

REGULAR ARTICLE

Active feeding of downstream migrating juvenile pink salmon (*Oncorhynchus gorbuscha*) revealed in a large Barents Sea river using diet and stable isotope analysis

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Abstract

The recent, rapid spreading of non-native pink salmon *Oncorhynchus gorbuscha* in the North Atlantic area has raised concerns about their possible negative impacts on native salmonid species. Potential interactions include competition for food resources during the short freshwater phase of juvenile *O. gorbuscha*, but little is known about their feeding behavior in the newly occupied North Atlantic rivers. Using stable isotope and stomach content analyses, patterns of freshwater feeding of non-native *O. gorbuscha* fry were studied in a large Fennoscandian river, the Teno, that discharges to the Barents Sea. Changes in stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$) and stomach contents from the period of emergence (April to mid-May) to estuarine entry (late May/June) were examined and provided both temporally integrated and short-term indicators of freshwater feeding dependency. In addition, the occurrence of juvenile *O. gorbuscha* and changes in their length and weight during their emergence/migration period were investigated. Juvenile *O. gorbuscha* were at the spawning grounds from April through to mid-May with abundance peaking in mid-May. Fish moved to the estuary by late May and their abundance decreased toward June, and their body size increased concurrently. Stomach analyses indicated no feeding activity in April–early May in the spawning areas, but the stomach fullness indices increased markedly in fish sampled in the estuary in May and June. The most important prey items in stomachs were Chironomidae and Ephemeroptera larvae. Significant changes in all analysed stable isotopes were detected among sample periods, with a peak in mid-May and June showing significantly lower values than other sample periods. A change from the higher values reflective of parental marine feeding to the lower values reflective of freshwater feeding indicated active in-river feeding by juveniles during the study period. The documented active freshwater feeding of non-native juvenile *O. gorbuscha* suggests potential resource competition with native fluvial fishes, particularly salmonids.

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KEYWORDS

Barents Sea, Finland, freshwater feeding, invasive species, juvenile growth, Norway, pink salmon, stable isotopes

1 | INTRODUCTION

Pacific pink salmon (*Oncorhynchus gorbuscha* Walbaum) are native to western North America and the eastern Pacific and are found commonly as breeding populations between 48°N and 64°N in North America and 44°N to 65°N in Asia (Heard, 1991). Currently *O. gorbuscha* can be commonly found throughout western Europe, the Great Lakes basin of eastern North America, and many rivers in South America (Behnke, 2002; Crawford & Muir, 2008; ICES, 2022; NHPSEG, 2023). Although expansion beyond the native range has often resulted from purposeful introductions, diffusion dispersal from aquaculture escapement has been the principal means by which *O. gorbuscha* have come to acquire invasive status in the river systems of western Europe (Welcomme, 1988), principally those also containing valued Atlantic salmon (*Salmo salar* L.) stocks (ICES, 2022; NHPSEG, 2023). In addition to the arbitrary introduction of *O. gorbuscha* to different areas in the Northern Hemisphere, the species has recently extended its natural distribution range into the Canadian and Russian Arctic (NHPSEG, 2023). The introduction of *O. gorbuscha* in northwestern Russia (Kola Peninsula, White Sea area) in the late 1950s paved the way for the recent rapid expansion of distribution and abundance of *O. gorbuscha* in the northeast Atlantic area (ICES, 2022; NHPSEG, 2023; Sandlund et al., 2019).

O. gorbuscha is a semelparous anadromous species that spawns in rivers in the autumn. Eggs normally hatch the following spring, with emergent fry leaving fresh water soon thereafter. *O. gorbuscha* thus has the shortest period of freshwater residency of any salmon species and was generally thought to complete minimal feeding in fresh water (e.g., Bailey et al., 1975; Frolenko, 1970; Hart, 1973; Wydoski & Whitney, 1979). More recent work in Scandinavia and northwestern Russia has shown that *O. gorbuscha* fry commence external feeding before migration as smolts (Gordeeva et al., 2015; Sandlund et al., 2019), with the intensity and duration of feeding depending in part on the required migration length and river hydrodynamic conditions (Veselov et al., 2016). Outside of their native range such differences in the start timing of exogenous feeding may have competitive implications for native species such as *S. salar*, particularly when and where there are high densities of *O. gorbuscha* fry (e.g., Mo et al., 2018).

After its introduction to the Atlantic area (Sandlund et al., 2019), *O. gorbuscha* have been present irregularly throughout northern Norway and Finland in small numbers for many years, being first reported in the early 1960s (Berg, 1961; Sandlund et al., 2019). More recently, *O. gorbuscha* numbers have increased dramatically across the North Atlantic, but particularly in the northeastern Atlantic rivers of Norway, Russia, and Finland (ICES, 2022; NHPSEG, 2023). Of particular concern has been the rise in the numbers of *O. gorbuscha* observed

in the Teno River, Finland/Norway. The Teno River is one of Europe's last great *S. salar* rivers (cf. Erkinaro et al., 2019), although recent evidence of low spawning stocks and low estimates of pre-fishery abundance have prompted closure of the fishery in the river and in nearby coastal areas as a precautionary approach (Anon., 2021). Observations of *O. gorbuscha* spawning in several reaches of the Teno main stem and in its tributaries (Anon., 2021; Erkinaro et al., 2022; Fossøy et al., 2022; Muladal & Fagard, 2021), and the subsequent documented development and hatching of spawned eggs, have made understanding the occurrence and extent of freshwater feeding by emergent *O. gorbuscha* fry of increased importance because of the role feeding may play in competitive interactions with native *S. salar* juveniles (VKM, 2020).

Using samples obtained from the 2021 spawning event, we examine patterns of feeding in *O. gorbuscha* fry from the period of emergence during spring 2022 to estuarine entry as a means of establishing the nature and extent of their feeding in the fresh waters of the Teno River. Specifically we test the hypotheses that migrating *O. gorbuscha* fry evidence consistent freshwater prey consumption by examining the fullness of their stomachs at discrete points in time and changes in their stable isotope values, expecting to find that (1) the stomachs of sampled fry consistently contain freshwater prey; and (2) the stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$) of the fry equilibrate from the isotopic values consistent with the use of maternally derived nutrients obtained from marine feeding to values reflective of freshwater feeding; that is, that isotopic values eventually decline with time. Combined, the data will present the first view of freshwater feeding of invasive *O. gorbuscha* progeny in one of the Europe's most important *S. salar* rivers and illustrate the potential for competitive interactions with the native species. In addition, we document the occurrence of juvenile *O. gorbuscha* at spawning grounds and in the estuary during their emergence/migration period in the spring/early summer, together with the development of their body size.

2 | MATERIALS AND METHODS

2.1 | Study area

The subarctic Teno River (Tana in Norwegian, Deatnu in Sámi) forms the border between northernmost Norway and Finland (70° N, 28° E), and the river drains a catchment area of 16,386 km² (Figure 1) into the Barents Sea. More than 1100 km of the different branches of the system are accessible to anadromous salmonid fish, including the main stem and numerous tributaries. The *S. salar* population of the Teno River is among the largest within

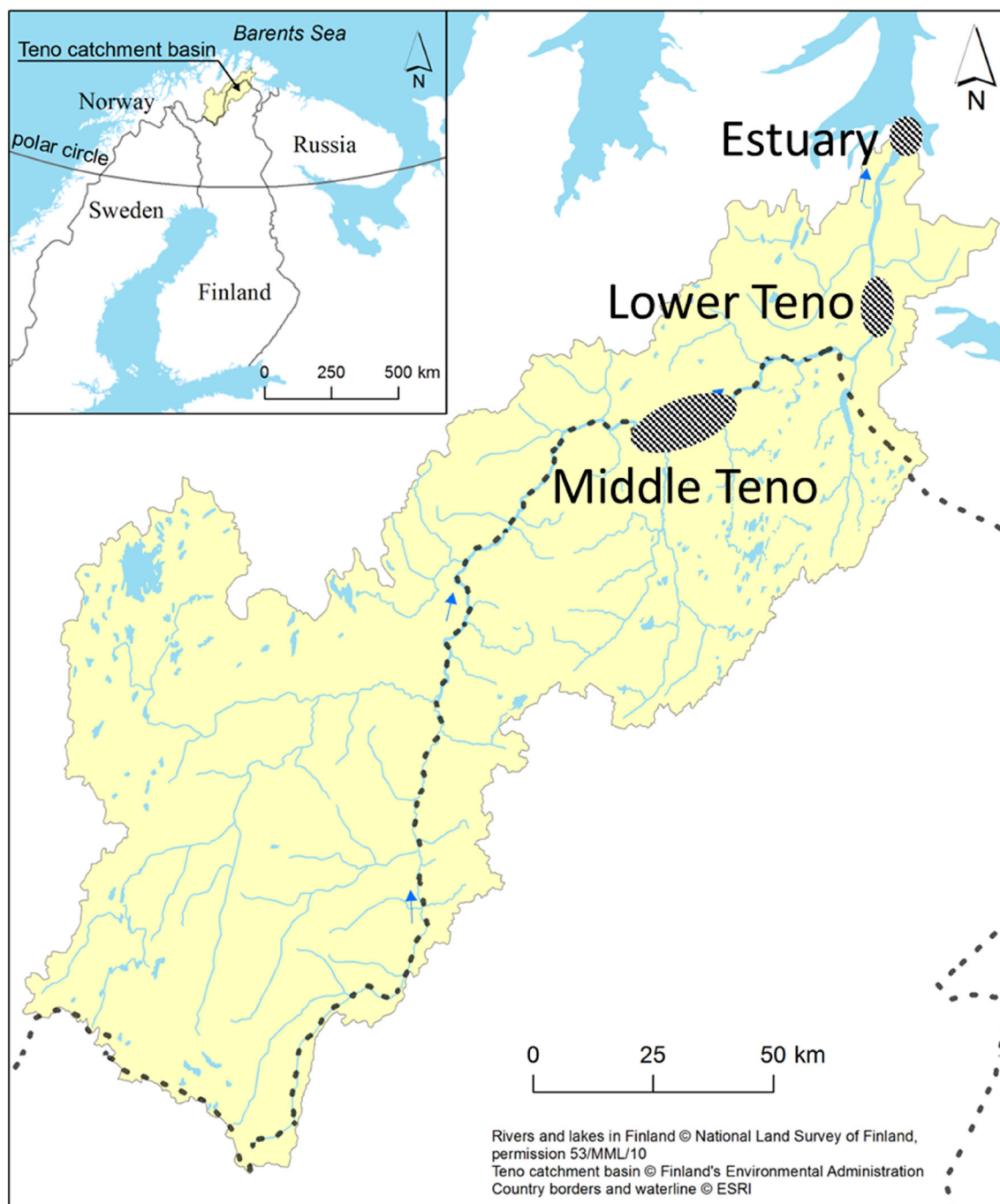


FIGURE 1 The Teno River catchment in northern Finland and Norway. Sampling areas for juvenile *Oncorhynchus gorbuscha* in the middle Teno main stem, lower Teno main stem, and in the estuary are indicated.

the geographic distribution range of the species, producing large catches, and showing an extremely wide diversity in life histories (Erkinaro et al., 2019) and distinct genetic populations (Vähä et al., 2017).

After the introduction of the *O. gorbuscha* to the White Sea Basin in Russia, occasional individuals were caught in the Teno River starting in the 1960s. In some years in the 1970s catches were higher after the release of large numbers of juveniles in Russian waters (Sandlund

et al., 2019). The estimated numbers of *O. gorbuscha* entering the Teno River system in the early 2000s varied between tens and hundreds, but in 2017 c. 5000 *O. gorbuscha* were estimated to have entered the Teno River, and at least the same number of fish were detected by sonar in 2019. In 2021, the sonar count was c. 50,000 individuals (Erkinaro & Orell, 2022), and increased again in 2023, with preliminary estimates suggesting approximately thrice the estimated 2021 abundance.

2.2 | Sampling

We sampled eggs and alevins of *O. gorbuscha* from spawning redds in the mid-part of the Teno River during and after their unprecedented run in September–October 2021 (see Erkinaro et al., 2022). Sampling of emerged juveniles at spawning grounds was continued in April–May 2022 by electrofishing and by hand excavation of redds with a shovel once ice conditions permitted access to open water areas in the middle and lower parts of the Teno River (Figure 1), which was still mostly frozen. Sampling of migrating juveniles was further conducted at the estuary of the Teno River (Figure 1) in May–June 2022 using a small beach seine (wings: 10 m and 7 m long, 1.5 m high; mesh-size, knot to knot: 8 mm in wings, 1 mm in the cod end). Abundance estimates of juvenile *O. gorbuscha* based on the catch data were computed as an “apparent” catch per unit effort (CPUE) by standardizing the sample sizes at the spawning areas as fish sampled per spawning redd, and at the estuary as fish caught per seine haul of a standard area of 300 m².

Individual fish were measured (to the nearest millimeter, total length) and weighed (nearest 0.1 g) in the laboratory after sampling and preserved in 80% ethanol. Fish samples were split for diet analyses, stable isotope analyses (SIA), and genetic purposes.

Data and results are presented by sampling period as follows: April (21–27), early-May (2–10), mid-May (11–18), late-May (23–31), and June (8–26). In addition, data from alevins in the pre-spawning period in October and November 2021 are presented in some cases (cf. Erkinaro et al., 2022).

2.3 | Diet analyses

Fish stomachs were preserved in 80% ethanol for laboratory analyses and identification of prey items. The relative volume of the stomach contents was estimated with the point scale used for juvenile *S. salar* in the Teno River and described by Erkinaro and Erkinaro (1998): 0 (empty), 1 (<25%), 5 (25%), 10 (50%), 15 (75%), 20 (full), and 25 (distended). The identification of invertebrate prey was completed to the lowest practical taxonomic level, usually order, with larvae, pupae, and adults identified separately. The numbers of individuals in each taxon were counted, and the frequency of occurrence (%F) and relative abundance (%A) of each taxon in stomachs were calculated for the different periods of spring and early summer coincident with when sampling was completed.

2.4 | Stable isotope analyses

For SIA, the head, tail, and gut from each specimen were removed prior to drying for 48 h at 60°C in a conventional laboratory drying oven (Yamota DX 600, Yamato Scientific Co. Ltd., Tokyo, Japan). Dried samples were then ground using a mortar and pestle, and the resulting homogenized tissues were used for SIA ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$). For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ sample material was weighed into 5 × 3.5 mm tin capsules (Elemental Microanalysis, Okehampton, UK) using an

analytical balance (XP205 DeltaRange, Mettler-Toledo GmbH, Greifensee, Switzerland) and subsequently analysed at the Environmental Isotope Laboratory, University of Waterloo, Ontario, Canada. Analyses were completed using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to an ECS 4010 Elemental Analyzer (Costech Analytical Technologies Inc. Valencia, CA, USA) with a reportable analytical precision of $\pm 0.2\text{‰}$ ($\delta^{13}\text{C}$) and $\pm 0.3\text{‰}$ ($\delta^{15}\text{N}$). Analytical precision was verified by the repeated measurement of internal laboratory standards cross-calibrated against certified International Atomic Energy Agency (IAEA) reference materials (IAEA-N1 + N2 for $\delta^{15}\text{N}$ and IAEA-CH3 + CH6 for $\delta^{13}\text{C}$). In any given batch of samples, no less than 20% of the samples analysed consisted of internal laboratory standards or reference materials. As a result of initial ethanol preservation most sample C:N ratios (>95%) were uniformly low (i.e., C:N <4), and there was no significant correlation between $\delta^{13}\text{C}$ and C:N ($r = -0.07$, $p = 0.67$). Thus, tissues were not lipid extracted or lipid-corrected (e.g., Jardine et al., 2013). All results are reported in standard per mil (‰) notation against the primary reference scale of Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}\text{C}$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (Mariotti, 1983).

Any remaining sample material was used for $\delta^{34}\text{S}$ analysis, also completed at the University of Waterloo, on an Isochrom Continuous Flow Stable Isotope Ratio Mass Spectrometer (GV Instruments, Micromass, Manchester, UK) connected to a Costech Elemental Analyzer (CNSO 4010, Costech Analytical Technologies Inc.). Results are reported in standard per mil (‰) notation expressed against the international Vienna-Canyon Diablo Troilite meteorite standard (Rees et al., 1978). Reportable analytical precision ($\pm 0.3\text{‰}$) was assured by monitoring and corrections made using international references and in-house standards calibrated against the certified international reference materials: IAEA-SO-5, IAEA-SO-6, NBS-127, NBS-123, and IAEA-S1 to-S3.

2.5 | Statistical analyses

Differences in stable isotope and biological measures between sampling periods were established using one-way ANOVA followed by application of the Spjøtvoll-Stoline extension to the Tukey's honestly significant differences multiple comparisons test that accounts for groups with unequal sample sizes (Spjøtvoll & Stoline, 1973) using the Statistica (StatSoft 2008) statistical analytical package). LOWESS smoothing was used to estimate the “average” temporal changes in stable isotope values and used for figure presentation. All statistical testing was completed at the 0.05 level of significance.

3 | RESULTS

Newly emerged *O. gorbuscha* juveniles were present in the spawning areas in the middle and lower parts of the Teno River main stem from initial sampling in April through to mid-May, with abundance peaking in mid-May (Figure 2). No *O. gorbuscha* were caught in the spawning

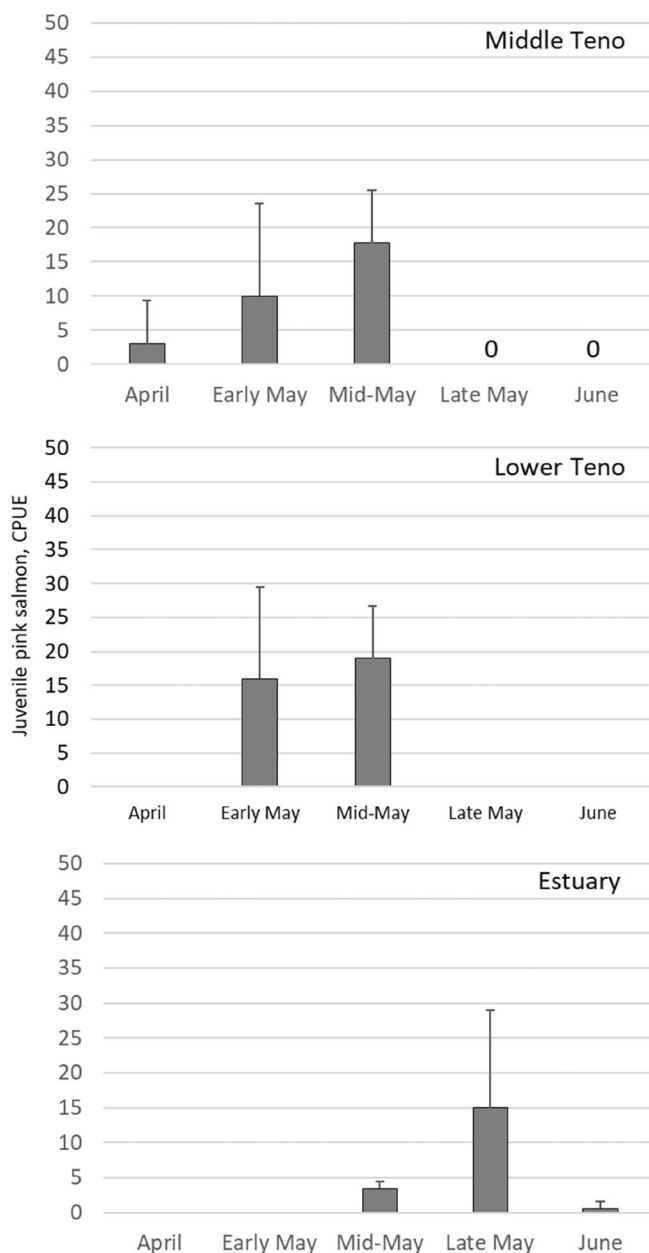


FIGURE 2 Occurrence and relative abundance (apparent catch per unit effort, CPUE; mean + S.D.) of juvenile *Oncorhynchus gorbuscha* in the Teno River in the middle, lower, and estuarine reaches of the river during the spring–early summer of 2022. A zero (0) indicates sampling effort with no catch.

areas in late May and June. The first sampling in the estuary was carried out in mid-May, and the highest catches of juvenile pink *O. gorbuscha* were caught in late May, and the abundance fell significantly toward June. In late June, no *O. gorbuscha* were captured in the estuary. Throughout the sampling period juveniles increased in both length (ANOVA $F_{6,298} = 428.01$, $p < 0.001$) and weight (ANOVA $F_{4,248} = 45.06$, $p < 0.001$; Figure 3). Juveniles caught in the estuary were significantly larger in June than those captured in May (Tukey's post hoc $p < 0.001$).

A total of $n = 88$ stomach samples of juvenile *O. gorbuscha* were analysed. Feeding activity of juveniles increased when they left the

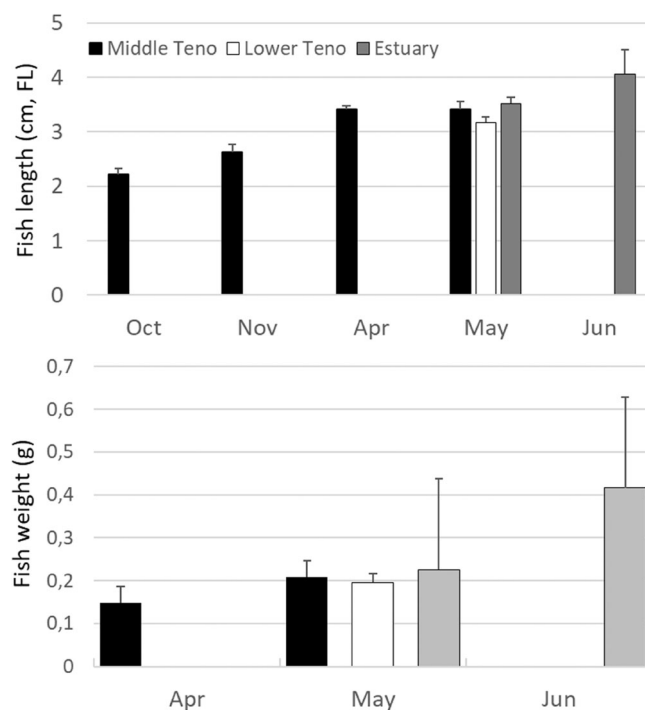


FIGURE 3 Total length (cm, upper panel) and weight (g, lower panel) of juvenile *Oncorhynchus gorbuscha* sampled from the different areas of the Teno River. Bars: mean; whiskers +S.D.

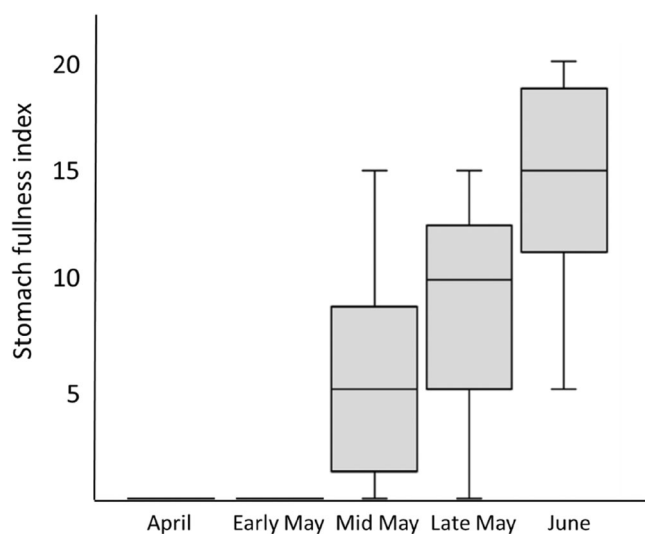


FIGURE 4 Stomach fullness index (0 = empty; 10 = 50% full; 20 = 100% full) of juvenile *Oncorhynchus gorbuscha* sampled in spawning areas in the Teno River (April–Mid-May) and in the estuary of the river (late May–June). The center line denotes the median value, the box contains the 25th to 75th percentiles of dataset, and the whiskers mark the 5th and 95th percentiles.

spawning grounds in the mid-parts of the Teno River. Stomach analysis revealed no feeding activity in early May in the spawning areas, but the stomach fullness indices increased markedly in fish sampled in the estuary later in May and especially in June (Figure 4). Overall, both the relative abundance among all prey items and the frequency of

TABLE 1 Frequency of occurrence (%F) and relative abundance (%A) of invertebrate prey categories identified in the stomachs of juvenile *Oncorhynchus gorbuscha* captured during their emigration from the Teno River.

	Mid-May		Late-May		June	
	%F	%A	%F	%A	%F	%A
Chironomidae l.	0.21	0.35	0.79	0.81	0.14	0.04
Chironimidae p.	0	0	0	0	0,57	0,36
Simuliidae l.	0	0	0.08	0.01	0	0
Ephemeroptera l.	0.32	0.35	0.5	0.15	0.14	0.04
Plecoptera l.	0	0	0	0	0.14	0.04
Insecta misc.*	0.32	0.3	0.25	0.03	0.86	0.52

Abbreviations: l., larvae; p., pupae.

*Mostly Diptera l. and p.

	April	Mid-May	Late-May	June
$\delta^{13}\text{C}$	-20.92 ± 0.54	-20.57 ± 0.51	-21.31 ± 0.71	-24.19 ± 1.17
$\delta^{15}\text{N}$	12.33 ± 0.61	11.54 ± 0.41	11.86 ± 0.81	10.17 ± 1.22
C:N ratio	3.14 ± 0.05	3.14 ± 0.21	2.99 ± 0.12	2.85 ± 0.22
$\delta^{34}\text{S}$	18.29 ± 0.30	18.07 ± 0.35	17.90 ± 0.50	11.88 ± 2.04

TABLE 2 Mean \pm S.D. stable isotope measures of juvenile *Oncorhynchus gorbuscha* captured during their emigration from the Teno River, Finland/Norway.

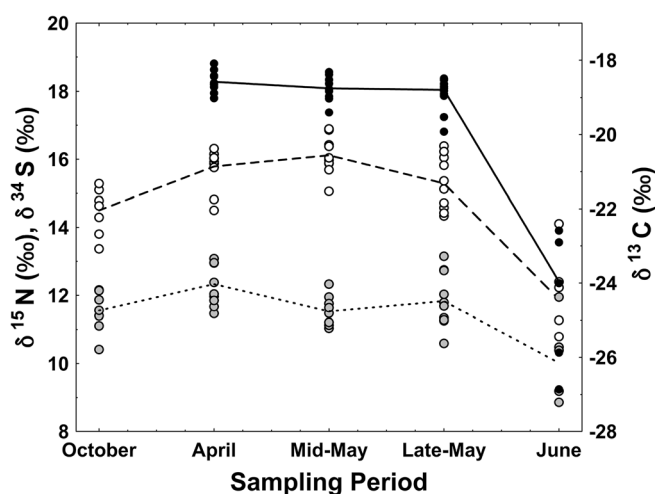


FIGURE 5 Changes in the stable isotope values of sampled juvenile *Oncorhynchus gorbuscha* across time in the Teno River from October to June the following year. $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ are plotted, respectively, with filled black, open, and gray circles. Lines plot the locally weighted scatterplot smoothing (Lowess) line for the $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ data. Note the sharp decline in all stable isotope values after late-May as *O. gorbuscha* evidence approaching isotopic equilibrium with freshwater resource pools.

occurrence were highest for Chironomidae and Ephemeroptera larvae in diets of juvenile *O. gorbuscha* (Table 1). In June, the role of both Plecoptera larvae and Chironomidae pupae increased in diets compared to the May samples. The unidentifiable prey items consisted mostly of dipteran remnants (larvae in May and pupae and adults in June) among which chironomids were the most common. Both the occurrence and abundance of the unidentifiable prey were highest in June (Table 1).

A total of $n = 44$ juvenile *O. gorbuscha* captured were analysed for stable isotopes over the period October 2021 to June 2022 (Table 2). Early October and November samples consisting of eggs ($n = 9$) and were too small to analyse for $\delta^{34}\text{S}$ but yielded sufficient sample material for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\delta^{13}\text{C}$: 22.01 ± 0.57 ‰; $\delta^{15}\text{N}$: 11.64 ± 0.68 ‰; C:N ratio: 3.92 ± 0.26 ‰). All other samples ($n = 35$) consisted of juvenile fish and were analysed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ (Figure 5). There were significant $\delta^{13}\text{C}$ differences among sample periods (ANOVA $F_{3,31} = 33.193$, $p < 0.001$), with June being significantly lower (Tukey's post hoc $p < 0.001$) than any of the other sample periods among which there were no significant differences (Tukey's post hoc $P \geq 0.104$). Similarly, for $\delta^{15}\text{N}$, there were among sample period differences (ANOVA $F_{3,31} = 9.970$, $p < 0.001$), with June being significantly lower (Tukey's post hoc $P \leq 0.030$) than any of the other sample periods among which there were no significant differences (Tukey's post hoc $P \geq 0.095$). The same pattern was repeated for $\delta^{34}\text{S}$ (ANOVA $F_{3,31} = 82.526$, $p < 0.001$), with June again differing significantly (Tukey's post hoc $p < 0.001$) from all the other periods, which did not differ from one another (Tukey's post hoc $P \geq 0.721$). Temporally all three stable isotope values peaked in mid-May before declining significantly thereafter through early June (Figure 5), with the shifts in $\delta^{13}\text{C}$ (3.62 ‰) and $\delta^{34}\text{S}$ (6.19 ‰) being largest.

4 | DISCUSSION

Juvenile *O. gorbuscha* sampled between April and June indicated recent feeding on freshwater prey, largely chironomid larvae, after early May. Samples obtained from the same individuals further evidenced distinctive changes in their isotopic values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$),

moving from the higher values reflective of the marine-derived nutrients of parental stock to the lower values reflective of freshwater feeding. The nature and extent of the observed changes in *O. gorbuscha* stable isotope values over time (here 4–6 weeks) were large enough to be both indicative of persistent freshwater feeding and reflective of the process of isotopic equilibration by the juveniles with the isotopic values typical of freshwater prey. In contrast, stomach samples obtained from the same individuals indicated recent (i.e., short-term) feeding on freshwater prey immediately prior to probable out-migration. Together the changes in juvenile isotope values and stomach contents reflect a persistent and consistent use of freshwater prey by juvenile *O. gorbuscha* during the period of their freshwater residency in the Teno that starts with the commencement of exogenous feeding and continues until fish reach the estuary. The use of freshwater resources was also reflected in the significant and consistent increase in the length and weight of juvenile fish size during their migration period to the river estuary.

Although *O. gorbuscha* are typically reported to reside in fresh waters for only a short period of time after hatching (Heard, 1991; Quinn, 2018) and are generally thought to proceed directly to sea from many invaded European rivers (e.g., Armstrong et al., 2018), the evidence from the Teno River indicates they can remain in fresh water for periods of weeks to months, that is, long enough for stable isotope values to approximately equilibrate with freshwater prey resources. In novel habitats, such as tributary rivers of the North American Great Lakes (Kwain, 1982), rivers in Scotland (Skóra et al., 2023) and on the west coast of Norway (Sandlund et al., 2019), and rivers to which they have been introduced in northwestern Russia (Gordeeva et al., 2015), *O. gorbuscha* fry have been noted to remain in fresh water for weeks to months. These periods are long enough for fast-growing fry to evidence a shift in their stable isotope values if freshwater feeding is occurring. Residency, however, appears to depend on how far up a given river system spawning and emergence occurs (Sandlund et al., 2019) and on river water levels, with low waters creating multidirectional flow fields favoring the formation of hydrodynamic pockets abounding in prey that slow out-migration of fry and promote feeding (Veselov et al., 2016).

Although it has been suggested that *O. gorbuscha* are likely to have little interaction with native *S. salar* because of the limited time spent in fresh waters (e.g., Nielsen et al., 2013), the dependence of out-migration speed on water levels suggests increasing risks of negative interactions as a result of climate-induced changes in seasonal hydrology. Although projected changes in annual river discharges are expected to be moderate in Finnish rivers (Olsson et al., 2015), the seasonal distribution of discharges will change significantly, decreasing in both spring and summer due to increased evapotranspiration and decreasing notably over the April to June period when *O. gorbuscha* out-migration might be expected to occur.

Feeding during out-migration has been known for some time, having been demonstrated in *O. gorbuscha* fry in the Skeena River, Canada, where fish were found to begin feeding at a fairly early stage of the migration (McDonald, 1960) on freshwater mayflies, stoneflies, craneflies, and midges, with the proportion of individuals found to be

feeding increasing in the lower reaches of the river. Literature for Russia similarly reports freshwater feeding in the rivers of the Pacific, White, and Barents seas where large *O. gorbuscha* smolt sizes have been related to intensive in-river feeding (e.g., Veselov et al., 2016 and references therein). The observed positive correlation between feeding intensity and in-river water temperatures (Veselov et al., 2016) suggests further climate-related risks associated with the establishment of *O. gorbuscha* in northern European rivers, with warming temperatures and lower flows leading to higher feeding intensities, delayed out-migration, and larger migrating *O. gorbuscha* smolts.

In the Indera River on the Kola Peninsula, the food spectrum of *O. gorbuscha* juveniles overlaps with that of juvenile *S. salar* and brown trout (*Salmo trutta* L.), consisting largely of Copepoda, Cladocera, and Chironomidae larvae (Veselov et al., 2016). Similarly, in the Malaya Huzi River, Sakhalin Island, the feeding of juvenile *O. gorbuscha* in the lower reaches of the river is dominated by the imagoes of various small insects and chironomid larvae (Pavlov et al., 2015). Chironomid larvae, in particular, are important prey for both juvenile *S. salar* and *S. trutta*, with newly emerged *S. salar* having been shown to feed primarily on chironomid larvae in Catamaran Brook, New Brunswick (Keeley & Grant, 1997) and smaller *S. salar* parr tending to selectively feed on chironomid larvae in different parts of the Teno River watershed (Erkinaro & Erkinaro, 1998). Similarly, in the Matamek River, Quebec, post-emergent *S. salar* were noted to feed extensively on adult chironomids (Williams, 1981). Studies of post-emergent feeding on *S. trutta* have likewise reported findings indicating small prey, such as chironomid larvae, being positively selected for (Sánchez-Hernández et al., 2011) or noted as dominant in the diet (Skoglund & Barlaup, 2006) across much of the natural range for the species.

The potential impact of fluvial fish on benthic invertebrate abundance and communities has been under debate for decades (e.g., Wooster, 1994). A number of studies have shown negative impacts on zoobenthos, whereas others have documented little or no effect at all (e.g., Dahl & Greenberg, 1996). Many studies have been based on experimental enclosures, and the integration of small-scale experiments with large-scale surveys has been suggested to improve applicability of study results in natural, real-life conditions (Meissner & Muotka, 2006). It has been shown that predation effects of fish on stream invertebrates are size-selective (Meissner & Muotka, 2006) and dependent on whether the fish utilize predominantly drifting or benthic prey (Dahl, 1998). In their experiments with c. 15-cm-long juvenile *S. trutta*, Meissner and Muotka (2006) identified the strongest effect of fish predation on relatively large benthic animals, for example, invertebrate predators and cased caddis larvae, whereas small-sized mayfly and chironomid larvae were unaffected. In our data, small-sized *O. gorbuscha* juveniles obviously fed on small-sized prey, especially chironomid larvae, and in May–early June with relatively low water temperatures, feeding on drifting prey items is unlikely (see Erkinaro & Erkinaro, 1998). Nevertheless, the question still remains as to whether a local heavy, size-selective predation on small-sized benthic animals has the potential to locally decrease their abundance to

the extent that it might affect the feeding opportunities of native juvenile salmonids.

The increasing incidence of reproductively viable adults in the Teno River (Erkinaro & Orell, 2022) and the use of spawning habitats by the adults for reproductive purposes (Erkinaro et al., 2022) suggests an ever-increasing number of successfully spawned juvenile *O. gorbuscha* are likely to occur in the Teno River. The concomitant increase in the demand for invertebrate prey is also likely to have local negative effects on overall invertebrate prey abundance and native salmonids through competition for food, particularly given the observations in Russian rivers linking high densities of *O. gorbuscha* fry to reductions in river zoobenthos (Veselov et al., 2016).

The potential negative effects on native salmonids resulting from exploitative competition with *O. gorbuscha* may, in part, be offset by the nutrient subsidy effects of adult spawners. For example, the eggs of *O. gorbuscha* may provide an energetic subsidy for juvenile native fish preying on them (Dunlop et al., 2021). Post-spawning mortalities may also benefit in-river fish production (e.g., Larkin & Slaney, 1997; Schmidt et al., 1998), and existing predators may successfully exploit juvenile *O. gorbuscha* as a prey resource. Thus, the anadromous *S. trutta* population using the Teno estuary as their feeding area (Orell et al., 2017) may take advantage of the new plentiful prey resource in the estuarine area in early summer. Resident northern pike (*Esox lucius* L.) may also pose a threat to *O. gorbuscha* both as a potential freshwater predator and from overlapping habitat use given the demonstrated vulnerability of *O. gorbuscha* to *E. lucius* resulting from the species' high habitat requirement overlaps (Jalbert et al., 2021).

Our analysis suggests there is an existing and growing risk of *O. gorbuscha* negatively affecting the native salmonids in the Teno River as a result of their active feeding during their freshwater residency and a possible reduction in the local prey base. The repeatedly noted tendency of *O. gorbuscha* across their introduced range to remain in river to feed and the possible climate-induced shifts in juvenile rearing habitats (i.e., warmer waters with lower flows) that have been linked with increased feeding activity in *O. gorbuscha* are only likely to further increase the competitive threat of *O. gorbuscha* juveniles to native salmonids. Nevertheless, given the variable dynamics of the species invasion processes (e.g., Moyle & Light, 1996), more research studies, including controlled experiments, are needed to understand the broader ecological implications, that is, exploitative competition effects, of *O. gorbuscha* reproduction and rearing for native fishes in the Teno River and other northern Atlantic river ecosystems in which they are repeatedly and increasingly being found.

AUTHOR CONTRIBUTIONS

Jaakko Erkinaro and Panu Orell conceptualized the study. Mikko Kytökorpi, Jan-Peter Pohjola, Panu Orell, and Jaakko Erkinaro conducted the fieldwork. Michael Power conducted the SIA analysis. Mikko Kytökorpi analysed the stomach samples. Jaakko Erkinaro and Michael Power drafted the manuscript. All authors edited and commented on the manuscript.

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DATA AVAILABILITY STATEMENT

The data used in this study (fish size, abundance, diet, isotopic data) are available in Dryad repository (doi:10.5061/dryad.931zcrjsb).

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