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Combining kinship analysis and otolith geochemistry to investigate homing and straying of invasive pink salmon (*Oncorhynchus gorbuscha*)

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Pink salmon (*Oncorhynchus gorbuscha*) are rapidly expanding beyond their native North Pacific range and invading rivers around the North Atlantic and Arctic. Determining whether adult occurrences in recently invaded rivers reflect recurrent immigration or local production is critical for assessing establishment and predicting further spread. DNA-based kinship analyses can identify family-level patterns of homing and straying, whereas otolith geochemistry can reconstruct the freshwater environments in which individuals were produced. Here, we combined these approaches to investigate natal return in invasive pink salmon in northern Norway. Kinship analysis revealed non-random spatial clustering of related individuals within rivers, and otolith strontium isotope analysis provided evidence consistent with natal return by a small proportion of adults in Kongsfjordelva. Although sample sizes were limited and the methods were not applied to the same individuals, these findings represent a methodological proof-of-concept showing how genetic and geochemical tools can help distinguish recurrent immigration from local recruitment.

Introduction

Natal homing is a defining feature of salmonid life history and provides the demographic foundation for the development of locally adapted populations (Taylor 1991; Quinn 2018). At the same time, straying allows salmon to disperse and quickly take advantage of new habitats in response to landscape and climatic changes (Schtickzelle and Quinn 2007; Milner *et al.* 2008). The balance between homing and straying is therefore central to understanding how salmonid populations establish, persist, and expand. This balance is particularly relevant for pink salmon (*Oncorhynchus gorbuscha*), which are rapidly expanding beyond their native range in

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the North Pacific and have invaded watersheds across the northwestern and northeastern Atlantic and Arctic, following repeated intentional introductions to northwestern Russia beginning in the 1950s (Mo *et al.* 2018; Sandlund *et al.* 2019; Lennox *et al.* 2023; Staveley *et al.* 2025; Dunmall *et al.* 2025). In Norway, pink salmon are considered an invasive species that may threaten Atlantic salmon (*Salmo salar*) and other native species (VKM 2020; Lennox *et al.* 2023; Thorstad *et al.* 2024). The threat from pink salmon adds to a wide variety of other anthropogenic changes threatening the native salmonids (Forseth *et al.* 2017; Fiske *et al.* 2024), which are facing dramatic declines in the North Atlantic (ICES 2026).

Biological invasions can be understood as a sequence of transitions in which species overcome barriers to transport, introduction, establishment, and spread (Blackburn *et al.* 2011). For pink salmon in the North Atlantic, the key uncertainty is no longer whether adults can arrive and spawn, but whether reproduction in individual rivers leads to locally produced adults that return to their natal watershed and contribute to self-sustaining populations. Distinguishing recurrent immigration from local recruitment is therefore central to placing individual watersheds along the invasion continuum and predicting whether they function primarily as recipient habitats or emerging sources for further spread. Pink salmon in their native range in the Pacific are generally thought to home less precisely than other salmonids, which could facilitate rapid spread through higher rates of straying (Keefer and Caudill 2014; Salmenkova 2017). However, homing rates vary among pink salmon populations, and some populations show fine-scale spatial site fidelity (May *et al.* 2023). Determining whether pink salmon in a given watershed are primarily recurrent strays or members of an emerging self-sustaining population is therefore critical for predicting future invasion trajectories and designing effective management responses. Recent observations of successful spawning and juvenile outmigration in several rivers in northern Norway (Erkinaro *et al.* 2023) and the North Atlantic region (Skóra *et al.* 2023, 2024) suggest that pink salmon have the potential to establish local populations beyond northwestern Russia, where the species was introduced (Alekseev *et al.* 2019; Sandlund *et al.* 2019). Recent work has also shown substantial regional and interannual variation in marine growth and adult body size of invasive pink salmon in Norway, highlighting that both freshwater recruitment and marine conditions are likely to influence invasion dynamics and establishment potential (Simmons *et al.* 2026).

Understanding natal origin and homing is especially important because current management efforts in Norway focus largely on preventing adult pink salmon from reaching spawning areas. Following the large invasion event in 2017, removals of migrating adults were initially led primarily by local volunteer groups (Thorstad *et al.* 2025). From 2023 onward, the Norwegian Environment Agency (*Miljødirektoratet*) and other government agencies coordinated broader efforts to limit pink salmon spread using traps designed to remove pink salmon while allowing native salmonids to enter rivers (Thorstad *et al.* 2025). However, trap operation is not possible in all watersheds and is strongly affected by river characteristics, discharge, and other environmental conditions. In addition, traps may be ineffective where pink salmon spawn downstream of the trap location and may potentially impact the migration success of native salmonids. Identifying whether pink salmon return to specific natal rivers, and which rivers may already support local production, is therefore essential for evaluating the effectiveness of removal efforts and for prioritizing management across watersheds.

At present, we lack the data needed to determine whether pink salmon in northern Norway show consistent natal homing or whether returning adults include a high proportion of strays from other rivers, potentially including rivers outside Norway. Homing behaviour and population establishment are commonly investigated using field observations, tagging, and genetic or geochemical analyses. However, each approach has limitations in the context of a recent and rapidly expanding invasion.

Traditional population genetic analyses often rely on the assumption that genetic drift and gene flow have approached equilibrium, allowing genetic differentiation among subpopulations to be interpreted in terms of population structure

and connectivity. The recent expansion of pink salmon into many Norwegian rivers violates this assumption (Fitzpatrick *et al.* 2012). At this stage of the invasion, genetic differentiation between populations may reflect shared or different source populations rather than the degree of homing and local establishment. Kinship analysis offers a useful alternative because it can identify individuals that share one or both parents without requiring long-term genetic equilibrium among populations. Although such analyses require sufficiently large sample sizes, genetic tools for detecting full- and half-sibling relationships are increasingly accessible. For pink salmon, this approach is particularly promising because the species has a predominantly two-year life cycle, meaning that most adults returning in a given year belong to the same cohort. Kinship analysis can therefore provide insight into the behavioural component of dispersal by revealing whether individuals returning to the same river reflect family-level patterns of homing or independent straying events. For example, kinship analysis has recently revealed fine-scale homing of pink salmon within natal rivers (May *et al.* 2023). However, identifying sibling pairs alone does not necessarily establish where those siblings were produced, because related individuals captured in the same river may still have originated elsewhere.

Otolith geochemistry provides complementary information by reconstructing the environmental history and natal origin of individual fish. Otoliths (*ear stones*) are calcium carbonate structures in the inner ear that grow continuously and are metabolically inert, preserving a chronological record of age, growth, and environmental history (Campana 1999; Campana and Thorrold 2001). Strontium isotope ratios ($^{87}Sr/^{86}Sr$) in otoliths reflect the waters experienced during otolith formation and can be used to infer freshwater origin because $^{87}Sr/^{86}Sr$ varies primarily with watershed geology and is incorporated into otoliths with little biological fractionation (Barnett-Johnson *et al.* 2008; Brennan *et al.* 2015). Furthermore, $^{87}Sr/^{86}Sr$ in river waters is generally temporally stable at a given location, with seasonal and interannual variability typically small relative to spatial differences among watersheds, supporting its use as a natural geochemical tracer of fish provenance (Brennan *et al.* 2015; Ciepiela and Walters 2019). Combining kinship analysis and otolith geochemistry therefore allows stronger inference than either method alone, because kinship analysis informs the behavioural and familial structure of dispersal, while otolith geochemistry helps identify the geographic environment in which individuals were produced.

Here, we applied genetic kinship analysis and geochemical tracing to pink salmon collected from rivers in Norway (Fig. 1). We provide results on kinship analysis from a broad range of rivers and a more focused geochemical dataset from Kongsfjordelva, an important watershed in Finnmark. Because of the lack of a systematic long-term monitoring and science program, the available samples were limited, and importantly, we could not apply the kinship analysis and the geochemical tracing to the same individuals. Therefore, this limited set of samples should be viewed as a methodological proof-of-concept for studying fish species showing rapid range expansion rather than a comprehensive quantitative study on homing rates in Norway.

Material and methods

Kinship analysis

Scales from pink salmon were collected from 368 adult fish caught in 31 rivers along the Norwegian coast in 2019 (Table S1 found in Supplementary Information, SI). DNA from the scale samples was extracted using the DNeasy Tissue Kit (QIAGEN) at the Norwegian Institute for Nature Research (NINA). The samples were then assayed for genetic variation at 298 SNP-markers using genotyping-in-thousands by sequencing (Campbell *et al.* 2015) at the Alaska Department of Fish and Game (ADF&G) Gene Conservation Lab, with selection of SNP-markers (Shedd *et al.* 2022). Of 368 samples from 31 rivers genotyped, 329 samples from 30 rivers were retained for further analyses (Table S1 in SI). Thirteen samples had a scoring rate less than 80%, and these were excluded from further analyses. Three pairs of individuals had (almost) identical genotypes, suggesting contamination and one individual from each pair was excluded

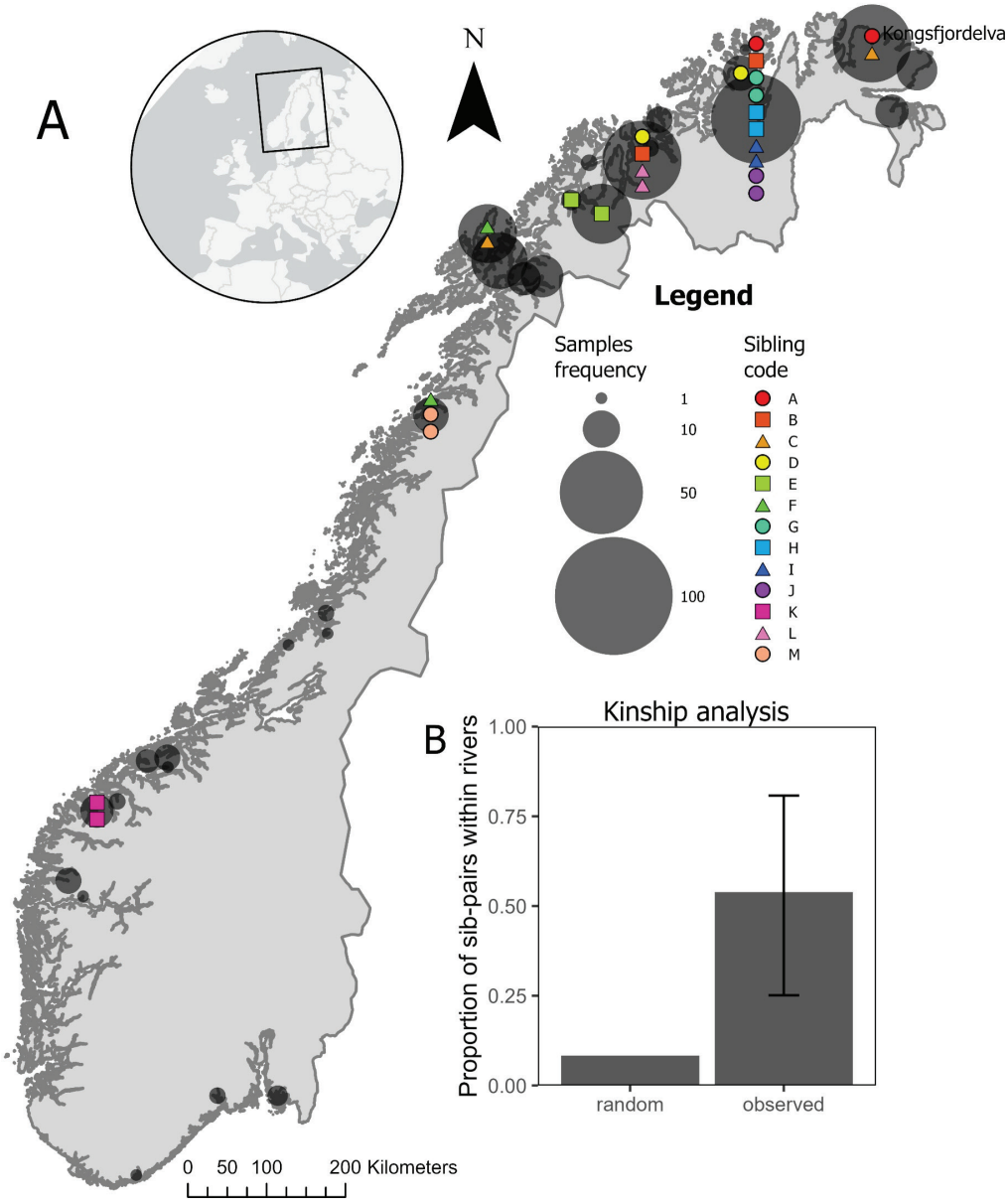

Fig. 1. a) Overview map showing sampling locations and sample frequency by river. Grey circles indicate the number of sampled individuals per location, while coloured symbols identify sibling groups detected in the kinship analysis (sibling codes A through M). Sibling pairs (half- and full-sibs) were determined among 329 adult pink salmon caught in 30 Norwegian rivers in 2019. **b**) Proportion of sibling pairs found within rivers for the 13 observed pairs and as expected under random distribution of siblings among sampled individuals.

from further analysis. We also excluded 23 individuals with an excess of heterozygosity, defined as observed heterozygosity exceeding the mean by more than two standard deviations (total mean observed heterozygosity: 0.340; total mean +2SD: 0.540). We used the R package, CKMRsim (Anderson 2024) to identify full- and half-sibling pairs (R Core Team 2025). CKMRsim was used to simulate kinship pairs based on observed allele frequencies and to estimate false

positive and false negative rates under different log likelihood ratio thresholds for the assignment of kinship. Simulations were conducted assuming no physical linkage between markers. To avoid the incorrect identification of any unrelated individuals as half-sibs, Anderson (2024) suggested that sibling pairs should be assigned with a log likelihood ratio (LLR) threshold that allows for a false positive rate ~10 times smaller than the reciprocal of the number of comparisons (53 956 pairwise comparisons). We allowed for a slightly higher false positive rate (LLR threshold: 8.0; false positive rate: 2.95×10^{-5}), to avoid an overly high false negative rate. Notably, the inclusion of false positives would result in a more conservative analysis of homing.

Geochemical analyses of otoliths

For the geochemical analysis, otoliths from pink salmon juveniles (June-July 2022, $n = 5$) and migrating adults (July 2023, $n = 36$), representing the same cohort, were collected from Kongsfjordelva (Table S2 in SI). The juveniles were collected using hand nets and were all free swimming in the water column without visible yolk-sack. The adults were collected using a fish trap (Fig. 1a). Samples were prepared at the Norwegian Institute for Nature Research (NINA) in the sagittal plane to allow for the analysis of their natal origin following established protocols (Barnett-Johnson *et al.* 2008). $^{87}Sr/^{86}Sr$ analyses were carried out at the MiMaC (Norwegian Laboratory for Mineral and Materials Characterisation) laser-ablation facility at the Geological Survey of Norway (NGU) using a Teledyne-Cetac Analyte excite 193 nm excimer laser coupled with a Nu Plasma 3 multi-collector inductively coupled plasma mass spectrometer. Ablations were carried out as lines with a laser diameter of 40 µm from the core of the otolith to the edge with a speed of 3 µm s^{-1} and all isotopes from mass 82–88 and the half masses in between were measured. This instrument setup allowed us to measure otolith $^{87}Sr/^{86}Sr$ at a high spatial resolution, providing sub-weekly life history information necessary to detect the potentially short time the fish spent in the freshwater before moving to the ocean. The natal portion of the otoliths was identified as the region immediately outside of the core, typically 50–100 µm and 40 µm wide. A marine mollusk was used as the primary reference material. Data reduction was carried out using the data reduction scheme "Sr isotopes universal" (Mulder *et al.* 2023) in Iolite 4 (Paton *et al.* 2011) with interference corrections for Kr, Rb and CaAr or ArAr dimers. More details about instrument parameters, data reduction and quality control can be found in Table S3 in SI.

Geochemical analysis of water samples

Water samples from 31 Norwegian rivers (Fig. 2a) were collected by volunteers below pink salmon traps or at river reaches where pink salmon have been observed. Water was passed through a 0.45 µm MCE filter and collected in 15 ml sterile metal-free centrifuge tubes. $^{87}Sr/^{86}Sr$ analysis of water samples to establish a regional strontium isoscape for northern Norway was carried out at the Archaeology, Environmental Changes & Geo-Chemistry (AMGC) laboratory at Vrije Universiteit Brussel using a Nu Plasma 3 (Snoeck *et al.* 2015; Gerritzen *et al.* 2024) in dry mode with an Apex Omega desolvator. This instrument setup allowed for the measurement of $^{87}Sr/^{86}Sr$ in low concentration samples (< 75 ppb), and more details about the instrument conditions can be found in Table S4 in SI. Repeated measurements of the standard reference material NBS987 returned a value of 0.710248 ± 0.000028 (2SD).

Reconstructing natal river origin from otoliths

To use otolith geochemistry to infer natal origin, we first established a regional $^{87}Sr/^{86}Sr$ reference baseline for northern Norway. This baseline included water samples from 31 watersheds, including Kongsfjordelva, and was supplemented for Kongsfjordelva by five juvenile pink salmon otoliths of known local origin. Because a comprehensive strontium isoscape is not yet available for Norway, we did not assign adults to specific non-local rivers. Instead, we classified adult fish as either consistent with Kongsfjordelva origin or consistent with other possible sources, based

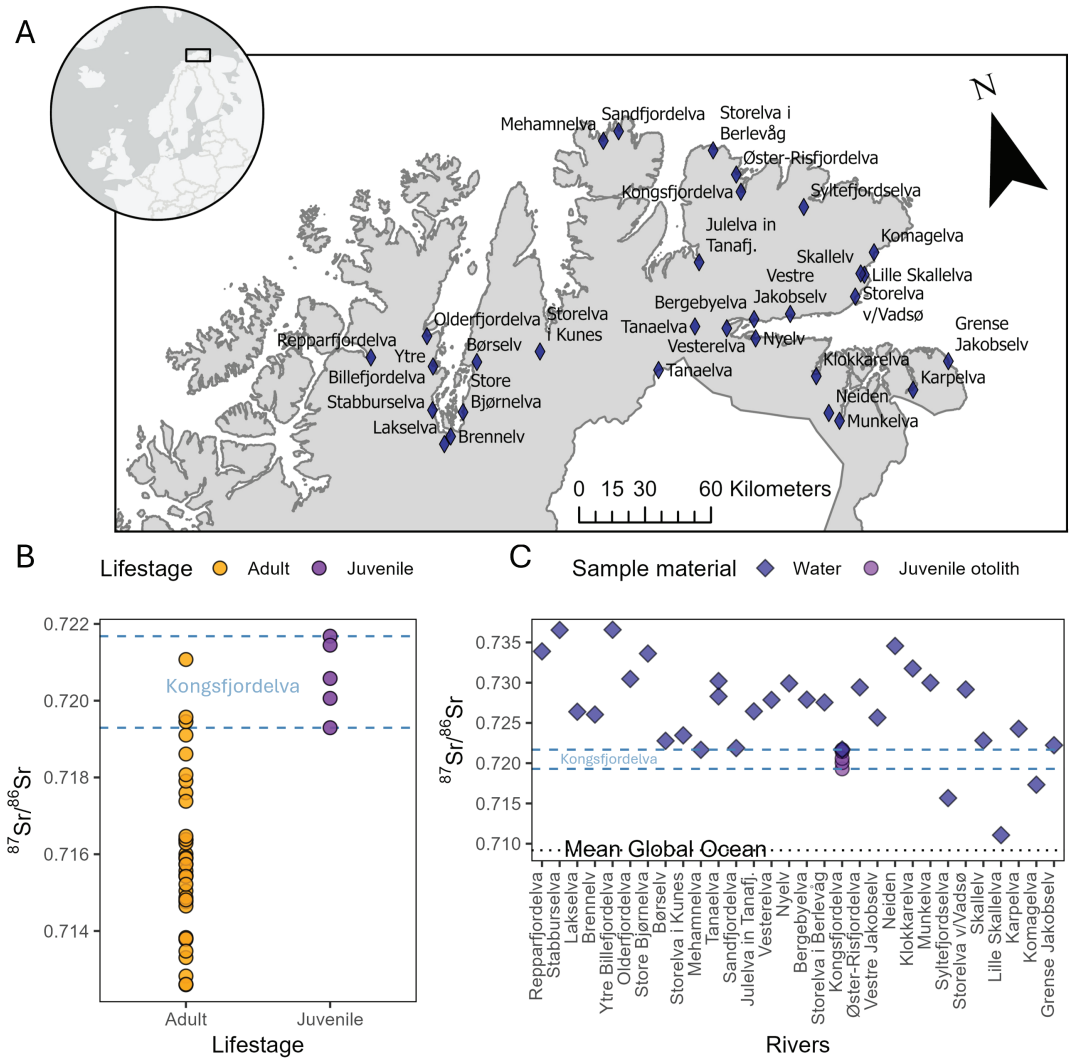

Fig. 2. a) Overview map showing the location of the 31 rivers sampled for strontium isotope ($^{87}Sr/^{86}Sr$) analysis in northern Norway. **b**) Comparison of $^{87}Sr/^{86}Sr$ results for 36 adult fish (orange circles) of unknown origin collected in Kongsfjordelva and five juvenile fish (purple circles) with known origin from Kongsfjordelva. Dashed line indicates the upper and lower bounds of the $^{87}Sr/^{86}Sr$ range for Kongsfjordelva based on both juvenile otoliths and a water sample. **c**) $^{87}Sr/^{86}Sr$ from water samples (blue diamonds) for 31 rivers from northern Norway, sorted from west to east and juvenile pink salmon otoliths (purple circles) for Kongsfjordelva.

on whether their natal otolith $^{87}Sr/^{86}Sr$ overlapped with the observed Kongsfjordelva $^{87}Sr/^{86}Sr$ reference range.

Results

We identified a total of 13 sibling pairs (half- and full-sibs) among the 329 pink salmon sampled from 30 rivers along the Norwegian coast (Table S1 in SI). Sibling pairs were assigned with a low false positive rate (~0.00003) and a high false negative rate (~0.381) (Fig. S1 in SI). The assignment was expected to result in few unrelated pairs to be assigned as half-sibs (53 956 pairwise comparisons × 0.00003 = 1.6 pairs). Out of the 13 sibling pairs identified, 7 pairs (54%) were

found between fish caught in the same river (*within rivers*), and 6 pairs (46%) were found between fish caught in different rivers (*between rivers*) (Fig. 1b). The maximum distance of siblings caught between rivers in our sample was ~700 km. The proportion of sibling pairs found within rivers (54%; 95% CI: 25–81%) was higher than expected given a random distribution of siblings among sampled fish (8%) (Fig. 1b). Two out of 13 sibling pairs were identified as full-sibling pairs, and both were found between rivers. Full-sibling pairs were differentiated from half-sibling pairs with a false positive rate (identifying half-sibs as full-sibs) of 0.002 and a false negative rate of 0.009.

The Kongsfjordelva strontium isotope range from the juvenile salmon is 0.7193–0.7217 (n = 5), which matches well with the single water sample from the river with a value of 0.7217 (n = 1). Measurements of the adults from the same cohort year showed that a small proportion of the studied fish (n = 3, ~8%) have natal $^{87}Sr/^{86}Sr$ consistent with the $^{87}Sr/^{86}Sr$ range of Kongsfjordelva (Fig. 2b). Based on our limited available data, the only other source matching this $^{87}Sr/^{86}Sr$ range is Mehamnelva (0.7217), with Sandfjordelva (0.7218) falling very close (Fig. 2c). Most adult fish (n = 33, ~92%) have natal $^{87}Sr/^{86}Sr$ of 0.7126–0.7191 that do not match Kongsfjordelva. The closest $^{87}Sr/^{86}Sr$ matches for these fish are rivers such as Syltefjordselva (0.7157) or Komagelva (0.7173) (Fig. 2c), but they could also come from other unsampled rivers in northern Norway or beyond. Two of the adult otolith samples are close in their $^{87}Sr/^{86}Sr$ (0.7191, 0.7186) to the $^{87}Sr/^{86}Sr$ range of Kongsfjordelva, which may represent homing individuals that were produced in a different (unsampled) reach of Kongsfjordelva.

Discussion

The progression of pink salmon from repeated arrival to local establishment and spread depends on the balance between straying and natal homing (Keefer and Caudill 2014; Quinn 2018). Within the invasion-continuum framework, this distinction is critical because adult occurrence alone does not demonstrate establishment (Blackburn *et al.* 2011). Rivers may receive recurrent immigrants without producing adults that return to the same watershed, reflecting continued immigration rather than local recruitment (Lockwood *et al.* 2005; Schtickzelle and Quinn 2007). Here, we demonstrate how genetic kinship analysis and otolith geochemistry can be combined to evaluate this transition from repeated immigration toward local recruitment and population establishment. Although sample sizes were limited and the two methods were not applied to the same individuals, our results provide evidence consistent with natal return by some individuals in northern Norway. These findings should therefore be interpreted as a methodological proof-of-concept illustrating how complementary tools can be used to detect local recruitment and quantify natal return in fish populations undergoing rapid range expansion.

Kinship analysis revealed that siblings occurred within rivers more often than expected by chance, indicating non-random spatial clustering of related individuals at the watershed scale. However, kinship alone cannot confirm local origin as within-river sibling pairs could arise either from natal homing or from siblings dispersing together and subsequently returning to the same non-natal river. Moreover, the proportion of related spawners detected depends on spawning population size, variance in reproductive success, and sampling intensity (Anderson 2024). Thus, while kinship analysis is a powerful and scalable screening tool for detecting structure in dispersal patterns, it does not directly quantify the proportion of returning adults that were locally produced.

Otolith geochemistry provides complementary information by linking individual fish to the freshwater environments in which they were produced (Campana 1999; Campana and Thorrold 2001; Barnett-Johnson *et al.* 2008; Brennan *et al.* 2015). Geochemical analyses showed that most adults captured in Kongsfjordelva likely originated elsewhere, while a small proportion (~8%) had natal $^{87}Sr/^{86}Sr$ consistent with the observed local reference range. Given the limited sample size and restricted $^{87}Sr/^{86}Sr$ baseline, this proportion should not be interpreted as a representative homing rate for Kongsfjordelva. Instead, the result provides evidence that pink

salmon can reproduce in this watershed and that at least some individuals may return, while also suggesting substantial straying at this stage of the invasion. Similar patterns of high dispersal have been reported in other recently expanding pink salmon populations (Gorman *et al.* 2024), consistent with expectations that early population establishment may be characterized by high straying rates. Importantly, our study and Gorman *et al.* (2024) show that geochemical tools can provide evidence of natal origin and thereby help distinguish locally produced adults from strays, despite the often short freshwater rearing period of juvenile pink salmon that can complicate natal river assignments. The pronounced variability in $^{87}Sr/^{86}Sr$ among rivers in northern Norway (Fig. 2c) highlights the strong potential of this approach for tracking dispersal and assessing population establishment. At present, however, limited baseline sampling restricts our ability to assign individuals to specific source rivers with high confidence. For example, it is possible that Kongsfjordelva shares a $^{87}Sr/^{86}Sr$ range with other unsampled rivers in Norway or northwestern Russia. Furthermore, it is likely that our limited sampling has not captured the full within-river $^{87}Sr/^{86}Sr$ range. Expanding the spatial extent of the isotope baseline using multiple water and, where possible, juvenile fish samples per river would allow probabilistic assignment of natal origins across watersheds and enable estimation of dispersal rates and distances.

Such regional-scale inference is difficult to achieve with direct methods alone. Although tagging and biotelemetry can provide detailed information on movement, survival, and return timing within individual rivers (Cooke *et al.* 2004), applying it across numerous remote watersheds would require large-scale capture and tagging of outmigrating juveniles, followed by the recapture of returning adults and systematic scanning for tags. In addition, outmigrating pink salmon juveniles are small and migrate shortly after emergence, which constrains tag size and retention and makes large-scale juvenile tagging technically challenging. In contrast, genetic and geochemical approaches do not require prior marking and can be applied retrospectively to fish collected during routine removal efforts or carcass surveys. This enables scalable assessment of natal return across many rivers without river-specific infrastructure.

Combining kinship analysis with otolith geochemistry provides complementary insight into both the behavioural and geographic dimensions of dispersal. Kinship analysis can reveal whether returning individuals reflect family-level patterns of homing or straying, whereas otolith geochemistry can identify the freshwater environments in which individuals were produced. Together, these methods allow stronger inference about natal origin, local recruitment, and population establishment than either approach alone. To move beyond proof of concept and estimate dispersal distances and rates over time, systematic sampling of returning adults in selected rivers would be required. Sampling several hundred individuals per river and cohort would substantially improve our power to detect sibling pairs and quantify within- versus between-river return patterns. Geochemical analyses could then be applied to inferred sibling pairs and to a representative subset of individuals to estimate the proportion of locally produced fish. Repeated sampling across cohorts, particularly given the two-year life cycle of pink salmon, would allow rapid detection of temporal changes in natal return and progression toward population establishment.

From a Norwegian management perspective, identifying where individual rivers fall along the invasion continuum is essential for prioritizing mitigation. Rivers dominated by non-local adults may function primarily as recipient habitats maintained by continued immigration, whereas rivers with increasing proportions of locally produced returning adults would indicate progression toward establishment and potential source populations for further spread. Integrating genetic and geochemical monitoring therefore provides a practical framework for tracking the balance between homing and straying, evaluating the effectiveness of control measures, and identifying watersheds where management actions should be intensified as pink salmon continue to expand in the North Atlantic and Arctic.

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Open research statement: The code and supporting data used in this study are publicly available in the GitHub repository (https://github.com/MalteWillmes/GeneticsGeochemPinkSalmonDispersal) and have been archived on Zenodo (DOI:10.5281/zenodo.21069909). The archived repository includes all scripts and input files needed to reproduce the analyses, summary tables, and figures presented in the manuscript.

Supplementary Information: The supplementary information related to this article is available online at: https://doi.org/10.60910/ber2026.9mgy-5v85

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