

Seasonal variation in the relative strength of bottom-up vs top-down effects in pelagic cladoceran populations identified through contribution analysis of birth rate

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ABSTRACT

Pelagic freshwater communities are characterized by the presence of strong trophic interactions, with the dominance of either food limitation (bottom-up effect) or predation pressure (top-down effect) alternating in time. Though this temporal variation should have a major impact on zooplankton dynamics, few studies have examined it. We consider here an approach that involves identifying signatures of food availability and size-selective fish predation based on the demographic characteristics of cladoceran populations. The relative strength of top-down vs bottom-up effects was assessed on short sampling intervals as contributions of the proportion of adults and fecundity, respectively, to the resulting change in birth rate. The dominant effect on each sampling interval was determined based on the absolute value of the ratio of those contributions (R). From previous experiments, we expected that under the dominant effect of food, R should be less than unity, while under fish predation it should be $1 < R < 3.4$. We analyzed two datasets – one collected for a

pelagic cladoceran community of three species, and another retrieved from the published data for *Daphnia catawba* in 1986. In the former case, the temporal variation in the dominant effect was assumed from the pattern of cladoceran population dynamics as well as limited data on zooplankton consumption by planktivorous fish; in the latter case, the seasonal change in predation pressure by fish on the daphnids was known from the original data. Our results show that the probability density functions for R values from the two datasets indicate an increased probability of the ratio values associated with the abovementioned ranges, suggesting that both bottom-up and top-down effects should have been driving cladoceran population dynamics during the study periods. Based on the results of the Generalized Additive Models (GAMs), the fitted R values for the most abundant species from the first dataset – *Bosmina longirostris* – changed from the values indicative of strong food effect at the beginning of the study period to those indicative of strong top-down effect when fish with substantial numbers of bosminids in the gut were caught. In the second dataset, for the two time intervals associated with increased predation pressure by fish, the fitted R values were predominantly located between 1 and 3.4, as expected. For both datasets, our results indicate that contribution analysis of birth rate can be used as an informative, albeit preliminary, tool to identify trophic interactions driving zooplankton seasonal population fluctuations in freshwater communities.

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Key words: trophic interactions; bottom-up; top-down; zooplankton; birth rate.

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INTRODUCTION

Interactions, including trophic interactions that cause changes in species' local abundance and distribution, are generally accepted to be the main subject of ecology (Krebs, 1972). It has been acknowledged that the pattern of distribution of the interactions' strength in food webs can significantly affect community dynamics (May, 1972; de Ruiter *et al.*, 1995; Wootton and Stouffer, 2016). Specifically, stability has been shown to depend on the presence of multiple weak trophic interactions counterbalancing the destabilizing effect of the limited

number of strong trophic interactions within the community (Paine, 1992; Hastings and Powell, 1991; McCann *et al.*, 1998; Berlow *et al.*, 2004; but see Allesina and Tang, 2012). However, it is the strong trophic links that should have an immediate effect on population and community dynamics at a given place and time (Paine, 1992; Rooney *et al.*, 2006; Polishchuk and Kasparson, 2023).

Aquatic ecosystems, and their pelagic compartment in particular, have a relatively higher number of interactions that are potentially strong, compared to terrestrial ecosystems (Strong, 1992; Rooney *et al.*, 2006; Shurin *et al.*, 2006; Rip and McCann, 2011). These strong interactions are often non-species-specific, what allows ecologists to aggregate functional groups of species into separate trophic levels treated as a linear trophic chain: phytoplankton, zooplankton and planktivorous predators (Strong, 1992; Riede *et al.*, 2011). The effective flow of energy between these trophic levels of pelagic freshwater communities results in pronounced effects of phytoplankton and planktivorous predators on zooplankton populations (Carpenter *et al.*, 1985; Elser *et al.*, 2000; Gliwicz, 2003; Borer *et al.*, 2005; Shurin *et al.*, 2006). Though both these effects can operate in a given cladoceran community, their contributions are likely not equal at any given moment, and the relative strength of the effects varies over time (Lampert, 1988; Matveev, 1995; Polishchuk *et al.*, 2013). Indeed, a general pattern of seasonal succession in freshwater zooplankton communities driven by the interplay of resource availability and predation by fish has been generally acknowledged as the Plankton Ecology Group model (PEG-model; Sommer *et al.*, 1986, 2012). However, accumulating data from various limnological studies have shown that a variety of factors can cause deviations from the PEG-model that are important for both short- and long-term community dynamics (Sommer *et al.*, 2012; Moustaka-Gouni *et al.*, 2014; Liu *et al.*, 2022).

Though this temporal variation should have a major impact on zooplankton dynamics, the number of studies focused on such variation remains limited (George, 2021). This may be because such investigations require detailed information on interactions between species, *i.e.*, collection of data on edible phytoplankton concentration and abundance of fish feeding on zooplankton, gut analysis for the fish etc., which can be labor- and time-consuming to obtain (Tessier, 1986; McQueen *et al.*, 1989; Wu and Culver, 1994; Jeppesen *et al.*, 2004). Here, we use an alternative approach – contribution analysis of birth rate – that does not require such detailed information for identification of the driving factor behind zooplankton dynamics. Specifically, this analysis involves standard demographic characteristics of zooplankton that are routinely estimated in research on cladoceran seasonal dynamics: fecundity, population size (age) structure and

egg development rate. Within the framework of our approach, the relative strength of the two factors that can drive cladoceran population dynamics – food vs. predation by planktivorous fish – is estimated as the ratio of contributions of demographic characteristics primarily associated with either of these two factors to the population birth rate. A modified version of the original Edmondson-Paloheimo model (Edmondson 1968; Paloheimo 1974) is used to calculate per capita birth rate b in order to make it more suitable for contribution analysis (Polishchuk 1995):

$$b = V \times \ln(1 + F A) \quad (\text{eq. 1})$$

where V is egg development rate, $F = E/N_a$ – fecundity calculated as the number of eggs (E) divided by the number of adult females (N_a), and $A = N_d/N$ – proportion of adults; $N = N_j + N_a$ – total population density calculated as the sum of the numbers of juveniles (N_j) and adults (N_a) per one liter. Written in such form the model allows one to relate birth rate to the quantity and quality of food (through F), predation pressure (through A ; because planktivorous predators are generally size-selective) and temperature (through V) (Polishchuk 1995; Polishchuk *et al.*, 2013).

Here, we have performed an initial test on whether contribution analysis of birth rate can detect signatures of the effects of food limitation and predation by fish in seasonal time series of freshwater cladoceran population dynamics. We analyzed two datasets – one collected for a pelagic cladoceran community of three species, and another retrieved from the published data for *Daphnia catawba* by Tessier (1986). In the former case the temporal variation in the dominant effect was assumed from the pattern of cladoceran population dynamics as well as the gut contents of planktivorous fish; in the latter case the seasonal change in predation pressure by fish on the daphnids had been known from the original data. We show that for two different datasets birth rate analysis can trace the general pattern of change in the relative strength of the effects of food and predation on pelagic cladoceran dynamics. The results are consistent with data on the likely factors driving zooplankton dynamics, as well as the previously obtained computer simulations' results for modeled cladoceran population dynamics under alternative scenarios of decreased standard egg number (indicative of the bottom-up effect of food limitation) vs increased mortality of large individuals (indicative of the top-down effect due to size-selective elimination by fish; Polishchuk *et al.*, 2013). Based on our results, we consider contribution analysis of birth rate to be a useful, albeit preliminary, tool that can highlight the likely temporal pattern of change between the predominant effects of food vs size-selective predation by fish on the focal cladoceran

populations and could precede a required more detailed analysis of pelagic freshwater food web dynamics.

METHODS

First dataset - Sterlyazhii Pond

Study site

The first dataset was collected during the summer of 2014 at Sterlyazhii Pond (55°41'53" N; 36°43'52" E), located at the Skadovsky Zvenigorod Biological Station of Lomonosov Moscow State University, Moscow Region. Data were collected from 13 June to 22 August 2014. The first day of sampling is further referred to as Day 0 of the study period. Three species of pelagic cladocerans were present in the pond during the study period: *Bosmina longirostris* (Müller, 1785), *Ceriodaphnia pulchella* (Sars, 1862) and *Dyaphanosoma brachyurum* (Liévin, 1848). Before the start of data collection, we had already known that planktivorous fish that might have potentially been feeding on these cladocerans were present in the pond. Our primary aim for this dataset was, relying on the demographic characteristics – fecundity and proportion of adults – of the cladoceran populations, to estimate the relative strength of the effects of food and fish predation on them using birth rate analysis. Next, we examined whether the results of this analysis were consistent with the limited data on food and predators available.

Sterlyazhii Pond was formed by a small dam constructed on a brook flowing into the Moscow River. It is a small shallow water body with a maximum depth of about 2.5 m and a surface area of 0.1 ha. A number of macrophytes that are relatively uniformly distributed within the area of the pond are present: the white waterlily *Nymphaea alba* (Linnaeus, 1753), yellow waterlily *Nuphar lutea* (Smith, 1809), as well as abundant pondweed *Potamogeton* sp.

On every sampling occasion, we measured the water temperature at three depths: 0.1, 0.5 and 1 m below the surface. During the study period, the average water temperature was relatively constant and fluctuated around

the value of $17.0 \pm 0.4^\circ\text{C}$ (mean $\pm$ SE, $n=19$). No vertical gradient of water temperature was observed.

On two occasions (27 June and 25 August) the nutrient concentrations in the water were measured (Tab. 1). The concentration of nitrate, nitrite and ammonium correspond to the oligo-mesotrophic state, while the concentration of phosphates corresponds to the mesotrophic state (Oksiyuk *et al.* 1993). The results of the analysis show that the concentrations of all measured nutrients were higher at the end of the study season. No estimation of water transparency was performed as even at the deepest part of the pond (2.5 m) the transparency was full.

The species composition of the fish community inhabiting Sterlyazhii Pond had been changing. Through the 1970s and 1980s a number of teleost fishes were introduced into the pond: carp *Cyprinus carpio* (Linnaeus, 1758), common chub *Squalius cephalus* (Linnaeus, 1758), common roach *Rutilus rutilus* (Linnaeus, 1758), Chinese sleeper *Perccottus glenii* (Dybowski, 1877), sunbleak *Leucaspius delineates* (Heckel, 1843). In 2006 the following species were registered ($n=102$ ind.): the most abundant species was the common roach (61% of the caught individuals), European perch *Perca fluviatilis* (Linnaeus, 1758; 21%), sunbleak (16%), while common chub and common dace *Leuciscus leuciscus* (Linnaeus, 1758) made up just 2% (Yelnikov *et al.*, 2006).

Data collection and analysis

During the study period, zooplankton samples were taken every 2 to 5 days, 4 days on average ($n=19$). Samples were collected from five stations distributed approximately evenly over the area of the pond, using a plankton net (mesh size: 140 μm , mouth diameter: 14 cm) towed vertically from near the bottom to the surface. The five samples, one per station, were mixed together and then concentrated to the volume of 500 mL. This mixed sample was transferred to the laboratory for further analysis. On one occasion (25 August) the statistical error of population-density estimates caused by horizontal heterogeneity was assessed, with each sample treated individually ($n=4$). The coefficient of variation was used

Tab. 1. Nutrient concentration in water samples taken from Sterlyazhii Pond in 2014. On both dates, the water samples were taken from a depth of 0.5 m below the surface.

Nutrient ion	Nutrient concentration (as mg N or P L ⁻¹)	
	27 June	25 August
NH ₄ ⁺	0.12	0.09
NO ₂ ⁻	0.005	0.007
NO ₃ ⁻	<0.02	0.16
PO ₄ ³⁻	0.075	0.12

to estimate standard deviation for cladoceran population density during the season.

To count animals and eggs, a 5- to 20-mL subsample of the total sample, depending on the abundance of zooplankton, was placed in a Bogorov tray, fixed with several drops of 4% buffered formalin and counted at 32× under a stereomicroscope. Only female cladocerans were found in the samples. To distinguish between juveniles and adults, the animals were measured using an ocular micrometer (to the nearest 50 μm). The number of eggs in the brood chambers of adults was also determined. We thus obtained the numbers (expressed per liter) of eggs E , juveniles N_j and adults N_a on every sampling date. Finally, based on water temperature and using a general formula from Bottrell *et al.* (1976), we calculated egg development time D (in days) and its reciprocal, egg development rate $V = 1/D$ ($[V] = \text{day}^{-1}$).

Phytoplankton samples were collected approximately once a week using a 1-L Ruttner sampler at depths of 0.1, 0.5 and 1 m. Three phytoplankton samples, one from each layer, were mixed, and 1 L of the resulting sample was fixed with Lugol's iodine and decanted for two weeks after the fixation. The samples were then analysed using a Nageotte counting chamber under a Zeiss Axiovert 200 microscope (Carl Zeiss, Germany). All samples were dominated by cyanobacteria and small unidentified cells of cocci and flagellates with a cell size of less than 10 μm in diameter. Some larger flagellates (*Peridinium spp.*) were also found, though in low numbers. Only pico- and nanoplankton fractions (size < 20 μm) were considered edible for the studied cladoceran species. The standard error of the edible phytoplankton concentration was estimated on the basis of counts of three subsamples taken from the sample pertinent on a given date.

On 25 July twelve 3- to 4-year-old individuals of the common roach were caught. The fish were put in a freezing chamber, and their gut contents were analyzed later in the lab under a stereomicroscope.

Second dataset - Lake Lacawac (from Tessier, 1986)

Data on seasonal dynamics of abundance and demographic characteristics in *Daphnia catawba*

The second dataset was built based on previously published data from Lake Lacawac, Pennsylvania, USA, collected in 1980 (Tessier, 1986). These data refer to population dynamics of the cladoceran *Daphnia catawba* (Coker, 1926), for which a detailed seasonal pattern of interactions with its primary resource competitor – the cladoceran *Holopedium gibberum* (Zaddach, 1855), and its predator, the yellow perch (*Perca flavescence* (Mitchill, 1814)) fry, – was known (Tessier, 1986). Our choice of this dataset is motivated by the fact that the limited data on planktivorous fish collected from

Sterlyazhii Pond were insufficient to conclude whether contribution analysis of birth rate could detect the top-down effect of fish predation on cladoceran population dynamics. The data were obtained by digitizing the graphs provided in the original paper (Tessier, 1986). The GetData Graph Digitizer (version 2.26) was used to extract data from the figures.

Lake Lacawac is a mesotrophic lake with a maximum depth of 12 m and a surface area of 20 ha (Berninger *et al.*, 1992). Detailed background information on the hydrological and ecosystem characteristics of Lake Lacawac can be found in the original paper (Tessier, 1986). Here we only briefly describe the data that we used in birth rate analysis. Lake Lacawac is characterized by a stable zooplankton community with *D. catawba* exhibiting two peaks of population abundance – in spring and in autumn – while during summer its abundance is suppressed (Tessier, 1986). The summer decrease is primarily associated with the consecutive appearance of two cohorts of the young-of-the-year (YOY) yellow perch, which feeds on *D. catawba*. Here we used the time series data on *D. catawba* population density and fecundity (measured as the number of eggs per an adult female, $F = E/N_a$) collected from 6 May (considered as Day 0 for the dataset) to 30 September 1980 with an average sampling interval of 4 days ($n=39$). The data on the proportion of adults were provided for 10 dates during the time period considered (Tessier, 1986). In order to perform birth rate analysis, the time steps between consecutive values of demographic characteristics should be relatively small – about 3 days (Polishchuk *et al.*, 2013). Thus, in those cases when the sampling intervals were considerably longer, we estimated the intermediate values of fecundity and proportion of adults using interpolation between two consecutive data points. The water temperature needed to calculate the egg development rate was estimated based on the data provided for 1979, as no such data were provided for 1980 (Tessier, 1986). We found this approximation relevant, as it has been reported that temporal changes in the water temperature of Lake Lacawac during the ice-free season showed a similar pattern between years (Moeller and Williamson, 1994). However, the vertical gradient of water temperature was pronounced in Lake Lacawac for each year and could have significantly affected the estimates of the egg development rates (Moeller and Williamson, 1994; Heinze *et al.*, 2013). Thus, we assumed the water temperature distribution between two consecutive years to be similar and used data on the vertical distribution of *D. catawba* combined with the data on the seasonal and vertical gradient of water temperature provided for 1979 to estimate the egg development rate for *D. catawba* during the focal time period in 1980.

Calculations and statistics

Birth rate analysis - contributions and the ratio of contributions

The strength of the effects of the environmental factors (food, predation by fish and water temperature) associated with a given demographic characteristic, is measured as a contribution of the change in this characteristic to the change in cladoceran birth rate (Polishchuk *et al.*, 2013):

$$\text{Con}X = \frac{\partial b}{\partial X} \times \frac{dX}{dt} \quad (\text{eq. 2})$$

where $X = V, F$ or A from eq. 1. The detailed description of the calculation procedure for the ratio of contributions (and a QBasic program to calculate contributions by numerical integration) used in the analysis can be found elsewhere (Polishchuk *et al.*, 2013). In order to estimate the relative strength of bottom-up vs top-down effects on a focal population we used the ratio of the absolute values of per-day contributions of the proportion of adults and fecundity into the change in cladoceran birth rate:

$$R = \frac{|\text{Con}A|}{|\text{Con}F|} \quad (\text{eq. 3})$$

In the case of the dominant effect of food limitation, the value of the ratio is expected to be $R < 1$, as the absolute value of the contribution of fecundity should exceed that of the proportion of adults. On the contrary, in the case of the dominant effect of predation by planktivorous fish, the ratio is expected to be $R > 1$. In the previously conducted microcosm and computer experiments it was shown that under food limitation R value varied between 0.59 and 0.84 and between 0.33 and 0.9, respectively; under the predominant effect of size-selective elimination that mimicked the effect of fish, *i.e.*, targeted relatively large adult individuals, the ratio varied between 1.7 and 2.77 in microcosm experiments and between 1.23 and 3.42 in computer experiments (Polishchuk *et al.*, 2013).

Statistical analysis

The statistical analysis was performed using the R statistics software (R Development Core Team, 2022). The cointegration test for the cladoceran population density and phytoplankton concentration was performed using the *dynlm* (Zeileis, 2019) and *urca* (Pfaff, 2008) packages. Generalized Additive Models (GAMs) were used as functions of time to estimate trends in temporal variation in the ratio of contributions R during the study periods (Simpson, 2018). We also fitted generalized linear models (GLMs) to the same datasets and used the F-test to see if the more complex GAMs would fit the R time series data better than the GLMs. The models were fitted using the *bam()* function in the *mgcv* package (Wood, 2017). Penalized cubic regression splines were used for

the smoothing. Generalized cross-validation criterion (GCV) was used for smoothness selection. The first-order correlation model (AR1) was used for the residuals of the R time series (Wood, 2017).

RESULTS

Here, we analyze two datasets – one collected in the field and one retrieved from the previously published results (Tessier, 1986) – in order to find out whether the temporal dynamics of the ratio of contributions are consistent with the anticipated pattern based on seasonal dynamics of the relative strength of top-down vs bottom up effects in cladoceran populations, as well as previous experimental results (Polishchuk *et al.*, 2013).

Seasonal dynamics in the pelagic cladoceran community of Sterlyazhii Pond

Population dynamics of three species of pelagic cladocerans (*Bosmina longirostris*, *Ceriodaphnia pulchella* and *Diaphanosoma brachyurum*) exhibited fluctuations of various amplitude during the study season (Fig. 1). Population density of all three species was generally consistent with seasonal change in edible phytoplankton concentration (Fig. 1). However, the augmented Dickey-Fuller test demonstrated significant cointegration between population density and phytoplankton concentration only for *B. longirostris* ($t = -2.07$, $p < 0.05$), but not for the other two species. The pattern of *B. longirostris* population dynamics demonstrated two peaks – the first on Day 0 of the study period and the second on Day 39; on both dates, population density exceeded 200 ind. L⁻¹. The local maximum of phytoplankton concentration on Day 42 was followed by a decrease in phytoplankton concentration that was: i) characterized by the relatively higher average values of phytoplankton concentration comparing to the local minimum preceding this peak (mean $\pm$ SE: $11 \pm 3 \times 10^6$ cells L⁻¹ and $17 \pm 3 \times 10^6$ cells L⁻¹ for Days 7-32 and Days 42-70 of the study period, respectively; $n=4$ for both time intervals); ii) associated with population increase *C. pulchella* and *D. brachyurum* (Fig. 1). In addition, the relatively higher phytoplankton concentration was associated with higher concentrations of nitrite-, nitrate- and phosphate-ions (Tab. 1). This might suggest that though during the second half of the study period, in consistence with the PEG-model, the pelagic cladocerans experienced food limitation, predation by planktivorous fish might have also been affecting the cladoceran community dynamics. This predation would have prevented extensive depletion of edible phytoplankton by *B. longirostris* and allowed the two other cladoceran species to increase in abundance. The results of the regression analysis suggest that the negative relationship between per capita growth rate (calculated as

$r = [\ln N(t+T) - \ln N(t)]/T$ and population density $N(t)$ associated with general trends of population increases and decreases for the three studied zooplankton species could be expected only for the most abundant species *B. longirostris* during the period of population increase (Days 23 to 39 of the study period; $R^2 = 0.704$, $p=0.037$). No statistically significant patterns of density dependence were identified for the rest of the time-series data either for *B. longirostris* or the other two species. This, again, suggests the possibility of the interplay between intra- and interspecific competition and potential predation by fish affecting the dynamics of the pelagic cladoceran community during the study season. The analysis of the gut contents of the common roach caught on a single occasion (25 July 2014, or Day 42 of the study period; $n=12$) indicated a wide range of dietary items, including cladocerans, copepods, insects and plants. All three studied cladoceran species were represented in the ration of the fish. The remains of individuals of either of the three

species were registered in the gut of five individuals. In two fish out of these five, the guts contained hundreds of *B. longirostris* individuals. This, together with the data on cladoceran population dynamics and resource concentration during the study period, suggests that the cladocerans, *B. longirostris* in particular, should have experienced predation pressure associated with the general trend of food limitation. However, we expected only one of these two effects – either top-down or bottom-up – to be predominant on a given sampling interval.

Seasonal dynamics in the pelagic cladoceran community in Lake Lacawac

In order to test to what extent the ratio of contributions R could be informative of the seasonal dynamics in the relative effect of food shortage and predation by the yellow perch fry, we used previously published data (Tessier, 1986). In this study, the pelagic cladoceran community included two species – *Daphnia catawba* and *Holopedium*

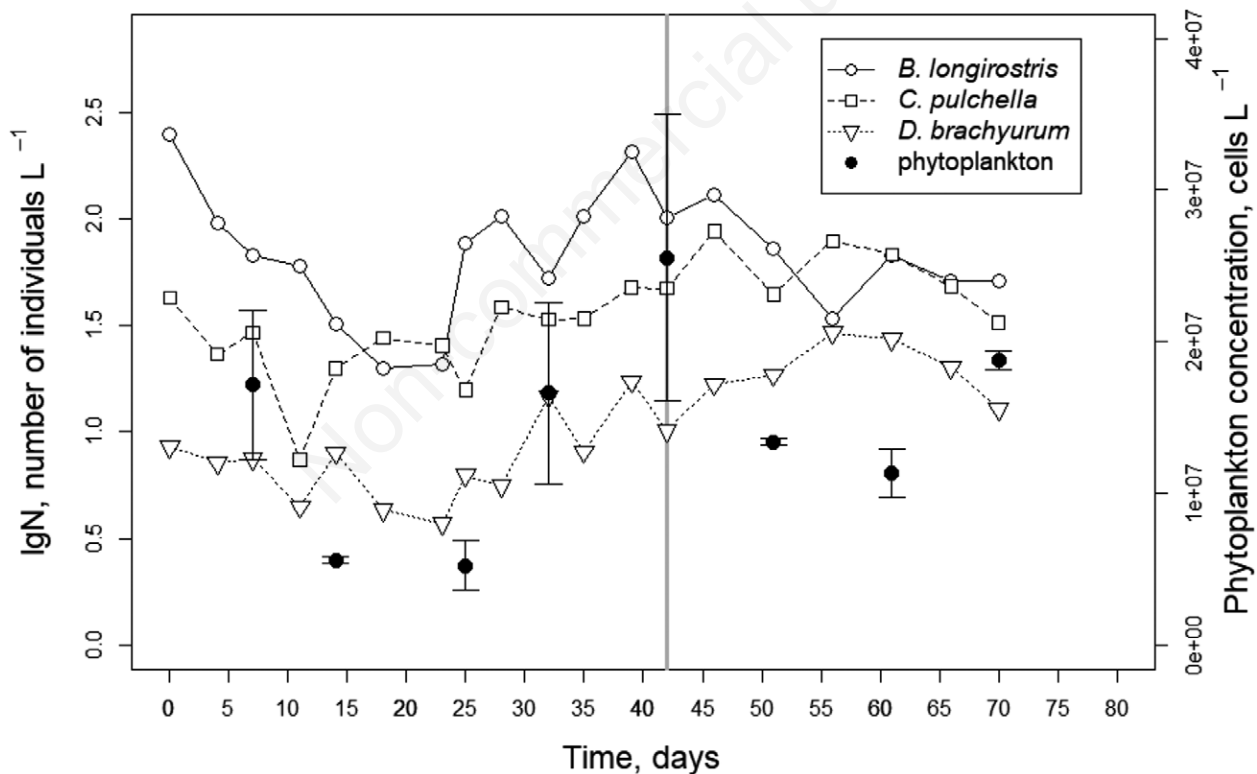


Fig. 1. Population dynamics of three pelagic cladocerans in Sterlyazhii Pond during the 2014 study period. The day on which the first zooplankton sample was collected (13 June) is considered Day 0 of the time series. Note that the population density of zooplankton is given on a logarithmic scale. The vertical line indicates the sampling date on which individuals of the common roach (*Rutilus rutilus*) feeding on the three cladoceran species were caught. Also shown are seasonal changes in edible phytoplankton concentration. For phytoplankton, the error bars are associated with between-subsample variance. For zooplankton, error bars are not provided; however, the coefficients of variation estimated from the horizontal heterogeneity of species distribution (0.65 for *B. longirostris*, 0.60 for *C. pulchella* and 0.52 for *D. brachyurum*) suggest that standard deviation was about 0.5-0.6 of the population density estimate for a given sampling date (see Methods section for more detail).

gibberum – that both experienced elimination by ichthyoplankton. While the planktivorous fish consumed adult individuals of *D. catawba*, only juveniles of *H. gibberum* were eliminated by the fish. During the study season 1980, two cohorts of YOY fish were present in Lake Lacawac. The first hatched in April and fed on *D. catawba* in June (Fig. 2, Days 30 to 70). After YOY individuals had reached about 20 mm in length, they shifted to feeding in the littoral zone of the lake (Tessier, 1986). At the same time, presumably in July, the second cohort of the yellow perch appeared that started feeding extensively on *D. catawba* in August (Fig. 2, Days 90 to 130). These two-time intervals of the relative increase in predation pressure are associated with a decline in *D. catawba* abundance, a simultaneous increase in *D. catawba* fecundity due to relaxation of resource limitation, and an increase in the abundance of its competitor *H. gibberum* (Fig. 2). The time interval between maximum abundance of the YOY yellow perch fry in the open water of Lake Lacawac in late July and early August (Fig. 2, Days 70 to 90) was likely associated with a decline in predation pressure on *D. catawba*, apparently both due to the decrease in the YOY fish of the first cohort abundance in the pelagic zone, and the preference of the newly hatched individuals of the second cohort for neonates of *H. gibberum* (Fig. 2; Tessier, 1986). Thus, the time-series data for *D. catawba* provided

by Tessier (1986) indicate that during the 1980 study season, we could expect the following sequence of changes in the relative strength of bottom-up vs. top-down effects on this species: i) food limitation followed by ii) top-down effect of the YOY yellow perch of the first cohort; iii) the relaxation of top-down effect when the abundance of yellow perch individuals was relatively low in the pelagic zone; iv) the second increase in the top-down effect by YOY yellow perch of the second cohort; v) an increase in food limitation at the end of the time series after the YOY yellow perch of the second cohort had also left the pelagic zone (Fig. 2).

Probability density distribution of the ratio of contributions

In the following step, we analyzed the probability density function (PDF) for the R values for both datasets. In the case of the Sterlyazhii Pond dataset, we calculated the ratio of contributions of changes in the proportion of adults and fecundity to the change in the species' birth rate $R = |ConA|/|ConF|$ for each sampling interval. We then aggregated all the per-sampling-interval R values estimated for the three zooplankton species in a single dataset ($n=54$; Fig. 3a). We can observe two local maxima of PDF for these data: one located between zero and unity, and the

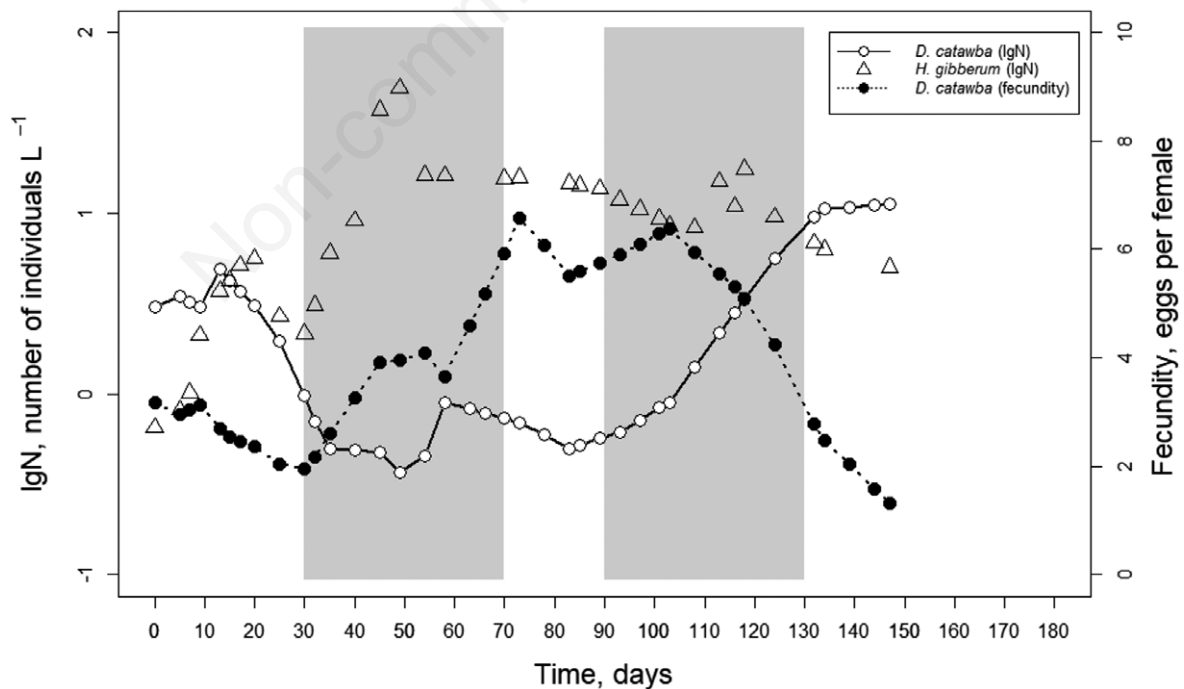


Fig. 2. Seasonal dynamics of *Daphnia catawba* population density (N , number of individuals L^{-1}), and *D. catawba* fecundity (F , eggs per female) during the 1980 study season (data retrieved from Tessier, 1986). Note that the population density of zooplankton is given on a logarithmic scale. The shaded areas indicate the approximate time intervals on which YOY individuals of the yellow perch *Perca flavescens* from two consecutive cohorts were expected to have a pronounced top-down effect on the *D. catawba* population.

second associated with R values of about 3. These maxima are consistent with the expected R values in the case of food limitation and predation pressure, respectively, as estimated in previously conducted computer experiments (Fig. 3a, shaded areas; see section Methods and Polishchuk *et al.*, 2013, for more detail). The rest of the R values do not seem to appear in the pooled dataset consistently and are most likely associated with estimation errors. We then repeated the same procedure for the data on the per-sampling-interval R values ($n=38$) for *D. catawba*, calculated from the estimates of fecundity and proportion of adults in the population in 1980 (Tessier, 1986). The distribution again demonstrated two local maxima: one below 1, apparently also associated with pronounced food limitation of the population, and the second associated with the ratio values located roughly between 2 and 3 that was consistent with a dominant top-down effect (Fig. 3b).

Temporal variation in the ratio of contributions for the Sterlyazhii Pond data

In order to estimate the dynamics of the relative strengths of the effects of food and fish predation in Sterlyazhii Pond for the focal cladoceran species, we analyzed temporal variation in the per-sampling-interval R values for the study season and compared the results with those of the previously conducted experiments (Fig. 4). We identified the outliers within the R distribution with the boxplot method using the interquartile range (IQR) criterion, *i.e.*, as values that were 1.5 times the interquartile range beyond the first and third quartile values. Then, we

eliminated these outliers from the original dataset of the calculated R values ($n=18$ for each of the three cladoceran species). In the next step, we fitted GAMs to the resulting R time series ($n=16$ for *B. longirostris*, $n=14$ for *C. pulchella* and $n=17$ for *D. brachyurum*; the basis dimension (k) was set to 10). The comparison to the linear model results using the F-test showed that the GAMs were a better description of the R temporal dynamics during the study period than the GLMs for *B. longirostris* and *D. brachyurum* (Fig. 4; $p<0.05$). The smooth terms used in the GAMs were significant ($p<0.05$ for both time series; deviance explained: 62.6% and 75.8%; GCV score: 3.7 and 1.6 for these two species, respectively). Based on the GAM results, the fitted values of the R ratio for the most abundant species – *B. longirostris* – changed from those associated with strong food limitation (Fig. 4, $R < 1$, marked with a horizontal red line) at the beginning of the study period to those associated with the effect of predation before the fish that had consumed substantial numbers of *B. longirostris* individuals were caught (Fig. 4, Day 42 marked with a grey vertical line), and then slightly decreased at the end of the study period. The fitted R values for *D. brachyurum* showed a similar pattern of those located between 1 and 3.4 when the planktivorous fish had been caught, if only slightly shifted in time, compared to *B. longirostris*, and with an additional instance of the R values associated with the potential effect of predation by the fish at the beginning of the study season (Fig. 4, Days 5 to 10). In the case of the data on R temporal variation for *C. pulchella*, the smooth terms of the fitted GAM were not significant ($p=0.61$; deviance explained: 9.8%; GCV score = 1.5) and its

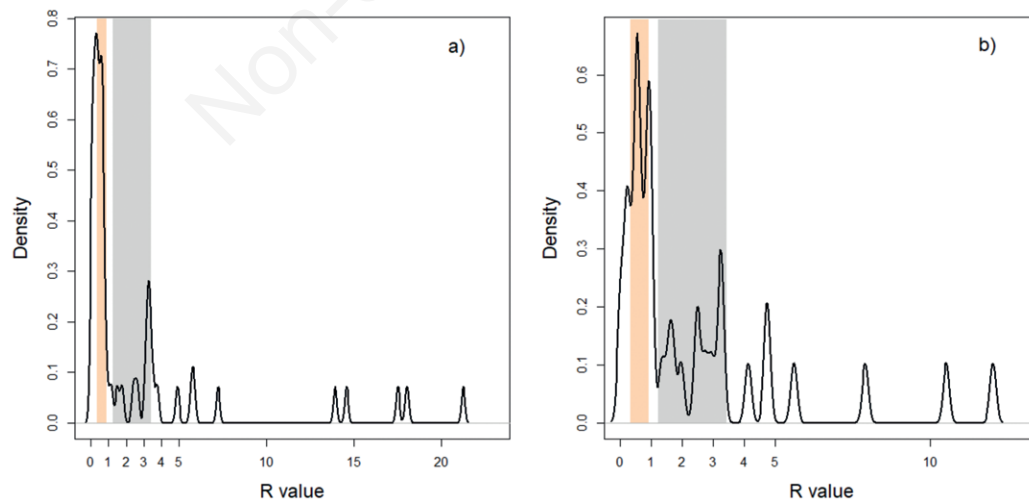


Fig. 3. Probability density function (PDF) for the R datasets. a) PDF calculated for single sampling intervals from the pooled dataset for the three studied pelagic cladoceran species (*Bosmina longirostris*, *Ceriodaphnia pulchella* and *Diaphanosoma brachyurum*; $n=54$) from Sterlyazhii Pond. b) PDF calculated based on the previously published data for *Daphnia catawba* ($n=38$; Tessier, 1986). Bandwidth = 0.1. The pink and grey shaded areas indicate the R confidence intervals for experimental regimes with the predominant effect of food limitation and size-selective elimination of cladocerans: (0.33; 0.90) and (1.23; 3.42), respectively (Polishchuk *et al.*, 2013).

prediction did not differ from those of GLM ($p = 0.26$). Though two of the R values in the time series for *C. pulchella* were located between 1 and 3.4 (Fig. 4, Days 44 to 54), the GAM failed to highlight them. The R temporal variation for the studied cladocerans is consistent with the data on zooplankton population density and phytoplankton concentration (Fig. 1), as well as data on the common roach food preference. The results suggest that following an increase in population density *B. longirostris* that was initially limited by food, should have experienced significant elimination by fish, the common roach in particular, and was not limited by food supply as evident from the data on edible phytoplankton concentration associated with the maximum in *B. longirostris* population density (Fig. 1). On the contrary, *D. brachyurum* that might have experienced predation at the beginning and at the end of the study period, was limited by food when *B. longirostris* population density reached its maximum (Figs. 1 and 4; Days 35 to 43).

Temporal variation in the ratio of contributions for *D. catawba*

In order to further test the ratio of contributions as being indicative of the relative strength of top-down versus bottom-up effects, we repeated the same procedure for seasonal change in the estimated per-sampling-interval *D. catawba* R values ($n=35$; $k = 14$), as for this species

the exact sequence of change in the relative strength of bottom-up vs top-down effects had been outlined (Fig. 5; data from Tessier, 1986). As was done previously, the outliers were eliminated from the original dataset based on the boxplot method under the IQR criterion (the number of R values in the original dataset was $n=38$). GAM smooth terms were significant ($p=0.61$; deviance explained: 80.2 %; GCV score = 1.1), and the results of the F-test suggest that the GAM provided a better fit to the data, compared to the GLM ($p<0.05$). The fitted R values generally followed the alteration sequence in the relative strength of the driving factors outlined above (Fig. 2). Specifically, for the two-time intervals associated with a high probability of predation by YOY yellow perch (Fig. 5, shaded areas) the fitted values of R were more often located between 1 and 3.4, what is consistent with the effect of predation by fish (Polishchuk *et al.*, 2013). On the contrary, for the time intervals associated with the lack of intensive predation (Fig. 5, non-shaded areas) the estimated R values were generally less than unity, which is consistent with the presence of food limitation. Thus, we have shown that the pattern of temporal variation of R values calculated for two separate datasets – one with an unknown pattern of food vs. predation effects and another based on the previously published data with the outlined sequence of alterations between the effects of food and fish predation on populations of pelagic cladoceran species – was in both cases generally consistent with data

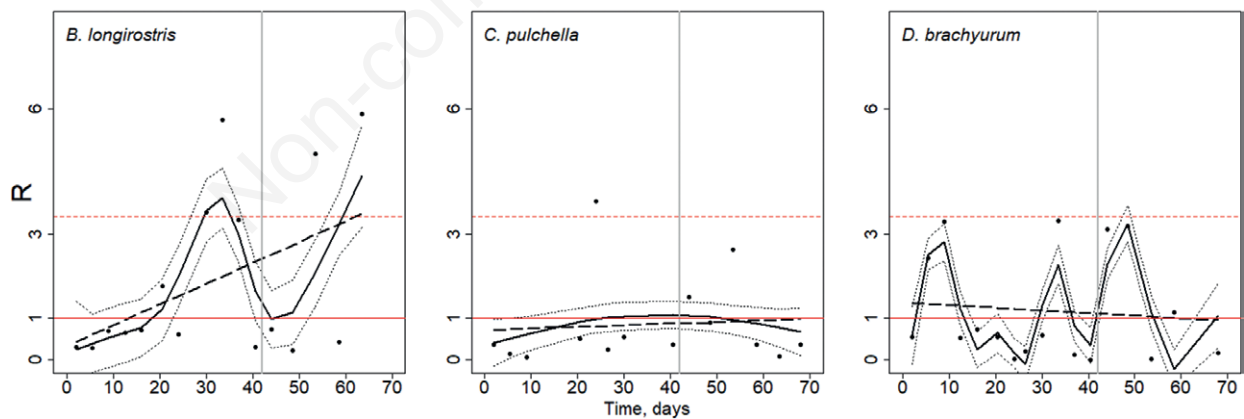


Fig. 4. Temporal variation of the ratio of contributions $R = |ConA|/|ConF|$ for the Sterlyazhii Pond dataset. By its meaning an R value refers to a certain sampling interval (because it reflects changes in the proportion of adults A and in fecundity F over that interval), and a set of R values corresponds to consecutive sampling intervals (see Polishchuk *et al.*, 2013 for more detail). In this figure, however, in order to make the timescale consistent with that of cladoceran population dynamics in Fig. 1, each R value is plotted against the middle of the corresponding sampling interval. GAMs (black solid lines) and GLMs (black dashed lines) were fitted to the data after the R values considered to be outliers had been removed from the datasets (See Results for more detail). The black dotted lines indicate $\pm$ SE of the GAM fit. The number of R data points: *Bosmina longirostris*, $n=16$; *Ceriodaphnia pulchella*, $n=14$; *Diaphanosoma brachyurum*, $n=17$. The vertical grey line indicates the sampling date on which individuals of *Rutilus rutilus* feeding on the three cladoceran species were caught. The horizontal red line indicates $R = 1$ that separates the R values associated with the predominant effect of food ($R < 1$) and those associated with predation pressure ($1 < R < 3.42$). The horizontal dotted red line marks the upper confidence interval ($R = 3.42$) from the previously conducted experiments with the predominant effect of size-selective elimination of cladocerans (Polishchuk *et al.*, 2013).

on phytoplankton and predation by fish, as well as with the results of previously conducted computer experiments (Polishchuk *et al.*, 2013).

DISCUSSION

Knowledge of interaction strength distribution is of great importance in understanding community functioning (McCann *et al.*, 1998). While some studies have treated individual between-species interaction strengths as numbers that are constant in time (May, 1972; Paine, 1992; Allesina and Tang, 2012), it has also been suggested that interaction strength depends on population dynamics of species composing a given community and that it should demonstrate temporal variation (Pimm and Lawton, 1980; Abrams, 2001; Sarnelle 2003; Wootton and Emmerson, 2005). These two approaches do not

contradict one another – while theoretical modeling requires sufficient simplification, it is widely acknowledged that theoretical ecology should build up on explicit detailed empirical research that takes such temporal variation into account (Berlow *et al.*, 2004; Wootton and Emmerson, 2005; Downing *et al.*, 2020).

In this study, we focused on seasonal variation in the relative strength of the effects of resource availability and predation pressure on pelagic cladoceran species. Both these effects are known to be strong drivers behind zooplankton dynamics, and their variation can cause critical transitions in freshwater communities (Collie *et al.*, 2004; Gsell *et al.*, 2016). Though weak species interactions characteristic of species-rich benthos play an important role in freshwater community dynamics (Rooney and McCann, 2012), it has been shown that freshwater pelagic species form a well-defined compartment that has limited energy and nutrient

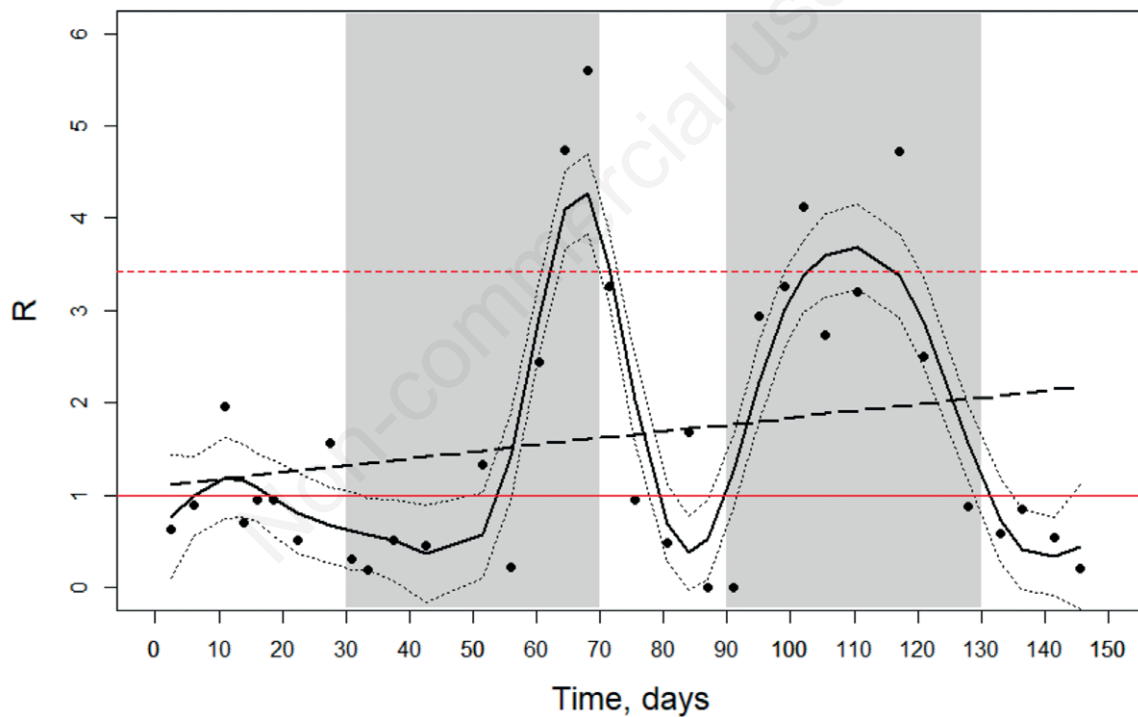


Fig. 5. Temporal variation of the ratio of contributions $R = |ConA|/|ConF|$ for *D. catawba* published data on population fecundity and proportion of adults change in 1980 (data retrieved from Tessier, 1986). By its meaning an R value refers to a certain sampling interval (because it reflects changes in the proportion of adults A and in fecundity F over that interval), and a set of R values corresponds to consecutive sampling intervals (see Polishchuk *et al.*, 2013 for more detail). In this figure, however, in order to make the timescale consistent with that of cladoceran population dynamics in Fig. 2, each R value is plotted against the middle of the corresponding sampling interval. GAM (black solid line) and GLM (black dashed line) were fitted to the data after the R values considered to be outliers had been removed from the dataset (See Results for more detail). The black dotted lines indicate $\pm$ SE of the GAM fit. The shaded areas indicate the approximate time intervals, on which YOY individuals of the yellow perch *Perca flavescens* from two consecutive cohorts were expected to have a pronounced top-down effect on the *D. catawba* population (Tessier, 1986). The horizontal red line indicates $R = 1$ which separates the R values associated with the predominant effect of food ($R < 1$) and those associated with predation pressure ($1 < R < 3.42$). The horizontal dotted red line marks the upper confidence interval ($R = 3.42$) from the previously conducted experiments with the predominant effect of size-selective elimination of cladocerans (Polishchuk *et al.*, 2013).

exchange with the benthic compartment (Rooney *et al.*, 2006; Wang *et al.*, 2020), and thus such indirect interactions were not taken into account in our study. It has been acknowledged that the studies on the dynamics of the relative strength of top-down vs bottom-up effects should also explicitly take into consideration the spatial scale on which the interactions are taking place (Wootton and Emmerson, 2005; Benoit-Bird and McManus, 2012). While pelagic communities of ponds and lakes are generally closed to migration, they can exhibit small-scale spatial heterogeneity that can potentially affect the strength of trophic interactions (Tessier, 1983, 1986; Lampert, 1989; Urmy and Warren 2019). However, we assume that such heterogeneity within cladoceran communities of small lakes and ponds in the absence of extensive migration should exhibit itself in the seasonal variation of the relative strength of top-down vs. bottom-up effects (Tessier, 1986).

Within the framework of contribution analysis of birth rate, it is assumed that changes in cladoceran fecundity are primarily affected by food availability, while changes in population age structure are primarily determined by size-selective fish predation (Polishchuk *et al.*, 2013). Though on certain occasions the situation can be different, *e.g.*, predation can affect fecundity due to the elimination of more conspicuous egg-bearing females, while food limitation can lead to changes in population age structure, these indirect effects are relatively minor, compared to the direct strong impacts of resource availability and size-selective elimination by fish on cladoceran demography (Polishchuk *et al.*, 2013).

The presence of direct strong trophic interactions in pelagic freshwater communities is thought to be reflected in relatively high temporal variability of population abundance (Gellner and McCann, 2016). Indeed, within the framework of the original PEG-model seasonal pelagic community dynamics were triggered by abiotic factors, and after that the fluctuations in zooplankton abundance were driven by temporal variation in the relative effects of resource availability and predation pressure (Sommer *et al.*, 1986). However, initially, the top-down suppression of the zooplankton community by fish predation was given a minor role as a factor accelerating zooplankton decline due to resource depletion (Sommer *et al.*, 1986). In line with the original version of the PEG-model, the results of contribution analysis for the data on seasonal dynamics of the four cladoceran species presented here suggest that food availability has a significant effect on population dynamics. This can be seen from the PDFs for the R values, with the highest probability corresponding to the R values below unity, which point to the resource limitation of the focal populations (Fig. 3). The pronounced cointegration of the *B. longirostris* population

density and edible phytoplankton concentration time series also supports the assumption on the dominant role of food availability in cladoceran seasonal dynamics.

In the more recent version of the PEG-model it has been acknowledged that top-down effects of strong fish predation can play a major role in zooplankton dynamics and show considerable seasonal variation (Sommer *et al.*, 2012). In case of the Sterlyazhii Pond dataset, the results on temporal variation of the ratio of contributions R can provide an insight into such seasonal dynamics of the relative strength of top-down effects for the studied cladoceran species (Fig. 4). Notably, the maximum of *B. longirostris* population density observed in the middle of the study period was associated with the strong effect of fish predation on that species, rather than food limitation. This suppression of *B. longirostris* population might have led to an increase in abundance of the other two cladoceran species – *C. pulchella* and *D. brachyurum*, apparently due to an associated increase in food availability (Fig. 1). As different from *B. longirostris*, *C. pulchella* and *D. brachyurum* were likely experiencing the predominant effect of food limitation between Days 20 and 40, rather than strong predation by planktivorous fish, as suggested by the results of contribution analysis (Fig. 4). The GAM fit indicates that following the period of increase in abundance, *D. brachyurum* population could have experienced the strong top-down effect of fish predation between Days 40 to 50 of the study period (Fig. 4). In case of *C. pulchella* the R values most likely associated with the effect of size-selective predation by fish (Fig. 4, Days 40 to 55) were not detected by the GAM predictor function. That was most likely caused by the limited number of observations ($n=14$) and the penalization procedure involved in the GCV smoothness selection, as the distribution of residuals for this dataset continuously indicated the underfitting that was not associated with the number of basic functions used and could be overcome once a regression spline of fixed degrees of freedom was fit instead of a penalized regression spline. This indicates that there might be a minimum number of sampling intervals required for the identification of driving factors behind zooplankton birth rate change and that in certain instances GAMs might fail to indicate strong predation pressure when it does affect seasonal dynamics of cladoceran populations.

It should be noted here that while the newly hatched yellow perch larvae initially fed on juvenile *D. catawba* individuals due to the gape limitation (Tessier, 1986; Wahl *et al.*, 1993), it was shown that YOY yellow perch larvae exceeding 10 mm in body length consume adult *D. catawba* individuals (Tessier, 1986), as well as practically do not consume prey of less than 0.5 mm in size (Wahl *et al.*, 1993). Moreover, for the European perch (*Perca fluviatilis*; Linnaeus, 1758) of 28 mm in body length, a

strong preference for comparatively larger adult *Daphnia hyalina* (Leydig, 1860) adult individuals was demonstrated experimentally (Furnass, 1979). The same pattern of preference of adult individuals by yellow perch fry can be seen from the seasonal dynamics in the size structure of *D. catawba* population included in our second dataset, as well as results of the fish gut contents provided in the original paper (Tessier, 1986). Thus, we expect that the YOY yellow perch individuals of the two cohorts exhibited strong size-selective predation before switching to feeding in the littoral zone (Tessier, 1986), and hence the comparison of the R values estimated for the time intervals associated with the YOY yellow perch larvae feeding in the pelagic zone with the reference R values from the previously conducted experiments with selective elimination of adult individuals seems reasonable for this dataset (Fig. 5; Polishchuk *et al.*, 2013).

Though our analysis of data collected in Sterlyazhii Pond shows that R values were generally consistent with those previously obtained in laboratory and computer experiments (Polishchuk *et al.*, 2013), we failed to collect sufficient data directly demonstrating the rate of consumption of the three studied species by the zooplanktivorous fish present in the pond. Based on the data collected at Sterlyazhii Pond previously (Yelnikov *et al.*, 2006), we expected that three planktivorous fish species could have been present in the pond in 2014: the sunbleak, European perch and common roach. In 2006 the common roach was the most abundant species in the pond (Yelnikov *et al.*, 2006). The fact that in 2014 twelve individuals were caught in the pond from a single sampling station by rod fishing within an hour or two indicates that the common roach of one particular age class (3 to 4 years) was present in relatively high numbers. Thus, it could have significantly affected the population numbers of the most abundant of the three species the common roach was known to be consuming – *B. longirostris*. The other two cladoceran species from Sterlyazhii Pond were not registered in the gut contents of the common roach individuals in high numbers. The diet of the sunbleak and European perch that could have also been present in Sterlyazhii Pond in 2014 also included cladocerans (Yelnikov *et al.*, 2006); however, the feeding of these two species on the studied cladocerans was not examined in 2014. This lack of explicit data on fish predation pressure on pelagic cladocerans in Sterlyazhii Pond was the reason why we have added a second dataset, that for *D. catawba*, retrieved from Tessier (1986). Thus, we used this second dataset to test whether contribution analysis of birth rate can indeed pinpoint the periods of the dominant effect of fish predation in seasonal population dynamics of cladocerans.

The population of *D. catawba* was known to be strongly affected by predation by YOY yellow perch that

appeared in two pulses during the season (Tessier, 1986). We tested whether the estimated R values for this species would follow the known seasonal pattern of change in the driving factor of cladoceran population dynamics and found that ratio R successfully highlighted the two focal time intervals when the *D. catawba* population was experiencing fish predation. Though data on phytoplankton concentration were not published for the whole study season in 1980 by Tessier (1986), additional data on seasonal dynamics of the Lipid-Ovary (L-O) index provided in the paper indicate that *D. catawba* population was not limited by food during the time periods when the two consecutive cohorts of YOY yellow perch were feeding on the daphnids (Tessier, 1986; Fig. 6 in that study). Though both datasets used in the present study lack direct data on either of the two environmental factors affecting the cladoceran populations (fish consumption or food availability), we suggest that the two datasets complement each other and provide enough support for the general conclusion of the work. The first dataset was specifically collected to perform contribution analysis of the birth rate for the three cladoceran species present in Sterlyazhii Pond in 2014, while the second dataset allowed us to complete the test of the method, as in that case the specific temporal pattern of the occurrence of predation by fish had been outlined beforehand. Together these datasets show that contribution analysis of birth rate can provide important, albeit preliminary, information on the temporal variation of top-down vs. bottom-up effects in cladoceran populations that could be further used in more elaborate studies of freshwater community dynamics.

The high temporal resolution of the methods used to highlight variation in the relative strength of direct trophic interactions has been shown to be crucial for the detection of factors affecting community dynamics and should not allow for indirect effects to come into action (Berlow, 1999; Wootton and Emmerson, 2005). In this work, we used per-sampling-interval (4 days on average) values of the ratio of contributions to track seasonal changes in the effects of food and predators on cladoceran populations. Though using such short sampling intervals should provide detailed information on temporal variation in the interaction strengths, the values of the ratio of contributions are associated with estimation errors that add considerable noise. The presence of such incongruent R values that are beyond the confidence intervals of experimental results (Polishchuk *et al.*, 2013) can be seen from the probability density functions built for both datasets (Fig. 3). This can be overcome by averaging R values over consecutive sampling intervals (Polishchuk and Kasparson, 2023). However, the trade-off between the thoroughness of the acquired information and its reliability that should define the temporal grain of contribution analysis remains the subject of future research.

Finally, contribution analysis of birth rate is built on the estimation of partial derivatives of cladoceran birth rate with respect to fecundity and proportion of adults, used as proxies of interaction strengths of the effects of food limitation and size-selective predation by fish. In such form, contributions are similar to the elements of the Jacobian matrices used in the analysis of community stability and allow us to include the dynamical aspect of interaction strengths in theoretical studies, as has been previously suggested (Novak *et al.*, 2016). This puts contribution analysis in a broader perspective of linking empirical studies on temporal variation in trophic interactions with theoretical research on freshwater community dynamics.

CONCLUSIONS

Seasonal fluctuations are characteristic of cladoceran population dynamics and are associated with temporal variation in the relative strength of the direct effects of food limitation and predation pressure in freshwater communities. Birth rate analysis has been shown to possess sufficient temporal resolution and manage to highlight these two types of effects during their time of existence. Here, we show that seasonal variation in the ratio of contributions to the birth rate of cladoceran demographic characteristics associated with the two types of trophic interactions (top-down vs. bottom-up) is consistent with expected seasonal variation in the relative strength of these interactions in two separate datasets. We suggest that contribution analysis of birth rate can provide a much-anticipated link between empirical studies of natural freshwater communities and theoretical research on community dynamics.

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