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Lake food web structure in Teici Nature reserve, Latvia: fish presence shapes functioning of pristine bog lake food webs

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Abstract   Studies on the effects of fish presence on lake ecosystems are widespread but only a few have been conducted in pristine aquatic environments. We employed Ecopath model for assessing food web structure in two fish-inhabited and one fishless lake in a pristine bog area. We hypothesized that: (a) fish absence will raise trophic positions of macroinvertebrate predators; (b) fish predation will lead to higher overall predation rates on zooplankton; (c) fish predation on large bodied zooplankton will result in top-down cascading effect, increasing phytoplankton biomasses. We found that fish have direct and indirect effects on zoobenthic communities. Chironomid biomass was greater and predatory macroinvertebrate groups had a higher trophic level in the fishless lake than in fish-inhabited lakes. Consumption rates of the benthic consumer fraction were greater than that of the planktonic fraction in the fishless lake; the opposite was found in the two lakes with fish. No effects of fish presence on zooplankton were found and we explain this partly by the low water transparency masking the impact of fish. Terrestrial insects constituted a crucial part of adult fish diet and we conclude that terrestrial secondary production contributes to the trophic support of fish communities in pristine bog lakes.

Keywords   Bog lakes · Food web · Ecopath · Latvia · Fishless lakes

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Introduction

With the increase in human population and the resulting need for resources stocking of fish to natural waterbodies has been growing in intensity during the last centuries (Rahel, 2000; Knapp et al., 2001). Thus, many originally fishless lakes have experienced native and non-native fish introductions that have resulted in major changes in the functioning of these rare and unique ecosystems (reviewed in Eby et al., 2006).

Presence/absence of fish is known to have very variable direct and indirect effects on lake ecosystem

structure and functioning (Eby et al., 2006). The effects of fish predation are known to shape the composition and abundance of zooplankton and benthic macroinvertebrate communities. It has previously been found that introduction of fish can lead to decrease in large, non-burrowing macroinvertebrate abundance (Tiberti et al., 2014) and a rapid and or even total elimination of certain taxa (Schilling et al., 2009a). Studies in naturally fishless lakes have demonstrated that they harbor unique macroinvertebrate communities; for that reason, it is extremely important to preserve and study such ecosystems (Schilling et al., 2009b; Drouin et al., 2011). Zooplankton communities are also known to be influenced by the presence of fish as the abundance of larger taxa declines when facing fish predation (Tiberti et al., 2014; Holmes et al., 2017). This in its turn often results in the release of phytoplankton from grazing pressure and a respective rise in algal biomass in a top-down trophic cascading (Scavia et al., 1986; Christoffersen et al., 1993; Jeppesen et al., 2000). The indirect effects of fish on lake food web structure are known to also include changes in trophic position of invertebrate predators (Tate & Hershey, 2003) and a decrease in the trophic efficiency of food webs (Eby et al., 2006).

However, some authors have found that local environmental conditions can play an important role when shaping ecosystem response to presence/absence of fish. It has been suggested that such factors as the size of an ecosystem (Eby et al., 2006), the presence of invertebrate predators (Anas et al., 2015) and littoral habitat complexity (Zaharescu et al., 2016) can serve to mask the effects of fish on the structure of lake food webs.

Most studies comparing the characteristics of fishless and fish inhabited lakes have focused on the effects of fish on certain taxonomic groups (e.g. Schilling et al., 2009b; Harper et al., 2021). Thus, there are fewer studies that have attempted elucidating the effects of fish presence has on all the food web components and their interactions. The Ecopath with Ecosim model (hereafter "Ecopath") has been used since the 1980s (Polovina, 1984), with more than 400 models published to date (Heymans et al., 2016) mostly for studying marine ecosystems. Several studies have demonstrated, however, that Ecopath suits to lacustrine ecosystems as well. Food web structure and functioning (Darwall et al., 2010), carbon fluxes, and the effects of trophic cascading have been studied in lakes under varying degrees of

anthropogenic pressures using Ecopath (Cremona et al., 2018; Bhele et al., 2022).

The studies on the effects of fish introductions on lake ecosystems are widespread but only a few have addressed the differences between the functioning of naturally fishless and fish inhabited lakes. Latvian territory holds some of the last pristine ombrotrophic bogs in Europe affording a chance to study diverse bog lakes untouched by direct human activities.

The Teici Nature reserve comprises 198 km^2 of raised bog habitat in the Eastern part of Latvia. Eighteen lakes are found in the territory of the reserve. Teici bog complex started forming after the last glacial period. Shallow lakes in depressions created by receding glaciers filled with organic sediment resulting in the gradual formation of domed peatlands. The lakes were formed on bog domes and their slopes as a result of accumulated peat breaking due to gravitational pull and forming depressions where water gradually collected (Lācis & Kalniņa, 1998). Most of the small and isolated seepage lakes in the bog complex harbor fish communities (Druvietis et al., 1998). However, five of the lakes are naturally fishless and no attempts to introduce fish have taken place (Druvietis, personal communication). These lakes have never been studied in their entirety but basic parameters such as oxygen and temperature profiles, N and P concentrations and phytoplankton community descriptors measured back in time are available (e.g. Druvietis et al., 1998). Recently, we conducted an intense multi-parameter sampling program over two years.

In this study, we employed Ecopath model for assessing organic matter fluxes and food web structure in two lakes inhabited by fish and one fishless lake for which we had an extensive data set of abiotic and biotic parameters. We hypothesized that: (a) fish absence will raise trophic positions of macroinvertebrate predators, (b) fish predation will lead to higher overall predation rates on zooplankton, and (c) fish predation on large bodied zooplankton will result in top-down cascading effect, increasing phytoplankton biomass.

Materials and mathods

Two lakes with fish communities (Lake Ciematnieka, Lake Tolkajas) and one fishless lake (Lake Vertezis)

were chosen as study lakes and are referred to as "Ciematnieka", "Tolkajas", "Vertezis" hereafter. All the study lakes (Table 1) are in the same general area of the ombrotrophic bog ecosystem and are surrounded by the sphagnum moss mat and scattered groves of *Pinus sylvestris* L., 1753. Northwesterly wind direction predominates (Center for Environment, Geology and Meteorology of Latvia, 2023). All the study lakes are seepage lakes, there are no inflowing or outflowing rivers or ditches.

Sampling took place during 2021 and 2022 and each lake was sampled multiple times over the period and covered all seasons (Table 2).

Vertical dissolved oxygen and temperature profiles were taken at 0.5 m intervals at the deepest location in each lake while pH and specific conductivity were measured at 0.5 m depth. These measurements were performed using a calibrated Hach HQ40D multi meter. Secchi depth was recorded using a standard 30 cm diameter Secchi disc.

Two parallel depth integrated water samples were collected at 1 m intervals from 0.5 m below the surface to 0.5 m above the bottom using a Ruttner sampler) at the deepest part of each study lake. Subsequent sub-sampling of the pooled water included 2 l for hydrochemistry and 1 l for phytoplankton. The second water sample was used for collecting zooplankton. Sub-surface water samples were collected in the littoral areas (littoral samples).

In the laboratory nutrient concentrations were determined according to standard protocol (e.g. Grasshof et al., 1983) The concentrations of ammonium (NH_4^+), phosphate (PO_4^{3-}), nitrite (NO_2^-), nitrate (NO_3^-), total nitrogen (TN), total phosphorus (TP) and chlorophyll-a (Chla) were measured. Data on pH, electrical conductivity (EC (µS/cm)), DOC (mg/l), Secchi depth (m) and nutrient concentrations (mg/l) is reported in Table 1 and Supplementary Table 5.

The phytoplankton samples were fixed with acid Lugol's solution. Subsamples of 25 ml of fixed samples were settled in a sedimentation chamber for 12 h and counted according to the Uthermöl technique using an inverted microscope (Leica DMI 3000, Leica Microsystems GmbH, Germany) at × 400 magnification. For each phytoplankton taxon (Tikkanen et al., 1992), at least 20 individuals were measured, except some species that had less than 3–5 individuals to calculate phytoplankton size and biovolume.

Table 1 Basic characteristics of the study lakes

Lake	Presence of fish	Size (ha)	Average depth (m)	Max. depth (m)	pH	EC (µS/cm)	DOC (mg/l)	Secchi depth (m)	TP (mg/l)	Chl a (µg/l)
Ciematnieka	Yes	54.7	1.3	2	4.1–4.3	36–38	29.6–33.1	0.3–0.5	0.105–0.125	0.9–52.4
Tolkajas	Yes	14.3	5.2	7.5	4.7–5.2	21–25	13.5–16.0	0.7–1.0	0.018–0.029	0.6–13.8
Vertezis	No	18.6	4.2	6.4	5.0–5.5	16–17	16.9–24.2	0.4–1.0	0.034–0.098	6–292.3

The total range of values for all the measurements provided for pH, EC, DOC, Secchi depth, TP and Chla

Table 2 Sampling periodicity

Item	Number of stations (location)	Sampling intensity	Time period
Hydrochemistry	1 (at the deepest point in a lake)	Every 4–8 weeks	May 2021–October 2022
Phytoplankton	2 (littoral and pelagial)	May, August, November	2021–2022
Zooplankton	2 (littoral and pelagial)	May, August, November	2021–2022
Macrozoobenthos	3–4 (littoral and pelagial)	May, August, November	2021–2022
Fish community	8–10 (different depth zones)	July	2021

Zooplankton sampling from the pelagic was performed by filtering the depth integrated water sample (8–10 l) through a conventional plankton net (50 cm diameter, 50 μm mesh size). In the littoral zone 50 l of water was collected from 0.3 to 0.5 m depth and filtered through the zooplankton net. Care was taken not to disturb the sediment. These samples were preserved with 96% ethanol. The entire sample was washed and adjusted to have a total volume of 100 ml, and thereafter counted to get the relative species' distribution. For identification and taxonomy, Flössner (2000) and Hudec (2010) were used. The individual biomass of dominant Cladocera and Copepoda species was estimated from length–weight relationships (Balushkina & Winberg, 1979) based on length measurements of 20 individuals of each species, or fewer if abundance was low.

Macrozoobenthos was sampled at three independent and pre-determined stations, covering both littoral and open water areas. Pelagic samples were collected using an Ekman sediment grabber (sampling area 0.0225 m^2). A total of five replicates per station were collected and pooled. Littoral samples were collected using a scraper (sampling area 0.25 m^2, mesh size 0.5 mm), two replicates per station were collected and pooled. Samples were sieved in the field with 0.5 mm sieve and preserved with 96% ethanol. Identification was performed according to Timm (2015). The number of macrozoobenthos taxa, and their abundance per square meter was calculated and their biomass was estimated from their weight.

For fish community sampling NORDIC multimesh survey nets were used and stratified random sampling was applied proportional to the area of the depth zones (CEN, 2015). Additional gillnets with 60 and 70 mm mesh size (30 × 1.5 m) were used concurrently and in the same manner. Species, total length, and weight of each individual fish were recorded. Bony structures for age determination were collected from up to five individuals from each 1 cm size class. Opercular bones were used for perch and scales for roach age determination. Stomach contents were collected from up to 5 individuals from each 1 cm size class of all the fish species. The samples were preserved in 96% ethanol, prey items were identified to the lowest possible taxon, enumerated, and weighed.

Model definition

We employed Ecopath model for assessing organic matter fluxes and food web structure in Lake Tolkajas, Ciematnieka and Vertezis. Ecopath main equations are described in Christensen and Walters (2004) and are briefly summarized in the supplementary material. The first Ecopath master Eq. (1) describing the production of group i considers that production is equal to the biomass taken by predation, fishing, natural mortality and export:

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + M0_i \times B_i \qquad (1)$$

where P_i is the production, Y_i the fishery catch rate, $M2_i$ the predation mortality of biomass B_i, E_i—the net migration rate, BA_i—the biomass accumulation rate, and $M0_i$—the mortality (other than predation or fishing). Ecotrophic Efficiency (EE_i), which is the fraction of the production that is used in the system can be employed for calculating $M0_i$ based on production and biomass, as in Eq. (2):

$$M0_i = \frac{P_i \times (1 - EE_i)}{B_i} \qquad (2)$$

Predation on i ($M2_i$, Eq. 1) is obtained from consumption and prey composition as in Eq. (3):

$$M2_i = \sum_{j=1}^{n} \frac{Q_j \times DC_{ji}}{B_i} \tag{3}$$

where n predator groups j feed on i. The total consumption rate of j is Q_j, DC_{ji} being the fraction of predators' diet contributed by i. The gross food conversion efficiency, g_i is given by Eq. (4):

$$g_i = \frac{(P/B)_i}{(Q/B)_i} \tag{4}$$

The production to biomass of i (P_i/B_i) value is calculated with Eq. (5):

$$\frac{P_i}{B_i} = \frac{Y_i + E_i + BA_i + \sum_j Q_j \times DC_{ji}}{B_i \times EE_i} \tag{5}$$

Finally, EE_i is calculated with the Eq. (6) below:

$$EE_i = \frac{Y_i + E_i + BA_i + B_i \times M2_i}{P_i} \tag{6}$$

The model requires three of the five Ecopath input parameters (B_i, P_i/B_i, P_i/Q_i, Q_i/B_i, EE_i) to be known to estimate the missing ones. Generally, EE_i is the parameter that is left to model estimation because it is the most difficult to assess independently. We followed the same approach during the modelling process and used B_i, P_i/B_i, and Q_i/B_i as inputs (Christensen & Walters, 2004) except in the case of terrestrial insects. As the biomass of terrestrial insects had not been measured, we assumed an EE of 0.99 considering aerial organic matter fluxes are heavily subsidizing seepage, nutrient poor lakes with small catchments (Cremona et al., 2019).

Fish were sampled by gillnetting which is not a quantitative method. Fish biomass (per surface unit) in both study lakes comprising perch was considered similar to that of other monospecific small lakes from the Baltic region and set at 0.2 t/km^2 (Ojaveer et al., 2003; Cremona et al., 2018).

Parametrization

We modeled 10, 12 and 8 functional biotic groups in lakes Tolkajas and Ciematnieka, and Vertezis respectively, and one group of detritus in every lake. Functional groups were the following: phytoplankton, zooplankton (copepods, cladocerans), benthic macroinvertebrates (chironomids, odonate larvae,

trichopterans, isopods, chaoborids, dytiscids), two stanzas of perch (juvenile (< 13 cm), adult), and one group of terrestrial insects falling on the lake surface. Groups that were specific to Ciematnieka and Vertezis were two macroinvertebrate taxa: chaoborids and dytiscids. The first group is specialized in capturing zooplankton (Rudstam, 2009) while the second one is a generalist predator. Because of the high-DOC content associated with bog lakes, high light extinction coefficients as well as low pH, periphytic and macrophyte primary production in the study lakes was observed to be very low. We therefore decided to model phytoplankton as the only primary producer in these lakes. As lakes Tolkajas and Ciematnieka hosted only one fish species (perch), we split that group into the two above-mentioned stanzas to capture changes in growth, mortality, recruitment processes and ontogenic diet shifts better (Christensen & Walters, 2004). Growth rate (von Bertalanffy, 1938)) of perch in small bog lakes is expected to be low, we consequently used for this parameter the values from the littoral zone in Lake Võrtsjärv, Estonia (Cremona et al., 2018) where perch growth rates were the lowest and comparable to that of small lakes (Ojaveer et al., 2003). As there is no migration of fish in these seepage lakes, recruitment power was set to 1. The other parameters such as relative biomass accumulation rate (BA_i/B_i) and the ratio of weight at maturity by asymptotical weight (W_m/W_∞) were calculated from the life-history tool in Fishbase (Froese & Pauly, 2023).

Detritus biomass was assessed with the empirical Eq. (7) from Christensen and Pauly (1993):

$$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} z_{eu} \tag{7}$$

with D being the biomass of detritus (g/C/m^2), PP the primary production (g/C/m^2/y) and z_{eu} the euphotic depth (m).

Phytoplankton primary production was assessed from chlorophyll a by calculating the positive slope of chla growth during the growing season. For invertebrates (zooplankton and benthos), P/B was calculated with the empirical relationship from Brey (2001) with weight conversion factors of 0.209 and 0.16 for zooplankton and macroinvertebrates, respectively (Ricciardi & Bourget, 1998). Natural mortality rates ($M0 + M2$) of fish were assessed from Fishbase life history tool (Pauly, 1980; Palomares & Pauly, 1998)

using temperature measurements from May as input values.

Diet composition (*DC*) of fish was assessed from stomach contents (in grams) surveys conducted in the two lakes. Diet of invertebrates were assigned based on specialist knowledge and following broadly the literature: zooplankton feed on phytoplankton, chaoborids on zooplankton, odonates and dytiscids on benthos and zooplankton, detritivores (chironomids, isopods, trichopterans) on detritus and phytoplankton, and terrestrial insects falling on lake surface were assigned only to detritus so that they do not affect lower trophic levels (in Ecopath, every group must be assigned a diet). The *DC* of groups for the three study lakes are compiled in the Supplementary Tables 2–4.

To constrain model outputs within realistic ranges during model calibration, group biomass and fish diet were considered "hard" parameters whereas *P/B* and diet composition of other groups were "soft" parameters. "Hard" parameters are reliable measurements and calculations that were not modified in the first stages of the calibration. "Soft" parameters on the other hand were adjusted first for calibrating the model in case of a group *EE* exceeded 1. In order to achieve *EE* values lower than 1 (which is mandatory from a thermodynamic perspective and a *sine qua non* condition for model running) we changed *DC*, first of the group with the highest *EE*. This procedure was repeated until all *EE* were lower than the unity. We followed Heymans et al. (2016) guidelines about the best practice in Ecopath, which include checking if the recommended prebalance diagnostics ("PREBAL") were satisfying thermodynamically (Link et al., 2010).

Results

Food web structure

The largest discrepancy between the functional groups of the study lakes lied in their phytoplankton biomass (Fig. 1). The biomass of Vertezis (120 t km^2) was ten times larger than that of Ciematnieka and twenty times more than that of Tolkajas. The primary-consumer-to-primary-producer biomass ratio was 0.18 in Tolkajas, 0.42 in Ciematnieka and only 0.02 in Vertezis. Although differing by the biomass of their functional groups, the three lakes exhibited similar structures in the lower trophic levels (from primary to producers to primary consumers) where zooplankton and Chironomids were the main primary consumers. They differed markedly in the secondary and tertiary consumer guilds (i.e. trophic levels > 2, Fig. 1). Perch, which is the top predator in Tolkajas and Ciematnieka occupied different trophic levels: in Ciematnieka perch had a higher trophic level (TL = 3.8 for juvenile, 3.3 for adults) than in Tolkajas (TL = 3 for juvenile, 3.1 for adults). In the fishless lake (Vertezis), the invertebrate top predators such as dytiscids and odonates occupied the same trophic levels (TL = 3.37 and 3.31 respectively) as adult perch do in lakes with fish. The trophic level of zooplankton did not differ between the fishless and the fish-inhabited lakes (Table 3).

Trophic linkages were strongest between phytoplankton and the four main grazer groups (copepods, cladocerans, trichopterans, chironomids; Fig. 1). Conversely, with the exception of detritivorous isopods, detritus made up no more than 30% of the *DC* for all consumer groups in the three lakes (Supplementary Tables 2–4). In the upper trophic levels, trophic linkages were the strongest between Chironomids and Odonates in Tolkajas, whereas Cladocerans and Chaoborids in Vertezis. The diversity of predatory groups increased food web connectivity in Ciematnieka as compared to the other two lakes and no trophic relationship dominated in the two upper trophic levels. The *EE*'s (a proxy of live biomass consumption by the ecosystem) of trichopterans and chironomids was greater in Ciematnieka and Vertezis relative to Tolkajas. The two study lakes hosting fish displayed low predation rates and *EE*'s of zooplankton (*EE* < 0.15). In both lakes, perch had only a limited impact on zooplankton biomass. Conversely, *EE*'s were close to 1 for all consumer groups in fishless lake Vertezis except for phytoplankton of which grazing pressure was consistently weak (Tables 4, 5, 6).

Organic matter fluxes

Modelled production fluxes differed strongly between the three lakes. In Tolkajas, the ratio between primary production from phytoplankton and production from primary consumers was 0.11, whereas it was 0.2 in Ciematnieka, and only 5×10^{-3} in Vertezis (Fig. 1). The lower trophic levels (primary producers and consumers)

Fig. 1 Flow diagram of Tolkajas (top), Ciematnieka (center) and Vertezis (bottom) food webs. Trophic levels are indicated by the numbered horizontal lines. Group node size is proportional to its top-down cascading effect, increasing phytoplankton biomasses production whereas color and thickness of lines are correlated to the intensity of linkages (thicker > thinner, red > blue). B denotes biomass
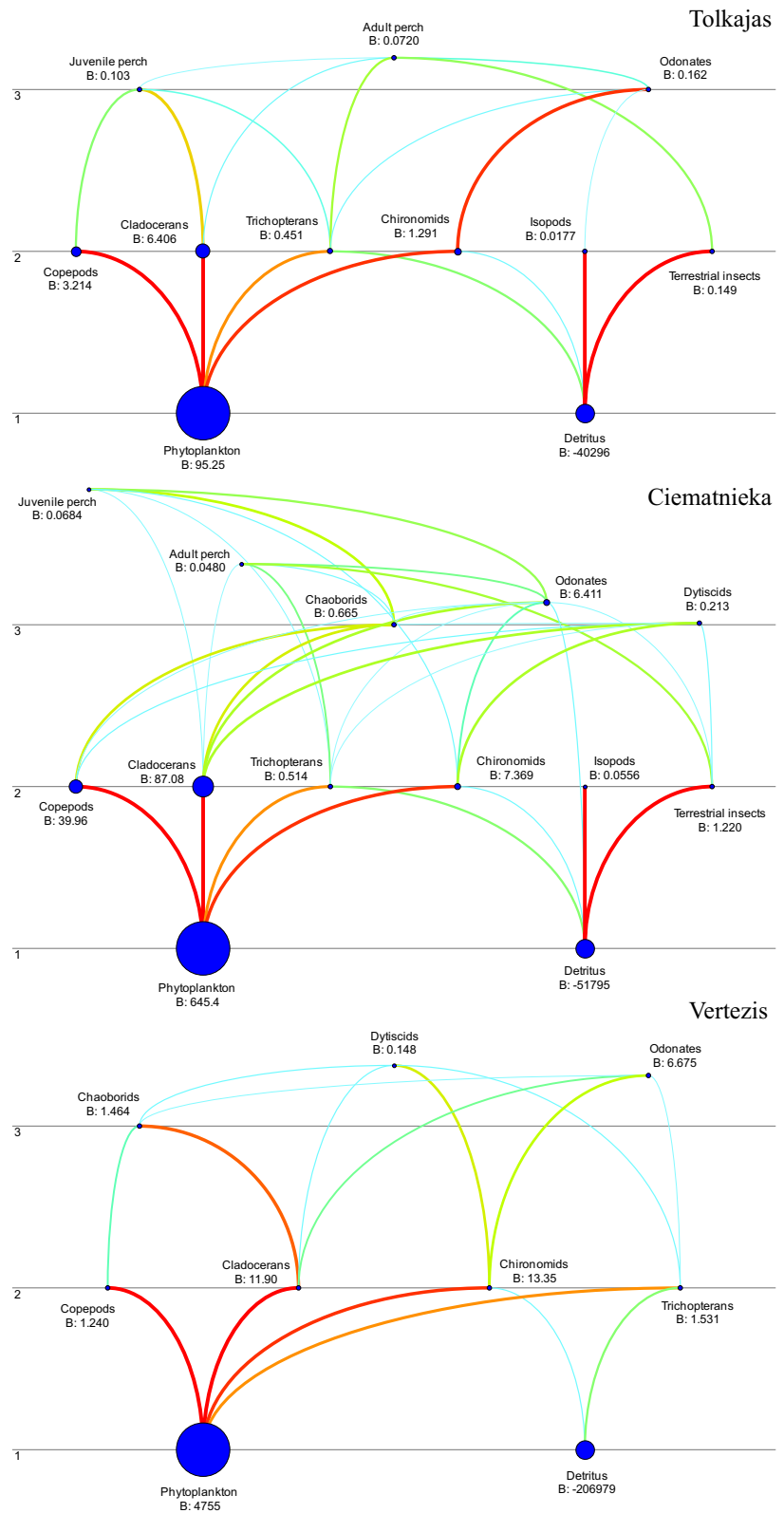
Table 3 Outputs of organics matter fluxes in the three study lakes

Parameter	Vertezis	Tolkajas	Ciematnieka	Unit
Sum of all consumption	145	47	574	t/km^2/year
Sum of all exports	4675	68	329	t/km^2/year
Sum of all respiratory flows	79	26	316	t/km^2/year
Sum of all flows into detritus	4682	70	340	t/km^2/year
Total system throughput	9583	213	1560	t/km^2/year
Sum of all production	4791	107	789	t/km^2/year
Calculated total net primary production	4755	95	645	t/km^2/year
Total primary production/total respiration	59	3.60	2.04	
Net system production	4675	68	329	t/km^2/year
Total primary production/total biomass	37	11	32	
Total biomass/total throughput	0.01	0.03	0.01	year^{-1}
Total biomass (excluding detritus)	128	8.22	20	t/km^2
Connectance Index	0.28	0.2	0.236	
System Omnivory Index	0.05	0.01	0.06	
Ecopath pedigree index τ	0.5	0.47	0.47	
Measure of fit, t^*	1.41	1.52	1.72	

Table 4 Basic input data and ecological output values estimated by Ecopath for Lake Tolkajas (left columns) food web

Group no.	Group name	B_i (t)	P_i/B_i (year^{-1})	Q_i/B_i (year^{-1})	EE_i	g_i (= P_i/Q_i)	Trophic level
1	Perch juvenile	0.12	0.8	.4.89	*0.05*	*0.16*	3
2	Perch adult	0.18	0.4	2.5	*0.16*	*0.16*	3.19
3	Copepods	0.15	20.6	*82.4*	*0.05*	0.25	2
4	Cladocerans	0.36	17.6	*70.4*	*0.06*	0.25	2
5	Odonates	0.10	1.48	*5.92*	*0.41*	0.25	3
6	Trichopterans	0.23	1.96	*7.84*	*0.68*	0.25	2
7	Chironomids	0.45	2.87	*11.48*	*0.45*	0.25	2
8	Isopods	0.01	1.66	*6.64*	*0.36*	0.25	2
9	Terrestrial insects	*0.07*	2.1	*8.4*	*0.99*	0.25	2
10	Phytoplankton	6.52	14.6	–	*0.46*	–	1
11	Detritus	4.03	–	–	*0.02*	–	–

All terms are defined in Eqs. (1) to (7). Values in italics are calculated by the model

monopolized 65% and 76% of the total system throughput in Tolkajas and Ciematnieka, respectively but only 51% in Vertezis. Flows above trophic level III in Tolkajas and trophic level IV in Ciematnieka and Vertezis were virtually non-existent. In Tolkajas and Ciematnieka, detritus was a relatively minor component of the carbon flow, contributing to 33% and 22% of the total system throughput in, respectively. Conversely, in Vertezis, detritus represented nearly half (49%) of the total throughput owing to the large unexploited phytoplankton biomass.

The scale of organic matter fluxes was markedly different between the three lakes, with Ciematnieka processing one order of magnitude more organic matter than Tolkajas (Table 3) and Vertezis processing much more than Ciematnieka. If the two fish lakes were solid net exporters of organic matter (68 and 329 t km^2 year for Tolkajas and Ciematnieka, respectively), the fishless lake exported 4675 t km^2 year. Although Ciematnieka food web net primary production was six times greater than that of Tolkajas, respiration flows were also much higher in that lake, so Tolkajas was more autotrophic than Ciematnieka.

Table 5 Basic input data and ecological output values estimated by Ecopath for Lake Ciematnieka food web

Group no.	Group name	B_i (t)	P_i/B_i (year^{-1})	Q_i/B_i (year^{-1})	EE_i	$g_i (= P_i/Q_i)$	Trophic level
1	Perch juvenile	0.08	0.8	4.891614	*0*	*0.16*	3.83
2	Perch adult	0.12	0.4	2.5	*0*	*0.16*	3.37
3	Copepods	1.08	37	*148*	*0.06*	0.25	2
4	Cladocerans	3.11	28	*112*	*0.13*	0.25	2
5	Chaoborids	0.06	11.08	*44.32*	*0.71*	0.25	3
6	Odonates	2.41	2.66	*10.64*	*0.83*	0.25	3.13
7	Dytiscids	0.03	6.67	*26.68*	*0*	0.25	3.01
8	Trichopterans	0.07	7.24	*28.96*	*0.72*	0.25	2
9	Chironomids	0.87	8.47	*33.88*	*0.74*	0.25	2
10	Isopods	0.01	5.56	*22.24*	*0*	0.25	2
11	Terrestrial insects	*0.17*	7.06	*28.24*	0.99	0.25	2
12	Phytoplankton	12.08	53.43	–	*0.83*	–	1
13	Detritus	5.18	–	–	*0.03*	–	–

All terms are defined in Eqs. (1) to (7). Values in italics are calculated by the model

Table 6 Basic input data and ecological output values estimated by Ecopath for Lake Vertezis food web

Group no.	Group name	B_i (t)	P_i/B_i (year^{-1})	Q_i/B_i (year^{-1})	EE_i	$g_i (= P_i/Q_i)$	Trophic level
1	Copepods	0.04	31	*124*	*0.94*	0.25	2
2	Cladocerans	0.35	34	*136*	*0.95*	0.25	2
3	Chaoborids	0.16	9.15	*36.6*	*0.95*	0.25	3
4	Dytiscids	0.02	7.39	*29.56*	*0.8*	0.25	3.37
5	Odonates	1.48	4.51	*18.04*	*0.8*	0.25	3.31
6	Chironomids	1.87	7.14	*28.56*	*0.92*	0.25	2
7	Trichopterans	0.26	5.89	*23.56*	*0.91*	0.25	2
8	Phytoplankton	124	38.35	*124*	*0.02*	0.25	1
9	Detritus	20.7	–	–	*0.0001*	0.25	–

All terms are defined in Eqs. (1) to (7). Values in italics are calculated by the model

Nevertheless, both lakes were solidly autotrophic ($PP/R = 3.6$ for Tolkajas, 2 for Ciematnieka) whereas the fishless lake Vertezis displayed the highest PP/R ratio of 59. All three lakes displayed very low omnivory indexes (< 0.07), indicating a strong specialization of consumers. Another indicator of ecosystem maturity, connectance index, was similar for the three systems and comprised between 0.2 and 0.28. Ecopath pedigrees were 0.47–0.5 for the three models.

Modelled consumption rates differed markedly between lakes and functional groups (Tables 7, 8, and 9). Lake Ciematnieka exhibited the largest consumption rates of all the studied systems, owing to the high activity level of its planktonic consumers.

Consumption rates of the planktonic fraction of consumers (copepods, cladocerans and chaoborids) were greater by one order of magnitude than those of the benthic fraction (chironomids, odonates, isopods, trichopterans, dytiscids) in Tolkajas (37 vs 7 t km^2 year) and in Ciematnieka (509 vs 57 t km^2 year). However, in the fishless lake Vertezis, consumption rates of the benthic fraction (86 t km^2 year was actually greater than that of the planktonic fraction (58 t km^2 year). In the two lakes where perch was present, consumption rates were within the same order of magnitude (1.07 t km^2 year in Tolkajas vs 0.71 t km^2 year in Ciematnieka). Detritus "consumption" which corresponds to the flux of organic matter that is not processed by consumers was much greater in

Table 7 Consumption rates (t/km²/year) by different biotic groups in Tolkajas as calculated by the model

Group no.	Group name	1	2	3	4	5	6	7	8	9	11
1	Juvenile perch		0.005								0.22
2	Adult perch		0.01								0.14
3	Copepods	0.18									5.59
4	Cladocerans	0.35	0.04								11
5	Odonates		0.06								0.22
6	Trichopterans	0.08	0.16			0.05					0.5
7	Chironomids					0.58					1.74
8	Isopods					0.006					0.02
9	Terrestrial insects		0.14								0.12
10	Phytoplankton			12	25		1.26	4.64			50
11	Detritus						0.54	0.51	0.07	0.59	
	Sum	0.62	0.45	12	25	0.64	1.80	5.16	0.07	0.59	**70**

Table 8 Consumption rates (t/km²/year) by different biotic groups in Ciematnieka as calculated by the model

Group no.	Group name	1	2	3	4	5	6	7	8	9	10	11	13
1	Juvenile perch												0.15
2	Adult perch												0.10
3	Copepods					1.32	1.02	0.08					69
4	Cladocerans	0.02	0.003			1.32	10	0.34					144
5	Chaoborids	0.18	0.02				0.25	0.008					0.71
6	Odonates	0.14	0.07				5.12						6.19
7	Dytiscids												0.38
8	Trichopterans	0.02	0.08				0.25	0.008					0.55
9	Chironomids	0.04					5.12	0.34					7.75
10	Isopods												0.1
11	Terrestrial insects		0.11				1.02	0.06					0.98
12	Phytoplankton			159	348				1.43	26			109
13	Detritus						2.56		0.61	2.94	0.22	4.88	
	Sum	0.41	0.3	159	348	2.65	25	0.85	2.05	29	0.22	4.88	340

Table 9 Consumption rates (t/km²/year) by different biotic groups in Vertezis as calculated by the model

| Group no.	Group name	1	2	3	4	5	6	7	9
1	Copepods			1.17					1.06
2	Cladocerans			4.68	0.05	6.67			10
3	Chaoborids				0.05	1.33			1.24
4	Dytiscids				0.11				0.14
5	Odonates					5.33			6.67
6	Chironomids				0.29	12			11
7	Trichopterans				0.05	1.33			1.36
8	Phytoplankton	4.96	47				48	4.28	4650
9	Detritus						5.34	1.83	
	Sum	4.96	47	5.85	0.59	26	53	6.12	4682

Vertezis compared to the other lakes (4682 t km^2 year vs 70 and 340 t km^2 year for Tolkajas and Ciematnieka respectively).

Mixed trophic impacts

According to the mixed trophic impacts (MTI) calculations, the trophic interactions in Tolkajas displayed a larger amount of negatively or positively impacted groups compared to Ciematnieka (Fig. 2), with stronger intraspecific competition also in this lake for perch and chironomids. Juvenile perch impact was strongly negative on zooplankton whereas that of adults was slightly positive. The trophic relationships between the two perch stanzas and zooplankton especially were less polarized in Ciematnieka with the exception of chaoborids which were actively preyed upon by juveniles in that lake. In Ciematnieka, the large odonate group impacted negatively nearly all invertebrate taxa with the exception of copepods and isopods. Phytoplankton carried a positive effect on groups consuming it in both lakes whereas some groups such as isopods and dytiscids (in Ciematnieka) had a too low biomass or connectivity to affect other groups in a significant way. The food web interactions of Vertezis were even more polarized than that of the two other lakes, with several groups (chironomids, odonates) carrying strongly negative effects on their prey (lower trophic levels) or competitors (equal trophic levels).

Discussion

The overall goal of this study was to analyze the effect of fish presence on the food web structure in undisturbed bog lakes. We modelled trophic interactions in the ecosystems to elucidate whether fish absence will change the trophic role of macroinvertebrate predators. We also explored if fish predation on zooplankton will result in top-down cascading effect, increasing phytoplankton biomass, as has been found in many temperate lakes. We discuss below the trophic structure of the study lakes and examine the three hypotheses presented in the introduction. Additionally, we discuss our findings that terrestrial secondary production plays an important role in supporting the lake food webs.
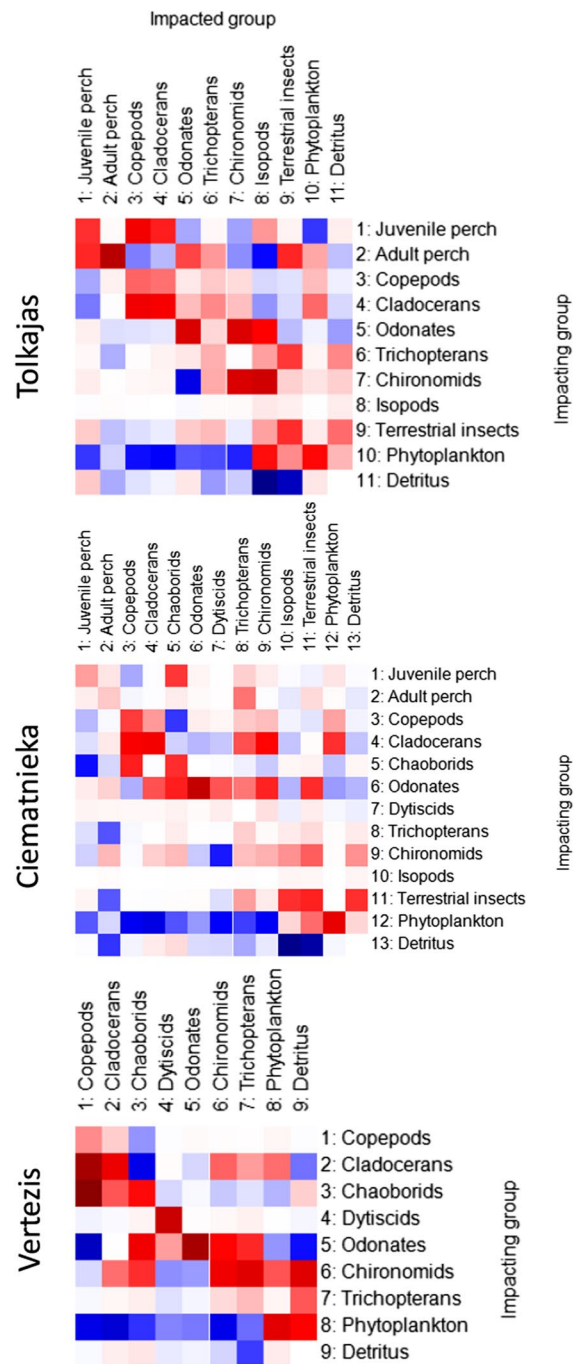
Fig. 2 Mixed Trophic Impacts (MTI) for Tolkajas (top), Ciematnieka (center), and Vertezis (bottom). Blue color corresponds to a positive impact, red to a negative one; color intensity indicating the impact strength. For example, juvenile perch impacted positively phytoplankton in Tolkajas and adult perch positively isopods

Trophic position of macroinvertebrates

The same invertebrate predators (dytiscids, odonates and, to a lesser extent, chaoborids) were found in all the study lakes. These predator groups are known to dominate zoobenthic communities across the spectrum of environmental conditions and to be able to tolerate highly acidic conditions (e.g. Rask et al., 1998; Kesti et al., 2022). The three lakes were also found to be very similar in the terms of pH, nutrient concentrations and other physicochemical parameters (Table 1 and Supplementary Table 5) but displayed different food web structures. The absence of fish in Vertezis corresponded with a higher trophic level of macroinvertebrate groups, making this lake distinct as compared to the other two study lakes. Thus, our findings agree with other studies that invertebrates reach greater population size and occupy wider trophic niches in the absence of fish predators (Johansson & Samuelsson, 1994; Tate & Hershey, 2003). Additionally, although some authors have not found significant effect of fish on macroinvertebrate trophic positions (Detmer & Lewis, 2019), it is generally accepted that fish suppress large-bodied invertebrate predators and interfere with their foraging and hunting patterns (e.g., Tate & Hershey, 2003; Schilling et al., 2009b). Finally, we also found that perch fed on benthic invertebrates throughout their ontogenetic development (Supplementary Figures 2 and 3) as in other studies from across Europe (Rask, 1986; Estlander et al., 2010). This combined information is consistent with a lower trophic level of macroinvertebrates in "fish-inhabited conditions".

Similarly, we found that consumers belonging to the benthic fraction (i.e. most macroinvertebrates with the exception of chaoborids) exhibited greater consumption rates in the fishless Lake Vertezis than in the two other lakes where planktonic consumers showed higher consumption rates than the benthic ones. These results agree with the literature in showing that benthic invertebrates are expected to exploit more trophic niches when fish are absent (Vadeboncoeur et al., 2005; Milardi et al., 2016).

Top-down cascading effects of fish predation on the lake food webs

Contrary to previous findings (Holomuzki et al., 1994; Fisher, 2013), vertebrate predators (and the presence of planktivorous chaoborids in Ciematnieka) did not modify the trophic position of zooplankton as it was the same in all the study lakes. Additionally, the EE's of zooplankton ($0.05 < EE < 0.15$) as well as their predation rates in the fish-inhabited lakes remained low and the zooplankton communities were similar in size and species distribution between fishless and fish-inhabited lakes (Zagars et al., 2023, in preparation). This combined information contradicts previous findings as it has often been described that juvenile perch exhibit high predatory pressure on zooplankton (Romare et al., 1999; Nunn et al., 2012) and fish predation in general is known to affect zooplankton abundance as well as communities' species and size distribution (Brucet et al., 2010; Tiberti et al., 2014; Holmes et al., 2017). We find that the effect of fish predation on zooplankton is highly dependent on local environmental conditions. Indeed, it has been found that in dark lakes with high DOC content visual predators'—such as perch' and chaoborids'—feeding efficiency on zooplankton is significantly hampered (Estlander et al., 2009; Estlander et al., 2010; Rask et al., 2014). Thus, the top-down trophic cascade does not seem to extend to the planktonic organisms of the food web. In eutrophic lakes, zooplankton cannot efficiently graze on phytoplankton because it is often dominated by large colonial or filamentous cyanobacteria (Cremona et al., 2018; Bhele et al., 2022), that were not found in the study lakes (Supplementary Table 6). In the humic study lakes this same effect is mostly due to the low visibility. Thus, as fish predation had no effect on zooplankton communities we found no cascading effect of fish predation on phytoplankton communities. The highest microalgal biomasses were observed in the fishless Vertezis.

Finally, according to Vadeboncoeur et al. (2005), top-down controls in lacustrine food webs are enabled by omnivory, especially when food webs are fueled by dual primary production from periphyton and phytoplankton. The observed low degree of omnivory (< 0.07) and the reliance of the food web on a unique autochthonous primary producer (phytoplankton) suggests furthermore that top-down mechanisms alone are not efficient enough to structure the study lakes' food webs.

The effects of a combination of bottom-up and top-down mechanisms on the lake food webs

We observed that the biomass of chironomids, which are the main benthic herbivores in the study lakes, is twice larger in fishless Vertezis than in fish inhabited Ciematnieka and four times larger than in Tolkajas. Chironomidae are known to exhibit high feeding plasticity and adaptability (Armitage et al., 1995) and to switch to feeding on algal food when it becomes available (Kesti et al., 2022). On the other hand, fish have been found to reduce chironomid densities via direct predatory pressure (Schilling et al., 2009a, b; Milardi et al., 2016). Thereby, we propose that the observed large biomasses of benthic herbivores in Vertezis were explained by a combination of bottom-up and top-down effects. Namely—high algal biomass that was driven by relatively high nutrient concentrations and light availability (Table 1 and Supplementary Table 5) as well as the lack of fish feeding pressure.

As illustrated by the high *EE* of Vertezis functional groups other than phytoplankton and the very low *EE* of phytoplankton, there is a discontinuity between primary and secondary production in the fishless lake that is not observed in the two other study lakes. On the one hand, high *EE* of consumers suggests Vertezis food web is already processing all the available live organic matter whereas, on the other hand, the low *EE* of phytoplankton is responsible for a decoupling of this group from the rest of the food web. The unconsumed production from phytoplankton is thus channeled through the detrital pathway. It has been hypothesized that food webs depending on both primary production and detritus recycling were more stable than those relying on only one organic matter source (Moore et al., 2004). Organic matter flow into detritus in Lake Vertezis were one order of magnitude greater than in the two other lakes and comparable to that of fish-inhabited eutrophic lakes (Cremona et al., 2016) which is raising questions about the contribution of the fishless lake to the regional carbon budget. Since Vertezis is exporting one order of magnitude more carbon than Ciematnieka and two orders more than Tolkajas, we need to investigate in the future if it is the absence of fish or the high phytoplankton biomass that is responsible for its large carbon exports.

Detritus accumulation would also increase primary production through mineralization. Future measurements of ecosystem respiration rates or biological oxygen demand are needed to further this line of research.

The role of secondary terrestrial production in bog lake food web functioning

Mehner et al. (2005) observed that terrestrial insects could constitute up to 84% of the diet in facultative insectivorous fish in mesotrophic low-land German lakes. It has also been shown that terrestrial insects support salmonid populations in rivers and high-altitude lakes (Baxter et al., 2007; Milardi et al., 2016). Additionally, small lakes exhibit a favorable periphery length to surface ratio for terrestrial inputs (Wilkinson et al., 2013; Cremona et al., 2019). However, most authors agree that terrestrial subsidies are not a quantitatively important resource in trophic support of whole lake fish communities (Cole et al., 2006; Mehner et al., 2007; Weidel et al., 2008). In our study terrestrial insects constituted a crucial part of adult fish diet in Tolkajas (up to 44% by mass) and Ciematnieka (up to 38% by mass). Furthermore, the model results suggest that, everything else being equal, without terrestrial organic matter contribution, fish in Tolkajas and Ciematnieka would reach a slower somatic build-up and the lakes would support a much smaller overall fish biomass, especially considering the observed high exploitation of benthic invertebrates. Interestingly, juvenile fish had higher trophic levels than adults in Tolkajas because adults consume 32.8% of terrestrial insects whereas juvenile did not consume them at all (Supplementary Tables 2 and 3). Thus, we propose that in dark water bog lakes with limited secondary benthic productivity and high connection to terrestrial habitats secondary terrestrial production plays an important role in trophically supporting whole-lake fish communities. Finally, an important consequence of high-terrestrial subsidy is that it partially releases zooplankton from predation by fish (Mehner et al., 2005) and this might be another reason behind the low predation rates on zooplankton in Tolkajas and Ciematnieka. Since Vertezis is a fishless lake, the best method to measure terrestrial contribution to its food web would be to measure insect subsidy directly which would require an enormous spatial and temporal sampling effort. Another, lower effort method would be to measure stable isotope composition of Vertezis consumers

to understand how secondary terrestrial production is channeled in the food webs of fishless lakes. We foresee this as a topic for future studies.

Conclusions

In summary, we found that the presence of fish was a key driver shaping functioning of pristine bog lake food webs. We suggest that fish predation has direct and indirect effects on zoobenthic communities` composition and abundance with benthic macroinvertebrates reaching higher trophic positions in the fishless lake Vertezis (hypothesis a). However, we found no apparent direct effects of fish presence on zooplankton and no top-down cascading effect resulting in increased phytoplankton biomasses (hypotheses b and c). We explain this by the local environmental conditions masking the impact of fish. Interestingly, we conclude that terrestrial secondary production contributes importantly to the trophic support of fish communities in small, pristine bog lakes.

Our study highlighted the strong structuring mechanisms that fish exhibit on the food webs and organic matter fluxes in pristine bog lakes. It also emphasizes the crucial trophic connectivity between the lakes and their surroundings.

Data availability The datasets analyzed during this study are available from the corresponding author on request.

Declarations

Conflict of interest The authors declare no competing interests.

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