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Ecological implications of fish removal: Insights from gut-content analysis of roach (*Rutilus rutilus*) and European perch (*Perca fluviatilis*) in a eutrophic shallow lake

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Abstract

Large reductions in fish biomass are common both as a method of managing lake ecosystems by fish removals (biomanipulation) and as naturally occurring fish kills. To further understand how fish reductions change feeding patterns of fish, we studied the diets of small- to medium-sized roach (*Rutilus rutilus*) and European perch (*Perca fluviatilis*) on a monthly basis using gut-content analysis during an 18-month period before and after a whole-lake fish removal in a eutrophic shallow lake. Further, we performed in-depth analyses of zoobenthos communities of the profundal and littoral zones, as well as analysed the zooplankton community in the littoral and pelagic parts of the lake to estimate abundance and biomass of potential diet items. We found that, in general, there was a trend toward increased zoobenthivory in both species and among all-sized fish after fish removal, regardless of prior diet preference. Reduced piscivory among larger perch (>150 mm) and reduced zooplanktivory among smaller perch and roach (<150 mm) were also observed. Moreover, during a short period of high zooplankton biomass after fish removal, both perch and roach (all sizes) shifted their diet toward daphnids, which likely caused a decrease in daphnid population. We suggest that such change toward periodical zooplanktivory across fish species and size groups may lead to unexpectedly high top-down control by fish after lake restoration by fish removal.

KEYWORDS

biomanipulation, diet choice, eutrophic, northern Europe, trophic cascade, zooplanktivory

1 | INTRODUCTION

Fish play a defining role in structuring lake food webs, provide important ecosystem services (Holmlund & Hammer, 1999; Thompson et al., 2012), and can influence all trophic levels through direct effects or trophic cascades (Kitchell & Carpenter, 1996). Understanding the role of fish populations is then essential to the understanding of lake ecosystems as a whole. The position of fish in lake food webs varies

considerably depending on lake type, species composition, and ecological state (Eloranta et al., 2015; Jeppesen et al., 2000). It is especially in the role of predators on zoobenthos and zooplankton that fish in shallow lakes are important for the structure of food webs (Bernes et al., 2015).

Some of the most common small- to medium-sized fish in northern Europe are the cyprinid, common roach (*Rutilus rutilus*) (hereafter roach), and the percid, European perch (*Perca fluviatilis*) (hereafter perch)

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(Kottelat & Freyhof, 2007). Both these fish species can occupy multiple trophic levels, but in the context of shallow lake restoration, they are often most important as medium-sized predators at similar trophic levels, enforcing top-down control on zoobenthos and zooplankton (Bernes et al., 2015; Jeppesen et al., 2007; Persson & Hansson, 1999; Sharma & Borgström, 2008). Perch and roach often occur together, and their presence can be used as an indicator of trophic structuring within lakes (Ritterbusch et al., 2022).

Roach possesses specialized digging and sieving mechanisms to separate macroinvertebrates from sediment and filter zooplankton from the water column (Lammens et al., 1987). Its feeding apparatus allows for a versatile diet, including detritus and plant material (Motta, 1984; Prejs & Blaszczyk, 1977), but its inefficiency in handling large prey limits its piscivorous capabilities (Lauder, 1988; Liem, 1973). In contrast, perch exhibits predatory adaptations such as teeth for prey restraint and a well-defined stomach with strong hydrochloric acid for nutrient release (Fish, 1960; Hirji & Courtney, 1979). With a selective foraging strategy and the ability to catch elusive prey (Chabot & Maly, 1986; Furnass, 1979), perch becomes a top predator through ontogenetic diet shifts toward piscivory, facilitating niche partitioning with roach (Mittelbach & Persson, 1998; Persson et al., 1996).

Mass fish depopulation can occur naturally, for example, through toxic algal blooms (Carmichael & Boyer, 2016), water-quality changes (Towrqseno et al., 1992), and anoxia (Müller & Stadelmann, 2004; Ruuhijärvi et al., 2010). However, biomanipulation of lakes, for example, removal of zooplanktivorous and benthivorous fish (hereafter fish removal), is also used extensively to induce clear-water ecological states by upsetting the in-lake balance (Bernes et al., 2015; Persson & Hansson, 1999; Scheffer et al., 1993). After fish removal, the expected changes are reduced phytoplankton concentrations and increased grazing by cladocerans, all contributing to decreased water turbidity (Olin et al., 2006). Estimating the effect of fish stock decimation on the food web, and the possibility of establishing a clear-water state, is important, not only to gauge the effect of lake restorations but also to understand natural lake processes.

Shallow nutrient-rich temperate lakes are often dominated by abundant smaller cyprinid fish and high pelagic primary production (Jeppesen et al., 2000). Small cyprinids have been found to effectively keep zooplankton biomass low and/or dominated by small-sized individuals, facilitating growth of phytoplankton (Jeppesen et al., 1997). However, the cascading effect of fish predation on phytoplankton biomass has been disputed (Post & McQueen, 1987). The purpose of fish removal is to reduce top-down control of fish predation on zooplankton, and in turn increase grazing on phytoplankton, and to reduce nutrient resuspension by larger bottom-feeding fish (Olin et al., 2006; Søndergaard et al., 2017). However, fish removals as a way to restore lakes rely on the major assumption that predation on zooplankton and/or nutrient resuspension by large bottom feeders decreases with reduced fish biomass. Perch and roach could react to competitive release by increased feeding rates on zooplankton, which would reduce the effect of fish removals. Therefore, understanding the dietary choices and responses of these two fish species is of immense value in managing eutrophic shallow lakes. The degree to

which the feeding niche of perch and roach has increased after fish removals has varied between studies. Syväranta and Jones (2008) found roach and perch to rely more on pelagic food sources as size and abundance of large *Daphnia* increased, whereas Persson and Hansson (1999) found all fish species to increase feeding on macroinvertebrates. Therefore, it is difficult to predict the effect of biomanipulation on fish diet choice based on current literature.

Our study investigates changes in roach and perch food preferences before, during, and after a whole-lake removal of fish, primarily roach, in a shallow eutrophic lake. We used a monthly resolution to gain a high-fidelity understanding of the driving forces behind small- to medium-sized fish diet choice after a major population removal. We expect that roach shifts from planktivory toward more benthivory given the potential for increased macroinvertebrate densities with lowered fish densities. Further, we predict perch shift toward more piscivory of especially 0+ roach. This was based on the expectation of recruitment compensation by roach population due to their reduced biomass, as was postulated by Persson and Hansson (1999).

2 | MATERIALS AND METHODS

2.1 | Study site

Our study site was Lake Ormstrup, which is a eutrophic shallow lake located in central Jutland, Denmark (56°19'34" N, 9°38'21" E). It is a small lake (11 ha) with a small catchment of mainly forest and agricultural area (Figure 1; Table 1). Lake Ormstrup has five confirmed fish species, where roach, perch, and northern pike (*Esox lucius*) are common and tench (*Tinca tinca*) and eel (*Anguilla anguilla*) are more rare. Further, the study lake has been shown to have frequent temporary summer stratifications and anoxia in the lower parts of the water column, which influence fish habitat use, periodically limiting fish to oxygenated upper waters (Søndergaard et al., 2022). Lake Ormstrup has been the subject of extensive monitoring of fish population, and physical and chemical parameters in the lake, both before and after a major roach removal. This makes it an ideal site for studying the effects of fish removal on diet.

2.2 | Fish removal

During fish removal campaigns by beach seine fishing in September/October 2020 and April 2021, an estimated 75%–80% roach biomass was removed from the lake, totaling over 4.5 t (4.1 t in September/October 2020 and 0.4 t in April 2021). The removed fish by percentage weight were roach (93%), perch (4%), and tench (3%).

The biomass of roach removed from the lake was estimated using a mark-recapture technique. Prior to or during a given sampling period, between 90 and 200 roach larger than 12 cm were PIT tagged (to minimize potential tag effects, smaller fish could not be tagged using 23-mm tags). The proportion of these tagged fish that were recaptured during seine-haul fishing was used as an indicator of the

FIGURE 1 Map of Lake Ormstrup. Littoral (green) and profundal (blue) invertebrate sampling areas are marked with points. Depth zones are indicated for profundal samples (shallow: 1.6–2 m, middle: 2.9–3.1 m, and deep: 4.1–4.5 m). Littoral samples were collected at 0.5–1 m depth. The location of the lake is indicated by a red circle on the smaller map of Denmark.

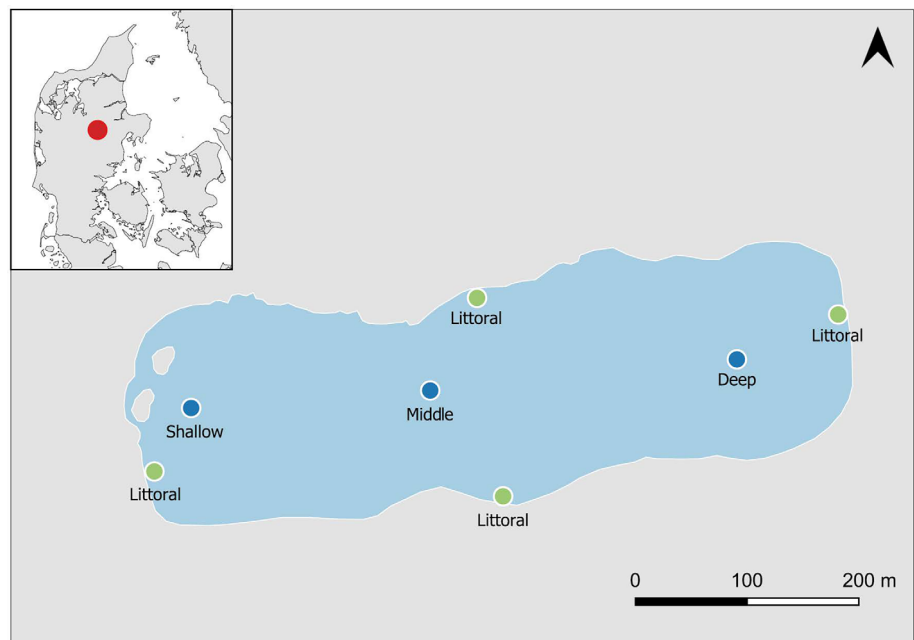


TABLE 1 Properties of Lake Ormstrup.

	2020	2021
Area (ha)	11	-
Maximum depth (m)	5.5	-
Mean depth (m)	3.4	-
Chlorophyll- <i>a</i> ($\mu\text{g/L}$)	52	42
Total-N (mg/L)	1.50	1.57
Total-P (mg/L)	0.58	0.53

Note: Summer averages of chemical properties and chlorophyll-*a* from May to September. Chemical values are from Søndergaard et al. (2022).

reduction in the roach population (at least for fish larger than 12 cm) (Table 2).

2.3 | Sampling of zooplankton and macroinvertebrates

Seasonal macroinvertebrate samples were collected on March 19 (winter), May 26 (spring), July 22 (summer), and October 27 (fall) 2021 in the littoral zone. Macroinvertebrates were also collected at three sampling stations of increasing depth in the lake (henceforth referred to as “profundal”) on February 17 (winter), June 1 (spring), July 22 (summer), and October 27 (fall). Littoral estimates of macroinvertebrate abundance, biomass, and individual weight were averages from four different sites in Lake Ormstrup, and triplicate samples were taken at each site (Figure 1). Littoral samples were collected at 0.5–1 m by placing a sample tube (0.039 m^2) in the sediment, effectively sealing the inside of the tube from the outside. The sediment, including macroinvertebrates and plant material from macrophytes, was then suspended in the tube using a scooping/cutting instrument.

Immediately after suspension, a net was inserted tightly under the sample tube, catching the suspended material and invertebrates. Extraordinarily, standardized macroinvertebrate samples were also taken from the littoral zone by triplicate kick-net sampling before and after fish removal, at the same four sites as the ordinary littoral macroinvertebrate samples. These samples were used to estimate whether abundance of macroinvertebrates increased after fish removal by comparing the number of macroinvertebrates per kick-net sample.

Profundal macroinvertebrate samples were averages from samples collected at the three sites of increasing depth (Figure 1) (shallow: 1.6–2 m, middle: 2.9–3.1 m, and deep: 4.1–4.5 m), using a sediment corer (diameter: 52 mm, 0.002 m^2 and the top 5 cm of the sediment) and 10 cores from each site. Individual macroinvertebrate samples were stored in 96% ethanol and brought to the laboratory. In the laboratory, the animals were sorted and determined to genus or lower taxonomic level. Each genus sample was counted, dried for 48 h at 60°C , and weighed. Because fewer invertebrates were found in the profundal, samples from different depths were pooled and weighed together for biomass estimates. Standard deviations for biomass were calculated per replicate by multiplying individual weight (total biomass/total individuals) and number of individuals in each replicate.

Weekly zooplankton data were available from 2020 to 2021 for both littoral and pelagic samples. In the littoral, samples were depth integrated at 1-m depth; pelagic samples were pooled surface-water samples (first meter) from three stations (same as profundal invertebrate stations in Figure 1). Zooplankton samples were collected during daytime. Zooplankton was filtered using a $20\text{-}\mu\text{m}$ mesh and stored in Lugol's solution until they could be counted and measured for biomass estimations in the laboratory. Lake water for chlorophyll-*a* analyses was sampled as part of the normal monitoring alongside zooplankton. Individual zooplankton weights were calculated by dividing

TABLE 2 Biomass (kg wet weight) of roach removed during fish removal, including the recapture rate of tagged fish during removal.

Removal period	Number of hauls	<60 mm	60–120 mm	120–180 mm	>180 mm	Recapture rate (%)
September/October, 2020	23 kg	33 kg	2707 kg	1243 kg	146 kg	66.70
April 2021	15 kg	13 kg	330 kg	91 kg	3 kg	31.80
Total	38 kg	46 kg	3037 kg	1334 kg	149 kg	

Note: A number of roach were tagged a few days before the removal was initiated and used as a proxy for the removed roach biomass. Only roach above 120 mm were tagged.

TABLE 3 Fishing methods used during the study period.

Month	2020	2021
January	N	N
February	N	N
March	N	E
April	N	E
May	E	E
June	E	E and G
July	E	G
August	G	E and G
September	S	S
October	N	N
November	E and G	N
December	E and G	N

Abbreviations: E, electrofishing; G, gillnet; N, no fishing; S, seine.

zooplankton sample abundance by zooplankton biomass from May to December.

2.4 | Sampling of roach fry

To compare the density of roach fry (0+) before and after fish removal, standardized sampling of fry was carried out in 2020 and 2021 using point abundance sampling by electrofishing (Copp, 2010; Copp & Peñáz, 1988). Sampling of roach fry occurred every 8–12 days between June 19 and August 9, 2020 (i.e., six sampling events), and between June 10 and August 31, 2021 (i.e., nine sampling events). At each sampling event, 80 sample points were electrofished from boats in the littoral zone. The sample points were distributed along the entire shoreline of the lake and alternately placed inside the reed vegetation and 1–2 m outside the outer edge of the reed belt (when present). The boat drifted slowly toward each sampling point before it was stopped and held in position. Subsequently, the electrofishing rod equipped with an anode ring was dipped into the water as deep as possible with the current switched on for 15 s. While shocking, the anode ring was steadily brought toward the surface by the electrofishing operator, all visible stunned fish were collected using a dip-net, and three dip-net hauls were made below the Secchi depth to sample nonvisible fry. The number of captured roach fry was noted for each sampling point.

2.5 | Fish stomach sampling

For the gut-content analysis, roach and perch were sampled monthly from May 2020 to September 2021 using small meshed sinking monofilament nylon gillnets, electrofishing, and beach seining (Table 3). With the exception of August, gillnets were specifically deployed for a single hour during the daytime as part of the monthly samplings. A short fishing time and a small mesh-size were chosen to reduce the effect of fish death on gut content and to reduce by-catch mortality of acoustically tagged large perch, roach, and pike used in monitoring of fish behavior running parallel to this study (e.g., Søndergaard et al., 2022). In August samplings, fish were taken as part of the yearly fish monitoring in the lake using standardized multimesh New Nordic Norm gillnets (12 meshes ranging from 5 to 55 mm). Electrofishing and gillnetting were the primary methods used for the collection of fish. During the period of fish removals (i.e., September 2020 and April 2021), fish were sampled from the beach seining catches constituting the September 2020 and April 2021 sampling. Sampling of fish was not done in October 2020 due to logistic challenges and in January and February 2021 due to ice cover. After catch, total length and weight were measured for all fish. Perch stomachs (from pharynx to pylorus) and roach guts were then stored individually in 96% ethanol.

2.6 | Stomach content analysis

All viable sampled stomachs ($n = 1282$) from May 2020 to September 2021 were analysed using the points method as described by Hynes (1950) and elaborated by Amundsen & Sánchez-Hernández (2019). For roach, lacking a distinct stomach, the first half of the stomach (elongated foregut) was used for analysis (from pharynx to second gut sling). The fullness of each stomach was determined by assignment of points, where 0 was completely empty and 5 was a full stomach. Using visual analysis, the item groups and their relative contribution to gut fullness were assigned a decimal fraction from 0 to 1, where 0 was completely lacking and at 1 the particular item was the only type found in the stomach. Gut samples for both perch and roach were divided into groups based on fish length (above or below 150 mm total length) as well as month in which they were caught.

2.7 | Data analysis

Statistical differences in abundance and biomass of littoral and profundal invertebrates, as well as monthly number of roach fry and

kick-net invertebrate samples, were analysed using a combination of analysis of variance (ANOVA) and Tukey's tests. Monthly number of roach fry caught was log transformed to achieve normality. We used Spearman's rank correlation to investigate the relationship between chlorophyll-*a* concentration and zooplankton biomass. The Spearman's rank correlation assesses the monotonic relationship between two variables by comparing their rank orders. The Spearman's rank correlation was chosen because data were not normally distributed.

For stomach content analysis, the relative contribution of the different prey items to diet was put in a square root-transformed Bray-Curtis similarity matrix. The square root transformation was chosen to reduce the effect of very common diet items. Fish groups were analysed for differences in stomach content using ANOSIM (analysis of similarities, a non-parametric ANOVA-like test) (Clarke, 1993) and calculated using Primer 7 software (version 7.0.21). The stomach content sample groups were further analysed using nonmetric multidimensional scaling (nMDS), based on fish groups rather than individuals. For the nMDS, fish were grouped based on species, month, and whether biomanipulation had occurred. The decision to divide fish into size categories at 150 mm was based on the length of ontogenetic dietary shift (Sánchez-Hernández et al., 2019) toward piscivory in perch and zooplanktivory/zoobenthivory in roach during the first 4 months of the study (before fish removal).

2.8 | Ethics statement

The care and use of experimental animals complied with Danish animal welfare laws, guidelines, and policies as approved by the Danish Ministry for Food, Agriculture and Fisheries and in accordance with the rules regarding removal of unwanted fish species.

3 | RESULTS

3.1 | Macroinvertebrates

We found the littoral biomass of macroinvertebrates to be significantly higher than profundal biomass across all four seasons (ANOVA, $F = 16.714$, $df = 1$, $p < 0.001$). Profundal macroinvertebrate biomass was less than 5 g total dry weight m^{-2} in all cases, whereas littoral biomass was higher at over 7 g total dry weight m^{-2} in all cases. Only the invertebrates most commonly found in fish diet (amounting to more than 95%) were included in the analysis of both profundal and littoral areas. In classification of invertebrates 'indet.' is short for indeterminate and indicates uncertain classification of species. For the profundal, these were chironomid larvae (Chironomidae indet.) in the shallow areas (<2-m depth) and phantom midges (Chaoboridae indet.) in the deeper areas (4–4.5 m depth) (Supplementary Material 1). For the littoral, the most common macroinvertebrates were chironomid larvae and pupae, water lice (*Asellus aquaticus*), caddisfly larvae (Trichoptera indet.), leeches (Hirudinea indet.), mayfly larvae

(Ephemeroptera indet.), and phantom midges (Supplementary Material 2).

Kick-net sampling from September (Table 4) revealed that the overall abundance of macroinvertebrates was significantly higher in 2021 (after fish removals in September/October 2020 and April 2021) than before fish removals in 2020 (ANOVA, $F = 16.714$, $df = 5$, $p < 0.001$).

3.2 | Zooplankton

The littoral zooplankton community changed significantly on an annual basis from small copepod and *Bosmina* dominance during June–July when zooplankton were most abundant in both years to dominance of larger *Daphnia* after fish removal (Figure 2; Table 5). In 2020, average individual weights of *Bosmina* (*Bosmina* spp.), copepod (*Copepoda* spp.), and *Daphnia* (*Daphnia* spp.) were 0.53, 0.47, and 2.09 μg per individual, respectively. In 2021 after biomanipulation, average individual weight of *Bosmina*, copepods, and *Daphnia* increased to 1.34, 1.15, and 3.43 μg per individual, respectively. Other zooplankton were abundant but consisted almost exclusively of small (<0.07 μg per individual in both 2020 and 2021) rotifers (*Rotifera*) and unidentifiable nauplii larvae that were not found in the diet of fish size categories included in this study. After fish removal, zooplankton biomass was low until June, then increased dramatically in June and July, and was again low from August. During the short period of increased zooplankton biomass, chlorophyll-*a* decreased to lower levels than what it had been at the same time the year before fish removal (Figure 2). However, we did not find any overall correlation between zooplankton biomass and chlorophyll-*a* concentration (Spearman's rank correlation, $p = 0.848$).

3.3 | Fish community

Fish length distribution is shown in Figure 3. For both species, large fish (over 150 mm) were less abundant than small fish (<150 mm), and were caught less frequently, especially after fish removal. In general, roach and perch above 300 and 200 mm, respectively, were rarely caught during sampling (Figure 3).

Roach fry density is presented in Table 4. There was no statistical difference in roach fry density before and after fish removal ($p = 0.223$; Table 4).

3.4 | Stomach content analysis

In total, 725 roach and 640 perch were caught for stomach content analysis during the study period. Stomach content changed significantly after fish removal. Prior to fish removal there was significant partitioning of resources (Figure 4; Table 6) between both species and size categories of fish (Figure 5). Before fish removal, large perch were mainly piscivorous, and their gut contained almost exclusively juvenile

Type	Sample	2020	SD	2021	SD
Littoral invertebrates (kick net)	Caddisfly larvae	0.75	0.18	5	-
	Chironomid larvae	234	79	494	120
	Leeches	4	1.2	6	1.4
	Mayfly larvae	83	53	48	29
	Water lice	95	-	661	-
Roach fry (PASE)	June	23	27	7	1
	July	3	3	1	1
	August	1	-	1	-

TABLE 4 Average abundance of littoral invertebrates during kick-net sampling (invertebrates/kick) and average catch of roach fry samples using PASE before (2020) and after (2021) fish removals.

Note: SDs are shown after the numbers. In both years, littoral invertebrates were sampled in September. Abbreviations: PASE, point abundance sampling by electrofishing; SD, standard deviation.

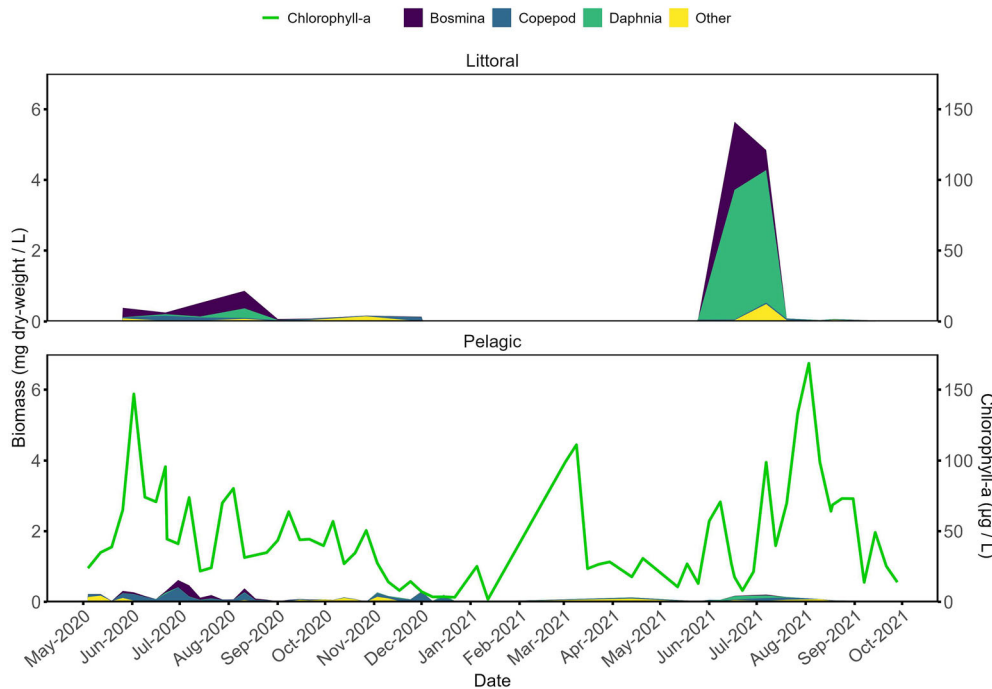


FIGURE 2 Stacked area chart of the total biomass per liter of major zooplankton groups in the littoral and pelagic zones of Lake Ormstrup from May 2020 to September 2021. Chlorophyll-*a* values are included from the pelagic zone with the green line in the lower plot.

TABLE 5 Summary statistics of ANOVA including the main effect of year, two-way interaction year:month, and three-way interaction year:month:type on zooplankton biomass in the littoral and pelagic.

	Coefficients	df	Sum squared	F-value	Pr (>F)
Littoral	Year	1	200.4	34.99	<0.001
	Year:month	11	123.5	1.9	0.037
	Year:month:type	36	63.2	2.61	<0.001
	Residuals	854	12.2		
Pelagic	Year	1	0.29	6.93	0.009
	Year:month	6	0.65	2.58	0.002
	Year:month:type	21	3.28	3.73	<0.001
	Residuals	289	12.1		

Note: Type is groups of zooplankton (i.e., copepods, *Bosmina*, and *Daphnia*). Abbreviation: ANOVA, analysis of variance.

roach (<85 mm, when intact enough to measure). After fish removal, large perch changed from piscivory to a macroinvertebrate-dominated diet (Figure 5). Because fewer large perch were caught after fish removal,

it was a concern that the decreased piscivory could be attributed to the “large” fish group being composed of smaller perch. However, piscivory still decreased significantly overall when only fish between 150 and

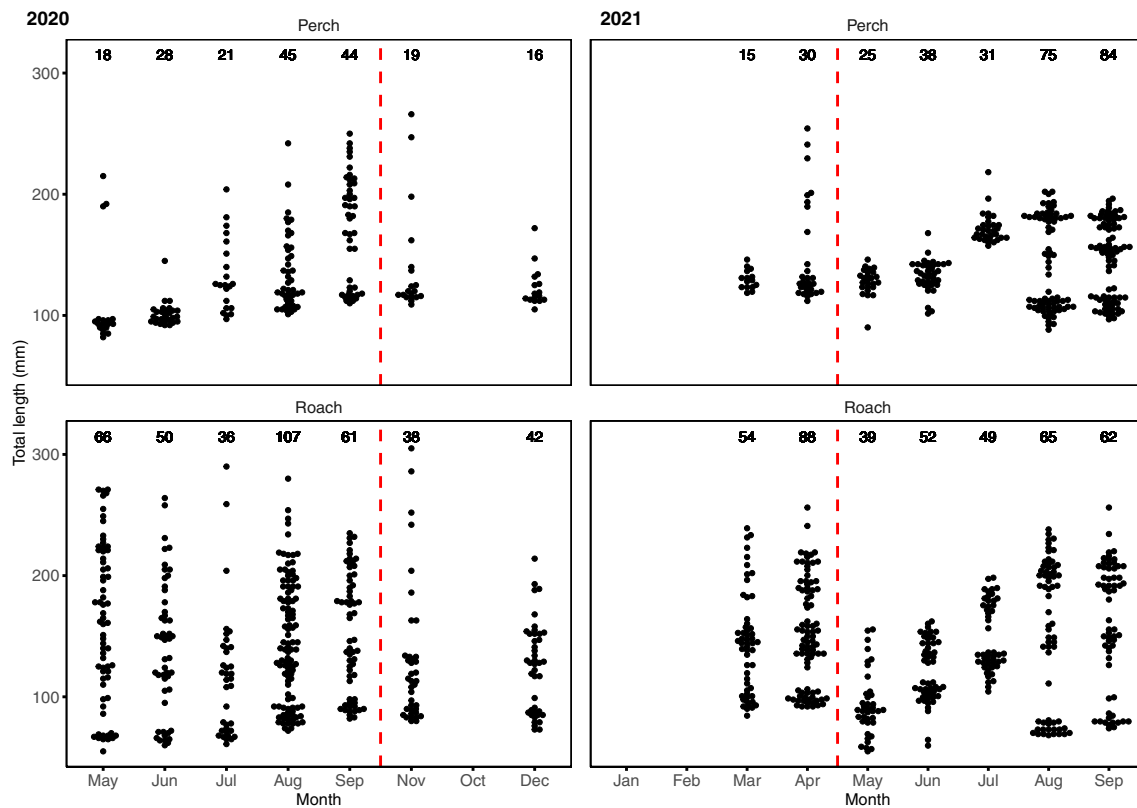


FIGURE 3 Beeswarm-style plot of fish total length (in mm) caught during fishing (see also Table 2). Numbers of fish caught in each month are indicated above each month. Points indicate individual fish. Dashed line indicates where fish removal occurred in both years.

200 mm were considered in months where comparison was possible (July–September) (ANOVA, $F = 11.052$, $df = 1$, $p = 0.001$).

Before fish removal, small perch had a decreasing amount of zooplankton (copepods, and to a lesser extent daphnids) in their diet, from the beginning of the study in May 2020 through September 2020 (Figure 6). After fish removal, small perch did not return to a zooplankton-rich diet but fed on macroinvertebrates throughout the year. The only exception to this was in June 2021, where small perch had a high fraction of *Daphnia* in their diet (Figure 6). Macroinvertebrates in the diet of perch of all sizes were diverse, with some seasonal variation. In fish diets, the prevailing macroinvertebrates comprised water lice; chironomid larvae and pupae; and mayfly larvae, caddisfly larvae, and leeches (Figure 7). Chironomids were the most common macroinvertebrates consumed overall. During the colder months (February–April) in 2021, caddisfly larvae were an important food source, coinciding with the time when biomass and individual weight of caddisfly larvae was highest (Supplementary Material 2). Chironomid pupae were prominent in the diet of both perch-size categories. However, biomass for chironomid pupae, as estimated by macroinvertebrate samples, was low in all cases (Figure 7).

Both before and after fish removal, large roach consumed mainly detritus, plant material, and macroinvertebrates (Figure 5). Large roach was the group of fish that changed diet the least after biomanipulation (Figure 7). However, there was an almost significant increase in

macroinvertebrates in the stomach content after fish removal (ANOVA, $F = 4.881$, $df = 1$, $p = 0.058$). This pattern was significant when June 2021, the month of very high zooplankton consumption, was excluded (ANOVA, $F = 7.15$, $df = 1$, $p = 0.037$). During June and July 2021 after biomanipulation, large roach also consumed daphnid zooplankton (Figure 6). This coincided with the time when *Daphnia* were very abundant in the system (Figure 2). Small roach had significantly more bosminid zooplankton in their diet before fish removal (ANOVA, $F = 89$, $df = 1$, $p < 0.002$) (Figure 6). After fish removal, small roach consumed mostly macroinvertebrates and detritus (Figure 5), except for May–July where they had significantly higher fractions of daphnid zooplankton in their diets (ANOVA, $F = 44$, $df = 1$, $p < 0.002$) (Figure 6).

4 | DISCUSSION

After biomanipulation, zooplankton community structure changed notably in Lake Ormstrup. Prior to fish removal, the lake was dominated by small bosminids, daphnids, and copepods but changed periodically toward high biomass of large daphnids after. These results are similar to those reported by He et al. (1994), Jeppesen et al. (2007), and Søndergaard et al. (2008), who studied similar removals of small- to medium-sized zooplanktivorous/benthivorous fish in small lakes. Fish removal most likely caused the shift in the zooplankton

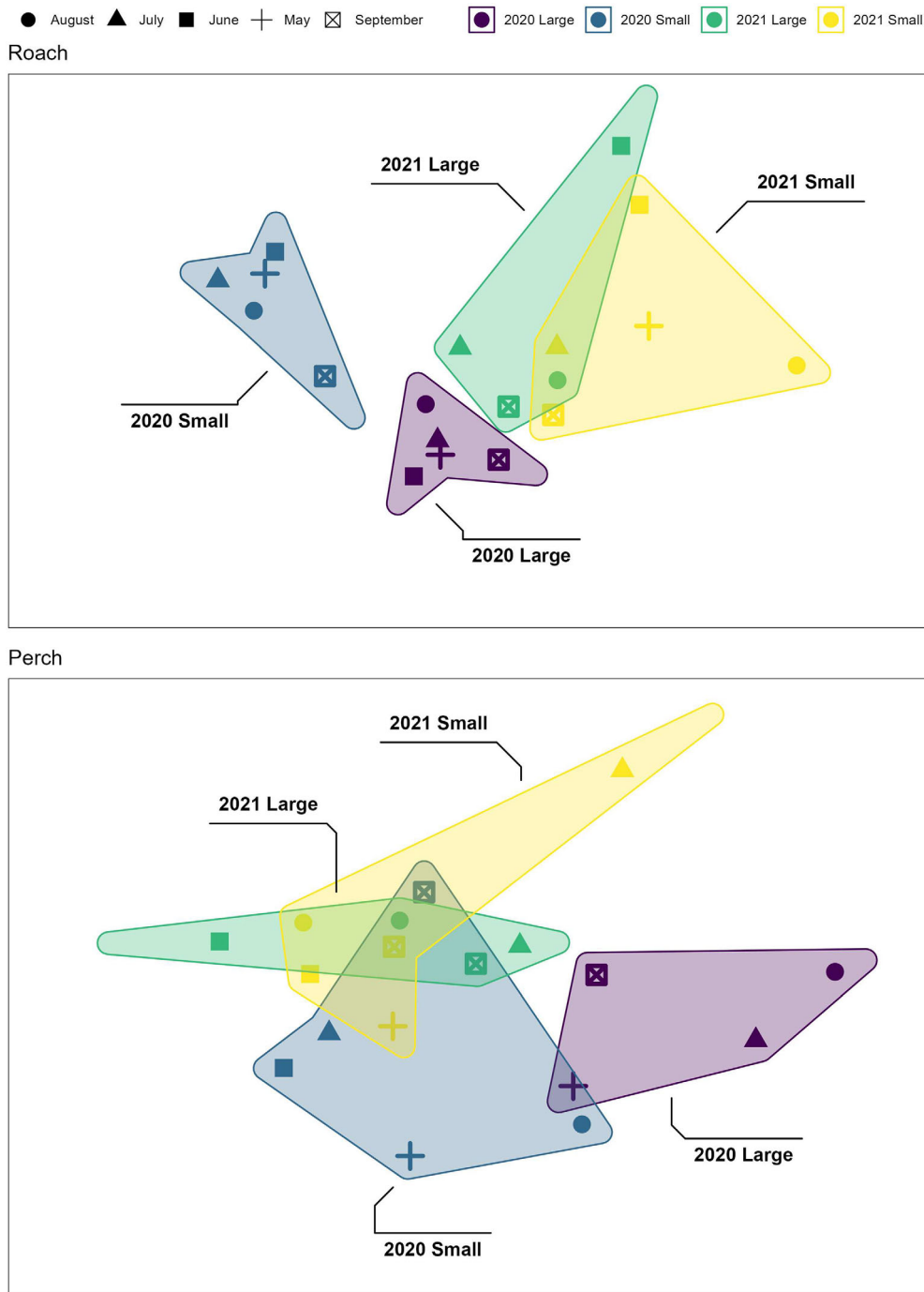


FIGURE 4 Nonmetric multidimensional scaling for small (7–15 and 4–15 cm total length) and large (15–26 and 15–30 cm total length) square root-transformed roach and perch diet before and after fish removal in directly comparable months May–September.

TABLE 6 Two-way crossed ANOSIM on the effect of size \times year on diet of roach and perch between the comparable months May–September before and after fish removal.

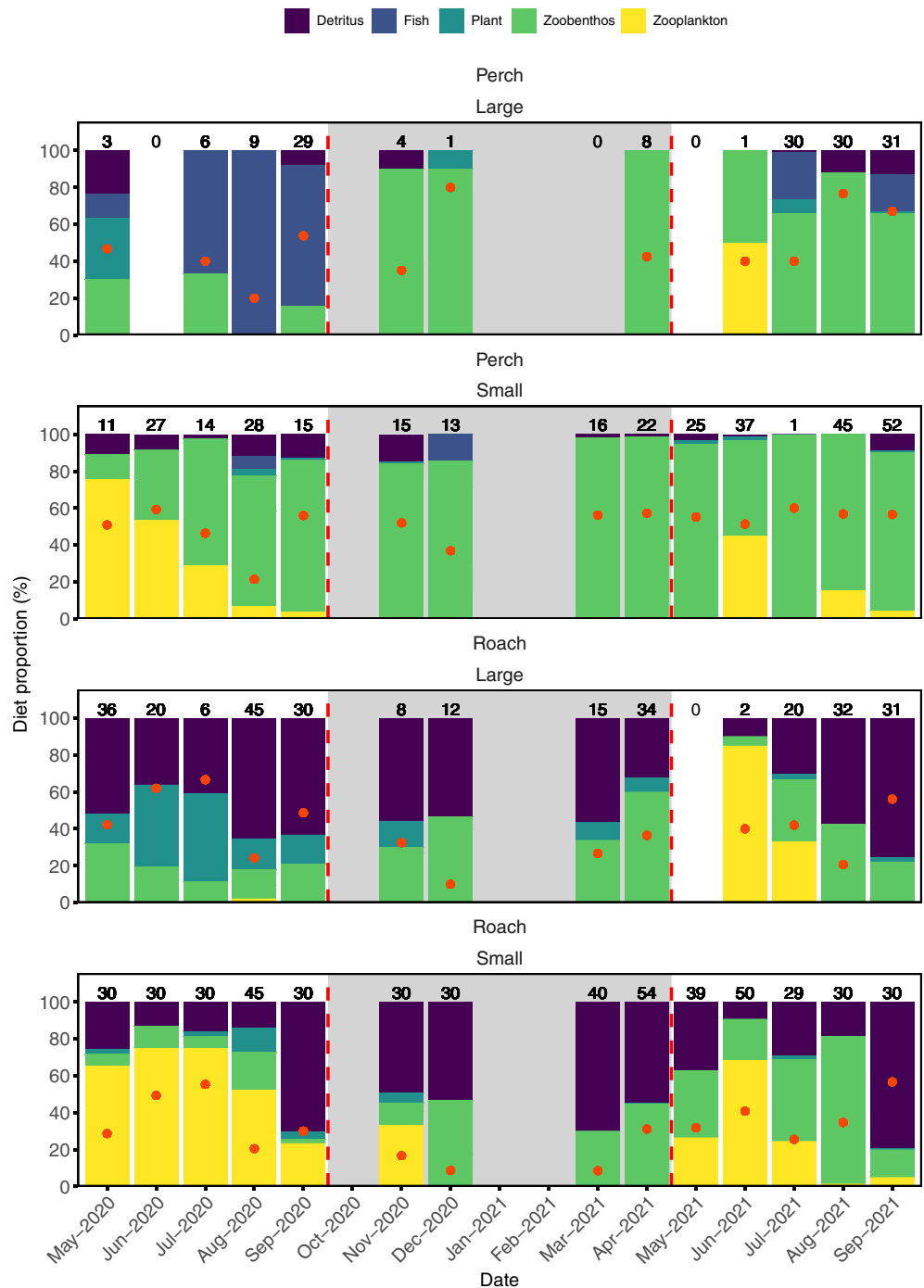
Species	Factor	R	P	Permutations
Roach	Year	0.491	0.007	999
	Size	0.696	0.001	999
Perch	Year	0.291	0.015	999
	Size	0.33	0.003	999

Abbreviation: ANOSIM, analysis of similarities.

community of the study lake, as top-down control is very strong in eutrophic shallow lakes (Jeppesen et al., 1997).

Large zooplankton control phytoplankton biomass more effectively than smaller species (Vakkilainen et al., 2004). The effect of this was observed in Lake Ormstrup where chlorophyll-*a* concentration was low during the period with high daphnid biomass. The period of high zooplankton biomass, after the second fish removal period in 2021, lasted less than 2 months, after which chlorophyll-*a* concentration increased to the highest observed values in the study period. We propose that this sudden increase, and subsequent decrease, in zooplankton biomass was

FIGURE 5 Stacked bar plot of percentual stomach content of small (7–15 and 4–15 cm total length) and large (15–26 and 15–30 cm total length) perch and roach, respectively. Dashed line indicates where fish removal occurred in both years. Orange dots show percentual average fullness. Number of samples (N) is marked above each bar. Shaded gray area highlights the period between directly comparable months in the 2 years. Orange dots show average fullness.



caused by an increase in daphnids due to low predation pressure and high food availability, as was also observed by Vanni (1987) and Vakkilainen et al. (2004). In turn, this caused a major diet shift toward zooplanktivory by all sizes of roach and perch, which eventually caused the daphnid stock to collapse. These conclusions are supported by gut-content analysis, which shows that all fish groups had high percentages of *Daphnia* in their gut during the months of high zooplankton biomass, regardless of size category or species. This provides evidence that fish respond immediately to changes in food abundance/composition and might have prevented the lake from switching from a turbid to a clear-water state or at least reducing the period where the shift is present by

enforcing top-down control on pelagic phytoplankton grazers. The reason this top-down control was observed in our study was likely that not enough roach were removed from the lake to sufficiently reduce predation on zooplankton under the given conditions. Further, we saw increased zooplanktivory among fish groups not expected to feed heavily on zooplankton (i.e., large-size classes of roach and perch), which might have led to an underestimation of the needed reduction in roach biomass. The effect of fish predation might be enhanced by periodic stratification, as described for the study lake by Søndergaard et al. (2022). This periodic stratification might increase zooplanktivory by confining both zooplankton and fish to the upper water column.

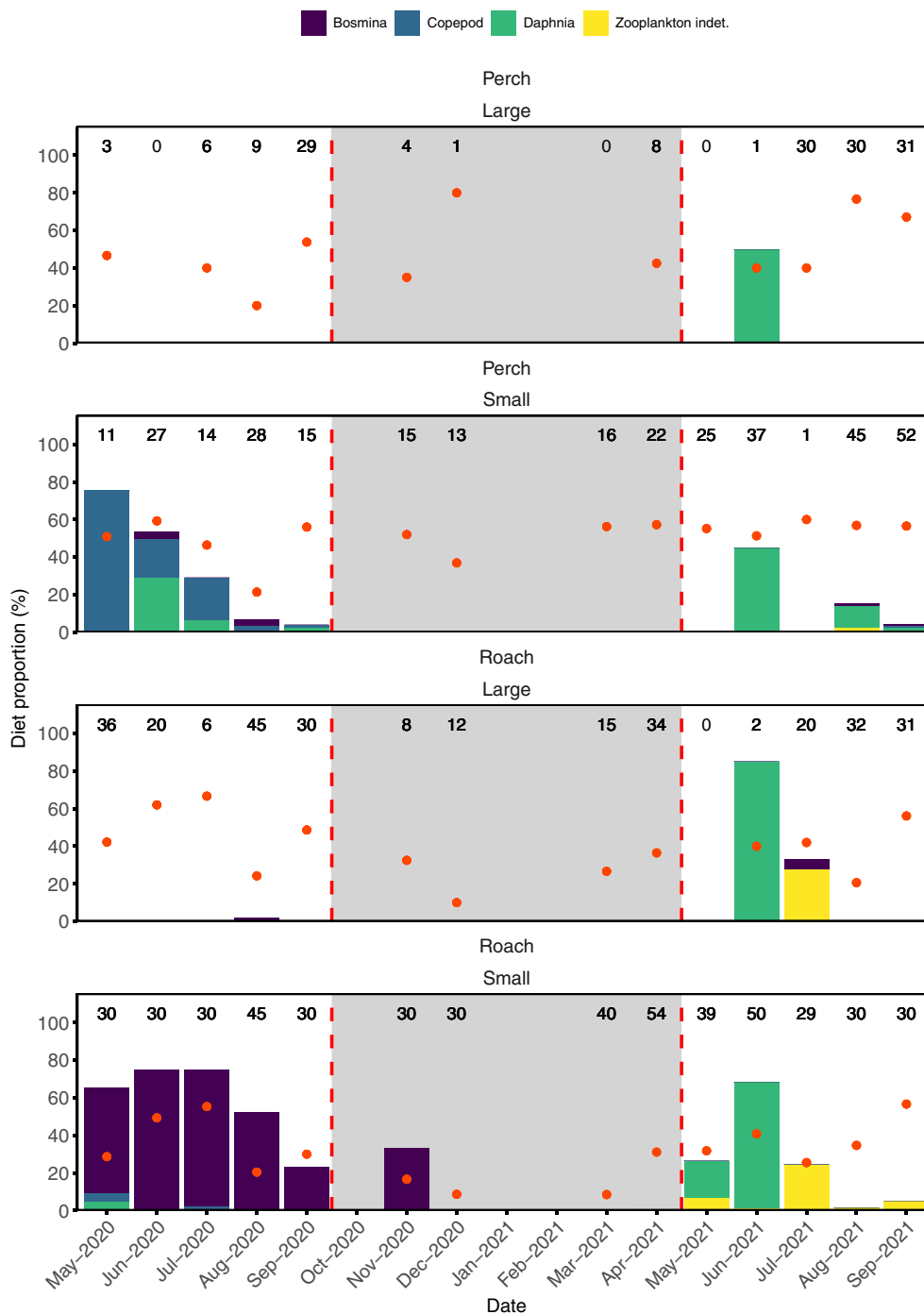


FIGURE 6 Stacked bar plot of zoobenthos in the diet of small (7–15 and 4–15 cm total length) and large (15–26 and 15–30 cm total length) perch and roach during the study period. Dashed line indicates where fish removal occurred. Number of samples (N) is marked above each bar. Orange dots show the average stomach fullness for each month. Shaded gray area highlights the period between directly comparable months in the 2 years.

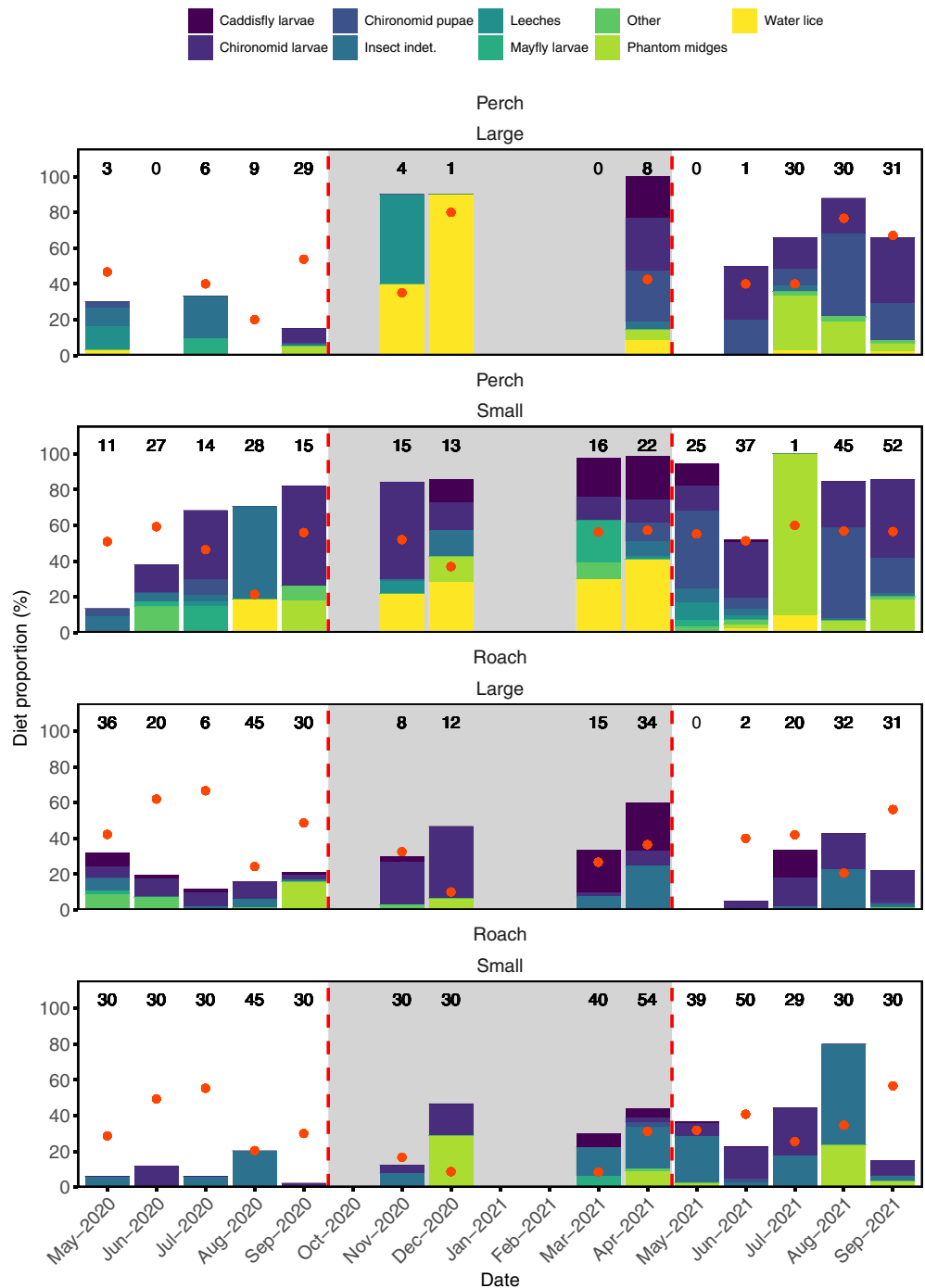
Moreover, we found small roach and perch consumed a high fraction of zooplankton before fish removal. In particular, roach fed heavily on bosminids, whereas perch fed mainly on copepods that are more elusive, supporting the findings of Peterka and Matěna (2011), who found that perch feed more successfully on smaller and fast-moving prey. This behavioral pattern also carried to foraging on macroinvertebrates, where we found perch to have a more diverse macroinvertebrate diet than roach, as well as having more macroinvertebrates in their diet in general. The macroinvertebrates in perch stomachs were not abundant in terms of biomass estimates (Supplementary Material) or found in roach diet. We largely attribute this to differences in foraging strategy and feeding

apparatus morphology, which differ significantly between roach and perch as found by Diehl (1988), Stolbunov and Pavlov (2006), and Peterka and Matěna (2009).

We found chironomid pupae in diets of both size categories of perch; however, biomass of these pupae in macroinvertebrate samples was low. Low biomass of chironomid pupae in benthic sediment samples was not surprising as these are commonly associated with the water column and surface waters, and thus, the true abundance of these is not captured well by this method.

When invertebrates in diet were identifiable, large roach had mostly sediment-burrowing chironomid larvae and house-building

FIGURE 7 Stacked bar plot of zooplankton in the diet of small (7–15 and 4–15 cm total length) and large (15–26 and 15–30 cm total length) perch and roach during the study period. Dashed line indicates where fish removal occurred in both years. Number of samples (N) is marked above each bar. Zooplankton marked indeterminate when stomach content was too deteriorated to determine.



caddisfly larvae in their gut, whereas small roach had chironomid larvae. Both chironomids and caddisfly larvae are not fast moving, relying on camouflage and “armored” houses to prevent predation. Both these strategies are presumably not very effective against the well-developed sucking (Osse, 1985) and mastication (Hjelm et al., 2003) apparatus of roach, which is likely why these organisms were most abundant in roach diet. Further, before fish removal, there was significant partitioning of diet resources in the gut content of both different species and size categories of fish. After fish removal, however, gut content of all fish groups shifted significantly toward increased zoobenthivory, which is consistent with a study by Persson and Hansson

(1999). They concluded that this shift was largely caused by reduced competition of large benthivorous bream (*Abramis brama*). Because our study lake does not contain bream, it seems that other mechanisms could also play a role, for example, reduced inter- and intraspecific competition among roach and perch. This is consistent with findings from other fish populations, where reduced fish biomass led to reduced individual diet specialization (Klemetsen et al., 2002; Prati et al., 2021).

Large perch were mainly piscivorous before fish removal, but shifted to zoobenthivory after, almost eschewing piscivory completely. It must be noted that perch caught before fish removal

were generally larger. By contrast, studies by Persson and Hansson (1999), Sharma and Borgström (2008), and Syväranta and Jones (2008) found piscivory in perch above 150 mm to increase after whole-lake fish removals. The reason for this increase in piscivory in their studies is largely attributed to increased reproduction in cyprinid fish, leading to increased density of fry. We did not observe a significant increase in roach fry abundance after fish removals, and this could explain why perch shifted from piscivory to zoobenthivory. This is based on the optimal foraging theory (Pyke et al., 1977; Sih & Christensen, 2001), stating fish will consume the most beneficial prey at the given situation. Presumably, macroinvertebrates and, at times, zooplankton were so abundant that this diet resource was preferable. We argue this because roach biomass, and thus the dominating prey fish, was reduced severely after fish removal and, further, because macroinvertebrate biomass increased significantly after fish removal. This is consistent with Nurminen et al. (2017) who found macroinvertebrate density to decrease with total fish density. The observed abundance of invertebrates in kick samples is also indicative of increased invertebrate abundance in the lake, likely stemming from reduced predation from fish.

Manipulations of fish biomass are often used to improve the state of lakes. However, fish populations and trophic state of lakes often react in unpredictable ways (Persson & Hansson, 1999; Syväranta & Jones, 2008). Despite intense monitoring of the lake, we found it difficult to anticipate how fish food selection was affected by fish removal.

Our study found a general trend toward increased zoobenthivory among all fish groups after fish removal, regardless of prior diet preference. There was reduced zooplanktivory among small perch and roach except for when biomass of large-bodied zooplankton was high. This shows that both small- to medium-sized roach and perch changed diet preferences in an opportunistic way in response to prey abundance. Diet shifts based on prey abundance are supported well by current literature (Persson & Hansson, 1999; Prati et al., 2021). Further, there was reduced piscivory among large perch (>150 mm) after fish removal, which was unexpected and not found by previous studies. Consequently, large perch did not increase the strength of fish removal by increasing predation mortality of smaller zooplanktivorous fish.

The goal of fish removal was to reduce top-down control of large zooplankton. This goal was achieved briefly; however, fish diets rapidly changed toward zooplanktivory in response to increased daphnid biomass. We propose that such a change toward periodical zooplanktivory across fish species and size groups may lead to higher top-down control on zooplankton than expected. Despite 75%–80% roach biomass was removed over a short period, in this specific lake this was not enough in the given situation for sustained suppression of zooplanktivorous top-down control throughout the summer. In addition, top-down control was enforced by fish size groups not originally thought to be planktivorous, suggesting that fish may be more plastic in their feeding behavior than expected. Changes toward periodical zooplanktivory across fish species and size groups may lead to high top-down control on zooplankton, which may challenge the use of fish removal to restore lakes.

AUTHOR CONTRIBUTIONS

Conceptualization: Andreas S. Berthelsen, Torben L. Lauridsen, and Christian Skov. Developing methods: Andreas S. Berthelsen, Torben L. Lauridsen, Christian Skov, and Martin H. Larsen. Data analysis: Andreas S. Berthelsen. Preparation of figures and tables: Andreas S. Berthelsen. Conducting research, data interpretation, and writing: Andreas S. Berthelsen, Torben L. Lauridsen, Christian Skov, Martin Søndergaard, and Martin H. Larsen.

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We used data from Forvaltningstjenesten 2.0 to create the map of the study area. These data are publicly available from the Danish Agency for Data Supply and Infrastructure. The authors have no conflicts of interest to declare.

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DATA AVAILABILITY STATEMENT

Data are available from the authors on reasonable request.

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