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How Do Eutrophication and Temperature Interact to Shape the Community Structures of Phytoplankton and Fish in Lakes?

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Abstract: Freshwater ecosystems are among the systems most threatened and impacted by anthropogenic activities, but there is still a lack of knowledge on how this multi-pressure environment impacts aquatic communities in situ. In Europe, nutrient enrichment and temperature increase due to global change were identified as the two main pressures on lakes. Therefore, we investigated how the interaction of these two pressures impacts the community structure of the two extreme components of lake food webs: phytoplankton and fish. We modelled the relationship between community components (abundance, composition, size) and environmental conditions, including these two pressures. Different patterns of response were highlighted. Four metrics responded to only one pressure and one metric to the additive effect of the two pressures. Two fish metrics (average body-size and biomass ratio between perch and roach) were impacted by the interaction of temperature and eutrophication, revealing that the effect of one pressure was dependent on the magnitude of the second pressure. From a management point of view, it appears necessary to consider the type and strength of the interactions between pressures when assessing the sensitivity of communities, otherwise their vulnerability (especially to global change) could be poorly estimated.

Keywords: global change; nutrients; anthropogenic pressure stressor; interaction; multiple stressors; lake systems

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1. Introduction

Freshwater ecosystems are among the systems most threatened and impacted by anthropogenic activities [1]. They are characterized by their high biodiversity [2], the erosion of which is considered to be steeper than that of terrestrial ecosystems [3], which makes them more vulnerable. Aquatic ecosystems are exposed to numerous anthropogenic stressors, be they physical (i.e., habitat degradation), chemical, or biological (i.e. invasive species), which interact with global change and lead to additional perturbations [4–8]. These multiple stressors compromise freshwater biodiversity and its associated biological functions, and ultimately the services provided by these systems to our society [9,10].

In Europe, monitoring associated with the implementation of the Water Framework Directive (WFD; an environmental policy that aims to protect and restore continental aquatic systems) showed that numerous aquatic ecosystems are impaired by human activities, with their ecological status ranging from bad to moderate [4,11]. While the WFD calls for lakes (like all bodies of water) to be in 'good ecological status', the latest evaluation (2nd River Basin Assessment) showed that 45% of lakes did not reach this status [12]. Unfortunately, in certain hydrographic basins, this percentage may even reach 100%. The report of the European Environmental Agency [12] emphasized that lakes are particularly impacted by nutrient enrichments, and also by climate change, more specifically by temperature increases [4,12,13]. The impact of these two stressors is also the most studied. In their review based on 219 studies, Nõges et al. [10] revealed that 78% dealt with nutrient impacts and 31% with temperature effects, either solely or jointly.

Nevertheless, although lakes rarely face a single pressure, few studies have looked at the combined effects of several pressures, and even fewer have examined their interactions. Some results concerned the cumulative effects of temperature and eutrophication on phytoplankton. Both pressures affect phytoplankton abundance and composition [14–17]. For instance, Krosten et al. [18] showed that temperature and nutrients both increase the relative abundance of cyanobacteria. However, in some cases, related by Richardson et al. [19], this relation can be different, depending on the lake type (morphological characteristics of the lake). Similarly, Jeppesen et al. [20] observed that fish community composition changed as a result of these two pressures. Coldwater species were replaced by warm-water-tolerant species owing to longer warm periods in summer and lower oxygen concentrations.

In most of these studies, when multi-stressors were considered, their combined effect was commonly assumed to be additive, i.e., equal to the sum of the individual effects of the stressors acting in isolation. This additive model is increasingly discussed in ecological systems in terms of antagonistic and synergistic interactions [4,7,10,21,22]. Stressors can act in synergy when the combined effect of stressors is greater than the sum of the impacts of individual stressors, whereas antagonistic interactions occur when the combined effect of stressors is less than expected based on their individual effects [23]. In situ, temperature and nutrient enrichment interaction is very often assumed to impact biological communities, but it is rarely quantified or modelled (see Rigosi et al. [24] for exceptions). This phenomenon is better studied in experimental conditions under which nutrient concentrations and temperature can be controlled [21,25–27]. Nevertheless, from a management point of view, the value of a study of this kind could be limited (e.g., the discrepancy between scales, other factors involved, etc.), and without taking into account these interactions (if verified), the evaluation of the lake status could be biased (e.g., [28]). In addition, knowledge of these interactive effects can be useful in the implementation of management plans, with the ecological benefit resulting from efforts to reduce interactive multi-stressors possibly giving rise to some 'ecological surprises' [5,29,30].

The aim of this study was to assess whether: (i) temperature and eutrophication impact various components (metrics) of the lake community, such as productivity and size structure, (ii) whether these effects are additive, (iii) or whether they are multiplicative, i.e., whether the effect of one pressure depends on the other pressure. We focused on two biological groups at the two ends of the trophic chain that are representative of the lake community, are often used in bioindication, and are studied in multi-stress conditions: phytoplankton and fish [7,10,31–34]. Moreover, a given pressure could impact each biological element either directly or indirectly through cascade effects along the trophic chain [17,35–37]. Hence, we could hypothesize similar responses to pressure from both trophic levels expressed by the increase in primary productivity and, thus, fish productivity with temperature and nutrients [37–40]. Similarly, we expected change to the community and a negative relationship between temperature and sizes [35,41–43].

This study was conducted at the macro-ecological scale, on a consistent dataset of 204 French lakes to ensure large diversity in thermal and trophic conditions. The combined effect of temperature and eutrophication was studied by comparing three statistical models: one considering only the effect of lake morphology, a second model considering an additive effect of the two pressures, and a more complex model considering the interaction between pressures.

2. Materials and Methods

2.1. Biological Data

The dataset comprised 204 French lakes, 48 natural lakes, and 156 reservoirs, for which biological and environmental data were available and collected in a standardized manner.

Fish samples were collected according to the Norden gillnet standardized protocol [44] during the period between July and mid-October. This protocol is based on a randomly stratified sampling design. Benthic gillnets, 30 m in length, 1.5 m in height, composed of 12 panels with mesh sizes ranging from 5 to 55 mm knot-to-knot, were randomly distributed in the depth strata of the lakes. The gillnets were set before sunset and lifted after sunrise to cover peaks of maximal fish activity [45,46]. All fish caught were identified at the species level, then measured (total length in millimeters) and weighed (to the nearest gram).

Phytoplankton was collected using a standardized method [47] and processed in laboratory following the counting process of the European Standard NF15204 [48]. Four sampling campaigns a year are recommended for each lake: three during the warmer period (between May and October) and one in late winter. Phytoplankton was collected at the deepest point of the lakes, in the euphotic part of the water column. Taxa were determined at the species level in the laboratory and their abundances were weighted by taxa biovolume [49] using standard cell values defined in the software Phytobs [50], or measured directly from the sample if the values were lacking. Additionally, chlorophyll-a was collected from the euphotic zone during each sampling event and measured using the standard methods NF-T 90-117 [49,51,52].

2.2. Biological Characterization

For each sampling occasion, ichthyofauna was characterized by eight metrics related to its density, by its composition, and by the size of the individuals making up the communities. Density was estimated by the number of individuals caught per sampling unit effort (expressed in square meters of nets set during a 12-h night period; CPUE) and the total biomass caught per sampling unit effort (BPUE). The ratio between the abundance of a predator, the perch (*Perca fluviatilis*), and the abundance of a prey, the roach (*Rutilus rutilus*), was used as a proxy of the trophic equilibrium of the lakes [53,54]. These two species are very common in French temperate lakes and generally abundant [55,56]. BPUEs and CPUEs were calculated for both species and their ratios (BPUE_Perch/Roach and CPUE_Perch/Roach) were computed for all the lakes where the two species occurred. In addition, the ratio of average perch to roach body size (Average Perch/Roach Body Size) was calculated for each lake to measure the evolution of ichthyofauna composition. The overall size of the fish community was assessed by the average size of all the fish caught in the benthic gillnets in a lake. This metric is useful for comparing the average difference in fish size between communities without differentiating between the processes behind it (loss of the largest individuals, decrease in the size of all fish, increase of small species or individuals, etc.) [57,58]. To investigate the processes involved in the change in size structure, the community size spectra (CSS) were considered [59]. CSS represent a frequency distribution of individual body sizes across size classes (defined on a log-scale) irrespective of taxonomy, through a linear regression relating abundances to size classes on log scales. Two metrics were calculated: the midpoint and the slope of the regression. The midpoint (CSS_Midpoint) value is an indicator of productivity of the system and determines the level of richness of ecosystems. For instance, two communities can display the same slope but different midpoints if the one has more fish than the other [60]. Slope (CSS_Slope) is an indicator of the health of the community [60], for example, fish overexploitation will reduce the abundance of large fish traduced by a high slope value.

Four metrics relating to density, composition, or size of phytoplankton communities were considered. Phytoplankton total biomass was surrogated by the concentration of chlorophyll-a (Chl-a, μg/L) in the euphotic zone. To limit the impact of seasonal variability, the Chl-a concentrations of the three summer samples were averaged. The composition of phytoplankton was assessed by the abundances of cyanobacteria and golden alga (Chrysophytes). Cyanobacteria are assumed to benefit from warmer temperatures and become dominant in higher nutrient concentrations, whereas Chrysophyceae are assumed to prefer colder and less eutrophic conditions [41,61–63]. Their abundances were weighted by taxa biovolume (considered as fixed) in order to calculated their respective biomass (Cyano_Biovolume and Chryso_Biovolume), and expressed in cubic millimeters per liter (mm^3/L). We then defined two size classes of phytoplankton, each taxon was classified as large or small, irrespective of whether the taxon was considered larger or smaller than microphytoplankton, as defined in the literature [64]. The ratio of the biomasses of large taxa on the biomasses of small taxa in each lake was then calculated. This metric (phytoplankton size class) allows us to see, as with ichthyofauna, whether the size structure of the phytoplankton community is affected by thermal and/or eutrophic stress [41,42,62,65,66].

2.3. Environmental Data

The lakes were characterized by natural environmental variables potentially influencing the structure of biological assemblages [67,68], i.e., physical/morphological characteristic of their environment, and by stressors.

The dataset comprised 204 French lakes, 48 natural lakes and 156 reservoirs. This corresponds to a diversity of lake throughout the French territory with morphological characteristics, ranging from the plain lake to the mountain lake, from the shallow lake to the deep lake, and very varied in terms of surface, area, the shape of the lake basin, and mean temperature or trophy level (details of the calculation of the index below) (Table 1, see Supplementary Materials for more details).

Table 1. Characterization of the environmental variables of the lakes studied.

Environmental Variable	Minimum–Maximum	Mean (sd)
Altitude (m)	0–2061	404.8 (382.4)
Perimeter (m)	1.5×10^3–1.9×10^5	1.7×10^4 (2.1×10^4)
Depth (m)	0.3–154.2	12.7 (16.6)
Area (km^2)	0,1–577,1	6,1 (40.9)
Volume (m^3)	1.3×10^5–8.9×10^{10}	5×10^8 (6.2×10^9)
Ig (m/km)	0.1–155.7	8.1 (16.8)
Temperature (°C)	2.9–16.3	11.1 (2.2)
Eutrophication	−2.0–3.1	−0.01 (1.1)

In order to limit the multi-collinearity between predictors (thus the redundancy between physical variables), we ran a principal component analysis. Four variables emerged from this analysis and characterized lake morphology: the mean depth (Depth, m), the area (Area, km^2), the water volume (Volume, m^3), and the overall hill index (Ig, m/km). Ig was calculated from the maximum depth, perimeter, and area [69,70] that characterizes the shape of the lake basin, according to the following Equation (1):

$$I_g = \frac{Pmax}{Lr}, \tag{1}$$

with

$$Lr = Plake \times \frac{0{,}282}{1{,}128} \times \left(1 + \sqrt{1 - \left(\frac{1{,}128}{K_C}\right)^2}\right), \tag{2}$$

and

$$\mathrm{K_C} = 0{,}282 \times \frac{\mathrm{Plake}}{\sqrt{\mathrm{Alake}}}, \tag{3}$$

where *Pmax* is the maximum depth of the lake (m), *Plake* is its perimeter (km) and *Alake* its area (km^2).

Two stressors were considered: temperature and eutrophication. Because water temperatures were not available for all the lakes but are strongly correlated with air temperatures [71,72] ($R^2 = 0.82$), we used the latter to characterize lake temperatures. To this end we used data from the SAFRAN reanalysis [73,74], available at a spatial resolution of 8 km × 8 km. To integrate the difference of altitude between grid cells and lakes, a correction of 6.5×10^{-3} C/m was applied.

Eutrophication was described by three variables: total phosphorous concentration (TP, μg/L), nitrate concentration (NO_3, μg/L) and importance of non-natural land cover in the catchment area (NNLC, percentage of the total catchment area). Phosphorus values range from 5 μg/L to 464 μg/L, corresponding to trophic states classified from oligotrophic to hyper-eutrophic [75]. The nutrients were sampled in the euphotic zone during the four same annual campaigns as for phytoplankton, according to a standard sampling method. NNLC was defined as the percentage of non-natural areas in the catchment and derived from the Corine Land Cover database [76]. This encompassed the CLC categories: (1) artificial territories and (2) agricultural territories (without 23 grasslands) [77]. We summarized the information of these eutrophication measures in a synthetic index of eutrophication. First, TP and NO_3 were log-transformed, NNLC was transformed by the arcsin of the square root, and then each variable was centered and reduced. The three transformed variables were averaged and these values were centered and reduced to produce the synthetic index.

All the data used in this study were collected between 2005 and 2017 by research institutes or water agencies, and centralized in a database by our laboratory.

To reduce the skewness of their distribution we log transformed maximum depth, lake area, lake volume, Ig, BPUEs, CPUEs, Chl-a, and the biovolumes of cyanobacteria and Chrysophyceae.

2.4. Data Analysis

To assess the significance of the interactions of pressures on biological metrics we defined three nested linear models related to three hypotheses [78]: (i) no pressure effect, (ii) additive effect of pressures, and (iii) interaction of pressures (multiplicative effect of pressures). The first model related the variability of biological metrics to physical variables only, metric ~ depth + area + Volume + Ig corresponds to the environmental data block (called 'environment' in the next formulae); the second model integrated the physical variables and the variable of pressures in an additive manner, metric ~ environment + temperature + eutrophication; the more complex model integrated the interaction between temperature and eutrophication, metric ~ environment + temperature + eutrophication + temperature interacting with eutrophication. The first model assumed that biological metric variability depends only of the environmental conditions. The second model hypothesizes that the effect of each pressure is independent of the other. In other words, whatever the level of the second pressure, the magnitude of response to the first pressure will always be the same. Conversely, the interaction included in the third model assumed that the effect magnitude of one pressure depends on the intensity of the second pressure.

The effect of pressures and their behavior (additive or multiplicative) were tested on each fish and phytoplankton metric by comparing models two by two with ANOVA (*F*-tests). First, we tested model 3 vs. model 2, then, if the interaction was not significant, we tested model 2 vs. model 1 to verify the significance of the pressure effect on the metric variability (*F*-tests). Once the most explanatory model was selected, we visually checked whether the linear model assumptions were verified (i.e., homoscedasticity, normality of residuals). Only metrics for which more than 10% of the variability of the biological metrics was explained were retained.

Finally, because it would have been difficult to forecast from coefficient values, if the interaction was significant, we looked at its effect in graph form using graph effect display representation [79]. For each graph, we represented how the expected metric values varied along the pressure gradients by leaving pressure values and fixing the values of the environmental variable to their averages. For each metric, two sets of graphs were drawn. One graph was compiled by allowing pressure values vary across their observed range of values, and one graph was drawn by restricting pressures to their observed combination of values.

3. Results

3.1. Environment and Pressures

The two metrics describing the pressures were weakly correlated with each other and with the natural environmental variables (Table 2). Temperature varied between 2.9 °C and 16.3 °C and eutrophication between −2 (low level of eutrophication) and 3.1 (high level of eutrophication) (Table 1). Not all possible combinations of pressure values were observed (white space in the right lower part of Figure 1). For instance, no lakes with an index value of eutrophication greater than −0.5 had a temperature lower than 8 °C, or an eutrophication greater than 1 with a temperature lower than 8 °C. Finally, only a few were present at a temperature below 6 °C. These limitations of our dataset conditions will be taken into account in the following interaction analyze of pressure effects on biological metrics.

Table 2. Pearson correlation of lake characteristics with temperature and eutrophication pressures.

Environmental variable	Temperature	Eutrophication
Depth (m)	−0.22	−0.43
Area (km^2)	0.14	−0.21
Volume (m^3)	−0.01	−0.37
Ig	−0.39	−0.41
Temperature (°C)	–	0.32
Eutrophication	0.32	–

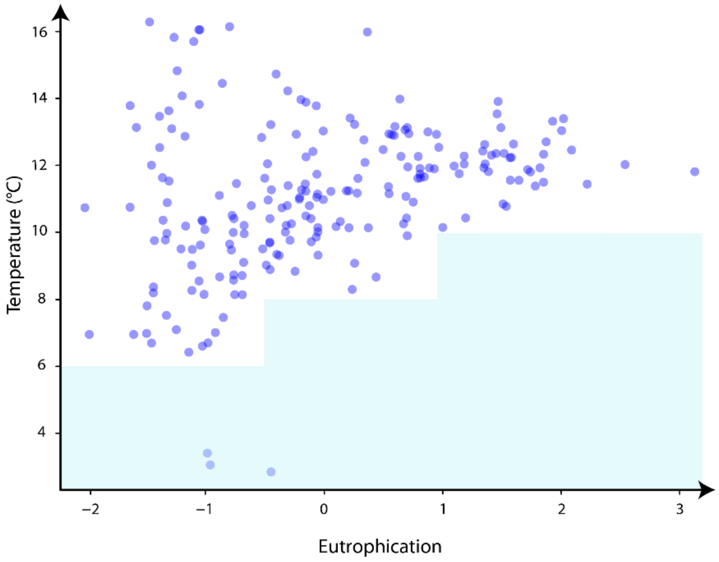

Figure 1. Relationship between temperature and eutrophication of lakes.

3.2. Pressure Effects

Of the 12 metrics, four (CSS_Slope, Phytoplankton Size Class, Average Perch/Roach Body Size, Cyano_Biovolume) were not sufficiently explained by the environmental and pressure variables ($R^2 < 10\%$) and were not considered further.

One model (CPUE_Perch/Roach) with the only environmental effect, five models (BPUE, CPUE, CSS_Midpoint, Chl-a, Chryso_Biovolume) with an additive effect of pressure and two models (Average Fish Body Size, BPUE_Perch/Roach) with a significant interaction of pressures were selected (Table 3).

Table 3. : Model comparisons two by two (ANOVA) with the final model selected and its associated adjusted R^2 ('-' if the R^2 was lower than 0.1). F-test results: *** $p < 0.001$, ** $p < 0.01$ and * $p < 0.05$. BPUE, biomass caught per sampling unit effort; CPUE, catch per sampling unit effort; CSS, community size spectra; Chl-a, chlorophyll-a; Cyano, cyanobacteria; Chryso, Chrysophyceae.

Metric	Model 2 vs. Model 3	Model 1 vs. Model 2	Selected model	R^2
BPUE	$F_{1,196} = 1.06$	$F_{1,197} = 11.86$ ***	Model 2	0.47
CPUE	$F_{1,196} = 0.88$	$F_{1,197} = 10.67$ ***	Model 2	0.32
BPUE_Perch/Roach	$F_{1,174} = 6.69$ **	$F_{1,175} = 1.11$	Model 3	0.22
CPUE_Perch/Roach	$F_{1,174} = 2.58$	$F_{1,175} = 0.70$	Model 1	0.15
Average Perch/Roach Body-Size	$F_{1,174} = 0.27$	$F_{1,175} = 0.91$	−	0
Average Fish Body Size	$F_{1,196} = 8.30$ **	$F_{1,197} = 5.72$ **	Model 3	0.12
CSS_Midpoint	$F_{1,196} = 0$	$F_{1,197} = 4.40$ *	Model 2	0.26
CSS_Slope	$F_{1,196} = 0.35$	$F_{1,197} = 0.02$	−	0.04
Chl-a	$F_{1,196} = 0.19$	$F_{1,197} = 20.32$ ***	Model 2	0.41
Cyano_Biovolume	$F_{1,196} = 2.06$	$F_{1,197} = 1.60$	−	0.09
Chryso_Biovolume	$F_{1,196} = 0.28$	$F_{1,197} = 9.90$ ***	Model 2	0.10
Phytoplankton size class	$F_{1,196} = 0.27$	$F_{1,197} = 4.57$ *	−	0.07

When an additive effect of pressure was significant, eutrophication was always positively related to the metric values (positive coefficient; Table 4), with the exception of Chryso_Biovolume, which decreased with eutrophication (Table 4). Fish metrics influenced only by eutrophication pressure were BPUE and CSS_Midpoint. The R^2 value indicated that the models explained 47% and 26% of variability, respectively. When the eutrophication index was removed from these models, the explained variance decreased by 6% and 3%. Metrics of phytoplankton influenced only by eutrophication were Chl-a and Chryso_Biovolume, with explained variances of 41% and 10%, respectively. Compared with the environmental model (model 1), including the eutrophication index, the explained variability increased by 11% and 8%, respectively. Fish CPUE was the only metric significantly influenced by the additive effect of the two pressures considered and with positive relationships. The model explained 32% of the variability of the metric (Table 3) and 7% of the variance was explained only by the combined effect of pressures.

Table 4. : Model coefficient (positive + or negative −) of pressure (temperature, eutrophication and interaction) for biological metrics selected. Bold: the impact of pressure or interaction on metric is significant.

Metric	Temperature	Eutrophication	Interaction
BPUE	+0.03	**+0.14**	No interaction
CPUE	**+0.06**	**+0.22**	No interaction
BPUE_Perch/Roach	**−0.17**	**+1.91**	**−0.16**
Average Fish Body-Size	**−0.43**	**−50.56**	**+4.04**
CSS_Midpoint	+0.04	**+0.13**	No interaction
Chl-a	+0.05	**+0.43**	No interaction
Chryso_Biovolume	+0.06	**−0.90**	No interaction

3.3. Interaction of Pressures

A significant negative effect of the interaction between eutrophication and temperature was measured on the BPUE_Perch/Roach metric, but a positive effect of the interaction between these two pressures was measured on the Average Fish Body Size metric. In these models, BPUE_Perch/Roach was negatively related to temperature and positively to eutrophication. Average Fish Body Size was negatively related to both temperature and eutrophication (Table 4). The interactive models explained 22% and 12% of the variability of the BPUE_Perch/Roach and Average Fish Body Size metrics, respectively. Compared with the R^2 value of the additive model (19% and 9%), the gain in explained variability relative to the interaction model represented an increase of 3% for both.

The interaction effects between temperature and eutrophication on BPUE_Perch/Roach and Average Fish Body Size metrics were assessed graphically (Figure 2, Figure 3). In the case of BPUE_Perch/Roach, we observed an interval of values approximately three times lower at low levels of eutrophication than at high levels, which means a higher effect of temperature at high eutrophication levels (Figure 2b). This corresponds to a small increase in BPUE_Perch/Roach with temperature for low levels of eutrophication and a large decrease with temperature at high levels of eutrophication. At low temperatures (<10–12 °C) we observed higher BPUE_Perch/Roach values than at higher temperatures (Figure 2c), which is accompanied by an increase in the metric with eutrophication at low temperatures and a decrease at high temperatures.

By looking at the interaction only on the combination of pressure values observed in lakes, the magnitude of response was limited (Figure 2d). We saw a small increase in the ratio of temperature to the low level of eutrophication (Figure 2e) and a significant decrease with the temperature for high levels of eutrophication (Figure 2f), reaching lower ratio values than at low temperatures. The high values of the BPUE_Perch/Roach ratio visible on the full model (Figure 2a) at low temperature–high eutrophication were not visible with the *in situ* pressure values (Figure 2d).

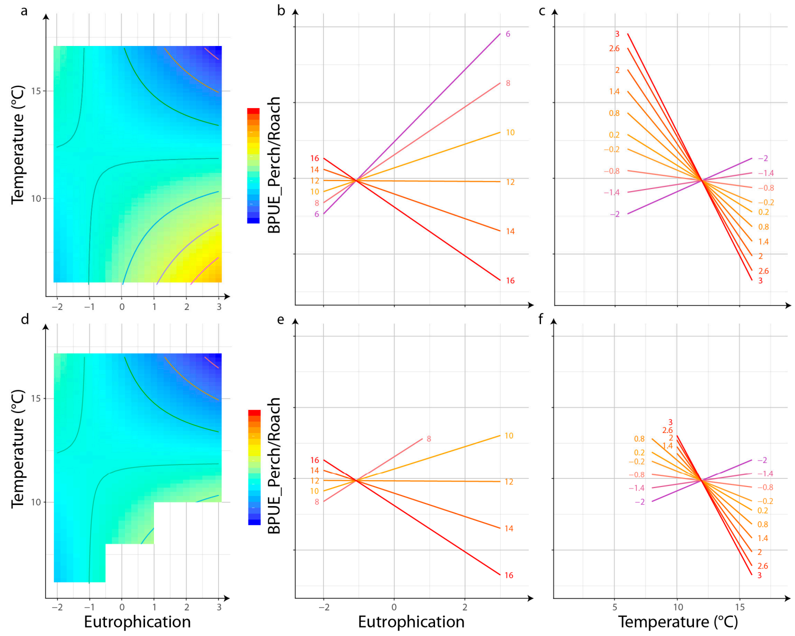

Figure 2. Effect of interaction between average temperature and eutrophication level on BPUE_Perch/Roach metric (log) when considering all possible combinations of pressures (**a**–**c**), or when considering only the observed combination of pressures (see Figure 1) (**d**–**f**). (**a**,**d**) Low theoretical values are represented in blue and high theoretical values in red.

When temperature increased, Average Fish Body Size decreased at low eutrophication levels, and increased strongly at high levels of eutrophication (Figure 3b). We observed higher Average Fish Body Size at low eutrophication, whereas we observed the lowest values in high eutrophication and low temperature conditions. At low temperatures (2–12 °C), body size varied widely with eutrophication and the highest values were observed when eutrophication was low (Figure 3c). Conversely, when temperatures were high (12–17 °C), the highest values of fish body size were measured when eutrophication was significant. Average Fish Body Size decreased with eutrophication at low temperatures and increased with eutrophication at high temperatures.

When analysis was limited to the pressure values observed, we essentially detected an increase in size with eutrophication for high temperatures (>13 °C) (Figure 3e) and a decrease in body size with temperature for low levels of eutrophication (Figure 3f). Compared with Figure 3a, the amplitude of body size in response to pressure conditions was reduced. The lowest values associated with an increase in temperature at low eutrophication were not observed with the observed pressure values (Figure 3d).

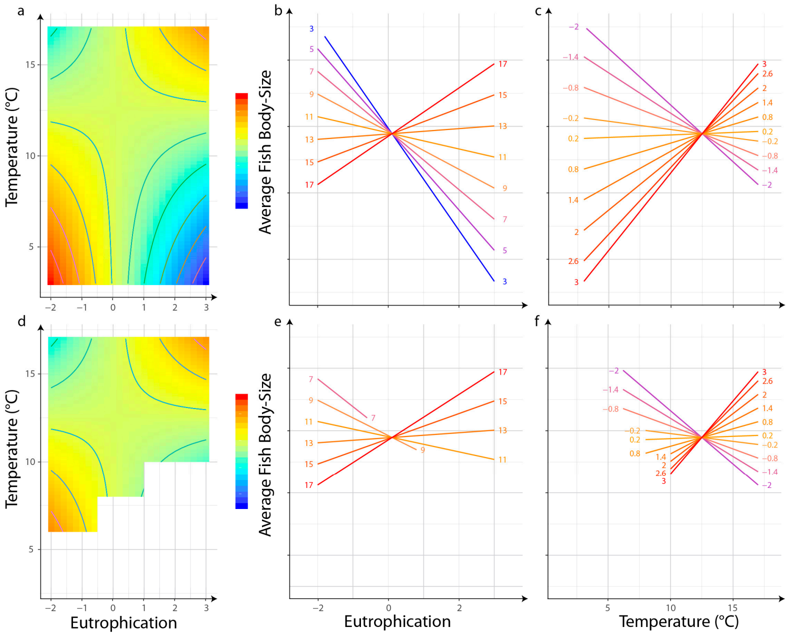

Figure 3. Effect of interaction between average temperature and eutrophication level on Average Fish Body Size when considering all possible combinations of pressures (**a–c**), or when considering only the observed combination of pressures (see Figure 1) (**d–f**). (**a**,**d**) Low theoretical values are in blue and high theoretical values in red.

4. Discussion

The objective of our study was to assess the interactive effect of temperature and eutrophication on the structure of fish and phytoplankton communities. Among the twelve pressure/impact models developed, an additive effect and an interactive effect were detected for, respectively one and two fish metrics, while most of the models reveal a significant effect of one stressor.

The impact of eutrophication on biological communities has long been observed [41]. For example, the effects of phosphorus loadings on primary production have largely been described in the scientific literature [80–82]. Algal blooms in response to eutrophication are also well-documented [83], as well as the changes in community structure [34,42,66,84,85]. The impact of temperature has been explored in detail, and is often still studied, especially since climate change has become evident [86]. The effect of an increase in temperature could be manifold and complex (see, for instance, Keller [87] and Richardson et al. [19]), but many authors agree on an increase in productivity [38,88,89] or on a decrease in ectothermal size [57,90,91]. Most of our results are in accordance with these observations. Fish density expressed in occurrence (CPUE) was shown to be positively correlated with an increase in both temperature and eutrophication. Similarly, the biomass of fish per capture effort (BPUE) and Chl-a were positively related to nutrient enrichment. This increasing productivity of phytoplankton and fish with eutrophication [36,38,92] is generally associated with the shift in community composition and structure [35], which is also observed in our case, through the ratio of perch vs. roach biomasses and Chrysophytes biomass. The biomass of Chrysophytes was shown to decrease when eutrophication increases, which is consistent with our hypothesis and previous results [34,35,85].

Of the two metrics related to CSS, slope and midpoints, only the latter was shown to increase with eutrophication. Finally, four metrics for which response to eutrophication and/or temperature were expected, were not explained by our models: CSS_Slope, Phytoplankton Size Class, Average Perch/Roach Body Size, and Cyano_Biovolume. The absence of impact of the stressors can be attributed to sampling protocol (reduction of the size range variability by gillnet selectivity for fish) and to size assessment for phytoplankton (very simplified and coarse) [41,42,66]. In addition, the high temporal and spatial variability of the abundance of cyanobacteria is a limit to this type of analysis [93,94].

In addition to the effect of pressures, we saw the significant proportion of model variability explained by the environmental characteristics of lakes confirming previous results and patterns when focusing on pressures [67,68].

More interestingly, two metrics were sensitive to the interaction of temperature and eutrophication: BPUE ratio between perch and roach and average community size. The interaction of these two pressures on the BPUE ratio between perch and roach highlighted the role played by temperature on the magnitude of this relationship. This was even more evident when graph effect displays were represented only on the observed range of values of these pressures (Figure 2d–f). The slope of the relation between eutrophication and BPUE ratio increased as the temperature increased (especially between 12 and 16 degrees). When all possible combinations of the pressures (Figure 2a–c) are used to visualize the estimated effect of each pressure (taking into account the second pressure due to the interaction between the two), some unexpected relationship may appear: for instance, a positive relationship between the ratio of perch/roach biomasses and nutrient enrichment for cold lakes (see Figure 2b). This is probably due to deep extrapolations for non-observed pressure conditions. Unlike an experimental design, for which environmental conditions are controlled and a perfect crossover of pressures can be used, the cold lakes in our dataset were mainly oligotrophic. Eutrophic lakes were predominantly observed under cool and warm conditions (Figure 1). However, interactive effects of temperature and nutrients on community dynamics are very often studied and observed on phytoplankton [37,84,85], but poorly tested for fish.

The relationship between fish size and temperature has been well studied, especially in the context of global warming (e.g., [57]). The significant interaction between eutrophication and temperature suggested that the magnitude as well as the sign of the relationship between temperature and average community size depends on trophic level. In oligotrophic conditions, community size was estimated to decrease along thermal gradients. This pattern has already been observed for fish [57,91], especially in lakes [95]. Ectothermal individuals could be smaller in warmer conditions, according to the temperature size rule theory [90], and/or smaller species could be preferentially selected as temperature increases [57,91]. With nutrient enrichment, the model predicted that average community size would increase with temperature, which is contradictory to the theory prediction. Nonetheless, fish in fisheries would grow faster and larger when the temperature increases, but when they are fed ad libitum [96]. This could also be explained by a more efficient trophic transfer and more available resources amplified through the trophic level with warming, as predicted by metabolic theory in nutrient-replete systems [97].

The fact that some components of community structure are impacted by different pressures and, in particular, their interaction should provide water managers with strong insight. Until recently in Europe, water managers mainly focused on pressure–impact relationships through multi-metric indices [98,99] to assess the ecological status of lakes [100,101] owing to the WFD. Such interaction could influence the scoring values of metrics, then metric index values and ecological assessment, but Miguet et al. [28] evaluated it at a small deviation. More recently, rather than focusing on ecological status, which is a current evaluation, some authors have worked on the vulnerability of lake ecosystems (e.g. [102]). This concept was designed around three components—sensitivity (the degree to which communities are affected, either adversely or beneficially, by pressure), exposure (contact between communities and stressors) and capacity to adapt (the ability of communities to adjust to potential hazards, to take advantage of opportunities or to respond to consequences) [103]—and seems very interesting for anticipating/forecasting lakes that will suffer from global warming. Addressing the vulnerability of communities to multiple stressors appears necessary in order to prevent future alterations in aquatic ecosystems by prioritizing the protection of the most vulnerable structures [104,105]. Our study shows that the sensitivity of communities is modulated both by the level of exposure to pressures and by the coupling of these pressures. If the interaction of pressures is seen as an additive effect, while multiple interactions could occur [7], then the sensitivity of the communities might be inconsistently evaluated, since the actual effect of a pressure would be related to the level of the other pressures. Thus, by ignoring interaction, there is a risk of an unexpected ecological effect by underestimating the effect of pressure, or even concluding that an effect in the opposite direction depends on the exposure level to another pressure [5,6]. This could lead to the adoption of an inappropriate strategy to manage lakes or to not prioritizing management actions for lakes that could actually be much more vulnerable than expected. With the increase of stress on freshwater ecosystems such as lakes, it will be necessary to pursue our monitoring on these systems to study their combined effects with global change and how this will impact aquatic communities [7,106].

To conclude, we highlight in situ interactive effects of eutrophication and temperature on lake fish communities. Therefore, in light of these unexpected effects, future management plans should consider the type and strength of interactions in order to avoid underestimating the vulnerability of these environments [105,107]. Finally, a consideration of pressure interaction in the study of environmental vulnerability could help to identify priorities for action to conserve and restore aquatic environments.

Supplementary Materials: The following are available online at www.mdpi.com/2073-4441/12/3/779/s1, Table S1: Linear Model Coefficients of biological metrics, Table S2: Environmental characteristic of the 204 lakes in the dataset.

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References

1. Dudgeon, D.; Arthington, A.H.; Gessner, M.O.; Kawabata, Z.-I.; Knowler, D.J.; Lévêque, C.; Naiman, R.J.; Prieur-Richard, A.-H.; Soto, D.; Stiassny, M.L.J.; et al. Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biol. Rev.* **2006**, *81*, 163.
2. Lundberg, J.G.; Kottelat, M.; Smith, G.R.; Stiassny, M.L.J.; Gill, A.C. So Many Fishes, So Little Time: An Overview of Recent Ichthyological Discovery in Continental Waters. *Ann. Mo. Bot. Gard.* **2000**, *87*, 26.
3. Sala, O.E. Global Biodiversity Scenarios for the Year 2100. *Science* **2000**, *287*, 1770–1774.
4. Hering, D.; Carvalho, L.; Argillier, C.; Beklioglu, M.; Borja, A.; Cardoso, A.C.; Duel, H.; Ferreira, T.; Globevnik, L.; Hanganu, J.; et al. Managing aquatic ecosystems and water resources under multiple stress—An introduction to the MARS project. *Sci. Total Environ.* **2015**, *503–504*, 10–21.
5. Jackson, M.C.; Woodford, D.J.; Weyl, O.L.F. Linking key environmental stressors with the delivery of provisioning ecosystem services in the freshwaters of southern Africa: Environmental stress and ecosystem services. *Geo Geogr. Environ.* **2016**, *3*, e00026.
6. Ormerod, S.J.; Dobson, M.; Hildrew, A.G.; Townsend, C.R. Multiple stressors in freshwater ecosystems. *Freshw. Biol.* **2010**, *55*, 1–4.
7. Schinegger, R.; Palt, M.; Segurado, P.; Schmutz, S. Untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. *Sci. Total Environ.* **2016**, *573*, 1079–1088.
8. Wagner, T.; Erickson, L.E. Sustainable Management of Eutrophic Lakes and Reservoirs. *J. Environ. Prot.* **2017**, *08*, 436–463.
9. Côté, I.M.; Darling, E.S.; Brown, C.J. Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B Biol. Sci.* **2016**, *283*, 20152592.

10. Nõges, P.; Argillier, C.; Borja, Á.; Garmendia, J.M.; Hanganu, J.; Kodeš, V.; Pletterbauer, F.; Sagouis, A.; Birk, S. Quantified biotic and abiotic responses to multiple stress in freshwater, marine and ground waters. *Sci. Total Environ.* **2016**, *540*, 43–52.
11. Poikane, S.; Ritterbusch, D.; Argillier, C.; Białokoz, W.; Blabolil, P.; Breine, J.; Jaarsma, N.G.; Krause, T.; Kubečka, J.; Lauridsen, T.L.; et al. Response of fish communities to multiple pressures: Development of a total anthropogenic pressure intensity index. *Sci. Total Environ.* **2017**, *586*, 502–511.
12. Kristensen, P.; Whalley, C.; Zal, F.; Christiansen, T.; Schmedtje, U.; Solheim, A.; Austnes, K.; Kampa, E.; Rouillard, J.; Prchalova, H.; et al. *2018 EEA European Waters Assessment*; European Waters Assessment; Office for Official Publications of the European Union: Copenhagen, Denmark, 2018; Volume 7.
13. Kristensen, P.; Vanneuville, W. In *Climate Change, Impacts and Vulnerability in Europe 2012: An Indicator-Based Report Section 3.3: Freshwater Quantity and Quality*; European Waters Assessment; Office for Official Publications of the European Union: Luxembourg, 2012; Volume 12, pp. 119–127.
14. Chen, X.; Yang, X.; Dong, X.; Liu, E. Environmental changes in Chaohu Lake (southeast, China) since the mid 20th century: The interactive impacts of nutrients, hydrology and climate. *Limnologica* **2013**, *43*, 10–17.
15. Salmaso, N. Interactions between nutrient availability and climatic fluctuations as determinants of the long-term phytoplankton community changes in Lake Garda, Northern Italy. *Hydrobiologia* **2011**, *660*, 59–68.
16. Scheffer, M.; van Nes, E.H. Shallow lakes theory revisited: Various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia* **2007**, *584*, 455–466.
17. Shurin, J.B.; Winder, M.; Adrian, R.; Keller, W.; Matthews, B.; Paterson, A.M.; Paterson, M.J.; Pinel-Alloul, B.; Rusak, J.A.; Yan, N.D. Environmental stability and lake zooplankton diversity—Contrasting effects of chemical and thermal variability. *Ecol. Lett.* **2010**, *13*, 453–463.
18. Kosten, S.; Huszar, V.L.M.; Bécares, E.; Costa, L.S.; Donk, E.; Hansson, L.-A.; Jeppesen, E.; Kruk, C.; Lacerot, G.; Mazzeo, N.; et al. Warmer climates boost cyanobacterial dominance in shallow lakes. *Glob. Chang. Biol.* **2012**, *18*, 118–126.
19. Richardson, J.; Miller, C.; Maberly, S.C.; Taylor, P.; Globevnik, L.; Hunter, P.; Jeppesen, E.; Mischke, U.; Moe, S.J.; Pasztaleniec, A.; et al. Effects of multiple stressors on cyanobacteria abundance vary with lake type. *Glob. Chang. Biol.* **2018**, *24*, 5044–5055.
20. Jeppesen, E.; Mehner, T.; Winfield, I.J.; Kangur, K.; Sarvala, J.; Gerdeaux, D.; Rask, M.; Malmquist, H.J.; Holmgren, K.; Volta, P.; et al. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia* **2012**, *694*, 1–39.
21. Crain, C.M.; Kroeker, K.; Halpern, B.S. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* **2008**, *11*, 1304–1315.
22. Piggott, J.J.; Townsend, C.R.; Matthaei, C.D. Reconceptualizing synergism and antagonism among multiple stressors. *Ecol. Evol.* **2015**, *5*, 1538–1547.
23. Folt, C.L.; Chen, C.Y.; Moore, M.V.; Burnaford, J. Synergism and antagonism among multiple stressors. *Limnol. Oceanogr.* **1999**, *44*, 864–877.
24. Rigosi, A.; Carey, C.C.; Ibelings, B.W.; Brookes, J.D. The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic state and varies among taxa. *Limnol. Oceanogr.* **2014**, *59*, 99–114.
25. Matthaei, C.D.; Piggott, J.J.; Townsend, C.R. Multiple stressors in agricultural streams: Interactions among sediment addition, nutrient enrichment and water abstraction: Sediment, nutrients & water abstraction. *J. Appl. Ecol.* **2010**, *47*, 639–649.
26. Piggott, J.J.; Lange, K.; Townsend, C.R.; Matthaei, C.D. Multiple Stressors in Agricultural Streams: A Mesocosm Study of Interactions among Raised Water Temperature, Sediment Addition and Nutrient Enrichment. *PLoS ONE* **2012**, *7*, e49873.
27. Townsend, C.R.; Uhlmann, S.S.; Matthaei, C.D. Individual and combined responses of stream ecosystems to multiple stressors. *J. Appl. Ecol.* **2008**, *45*, 1810–1819.
28. Miguet, P.; Logez, M.; Argillier, C. *Incertitudes Liées aux Interactions de Pressions. Effet des Interactions Entre les Pressions sur les Métriques Constitutives des Indicateurs IIL et IIR—Rapport AQUAREF. Personal Communication*; Irstea: Aix-en-provence, France, 2018.
29. Paine, R.T.; Tegner, M.J.; Johnson, E.A. Compounded Perturbations Yield Ecological Surprises. *Ecosystems* **1998**, *1*, 535–545.

30. Villar-Argaiz, M.; Medina-Sánchez, J.M.; Biddanda, B.A.; Carrillo, P. Predominant Non-additive Effects of Multiple Stressors on Autotroph C:N:P Ratios Propagate in Freshwater and Marine Food Webs. *Front. Microbiol.* **2018**, *9*, 69.
31. Lange, K.; Townsend, C.R.; Matthaei, C.D. Inconsistent Relationships of Primary Consumer N Stable Isotope Values to Gradients of Sheep/Beef Farming Intensity and Flow Reduction in Streams. *Water* **2019**, *11*, 2239.
32. Walters, A.W.; Bartz, K.K.; Mcclure, M.M. Interactive Effects of Water Diversion and Climate Change for Juvenile Chinook Salmon in the Lemhi River Basin (U.S.A.): Water Diversion and Climate Change. *Conserv. Biol.* **2013**, *27*, 1179–1189.
33. Wenger, S.J.; Isaak, D.J.; Luce, C.H.; Neville, H.M.; Fausch, K.D.; Dunham, J.B.; Dauwalter, D.C.; Young, M.K.; Elsner, M.M.; Rieman, B.E.; et al. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 14175–14180.
34. Winder, M.; Reuter, J.E.; Schladow, S.G. Lake warming favours small-sized planktonic diatom species. *Proc. R. Soc. B Biol. Sci.* **2009**, *276*, 427–435.
35. Jeppesen, E.; Sondergaard, M.; Jensen, J.P.; Havens, K.E.; Anneville, O.; Carvalho, L.; Coveney, M.F.; Deneke, R.; Dokulil, M.T.; Foy, B.; et al. Lake responses to reduced nutrient loading - an analysis of contemporary long-term data from 35 case studies. *Freshw. Biol.* **2005**, *50*, 1747–1771.
36. Jeppesen, E.; Peder Jensen, J.; SØndergaard, M.; Lauridsen, T.; Landkildehus, F. Trophic structure, species richness and biodiversity in Danish lakes: Changes along a phosphorus gradient: A detailed study of Danish lakes along a phosphorus gradient. *Freshw. Biol.* **2000**, *45*, 201–218.
37. Kratina, P.; Greig, H.S.; Thompson, P.L.; Carvalho-Pereira, T.S.A.; Shurin, J.B. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology* **2012**, *93*, 1421–1430.
38. Bucak, T.; Saraoğlu, E.; Levi, E.E.; Nihan Tavşanoğlu, Ü.; İdİl Çakiroğlu, A.; Jeppesen, E.; Beklioğlu, M. The influence of water level on macrophyte growth and trophic interactions in eutrophic Mediterranean shallow lakes: A mesocosm experiment with and without fish: Effects of water level in warm shallow lakes. *Freshw. Biol.* **2012**, *57*, 1631–1642.
39. Downing, J.A.; Plante, C.; Lalonde, S. Fish Production Correlated with Primary Productivity, not the Morphoedaphic Index. *Can. J. Fish. Aquat. Sci.* **1990**, *47*, 1929–1936.
40. Kronvang, B.; Jeppesen, E.; Conley, D.J.; Søndergaard, M.; Larsen, S.E.; Ovesen, N.B.; Carstensen, J. Nutrient pressures and ecological responses to nutrient loading reductions in Danish streams, lakes and coastal waters. *J. Hydrol.* **2005**, *304*, 274–288.
41. Meerhoff, M.; Teixeira-de Mello, F.; Kruk, C.; Alonso, C.; González-Bergonzoni, I.; Pacheco, J.P.; Lacerot, G.; Arim, M.; Beklioğlu, M.; Brucet, S.; et al. Environmental Warming in Shallow Lakes. In *Advances in Ecological Research*; Elsevier: London, UK, 2012; Volume 46, pp. 259–349.
42. Moss, B.; Stephen, D.; Balayla, D.M.; Becares, E.; Collings, S.E.; Fernandez-Alaez, C.; Fernandez-Alaez, M.; Ferriol, C.; Garcia, P.; Goma, J.; et al. Continental-scale patterns of nutrient and fish effects on shallow lakes: Synthesis of a pan-European mesocosm experiment. *Freshw. Biol.* **2004**, *49*, 1633–1649.
43. Persson, L.; Diehl, S.; Johansson, L.; Andersson, G.; Hamrin, S.F. Shifts in fish communities along the productivity gradient of temperate lakes-patterns and the importance of size-structured interactions. *J. Fish Biol.* **1991**, *38*, 281–293.
44. C.E.N. *Water Quality—Guidance on the Scope and Selection of Fish Sampling Methods (English Version EN 14757:2015)*; European Committee for Standardization; BSI Standards: Brussels, Belgium, 2015.
45. Prchalová, M.; Mrkvička, T.; Kubečka, J.; Peterka, J.; Čech, M.; Muška, M.; Kratochvíl, M.; Vašek, M. Fish activity as determined by gillnet catch: A comparison of two reservoirs of different turbidity. *Fish. Res.* **2010**, *102*, 291–296.
46. Šmejkal, M.; Ricard, D.; Prchalová, M.; Říha, M.; Muška, M.; Blabolil, P.; Čech, M.; Vašek, M.; Jůza, T.; Monteoliva Herreras, A.; et al. Biomass and Abundance Biases in European Standard Gillnet Sampling. *PLoS ONE* **2015**, *10*, e0122437.
47. Laplace-Treyture, C.; Rimet, F.; Anneville, O.; Druart, J.-C.; Barbe, J.; Dutartre, A. *Protocole Standardisé D'échantillonnage, de Conservation, D'observation et de Dénombrement du Phytoplancton en Plan D'eau Pour la Mise en Œuvre de la DCE: Version 3.3.1. Personal Communication.*; Cemagref: Cestas, France, 2009; p. 44.
48. A.F.N.O.R., N.E. 15204 *Qualité de l'eau—Norme Guide Pour le Dénombrement du Phytoplancton par Microscopie Inversée (Méthode Utermöhl). [Water Quality. Guidance Standard on the Enumeration of Phytoplankton Using*

Inverted Microscopy (Utermöhl Technique)]. AFNOR Normalisation: La plaine Saint-Denis, France, 2006; p. 39.

49. Derot, J.; Jamoneau, A.; Teichert, N.; Rosebery, J.; Morin, S.; Laplace-Treyture, C. Response of phytoplankton traits to environmental variables in French lakes: New perspectives for bioindication. *Ecol. Indic.* **2020**, *108*, 105659.
50. Laplace-Treyture, C.; Hadoux, E.; Plaire, M.; Dubertrand, A.; Esmieu, P. *PHYTOBS v3.0: Outil de Comptage du Phytoplancton en Laboratoire et de Calcul de l'IPLAC. Version 3.0. Application JAVA. Personal Communication*; Irstea: Cestas, France, 2017.
51. Laplace-Treyture, C.; Feret, T. Performance of the Phytoplankton Index for Lakes (IPLAC): A multimetric phytoplankton index to assess the ecological status of water bodies in France. *Ecol. Indic.* **2016**, *69*, 686–698.
52. A.F.N.O.R., N.T. 90-117 *Qualité de l'eau—Dosage de la Chlorophylle a et d'un Indice Phéopigments. Méthode par Spectrométrie D'absorption Moléculaire [Water Quality—Determination of Chlorophyll a and of a Pheopigments Index. Molecular Absorption Spectrometric Method]*. AFNOR Normalisation: Paris, France, 1999; p. 11.
53. Bergström, L.; Karlsson, M.; Bergström, U.; Pihl, L.; Kraufvelin, P. Relative impacts of fishing and eutrophication on coastal fish assessed by comparing a no-take area with an environmental gradient. *Ambio* **2019**, *48*, 565–579.
54. Van Dorst, R.M.; Gårdmark, A.; Svanbäck, R.; Beier, U.; Weyhenmeyer, G.A.; Huss, M. Warmer and browner waters decrease fish biomass production. *Glob. Chang. Biol.* **2019**, *25*, 1395–1408.
55. Deceliere-Vergès, C.; Argillier, C.; Lanoiselée, C.; De Bortoli, J.; Guillard, J. Stability and precision of the fish metrics obtained using CEN multi-mesh gillnets in natural and artificial lakes in France. *Fish. Res.* **2009**, *99*, 17–25.
56. Irz, P.; Odion, M.; Argillier, C.; Pont, D. Comparison between the fish communities of lakes, reservoirs and rivers: Can natural systems help define the ecological potential of reservoirs? *Aquat. Sci.* **2006**, *68*, 109–116.
57. Daufresne, M.; Lengfellner, K.; Sommer, U. Global warming benefits the small in aquatic ecosystems. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 12788–12793.
58. Ohlberger, J. Climate warming and ectotherm body size—From individual physiology to community ecology. *Funct. Ecol.* **2013**, *27*, 991–1001.
59. White, E.P.; Ernest, S.K.M.; Kerkhoff, A.J.; Enquist, B.J. Relationships between body size and abundance in ecology. *Trends Ecol. Evol.* **2007**, *22*, 323–330.
60. Guiet, J.; Poggiale, J.-C.; Maury, O. Modelling the community size-spectrum: Recent developments and new directions. *Ecol. Model.* **2016**, *337*, 4–14.
61. Bartosiewicz, M.; Przytulska, A.; Deshpande, B.N.; Antoniades, D.; Cortes, A.; MacIntyre, S.; Lehmann, M.F.; Laurion, I. Effects of climate change and episodic heat events on cyanobacteria in a eutrophic polymictic lake. *Sci. Total Environ.* **2019**, *693*, 133414.
62. Korkonen, S.; Weckström, J.; Korhola, A. Biogeography and ecology of freshwater chrysophyte cysts in Finland. *Hydrobiologia* **2019**, *847*, 497–499.
63. Moss, B.; Kosten, S.; Meerhoff, M.; Battarbee, R.W.; Jeppesen, E.; Mazzeo, N.; Havens, K.; Lacerot, G.; Liu, Z.; De Meester, L.; et al. Allied attack: Climate change and eutrophication. *Inland Waters* **2011**, *1*, 101–105.
64. Ignatiades, L. Redefinition of cell size classification of phytoplankton—A potential tool for improving the quality and assurance of data interpretation. *Mediterr. Mar. Sci.* **2015**, *17*, 56.
65. Kruk, C.; Huszar, V.L.M.; Peeters, E.T.H.M.; Bonilla, S.; Costa, L.; LüRling, M.; Reynolds, C.S.; Scheffer, M. A morphological classification capturing functional variation in phytoplankton. *Freshw. Biol.* **2010**, *55*, 614–627.
66. Stephen, D.; Balayla, D.M.; Becares, E.; Collings, S.E.; Fernandez-Alaez, C.; Fernandez-Alaez, M.; Ferriol, C.; Garcia, P.; Goma, J.; Gyllstrom, M.; et al. Continental-scale patterns of nutrient and fish effects on shallow lakes: Introduction to a pan-European mesocosm experiment. *Freshw. Biol.* **2004**, *49*, 1517–1524.
67. Irz, P.; Michonneau, F.; Oberdorff, T.; Whittier, T.R.; Lamouroux, N.; Mouillot, D.; Argillier, C. Fish community comparisons along environmental gradients in lakes of France and north-east USA. *Glob. Ecol. Biogeogr.* **2007**, *16*, 350–366.
68. Mehner, T.; Holmgren, K.; Lauridsen, T.L.; Jeppesen, E.; Diekmann, M. Lake depth and geographical position modify lake fish assemblages of the European 'Central Plains' ecoregion. *Freshw. Biol.* **2007**, *52*, 2285–2297.
69. Danis, P.-A.; Ferrer, R.; Gevrey, M.; Argillier, C. *Seuils des Paramètres Physicochimiques Soutenant la Biologie—Plans d'eau Naturels—Rapport D'avancement. Personal Communication*; Irstea: Aix-en-Provence, France, 2012.

70. FAO. CEMAGREF. In *Crues et Apports: Manuel Pour L'estimation des Crues Décennales et des Apports Annuels Pour les Petits Bassins Versants non Jaugés de L'AFRIQUE Sahélienne et Tropicale Sèche*; Food and Agriculture Organization of the United Nations: Rome, Italy, 1996; pp. 61–77.
71. Livingstone, D.M.; Lotter, A.F. The relationship between air and water temperatures in lakes of the Swiss Plateau. *J. Paleolimnol.* **1998**, *19*, 181–198.
72. Prats, J.; Danis, P.-A. An epilimnion and hypolimnion temperature model based on air temperature and lake characteristics. *Knowl. Manag. Aquat. Ecosyst.* **2019**, 8, doi:10.1051/kmae/2019001.
73. Quintana-Seguí, P.; Le Moigne, P.; Durand, Y.; Martin, E.; Habets, F.; Baillon, M.; Canellas, C.; Franchisteguy, L.; Morel, S. Analysis of Near-Surface Atmospheric Variables: Validation of the SAFRAN Analysis over France. *J. Appl. Meteorol. Climatol.* **2008**, *47*, 92–107.
74. Vidal, J.-P.; Martin, E.; Franchistéguy, L.; Baillon, M.; Soubeyroux, J.-M. A 50-year high-resolution atmospheric reanalysis over France with the Safran system. *Int. J. Climatol.* **2010**, *30*, 1627–1644.
75. Vollenweider, R.A. Global problems of eutrophication and its control. *Symp. Biol. Hung* **1989**, *38*, 19–41.
76. European Union—SOeS Corine Land Cover. Available online: https://www.statistiques.developpement-durable.gouv.fr/corine-land-cover-0 (accessed on 2 December 2019).
77. Launois, L.; Veslot, J.; Irz, P.; Argillier, C. Selecting fish-based metrics responding to human pressures in French natural lakes and reservoirs: Towards the development of a fish-based index (FBI) for French lakes: Response of fish-based metrics to human pressures in French lakes. *Ecol. Freshw. Fish* **2011**, *20*, 120–132.
78. Logez, M.; Pont, D.; Ferreira, M.T. Do Iberian and European fish faunas exhibit convergent functional structure along environmental gradients? *J. N. Am. Benthol. Soc.* **2010**, *29*, 1310–1323.
79. Fox, J. Effect Displays in R for Generalised Linear Models. *J. Stat. Softw.* **2003**, *8*, 27.
80. Elser, J.J.; Bracken, M.E.S.; Cleland, E.E.; Gruner, D.S.; Harpole, W.S.; Hillebrand, H.; Ngai, J.T.; Seabloom, E.W.; Shurin, J.B.; Smith, J.E. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* **2007**, *10*, 1135–1142.
81. Rader, R.B.; Richardson, C.J. The effects of nutrient enrichment on algae and macroinvertebrates in the everglades: A review. *Wetlands* **1992**, *12*, 121–135.
82. Smith, V.H.; Tilman, G.D.; Nekola, J.C. Eutrophication: Impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* **1999**, *100*, 179–196.
83. Anderson, D.M.; Glibert, P.M.; Burkholder, J.M. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* **2002**, *25*, 704–726.
84. Jeppesen, E.; Kronvang, B.; Meerhoff, M.; Søndergaard, M.; Hansen, K.M.; Andersen, H.E.; Lauridsen, T.L.; Liboriussen, L.; Beklioglu, M.; Özen, A.; et al. Climate Change Effects on Runoff, Catchment Phosphorus Loading and Lake Ecological State, and Potential Adaptations. *J. Environ. Qual.* **2009**, *38*, 1930.
85. Moss, B.; Mckee, D.; Atkinson, D.; Collings, S.E.; Eaton, J.W.; Gill, A.B.; Harvey, I.; Hatton, K.; Heyes, T.; Wilson, D. How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in shallow lake microcosms: Climate change and phytoplankton. *J. Appl. Ecol.* **2003**, *40*, 782–792.
86. Pörtner, H.-O.; Roberts, D.C.; Masson-Delmotte, V.; Zhai, P.; Tignor, M.; Poloczanska, E.; Mintenbeck, K.; Alegría, A.; Nicolai, M.; Okem, A.; et al. *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*; IPCC: Geneva, Switzerland, 2019.
87. Keller, W. Implications of climate warming for Boreal Shield lakes: A review and synthesis. *Environ. Rev.* **2007**, *15*, 99–112.
88. Binzer, A.; Guill, C.; Rall, B.C.; Brose, U. Interactive effects of warming, eutrophication and size structure: Impacts on biodiversity and food-web structure. *Glob. Chang. Biol.* **2016**, *22*, 220–227.
89. Downing, J.A.; Plante, C. Production of Fish Populations in Lakes. *Can. J. Fish. Aquat. Sci.* **1993**, *50*, 110–120.
90. Atkinson, D. Temperature and Organism Size—A Biological Law for Ectotherms? In *Advances in Ecological Research*; Elsevier: London, UK, 1994; Volume 25, pp. 1–58.
91. Sentis, A.; Binzer, A.; Boukal, D.S. Temperature-size responses alter food chain persistence across environmental gradients. *Ecol. Lett.* **2017**, *20*, 852–862.
92. Dodson, S.I.; Arnott, S.E.; Cottingham, K.L. The Relationship in Lake Communities between Primary Productivity and Species Richness. *Ecology* **2000**, *81*, 19.
93. Bosse, K.R.; Sayers, M.J.; Shuchman, R.A.; Fahnenstiel, G.L.; Ruberg, S.A.; Fanslow, D.L.; Stuart, D.G.; Johengen, T.H.; Burtner, A.M. Spatial-temporal variability of in situ cyanobacteria vertical structure in Western Lake Erie: Implications for remote sensing observations. *J. Gt. Lakes Res.* **2019**, *45*, 480–489.

94. Dalu, T.; Wasserman, R.J. Cyanobacteria dynamics in a small tropical reservoir: Understanding spatio-temporal variability and influence of environmental variables. *Sci. Total Environ.* **2018**, *643*, 835–841.
95. Emmrich, M.; Pédron, S.; Brucet, S.; Winfield, I.J.; Jeppesen, E.; Volta, P.; Argillier, C.; Lauridsen, T.L.; Holmgren, K.; Hesthagen, T.; et al. Geographical patterns in the body-size structure of European lake fish assemblages along abiotic and biotic gradients. *J. Biogeogr.* **2014**, *41*, 2221–2233.
96. Pickering, A.D. Growth and stress in fish production. *Aquaculture* **1993**, *111*, 51–63.
97. O'Gorman, E.J.; Ólafsson, Ó.P.; Demars, B.O.L.; Friberg, N.; Guðbergsson, G.; Hannesdóttir, E.R.; Jackson, M.C.; Johansson, L.S.; McLaughlin, Ó.B.; Ólafsson, J.S.; et al. Temperature effects on fish production across a natural thermal gradient. *Glob. Chang. Biol.* **2016**, *22*, 3206–3220.
98. Logez, M.; Pont, D. Global warming and potential shift in reference conditions: The case of functional fish-based metrics. *Hydrobiologia* **2013**, *704*, 417–436.
99. Mondy, C.P.; Villeneuve, B.; Archaimbault, V.; Usseglio-Polatera, P. A new macroinvertebrate-based multimetric index (I2M2) to evaluate ecological quality of French wadeable streams fulfilling the WFD demands: A taxonomical and trait approach. *Ecol. Indic.* **2012**, *18*, 452–467.
100. Argillier, C.; Caussé, S.; Gevrey, M.; Pédron, S.; De Bortoli, J.; Brucet, S.; Emmrich, M.; Jeppesen, E.; Lauridsen, T.; Mehner, T.; et al. Development of a fish-based index to assess the eutrophication status of European lakes. *Hydrobiologia* **2013**, *704*, 193–211.
101. Blabolil, P.; Logez, M.; Ricard, D.; Prchalová, M.; Říha, M.; Sagouis, A.; Peterka, J.; Kubečka, J.; Argillier, C. An assessment of the ecological potential of Central and Western European reservoirs based on fish communities. *Fish. Res.* **2016**, *173*, 80–87.
102. Teichert, N.; Lepage, M.; Sagouis, A.; Borja, A.; Chust, G.; Ferreira, M.T.; Pasquaud, S.; Schinegger, R.; Segurado, P.; Argillier, C. Functional redundancy and sensitivity of fish assemblages in European rivers, lakes and estuarine ecosystems. *Sci. Rep.* **2017**, *7*, 17611.
103. Turner, B.L.; Kasperson, R.E.; Matson, P.A.; McCarthy, J.J.; Corell, R.W.; Christensen, L.; Eckley, N.; Kasperson, J.X.; Luers, A.; Martello, M.L.; et al. A framework for vulnerability analysis in sustainability science. *Proc. Natl. Acad. Sci. USA* **2003**, *100*, 8074–8079.
104. Parravicini, V.; Villéger, S.; McClanahan, T.R.; Arias-González, J.E.; Bellwood, D.R.; Belmaker, J.; Chabanet, P.; Floeter, S.R.; Friedlander, A.M.; Guilhaumon, F.; et al. Global mismatch between species richness and vulnerability of reef fish assemblages. *Ecol. Lett.* **2014**, *17*, 1101–1110.
105. Teichert, N.; Argillier, C.; Lepage, M.; Segouis, A.; Schinegger, R.; Palt, M.; Schmutz, S.; Segurado, P.; Ferreira, M.T.; Chust, G.; et al. *Deliverable D5.1-5: Reports on Stressor Classification and Effects at the European Scale: New Functional Diversity Indices Allowing Assessing Vulnerability in Abiotic Multi-Stressor Context*; MARS Project, Department of Aquatic Ecology/Faculty of Biology, Centre for Water and Environmental Research (ZWU): Duisburg-Essen, Germany, 2016; pp. 515–543.
106. Allan, J.D.; McIntyre, P.B.; Smith, S.D.P.; Halpern, B.S.; Boyer, G.L.; Buchsbaum, A.; Burton, G.A.; Campbell, L.M.; Chadderton, W.L.; Ciborowski, J.J.H.; et al. Joint analysis of stressors and ecosystem services to enhance restoration effectiveness. *Proc. Natl. Acad. Sci. USA* **2013**, *110*, 372–377.
107. Brown, C.J.; Saunders, M.I.; Possingham, H.P.; Richardson, A.J. Managing for Interactions between Local and Global Stressors of Ecosystems. *PLoS ONE* **2013**, *8*, e65765.