



Large fish forage lower in the food web and food webs are more truncated in warmer climates

Gissell Lacerot · Sarian Kosten · Raquel Mendonça · Erik Jeppesen · José Luiz Attayde · Néstor Mazzeo · Franco Teixeira-de-Mello · Gilbert Cabana · Matías Arim · José Henrique Cantarino Gomes · Sh Tserenpil · Marten Scheffer

Received: 31 May 2021 / Revised: 26 November 2021 / Accepted: 27 November 2021 / Published online: 9 December 2021
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2021

Abstract Body size is usually considered a good indicator of trophic position in fish communities. Indeed, the proverbial wisdom that “Big Fish Eat Little Fish” is consistent with observations from marine systems where systematic removal of the largest individuals has occurred, with cascading effect in the ecosystems. Trophic cascades are also well documented in temperate lakes but may not be as pronounced in (sub)tropical lakes due to higher degree of fish omnivory. We analysed fish communities along

a climatic gradient and showed the classical correlation between body size and relative trophic position disappears in warmer climates where large fish appear to be feeding systematically on the lowest trophic levels. This concurs with experimental findings demonstrating that omnivorous fish tend to include more plant and less animal matter in their diet at higher temperatures. Accordingly, the community-wide trophic web indicators, calculated based on stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), showed that the average degree of trophic diversity declined from cold to warm lakes and that the trophic webs become more truncated towards warmer climates. This has implications for lake restoration approaches in warmer climates and in temperate lakes within the context of global warming.

Handling Editor: Sidinei M. Thomaz

Guest editors: José L. Attayde, Renata F. Panosso, Vanessa Becker, Juliana D. Dias & Erik Jeppesen / Advances in the Ecology of Shallow Lakes

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10750-021-04777-6>.

G. Lacerot (✉)
Ecología Funcional de Sistemas Acuáticos, Centro Universitario Regional del Este, Universidad de la República, Rocha, Uruguay
e-mail: glacerot@cure.edu.uy

S. Kosten
Department of Aquatic Ecology & Environmental Biology; Radboud Institute for Biological and Environmental Sciences (RIBES), Radboud University, Nijmegen, The Netherlands

Keywords Trophic diversity · Stable isotopes · Trophic webs · Body size · Temperature · Latitude

R. Mendonça
Laboratório de Ecologia Aquática, Universidade Federal de Juiz de Fora, Juiz de Fora, MG, Brazil

E. Jeppesen
Department of Ecoscience and WATEC, Aarhus University, Silkeborg, Denmark

E. Jeppesen
Sino-Danish Centre for Education and Research, University of the Chinese Academy of Science, Beijing, China

Introduction

In aquatic trophic webs, most predators are not particularly selective, and gape-size puts a limit to the size of the prey (Cohen et al., 1993; Brose et al., 2006; Otto et al., 2007). Indeed, the proverb “Big Fish Eat Little Fish”, famously depicted by the Flemish painter Pieter Bruegel the Elder, reflects well how food web relations are established within fish communities in different ecosystems (Cohen et al., 1993; Romanuk et al., 2011; Jennings & van der Molen, 2015). An implication is that selective fishing on the largest individuals causes a systematic alteration of trophic structure as the suppression of top predators often has profound effects on the lower trophic levels (Pauly et al., 1998; Worm & Meyers, 2003). The biomass of small fish may increase, resulting in a decrease of large herbivorous zooplankton but an increase in microalgae biomass (Worm & Meyers, 2003; Frank et al., 2005; Scheffer et al., 2005). While for marine systems debate remains over the causal relationships behind trophic cascades, the phenomenon is well elucidated for temperate lakes (Brett & Goldman, 1996; Carpenter & Kitchell, 1996). In fact, manipulation of fish communities is a commonly used tool in temperate regions to reduce phytoplankton biomass through the cascading effects from fish

over zooplankton to algae (Gulati et al., 1990; Søndergaard et al., 2008; Abell et al., 2020).

How the trophic webs are functioning in subtropical and tropical lakes is less understood. So far, results suggest that a reduction of top predator fishes does not have the same strong effects in warmer lakes as in temperate lakes (Jeppesen et al., 2005; Jeppesen et al., 2007), because of higher prevalence of herbivory and omnivory in warm lakes (Wootton & Oemke, 1992; Lazzaro, 1997), and alterations in food web structure (Layman et al., 2005; Meerhoff et al., 2007, 2012; Havens et al., 2009; Teixeira de Mello et al., 2009), resulting in a weaker top-down response from fish to algae (Pujoni et al., 2016). Multiple theoretical approaches also suggest that omnivory results in a shorter food web length and increased connection strength of organisms within the food web (Layman et al., 2005; Arim et al., 2007a; Post & Takimoto, 2007; Takimoto et al., 2012). This is supported by a meta-analysis of fish diets in freshwater, brackish and marine waters (González-Bergonzoni et al., 2012) as well as a comparative analysis of nitrogen stable isotopes between subtropical lakes in Uruguay and temperate shallow lakes in Denmark (Iglesias et al., 2017) that indicated a higher prevalence of omnivory and shorter food chain lengths in warmer systems. Different causal mechanisms may explain the larger degree of omnivory

E. Jeppesen

Limnology Laboratory, Department of Biological Sciences and Centre for Ecosystem Research and Implementation, Middle East Technical University, Ankara, Turkey

E. Jeppesen

Institute of Marine Sciences, Middle East Technical University, Mersin, Turkey

J. L. Attayde

Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, RN, Brazil

N. Mazzeo · F. Teixeira-de-Mello · M. Arim

Departamento de Ecología y Gestión Ambiental, Centro Universitario Regional del Este, Universidad de la República, Maldonado, Uruguay

N. Mazzeo

Instituto SARAS, Bella Vista, Maldonado, Uruguay

G. Cabana

Département de chimie-biologie, Université du Québec à Trois-Rivières, Trois-Rivières, QC, Canada

J. H. Cantarino Gomes

Petrobras Transporte SA, Transpetro, Rio de Janeiro, Brazil

S. Tserenpil

Nuclear Research Center, National University of Mongolia, Ulaanbaatar, Mongolia

M. Scheffer

Department of Aquatic Ecology and Water Quality Management, Wageningen University, Wageningen, The Netherlands

of fish in warm systems (reviewed by González-Bergonzoni et al., 2012). Fish communities in warmer lakes tend to be more diverse, causing higher food competition and food partitioning (González-Bergonzoni et al., 2012; Schemske et al., 2009). Moreover, metabolic rates increase with warmer temperature and diminish the beneficial effect of digesting animal material, while enhancing the nutritional gain obtained from vegetal material (Behrens & Lafferty, 2007). In this sense, aquatic ectotherms omnivores have been shown to increase herbivory at higher temperatures, and the analysis of a global dataset of freshwater fish species revealed that larger tropical fish presented a significantly lower trophic position than their temperate counterparts, suggesting a compensating mechanism for higher energetic constraints feeding at a lower trophic position (Dantas et al., 2019).

Here, we aim to evaluate possible variations in the structure of food webs along a climate gradient. We hypothesise that food webs in cooler lakes follow the classical food chain concept with larger fish eating the smaller, whereas in warmer lakes the high dominance of omnivorous fish alters these relationships and shortens the length of the food web. For this, we analysed the relationship between body length and relative trophic position (given by $\delta^{15}\text{N}$ signal) in fish communities of 17 lakes, spanning over a latitudinal gradient (from 5° S to 54° S) of climate and temperature in South America. This relation between $\delta^{15}\text{N}$ and fish size is expected to be steeper in classical food webs than in more omnivorous ones (Fig. 1). We

also applied Layman's community-wide metrics based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope signatures of fish and other aquatic communities, to assess the characteristics of the lake's food webs. Food web characteristics are, however, not only dependent on temperature but may also vary with system size (Post et al., 2000; Arim et al., 2010), productivity (e.g. Meerhoff et al., 2012; Takimoto & Post, 2013) and macrophyte structure and coverage (Crowder & Cooper, 1982). To avoid potential confounding effects of these variables, and to better segregate the role of climate in the trophic structure of fish communities, we selected lakes within a narrow size range, and we estimated their nutrient concentrations and macrophyte coverage (Table S1). The presence of exotic fish species might alter local fish community composition through predation and resource competition with native species (Fernando, 1991) and modify the native fish' dietary resources and trophic position (e.g. Mazumder et al., 2012). As this can potentially alter the body length-trophic position relation, we conducted all analyses using the dataset including all lakes as well as using a subset of lakes without exotic species.

Materials and methods

Sampling

17 lakes selected along a latitudinal gradient (5 – 55° S) in South America were sampled once during summer

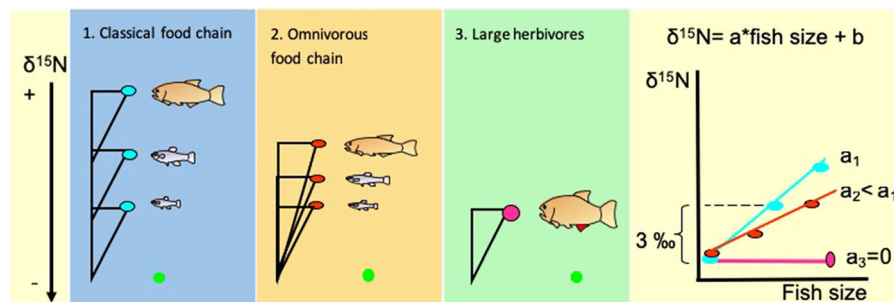


Fig. 1 Conceptual diagram depicting the relation between $\delta^{15}\text{N}$ (as an indicator of trophic position) and fish size. Dots of different colours indicate the $\delta^{15}\text{N}$ signal for each case. (1) In a classical food chain, large fish predate on smaller fish (blue dots), which feed on primary producers or consumers (green dot). This relation is expected to produce a slope with the characteristics of a_1 in the $\delta^{15}\text{N}$ vs fish size graph in the panel on the far right. (2) In a more omnivorous food web, fish forage on

different trophic levels, resulting in lower $\delta^{15}\text{N}$ signals of the larger fish (red dots), which is expected to produce a slope (a_2) less steep than a_1 . (3) When large fish are herbivorous, their $\delta^{15}\text{N}$ signal is similar to that of small fish with a similar diet, which is expected to produce a slope 0 ($a_3 = 0$). When intermediate-sized fish are piscivorous or omnivorous, this may result in $a < 0$ (not shown)

in Uruguay and Argentina or dry season in Brazil between November 2004 and March 2006 by the same team (Table S1). The temperature gradient corresponds to the average yearly air temperature at each lake location (Leemans & Cramer, 1991).

We collected integrated water samples at 20 random points in each lake. Two litres of each integrated sample were gathered in a bulk sample totalling 40 L. Filtration for various analyses was conducted directly after collection. Total phosphorus (TP) concentration in the water, which is an indicator of trophic state, was determined using a continuous flow analyser (Skalar Analytical BV) following NNI protocols (NNI, 1986) with the exception of UV/Persulfate destruction, which was not executed beforehand but integrated in the system. Submerged macrophyte coverage was estimated based on observations of macrophyte presence/absence at 20 random points in the lake combined with coverage estimations of macrophytes at 13–47 points (average 22) equally distributed on 3–8 parallel transects. The number of transects varied with the shape and size of the lake. Observations were made from a boat using a grapnel when water transparency prevented a clear view of the bottom. The percentage of the lake's volume filled with submerged vegetation (PVI) was determined analogously to classical studies (Canfield et al., 1984). First, we calculated the PVI of the individual sampling locations by multiplying the coverage percentage by the average length of the macrophytes divided by the depth. The PVI of the entire lake was then calculated by multiplying the area of the lake covered by macrophytes (m^2) by the average height of vegetation in the vegetated locations that were sampled (m) divided by the total volume of the lake (m^3).

The fish community was sampled in each lake using a stratified random approach with multi-mesh-size gillnets (Appelberg, 2000). Each net was 30 m long and 1.5 m deep and consisted of 12 different mesh sizes ranging from 5 to 55 mm (knot to knot), randomly distributed in 2.5 m sections. We recorded the length and weight and took a white muscle sample for stable isotopes analysis from at least one individual from each mesh size (if caught) for all species found. If the fish were too small to obtain enough material (< 6 cm), we used the whole body minus head, tail, skin and guts.

All samples were stored on ice immediately and frozen within a couple of hours. All remaining fish

caught were counted, measured (total length), and weighed. Fish abundance was estimated as the average catch among nets and expressed as catch per unit of effort (CPUE; individuals $net^{-1} 12 h^{-1}$). Bulk zooplankton was collected with a 68 μm mesh net towed at the water surface in at least two different points in the lake, integrating pelagic and macrophyte-dominated areas. The organisms were then transferred into flasks with filtered lake water to allow zooplankters evacuate their gut contents. Macroinvertebrates were collected from the lake shore and at deeper water sites where they adhered to submerged macrophytes, using a hand net.

Stable isotope analysis

For the carbon and nitrogen stable isotope analysis, fish muscle and zooplankton were freeze-dried and powdered. Macroinvertebrates were dried in an oven for about 48 h at 60°C. To remove carbonates from the macroinvertebrate sample, carapaces of crustaceans and shells of big molluscs were removed manually. Molluscs that were too small to handle manually were ground and treated by an acid (HCl). Subsequently, 0.5–2 mg aliquots (depending on sample type) were placed in tin capsules. The capsules were loaded into an elemental analyser for combustion (Carlo Erba EA). The carbon dioxide and nitrogen gas (N_2) generated from the combustion were purified in a gas chromatographic column and passed directly to the inlet of a gas isotope ratio mass spectrometer (Delta Plus, Finnigan Mat). One replicate sample and standards were analysed after every set of 10 samples. The carbon and nitrogen isotopic ratios were expressed as $\delta^{13}C$ and $\delta^{15}N$ in relation to Pee Dee Belemnite and atmospheric N_2 standards, respectively (Mendonça et al., 2013).

Data analysis

The relation between average and maximum body length with temperature and latitude was explored using simple regression analysis. Fish length range was calculated as the difference between the largest and smallest fish for each lake. To explore the relative importance of omnivory in our latitudinal gradient, fish were divided into four functional groups according to their diet (omnivores, detritivores, herbivores and piscivores) based on literature (Mazzeo et al.,

unpublished data). Non-parametric Spearman correlations (r_s) were applied to check relations between yearly average temperature, fish average and maximum length, fish length range, $\delta^{15}\text{N}$ and fish abundance by functional groups. To check if the presence of exotic species affected the relationship between body length and temperature, data were analysed including and excluding lakes with exotic species.

To test the association between the relative trophic position (as $\delta^{15}\text{N}$), body length and temperature, we compared a series of generalised linear models (GLM) depicting linear and quadratic terms for the explanatory variables as well as their interactions using lake as a covariable (Table 1). The use of lake as a covariable allows us to compare the relative trophic positions of fish from different lakes across a body length gradient, independently of a $\delta^{15}\text{N}$ baseline. We then compared the best model with other lake characteristics including area, depth, oxygen, nutrients and macrophyte coverage. To choose the more parsimonious model, we compared the different models using their Akaike Information Criteria (AIC) values and calculated their Akaike weights. According to Burnham and Anderson (2004), this can be interpreted as the “weight of evidence” in favour of a model.

For the comparison of trophic structure between different lakes, we applied Layman’s community-wide metrics based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope signatures (Layman et al., 2007; Jackson et al., 2011) to the food webs, including fish, macroinvertebrates and zooplankton but excluding basal resources (as data were available only for a subset of the lakes). The metrics analysed were: (1) carbon range ($\delta^{13}\text{C}$ range, CR), as a measure of the diversity of food sources exploited, and nitrogen range ($\delta^{15}\text{N}$ range; NR), as a measure of the vertical structure within each food web, (2) mean distance to centroid (CD), as a measure of the average degree of trophic diversity within a food web,

which is calculated as the average Euclidean distance of each species to the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ centroid, where the centroid is the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all species in the food web., and (3) trophic niche space calculated as Standard Ellipse Area (SEA). SEA is developed in a Bayesian framework, rendering this method unbiased with respect to sample size and thus more robust than the convex hull area-based TA metrics (Jackson et al., 2011). Multiple stepwise regression analysis was used to evaluate the influence of lake characteristics including area, depth, nutrients, macrophyte coverage, latitude, temperature, and fish community characteristics on the community-wide metrics.

Simple regression analyses were used to evaluate the relation between fish body length and the community-wide metrics with latitude and temperature. Data were transformed with $\log x$ or $\log x + 1$ to approach normality. All statistical analyses were performed using SPSS for Windows v. 15.0 (SPSS Inc., Chicago, IL, U.S.A.), except of the GLM analyses, which were conducted in R v. 3.4.1 with the GLM function, package ‘stats’ version 3.5.2. and the Layman’s metrics, which were calculated using the “SIBER package” in R.

Results

The average and maximum body length of individual fish in our lakes decreased towards the equator (Fig. 2A) and with increasing temperature (Fig. 2B). No significant Spearman correlations between fish length range (Table S1) and latitude ($r_s = 0.431$, $P = 0.084$) or temperature ($r_s = -0.438$, $P = 0.079$) occurred in any of the lakes. Also, in our dataset, species with documented omnivorous diets became relatively more abundant in warmer climates

Table 1 Summary of the different models tested with generalised linear model analysis. (+) indicates the terms included in the model

Models	Size	Size ²	Temp	Lake	Size*Temp	Size ² *Temp	Size*lake	Size ² *lake
Model 1	+		+	+				
Model 2	+		+	+	+			
Model 3	+	+	+	+				
Model 4	+	+	+	+	+	+		
Model 5	+	+	+	+			+	+
Model 6	+	+	+	+	+	+	+	+
Model 7	+	+		+			+	+

Size = fish average total length (cm),

Temp = temperature

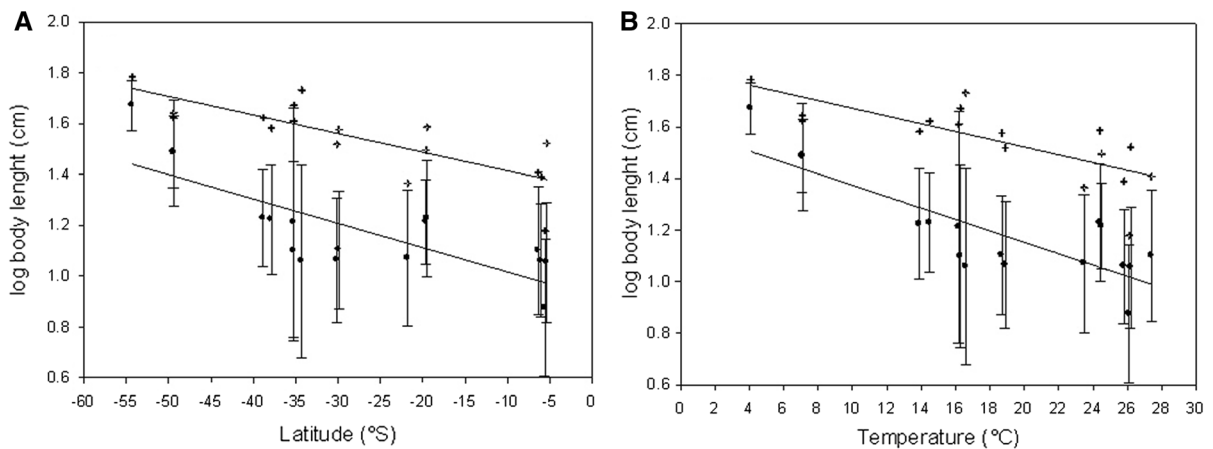


Fig. 2 Average log body length of individual fish in each lake relative to: **(A)** latitude ($R^2 = 0.61$, $P < 0.0001$, $n = 17$, regression line shown), + sign shows maximum log fish length (cm) for each lake ($R^2 = 0.63$, $P < 0.0001$, $n = 17$, regression line shown); **B** average yearly temperature ($R^2 = 0.68$,

$P < 0.0001$, $n = 17$, regression line shown), + sign shows maximum log fish length (cm) for each lake ($R^2 = 0.56$, $P < 0.0001$, $n = 17$, regression line shown). Bars indicate standard deviations

($r_s = 0.499$, $P = 0.04$ for CPUE of omnivorous fish and temperature) (Fig. S1).

The GLMs associating $\delta^{15}\text{N}$ with fish length (Size) and temperature (Temp) show that the inclusion of the interaction term Size*Temp increases the variance explained (Model 2; Table 2). The addition of a quadratic term for fish size alone (Size²) did not improve the model. However, the addition of the interaction (Size²*Temp) increased the explained variance further (Model 4; Table 2). Model 4 also shows the lowest AIC value and the largest Akaike weight (78%). It displays an increase of relative trophic position with fish body length in colder climates, changing to a less positive relationship with a lower slope at intermediate temperatures and finally to absent or even negative association at warmer temperatures (Table 3; Fig. 3).

The weaker relationship between the relative trophic position and fish body length in warmer regions is also reflected in the Spearman correlation coefficients of $\delta^{15}\text{N}$ versus length in the individual lakes as the coefficient decreases and even becomes negative at higher temperatures (Fig. S2). The inclusion of different environmental variables (TP, Area, Depth, PVI) to Model 4 did not result in a further lowering of the AIC values (AIC = 629 for TP, Area and Depth; AIC = 626.9 for PVI).

All community-wide Layman metrics calculated from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes showed a declining trend towards the equator and with increasing average yearly temperature, only significantly so for the proxies of trophic niche space (SEA) and mean distance to centroid (CD) (Fig. 4). In a stepwise multiple regression analysis with lake area, TP, PVI,

Table 2 Likelihood ratio test of the generalised linear models tested

Model	Residual df	Residual deviance	df	Deviance (χ^2)	P value	AIC	df	Akaike weights
1	161	309				647.9	20	$2.18 e^{-5}$
2	160	276	1	33.1	$1.81 e^{-5}$	629.5	21	$2.15 e^{-1}$ (21.5%)
3	160	305	0	-29.6		647.9	21	$2.21 e^{-5}$
4	158	266	2	39.5	$1.71 e^{-5}$	626.9	23	$7.84 e^{-1}$ (78.4%)
5	128	229	32	76.7	0.09	659.8	53	$5.8 e^{-8}$
6	127	229	31	37.2	0.92	661.8	54	$2.14 e^{-8}$

Table 3 Results of generalised linear model 4

Parameters	Estimate	SE	<i>t</i> value	<i>P</i> value
Intercept	332.6	197.6	1.7	0.09
Size	29.8	9.3	3.2	0.001
Size ²	− 9.3	3.9	− 2.4	0.02
Temp	17.1	10.4	− 1.6	0.11
Size*Temp	− 1.49	0.5	− 3.2	0.002
Size ² *Temp	0.49	0.2	2.4	0.02

Size = fish average total length (cm), Temp = the average yearly air temperature at the particular lake location (°C)

average and maximum fish length and fish species richness (S), and average yearly temperature we found that both temperature and TP contributed significantly to the variation in nitrogen range as a measure for vertical structure in the food web (NR: $R^2 = 0.54$, $F = 7.7$ $P = 0.006$; $- 0.20Temp + 0.64TP + 11.84$) and SEA ($R^2 = 0.66$, $F = 12.8$ $P = 0.001$; $- 0.52Temp + 0.44TP - 0.711$).

We found non-native species in 7 lakes of our dataset (Table S2). The exotic species usually represented less than 7% of the total CPUE (Table S2). However, even though the presence of exotics was not restricted to a specific climatic region or functional

Fig. 4 Layman metrics with latitude (left) and average yearly temperature (right). Linear regressions with latitude: nitrogen range (NR $R^2 = 0.15$, $P = 0.11$); carbon range (CR $R^2 = 0.06$, $P = 0.35$); Standard Ellipse Area (SEA $R^2 = 0.48$, $P = 0.002$); mean distance to centroid CD (CD $R^2 = 0.22$, $P = 0.05$). Linear regressions with temperature: NR ($R^2 = 0.15$, $P = 0.11$); CR ($R^2 = 0.05$, $P = 0.36$); SEA ($R^2 = 0.54$, $P = 0.00005$); CD (CD $R^2 = 0.30$, $P = 0.02$). Continuous lines indicate significant regressions

group, percentages tended to be higher in the coldest lakes (Table S2). Removing the lakes with exotic species resulted in a dataset with a smaller latitudinal and temperature range (Fig. S3). Analyses using the exotic-free dataset, showed a similar trend of decrease in body length with temperature as the full dataset, albeit this was non-significant in the case of average fish length. A reanalysis of the GLM Model 4 after eliminating lakes with exotic species did not change the AIC value (AIC = 626.95).

Discussion

The spatial patterns analysed in our study showed that the expected classical relation between body size and trophic position in fish communities disappeared in

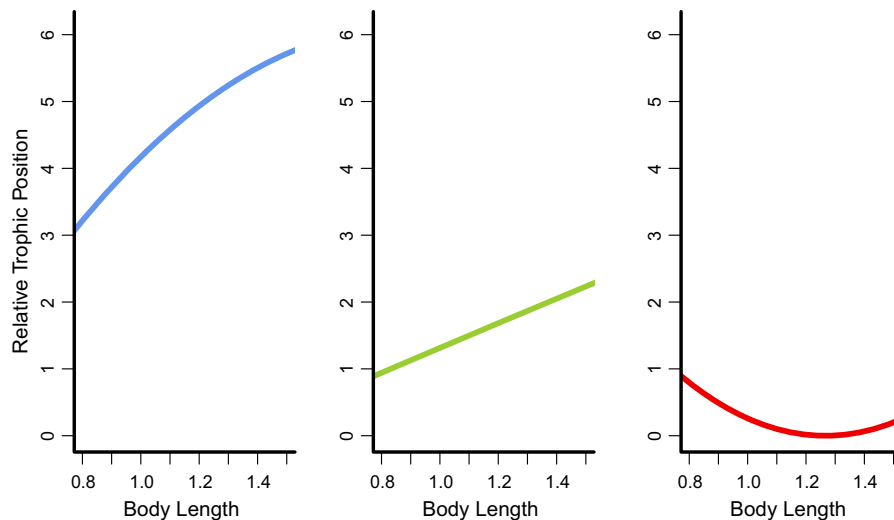
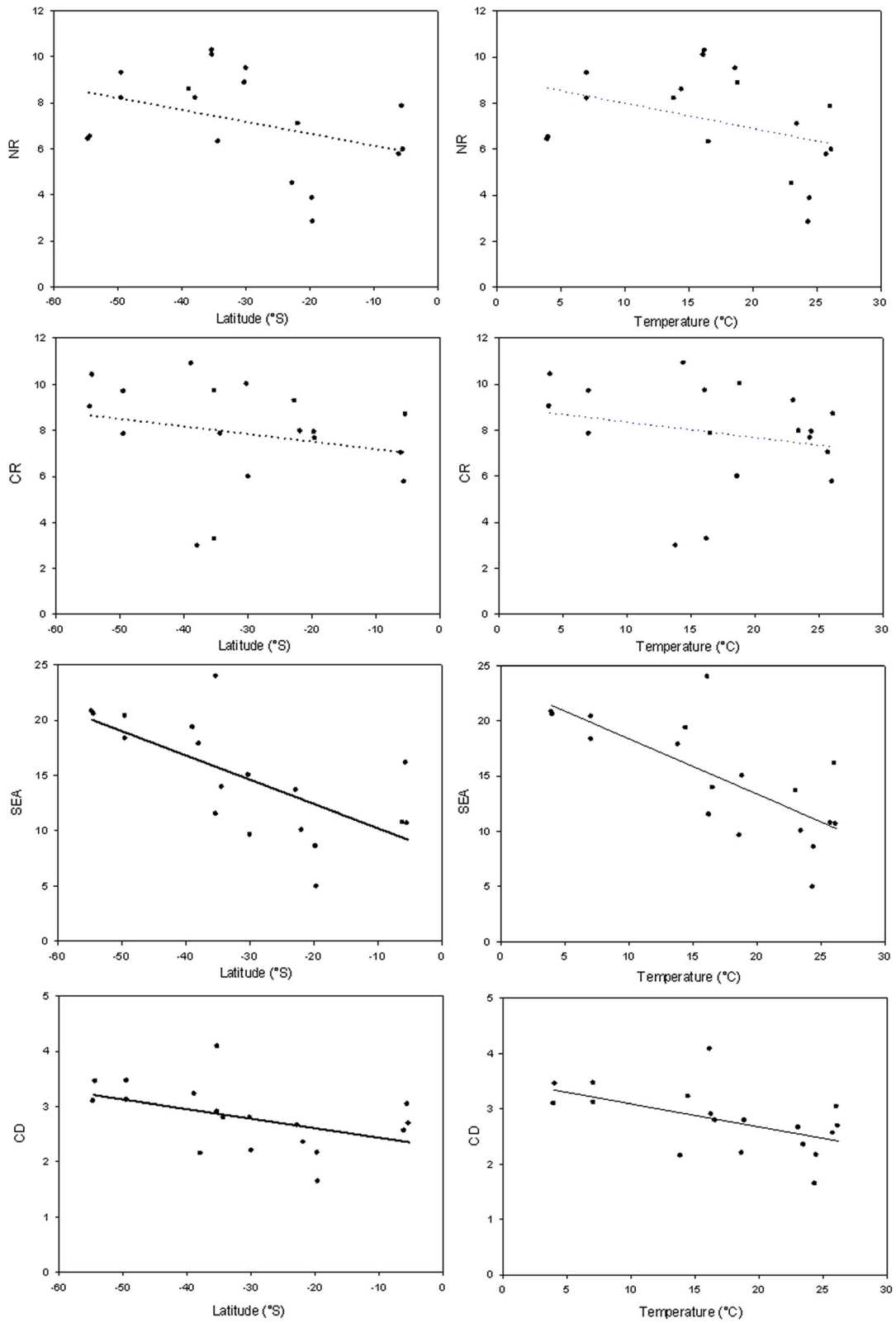


Fig. 3 Graphical representation of the generalised linear model $\delta^{15}N = \beta_0 + \beta_1Size + \beta_2(Size)^2 + \beta_3Temperature + \beta_4(-Size*Temp) + \beta_4(Size^2*Temp) + \beta_{5i}lake$ (Model 4) for the lowest temperatures (blue), the median (0.5 percentile, green) and the warmest (0.95 percentile, red) temperatures. The y-axis

shows the Relative Trophic Position which is not a direct measure of trophic level, but rather a lake-normalised relationship between fish average length and $\delta^{15}N$ (achieved by using lake as a covariable in the GLM analysis)



warmer lakes, where the relation between body length and relative trophic position flipped direction along the climatic gradient, being positive in cooler lakes and negative in warmer lakes. This is consistent with our hypothesis stating that large fish in cooler systems feed on smaller fish, whereas large fish in warmer systems would feed on lower trophic levels. The results agree with recent studies showing that larger freshwater fish forage lower in the food web in a warmer tropical climate than in cooler temperate climates (Iglesias et al., 2017; Dantas et al., 2019). The change in the relation between the relative trophic position and body length was, according to our results, not caused by a change in the length range of the fish, which did not differ along the temperature gradient. However, both the average and the maximum length of the fish decreased with increasing temperature (and decreased towards the equator) (Fig. 2). These results are in line with how temperature decreases the body size of ectotherms in warmer environments, as indicated by the significant interaction term between fish body length and temperature in the GLM analysis (Atkinson, 1994) and fit with earlier evidence that small fish tend to be dominant in warm lakes (Teixeira de Mello et al., 2009; Meerhoff et al., 2012). Moreover, the larger fish showed reduced $\delta^{15}\text{N}$ signals with increasing temperatures, as shown by the transition from a positive to an absent or even negative association between $\delta^{15}\text{N}$ and fish length near the equator. As revealed in other studies (e.g. Iglesias et al., 2017), the $\delta^{15}\text{N}$ range (NR) also tended to decrease towards the equator and with temperature, though the relationship was rather weak and not significant. Instead, NR increased significantly with TP in our study, perhaps because the relaxation of competition when food is abundant gives space for a higher degree of carnivory (Arim et al., 2007b). All other food web metrics also tended to decline from cold to warm lakes, but only significantly so for the mean distance to centroid (CD), which is a measure of the average degree of trophic diversity within a food web, and the trophic niche space calculated as SEA. Lower CD and SEA in the warm lakes may reflect that the species in our study, as well as the majority of subtropical and tropical fish species are omnivores and have a strong degree of feeding niche overlap (Arim et al., 2007a, b; Post and Takimoto, 2007). However, SEA also increased with TP, which might indicate more resource availability. The predominance of

omnivore fish affects the functioning of aquatic trophic webs at lower latitudes, particularly regarding the magnitude of their cascading trophic interactions. Studies have found that depending on their feeding mode (i.e. filter feeder or visual particulate feeder, Lazzaro, 1987) or biomass, omnivore fish can either control or promote algae growth, through complex direct and indirect feeding interactions (Lazzaro et al., 1992; Boveri & Quirós, 2007; Attayde & Menezes, 2008; Attayde et al., 2010), but the overall strength of the cascading effects is rather weak (Attayde & Menezes, 2008; Pujoni et al., 2016).

The introduction of exotic fish species is common in many aquatic systems and our lakes are no exception (Menezes et al., 2012). The analysis of the exotic-free dataset decreased the number of lakes and the temperature range to analyse, which made difficult to separate this effect from a possible exotic fish effect on the trophic web of each lake. Hence a larger dataset is needed to further study the possible effect of exotic fish introduction in warmer lakes. Despite this, we found no differences in the GLM selected, with this data subset. This suggests that the systematic relationship between trophic size structure and climate is not a result of variation in exotics along the climate gradient.

The key question remains: which factors explain the systematic change in size and trophic structure of freshwater fish communities with climate? One hypothesis is that energetic limitations play an increasingly important role at higher temperatures. Larger animals have higher energetic demands (McNab, 2002). Food availability decreases as we go up the food web due to the limited efficiency with which energy is transferred from one trophic level to the next, implying that the energetic demands of large animals are more easily met at lower trophic levels (Elton, 1927; Arim et al., 2007a). Since gape limitation tends to result in larger carnivores, energy limitation is expected to promote the opposite pattern (Arim et al., 2007a). In ectothermic animals such as fish, energy demands rise steeply with increasing temperature (Atkinson, 1994). Therefore, energy limitation is expected to rise with increasing temperature (at similar productivity), potentially explaining why in warmer lakes average and maximum body sizes are smaller and why omnivores that are potential predators prefer foraging on lower trophic levels in warm lakes. Another potential explanation is that plant

material may be more easily assimilated by fish at warmer temperatures, as suggested by an experimental study where adding animal matter to the diet of an omnivorous fish promoted performance at low but not at high temperatures (Behrens & Lafferty, 2007). Additionally, fish can consume a higher proportion of plant material in summer than in winter (González-Bergonzoni et al., 2016).

Our results thus indicate that the classical perception of the big fish eat the small does not hold for lakes in warm climates. Although this finding cannot be considered an absolute proof due to the number of lakes included in this study, it does suggest that the top-down control of small fish is likely to be substantially weaker in warmer than temperate conditions, which is further corroborated by the high numbers of small omnivorous fish recorded in warmer lakes compared with cooler lakes (Kosten et al., 2009; Teixeira de Mello et al., 2009). As a consequence, small fish may well exert a higher predation pressure on zooplankton, resulting in reduced top-down control on phytoplankton in warm climates (Jeppesen et al., 2009; Kosten et al., 2009). This shift in trophic structure is of more than academic interest as managing the trophic cascade in lakes is an important part of combating excessive phytoplankton growth (Jeppesen et al., 2012).

Acknowledgements We thank the SALGA (South America Lake Gradient Analysis) group for invaluable support before, during and after fieldwork. We deeply thank all students and researchers involved in the sampling. Special thanks to David da Motta Marques (UFRGS) for his great contribution to the project, Mario Vinicius Condini from the Laboratório de Ictiologia (FURG) for analysing the fish samples from lakes in Rio Grande do Sul, and Dr. Carolina Crisci (CURE-UdelaR) for statistical advice. We are grateful to all lake owners for giving us access to the lakes and valuable information. We thank the reviewers for their thoughtful comments towards improving our manuscript.

Author contributions MS, GL, SK, EJ and NM contributed to the conceptual and methodological development of the project within the framework of the ‘South American Lake Gradient Analysis’ project (SALGA). GL and SK co-coordinated the fieldwork. GL, SK, RM, EJ, NM, JLA, DMM and MS conducted the fieldwork. RM analysed the stable isotope samples. FTM, JHG, JLA and GL analysed the fish samples. MA, TS and GC contributed with data analysis and theoretical background. GL, EJ, SK and MS wrote the manuscript. All authors discussed the results, commented and approved the manuscript.

Funding This research was financed by The Netherlands Organization for Scientific Research (NWO) Grant W84-549 and WB84-586, The National Geographic Society Grant 7864-5; in Brazil by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) Grants 480122, 490409, 311427; in Uruguay by PEDECIBA, Maestría en Ciencias Ambientales, Aguas de la Costa S.A., Banco de Seguros del Estado, and the SNI of the Agencia Nacional de Investigación e Innovación (ANII). EJ was supported by the MARS project (Managing Aquatic ecosystems and water Resources under multiple Stress) funded under the 7th EU Framework Programme, Theme 6 (Environment including Climate Change), Contract No.: 603378 (<http://www.mars-project.eu>) and the TÜBITAK program 2232 (Project 118C250). MA was supported by FONDAP-FONDECYT to CASEB.

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

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed by the authors.

Informed consent Not applicable.

References

- Abell, J. M., D. Özkundakci, D. P. Hamilton & P. Reeves, 2020. Restoring shallow lakes impaired by eutrophication: approaches, outcomes, and challenges. *Critical Reviews in Environmental Science and Technology*. <https://doi.org/10.1080/10643389.2020.1854564>.
- Appelberg, M., 2000. Swedish Standard Methods for Sampling Freshwater Fish with Multi-mesh Gillnets. *Fiskeriverket Information I*, 3–32 Karl Olov Öster, Drottningholm.
- Arim, M., F. Bozinovic & P. A. Marquet, 2007a. On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis. *Oikos* 116: 1524–1530.
- Arim, M., P. A. Marquet & F. M. Jaksic, 2007b. On the relationship between productivity and food chain length at different ecological levels. *The American Naturalist* 169: 62–72.
- Arim, M., S. R. Abades, G. Laufer, M. Loureiro & P. A. Marquet, 2010. Food web structure and body size: trophic position and resource acquisition. *Oikos* 119: 147–153.
- Attayde, J. L., G. Corso & A. Araujo, 2010. Omnivory by planktivores stabilizes plankton dynamics, but may either

- promote or reduce algal biomass, 2010. *Ecosystems* 13: 410–420.
- Atkinson, D., 1994. Temperature and organism size: a biological law for ectotherms? *Advances in Ecological Research* 25: 1–58.
- Behrens, M. D. & K. D. Lafferty, 2007. Temperature and diet effects on omnivorous fish performance: implications for the latitudinal diversity gradient in herbivorous fishes. *Canadian Journal of Fisheries & Aquatic Sciences* 64: 867–873.
- Boveri, M. B. & R. Quirós, 2007. Cascading trophic effects in panmpean shallow lakes: results of a mesocosm experiment using two coexisting fish species with different feeding strategies. *Hydrobiologia* 584: 215–222.
- Burnham, K. P. & D. R. Anderson, 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33: 261–304.
- Brett, M. T. & C. R. Goldman, 1996. A meta-analysis of the freshwater trophic cascade. *Proceedings of the National Academy of Science USA* 93: 7723–7726.
- Brose, U., T. Jonsson, E. L. Berlow, P. Warren, C. Banasek-Richter, L.-F. LixBersier, J. L. Blanchard, T. Brey, S. R. Carpenter, M.-F. CattinBlandenier, L. Cushing, H. A. Dawah, T. Dell, F. Edwards, S. Harper-Smith, U. Jacob, M. E. Ledger, N. D. Martinez, J. Memmott, K. Mintenbeck, J. K. Pinnegar, B. C. Rall, T. S. Rayner, D. C. Reuman, L. Ruess, W. Ulrich, R. J. Williams, G. Woodward & J. E. Cohen, 2006. Consumer–resource body-size relationships in natural food webs. *Ecology* 87: 2411–2417.
- Canfield, D. E., Jr., J. V. Shireman, D. E. Colle, W. T. Haller, C. E. Watkins & M. J. Maceina, 1984. Prediction of chlorophyll-a concentrations in Florida lakes: importance of aquatic macrophytes. *Canadian Journal of Fisheries & Aquatic Sciences* 41: 497–501.
- Carpenter, S. R. & J. F. Kitchell (eds), 1996. *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge.
- Cohen, J. E., S. L. Pimm, P. Yodzis & J. Saldaña, 1993. Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology* 62: 67–78.
- Crowder, L. B. & W. E. Cooper, 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63: 1802–1813.
- Dantas, D. D. F., A. Caliman, R. D. Guariento, R. Angelini, L. S. Carneiro, S. M. Q. Lima, P. A. Martinez & J. L. Attayde, 2019. Climate effects on fish body size-trophic position relationship depend on ecosystem type. *Ecography* 42: 1579–1586.
- Elton, C., 1927. *Animal Ecology*, University of Chicago Press, Chicago.
- Fernando, C. H., 1991. Impacts of fish introductions in tropical Asia and America. *Canadian Journal of Fisheries and Aquatic Science* 48(1): 24–32.
- Frank, K. T., B. Petrie, J. S. Choi & W. C. Leggett, 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308: 1621–1623.
- González-Bergonzoni, I., M. Meerhoff, T. A. Davidson, F. Teixeira-de Mello, A. Baattrup-Pedersen & E. Jeppesen, 2012. Meta-analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. *Ecosystems* 15: 492–503.
- González-Bergonzoni, I., E. Jeppesen, N. Vidal, F. Teixeira-de Mello, G. Goyenola, A. López-Rodríguez & M. Meerhoff, 2016. Potential drivers of seasonal shifts in fish omnivory in a subtropical stream. *Hydrobiologia* 768: 183–196.
- Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer, & E. van Donk, 1990. Biomanipulation-tool for water management. In Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer & E. van Donk (Eds) *Developments in Hydrobiologia*. 628 pp.
- Havens, K. E., A. C. Elia, M. I. Taticchi & R. S. I. I. I. Fulton, 2009. Zooplankton-phytoplankton relationships in shallow subtropical versus temperate lakes Apopka (Florida, USA) and Trasimeno (Umbria, Italy). *Hydrobiologia* 628: 165–175.
- Iglesias, C., M. Meerhoff, L. S. Johansson, I. González-Bergonzoni, N. Mazzeo, J. P. Pacheco, F. Teixeira-de Mello, G. Goyenola, T. L. Lauridsen, M. Søndergaard, T. M. Davidson & E. Jeppesen, 2017. Stable isotope analysis confirms substantial differences between subtropical and temperate shallow lake food webs. *Hydrobiologia* 784(1): 111–123.
- Jackson, A. L., R. Inger, A. C. Parnell & S. Bearhop, 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* 80: 595–602.
- Jennings, S. & J. van der Molen, 2015. Trophic levels of marine consumers from nitrogen stable isotope analysis: estimation and uncertainty. *ICES Journal of Marine Science* 72: 2289–2300.
- Jeppesen, E., M. Søndergaard, N. Mazzeo, M. Meerhoff, C. C. Branco, V. Huszar & F. Scasso, 2005. Lake restoration and biomanipulation in temperate lakes: relevance for subtropical and tropical lakes. Chapter 11. In Reddy, M. V. (ed), *Tropical Eutrophic Lakes: Their Restoration and Management Science Publisher, INC, Enfield*: 331–359.
- Jeppesen, E., M. Meerhoff, B. A. Jacobsen, R. S. Hansen, M. Søndergaard, J. P. Jensen, T. L. Lauridsen, N. Mazzeo & C. W. C. Branco, 2007. Restoration of shallow lakes by nutrient control and biomanipulation – the successful strategy varies with lake size and climate. *Hydrobiologia* 581: 269–285.
- Jeppesen, E., B. Kronvang, M. Meerhoff, M. Søndergaard, K. M. Hansen, H. E. Andersen, T. L. Lauridsen, L. Liboriussen, M. Beklioglu, A. Ozen & J. E. Olesen, 2009. Climate change effects on runoff, catchment phosphorus loading and lake ecological state, and potential adaptations. *Journal of Environmental Quality* 38: 1930–1941.
- Jeppesen, E., M. Søndergaard, T. L. Lauridsen, T. A. Davidson, Z. Liu, N. Mazzeo, C. Trochine, K. Özkan, H. S. Jensen, D. Trolle, F. Starling, X. Lazzaro, L. S. Johansson, R. Bjerring, L. Liboriussen, S. E. Larsen, F. Landkildehus & M. Meerhoff, 2012. Biomanipulation as a restoration tool to combat eutrophication: recent advances and future challenges. *Advances in Ecological Restoration* 47: 411–487.
- Kosten, S., G. Lacerot, E. Jeppesen, D. da Motta Marques, E. H. van Nes, N. Mazzeo & M. Scheffer, 2009. Effects of submerged vegetation on water clarity across climates. *Ecosystems* 12: 1117–1129.
- Layman, C. A., K. O. Winemiller, D. A. Arrington & D. B. Jepsen, 2005. Body size and trophic position in a diverse tropical food web. *Ecology* 86: 2530–2535.

- Layman, C. A., D. Albrecht Arrington, C. G. Montaña & D. M. Post, 2007. Can stable isotopes ratios provide for community-wide measurements of trophic structure. *Ecology* 88: 42–48.
- Lazzaro, X., 1987. A review of planktivorous fishes: their evolution, feeding, behaviours, selectivities, and impacts. *Hydrobiologia* 146: 97–167.
- Lazzaro, X., 1997. Do the trophic cascade hypothesis and classical biomanipulation approaches apply to tropical lakes and reservoirs? *Verhandlungen Der Internationalen Vereinigung Für Theoretische Und Angewandte Limnologie* 26: 719–730.
- Lazzaro, X., R. W. Drenner, R. A. Stein & J. D. Smith, 1992. Planktivores and plankton dynamics: effects of fish biomass and planktivore type. *Canadian Journal of Fisheries and Aquatic Science* 49: 1466–1473.
- Leemans, R. & W. Cramer, 1991. The IIASA database for mean monthly values of temperature, precipitation and cloudiness on a global terrestrial grid. Research Report RR-91-18. International Institute of Applied Systems Analyses, Laxenburg, pp. 61.
- Mazumder, D., M. Johansen, N. Saintilan, J. Iles, T. Kobayashi, L. Knowles & L. Wen, 2012. Trophic shifts involving native and exotic fish during hydrologic recession in floodplain wetlands. *Wetlands* 32: 267–275.
- McNab, B. K., 2002. *The Physiological Ecology of Vertebrates*, Cornell University Press, New York.
- Meerhoff, M., J. M. Clemente, F. Teixeira de Mello, C. Iglesias, A. R. Pedersen & E. Jeppesen, 2007. Can warm climate-related structure of littoral predator assemblies weaken clear water state in shallow lakes? *Global Change Biology* 13: 1888–1897.
- Meerhoff, M., F. Teixeira-de Mello, C. Kruk, C. Alonso, I. González-Bergonzoni, J. P. Pacheco, G. Lacerot, M. Arim, M. Beklioglu, S. Brucet, G. Goyenola, C. Iglesias, N. Mazzeo, S. Kosten & E. Jeppesen, 2012. Environmental warming in shallow lakes: a review of potential changes in community structure as evidenced from space-for-time substitution approaches. *Advances in Ecological Research* 46: 259–349.
- Mendonça, R., S. Kosten, G. Lacerot, N. Mazzeo, F. Roland, J. P. Ometto, E. A. Paz, C. P. Bove, N. C. Bueno, J. H. C. Gomes & M. Scheffer, 2013. Bimodality in stable isotope composition facilitates the tracing of carbon transfer from macrophytes to higher trophic levels. *Hydrobiologia* 710: 205–218.
- Menezes, R. F., J. L. Attayde, G. Lacerot, S. Kosten, L. Coimbra e Souza, L. S. Costa, E. H. Van Nes & E. Jeppesen, 2012. Lower biodiversity of native fish but only marginally altered plankton biomass in tropical lakes hosting introduced piscivorous *Cichla cf. ocellaris*. *Biological Invasions* 14: 1353–1363.
- NNI, 1986. Water - Photometric determination of the content of dissolved orthophosphate and the total content of phosphorus compounds by continuous flow analysis, p. 8. Normcommissie 390 147 “Waterkwaliteit”, Nederlands Normalisatie-instituut.
- Otto, S. B., C. R. Björn & U. Brose, 2007. Allometric degree distributions facilitate food-web stability. *Nature* 450: 1226–1230.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese & F. Torres Jr., 1998. Fishing down marine food webs. *Science* 279: 860–863.
- Post, D. & G. Takimoto, 2007. Proximate structural mechanisms for variation in food-chain length. *Oikos* 116: 775–782.
- Post, D. M., M. L. Pace & N. G. Hairston, 2000. Ecosystem size determines food-chain length in lakes. *Nature* 405: 1047–1049.
- Pujoni, D. G. F., P. M. Maia-Barbosa, F. A. Rodrigues Barbosa, C. R. Jr. Fragoso & E. H. van Nes, 2016. Effects of food web complexity on top-down control in tropical lakes. *Ecological Modelling* 320: 358–365.
- Romanuk, T. N., A. Hayward & J. A. Hutchings, 2011. Trophic level scales positively with body size in fishes. *Global Ecology and Biogeography* 20: 231–240.
- Scheffer, M., S. R. Carpenter & B. De Young, 2005. Cascading effects of overfishing marine systems. *Trends in Ecology & Evolution* 20: 579–581.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel & K. Roy, 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics* 40: 245–269.
- Søndergaard, M., L. Liboriussen, A. R. Pedersen & E. Jeppesen, 2008. Lake restoration by fish removal: long-term effects in 36 Danish lakes. *Ecosystems* 11: 1291–1305.
- Takimoto, G. & D. M. Post, 2013. Environmental determinants of food-chain length: a meta-analysis. *Ecological Research* 28: 675–681.
- Takimoto, G., D. Post, D. Spiller & R. Holt, 2012. Effects of productivity, disturbance, and ecosystem size on foodchain length: insights from a metacommunity model of intraguild predation. *Ecological Research* 27: 481–493.
- Teixeira de Mello, F., M. Meerhoff, Z. Pekcan-Hekim & E. Jeppesen, 2009. Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. *Freshwater Biology* 54: 1202–1215.
- Wootton, J. T. & M. P. Oemke, 1992. Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream. *Environmental Biology of Fishes* 35: 311–319.
- Worm, B. & R. A. Myers, 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84: 162–173.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.