Potential migration routes for the alien species, pink salmon (*Oncorhynchus gorbuscha*)

Investigating access in west and south coast rivers of Sweden

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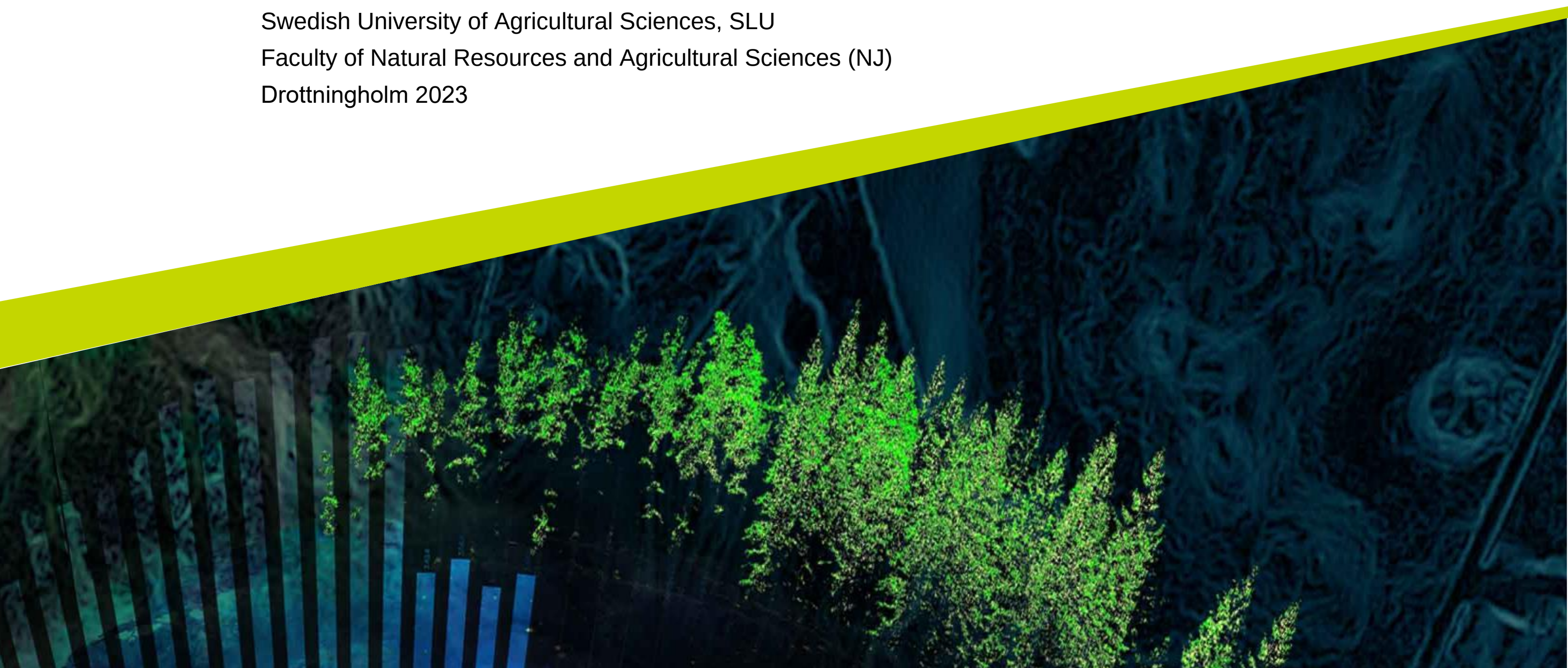

Potential migration routes for the alien species, pink salmon (*Oncorhynchus gorbuscha*). Investigating access in west and south coast rivers of Sweden

Potentiella vandringsvägar för den främmande puckellaxen. En utredning om tillgång på vattendrag på Sveriges väst- och sydkust

Rebecca Martin

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Abstract

Invasive alien species are one of the main drivers of ecosystem change globally, presenting challenges to biodiversity that take many forms Pink salmon, *Oncorhynchus gorbuscha*, has recently been observed on the Swedish west coast where its presence is the result of secondary spreading from populations introduced to the White and Barents Seas in northwestern Russia. In Sweden, *O. gorbuscha* is recognised as having high invasion potential but is not presently classed as invasive. Potential problems arising from an established pink salmon distribution on the Swedish west and south coasts are speculated to relate to instances where habitat use by the alien species overlaps with that of Sweden's native salmonids.

Aiming to facilitate further research into pink salmon distribution, this study investigates 29 rivers on Sweden's south and west coasts with regards to accessibility for migrating pink salmon looking to spawn. Mapping of potential migration routes for pink salmon was performed using GIS to explore, extract, analyse and process existing data on migratory barriers, fishways, Atlantic salmon distribution and pink salmon observations. The resulting maps were analysed alongside data on physical characteristics of each river drainage basin and existing literature on pink salmon to comment on potential impacts of the alien species on native ecosystems.

The study concludes that the most severe potential impacts are posed by pink salmon migrating further upstream than expected. This could give rise to competition between pink salmon and indigenous salmonids for optimal spawning grounds as well as exacerbate nutrient loading in rivers. Furthermore, factors contributing to vulnerability of each river drainage basin to pink salmon establishment were recognised as highly complex. A first step to assessing vulnerability was identified as prioritising either the native salmonid populations or the RDB's ecosystem.

The prospect of intentionally introduced pink salmon establishing in Sweden highlights other challenges forced upon natural systems by humans. It is however, quite paradoxically, man-made barriers in the form of hydropower dams that currently constitute the largest preventative measure to pink salmon spreading in most river drainage basins.

Keywords: Invasive, alien species, pink salmon, anadromous, migration barriers

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Introduction

Invasive alien species are recognised as one of the main direct drivers of change in ecosystems globally, posing serious challenges to biodiversity (Millennium Ecosystem Report, MA 2005). Introductions of alien species most often prove unproblematic due to the fact that the newcomer either does not establish or that their effects on the novel system are non-damaging (Simberloff 2009; Sandlund et al. 2019). However, potential impacts of alien species on the biodiversity of recipient ecosystems include changes to indigenous species richness, abundance and genetic diversity as well as extinction risks resulting from modifications to trophic systems, system productivity and nutrient cycling for example (Hawkins et al. 2015; Sandvik et al. 2013). Inland water and coastal ecosystems have been highly affected by invasive species over the last 50-100 years, leading to trends of increasing (coastal) or rapidly increasing (inland water) impacts due to this driver. Impacts of invasive species on marine systems seem, however, to be stable and low over time, although this represents the global situation meaning local variations are not accounted for (MA 2005).

Alien species are often intentionally introduced with incentives rooted in economic gain or recreation (Diaz Pauli et al. 2022; Sandlund et al. 2019). This study focuses on one such example, *Oncorhynchus gorbuscha*, pink salmon. This species is native to the North Pacific Ocean, where it constitutes an important subsistence, recreational and commercial resource (Quinn 2018). This makes it an attractive prospect for introductions outside its natural distribution, as seen in the operations most likely responsible for its presence in Sweden (Sandlund et al 2019; Diaz Pauli et al. 2022). In attempts to support commercial fishing around the White and Barents Seas, Russian efforts transferred millions of pink salmon eggs and young to this region from sites on the country's Pacific coast (fig. 1a). Introductions from Sakhalin, (1955-79), were unsuccessful in establishing persisting populations (Gordeeva et al. 2015). However, translocation of embryos from the River Ola population, north of Sakhalin, (1985-99) (fig 1a), brought about self-sustaining populations and it is secondary spreading of these populations that is the most probable cause of pink salmon in Sweden (fig. 1b) (Sandlund et al. 2019).

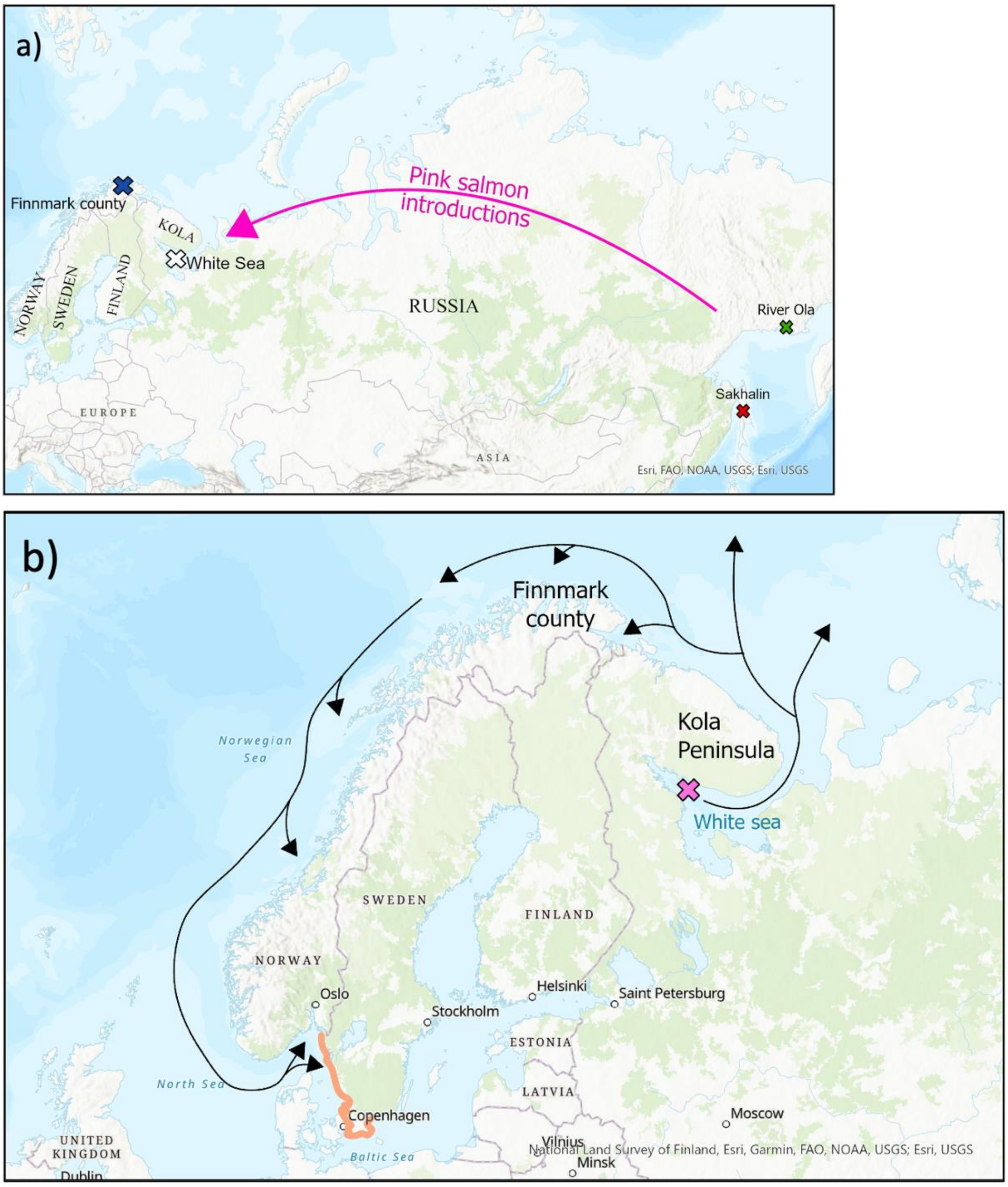

Figure 1. a) Native sites of transplanted pink salmon in the western Pacific Ocean, the arrow points to the sites of introduction in the rivers draining into the White Sea. b) Secondary spreading of pink salmon from the site of introduction around the White Sea (pink cross). Over time, pink salmon have spread to the northern side of the Kola Peninsula and into Finnmark county in northern Norway where self-reproducing populations now exist. Distribution has since continued to spread westwards and southwards along Norway's coast and to the west coast of Sweden. The geographic area of study is highlighted in orange.

Assessments in Sweden have signalled that pink salmon are capable of severe impact with regards to invasion potential and ecological impact although, currently, the species is neither established nor classified as invasive in this country (Strand et al. 2018). Regular observations of pink salmon are a relatively new phenomenon in Sweden where, as in Norway, potential impacts can only be speculatively accounted for (Sandlund et al 2019; Staveley & Ahlbeck Bergendahl 2022).

Where relevant, this study also discusses *Salmo salar*, Atlantic salmon, and *Salmo trutta*, brown trout, both native to Sweden (Jonsson & Jonsson 2009). All three species belong to the Salmonidae family and therefore share a number of behavioural and ecological characteristics (Quinn 2018; Klemetsen et al. 2003).

1.1 Alien establishment and invasions

Ideas underpinning the potential of alien species to establish self-reproducing populations in novel environments belong to the theories of *ecological niches* and *propagule pressure*.

Both concepts recognise two primary stages necessary for an introduced species to establish in a novel location. Firstly, the species must arrive at the new site and secondly, it must successfully reproduce there (Shea & Chesson 2002; Simberloff 2009). A third stage may follow whereby secondary spread from the initial site of introduction occurs into the surrounding region (Seah & Chesson 2002). Likewise, the theories of ecological niches and propagule pressure both recognise habitat specialisation as fundamental to the fates of alien species. This being the notion that a species may only establish populations in places with ecological conditions in line with those found in their native habitats (Peterson 2003).

Simberloff (2009) proposes that establishment of an introduced species relies on the amount of individuals arriving and the regularity of arrivals, the so-called propagule pressure. Here, a propagule is an individual or group of individuals and propagule pressure is defined by propagule size (number of individuals) and propagule number (how often propagules arrive). The larger the propagule size and the higher the propagule number, the more likely it is that an introduced species will establish.

Niche theory relates to the problems arising from introduction of alien species in so much as the species' capacity to colonise is highly dependent on its *responses* to the biological and physical conditions at the time and place of introduction and furthermore, its invasive capacity depends on its outward *effects* on the receiving system (Shea & Chesson 2002). Responses affect the overall rate of population growth whereas effects include interactions with other species, (e.g., competition, predation) and resource use, (e.g., feeding, shelter), becoming more important with increasing abundance (Shea & Chesson 2002).

Concerning the spread and potential colonisation of pink salmon in west and south coast rivers of Sweden, the concept of propagule pressure maintains that abundance and frequency of non-indigenous arrivals are vital factors to their succeeding or failing to establish. Moreover, niche theory highlights the importance of available resources and species interactions at arrival sites.

1.2 Salmonids

The species highlighted in this study are members of the Salmonidae family, often referred to as salmonids or salmon fish (Eschmayer 1998). Both pink and Atlantic salmon display, almost without exception, an anadromous lifestyle: spawning and early life stages occur in freshwater whilst migration to the open ocean allows for growth rates far exceeding those achieved in freshwater (Jonsson & Jonsson 2010; Quinn 2018:28). Brown trout display a higher mixture of anadromous behaviour and freshwater residence (Klemetsen et al. 2003).

In salmonids, spawning takes place in the autumn in streams where the female digs *redds* in the gravel into which embryos are deposited. After spawning, some adult fish die whilst others migrate back to the ocean or remain in freshwater systems, this varies between species (fig. 2). *Alevins* metabolise the yolk-sac prior to emerging from the gravel as *fry*, sometime during spring. Fry of some species, including pink salmon, migrate to the ocean directly whilst those fish remaining in freshwater systems become *parr* (fig. 2): this is the behaviour most common to salmonids. The contrasting conditions between fluvial systems and the ocean require significant physiological changes in migrating individuals, a phase known as *smolting*. Anadromous salmonids spend varying periods of time feeding at sea prior to migrating back to freshwater in order to spawn (fig. 2) (Quinn 2018).

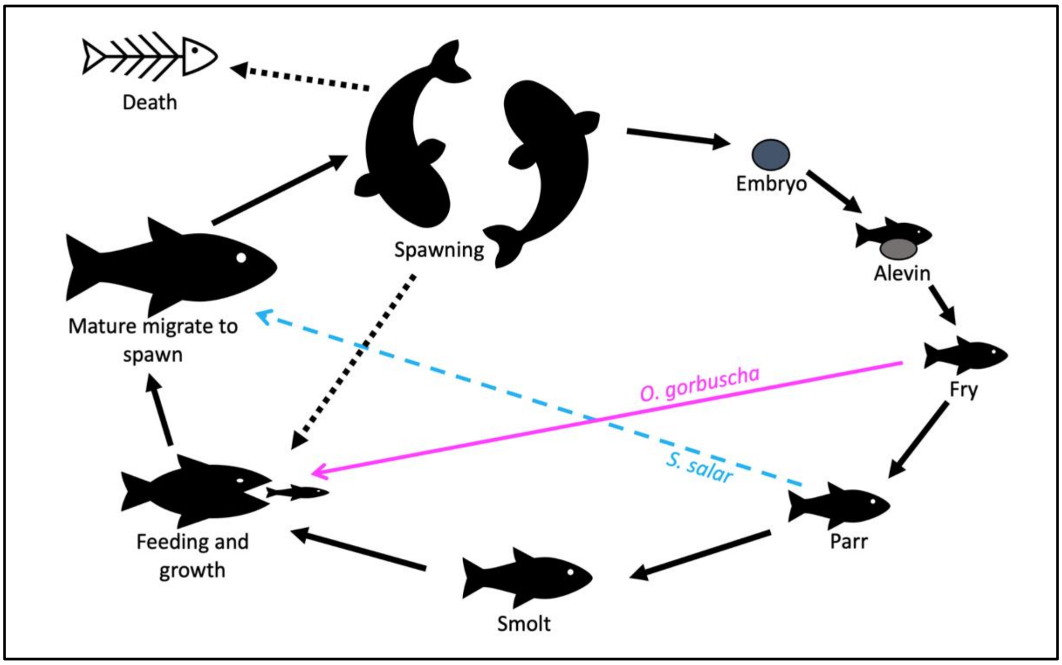

Figure 2. Generic life-cycle of salmon and trout. The pink arrow represents the readiness of pink salmon fry for seaward migration (Quinn 2018). The dashed blue arrow represents the occurrence of maturing parrs in Atlantic salmon (Klemetsen et al. 2003).

1.3 Pink salmon, *Oncorhynchus gorbuscha*

Whilst salmonids do share many traits and behaviours, it is apparent that differences, both small and large occur between species (Gedrem & Gunnes 1973; Klemetsen 2003; Quinn 2018). The following sections concern pink salmon whilst highlighting the differences between this species and Atlantic salmon and brown trout most pertinent to this study.

Two features of pink salmon appearance offer simple distinction from Atlantic salmon. These are important in facilitating the increase of public awareness and reporting. Firstly, pink salmon of both sexes have a black tongue in contrast to all the pink mouth of Atlantic salmon. Secondly, when ready to spawn, males develop a hump on their backs (SLU 2023a).

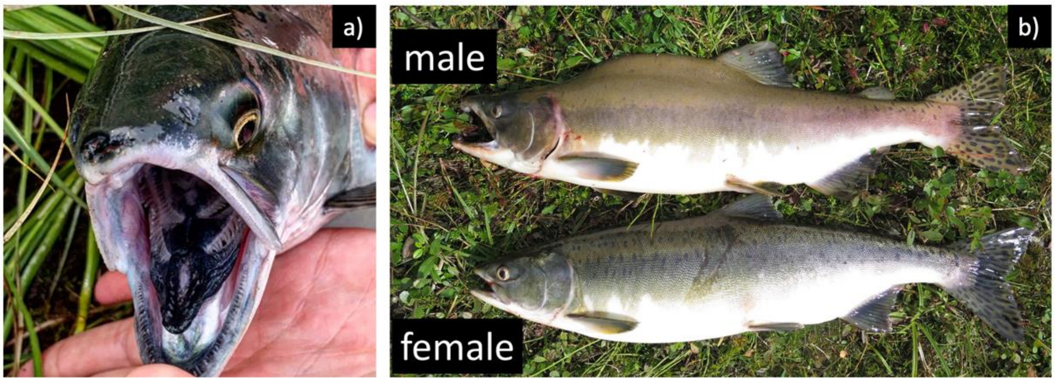

Figure 3. Identification of pink salmon is facilitated by a) the black tongue in both sexes and b) the development of a hump in front of the dorsal fin of spawning males. Photo: a) Hårvard Vistnes, b) Eva Thorsted, NINA.

1.3.1 Life-cycle

Pink salmon tend not to migrate far upstream, often spawning in the lower reaches of river systems and sometimes even in the intertidal zone (Quinn 2018). Additionally, indications of pink salmon spawning activity in Norway have been observed from early August into early September (Sandlund et al. 2019). Atlantic salmon and trout prefer however to spawn further upstream (Petersson et al. 2018) and spawn later in the autumn and into winter (Mo et al. 2018). As pink salmon fry spend little time in fluvial systems their impact here is limited. In contrast to juvenile Atlantic salmon and brown trout, which remain in freshwater habitats (Jonsson & Jonsson 2009), this also means that the capacity of a suitable pink salmon spawning site is defined by the space available for redds rather than e.g., nutrition or shelter. For this reason pink salmon can display incredibly dense spawning (Quinn 2018).

Almost without exception pink salmon mature at their second summer and despite rapid growth, *O. gorbuscha* is the smallest salmon species at maturity (c. 2 kg) (Quinn 2018). Longer lifetimes in Atlantic salmon and sea trout contribute to these species being capable of reaching much larger sizes compared to pink salmon (Klemetsen et al. 2003).

Pink salmon are entirely *semelparous*, spawning once and dying in the stream a short time afterward. Hence they do not require spared energy reserves for continued life after spawning. This trait allows mature pink salmon to devote all their energy to migration, spawning and even to parental care, which is more restricted in *iteroparous* (repeated spawning events) salmon such as Atlantic salmon and brown trout (Klemetsen et al. 2003). This is exemplified by pink salmon females aggressively guarding nests after spawning (Quinn 2018). Another aspect of semelparity is the transfer of nutrients from oceans to freshwater systems provided by the decomposition of carcasses after spawning (Quinn 2018). This trait in Pacific salmon has been shown to benefit entire ecosystems in the native range: The provision of nutrients is significant to the generally unproductive streams and lakes of northern latitudes where either nitrogen or phosphorus are often limiting (Quinn 2018).

In tandem with semelparity, the two year maturity cycle results in odd and even year *broodlines* (Gordeeva & Salmenkova; Quinn 2018). Across the pink salmon's native range, either odd *or* even year broodlines tend to dominate, with some rivers accommodating populations with seemingly *only* odd or *only* even year broodlines (Quinn 2018). Reasons for this remain unclear but what is certain is that *O. gorbuscha's* life-history traits prove effective: pink salmon is the most abundant salmon species, both in numbers and biomass (Quinn 2022). Additionally, in contrast to trends seen in both Atlantic salmon and brown trout in the North Atlantic in recent decades, pink salmon have displayed increasing abundance in the northern extent of their native range (HaV 2022; Quinn 2022).

1.3.2 Homing, straying and colonisation

Upon maturity pink salmon will return rather quickly to coastal waters where they may linger for a time before *homing*: swimming upstream their natal river in order to spawn (Quinn 2018).

Although the mechanisms behind the straying from the homing route are not well-understood, it is a fairly common phenomenon among salmonids (Quinn 2018). Both homing and straying infer evolutionary advantages. Homing will probably ensure that suitable redd sites can be found whereas straying will distribute a population and provide insurance against disturbances to the natal site. Straying is also a necessity for spreading and colonising new areas as part of natural succession. Pink salmon are more prone to extensive straying than other, longer living species and pink salmon in the early stages of colonisation may be inclined to an even higher degree of straying (Quinn 2018).

Despite numerous unsuccessful introduction attempts within the native range, Quinn (2018) concludes that pink salmon have a quite good track record of successful colonisations of areas made newly accessible, both naturally and by humans. For example, glacial retreat in Glacier Bay, Alaska, provided conditions for rapid colonisation of Wolf Point Creek within just four generations. The establishment and expansion of the species in all five of the Great Lakes is remarkable in a number of facets: Firstly, this is a freshwater network and pink salmon are naturally anadromous; secondly, the fish displayed extensive straying in the first years after introduction; and thirdly, the two year life-cycle was not rigid (Quinn 2018). Similarly, colonising of newly accessible areas is also seen in pink salmon's novel range around the North Atlantic, indicating the role of straying as a possible facilitator for pink salmon invasions (Sandlund et al 2019). What this and the other examples of colonisation demonstrate is the opportunistic, volatile and highly adaptable nature of pink salmon populations (Quinn 2018).

1.3.3 Potential impacts on native salmonids and ecosystems

As a close relative to Atlantic salmon and sea trout, pink salmon presents a potential threat to native populations due to their shared requirements (Petersson et al. 2018). The actual impacts of pink salmon establishing populations in Swedish rivers remains uncertain. Potential problems are closely tied to questions raised by niche theory, namely effects of interactions between species and competition for resources as well as responses to physical conditions at the time of arrival.

Competition with native salmon and trout for food and spawning sites will depend on when and how far up river systems pink salmon spawn (Pertersson et al. 2018). Problems may arise where pink salmon are not restricted to lower regions of rivers as expected from behaviour in the native range, this behaviour has been seen in Norway (Mo et al. 2018). Pink salmon females are known to aggressively guard their redds after spawning which chould overlap with Atlantic salmon and brown trout looking to spawn. This aggressive behaviour could interfere with native salmonid spawning at optimal sites (Sandlund et al. 2019; Armstrong et al. 2018). In addition, fry emerging further upstream would have further to migrate out to sea therefore spending longer in rivers and hence burdening the ecosystem (Sandlund et al. 2019).

Another uncertain prospect is the effect of nutrient contribution by decomposing pink salmon carcasses post-spawning. Enrichment may benefit nutrient-poor systems, with positive knock-on effects up the trophic system, but pose an exacerbating factor to rivers affected by or at risk of eutrophication (Armstrong et al. 2018; Sandlund et al. 2019).

Spread of disease to and potential hybridising with native salmonids are additional questions that require addressing (Petersson et al. 2018). However, pink salmon in the Atlantic have not been shown to carry any viruses from the Pacific Ocean that might have raised concern with regards to native species (Sandlund et al. 2019).

Causes behind the pink salmon boom witnessed in 2017 are not entirely confirmed, although it is apparent that offspring from 2015's spawning met with beneficial conditions (Mo et al. 2018). If these conditions were the product of ongoing climate change then it can be expected that increasing abundance of pink salmon to the west and south of the Russian border will be a progressive trend (Armstrong et al. 2018).

1.3.4 Pink salmon in Norway

Between the west coast of Sweden and sites of Russian translocations, as the fish swims, lies the entirety of Norway's mainland coast and observations of pink salmon have been much more prevalent there in comparison to Sweden. The story in Norway continues to unfold and tells of pink salmon's behaviour in the North Atlantic as well as its progress towards Sweden. It is from here that much of the research studied for this paper is fetched.

Since the 1970s pink salmon have been observed in Norway in varying but low numbers in both odd and even years, with maximum catches reaching not more than 1700 fish and, apart from straying individuals, restricted to a few rivers in eastern Finnmark county which borders Russia (Berntsen et al. 2022). Between 2000 and 2007 high numbers of pink salmon were observed in Norway before dropping off considerably until 2017 when c. 12 000 observations were made. Abundance rapidly increased abundance for every odd year spawning event from 2017 onwards and in 2021 over 200 000 fish were caught in 271 rivers of very varying sizes, spanning the entire length of the country as well as in coastal fisheries (Berntsen et al. 2022). Reports necessitate observations and hence the data reported must be interpreted as an indication of what is occurring on a larger scale (Sandlund et al. 2019).

Pink salmon remain largely concentrated to Finnmark and with increasing distance to the west and south of the border, abundance and proportions of pink salmon decline (Berntsen et al. 2022).

River preference of returning pink salmon appears to be affected by a number of factors in combination and of varying geographic and temporal importance (Berntsen et al. 2021). Modelling of these factors integrated with the Norwegian data collected for 2017 and 2019 showed that the most significant factors proved to be proximity to Russia, the size of the river and the size of the Atlantic salmon population. Additionally, the size of the river was more important both in the south versus the north and in 2017 versus 2019 (Berntsen et al. 2021).

1.3.5 Pink salmon in Sweden

As previously noted, the expansion of pink salmon distribution to Swedish waters has occurred unexpectedly quickly. As yet there is no national monitoring over the species but Staveley and Ahlbeck Bergendahl (2022) have summarised the situation from the Swedish perspective. Typical for the region, Sweden reported highest to date abundances of pink salmon in 2021. Pink salmon were observed at Trollhättan, almost 80 kilometres up Göta älv, although to date there have been no reports of successful spawning in Swedish waters. As the majority of the 2021 observations, (n = 45 of total n = 70), were made by a single camera system at Herting in the River Ätran, coupled with the fact that there is no commercial fishery for Atlantic salmon on the west coast and no national monitoring system for pink salmon, it must be assumed that substantial numbers go unnoticed each year. As mentioned, observations made in Sweden in 2019 were markedly less than those in both 2017 and 2021, only five observations were made in 2019 and of these all via the camera at Herting. 2017 had the second highest abundance of pink salmon in Sweden with 46 observations. In recent years, the southernmost record of pink salmon on the Swedish west coast was observed in 2021 in the River Lagan in Halland county, note that this record is anectdotal (Blomberg 2021).

1.4 Aims & research questions

This study is part of a larger research project, *Pink salmon in Sweden*, being carried out at SLU Aqua, the Department of Aquatic Resources at the Swedish University of Agricultural Sciences (SLU 2023b). The project aims to understand distribution and spawning success on the Swedish west coast as well as raise public awareness and reporting of observations.

The main objective of this study is to map potential migratory routes for pink salmon looking to spawn on the west and south coasts of Sweden and assess the potentially accessible range within the river drainage basins studied. It is hoped that this work will facilitate further research and efforts with regards to planning and management. The study also attempts to highlight potential impacts of pink salmon on these routes and comments on prospects of interactions between the alien and native species. With this in mind the following research questions are posed:

1. In the drainage basins of the selected rivers, where are potential routes for migrating pink salmon looking to spawn and how much of each river drainage basin (RDB) is accessible to pink salmon?
2. What are the potential impacts of pink salmon navigating these routes and spawning?
3. With regards to questions 1 & 2, what contributes to vulnerability in RDBs?

Material & Method

2.1 Approach

Mapping and visualisation of potential migration routes for pink salmon used geographical information systems (GIS) software to analyse existing, open access data. Comparison of results from this method with background knowledge and current literature on pink salmon in both its native range and in the North Atlantic was used to indicate potential impacts of the alien species and to comment on river drainage basin vulnerability to pink salmon.

2.1.1 Geographical area of study and study depth

The study selected the 24 rivers on the Swedish west coast with wild salmon populations (Ahlbeck Bergendahl & Staveley 2023) plus five rivers on the south coast (fig. 4). The west coast of Sweden is closest to the *invasion front* (i.e. the foremost edge of the distribution of the spreading population), as seen in the Norwegian literature (Berntsen et al. 2022) and recent observations of pink salmon in Sweden are concentrated in this region (Staveley & Ahlbeck Bergendahl 2022). The five rivers on the south coast have been chosen due to their size and geographical spread along the coast. In line with the larger research project of which this study is a part, it is thought that the rivers in this selection give the highest chance of detecting pink salmon that migrate into south coast rivers.

The study presents a relatively simple overview of the entire coastline. At this early stage in the assessment of the potential impacts of pink salmon in Sweden and in combination with the timeframe of the study, this objective was deemed more interesting and helpful rather than a detailed assessment of a handful of sites.

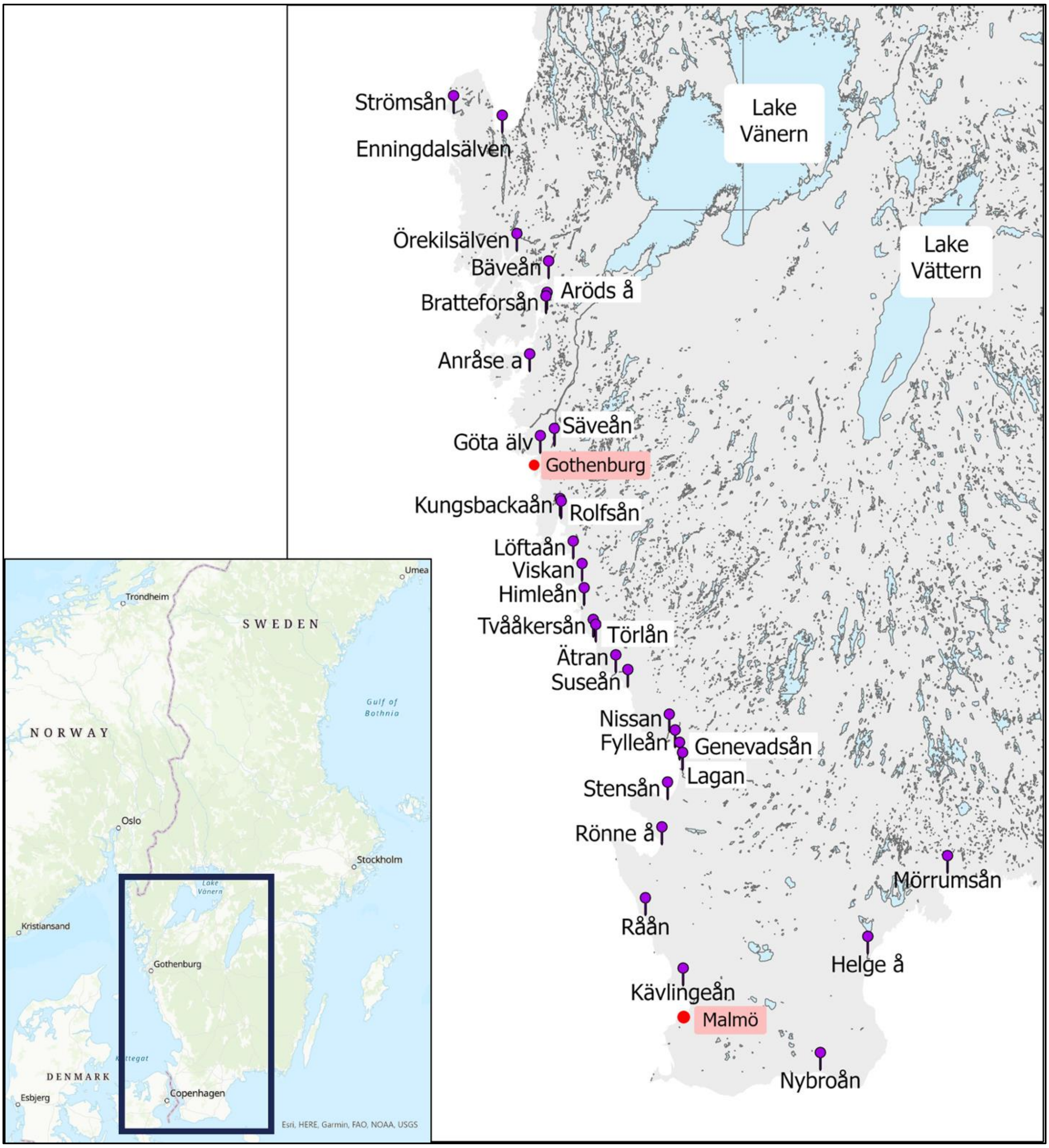

Figure 4. The geographical area of study. Pins mark the mouths of the rivers in focus for this study. *For Enningdalsälven, due west of Strömsån to the north, the pin is located at the border with Norway, the rivermouth is a further c. 15 km downstream. Map: SMHI © Översiktskarta © Lantmäteriet*

2.1.2 Materials and software

Geovisualisation and simple manipulation of the data used was performed in ArcGIS Pro ®, © Esri. Data on migratory barriers, fishways and electrofishing surveys, plus basemaps used to facilitate analysis and orientate the viewer were collected as shapefiles, (ready to open in GIS), from various national databases (table 1).

Table 1. Input data sets, (existing shapefiles) used in GIS.

Data, format	**Use**	**Source, year**
Migratory barriers, vector	Partial and definite migratory barriers to brown trout	Länsstyrelsen [Directorate of counties], 2021
Fishways, vector	Aid: Fishways targeting brown trout and Atlantic salmon	Åtgärder i Vatten, [National database over restaurative measures in aquatic environments], n.d.
Electrofishing samples, vector	Salmon observations	Swedish electrofishing register (SERS), 2023.
Key/base maps, vector	Base map: Lakes	Lantmäteriet, n.d.

GIS

In order to aid the uninitiated in navigating the rest of the Method section, here follows a short introduction to working with data sets in GIS.

In GIS software, data sets formatted as so-called *shapefiles* may be projected onto a digital map using northing and easting coordinates (fig. 5). Each set of coordinates bears with it the corresponding information from the data set and this can be viewed point for point in pop-up windows, or as the complete data set. The complete data set may be opened for exploration within the software under the alias *attribute table*. Hence, the attribute table is made up of the attributes or properties of each data point. Shapefiles are often available directly from authorities and within GIS are often called *layers*. *Input layers* are used to isolate and analyse datapoints and *output layers* are constructed by the user via *processes* (fig.5). Ouput layers can then become input layers for further analysis (fig. 5). Multiple layers may be viewed at the same time, allowing visual comparison and analysis by the user.

2.2 Procedure

2.2.1 ArcGIS Pro

The analysis of datapoints and working-procedure within GIS made the following assumptions:

- With regards to migratory barriers, pink salmon share the same navigating ability as brown trout.
    - Definite barrier: pink salmon can most likely not pass upstream under any circumstances (Biotopkartering 2002).
    - Partial barrier: pink salmon may pass under beneficial conditions (Biotopkartering 2002)
- With regards to electrofishing observations, pink salmon have access to the same sites as Atlantic salmon.
- Where no definite migratory barrier is present in a waterway, knowledge of partial barriers may be of use.

The output layer *Salmon furthest upstream* resulted from the isolation of data points in the input layer *Electrofishing* representing the Atlantic salmon observation occurring furthest upstream from the river mouth, (fig. 5a). This was repeated for each river and its tributaries. Information for the isolated data points was extracted to Excel in order to collate a new data set containing: coordinates; principal river drainage basin; place description; most recent salmon observation.

The output layer *Defining barriers* resulted from isolation of data points in the input layer *Migratory barriers*, (fig. 5b), representing: the first definite migratory barrier occurring upstream from the river mouth for each river and its tributaries; and, for waterways with no definite barrier, the last partial migratory barrier occurring upstream from the river mouth with no salmon observations upstream. For this stage, the layers *Fishways* and *Electrofishing* were useful aids. Information for the isolated data points was extracted to Excel in order to collate a new data set containing: coordinates; principal river drainage basin; place description; type of barrier; passability of barrier; comments regarding e.g., fishways, planned improvements to benefit fish migration. Visualisation of barriers used passability to distinguish definite from partial barriers.

Data sets collated in Excel were imported to GIS using the *Geoprocessing* data management tool *XY Table to point* which created the output layers described above. This function was also used to create datapoints for the output layer *Pink salmon observations* from the accessed data set (fig. 5a). Visualisation of *Defining barriers* layer used categorised symbology to distinguish between definite and partial barriers to migration.

The output layer *Confirmed salmon route* was created using the geoprocessing data management tool *Create feature class*. This required manually tracing the waterways, drawing a digital line to highlight the stretches of river downstream of pink and Atlantic salmon observations. The distance from the river mouth to the end of the route upstream was calculated using the *Measure distance* tool in the *Inquiry* section of the *Map* menu bar.

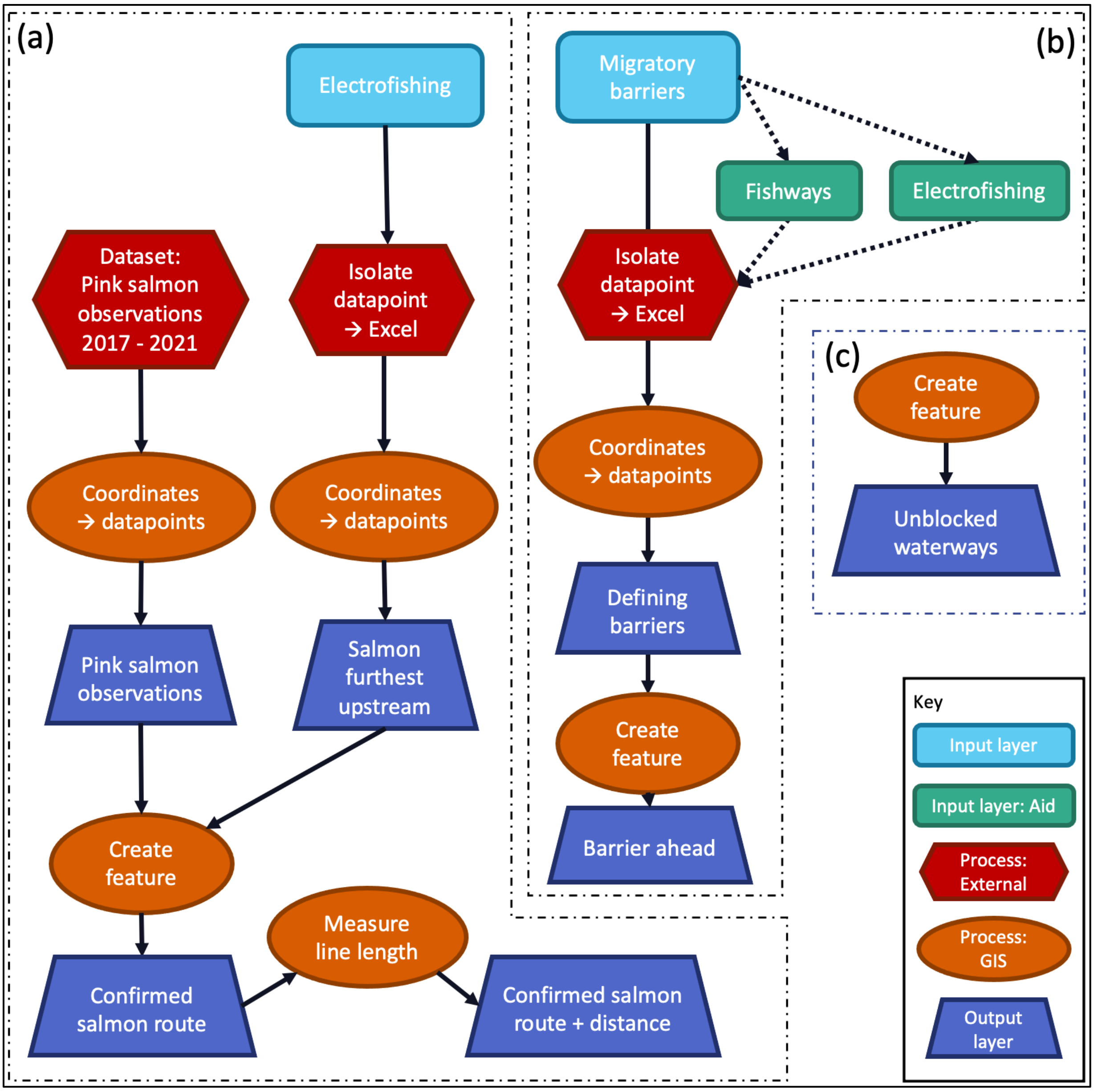

Figure 5. Workflow schematic of processes performed in GIS. Starting as Input layers at the top of the figure, data points undergo a series of processes, both within the GIS software and externally. This results in new layers which may, in turn, be subjected to further analysis and processes. The appearance of input and output layers can be optimised to facilitate its purpose.

Complementary data

River discharge was calculated as the average over the years 2010-2021 (SMHI u.d.).

Length of river drainage basins (RDB) was measured using the *Measure* tool in ArcGIS Pro ®, © ESRI which uses points and straight lines. Depending on the geometry of the RDB either one single or two joined lines were made between the rivermouth and the farthest edge of the RDB. Two lines were used where a single line would have crossed the RDB border.

The proportions of RDB accessible to pink salmon were roughly estimated by calculating the areas of polygons created using the *Measure* tool and comparing with the area of the RDB.

Results & Analysis

3.1 Potential migration routes for pink salmon

Potential routes upstream for migrating pink salmon looking to spawn were deduced as being those where:

- Pink salmon had been observed in recent years (Staveley & Ahlberg Bergendahl 2022)
- Atlantic salmon had been observed (electrofishing)
- It could be determined that upstream migrating sea trout were able to reach (migratory barriers, fishways)

Figure 6 over Bäveån represents a good example of the geovisualisation of results for a single river drainage basin although much more refined exploration of the results is possible using GIS. The most cautious interpretation of the data results in potential pink salmon routes stopping only at definite barriers but passing partial barriers and proceeding up unblocked waterways (fig. 6). Routes where barriers occur are also defined in the visualisation and indicate the presence of a migratory barrier, (definite or partial), upstream. The confirmed presence of salmon, pink or Atlantic, upstream is also visualised and unblocked routes are also highlighted (fig. 6). Much more refined exploration of the results is possible using GIS software.

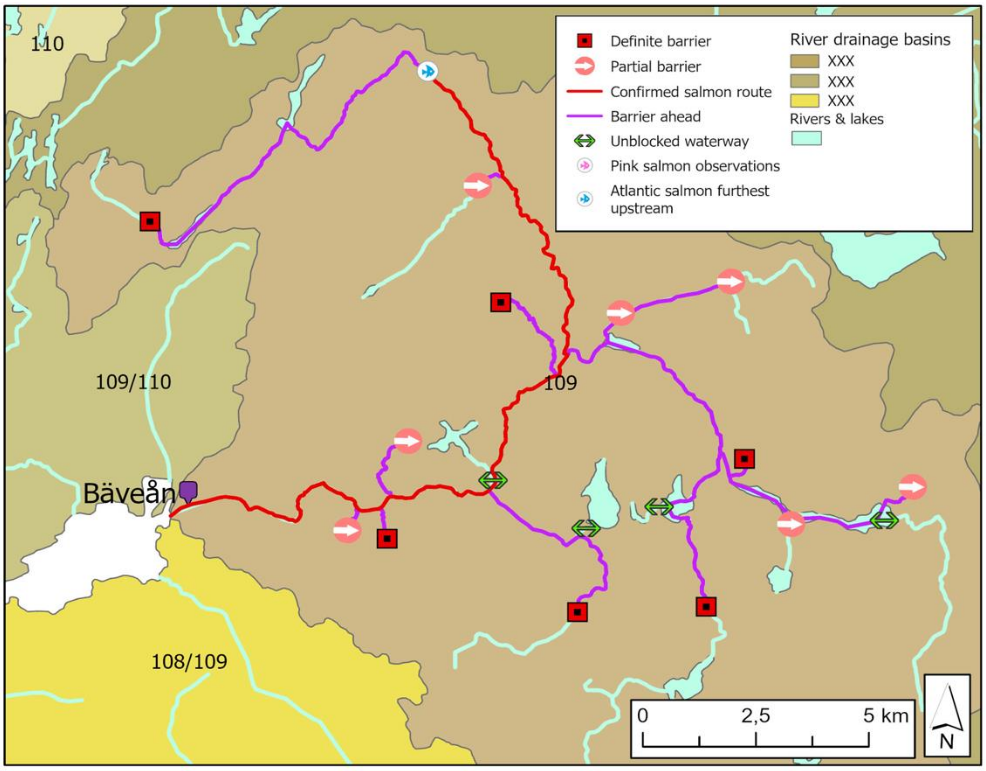

Figure 6. Potential migratory routes for pink salmon in Bäveån. Routes with confirmed salmon observations upstream are red and end at a pink (pink fish) or Atlantic (blue fish) salmon. Routes with berries ahead are purple and end at definite barriers, (red square), indicating an impassable obstacle for pink salmon or at partial barriers, (pink circle with white arrow) which are interpreted as passable. Green arrowheads signify that passage upstream is unblocked.

3.2 Drainage basins

3.2.1 Strömsån, Enningdalsälven, Örekilsälven and Bäveån

Much of Strömsån's drainage basin is unblocked or partially blocked, definite barriers are mostly present towards the heads of tributaries (fig. 7). An estimated 67 percent of this RDB is deemed accessible to pink salmon and Atlantic salmon have been observed 18 kilometres upstream (fig. 7; tables 2 & 3).

Most of Enningdalsälven runs through Swedish territory although the river crosses the border with Norway around 15 kilometres upstream of the rivermouth. In the Swedish part of this RDB, tributaries are more often blocked by definite barriers making much of its breadth inaccessible to pink salmon (fig. 7). The mainstem however is unblocked leaving the length of the RDB open for migration (c. 20 percent of the Swedish area) (fig. 7; table 3). Pink salmon have been observed here in 2021 although it is not recorded where and Atlantic salmon have been recorded 31 kilometres from the rivermouth (tables 2 & 3; fig. 7).

Örekilsälven's drainage basin is effectively split into two halves, with the mainstem continuing northwest whilst tributary Munkedalsälven occupies the southeastern half of the RDB. The mainstem remains unblocked but Munkedalsälven is obstructed by a definite barrier around seven kilometres from Örekilsälvens rivermouth so this half of the RDB is not open to pink salmon (fig. 7). Roughly 67 percent of this RDB is estimated accessible to pink salmon and the species was observed in Örekilsäven in both 2017 and 2021, with ten individuals detected in the latter but at unknown distances from the rivermouth (tables 2 & 3). The furthest upstream Atlantic salmon in this RDB was recorded just nine kilometres from the rivermouth (fig. 7; table 3).

Around half of Bäveån's drainage basin is assessed as accessible to pink salmon (table 3), this is due to the mainstem being unblocked until near the head of the river, and much of the central region containing several partial barriers and unblocked tributaries (fig. 7). Atlantic salmon have been observed 36 kilometres upstream in the mainstem but the southerly half of this RDB is barred by definite barriers (table 3; fig. 7).

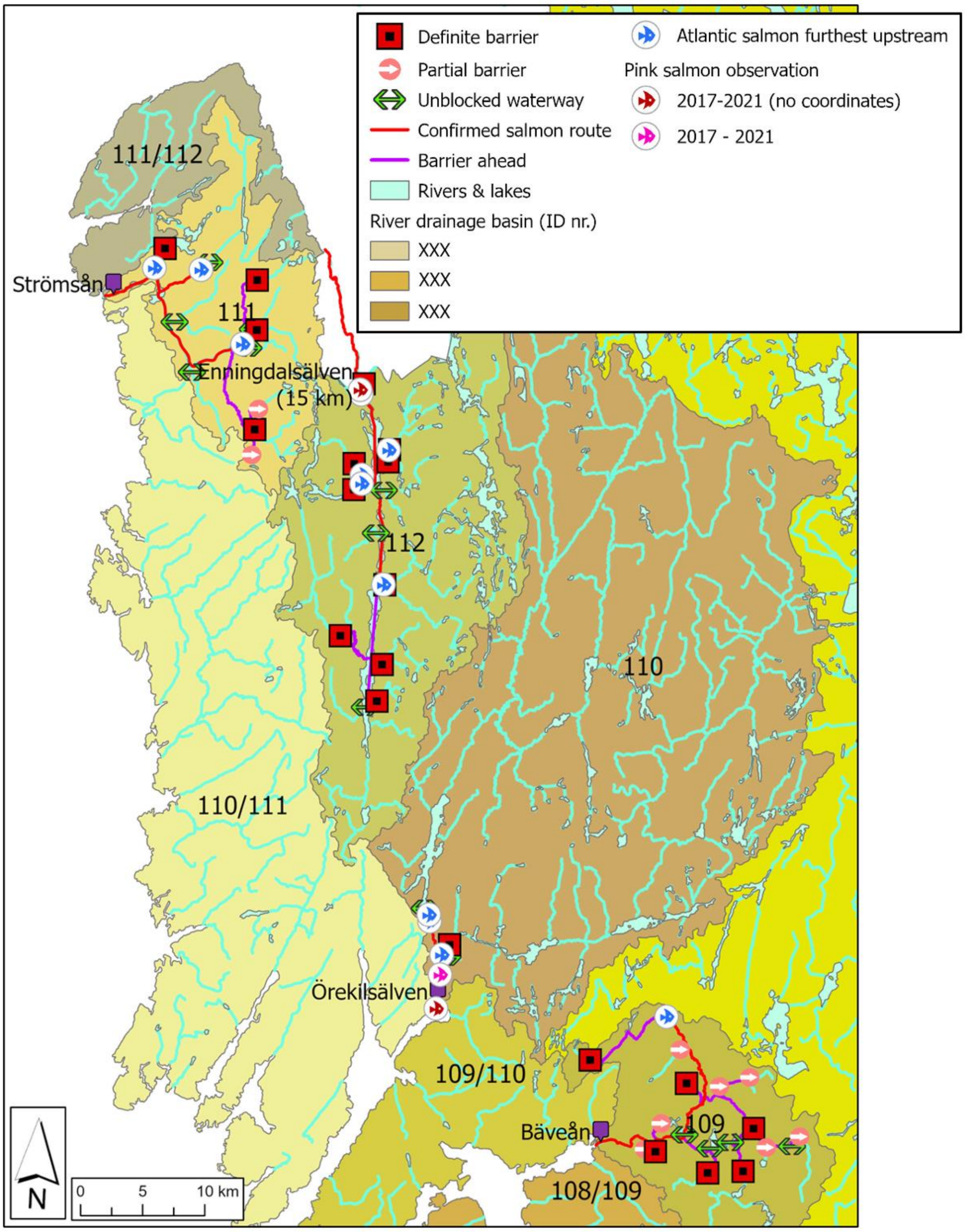

Figure 7. Potential migratory routes for pink salmon in Strömsån, Enningdalsälven, Örekilsälven and Bäveån.

3.2.2 Between Göta älv and Bäveån (108/109) - Aröds å, Bratteforsån and Anråse

There are a number of smaller streams in the drainage basin between Göta älv and Bäveån unaccounted for by this study (fig. 8). That said the rivers studied are responsible for much of the drainage so it may be stated that definite barriers in the mainstems of Aröds å, Bratteforsån and Anråse å prevent pink salmon passage into much of the drainage basin (fig. 8). In 2017 a pink salmon was observed in coastal waters of Ljungskileviken near the mouths of Aröds å and Bratteforsån (fig. 8; table 2). Atlantic salmon observed furthest upstream reached less than ten kilometres from the rivermouth in all three rivers (fig. 8; table 3).

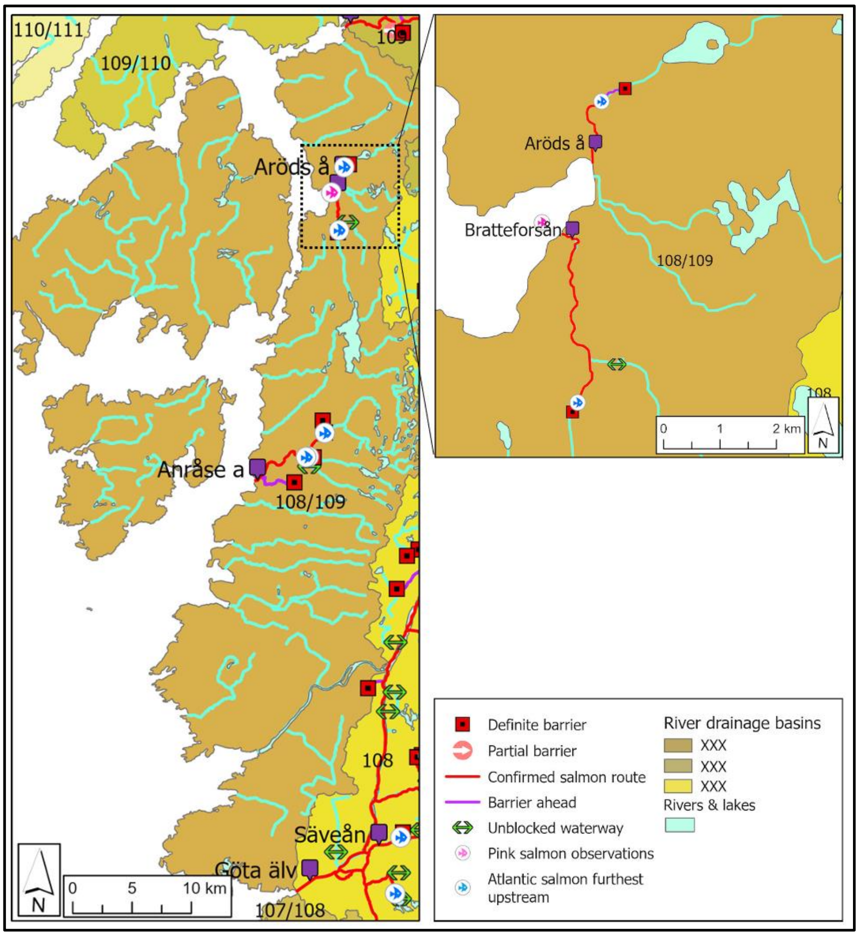

Figure 8. Potential migratory routes for pink salmon in Rriver drainage basin 108/109 (between Göta älv and Bäveån), with Aröds å, Bratteforsån and Anråse å.

3.2.3 Göta älv

A dam at Floda hydropower station in Säveån, c. 35 kilometres from the confluence with Göta älv blocks most of the very southeasterly region of the RDB . Four pink salmon were abserved in Säveån in 2021 (fig 9b; table 2).

The mainstem of Göta älv passes close to the western border of the drainage basin and is open up to Trollhättan (fig. 9c). Several tributaries south of Trollhättan are not passable for pink salmon, often with barriers close to the confluence with the mainstem. A number of tributaries, extending tens of kilometres, are however unblocked (fig 9b). The hydropower dams at Trollhättan block passage further upstream and into Sweden's largest lake, Vänern, via which the large majority of drainage for the entire basin occurs. Pink salmon have been observed in relatively high numbers in Göta älv, (table 2), the majority of these at Lilla Edet, 56 kilometres from the rivermouth. Lilla Edet is also the site of hydropower production and passage past this site is only possible via a fishway.

The results show that pink salmon have migrated almost 80 kilometres upstream Göta älv to Trollhättan, where four individuals were observed in 2021(fig. 9b & c; table 2). Assuming that the data over pink salmon observations used in this study are complete then this marks the furthest upstream pink salmon observation in Sweden to date. Additionally, it matches Atlantic salmon observations furthest upstream in this river (table 3).

Note that Göta älv's drainage basin is by far the study's largest (fig 9a) (50 038 km^2), has the greatest freshwater discharge and is home to the second highest number of pink salmon observations after Ätran (tables 2 & 3). Despite access proven possible 80 kilomtres upstream Göta älv, due to its size the unblocked proportion of the drainage basin is estimated to be just 2 percent (table 3).

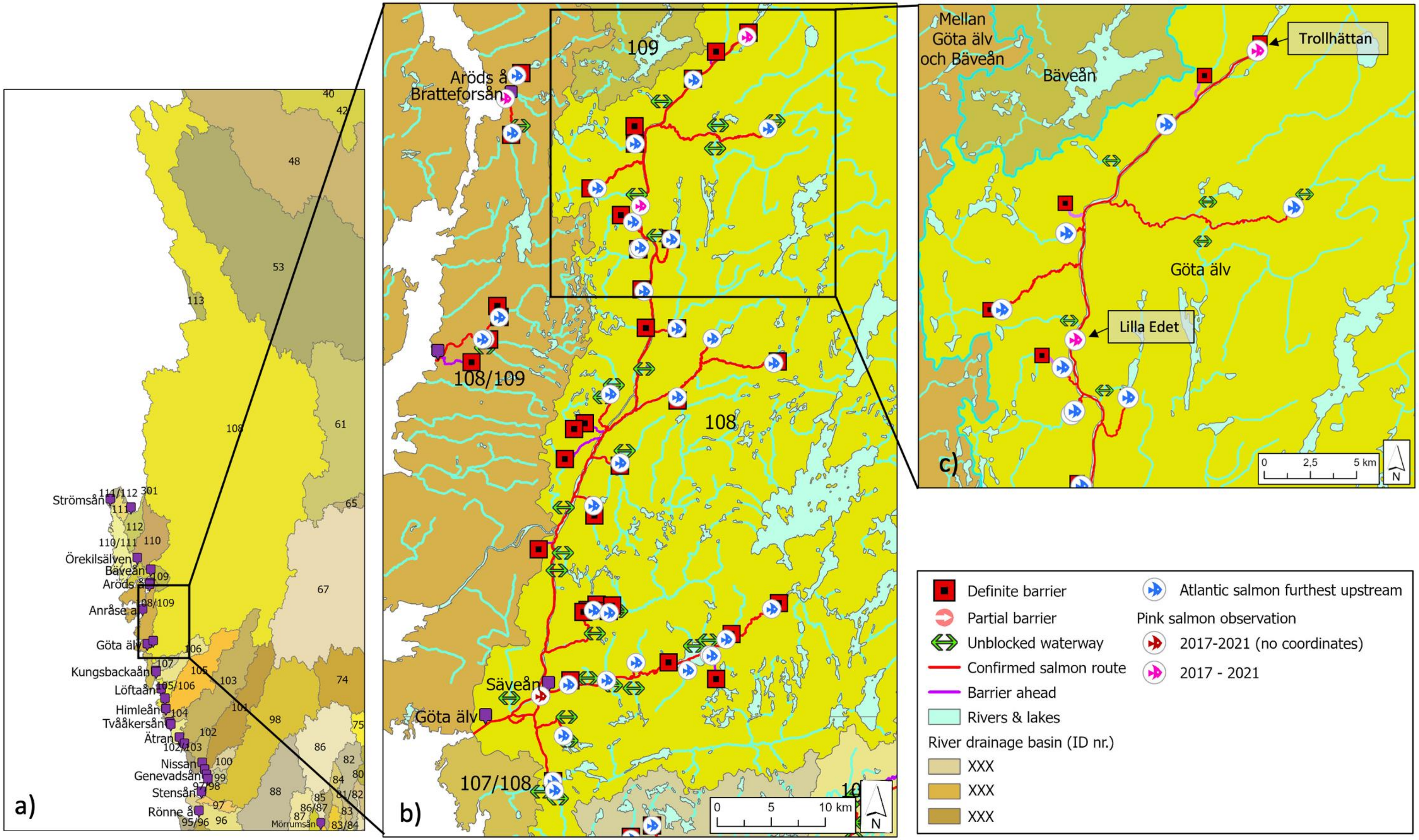

Figure 9. Potential migratory routes for pink salmon in RDB 108, highlighting Göta älv's mainstem and large tributary, Säveån. 9a highlights the size of the RDB, at 55 038 km^2 it is by far the largest in the study region. 9b shows the extent of the RDB containing defining barriers and salmon observations. 9c magnifies the northernmost region of the mainstem including the definite barrier at Trollhättan (red square furthest north) which pink salmon have reached in recent years.

3.2.4 Kungsbackaån, Rolfsån, Löftaån and Viskan

Apart from a pocket of lakes in the north of the RDB, Kungsbackaån's drainage basin is largely accessible (c. 75 %) to pink salmon and the mainstem is unblocked (fig. 10; table 3). The same is true for Rolfsån where impassable barriers block the innermost third of the drainage basin (fig. 10). Atlantic salmon have been observed in both of these rivers in recent years (fig. 10) and as far 68 kilometres upstream in Rolfsån (table 3). This is the third longest distance from the rivermouth for Atlantic salmon seen in this study.

Löftaån accounts for the most part of the drainage basin between Viskan and Rolfsån (ID nr. 105/106) (table 3); other waterways in this drainage basin were not studied. A definite barrier in Löftaån's mainstem prevents passage further upstream into the northeastern region of the RDB (fig. 10) and Atlantic salmon have been observed as far as 17 kilometres upstream (table 3).

The mainstem of Viskan is unblocked until Kungfors hydropower station around 60 kilometres upstream, restricting migration to the northernmost two thirds of the RDB (fig. 10). Many tributaries to the southeast of Kungfors are unblocked and the west-northwestern edge of Viskan's drainage basin is also largely unblocked until a definite barrier (fig. 10), this is in the tributary Surtan. Atlantic salmon have been observed in this vicinity, around 73 kilometres upstream (table 3) and pink salmon were observed here in 2017 although details on where and how many are not recorded in the dataset used (table 2).

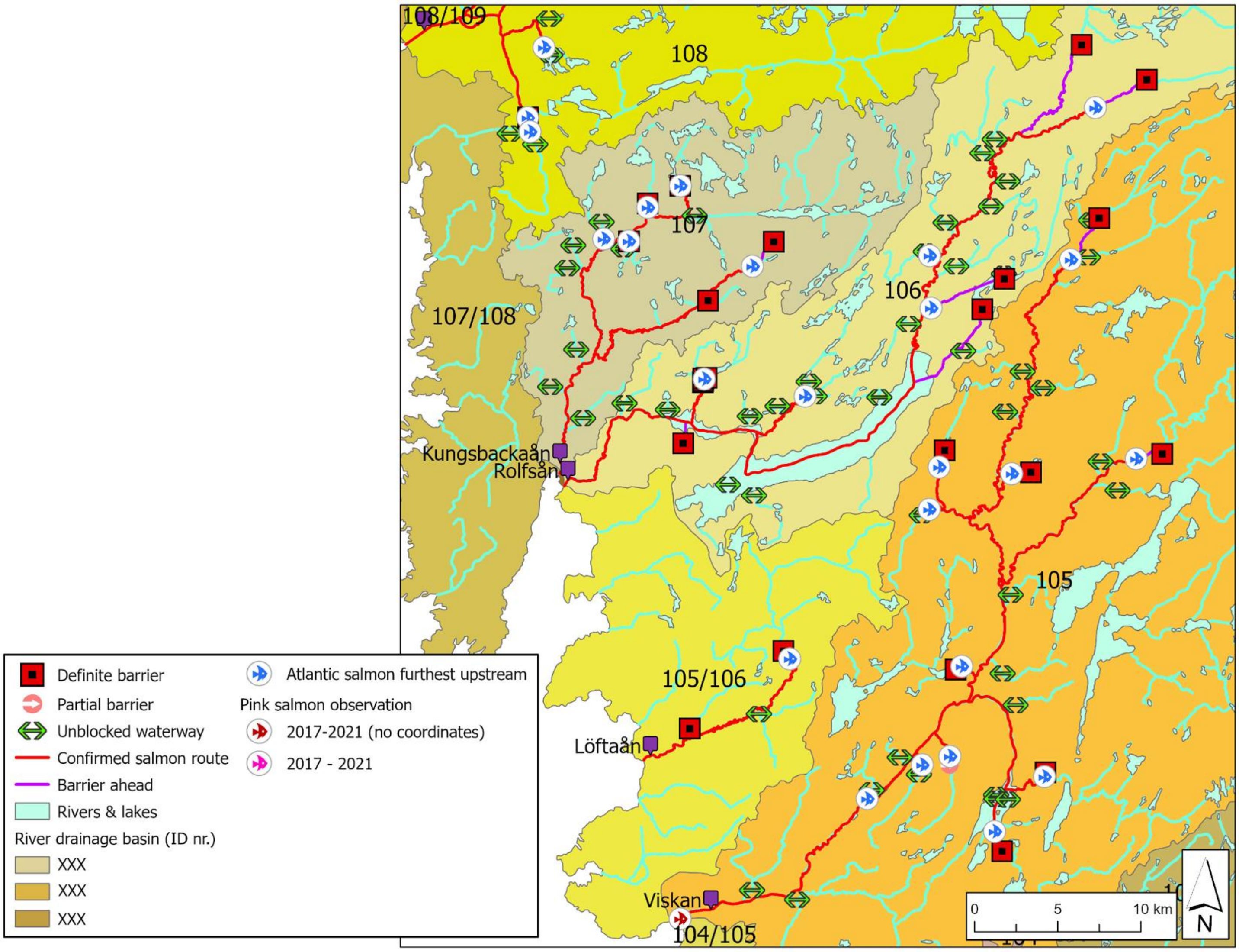

Figure 10. Potential migratory routes for pink salmon in Kungsbackaån, Rolfsån, Löftaån and Viskan.

3.2.5 Himleån, Tvååkersån, Törlån and Suseån

There are no barriers affecting migration in Himleån, Tvååkersån or Törlån and Atlantic salmon occur here as far as 19, eight and five kilometres upstream respectively (fig. 11; table 3).

Ätran's mainstem accounts for drainage of almost the entirety of the RDB, it is blocked at Ätrafors slightly upstream of the confluence with the large tributary Högvadsån (c. 35 kilometres from the rivermouth) (fig 11). Much of the portion of the RDB draining into Högvadsån, (northwestern edge), is unblocked to pink salmon (fig11). For reference, Ätrans drainage basin stretches c. 150 kilometres inland from the coast, the second longest and fourth largest (3 339 km^2) RDB in the study (table 3). Ätran is responsible for the highest number of pink salmon observations in Sweden, a large deal of these occurred at the camera trap at Herting, around four kilometres up the Ätran (fig. 11; table 2). RDB accessibility to pink salmon is estimated to c. 25% and the species has also been observed at around 21 kilometres upstream at Vessingebro and around 35 kilometres from the river mouth at Nydala in Högvadsån (fig. 11; table 2). Nydala is home to the national monitoring site for Atlantic salmon which are regularly observed throughout much of this drainage basin.

Suseån's drainage basin is widely accessible to pink salmon, c. 75 percent (table 3). A total of three definite barriers block only three smaller waterways (fig. 11).

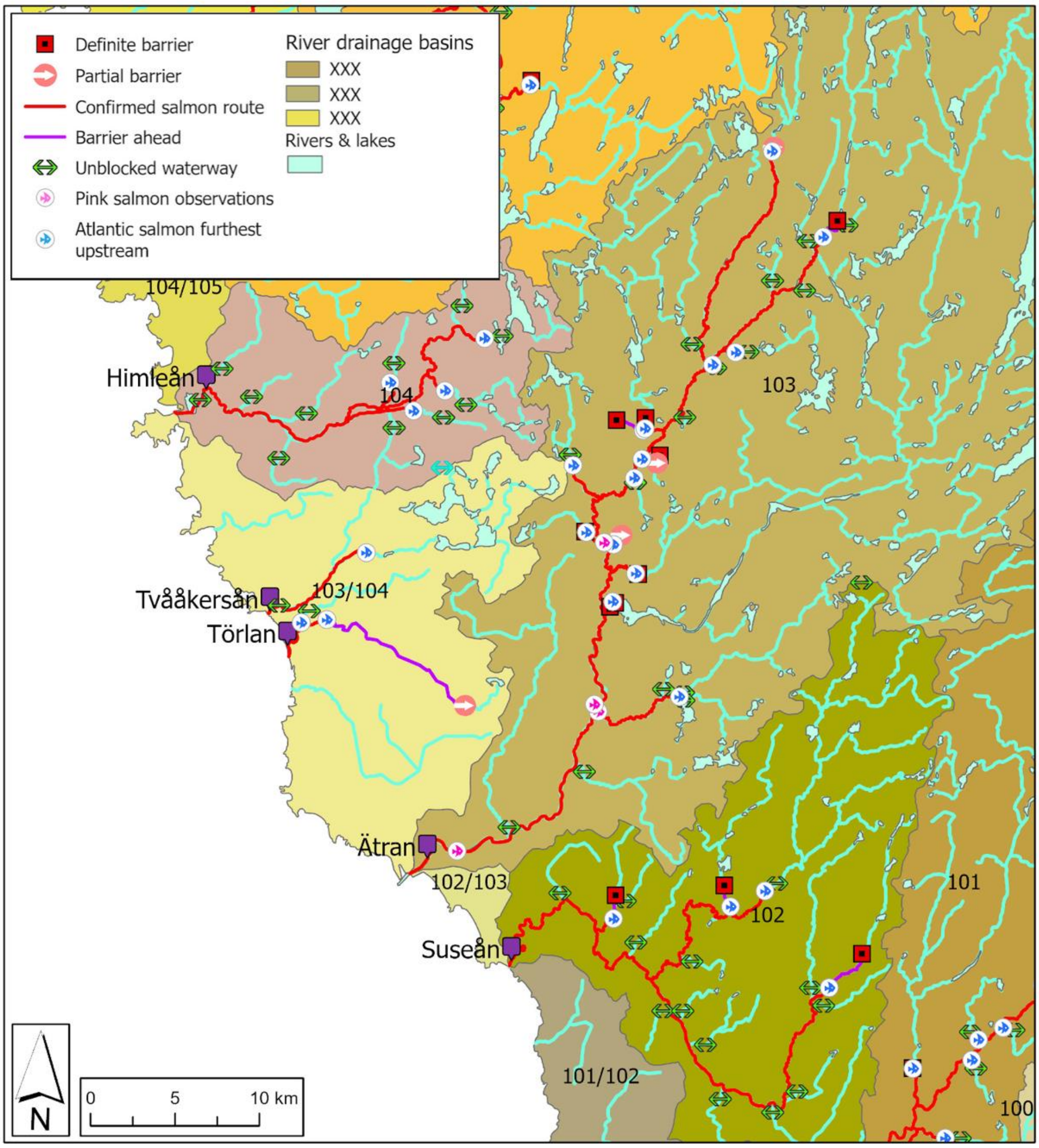

Figure 11. Potential migratory routes for pink salmon in Himleån, Tvååkersån, Törlån. Ätran and Suseån.

3.2.6 Nissan, Fylleån, Genevadsån, Lagan and Stensån

Atlantic salmon are regularly observed by fishing surveys in Nissan and its tributaries (fig. 12). The mainstem flows down the western side of the RDB and is blocked around 25 kilometres from the river mouth (fig. 12). The tributary Sennan to the southeast is also blocked leaving only the very southeasterly extent, roughly eight percent, of the c. 145 kilometre long drainage basin open (fig. 12; table 3).

Approximately halfway up the mainstem of Fylleån is a barrier about which information is lacking so a cautious interpretation has been made and it is classed as partial (fig. 12). Both pink and Atlantic salmon have been observed in Fylleån and although these have occurred only downstream of the barrier precautious interpretation of these results leads to the conclusion that almost the entire RDB is deemed accessible to migrating pink salmon (fig. 12; tables 2 & 3).

In Genevadsån's drainage basin there are only two definite barriers and these do not block substantial parts of the basin; this RDB is largely unblocked to pink salmon and Atlantic salmon have been observed far into the basin at 26 kilometres upstream (fig. 12; table 3).

Lagan's RDB is the second largest in the study (6445 km^2) (table 3). It is around 165 kilometres long but most of it is barred by definite barriers, the most effective being in Lagan's mainstem at Laholm's hydropower station around 15 kilometres from the rivermouth which blocks access to all of the RDB apart from the very southern edge (fig. 12; table 3). Lagan is also the southernmost river to witness pink salmon migration in recent years (fig. 12; table 2): an individual was caught c. 7.5 kilometres from the Lagan's rivermouth in 2021 and there was also an observation in this river in 2017 although details are lacking.

Stensån has a short narrow drainage basin which is mostly unblocked and where Atlantic salmon have been observed relatively close to the basin's inner extent around 37 kilometres upstream (fig. 12; table 3).

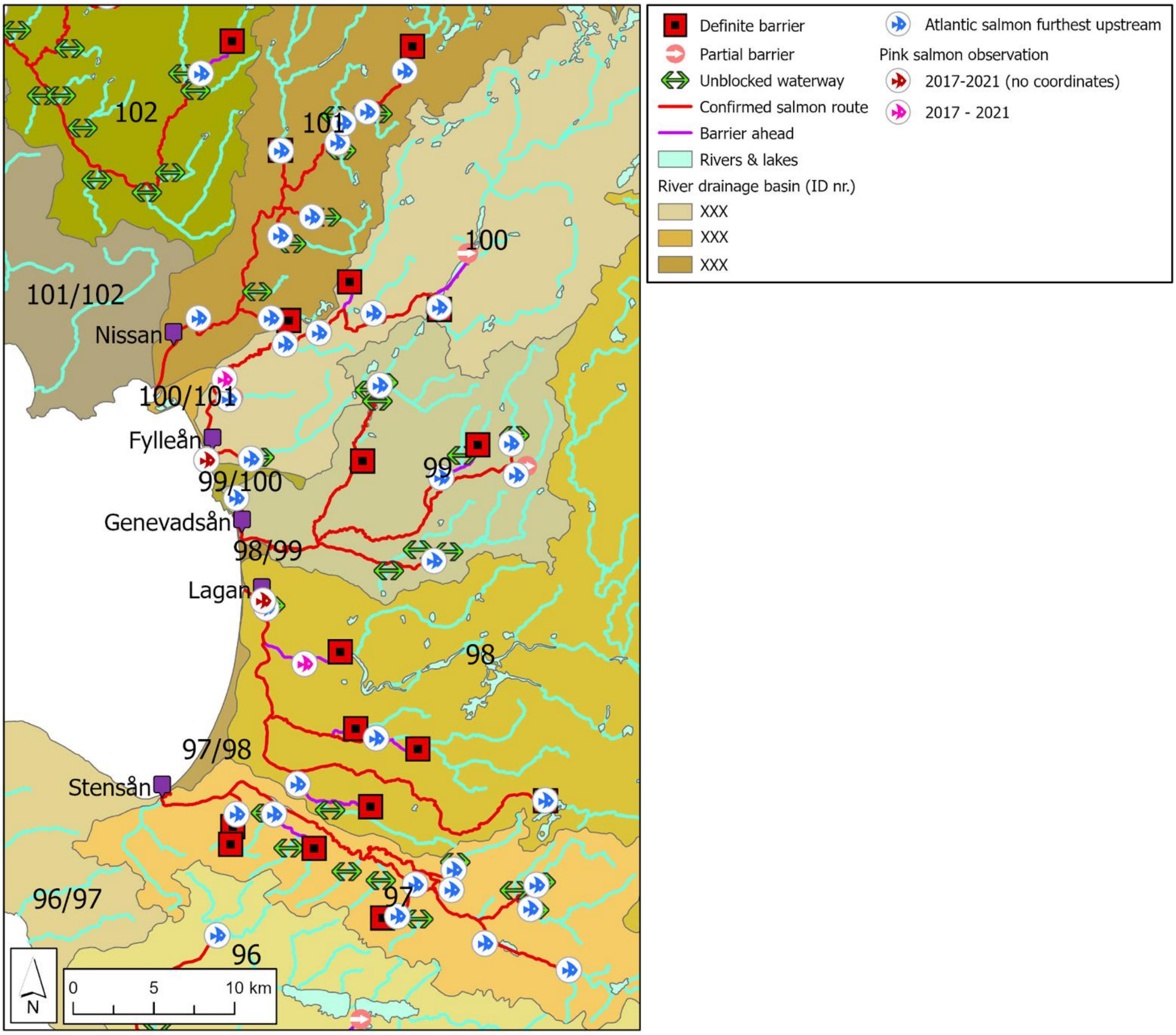

Figure 12. Potential migratory routes for pink salmon in Nissan, Fylleån, Genevadsån, Lagan and Stensån.

3.2.7 Rönne å and Rååån

Rönne å is the most southerly west coast river studied and Rååån marks the crossover to the study's south coast rivers.

Much of the northern half of Rönne å's drainage basin is interpreted as accessible to pink salmon (fig. 13). A dam at Forsmöllan in the mainstem restricts access into the south of the RDB, although many tributaries downstream (north of the definite barrier) remain unblocked (fig. 13) leaving around 33 percent of the RDB accessible to pink salmon (table 3). Atlantic salmon are regularly observed all the way up to definite barriers (fig. 13), the furthest upstream at 61 kilometres from the rivermouth (table 3).

Rååan is unblocked (fig. 13), this drainage basin is the smallest in the study (193 km^2) (table 3).

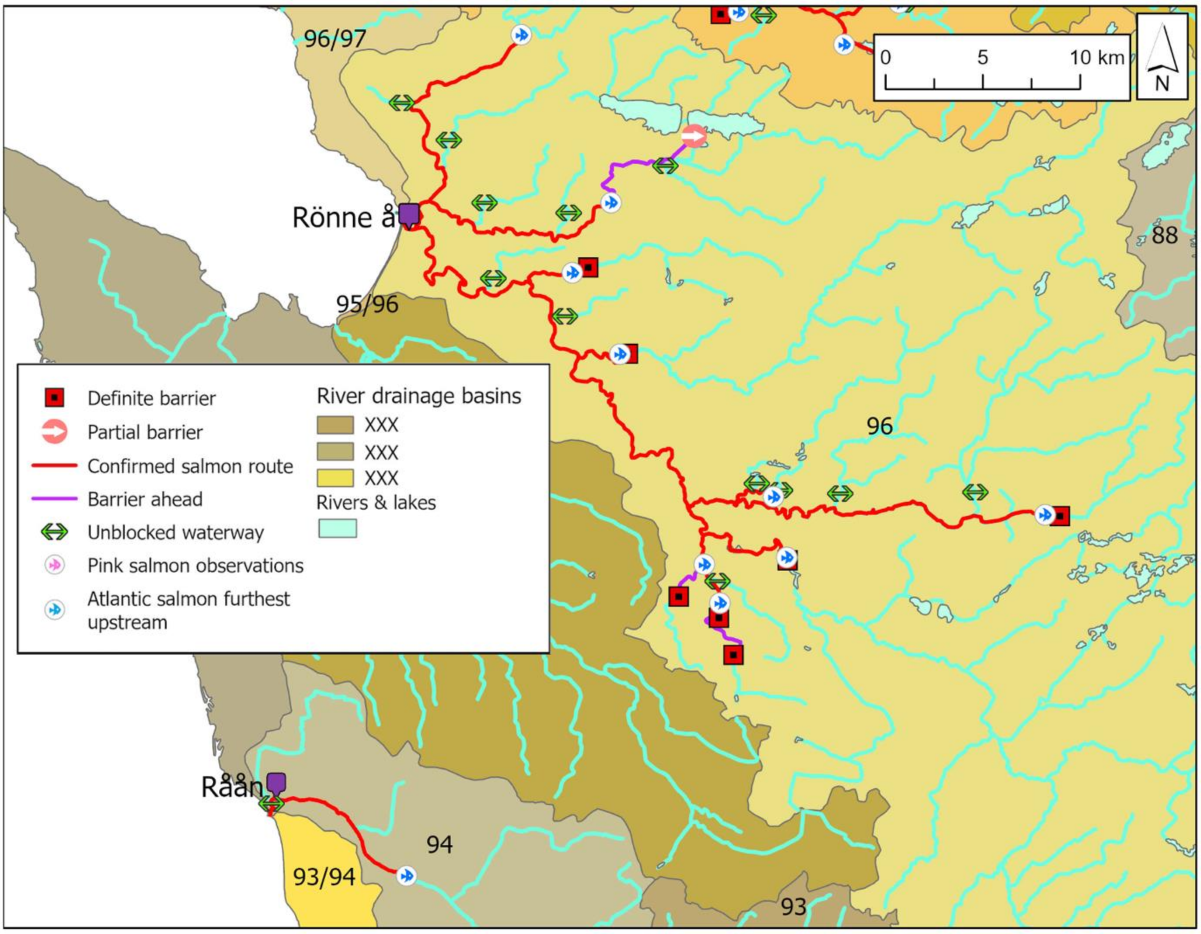

Figure 31. Potential migratory routes for pink salmon in Rönne å and Råån.

3.2.8 Kävlingeån and Nybroån

Much of Kävlingeån's drainage basin is blocked by definite barriers leaving only a small section of accessible waterways, these join the mainstem between around 25 to 35 kilometres upstream from the rivermouth (fig. 14) and result in roughly 20 percent of the RDB being open to pink salmon (table 3).

Nybroån is totally unrestricted to migrating pink salmon (fig.14).

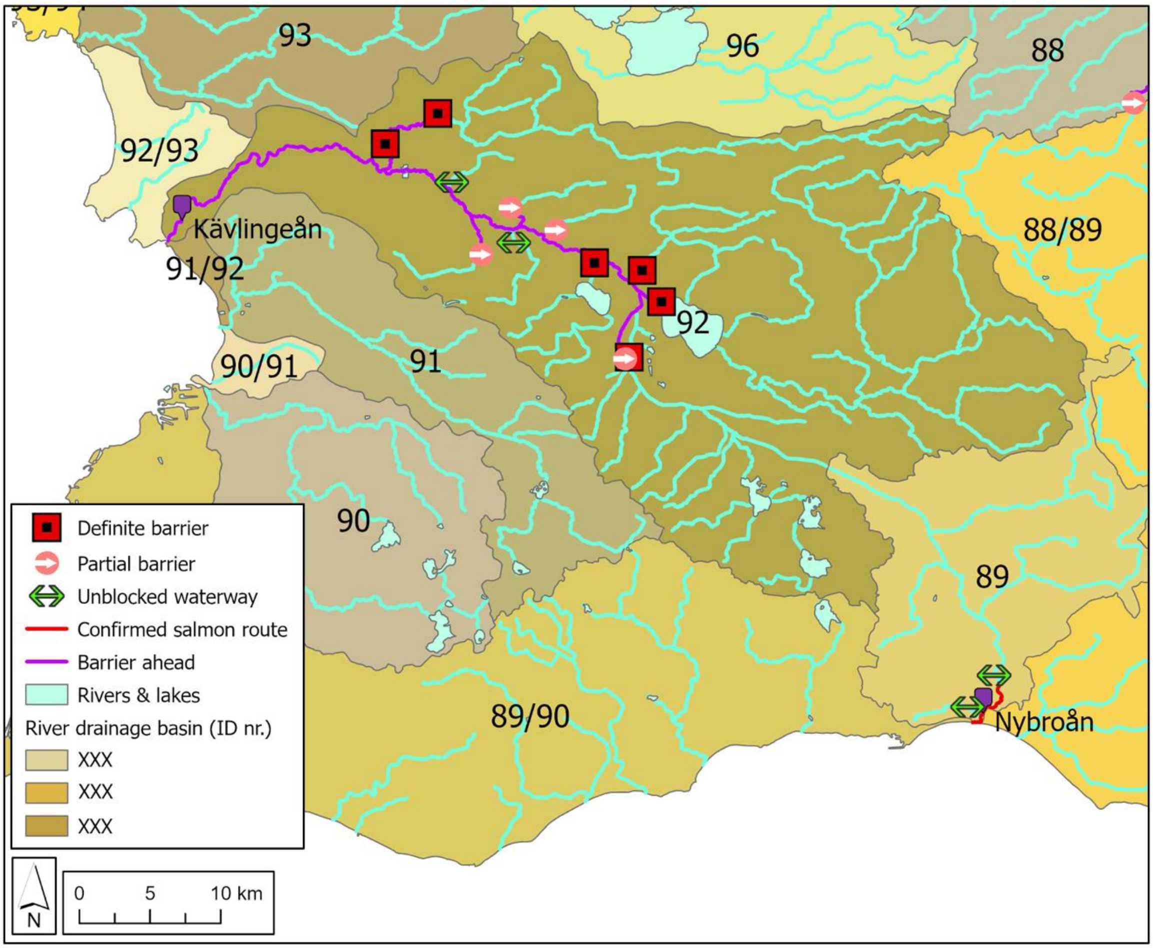

Figure 32. Potential migratory routes for pink salmon in Kävlingeån and Nybroån

3.2.9 Helge å and Mörrumsån

The very south of Helge å's drainage basin is accessible to pink salmon (fig. 15) but this does not account for a large proportion of the entire RDB, which is the study's third largest (4 720 km^2) (table 3). A dam blocks the mainstem c. 60 kilometres from the river mouth and two other tributaries are also barred by dams a little further into the 135 kilometre long RDB (fig. 15; table 3). Atlantic salmon have been observed in the vicinity of these dams, 71 kilometres from the rivermouth (fig. 15; table 3). This distance represents the second highest recording of Atlantic salmon furthest upstream in the study (table 3).

Towards the rivermouth, Mörrumsån's river basin is very narrow and only a relatively small stretch of the mainstem is open to pink salmon, leaving an estimated 8 percent of the realtively large (3 366 km^2) RDB accessible (fig. 15; table 3). Definite barriers occur at Fridafors, around 50 kilometres into the RDB near which Atlantic salmon have been observed (fig. 15; table 3).

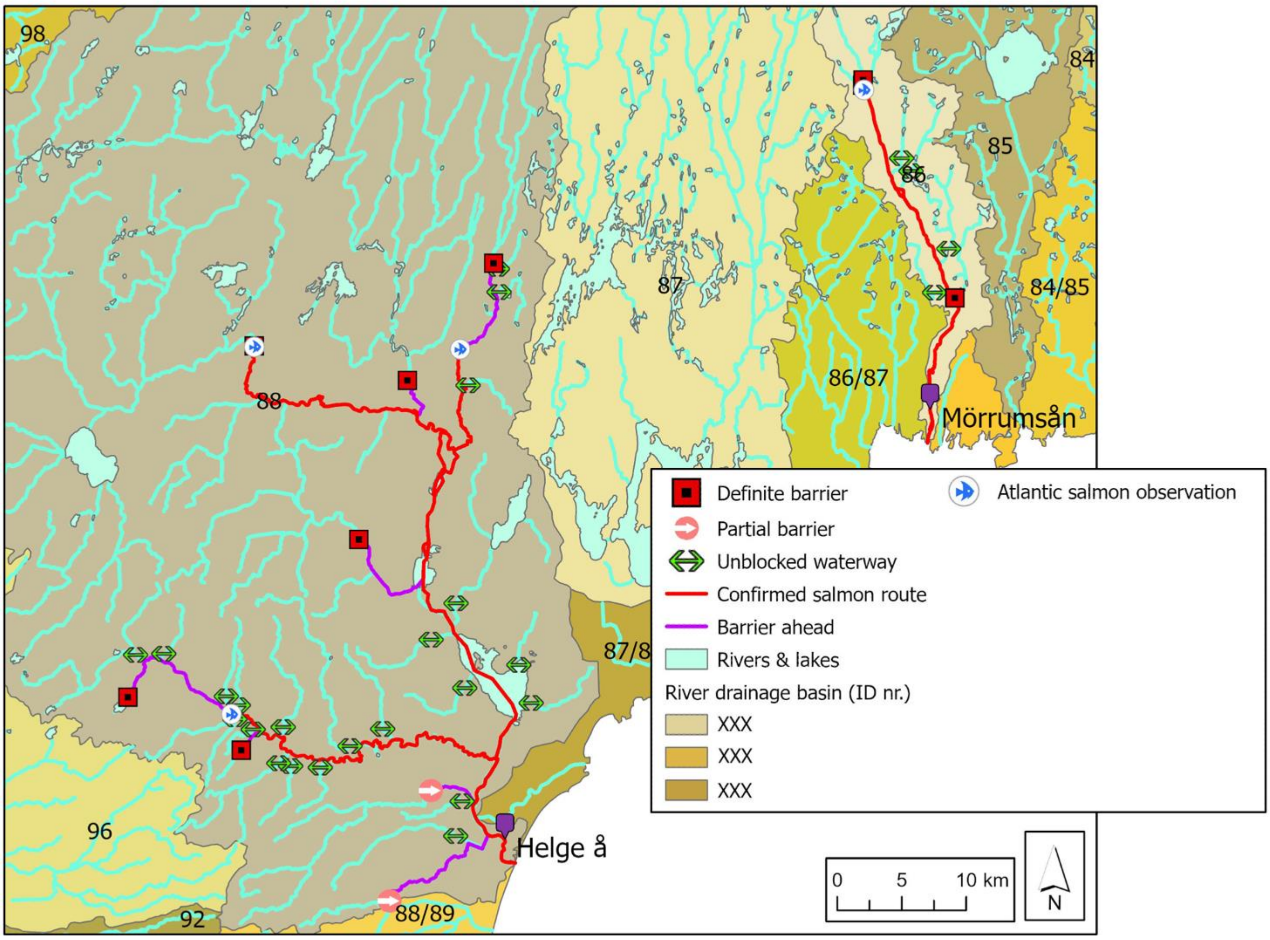

Figure 47. Potential migratory routes for pink salmon in Helge å and Mörrumsån.

Table 2. Pink salmon observations in Sweden 2017 – 2021, by river, site and distance upstream from rivermouth (data source: Petersson et al. (2018); Staveley & Ahlbeck Bergendahl (2022); Blomberg (2021)).

River	**Site**	**Distance from rivermouth, km**	**Nr. Pink salmon observed**		
			2017	**2019**	**2021**
Ätran	Herting	4	18	5	45
	Vessingebro	21	1		1
	Nydala	35	1		2
Säveån	Unknown	n/a			4
Göta älv	Trollhättan	78			4
	Lilla Edet	56	20		3
Örekilsälven	Unknown	n/a			10
	Kvistrum	3	2		
Fylleån	Unknown	5	1		
Enningdalsälven	Unknown	n/a			1
Lagan	Unknown	n/a	Unknown		
	Laholm	7.5			1
Viskan	Unknown	n/a	Unknown		
Coastal	Ljungskileviken	n/a	1		

Table 3. An overview of each river studied: the RDB ID nr.; mean annual discharge at the rivermouth for 2010-2021 (SMHI u.d.); distance upstream (from rivermouth) of furthest upstream Atlantic salmon observations; occurrence of pink salmon observation 2017 – 2021 (data source: Staveley & Ahlbeck Bergendahl (2022); Petersson et al. (2018)).

River (RDB ID nr.)	**RDB Area, km^2**	**RDB length, km**	**Mean annual discharge, m^{3}s^{-1}**	***S. salar* furthest upstream, km from rivermouth**	***O. gorbuscha* observed in RDB (2017-2019)**	**Proportion of RDB unblocked, %***
Anråse a (108/109)	n/a	n/a	2	9		n/a
Aröds å (108/109)	n/a	n/a	0.5	2		n/a
Bratteforsån (108/109)	n/a	n/a	1	4		n/a
Bäveån (109)	300	30	4	36		50
Enningdalsälven (112)	554**	40**	14	31	x	20
Fylleån (100)	393	45	8	27	x	80
Genevadsån (99)	228	25	4	26		80
Göta älv (108)	50 038	550	220	79	x	2
Helge å (88)	4 720	135	43	71		25
Himleån (104)	208	25	4	19		100
Kungsbackaån (107)	301	35	6	25		75
Kävlingån (92)	1 202	55	10	n/a		20
Lagan (98)	6 445	135	82	39	x	8
Löftaån (105/106)	n/a	n/a	3	17		n/a
Mörrumsån (86)	3 366	130	27	32		8
Nissan (101)	2 683	145	47	35		8
Nybroån (89)	316	30	3	n/a		100
Rolfsån (106)	692	60	14	68		50
Råån (94)	193	20	2	9		100
Rönne å (96)	1 894	80	21	61		33
Stensån (97)	284	35	4	37		80
Strömsån (111)	257	30	4	18		67
Suseån (102)	449	30	8	44		75
Säveån (108)	n/a	n/a	n/a	36	x	n/a
Tvååkersån (103/104)	n/a	n/a	2	8		n/a
Törlan (103/104)	n/a	n/a	1	5		n/a
Viskan (105)	2 200	105	43	73		33
Ätran (103)***	3 339	155	60	69	x	25
Örekilsälven (110)	1 338	70	24	9	x	67

* Rough estimate - using area of RDB (SMHI u.d.) and Measure tool in ArcGIS Pro ®, © ESRI.
** 554km^2 of the area and c. 40 km of the length of Enningsdalsälven’s drainage basin lies within Sweden, from the Norwegian border the river flows a further 15 km.
*** Ätran is home to two monitoring sites: a camera trap 4.3 km upstream at Herting; and the national monitoring site for *S. salar* 32 km upstream at Nydala in tributary Högvadsån.

Discussion

4.1 Discussion of results

4.1.1 Migrations far upstream

In contrast to behaviour in the native range where they spawn low down in river systems (Quinn 2018), pink salmon have been observed nearly 80 kilometres upstream Göta älv at Trollhättan. These Swedish findings reflect a number of other pink salmon observations around the North Atlantic where individuals have occurred tens of kilometres upstream in Norway and as far as 81 kilometres in Scotland (Mo et al. 2018; Armstrong et al. 2018). Sandlund et al. (2019) states that pink salmon spawning in larger rivers may occur hundreds of kilometres upstream. These sites are therefore vulnerable to the impacts that hosting pink salmon spawning may entail, that is to say the *effect aspect* of the species' niche (Shea & Chesson 2002). With regards to pink salmon far upstream Swedish rivers this concerns primarily three factors: overlapping of desired spawning sites between pink salmon and native species; pink salmon dying after spawning; and fry spending time in river systems.

Competition for redd sites

Atlantic salmon and brown trout naturally spawn further upstream than pink salmon are usually seen to do in their native range (Petersson et al. 2018; Quinn 2018). Longer migration by pink salmon means that, compared to expectations based on native range behaviour, they are more likely to use the same spawning grounds as indigenous salmonids. In line with timing in their home range, pink salmon in Norway have been seen to migrate and spawn earlier than Atlantic salmon and trout (Sandlund et al. 2019; Mo et al. 2018)). This in itself may bode well for the native species if they are able to disturb pink salmon redds in the process of spawning themselves. That said, pink salmon are seen to guard their redds post-spawning, exhibiting aggressiveness towards other fish (Mo et al. 2018; Quinn 2018). It is even plausible that this may affect migrating salmon and trout attempting to reach sites upstream of spawning pink salmon. Pink salmon laying claim to redd sites in this manner could lead to native species being forced to spawn at less suitable sites, at least for the first weeks of the spawning period, and consequently lower rates of embryo survival to hatching for Atlantic salmon and brown trout (Sandlund et al. 2019).

This would illustrate the effect aspect of pink salmon taking to their ecological niche in the novel range, (out-competing natives for redd sites), expressing itself in the response aspect of indigenous salmonids (lower birth rate) (Shea & Chesson 2002). It also echoes the elements of propagule pressure: pink salmon in this scenario occupy and defend the better spawning grounds and in doing so give their offspring a greater chance of survival and hence better odds of returning in greater numbers (increased propagule size) to spawn later (repeated arrivals: propagule number) (Simberloff 2009).

Pink salmon carcasses

The energy expended by pink salmon on parental care, expressed as redd-guarding, is afforded to this species due to their semelparous nature whereby all energy reserves are available for devotion to one single spawning event (Quinn 2018). Another aspect of semelparity is that all pink salmon individuals die shortly after spawning and their carcasses decompose in the vicinity of spawning grounds. This phenomenon transfers large quantities of nutrients and energy, taken up by the fish during the rapid growth stage at sea, to the river systems and the ecosystems the spawning grounds are part of. In other words, these systems that naturally drain nutrients away from the landscape rapidly become considerable sources of nutrients (Quinn 2018).

Rivers in pink salmon's native range are often nutrient poor and this nutrient transfer via carcass decomposition can deliver significant benefits to ecosystems (Quinn 2018). It is not impossible that the same could be true for rivers in northern Norway as they share similar nutrient poor profiles (Mo et al. 2018). This would probably not be the case for the south of Sweden which is home the country's most intensive agriculture. Here, eutrophication is a problem or a risk in many waters, especially lower down in systems and lakes draining many rivers (Länsstyrelserna n.d.). Whatever the status of the rivers, it follows that extra nutrients contributed to the ecosystem constitute an effect and may alter ambient productivity and nutrient cycling that native species are well-adapted to, a challenge to local biodiversity lifted by Hawkins et al. (2015). However, the amount of nutrients transferred upstream by pink salmon may need to be rather considerable in order to be significant: Although Atlantic salmon are known to be iteroparous, the actual proportion of individuals in each population spawning twice or more is far from 100 percent and dying shortly after spawning is widespread even in Atlantic salmon (Persson et al. 2023).

A recent study by Persson et al. (2023) investigated Norwegian salmon and showed that the proportion of repeat spawners varied from zero to 26 percent between populations. This indicates that pink salmon carcasses in Swedish rivers do not pose a novel impact on spawning grounds and their ecosystems but that the situation in each RDB must be closely monitored with regards to the numbers of pink salmon relative to numbers of Atlantic salmon. This relates to pink salmon not being limited at spawning grounds by the same resources as native salmonids due to the fact that fry rely on neither nourishment nor shelter there (Quinn 2018). As a consequence, pink salmon, limited only by space for redds, can spawn in extremely dense numbers which could potentially cause nutrient transfer to become a significant impact on productivity.

Fry spending time in rivers

One more cause of potential problems due to pink salmon spawning far upstream is that, as a result of hatching farther upstream than in the native range, pink salmon fry would naturally spend longer in the river system (Sandlund et al. 2019). In contrast to their negligible impacts on rivers in the home range (Quinn 2022), other species would be exposed to the effects of pink salmon fry feeding during the time spent migrating downstream to the coast, e.g., predation and competition interactions. The concept of propagule pressure would then dictate that the longer the journey and the more numerous the fry, the more these interactions may have negative consequences for native species of the river systems involved and hence the greater the likelihood that pink salmon could establish there.

4.1.2 Migration to Lagan

In recent years, the most southerly pink salmon observations in Sweden have been made in the Lagan, a large river, (82 m^3s^{-1}), in Halland county. Lagan's rivermouth lies close to the south coast of Sweden, around 100 kilometres from Öresund bridge which marks the border between the North Sea and the Baltic Sea (Google Maps n.d.). It is currently thought that pink salmon have established only in eastern Finnmark county (Sandlund et al. 2019), if this is correct then these rivers must represent the closest possible natal source of pink salmon migrating to Lagan. The distance by sea from the coastal waters off Finnmark to the Lagan's rivermouth is around 2 500 kilometres (Google Maps n.d.). Note that this is not the farthest pink salmon individuals from these populations appear to have strayed, with observations occurring as far away as the east coast of Canada (ICES 2022). This mirrors Quinn's (2018) sentiments that pink salmon in their natural range are seen to stray considerable distances and furthermore, that an even higher degree of straying may be witnessed in the early stages of colonising. Berntsen et al. (2022) showed that the spread of pink salmon has been progressively moving eastward from the southwest coast of Norway, with higher abundances of pink salmon seen on Norway's south coast in 2021 than in 2017. The odd finding of pink salmon at in the Lagan appears to concur with this illustration of the invasion front, where pink salmon are attracted to larger rivers (Berntsen et al. 2021). Although, as discussed below, reliable data on abundance of pink salmon is lacking so comparisons of mean annual discharge and pink salmon abundance are not yet possible in Sweden.

4.1.3 The camera trap at Herting

The River Ätran was home to the most pink salmon observations from 2017 to 2021 although these high numbers are due to the camera trap at Herting, four kilometres from the river mouth (Staveley & Ahlbeck Bergendahl 2022). The trap allows for simple and effective counting and measuring of all fish passing the trap and salmon species may also be distinguished (Fiskdata n.d.). This means that the observations at Herting account for every pink salmon passing through - something that is not possible at other sites. This factor, in combination with the speculative nature of pink salmon research in Sweden at this time implies that for other rivers, as stressed by Sandlund et al. (2019), observations should be interpreted as mere indications of the bigger picture.

As previously noted, the national monitoring site for west coast Atlantic salmon populations is also located in this RDB, at Nydala on Högvadsån (Staveley & Ahlbeck Bergendahl 2022). In contrast to neighbouring Norway where abundance of pink salmon was seen to increase successively from 2017 to 2019 and then to 2021 (Mo et al. 2018; Sandlund et al. 2019), the number of observations at Herting mirrored other locations around the North Atlantic such as the UK and Ireland (Skóra et al. 2023). Other Swedish locations with pink salmon observations in both 2017 and 2021, e.g., Lilla Edet, did not always follow this pattern, indicating the importance of the Ätran's monitoring sites, especially Herting, in giving insight into the status of pink salmon in Sweden.

Whilst these figures may also be interpreted to reflect the situation across other RDBs, care must be taken to consider the varying conditions between drainage basins. Berntsen et al. (2022) highlight that a number of factors in combination appear to affect the abundance of pink salmon observed in a river including: the size of the river; the size of the native salmon population; and distance from the Russian border.

4.1.4 Annual mean discharge

High numbers of pink salmon in Göta älv may reflect findings by Berntsen et al. (2021) regarding the preference for larger rivers by migrating pink salmon at the invasion front. Results for this study show that mean annual discharge for the rivers where pink salmon observations have been made in recent years ranges from 8 – 220 m^3s^{-1}. In the study's second and third largest rivers, Lagan (82 m^3s^{-1}) and Ätran (60 m^3s^{-1}), very few pink salmon observations have been made in recent years (apart from at Herting). As most pink salmon recordings away from Herting are due to chance catches by members of the public (Staveley and Ahlbeck Bergendahl 2022), higher numbers of observations in Göta älv may reflect a bias in terms of fishing efforts or the spread of awareness and reporting. In addition, the low numbers of observations also indicate that the existing data are not sufficient to comment with any certainty on preference for larger rivers at the invasion front in Sweden.

4.1.5 Vulnerability in RDBs

By *vulnerability*, the study refers to how at risk each RDB is to potential impacts of pink salmon establishment. Berntsen et al. (2021) showed that river size, distance from the Russian border and the size of the native salmon population were important factors in the occurrence of pink salmon in Norwegian rivers. Data on these factors is easily accessed although this study has looked only at river size. Combining the results of this study with other factors affecting pink salmon migration in order to identify RDBs on a sort of vulnerability-scale would require dealing with a number of challenges and trade-offs. Subsequently, knowledge of the relative importance of the factors involved would be required. These are demands that cannot be met by this study. However, a number of other factors contributing to vulnerablilty in RDBs can be identified.

In terms of potential impacts to its ecosystems, the proportion of a river drainage basin accessible to pink salmon may be thought of as directly related to its vulnerability. According to the assumptions made for this study, native Atlantic salmon and migratory brown trout are constrained by the same limits as the pink salmon: they all share the same access. Hence, in terms of only this factor – all wild Atlantic salmon and migratory brown trout populations are equally exposed to pink salmon. It is therefore clear that vulnerability of RDBs in terms of their native salmonid populations, is not directly relative to the proportion accessible to pink salmon but probabaly moreso to the status of the native salmonid populations: Where, as Sandlund et al. (2019) indicate, weaker native salmonid populations are more vulnerable.

As the 2017 migrations in Norway proved, pink salmon young experiencing beneficial conditions result in large numbers of mature pink salmon returning and utilising rivers of all sizes (Sandlund et al. 2019). The increased abundance appears to be a positive feedback to a change in environmental conditions (Berntsen 2022), described by Simberloff (2009) as environmental *stochasticity* or unpredictability. Simberloff (2009) highlights the negative effects that environmental disturbances can have on the establishment of non-indigenous propagules but in this instance, the opposite reaction is seen: changes in the environment favour the alien species.

This indicates that identifying the most vulnerable RDBs should also consider different climate and environmental scenarios.

4.2 Limitations and assumptions

Data used refers to native species

As pink salmon are an alien species to the area of study, data on their closest native relatives has been used to interpret accessibility. Whilst it is clear from existing literature that salmonids do share many traits, it is also apparent that differences between species can be considerable (Gjedrem & Gunnes 1973; Klemetsen 2003; Quinn 2018). Factors particularly relevant to the interpretation of this study's results concern data dealing with passability of migratory barriers and fishways as salmonids have varying swimming capabilities.

Passability of migratory barriers is classified after brown trout which are on average around 1.5 times larger than pink salmon (Curry-Lindahl 1985; Quinn 2018). For fishways, if the target species was Atlantic salmon or brown trout then the study assumed that pink salmon are also capable of navigating it. Atlantic salmon are on average about twice as large as pink salmon (Curry-Lindahl 1985). It is likely that both brown trout and Atlantic salmon can navigate higher obstacles and higher rates of flow as maximum speeds and leaping heights in salmonids are positively correlated to length (Beach 1984).

This allows the results to maintain a degree of precaution with regards to large obstacles and fishways as assumptions have been made that pink salmon are capable of navigating the same obstacles as brown trout and Atlantic salmon. According to Simberloff et al. (2013) the whole aim of research on invasive alien species is to be precautionary, thus facilitating the prevention of negative impacts.

Data completeness and verification

Huisman and de By (2009) mention completeness as a component of spatial data quality; this refers to the capacity of the data to represent all relevant features of reality. Data regarding pink salmon observations have already been mentioned with regards to this issue but the remaining data sets also lack completeness. Electrofishing data represent points in time and space where salmon are confirmed to have been found although observations do not exclude the possibility that salmon are found elsewhere or at the same site at other times. Furthermore, data sets on migratory barriers and fishways are likely to be outdated in many instances, especially considering efforts in recent years to review and improve connectivity and environmental quality in river systems in line with EU legislation (HaV, Energimyndigheten & Svenska kraftnät 2019). Verification of these data sets for the entire study area would have been extremely time-comsuming which, in tandem the project's aim to analyse all 29 selected rivers, was not a possibility within the timeframe at hand.

In addition to the question of completeness in the electrofishing data it is assumed that all plausible Atlanctic salmon observations are the result of migration to spawn or of successful, *in situ* spawning. This may however not be the case as a number of rivers (i.e., Göta älv, Lagan and Nissan) host smolt releases (HaV 2022). If this was to be an issue at a later time then comparison of electrofishing data with information on smolt releases would allow for verification.

Generalisation

As each RDB must be separately investigated, generalisation of these results beyond the rivers studied is not possible. Potential migration routes for pink salmon can be said to depend on connectivity. However, potential impacts rely on many other factors including interaction between pink salmon and its novel environment and with other species as well as the physical conditions of the RDB.

4.3 Improvements and further research

A few simple although time consuming improvements to this study could contribute greatly to the usefulness of its results. Verification of existing data, as mentioned above, is one example. In addition, more detailed investigation of electrofishing data, in combination with information from population status reports could highlight important sites for native salmonids giving further indication of vulnerability.

The volume and characteristics of data currently available for pink salmon in Sweden do not allow for statistical analysis. This study demanded speculative conclusions in hope of facilitating precautionary prevention strategies. That said, lack of species-specific information led to extremely precautious interpretation of results. This was felt, in part, to benefit the study. However, further investigation of both migratory barriers and the swimming abilities of pink salmon are aspects where more detail could provide a far better idea of the migratory possibilities for pink salmon.

A direct development of this study would be more precise calculations of the accessible proportions of each RDB. This could be readily achieved by creating a new layer in GIS where more intricate polygons are formed over the accessible or inaccessible parts of the RDB whereby GIS can then calculate their area.

A natural next step for research into potential pink salmon establishment would be to perform the modelling utilised by Berntsen et al. (2021) to predict future spreading in west and south coast rivers in Sweden. In combination with the eDNA sampling planned by the research project, Pink salmon in Sweden (Staveley & Ahlbeck Bergendahl 2022), this could create a much more comprehensive picture the current and future trends in pink salmon distribution compared the the Swedish data available at this point in time. By highlighting vulnerable RDBs, this would also facilitate the prioritising of sites for deployment of measures against pink salmon migration.

Conclusions

The appearance of pink salmon in Swedish waters in any discernable abundance is such a recent phenomenon that their distribution and occurrence is estimated to be vastly underestimated by the existing data. This study shows that river drainage basins on the west and south coasts of Sweden vary greatly in their accessibility and vulnerability to pink salmon migration.

Accessibility for pink salmon is assumed to match that for native anadromous salmonids whereas vulnerability depends on a variety of combining factors. These factors include easily obtainable data such as proximity to the source populations and the size of the river, but they also encompass many other biotic and abiotic aspects of river drainage basins that are much more difficult or time-consuming to investigate. In addition, the existing data on pink salmon observations in Sweden is too incomprehensive to draw definite conslusions on the actual distribution of the species.

Potential impacts of pink salmon spawning in the routes identified by the study are mostly concerned with adults spawning farther upstream than expected from behaviour in the native range. For example, competition for redd-sites could negatively impact native species' birth rate and decomposing carcasses of post-spawned pink salmon pose a threat to nutrient-loaded river systems, especially considering pink salmon's capacity for spawning at high denisties.

The prospect of intentionally introduced pink salmon resulting in established populations in Sweden highlights the combination of challenges forced upon natural systems by humans, including nutrient loading and fishing pressures. It is however, quite paradoxically, man-made barriers in the form of hydropower dams that currently constitute the largest preventative measure to pink salmon spreading in most river drainage basins.

Further research should combine modelling with eDNA sampling and use the most comprehensive data that time allows for in order to inform the most appropriate action for each RDB. It is hoped that the precautious nature in which the results of this study were interpreted contributes useful information to the next stages of work in this field.

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