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Long-Term Changes in Fish Community Composition of a Coregonid Dominated Oligotrophic Lake

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Abstract: Cold-water lakes in high-latitude regions are experiencing rapid changes in community structure and functioning associated with local and global stressors (e.g., climate change, hydropower and invasive species). However, the long-term ecological responses of cold-adapted top predators are relatively poorly monitored despite their high importance for structuring ecological communities and for the provisioning of ecosystem services. We studied long-term changes (2010–2021) in the population structure and trophic niche of two cold-adapted coregonid fishes in oligotrophic Lake Osensjøen, southeastern Norway. Our gillnet surveys indicated that the whitefish (*Coregonus lavaretus*) population declines simultaneously with the increasing population density of roach (*Rutilus rutilus*), whereas vendace (*Coregonus albula*) showed more stable densities. Both whitefish and vendace became increasingly dominated by small-sized individuals following the increase in coexisting roach and perch (*Perca fluviatilis*) populations. Our stomach content and stable isotope data indicated a marked overlap in the trophic niches of whitefish and roach, with both species showing high among-individual variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as compared to the more specialized zooplanktivorous vendace. Our study provides further evidence that the ongoing environmental changes in high-latitude lakes may induce rapid changes in community structures and lead to the population declines of cold-adapted fishes, likely associated with strong resource competition with warm-adapted cyprinid and percid fishes. Such shifts in fish community structure may, in turn, affect the benthic and pelagic food-web compartments and reduce valuable ecosystem services such as local fisheries targeting salmonids.

Keywords: salmonid fishes; environmental change; stable isotope analysis; nutrition; isotopic niches; population dynamics; cyprinification



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1. Introduction

Freshwater ecosystems are among the most vulnerable habitats on Earth, experiencing rapid biodiversity loss and impaired ecological functions with potential cascading impacts across the connected freshwater, marine and/or terrestrial ecosystems and their associated ecosystem services [1,2]. Lakes in high-latitude regions are particularly sensitive to global warming and abrupt changes in species assemblages due to the limited potential of native cold-adapted species to evade or alleviate negative interactions with competitively superior warm-adapted species spreading towards higher latitudes and altitudes [3–5]. For example, the ongoing changes in community compositions and habitat conditions are causing marked declines in highly valued, cold-adapted salmonid fish populations in North

European lakes [4,6,7]. These salmonids include pelagic zooplankton feeding fishes, usually occurring at moderate densities (<1000 fish/ha) [8] preying on herbivorous zooplankton that may control algae biomass. At high densities of planktivorous fish, and especially when cyprinids are abundant [4,8–10], the density and individual size of herbivorous zooplankton may be reduced [11–14], leading to increased algae growth and degraded water quality.

As compared to the larger and more generalist *Salmo* and *Salvelinus* species, coregonid fishes like vendace (*Coregonus albula*) and European whitefish (*Coregonus lavaretus*) are considered more specialized zooplanktivores which may induce strong top-down control on zooplankton communities but show limited resource competition with more littoral-oriented benthivorous fishes [15,16]. However, in some lakes, whitefish show resource polymorphism, with phenotypically distinct ecotypes utilizing predominantly pelagic, profundal or littoral food and habitat resources [17]. This resource polymorphism, together with lake morphometry, are important factors determining niche overlap between cold-water coregonids and more warm-adapted competitive fishes, with deeper lakes providing a vacant pelagic niche for zooplanktivorous whitefish [18]. Although the competitive interactions between native coregonids and invasive percid or other coregonid fishes have been widely studied in subarctic lakes [16,19–22], there is limited evidence for long-term changes in the trophic niches and population structures of sympatric whitefish and vendace populations in more southern lakes subject to recent environmental changes, e.g., in fish community composition.

We studied the long-term changes in population structure and trophic niches of sympatric whitefish and vendace in Lake Osensjøen, southeastern Norway. The lake has been an important target for local inland fisheries targeting relatively large-sized whitefish and vendace. However, in recent years, the coregonid populations seem to have undergone substantial changes in abundance and size, with negative impacts on local fisheries [23,24]. Here, we compile data from fish monitoring surveys (hydroacoustic and survey gillnet catches), as well as stomach content and stable isotope analyses conducted over multiple years (2009–2021), to elucidate the potential competitive interactions between the coexisting cold-water-adapted coregonid and more warm-water-adapted percid and cyprinid fishes. The body sizes of important groups of herbivorous zooplankton were measured to assess the potential effects of changes in fish predation pressure. We expected vendace to retain relatively large population sizes due to the highly specialized pelagic zooplanktivorous niche of the species and thus limited resource competition with the more littoral-oriented sympatric percid and cyprinid fishes. In contrast, we expected the more generalist whitefish to show substantial niche overlap with the coexisting percid and cyprinid fishes, potentially causing a decline in the whitefish population.

2. Materials and Methods

2.1. Study Area

Lake Osensjøen (61°15' N, 11°45' E) is an oligotrophic (total phosphorous = 7.5 µg/L) and slightly humic (color = 79 mg Pt/L) [25] lake situated at 435 m a.s.l. in Trysil and Åmot municipalities, Innlandet County in southeastern Norway (Figure 1). Since 1930, the lake has been regulated with a dam on the natural outlet, and before 1981, the regulation only supplied two small river plants in the outlet river. Since 1981, the lake has been tapped through a tunnel from the bottom at the northwestern end of the lake, 20–25 m below the surface, to a power plant below. The minimum discharge in the outlet river is now 6.0 m³/s from 1 June to 15 September and 2.5 m³/s the rest of the year [26], and up to 25 m³/s is tapped through the tunnel, most of it during autumn and winter. The new regime has possibly had an impact on the recruitment of whitefish, as important spawning grounds are

localized in areas close to the tunnel [27], and larvae and fry or their nutrition crustaceans may be entrained. The annual regulation amplitude of 6.6 m (431.2–437.8 m a.s.l.) has led to the nearly complete disappearance of littoral macrophytes. The lake surface area is 43.6 km², with a maximum depth of 117 m and an average Secchi depth of 2–2.5 m in 2021. The water surface temperature is typically below 15 °C in summer but may reach 17 °C in August. The mean air temperature in July–August at the closest meteorological station (Haugedalen, 20 km west of Lake Osensjøen) was 14.1 °C, and it increased significantly with the year (Temp., °C = 0.044 × Year + 73.38, $r = 0.45$, d.f. = 40, $p < 0.01$) in the period 1970–2011 (the station was closed down) but seemed to level out after 2002. At another meteorological station, Flisa (56 km south of Lake Osensjøen), there was no correlation for the period 2004–2024 (Temp., °C = $-0.0073 \times \text{Year} + 30.70$, $r = -0.05$, d.f. = 19, $p > 0.05$), so the summer temperature seems to have stabilized after 2000, though with a peak in 2002 and 2006.

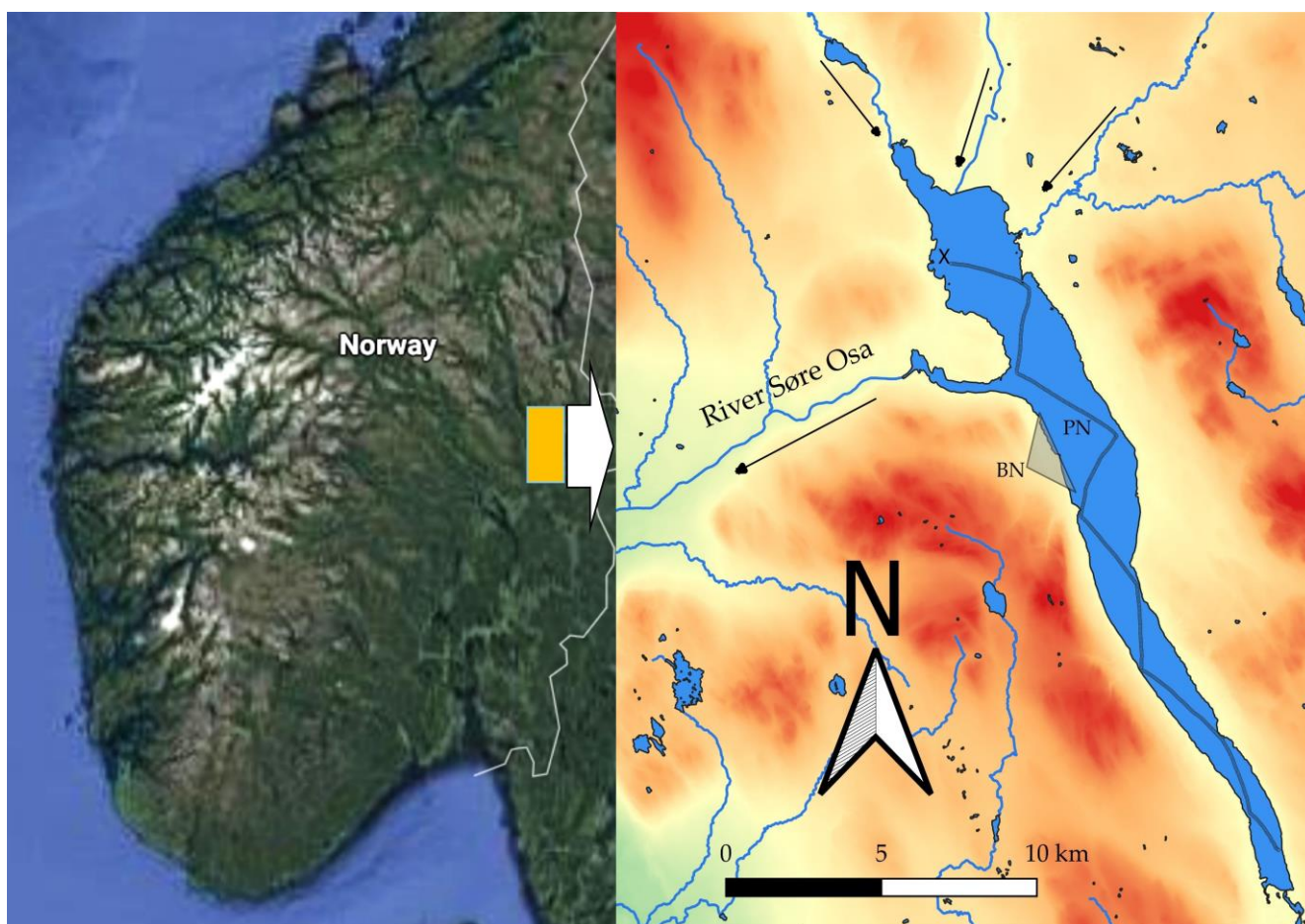


Figure 1. The location of Lake Osensjøen in southeastern Norway. PN and BN indicate the sites where repeated sampling with pelagic (PN) and benthic (BN) nets were conducted. Lake-crossing transects of hydroacoustic recordings were indicated by plotting the position of every 50th signal transducer. X in the northwestern part of the lake marks the approximate position of the tunnel exit. Colors indicate topography.

Lake Osensjøen harbours nine fish species: vendace, European whitefish, roach (*Rutilus rutilus*), perch (*Perca fluviatilis*), burbot (*Lota lota*), brown trout (*Salmo trutta*), northern pike (*Esox lucius*), European grayling (*Thymallus thymallus*), and the common minnow (*Phoxinus phoxinus*). Vendace originating from Lake Mjøsa and whitefish originating from several sources were introduced to the lake in the early 20th century [28,29], whereas the other species are native. The vendace in Lake Osensjøen has, on average, 44 gillrakers as

compared to the whitefish, with a mean of 30 gillrakers [29]. The exploitation of vendace and whitefish has been low to moderate since the 1970s, but has decreased since 2000, partly due to the reduced size of vendace and *Triaenophorus robustus* cestode infections in whitefish.

2.2. Sampling

Hydroacoustic assessment of the pelagic fish density was conducted using a SIMRAD EY-M [30] echosounder in 2009–2011, whereas a SIMRAD EK 15 echosounder [31] was used in 2018 and 2021. A comparison of the devices with beam angles 11.2° and 9° produced corresponding results [32]. The hydroacoustic recordings were conducted along the same nine transects (Figure 1) crossing the lake at daytime in spring and at nighttime in autumn with a degree of coverage of $S = 3.1$ [33]. The data were analyzed in one depth layer, i.e., from 20 m to approximately 40 m in May and from 2 to 20 m in autumn, in which more than 95% of the recorded fish were observed. Fish density ≥ 5 cm (corresponding to target strength ≥ -54 dB [30]) and length distributions were calculated by means of relevant (see below) software. Total abundance of pelagic fish was calculated by multiplying the estimated density at depth 20–40 and 2–20 m with the lake area covering the depth > 20 and > 2 m, respectively.

Fish samples were collected in June, August and September 2010, 2013, and 2021, using 1.5 m high and 30 m long benthic and 6 m high and 30 m long pelagic multi-mesh Nordic gillnets, both consisting of 12 randomly distributed 2.5 m long panels with knot-to-knot mesh sizes of 5, 6.25, 8, 10, 12.5, 16, 19.5, 24, 29, 35, 43, and 55 mm [34]. The pelagic nets were used only in August and September. The gillnet effort was supplemented by two sets of 1.5 m high and 25 m long benthic gillnets of mesh sizes 10, 13.5, 16.5, 19.5, 22.5, 24, 29, 35, 42, and 52 mm and 10, 13.5, 16.5, 19.5, 24, 29 and 35 mm, as well as one set of 6 m high and 25 m long pelagic nets with mesh sizes 10, 12.5, 16.5, 19.5, 24, 29, 35, and 39 mm. The benthic nets were set on the western shore of the lake (Figure 1) from close the shore towards the deeper areas, either as separate sets or by combining two nets with different mesh sizes. Pelagic nets were set at 2–8 m and 12–18 m depths. Species fish length was measured (mm) from the tip of the snout to end of the tail held in the natural position and wet mass (g) was recorded from all 992 captured fish (Table S1). To analyze the recently ingested prey items, stomach samples were dissected from vendace and whitefish in 2010 and 2021, supplemented with roach stomach samples in 2021.

For stable isotope analysis (SIA), a small sample of dorsal muscle tissue was dissected from random subsamples of fish and stored at -20 °C. Whenever gillnet catches permitted, almost equal numbers of individuals were included from each habitat to make the subsamples representative of the whole fish population. Qualitative samples of putative littoral and pelagic food sources were collected for SIA. Zooplankton was collected from the pelagic zone close to the pelagic nets in August (2010, 2013, 2018 and 2021) by taking several hauls through the water column with a 100 μ m mesh plankton net until sufficient material was obtained. The samples were later sieved through a 200 μ m mesh to obtain pure samples of adult cladocera and copepods. The body length of *Bosmina* sp. and *Daphnia* sp. was measured (0.01 mm). Benthic macroinvertebrates were collected in July and August (2010, 2013 and 2021) from the littoral zone in the same area as the benthic gillnetting (BN), using a kick net in the shallow water (0–1 m) and an Ekman grab or a benthic sledge in deeper areas. All benthic macroinvertebrate samples were sieved through a 500 μ m mesh. Both benthic and pelagic invertebrates were sorted to genus level. Only the soft body tissues from mollusks were prepared for SIA.

Fish (Table S2), benthic macroinvertebrates and zooplankton samples were dried (48 h in a freeze-drier or at 60 °C in an oven), ground to a fine powder, and weighed

(0.500–0.600 mg) into encapsulated tin cups for subsequent SIA. Stable carbon and nitrogen isotope ratios (expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) were analyzed by an elemental analyzer coupled to a continuous flow isotope ratio mass spectrometer at the University of Jyväskylä, Finland. Vienna PeeDee Belemnite and atmospheric nitrogen were used as international references for carbon and nitrogen, respectively (see Eloranta et al. [15] for more details of SIA procedures).

2.3. Data Treatment and Statistical Analysis

SIMRAD EY-M stored the data on magnetic tape, and the tapes were digitalized and analyzed by means of the HADAS software (ver. 3.9) [35]. SIMRAD EK15 used an ordinary pc running SIMRAD ER15 (ver. 1.2.4) software for the control and sorting of data. The EK15/ER15 system was set up to store raw data, and these data were later analyzed with the Sonar5-Pro software (ver. 608.53) [36].

Assuming negatively distributed N (as based on counting data), confidence intervals of estimates were calculated from \ln transformed variables $y = \ln x$, and the 95% confidence interval of transformed values: $\text{C.I.}_y = \hat{y} \pm t_{0.025} \times \text{S.E.}$ For untransformed x , lower $\text{C.L.}_x = N_{\text{mean}} \times (e^{\text{Lower C.L.}_y} / e^{-\hat{y}})$ and Upper $\text{C.L.}_x = N_{\text{mean}} \times (e^{\text{Upper C.L.}_y} / e^{-\hat{y}})$, according to Elliot [37]. Mean values across years were normally distributed (as mean values are) and confidence intervals were calculated as $\text{mean} \pm 1.96 \times \text{S.E.}$

The gillnet catch per unit effort (CPUE) was calculated as the number of fish caught per 100 m^2 gillnet and night (approximately 12 h). Zooplankton samples were counted and presented as a proportion (%) by numbers. Food items in fish stomachs were counted and presented as the mean frequency of the item group in species and year.

Frequencies of species in the gillnet samples were analyzed for differences between years, and taxonomic groups (summarized over individuals of fish) in stomach samples were analyzed for differences between populations/species by means of Pearson's chi-square test in R software [38,39]. The pairwise proportional similarity index D between populations/species was estimated by the following formula [40]:

$$D = 1 - 0.5 \times \sum_{i=1}^{\infty} |p_{x,i} - p_{y,i}|$$

where $p_{x,i}$ and $p_{y,i}$ are the frequencies of the taxonomic group i recorded in stomachs of species x and y , respectively. D may range from close to 0 to close to 1, and a high value means high similarity/overlap, indicating competition for food.

We used the SIBER package (Jackson et al., 2011), the jags package [41] and the ggplot2 packages [42] in R software [38] to estimate the sizes and overlaps of isotopic niche areas of vendace, whitefish, perch and roach sampled in different years. The isotopic niches were visualized by prediction ellipses containing approximately 95% of the data [42]. Total convex hull areas (TAs) and the sample size-corrected standard ellipse areas (SEAc) depict the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of all individuals and the core group of individuals (i.e., 95%), respectively, thus reflecting individual variation in long-term assimilated diets and the population-level trophic niche of each fish species.

Linear modelling was conducted by means of R software [38] to explore the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (successively, as response variable y) in four linear models (lm), adding the sampling year and species as categorical predictors and fish length as a continuous predictor, starting with including three-way interaction terms:

- Model 1: $y = \text{factor}(\text{Year}) * \text{Species} * \text{Fish length};$
- Model 2: $y = \text{factor}(\text{Year}) * \text{Species} + \text{Fish length};$
- Model 3: $y = \text{factor}(\text{Year}) * \text{Fish length} + \text{Species};$
- Model 4: $y = \text{factor}(\text{Year}) + \text{Fish length} + \text{Species}.$

The term $x_1 * x_2$ includes three predictor terms: x_1 , x_2 and the interaction $x_1:x_2$.

The model with the lowest Akaike's information criterion (AIC) was selected. The variation between species within year was tested pairwise with one-way ANOVA and the Tukey post hoc test [39].

3. Results

3.1. Fish Density and Spatial Distribution

The estimated density of pelagic fish increased from 193 (95% C.I.: 111–338) fish/ha in 2010 and remained stable from 2011 to 2018, 611 (95% C.I.: 272–1372) fish/ha and 689 (95% C.I.: 297–1081) fish/ha, respectively. The confidence intervals are wide and overlapping, and the difference between 2011 and 2018 is non-significant. A significant (non-overlapping C.I.) increase to 3650 fish/ha (95% C.I.: 2914–2385) was recorded in May 2021, whereas in September the same year, the density decreased to 378 (277–479), i.e., below that of 2011 and 2018 (Appendix A). The mean density of the estimates of 2011, 2018 and September 2021 was 559 fish/ha (95% C.I.: 376–742), with an upper C.L. limit substantially lower than the lower C.L. limit of the May estimate, so the May estimate was significantly higher. The pelagic fish were recorded at a greater depth (>20 m) in May than in September, and by multiplying the recorded density with the area of the lake covering depths > 20 m, we determined that there were 5,475,000 fish. The density in September at a depth > 2 m yields 1,512,000 fish, or less than one-third of the May estimate.

Pelagic gillnet catches at a 2–10 m depth in autumn gave mostly vendace and whitefish, although with a decreasing number of whitefish from 2013 to the near absence of them in 2021, when a few roach fish were also caught from the pelagic zone (Figure 2). A few vendace but no other fishes were caught deeper than 10 m. Benthic catches of vendace increased slightly, whereas whitefish catches decreased steadily from 2010 to 2021. At the same time, the benthic catches of roach increased, and the species was numerically dominant in 2021, with the roach CPUE being more than three times that of the other species, i.e., making up 75% of the catches. Perch catches also increased slightly in 2021, whereas grayling was caught in 2010 and 2013, but not in 2021 (Table S1). The proportions of vendace, whitefish and roach in the benthic catches were significantly different between years ($\chi^2 = 11.3, 228.2$ and 172.2 , respectively, d.f. = 2, $p < 0.0001$ – 0.01), but not so for perch ($\chi^2 = 3.1, p > 0.05$). The proportion of perch increased from 2010 to 2013 but decreased in 2021.

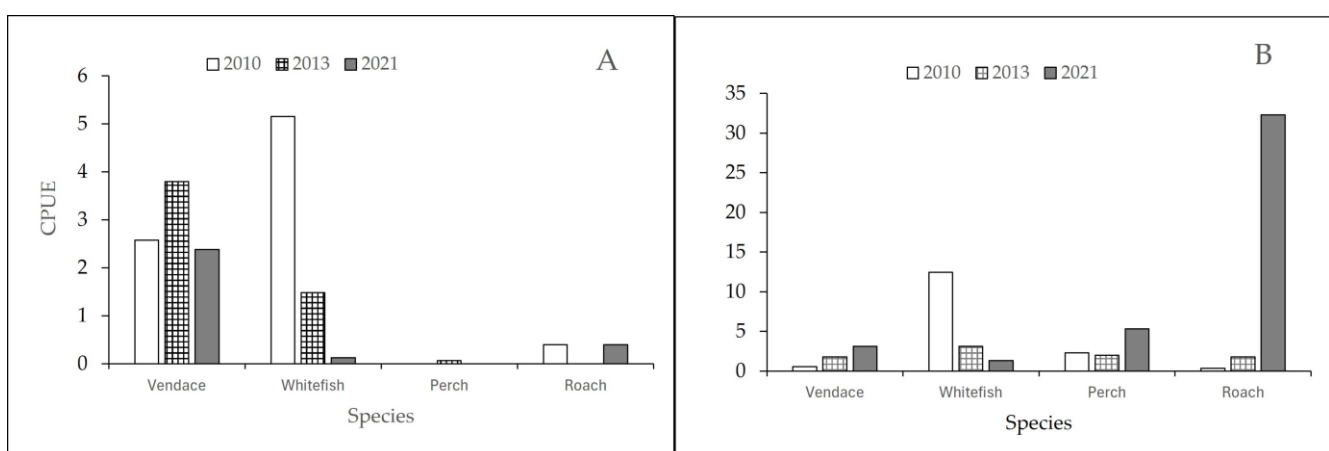


Figure 2. Relative densities of vendace, whitefish, perch and roach in the pelagic (A) and benthic (B) habitats of Lake Osensjøen in 2010, 2013 and 2021, presented as number of fish caught per 100 m² gillnet per night (catch per unit effort, CPUE).

3.2. Fish Size

Vendace showed a dramatic change in length distribution from 2010, when all specimens caught were larger than 200 mm, to 2013, when lengths ranged from 150 to 250 mm, decreasing further in 2021 when lengths ranged from 100 to 160 mm (Figure 3A). Whitefish showed a similar decline in body size, with a dominance of specimens larger than 300 mm in 2010 and 250 mm in 2013 and smaller than 270 mm in 2021 (Figure 3B).

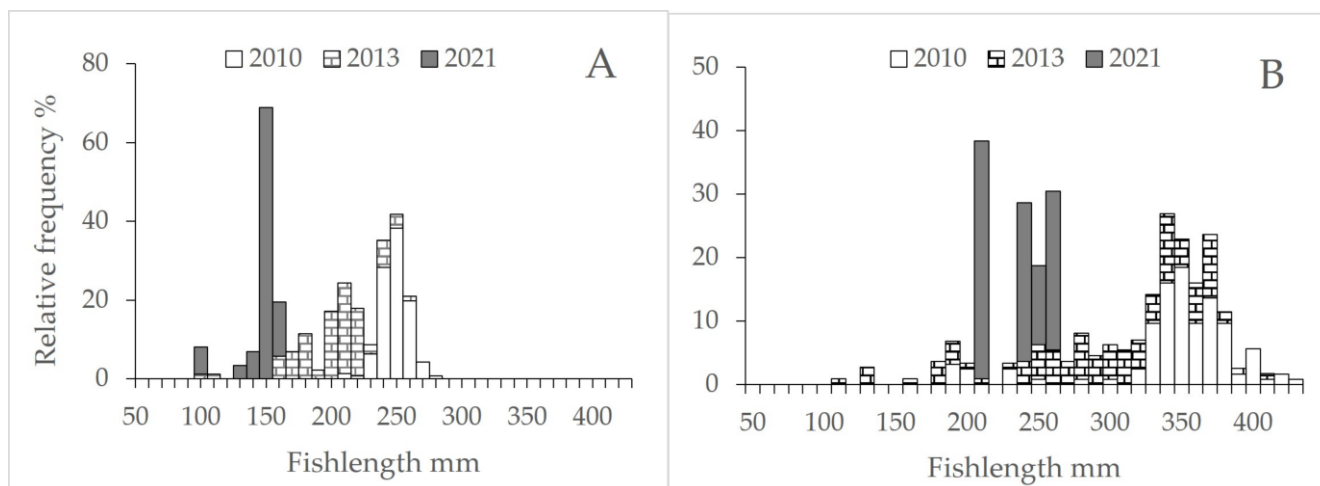


Figure 3. Length distributions of vendace (A) and whitefish (B) caught in Lake Osensjøen in 2010, 2013 and 2021.

The vendace and whitefish catches were divided into three length groups (to avoid null groups), and chi square tests revealed highly significant differences between years for both vendace ($\chi^2 = 224.4$, d.f. = 4, $p < 0.0001$) and whitefish $\chi^2 = 72.1$, d.f. = 4, $p < 0.0001$). In 2010, only one 290 mm roach was caught, whereas in 2013 and 2021, the roach length ranged from 120 to 290 mm and from 90 to 270 mm, respectively. Perch caught in 2010 were larger (240–290 mm) than those caught in 2013 (130–230 mm) and 2021 (90–230 mm), indicating increasing recruitment.

3.3. Diet

Cladocera (*Bosmina*, *Daphnia* and *Bythotrephes* sp.) was the most important zooplankton prey group for vendace and pelagic-caught whitefish, as well as for benthic-caught whitefish, which also consumed benthic insects (caddisfly and mayfly larvae) and molluscs (Figure 4). *Bosmina* sp. was the most important zooplankton prey for vendace and roach in 2021. *Daphnia* sp. was an important prey for vendace and whitefish but was not found in roach stomachs. *Chydoridae* were important prey only for whitefish, whereas copepods were consumed by all three species, though most frequently by vendace. *Bythotrephes* sp., mussels and snails were not recorded in the fish stomachs in 2021. Unlike for zooplanktivorous vendace, insects were also important prey for whitefish and roach. The frequency of taxonomic groups in the stomach samples differed significantly between species. For planktonic food (benthic items were only found in benthic whitefish) items in 2010, the frequencies of taxonomic groups in stomachs were significantly different between benthic and pelagic whitefish $X^2 = 25.0$, d.f. = 1, $p < 0.001$), between pelagic whitefish and vendace $X^2 = 57.9$, d.f. = 1, $p < 0.001$), and more between benthic whitefish and vendace $X^2 = 10.8$, d.f. = 1, $p < 0.01$). There were also significant differences between vendace, whitefish and roach stomachs in 2021, $X^2 = 44.3$, d.f. = 4, $p < 0.0001$).

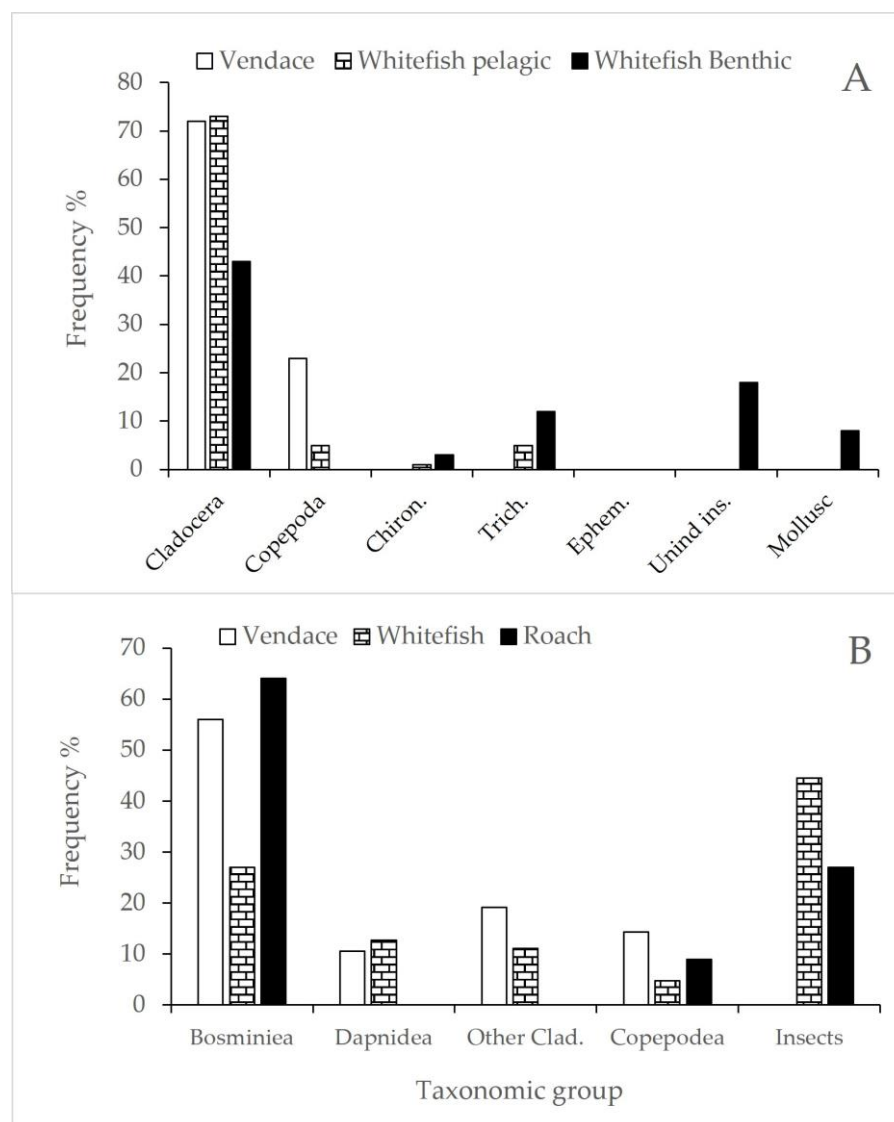


Figure 4. The relative occurrence of different prey categories in the stomach contents of vendace, pelagic and benthic whitefish sampled in 2010 (A), as well as in the stomach contents of vendace, whitefish and roach sampled in 2021 (B).

The highest pairwise similarity $D = 0.94$ was found between benthic and pelagic whitefish. It was lower between pelagic whitefish and vendace $D = 0.82$, and the lowest $D = 0.76$ was found between benthic whitefish and vendace in 2010. In 2021, the similarity was surprisingly the highest between vendace and roach $D = 0.66$, and the second highest $D = 0.54$ was found between roach and whitefish, whereas the lowest value $D = 0.54$ was found between vendace and whitefish.

3.4. Zooplankton

Cladocera dominated the zooplankton communities both in 2013 and 2021 (Figure 5). The proportion of *Daphnia* sp. was higher in 2021, whereas the proportion of other cladocera was lower. The proportion of copepods was quite similar in the two sampling years. The body lengths of *Daphnia* sp. and *Bosmina* sp. decreased from 2010 to 2018 and then increased from 2018 to 2021.

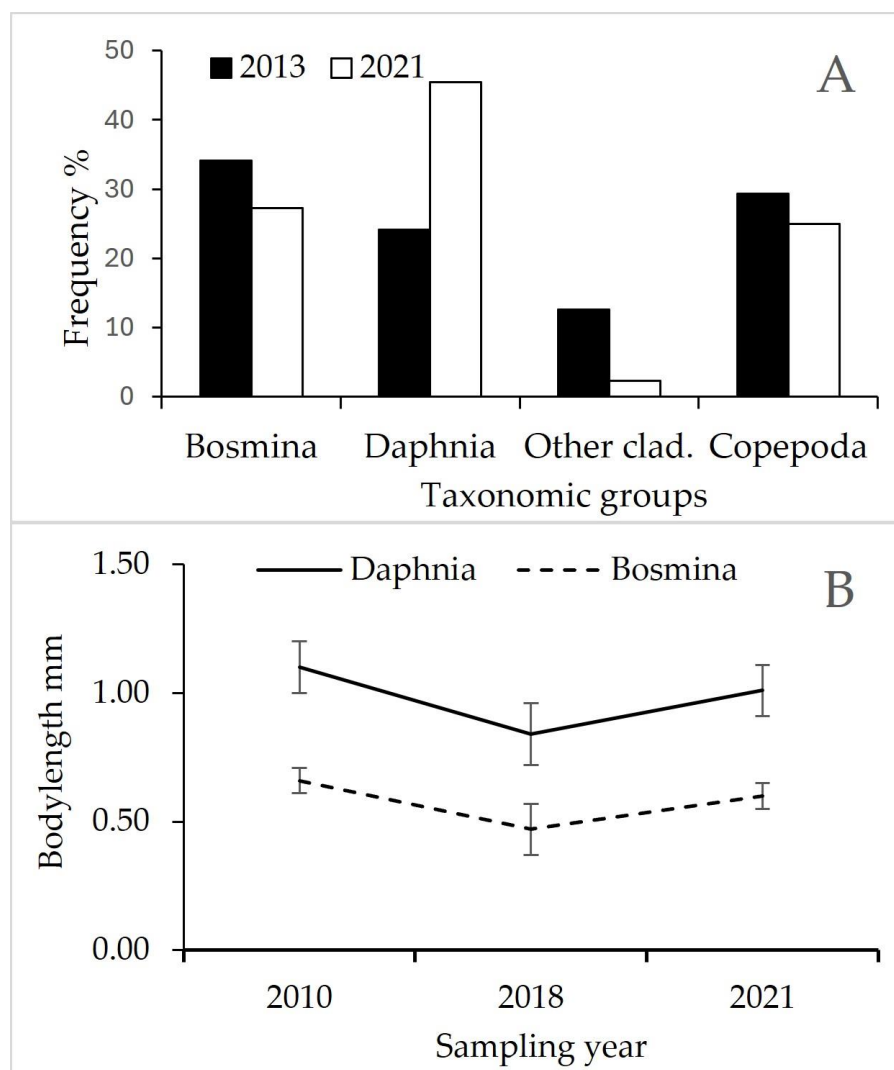


Figure 5. Frequency of important taxa in the zooplankton samples collected from Lake Osensjøen in 2013 and 2021 (A), and the mean body length of *Daphnia* sp. and *Bosmina* sp. collected in 2010, 2018 and 2021 (B). Vertical lines show 95% confidence limits.

3.5. SIA

The $\delta^{13}\text{C}$ values of vendace and whitefish ranged from -32.4 to -25.9‰ and from -30.2 to -25.9‰ , respectively (Table 1). The $\delta^{13}\text{C}$ values of roach and perch ranged from -30.0 to -25.9‰ and from -31.1 to -25.0‰ , respectively. The $\delta^{13}\text{C}$ values of brown trout, grayling, burbot and pike varied between -34.3 and 25.1‰ , with the littoral-dwelling grayling showing the highest $\delta^{13}\text{C}$ value.

The $\delta^{15}\text{N}$ values of vendace and whitefish ranged from 6.2 to 10.6‰ and from 6.1 to 10.2‰ , respectively. The $\delta^{15}\text{N}$ values of roach and perch ranged from 6.7 to 11.1‰ and from 6.7 to 9.7‰ , respectively. The $\delta^{15}\text{N}$ values of brown trout, grayling, burbot and ranged from 5.6 to 10.6‰ .

Zooplankton typically showed lower $\delta^{13}\text{C}$ values than zoobenthos (Table 2). The $\delta^{13}\text{C}$ values of zooplankton showed between-year variation: -29.9‰ in 2010, -33.0 to -31.1‰ in 2013, and -28.3 to -26.5‰ in 2021). Zooplankton also showed lower $\delta^{15}\text{N}$ values (-0.9 – 4.8‰) than littoral zoobenthos (5.3 – 12.5‰).

Table 1. Mean, range and standard deviation (S.D.) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of different fish species sampled from Lake Osensjøen.

Year	Species	n	$\delta^{13}\text{C}$ (‰)			$\delta^{15}\text{N}$ (‰)			TA	SEA _c
			Mean	Range	S.D.	Mean	Range	S.D.		
2010	Vendace	16	−31.0	−32.2–−30.1	0.7	8.5	10.4–10.6	0.3	1.39	0.62
	Whitefish	25	−28.7	−30.2–−26.0	1.1	7.5	6.1–8.8	0.7	7.23	2.56
	Roach	1	−27.8	-	-	7.8	-	-	-	-
	Perch	5	−27.3	−28.8–−26.4	0.9	8.2	7.7–8.5	0.3	0.87	1.12
	Brown trout	2	−27.8	−28.0–−27.7	0.2	8.7	8.1–9.4	0.9	-	-
	Grayling	1	−25.1	-	-	7.8	-	-	-	-
	Burbot	2	−28.4	−28.4–−28.4	0.0	10.5	10.4–10.6	0.1	-	-
	Pike	3	−28.4	−28.5–−28.3	0.1	9.1	8.6–9.5	0.5	-	-
2013	Vendace	22	−31.6	−32.4–−30.8	0.4	9.0	8.1–9.5	0.3	1.28	0.47
	Whitefish	7	−28.3	−29.0–−27.1	0.7	8.7	7.0–10.2	1.3	3.54	3.05
	Roach	7	−28.4	−29.5–−27.6	0.7	7.5	7.0–7.9	0.3	1.09	0.82
	Perch	8	−28.4	−31.1–−25.0	2.1	8.4	6.7–9.7	1.2	7.96	5.72
	Brown trout	12	−28.0	−31.2–−26.5	1.3	8.9	7.7–10.2	0.8	-	-
	Grayling	12	−26.0	−28.1–25.2	0.7	7.8	6.9–8.7	0.6	-	-
	Burbot	12	−28.0	−34.3–−25.6	1.3	8.9	5.7–10.7	0.8	-	-
	Pike	4	−29.2	−31.2–−27.6	1.6	8.3	7.4–9.2	0.9	-	-
2021	Vendace	25	−29.7	−32.4–−25.9	0.2	8.4	6.2–10.4	1.2	1.91	0.65
	Whitefish	11	−27.4	−29.6–−25.8	1.1	7.8	6.9–10.2	0.7	3.84	1.94
	Roach	26	−28.3	−30.0–25.9	1.3	8.3	6.7–11.1	1.1	11.22	3.85

Table 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of different benthic macroinvertebrate (ZooB) and pelagic zooplankton (ZooP) taxa sampled from Lake Osensjøen.

Year	Item Group	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
2010	ZooB bulk	1	−25.93	5.32
	ZooP bulk	1	−29.89	3.71
2013	<i>Bosmina/Daphnia</i> mixture	1	−33.01	1.68
	<i>Bosmina</i>	1	−32.59	2.09
	<i>D. cristata</i>	1	−31.14	−0.87
	<i>Daphnia</i> sp.	1	−32.51	2.79
	ZooP bulk.	1	−32.57	1.82
2021	Annelida	1	−26.36	7.23
	Coleoptera	1	−26.61	15.13
	<i>Chironomidae</i>	1	−27.62	11.52
	<i>Ephemer.</i>	1	−27.26	12.64
	<i>Trichopt</i>	1	−26.93	12.32
	<i>Daphnia</i>	1	−28.29	4.77
	<i>Bosmina</i>	1	−26.52	3.11

The shapes and sizes of the isotopic niche areas of vendace and whitefish changed to some extent following the establishment of perch and roach (Figure 6). In general, vendace showed the most pelagic (low $\delta^{13}\text{C}$ values) and specialized (least variable) isotopic niche, with some individuals attaining a lower trophic position (low $\delta^{15}\text{N}$) in 2021 following roach and perch establishment in the lake. In contrast, whitefish and perch showed more littoral (high $\delta^{13}\text{C}$ values), highly overlapping and highly variable isotopic niches, with some individuals likely having specialized to feeding on littoral benthic macroinvertebrates (high $\delta^{13}\text{C}$), pelagic zooplankton (low $\delta^{13}\text{C}$) or smaller fish (high $\delta^{15}\text{N}$).

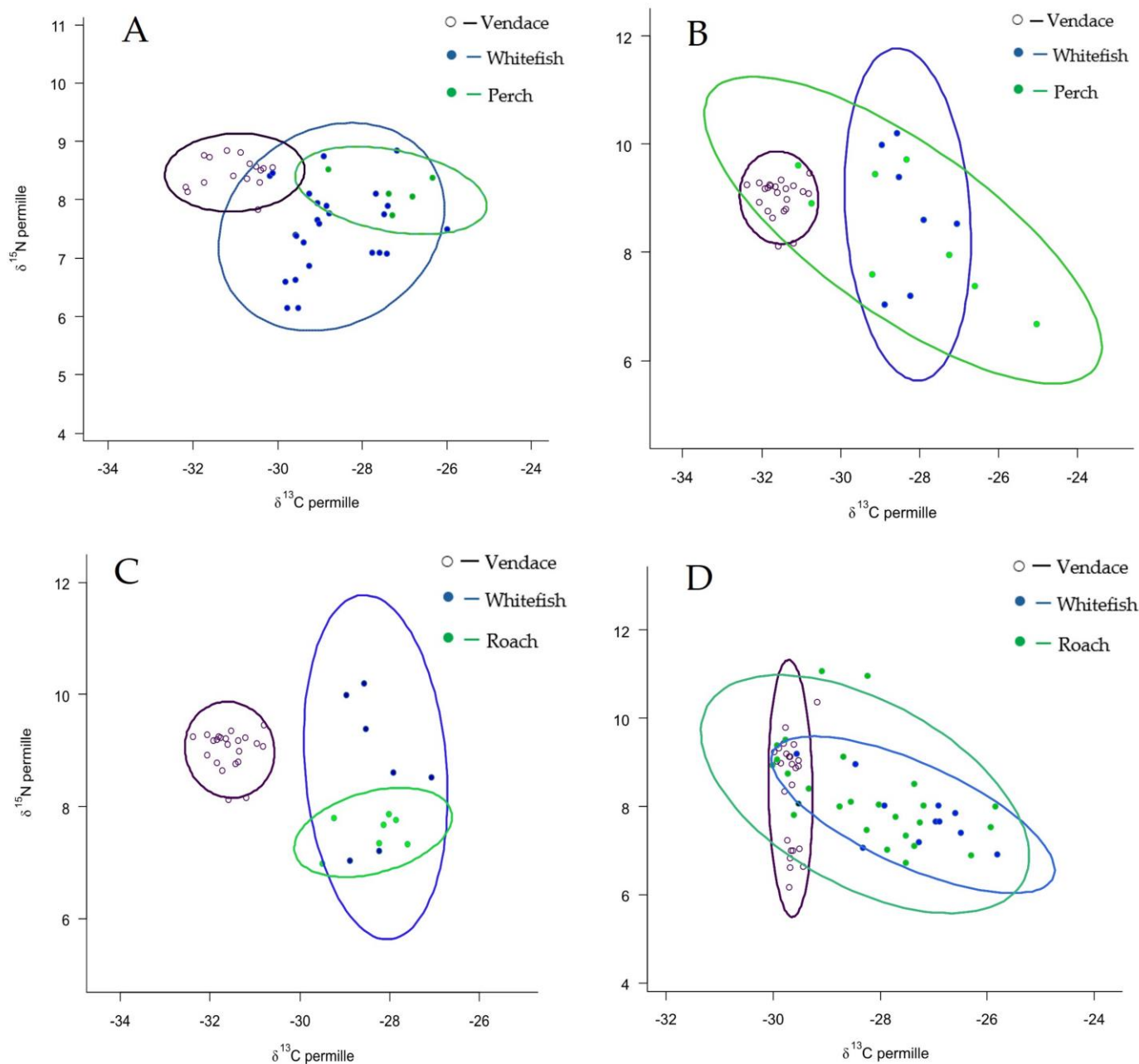


Figure 6. Stable isotope biplots showing the individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and the standard ellipse areas (SEAs) depicted for vendace, whitefish and perch sampled from Lake Osensjøen in 2010 (A) and 2013 (B), and for vendace, whitefish and roach sampled in 2013 (C) and 2021 (D).

The isotopic niche area (SEAc) of vendace was consistently lower than that of whitefish across the study years (Table 1), whereas that of perch increased by $5\times$ from 2010 to 2013, as did that of roach from 2013 to 2021, when both species had larger isotopic niches than vendace and whitefish.

The isotopic niche area (SEAc) of whitefish overlapped more with that of vendace in 2010, and vice versa (Figure 7). However, a contrasting pattern was observed in 2013 when the perch isotopic niche overlapped more than 50% with those of vendace, whitefish and roach. The whitefish niche overlapped close to 100% with that of roach. In 2021, the isotopic niche area of roach overlapped those of vendace and whitefish, by 80% and 94%, respectively.

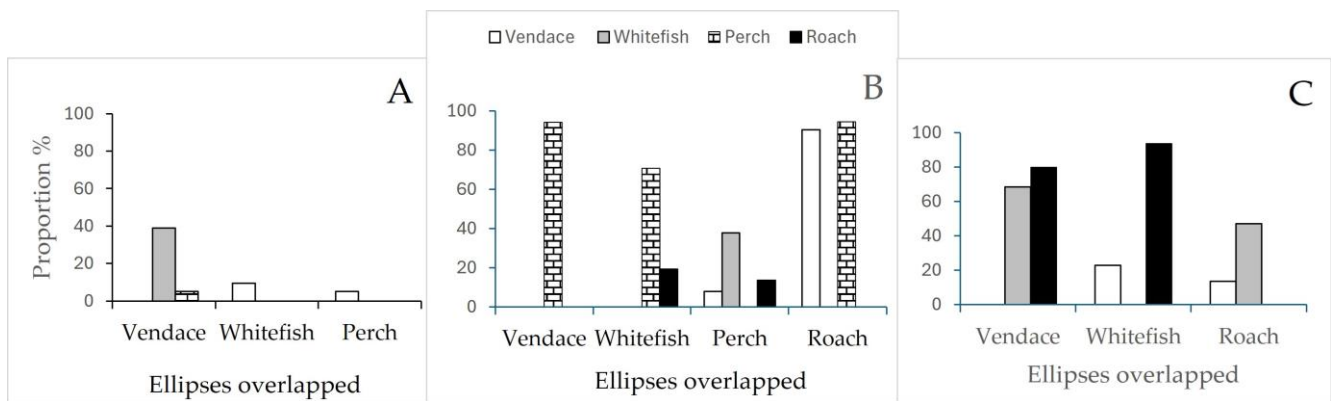


Figure 7. Overlaps in the isotopic niche areas (SEAc) of vendace, whitefish, perch and roach sampled from Lake Osensjøen in 2010 (A), 2013 (B) and 2021 (C).

When exploring the $\delta^{13}\text{C}$ variation of fish with linear modelling, Model 2 gave the lowest AIC = 370.7, i.e., including the categorical interaction term (year): Species (as compared to AIC = 379.4, 393.6 and 391.3, respectively, with Model 1, 3 and 4). Model 1 gave the lowest AIC = 292.0 describing the $\delta^{15}\text{N}$ variation, i.e., including all interaction terms (as compared to AIC = 312.2, 305.0 and 306.9 with Model 2, 3 and 4). The best model revealed some differences between years and species for both elements (Table 3), mostly for the mean $\delta^{13}\text{C}$, which was significantly higher in 2021 than in 2010 and 2013. It was significantly higher for perch than for the other species, and there was a significantly positive effect of fish length. Only one interaction term had a significant effect, i.e., the 2013 and Roach interaction, showing that the $\delta^{13}\text{C}$ value was higher for roach than for perch this year. The model showed significantly higher values of $\delta^{15}\text{N}$ in 2021 than in 2010 and 2013, but there were no significant main effects of either species or fish length. The mean $\delta^{15}\text{N}$ was significantly lower for vendace than for perch in 2021, when the $\delta^{15}\text{N}$ of vendace was also significant positively related to fish length, different from the other years and species.

Table 3. Results from the best linear model of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with predicting variables: year, species, Year:Species interaction, and fish length. (NA = not calculated due to few data). Significant p -values (<0.05) are in boldface.

Coefficients	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	Estimate	S.E.	t	p	Estimate	S.E.	t	p
Intercept (Pch 2010)	−29.03	0.63	−46.31	<0.001	5.96	4.35	1.37	>0.05
2013	−0.66	0.52	−1.28	>0.05	−0.22	4.46	−0.05	>0.05
2021	2.06	0.38	5.46	<0.001	5.72	2.37	2.41	<0.05
Roach	−2.40	0.56	−4.28	<0.001	−3.88	5.00	−0.78	>0.05
Vendace	−3.51	0.45	−7.75	<0.001	2.06	4.99	0.41	>0.05
Whitefish	−1.85	0.45	−4.13	<0.001	−0.62	4.40	−0.14	>0.05
Fish length	0.01	0.00	3.50	<0.001	0.01	0.02	0.51	>0.05
2013:Roach	2.98	0.74	4.03	<0.001	4.65	5.20	0.89	>0.05
2021:Roach	NA	NA	NA	NA	NA	NA	NA	NA
2013:Vendace	0.30	0.58	0.52	>0.05	0.65	5.55	0.12	>0.05
2021:Vendace	−0.07	0.42	−0.16	>0.05	−9.02	3.44	−2.62	<0.01
2013:Whitefish	1.19	0.63	1.87	>0.05	0.00	4.73	0.00	>0.05
2021:Whitefish	NA	NA	NA	NA	NA	NA	NA	NA
2013:Fish length					0.01	0.02	0.31	>0.05
2021:Fish length					−0.02	0.01	−2.04	<0.05
Roach:Fish length					0.01	0.02	0.70	>0.05
Vendace:Fish Length					−0.01	0.02	−0.33	>0.05
Whitefish:Fish length					0.00	0.02	−0.11	>0.05

Table 3. Cont.

Coefficients	$\delta^{13}\text{C}$				$\delta^{15}\text{N}$			
	Estimate	S.E.	<i>t</i>	<i>p</i>	Estimate	S.E.	<i>t</i>	<i>p</i>
2013:Roach:Fish length					−0.02	0.02	−0.83	>0.05
2021:Roach:Fish length					NA	NA	NA	NA
2013:Vendace:Fish length					0.00	0.02	−0.20	>0.05
2021:Vendace:Fish length					0.046	0.02	3.08	<0.001
2013:Whitefish:Fish length					0.00	0.02	−0.03	>0.05
2021:Whitefish:Fish length					NA	NA	NA	NA
Model statistics	$F = 35.2, \text{d.f.} = 10,128, p < 0.001, R^2 = 0.73$				$F = 8.9, \text{d.f.} = 19,119, p < 0.001, R^2 = 0.59$			

The post hoc tests showed that the mean value of $\delta^{13}\text{C}$ was significantly ($p < 0.05$) lower for vendace as compared with the other species in all years, whereas the differences between the other species varied (Table S3). It was significantly lower for whitefish than for perch in 2010, but not in 2013, and it was non-significantly higher than that for roach in 2013, whereas this difference was significant in 2021. The mean $\delta^{15}\text{N}$ of vendace was significantly higher than that of whitefish in 2010 only, and significantly higher than that of roach in 2013. The mean $\delta^{15}\text{N}$ of whitefish was significantly higher than that of roach in 2013 but not in 2021. No pairwise differences in $\delta^{15}\text{N}$ were significant in 2021, and there was no significant difference between perch and roach or between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in 2013.

4. Discussion

High-latitude lakes are subjected to rapid environmental changes, such as the increasing abundance and competitive dominance of warm-adapted fish species that may have negative impacts on the recruitment and resource use of coexisting cold-adapted salmonids. Our study demonstrates the relatively stable abundance, size structure and specialized zooplanktivorous niche of vendace in Lake Osensjøen, whereas the more generalist whitefish showed reduced abundance, body size and trophic niche width following the increasing abundances and niche widths of coexisting perch and roach from 2011 and 2013 onwards, respectively. Although we found evidence for only minor changes in the zooplankton communities, the long-term changes in the fish community may have cascading impacts on the structure and functioning of the pelagic and benthic food-web compartments, as well as for important ecosystem services associated with local fisheries traditionally targeting salmonids, for example.

4.1. Abundance and Spatial Distribution of Fish

The abundance of pelagic fish in Lake Osensjøen roughly tripled from the 1990s to 2010 [8,23] but seems to have stabilized after 2011, excluding an exceptional peak in May 2021. Whitefish earlier shared the pelagic zone with vendace in approximately equal amounts [23,33], but decreased in number drastically during our study years and were not caught from the pelagic zone in 2021. Simultaneously, benthic catches of perch increased from 2010 to 2013, and further in 2021, although the proportion of perch decreased. Roach also increased substantially from 2013 to 2021 and became the numerically dominant species, comprising 75% of the benthic catches.

The estimated number of fish in the pelagic zone in May 2021 was extremely high (3650 fish/ha) as compared to recordings in previous years, with a mean of 79 fish/ha (95% C.I.: 49–109) during 1986–1998 [8], as well as compared to the mean of 559 fish/ha (95% C.I.: 376–742) over 2011, 2018 and Sep. 2021. Linløkken [8] recorded 34–4720 fish/ha in 17 lakes in southeastern Norway, with densities below 900 fish/ha observed in all salmonid- and coregonid-dominated lakes. Densities above 1000 fish/ha were only recorded in lakes

harbouring perch and cyprinids, such as roach, common bleak (*Alburnus alburnus*), and common bream (*Abramis brama*). As roach is the only cyprinid species besides minnow in Lake Osensjøen, the exceptionally high density in May 2021 was probably made up by roach and perch in an overwintering “modus” dwelling stage at depths below 20 m, whereas in autumn, the pelagic zone was dominated by true pelagic plankton-feeding vendace at depth above 20 m depth.

The observed fluctuations in relative fish abundances in Lake Osensjøen were possibly driven by changes in abiotic factors. For example, warm summers (July–August) may have supported relatively high vendace recruitment after 2000, whereas the recruitment of whitefish spawning in relatively shallow water may have been reduced by early ice break during the spring low-water-level period. The new regulation regime of 1981, with a tunnel outlet on the lake bottom in a previously important spawning area, may also have had a negative effect on whitefish recruitment [23]. Whitefish has been shown to predate on the larvae and fry of vendace and other species [43]. Thus, reduced whitefish densities may have supported the increased recruitment of other lake spawning fishes. In addition, the recruitment of perch [44–46] and roach [46–48] may be supported by increasing water temperature, depending on the prevailing predation pressure [46,49]. Perch can also predate on the larvae of vendace [50] and whitefish [16,51], thus potentially reducing the recruitment of coregonid fishes in Lake Osensjøen through direct predatory impacts.

Declining whitefish populations have also been recorded in other previously whitefish dominated lakes following invasions of competitively superior pelagic zooplanktivorous vendace [52,53]. The increased abundance of perch in Lake Osensjøen has likely intensified interspecific competition for benthic food and habitat resources, as also demonstrated by Hayden, Holopainen [16] in six lakes in northwestern Fennoscandia. This competition for benthic resources has likely intensified following the increased abundance of roach after 2013, thus potentially contributing to the reduced whitefish catches in the benthic gillnets. The shift from the dominance of coregonids to a cyprinid (roach)- and a percid (perch)-dominated fish community observed here in Lake Osensjøen and also elsewhere, often referred to as cyprinidification [54–56], may have been further supported by increasing water temperatures and/or nutrient concentrations [4,56,57]. However, Lake Osensjøen is still an oligotrophic lake, and thus increasing water temperature is likely a more important abiotic driver than changes in water quality, although the summer temperatures in the study region have remained relatively stable after 2010.

4.2. Food and Niches

Vendace, whitefish and roach all consumed zooplankton, with cladocera and copepods being the most frequently observed taxa in the stomach contents of vendace and pelagic-caught whitefish. Benthic whitefish also fed on zooplankton, but additionally on zoobenthos (i.e., insect larvae and molluscs), as also observed in other lakes with sympatric vendace and whitefish populations [52]. Roach and perch are typically zooplanktivores at small sizes (<150 mm), but perch tend to shift to piscivory with increasing body size [46,51,58,59]. In contrast to the coexisting coregonids, roach in Lake Osensjøen fed on *Bosmina* sp., but not on *Daphnia* sp.. We found no significant changes in the body sizes of these two zooplankton taxa, suggesting that the roach expansion probably did not reduce the algae grazing capacity of herbivorous zooplankton. *Daphnia cristata* has been shown to be the dominant *Daphnia* species in Lake Osensjøen [24], with the species’ smaller size and lower visibility (hyaline body and small eyespot) likely reducing fish predation as compared to the more visible *D. galeata* and *Bosmina longispina*, though *Bosmina* is only half as long [8,60]. The stomach contents of whitefish showed a diverse diet comprising several prey taxa, including molluscs in 2010 but not in 2021 when benthic insects were

observed in smaller amounts in the fish diets. The increased perch and roach abundance probably reduced the already low biomass of zoobenthos in this oligotrophic regulated lake. The lack of predatory *Bythotrephes* and the reduction in Chydoridae abundance in the fish stomachs in 2021 may also be the result of increased predation from perch and roach on crustaceans. The similarity index D indicated greater similarity between roach and the coregonid species than between the coregonids, indicating that the expanding roach affected both vendace and whitefish negatively; however, vendace avoids this as long as roach dwells in the benthic habitat.

Our stable isotope data indicated the most pelagic and specialized zooplanktivorous niches for vendace as compared to the more littoral and variable trophic niches of whitefish, perch and roach. The $\delta^{13}\text{C}$ values increased with body length, indicating a general ontogenetic niche shift from pelagic zooplanktivorous to more littoral-based diets as fish grew larger. These size-related niche shifts were less evident in 2013 and 2021 when large coregonid individuals became sparse. The increasing $\delta^{15}\text{N}$ values with the fish length of vendace in 2021 suggested a change in prey selection, probably from the consumption of more copepods, of which there are many predatory species [61]. Such size-related shifts in the resource use of generalist top consumers commonly shape intra- and interspecific interactions within and between coexisting fish populations, with potential cascading effects on the benthic and pelagic communities [20].

The overlapping isotopic niches of whitefish and perch suggest resource competition between these two generalist fishes. In contrast, as hypothesized, vendace showed a narrow and more stable pelagic niche throughout the study period. Whitefish showed a wider and more variable isotopic niche, with a slight increase from 2010 to 2013 followed by a decrease in 2021. The observed slight niche expansion in 2013 likely results from increased individual specialization that may reduce intraspecific competition [62–64]. However, the increased abundance of perch in Lake Osensjøen may have forced whitefish individuals to use alternative food and habitat resources, thereby diversifying the population-level niche. At the same time, whitefish seemed to reduce the use of pelagic resources dominated by vendace. The population-level niche of whitefish was particularly narrow in 2021 when the benthic food and habitat resources were likely dominated by the abundant roach. Eloranta et al. [65] found that the isotopic niche of whitefish showed a humped-shaped relationship with the increasing relative abundance of sympatric competitors, suggesting the widest population niche at an intermediate intensity of interspecific interactions in lakes hosting perch. The isotopic niche width of whitefish tended to decrease with increasing altitude, suggesting reduced niches in colder, less productive lakes. As hypothesized, we found perch and roach to expand their trophic niches from 2010 to 2013 and from 2013 to 2021, respectively, following their increasing abundances in Lake Osensjøen. However, it should be noted that the perch and roach samples caught in later years included more small individuals with contrasting diets to those of their larger conspecifics, therefore causing an apparent niche expansion of the fish populations.

The largely overlapping trophic niche of whitefish with perch and later with roach probably increased resource competition and reduced the growth and recruitment of whitefish, whereas the more specialized zooplanktivorous vendace showed a minor response, although the population became dominated by smaller individuals.

Our hydroacoustic surveys demonstrated record-high fish biomasses in Lake Osensjøen in May 2021, with the high roach abundances likely leading to increased predation pressure on benthic resources. The abundant roach is of minor interest to fisheries, but it has an ability to cause substantial bioturbation and resuspension of sedimented nutrients and detritus, leading to decreased water quality [66–68]. While the previously abundant and large-sized whitefish is now nearly vanished from Lake Osensjøen, the small-sized

(100–150 mm) vendace may still support the local fishery, also by providing a suitable small prey fish for the popular large-sized piscivorous brown trout [69,70].

5. Conclusions

Like several other oligotrophic cold-water high-latitude lakes, Lake Osensjøen has undergone dramatic changes in the past decades. From being a lake dominated by formerly (i.e., 120 years ago) introduced coregonid fishes, perch and, in particular, roach have now become the most abundant fish species. The whitefish was first suppressed in the pelagic zone and later also become sparse in the benthic habitats. The typical littoral benthivorous grayling was not caught at all in 2021, possibly due to the marked expansions of the perch and roach populations. These two species are native to the lake and constituted a significant part of the fish stock before the lake water level became regulated for hydropower production, causing dramatic losses of previously vegetated shallow littoral spawning habitats. In recent decades, the increased temperatures may have supported increased vendace recruitment, leading to a dense population of small-sized individuals. In contrast, the expected earlier ice break up is assumed to reduce whitefish recruitment, whereas the reduced predation on fish eggs and larvae by whitefish and the increasing water temperatures may in turn have supported the boom of warm-adapted perch and roach populations.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/hydrobiology4020010/s1> or <https://zenodo.org/uploads/14772260> (accessed 30 January 2025): Table S1. Total annual catches of fish in Lake Osensjøen in pelagic (P) and benthic (B) gillnets in 2010, 2013 and 2021. Table S2. Number of stable isotope analyses of species in 2010, 2013 and 2021. Table S3. Results of pairwise testing between vendace (Vd), whitefish (Wf), perch (Pch) and roach (Rch) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between species by means of one-way ANOVA and Tukey post hoc test.

Author Contributions: Conceptualization, A.N.L., A.B.G. and A.P.E.; methodology, A.N.L.; software, A.N.L.; validation, A.N.L. and A.B.G.; formal analysis, A.N.L. and A.B.G.; investigation, A.N.L. and A.B.G.; resources, A.N.L. and A.P.E.; data curation, A.N.L. and A.B.G.; writing—original draft preparation, A.N.L., A.B.G. and A.P.E.; writing—review and editing, A.N.L., A.B.G. and A.P.E.; visualization, A.N.L.; supervision, A.N.L.; project administration, A.N.L.; funding acquisition, A.N.L. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement: Sampling for this study (registered in Cristin-prosjekt-ID: 354592) was in part conducted before our present institution, Inland Norway University of Applied Sciences, and its Research Ethics Committee, were founded, and the Norwegian Act on Experiments on Animals includes only animals kept alive, for some purpose, after catching. The gill net sampling, nevertheless, was conducted in accordance with Norwegian law for salmon and inland fishery, in agreement with, and partly in cooperation with, the fishing rights holders.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data available on request.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

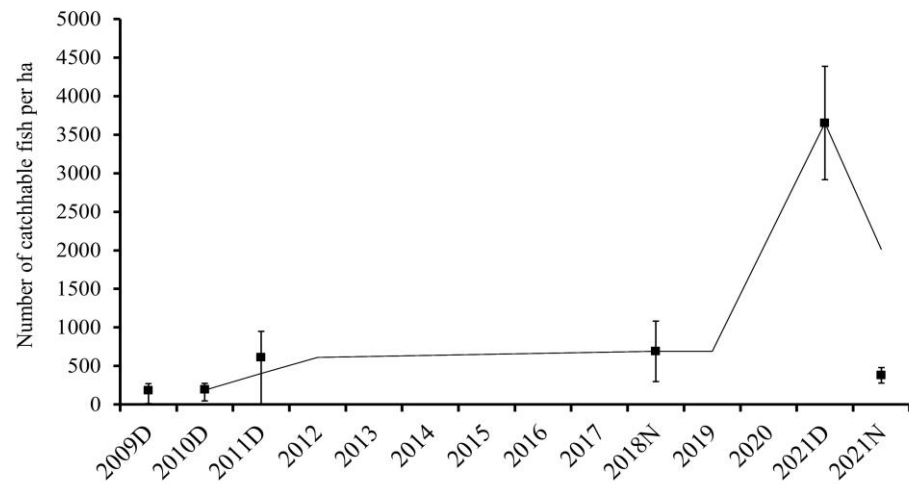


Figure A1. Estimated pelagic fish densities in Lake Osensjøen based on hydroacoustic surveys, with the line representing the moving average and the filled squares and whiskers showing the mean and 95% confidence intervals of estimated numbers of catchable fish per hectare. Abbreviations: D = daytime and N = nighttime recordings.

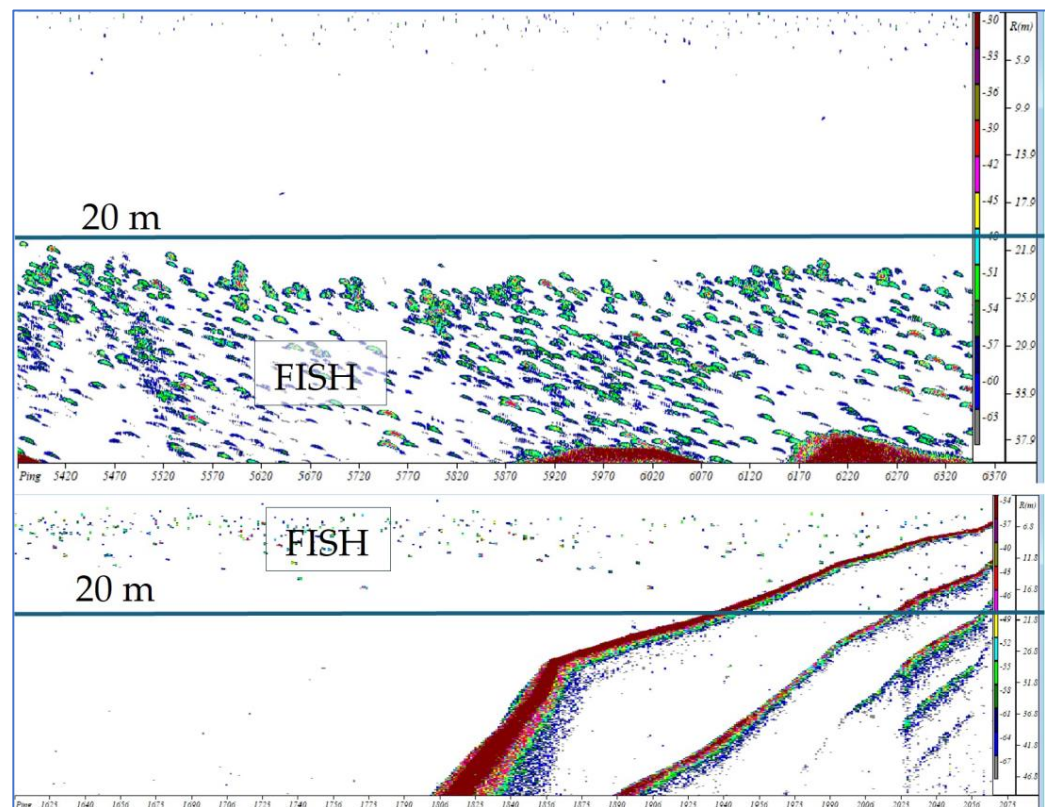


Figure A2. Echograms showing the fish distributions and abundances in Lake Osensjøen in May (upper) and in September (lower) 2021, based on echosounder recordings. The size of the target (fish) drawn depends on the number of hits by the sound beam, which depends on fish size and its distance from the sound source (i.e., depth), due to the sound beam's cone shape.

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