



Energy-based top-down and bottom-up relationships between fish community energy demand or production and phytoplankton across lakes at a continental scale

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Abstract

Fish community feeding and production rates may differ between lakes despite similar fish biomass levels because of differences in size structure and local temperature. Therefore, across-lake comparisons of the strength and direction of top-down and bottom-up fish–phytoplankton relationships should consider these factors. We used the metabolic theory of ecology to calculate size- and temperature-corrected community energy demand (CED_{om}) and community production (CP) of omnivorous fishes in 227 European lakes from major habitat types (MHTs) of polar freshwaters, temperate floodplain rivers and wetlands, and temperate coastal rivers. We related CED_{om} with total phosphorus (TP)-corrected chlorophyll *a* (Chl *a*) concentrations to evaluate a potential top-down directed trophic cascade from fish to phytoplankton. Furthermore, we related Chl *a* with CP to demonstrate potential bottom-up effects of phytoplankton on fish. For both analyses, we added the CED of piscivorous fishes (CED_{pi}) as a predictor to account for potential predation effects on the omnivorous fish community. CED_{om} was weakly positively related with TP-corrected Chl *a*, but the strength of the relationship differed between MHTs. In contrast, CP was consistently positively related with Chl *a* in the entire dataset. CED_{pi} did not contribute to top-down or bottom-up relationships. The application of metabolic variables characterizing fish community feeding and production rates makes these results robust because the approach accounted for the usually neglected effects of fish size and temperature in across-lake comparisons. Our results suggest that bottom-up effects from phytoplankton on fish secondary production in lakes are substantially stronger than top-down effects from fish on phytoplankton biomass.

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Trophic cascades, that is, biotic interactions that affect more than just two adjacent trophic levels, can strongly modify the functioning of ecosystems (Carpenter et al. 1985). In lakes, a top-down trophic cascade can be induced by high abundances of zooplanktivorous fish, which exert a strong predation

pressure on zooplankton, with the consequence that phytoplankton biomass increases (Carpenter et al. 1985; Burghardt and Schmitz 2015). In turn, a bottom-up trophic cascade can be expected if high nutrient concentrations favor high phytoplankton, zooplankton, and ultimately high fish biomasses (McQueen et al. 1986; Jeppesen et al. 1999). Single-lake studies often find strong top-down cascades (Tonn et al. 1992; Carpenter 2001; Potthoff et al. 2008), and bioenergetics models have helped to quantify the consumption of zooplankton by planktivorous fish (e.g., Luecke et al. 1990). However, across-lake comparisons have shown ambiguous results where the highest phytoplankton biomasses are not always found in lakes characterized by the highest fish biomasses (Persson et al. 1992; Brett and Goldman 1996; Drenner and Hambright 2002; Mehner 2010; Detmer et al. 2017), suggesting that the typically strong negative interactions between planktivorous fish and zooplankton (Jeppesen et al. 2003) do not always cascade to phytoplankton. In contrast, strong bottom-up effects have in particular been described for the trophic link between phytoplankton and zooplankton, whereas the effects of high phytoplankton biomass usually become weaker at the fish trophic level (McQueen et al. 1986; Brett and Goldman 1996; Hulot et al. 2014).

One reason for the differing outcome of the comparative approaches may be the effects of confounding factors on lake-specific cascades. In addition to lake depth or area (Olin et al. 2002; Garcia et al. 2006), the size structure of the fish community may be important (Brose et al. 2006; O’Gorman et al. 2010; DeLong and Walsh 2015; Hatton et al. 2015). Both predation and production rates of fish scale with fish size (Brown et al. 2004). In particular, the fish production rate per unit biomass (P/B) ratio varies inversely with size-at-maturity and longevity and is therefore specific for species and populations (Randall and Minns 2000). Hence, similar fish abundances or biomasses in two lakes may translate into strongly differing energetic demands or production rates of the communities if these differ notably in size structure. A second strong effect on fish consumption and production rates can be expected from differences in local temperature (Brown et al. 2004). However, local temperature has rarely been taken into account when comparing the strength of trophic cascades between lakes even though several studies suggest that top-down control by fish increases from temperate to (sub)tropical lakes, leading to higher chlorophyll *a*:total phosphorus (Chl *a* : TP) ratios in warm lakes (Gyllström et al. 2005; Meerhoff et al. 2012).

The metabolic theory of ecology (MTE; Brown et al. 2004)—a quantitative theory that addresses the temperature and size dependency of almost all ecological rates—provides a concept that facilitates integration of fish body size distribution, biomass, and temperature into a single metric, thus supporting an evaluation of the strength of trophic cascades across lakes. The MTE summarizes the relationships of metabolic rate, development time, population growth rate, or rate of molecular evolution with body mass (Brown et al. 2004). It also positively and

exponentially relates almost all biological activity rates to temperature, including biochemical reactions and metabolic rates (Brown et al. 2004). Accordingly, the MTE allows standardizing biological rates across taxa, organismal sizes, and locations. Hence, MTE-standardized rates are assumed to be robust against the effect of confounding factors, which otherwise typically may bias large-scale comparisons of trophic cascades. Linear and unimodal responses of consumption rates of ectotherms to temperature are possible (Knies and Kingsolver 2010; Englund et al. 2011), but the linear form is more appropriate when the lake temperatures are below the thermal optima of the ectotherms, which is also the case in this study.

Here, we apply the MTE framework to determine the strength and directionality of top-down and bottom-up trophic cascades between fish and phytoplankton in lakes at a continental scale in Europe. Specifically, we calculated the size- and temperature-corrected energy demand of the omnivorous fish community (i.e., community energy demand, CED_{om}) (Nelson et al. 2017a) and the size- and temperature-corrected production of the omnivorous fish community (i.e., community production, CP_{om}) (Nelson et al. 2017b) to evaluate whether phytoplankton biomass measured as Chl *a* concentration is a predictor of omnivorous fish CP_{om} (bottom-up) or a response to omnivorous fish CED_{om} (top-down) across 227 European lakes. The CED of piscivorous fish (CED_{pi}) was added to both top-down and bottom-up models as explanatory variable to account for potential control of omnivorous fish communities by fish predation. For the relationships with fish CED_{om} , we used the residual variance from the Chl *a* vs. TP regression as an approximation of phytoplankton biomass not explained by TP. This large dataset accounts for substantial variation in environmental conditions between the lakes (Brucet et al. 2013). It does not contain information on zooplankton biomasses and size distributions because zooplankton was excluded as biological quality element in the European Water Framework Directive, 2000/60/EC, and we can, therefore, only evaluate the indirect effects between fish and phytoplankton.

We hypothesized that metabolic metrics of the fish community would reveal both top-down and bottom-up trophic cascades in lakes. The integration of fish abundance and size structure into CED or CP, while accounting for local temperature differences between lakes, may allow for a more systematic exploration of indirect food web interactions between fish and phytoplankton than the commonly applied metrics of fish abundance or biomass. We expected that a high energy demand of the omnivorous fish community, expressed as high fish CED_{om} , would cascade down to phytoplankton. Therefore, at high CED_{om} , the realized phytoplankton biomass (measured through the residuals of the Chl *a* to TP relationship: TP-corrected Chl *a*) was expected to be higher than at low CED_{om} . In turn, we expected that phytoplankton biomass (Chl *a*) would also be a good predictor of fish community production (CP_{om}) so that a bottom-up trophic cascade would cause increased production of

the fish community in phytoplankton-rich lakes, as described in terms of community composition and biomass (Bruce et al. 2013; Arranz et al. 2015; Matsuzaki et al. 2018).

Material and methods

Fish database and sampling

We used the dataset from the EU project WISER (Water bodies in Europe: Integrative Systems to assess Ecological status and Recovery) created during a European Water Framework Directive intercalibration process, encompassing 1922 lakes (Argillier et al. 2013; Bruce et al. 2013; Mehner et al. 2017), and data from 57 lakes located in Western and Central Turkey (Boll et al. 2016). Among these lakes, Chl *a* concentrations and fish size distributions were available only for 227 lakes located in 10 countries (Czech Republic, Estonia, France, Germany, Italy, Norway, Slovenia, Sweden, Turkey, and United Kingdom) along a latitudinal gradient between 36.7 N and 67.1 N and a longitudinal gradient between 4.2 W and 36.2 E (Fig. 1). The selected lakes covered three freshwater major habitat types (MHTs: polar freshwaters, temperate floodplain rivers and wetlands, and temperate coastal rivers, Fig. 1); these reflect groupings of ecoregions with similar biological, chemical, and physical characteristics and are equivalent to biomes for terrestrial systems (<http://feow.org/mht>). For all lakes, fish abundance and biomass, individual fish body size distribution, Chl *a*, and TP concentrations were available (Table 1).

Fish communities in lakes were sampled using a standardized procedure according to the European Committee for

Table 1. Overview of variable characteristics of the lakes included in the study. $BPUE_{om}$ and $BPUE_{pi}$ refer to biomass per unit effort of omnivorous and piscivorous fish, $NPUE_{om}$ and $NPUE_{pi}$ to number per unit effort of omnivorous and piscivorous fish, Chl *a* refers to chlorophyll *a* and Total P refers to total phosphorus.

	Median	1st quartile	3rd quartile
$BPUE_{om}$ (g net ⁻¹ night ⁻¹)	1798	1067	2635
$BPUE_{pi}$ (g net ⁻¹ night ⁻¹)	501	298	849
$NPUE_{om}$ (fish net ⁻¹ night ⁻¹)	41	21	91
$NPUE_{pi}$ (fish net ⁻¹ night ⁻¹)	3	2	6
Lake altitude (m a.s.l.)	81	41	257
Lake area (km ²)	1.1	0.5	2.5
Lake maximum depth (m)	14	7	25
Lake mean depth (m)	5	3	9
pH	8.0	6.9	8.4
Chl <i>a</i> (mg m ⁻³)	6.6	2.9	17.0
Total P (mg m ⁻³)	19.5	8.2	49.7
Mean annual air temperature (°C)	8.3	6.6	9.1

Standardization (Appelberg et al. 1995; CEN 14757: 2015) during late summer and early autumn along the years 1993 to 2012. The fish were caught using benthic Nordic multi-mesh gillnets (length 30 m, height 1.5 m, 12 mesh-size panels of 2.5 m length each, knot to knot dimensions in a geometric

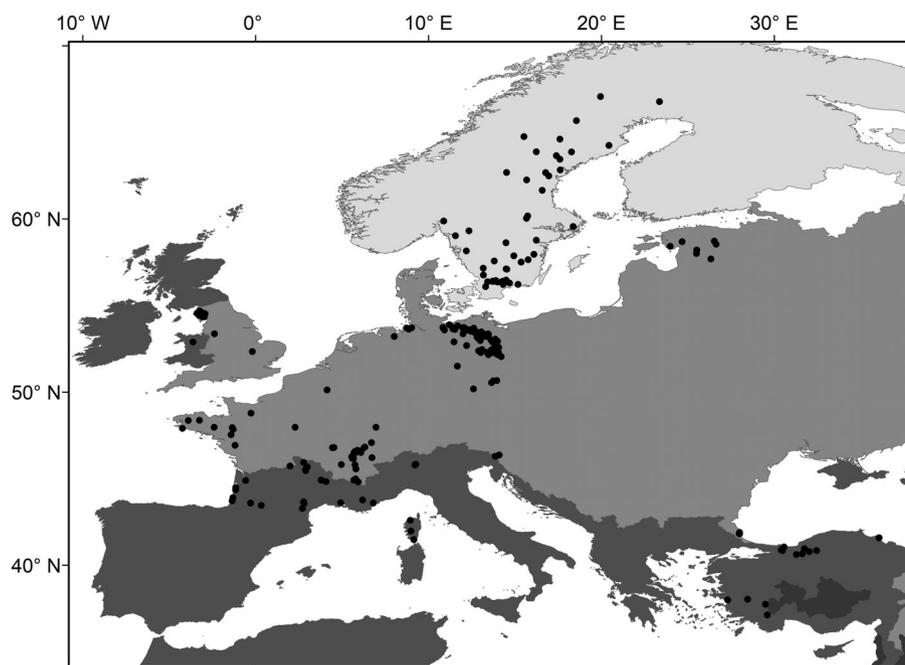


Fig. 1. Map of the 227 lakes studied. The lakes are located across three freshwater major habitat lake types (MHT) of the world (<http://feow.org/mht>)—light gray area: polar freshwaters ($n = 50$), medium gray area: temperate floodplain rivers and wetlands ($n = 135$), dark gray area: temperate coastal rivers ($n = 42$).

scale between 5 and 55 mm) and pelagic multi-mesh gillnets (length 27.5 m, height 3 or 6 m, similar mesh-size panels as the benthic ones without the 5 mm mesh panel) designed to catch lake fish communities in a representative way with respect to fish abundance, fish species composition, and size distribution (Appelberg et al. 1995; CEN 14757: 2015). The total number of benthic and pelagic nets per lake and their distribution across the depth zones followed the European Standard. Pelagic nets were set only in lakes with more than 6 m maximum depth (CEN 14757: 2015). The nets were left approximately 12 h overnight to include both evening and morning phases of high fish activity (Prchalová et al. 2010). All fish caught were individually measured (rounded to cm total length, TL) and directly weighed (g wet mass, WM) in most cases. For some lakes, WM was calculated from TL by regional species-specific regressions. For more details, see Bruce et al. (2013).

We split the fish species into omnivores and piscivores. Piscivores undergo ontogenetic niche shifts, and hence piscivory is the dominant feeding strategy only beyond a certain fish size. Therefore, all individuals $> 2^5 = 32$ g (~ 15 cm total length) of common eel (*Anguilla anguilla*), asp (*Aspius aspius*), pike (*Esox lucius*), ide (*Leuciscus idus*), largemouth bass (*Micropterus salmoides*), perch (*Perca fluviatilis*), Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), lake charr (*Salvelinus umbla*), pikeperch (*Sander lucioperca*), Wels catfish (*Silurus glanis*), European chub (*Squalius cephalus*), Aegean chub (*Squalius fellowesii*), *Squalius* spp., and rainbow trout (*Oncorhynchus mykiss*) were defined as piscivores according to Mehner et al. (2016). Smaller individuals of these piscivorous species and all other fishes were considered omnivores but with major contributions of zooplankton to their diet. The list of fish species present in each lake, the biomass per unit effort (BPUE), and maximum mass and length are shown in Table S5.

TP (mg m^{-3}) was measured as the mean of a minimum of four samples taken in the sampling year (one for each season) for all lakes. Mean annual air temperature ($^{\circ}\text{C}$) per lake was calculated using the Climatic Research Unit model proposed by New et al. (2002). This specific model can obtain a spatial resolution of $10'$ latitude and (or) longitude and takes into account elevational differences between stations. The close coupling between air temperature and surface water temperature (McCombie 1959; Livingstone and Lotter 1998) facilitates the use of mean annual air temperature at the lake location as an adequate approximation of mean surface water temperature across large geographic scales.

Variables characterizing anthropogenic pressures were available only for a small subset of the lakes (Table S4) and consequently could not be included into the top-down and bottom-up models. Land use in the lake catchment was estimated using Corine Land Cover, population density in the catchment according to expert judgment on a four-step scale (low, medium, high, and very high), and shoreline bank

modification according to expert judgment on a ranked scale of five classes (1: no modification to 5: highly modified). More information can be found in Bruce et al. (2013).

Fish metrics

Size spectrum slopes were modeled to calculate the metabolic metrics of the omnivorous fish communities. Size groups of the omnivorous fishes were based on \log_2 class intervals of wet mass (g). The smallest individuals of ≤ 8 g (i.e., fish in first year of life) were summed in the first wet mass class (2^1 – 2^3 g) because it has been shown that gillnets consistently underestimate small fish (Prchalová et al. 2009; Arranz et al. 2015). All fish > 4096 g were also summed in the last wet mass class (2^{13} g) due to the underestimation of very large fish in the catches (Prchalová et al. 2009; Arranz et al. 2015; Šmejkal et al. 2015). The linear size spectrum was calculated for each omnivorous fish community through ordinary least square regression between the \log_2 midpoint of size classes (axis x) and the \log_2 of the total number or biomass per size class (axis y). This relationship is usually described by a decreasing linear function in fish numbers or biomass as midpoint size class increases, and the size spectrum slope was used to calculate the metabolic metrics of the fish community (see below).

Energy-based fish community attributes

We estimated the metabolic rate (I_i) of an individual i relating its body mass (M , g) with temperature (T , K) through the equation:

$$I_i = I_0 [M]^{3/4} e^{-E/kT}, \quad (1)$$

where I_0 ($e^{19.65}$ W $\text{g}^{-3/4}$) is a normalization constant independent of body size and temperature (Brown et al. 2004), E (0.65 eV) is the activation energy of cellular respiration, k ($8.6173 \cdot 10^{-5}$ eV K^{-1}) is the Boltzmann constant, and T is absolute air temperature in K (constrained to a temperature range of 0–40 $^{\circ}\text{C}$).

To extrapolate the metabolic rate of an individual fish to the whole omnivorous community (CED_{om} , Nelson et al. 2017a) by accounting for local size distribution, we used the abundance per size class as predicted from slope and intercept of the lake-specific size spectrum multiplied by the metabolic rate of a midpoint-sized fish and finally summed the metabolic rates across all size classes:

$$\text{CED} = \sum (I_i \times N_i), \quad (2)$$

(unit $\text{W net}^{-1} \text{night}^{-1}$), where I_i is the metabolic rate of a midpoint sized fish (Eq. 1) and N_i is the predicted abundance of that size class as calculated from the slope and intercept of the local size-abundance relationship. To calculate the CED_{om} , we included all fish ≥ 1 g distributed over \log_2 size classes up to the maximum size of omnivorous fish found in the catches of that lake. By applying predicted instead of observed numbers

per size class, we removed the potential bias from size-selective fishing, which may result in under- or overrepresentation of certain size classes according to differing net selectivity. In particular, this procedure corrects for the underestimation in gillnet catches of fishes that are omnivorous in their first year of life (Prchalová et al. 2009; Arranz et al. 2015) and which can contribute substantially to predation on zooplankton and to trophic cascades (Mehner and Thiel 1999). When estimating the abundance per each size class from the size-spectrum slope and intercept, we considered the random error term in the de-log transformation of the abundance because the simple exponential of the predicted log variable does not consider specification and estimation uncertainty (Bårdsen and Lütkepohl 2009).

Due to the clipping of the size distribution for piscivorous fishes at 32 g, we did not obtain linear size distributions for piscivores. Therefore, we calculated CED_{pi} from I_i of each individual piscivore (Eq. 1) and summed all values per lake to obtain the CED_{pi} .

Furthermore, we estimated the community production of omnivorous fish (CP_{om} , non-normalized values) by summing the product of the mean annual biomass per each size class (B , predicted biomass per size class from the calculated biomass spectrum) and the biomass turnover rate (production to biomass ratio, $P : B$), calculated within the MTE framework and according to Nelson et al. (2017b):

$$P : B \propto M^{-1/4} e^{-E/kT}, \quad (3)$$

$$P \approx B \times P : B, \quad (4)$$

$$CP = \sum P_i, \quad (5)$$

where M (g) is the body mass of a size class, E (0.65 eV) is the activation energy of cellular respiration, k ($8.6173 \cdot 10^{-5}$ eV K^{-1}) is the Boltzmann constant, and T is the absolute air temperature in K (constrained to a temperature range of 0–40°C).

Statistical analyses

We used linear mixed-effects models to estimate top-down and bottom-up trophic cascades across all lakes, while accounting for the systematic spatial autocorrelation in the variables. The relationship between Chl a (dependent variable) and CED_{om} , CED_{pi} , and TP (independent variables) was used as an indicator of top-down control on phytoplankton. To avoid regressing CED_{om} on the Chl $a : TP$ ratio to account for the top-down effect (as done for example by Jeppesen et al. 2003), we used TP as additional predictor variable for Chl a and calculated its partial regression coefficient to account for the effect of TP on Chl a . By this approach, the relationship between CED_{om} and the residuals of the Chl a vs. TP regression is evaluated and indicates if phytoplankton biomass in lakes with many fish is higher than predicted by TP alone. The relationship between CP_{om} (dependent variable) and Chl

a and CED_{pi} (independent variables) was used as an indicator of bottom-up control on fish (Jeppesen et al. 2000; Hessen et al. 2003). CED_{pi} was added to both regressions to account for the effect of piscivorous predation on omnivorous fish. Data were \log_{10} -transformed as necessary to satisfy assumptions of normality. We checked for normality and homogeneity of variances by visual inspection of residuals plotted against fitted values. The models did not contain random factors, but accounted for spatial autocorrelation structure.

Spatial autocorrelation was tested in the model by adding a covariance matrix that depends on the Euclidean distance between sites in the residual variation equation (corExp function in the nlme package, Pinheiro et al. 2019) in the R platform (R Development Core Team 2019). We estimated the range (scales the distance between sites at which there is spatial autocorrelation among residuals) and the nugget (scales the non-spatial variance in the residuals) during the fitting process.

To account for differing numbers of lakes per MHT, we reran the models on a random sampling of lakes with replacement per each MHT (1000 bootstraps, equal amount of 42 lakes selected per each MHT each time: $n = 126$ lakes). To account for the regional differences in the variables studied, we split the total dataset in the three freshwater MHTs and ran all the analyses again for each freshwater MHT.

Variation per MHT in environmental variables (temperature, maximum depth, TP, and Chl a ; Fig. S3) and variables characterizing anthropogenic pressures (Table S4) were further analyzed by Kruskal–Wallis test with MHT as a fixed effect for each environmental variable. Dunn post hoc tests were used for multiple comparisons among MHTs. Data were analyzed using R v. 3.4.3 (R Development Core Team 2019) and the R package *nlme* (Pinheiro et al. 2019). The map was generated using ArcGIS Desktop: Release 10 (ESRI 2011).

Results

The CED_{om} was positively related to the realized Chl a concentration (TP-corrected Chl a) across the 227 lakes ($R^2_{\text{partial}} = 0.10$, $p < 0.001$, Fig. 2B, Table 2). CED_{pi} was not a significant predictor of Chl a ($R^2_{\text{partial}} = 0.002$, $p = 0.5$, Fig. 2A, Table 2). CP_{om} was predicted by Chl a across the lakes ($R^2_{\text{partial}} = 0.28$, $p < 0.001$, Fig. 2B, Table 2). CED_{pi} was not a significant predictor of CP_{om} ($R^2_{\text{partial}} = 0.001$, $p = 0.6$, Fig. 2B, Table 2).

One thousand resamplings of 42 lakes from each freshwater MHT confirmed the previous results despite a significantly reduced number of lakes (126 instead of 227) (Fig. S1, Table S1). The standard error of the 1000 slopes from the resampling of the Chl a to CED_{om} (0.10 ± 0.04) and CP_{om} to Chl a (0.66 ± 0.10) relationships included the slopes of the Chl a to CED_{om} (0.14 ± 0.03) and CP_{om} to Chl a (0.58 ± 0.07) relationships for the total dataset. Spatial autocorrelation between lakes was significant in all models ($p < 0.001$, see Table 2 for range and nugget). To understand the implication

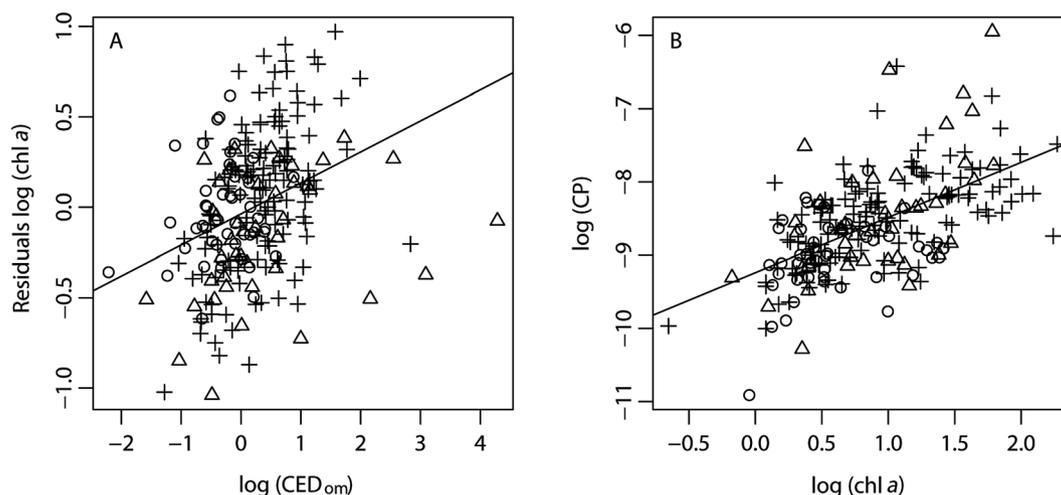


Fig. 2. Linear model plot between the residuals of the Chl *a* (mg m^{-3}) to TP (mg m^{-3}) relationship (TP-corrected Chl *a*) and omnivorous fish community energy demand (CED_{om} , $\text{W net}^{-1} \text{ night}^{-1}$) (A) and between omnivorous fish community production (CP, non-normalized values) and Chl *a* (mg m^{-3}) (B). Model outputs are shown in Table 2. Different symbols represent the three freshwater major habitat lake types (MHTs): polar freshwaters (circles), temperate floodplain rivers and wetlands (pluses), and temperate coastal rivers (triangles).

Table 2. Output of the models relating Chl *a* (mg m^{-3}) with community energy demand of omnivorous (CED_{om} , $\text{W net}^{-1} \text{ night}^{-1}$) and piscivorous fish (CED_{pi} , $\text{W net}^{-1} \text{ night}^{-1}$) and TP (mg m^{-3}), and omnivorous fish community production (CP, non-normalized values) with Chl *a* (mg m^{-3}) and community energy demand of piscivorous fish (CED_{pi} , $\text{W net}^{-1} \text{ night}^{-1}$). R^2 is given with lower and upper 95% confidence limits in brackets. Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

	Value	SE	df	t value	F value	R^2_{partial}
Top-down: $\text{Log}(\text{Chl } a) \sim \text{Log}(\text{CED}_{\text{om}}) + \text{Log}(\text{CED}_{\text{pi}}) + \text{Log}(\text{TP})$						
(Intercept)	0.01	0.13	223	0.1	0.01	
$\text{Log}(\text{CED}_{\text{om}})$	0.14	0.03	223	4.1***	16.5***	0.10(0.04–0.18)
$\text{Log}(\text{CED}_{\text{pi}})$	0.04	0.06	223	0.6	0.42	0.002(0.00–0.03)
$\text{Log}(\text{TP})$	0.62	0.05	223	12.6***	160.0***	0.48(0.40–0.56)
Range (km)	531***	Nugget (km)	68***		R^2_{model}	0.62(0.55–0.68)
Bottom-up: $\text{Log}(\text{CP}) \sim \text{Log}(\text{Chl } a) + \text{Log}(\text{CED}_{\text{pi}})$						
(Intercept)	−9.04	0.18	224	−46.3***	2428.5***	
$\text{Log}(\text{Chl } a)$	0.58	0.07	224	8.1***	65.2***	0.28(0.19–0.38)
$\text{Log}(\text{CED}_{\text{pi}})$	0.05	0.09	224	0.5	0.2	0.001(0.00–0.03)
Range (km)	191***	Nugget (km)	39***		R^2_{model}	0.29(0.20–0.38)

of spatial autocorrelation in the results, we ran the models without accounting for spatial autocorrelation. The significance of all values remained unchanged with slight modifications of the partial R^2 values (Table S2).

We reran the analyses in subsets from the three freshwater MHTs: polar freshwaters ($n = 50$), temperate floodplain rivers and wetlands ($n = 135$), and temperate coastal rivers ($n = 42$). The results were largely similar to those found in the entire dataset except in the case of the Chl *a* to CED_{om} relationship that was only significant in the temperate floodplain rivers and wetlands MHT (Fig. S2, Table S3). Lakes in this MHT tended to be deeper than in the other two MHTs (Fig. S3) and were exposed to stronger human impact, in particular a

higher percentage of agricultural land use in the catchment (Table S4).

Discussion

Metabolic variables reflecting fish energy demand or production were related with phytoplankton (expressed as Chl *a*) across 227 European lakes. The estimated top-down effects of fish on phytoplankton were weaker than the bottom-up effects of phytoplankton on fish in models run either with all data together or with the data split by ecoregion. The bottom-up patterns were robust and found also by accounting for spatial autocorrelation and by statistical resampling of an equal

number of lakes from the three freshwater MHTs. The top-down patterns were less robust in the different set of models and only significant in the temperate floodplain rivers and wetlands when the data were split by MHT. This new approach suggests that fish and phytoplankton are trophically connected in lakes, and metabolic variables can detect these relationships across lakes despite a variety of potentially confounding effects.

The novelty of our approach is the integration of fish abundance, size, and temperature into metabolic metrics, which should allow a more robust estimation to be made of trophic cascades over large geographical and lake-morphometry ranges and over broad taxonomic variability of the fish communities. By using this approach, we confirmed the occurrence of fish-induced trophic cascades as similarly demonstrated in many single-lake studies (Hairton et al. 1960; Carpenter et al. 1985; McQueen et al. 1986; Paine 2006; DeLong and Walsh 2015). However, when comparing the trophic cascades across many lakes from the European continent, the top-down effect found in our study was weaker than that in most of the previous single-lake studies. In a study focusing on the effect of piscivores on prey density and size and indirectly on Chl *a* in more than 60 lakes in northern Germany, Mehner (2010) found a weak top-down control of fish on Chl *a*. In a recent study in 138 Finnish oligo-eutrophic lakes populated by piscivorous pikeperch (*Sander lucioperca*), Kokkonen et al. (2019) demonstrated that bottom-up effects of phytoplankton on fish were much stronger than the top-down effects by fish on phytoplankton. We suggest that our results complement these earlier studies and support the suggestion of a relatively weak top-down effect of fish on phytoplankton biomass in across-lake comparisons. However, weaker effects on Chl *a* by fish (top-down control) than by Chl *a* on fish (bottom-up control) were expected, considering that most of the fish species found in the lakes were omnivores occurring in both pelagic and benthic habitats. The feeding on both zooplankton and benthic macroinvertebrates by omnivorous fish may weaken top-down cascades on pelagic zooplankton and phytoplankton relative to bottom-up cascades where high phytoplankton biomasses induce high zooplankton biomasses, and omnivorous fish use this resource directly. The effect of piscivorous fish on top-down and bottom-up cascades was not significant, confirming earlier studies showing that the control of omnivorous fishes by piscivore predation is usually weak (Mehner 2010; Mehner et al. 2016; Kokkonen et al. 2019).

When we split the dataset according to the freshwater MHTs, a significant top-down effect of CED_{om} on Chl *a* was found in the temperate floodplain rivers and wetlands region, whereas no effect emerged for polar freshwaters and the temperate coastal river region. However, TP was a significant predictor of Chl *a* in all MHTs. This pattern suggests that Chl *a* in these lakes is primarily controlled by nutrient concentrations, with negligible effects by fish on the Chl *a* to TP residuals ratio. Productivity (Chl *a* and TP) in the lakes in the temperate

floodplain rivers and wetlands region was intermediate, polar freshwaters being less productive and lakes in the temperate coastal river region more productive. Overall, however, the majority of the lakes included in this study fall within the oligotrophic and weakly mesotrophic range (62% of the lakes had a Chl *a* lower than 10 mg m⁻³). Therefore, it is rather unlikely that the differences in top-down control between the MHTs are attributable to the slightly differing trophic state of the lakes, as suggested, for example, by Jeppesen et al. (2003). By using a large dataset (466 lakes) from Greenland, Denmark, Norway, and New Zealand, these authors concluded that top-down control on large-bodied zooplankton by fish is strong in oligotrophic and hypertrophic lakes but weak at intermediate TP concentrations.

However, the lakes in the temperate floodplain rivers and wetlands region were, on average, substantially deeper and therefore the higher proportion of pelagic planktivores among the omnivorous fish exerted a stronger pelagic top-down control on phytoplankton than the omnivorous fish in the shallower lakes of the two other MHTs. This difference between the MHTs is shown by the significance of CED_{om} as predictor in the temperate floodplain rivers and wetlands region. In contrast to many previous studies, our calculations explicitly included fish catches in pelagic gill nets in deep lakes where planktivorous fish usually dominate. There are several studies pointing to the fact that inclusion of the pelagic fish community may result in more reliable estimates of fish community composition in deep lakes (e.g., Diekmann et al. 2005; Alexander et al. 2015). Accordingly, the stronger consideration of pelagic planktivores in our study may also explain why we found stronger top-down control by fish in the deeper lakes, in contrast to earlier studies showing that fish exert strong trophic cascades in shallow lakes because of the higher fish biomass per volume, maintained by a higher benthic invertebrate production (Jeppesen et al. 2003).

In addition, the human impact related to agriculture land use was higher in the temperate floodplain rivers and wetlands region than in the two other MHTs. High agricultural land use may cause higher nutrient concentrations, increased turbidity and reduced benthic primary production in adjacent lakes, with potentially further consequences for fish-induced trophic cascades (Vadeboncoeur et al. 2003). However, average TP and Chl *a* concentrations were intermediate in lakes of this MHT, but higher in lakes of the temperate coastal river region despite low agricultural land use there. Therefore, a direct nutrient effect of anthropogenic land use could not be found, and we conclude that the differing land-use characteristics in the three MHTs had only a minor effect on differences of trophic cascades between lakes.

We acknowledge that the lack of zooplankton data from the lakes challenges the mechanistic understanding of our results. Zooplankton was excluded as biotic quality element in the European Water Framework Directive, 2000/60/EC, and zooplankton data are therefore not included in this dataset.

Thus, we do not know whether high Chl *a* values were related with high zooplankton biomasses, ultimately leading to high fish community production. Other studies, however, show a strong relationship between phytoplankton and zooplankton biomasses (Hanson and Peters 1984; Jeppesen et al. 1997). Even though we cannot evaluate whether zooplankton biomasses were low in those of our study lakes where the fish CED_{om} was high, the consistently positive relationship between Chl *a* and CP_{om} suggests that trophic links between fish and phytoplankton exist and are detectable across almost 250 lakes.

We calculated CP via the *P* : *B* ratio according to the framework of the MTE (Nelson et al. 2017b). However, in contrast to the CED calculations, we obtained only a scaling relationship and were not able to calculate the absolute production of the fish community per lake. The reason is the lack of a normalization constant for *P* : *B* ratios, which, in contrast, was available for the metabolic rate of fish and hence for the CED. The next step here would be to accumulate empirical data on fish secondary production and size structure from a larger set of lakes and to compare these with the CP estimates based on the MTE. Furthermore, we acknowledge that Chl *a* is only an approximation to phytoplankton biomass. Chl *a* does not account for differences between lakes in primary production attributable to size structure differences of phytoplankton species or phytoplankton community composition, with variation in Chl *a* per cell or variation in prey selectivity by zooplankton (Kasprzak et al. 2008; Canfield et al. 2019). Moreover, we acknowledge that Chl *a* : TP is a crude estimate of top-down control effects; several biomanipulation studies in eutrophic lakes have shown that reducing the abundance of planktivorous and omnivorous fish causes a reduction of the Chl *a* : TP ratio but less than would be expected from simple top-down control because not only Chl *a* but also TP decrease in these lakes (Jeppesen et al. 2012). However, we assume that this effect is weak in the present dataset that represents mainly oligotrophic and mesotrophic lakes. The rather indirect approach of determining top-down control needs to be verified by more direct analyses of data on the size and abundance of zooplankton, the zooplankton : phytoplankton biomass ratio or data on zooplankton grazing rates, which were not available in the present study.

This is the first time that MTE has been used to assess the strength of trophic cascades across lakes. The integration of the size structure and biomass of the fish community with temperature makes metabolic metrics very suitable for the study of food web processes across lakes exhibiting very different characteristics, at least from a bottom-up control perspective. Metabolic metrics add further robustness to the bottom-up control theory that has principally been developed by using fish density and biomass metrics (McQueen et al. 1986; Power 1992; Jeppesen et al. 2000; Bruce et al. 2013). The dependence of top-down control on many other factors such as the homeostasis of secondary production (Detmer et al. 2017), producer quality and

defense (Borer et al. 2005; Cebrian et al. 2009), ecosystem complexity (Hillebrand and Cardinale 2004), zooplankton community composition (Hansson et al. 1998), and rates of exogenous inputs (Leroux and Loreau 2008) challenges the detection of such a mechanism when comparing multiple lakes with very different characteristics. As a next step in research, it would be informative to determine the effect of fish metabolism on lake top-down and bottom-up control in other biomes of the world in order to confirm and generalize the patterns found here for an expansive set of European lakes.

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Conflict of Interest

None declared.

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