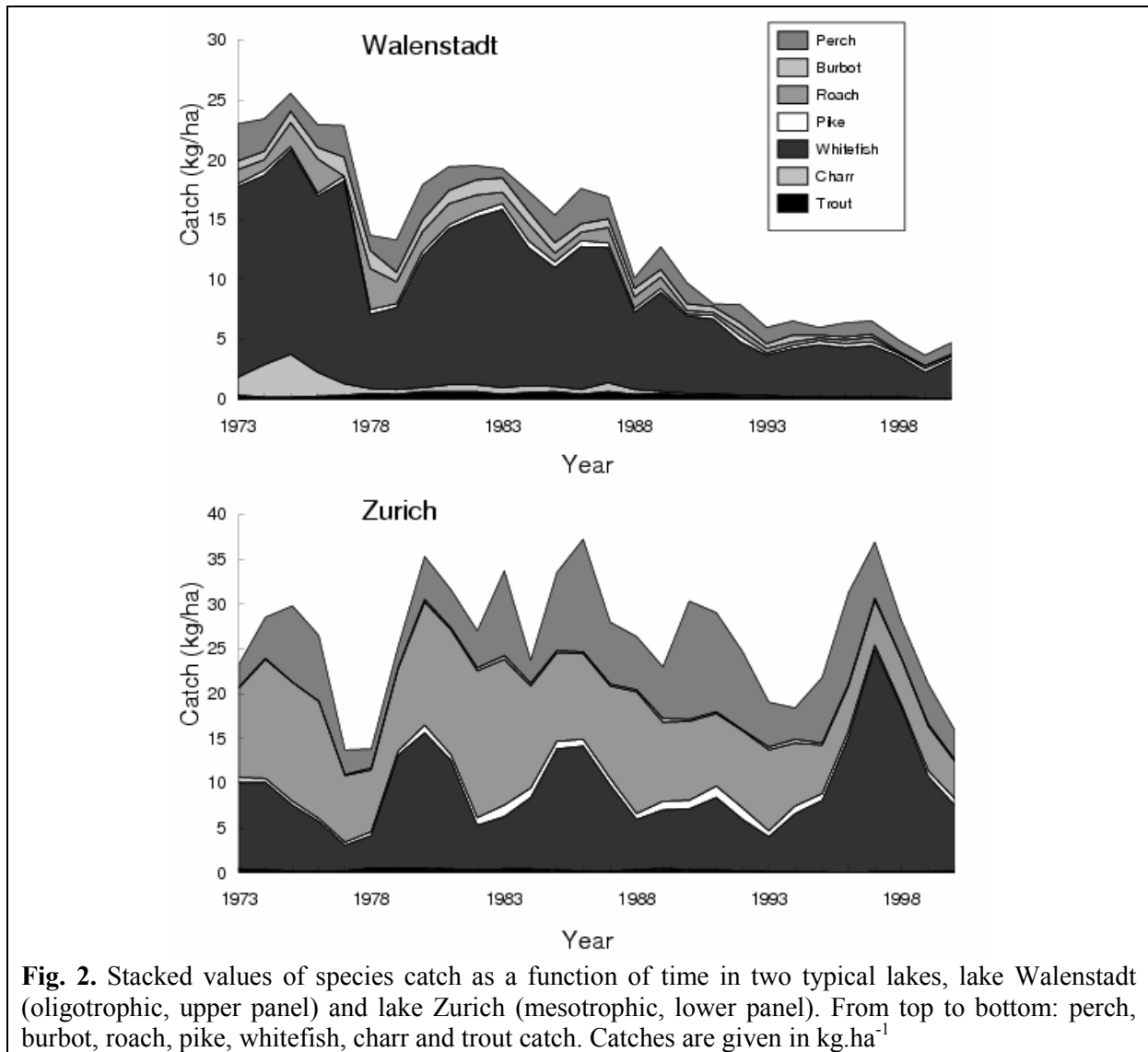
Fig. 2. Stacked values of species catch as a function of time in two typical lakes, lake Walenstadt (oligotrophic, upper panel) and lake Zurich (mesotrophic, lower panel). From top to bottom: perch, burbot, roach, pike, whitefish, charr and trout catch. Catches are given in kg.ha^{-1}

Models

We used nonlinear regression models to assess the dependency of log B on two environmental variables: TP and AWT. We assume that B is proportional to adult abundance (A) within a given lake, although capturability may vary among lakes. Two families of regression models were used: (i) Autoregressive Ricker-type log-model (ARL model), and (ii) quasi-equilibrium model with moving average error incorporating the effect of total community biomass Z (QEMAZ model). Both families take into account the temporal autocorrelation usually found in ecological time series. The two families of models are linked, but QEMAZ models are based on the assumption of quasi-equilibrium whereas ARL models are not. Both families of models were studied because they return different pieces of information.

The ARL model is based on the following equation, for each species and lake:
$$\log B_t = \log\left(sB_{t-1}e^{dTP+eTP^2+fAWT} + \alpha B_{t-3}e^{-\beta_{lake}B_{t-3}+aTP+bTP^2+cAWT}\right)+\varepsilon_t \qquad (1)$$
where s and α are baseline adult survival and recruitment respectively, a, d, b, e represent linear (a, d) and quadratic (b, e) effects of TP on adult survival (d, e) and on recruitment (a, b), f and c represent linear effects of AWT on survival and recruitment respectively, β_{lake}, is a lake-specific parameter that represents density-dependent inhibition of recruitment and ε_t is a

white noise process. All parameters are species-specific. The rationale behind equation (1) is based on the fact that adults at time t come from two sources: individuals that were adults at time t - 1 and have survived, and individuals that were born at time t - 3 and became adults at time t (the average maturation time for female of the studied species; justification in Online Appendix S2 and see also next section). Noting s the adult survival, T the maturation delay (here T=3 years in all species) and φ the recruitment factor (i.e. the probability that a newborn survives T years and becomes adult times the per-capita adult fecundity), catches of adult fishes can be written as:

$$B_t = s_{t-1}B_{t-1} + \varphi_{t-T}B_{t-T} \tag{2}$$

The classical Ricker stock-recruitment model (Ricker, 1954) can be used to model recruitment as a density-dependent function of adult abundance:

$$\varphi_t = \alpha(t)\mathrm{e}^{-\beta B_t} \tag{3}$$

where $\alpha(t)$ is the baseline recruitment. β incorporates both the dependency of recruitment on adult density and local capturability, since fish catches B_t are proportional, but not equal, to adult densities. Thus, β must be allowed to differ among lakes to account for differences in capturability.

Finally, we introduced the effect of TP and AWT on survival and recruitment, using exponential terms $se^{dTP+eTP^2+fAWT}$ and $\alpha e^{aTP+bTP^2+cAWT}$ as the expressions of the *survival* and *recruitment* functions respectively. Quadratic effects of TP were allowed because its range of variation was so large that nonlinear effects could reasonably be expected based on knowledge of the species' biology. This yields equation (1), from which a family of sub-models can be constructed by imposing various combinations of constraints such as a=b=0, c=0 etc. Model (1) (without constraint) can be thought of as the complete ARL model incorporating TP and AWT as explanatory variables of both survival and recruitment. From a statistical viewpoint, however, it is not possible to obtain informative fits of this complete model because abundance data are temporally autocorrelated (i.e. B_{t-1} and B_{t-3} are expected to be relatively similar). Thus, the likelihood surface on which to estimate jointly a and d, for instance, is bound to be quite flat and these estimates will have large error variance and covariance. Our analysis was therefore restricted by exploring only models derived from (1) that respect the following constraints:

- either (a, b) or (d, e) equals (0, 0) ;
- either $c = 0$ or $f = 0$.

We also explored a second family of regressions (QEMAZ model) that can be written as :

$$\log B_t = \mu_{lake} + a'TP + b'TP^2 + c'AWT + d'\left(Z_{t-3} - \overline{Z}_{Lake}\right) + \varepsilon_t \tag{4}$$

where μ_{lake} is a lake-specific constant, Z_t is the natural logarithm of total community catch in year t, $\overline{Z}_{Lake}$ is the average value of Z_t in a given lake, and ε_t is a moving average error (Brockwell & Davis, 1991; Pierce, 1971) that takes into account the temporal autocovariance of the data at lags up to three:

$$\varepsilon_t = E_t + \theta_1 E_{t-1} + \theta_2 E_{t-2} + \theta_3 E_{t-3} \tag{5}$$

and E_t is a white noise process (i.e. a sequence of independent identically distributed Gaussian variables). Model (4) can be derived from model (1) by assuming that $\log B_t$ oscillates around a stable equilibrium and adding the assumption that not only the biomass of the species itself but the whole community in the previous years may influence species biomass at time t. We derived the θ_i's from autocovariance functions arising from model (1), neglecting autocovariances at lags > 3 (for details on the method, see Brockwell *et al.*, 1991; for details on the method, see Pierce, 1971). Because we avoid introducing too many parameters and because interspecific effects are likely to be more important on the juvenile stages, e.g.

through crowding and intraguild predation, a three-year delay to the effect of community biomass on log B was retained. The imposed autocovariance lag is indeed a maximum maturation delay, and the autocovariance coefficient θ_3 would be 0 if maturation occurs before 3 years. The robustness of QEMAZ models to variation in maturation delay was also checked by re-running them using 2, 3 and 4-year maturation delays and the downgraded dataset. The biomass of a species with positive d' increases when the community biomass increases. A family of sub-models was generated as above for each species. We also analyzed similar models for Z ($d' = 0$ in these models). Z is an approximate proxy for total community biomass because capturabilities differ among species and lakes. However, when restricted to lake-specific analyses (as in QEMAZ models), this inaccuracy is only due to differences of capturabilities among fish species, so that Z well qualifies community biomass when the most abundant species is also the one on which fishing focuses (whitefish in almost all lakes).

In both families of models, the maturation delay was assumed to be equal to 3 in all species. This choice was justified based on a literature survey (Online appendix S2). However, we further checked our results when this assumption was relaxed, i.e. using maturation delays of 2, 3 and 4 years. This was performed using a downgraded database (i.e. we did not use year 1973 when testing to allow for 4-year maturation delays). Changing maturation delays induced limited changes that are mentioned in the result section.

Statistical analyses: fitting procedures
Missing data in TP records were fitted based on local regressions. This model fits a locally quadratic temporal trend on TP time series per lake, using an interpolation method with Gaussian error and tri-cube weighting function (Cleveland & Devlin, 1988). Local regressions were computed using the loess function in S-PLUS (Insightful, 2004) and half of the data points as neighbours (span = 0.5). All local regressions had multiple coefficient of regression (R^2) higher than 0.87 (Table 1), indicating appropriate fit. Further analyses using TP as an explanatory variable make use of loess-fitted TP.

The abundance table and total community biomass were obtained by log-transforming catches per species and of all species respectively. Null annual catch for a given species was treated as missing data. TP, TP² and AWT were chosen as environmental explanatory variables. As ARL models required data on B_{t-3} to compute B_t, the study period was restricted to 1973-2000. All models were fitted using Generalized Nonlinear Least Squares regressions (GNLS, for ARL models) and Generalized Least Squares regressions (GLS, for QEMAZ models) based on maximum likelihood, implemented in S-PLUS (Insightful, 2004). We discarded data from lake Bourget when fitting ARL models of whitefish abundance because the lake-specific β was found negative using unconstrained GNLS modelling. We also discarded burbot and charr from the ARL model analysis because these models failed to converge.

Model selection and multimodel inference
Both families of models (ARL, QEMAZ) were represented by various sub-models (respectively 15 and 12 per species, and 6 for Z in the latter case). The goodness-of-fit of these sub-models can be compared within each family using the bias-corrected Akaike Information Criterion (AICC, Hurvich & Tsai, 1989). The best model within each family is the one with the highest AICC (Akaike, 1973; Brockwell *et al.*, 1991; Hurvich *et al.*, 1989), and the information content of all other models is measured in relative units as the difference in AICC compared to the best model, noted ΔAICC. ΔAICC higher than 2 is usually taken as evidence for a significant difference. However, restricting the analysis to the best model and significance tests based on model simplification involve a loss of information when: (i) non-

nested series of models are compared, and (ii) many AICC are similar (small ΔAICC). In the latter case, inference and hypothesis tests based on the best model ignore the uncertainty associated with model identification (Burnham & Anderson, 2002). Such problems may be circumvented using Akaike weights and multi-model inference (Burnham *et al.*, 2002; Burnham & Anderson, 2004). The Akaike weight w_i of model *i* within a given family of models (ARL or QEMAZ) was computed as (Burnham *et al.*, 2002, , 2004):

$$w_i = \frac{e^{-\Delta_i/2}}{\sum_j e^{-\Delta_j/2}} \qquad (6)$$

where Δ_i is the ΔAICC of model *i* and the sum is over all models of the same family. An Akaike weight can be interpreted as the probability for a model to be the best one in the family (Burnham *et al.*, 2002, , 2004).

Within each family of models, Akaike weights can also be summed over all models that share part of their parameter constraints. For instance, the Akaike weights of all models that did not incorporate TP as an explanatory variable were added together. This sum (w_H) was used to evaluate the plausibility of the hypothesis (*H*) that TP had no effect. To this end, we calculated the evidence ratio of *H* as:

$$ER_H = \frac{w_H}{1 - w_H} \qquad (7)$$

The null expectation of the ER_H (i.e. total uncertainty on *H*) is $ER_{null} = \dfrac{k}{n-k}$ if the total number of models in that family is *n* and the number of models compatible with hypothesis *H* is *k*. The evidence ratio can be interpreted following Burnham and Anderson (2002, 2004): an hypothesis is considered *plausible* when $ER > ER_{null}$, *implausible* otherwise, *likely* when it is so high that it corresponds to a δAICC value of 2 or higher, i.e. when $ER > 2.72\ ER_{null}$ (Burnham *et al.*, 2002), and *unlikely* when it corresponds to a δAICC value of –2 or lower, i.e. when $ER < 0.37\ ER_{null}$.

Akaike weights can be used to incorporate uncertainty in model choice into prediction formulae. This is done by computing the arithmetic mean of all models of a given family weighted by their respective Akaike weights (Burnham *et al.*, 2002, , 2004). For linear models (such as QEMAZ models), it is possible to average values of parameters in order to obtain average recruitment and survival functions of TP and AWT. Although this procedure only yields approximate average values of parameters in non-linear models (such as ARL models), the computation of average responses of the sub-models is still exact (Burnham *et al.*, 2004). Moreover, because $\log \beta$ has the same dimension as $\log B$ (i.e. the response in ARL models), its average value corresponds exactly to $\log \beta$ value in the average model.

Predicted equilibrium abundances *μ'* were estimated by averaging sub-model equilibrium abundances in each family. In the ARL family, equilibrium abundance within each lake is given by (equation 1):

$$\mu'_{lake} = \log\left(\log\left(\frac{\alpha}{1 - se^{dTP + eTP^2 + fNAO}} \right) + aTP + bTP^2 + cAWT \right) - \log \beta_{lake} \qquad (8)$$

while in the QEMAZ models it is simply (equation 4):

$$\mu'_{lake} = \mu_{lake} + a'TP + b'TP^2 + c'AWT \qquad (9)$$

in which all coefficients (*a, b, ...*) were obtained from the average model (the term in *Z* is neglected in (9) since we are interested in the equilibrium abundance at mean *Z*).

We computed 95% confidence intervals around these predictions ($\mu' \pm 1.96\sigma$), where σ is the square root of the unconditional variance. σ^2 is the sum of two independent components of variance (Burnham *et al.*, 2002, , 2004): the first represents the variance due to the uncertainty in model choice σ_{Inter}^2, which is simply the variance of predicted log-abundances among all models ; the second is the average error variance of one model $\sum_i w_i(\sigma_i^2 + \sigma_{lakes,i}^2)$, which

comprises for each model *i*, a between-lakes component of variance ($\sigma^2_{lakes,i}$, variance in predicted μ' among lakes) and a within-lake residual variance (σ^2_i).

All data transformations and model fitting were performed using S-PLUS 6.2 (Insightful, 2004).

Results

ARL model

ARL modelling of log-abundance data converged for five species (trout, whitefish, pike, roach and perch). The best model for each species fitted observed data with an adjusted squared correlation coefficient larger than 0.80 (Table 2). The proportion of acceptable models (i.e. with $\Delta AICC < 2$) was less than 0.33 in each species.

Predicted equilibrium abundances suggested that trout and roach responded positively to increases in TP, pike responded slightly negatively, whitefish had a peak of abundance at intermediate TP values (*c.* 40-50 μg.l^{-1}) and perch was not affected by TP at all (Fig. 3 and S1). TP effect on log-abundance was unlikely for perch and implausible for pike, and plausible for all other species (Table 2). No strong AWT effect on equilibrium abundances was detected (implausible in all species, Table 2).
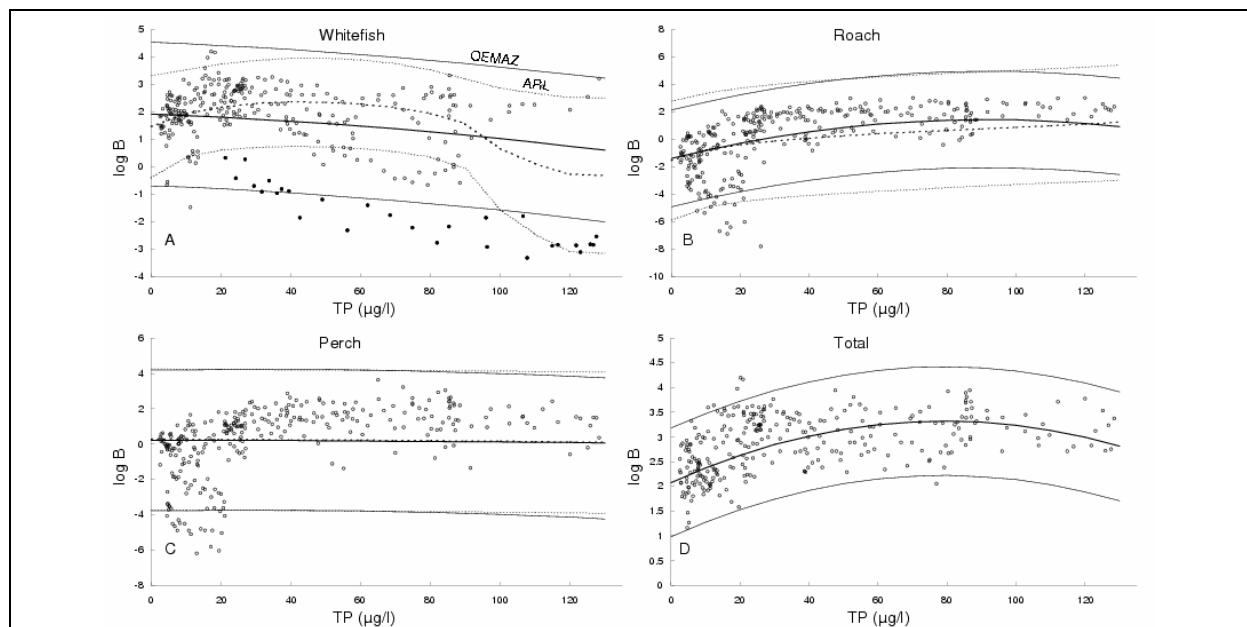
Fig. 3. Equilibrium abundances estimated using average model predictions at average winter temperature set to 0. Empty circles correspond to observed data (full circles point out data from lake Bourget). Dotted and continuous lines indicate the mean expected value and confidence bounds using total variance of the ARL and QEMAZ models respectively. Equilibrium log-abundance of (A) whitefish, (B) roach, and (C) perch. (D) Equilibrium total biomass in the communities.

Recruitment was affected by TP in all species, except perch (not robustly for whitefish). A linear effect of TP on the recruitment of trout was likely, while it was plausible for roach and pike. A quadratic effect of TP on recruitment was plausible (but not robustly so) for whitefish and for trout, and unlikely for all others. Recruitment decreased with TP for pike, while it increased for trout, roach and perch (Fig. 4 A). Whitefish recruitment peaked at intermediate TP levels (*c.* 50 µg.l^{-1}) and decreased steeply for higher TP values. Survival was affected by TP in few species. It is likely that TP had no effect on the survival of trout, and plausible that it had no effect on pike, roach and perch, a linear effect on roach and perch, and a quadratic effect on whitefish (Table 2). Survival functions were not severely affected by changes in TP (Fig. 4 B): whitefish survival peaked at TP $\approx$ *c.* 40µg.l^{-1}, trout survival increased slightly, pike survival decreased slightly, while perch survival more pronouncedly decreased and roach survival increased. It was likely that TP affected more recruitment than adult survival in trout (Table 2), and this hypothesis was also plausible for pike and roach, but not for whitefish and perch (compare also Figures 4 A and 4 B).

Fig. 4. Variations of recruitment (A) and survival (B) functions with total phosphorus (TP) at average winter temperature set to 0 for trout (continuous line), whitefish (dashed line), pike (dotted line), roach (dashed and dotted line) and perch (dashed and double-dotted line) as computed by model averaging of ARL models. Note the difference in scale between the two panels.
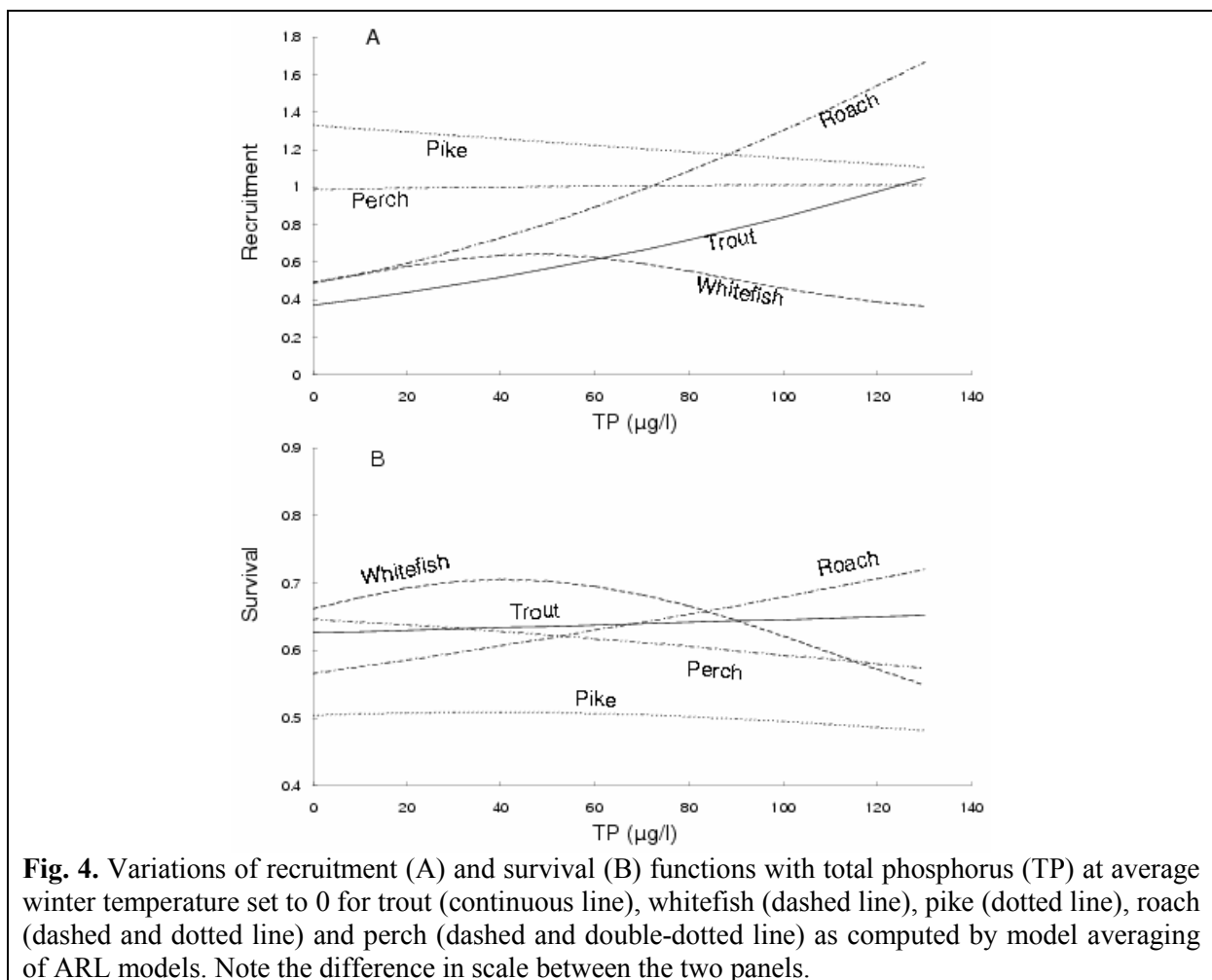
AWT effects on recruitment and survival were generally unlikely (Table 2). However, it was plausible that AWT affected the recruitment of pike (positively) and perch (negatively, Table 2 and Fig. S2 A). It was plausible that AWT affected more recruitment than adult survival in all species (Table 2 and Fig. S2).

All results obtained from ARL models were generally robust to changes in maturation delay (Table 2), except for whitefish dependence on TP, as mentioned above.

Table 2. Best ARL models and multimodel inference for the five species for which model convergence was achieved. Lag indicates the maturation delay used in the model. The number of observations used for model fitting (N) is given accordingly (depending on the number of null abundance record, excluding lake Bourget for whitefish, and depending on whether the full or downgraded dataset was used; see Material and Methods). The explanatory variables for s and φ, the adjusted squared correlation coefficient (R^2) and the number of degrees of freedom (df) of the best model are given under the "best model" header. The other columns give the evidence ratio (ER) associated with hypotheses on the effect of TP or AWT on survival or recruitment. Columns "no TP" and "no AWT" present the ER associated with the absence of any effect of TP or AWT index on specific log-abundance modelling. In the last two columns are given the evidence ratios of all models that incorporate an effect of TP (resp. AWT) on the recruitment function versus all models that incorporate an effect of TP (resp. AWT) on the adult survival function. The last three rows give the ER limits for unlikelihood, plausibility and likelihood of hypotheses. Underlined and bold values represent plausible and likely hypotheses, respectively.

			Best model				TP effect on survival			AWT effect on survival		TP effect on recruitment			AWT effect on recruitment		no TP	no AWT	TP	AWT
Species	lag	N	s	φ	adjusted R^2	df	no effect $d=e=0$	linear $e=0$	quadratic	no effect $f=0$	linear	no effect $a=b=0$	linear $b=0$	quadratic	no effect $c=0$	linear	effect	effect	φ/s	φ/s
Trout	3	301	-	TP	0.87	15	**8.17**	0.09	0.03	3.65	0.27	0.18	**1.58**	0.31	3.50	0.29	0.05	1.29	**7.77**	1.03
Trout	2	292	-	TP, TP²	0.87	16	**61.45**	0.00	0.01	2.97	0.34	0.02	0.25	**3.69**	3.19	0.31	0.00	1.04	**61.45**	0.95
Trout	3	292	-	TP	0.87	15	**7.19**	0.10	0.03	3.46	0.29	0.20	**1.36**	0.35	3.41	0.29	0.04	1.22	**6.85**	1.01
Trout	4	292	-	TP	0.86	15	**5.38**	0.12	0.05	4.09	0.24	0.20	**1.57**	0.29	3.35	0.30	0.01	1.34	5.33	1.17
Whitefish	3	273	-	TP, TP²	0.80	15	1.28	0.10	0.53	2.12	0.47	1.29	0.05	0.63	3.88	0.26	0.14	0.90	0.99	0.64
Whitefish	2	265	TP, TP²	-	0.80	15	0.22	0.04	**3.57**	4.05	0.25	**6.00**	0.01	0.15	3.29	0.30	0.04	1.32	0.17	1.18
Whitefish	3	265	TP, TP²	-	0.80	15	0.25	0.03	**3.42**	3.15	0.32	**4.72**	0.01	0.20	3.58	0.28	0.02	1.18	0.22	0.91
Whitefish	4	265	TP, TP²	-	0.80	15	0.12	0.02	**6.97**	4.43	0.23	**10.58**	0.01	0.09	1.59	0.63	0.02	0.76	0.10	2.09
Pike	3	301	-	TP	0.93	15	3.24	0.14	0.13	4.67	0.21	0.90	0.65	0.15	1.90	0.53	0.31	0.92	2.23	1.96
Pike	2	292	-	TP	0.93	15	2.55	0.16	0.17	4.20	0.24	0.97	0.62	0.14	1.48	0.68	0.27	0.68	1.80	2.10
Pike	3	292	-	TP	0.93	15	2.37	0.13	0.22	4.09	0.24	1.36	0.45	0.13	1.77	0.56	0.39	0.80	1.43	1.83
Pike	4	292	-	-	0.93	14	1.84	0.19	0.24	3.66	0.27	2.18	0.28	0.11	1.94	0.52	0.50	0.80	0.89	1.59
Roach	3	297	-	TP	0.89	15	1.81	0.36	0.10	4.22	0.24	0.76	0.61	0.23	2.70	0.37	0.08	1.17	1.59	1.41
Roach	3	288	-	TP	0.89	15	1.93	0.34	0.09	4.29	0.23	0.72	**0.71**	0.20	2.54	0.39	0.08	1.12	1.71	1.50
Roach	4	288	-	TP	0.89	15	1.46	0.44	0.11	4.64	0.22	0.96	0.62	0.15	2.08	0.48	0.09	0.99	1.25	1.83
Perch	3	301	-	-	0.90	14	1.70	0.37	0.11	3.72	0.27	4.03	0.17	0.05	1.98	0.51	**0.76**	0.83	0.54	1.59
Perch	3	292	-	-	0.90	14	1.92	0.34	0.09	4.65	0.22	3.73	0.19	0.06	1.78	0.56	**0.81**	0.86	0.62	2.03
Perch	4	292	-	-	0.89	14	3.76	0.19	0.05	4.16	0.24	1.66	0.19	0.27	2.96	0.34	**0.71**	1.24	1.79	1.30
Limit ER for unlikelihood							0.55	0.09	0.09	0.74	0.18	0.55	0.09	0.09	0.74	0.18	0.09	0.18	0.37	0.37
Limit ER for plausibility							1.50	0.25	0.25	2.00	0.50	1.50	0.25	0.25	2.00	0.50	0.25	0.50	1.00	1.00
Limit ER for likelihood							4.08	0.68	0.68	5.44	1.36	4.08	0.68	0.68	5.44	1.36	0.68	1.36	2.72	2.72

Table 3. Best QEMAZ models and multimodel inference for each species and for total community biomass (Z). Lag indicates the maturation delay used in the model. The number of observations used for model fitting (N) is given accordingly (depending on the number of null abundance record, and on whether the full or downgraded dataset was used; see Material and Methods). The explanatory variables for μ', the adjusted squared correlation coefficient (R^2), and the number of degrees of freedom (df) of the best model are given under the "best model" header. The other columns give ER associated with hypotheses on the effect of TP, AWT or total community biomass (Z) on log-abundances. Model averaging estimation of d' is given in the last column. When modelling Z as a function of environmental variables, d' was set to 0. Underlined values represent plausible hypotheses ; in bold, likely ones. The last three rows give the ER limits for unlikelihood, plausibility and likelihood of proposed hypotheses.

Species	lag	N	Best model μ'	adjusted R^2	df	TP effect no effect $a'=b'=0$	TP effect linear $a'=0$	TP effect quadratic	AWT effect no effect $c'=0$	AWT effect linear	Z effect no effect $d'=0$	Z effect linear	d'
Trout	3	301	TP, TP², AWT	0.77	19	0.00	0.03	**35.19**	0.44	2.29	2.36	0.42	0.016
Trout	2	292	TP, TP², AWT	0.78	19	0.00	0.00	**339.55**	0.62	1.62	2.84	0.35	0.008
Trout	3	292	TP, TP², AWT	0.78	19	0.00	0.01	**74.44**	0.28	3.51	2.52	0.40	0.014
Trout	4	292	TP, TP², AWT	0.78	19	0.00	0.03	**31.18**	0.41	2.42	3.10	0.32	-0.002
Charr	3	283	TP, TP²	0.75	18	0.01	1.00	0.97	1.23	0.82	3.09	0.32	-0.004
Charr	2	276	TP, TP²	0.77	18	0.00	0.19	**5.29**	1.12	0.90	2.91	0.34	-0.012
Charr	3	276	TP, TP²	0.76	18	0.00	0.55	**1.78**	1.10	0.91	3.00	0.33	-0.009
Charr	4	276	TP, TP²	0.76	18	0.01	0.78	1.25	1.07	0.93	2.30	0.43	0.032
Whitefish	3	301	TP	0.79	17	0.01	1.46	0.67	2.96	0.34	2.84	0.35	0.011
Whitefish	2	292	TP, TP²	0.80	18	0.00	0.25	**4.06**	3.05	0.33	2.37	0.42	-0.027
Whitefish	3	292	TP, TP²	0.80	18	0.00	0.79	1.26	2.28	0.44	2.23	0.45	0.025
Whitefish	4	292	TP, Z	0.80	18	0.00	1.44	0.69	2.66	0.38	0.04	22.44	0.267
Pike	3	301	TP, Z	0.90	18	0.55	0.95	0.19	1.62	0.62	1.03	0.97	0.043
Pike	2	292	TP, Z	0.91	18	0.26	1.42	0.26	1.36	0.73	0.32	3.12	0.092
Pike	3	292	TP	0.91	17	0.54	0.90	0.21	1.95	0.51	1.57	0.64	0.026
Pike	4	292	TP	0.91	17	0.65	0.80	0.19	2.03	0.49	2.59	0.39	0.010
Roach	3	297	TP, TP²	0.84	18	0.00	0.01	**146.82**	2.74	0.36	2.95	0.34	-0.012
Roach	2	288	TP, TP²	0.84	18	0.00	0.01	**102.25**	2.65	0.38	2.54	0.39	-0.027
Roach	3	288	TP, TP²	0.84	18	0.00	0.02	**66.58**	2.60	0.38	2.88	0.35	-0.015
Roach	4	288	TP, TP², Z	0.84	19	0.00	0.01	**91.92**	2.20	0.45	0.66	1.52	-0.163
Burbot	3	300	TP, TP², AWT	0.72	19	0.23	0.08	**2.85**	0.17	**6.02**	2.22	0.45	-0.029
Burbot	2	291	TP, TP², AWT	0.72	19	0.06	0.02	**11.38**	0.17	**5.73**	1.31	0.76	0.066
Burbot	3	291	TP, TP², AWT	0.72	19	0.14	0.05	**5.03**	0.28	**3.57**	2.91	0.34	-0.010
Burbot	4	291	TP, TP², AWT	0.72	19	0.20	0.07	**3.32**	0.24	**4.20**	2.77	0.36	-0.015

(Table 3 continued)

Species	lag	N	μ'	adjusted R²	df	TP effect no effect $a'=b'=0$	TP effect linear $a'=0$	TP effect quadratic	AWT effect no effect $c'=0$	AWT effect linear	Z effect no effect $d'=0$	Z effect linear	Z effect d'
				Best model									
Perch	3	301	-	0.86	16	**1.39**	0.42	0.14	1.85	0.54	**2.88**	0.35	0.011
Perch	2	292	-	0.86	16	**1.54**	0.38	0.14	2.50	0.40	1.32	0.76	-0.065
Perch	3	292	-	0.86	16	**1.46**	0.41	0.13	2.21	0.45	**3.04**	0.33	0.005
Perch	4	292	Z	0.87	17	**1.73**	0.27	0.18	2.47	0.40	0.01	**96.55**	-0.395
Z	3	301	TP, TP²	0.57	18	0.00	0.00	**315.24**	**2.99**	0.33	-	-	-
Z	2	292	TP, TP²	0.57	18	0.00	0.00	**3430.20**	**2.76**	0.36	-	-	-
Z	3	292	TP, TP²	0.57	18	0.00	0.00	**318.78**	**3.06**	0.33	-	-	-
Z	4	292	TP, TP²	0.57	18	0.00	0.00	**263.13**	**3.08**	0.32	-	-	-
Limit ER for unlikelihood							0.18		0.37		0.37		
Limit ER for plausibility							0.50		1.00		1.00		
Limit ER for likelihood							1.36		2.72		2.72		

QEMAZ model

QEMAZ modelling of observed log-abundance converged both for all species and for total community biomass. All species (except pike) had less than 33% of their models performing at ΔAICC < 2, ensuring a restricted choice of competing best models. The best model for each species fitted observed data quite well (adjusted R^2 between 0.72 and 0.91; Table 3). Total community biomass was fitted with a maximum adjusted squared correlation equal to 0.57 (only one model had ΔAICC < 2).
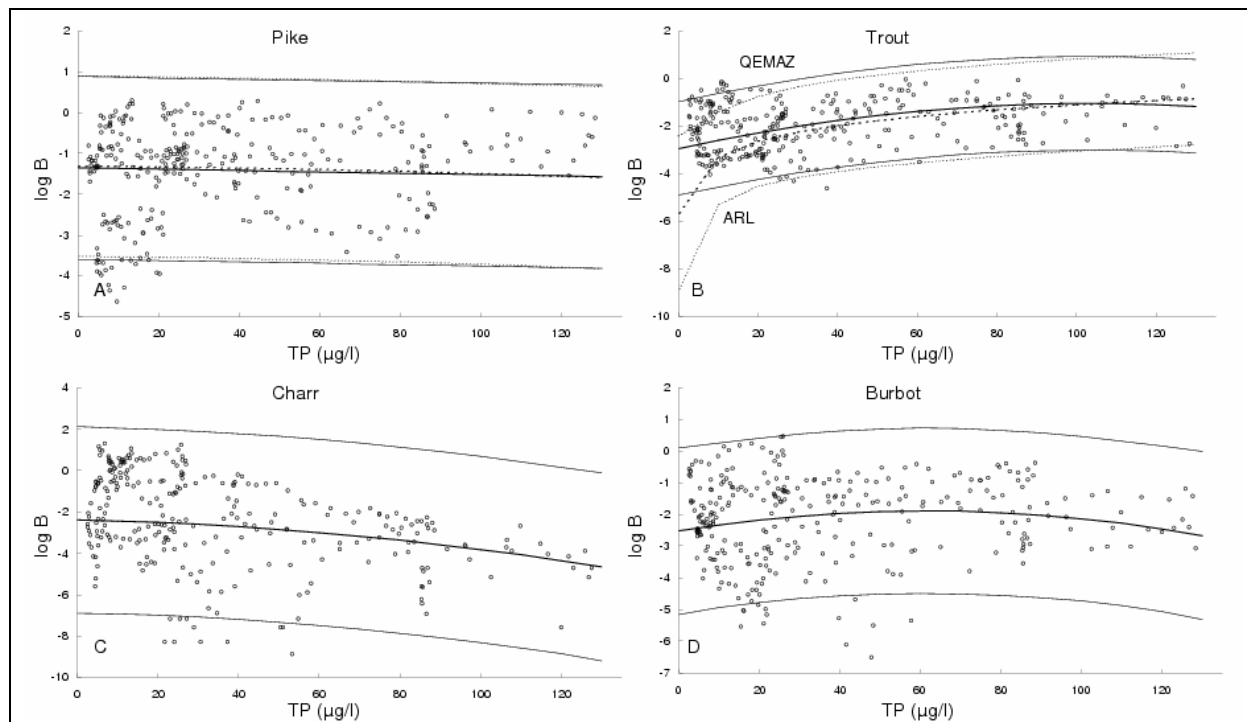

Fig. S1. Equilibrium abundances estimated using average model predictions at average winter temperature set to 0. Circles correspond to observed data. Dotted and continuous lines indicate the mean expected value and confidence bounds using total variance of the ARL and QEMAZ models respectively. Equilibrium log-abundance of (A) pike, (B) trout, (C) charr, and (D) burbot.

Trout and roach responded positively to increases in TP, while whitefish and burbot abundances and total community biomass first increased then decreased with TP, charr responded negatively to TP, and both pike and perch were almost not affected by TP (Fig. 3 and S1).

It is likely that TP had no effect on perch (Table 3). A linear effect of TP on whitefish abundance was likely (but not robustly so), and it was also plausible for charr and pike. A quadratic TP effect was likely for trout, roach, burbot and community biomass, and plausible for charr and whitefish. On the other hand, AWT effects were unlikely in whitefish, roach and for community biomass, implausible in charr, pike and perch, plausible in trout and likely in burbot. Burbot and trout log-abundances slightly increased with increasing AWT values (multimodel $c' = 0.073$ and 0.030 resp.). Community biomass affected log-abundances in a very erratic way, depending on the maturation lag (Table 3). Based on 3-year maturation and use of the full dataset, community biomass effect was unlikely in charr, whitefish, roach and perch, and implausible for trout, pike and burbot. Model averaging estimation of d' showed that Z effect on specific log-abundance is negative for charr, roach and burbot and positive for trout, whitefish, pike and perch (Table 3).

Results obtained from QEMAZ models were quite robust to changes in maturation delays (Table 3), except the dependence of whitefish on TP (not robustly linear), and of whitefish, pike and perch on total community biomass, as mentioned above.
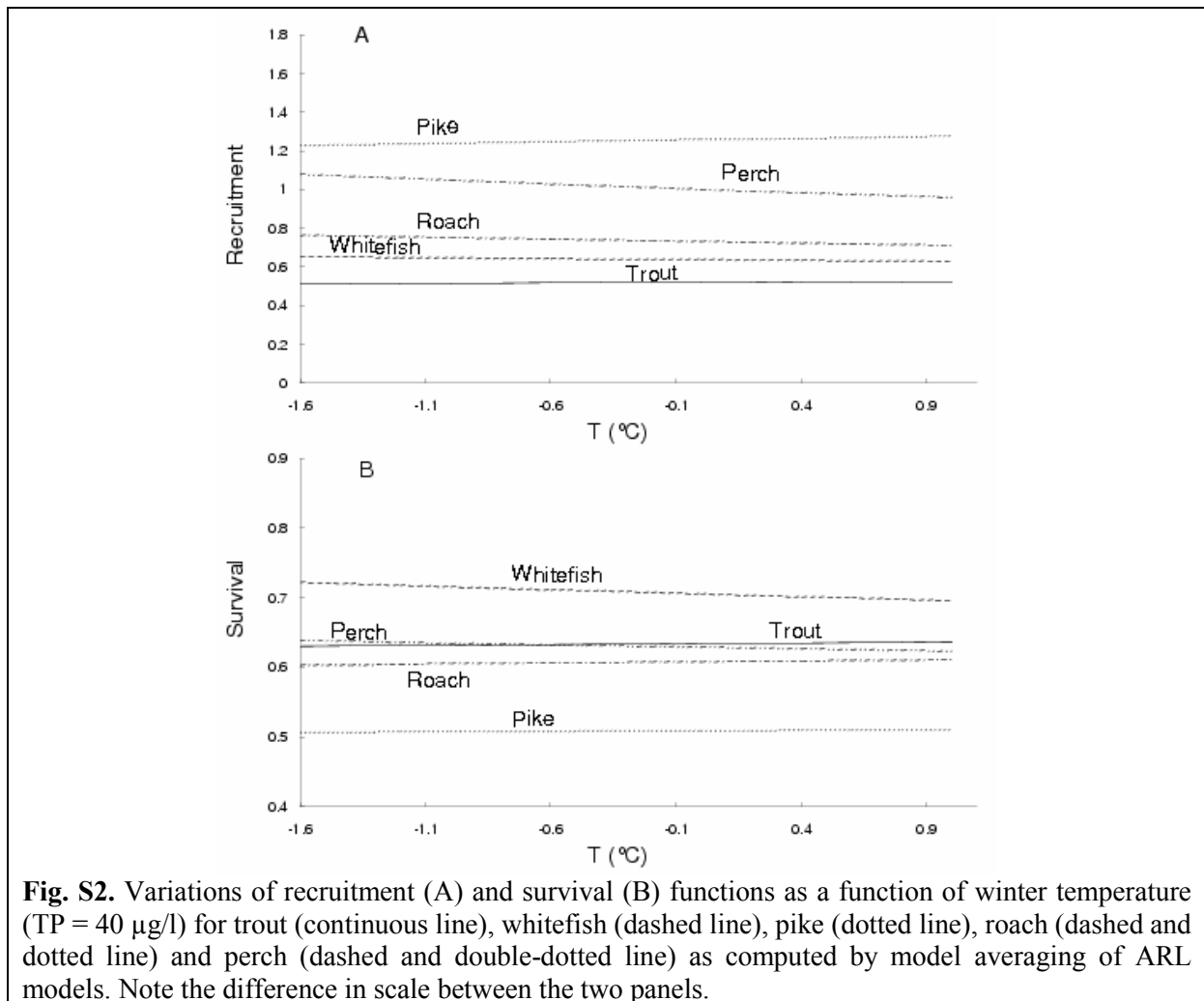
Fig. S2. Variations of recruitment (A) and survival (B) functions as a function of winter temperature (TP = 40 µg/l) for trout (continuous line), whitefish (dashed line), pike (dotted line), roach (dashed and dotted line) and perch (dashed and double-dotted line) as computed by model averaging of ARL models. Note the difference in scale between the two panels.

Discussion

The influence of eutrophication on survival and recruitment

Our analyses suggest that TP affects the abundance of all species, except perch. These effects are more likely to be predicted by recruitment than by adult survival in trout, pike and roach. Indeed, only three TP effects on s were reported as plausible, while there were four plausible and one likely effects of TP on recruitment. Comparisons of hypotheses using ER indicated that a mediation of TP effects through recruitment rather than survival was at least plausible for pike and roach, and likely for trout (Table 2). This hypothesis can be rejected for perch, which was unlikely to be affected by TP in all models anyway, and for whitefish since the best model depends on maturation delay. Overall, this hypothesis is best supported for trout and pike, and should be accepted with caution in whitefish and roach.

Our results on the influence of TP on recruitment make sense from an empirical point of view. First, whitefish recruitment peaks at intermediate TP level (Table 2, Fig. 4 A). This corroborates work suggesting that lake-dwelling salmonid egg survival could be impaired by eutrophication (Müller, 1992). Interestingly, trout recruitment increased with TP, which does not contradict Müller's results because trouts do not reproduce in lakes but in tributary

streams, and thus are not expected to be affected by eutrophication. Second, pike recruitment is negatively affected by eutrophication (Table 2, Fig. 4 A). This agrees with the hypothesis that egg survival in pike increases in the presence of oligotrophic water-attuned macrophytes (Gerdeaux, pers. obs.). Third, both recruitment and survival in roach are improved by eutrophication (Table 2 and Fig. 4). However, recruitment is more affected by changes in TP (Table 2), which arguably supports the idea that roach juveniles experience starving conditions in oligotrophic waters. According to studies on zooplankton dynamics changes in Perialpine lakes (see Gerdeaux *et al.*, 2006), perch, roach and whitefish juveniles compete with each other for resources in spring. Our results suggest that competition may favour roach in eutrophic conditions. This argument could be applied to analyze TP effect on recruitment and survival functions in trout, with extra caution due to potential stocking biases.

One *caveat* should be kept in mind when interpreting these results: efficient fish stocking (i.e. introduction of larvae or juveniles) shifts natural patterns towards a greater importance on abundances of adult survival over recruitment. Indeed, if a species is regularly stocked, autocorrelation of adult abundances at lag one increases, and changes in adult survival with TP or AWT are less likely than changes in recruitment. The effect of recruitment might therefore be more marked than implied by our analyses. Four species (whitefish, trout, pike and charr) have been stocked to some extend in the lakes studied. However, stocking does not account for more than 10% of the fished biomass in whitefish, trout and pike. Indeed, trout stocking is known to be quite inefficient (Champigneulle & Cachera, 2003), while whitefish stocking is not required to maintain sustainable populations (Gerdeaux, 2004). Pike stocking is not expected to change abundance importantly because of strong density-dependent mortality in this cannibalistic species (Bry, 1992). In charr, stocking can represent up to 80% of fished biomass, but this figure varies among lakes (D. Gerdeaux, unpublished data). Thus, we must be most cautious when interpreting results for charr.

The influence of climate change on survival and recruitment
Climate change, assessed using AWT, has very little observable effect on the recruitment and survival functions of the five ARL-modelled species. Pike recruitment is slightly positively affected by AWT (multimodel $c = 0.015$), while perch recruitment is slightly impaired (multimodel $c = -0.009$). However, there is no likely support either against or for AWT effects on any fitness component. Interestingly, we obtained very similar results when using the winter North Atlantic Oscillation Index (NAOI, Hurrell, 1995) as a proxy to temperature, further suggesting that climatic change affects little fitness components (results not shown).

Mesocosm and in situ experiments are required to assess such fine-grained effects as those of climate change on survival and recruitment (e.g., Gillet *et al.*, 2006). Yet, significant effects of climate change on recruitment or survival in other species have already been reported in the field (e.g. Grosbois & Thompson, 2005; Ward *et al.*, 2005). In fact, the absence of any likely AWT effect on fitness components of studied fish species is true only relatively to the effects due to TP. The presence of a slightly negative (but not robust) effect of AWT on perch recruitment is nevertheless interesting because it matches expected patterns due to changes in zooplankton peaks: as climatic warming proceeds, zooplankton peaks happen earlier in the year (Straile, 2002), and roach hatching time also follows this trend (Gillet *et al.*, 2006), while perch hatching time remains constant (Gerdeaux, pers. obs.). These phenomena result in increased competition between roach and perch larvae, which in general profits to the former (Persson & Greenberg, 1990), and thus in decreased perch recruitment.

The effects of climate change on species at the boundary of their climatic range
The distribution boundaries of Northern species are expected to be displaced northwards as temperature increases (e.g. in fish species, see Magnuson *et al.*, 1990; Meisner, 1990; Shuter *et al.*, 1990). Abundances of species at their Southernmost distribution boundary (here, burbot and charr) are therefore expected to be negatively affected by AWT, since a northwards displacement should go with a substantial decrease in abundance at actual peripheral populations (see Gaston, 2003, chapter 4). QEMAZ models did not support this prediction (Table 3): an AWT effect on charr is implausible, while burbot abundances are positively affected by the AWT (multimodel $d' = 0.073$), contrary to expectations. Here again, the same results were obtained when using the NAOI instead of AWT (results not shown).

Discrepancies between results and expectations might be explained as follows. Total biomass and the AWT are positively correlated (multimodel $d' = 0.001$), so that a positive effect of the AWT might be easily traded-off (in the GLS modelling) for a positive effect of total biomass and *vice versa*. That such an effect is due to convex yield-per-effort function is thus equivalent to a positive AWT effect. However, this interpretation is only valid if the GLS modelling procedure is unable to assign the effect to AWT or to Z, and thus is dependent upon the extent of total biomass and temperature covered by existing data. Charr and burbot are essentially present in oligotrophic lakes (e.g. Annecy, Brienz, Lucerne, Thun, and Walenstadt), and only experience a restricted scale of total biomass values. Our analyses might therefore fail to detect the expected patterns of climatic dependence on burbot and charr abundance. This seems all the more realistic since we found negative d' values for both charr and burbot, while positive values were expected for piscivorous and omnivorous species.

Another potential explanation may be that the thermal niche of a given species may not correspond to optimal conditions for the development and/or reproduction of that species. Indeed, the thermal niche achieved by a species might be dictated jointly by its thermal preferences and by competition pressures due to the geographic distribution of other species (Munoz, 2006). This explanation seems to fit the case of burbot quite well since experimental evidence indicates that burbot consumption rates benefit from warming in Perialpine lakes (Hofmann & Fischer, 2003).

Our results may also be blurred for two reasons. First, some species buffer the effects of global warming by modifying their position in the water column, in order to stay at optimal temperature (behavioural thermoregulation, see de Stasio *et al.*, 1996; behavioural thermoregulation, see Hill *et al.*, 1990; Shuter *et al.*, 1990). Behavioural thermoregulation is less likely for juveniles, which mostly dwell in the littoral zone. This phenomenon is therefore expected to blur temperature effects on adult survival only. Actually, the only observed effects of AWT were reported on recruitment rather than on survival. Second, climatic warming has multiple effects on lake ecosystems through different mechanisms. For instance, increasing air temperature may lead to hypolimnion anoxia, decreased imports, increased water renewal time or modified zooplankton peaks (Schertzer *et al.*, 1990; Schindler *et al.*, 1990; Straile, 2002). All these processes can theoretically affect fish communities through habitat or resource competition. They may interact synergistically or antagonistically, potentially hiding causal relationships.

The effect of environmental variables on total community biomass
QEMAZ models revealed that total community biomass peaked at relatively high level of TP (*c*. 80 µg.l^{-1}; Table 3 and Fig. 3 D). This is consistent with the fact that eutrophication non-linearly affects primary productivity (Vadeboncoeur *et al.*, 2003). In eutrophic lakes, benthic

primary productivity is inhibited by phytoplankton density, and thus saturates with increasing TP. Combined with an increase in the density of inedible algae at high TP, these might result in zooplankton density peaking at intermediate TP values, and this pattern could be transmitted to the fish community through bottom-up effects. Total fish biomass is not affected by changes in the AWT (Table 3), which corroborates predictions made under the hypothesis of high consumption of zooplankton by fishes (Vasseur *et al.*, 2005).

Differential effects of total community biomass on fish species
Total community biomass did not have any robust plausible effect on equilibrium log-abundances (Table 3). Instead of comparing probabilities of effect, we might compare multimodel d' scores (Table 3). Piscivores (pike) and omnivores (trout, perch) are positively (but not strongly) affected by total biomass, while planktivores (roach) are slightly negatively affected by community biomass. These patterns corroborate theoretical predictions from food chain models (Oksanen *et al.*, 1981), predicting that an increase in primary productivity benefit species at the highest trophic level and enhance total community biomass. The cases of whitefish, charr and burbot suggest discrepancies between our results and theoretical outcomes (Mylius *et al.*, 2001; Oksanen *et al.*, 1981; Persson *et al.*, 1992). For instance, total biomass does not affect positively the abundance of burbot, a piscivorous species. It remains possible though that relative capturabilities of different species depend on community biomass: if the overall fishing effort is constant, this effort might be diverted towards species that have more convex yield per effort functions. In other words, if fishing one burbot is easier than fishing one trout, but that fishing ten burbots is less easy than ten trouts, fishermen are expected to shift fishing efforts from burbot to trout with increasing total community biomass (e.g. in Salas, Sumaila & Pitcher, 2004). This explanation may also hold for charr (for which d' was found slightly negative). Charr and burbot are both attuned to the hypolimnion (deep pelagic and benthic zones) in Perialpine lakes, and so could have less convex yield-per-effort functions than littoral or pelagic species in deep lakes (e.g. trout and whitefish).

Interestingly, no planktivore was likely to be affected by community biomass, whereas some theories (Mylius *et al.*, 2001) imply that omnivores should outcompete planktivores in eutrophic waters. According to food chain models, piscivore abundances increase with resource density while planktivore abundances remain constant (Oksanen *et al.*, 1981). Our data support Oksanen's hypothesis, though not strongly since roach had slightly negative d' values. Further evaluations of both theories would require exploring a wider scale of TP changes, or experimental approaches (e.g. mesocosm manipulation of community biomass).

The influence of local and global factors on communities
Fish communities in Perialpine lakes are mainly affected by four external processes, namely climatic warming, oligotrophication, artificial fish stocking and selective fishing, which may be categorized as either local or global processes. Climatic warming is a global pattern, and affects terrestrial as well as marine ecosystems worldwide (Blenckner *et al.*, 2002; Ottersen *et al.*, 2001). On the other hand, oligotrophication, stocking and fishing are local processes with consequences at a much smaller scale. They are expected to have a more significant impact than climatic warming over short periods. This global process was here estimated using a regional index (the AWT) of a global phenomenon, which may indeed lack explanatory power at short temporal scale (Carpenter *et al.*, 1992). This might explain why TP is a better predictor than the AWT in our models. However, the lack of patterns consistent with theoretical expectations may not be entirely imputable on the geographic scale of the climatic proxy given that we used a regional (rather than global) indicator of climatic warming.

Moreover, we also performed the same analyses using the NAOI, a global climatic index, instead of AWT, and results were quite similar (results not shown). Dependencies of fish abundances on climate thus seem quite weak using both a regional and a global climatic index.

Acknowledgements

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Appendix S1 Climatic proxy for Perialpine lakes

Here, we show that monthly air temperature values around the eleven lakes studied have remained very similar over the 1970-2000 period. We used monthly temperature reconstructions (Casty, 2005; Casty *et al.*, 2005), to assess whether air temperature was similar around the 11 studied lakes during this period. Reconstructed temperature time series are highly correlated (Table S1). However, high correlations are expected because of the common seasonality component of all time series. We tested for parallel year-to-year variation among sites using the following Generalized Linear Model (GLM) :

$$T \sim Site*Month + Site*Year$$

where the *Month* and *Year* factors account for seasonal and annual variations respectively. Interactions with the *Site* factor quantify variation of seasonal or inter-annual thermal regimes among sites. Removing the site by year interaction did not change significantly the deviance (change in deviance : 48.53, df = 270, p = 1.0). The best model according to the Akaike criterion is by far $T \sim Site*Month + Year$ (Table S2), showing that although seasonal thermal regimes do vary among sites (indicating microclimatic effects), the inter-annual component of variation is common to all sites.

Table S1. Correlations and covariances among reconstruction temperature time series. Values above the diagonal are correlation coefficients, those on the diagonal (underlined values) are variances, and those under the diagonal are covariances. Headers of rows and columns refer to latitude/ longitude coordinates.

	47.25N 7.25E	47.25N 8.25E	47.25N 9.25E	46.75N 6.75E	46.75N 8.25E	46.25N 6.25E	46.25N 7.25E	46.25N 7.75E	45.25N 5.75E	45.25N 6.25E
47.25N/7.25E	<u>40.22</u>	1.00	0.99	1.00	0.99	1.00	0.99	0.98	0.99	0.99
47.25N/8.25E	40.14	<u>40.18</u>	0.99	1.00	0.99	1.00	0.98	0.98	0.99	0.98
47.25N/9.25E	39.77	39.74	<u>39.80</u>	0.99	0.99	0.99	0.99	0.98	0.99	0.99
46.75N/6.75E	39.79	39.66	39.45	<u>39.51</u>	0.99	1.00	0.99	0.99	1.00	0.99
46.75N/8.25E	35.30	35.26	35.13	35.01	<u>31.48</u>	0.99	0.99	1.00	0.99	0.99
46.25N/6.25E	40.09	40.00	39.74	39.77	35.27	<u>40.21</u>	0.99	0.98	1.00	0.99
46.25N/7.25E	35.50	35.36	35.38	35.40	31.70	35.55	<u>32.29</u>	1.00	0.99	1.00
46.25N/7.75E	33.80	33.69	33.62	33.63	30.32	33.86	30.71	<u>29.45</u>	0.99	0.99
45.25N/5.75E	39.65	39.52	39.37	39.41	35.05	39.77	35.47	33.80	<u>39.65</u>	1.00
45.25N/6.25E	36.94	36.79	36.73	36.78	32.92	37.04	33.41	31.89	37.07	<u>34.92</u>

Table S2. Akaike Information Criterion (AIC) for the four models compared in appendix S1.

Model	Degrees of freedom used	AIC
1: *T ~ Year + Site*Month*	151	13240
2: *T ~ Site*Year + Site*Month*	421	13732
3: *T ~ Year + Month*	43	20273
4: *T ~ Site*Year + Month*	322	14001

Appendix S2 Maturation delays of the species studied

This appendix deals with the justification of the use of a three-year maturation delay for all studied species. We gather all potential pieces of information which indicate that this delay is likely for most species from existing literature and databases.

A constant 3-year time lag between hatching and recruitment in all species and all lakes was used in our analyses (we mentioned in the result section that assuming a 2 or 4-year time lag did not yield substantial modifications of the results). This choice is justified by data collected in the literature. Ages at maturity indeed essentially agree with this assumption for Arctic charr (Hesthagen *et al.*, 1997; Roff, Heibo & Vollestad, 2006), brown trout (Froese & Pauly, 2006; Hesthagen *et al.*, 1997; Keith & Allardi, 2001; Klemetsen *et al.*, 2003), whitefish (Froese *et al.*, 2006; Keith *et al.*, 2001), Northern pike (Bry, 1992; Craig, 1996; Froese *et al.*, 2006; Keith *et al.*, 2001; Roche, O'Grady & Bracken, 1999), Eurasian perch (Froese *et al.*, 2006; Keith *et al.*, 2001; Roff *et al.*, 2006; Thorpe, 1977), roach (Froese *et al.*, 2006; Keith *et al.*, 2001; Papageorgiou, 1979; Tarkan, 2006), and burbot (Froese *et al.*, 2006). From the literature, the only factors that strongly affect age at maturity are fast adaptation to heavy harvesting conditions, temperature, and diet possibilities. The first factor can be excluded since fisheries exploitation in the Perialpine lakes considered is strictly defined and rules well enforced (D. Gerdeaux, pers. obs.). Changes in temperature are presumably unlikely to result in a variation of a year (or more) in age at maturity over the time period studied. Moreover, temperature anomalies oscillate around their trend, which would rather result in increased variability in age at maturity rather than increased median age at maturity. The role of diet possibilities are likely to affect age at maturity only in omnivorous species (perch, charr and trout).

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