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The effect of inter- and intraspecific competition on individual and population niche widths: a four-decade study on two interacting salmonids

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Competition is assumed to shape niche widths, affecting species survival and coexistence. Expectedly, high interspecific competition will reduce population niche widths, whereas high intraspecific competition will do the opposite. Here we test in situ how intra- and interspecific competition affects trophic resource use and the individual and population niche widths of two lacustrine fish species, Arctic charr and brown trout, covering a 40 year study period with highly contrasting competitive impacts prior to and following a large-scale fish culling experiment. Initially, an overcrowded Arctic charr population dominated the study system, with brown trout being nearly absent. The culling experiment reduced the littoral Arctic charr density by 80%, whereupon brown trout gradually increased its density in the system. Thus, over the study period, the Arctic charr population went from high to low intraspecific competition, followed by increasing interspecific competition with brown trout. As hypothesized, the relaxed intraspecific competition following the experimental culling reduced individual diet specialization and compressed population niche width of Arctic charr. During the initial increase of the brown trout population, there was a large dietary overlap between the two species. Over the subsequent intensified interspecific competition from the population build-up of brown trout, their trophic niche overlap chiefly declined due to a dietary shift of Arctic charr towards enhanced zooplankton consumption. Contrary to theoretical expectations, the individual and population niche widths of Arctic charr increased with intensified interspecific competition. In contrast, the diet and niche width of brown trout remained stable over time, confirming its competitive superiority. The large-scale culling experiment and associated long-term research revealed pronounced temporal dynamics in trophic niche and resource use of the inferior competitor, substantiating that intra- and interspecific competition have large and contrasting impacts on individual and population niches.

Keywords: competitive interactions, long-term studies, niche theory, *Salmo trutta*, *Salvelinus alpinus*, trophic ecology

Introduction

The feeding of animals is a fundamental element in their ecological performance and life maintenance and has been integral in studies of competition and niche theories (Schoener 1974, Ross 1986, Araújo et al. 2008, Bolnick et al. 2010). The trophic ecology of animal populations may vastly change over time with variations in e.g. conspecific abundance and interactions with other species (Bøhn et al. 2008, Amundsen et al. 2019). When resources are limited, niche differentiation plays a key role in species coexistence (Gause 1934, Hardin 1960, Johnson and Bronstein 2019). However, coexistence and competitive exclusion are strongly dependent on the amount of individual niche variation among competing species (Barabás and D'Andrea 2016, Hart et al. 2016, Xia et al. 2020). The degree of individual niche variation in wild populations is furthermore often subject to temporal variation in response to shifts in the ecological contexts (Araújo et al. 2011, Costa-Pereira et al. 2018), which impact the outcome of competitive interactions and long-term coexistence (Barabás and D'Andrea 2016, Hart et al. 2016, Costa-Pereira et al. 2018).

Competitive interactions among species play a major role in directly or indirectly determining the structure of ecological communities across biomes (MacArthur 1958, MacArthur and Levins 1967, Chase et al. 2002). A central aspect of competition ecology has been determining the consequences of competition on the niche widths (compression or expansion) of individuals and populations (Svanbäck and Persson 2004, Tinker et al. 2008, Costa-Pereira et al. 2019). Theory predicts that intra- and interspecific competition respectively expand and constrain individual and population niche widths (Roughgarden 1972, Bolnick et al. 2010). For instance, an increase in interspecific competition might constrain resource availability reducing individuals and population niche widths (Roughgarden 1974). However, such resource limitation might also cause an expansion of the overall population niche width, as individuals are forced to feed on alternative low-value prey (Bolnick 2001, Svanbäck and Bolnick 2005, Svanbäck and Persson 2009, Svanbäck et al. 2011). On the other hand, a reduction of interspecific competition might either expand the population niche width if newly or previously depleted resources are added to the diet or contract the width if individuals specialize toward a smaller set of preferred resources (Bolnick et al. 2010). Under a high intraspecific competition scenario, the preferred resources might be overexploited, leading to niche expansion resulting from enhanced inter-individual variation (Amundsen 1995, Bolnick et al. 2003, Svanbäck and Persson 2004, Araújo et al. 2011). The suggested mechanism for the population niche expansions is related to increased individual specialization via among-individual variation rather than niche expansion at the individual level (i.e. the individual niche widths remain constant, Svanbäck and Bolnick 2007, Bolnick et al. 2010). However, Jones and Post (2016) demonstrated with an extensive meta-analysis that intraspecific competition can have either restricting or diversifying effects on population niche width and individual specialization. Costa-Pereira et al. (2018) similarly suggested that the effects of intraspecific competition on individual specialization may be less obvious than commonly assumed.

Changes in population niche and individual specialization across seasons or short time periods have previously been addressed (Bolnick et al. 2010, Araújo et al. 2011, Costa-Pereira et al. 2019). There is, however, a lack of knowledge about how long-term shifts in ecological factors affect the niches of individuals in competing species, even though long-term temporal changes might better elucidate variations in dietary niches and resource partitioning among competing species (Hampton et al. 2019).

The potential for inter-annual niche width plasticity differs between generalist and specialist species. Dietary shifts are a common response to changes in the prey abundance and availability and may chiefly impact survival, growth and reproductive capacity of the species (Amundsen et al. 2007, 2019). Specialized species tend to be more vulnerable to environmental changes, while more generalist species have a higher capacity to adapt to altered conditions (Brooker et al. 2014). However, even highly specialized species may opportunistically include prey resources that are intrinsically easy to use if these are available in high abundances (Robinson and Wilson 1998). Since many species undergo ontogenetic dietary shifts (Werner and Gilliam 1984), the susceptibility to environmental changes may vary throughout their life cycle. Furthermore, inherent changes in feeding along ontogeny might affect temporal resource overlap within and among species as only a certain subset of individuals may compete with each other at a given time (Werner and Gilliam 1984, Woodward and Hildrew 2002).

In the present study, we explore dietary shifts in two sympatric salmonids; Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* (hereafter referred to as charr and trout), over a four-decade period following the recovery of the latter after a large-scale perturbation experiment in a pristine subarctic lake (Lake Takvatn). This species pair has been the study system of classical work on competition and interactive segregation (Nilsson 1963, 1965, 1967), with trout typically being considered as competitively superior to charr in the littoral habitat (Forseth et al. 2003, Klemetsen et al. 2003, Sánchez-Hernández and Amundsen 2015). In allopatry, the two fish species often feed on relatively large benthic prey in the littoral zone (Nilsson 1963, 1967). In sympatry, trout being a more aggressive and inflexible territorial feeder, typically continue to feed on the preferred littoral prey, forcing charr to feed on alternative prey such as zooplankton (Nilsson 1963, Langeland et al. 1991). However, in our study system, such naturally occurring dynamics were altered by anthropogenic disturbance. Trout was originally the only fish species present in Lake Takvatn, but due to selective fishing with large meshed-gill nets, the population drastically declined. Arctic charr was subsequently introduced to the lake in 1930, and continued selective removal of large individuals in the already overfished trout population led charr to become the dominant species in the system, forming an overcrowded population,

whereas the trout nearly vanished (Klemetsen et al. 1989, 2002). Between 1984 and 1991, an intensive experimental culling of the overpopulated and dominant charr population took place in the lake, removing around 700 000 individuals in total and reducing their density to 20% (Amundsen et al. 2019). This resulted in a gradual long-term recovery of the trout population (Klemetsen et al. 2002, Persson et al. 2007, 2013), which at present makes up about half of the littoral catches (Amundsen et al. 2019, Fig. 1). The experimental culling also strongly reduced intraspecific competition in the charr population, resulting in enhanced food consumption rates as the density declined (Amundsen et al. 2007). Compared to the pre-culling period, the total density of fish (charr and trout) in the littoral area halved. Densities of conspecifics and heterospecifics are respectively good proxies for intra- and interspecific competition as resource availability is affected by consumer's abundances (Bohlin et al. 2002, Hasegawa 2016). Hence, over a forty-year period, the charr in the lake has gone from a state of high intraspecific competition to low competition post culling, followed by enhanced interspecific competition from the increasing trout population over the last couple of decades. This provides a unique opportunity to test predictions from niche and competition theory both within and between species using long-term data from the pre- and post-perturbation periods of a full-scale density-manipulation experiment in a natural ecosystem.

The aim of the study was to investigate how intra- and interspecific competition affects the individual and population niche widths of two competing species prior to and after a whole-lake manipulation experiment that resulted in a gradual shift from a numeric dominance of one of them to more equal densities of both competitors. We firstly hypothesized that relaxation of intraspecific competition as a consequence of the charr culling reduced inter-individual variation in resource use, resulting in a similar or narrower population niche width of charr. Secondly, we hypothesized that enhanced interspecific competition from trout in the post-culling period as an increasingly abundant and superior trophic specialist forced charr, the inferior generalist predator, to undertake dietary niche shifts, resulting in narrower individual and population niche widths. Thirdly, we hypothesized

Figure 1. Average catch per unit effort ±SD (CPUE, calculated as the mean number of fish per 100 m² gillnets per night) of Arctic charr and brown trout over the four-decade study duration.

that the trophic niche of trout, being a more aggressive and territorial feeder, remained stable throughout the whole study period both at the individual and population level by gradually overtaking resources previously used by charr. Although theory predicts effects of increased intraspecific competition on population and individual niches, we expected these to remain stable for trout following its recovery due to a much lower overall density of consumers in the littoral zone in the post-culling compared to the pre-culling period.

Material and methods

Study site

The study was conducted in Takvatn (67°54′N, 15°42′E), a 15.2 km² dimictic and oligotrophic lake situated at 215 m a.s.l. in northern Norway. There are two months of midnight sun and two months of polar night at this latitude, and the lake is covered by ice and snow for 5–6 months (December–June). The littoral zone extend down to ca 15 m depth and covers about one-third of the lake area. The maximum depth is 88 m. Due to strong wave action, the upper (0–3 m) littoral habitat has hard bottoms without emergent vegetation. The middle littoral from 3 to 10 m depth has a belt of scattered submerged vegetation dominated by *Nitella* algae but also some *Isoetes lacustris*, *Myriophyllum* and *Potamogeton*. Secchi depths range between 14 and 17 m, maximum epilimnic temperatures are about 14°C, and phosphorous levels do not exceed 5 ppm (Eloranta et al. 2013).

The zooplankton community comprises ten rotifers, seven cladocerans and two copepods species (Dahl-Hansen et al. 1994, Primicerio and Klemetsen 1999, Amundsen et al. 2009, 2013). The upper littoral benthos community has a richness of 25 macroinvertebrate taxa, composed of 18 insects and seven non-insects (Klemetsen et al. 1992, 2020, Klemetsen and Elliott 2010, Frainer et al. 2016; see the Supporting information for more details on the zooplankton and benthic invertebrate community of Lake Takvatn). The current fish community comprises trout, charr and three-spined stickleback *Gasterosteus aculeatus*. Historically, trout was the only fish present, but due to overfishing, the population declined, and charr was introduced in 1930 from Fjellfrøsvatn, a lake situated in a tributary to the downstream river from Takvatn (Klemetsen et al. 1989). The density of charr increased exponentially over time, reaching an overcrowded state dominated by small-sized mature individuals by 1980, while trout almost disappeared from the lake (Klemetsen et al. 2002). In 1950, three-spined stickleback was introduced from Sagelvvatn, a lake not far from Takvatn but in a separate river system. The massive culling of the overcrowded charr population during the perturbation experiment was done by double-funneled wire traps baited with cod roe (Amundsen et al. 1993). The funnel opening prevented the entry of large fish, and the wire mesh prevented the escape of small fish. Up to 150 traps were used over the entire lake in spring and summer but, most effectively, in late winter (April–May), at a time when almost
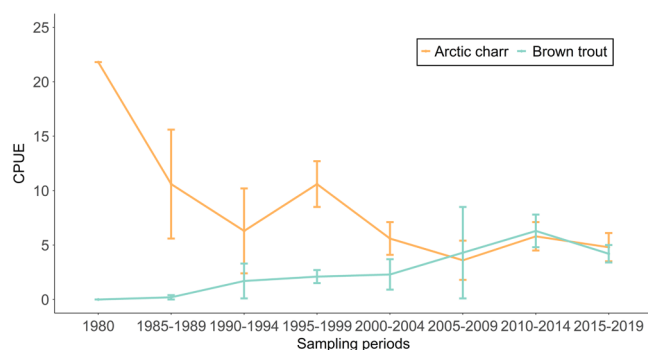
the whole population was concentrated under the ice in the littoral zone (Klemetsen et al. 2003).

Fish sampling and processing

Charr and trout were sampled annually from the littoral habitat (< 15 m depth) in August from 1980 to 2019 using single-meshed gillnets of various mesh sizes prior to 1989 and thereafter multi-meshed gillnets with panels of eight different mesh sizes ranging from 10 to 45 mm, knot to knot (Table 1). The nets fished in the lake overnight for approximately 12 h. Fork length and other parameters not used in the current study (weight, sex and gonad maturation) of all fish were recorded in the field and stomach samples were collected. Catch per unit effort (CPUE), defined as the number of fish caught per 100 m² gillnets per night, was estimated as a proxy for the littoral abundance of charr and trout.

In the lab, stomachs were opened, and the fullness degree was determined on a scale from 0 to 100% (Amundsen and Sánchez-Hernández 2019). Prey items were identified at the lowest taxonomical level, and their relative contribution to total stomach fullness (expressed in percentage) was calculated according to Amundsen (1995). Prey taxa were then grouped into twelve categories: 1) small cladoceran zooplankton (*Bosmina* spp.), 2) large cladoceran zooplankton (*Daphnia* spp. and *Holopendium gibberum*), 3) predatory cladoceran zooplankton (*Bythotrephes longimanus* and *Polyphemus pediculus*), 4) copepod zooplankton (cyclopoid and calanoid copepods), 5) amphipods (*Gammarus lacustris*), 6) mollusks (*Radix peregra*, *Planorbis* sp., *Valvata* sp. and

Pisidium sp.), 7) pleuston (terrestrial and hatching aquatic insects), 8) Chironomidae pupae, 9) Chironomidae larvae, 10) Trichoptera larvae (house-living and free-living), 11) other benthos (Ephemeroptera nymphs, Plecoptera nymphs, Megaloptera larvae, Tipulidae larvae, Coleoptera and the chydorid cladoceran *Eurycercus lamellatus*) and 12) fish (three-spined stickleback, charr and unidentified fish remains). These prey categories were used for a simplified visualization of temporal dietary changes, whereas un-pooled prey data were used for the subsequent dietary analyses.

For the dietary analyses, stomachs with a fullness degree below 10% or containing only unidentified prey were removed from the dataset. Each individual stomach content was then standardized to estimate prey abundance as the mean contribution of each prey category to the diet. The fish were divided into the three size classes (< 150, 150–299 and > 300 mm) to study ontogenetic dietary shifts over the 40 year study period and if these shifts might be influenced by an increase in individual dietary specialization as explained earlier, where individuals switch to alternative resources to mitigate the effects of competition (Araújo et al. 2011). By pooling data in five-year sampling periods, the 150 and 299 mm size class provided large enough sample sizes for temporal comparisons. Since the number of samples in this size class ranged from 86 to 200 individuals for charr and 60 to 129 for trout, 86 charr and 60 trout stomachs were randomly selected from each sampling period to avoid sample size bias in subsequent analyses. No significant size differences among sampling periods (ANOVA, all p > 0.05) were detected within each size group. A total of 1424 charr and 621 trout were included in the analyses.

Statistical analysis

Descriptive and inferential analyses were performed with the open-source software Rstudio (ver. 1.1.423, Rstudio Inc.), based in R ver. 3.5.1 (<www.r-project.org>). We used a permutational multivariate analysis of variance (PERMANOVA) to assess dietary composition differences between sampling periods and host species (Anderson 2005). A Bray–Curtis based non-metric multidimensional scaling (NMDS) was further used to graphically illustrate any dietary differences between charr and trout among different sampling periods. To determine which prey contributed the most to the observed differences, we opted for Sum-of-*LR*, a multivariate method based on generalized linear model with negative binomial errors (Wang et al. 2012, Warton et al. 2012). We chose this method over the more widely used similarity percentage (SIMPER) analysis as the latter can confound strong between-group effect with large within-group variance, yielding misleading results (Warton et al. 2012).

We measured the total niche width (TNW) of populations applying the Shannon index of diversity to the population's distribution of resource use (Roughgarden 1979). We then partitioned TNW into the within-individual component of niche width (WIC), which is the average individual niche width, and the between-individual component of niche

Table 1. Number (n) and average (Av.) fork length in mm ± SD of the three size groups of Arctic charr and brown trout sampled throughout the sampling periods.

Sampling periods	Size classes in mm	Arctic charr		Brown trout	
		n	Av. length ± SD in mm	n	Av. length ± SD in mm
1980	150–299	86	204.9 ± 18.2	–	–
1985–1989	< 150	20	129.0 ± 15.7	–	–
1985–1989	150–299	86	209.0 ± 41.4	–	–
1985–1989	> 300	24	337.5 ± 27.0	–	–
1990–1994	< 150	86	124.3 ± 14.3	17	129.4 ± 11.7
1990–1994	150–299	86	209.9 ± 46.2	60	201.0 ± 34.1
1990–1994	> 300	62	353.6 ± 38.3	2	362.5 ± 53.0
1995–1999	< 150	69	125.2 ± 15.7	4	137.5 ± 7.4
1995–1999	150–299	86	209.4 ± 40.2	60	207.6 ± 37.0
1995–1999	> 300	22	348.2 ± 42.1	1	311
2000–2004	< 150	86	121.6 ± 15.9	16	128.4 ± 13.4
2000–2004	150–299	86	206.4 ± 32.5	60	207.7 ± 38.4
2000–2004	> 300	11	352.2 ± 30.8	9	337.3 ± 34.7
2005–2009	< 150	86	122.3 ± 17.8	60	128.6 ± 17.7
2005–2009	150–299	86	208.5 ± 37.8	60	210.6 ± 40.4
2005–2009	> 300	17	353.0 ± 31.2	14	344.3 ± 37.2
2010–2014	< 150	68	119.3 ± 15.4	60	131.3 ± 12.6
2010–2014	150–299	86	208.8 ± 43.9	60	209.2 ± 42.0
2010–2014	> 300	28	345.6 ± 38.5	7	347.7 ± 51.1
2015–2019	< 150	86	124.4 ± 15.7	53	129.8 ± 17.6
2015–2019	150–299	86	198.8 ± 33.7	60	205.8 ± 41.1
2015–2019	> 300	71	349.2 ± 29.5	19	343.9 ± 33.0

width (BIC), which is the variation between individuals' niche positions, such that $TNW = WIC + BIC$ (Roughgarden 1972). To assess the impact of trout density on charr's niche, we correlated TNW, WIC and BIC values with CPUE using Spearman's correlation coefficient with Bonferroni's correction. To evaluate the degree of individual diet specialization, we used multiple measures for a more robust assessment of this multifaceted trait than can be accomplished using a single metric. Individual diet specialization can be expressed as the variation between an individual diet and the population diet or between an individual and other individuals. We therefore calculated the WIC/TNW ratio, which provides a measure of specialization by individuals within a population, with specialization being high when WIC/TNW is low. Additionally, the degree of individual diet specialization was assessed with the level of diet variation (E; Araújo et al. 2008), the proportional similarity index (PS_i; Bolnick et al. 2003) and the individual specialization index (IS and V; Bolnick et al. 2002, 2007).

We used variance inflation factor (VIF) to detect multicollinearity (correlation between predictors) among individual specialization indexes. A VIF value < 3 indicate lack of collinearity (Zuur et al. 2010). Collinearity was detected among indexes (all VIF values > 3); hence, we opted to use WIC/TNW values to represent individual specialization. Finally, we tested relationships between sampling periods, WIC, BIC and WIC/TNW values using a generalized least squares model (GLS) using the nlme package (Pinheiro et al. 2021). To account for temporal autocorrelation, we used the autoregressive term AR1. Model fit was evaluated with the autocorrelation function ACF and partial autocorrelation function PACF and the fit between residuals versus fitted values. Data from all sampling periods were used to assess the first two hypotheses with the intent of inferring if temporal changes in individual and population niche widths in charr were likely due to decreased intra-specific competition or increased inter-specific competition. To assess the impact of trout density on charr's individual specialization, we correlated WIC/TNW values with CPUE using Spearman's correlation coefficient with Bonferroni's correction. Calculation of TNW, WIC, BIC, WIC/TNW, E, PS_i and IS were performed with the RInSp package (Zaccarelli et al. 2013).

Interspecific diet overlap was calculated with the Schoener's overlap index $\alpha = 1 - \frac{1}{2} \left(\sum \left| P_{xj} - P_{yj} \right| \times 100 \right)$ (Schoener 1970), where P_{xj} and P_{yj} are the relative abundance of diet item j in the stomach of species x and y, respectively. The index ranges from 0 to 100% with values of 0 indicating absence of diet overlap and values of 100% indicating a complete dietary overlap. Additionally, for the 150–299 mm size classes of charr and trout, we calculated the pairwise diet similarity (PS_{ij}) between each pair of heterospecific individuals i and j: $PS_{ij} = \sum_k \min(P_{ik}, P_{jk})$, where P_{ik} and P_{jk} are the proportions of the Kth prey type in individual i's and j's diet (Bolnick and Paull 2009). A value of 0 indicates that the paired individuals do not share common prey, while values close to 1 indicate that they consume the same prey in identical proportions. PS_{ij} was calculated with the RInSp package (Zaccarelli et al. 2013).

Effects of resource pulses

We run additional analyses in order to test whether the outcomes remain the same after excluding a resource pulse, i.e. infrequent, large-magnitude and short-duration events of increased resource availability (Yang et al. 2010). Temporally superabundant food sources might lead to a convergence in the resource use of co-occurring predators, altering their immediate trophic interactions (Lack 1946, Croxall et al. 1999, Selva et al. 2012). More specifically, the superabundance of a single prey potentially may temporally influence individual specialization and resource partitioning (Meyer 1989, Malmquist et al. 1992, Robinson and Wilson 1998). In subarctic lakes, hatching chironomid pupae cyclically occur in superabundance during midsummer, constituting a resource that is typically included in the fish diet when abundantly present (Adalsteinsson 1979, Amundsen and Klemetsen 1988). A superabundance of Chironomidae hatching and emergence were observed in the field within several of the sampled years (1980, 1986, 1994, 2002, 2007, 2011, 2014 and 2018). This massive hatching is mainly by a single species, *Heterotrissocladius subpilosus* and lasts for only 2–3 weeks in early summer. The species strongly dominates the profundal benthos as larvae (Klemetsen et al. 1992). Given a particularly strong presence of Chironomidae pupae in 1980, which was the only observation available for the pre-culling period, we also addressed our research hypotheses following the exclusion of this prey type. We excluded Chironomidae pupae to reduce bias in interspecific competition metrics among sampling periods as events of Chironomidae pupae superabundance would have been more diluted among pooled periods compared to a single event. Hence, we repeated the above procedures and analysis on a subset of 464 charr and 294 trout excluding this prey from the diet.

Results

Fish abundances

Major changes occurred in the abundance and structure of the littoral fish community of lake Takvatn over the four decades (Fig. 1). In 1980, the charr population was in an overcrowded state, while trout was almost absent. During the culling experiment, the charr density vastly declined in the littoral zone. In the post-culling period (1990–2019), the charr density remained at a relatively low level while that of trout gradually increased, reaching equal densities as the charr in the littoral zone from the early 2000s and onwards (Fig. 1).

Diet composition

A total of twenty-seven prey taxa were identified from the examined samples. Between the two salmonids, charr had the most diverse diet in all sampling periods and size classes (mean 13.8 ± 4.2 SD versus 9.4 ± 4.9 SD prey taxa for trout). Overall, charr consumed on average 2.57 (range 1–8) prey taxa per individual while trout only 1.95 taxa (range 1–7). Twenty-five taxa were common to both species, whereas two taxa (*Daphnia* spp. and calanoid copepods) were found only in charr. The most abundant prey in the diet of charr between 150 and 299 mm were Chironomidae pupae and other pleuston, whereas small cladocerans (*Bosmina* spp.) were most abundant in individuals below 150 mm, and mollusks (mainly *R. peregra*) in individuals larger than 300 mm (Fig. 2A). In trout, pleuston dominated the diet in fish below 300 mm, while fish (primarily three-spined stickleback) was the main prey in individuals over 300 mm (Fig. 2B).

Temporal changes in population diets

At the population level, the diets of charr and trout between 150 and 299 mm differed significantly between the sampling periods (PERMANOVA, F = 10.174, df = 7, p < 0.001 and F = 2.509, df = 5, p = 0.003 respectively). In 1980, before the culling experiment, Chironomidae pupae and fish (three-spined stickleback) had a major contribution to the charr diet. During the prime culling period (1984–1989), fish consumption distinctly diminished while pleuston became a major food source. In the post-culling period (1990–2019), the importance of pleuston gradually decreased while that of small, large and predatory cladocerans increased, with the latter first appearing in 2008 (Fig. 2A). A similar increase in the consumption of large and predatory cladocerans over the post-culling period was also seen for charr < 150 mm, whereas charr larger than 300 mm showed a consistent dominance of mollusks. For 150–299 mm charr, significant dietary changes occurred for eight out of the twelve pooled prey categories, with predatory and large cladocerans showing the largest variations over time (Table 2). The diet of 150–299 mm trout compared to that of charr varied to a lower degree without showing any distinct temporal pattern (Table 2, Fig. 2B). Out of the twelve prey categories, only predatory cladoceran zooplankton and other benthos showed significant variation over time (Table 2). Pleuston dominated the diet of trout below 300 mm in all sampling periods while fish that of trout larger than 300 mm (Fig. 2B).

Interspecific niche overlaps

The dietary niche overlap reflected temporal changes in feeding behavior between the two salmonids (Table 3). In 1990–1994, the 150–299 mm charr diet significantly overlapped (0.95) with that of trout of similar size. Over the subsequent study periods, the interspecific dietary overlap decreased sixfold, suggesting that extensive dietary segregation occurred between them as the trout population increased (Fig. 3, Supporting information). Interspecific dietary overlap was generally lower than the intraspecific dietary overlap in all sampling periods and for both fish species (Table 3A, Supporting information). In 150–299 mm charr, the average individual overlap prior to the culling experiment was lower than that observed in the following sampling periods except for 2005–2009 (Table 3B). In every sampling period the intraspecific dietary overlap was higher in trout than in charr.

Niche width and individual specialization

The total niche width (TNW) of 150–299 mm charr and trout showed similar patterns over time before and after excluding Chironomidae pupae from the analysis (Supporting information). The TNW of trout was chiefly stable over time, whereas for charr there was a decrease in TNW during and following the experimental culling before stabilizing after the recovery of the trout population (Fig. 3, Supporting information). The within-individual component (WIC) of charr significantly increased over time (GLS, df = 29, p = 0.044, slope = 0.012 ± 0.004 SE), while the between-individual component (BIC) showed a slight but not significant decline (GLS, df = 29, p = 0.115, slope = −0.014 ± 0.009 SE) (Fig. 3, Supporting information). There was a strong positive correlation between the observed increase of WIC in charr and the increase in trout density (R = 0.88, p = 0.004), whereas no significant correlations were observed for TNW (R = 0.06, p = 0.89) and BIC (R = −0.4, p = 0.32). Both WIC and BIC of 150–299 mm trout remained relatively stable over time (GLS, df = 23, p = 0.386, slope = −0.003 ± 0.004 SE and p = 0.574, slope = 0.005 ± 0.009 respectively). Charr had a more generalist diet than trout, as indicated by higher TNW values (Fig. 3, Supporting information). The more generalist diet of charr was also reflected by NMDS (Fig. 4).

Effects of resource pulses

After the exclusion of chironomid pupae from the analysis, changes in individual specialization were more evident. The WIC/TNW values of charr significantly increased over time (GLS, df = 29, p = 0.016 , slope = 0.007 ± 0.003 SE) indicating a temporal reduction in individual specialization. On the contrary, WIC/TNW values in trout slightly decreased over time, but this trend was not significant (GLS, df = 23, p = 0.166, slope = −0.003 ± 0.002 SE) and the values remained fairly stable over time (Fig. 3, Supporting information). The degree of individual specialization in charr was at the highest in the pre-culling period, decreased during the culling period, and remained relatively stable in the post-culling period until 2010–2014, before reaching its minimum in 2015–2019 (Fig. 3, Supporting information). There was a strong positive correlation between the observed increase of WIC/TNW values in charr and the increase in trout density (R = 0.78, p = 0.022).
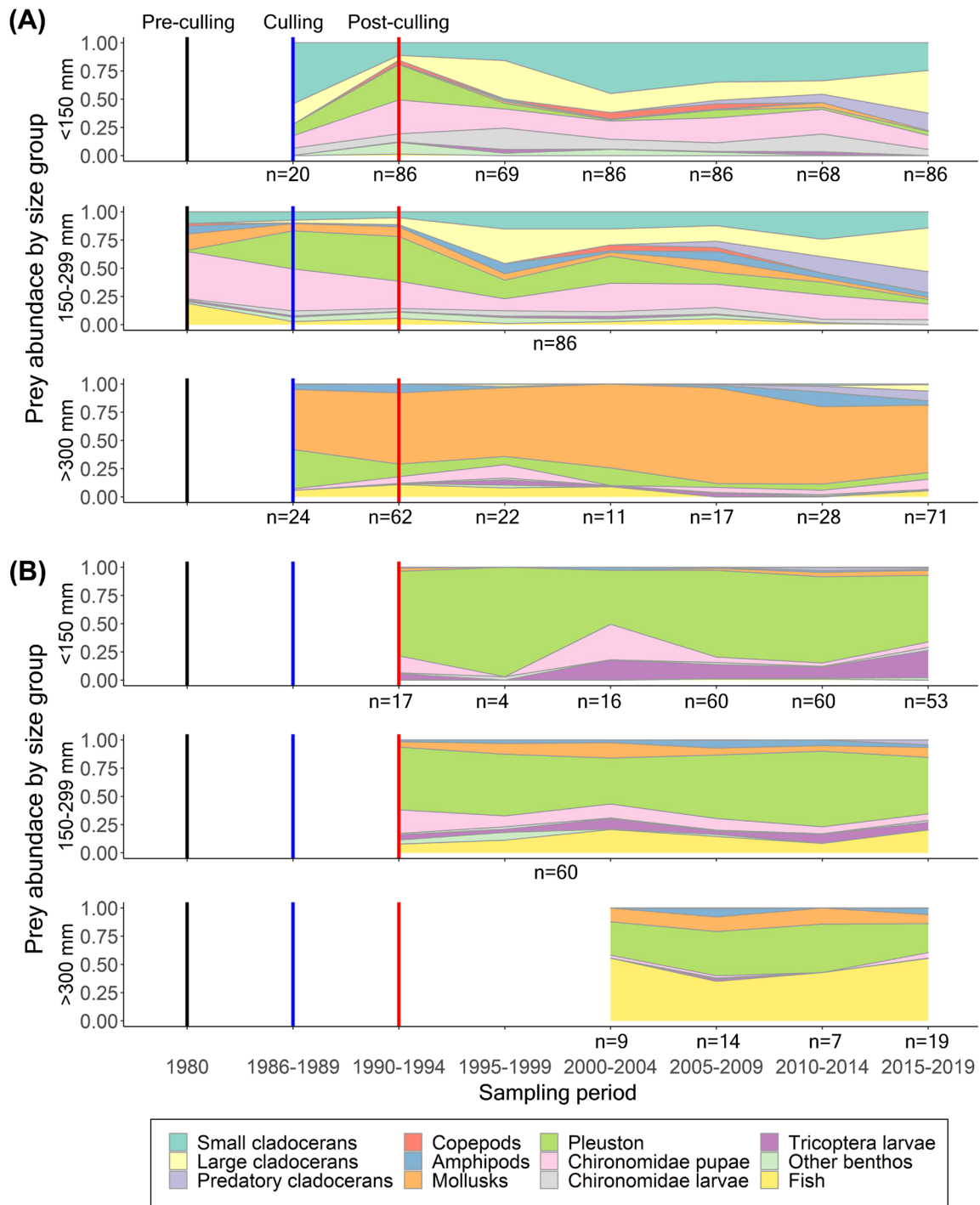
Figure 2. Temporal variation in main dietary composition within three main size groups of (A) Arctic charr and (B) brown trout over the four-decade study period.

Discussion

Our 40 year long time-series provided a unique opportunity to test assumptions from classic ecological theory on competition and niche width. Via a large-scale manipulation experiment we demonstrate that different levels of both intra- and interspecific competition affect individual and population niches with diverse impacts across species and size classes. With a relaxation in intraspecific competition from the fish culling, the individual niche width of charr expanded, whereas the population niche width declined from reduced among-individual variation. Post-culling, trout became

Table 2. Changes in pooled prey categories and single prey calculated separately with Sum-of-*LR* on multivariate GLM negative binomial analysis of deviance. *p < 0.05.

	Prey category	Arctic charr		Brown trout	
		LR	p	*LR*	p
1	Small cladoceran zooplankton	15.992	0.024*	–	–
	Bosmina spp.	15.997	0.175	–	–
2	Large cladoceran zooplanton	118.214	< 0.01*	3.605	0.839
	Daphnia spp.	130.694	< 0.001*	–	–
	Holopendium gibberum	67.108	< 0.001*	3.605	0.888
3	Predatory cladoceran zooplankton	251.962	< 0.01*	23.940	< 0.001*
	Bythotrephes longimanus	243.686	< 0.01*	23.939	0.002*
	Polyphemus pediculus	61.364	< 0.01*	–	–
4	Copepod zooplankton	42.432	< 0.01*	3.605	0.839
	Calanoid copepods	35.497	< 0.01*	–	–
	Cyclopoid copepods	16.347	0.171	3.605	0.888
5	Amphipods	5.765,	0.132	1.370	0.839
	Gammarus lacustris	5.765	0.603	1.371	0.888
6	Mollusks	6.458	0.132	2.437	0.839
	Radix peregra	5.493	0.603	1.306	0.888
	Planorbis sp.	14.039	0.329	1.959	0.888
	Valvata sp.	8.513	0.603	6.824	0.724
	Pisidium sp.	12.206	0.487	5.064	0.888
7	Pleuston	50.854	< 0.01*	3.552	0.839
	Terrestrial insects	49.793	< 0.01*	2.628	0.888
	Trichoptera pupae	39.671	< 0.01*	46.153	< 0.01*
8	Chironomidae pupae	29.153	< 0.01*	6.743	0.364
	Chironomidae pupae	29.152	< 0.01*	6.744	0.724
9	Chironomidae larvae	10.347	0.132	4.434	0.603
	Chironomidae larvae	10.365	0.589	4.442	0.888
10	Trichoptera larvae	11.768	0.132	2.463	0.839
	House-living Trichoptera larvae	10.865	0.589	19.616	0.012*
	Free-living Trichoptera larvae	14.500	0.298	17.219	0.029*
11	Other benthos	20.870	0.006*	22.591	< 0.01*
	Coleoptera	14.141	0.329	20.532	0.011*
	Ephemeroptera nymphs	4.147	0.603	7.465	0.642
	Eurycercus lamellatus	23.478	0.060	4.472	0.888
	Megaloptera larvae	8.396	0.603	10.951	0.180
	Plecoptera larvae	8.956	0.603	7.249	0.642
	Tipulidae larvae	11.363	0.578	16.654	0.031*
12	Fish	18.103	0.012*	1.899	0.839
	Arctic charr	11.202	0.578	–	–
	Three-spined stickleback	26.44	0.003*	2.616	0.888
	Unidentified fish remains	8.956	0.603	11.321	0.156

gradually more abundant, increasing the interspecific competition with charr. The charr responded by segregating in diet use from the superior trout, but contrary to expectations there was an increase in the individual and population niche widths of charr along with the increasing trout abundance. The trout population in contrast showed relatively stable resource use and population and individual niche widths over time. Overall, resource specialization, niche width and niche overlap changed with altered competitive interactions following the charr culling experiment as the system shifted from high to low densities of charr as the dominant species to a distinctive recovery of the trout population to equal densities of the two competitors. Our finding further emphasizes the importance of long-term studies to detect temporal changes in trophic niches. Interactions among species and environmental conditions may vary over time, influencing both individual and population niches. Our study, brings novel insights to the understanding of individual and population niche variation of animals on a large time perspective through changes in competition levels, whereas the majority of studies primarily focus on short and seasonal dynamics (Bolnick et al. 2010, Araújo et al. 2011, Cloyed and Eason 2016, Costa-Pereira et al. 2019, Xia et al. 2020).

The findings supported our first hypothesis that relaxed intraspecific competition decreases individual diet specialization and inter-individual variation resulting in a reduced population niche width. This response to a reversal of the intensity of intraspecific competition is in accordance with both theoretical considerations (Roughgarden 1972, Svanbäck and Bolnick 2005) and observational and experimental studies (Svanbäck and Bolnick 2007, Huss et al. 2008, Araújo et al. 2011), which have shown that high intraspecific competition

Table 3. (A) Intraspecific dietary overlap among different size classes (150–229 mm versus < 150 mm and > 300 mm, respectively), and (B) intraspecific average pairwise diet similarity among 150–299 mm individuals in both Arctic charr and brown trout. Chironomidae pupae and sample with less than ten individuals were excluded from the analysis.

(A)	Arctic charr		Brown trout	
Sampling periods	< 150 mm	> 300 mm	< 150 mm	> 300 mm
1985–1989	0.40	0.68	–	–
1990–1994	0.86	0.37	0.96	–
1995–1999	0.85	0.24	–	–
2000–2004	0.50	0.32	0.87	–
2005–2009	0.82	0.28	0.98	0.90
2010–2014	0.79	0.93	0.99	–
2015–2019	0.83	0.24	0.89	0.75

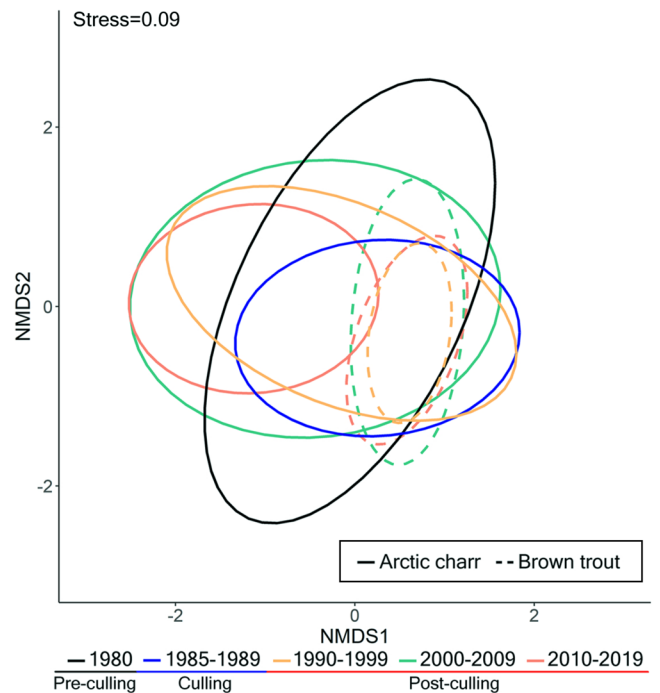| (B)	150–299 mm	150–299 mm
1980	0.16	–
1985–1989	0.27	–
1990–1994	0.30	0.50
1995–1999	0.23	0.41
2000–2004	0.23	0.24
2005–2009	0.13	0.44
2010–2014	0.21	0.46
2015–2019	0.25	0.34

Figure 4. Non-metric multidimensional scaling (NMDS) plot on Bray-Curtis distances (95% confidence intervals ellipses) showing dietary differences between 150-299 mm Arctic charr and brown trout over the four-decade study span using ten years sampling intervals in the post-culling period. Chironomidae pupae were excluded from the analysis.
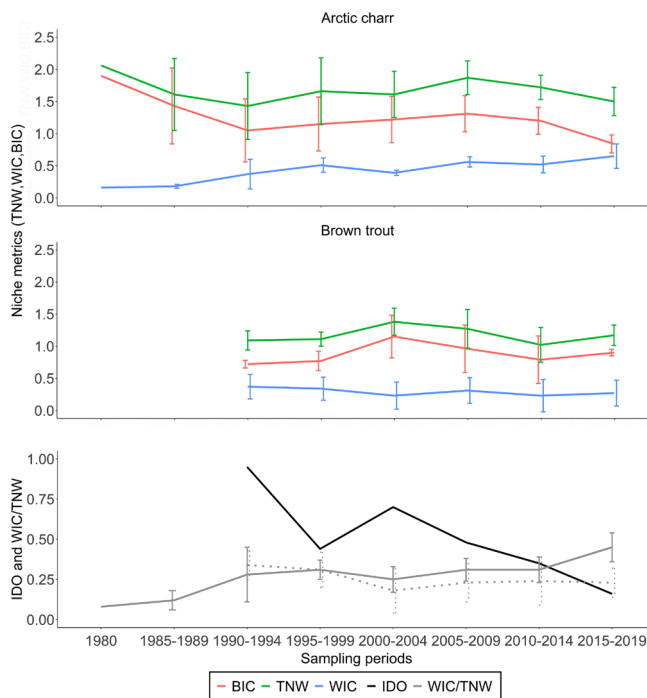

Figure 3. Average total niche width (TNW), within-individual component (WIC), between-individual component (BIC), individual specialization (WIC/TNW) ±SD, and interspecific dietary overlaps (IDO) of 150-299 mm Arctic charr (solid line) and brown trout (dotted line) over the four-decade study period.

promotes increased population niche width via individual specialization and greater between-individual variation. The individual diet specialization towards different prey types increases the diversity and inter-individual differences in prey utilization, thereby promoting resource partitioning among conspecific individuals, which may alleviate the effects of strong intraspecific competition (Xia et al. 2020).

Our second hypothesis, that stronger interspecific competition from the increasing trout population should result in dietary niche shift and narrower individual and population niche widths of the competitively inferior charr, was in contrast only partly supported. The expected dietary niche shift of charr occurred through an enhanced inclusion of zooplankton prey, in particular large and predatory cladocerans, resulting in reduced niche overlap and increasing resource partitioning as the trout densities increased. Classic niche theory suggests that with an increase in interspecific competition between asymmetric competing species, i.e. one being a superior competitor, the weaker competitor might be competitively relegated (Tran et al. 2015), leading to niche displacement, reduced growth and reduced abundance (Bøhn et al. 2008). However, if the inferior competitor can utilize other prey types that are unexploited or underutilized by the otherwise superior competitor, the increased exploitation of such resources will lead to a resource partitioning that may alleviate the effects of interspecific competition (Juncos et al. 2015). Zooplankton represents such

alternative prey for charr and is a characteristic prey resource for charr living in sympatry with trout (Nilsson 1963, 1965, 1967, Forseth et al. 2003, Eloranta et al. 2013). This was also confirmed by the present study, where charr increased their utilization of zooplankton in line with the post-culling increase in trout abundance. Zooplankton was, however, also a relatively important prey in the pre-culling, overcrowded charr population when trout was nearly absent, but at this point only small-sized cladocerans (*Bosmina longispina*) and copepods (*Cyclops scutifer* and *Eudiaptomus graciloides*) were present in the charr diet (Fig. 2; Amundsen and Klemetsen 1988). Following the charr culling, large-sized and predatory cladocerans (mostly *Daphnia* sp. and *B. longimanus*) became the dominant zooplankton prey, demonstrating that the zooplankton community was severely down-grazed by the overcrowded charr population, thus contributing to the severe pre-culling intraspecific competition. Hence, the reduced population density and intraspecific competition following the experimental charr culling enhanced prey availability in the study system and thus the ecological opportunity (Sánchez-Hernández et al. 2021), thereby apparently facilitating a comprehensive resource partitioning with trout as the trout density and impact of interspecific competition increased. Enhanced ecological opportunity in the system in the post culling period is also supported by the disappearance of ontogenetic habitat shift in charr even in the presence of trout (Klemetsen et al. 2002). Before the culling juvenile charr were confined to the profundal and pelagic zone due to high intraspecific competition whereas following the intensive charr culling they also started to utilize the littoral zone (Klemetsen et al. 2002).

Contradictory to our second hypothesis, the population and individual niche widths of charr did not decline with the increasing interspecific competition from trout, even though niche constrictions commonly are found as a response to increased interspecific competition in both natural populations and experimental setups (Trewby et al. 2008, Bolnick et al. 2010, De Santis et al. 2021). As a generalist and highly plastic predator, the charr may seemingly have escaped interspecific competition with the increasingly abundant trout not only by enhanced feeding on large and predatory cladocerans, but also by including a variety of other prey in their diet, resulting in large dietary niche widths both at the individual and population levels. Accordingly, both under high intraspecific and interspecific competition the charr had a broad population niche width. The fact that the first hypothesis was more strongly supported than the second may indicate that intraspecific competition was stronger than interspecific competition, likely because the new-gained post-culling accessibility of large and predatory cladocerans and other suitable prey for charr remained available also after the trout population recovered, thereby facilitating a high diet flexibility of the individual charr. Accordingly, under the pre-culling high intraspecific competition of charr, the large population niche width was the result of individual specialization and high inter-individual variation, whereas broad individual niches and a high within-individual contribution

to the niche width prevailed under the impact of interspecific competition from trout. The latter finding contradicts the general expectations from niche theory (Van Valen 1965, Roughgarden 1972, Schoener 1974), but is in accordance with the conclusion of Bolnick et al. (2010) and Araújo et al. (2011) that interspecific competition may increase or decrease individual specialization depending on the context. In the present scenario with charr and trout, the generalist nature of charr (Amundsen 1995) may respond to a combination of inter- and intraspecific competition by rather expanding than decreasing the individual niche width. Such a response would be in line with optimal foraging theory (Stephens and Krebs 1986), postulating that individuals will expand their trophic niche when preferred resources are scarce, which could be the case with inter- and intraspecific competition in co-action (Gabler and Amundsen 2010).

Our findings in respect to temporal and ontogenetic dynamics in diet, niche parameters and feeding similarity (NMDS plot), revealed that the niche width and dietary composition of the superior competitor brown trout was chiefly stable through time, as predicted by our third hypothesis. Hence, the resource utilization of the superior competitor was mainly independent of both intra- and interspecific interactions. A dominance of trout over charr for littoral resources has also been previously observed in the system (Eloranta et al. 2013). This supports previous notions about asymmetric competition between charr and trout, where trout is considered the superior competitor (Persson et al. 2007, Jonsson et al. 2008). A similar pattern was also found when contrasting these two competitors in allopatry versus sympatry (Nilsson 1963, 1965, 1967). The allopatry–sympatry scenario is reflected in the present long-term study with a gradual transition from a complete dominance of one species (practically allopatry) to equal densities of the two competitors (sympatry) within the same lake habitat. In the overcrowded state of the charr population, the superior competitor, trout, was constrained by recruitment and low resource availability (Persson et al. 2007). The substantial ecological release following the culling increased the number of trout but did only to a minor degree affect the resource utilization of the trout population, which chiefly remained constant throughout the whole study period. The temporal stability in the diet utilization of trout size groups relative to the marked dietary changes of charr (increase in the consumption of large and predatory cladocerans over the post-culling period in most size groups) confirms the competition asymmetry between the two species, with trout having the upper hand in the littoral habitat (Forseth et al. 1994, Jonsson et al. 2008). In addition, this asymmetrical competition is expected to vary over ontogeny (Sánchez-Hernández et al. 2019). The current study shows that charr individuals switch to alternative resources over ontogeny, likely to mitigate the effects of competition, and leading shifts in the degree of individual specialization in agreement with previous considerations (Araújo et al. 2011). However, the current study provides novel knowledge on the temporal dimension of individual niche specialization as earlier studies have been primarily focused on short

temporal and seasonal dynamics so far (Bolnick et al. 2003, Araújo et al. 2011, Costa-Pereira et al. 2018). In this regard, we observed contrasting responses from two salmonid species (charr showing temporal reduction in individual specialization, whereas it remained stable in trout), emphasizing the importance of dominant-subordinate status for understanding temporal trends in niche variation among animals.

In conclusion, our study substantiates that competition shapes population niche widths diversely affecting species and size classes. Trout, the superior competitor, had a stable resource utilization chiefly independent of any intra- or interspecific interactions. In contrast, the trophic ecology and resource utilization of the competitively inferior charr varied with decreasing intra- and increasing interspecific competition. Our findings thus reveal that there may be large temporal variations in resource use and population and individual niche widths within the same population. Furthermore, our long-term scrutiny of the impacts of the charr culling experiment chiefly corroborate expectations from classic niche and competition theory, with a notable exception for the increased individual and population niche widths of charr observed under interspecific competition with trout. Apparently, the coexistence of the two competing predators is strongly dependent on the niche variation and trophic plasticity of the inferior competitor, charr.

Author contributions

Sebastian Prati: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Eirik Haugstvedt Henriksen**: Conceptualization (supporting); Investigation (equal); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Aslak Smalås**: Conceptualization (supporting); Investigation (equal); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Rune Knudsen**: Conceptualization (supporting); Investigation (equal); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Anders Klemetsen**: Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Javier Sánchez-Hernández**: Formal analysis (supporting); Writing – original draft (equal); Writing – review and editing (equal). Per-Arne **Amundsen**: Conceptualization (equal); Investigation (equal); Methodology (supporting); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.95x69p8jx> (Prati et al. 2021).

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