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An allometric niche model for species interactions in temperate freshwater ecosystems

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Abstract. Trophic interactions are central in understanding ecosystem processes and the management of natural ecosystems but are frequently complex to estimate. To address this issue, body size has been shown to be a useful trait to reconstruct species interactions, particularly in aquatic ecosystems. An allometric niche model (aNM) considering body size as a niche trait is proposed to predict trophic interactions in temperate freshwater ecosystems. The aNM calibration was based on 26 ubiquitous freshwater species with known minimal and maximum prey body sizes that permitted the establishment of prey body size ranges for vertebrate and invertebrate consumers. The aNM inferences were validated for 13 empirical freshwater food webs, and the model was applied to an extensive inventory of 474 species (spanning six orders of body size magnitude) from the largest natural French lake (Lake Bourget). This application permitted to strengthen the aNM validation with predator-prey mass ratio comparisons, predicted diet analyses, and allowed the exploration of the lake food web structure. The aNM provided appreciable intrinsic validity (specificity = 87 ± 12%, sensitivity = 59 ± 29%, accuracy = 81 ± 10%), and departures among inferred and empirical trophic interactions were explained by foraging specificities or limited sampling of stomach contents. In Lake Bourget, 26,037 trophic links were inferred. Predator–prey mass ratios for vertebrates and invertebrates were consistent with those empirically established and were occasionally higher for invertebrates as the aNM considers small prey (e.g., bacteria) as possible resources for invertebrates. The inferred diets for three species selected for their well-known foraging ecology also revealed plausible outcomes of the aNM. The nested structure of the lake food web was determined by highlighting different topologies among the benthic and the pelagic food sub-webs and the role of top predator fish in the coupling of both food sub-webs. Due to the large number of species inventories available worldwide for freshwater ecosystems anchored in the ecological monitoring, the aNM may represent a valuable tool for both ecologists and managers to address complementary facets of applied biodiversity studies (e.g., reconstruct highly resolved food webs, predict pressures on important species or new interactions with invasive species).

Key words: allometry; body size; food web; freshwater; niche model; species inventories; trophic interactions.

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INTRODUCTION

Trophic interactions are one of the most evident and constraining ecological interactions that shape species abundances and influence food web structure and ecosystem processes (Beckerman et al. 2006, Otto et al. 2007, Allesina and

Tang 2012). However, their identification among co-occurring species using either direct (Hyslop 1980) or indirect methods (Laska and Wootton 1998) remains difficult, particularly for small organisms (e.g., invertebrates). Several inherent limitations of empirical studies can hinder the resolution of exhaustive trophic interactions among species living within an ecosystem. These limitations are mainly related to the limited taxonomic resolution and/or the misidentification of consumers' prey as well as the sampling effort. These factors can influence the characterization of consumers' diet range, where the number of actual prey for a species tends to continuously increase with the number of individuals analyzed (Woodward et al. 2010). Additionally, ethical considerations can further limit the possibility of sacrificing or manipulating individuals to access their stomach contents (Light et al. 1983, Kamler and Pope 2001).

To address these difficulties, different methods have been proposed to reconstruct species trophic interactions. Extrapolations from existing published species interactions based on phylogenetic relationships (Gray et al. 2015) have provided plausible results but were dependent on the data quality and the species taxonomic resolution. Predictive models such as the allometric diet breadth model (Petchey et al. 2008) or a composite model of phylogenetic and species trait distributions (Pomeranz et al. 2019) have provided a better understanding of trophic interaction mechanisms and insights into food web structures while requiring specific parameters that are challenging to retrieve, such as handling time or attack rate. In most accurate predictive models, species body size is used as a strong predictor of trophic interactions (Brose et al. 2006*a*, Reum et al. 2018, Portalier et al. 2019), and this factor is especially valuable in aquatic ecosystems (Warren and Lawton 1987) and simple to retrieve from species monitoring programs or the literature. Gravel et al. (2013) successfully took advantage of the niche model principles (Williams and Martinez 2000) to predict trophic interactions from this trait for fish species in the Mediterranean Sea. These authors used species body size as a unidimensional trait to characterize the species trophic niches leading to allometric relationships between predator–prey body sizes. This approach has recently been used to explore the connectivity of the global marine food web by considering complementary ecological traits such as habitat (Albouy et al. 2019).

Among aquatic ecosystems, freshwater ecosystems contain significant biodiversity and support numerous ecosystem services (e.g., drinking water, fish production, and recreational activities; Schallenberg et al. 2013, Costanza et al. 2014), consequently having important patrimonial and conservation values. A prerequisite for efficient conservation is to embrace the complexity of species interactions among which trophic interactions are expected to be primarily involved (Cumming et al. 2010). Hence, we expanded the approach of Gravel et al. (2013) to freshwater ecosystems and generalized its original application focused on vertebrates (fish) by including invertebrate consumers. Thus, we could benefit from a predictive allometric niche model (aNM) that would allow the reconstruction of trophic interactions from primary producers to top predator fish in temperate freshwater ecosystems. Importantly, this model involves species inventories, which are among the most commonly available and shared ecological data, and would consequently offer substantial application opportunities in various fields of research for both ecologists and managers.

In this study, the aNM was first calibrated using species widely distributed among freshwater ecosystems whose diets and/or feeding ranges have been extensively studied. The intrinsic validity of the model was tested by comparing the aNM inferences to the empirical trophic interactions in 13 freshwater food webs by classification metrics (Tharwat 2018). The aNM was then applied to an extensive species inventory from the largest natural French lake (Lake Bourget). The consistency of the aNM inferences was first investigated through the calculation of predator–prey body mass ratios and compared with empirical body mass ratios. The inferences were then used to analyze the predicted diets for three selected common species: the European catfish (*Silurus glanis*, an invasive species in many ecosystems, recently established in Lake Bourget), the whitefish (*Coregonus lavaretus*, presenting a significant economic value), and the gammarid shrimp (*Gammarus pulex*, occupying a functional role in organic matter decomposition). Finally, the aNM was used to explore the whole food web structure of Lake Bourget by characterizing its underlying nestedness induced by its respective benthic and pelagic food sub-webs and to determine how species were involved in this coupling. We specifically expected to identify a structural asymmetry between these two food sub-webs (Rooney et al. 2006, McCann and Rooney 2009, Rooney and McCann 2012) and suspected that top predator fish would play a crucial role in their coupling.

MATERIAL AND METHODS

Fitting the aNM

The niche model (Williams and Martinez 2000) is a stochastic model stating that a consumer of body size n_i forages on a continuous feeding range r_i, centered on c_i. This model fairly predicts the structural properties of complex food webs (Camacho et al. 2002, Williams et al. 2010) and suggests that the trophic niche of consumers could be approximately unidimensional. Gravel et al. (2013) proposed using the niche model principles to predict species trophic interactions by considering species body size as a descriptor of the unidimensional trophic niche. Specifically, consumer i whose niche position is n_i (i.e., consumer body size) would consume any species within the body size range r_i (i.e., a continuous feeding range for consumers defined by $r_{i\min}$ and $r_{i\max}$). We used quantile regressions (QRs; Koenker 2005) to infer the feeding ranges of consumers. Quantile regressions differ from linear models by estimating the conditional distribution (i.e., any quantiles) of a response variable instead of focusing on its mean. In the present context, $\log_{10}$ (predator body size) was the explanatory variable and $\log_{10}$ (prey body size) was the response variable and we retained the 5% and 95% quantiles to characterize the lower ($r_{\min}$) and the higher ($r_{\max}$) bounds of the predator feeding range, similarly to Gravel et al. (2013).

These QRs were fitted using 26 ubiquitous species living in temperate lakes and rivers, whose diets and/or feeding ranges were known (Appendix S1) and covered a large body size range (i.e., from protists to piscivorous fish). Both QRs ($QR_{5\%}$ and $QR_{95\%}$) were fitted for invertebrate and vertebrate consumers separately to account for their inherent differences in feeding ranges, leading to two specific relationships for both QRs.

aNM predictions and refinement

Based on the QRs, the consumers feeding ranges were inferred using their body size as the niche position n_i and trophic links were predicted for any species falling within r_i, leading to a binary adjacency matrix of potential trophic interactions $\mathbf{M_{bp}}$ (filled with 1 if consumer i had a trophic interaction with a prey or 0 if there was no interaction). Complementary ecological criteria were considered to refine $\mathbf{M_{bp}}$ in the application below by deleting trophic links to account for species spatial co-occurrence (i.e., habitat traits) and a priori knowledge regarding the trophic ecology of consumers (e.g., piscivory). For the habitat trait, species were classified as strictly pelagic, strictly benthic or pelagic/benthic and trophic links involving species from different habitats (i.e., strictly pelagic or strictly benthic) were deleted similarly to the method in Albouy et al. (2019). Complementarily, trophic links associating strict piscivorous fish to organisms other than fish (i.e., macroalgae, mollusks, or oligochaetes) were deleted (Serveau and Raymond 2007, Keith et al. 2011). These refinements led to the final binary adjacency matrix $\mathbf{M_{bf}}$ that included all the expected trophic interactions within the food web of the studied ecosystem.

Binary trophic links were also weighted according to the positioning of the prey body size within the consumer feeding range to obtain the weighted adjacency matrix $\mathbf{M_{wf}}$. We first considered a normal density distribution with a mean equal to the center of r_i (c_i, Eq. 1) and a standard deviation equal to the standard deviation (SD) of 100 simulated points evenly spaced over r_i, so that the normal distribution was scaled to r_i. The resulting values were then normalized by the maximum value of the normal density distribution to obtain maximum weighted links equal to 1 at c_i in accordance with the probabilistic niche model (Williams et al. 2010), providing higher feeding probabilities at the niche center (optimal body size ratio) that decline consistently with the distance from the center. The center c for consumer i was estimated as follows:

$$c_i = r_{i\min} + (r_{i\max} - r_{i\min})\frac{1}{2} \qquad (1)$$

Finally, we calculated prey proportions, comparable between consumers, by dividing each weighted link associated with prey j inferred in the diet of consumer i by the sum of the weighted links associated with all prey inferred in the diet of consumer i, so that columns corresponding to consumers summed to 1. These final prey proportions in $\mathbf{M_{wf}}$ were expected to provide possible estimates of prey preferences for each consumer according to its niche center (i.e., the likelihood that consumer i consumes prey j considering all prey equally available in the ecosystem).

Empirical validation of aNM predictions

Binary adjacency matrices of trophic links for 13 empirical freshwater food webs originating from different temperate ecosystems (i.e., lakes, ponds, and streams; Table 1) were retrieved from Global webs (https://www.globalwebdb.com) and from the Cheddar R package (Hudson et al. 2013). An average body size was attributed to each species in these food webs by two main sources (FishBase, Tachet et al. 2010). The aNM was then applied to each food web, and habitat refinements were considered for the lakes to obtain their respective binary matrix $\mathbf{M_{bf}}$. Columns, conventionally representing consumers, assigned to primary producers in the $\mathbf{M_{bf}}$ were deleted as they necessarily summed to 0. The resulting matrices were compared with the empirical matrices to quantify the aNM intrinsic validity using three metrics (Tharwat 2018): (1) sensitivity (i.e., proportion of correctly predicted existing links; Eq. 2), (2) specificity (i.e., proportion of correctly predicted absent links; Eq. 3), and (3) accuracy (i.e., proportion of correctly predicted both present and absent links; Eq. 4).

$$\text{sensitivity} = 100\frac{\text{TP}}{(\text{TP}+\text{FN})} \tag{2}$$

$$\text{specificity} = 100\frac{\text{TN}}{(\text{TN}+\text{FP})} \tag{3}$$

$$\text{accuracy} = 100\frac{\text{TN}}{(\text{TP}+\text{FP}+\text{TN}+\text{FN})} \tag{4}$$

where TP represents true positives (i.e., predicted links empirically present), TN represents true negatives (i.e., not predicted links empirically absent), FP represents false positives (i.e., predicted links empirically absent), and FN represents false negatives (i.e., not predicted links empirically present).

Application to Lake Bourget

Study site and data set.—Lake Bourget (45°43′46.842″ N, 5°52′10.484″ E) is the largest natural French lake located in the Alps. This lake supports significant ecosystem services, providing 50–100 tons of harvested fish per year, drinking water for cities of several thousands of people and recreational activities, generating several millions euros per year to the local economy (Jacquet et al. 2020).

A detailed inventory of the species living in this lake was obtained from the long-term

Table 1. Characteristics of the 13 empirical food webs used to validate the aNM.

Food webs	Location	Ecosystem	Taxonomic categories and species richness	References
Allta'Mharcaidh Stream	UK	Stream	De, Pb, Ia, Fi (n = 40)	Layer et al. (2010) (1)
Bakersfield Ponds	USA	Pond	De, Pk, Zo, Ia (n = 30)	Hurlebert et al. (1972) (2)
Bere Stream	UK	Stream	Pb, Ia, Fi (n = 65)	Layer et al. (2010) (1)
Constance Lake	Europe	Lake	Ba, Pk, Ci, Zo, Fi (n = 23)	Boit et al. (2012) (2)
Crescent Lake	USA	Lake	Zo, It, Ia (n = 13)	Hampton et al. (2011) (2)
Dorset Streams	UK	Stream	Ba, De, Fu, Pb, Pk, Zo, Ia (n = 65)	Ledger et al. (2011) (1)
Hard Knott Gill	UK	Stream	De, Pb, Ia, Fi (n = 44)	Layer et al. (2010) (1)
Mill Stream	UK	Stream	De, Pb, Ia, Fi (n = 86)	Layer et al. (2010) (1)
Old Lodge Stream	UK	Stream	De, Pb, Ia, Fi (n = 23)	Layer et al. (2010) (1)
Ovre Heimdalsvatn Lake	Norway	Lake	De, Pk, Pb, Ma, Zo, Fi (n = 39)	Larsson et al. (1978) (2)
Skipwith Common Ponds	UK	Pond	De, Zo, Ia (n = 35)	Warren (1989) (2)
Tuesday Lake	USA	Lake	Pk; Zo, Ia, Fi (n = 51)	Cohen et al. (2003) (1)
Villas County Ponds	USA	Pond	De, Zo, Ia (n = 77)	Schneider (1997) (2)

Notes: (1) correspond to data retrieved from the Cheddar package and (2) are food webs from the website Global Web (https://www.globalwebdb.com). Ba is for bacteria, Ci is for ciliates, De is for detritus, Fu is for fungus, Fi is for fish, It is for terrestrial invertebrates, Ia is for aquatic invertebrates, Ma is for macrophytes, Pb is for phytobenthos, Pk is for phytoplankton, and Zo is for zooplankton.

monitoring survey conducted for several decades (SOERE OLA-IS, INRAE Thonon-les-Bains, CISALB; Rimet et al. 2020) as well as from complementary studies (Appendix S2).

A large reference array was used to attribute a lake compartment (i.e., pelagic, benthic, pelagic/benthic) to each species according to its habitat and to estimate body sizes for all species, considering research papers, reference Web sites such as AlgaeBase (https://www.algaebase.org/), FishBase (https://www.fishbase.se/), or EOL (https://eol.org/) and technical reports (e.g., average fish body size from the long-term monitoring survey). For fish, average adult body size was considered and obtained either directly by the references indicated above or estimated from an average of the maximum and the minimal body sizes reported. Different life stages (i.e., juveniles and adults) were only considered for fish supporting important economic and ecological values for the lake (i.e., *Perca fluviatilis*, *Coregonus lavaretus*, *Salmo trutta,* and *Esox lucius*). Apart from these fish, each species represented a unique node within the food web. The aNM was then applied to all consumers to obtain the binary matrix $\mathbf{M_{bf}}$ and the weighted matrix $\mathbf{M_{wf}}$.

*Body mass ratios.—*Body mass ratios between consumers and their prey are of primary importance for food web stability and are highly constraining in most ecosystems (Emmerson and Raffaelli 2004, Loeuille and Loreau 2005, Otto et al. 2007). We calculated $\log_{10}$ (predator–prey body mass ratio; hereafter called mass ratios) for each predator–prey pair inferred by the aNM. Those were compared with the estimates of Brose et al. (2019), calculated from the available open-access database (https://doi.org/10.25829/iDiv.283-3-756) for lake invertebrate consumers (number of trophic interactions = 5663; mean = 3.28 ± 2.17) and lake ectotherm vertebrate consumers (number of trophic interactions = 2805; mean = 5.31 ± 2.57). Trophic links inferred by the aNM exhibiting mass ratios falling within Brose's estimates ± 1 SD were suggested as plausible, providing a way to validate the aNM inferences. Species body sizes were converted to body masses according to different empirical relationships (Appendix S3).

*Trophic niches.—*We examined the inferred diets for three species not used in the calibration and whose actual diets have been widely described: the European catfish (*Silurus glanis*), the whitefish (*Coregonus lavaretus),* and the gammarid shrimp (*Gammarus pulex*). The gammarid shrimp can feed on diverse food resources ranging from fragments of decaying terrestrial organic matter, fungi, bacteria, and algal biofilms (Graça et al. 1993, MacNeil et al. 1997, Maltby et al. 2002, Franken et al. 2005), the whitefish is zooplanktonophagus with a diet mainly composed of cladocerans and chironomids (Amundsen et al. 2010, Anneville and Hamelet 2018), and the European catfish is omnivorous, feeding on various prey from invertebrates to fish (Carol et al. 2009, Copp et al. 2009, Ferreira et al. 2019). We explored their inferred prey characteristics (i.e., identity, body size, prey preferences, and habitats) to complementarily evaluate how the aNM inferences would provide plausible trophic niches in relation to previous diet studies.

*Food web topologies.—*Following the approach of Bersier et al. (2002), an array of food web metrics was calculated for the whole food web as well as for the benthic (i.e., strictly benthic species) and pelagic (i.e., strictly pelagic species) food sub-webs based on the $\mathbf{M_{bf}}$ and $\mathbf{M_{wf}}$ matrices: the total number of links (L), the linkage density (LD, the proportion of realized connections per species), and the directed connectance (C, the proportion of all possible trophic links that are actually realized). The species trophic positions (TP) were estimated according to the method of Levine (1980) in which primary producers were set to TP = 1 while TP for consumers were calculated as 1 plus the mean prey TP. The proportions of top predators (%T), intermediate species (%I), and basal species (%B) were then calculated.

In lakes, studying the coupling between the benthic and pelagic food sub-webs appears essential to understand the real structure of whole food webs and the dependence of consumers on the resource production of the different lake compartments (Vander Zanden and Vadeboncoeur 2002, McCann et al. 2005). This coupling was studied by quantifying the benthic reliance of each consumer as the percentage of benthic prey in their inferred diets. The relationship between benthic reliance and species TP was then modeled using a generalized additive model (GAM; Wood 2017). Invertebrates that could feed in both benthic and pelagic habitats (e.g., chironomids) were not accounted for in the GAM because benthic reliance depends on habitat.

All statistical and graphical displays were performed using R.3.5.1 (R Core Team Development 2018) with the packages cheddar (Hudson et al. 2013), SparseM (Koenker and Ng 2003), quantreg (Koenker 2021), igraph (Csárdi and Nepusz 2006), NetIndices (Kones et al. 2009), foodweb (Perdomo 2015), ggplot2 (Wickham 2016), and mgcv (Wood 2017).

R codes example are provided in Appendix S4, detailing in a step-by-step manner the inference of trophic links, the weighting procedure, the extraction of species metrics, and the export to Network3D (Yoon et al. 2004) based on a simplified example. Codes, functions, and data are available at: https://github.com/chloevagnon/aNM_method.

RESULTS

aNM fitting and intrinsic validity

The QR slopes clearly differed among the vertebrates and invertebrates (Fig. 1; Table 2). The slopes were ~7.7-fold higher for the $QR_{5\%}$ and ~1.5-fold higher for the $QR_{95\%}$ of vertebrates compared with those of invertebrates. Consequently, the slope of c was also higher for vertebrates than for invertebrates.

The aNM correctly predicted the large majority of absent trophic links for the different ecosystem types with an average specificity of 87 ± 12% ranging from 78% to 99% (Table 3),

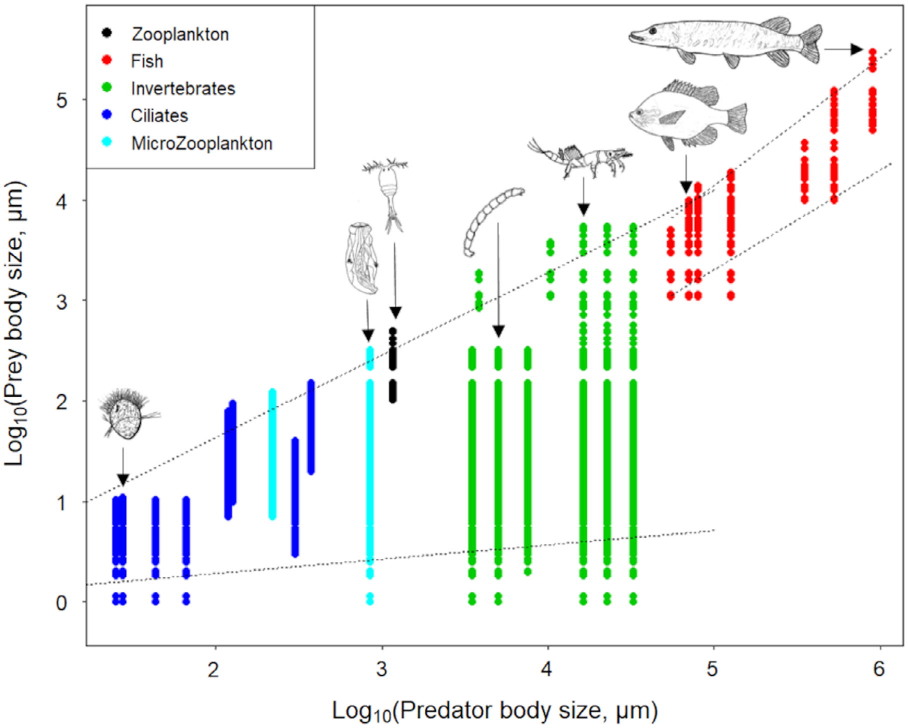

Fig. 1. Log_{10} (predator–prey size) relationships for the 26 reference species ubiquitous in temperate freshwaters used in the aNM calibration. Predators (x-axis) are segregated among five taxonomical groups (i.e., fish, macroinvertebrate, zooplankton, ciliate, and microzooplankton). Prey body size ranges were obtained from the literature and empirical observations (Appendix S1). Points correspond to prey inferred by the aNM for each reference species in Lake Bourget. The dotted gray lines indicate $r_{\max}$ ($QR_{95\%}$) and $r_{\min}$ ($QR_{5\%}$) of the feeding range of predators according to their body size and differed for invertebrates and vertebrates (i.e., fish). Species drawings show the diversity of predators considered by the aNM from left to right: *Lohmaniella* sp., *Asplanchna priodonta, Megacyclops viridis, Cladotanytarsus* sp., *Ephemera* sp., *Lepomis gibbosus,* and *Esox lucius*.

Table 2. Coefficients of the aNM for the invertebrate and vertebrate consumers based on quantile regressions (QRs).

	Upper range ($r_{\max}$ = QR$_{95\%}$)		Lower range ($r_{\min}$ = QR$_{5\%}$)	
Consumer category	Intercept	Slope	Intercept	Slope
Invertebrates	. . .	0.82	. . .	0.14
Vertebrates	–2.17	1.26	–2.07	1.08

except for Tuesday Lake (specificity = 55%). The aNM capacity to correctly predict the trophic link occurrences was also appreciable (Table 3), although the results were variable among food webs as indicated by the high standard deviation associated with the average sensitivity (59 ± 29%). For five food webs, the aNM clearly omitted a significant trophic link fraction (sensitivity of 11%, 15% 20%, 35% and 48%), while for 8 food webs, the sensitivity was higher than 75%. The aNM capacity to predict both absent and present links was high, with an average accuracy of 81 ± 10% (Table 3). An accuracy below 70% was found for only two food webs (Tuesday Lake and Skipwith common ponds with accuracies of 62% and 69%, respectively). The aNM presented a low ability to predict absent trophic links for Tuesday Lake (i.e., low specificity) and a high ability to predict existing links (i.e., high sensitivity), while the opposite scenario occurred for Skipwith common ponds. For the three ecosystem types, the most consistent results were obtained for the most detailed interaction matrices (e.g., food webs from the Cheddar package), and the accuracy was similar among the different ecosystems but slightly higher for stream food webs than for lakes and ponds.

Inference of Lake Bourget food web

The species inventory of Lake Bourget included 474 species, covering six orders of magnitude of body size with species from primary producers to large fish (Fig. 2a). The smallest species corresponded to the bacteria *Methanoregula boonei* (1.10^{-4} cm), and the largest species was the European catfish *Silurus glanis* (115 cm). The species distribution among lake habitats was well balanced, with strictly benthic species accounting for 42.6% (Fig. 2b), strictly pelagic species accounting for 43.7% (Fig. 2c), and pelagic/benthic species accounting for 13.7%. The aNM application to the species inventory of Lake Bourget permitted to infer a total of 26,037 trophic links.

Predator–prey mass ratios

The mass ratios calculated from the predicted trophic links in Lake Bourget provided satisfying consistency with those from Brose et al. (2019) for invertebrates and vertebrates. The mass ratios for invertebrates were calculated from 24,494 trophic links and were higher than those obtained by Brose et al. with a mean mass ratio of 4.5 ± 1.9 (Fig. 3a). On average, 73.3% of the mass ratios fell within Brose's estimates ± 1 SD.

Table 3. Specificity, sensitivity, and accuracy of the aNM inferences for the 13 empirical food webs of temperate freshwater ecosystems.

Food webs	Ecosystem	Specificity (%)	Sensitivity (%)	Accuracy (%)
Allta'Mharcaidh Stream	Stream	96	77	92
Bakersfield Ponds	Pond	87	34	72
Bere Stream	Stream	94	81	91
Constance Lake	Lake	86	47	77
Crescent Lake	Lake	88	11	80
Dorset Streams	Stream	78	85	79
Hard Knott Gill	Stream	95	81	92
Mill Stream	Stream	95	84	93
Old Lodge Stream	Stream	100	73	92
Ovre Heimdalsvatn Lake	Lake	78	73	77
Skipwith Common Ponds	Pond	92	19	68
Tuesday Lake	Lake	56	88	62
Villas County Ponds	Pond	90	15	78

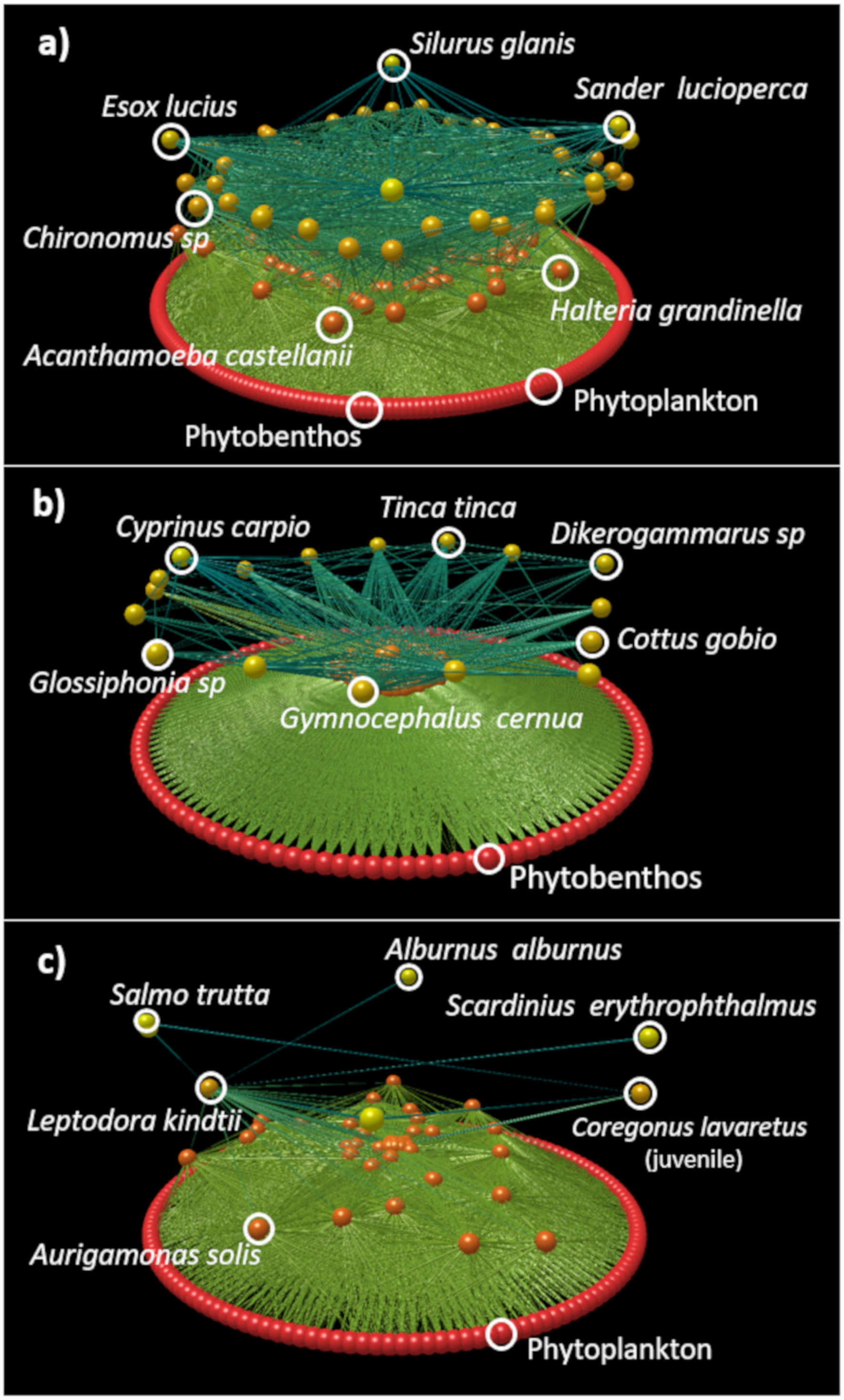

Fig. 2. 3D-visualizations of the whole food web of Lake Bourget (a), the benthic food sub-web (b), and the pelagic food sub-web (c). Species are represented by spheres. Colors depend on trophic positions, red being the lower trophic position (i.e., autotrophic species at the bottom of the food webs), and yellow being the more elevated trophic position. Lines represent trophic links.

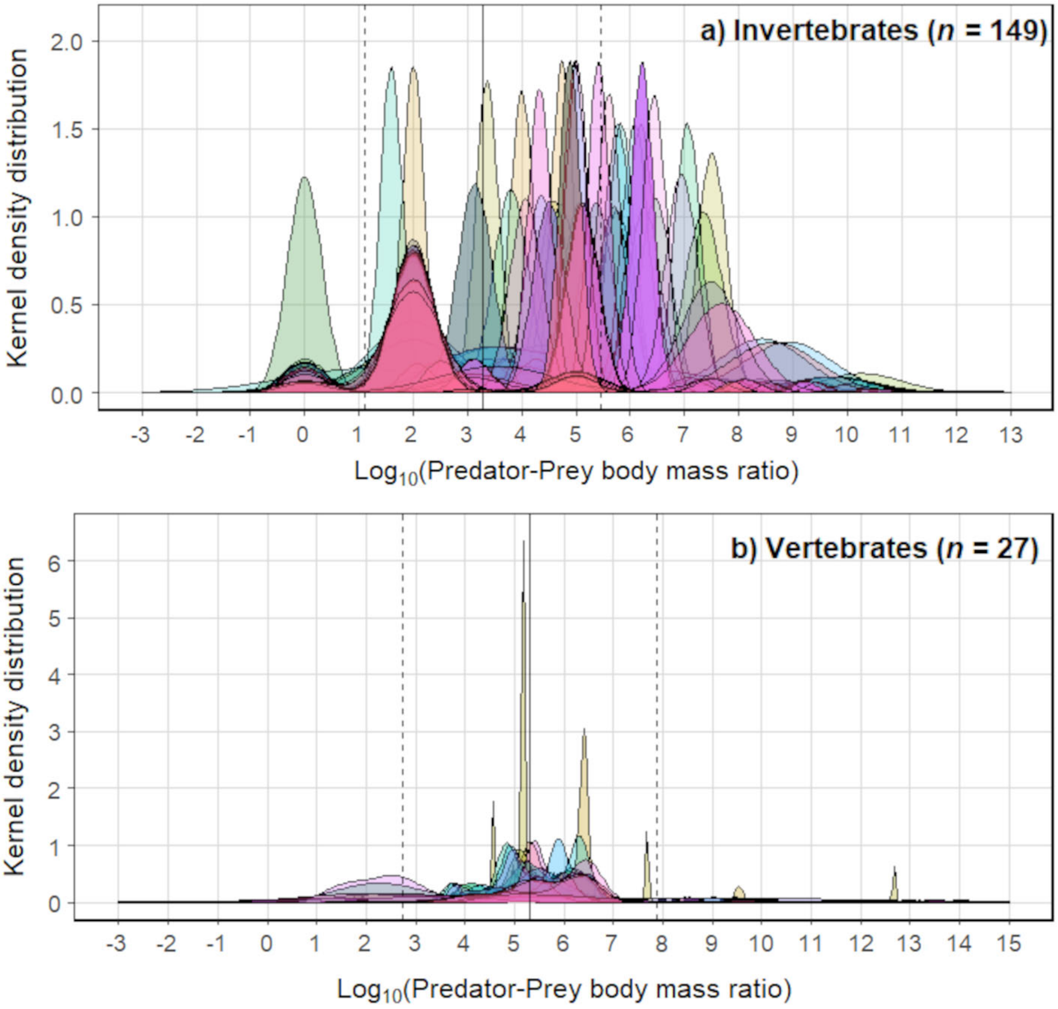

Fig. 3. Kernel density distributions of $\log_{10}$ (predator–prey mass ratios) for the 103 invertebrates (a) and the 27 vertebrates (b) in the dataset. Full vertical black line represents the mean of the $\log_{10}$ (predator–prey mass ratios) from Brose et al. (i.e., $\text{mean}_{\text{invertebrates}} = 3.28$ and $\text{mean}_{\text{vertebrates}} = 5.31$; 2019), and the dashed vertical black lines represent the SD of the $\log_{10}$ (predator–prey body mass ratios) from the same study (i.e., $\text{SD}_{\text{invertebrates}} = 2.17$ and $\text{SD}_{\text{vertebrates}} = 2.57$).

Concerning vertebrates, the 1543 inferred mass ratios were in accordance with Brose's estimates with an average of 5.4 ± 1.3 (Fig. 3b), leading to 94.4% of the mass ratios being within Brose's estimates ± 1 SD.

Trophic niche predictions

Diets inferred by the aNM for the three well-studied species were highly consistent with those empirically observed. Specifically, 72%, 70%, and 95% of the inferred prey (for the European catfish, whitefish and gammarid shrimp respectively) were observed in previous diet studies (Appendix S5: Tables S1–S3). The aNM inferred 18 prey for the European catfish with prey body sizes ranging from 5.5 to 30 cm and most prey measuring approximately 10 cm. This prey body size corresponds to species such as crayfish that are actually highly predated by the European catfish and for which prey preference was expected to be maximum (Fig. 4a,b). Inferred prey mostly occurred in the benthic habitat (nine prey), while four prey were associated with the pelagic habitat and five others

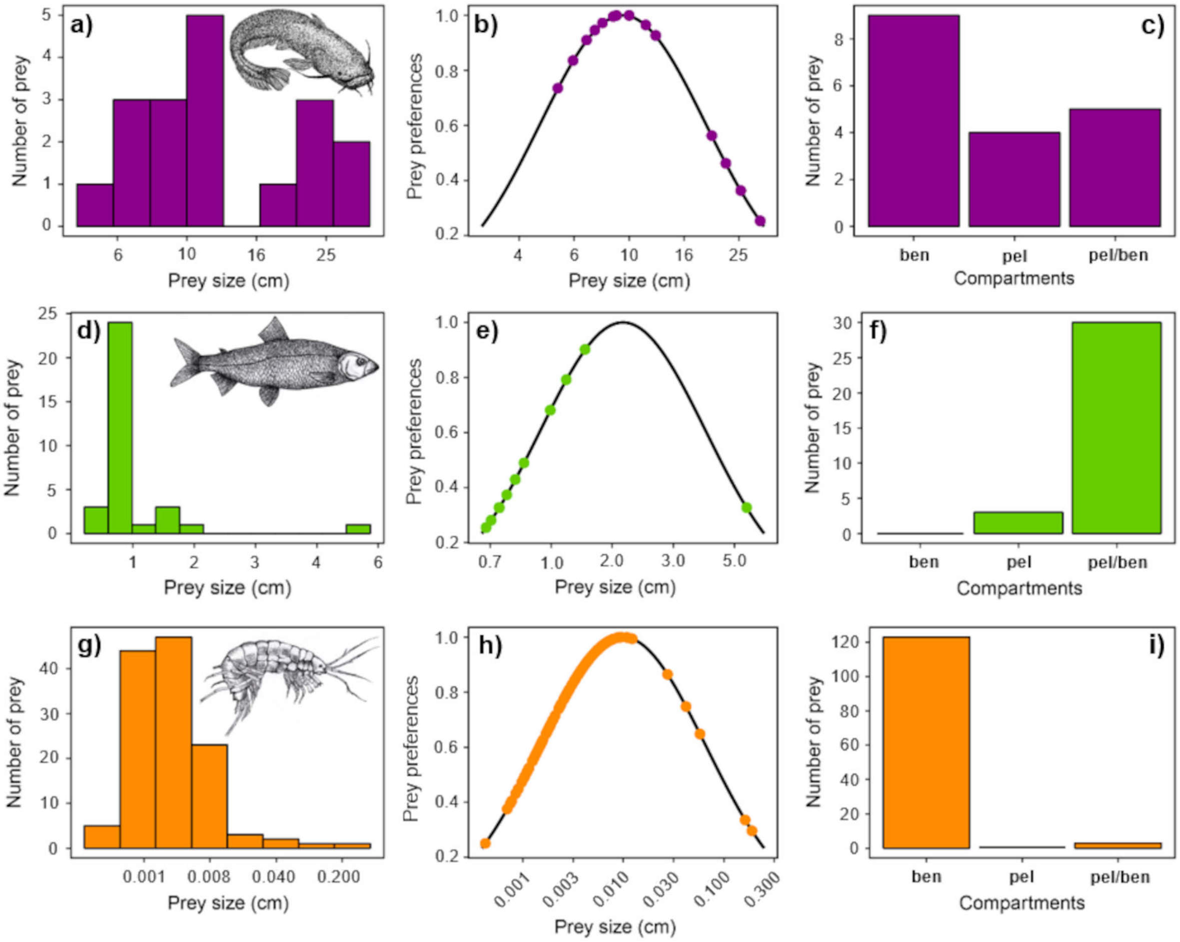

Fig. 4. Inferred prey attributes by the aNM for *Silurus glanis* (a, b, c), *Coregonus lavaretus* (d, e, f), and *Gammarus pulex* (g, h, i). Barplots in the first column show the prey size distributions. The black lines in the second column refer to weighted trophic links and the points relate to individual prey. The barplots in the third column indicate prey compartments (pel = pelagic, ben = benthic, pel/ben = pelagic/benthic).

corresponded to both (Fig. 4c), supporting the affinity of the European catfish for the benthic habitat.

For the whitefish, 33 prey species were inferred, measuring between 0.8 and 5.5 cm. Most prey measured approximately 0.9 cm in Lake Bourget, with the highest prey preference predicted for prey measuring 2 cm (Fig. 4d, e). A total of 30 prey belonged to the pelagic/benthic habitat, while only three were strictly pelagic; no species was exclusively benthic (Fig. 4f). Chironomid and zooplankton species, important in the whitefish diet, were predicted as prey for this predator. However, the predicted feeding range of the whitefish was higher than the empirical range, as *Daphnia* sp. was not included in the predicted diet. *Coregonus* juveniles were also predicted as prey, while cannibalism for this species has been reported only for adults on larvae.

For the gammarid shrimp, 127 prey species were found ranging from 7.10^{-4} cm to 0.2 cm. Most of the prey measured between 1.10^{-3} cm and 0.031 cm (60 prey; Fig. 4g,h). The inferred prey corresponded mainly to benthic algae and detritus therefore belonging to the benthic habitat (124 species) while only three were pelagic/benthic (*Cocconeis placentula*, particulate organic matter and *Ulnaria ulna*; Fig. 4i). The general diet of the gammarid shrimp was hence in agreement with those actually observed in the field.

Food web topology

The connectance C and the linkage density LD of the whole food web were 0.1 and 54.9, respectively (Table 4). Basal species were clearly dominant (60.7%), followed by intermediate species (36.8%), while top predators only represented 5% of the total species inventory. By considering a species habitat trait, the whole food web of Lake Bourget was split into benthic and pelagic food sub-webs. This splitting revealed clear topological differences, particularly for the number of links, the linkage density LD, and the connectance C (Table 4). The benthic food sub-web appeared denser than the pelagic food sub-web with 1668 additional links and a 1.4-fold higher LD. There was a greater percentage of top and intermediate species, and consequently less basal species, in the benthic food sub-web than in the pelagic food sub-web. These two food sub-webs were clearly connected by a set of invertebrates and vertebrates found in both habitats. For the whole food web, a total of 14,145 trophic links characterized the coupling of the pelagic and benthic habitats.

By relating species benthic reliance to their trophic position, a bell-shaped pattern was identified with the fitted values of the GAM (total deviance explained = 73.5%, edf = 2.9, P value < 0.001; Fig. 5). This pattern clearly highlighted differences among the benthic and pelagic food sub-webs within the whole food web that tended to be connected by species with high trophic positions (i.e., fish). Nonetheless, most fish exhibited more than 50% of benthic reliance (up to 90% for some species).

Table 4. Topological metrics of the whole food web and the pelagic and benthic food sub-webs in Lake Bourget.

Topological metrics	Whole food web	Pelagic food sub-web	Benthic food sub-web
Richness	474	207	202
Links (L)	26,037	5112	6780
Directed connectance (C)	0.1	0.1	0.2
Linkage Density (LD)	54.9	24.7	33.6
% Top species (%T)	2.5	2.5	3.2
% Intermediate species (%I)	36.8	23.1	32.9
% Basal species (%B)	60.7	74.4	63.9

DISCUSSION

aNM principle and calibration

We introduced the aNM to infer trophic interactions among aquatic organisms in temperate freshwater ecosystems that necessitate two widely available ecological data: species inventories and their associated body sizes. The model well predicted trophic interactions found in empirical food webs for both vertebrates and invertebrate consumers. Inferences of the mass ratios between prey and predators in Lake Bourget as well as trophic niches for known species were also consistent with those in empirical studies. Finally, the aNM permitted to investigate the structures of food webs and food sub-webs that highlighted the nestedness of the food sub-webs connected by consumers with high trophic positions.

This model expands the approach proposed by Gravel et al. (2013), initially developed for marine fish species, to aquatic freshwater organisms. In contrast to previous allometric models predicting trophic interactions (Gravel et al. 2013, Albouy et al. 2019, Pomeranz et al. 2019), the aNM considers different allometric relationships (i.e., QRs) for invertebrates and vertebrates therefore spanning a large range of consumer body sizes. The inclusion of invertebrates as consumers allowed moving toward a comprehensive approach to characterize temperate freshwater aquatic food webs including primary producers to top predator fish. Another specificity of the aNM relates to the species niche center estimation. Gravel et al. (2013) used the linear model between $\log_{10}$ (prey body size) and $\log_{10}$ (predator body size) to estimate the niche center (c_i) of consumer feeding ranges, while we calculated it as $r_{i\min} + ½\ r_i$ to ensure that c_i corresponds to the niche center regardless of the distribution of prey body sizes. A weighting procedure of trophic links was proposed as a possible means to switch from the binary adjacency matrix $\mathbf{M_{bf}}$ to the weighted adjacency matrix $\mathbf{M_{wf}}$, providing a wide variety of network indices calculation and dynamic modeling where these weighted links may be considered as prey preferences and could be associated with allometric handling times and attack rates to represent potential interaction strengths (Emmerson and Raffaelli 2004).

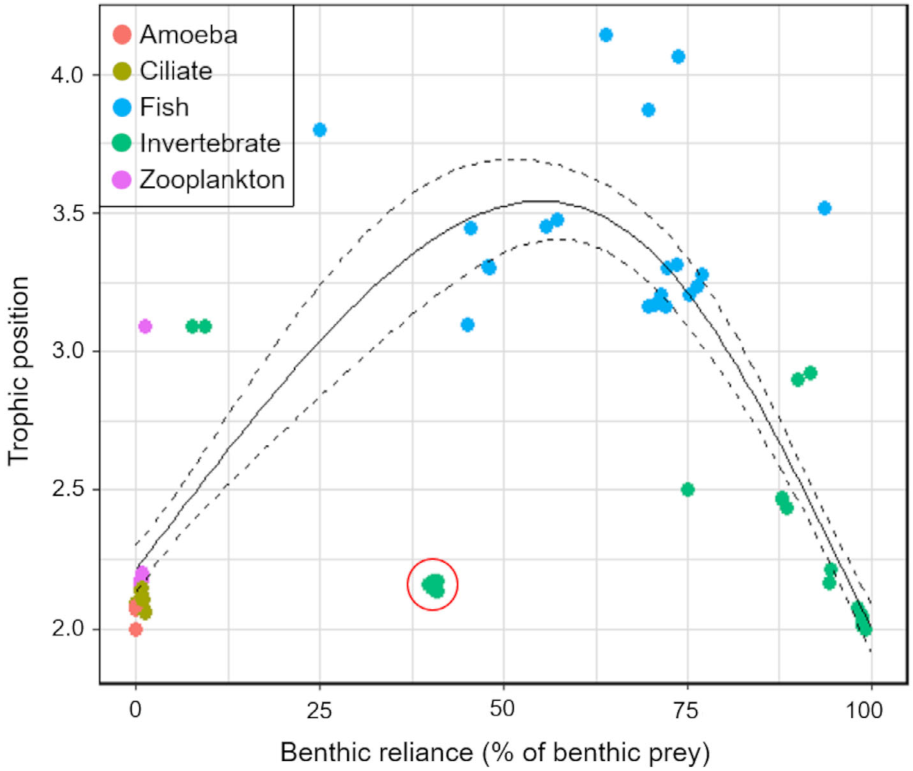

Fig. 5. Benthic reliance of Lake Bourget consumers in relation to their trophic position. The lines represent the GAM fitted values, and the dotted lines represent confidence intervals at 5% and 95%. Primary consumers that can feed on benthic and pelagic resources, circled in red, were not considered in the GAM calculation because they belong to the benthic/pelagic compartment.

The aNM calibration was based on predator-prey body size relationships identified from the diet ranges of ubiquitous species in temperate freshwaters. However, several limitations should be considered for the application of the aNM to ecosystem types other than temperate freshwaters due to local adaptation of trophic behaviors that may lead to significant diet range dissimilarities. For instance, specific mouth shapes allow endemic fish in tropical ecosystems to graze on phytobenthos (e.g., *Tropheus* sp. in Lake Tanganyika; Sturmbauer et al. 1992) or to feed on corals (e.g., *Scaridae*; Bellwood 1985). Models considering complementary parameters such as the allometric diet breadth model of Petchey et al. (2008) seem to be more suitable to infer trophic interactions in specific ecosystems (e.g., substantial inferences for terrestrial, marine or reef ecosystems) but perform better when each food web is fitted separately. In contrast, the aNM requires only limited data and provides comparable temperate freshwater food webs considering the same relationships applied to different species inventories.

aNM validation

The intrinsic validity of the aNM tested among the 13 empirical food webs indicated a satisfactory ability to predict the overall pattern of the empirical food webs with an average accuracy of 81 ± 10% despite variability across food webs. More precisely, the absence of links was better predicted than the presence of links (i.e., higher specificity than sensitivity). The limited sensitivity for five food webs (lower than 50%, two lakes and three ponds) could be explained by two factors inducing link omissions. First, the consumption by microzooplankton of large phytoplankton, both presenting similar body sizes, was not predicted by the aNM. However, this trophic feature is seldomly observed for microzooplankton species that usually feed preferentially on small phytoplankton species (Knisely and Geller 1986, Colina et al. 2016). Second, zooplanktonophagus fish tend to forage on smaller prey than predicted by the aNM. This trophic feature could be accounted for by lowering the feeding range for these species as a complementary trophic niche trait in the refinement process.

The limited aNM specificity was mostly due to the continuous feeding range of consumers inducing false positives compared with empirical data. Nonetheless, empirical studies for food webs may have not identified all possible prey for consumers due to limited sampling efforts (Woodward et al. 2010). If predictions for primary producers were considered in the calculation of the classification metrics (i.e., no trophic links when considered as consumers that increases the true negatives), the average specificity (+3.44) and accuracy (+3.24) would be improved as well as the standard deviations (−5.97 and −2.56, respectively).

Application to Lake Bourget

*Mass ratio.—*The inferred mass ratios for the vertebrates were highly similar to those from Brose et al. (2019; i.e., falling within Brose's estimates ± 1 SD) suggesting plausible inferences of predator–prey trophic links. These results were also in relative agreement with the empirical mass ratios recently reported by Gaeta et al. (2018) for freshwater fish. For invertebrates, the majority of mass ratios were consistent with those in the study of Brose et al. (2019), supporting the plausible predictions for different invertebrate consumers, while 27% of the inferred mass ratios were higher than those reported by Brose et al. (2019) and other previous studies (e.g., Warren and Lawton, 1987, Brose et al. 2006*b*). This divergence originated from the aNM calibration that allows invertebrates to feed on small unicellular organisms such as bacteria and protists. These small prey have been reported in different invertebrate diets, using DNA and isotopic analysis (Deines et al. 2007, Grey 2016), but are rarely identified in common diet analyses (e.g., stomach content analyses). These higher mass ratios compared with those in other studies would thus be plausible in regard to new advances in trophic ecology of invertebrates and in rare previous studies that underlined invertebrates feeding on protists (Layer et al. 2010).

*Trophic niches.—*For the three species studied in Lake Bourget, a vast majority of their inferred prey could be validated by empirical observations (i.e., more than 70% of correct trophic links) representing similar inferences to those in other studies using body size as a niche dimension (Williams et al. 2010, Gravel et al. 2013, Albouy et al. 2019). The empirical omnivorous diet of the European catfish was hence congruent with aNM predictions inferring species from different lake habitats and taxonomical categories (i.e., invertebrates (crayfish) and vertebrates (common perch); Carol et al. 2009, Guillerault et al. 2017). The detritivorous diet of the gammarid shrimp was also correctly predicted with phytobenthos and detritus predominance in accordance with the results in empirical studies (Maltby et al. 2002). The inferred diet of the whitefish provided more ambiguous results. On the one hand, most prey were chironomid species as well as cladocerans (e.g., *Bythotrephes longimanus*) that constitute a large fraction of the whitefish diet. On the other hand, smaller cladoceran species, especially *Daphnia* sp., were not predicted in its diet while this species represents an important resource at different periods of the year. Prey larger than several centimeters (e.g., early perch, young of the year) are also anecdotal. Accounting for planktonophagy as a foraging trait to address this trophic characteristic may be easily implemented in the aNM. It may typically constrain the feeding range to be lower and narrower for zooplanktonophagus fish than for other fish species. However, in its current form, the lower range for whitefish was 0.8 cm, close to the *Daphnia* sp. body size set at 0.5 cm. These results strengthen the plausible inferences of the aNM for large body size range of consumers and could be used to identify potential prey and/or predators for a species.

*Food web topologies.—*The inferred food web exhibited several plausible topological properties compared with empirical ones in the literature. For instance, the connectance of the whole food web of Lake Bourget (0.1) was close to those observed by Dunne et al. (2002) for Lake Tahoe, Mirror Lake, and Bridge Brook Lake (i.e., 0.13, 0.15, and 0.17, respectively).

The examination of the food sub-webs revealed a higher number of links in the benthic habitat, leading to a higher directed connectance and a higher linkage density compared with those in the pelagic food sub-webs. These results indicated a more intricate and denser food sub-web in the benthic habitat than in the pelagic one, revealing the structural asymmetry of the whole food web as initially hypothesized. Such patterns may inform the stability properties for these food sub-webs and highlight a higher stability in the benthic food sub-web than in the pelagic one (Rooney et al. 2006, Rooney and McCann 2012, Landi et al. 2018).

The bell-shape highlighted by the variable benthic reliance of the lake organisms was another interesting outcome of the Lake Bourget food web that may reflect a pervasive feature of aquatic ecosystems (Rooney et al. 2006, McCann and Rooney 2009). Species with high trophic positions tend to be characterized by mixed benthic/pelagic diets, revealing their roles in coupling benthic and pelagic food sub-webs (McCann et al. 2005). High trophic position fish still conserved a dominant benthic reliance, suggesting that benthic production may be especially important to fuel fish populations in this lake. This assertion is in line with several studies that focused on the benthic reliance of fish species in lakes (e.g., Vander Zanden and Vadeboncoeur 2002).

CONCLUSIONS

The aNM was calibrated with empirical diets of ubiquitous freshwater species and exhibited a high intrinsic validity suggesting robust predictions of trophic interactions among a wide size range of consumers in temperate freshwater ecosystems.

The application of the aNM to Lake Bourget permitted us to appreciate the realism of trophic interaction inferences. The comparison of body mass ratios between predators and prey from Lake Bourget was highly consistent with those from a large empirical study referencing more than 8400 trophic links for lake ecosystems. Moreover, the inferred diets in Lake Bourget for three species presenting different body sizes and feeding habits were greatly representative of their diets described in previous studies. The analyses of food web and food sub-web topologies also revealed encouraging outcomes to identify their structures, their interconnections, and the role of fish species in this coupling that was not already studied in this lake.

The aNM depicts all possible trophic interactions that a species could display with its co-occurring species. It must be considered that all the predicted trophic links are obviously not always concomitantly active. Feeding behaviors following seasonal variations may modulate trophic interactions, causing lack of trophic links in empirical consumer diets depending on the sampling effort and prey taxonomic resolution. Thus, the aNM inferences, which do not depend on these variations, might represent long-term and exhaustive diets for aquatic consumers. Limitations could arise for species exhibiting particular trophic features, such as large fish zooplanktonophagy or small-consumer phagotrophy (e.g., smaller than 100 μm), for which additional refinements could be incorporated to account for these species-specificities (e.g., additional predator trait). Nonetheless, this consideration concerned a restricted set of species for the analyzed empirical food webs and for the case of Lake Bourget.

Overall, by considering two distinct relationships according to predator type, this model newly allows to reconstitute trophic interactions between species ranging from bacteria to large fish, that can be subsequently scaled up to the reconstruction of entire food webs, comparable between temperate freshwater ecosystems. Thus, the aNM may represent a valuable method for inferring species trophic interactions in temperate freshwater ecosystems from streams to lakes (e.g., diets, predation pressures, or resource depletion) as well as reconstructing plausible complex food webs only based on species inventories and associated body sizes, opening the way to a vast application area for both ecologists and managers.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3420/full