ORIGINAL RESEARCH

Exploring temporal patterns in fish feeding ecology: Are ontogenetic dietary shifts stable over time?

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Abstract Disentangling the causes and consequences of ontogenetic niche shifts has been a pivotal challenge in ecology, aiming to enhance the understanding of biological processes that function at the individual, population, and community levels. Studies on ontogenetic dietary shifts have traditionally focused on short time scales, mostly including sampling covering just one or a few consecutive years, thus neglecting possible aspects of temporal variation and ecosystem stability that can only be revealed on long-term scales. We address ontogenetic dietary shifts of two fish predators in an intraguild system (Arctic charr and brown trout) using a long-term dataset spanning 20 consecutive years. Our study revealed distinct ontogenetic niche shifts of the two intraguild predators and demonstrated that these patterns were stable over time, suggesting large stability in prey acquisition and resource partitioning despite changes in their abundances and relative species composition. Some interannual variation was observed, but this was primarily due to sampling bias from low observation numbers for some ontogenetic stages, reflecting a common methodical challenge for ontogenetic niche shift studies. The persistent patterns in the trophic ontogeny of intraguild predators likely facilitate population and community stability by reducing inter- and/or intraspecific competition, thereby having important consequences for ecosystem functioning and resilience. Our study provides a strong rationale for performing ontogenetic niche shift studies over several consecutive years, enabling important insights into temporal variation, enhancement of observation numbers by merging data from multiple years, and the facilitation of a less intrusive sampling scheme for more vulnerable populations.

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Introduction

Ontogenetic dietary niche shifts are common in nature, particularly in insects, amphibians, and fishes, and are essential for understanding ecological processes that function at the individual, population, and community levels (e.g., Werner and Gilliam 1984; Nakazawa 2015; Sánchez-Hernández et al. 2019a; Rudolf and Eveland 2021). Such shifts are beneficial for consumers, enhancing growth and lifetime fecundity, and reducing mortality risk (e.g., Olson 1996; Post 2003; Trakimas et al. 2011). Moreover, ontogenetic dietary shifts may have important implications for higher trophic levels and the overall community dynamics (e.g., de Roos and Persson 2013; Rudolf and Rasmussen 2013; Reichstein et al. 2015) by influencing energy pathways and food-web structures (e.g., Miller and Rudolf 2011; Nakazawa 2015; Sánchez-Hernández 2016). Several predators feeding on the same food resource can strongly destabilise a system, while ontogenetic dietary shifts may enhance community stability by facilitating coexistence among sympatric species through resource partitioning (Schellekens et al. 2010; Klecka and Boukal 2012; Wollrab et al. 2013; Nilsson et al. 2018; Rudolf and Eveland 2021). Hence, ontogenetic dietary shifts generally seem to balance consumer-resource dynamics and increase population and community resilience by reducing inter- and/or intraspecific competition (reviewed in Nakazawa 2015 and Sánchez-Hernández et al. 2019a). Besides, studies aiming to understand ontogenetic dietary shifts can provide important clues about fish population and community ecology by identifying the factors that enable stability in stage-structured food webs and assemblages (Sánchez-Hernández et al. 2019a).

There is currently a good comprehension of the nature, causes, and consequences of ontogenetic dietary shifts (German and Crompton 2000; Nakazawa 2015; Sánchez-Hernández et al. 2019a; Rudolf and Eveland 2021), but the knowledge is commonly biased towards popular or economically important species, possibly limiting the recognition of general theories applicable to fish biology and ecology of a range of model organisms (Sánchez-Hernández et al. 2019a). It should be expected that the niche shifts of consumers during their development are linked to the taxonomic and phylogenetic identity of the species (German and Horn 2006; Sánchez-Hernández

2020a), and similar ontogenetic patterns in feeding are thus likely to be observed in closely related species. In general, a suite of drivers of ontogenetic dietary shifts have been identified, including predation risk, competition, prey availability, habitat use, morphological constraints, swimming ability, gut length, and bioenergetic considerations (Sánchez-Hernández et al. 2019a). Still, much attention needs to be paid to possible combined effects (synergies) among the recognised driving mechanisms of ontogenetic dietary shifts. Thus, the understanding of ontogenetic dietary shifts is often complex as some processes (e.g., ontogenetic changes in habitat use) may be a driver of ontogenetic dietary shifts or emerge as a consequence of other drivers, such as changing predation risk or prey availability (Sánchez-Hernández et al. 2019a). There is further strong evidence that ontogenetic changes in habitat use linked to changes in prey availability may drive ontogenetic dietary shifts (Nakazawa 2015; Sánchez-Hernández et al. 2019a; Tierno de Figueroa and López-Rodríguez 2019).

An important handicap for the current knowledge regarding theory and key concepts in trophic theory is related to the sampling efforts and duration of research programs. Studies on, e.g., insects, amphibians, reptiles, mammals, and fishes typically cover short time frames spanning from one to a few consecutive years (e.g., Eloranta et al. 2010; Klecka and Boukal 2012; Schriever and Williams 2013; Luría-Manzano and Ramírez-Bautista 2019), whereas studies using long-term perspectives are scarcer in the literature despite some noteworthy exceptions from freshwater (e.g., L'Abée-Lund et al. 2002; Saksgård and Hesthagen 2004; Winfield et al. 2012; Riccialdelli et al. 2013; Hanson et al. 2018) and marine (e.g., Michalsen et al. 2008; Holt et al. 2019; Townhill et al. 2021) fish model organisms. Overall, long-term studies constitute a small fraction (5–6%) of research efforts in aquatic systems (Xenopoulos 2019). This is unfortunate as long-term aquatic studies have provided new insights into temporal ecological patterns that could not have been observed on short time scales (Hampton et al. 2019), particularly in relation to drivers of temporal dynamics and key mechanisms that may facilitate ecosystem stability.

We examined the ontogenetic dietary shifts of two coexisting salmonid model species, brown trout (*Salmo trutta* Linnaeus, 1758) and Arctic charr [*Salvelinus alpinus* (Linnaeus, 1758)], through a

long-term dataset spanning two decades. Generalist species, such as most salmonids, often forage on a wide range of aquatic invertebrates when small, but may include terrestrial invertebrates, fish, amphibians, or rodents at larger sizes (Grey 2001; Eloranta et al. 2010; Jensen et al. 2012; Prati et al. 2020, 2021). Previous short-term studies have demonstrated that early stages of brown trout mainly prey upon benthic macroinvertebrates and pleuston (zooplankton is commonly absent in most size classes) but switch to piscivory later in development (Jensen et al. 2012; Prati et al. 2020). Arctic charr, on the other hand, typically shifts from small prey (zooplankton) to larger prey (benthic macroinvertebrates) and finally to piscivory or cannibalism, depending on the fish community structure (Amundsen 1994; Eloranta et al. 2010; Prati et al. 2020). In addition, systems with brown trout and Arctic charr living in sympatry represent an example of intraguild predation (i.e., size-structured mixed competition–predation interactions) where the fish species interact both as competitors and as predator and prey (Hesthagen et al. 1997; Persson et al. 2007, 2013; Sánchez-Hernández et al. 2017). In these systems, brown trout is commonly the superior species (Nilsson 1963, 1967; Hesthagen et al. 1997; Prati et al. 2021). Large brown trout are generally able to feed on small Arctic charr, but similar-sized individuals of both fish species usually compete for the same food resources (Persson et al. 2013; Prati et al. 2021). In addition, fish community configuration is a key ecological factor determining the trophic position of salmonid species linked to their increasing piscivory due to the presence of suitable prey fish species such as three-spined stickleback (*Gasterosteus aculeatus* Linnaeus, 1758), European whitefish *Coregonus lavaretus* (Linnaeus, 1758) or European minnow *Phoxinus phoxinus* (Linnaeus, 1758) (e.g., L'Abée-Lund et al. 2002; Jensen et al. 2012; Eloranta et al. 2015; Sánchez-Hernández et al. 2017). Besides, in many lacustrine systems, the connection between these suitable prey fish species and the piscivory behaviour of the focal apex predators is pivotal to understand their individual niche specialisation (Sánchez-Hernández et al. 2017). In this respect, it was recently found that temporal changes in fish community dynamics (i.e., changes in species abundance) over long-term periods had contrasting impacts on the individual and population niches of Arctic charr, whereas the diet and niche width of

brown trout chiefly remained stable over time (Prati et al. 2021), thus demonstrating that temporal shifts in feeding habits of fish may be species-specific.

Temporal variation (i.e., year-to-year variation) in ecological conditions (e.g., prey availability and species interactions) may impose an important limitation in recognising meaningful conclusions about biological processes like feeding when studies are projected on short-time scale designs. More specifically, interannual variability might drive ecological research focused on short-term studies towards less reliable conclusions compared to studies conducted on a longer term (Purdom et al. 2015; Cauvy-Fraunié et al. 2020). In addition, a practical issue with ontogenetic niche shift studies is that the diversion of a population sample into ontogenetic subgroups often possesses a problem with respect to low sample sizes for some of the subgroups. This requires attention on sampling designs to reach balanced datasets with adequate sample sizes for less common ontogenetic subgroups. Thus, methodological developments in trophic ontogeny research need to be driven towards improving data quality and representativeness.

Here we explore and contrast the long-term variation in ontogenetic dietary shifts of two intraguild predators, Arctic charr and brown trout, using a long-term dataset that spans 20 consecutive years of annual studies from a subarctic lake system. The main objectives were to (i) contrast ontogenetic variation in the resource use of the two intraguild predators, (ii) explore whether their ontogenetic dietary shifts are stable over time, (iii) optimise sampling design for trophic ontogeny studies, and (iv) address the ecological consequences of these ontogenetic niche shifts and their species-specific and temporal variation for intra- and interspecific resource partitioning, community dynamics and ecosystem stability.

Material and methods

Study system

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. The study system is included in a long-term research program on the ecology and management of oligotrophic lake systems (Amundsen et al.

2019). The fish community comprises brown trout, Arctic charr, and three-spined stickleback. Prey species composition is well known, including nine crustacean zooplankton taxa and 25 macroinvertebrate taxa (see Prati et al. 2021 for further details).

Sampling

We collated annual sampling in August (between July 30 and August 19; mostly between August 6 and 18) over two decades (2001–2020) to form a long-term database. Fish were sampled in the littoral habitat using 40-m long multi-mesh survey gillnets set overnight (approximately 12 h). To obtain a suitable representation of size distribution among fish populations, we used multi-mesh gillnets with eight randomly distributed 5-m long panels of different mesh sizes (10, 12.5, 15, 18.5, 22, 26, 35, and 45 mm knot-to-knot) (Prati et al. 2021). A total of 2432 individuals (1312 Arctic charr and 1120 brown trout) were sampled. Catch per unit effort (CPUE), that is, the number of fish caught per 100 m^2 gillnet per night (~ 12 h), was estimated for each fish species (Fig. 1). Each individual was measured (fork length range: 68–775 mm and 85–467 mm for brown trout and Arctic charr, respectively; see Appendix S1 for further details) and sexed by gonad examination (Appendix S1), and stomachs were removed for diet analysis.

Stomach content analyses

In the lab, the stomachs were opened, and dietary analysis was implemented using the relative fullness method (Hyslop 1980; Amundsen and Sánchez-Hernández 2019). The total fullness of all stomach contents was first visually assessed and expressed on a scale from empty (0%) to full (100%). All prey items were identified to the lowest practical taxonomic level using a binocular microscope (magnification × 40), whereafter the fullness contribution of each prey taxon was assigned, summing up to the total stomach fullness. Prey abundance, i.e., the contribution of each prey type to the total stomach contents, was estimated on a percentage scale following Amundsen & Sánchez-Hernández (2019). The different prey taxa were grouped into four main dietary categories: (I) zooplankton (*Bosmina* spp., *Daphnia* spp., *Holopedium gibberum* Zaddach, 1855, *Bythotrephes longimanus* Leydig, 1860, *Polyphemus pediculus* (Linnaeus, 1758), and cyclopoid and calanoid copepods), (II) benthic prey (*Radix peregra* (Müller, 1774), Valvatidae snails, *Pisidium* spp., *Gammarus lacustris* Sars 1863, Chironomidae larvae, Trichoptera larvae, Ephemeroptera nymphs, Megaloptera larvae, Tipulidae larvae, Plecoptera nymphs, and the semi-benthic *Eurycercus lamellatus* (Müller, 1776) chydorid), (III) pleuston (chironomid pupae and exogenous prey items such as terrestrial insects, but also some pupae and aerial imagoes of aquatic insects) and (IV) fish. The

Fig. 1 Fish abundance over the study period (2001–2020) showing relative contribution (%) of brown trout compared to Arctic charr (blue line and primary y-axis) and catch per unit effort (CPUE) for both species (bars plot and secondary y-axis)
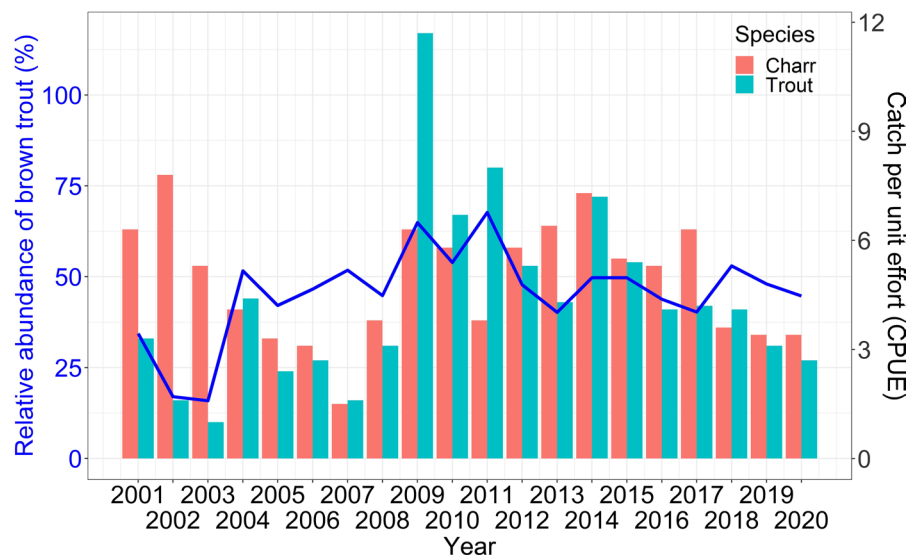
number of empty stomachs was low in both species, representing 2.1% and 1.3% of the total samples of Arctic charr and brown trout, respectively (Appendix S1).

The relative fullness method resembles the classic point method (Hynes 1950; Hyslop 1980), but the relative prey contribution in the stomach is visually scored in percentage rather than in points summing up to the total stomach fullness (Amundsen and Sánchez-Hernández 2019). Both methods have been criticised for being subjective, as the visual estimation of the bulk of food in the stomach does not have the measurement precision of, e.g., the numerical or gravimetric methods (Baker et al. 2014). However, a recent scrutiny of the relative fullness method demonstrated a high consistency and reliability of this approach (Amundsen and Sánchez-Hernández 2019). The practical execution of this method is also simple and fast relative to other approaches (Hyslop 1980), which allows for efficient processing of large sample sizes (Amundsen and Sánchez-Hernández 2019 and references therein). Stomach contents can provide valuable information about feeding habits and foraging modes of consumers in line with the biological traits of their prey (de Crespin de Billy and Usseglio-Polatera 2002; Sánchez-Hernández and Cobo 2018). In this regard, dietary observations of fish individuals can be used to extrapolate information about foraging modes (e.g., zooplanktivore or benthivore) based on the type of prey (limnetic or benthic) in the stomach contents (Knudsen et al. 2010; Sánchez-Hernández et al. 2021a), as prey communities in the study system chiefly differ between the littoral (large-bodied zoobenthos) and pelagic (small-bodied zooplankton) zones (Prati et al. 2021 and references therein). Thus, the above-mentioned prey categories (zooplankton, benthic prey, pleuston, and fish) were used as a proxy for different foraging modes (i.e., pelagic foraging, benthic foraging, water-surface foraging, and piscivory, respectively) to explore ontogenetic changes in both diet and foraging habits of the model organisms. Intra- and interspecific resource partitioning were calculated as percentage overlap (Pianka index) using the most detailed taxonomical resolution of the prey resources identified in the stomach contents. The Pianka index has a minimum of 0% (no prey overlap) and a maximum of 100% (all taxa in equal proportions), the overlap usually being considered biologically significant when the value of the index exceeds 60% (Wallace 1981).

Statistics

All data analyses and visualisation were carried out using R version 3.6.2 (R Core Team 2019). Prior to data analyses, individuals were divided into eight size groups to explore feeding differences over the ontogeny: (I) 50–100 mm, (II) 100–150 mm, (III) 150–200 mm, (IV) 200–250 mm, (V) 250–300 mm, (VI) 300–350 mm, (VII) 350–400 mm and (VIII) > 400 mm. A common challenge for ontogenetic niche shift studies is to cope with low sample sizes for certain size groups and years (particularly for large and small fish) due to the subdivision of population samples into ontogenetic sub-groups. To explore possible bias of low observation numbers in the analysis of interannual variation, we examined the relationship between two statistical variance estimators (variance and relative variance) of the mean prey abundance over the 20-yr study period versus the average annual sample sizes for the various ontogenetic stages over the same period.

Feeding analyses were performed using different time scales to test the research objective that ontogenetic dietary shifts are stable over time, i.e., with similar ontogenetic trends regardless of the time scales according to local polynomial regression (LOESS) curves, and to explore an optimisation of the sampling design for trophic ontogeny studies. The adopted time scales included: (I) a coarse-scaled approach comprising the full data set covering the complete sampling period (2001–2020), (II) an intermediate-scaled approach covering decadal periods (2001–2010 and 2011–2020), (III) a semi-fine-scaled approach covering five-year periods (2001–2005, 2006–2010, 2011–2015 and 2016–2020), and (IV) a fine-scaled approach covering two-year periods (2001–2002, 2003–2004, 2005–2006, 2007–2008, 2009–2010, 2011–2012, 2013–2014, 2015–2016, 2017–2018 and 2019–2020). Additionally, the annual-based data set has been explored as the baseline for our time-scale comparisons. Shapiro–Wilk tests indicated non-normality in the data, and thus nonparametric Kruskal–Wallis tests were used to analyse differences in prey abundance among size groups. Logistic regression models were fitted using the "popbio"

package in R (Stubben and Milligan 2007) to examine the switch in feeding (zooplankton, benthic prey, pleuston, and fish prey) of the model organisms as a function of fish length based on presence-absence data (1 = prey category consumed and 0 = no prey category consumed). The shift to a specific prey category can be assumed to occur when, according to the fitted curve of a logistic regression model, the probability of the category occurring in the diet is 50% (Kahilainen and Lehtonen 2003; Sánchez-Hernández and Cobo 2018). Hence, a 50% probability level was employed to investigate the body-length related timing of the dietary shift by the fish species. Probability levels of 25% and 75% were considered as threshold values for the range of sizes where the feeding shift occurs. Pianka index was calculated using the "spaa" package in R (Zhang 2016) to examine intra- and interspecific resource partitioning. To identify biologically significant values of this index (>60%), we built a heatmap of percentages in the gplot2 package (Wickham 2016). A significance level of $p = 0.05$ was used for all analyses.

Results

### Ontogenetic dietary shifts of Arctic charr and brown trout

Arctic charr showed clear ontogenetic dietary shifts that were stable over time despite some inter-period variation when data was analysed through finer-scaled approaches (especially in two-year periods) (Fig. 2). The most common prey resources for Arctic charr were zooplankton and benthic prey, but their contribution changed over the ontogeny (Figs. 2 and 3, Appendix S2). The consumption of zooplankton was higher in small fish, whereas the abundance of benthic prey increased with increasing body length (Fig. 2). Logistic regression models indicated that the ontogenetic shifts towards benthic prey and away from zooplankton occurred at body lengths of 24.8 cm and 25.3 cm, respectively (Fig. 3 and Appendix S3), but the specific size-related timing slightly varied among time periods (Fig. 4). Pleuston peaked in small and intermediate fish (Fig. 2), whereas the abundance of fish prey was very low although slightly increased for the largest size groups (Appendix S3). The observed ontogenetic dietary patterns remained stable regardless of the considered time periods, i.e., zooplankton decreasing and benthic prey increasing over the ontogeny (Fig. 2), despite a relatively
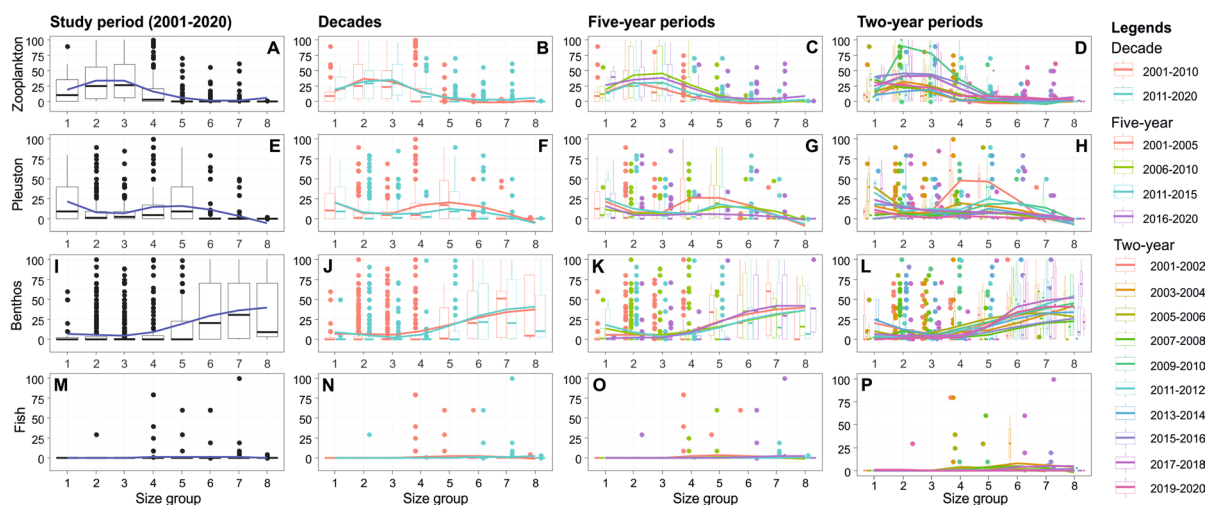
Fig. 2 Ontogenetic dietary shifts of Arctic charr over the study period (panels A, E, I and M), decades (panels B, F, J and N), five-years periods (panels C, G, K, and O) and two-year periods (panels D, H, L, and P). The boxplot indicates the median and the interquartile range with a 95% confidence interval for the median. Local polynomial regression (LOESS) curves are fitted to the data for illustrative purposes to show ontogenetic trends

Fig. 3 Probability of the ontogenetic dietary shift (zooplankton, pleuston, benthic prey, and fish) as a function of fork length of Arctic charr and brown trout over the study period (2001–2020). Only statistically significant results are shown, see Appendix S3 for all model configurations and outputs of all time periods. Bars represent histograms of occurrence frequencies across fish size spectrum grouped in five cm size classes for illustrative purposes of the size structure and based on presence–absence data (1 = prey consumed, 0 = no prey consumed). The red line represents the fitted curve of the logistic regression model
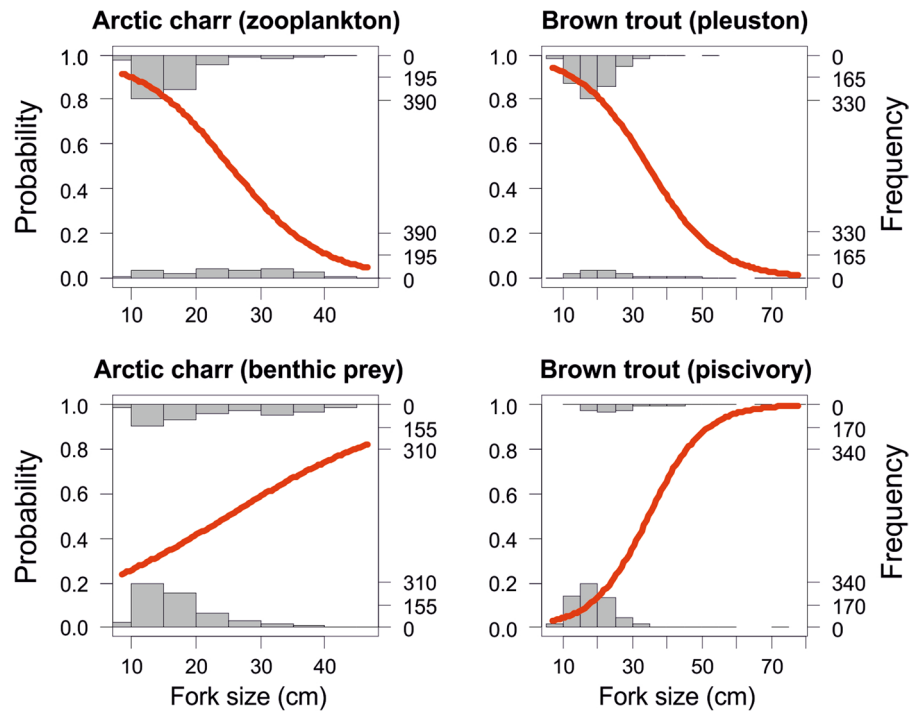

high degree of inter-annual variation (Appendix S4). However, small differences among five-year periods in the patterns for pleuston were observed; more specifically, the peak occurred earlier in the ontogeny in 2001–2005 compared to 2006–2010 and 2011–2015, whereas in 2016–2020, the pleuston contribution remained low without any changes over ontogeny (Fig. 2 and Appendix S2). This variability among sampling periods was most evident among two-year periods (Fig. 2), where also contrasting ontogenetic dietary directions in the consumption of pleuston could be seen, decreasing in most periods except in 2003–2004, when it was increasing (Fig. 4). The low level of piscivory observed in Arctic charr prevented us from exploring any differences in the ontogenetic patterns revealed among the various analytical approaches of differing time scales.

Like Arctic charr, brown trout also demonstrated clear ontogenetic dietary shifts that were stable over time but with some inter-period variations at the shorter time scales (i.e., two-year and inter-annual) (Fig. 5 and Appendix S4). Pleuston was the most important prey category for small and intermediate-sized fish but decreased over ontogeny, whereas the abundance of fish prey increased and constituted the most important prey for large fish (Fig. 5). Logistic

regression models showed that the ontogenetic shifts towards fish prey and away from pleuston occurred at body lengths of 34.5 cm and 34.6 cm, respectively (Fig. 3 and Appendix S3), with small variations among time periods (Fig. 4). In contrast, there were no severe ontogenetic dietary shifts in the consumption of benthic prey (Fig. 5 and Appendix S2), but logistic regression models revealed some contrasting outcomes among two-year periods (Fig. 4). The consumption of zooplankton was slightly higher in small fish, and these differences were also more pronounced in the second decade (2011–2020) and the last five-year period (2016–2020) (Fig. 5 and Appendix S2). Despite a seemingly high degree of inter-annual (Appendix S4) and biennial (Fig. 5) variation, ontogenetic dietary shifts in the utilization of pleuston and fish prey were always present at the adopted coarser time scales (i.e., full dataset, decade, and five-year period).

Both for Arctic charr and brown trout, the sample sizes were low for certain size groups and years, particularly for large and small fish (Appendix S1, Table S1C), which may explain some of the inter-annual variations that were observed for the single-year data (Appendix S4). The analysis of the impact of sampling size on the observed interannual
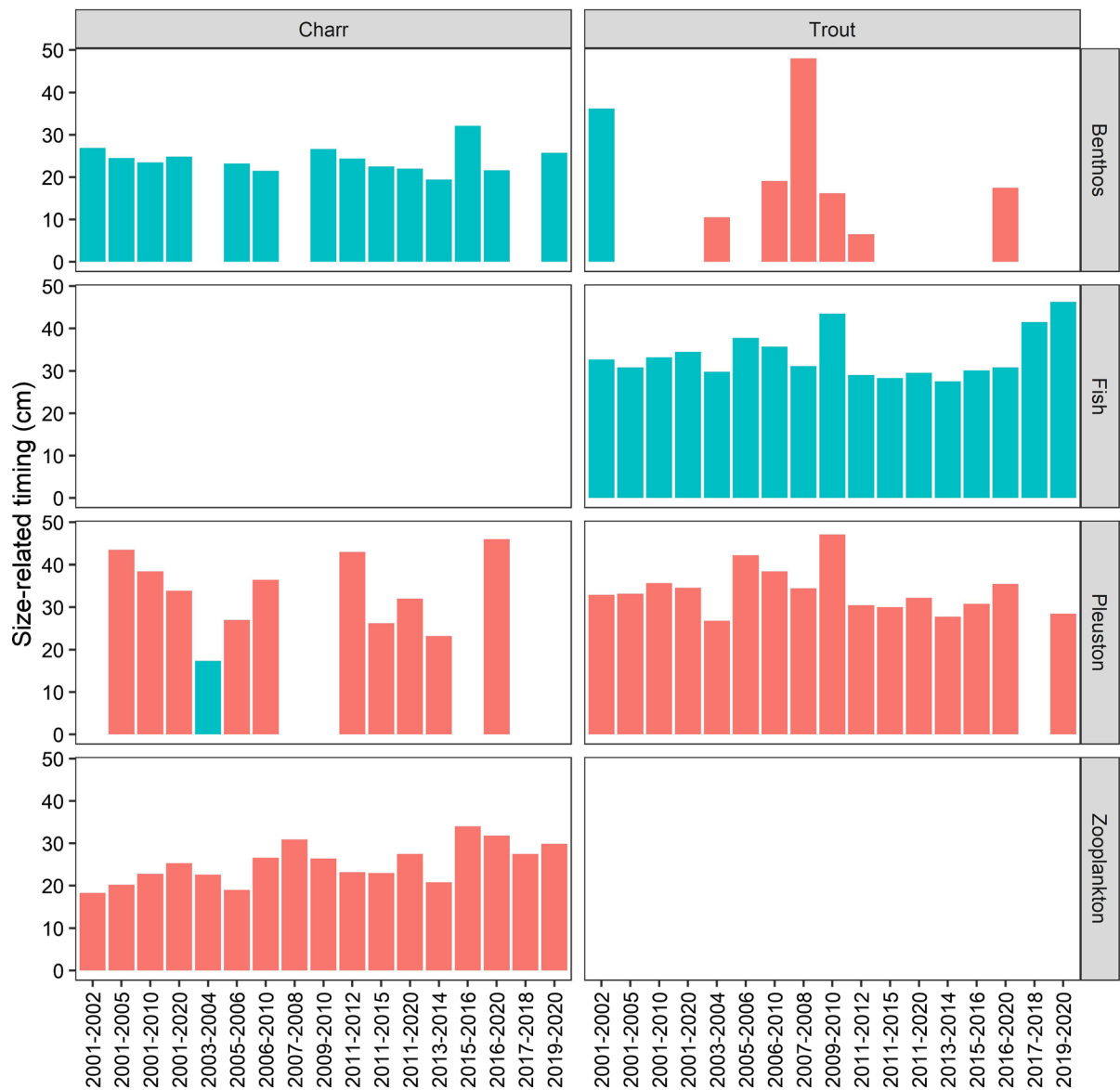
Fig. 4 Temporal changes in size-related timing (cm) of prey category according to logistic regression models of brown trout and Arctic charr. Colours show the direction of the ontogenetic shifts showing increasing (green) or decreasing (red) of the prey category over ontogeny (i.e. with fish size increases). Missing bars indicate that the logistic regression model did not provide any estimate of the 50% probability level or uneven/low events in the presence-absence data

variation revealed that the variance estimators were high for ontogenetic stages with low observation numbers, but rapidly declined and remained at low levels for average sample sizes larger than approx. 10 (Appendix S5), supporting the notion that low sample sizes for some of the ontogenetic subgroups may lead to biased conclusions about interannual variations. Correspondingly, when increasing the

observation number by merging data from consecutive sampling years, the observed temporal fluctuations declined. Still, for both species, some temporal variation could be seen from the merged datasets, including two-year, five-year, and even ten-year periods (Figs. 2 and 4), suggesting that these were not related to low sample sizes but represented distinct temporal changes.
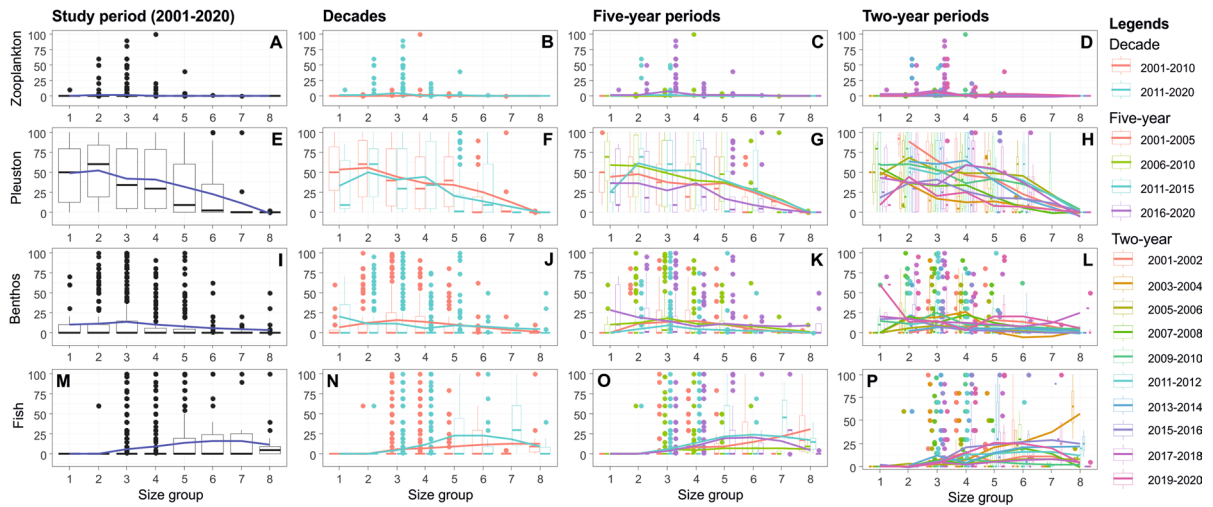
Fig. 5 Ontogenetic dietary shifts of brown trout over the study period (panels A, E, I, M), decades (panels B, F, J, and N), five-years periods (panels C, G, K, and O) and two-year periods (panels D, H, L, and P). The boxplot indicates the median and the interquartile range with a 95% confidence interval for the median. Local polynomial regression (LOESS) curves are fitted to the data for illustrative purposes to show ontogenetic trends

Fig. 6 Between-species overlaps (Pianka's percent overlap index) in diet use of Arctic charr (C) and brown trout (T) for the eight size groups (numbers from 1 to 8) over the study period (2001–2020). The overlap/similarity is considered high when the index value exceeds 60% (values in red), values below 60% are in green, and values equal to 60% are in white. See Appendix S6 for outcomes over all time periods
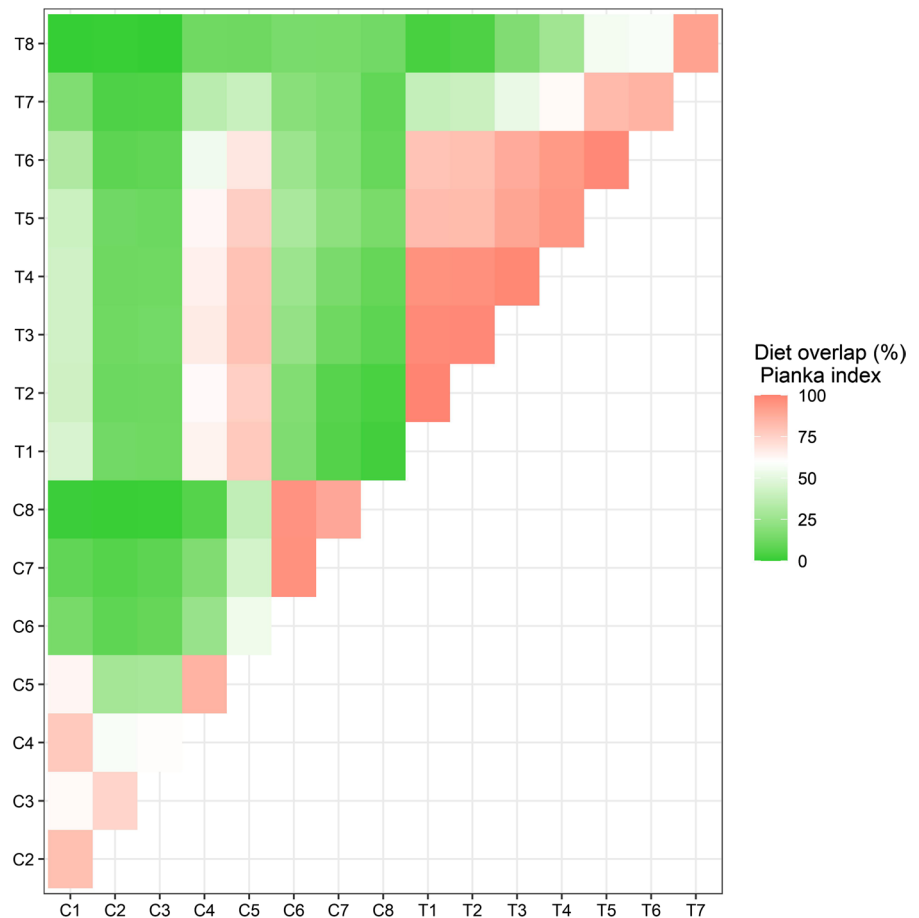
Intra- and interspecific resource partitioning

Intraspecific resource partitioning in Arctic charr increased over the ontogeny as diet overlap was higher among small and intermediate size groups in comparison to larger individuals (Fig. 6). Also, Arctic charr showed clear dietary segregation with brown trout, except between intermediate size groups of Arctic charr and small and intermediate size groups of brown trout where the diet overlap was high (>60%, Fig. 6). Intraspecific resource partitioning was less evident in brown trout than in Arctic charr, at least among small and intermediate-sized groups, whereas diet overlaps for large individuals were lower. However, intra- and interspecific resource partitioning were highly variable depending on the adopted time-scale approach (i.e., coarser versus finer scales) (Appendix S6).

Discussion

Although several authors have drawn conclusions about the feeding of animals based on long-term studies (e.g., L'Abée-Lund et al. 2002; Saksgård and Hesthagen 2004; Riccialdelli et al. 2013; Hanson et al. 2018), the current study represents to our knowledge the first attempt to evaluate temporal variation in ontogenetic dietary shifts using a long-term perspective with consistent sampling strategy and efforts to enhance representativeness and explore sampling design optimisation. Our findings reveal stable patterns in the ontogenetic dietary shifts of the two intraguild predators despite changes in their abundances and relative composition over the 20-yr study period. However, we also recognised some temporal changes, especially when the long-term dataset was explored using single- or two-year time scales. Still, most of the observed interannual variation can seemingly be ascribed to methodical issues related to low year-specific sampling sizes rather than representing true and biologically meaningful variation. Although our findings rely on stomach contents analysis representing diets over a short time scale, the temporal consistency of the observed patterns supports their reliability. Diet-tracing techniques such as stable isotopes may provide an enhanced seasonal representation of dietary data (Davis et al. 2012) and is thus an advisable complement for future temporal

studies of ontogenetic dietary shifts, but such analyses were unfortunately not included in the current long-term research program.

Our study shows that ontogenetic dietary patterns can remain stable over time regardless of the considered time periods. Unfortunately, most previous studies based on long-term feeding datasets have only focused on the description of temporal changes in the overall diet composition (e.g., L'Abée-Lund et al. 2002; Saksgård and Hesthagen 2004; Winfield et al. 2012; Riccialdelli et al. 2013; Townhill et al. 2021), whereas the limited cases that have covered trophic ontogeny did not include the temporal approach but rather merged interannual samples (e.g., Holt et al. 2019). Thus, it is pertinent to ask whether our observed stability in ontogenetic dietary trajectories is the common norm in nature. In this regard, numerous factors (predation risk, competition, prey availability, habitat use, morphological constraints, etc.) can influence trophic ontogeny, and the most influential of these may vary both spatially and temporally (Sánchez-Hernández et al. 2019a). Accordingly, further studies addressing long-term variation in the dietary ontogeny of fish are highly requested. Temporal stability in prey communities should also preferably be taken into account, as prey characteristics (availability, abundance, and typology) may shape predator niche variation via bottom-up mechanisms (Sánchez-Hernández et al. 2019b, 2021b).

Interannual variation in prey availability (i.e., temporal variations in prey communities) has frequently been observed in aquatic systems (e.g., Løvik and Kjellberg 2003; Hämäläinen et al. 2003; Frainer et al. 2016; Prati et al. 2021), likely shaping foraging and diet composition of predators (e.g., Ringler 1985; Baudrot et al. 2016). In the present study, even though most interannual variation observed with the single- and two-year time scales could be ascribed to bias from low sample sizes of certain ontogenetic stages, there were a few dietary changes that were consistent also for the five- and ten-year time scale approaches, supporting that these represent valid temporal variation. More specifically, the consumption of benthic prey and zooplankton by brown trout was slightly higher over the last five-year period (2016–2020) compared to the other periods, whereas for the same time period, the pleuston contribution was noticeably low for Arctic charr and remained low without any changes over the ontogeny. This result entails the

importance of the predatory cladoceran zooplankton (*Bythotrephes longimanus*) and benthic prey (mainly Coleoptera and Tipulidae larvae) to explain niche variation over time of brown trout and Arctic charr (Prati et al. 2021). In addition, these modest changes in prey consumption might indicate some ongoing alterations at the ecosystem level, possibly as a consequence of new environmental conditions related to increasing water temperatures driven by the ongoing climate warming, which have also been documented for our study lake (Smalås 2021). For example, it has recently been demonstrated that warmer-adopted, generalist fish species have a higher capacity than cold-adapted species to undergo reciprocal benthic–pelagic switches in feeding associated with environmental change (Sánchez-Hernández et al. 2021a), which may be key to understanding the functioning and stability of northern fish communities under a changing climate. Accordingly, it is possible that the cold-water adopted Arctic charr over the last years have avoided the warm upper-water layers in August as a consequence of climate warming impacts, making this ecological niche available for brown trout that over the same period were found to prey slightly more on zooplankton. In this regard, it should be kept in mind that high-latitude regions are one of the fastest warming areas of the world due to the Arctic amplification phenomenon (Coumou et al. 2018). Thus, species-specific readjustments in trophic ontogeny linked to new environmental conditions driven by the current climate warming (Smalås 2021) can be essential for understanding the coexistence of intraguild communities in a changing environment. This view supports recent theoretical considerations underlining the importance of intraguild predators with partial, rather than complete, ontogenetic dietary shifts as a key for understanding community reconfigurations and consumer coexistence for predictions about how warming may affect species composition and interactions (Thunell et al. 2021).

Although no consensus has previously been reached for a standardised time scale for studying ontogenetic dietary shifts of common-studied model organisms, our findings suggest that short-term studies, including one or a few years of sampling efforts, may constitute a reliable approach when addressing research objectives and questions related to dietary composition and trophic ontogeny, given that sufficient sample sizes can be obtained for the various ontogenetic stages. Long-term datasets are needed to disentangle ecological trends and processes responsible for ecosystem stability that could not have been observed on short time scales (Hampton et al. 2019). In this regard, it should be noted that the observed year-to-year variation, which chiefly was due to sampling bias from some low observation numbers, may hinder the ability to disentangle general patterns in feeding from single-year studies if the sample sizes are limited. Future studies aiming to disentangle ontogenetic dietary shifts of animals should take these methodological challenges into account and increase sampling efforts to overcome weaknesses and constraints of low sample sizes. This may be implemented by enhancing the sampling efforts within a specific study year. However, whenever feasible, there are strong reasons to enhance the efforts and observation numbers by performing the study over several consecutive years. This will provide insights into temporal variation, especially for ontogenetic stages that are numerously present in the samples, and will also enable an increase in observation numbers of less numerous ontogenetic stages by merging data from consecutive years. This approach will also facilitate a less intrusive sampling strategy for studies of more vulnerable populations as the sampling impact will be dispersed over multiple years. Thus, more attention needs to be paid to compile expansive datasets by merging data from multiple years to overcome possible pitfalls due to low sampling sizes for some ontogenetic stages, a limitation common to many studies focused on trophic ontogeny, in order to enhance our understanding of ontogenetic stability through time.

From an ecological standpoint, our findings also underline the importance of ontogenetic niche shifts in creating stability in aquatic systems. We demostrate that selective differences in feeding and asymmetrical competition between brown trout and Arctic charr, representing two predators in an intraguild system, are particularly important in understanding the distinct but stable ontogenetic feeding trajectories observed in the present study. The observed patterns may have a stabilising effect at the population, community and ecosystem levels. In terms of both diet and habitat utilisation, consistent ontogenetic niche shifts will stabilise population and community dynamics, which, in turn, enhance ecosystem stability by reducing overexploitation of prey as well as

inter and intraspecific interactions, as also suggested by earlier studies (Rudolf and Lafferty 2011; Nilsson et al. 2018; Sánchez-Hernández et al. 2019a). We argue that size-specific feeding patterns represent a key factor in preserving the stability of natural systems as they may mitigate perturbations arising from interactions among competing predators. In fact, ontogenetic dietary shifts commonly reduce interspecific competition between morphologically (and ecologically) similar species in a broad suite of model organisms (e.g., Céréghino 2006; Schellekens et al. 2010; Klecka and Boukal 2012; Wollrab et al. 2013). Our study demonstrates that intraguild predators display different ontogenetic dietary shifts, which may reduce both intra- and interspecific competition for food through enhanced resource partitioning and allow the two consumers to coexist despite asymmetrical competition. Arctic charr underwent ontogenetic dietary shifts from zooplankton to benthic prey, a pattern widely described in the literature (Klemetsen et al. 2003; Prati et al. 2020). For brown trout, we observed that the consumption of pleuston decreased over the ontogeny whereas fish predation increased, a finding in line with previous studies reporting that brown trout often switches to piscivory later in development (Grey 2001; Jensen et al. 2012; Prati et al. 2020; Sánchez-Hernández 2020b). In northern lakes, exogenous resources are typically a key energy source for brown trout during mid-to-late summer (Milardi et al. 2016a, 2016b). However, the present study reveals that exogenous resources were more important in small and medium brown trout (up to 350 mm) and thus not consistently used over the whole ontogeny.

Our overall findings revealed that the two study species displayed different ontogenetic dietary shifts; in brown trout, pleuston decreased and fish prey (including Arctic charr) increased over the ontogeny, whereas in Arctic charr, zooplankton decreased and benthic prey increased. These contrasting patterns suggest that stage-specific resource allocations of the consumers can reduce interspecific competition for food, as also demonstrated through our dietary comparisons using the Pianka index. These adaptations are an example of intraguild predation, where transitions to piscivory can be displayed because fish species in the study system interact as predator and prey (Hesthagen et al. 1997; Browne and Rasmussen 2009; Sánchez-Hernández et al. 2017). Brown trout is

considered a superior competitor compared to Arctic charr (Hesthagen et al. 1997; Prati et al. 2021), and the presence of profitable small fish prey (three-spine stickleback) and mixed competitor–prey interactions among the fish species in the study system are likely to support early piscivory in brown trout populations (Sánchez-Hernández et al. 2017). Although it is reasonable to posit that the resulting ecosystem stability of the studied system (Takvatn lake) will provide resilience to future multiple stressors like climate warming (favouring brown trout over Arctic charr in northern systems) or other anthropogenic impacts (e.g., overfishing, species introductions or pollution), these may in future have destabilising effects due to, e.g., loss of ontogenetic diversity within the populations (Rudolf and Eveland 2021) and increases in competition strength (Thunell et al. 2021), which eventually would lead to unpredictable ecosystem consequences.

In conclusion, we demonstrated long-term stability in the ontogenetic dietary niche shifts of Arctic charr and brown trout, and thereby in prey acquisition and resource partitioning of the two intraguild predators, despite the significant changes in their fish populations over the study period. These persistent patterns in ontogenetic niche shifts facilitate population and community stability by reducing inter and/or intraspecific competition and may thereby also have important consequences for ecosystem functioning and resilience to environmental and ecological changes. Our study also provides important insights into the common methodical challenge for ontogenetic niche shift studies from low sample sizes of some of the ontogenetic stages. In spite of our main conclusion of long-term stability in the ontogenetic dietary shifts of the two model species, we still like to emphasise that there are strong reasons to perform ontogenetic niche shift studies over several consecutive years as this provides important insights into temporal variation. Furthermore, it enhances observation numbers across all size classes and facilitates a less intrusive sampling scheme for small and vulnerable populations by merging data from multiple years. Thus, we suggest combining two or more years in those scenarios where the sample sizes can be compromised for various reasons, such as small populations or unbalanced data among ontogenetic stages. Overall, the described outcomes and methodological recommendations of the present study may be usefully extended to other

researchers with a broad interest in fish ecology and research questions of trophic ontogeny.

Data accessibility Data available from the Figshare Digital Repository (https://doi.org/10.6084/m9.figshare.20695489.v1).

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