

ORIGINAL ARTICLE OPEN ACCESS

Interactive Effects of Anthropogenic Stressors on the Temporal Changes in the Size Spectrum of Lake Fish Communities

Valentin Marin¹ | Julien Cucherousset¹ | Gaël Grenouillet^{1,2}

¹Centre de Recherche Sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS, IRD, Toulouse INP, Université Toulouse 3 – Paul Sabatier (UT3), Toulouse, France | ²Institut Universitaire de France, Paris, France

Correspondence: Valentin Marin (valentin.marin@inrae.fr)

Received: 19 August 2024 | **Revised:** 24 October 2024 | **Accepted:** 25 October 2024

Funding: This work was supported by Office Français de la Biodiversité.

Keywords: biological invasions | body size | community structure | eutrophication | fish ecology | global warming

ABSTRACT

The size spectrum represents a powerful approach for quantifying the effects of environmental changes from individuals to communities in aquatic ecosystems. However, our understanding of its temporal stability in freshwater ecosystems is still limited. In the present study, we used a size spectrum approach to investigate the responses of 126 lake fish communities to changes in the intensity of three common anthropogenic stressors (i.e., global warming, nutrient loading and biological invasions) in French natural lakes and reservoirs over an average 5-year time period. Using a backward selection on a full model including all possible effects of stressors on the size spectrum slope, we demonstrated that (i) increasing summer temperature shifted fish abundance towards the largest size classes, resulting in a flatter size spectrum slope and (ii) nutrient loading and biological invasions were associated with a shift towards smaller size classes in natural lakes, while the opposite effect was observed in reservoirs. In addition, these two stressors interacted in determining changes in the size structure of fish communities, complicating what the size spectrum can reveal about changes in stressor intensity during monitoring programs. All predictors accounted for a limited part of the observed changes in size spectra, and further investigations are needed to fully apprehend the interplay between natural and human-induced drivers of the temporal changes in size spectra in contrasting environmental conditions.

1 | Introduction

Freshwater ecosystems are subject to multiple anthropogenic stressors, such as global warming, eutrophication or non-native species introductions (Vörösmarty et al. 2010; Dudgeon 2019). Fish communities are particularly sensitive to these stressors and are commonly used as indicators of the ecological status of inland water bodies (Ritterbusch et al. 2022). Most fish species have a long lifespan, typically several years (López-López and Sedeño-Díaz 2015), making them a relevant choice for long-term monitoring of community dynamics (Cabral et al. 2022; Collingsworth

et al. 2017). Moreover, freshwater fish communities cover multiple trophic levels, offering the potential to study not only the direct effects of anthropogenic stressors on species, but also the consequences on trophic interactions in food webs (Sagouis et al. 2015; Cazelles et al. 2019; Donázar-Aramendía et al. 2019). For example, lower proportions of piscivorous fish are commonly observed in eutrophic lakes (Poikane et al. 2017). Although trophic guilds provide indirect measures of changes in trophic structures, they can provide a relevant and operational framework for improving our understanding of freshwater ecosystem functioning in response to anthropogenic stressors (Pont et al. 2006).

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Author(s). *Ecology of Freshwater Fish* published by John Wiley & Sons Ltd.

An alternative perspective is to consider the trophic structure through the biomass pyramid (Trebilco et al. 2013). Freshwater fish communities are strongly size-structured (Emmrich et al. 2011, 2014; Mehner et al. 2016; Brucet et al. 2017). Body size is a key ecological trait in communities because it determines how individuals interact with their biotic and abiotic environment (Woodward et al. 2005; Hildrew, Raffaelli, and Edmonds-Brown 2007). Fish ontogeny is commonly characterised by dietary shifts (Werner and Gilliam 1984) with, for instance, piscivorous species being typically invertivorous during their early life stages and becoming piscivorous when reaching sufficient gap size (Mittelbach and Persson 1998). Consequently, the trophic position generally increases with body size, with predatory fish less abundant than their prey because of energy loss at each trophic level (Trebilco et al. 2013). The rate of decrease in fish abundance as a function of body size (hereafter 'size spectrum slope') is related to the food web structure (such as predator abundance) and therefore independent of the taxonomic structure of communities (Emmrich et al. 2014; Mehner et al. 2016).

The fish size spectrum is commonly used to monitor the effects of fisheries activities on marine fish communities (Shin et al. 2005). In freshwater ecosystems, fish size has been also reported to covary with multiple anthropogenic stressors and represents a complementary biomonitoring approach (deBruyn, Marcogliese, and Rasmussen 2002; Benejam et al. 2016; Marin et al. 2023). For example, eutrophic lakes generally display lower abundance of larger fish and steeper fish size spectrum slopes (Chu et al. 2016; Arranz et al. 2021; Marin et al. 2023). Conversely, non-native species are generally larger than native fish species (Blanchet, Grenouillet, et al. 2010), and their high abundance can induce flatter slopes (Kopf et al. 2018; Arranz et al. 2021). Finally, natural drivers can also influence the fish size spectrum, such as warmer climates, leading to steeper slopes, and larger and more connected ecosystems are likely to support larger individuals and to display more resistance to anthropogenic stressors (Blanchet, Rey, et al. 2010; Emmrich et al. 2011; Pusey et al. 2020). However, despite accumulating evidence linking the spatial patterns in fish size spectra to biotic and abiotic environmental conditions, the temporal dynamics of fish size spectra in response to anthropogenic stressors have been overlooked. To our knowledge, only two studies have investigated the temporal variation of the fish size spectrum in response to environmental changes in freshwater ecosystems. Murry and Farrell (2014) demonstrated that the simple effect of change in temperature and nutrients had no effect on the size spectrum slope, which could partly be explained by the interactive effect of other anthropogenic stressors that disrupt the dynamics underlying the size spectrum as observed in Arranz, Grenouillet, and Cucherousset (2023a). Interestingly, these two studies were performed in lotic ecosystems and over large time scales (i.e., 30 years), which exceeds the standard duration of typical biomonitoring surveys aimed at quantifying the effectiveness of management measures (typically 5 years). Consequently, it is crucial to not only provide an assessment of the anthropogenic stressors that influence the temporal variation in the size spectrum slope, but also to determine whether it can respond to environmental changes over shorter periods of time.

In the present study, we used a large biomonitoring dataset to quantify the temporal changes in the fish size spectra in 126 French lakes exposed to different levels of anthropogenic stressors. Our specific objectives were (i) to test fish size spectrum responses to impacts related to changes in summer water temperature, phosphorus concentrations and biomass of non-native fish species and their interactive effects and (ii) to address the role of lake connectivity and size on the response of fish size spectra to these specific anthropogenic stressors. More specifically, we expected steeper fish size spectrum slopes with temperature and nutrient increases and flatter slopes with increased relative biomass of non-native fish species. We then expected that increasing connectivity and lake size would result in greater stability in slope to changes in anthropogenic stressors.

2 | Materials and Methods

2.1 | Study Design and Fish Data

Fish sampling was conducted between 2005 and 2019 as part of the European Water Framework Directive (Argillier et al. 2013). Studied ecosystems initially included 40 natural lakes and 90 reservoirs. Fish were sampled from June to October using benthic multi-mesh gillnets set overnight and completed with pelagic multi-mesh gillnets when the depth of the lake exceeded the height of the pelagic nets (CEN 2005). Sampling effort (number of nets, varying from 4 to 81) was determined according to the lake area to obtain standardised catch per unit effort among lakes (CEN 2005). The standardised protocol was updated in 2015 to ensure temporal replication of sampling points throughout successive campaigns within lakes (CEN 2015), but in our case, none of the lakes had both first and second fish samplings after 2015, making the two samplings comparable across all lakes. In all lakes, the average time interval between the two sampling events was 5 years (Figure S1). A total of 449,511 individuals were measured individually or grouped in batches per species when individuals were similar in body length. For these individuals (34.9% of the total number of fish individuals, primarily juveniles [7 cm on average] from highly abundant species), we randomly assigned body length between the maximum and the minimum of the batch using a uniform law (Marin et al. 2023). Individual body mass was then estimated using specific length-weight relationships calculated from the entire database.

2.2 | Environmental Conditions

2.2.1 | Hydro-Morphology

We first categorised the lakes into two main groups, natural lakes and reservoirs, considering that the fish size spectrum might exhibit varying responses to the same anthropogenic stressors in these two ecosystems (Marin et al. 2023). Subsequently, natural lakes and reservoirs were characterised by their size (ranging from 10^5 to 10^{11} m³) and the number of tributaries (ranging from 0 to 8 rivers and streams). Lake size and connectivity were log-transformed to mitigate the influence of extreme values and improve the normality assumption.

2.2.2 | Anthropogenic Stressors

For each lake, global warming was quantified with changes in air summer temperature (mean temperature from June to August) between the two fish sampling events using temperature data provided by *Météo France* at the national level in a 8×8 km grid. Specifically, temperature change was estimated by calculating the rate of change (expressed in percentage) in mean summer temperature measured for the two fish sampling events divided by the time interval (2–10 years). Similarly, change in phosphorus concentration was estimated by calculating the percentage of change in total phosphorus concentrations measured for the two fish sampling events and then dividing it by the time interval. Three water samples for each fish sampling event were collected (1 m under the surface, middle depth of the water column and 1 m above the bottom) in the center part of the lake and averaged. When natural lakes or reservoirs were shallow (max depth < 4 m), only sub-surface and near-bottom sampling were conducted. Phosphorus data are available in the *Naïades* database (<https://naiades.eaufrance.fr>). Finally, changes in the relative biomass of non-native to total fish species in the community were determined as the percentage of change in the proportion of non-native to total fish biomass between the two fish sampling events, standardised as other predictors above by the number of years between the two fish sampling events. Species status (native or non-native) was defined at the national scale following Keith, Persat, and Allardi (2011).

2.3 | Changes in the Fish Size Spectrum

We estimated the slope of the fish size spectrum using the maximum likelihood estimate (MLE) based on an underlying Bounded Power Law distribution (PLB) of individual fish masses (Edwards et al. 2017). The formula for estimating the negative exponent b of the size spectrum was derived from the `sizeSpectra` package (`negLL.PLB` in Edwards 2019, full code and functions available in the Supporting Information). To minimise sampling bias associated with the smallest size classes using standardised multi-mesh gillnets, we only considered fish individuals with a body size greater than 4 g (Mehner et al. 2016). This resulted in the exclusion of approximately half of individual lengths estimated from batches (see Section 2.1 above). Change in the Fish Size Spectrum (FSS) slope for each lake were then calculated using the Equation (1):

$$\text{FSS slope change} = \frac{\text{FSS slope}_{T2} - \text{FSS slope}_{T1}}{\text{Time}} \quad (1)$$

where T1 and T2 represent the first and second fish sampling events, respectively, and Time represents the number of years between these two events. To ensure the robustness of our estimations of changes in size structure, we also calculated the slope of the size spectrum from the historical binned approach using the Normalised Abundance Size Spectrum (NASS: Sprules and Barth 2016). We categorised all body masses into nine size classes following a geometric series of 2 (1st: 4–8 g, 2nd: 8–16 g, ..., 9th: 1024 g and more), ensuring equivalent spatial and temporal representation of all size classes while avoiding null occurrences (Marin et al. 2023). We then calculated

TABLE 1 | Effects of environmental drivers on changes in the fish size spectrum slope.

Predictors	Estimate	F	p
Summer temperature change	0.002	4.093	0.046
Total phosphorus change	−0.001	1.207	0.274
Non-native biomass change	−0.900	2.994	0.086
Lake type	−0.017	2.386	0.125
Lake size	< 0.001	0.092	0.763
Lake connectivity	−0.005	0.145	0.704
Total phosphorus change × Lake type	0.002	7.406	0.008
Non-native biomass change × Lake type	1.080	7.006	0.009
Non-native biomass change × Total phosphorus change	−0.040	5.864	0.017

Note: Only drivers from the final model after backward selection are displayed. Significant $p < 0.05$ are displayed in bold. Marginal $R^2 = 0.188$, conditional $R^2 = 0.256$. $n = 126$.

the variation rate (or slope) in abundances across size classes (\log_2 of normalised abundance) (Emmrich et al. 2014; Arranz et al. 2021; Marin et al. 2023). The normalisation of abundances was achieved by dividing fish abundance per size class by the width of each size class (Sprules and Barth 2016). We visually inspected lakes where the two methods showed major discrepancies (van Dorst et al. 2022), leading to the exclusion of four lakes (1 natural lake and 3 reservoirs) from the subsequent analyses (Figure S2). More importantly, we found qualitatively similar results using the MLE method (Tables 1 and S1).

2.4 | Data Analyses

First, the magnitude of anthropogenic stressors and size spectrum changes were quantified by comparing the changes in each parameter to the null expectation of 0 change using the bilateral Student test. Concerning slope variations, we conducted a Mantel test to assess potential spatial autocorrelation to preemptively address any need for an autocorrelation structure in the model (Figure S3). Then, the effects of anthropogenic stressors on slope changes were tested using linear mixed models using the `LmerTest` R-package (version 3.1–3; Kuznetsova, Brockhoff, and Christensen 2017). Because surveys were conducted between May and October and recruitment dynamics may have an important effect on fish sampling (Miguet, Logez, and Argillier 2021), we first used the seasonal trends of the sampling events as a random factor with three possible combinations (same season, summer for the first sampling event and autumn for the second and autumn for the first sampling event and summer for the second). Second, the time interval (in years) between the two sampling events was categorised into three factors (short: 2–4 years, medium: 5–7 years and long:

> 7 years) as a random effect in our analyses to account for any potential bias related to this variability in the sampling design. Finally, we used the year of the first sampling event as a third random effect, categorised in three time periods (2005–2007, 2008–2010 and > 2010). We built a full model incorporating single interactions between anthropogenic stressors and hydro-morphological variables using the following Equation (2):

$$\begin{aligned} \text{FSS slope change} = & \text{Temp}_{\text{change}} \times \text{Inva}_{\text{change}} \\ & + \text{Temp}_{\text{change}} \times \text{TP}_{\text{change}} + \text{Temp}_{\text{change}} \times \text{LT} \\ & + \text{Temp}_{\text{change}} \times \text{LC} + \text{Temp}_{\text{change}} \times \text{LS} \\ & + \text{Inva}_{\text{change}} \times \text{TP}_{\text{change}} + \text{Inva}_{\text{change}} \times \text{LT} + \text{Inva}_{\text{change}} \times \text{LC} \\ & + \text{Inva}_{\text{change}} \times \text{LS} + \text{TP}_{\text{change}} \times \text{LT} + \text{TP}_{\text{change}} \times \text{LC} \\ & + \text{TP}_{\text{change}} \times \text{LS} + \text{Temp}_{\text{change}} + \text{Inva}_{\text{change}} \\ & + \text{TP}_{\text{change}} + \text{LT} + \text{LC} + \text{LS} + (1 | \text{Season trend}) \\ & + (1 | \text{Time interval}) + (1 | \text{Year of the first sampling}) \end{aligned} \quad (2)$$

where $\text{Temp}_{\text{change}}$, $\text{Inva}_{\text{change}}$ and $\text{TP}_{\text{change}}$ represent the changes in summer temperature, biomass of non-native species and total phosphorus, respectively. LT, LC and LS denote lake type (natural lake or reservoir), lake connectivity (\log_{10} of tributary numbers) and lake size (\log_{10} of the total volume), respectively. There was little evidence for multi-collinearity among all initial predictors, with all variance inflation factors (VIF) below 4. We initially performed a backward selection on interactive fixed terms, prioritising the highest p -value, and stopped when the remaining interactions were significant ($p < 0.05$). We then conducted a random effects selection based on variance criteria to avoid excessive singularity in determining the conditional R^2 (Nakagawa and Schielzeth 2013). Ultimately, only the year of the first sampling factors was maintained (Table A2) and explained around one-fourth of the size spectrum slopes trends variance in the final model (marginal $R^2 = 0.188$, conditional $R^2 = 0.256$ including both fixed and random effects).

3 | Results

Across all locations, summer air temperature increased by 4.3% per year ($t = 7.381$, $p < 0.001$), although several locations displayed decreasing temperature (Figure 1a). Regarding total phosphorus concentrations, many lakes experienced a decrease over time (Figure 1b); however, these changes were too slight to induce a significant overall mean change across all lakes ($t = 0.708$, $p = 0.486$). Lastly, changes in biomass of non-native fish species ranged between -10% and $+10\%$ per year, with a significant overall decrease over the study period (Figure 1c, $t = -2.120$, $p = 0.036$).

The fish size spectrum slopes were all negative, ranging from -2.489 to -0.714 and from -2.743 to -0.544 for the first and second sampling event, respectively, and did not show geographical patterns in their temporal changes (Figures 2a and S3). Slope changes varied from -0.254 to $+0.175$ per year with an average variation that did not differ from zero ($t = -0.861$, $p = 0.391$, Figure 2b).

Regarding potential drivers of changes in fish size spectrum slopes, we identified a significant effect of the three tested stressors (Table 1). First, we observed a positive effect of increasing mean summer temperature in both lakes and reservoirs (Table 1, Figure 3a). Second, we found a negative effect of increasing biomass of non-native species and total phosphorus concentrations in natural lakes, while the opposite effect was observed in reservoirs (Table 1, Figure 3b,c). Third, we observed a significant interaction between these two stressors (Table 1). Specifically, a concomitant increase in non-native species biomass and total phosphorus concentration led to steeper slopes, while an increase in non-native species biomass when total phosphorus concentration decreased led to flatter slopes (Figure 4). Finally, we did not observe any significant effects of lake size and lake connectivity on slope changes (Table 1).

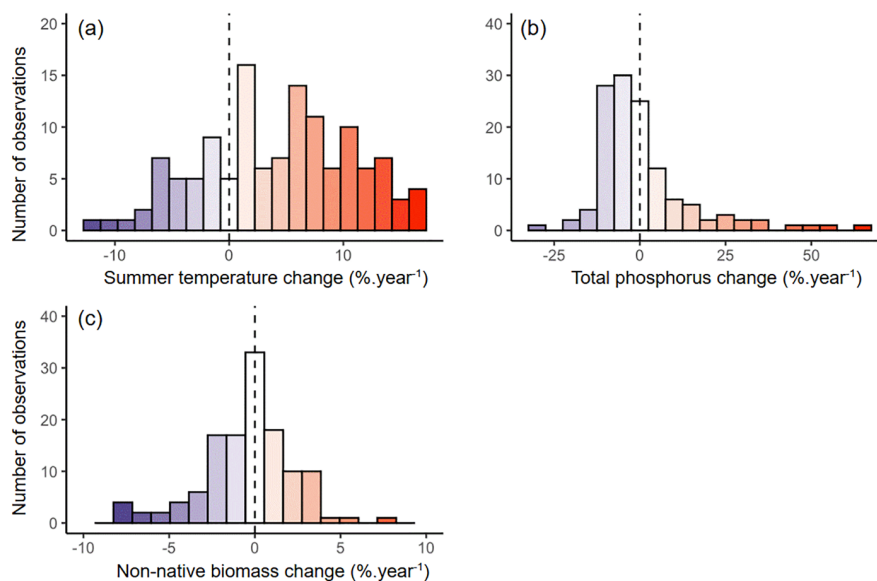


FIGURE 1 | Distribution of changes (%. year⁻¹) in (a) summer temperature, (b) total phosphorus concentration and (c) biomass of non-native species between the two fish sampling events in the studied lakes ($n = 126$). The intensity of the red colour indicates the magnitude of the increase in anthropogenic stressors, while the intensity of the blue colour indicates the magnitude of the decrease in anthropogenic stressors.

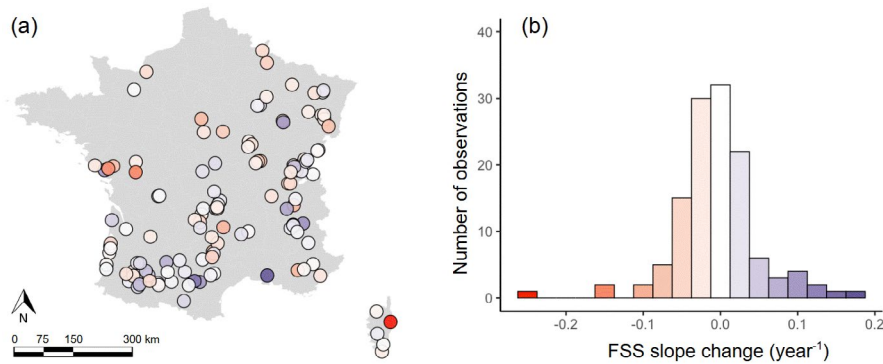


FIGURE 2 | Spatial distribution (a) and (b) relative frequencies of temporal changes in Fish Size Spectrum (FSS) slopes across France ($n=126$). The intensity of the red colour indicates the magnitude of the steepening of the size spectrum slope, while the intensity of the blue colour indicates the magnitude of the flattening.

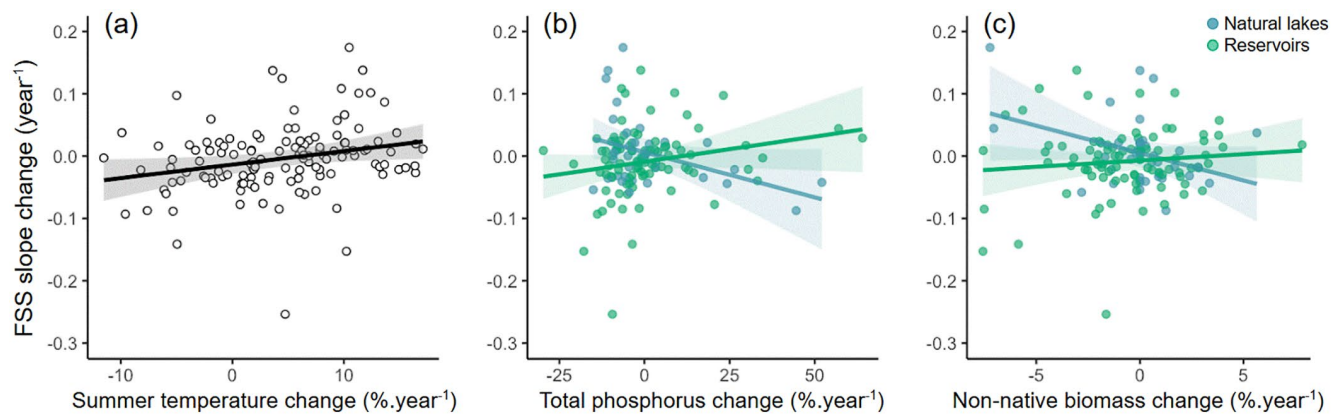


FIGURE 3 | Effect of changes in summer temperature (a), total phosphorus and biomass of non-native species, depending on lake type (b, c), on the Fish Size Spectrum slope (FSS).

4 | Discussion

In this study, we aimed to assess the effects of anthropogenic stressors on temporal changes in fish size spectra in natural lakes and reservoirs. Consistent with our first hypothesis, we observed significant effects of anthropogenic stressors on the fish size spectrum slope. However, changes in stressors explained a limited part of the temporal variation in the size spectrum (around 20%), and some of these responses differed from those found in previous studies. For example, while we expected a negative effect of warming on large body sized organisms, our study revealed a positive effect of increased water temperature on the slope, meaning that communities experiencing higher summer temperature showed a concurrent increase in the proportion of large fish. In addition, we demonstrated an interplay of nutrient loading and biological invasions in the temporal dynamics of the size spectrum. More specifically, increasing non-native species had a positive effect on size spectrum slopes when nutrient concentrations (total phosphorus) decreased. Regarding our second hypothesis, lake size and connectivity criteria did not significantly affect slope stability, but lake type (natural lake or reservoir) played a crucial role in modulating the responses of the slope to nutrient loading or biological invasions by non-native species.

In alignment with recent findings (Arranz, Grenouillet, and Cucherousset 2023a), our study highlights that the temporal

dynamics of community size distribution can yield variable, even unexpected results when compared to spatial patterns. These results can be explained by two mechanisms. First is the limited temporal scale of our study coupled with a lack of drastic changes in stressor intensity in the studied sites. The low intensity of stressors can also result in opposite responses of community dynamic to predicted ones. This pattern has been widely emphasised to describe biodiversity patterns with the Intermediate Disturbance Hypothesis (IDH), which suggests a peak in species diversity at intermediate-scale perturbations (Connell 1978). These ‘ecological surprises’ (sensu Paine, Tegner, and Johnson 1998) can often be encountered when biological structures are contingent on multiple trophic levels such as size spectrum (Thompson, MacLennan, and Vinebrooke 2018), as all organisms (or species) are interdependent and may not respond with the same strength or synchronously in time (Meerhoff et al. 2012). Second is the absence of strong changes in the size spectrum slopes. Although the changes in slope obtained using the maximum likelihood estimation may be slightly reduced compared to the binned approaches historically used (Figure S2), our estimates of changes ranged mainly between -0.1 and 0.1 per year, which correspond to annual variations rather than long-term trends. For example, Broadway et al. (2015) reported an average increase in the slope of the fish size spectrum in the Wabash River of 0.06 per year over 30 years, with a standard error around 0.30 due to high inter-annual variations. Similarly,

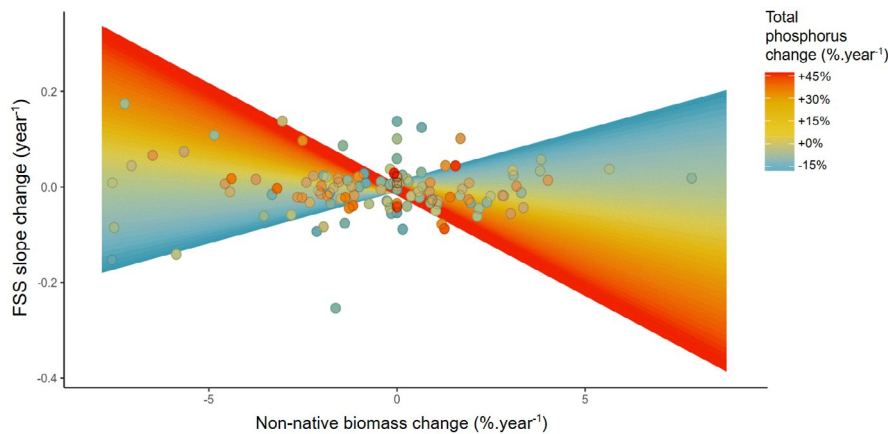


FIGURE 4 | Interactive effect of changes in biomass of non-native species and total phosphorus concentration on the fish size spectrum slope (FSS). The coloured lines, corresponding to different levels of total phosphorus change (% per year), are drawn using the coefficient estimates from the best linear mixed model to compute the slope for non-native biomass change, while holding the total phosphorus change at values ranging from -20% to $+50\%$ per year.

Murry and Farrell (2014) found a standard error of 0.18 over 30 years in the St. Lawrence River. Our results further suggest that other changes in environmental conditions at the national scale (including natural factors), which were not considered here, have affected the stability of size spectra, as the monitoring period (i.e., the year of the first sampling, treated as a random effect) explained a non-negligible proportion of the observed variation. Together, these observations suggest that some of the temporal variation in the slope could have been caused by natural fluctuations in biological processes and environmental conditions.

While the size spectrum slope may exhibit substantial inter-annual variations, we were able to link some variations to observed changes in environment conditions observed during the study period, including global warming. Following the Metabolic Theory of Ecology (MTE: Brown et al. 2004), we would expect steeper slopes with increasing temperature, as metabolic demands of larger individuals are exacerbated, and energy is further dissipated at each trophic level. While numerous studies support this hypothesis by reporting steeper slopes in warm climates (Emmrich et al. 2014; Chu et al. 2016; Marin et al. 2023), we observed flattening slopes with increasing temperature. O’Gorman et al. (2017) proposed that predators could compensate for their energy loss by increasing predation pressure if temperature increases were within their thermal tolerance, leading to flatter slopes. Following this hypothesis, the contrasting responses of the size spectrum slope to temperature between spatial and temporal patterns are therefore not exclusive and may depend on the velocity of warming, as well as the time scale, over which the response is observed. Indeed, the long-term consequences of increased predation by predators may manifest as reduced abundance due to prey depletion (Nagelkerken et al. 2020), resulting in steeper slopes, as observed for spatial patterns in response to warmer climates.

In addition to global warming, human alterations to freshwater systems also include the introduction of non-native species by removing natural geographical barriers (Ricciardi 2007). While non-native species compete with native species and often have larger body sizes (Blanchet, Grenouillet, et al. 2010), we expected

their increase to result in flatter slopes. However, this hypothesis was only partially verified, as an increase in the proportion of non-native species induced flatter slopes only if there was a concomitant decrease in nutrient concentration (Figure 4). Conversely, the simultaneous increase in non-native species and nutrients induced steeper slopes. We can suggest different non-native species assemblages in the two cases, and perhaps increasing nutrients favoured the establishment of more tolerant non-native species characterised by smaller size and fast reproductive strategies (Chu et al. 2016; Arranz et al. 2021). Conversely, large non-native species such as common carp (*Cyprinus carpio*) or European catfish (*Silurus glanis*) are generalists for habitat and resources and can be found in waters with low nutrient concentrations (Vejřík et al. 2017; Toussaint et al. 2018). More importantly, high abundance of these two species is known for flattening the size spectrum slopes in freshwater communities (Arranz et al. 2021). Although the interactive effects of temperature and invasion on size-based interactions are well-documented in freshwater ecosystems (Arranz, Grenouillet, and Cucherousset 2023b), our results suggest that the effects of non-native species on communities may also depend on the changes in nutrient levels. In fact, the addition of nutrients and the introduction of non-native species can modulate bottom-up and top-down forces, respectively (Sinclair and Arnott 2015). Given that bottom-up and top-down forces can strongly interact to shape trophic structures (La Pierre and Hanley 2015), we emphasise here the need for future studies to consider the interactive effects of biological invasions and eutrophication to accurately predict their impacts on community size structure.

Another important result is the necessity of considering the differences between lakes and reservoirs when assessing the response of fish communities to anthropogenic stressors. This distinction has already been pointed out in the development of biomonitoring programs, as different indices are used for lakes and reservoirs in France (Miguët et al. 2018). Indeed, lakes are generally less connected and shallower and have a lower shoreline development index (less circular) compared to reservoirs (Marin et al. 2023). However, our results indicate that connectivity and size criteria are unlikely to drive the differences in fish community responses between lakes and

reservoirs. Despite accumulating evidence of environmental factors influencing fish communities specifically in reservoirs (Bem et al. 2021; Pennock et al. 2021; Besson et al. 2023), the direct comparison of these potential differences between lakes and reservoirs remains understudied. Numerous factors, such as age, water discharge, or fluctuations, have been identified as potential determinants of the spatial distribution and temporal variations in fish community structure (Logez et al. 2016; dos Santos et al. 2017; Loures and Pompeu 2019). Interestingly, a recent study in seven tropical reservoirs showed that water discharge may partly explain the spatial distribution of the fish size structure (Murry et al. 2024). The authors also reported that the size structure response coincided with other community characteristics (e.g., species richness and evenness or functional metrics such as abundance of piscivorous individuals). Species colonisation or extinction may strongly influence changes in the size structure, but this can also be caused by demographic bursts of a single species (Murry et al. 2024). In line with these observations, additional analysis (Figure S4) revealed a correlation between species evenness or individuals piscivorous individuals and temporal changes in the size spectrum. Specifically, increasing species evenness and relative piscivorous biomass coincide with a flatter size spectrum slope. However, this relationship was less pronounced in reservoirs. As reservoirs represent the majority of our studied locations, we can confidently assert that including the stability of hydrological variables (e.g., water flow and level fluctuations) would enhance our ability to predict temporal changes in the fish size spectrum. Considering these factors when studying variations in size structure or other functional properties of communities would enable us to better adjust regulatory biomonitoring programs in these complex ecosystems, particularly in the context of climate change and future water use issues.

In conclusion, our study offers a short-term observation of changes in the size spectrum following a time scale consistent with mandatory biomonitoring surveys. We showed that anthropogenic stressors can induce changes in the size spectrum during a limited period, but the trends observed over 5 years can be transient and must be carefully extrapolated. We encourage future studies to develop the temporal analysis of community metrics reflecting biological interactions such as size spectra to improve our ability to predict how communities will adapt in a changing world.

Author Contributions

Conceptualisation: V.M., J.C. and G.G. Developing methods: V.M., J.C. and G.G. Data analysis: V.M. Conducting the research: V.M., J.C. and G.G. Data interpretation: V.M. and G.G. Writing: V.M., J.C. and G.G.

Acknowledgements

This work was funded by the Office Français de la Biodiversité (OFB) as part of the SPECTRA project. We are indebted to the OFB for providing the monitoring data. We are grateful to three anonymous referees for their major contribution to the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

- Argillier, C., S. Caussé, M. Gevrey, et al. 2013. "Development of a Fish-Based Index to Assess the Eutrophication Status of European Lakes." *Hydrobiologia* 704: 193–211. <https://doi.org/10.1007/s10750-012-1282-y>.
- Arranz, I., S. Brucet, M. Bartrons, C. García-Comas, and L. Benejam. 2021. "Fish Size Spectra Are Affected by Nutrient Concentration and Relative Abundance of Non-native Species Across Streams of the NE Iberian Peninsula." *Science of the Total Environment* 795: 148792. <https://doi.org/10.1016/j.scitotenv.2021.148792>.
- Arranz, I., G. Grenouillet, and J. Cucherousset. 2023a. "Human Pressures Modulate Climate-Warming-Induced Changes in Size Spectra of Stream Fish Communities." *Nature Ecology & Evolution* 1–7: 1072–1078. <https://doi.org/10.1038/s41559-023-02083-z>.
- Arranz, I., G. Grenouillet, and J. Cucherousset. 2023b. "Biological Invasions and Eutrophication Reshape the Spatial Patterns of Stream Fish Size Spectra in France." *Diversity and Distributions* 29: 590–597. <https://doi.org/10.1111/ddi.13681>.
- Bem, J. D., J. Ribolli, C. Röpke, K. O. Winemiller, and E. Zaniboni-Filho. 2021. "A Cascade of Dams Affects Fish Spatial Distributions and Functional Groups of Local Assemblages in a Subtropical River." *Neotropical Ichthyology* 19: e200133. <https://doi.org/10.1590/1982-0224-2020-0133>.
- Benejam, L., F. Teixeira-de Mello, M. Meerhoff, M. Loureiro, E. Jeppesen, and S. Brucet. 2016. "Assessing Effects of Change in Land Use on Size-Related Variables of Fish in Subtropical Streams." *Canadian Journal of Fisheries and Aquatic Sciences* 73: 547–556. <https://doi.org/10.1139/cjfas-2015-0025>.
- Besson, J. C., J. J. Neary, J. D. Stafford, C. G. Dunn, and L. E. Miranda. 2023. "Fish Functional Gradients Along a Reservoir Cascade." *Freshwater Biology* 68: 1079–1091. <https://doi.org/10.1111/fwb.14087>.
- Blanchet, S., G. Grenouillet, O. Beauchard, et al. 2010. "Non-Native Species Disrupt the Worldwide Patterns of Freshwater Fish Body Size: Implications for Bergmann's Rule." *Ecology Letters* 13: 421–431. <https://doi.org/10.1111/j.1461-0248.2009.01432.x>.
- Blanchet, S., O. Rey, R. Etienne, S. Lek, and G. Loot. 2010. "Species-Specific Responses to Landscape Fragmentation: Implications for Management Strategies: Species-Specific Responses to Fragmentation." *Evolutionary Applications* 3: 291–304. <https://doi.org/10.1111/j.1752-4571.2009.00110.x>.
- Broadway, K. J., M. Pyron, J. R. Gammon, and B. A. Murry. 2015. "Shift in a Large River Fish Assemblage: Body-Size and Trophic Structure Dynamics." *PLoS One* 10: e0124954. <https://doi.org/10.1371/journal.pone.0124954>.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85: 1771–1789. <https://doi.org/10.1890/03-9000>.
- Brucet, S., Ü. N. Tavşanoğlu, A. Özen, et al. 2017. "Size-Based Interactions Across Trophic Levels in Food Webs of Shallow Mediterranean Lakes." *Freshwater Biology* 62: 1819–1830. <https://doi.org/10.1111/fwb.12997>.
- Cabral, H. N., A. Borja, V. F. Fonseca, et al. 2022. "Fishes and Estuarine Environmental Health." In *Fish and Fisheries in Estuaries*, edited by A. K. Whitfield, K. W. Able, S. J. M. Blaber, and M. Elliott, 332–379. Wiley. <https://doi.org/10.1002/9781119705345.ch6>.
- Cazelles, K., T. Bartley, M. M. Guzzo, et al. 2019. "Homogenization of Freshwater Lakes: Recent Compositional Shifts in Fish Communities Are Explained by Gamefish Movement and Not Climate Change."

- Global Change Biology* 25: 4222–4233. <https://doi.org/10.1111/gcb.14829>.
- CEN. 2005. “Water Quality—Sampling of Fish With Multi-Mesh Gillnets.” *European Committee for Standardization* 14: 757.
- CEN. 2015. “Water Quality—Sampling of Fish With Multi-Mesh Gillnets.” *European Committee for Standardization* 14: 757.
- Chu, C., N. P. Lester, H. C. Giacomini, B. J. Shuter, and D. A. Jackson. 2016. “Catch-Per-Unit-Effort and Size Spectra of Lake Fish Assemblages Reflect Underlying Patterns in Ecological Conditions and Anthropogenic Activities Across Regional and Local Scales.” *Canadian Journal of Fisheries and Aquatic Sciences* 73: 535–546. <https://doi.org/10.1139/cjfas-2015-0150>.
- Collingsworth, P. D., D. B. Bunnell, M. W. Murray, et al. 2017. “Climate Change as a Long-Term Stressor for the Fisheries of the Laurentian Great Lakes of North America.” *Reviews in Fish Biology and Fisheries* 27: 363–391. <https://doi.org/10.1007/s11160-017-9480-3>.
- Connell, J. H. 1978. “Diversity in Tropical Rain Forests and Coral Reefs: High Diversity of Trees and Corals Is Maintained Only in a Nonequilibrium State.” *Science* 199: 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>.
- deBruyn, A. M. H., D. J. Marcogliese, and J. B. Rasmussen. 2002. “Altered Body Size Distributions in a Large River Fish Community Enriched by Sewage.” *Canadian Journal of Fisheries and Aquatic Sciences* 59: 819–828. <https://doi.org/10.1139/f02-056>.
- Donázar-Aramendía, I., J. E. Sánchez-Moyano, I. García-Asencio, J. M. Miró, C. Megina, and J. C. García-Gómez. 2019. “Human Pressures on Two Estuaries of the Iberian Peninsula Are Reflected in Food Web Structure.” *Scientific Reports* 9: 11495. <https://doi.org/10.1038/s41598-019-47793-2>.
- dos Santos, N. C. L., H. S. de Santana, J. C. G. Ortega, et al. 2017. “Environmental Filters Predict the Trait Composition of Fish Communities in Reservoir Cascades.” *Hydrobiologia* 802: 245–253. <https://doi.org/10.1007/s10750-017-3274-4>.
- Dudgeon, D. 2019. “Multiple Threats Imperil Freshwater Biodiversity in the Anthropocene.” *Current Biology* 29: 960–967. <https://doi.org/10.1016/j.cub.2019.08.002>.
- Edwards, A. M. 2019. “The ‘SizeSpectra’ Package.” <https://github.com/andrew-edwards/sizeSpectra>.
- Edwards, A. M., J. P. Robinson, M. J. Plank, J. K. Baum, and J. L. Blanchard. 2017. “Testing and Recommending Methods for Fitting Size Spectra to Data.” *Methods in Ecology and Evolution* 8: 57–67. <https://doi.org/10.1111/2041-210X.12641>.
- Emmrich, M., S. Brucet, D. Ritterbusch, and T. Mehner. 2011. “Size Spectra of Lake Fish Assemblages: Responses Along Gradients of General Environmental Factors and Intensity of Lake-Use: Size Spectra of Lake Fish Assemblages.” *Freshwater Biology* 56: 2316–2333. <https://doi.org/10.1111/j.1365-2427.2011.02658.x>.
- Emmrich, M., S. Pédrón, S. Brucet, et al. 2014. “Geographical Patterns in the Body-Size Structure of European Lake Fish Assemblages Along Abiotic and Biotic Gradients.” *Journal of Biogeography* 41: 2221–2233. <https://doi.org/10.1111/jbi.12366>.
- Hildrew, A. G., D. G. Raffaelli, and R. Edmonds-Brown. 2007. *Body Size: The Structure and Function of Aquatic Ecosystems*. Cambridge, UK: Cambridge University Press.
- Keith, P., H. Persat, and J. Allardi. 2011. “Les poissons d’eau douce de France.” In *Collection Inventaires & biodiversité*, edited by revue, augmentée et mise à jour, 2nd ed, 552, Mèze Paris: Biotope Muséum national d’histoire naturelle.
- Kopf, R. K., P. Humphries, N. R. Bond, et al. 2018. “Macroecology of Fish Community Biomass—Size Structure: Effects of Invasive Species and River Regulation.” *Canadian Journal of Fisheries and Aquatic Sciences* 76: 109–122. <https://doi.org/10.1139/cjfas-2017-0544>.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. “lmerTest Package: Tests in Linear Mixed Effects Models.” *Journal of Statistical Software* 82: i13. <https://doi.org/10.18637/jss.v082.i13>.
- La Pierre, K. J., and T. C. Hanley. 2015. “Bottom-Up and Top-Down Interactions Across Ecosystems in an Era of Global Change.” In *Trophic Ecology*, edited by T. C. Hanley and K. J. La Pierre, 365–406. Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/CBO9781139924856.015>.
- Logez, M., R. Roy, L. Tissot, and C. Argillier. 2016. “Effects of Water-Level Fluctuations on the Environmental Characteristics and Fish-Environment Relationships in the Littoral Zone of a Reservoir.” *Fundamental and Applied Limnology* 189: 37–49. <https://doi.org/10.1127/fal/2016/0963>.
- López-López, E., and J. E. Sedeño-Díaz. 2015. “Biological Indicators of Water Quality: The Role of Fish and Macroinvertebrates as Indicators of Water Quality.” In *Environmental Indicators*, edited by R. H. Armon and O. Hänninen, 643–661. Netherlands, Dordrecht: Springer. https://doi.org/10.1007/978-94-017-9499-2_37.
- Loures, R. C., and P. S. Pompeu. 2019. “Temporal Changes in Fish Diversity in Lotic and Lentic Environments Along a Reservoir Cascade.” *Freshwater Biology* 64: 1806–1820.
- Marin, V., I. Arranz, G. Grenouillet, and J. Cucherousset. 2023. “Fish Size Spectrum as a Complementary Biomonitoring Approach of Freshwater Ecosystems.” *Ecological Indicators* 146: 109833. <https://doi.org/10.1016/j.ecolind.2022.109833>.
- Meerhoff, M., F. Teixeira-de Mello, C. Kruk, et al. 2012. “4—Environmental Warming in Shallow Lakes: A Review of Potential Changes in Community Structure as Evidenced From Space-For-Time Substitution Approaches.” In *Advances in Ecological Research, Global Change in Multispecies Systems Part 1*, edited by U. Jacob and G. Woodward, 259–349. Cambridge, Massachusetts: Academic Press. <https://doi.org/10.1016/B978-0-12-396992-7.00004-6>.
- Mehner, T., C. Keeling, M. Emmrich, et al. 2016. “Effects of Fish Predation on Density and Size Spectra of Prey Fish Communities in Lakes.” *Canadian Journal of Fisheries and Aquatic Sciences* 73: 506–518. <https://doi.org/10.1139/cjfas-2015-0034>.
- Miguet, P., M. Logez, and C. Argillier. 2021. “Incertitudes liées à l’échantillonnage: Effet de la date de la campagne de pêche sur l’évaluation de l’état écologique des plans d’eau par l’ichtyofaune.” <https://doi.org/10.13140/RG.2.2.25527.44962>.
- Miguet, P., M. Logez, M. H. Lizée, and C. Argillier. 2018. “Développement de l’Indice Ichtyofaune pour l’évaluation du potentiel écologique des Retenues, l’IIR.” Programme 2016/2018—Thème 22.1 “Etat écologique, biodiversité et fonctionnement des écosystèmes lacustres”—Action n 12 “Indicateur ichtyofaune de l’état écologique pour les plans d’eau.”
- Mittelbach, G. G., and L. Persson. 1998. “The Ontogeny of Piscivory and Its Ecological Consequences.” *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1454–1465. <https://doi.org/10.1139/f98-041>.
- Murry, B. A., and J. M. Farrell. 2014. “Resistance of the Size Structure of the Fish Community to Ecological Perturbations in a Large River Ecosystem.” *Freshwater Biology* 59: 155–167. <https://doi.org/10.1111/fwb.12255>.
- Murry, B. A., M. D. L. Olmeda, C. Lilyestrom, D. S. Adams, K. Adase, and M. García-Bermudez. 2024. “Community Size-Spectra Applied to Recreational Freshwater Fisheries in Puerto Rican Reservoirs.” *Fisheries Management and Ecology* 31: e12671. <https://doi.org/10.1111/fme.12671>.
- Nagelkerken, I., S. U. Goldenberg, C. M. Ferreira, H. Ullah, and S. D. Connell. 2020. “Trophic Pyramids Reorganize When Food Web Architecture Fails to Adjust to Ocean Change.” *Science* 369: 829–832. <https://doi.org/10.1126/science.aax0621>.
- Nakagawa, S., and H. Schielzeth. 2013. “A General and Simple Method for Obtaining R² From Generalized Linear Mixed-Effects Models.”

- Methods in Ecology and Evolution* 4: 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>.
- O’Gorman, E. J., L. Zhao, D. E. Pichler, et al. 2017. “Unexpected Changes in Community Size Structure in a Natural Warming Experiment.” *Nature Climate Change* 7: 659–663. <https://doi.org/10.1038/nclim.ate3368>.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. “Compounded Perturbations Yield Ecological Surprises.” *Ecosystems* 1: 535–545. <https://doi.org/10.1007/s100219900049>.
- Pennock, C. A., B. A. Hines, D. S. Elverud, et al. 2021. “Reservoir Fish Assemblage Structure Across an Aquatic Ecotone: Can River-Reservoir Interfaces Provide Conservation and Management Opportunities?” *Fisheries Management and Ecology* 28: 1–13. <https://doi.org/10.1111/fme.12444>.
- Poikane, S., D. Ritterbusch, C. Argillier, et al. 2017. “Response of Fish Communities to Multiple Pressures: Development of a Total Anthropogenic Pressure Intensity Index.” *Science of the Total Environment* 586: 502–511. <https://doi.org/10.1016/j.scitotenv.2017.01.211>.
- Pont, D., B. Hugueny, U. Beier, et al. 2006. “Assessing River Biotic Condition at a Continental Scale: A European Approach Using Functional Metrics and Fish Assemblages: Biotic Integrity Assessment of European Rivers.” *Journal of Applied Ecology* 43: 70–80. <https://doi.org/10.1111/j.1365-2664.2005.01126.x>.
- Pusey, B. J., M. Douglas, J. D. Olden, S. Jackson, Q. Allsop, and M. J. Kennard. 2020. “Connectivity, Habitat, and Flow Regime Influence Fish Assemblage Structure: Implications for Environmental Water Management in a Perennial River of the Wet–Dry Tropics of Northern Australia.” *Aquatic Conservation: Marine and Freshwater Ecosystems* 30: 1397–1411. <https://doi.org/10.1002/aqc.3347>.
- Ricciardi, A. 2007. “Are Modern Biological Invasions an Unprecedented Form of Global Change?” *Conservation Biology* 21: 329–336. <https://doi.org/10.1111/j.1523-1739.2006.00615.x>.
- Ritterbusch, D., P. Blabolil, J. Breine, et al. 2022. “European Fish-Based Assessment Reveals High Diversity of Systems for Determining Ecological Status of Lakes.” *Science of the Total Environment* 802: 149620. <https://doi.org/10.1016/j.scitotenv.2021.149620>.
- Sagouis, A., J. Cucherousset, S. Villéger, F. Santoul, and S. Boulétreau. 2015. “Non-Native Species Modify the Isotopic Structure of Freshwater Fish Communities Across the Globe.” *Ecography* 38: 979–985. <https://doi.org/10.1111/ecog.01348>.
- Shin, Y. J., M. J. Rochet, S. Jennings, J. G. Field, and H. Gislason. 2005. “Using Size-Based Indicators to Evaluate the Ecosystem Effects of Fishing.” *ICES Journal of Marine Science* 62: 384–396. <https://doi.org/10.1016/j.icesjms.2005.01.004>.
- Sinclair, J. S., and S. E. Arnott. 2015. “Effects of an Invasive Consumer on Zooplankton Communities Are Unaltered by Nutrient Inputs.” *Freshwater Biology* 60: 161–173. <https://doi.org/10.1111/fwb.12482>.
- Sprules, W. G., and L. E. Barth. 2016. “Surfing the Biomass Size Spectrum: Some Remarks on History, Theory, and Application.” *Canadian Journal of Fisheries and Aquatic Sciences* 73: 477–495. <https://doi.org/10.1139/cjfas-2015-0115>.
- Thompson, P. L., M. M. MacLennan, and R. D. Vinebrooke. 2018. “An Improved Null Model for Assessing the Net Effects of Multiple Stressors on Communities.” *Global Change Biology* 24: 517–525. <https://doi.org/10.1111/gcb.13852>.
- Toussaint, A., N. Charpin, O. Beauchard, et al. 2018. “Non-Native Species Led to Marked Shifts in Functional Diversity of the World Freshwater Fish Faunas.” *Ecology Letters* 21: 1649–1659. <https://doi.org/10.1111/ele.13141>.
- Trebilco, R., J. K. Baum, A. K. Salomon, and N. K. Dulvy. 2013. “Ecosystem Ecology: Size-Based Constraints on the Pyramids of Life.” *Trends in Ecology & Evolution* 28: 423–431. <https://doi.org/10.1016/j.tree.2013.03.008>.
- van Dorst, R. M., C. Argillier, S. Brucet, et al. 2022. “Can Size Distributions of European Lake Fish Communities Be Predicted by Trophic Positions of Their Fish Species?” *Ecology and Evolution* 12: e9087. <https://doi.org/10.1002/ece3.9087>.
- Vejřík, L., I. Vejříková, P. Blabolil, et al. 2017. “European Catfish (*Silurus glanis*) as a Freshwater Apex Predator Drives Ecosystem via Its Diet Adaptability.” *Scientific Reports* 7: 15970. <https://doi.org/10.1038/s41598-017-16169-9>.
- Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, et al. 2010. “Global Threats to Human Water Security and River Biodiversity.” *Nature* 467: 555–561. <https://doi.org/10.1038/nature09440>.
- Werner, E. E., and J. F. Gilliam. 1984. “The Ontogenetic Niche and Species Interactions in Size-Structured Populations.” *Annual Review of Ecology and Systematics* 15: 393–425. <https://doi.org/10.1146/annurev.es.15.110184.002141>.
- Woodward, G., B. Ebenman, M. Emmerson, et al. 2005. “Body Size in Ecological Networks.” *Trends in Ecology & Evolution* 20: 402–409. <https://doi.org/10.1016/j.tree.2005.04.005>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.