Received: 8 October 2025 | Accepted: 5 March 2026

DOI: 10.1111/1365-2656.70260

BRITISH ECOLOGICAL SOCIETY Journal of Animal Ecology

RESEARCH ARTICLE

Biological invasions disrupt the relationship between size spectrum and trophic interactions in freshwater fish communities

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Funding information
Office Français de la Biodiversité

Handling Editor: Malte Jochum

Abstract

1. The size spectrum, which describes the relationship between abundance (or biomass) and body size, is an ataxic approach that can provide insights into energy fluxes across trophic levels. However, anthropogenic perturbations can alter the relationship between body size and trophic position, and therefore, the predator–prey mass ratio (PPMR).
2. In this study, we used body size distribution and stable isotope analyses to investigate the relationship between size spectrum and the PPMR in lake fish communities across various eutrophication and invasion levels.
3. Our results revealed that, although size spectrum and PPMR co-varied (i.e. resulting in flatter size spectrum when PPMR was low), this effect was modulated by the level of biological invasion in the community. This was likely caused by differences in trophic niche between native and non-native species: small non-native species exhibited higher trophic positions than small native species, while large non-native species can have lower trophic positions than their native counterparts.
4. These findings suggest that the relationship between size structure and trophic interactions in lake fish communities may be blurred by anthropogenic perturbations, challenging core assumptions of size-based ecology in estimating energy fluxes within freshwater food webs.

KEYWORDS
body size distribution, energy fluxes, predator prey mass ratio, stable isotope analyses, trophic position

1 | INTRODUCTION

Body size is a fundamental attribute of organisms that co-varies with many biological traits (Brown et al., 2004; Pianka, 1970) and shapes how organisms interact with their environment (Hildrew et al., 2007; Woodward et al., 2005). Numerous empirical studies in aquatic ecosystems have demonstrated that body size is a better predictor of individual trophic position than taxonomy (Al-Habsi et al., 2008; Jennings et al., 2001; Soler et al., 2016). This is because predator–prey relationships are largely determined by size constraints and the gape size of aquatic predators (Hairston & Hairston, 1993; Wainwright & Richard, 1995). As a result, aquatic food webs are strongly size-structured, with a positive relationship between body size and trophic position, and this pattern is commonly observed in both marine and freshwater ecosystems (Nakazawa et al., 2010; Potapov et al., 2019; Romanuk et al., 2011).

The community size spectrum, that is, the relationship between the abundance (or biomass) of organisms and their body size, represents an emergent property of communities, shaped by energy dynamics and predator–prey interactions (Reuman et al., 2008; Trebilco et al., 2013). Theoretically, it reflects some fundamental attributes of food webs, including their carrying capacity and trophic transfer efficiency (Brose et al., 2017). In this sense, approaches based on size spectrum are commonly used to indirectly quantify the response of food webs to anthropogenic perturbations in both marine (e.g. climate change: Heneghan et al., 2019, or fishing: Rochet & Benoît, 2012; Rogers et al., 2014) and freshwater (e.g. eutrophication: Emmrich et al., 2011, hydro-morphological alterations: Marin et al., 2023 or non-native species introduction: Arranz et al., 2021) ecosystems. However, it remains unclear how variations in community size spectrum caused by anthropogenic perturbations actually reflect changes in predator–prey interactions and energy flux within food webs (Leclerc et al., 2025; Mehner et al., 2018). Addressing this knowledge gap is particularly relevant as aquatic ecosystems are increasingly facing multiple stressors that may blur the role of body size in structuring predator–prey interactions (Carvajal-Quintero et al., 2024). Eutrophication, that is, the addition of nutrients from agricultural or domestic run-off, can simplify food webs by redirecting consumer diets towards basal resources, and reduce their mean trophic position (Nordström & Bonsdorff, 2017; van der Lee et al., 2021). This has been associated with shifts in biomass towards smaller size classes and steeper size-spectrum slopes (Arranz et al., 2021). At the opposite, biological invasions, that is, the introduction of non-native species into recipient communities, generally coincide with an increase in mean trophic position in freshwater food webs (Cucherousset et al., 2012; but see Leclerc et al., 2025) and flatter size spectrum slopes (Arranz et al., 2021). However, it has been recently demonstrated that the responses of size spectrum and trophic structure are not necessarily coupled (Leclerc et al., 2025). These findings highlight the need to empirically investigate the relationships between them, while explicitly accounting for environmental conditions faced by the communities.

Stable isotope analyses represent an integrative approach to empirically quantify energy origin and fluxes within food webs (Hertz et al., 2014; Jennings et al., 2008; Perkins et al., 2018). Nitrogen stable isotope ($\delta^{15}N$) is commonly used to assess the trophic position of organisms (Post, 2002) and can be used to quantify key food web properties such as the Predator–Prey Mass Ratio (PPMR), which is directly linked to energy flux in food webs (Jennings et al., 2008). Specifically, increasing PPMR (predators much larger than their prey) under constant trophic transfer efficiency (generally considered ~10%; Brown et al., 2004) will reduce the food chain length (Barnes et al., 2010; Jennings et al., 2002), resulting in a higher abundance of large individuals at the top of the food chain. Therefore, size spectrum slope and PPMR are linked theoretically as Equation (1):

$$\mathrm{TTE} = \mathrm{PPMR}^{\mathrm{SS}_{\mathrm{slope}}+0.75} \text{ or } \mathrm{SS}_{\mathrm{slope}} = \frac{\log \mathrm{TTE}}{\log \mathrm{PPMR}} - 0.75 \quad (1)$$

where TTE is trophic transfer efficiency. However, empirical support for this relationship remains limited.

Recently, Coghlan et al. (2022) reported evidence of a positive association between the proportion of large-bodied individuals and PPMR using stable isotope analysis in coastal reef fish communities, suggesting that size-spectrum slopes may provide a reliable proxy for inferring changes in energy fluxes within food webs. Importantly, the authors demonstrated that the relationship between PPMR and the size spectrum slope only emerged in tropical communities and not in temperate ones, and discussed the potential role of temperature or anthropogenic perturbations in exacerbating or blurring the role of body size in explaining predator–prey interactions (Coghlan et al., 2022). Although the relationship between trophic position and the size spectrum can combine size-based approaches and energy fluxes within aquatic food webs (Hertz et al., 2014), empirical studies investigating the co-variations of size spectrum and food web structure using stable isotope analyses are still missing, especially in freshwater ecosystems. Such evidence would not only help identify the ecological mechanisms through which the size spectrum responds to anthropogenic perturbations, but also clarify how they may disrupt the relationships between community structure and energy fluxes within food webs.

In this study, we tested whether anthropogenic perturbations alter the relationship between size spectra and trophic structure in freshwater fish communities. Using an empirical dataset based on fish communities sampled in 25 gravel pit lakes displaying strong gradients of eutrophication and biological invasion, we quantified the size spectrum slope and PPMR using body size distribution and stable isotope analyses in fish communities. We hypothesized that the relationship between the size spectrum slope and PPMR would differ depending on the levels of eutrophication and biological invasions, as these anthropogenic perturbations can disrupt size-based interactions (Arranz et al., 2023; Moi et al., 2025).

2 | MATERIALS AND METHODS

2.1 | Study sites and fish community sampling

The study was conducted in 25 gravel pit lakes (hereafter 'lakes') located in the Garonne floodplain (southwestern France), distributed within a maximum distance of 60 km. All lakes were disconnected from each other and from the river network and infilling was from the water-table (Alp et al., 2016; Jackson et al., 2017; Zhao et al., 2016). These artificial lakes are relatively small (mean = 0.135 km^2, SD = 0.096) and display a large variety of hydrobiological conditions (details in Table S1). For instance, lake maturation, that is, the time since excavation, correlates with a strong eutrophication gradient due to organic matter accumulation (Colas et al., 2021), whereas communities were mainly driven by lake management. Specifically, lake access may be restricted, open to the public or reserved exclusively for angling activities such as private fisheries (Zhao et al., 2016). Some lakes are regularly stocked with native and non-native fish (Garcia et al., 2023; Gimenez et al., 2023) and are also invaded by two non-crayfish species (red-swamp crayfish *Procambarus clarkii* and spiny-cheek crayfish *Faxonius limosus*; Alp et al., 2016). In brief, the studied ecosystem displays a unique gradient of community structures within a limited geographical area, with access-restricted lakes naturally colonized by pioneer native species through avian zoochory (Garcia et al., 2023), while managed lakes can exhibit higher taxonomic and functional diversity, including non-native species (Gimenez et al., 2023; Zhao et al., 2016).

Fish community monitoring was performed as part of the long-term Studies in Ecology and Evolution (SEE-Life) programme of the CNRS and projects of the Office Français de la Biodiversité (OFB). Fish sampling was performed under the authorizations 'Arrêtés Préfectoraux' 20140808, 20160706, 20170717, 20180717, 20190506, 20210618 and 20220912 from the Direction Départementale des Territoires (DDT) of the Préfecture de la Haute-Garonne. Fish communities were sampled once in each lake between 2014 and 2022 at the end of the growing season, from mid-September to mid-October. To ensure a representative sampling of the fish community, we used an integrative protocol combining gillnetting and electrofishing approaches to cover variability in habitat, body size and life stages (Zhao et al., 2016). Specifically, gillnets are efficient in deeper habitats (>1 m), while electrofishing is efficient in shallow and vegetated habitats (<1 m). Gillnetting was performed using 6 to 8 nets in the pelagic and littoral zones of the lakes, with the number of nets determined by lake area. Gillnetting started at sunrise (approx. 7:00 AM) with a duration of 2 h per net. A wide range of mesh sizes was used to ensure coverage of fish size distributions among species (Zhao et al., 2016, 2019). Electrofishing was performed in the early afternoon from a small boat, using a Point Abundance Sampling by Electrofishing (PASE) approach to sample the littoral habitat of each lake (Cucherousset et al., 2006). In each lake, a total of 25 PASE locations, spaced at least 20 m apart, were used (Zhao et al., 2016). Fish sampled were identified to species (except *Blicca bjoerkna* and *Abramis brama* which were pooled together as bream sp.) and measured for total body length (mm). Individual body mass (g) was then estimated using body length–mass relationships obtained in the study area (Zhao et al., 2019). In total, 10,099 individuals from to 23 species were sampled (Table S2). Species status (native or non-native, Table S2) was defined at regional scale (Adour-Garonne watershed) following Keith et al. (2011). Around half of the species were non-native (12 native and 11 non-native). Among the non-native species, three were piscivorous (largemouth bass *Micropterus salmoides*, pikeperch *Sander lucioperca* and European catfish *Silurus glanis*), while eight were non-piscivores (mosquitofish *Gambusia affinis*, ruffe *Gymnocephalus cernua*, pumpkinseed *Lepomis gibbosus*, black bullhead *Ameiurus melas*, goldfish *Carassius auratus*, grass carp *Ctenopharyngodon idella*, gibel carp *Carassius gibelio* and the common carp *Cyprinus carpio*). Three native species were piscivorous (northern pike *Esox lucius* and European perch *Perca fluviatilis* and eel *Anguilla anguilla*), while the nine others were non-piscivorous cyprinid species (bleak *Alburnus aburnus*, chub *Squalius cephalus*, roach *Rutilus rutilus*, rudd *Scardinius erythrophthalmus*, tench *Tinca tinca*, toxostome *Parachondrostoma toxostoma*, gudgeon *Gobio gobio*, barbel *Barbus barbus* and bream sp.). Individual fish with an estimated body mass <1 g were excluded from the analyses due to the limited sampling efficiency of electrofishing for smaller individuals (Copp, 1989), avoiding biases in size structure estimation (Mehner et al., 2016; Sutton & Jones, 2020). Individuals excluded were mainly mosquitofish with body lengths <30 mm (80% of total excluded individuals). The body mass of the individuals included in the subsequent analyses ranged from 1 to 31,625 g (mean = 112 g, SD = 741 g).

Across all lakes, species richness ranged from 2 to 15, with an average of seven species (SD = 3). Low species richness was mainly found in younger lakes (Table S1). Among the 25 studied fish communities, European perch was the most abundant species (35% of all individuals: Table S2), followed by roach (19%) and pumpkinseed (18%). Most of the biomass at the community level was represented by common carp (44%), followed by European catfish (12%) and European perch (11%: Table S2).

2.2 | Anthropogenic perturbations

The eutrophication level of each lake was assessed using the mean of three Trophic State Index (TSI) (Arranz et al., 2023), calculated using water clarity (Secchi depth), chlorophyll-a concentration (Chla, in mg.L^{-1}) and total phosphorus concentration (TP, in µg.L^{-1}). These variables were measured at three different locations in each lake (Zhao et al., 2016), and then averaged. Across all lakes, Secchi depth ranged from 15 to 242 cm, Chl-a ranged from 1 to 128 µg.L^{-1} and TP ranged from 13 to 157 µg.L^{-1}. Then, the averaged values was used to calculate TSI for each variable using the following formulas (Carlson, 1977):

$$\mathrm{TSI}_{\mathrm{Secchi}} = 10 \times \left(6 - \frac{\log(\mathrm{Secchi\ depth})}{\log(2)}\right) \tag{2}$$

$$\mathrm{TSI}_{\mathrm{Chla}} = 10 \times \left(6 - \frac{-0.68 \times \log(\mathrm{Chla})}{\log(2)}\right) \tag{3}$$

$$\mathrm{TSI}_{\mathrm{TP}} = 10 \times \left(6 - \frac{\log\left(\frac{48}{\mathrm{TP}}\right)}{\log(2)}\right) \tag{4}$$

Then, we used the average value for each lake as follows:

$$\mathrm{TSI}_{\mathrm{lake}} = \frac{\mathrm{TSI}_{\mathrm{Secchi}} + \mathrm{TSI}_{\mathrm{Chla}} + \mathrm{TSI}_{\mathrm{TP}}}{3} \tag{5}$$

TSI values varied from 45 to 78, indicating a strong eutrophication gradient ranging from mesotrophic (>40) to hypereutrophic (>70) lakes (Carlson, 2007). Finally, the level of biological invasion was determined as the relative biomass (%) of non-native individuals within the fish community. The proportion of non-native individuals ranged from 0% to 97%, highlighting a strong invasion gradient among the studied lakes. Importantly, eutrophication and invasion level were not correlated (Pearson$_r$ = 0.232, p = 0.264; Figure S1).

2.3 | Size spectrum

The size spectrum slopes of fish communities (hereafter size spectrum$_b$) were calculated in each lake based on the comprehensive sampling of the fish community using a binned method at a log–log space (Sprules & Barth, 2016). Fish sampled via gillnetting and electrofishing were combined to capture the variability in body sizes across habitats, as all lakes were sampled using a similar relative sampling effort. For each fish community, all individual body masses were categorized into 15 classes, based on a geometric series of 2 (1st: 1–2 g, 2nd: 2–4 g, …, 15th: >16,384 g; Mehner et al., 2016). We then calculated an ordinary-least-square regression to fit fish abundances across size classes ($\log_2$ of normalized abundance) (Arranz et al., 2023; Marin et al., 2023; Mehner et al., 2016). The normalization of abundances was achieved by dividing fish abundance per size class by the width of each size class (in g: Sprules & Barth, 2016). To ensure robustness of size spectrum$_b$ estimation by binned method, we also computed the size spectrum$_b$ using the maximum likelihood estimate (MLE) using 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 calculated using the *negLL.PLB* function available in the *sizeSpectra* package on the *Rstudio* software (Edwards, 2019). Importantly, there was a strong positive and significant correlation between the size spectrum$_b$ obtained using the MLE approach and the size spectrum$_b$ obtained using the binned method (Pearson correlation, r = 0.78, p < 0.001). The latter were used for subsequent analyses and we found qualitatively similar results when using the size spectrum$_b$ from the MLE approach (Table 1; Table S3).

2.4 | Predator–prey mass ratio (PPMR)

2.4.1 | Trophic positions of fish

The trophic position of fish was estimated using δ^{15}N of fish and invertebrates (Figure S2). During the sampling process, fish were fin-clipped for stable isotope analyses by covering the full range of body sizes for each species in each lake (Zhao et al., 2019). In total, 1079 fish were analysed, belonging to 17 species (representing the most abundant at our study scale: Table S2). On average, seven (SD = 2) individuals per species were analysed for δ^{15}N, corresponding to a mean of 44 (SD = 4) individuals per lake (Table S1). To allow comparison between lakes, we calculated the trophic positions of fish using benthic invertebrates (primary consumers) as baselines (Evangelista et al., 2019). Depending on their presence in the lakes, these included bivalves (*Corbicula fluminea* or *Dreissena polymorpha*), gastropods (*Physella* sp.) or insect larvae (mayfly Baetidae), which are commonly used as reliable baselines for freshwater fish (Anderson & Cabana, 2007). These baselines integrate the spatial and temporal variability in stable isotope values (Anderson & Cabana, 2007). Indeed, scrapers or filter feeders integrate both autochthonous and allochthonous energy channels through the consumption of bulk plankton and/or periphyton (e.g. algae and bacteria; Kristensen et al., 2016). In addition, we assumed limited differentiation between energy channels due to the small size and shallow depth of the studied lakes. Invertebrates were collected at three different locations in each lake, with a minimum of three individuals per taxon to ensure robust estimates of baseline stable isotope values (Jackson et al., 2017). The entire body was used for insect larvae, while only the foot muscle was used for molluscs for stable isotope analyses (Evangelista et al., 2019). All samples were dried and ground into a homogeneous powder prior to stable isotope analyses at the Cornell Isotope Laboratory (COIL). Nitrogen stable isotope values were then used to calculate the trophic position of each fish (TP$_{\text{fish}}$) following Post (2002):

$$\mathrm{TP}_{\text{fish}} = 2 + \left(\delta^{15}\mathrm{N}_{\text{fish}} - \delta^{15}\mathrm{N}_{\text{baseline}}\right) / 3.4 \tag{6}$$

where 2 is the trophic position of the primary consumers (benthic invertebrates), $\delta^{15}\mathrm{N}_{\text{fish}}$ is the nitrogen isotope ratio of fish, $\delta^{15}\mathrm{N}_{\text{baseline}}$ is the δ^{15}N value of the baseline invertebrates (pooled across insects and molluscs) and 3.4 is the fractionation factor between trophic levels (Post, 2002, Figure S2).

2.4.2 | PPMR estimation

We estimated a proxy of PPMR for each fish community using the relationship between body mass (X-axis in a $\log_2$ scale) and trophic position (Jennings et al., 2002). The slope (b) of this relationship can be used to estimate an average PPMR by quantifying the rate at which trophic position increases per unit body mass (Hertz et al., 2014; Jennings et al., 2002; Reum et al., 2020). Specifically, low values of b indicate that trophic position increases slowly with body mass (high PPMR). Conversely, high b values reflect a low PPMR, as trophic position increases rapidly with body mass. To ensure consistency with the size spectrum analysis, trophic position data were grouped into the same 15 size classes (based on $\log_2$-transformed body mass) used to calculate the size spectrum$_b$. We then determined the slope of the linear regression between the mean trophic positions (Y axis) and body mass classes (X axis) for each community (hereafter PPMR$_b$) using an ordinary-least-square regression.

2.5 | Statistical analyses

We first assessed the spatial auto- and cross-correlation of size spectrum$_b$ and PPMR$_b$ to determine whether spatial structure needed to be accounted for in subsequent analyses. Spatial autocorrelation was tested individually using Moran's test, based on geographical distances between sampling sites (*moran.test* function in the *spdep* R-package, version 1.3-3). Spatial cross-correlation was then estimated by computing the geographical distance matrix and pairwise difference matrix of size spectrum$_b$ and PPMR$_b$. A Mantel test was performed using the *mantel* function from the vegan package (version 2.6-8), with significance assessed through 999 permutations. Second, we tested the effects of PPMR$_b$, eutrophication, biological invasion and their interactions on the size spectrum$_b$ using a linear mixed model (*lme4* R-package version 1.1-34) as the following Equation (7):

$$\text{Size spectrum}_b = \beta_0 + \beta_1 \times \text{PPMR}_b + \beta_2 \times BI + \beta_3 \times E + \beta_4 \times \left(\text{PPMR}_b \times BI\right) + \beta_5 \times \left(\text{PPMR}_b \times E\right) + \beta_6 \times (E \times BI) + u_{\text{Year}} + \varepsilon_{\text{Lake}} \tag{7}$$

where β_0 is the model intercept; β_1, …, β_6 are the fixed-effect coefficients for single and interactive effects; BI and E the observed biological invasion and eutrophication level, respectively; u_{Year} the random effect of year and ε the residual error of each lake, both assumed ~ N(0, σ^2). Even though no temporal trend was detected in the size spectrum$_b$ or its predictors (Figure S3), sampling year was included as a random factor to account for interannual variability. No particular correction was applied to achieve normality assumption. A backward selection procedure based on a significance level of 0.05 was realized on the full model (Equation 7), removing non-significant interactions to obtain the final (best) model. Due to the low level of replication and the presence of extreme values that could influence model fitting, we tested each observation as a potential mean-shift outlier using the *outlierTest* function from the *car* R-package (version 3.1-3). No studentized residuals was identified as an outlier, with all Bonferroni $p > 0.05$. Given the significant interaction between PPMR$_b$ and biological invasions (see Results section), we further tested whether the relationship between body mass (BM) and trophic position (TP) differed between native and non-native species, using a linear mixed model following Equation (8):

$$\text{TP} = \beta_0 + \beta_1 \times \text{BM} + \beta_2 \times \text{Status} + \beta_3 \times (\text{BM} \times \text{Status}) + u_{\text{Lake}} + \varepsilon_i \tag{8}$$

where β_0 is the model intercept; β_1, β_2 and β_3 are the fixed-effect coefficients for single and interactive effects; BM the log$_2$-transformed body mass in (g) to assume a normal distribution and ensure consistency with PPMR calculation; Status as the native/non-native status of individuals (Table S2); u_{Lake} the random effect of lake and ε the residual error of each individuals, both assumed ~ N(0, σ^2). Lake was included as a random factor to account for intraspecific variation in foraging behaviour that may differ among lakes.

3 | RESULTS

The size spectra$_b$ were consistently negative (mean = −1.360, SD = 0.148, Figure 1a), with high regularity across size classes (mean $R^2 = 0.894$, SD = 0.060), indicating that lake fish communities were strongly size-structured. Variations of size spectrum$_b$ were associated with a simultaneous increase in small-body size class and a decrease in large size classes (Figure 1c). Regarding PPMR$_b$, we observed both positive and negative values (Figure 1b), indicating that individuals with lower trophic position could occur in the largest size classes (Figure 1d). We found no significant spatial autocorrelation for either size spectrum$_b$ and PPMR$_b$, supported by Moran values close to the expected value under spatial randomness ($I = -0.042$, $p = 0.500$ for both variables). Spatial projection of size spectrum$_b$ and PPMR$_b$ values revealed an unclear pattern in their covariation, as low PPMR$_b$ can be associated with both steep and shallow size spectrum$_b$ (Figure 2). Importantly, the relationship between size spectrum$_b$ and PPMR$_b$ was not related spatially (Mantel $r = 0.045$, $p = 0.324$).

We found a significant interaction between PPMR$_b$ and biological invasion in explaining the variation in size spectrum$_b$ (Table 1). Specifically, in lakes with low levels of biological invasions, PPMR$_b$ had a positive effect on size spectrum$_b$ (i.e. resulting in flatter size spectrum$_b$ when PPMR was low, Figure 3). Conversely, in lakes with high levels of biological invasions, PPMR$_b$ had a negative effect on size spectrum$_b$ (i.e. leading to steeper size spectrum$_b$ when PPMR was low, Figure 3). Finally, there was no significant effect of eutrophication on the size spectrum$_b$ (Table 1).

The relationship between body mass and trophic position differed significantly between native and non-native species, as indicated by the significant interaction between fish species status and body mass ($p = 0.030$, Table 2). Specifically, the trophic positions for small native individuals were lower than those of non-native individuals, but increased steeply (Figure 4a). This pattern was driven by small non-native species with relatively high trophic positions (e.g. pumpkinseed, mosquitofish or black bullhead, Figure 4b). At larger body sizes, trophic positions converged, resulting in similar estimates for native and non-native individuals (Figure 4a). This convergence was driven by both large-bodied non-native species with higher trophic position (e.g. largemouth bass and pikeperch) and by large-bodied non-native species with lower trophic positions (e.g. common and gibel carp) than native ones (Figure 4b). However, non-native species displayed a higher correlation between body mass and trophic position, with 66% exhibiting significant positive relationships (Figure 5). In contrast, only three of the seven native species analysed (European perch, chub and bream sp.) showed an increase in trophic position during ontogeny. Importantly, body mass and species status explained only a small part of the individual variation in trophic position in our study, which was largely accounted by lake identity (40.7% of variance: Table 2).

4 | DISCUSSION

Environmental conditions influenced by anthropogenic perturbations can affect the relationship between size distribution and energy flux within food webs (Trebilco et al., 2013). This study is the first to empirically explore these effects in freshwater ecosystems using stable isotope analyses. Our results partially validate the hypothesis that the relationship between size spectrum and predator–prey mass relationship (PPMR) would differ depending on the

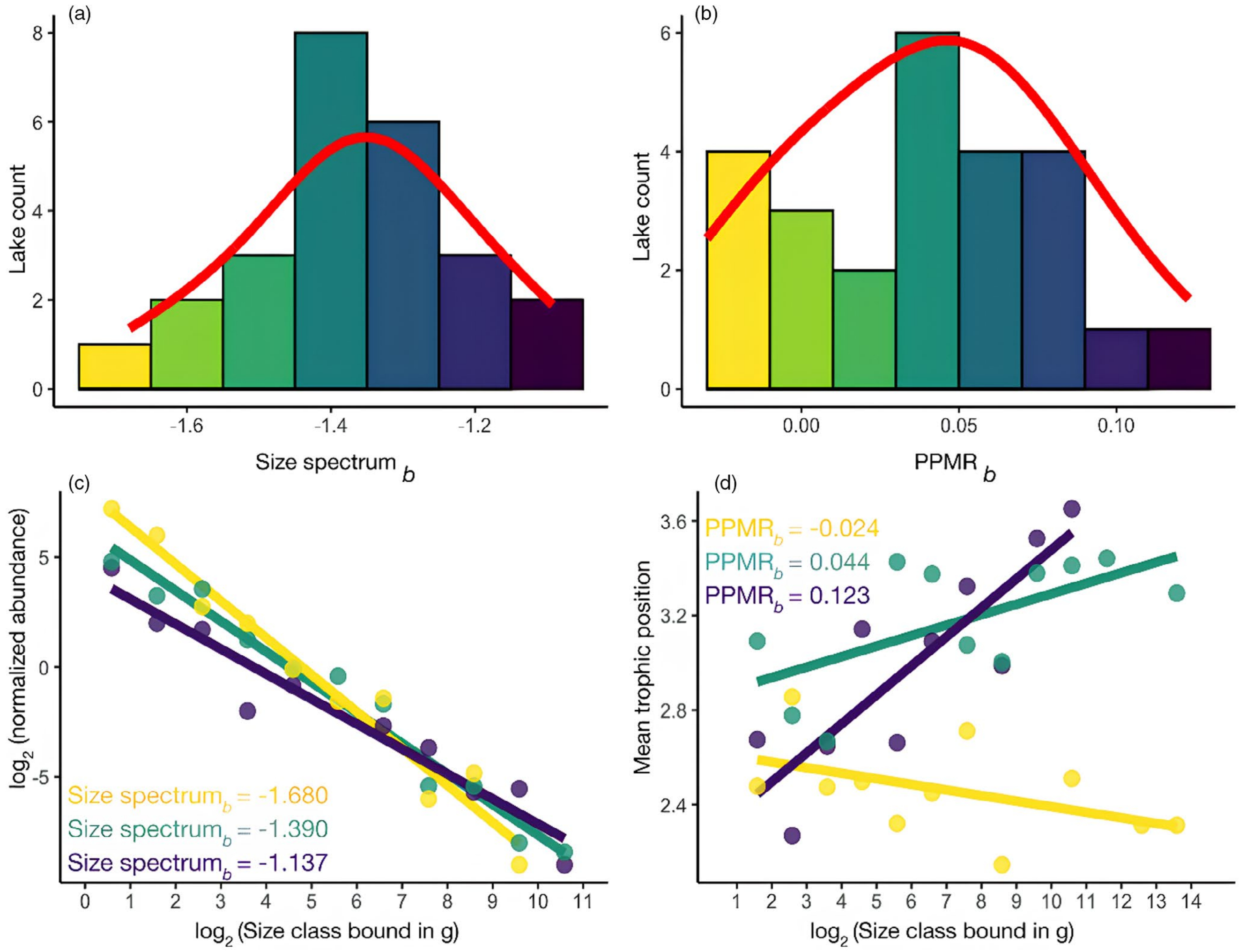

FIGURE 1 Distributions of size spectrum$_b$ (a) and PPMR$_b$ (b) across the 25 studies fish communities and representation of their minimum, median and maximum observed values (c, d), respectively. Red lines represent the estimated densities and colours the gradient from low to high values.

levels of eutrophication and biological invasions. Specifically, we found that biological invasions disrupted the relationship between size spectrum and PPMR, a result driven by the divergence in trophic niche between native and non-native species. However, no significant effect of eutrophication on the size spectrum was observed. This implies that changes in species composition may more profoundly affect energy fluxes within fish food webs rather than altering energy input through bottom-up effects.

The size spectrum is currently a common ecological approach to characterize community structure because it is grounded in allometric principles applicable across all biomes (Hatton et al., 2015; Petchey & Belgrano, 2010). However, the main assumptions of size-spectrum approach to estimate energy flux in food webs requires that body size governs the trophic position of organisms. Therefore, one of our most important findings is the considerable uncertainty in predicting trophic position based on body size in freshwater fish communities, particularly when non-native species are present. These results are not unexpected, as trophic interactions within temperate freshwater fish communities tend to be more size-structured compared to other freshwater ecosystems (Dalponti et al., 2024). While increases in trophic position during ontogeny were more common among non-native species, these species exhibited distinct relationships between mean body size and trophic position, which may confer a competitive advantage (Dijoux et al., 2024). Common carp, which significantly contributed to the community total biomass, is one of the most compelling examples. Common carp is a generalist species in terms of habitat (e.g. water flow, climate) and feeding preferences (e.g. plants, invertebrates) (Moyle & Marchetti, 2006; Toussaint et al., 2016). The common carp can simultaneously flatten the size spectrum slope by increasing the proportion of large individuals, while likely hindering the transfer of energy from basal resources to higher trophic levels (Arranz et al., 2021; Kopf et al., 2019). In this sense, the common carp is rapidly released from native predator pressure due to its large body size, thus representing a trophic dead-end. On the other hand, we observed non-native species with lower body sizes than native species, and occupying relatively high trophic positions. An example of this is the mosquitofish, which has been widely introduced across Europe

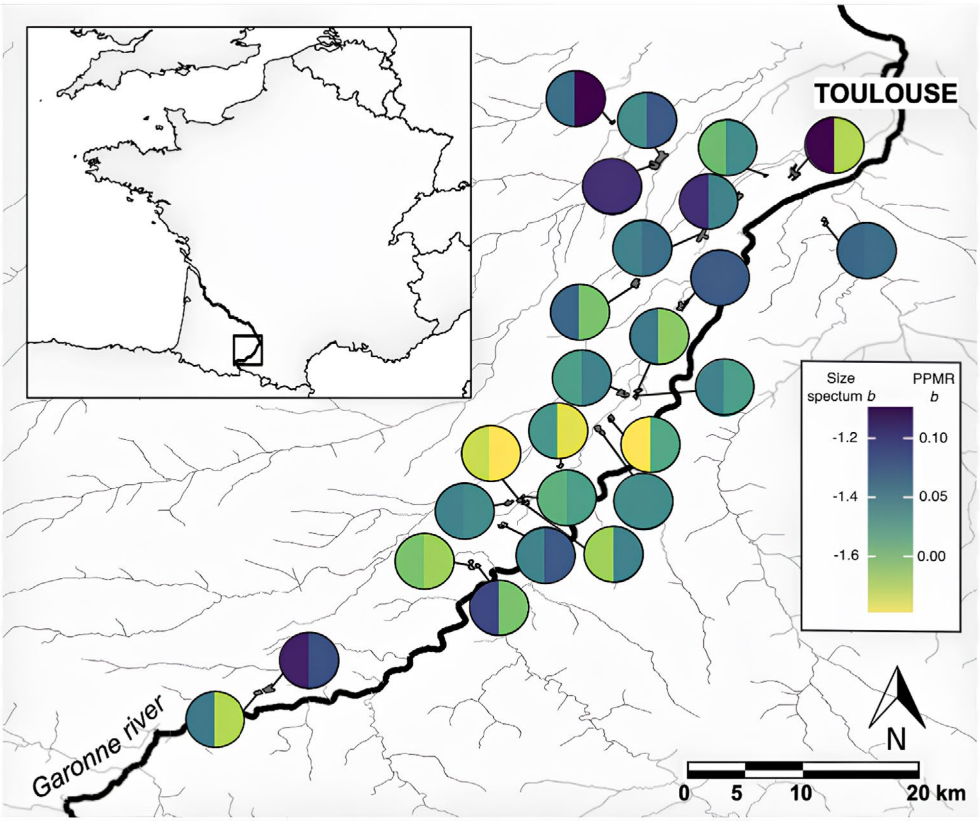

FIGURE 2 Geographical variation of the size spectrum and PPMR$_b$ in the 25 studied lakes. Colours on the left and right parts of the circles represent the gradient of size spectrum$_b$ and PPMR$_b$ values from low to high, respectively.

TABLE 1 Results of the final mixed model testing the effects of PPMR$_b$ and anthropogenic perturbations (i.e. eutrophication and biological invasion) on size spectrum$_b$.

Predictors	Estimate (β)	*F*-value	*p*-value
Eutrophication	0.002	0.727	0.407
PPMR$_b$	3.941	8.171	**0.014**
Biological invasion	0.276	4.117	0.060
PPMR$_b$ × Biological invasion	−5.723	6.033	**0.026**

Note: Significant *p*-value are indicated in bold. Fixed terms accounted for 24.6% of the variance (marginal R^2) and random effects (i.e. sampling year) for 23.6%.

for mosquito larvae control. However, its impact has exceeded initial expectations, resulting in direct predation on vertebrates, including amphibians (Vannini et al., 2018). Taken together, these observations highlight the challenge of using size spectra to estimate energy flux in food webs in ecosystems altered by non-native species. This is particularly problematic, as biological invasions now affect the majority of waterbodies worldwide (Petsch, 2016). In addition, biological invasions by prey species could also affect energy fluxes by modifying the trophic ecology of native fish. For instance, it is very likely that the weak ontogenetic shift observed for Northern pike is driven by the fact that individuals might consume invasive crayfish as they grow, and become less piscivorous than expected in non-invaded systems. Feeding specialization on invertebrates among Northern pike populations strongly influences their mean trophic position (Beaudoin et al., 1999) and, more generally, likely explains why lake identity largely determined the body size–trophic position relationship at the individual level in our study.

Although freshwater food webs tend to be less size-structured than marine food webs, where size spectrum theory was originally developed (Potapov et al., 2019), our results demonstrate for the first time empirically that variation in size spectrum remains meaningfully associated with changes in PPMR in native communities. Specifically, the steepest size spectrum was associated with higher PPMR in native fish communities. However, this finding does not align with the theory that high PPMR tends to shorten food chains' length, reducing energy loss across trophic levels, and results in a higher abundance of large individuals (Barnes et al., 2010; Jennings et al., 2002). This discrepancy can likely be explained by the fact that most individuals were distributed into two trophic levels, thus reducing the food chain by one link. In other words, predator abundance may increase when predators consume prey that are large relative to their own body size. This suggests that the abundance and biomass of predators are more constrained to the optimal foraging (trade-off between energy spent in foraging vs prey energy content: Petchey et al., 2008) than energetic constraints on the food chain at each trophic level in freshwater ecosystems. This unexpected relationship

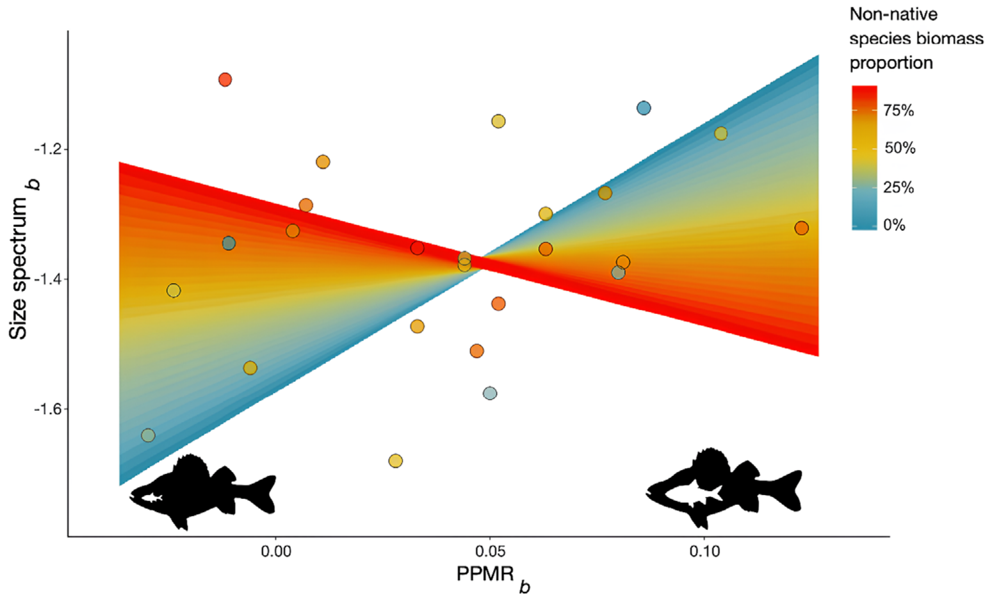

FIGURE 3 Interaction effect of biological invasion (i.e. non-native species proportion) on the relationship between PPMR_b and size $\mathrm{spectrum}_b$. Points represent observed values and are colour-coded based on their non-native biomass proportion, from high proportions in red to low proportions in blue. Rainbow lines presented behind the observations represent the predicted value of size $\mathrm{spectrum}_b$ by the final model, varying PPMR_b and non-native species proportion, with the mean value of eutrophication level and without the random effects (i.e. sampling year).

TABLE 2 Results of the final model testing the effects of species status (native or non-native) on trophic position.

Predictors	Estimate (β)	*F*-value	*p*-value
Body mass ($\log_2$)	0.061	123.246	**<0.001**
Species status$_{\text{non-native}}$	0.258	19.238	**<0.001**
Body mass (Log_2) × Specie status$_{\text{non-native}}$	−0.020	4.585	**0.030**

Note: Significant *p*-values are indicated in bold. Fixed term accounted for 7.7% of the variance (marginal R^2) and random effect (lake) for 40.7%.

between size spectrum and PPMR has recently been observed in European fish communities using trophic position defined at the species level (van Dorst et al., 2022). As mentioned by the authors, detailed and integrative empirical data on fish diet and trophic interactions are scarce, and their estimates of the PPMR could be biased because they derived theoretical trophic position according to the literature. Our results provide significant insight in this direction as we found a similar pattern using an empirical approach. Simply determining the body masses of piscivorous fish and their prey, identified at the species level, provides a reliable and realistic estimate of PPMR in these communities.

The more complex role of trophic interactions in governing the size spectrum derived from a monophyletic group in a freshwater ecosystem (i.e. fish) has been previously stated in the literature (Rossberg et al., 2019). Specifically, the decrease in abundance with increasing body size in fish communities may also reflect ontogenetic growth, while bottom-up and top-down effects become more apparent in the size spectrum when other trophic groups are included (i.e. phytoplankton and zooplankton). This can partly explain here the low importance of eutrophication in directly determining the size structure of our study, or by inducing changes in PPMR. These aspects have been previously discussed in the literature. For instance, changes in the slope of the fish size spectrum in response to eutrophication have been attributed to the higher physiological tolerance of small species rather than important changes in trophic structure (Arranz et al., 2021; Chu et al., 2016). Although the whole-community size spectrum, calculated across paraphyletic groups, offers a more realistic view of energy fluxes within food webs (Benoit et al., 2021; Heather et al., 2021; Rossberg et al., 2019), it may limit detection of intraspecific variation in size spectrum responses to environmental gradients (Rossberg et al., 2019). These observations raise serious important concerns about the simultaneous use of the size spectrum as an indicator of both trophic structure and anthropogenic perturbations in freshwater ecosystems (Marin et al., 2023). This is particularly important in light of the growing interest in using the size spectrum to indirectly quantify the effects of global changes on the functioning of aquatic ecosystems by changes in energy flux in food webs (Atkinson et al., 2024; Collyer et al., 2023; de Guzman et al., 2024).

In conclusion, our findings underscore the relationships between spatial variations in body size distributions and energy fluxes within freshwater fish communities, emphasizing the importance of considering the environmental context. We call for further empirical studies investigating the influence of anthropogenic perturbations on food web structure to better assess their interactions with the

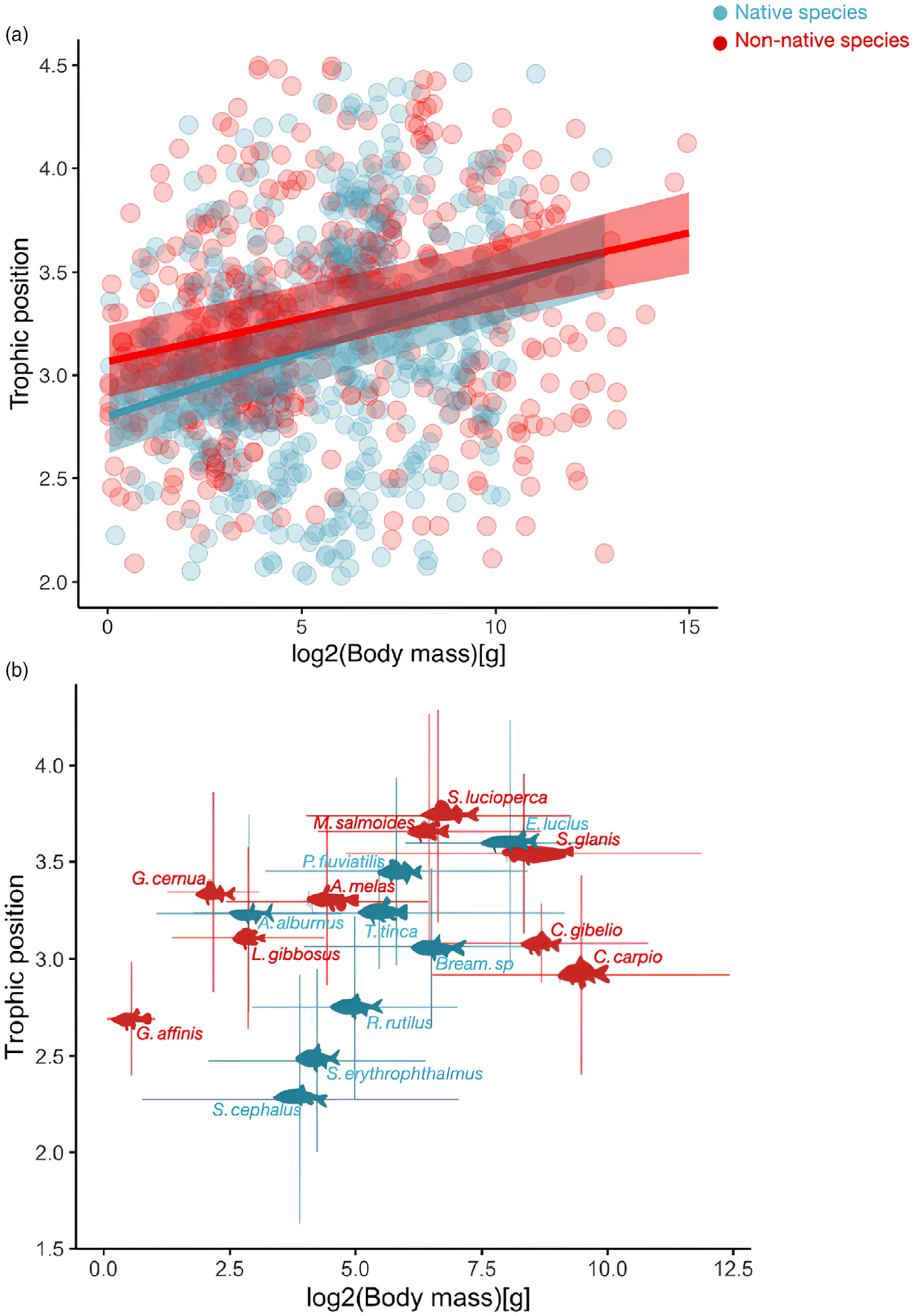

FIGURE 4 (a) Relationship between body mass and trophic position of native (blue) and non-native (red) individuals. The lines represent the relationships estimated for all individuals (±95% CI) from the linear mixed model. (b) Mean body mass and trophic position for each species and across all life stages. Error bars represent the standard deviation.

effect of invasive species. Such efforts would also enhance our understanding of the role of body size in interaction networks and shed light on how global changes are impacting ecosystem functioning.

AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed methodology. Valentin Marin, Ignasi Arranz and Julien Cucherousset collected the data. Valentin Marin analysed the data and led the writing of the manuscript. Ignasi Arranz, Gaël Grenouillet and Julien Cucherousset contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We are very grateful to the 'gravière' team for their help during field work, to lake owners and managers for allowing sampling. This work

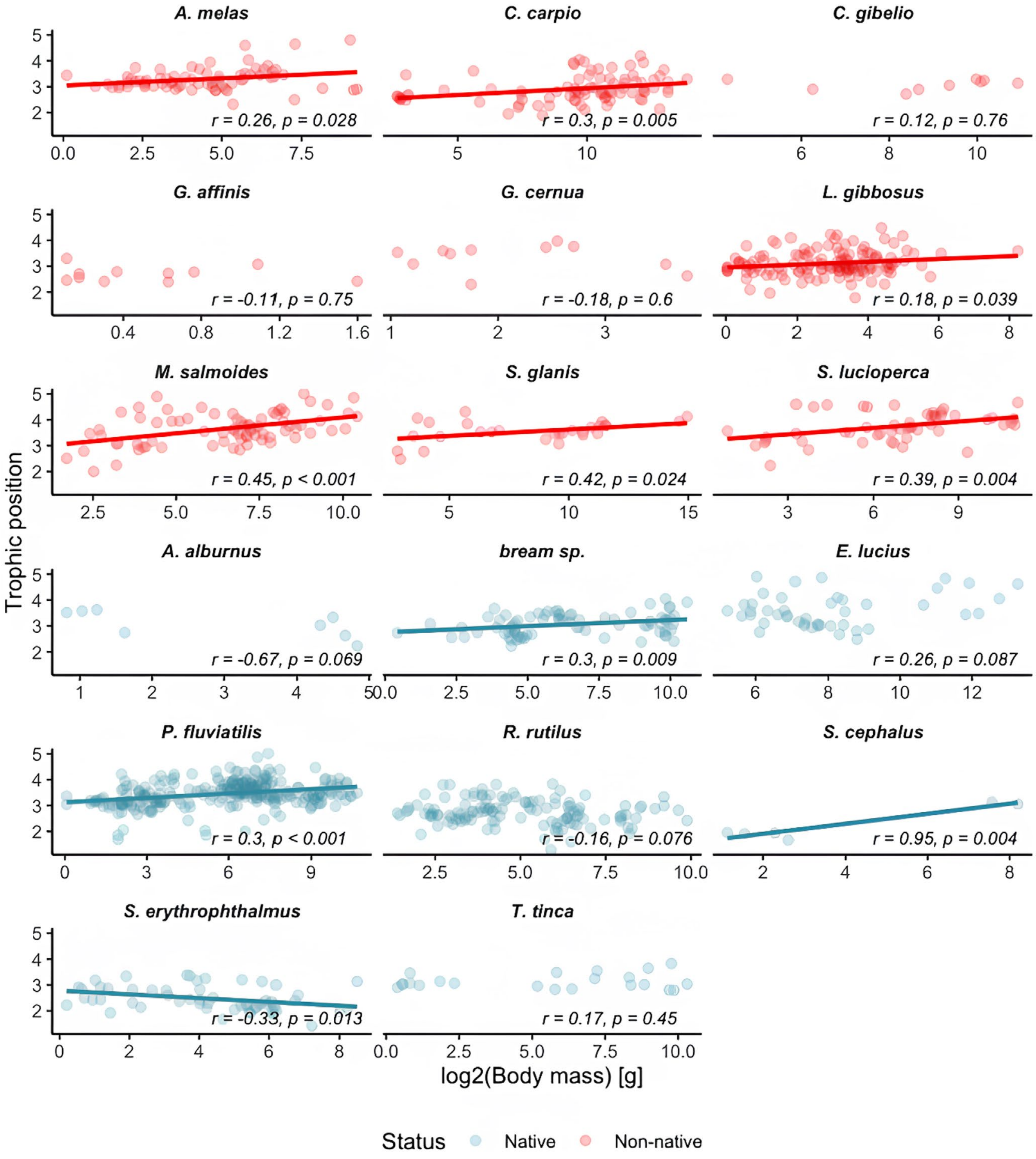

FIGURE 5 Relationships between trophic position and body mass in native (blue) and non-native species (red). Pearson correlation coefficients and associated *p*-values are provided.

was part of the STABLELAKE and SPECTRA projects funded by the Office Français de la Biodiversité (OFB). This work is part of the long-term Studies in Ecology and Evolution (SEE-Life) programme of the CNRS. We are also grateful to the three anonymous reviewers who made significant contributions to the manuscript. Open access publication funding provided by COUPERIN CY26.

CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.69p8cz9jd (Marin et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Hydrobiological characteristics of the 25 studied gravel pit lakes.

Table S2. Common and scientific names, status (native or non-native, defined at the country level), relative abundance (%) and relative biomass (%) of each fish species sampled in the studied gravel pit lakes. Relative abundance and biomass were calculated after removing individuals <1 g.

Table S3. Outputs of the final model testing the effects of PPMR_b and anthropogenic stressors (eutrophication and biological invasion) on the size $\mathrm{spectrum}_b$ estimated using the maximum likelihood method. Significant *p*-value are displayed in bold.

Figure S1. Geographical variation of invasion (% of non-native individuals) and eutrophication (trophic state index, TSI) level in the 25 studied lakes. Colours on the left and right parts of the circles represent the gradient of eutrophication and invasion level from low to high, respectively.

Figure S2. Distribution of the δ^{15}N values in each lake. Individual fish are represented in blue points and boxplots represent their distribution in each lake. Stable isotope values of baselines (primary consumers) used to calculate trophic position are displayed in orange and baseline (primary consumer) used in orange.

Figure S3. Plots between the sampling year and the size $\mathrm{spectrum}_b$ (a), as well as the predictors: predator–prey mass ratio (PPMR_b) (b), Trophic State Index (Eutrophication level) (c) and percentage of non-native individuals (Biological Invasion level) (d). Spearman correlation tests are also shown on the top right for each plot.

How to cite this article: Marin, V., Grenouillet, G., Arranz, I., & Cucherousset, J. (2026). Biological invasions disrupt the relationship between size spectrum and trophic interactions in freshwater fish communities. *Journal of Animal Ecology*, *00*, 1–13. https://doi.org/10.1111/1365-2656.70260