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RESEARCH ARTICLE

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Reintroducing Atlantic salmon in the river Rhine for decades: Why did it not result in the return of a viable population?

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Abstract

Freshwater species biodiversity is under threat. The average global decline for migratory fish species is estimated to be more than 75% since 1970. Atlantic salmon is one of these species with a steep decline in north-western Europe and it even went extinct in the river Rhine in the 1950s. The causes for this decline have been posted to habitat loss, pollution, climate change and overfishing. Annual stocking in the Rhine since the late 1980s resulted in an initial increase in the Atlantic salmon numbers after which numbers collapsed again. In this paper, we lay out the recent decline, estimate losses of smolts and adults at different sections in the freshwater habitat and elaborate on potential causes of the recent decline and these losses. We found that the salmon population of the river Rhine has declined rapidly over the past two decades, with a current estimated spawning population of only ~350–800 individuals. The percentage of salmon smolts returning as adults to spawning grounds is estimated at 0.5%–0.6%, well below the 3% supposedly needed to maintain a self-sustaining population. Many individuals disappear during their migrations, with the highest percentage of smolts disappearing in the German tributaries (44%) and the Dutch lower Rhine (71%), while the percentage of disappearing adults is highest in both the Dutch (74%) and the German (78%) Rhine. Causes for the losses per river section remain unclear and possible threats, some specific to the river Rhine, are being discussed. The large losses of smolts and adults in inland waters, compared with open sea losses, indicate that restocking the river Rhine might only result in a self-sustaining population with more ecological restoration than carried out so far along the intensively shipped and highly regulated river course and associated high levels of predation, and might be increasingly limited by future climate change.

KEYWORDS
freshwater mortality, predation, reintroduction, return rate, salmon stocking, self-sustaining population, (smolt) migration

1 | INTRODUCTION

Worldwide, freshwater biodiversity is under severe threat, showing decline rates that are higher than those of marine or terrestrial biodiversity (Harrison et al., 2018; WWF, 2018). These declines are mainly caused by five events: overexploitation, water pollution, flow modification, destruction or degradation of habitat, and invasion by exotic species (Dudgeon et al., 2006). All five are directly applicable to migratory freshwater fish, which, compared with other fish groups, are disproportionately threatened (Darwall & Freyhof, 2015). Globally, migratory freshwater fish, based on the Living Planet Index, have declined by an average of 76% between 1970 and 2016 (Deinet et al., 2020). In Europe, the average decline is even more pronounced with 93% in the same time period (Deinet et al., 2020). This includes diadromous species from the Eastern Atlantic like Atlantic salmon (*Salmo salar*), twaite shad (*Alosa fallax*) and allis shad (*Alosa alosa*) from the river Rhine in the Netherlands where the reported declines have been around 99% (Limburg & Waldman, 2009).

The Atlantic salmon is an iconic migratory fish and its historic population decline in north-western Europe has been studied in detail. At the end of the 1800s, adult salmon numbers in the Rhine system were at least in the 100,000 s, if not considerably more, making the Rhine system one of the most important salmon rivers in Europe (Ingendahl & Beeck, 2011; Lenders, 2017; Lenders et al., 2016). Around the turn of the previous century, salmon declined dramatically, despite stocking programmes that already took place during that time (Lenders, 2017). In the 1950s, like in other adjacent river systems (e.g., Elbe, Thames, Weser), salmon went extinct in the Rhine. Factors driving this extinction were chemical pollution (and with it the deterioration in water quality), obstructions in its migration routes, overfishing and loss of spawning areas (ICPR, 2015).

In the early 1970s, pollution levels had peaked in the river Rhine and since then water quality has significantly improved due to joint efforts of the riparian states that resulted in the upgrading and construction of new sewage treatment plans (Mostert, 2009; Uehlinger et al., 2009). The water quality improvements resulted in the initiation of a salmon reintroduction programme in 1988 where young salmon of different stages were released in the Rhine on a yearly basis. Between 1998 and 2009, 1–3 million young salmon per year were released (Ingendahl & Beeck, 2011), and this stocking of millions of young salmon is continuing till the present day. In 1990, the first adult salmon was caught again in upstream parts of the Rhine, and in 1994, the first occurrence of natural reproduction was documented (Ingendahl & Beeck, 2011). Despite these initial small successes, the current numbers of returning adult salmon (500–1000 in the main spawning areas) are believed to be too low to establish a self-sustaining population (Bijlsma et al., 2019; Ingendahl & Beeck, 2011; Schneider, 2011).

In this paper, we lay out the recent further decline, pinpoint where most disappearances of smolts and adult salmon occur and elaborate on possible contributing factors to these losses. Salmon on their way to their spawning sites in the upper reaches of the Rhine can migrate from the sea passing the Netherlands via three possible routes: (i) a northern route via the Wadden Sea, Lake IJsselmeer and the river IJssel down south to the main Rhine River branch, or a western route (ii) via the Haringvliet, or (iii) via the Nieuwe Waterweg (Figure 1). The latter is currently the only freely accessible route via seaport Rotterdam, whereas the Haringvliet and IJsselmeer can only be accessed by passing tidal gates. Spawning mainly takes place in the German section of the Rhine and in the tributaries Sieg, Dhünn, Wupper, Ahr, Saynbach, Nette, Agger and Wisper (Figure 1), but is also indicated for the Kinzig, Speyerbach and Wieslauter (A. Schrimpf, unpublished data), and to a lesser extent in France, for example, the tributaries Bruche and Lauter (ICPR, 2015). The Swiss part of the river Rhine also offers suitable spawning grounds, but these are mostly inaccessible. Based on telemetry data of migrating salmon smolts and adults, and numbers of young salmon released in stocking programmes, the size of the salmon population and mortality rates along these migration routes were estimated.

2 | MATERIALS AND METHODS

2.1 | Population trend

Since 1994, adult salmon and sea trout are monitored using salmon fyke nets designed to catch salmonids, during summer (June, July) and autumn (October, November), two periods of known salmon migration. For the trend of salmon through time, we selected data from the location of the river Waal (part of the river Rhine, Figure 1) as most salmon migrate through this river branch (Hop & Vriese, 2018). We selected data from 1997 onwards as fishing effort was not recorded before 1997. The catch per unit effort (CPUE) was calculated by summing the total number of salmon caught per year, divided by the total sum of the effort of that year. Effort is defined as the (number of gears * duration in hours)/24 h, resulting in the number of fyke net days.

2.2 | Population estimation

To estimate the number of salmon migrating from, and returning to, their spawning grounds, numbers of stocking programmes (provided by the International Commission for the Protection of the Rhine, ICPR) and data from telemetry studies were used. These telemetry studies made use of a unique infrastructure of detection stations to track tagged salmonids (NEDAP trail system) in the Netherlands and Germany. This infrastructure has been used to track upstream migrating adult salmonids since 1997 (Bij de Vaate & Breukelaar, 2001; Hop & Vriese, 2018; van Giels & Breukelaar, 2011; van Giels & Vriese, 2016; Vriese & Breukelaar, 2011). For this paper, data from 2001 to 2016 was used where 926 sea trout and 195 salmon were caught, tagged and released on the North Sea side (Voordelta) of the Haringvliet sluices near Stellendam (Hop & Vriese, 2018; van Giels & Breukelaar, 2011; van Giels & Vriese, 2016). In the period 2006–2016, 1305 salmon smolts were tagged and released in the rivers Sieg

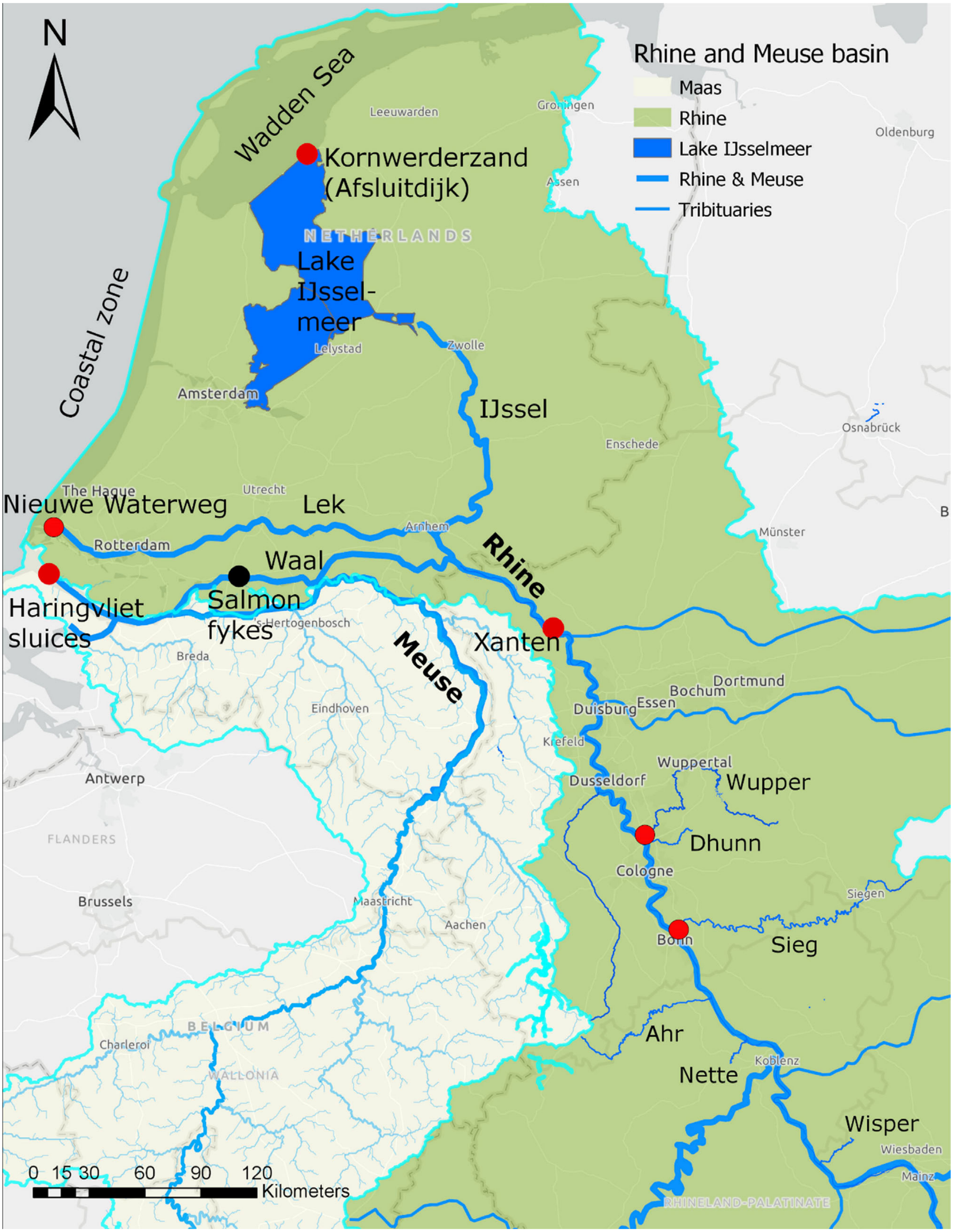

FIGURE 1 Map of Rhine and Meuse delta with the 11 different segments corresponding to different water bodies and river parts (1) Wadden Sea, (2) Lake IJsselmeer/Afsluitdijk, (3) river IJssel, (4) North Sea coastal zone, (5) Nieuwe Waterweg, (6) River Lek (Nederrijn), (7) Haringvliet sluices, (8) river Waal, (9 and 10) river Rhine (Dutch & German part), (11) Spawning grounds and major stocking tributaries (e.g., rivers Sieg, Wupper, Dhünn). Red dots indicate five important detection stations (Haringvliet sluices, Nieuwe Waterweg, Wadden Sea, Xanten, Wupper mouth, Sieg mouth), and black dot indicates the location of the salmon fyke monitoring in the river Waal. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Number of smolts tagged and detected per year.

Year	Tagged (*n*)	Detected (*n*)	Detected (%)
2006	10	5	50
2007	78	61	78
2008	120	80	67
2009	120	73	61
2010	120	86	72
2011	195	75	38
2012			
2013	120	52	43
2014	149	50	34
2015	194	120	62
2016	199	128	64
Total	1305	730	56

Note: No smolts were tagged in the year 2012.

(15.3 km from the detection station), Dhünn (8.9 km from the detection station) and Wupper (22.4 km from the detection station) to track their downstream migration towards the sea using the same infrastructure (Table 1).

To estimate salmon losses along their migration route, the Rhine delta was divided into 11 different segments corresponding to different water bodies and river parts (Figure 1). The telemetry data were then used to calculate which percentage of up−/downstream migrating salmon passes each segment.

2.3 | Smolts

Each year, several million salmon from different life stages are stocked in Germany, France, Luxembourg and Switzerland. Most of these salmon are still fry or parr when they are stocked. The different life stages of the stocked salmon make sure that not all of these individuals migrate downstream that same year as smolt. The ICPR developed a method to assess how many of these stocked fry/parr numbers attribute to migrating smolt numbers, the so-called 'smolt equivalents' (ICPR, 2009). In this article, we used the average yearly stocking data from 2010 to 2021 to calculate the number of smolts, based on smolt equivalents, that passes each segment.

In addition to stocking, natural spawning takes place in these rivers as well. Numbers of smolts from natural spawning were estimated from yearly electrofishing surveys (before stocking occurs) in the rivers Ahr, Sieg and Saynbach over the period 2010–2021 (Jörg Schneider, personal communication) and were averaged per year. Sampling took place in accessible spawning habitats. Population densities of naturally occurring young-of-the-year were projected according to estimated catch rates. In some cases, habitat-specific catch rates were calculated using the removal method (three successive fishing efforts). These numbers were added to the yearly number of smolt equivalents. It should be noted that a recent genetic parental analysis showed that the amount of smolts from natural spawning varies strongly between rivers and years. Preliminary data suggest that the percentage of smolts that originate from natural spawning ranges from less than 10% up to 50% of the collected fish samples (A. Schrimpf, unpublished data). This means that our estimates of natural spawning should be taken as an order of magnitude.

This provided us with a rough (maximum) estimate of the number of smolts that start their downstream seaward migration. The minimum number of smolts that start migrating was calculated by using the percentage of tagged smolts that are detected entering the river Rhine at the mouth of the Wupper (56%, Vriese, 2018). The study of Vriese (2018) also provides the percentages of tagged smolts reaching every segment. Using these percentages, we estimated the number of smolts that reached each segment. None of the tagged smolts reached the exit point in the Afsluitdijk of Lake IJsselmeer, probably because the percentage of smolts migrating through the river IJssel is very low. To estimate the survival of smolts crossing Lake IJsselmeer, we used a range of 0%–27% of smolts coming from the river IJssel where the 27% is based on the survival of smolts in the downstream river branches.

2.4 | Adults

The numbers of returning adult salmon per segment are back-calculated from the number of adult salmon that reach the spawning grounds in Germany per year over the period 2010–2021 (monitoring data provided by ICPR). As it is estimated that 35%–75% of returning salmon are observed at these monitoring stations (Buisdorf, Agger, river Dhünn, Armin Nemitz, personal communication), we applied these percentages to estimate the total number of salmon reaching the spawning grounds on a yearly basis over the period 2010–2021. It should be noted that information on return rates at other rivers (e.g., Wupper) is lacking on this matter.

3 | RESULTS

3.1 | Trend of salmon population

From the start of the monitoring in the river Waal, the numbers of salmon increased up to 2002 (Figure 2). After that year, salmon numbers dropped till 2007. The numbers increased again in 2008 and remained relatively stable till 2013. From 2014, a strong decline is visible with hardly any salmon being caught within the monitoring in the last 7 years (0–4 salmon per year). Most salmon caught in this survey are adults (>50 cm) returning towards their spawning grounds in Germany and France.

3.2 | Population estimates

3.2.1 | Smolts (downstream migration)

The number of salmon returning is dependent on the number of stocked salmon in the upper Rhine and its tributaries. This stocking

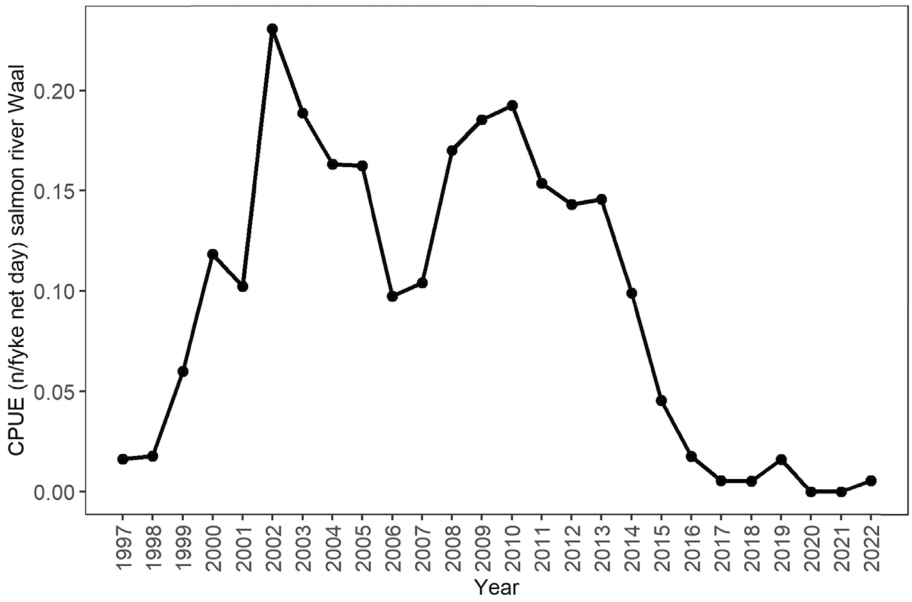

FIGURE 2 Catch per unit effort (CPUE, number of salmon per fyke net per day) of Atlantic salmon in the salmon monitoring with so-called 'zalmsteken'; fyke nets with large mesh sizes especially designed to catch salmonids. Most salmon caught in this survey are adults (>50 cm) returning towards their spawning grounds in Germany and France.

TABLE 2 Number of stocked eggs, fry, parr and smolts expressed in smolt equivalents (ICPR, 2009) in the Rhine and its tributaries in Germany, France and Switzerland.

Year	Eggs/fry	Parr/presmolt	Smolt	Total
2010	54,630	30,036	16,940	101,606
2011	56,108	19,180	15,229	90,516
2012	73,744	86,780	8500	169,024
2013	67,505	62,413	11,935	141,854
2014	83,049	61,101	15,604	159,754
2015	50,772	76,100	8738	135,610
2016	70,352	103,152	9468	182,971
2017	78,562	55,510	925	134,997
2018	70,815	41,867	19,276	131,958
2019	69,068	70,847	6104	146,019
2020	60,020	98,952	285	159,257
2021	69,886	36,032	656	106,574
Total	804,511	741,970	113,660	1,660,140
Average	67,043	61,831	9472	138,345

Note: Number of stocked individuals in the period 1997–2009 were comparable with those from 2010 to 2021 but not details on life stage could be obtained (ICPR, unpublished data).

started at the end of the 1980s when the first release of salmon was done in the river Sieg in 1988, and from 1995 onwards more than 500,000 salmon fry per year have been released (Schmidt & Feldhaus, 1999). In the last decade, millions of eggs, fry, parr and smolts have been released into the Rhine and its tributaries in Germany, France and Switzerland each year. The majority of fish were stocked in the German Rhineland-Palatinate and North Rhine-Westphalia states (e.g., rivers Sieg and Ahr). Smoltequivalents (ICPR, 2009) of these stockings have been calculated. On average, an estimated 138,345 stocked smolts per year are migrating towards the sea (Table 2).

Based on electrofishing data from 2010 to 2021, it is estimated that an additional 1886 smolts started their migration on a yearly base, as a result of natural spawning (Jörg Schneider, personal communication). This leads to an average (maximum) total of 140,231 smolts that start their seaward migration. The minimum number of smolts that start their seaward migration in the river Rhine is calculated by using the percentage (56%, Table 1) of tagged smolts that reach the mouth of the river Wupper where it meets the river Rhine (Vriese, 2018). This results in an estimated minimum of 78,529 (Table 3).

Migrating downstream from the river Rhine, smolts are divided over three branches (rivers Waal, Lek and IJssel, Figure 1, Table 2). The majority of the smolts use the river Waal for their seaward migration and only a small portion migrates through the river IJssel or river Lek (both 1% of the total number of smolts that start to migrate each year). From the river Waal, most smolts migrate through the Haringvliet sluices towards open sea although some choose to migrate through the Nieuwe Waterweg, which has an open connection to the North Sea, possibly joined by individuals that migrated through the river Lek. The higher percentages of smolts detected in the Nieuwe Waterweg compared with the river Lek indicate that some individuals, which are migrating through the river Waal towards the Haringvliet sluices, choose to migrate through the Nieuwe Waterweg instead. As no tagged smolts were detected at the Afsluitdijk in the study of Vriese (2018), we assumed a survival of 27% (conform survival at the downstream rivers) of smolt from the river IJssel, to estimate the maximum number of smolts reaching the Wadden Sea. In total, it is estimated that 10,994–19,632 smolts reach the sea, which equals 14% of the total number of smolt equivalents, including wild smolts (from natural reproduction).

TABLE 3 Number of smolts per area based on stocking, natural spawning and telemetry data.

Area	% detected	Minimum number	Maximum number
Stocking (and spawning) areas	56[a]	78,529	140,231
River Rhine (Xanten, Germany)	74	58,701	104,823
River Waal	49	38,479	68,713
River Lek (Nederrijn)	1	785	1402
Haringvliet sluices	12	9424	16,828
River Nieuwe Waterweg	2	1571	2805
River IJssel	1	785	1402
Afsluitdijk (enclosure dam Lake IJsselmeer)	0–0.27	0	379

Note: The numbers in this table are an indication of the order of magnitude and cannot be taken as an exact representation of the actual number of smolts. Detected percentages are retrieved from tagging data in Vriese (2018).
[a]56% is the percentage of the total number of detected salmon smolts at the detection station in the mouth of the river Wupper.

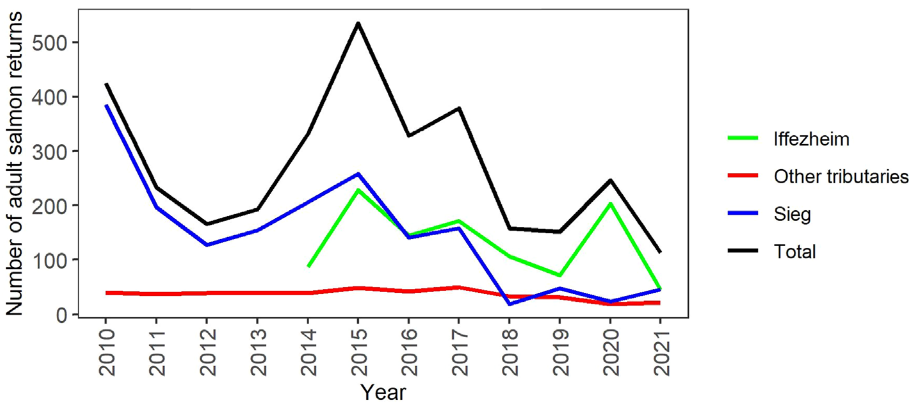

FIGURE 3 Numbers of adult salmon observed in the upstream tributaries or on the spawning grounds of the river Rhine. Iffezheim numbers from 2010 to 2013 were not used due to maintenance work on the fishway and numbers from 2021 are an underestimation as these numbers come from fish collected in the fishway and not from the video analysis like in other years. Note that these numbers are not corrected for catching/counting effort. [Color figure can be viewed at wileyonlinelibrary.com]

3.2.2 | Adults (upstream migration)

The monitoring program of the ICPR records adult salmon that have returned to the upstream tributaries of the river Rhine, the Rhine at Iffezheim and to the spawning grounds. Conform the population trend in the river Waal, numbers have been declining since 2010 (Figure 3). Most salmon used to be observed in the river Sieg but in recent years this number has decreased rapidly while observations at Iffezheim increased from 2014 which might be due to improvements to the fish trap. The other tributaries (Ahr and Saynbach) also show a decline from 2017 onwards. On average 53% of all salmon were observed in the river Sieg, 34% at the fishway in Iffezheim and 13% in other tributaries, equalling 279 salmon a year. As an estimated 1/3 to 3/4 of all salmon is estimated to be observed (Armin Nemitz, personal communication) during this monitoring, a range of 373–798 adult salmon are estimated to return to their spawning ground each year.

This range of returning salmon was used to back-calculate the number of salmon per segment using tagging data from three studies (Hop & Vriese, 2018; van Giels & Breukelaar, 2011; Vriese & Breukelaar, 2011). As the tagging data on adult salmon were limited (195 individuals tagged, 53 detected), we also used the tagging data from upstream migrating adult sea trout (926 individuals tagged, 259 detected), assuming survival/disappearance rates are similar for the two species. Jansen et al. (2008) calculated that this assumption is reasonable as similar percentages of salmon and sea trout reached the spawning grounds. The detected percentage of salmon (27%) and sea trout (28%) for the 2001–2016 tagging data also supported this assumption (Table 4). [Correction added on 11 May 2024, after first online publication: Table 3 was changed to Table 4 in this sentence.]

A total of 1100 adult salmonids were tagged in the studies of Hop and Vriese (2018), van Giels and Breukelaar (2011), Vriese and Breukelaar (2011) during three different time periods: 2001–2008, 2009–2010 and 2010–2016. The average detection percentage was 26% but differed between the three studies (Table 3). In 2001–2008 and 2009–2010, the detection percentages were 39% and 33%, respectively, while in 2010–2016 the detection percentage was only 13% (Table 4). This lower percentage could be due to a difference in release locations (Hop & Vriese, 2018). In the period 2010–2014, all tagged salmonids were released at the harbour in Stellendam and not in the Voordelta. Based on detection data of the past few years, detection percentage of salmonids released in the harbour of Stellendam was 11%, while for the ones released in the Voordelta, the percentage was 21%, indicating a large influence of release location (Hop & Vriese, 2018).

The highest percentage of detection was at the Haringvliet sluices followed by the Nieuwe Waterweg, most salmon migrate through the river Waal and only a small percentage through the river Lek, as was observed for smolts as well. Back-calculated from the number of salmons observed at the spawning grounds, 6512–13,933 adult salmon

TABLE 4 Number of tagged and detected upstream migrating adult Atlantic salmon and sea trout over three different time periods (Hop & Vriese, 2018; van Giels & Breukelaar, 2011; Vriese & Breukelaar, 2011) for all rivers (incl. the river Meuse).

	Adult	2001–2008	2009–2010	2010–2016	Total
Tagged	Trout	280	229	417	926
	Salmon	105	30	60	195
	Total	385	259	477	1121
Detected	Trout	117	81	61	259
	Salmon	35	11	7	53
	Total	152	92	68	312
% Detected	Trout	42%	35%	15%	28%
	Salmon	33%	37%	12%	27%
	Total	39%	36%	14%	28%

TABLE 5 Number of upstream migrating adult Atlantic salmon per area over three different time periods for the river Rhine.

	2001–2008	2009–2010	2010–2016	Total	% return	Min. Number salmon	Max. Number salmon
Total tagged	380	249	471	1100	100%	6512	13,933
Detected salmonids	147	82	62	291	26%	1723	3687
Haringvliet sluices	98	61	35	194	18%	1149	2458
River Nieuwe Waterweg	49	21	27	97	9%	574	1229
River Lek	9	4	1	14	1%	83	177
River Waal	41	28	15	84	8%	497	1064
River Rhine (NL)			11				
River Rhine/tributaries	37	24	2	63	6%	373	798

Note: The number of tagged individuals and return percentages are based on Atlantic salmon and sea trout excluding the river Meuse. The minimum and maximum numbers of returning salmon per area are back-calculated from the estimate 373–798 salmon that are estimated to have reached the spawning grounds. The numbers in this table are an indication of the order of magnitude and cannot be taken as an exact representation of the actual number of adult salmon.

entered the Netherlands to return to their spawning grounds (Table 5).

To visualize where the highest losses of smolts and adults take place we congregated the estimated number of migrating smolts, adults and the percentage loss into five areas: spawning grounds, river Rhine in Germany, river Rhine in the Netherlands, the coastal zone and the open sea (Figure 4).

For smolts, the highest disappearance rates occur in the transition from the Rhine to the coastal zone. For adults, this percentage is also high, when adult salmons reach the Dutch lower Rhine, 74% of them seem to have disappeared already. Of these adult salmons entering the lower Rhine, another 78% is lost trying to reach the German Rhine and their spawning grounds. The overall losses for adults in inland waters from the coastal zone to the spawning grounds are 94%. For smolts, the river sections between the spawning grounds and the German Rhine and between the German and Dutch lower Rhine are responsible for 26%–34% of the losses. However, when looking at absolute numbers, these parts have the highest losses with 20,417–36,460 smolts disappearing between the spawning grounds and the German Rhine and 19,632–35,058 smolts disappearing between the German Rhine and Dutch lower Rhine. On the other hand, smolt losses per km are actually quite similar between the German and Dutch stretches of the river Rhine, ranging from 0.17% to 0.24% per km for the German stretch and from 0.23% to 0.28% per km for the Dutch stretch (Table 6). The overall smolt losses in inland waters from the spawning grounds to the coastal zone are 86%.

The disappearance percentages of out-migrating smolts to adult salmon at open sea were calculated from the absolute estimated numbers leaving and arriving at the coastal zone (Figure 4) and range between 29% and 41%.

The overall percentage of adult salmon returning to their spawning grounds based on the total number of smolts that start their migration (78,529–140,231) and the numbers of adult salmon reaching the spawning grounds (373–798) is estimated at 0.5%–0.6%.

4 | DISCUSSION

4.1 | Salmon losses highest in rivers

In general, the recent decline of Atlantic salmon stocks has largely been attributed to poor survival in the marine environment (ICES, 2021; Olmos et al., 2020). Our results indicate that relatively high percentages of salmon are indeed lost in the marine stage (29%–41%). However, even higher percentages of losses were found in the inland waters; for smolts respectively 26%, 34% and, 71% for the

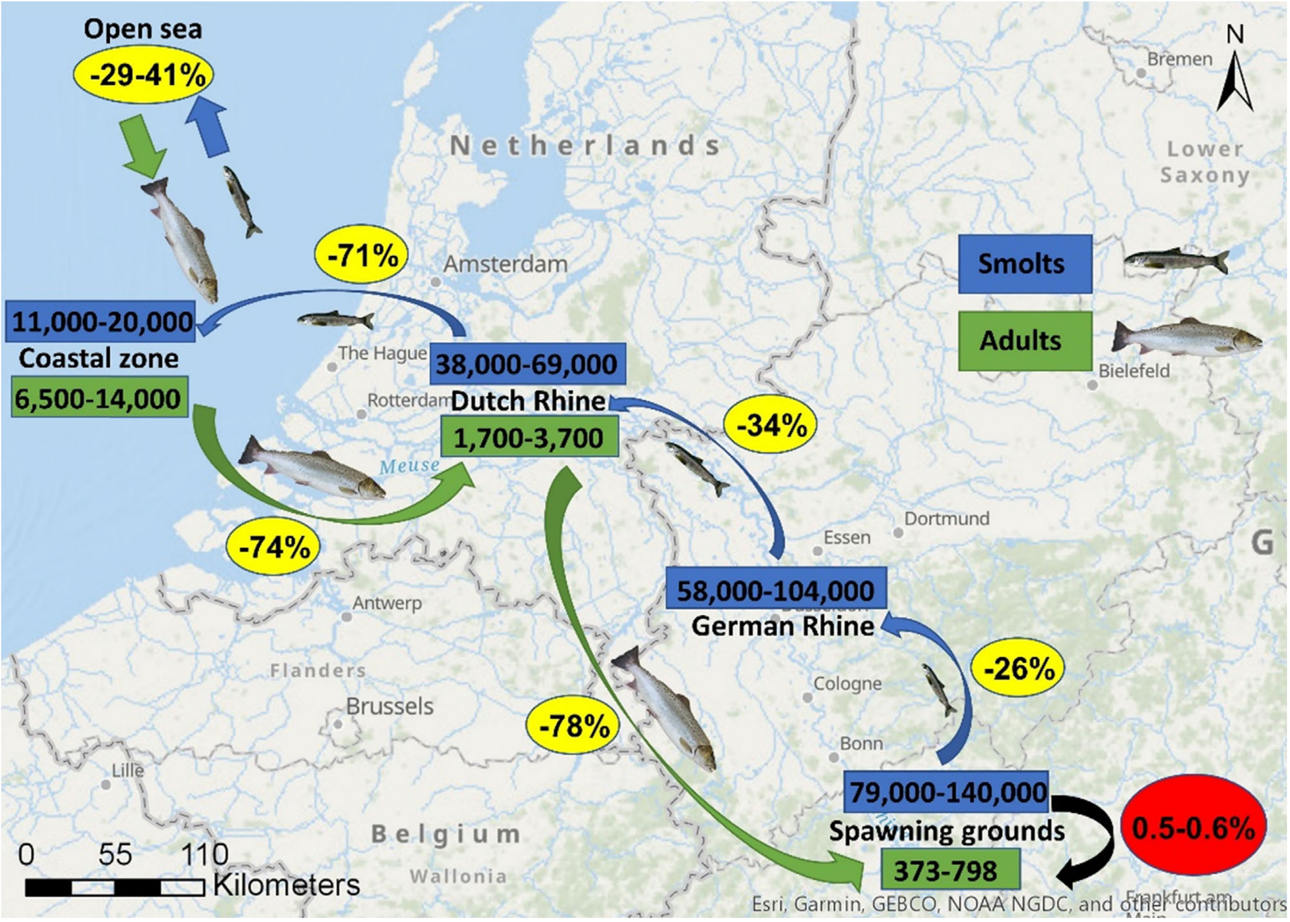

FIGURE 4 Estimated numbers of downstream migrating smolts (blue) and upstream migrating adult Atlantic salmon (green) in the river Rhine. Percentages of salmon disappearing per river section (yellow) are based on telemetry data, salmon stockings and observed adult salmon on the spawning grounds. The overall percentage of starting smolts that return as adults reaching the spawning grounds is estimated to be 0.5%–0.6% (red). The percentages of salmon disappearing at open sea are based on the estimated numbers in the coastal zone. The numbers in this figure are an indication of the order of magnitude and cannot be taken as an exact representation of the actual number of salmon. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 6 Percentage loss per km for smolts on the German and Dutch stretches of the river Rhine (from Vriese, 2018).

River stretch	Length (km)	% loss per km
Dhünn-Xanten	117	0.24%
Wupper-Xanten	117	0.17%
Sieg-Xanten	170	0.20%
Waal (Vuren)-Xanten	121[a]	0.23%[a]
Waal (Vuren-Haringvliet sluices/Nieuwe Waterweg)	261	0.28%

[a]The Nederrijn and IJssel stretches are excluded for this calculation as only few salmon smolts migrate via these routes and no loss percentage could be estimated for these stretches. Given the similar percentages for the different stretches, these were also assumed to hold for these stretches, although in absolute numbers, losses in these stretches are very low.

German Rhine, German/Dutch Rhine and Dutch Rhine (86% in total), and for adults respectively 74% and 78% for the coastal zone and Dutch/German Rhine (94% in total).

It has to be noted that the percentages of smolt disappearance reported in this study need to be considered with caution. The tagging studies of smolts were performed with relatively large (2+ age class, 29 cm on average, Vriese, 2018) smolts that were raised in hatcheries and therefore can show a different disappearance percentage compared with smolts that were raised in a natural environment without a tag. There is a growing amount of evidence suggesting that hatchery-reared Atlantic salmon smolts have a lower survival, lower return rate, slower growth and a lower fitness compared with wild smolts (Chaput, 2012; Long et al., 2023; O'Sullivan et al., 2020; Skaala et al., 2019). This needs to be considered when interpreting these results.

The high disappearance percentage of adult salmon, before they reach the Dutch lower Rhine (74%), could be a result of using tagging data from both salmon and sea trout, assuming that tagged sea trout and salmon have similar survival/disappearance chances. Sea trout forage in the Voordelta and in front of the Haringvliet sluices, and these fish do not necessarily have to migrate through the Haringvliet sluices shortly after being tagged and can enter freshwater at other freshwater entry points, even in other countries. As is confirmed by recaptures of tagged sea trout at fish traps in France and Scandinavia. However, based on our telemetry data, there is no significant difference between the percentage of salmon and sea trout entering the Rhine River system (Table 4). This makes it less likely that the high disappearance percentage is an overestimate due to sea trout entering at other freshwater entry points. Either way, if the disappearance percentages of either smolts or adults in inland stretches and coastal zone are overestimated, this would then lead to a higher estimate for open sea mortality but would not affect the overall return percentages of 0.5%–0.6%, because this was not based on the telemetry data, but on independently derived totals.

High percentages of smolt disappearance could partly be caused by natural mortality. A review that looked at salmon smolt natural mortality in rivers reported mortality rates of 0.3%–7% per kilometre (Thorstad et al., 2012). These percentages are in line with more recent studies on Atlantic salmon smolt river mortality (Chaput et al., 2019; Flavio et al., 2019, 2021; Lothian et al., 2018; Molina-Moctezuma et al., 2021). Assuming that most individuals need to swim down the river Rhine for more than 300 km to reach the North Sea, an assumed natural mortality rate of 1% per kilometre would result in a maximum of 6900 individuals reaching the North Sea (assuming a maximum of 140,000 smolt starting the downward migration). This estimate is in the same order of magnitude as the number of smolts reaching the North Sea in this study (11,000–20,000). Even higher percentages of natural smolt mortality seem to occur in estuaries and marine areas close to river mouths; 0.6%–36% per kilometre, where predation is considered to be a major factor (Flavio et al., 2020; Havn et al., 2020; Thorstad et al., 2012). Although the estimated percentage of smolt losses per km of the current study is at the lower end of the percentage losses found in the literature, the (heavily modified) river Rhine is a fairly long river. This means that even a relatively low percentage of losses per km can have a large effect on smolt number reaching the sea.

In addition to natural mortality, human-induced mortality is likely to be a large contributing factor as well. These, and other possible factors contributing to the high disappearance percentage of both smolts as adult salmon from the Rhine system are discussed below.

4.2 | Population trend and current threats to Atlantic Salmon in the Rhine system

Since 2013, the number of returning adult salmon has dropped drastically in the monitoring fykes in the river Waal (Figure 2), whereas the number of stocked young salmon remained high. So far, it remains unclear why this strong decrease has occurred. There are several environmental factors that have changed in the past decade that could have added to the already strong human-induced pressures from the (recent) past. In the past, habitat loss (especially damming and loss of spawning and nursery grounds), overfishing and pollution, are thought to have contributed to the decline of Atlantic salmon (de Groot, 2002; Lenders, 2017; Lenders et al., 2016; Limburg & Waldman, 2009). Here, we discuss a few more recent threads, such as climate change, and some additional threats, which may be specific to the river Rhine system.

4.2.1 | Weirs and turbines

Salmon that migrate through the Netherlands could encounter a series of three weirs when migrating through the river branch Nederrijn/Lek (Driel, Amerongen & Hagestein). The weirs at Amerongen and Hagestein also have hydropower stations, although the turbines of the latter are out of order since 2005. Fishways have been installed along these three large weirs in the Netherlands (2001–2004), and these have been shown to improve upstream migration (Winter & Jansen, 2007). However, these weirs can still act as a barrier for migration (de Leeuw & Winter, 2006; Winter, 2006) as fish are getting delayed while searching for a suitable passage route. Several tagging studies, salmonids of the river Rhine have shown this kind of searching behaviour (Hop & Vriese, 2018; Jurjens, 2006; van Giels & Breukelaar, 2011; Vriese, 2018; Vriese & Breukelaar, 2011). During the downstream migration, this delay could in turn lead to desmoltification (Aarestrup & Koed, 2003). The searching behaviour also leads to congregation of fish making them vulnerable to predation (see below). On the other hand, most salmon (both juvenile and adult) choose to migrate directly through the river Waal and tagging studies have shown that only a few percent choose the rivers Nederrijn/Lek to migrate and only these individuals will encounter these three major weirs.

In Germany however, many tributaries of the river Rhine have weirs, where some of these weirs are combined with hydropower stations with turbines (in the river Wupper alone there are eight hydropower stations). Especially the so-called 'Low-Head-Turbines' (e.g., Kaplan turbine) are dangerous for adult salmon. Despite the fishways that are sometimes present, some salmon choose to migrate upstream through the turbines and each year several adult salmonids are found with major head injuries inflicted by turbines (Schneider & Seufert, 2021). For smolts, a study on a power station in the river Sieg revealed an extra mortality due to the power station, including the reservoir, of 16%–25% of tagged salmon smolts entering the reservoir. This mortality occurred despite the power station being constructed with fish-friendly solutions such as bar racks in front of the turbine intakes, alongside several types of bypass routes being accessible for downstream migrating smolts (Havn et al., 2018). In a more recent study, Havn et al. (2020) found a salmon smolt mortality rate of 7.2% at the same power station while at the weir there was a mortality rate of 5.2%. In another study, Thorstad et al. (2017) found that tagged (hatchery-reared) salmon smolts in Kinzig, Germany had a combined mortality of 5%–8% (excluding delayed effects), due to a hydropower station with a movable bulb turbine. The studies of Havn et al. (2018, 2020) were based on fish that likely originated from stocking of 0^+ or 1^+ fry or parr by local hatcheries but could also be the result of natural spawning. This means that the aforementioned studies are mainly based on hatchery-reared and/or stocked smolts that might have a different (likely higher) mortality rate than wild smolts.

4.2.2 | Ship navigation

The river Rhine has a high intensity of ship traffic and is considered to be one of the busiest inland waters in the world in terms of ship navigation. It is estimated that on a daily basis in the German part of the river Rhine (from Iffezheim to the border with the Netherlands), 1600 ships travel back and forth (Schneider & Seufert, 2021). The estimate for the Dutch part of the river Rhine is 300 (de Laak, 2002). This number is confirmed by a recent study that quantified the number of ship movements between 2009 and 2018 in the river Waal (van de Ven et al., 2021). They found an average of 100,000 ship movements a year (averaging to 274 ship movements a day, close to the earlier reported 300 a day). This brings the total to about 1900 ships/ship movements a day on the river Rhine. Especially during periods of reduced discharge in the fall (and nowadays also in the summer) that often coincides with upstream adult salmon migration (June–November), the high amount of ship traffic can be detrimental to salmon as they either can be sucked in by the ship's propeller directly (suction force of 1–4 m, depending on the type and size of the ship) or by the hull which is supposed to have an even larger suction force (Schneider & Seufert, 2021). During dry years, there is even less discharge and the navigation depth of the river Rhine is only 2.5 m (Schneider & Seufert, 2021) while the overall average draft of ships at the river Waal is 2.2 m (van de Ven et al., 2021). The lower water levels in dry years also increase the ship traffic intensity. Due to these lower water levels, large ships need to carry less cargo and more (smaller) ships need to be used in order to maintain the same transport capacity resulting in a significant negative correlation between water level and ship traffic intensity (van de Ven et al., 2021). Although actual numbers of adult salmon injured by propellers remain uncertain, both Sportvisserij Nederland and the Büro für fischökologische Studien, Frankfurt occasionally receive photos of salmon, which are determined to be fatally injured by propellers (Schneider & Seufert, 2021), indicating that adult salmon are lost due to ship traffic.

4.2.3 | Higher chance of reduced discharge due to climate change

The reduced discharges seem to be the result of climate change and are expected to occur more frequently in the river Rhine in the future (Stahl et al., 2022). A reduced discharge can be detrimental to salmonids as it increases predation risks and risks of collision with either ship propellers or turbines. A reduction in discharge also seems to be detrimental to the number of returning salmon. Schneider (2009) found that, in the period from 2000 to 2008, higher discharges in the river Sieg (main spawning tributary of the river Rhine) resulted in a larger number of adult salmon returnees the next year and the year after, and vice versa. In a meta-analysis, Schneider and Seufert (2021) found that these correlations were still present using data up to 2018, albeit less pronounced. From this, they concluded that the migration corridor of Atlantic salmon increases with higher discharge. As a result, predation pressure from piscivorous fish (pikeperch, pike, asp, catfish) and birds (primarily cormorants) is distributed over a larger area with higher discharges. In addition, the increased turbidity associated with increased runoff should provide better protection from visual predators (such as pike and cormorant). The higher runoff also reduces the amount of time spent migrating the river Rhine and its tributaries. Especially for smolts that migrate from rivers that have hydropower stations (e.g., Sieg, Lahn, Main, Moselle, Oberrhein), high discharges will have a positive effect. High discharges increase the probability of smolts migrating over the weir rollers instead of through the turbines (Schneider & Seufert, 2021). Havn et al. (2020) also found that losses of salmon smolts due to a hydropower station in the river Sieg were lower in years with high discharge compared with years with low discharge during the smolt run. In the past decade, there have been years with very low discharge during the second half of the year (e.g., 2018). As these reduced discharges are likely to occur more often due to the changing climate, this will have a negative impact on the salmon population of the river Rhine.

4.2.4 | Higher temperatures due to climate change

Together with reduced discharge, an increase in water temperature in the river Rhine has occurred and is likely to increase further (Hardenbicker et al., 2017). The salmon population decrease seems to start after a substantial decrease in discharge and coinciding water levels (Figure 5). The population even collapses after a series of low discharge from 2014 onwards (Figure 5). This suggests that the number of returning salmon is correlated with discharge as suggested by Schneider (2009) and Schneider and Seufert (2021). Although the water temperature has increased, this does not directly correlate with the decrease or the collapse in the salmon population. An increase in water temperature can lead to earlier fry emergence and possibly to a mismatch in the timing of fry emergence and food availability (Thorstad et al., 2021). In addition, the growth of juvenile salmon in the river will generally increase with temperature increase, and the juveniles may reach smolt size earlier. Warmer river temperatures earlier in spring seem to influence the timing of migration, with smolts migrating to the ocean earlier in the year (Otero et al., 2014). This could create a mismatch between timing of smolt sea entry and favourable conditions at sea (Hawkes et al., 2017; Kennedy & Crozier, 2010). In addition, water temperatures in the river Rhine are, and are expected to continue to, periodically exceed the upper thermal tolerance limit for salmon. Also, energy depletion at high temperatures before spawning is higher in small than in large salmon, suggesting that smaller individuals may be more affected by these high temperatures (Lennox et al., 2018). This is of great concern as returning Atlantic salmon are getting smaller (Czorlich et al., 2022).

An in-depth analysis of all relevant (a)biotic factors possibly influencing the salmon population could shed some light on how these

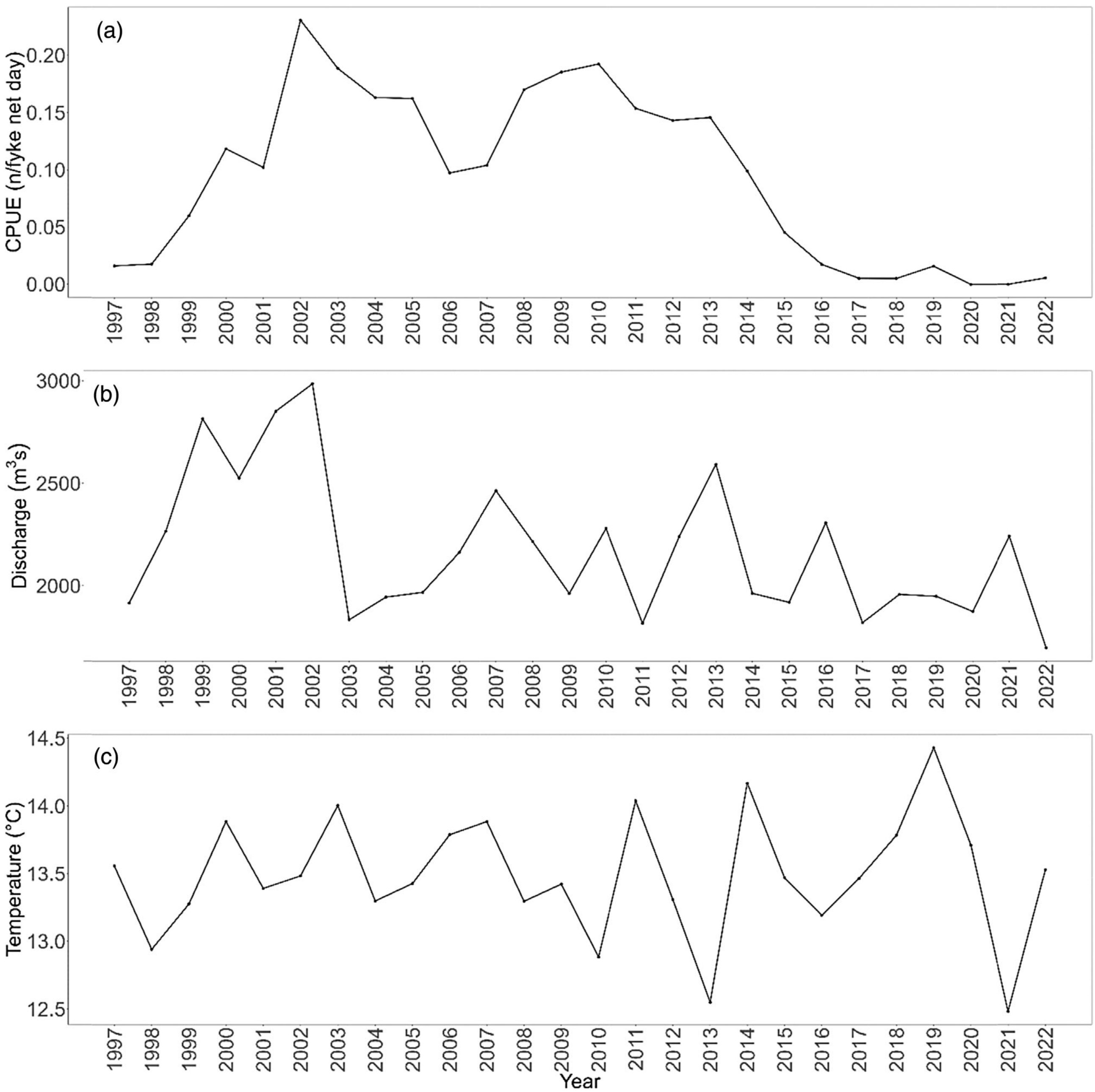

FIGURE 5 Trend of the salmon population in the river Waal (a), discharge (b) and temperature (c). Daily discharge and temperature data were measured at Lobith in the river Rhine and retrieved from www.waterinfo.rws.nl.

factors influence the number of returners. However, such an analysis is beyond the scope of this paper.

4.2.5 | Predation

Piscivorous birds (mainly cormorants)

The cormorant is an opportunistic predator that mainly feeds on fish that are abundant. The cormorant population has increased rapidly in Europe, from 225,000 in 1970 to more than 1.5 million in 2014, excluding Russia (Kohl, 2015). Especially at Lake IJsselmeer, the Dutch delta and the German part of the Rhine close to the Dutch border, the area where smolts need to migrate through, a sharp increase in numbers is observed, from only a few cormorants in the early 1980s to ~20.000 at the end of the 2010s (ICPR, 2020b). A study from Denmark summarized the effect of predation on salmonid smolt survival using 24 tagging studies. In all these studies, salmonid smolt mortality of cormorant predation was higher than 20% with an average of 47%, ranging from 23% to 88% (Jepsen et al., 2019). On the other hand, studies from Sweden and Czech Republic showed a mortality of 0%–2% of salmonid smolts due to cormorant predation (Boström, 2013; Boström et al., 2009; Lyach & Cech, 2017). So it seems that cormorant mortality varies a lot by location and environment.

At the spawning grounds of the river Sieg in Germany, 10 stomachs of overwintering cormorants were checked and 3 of them contained young salmon parrs (Schneider, 2005). Blasel (2004) claimed that predation pressure by cormorants is high in the most Southern part of the German Rhine ('Restrhein'), with 1200 cormorants overwintering in this part of the river Rhine in 2004, which led to a significant reduction of the fish stock in that part.

During the past years, in some cormorant colonies near stocking locations on the rivers Sieg, Wupper and Dhünn searching actions for tags of salmon smolts were carried out. Preliminary results show that at least about 10%–20% of the smolts were caught by cormorants staying in breeding colonies in the vicinity of the stocking locations. It must be taken into account however, that in this case, 2-year-old smolts from hatcheries were concerned, which have not yet been exposed to any natural environment and thus do not have any experience with predators (ICPR, 2018).

Based on restocking efficiency experiments, the Rheinischer Fischereiverband have shown that an average of 15%–25% of healthy 1-g parrs survive up to September after being stocked. Based on smolt output experiments, they concluded there must be a high mortality of smolts between September and March each year, which could be partly due to cormorant predation (Armin Nemitz, personal communication).

Piscivorous fish (mainly Wels catfish)

Both in Germany and in the Netherlands, the abundance of the Wels catfish (*Silurus glanis*) has increased significantly over the past decade (Schneider & Seufert, 2021; van Rijssel et al., 2021). Wels catfish are large, predatory fish and a study in the South-West of France found that in a fishway of the river Gironne, 35% of the 40 adult salmon passing through it were predated by Wels catfish (Boulêtreau et al., 2018). In the fishways of Iffezheim and Gambsheim in Germany, used by salmon to migrate through, the numbers of Wels catfish have increased from 75 in 2014 to over 300 in 2018. If predation rates of adult salmon are similar or only a quarter of the predation rate at the Gironne, this will have a profound impact on the spawning population of the river Rhine. Salmonids are occasionally reported to have clear bitemarks of Wels catfish (Claus et al., 2021; Schneider & Seufert, 2021). In addition, Wels catfish are known to congregate close to weirs and turbines waiting for disorientated fish to exit the turbines or leave the fishways (Schneider & Seufert, 2019, 2021). Although less is known about predation of Wels catfish on smolts, Koed et al. (2002) reported a mortality rate of 70% of tagged smolts around a hydropower plant where 19 out of 27 tags were retrieved in the stomachs of pikeperch (*Sander lucioperca*), pike (*Esox Lucius*) and grey heron. Congregations of smolts at weirs and turbines make it likely that smolts searching for a way to pass the migration barrier become a relatively easy prey for Wels catfish. In the lower sections of the Rhine, pike perch and pike are common and known predators of salmon smolts (Kennedy et al., 2018). In the downstream lakes Haringvliet and Hollandsch Diep, pikeperch biomass has increased since 2011 (van Rijssel et al., 2023).

Marine mammals (mainly seals). Since the 1990s, there has been a strong increase of both the harbour seal (*Phoca vitulina*) and the grey seal (*Halichoerus grypus*) in the Wadden Sea, from less than a 1000 counted harbour seals in the 1990s to 8245 in 2021 (Galatius et al., 2021). For grey seals, where data are available from 2008 onwards, the increase is from less than 2000 counted individuals in 2008 to 6788 individuals in 2021 (Brasseur et al., 2021). The counted numbers of harbour and grey seals in the Voordelta (the area of the North Sea that salmonids have to pass through while migrating from/towards the Haringvliet sluices; coastal zone) have increased drastically as well. From only a few harbour seals on average in the 1990s to more than 500 in 2020/2021. For grey seals, average counted numbers increased from 0 in the 1990s to over 1200 in 2020/2021 (Hoekstein et al., 2022). Upstream migration at the Haringvliet sluices is hampered and may lead to increased searching behaviour and residence time near the barrier, increasing vulnerability to predators that can catch adult salmon, like seals. There have been numerous studies indicating that seals actually do predate on Atlantic salmon (Falkegård et al., 2023). A study on the diet of harbour seals in the Wadden Sea based on otoliths from 103 faecal samples revealed that these seals predominantly fed on demersal fish, for example, flatfish species (flounder, sole, plaice, dab), but also on sand eel, cod, and whiting (Aarts et al., 2019). Although no otoliths of salmonids were found in this study, predation on these cannot be excluded. First, this study was performed on harbour seals in the Wadden Sea where the chance of an encounter with salmon is very small compared with the Voordelta. In addition, grey seals, which are more common in the Voordelta might have a different diet than harbour seals (although they are thought to mainly feed on sand eel in the North Sea, Brown et al. (2012)). Second, salmonid predation by seals can vary strongly on a fine spatial and temporal scale. For instance, the diet of harbour seals in southeast Scotland consisted of 0%–64% salmon (mainly grilse and smolts) depending on the time and location (Sharples et al., 2009). Third, the results of the aforementioned studies are based on otoliths in faecal samples. According to observations of several fishermen, the heads of mullets, sea bass and salmonids have been found in their nets supposedly bitten off by seals. If this behaviour is common feeding behaviour of seals in the Voordelta, no otoliths of salmonids will ever be detected in faecal samples. However, Suuronen and Lehtonen (2012) found that, based on otoliths, 20% of the grey seals in the Baltic Sea included salmonids in their diet during the migration time of salmonids. The authors did mention though, that there was one large 1-metre salmonid found in the stomach of a grey seal without a head. In addition, bitemarks from seals are also occasionally reported from salmonids in the river Rhine and at the fish trap of Iffezheim (Claus et al., 2021; Schneider & Seufert, 2021). It is likely that only the slightly wounded salmonids survive these attacks and probably means that the actual occurrence of seal attacks is higher than the number of observations.

4.2.6 | Genetic origin and suitability of stocked salmon

The ICPR evaluated the effect of stocking salmon from different populations. Over the past decades, salmon from different populations (Ireland, Sweden, Norway, Denmark, Scotland, France and Germany) have been stocked in the river Rhine (ICPR, 1999, 2004). On several occasions, the ICPR analysed the origin of salmon during different years at different locations.

In the Netherlands (Rhine delta), 46 of the 75 evaluated samples dating back to 1999–2013 could be associated with a probability >80% to a region of origin. Most individuals were of Irish origin, corresponding to donor populations from before 2003. Twelve individuals were of the river Loire origin and may thus presumably be traced back to stocking exercises in the upper Rhine and other systems like the Maas (river Allier strain; ICPR, 2018).

In 2016, samples of 700 salmon were taken of age classes 2004–2015 to analyse their origin. The individuals concerned returnees to the river Sieg and their descendants from the Wildlachszentrum Rhein Sieg and the fish hatchery Albaum (LANUV NRW). The results showed that most of the salmon originate from United Kingdom and Ireland (corresponding to donor populations in earlier years) and Sweden/Eastern Norway (including donor rivers Ätran and Lagan) corresponding with the donor populations that have been used in the river Sieg since 2003 and Saynbach since 1994. In individual cases, salmon were of French origin (rivers Loire/Allier, ICPR, 2018). The assignment of these returners to the Sieg was found to be low (Vonlanthen & Kreienbühl, 2017, 2018b). However, when the populations from the Sieg itself (returners) and from the Denmark Centre for Vildlaks (DCV, providing the Ätran strain for Sieg System) were added to the baseline, 34 out of 48 individuals that could be assigned with a probability of >70%, were assigned to the Sieg population, one to the DCV population, one to the Ätran population, one to the Loire/Allier population and 11 to other populations (mainly United Kingdom & Ireland, Vonlanthen & Kreienbühl, 2018a). Vonlanthen and Kreienbühl (2018a) also found that the Sieg population is genetically very similar to the DCV population. These results combined led Vonlanthen and Kreienbühl (2018a) to conclude that the Sieg population (returners to the Sieg) can now be considered as a unique genetic population. It mostly resembles that of the DCV but also has some genetic resemblance with populations from Scotland, probably as a result of earlier stocking. Vonlanthen and Kreienbühl (2018a) also noted that, in contrast with expectations, the DCV population was not very closely related to the Ätran population. This is probably due to the lack of many years living in confinement without the addition of new returners from the Ätran resulting in a genetic deviation from the Ätran population.

More recent (preliminary) data (2017–2021) confirm that most caught returnees in the Sieg originate from the donor populations from Sweden (DCV, Ätran, Lagan) followed by donor populations from Ireland and only a few from France (Loire, Allier, Figure 6). Interestingly, from most of the 'Irish salmon' from 2020 and 2021, a parental analysis could not detect the parents from hatchery samples, indicating natural reproduction of the 'Irish salmon'. In contrast, when returning salmon was of Swedish origin most parents could be detected originating from the hatchery Wildlachszentrum Rhein Sieg, fish hatchery Albaum or Salmon Centre Hasper Talsperre, indicating most 'Swedish returners' result from stocking. Preliminary genetic data from parr and smolts in the rivers Agger, Nister, Speyerbach or Wieslauter, where stocking is conducted, indicate that still a high percentage of sampled fish originate from stockings and to a lesser extend from natural reproduction (A. Schrimpf, unpublished data).

Ultimately, these kinds of studies might provide an answer to whether returning salmon have originated from stocking or from natural spawning and which stocking activities/strains are most successful. So far, it seems that the genetic variability is not lost due to breeding and stocking salmon (ICPR, 2018; Vonlanthen & Kreienbühl, 2017, 2018b). On the other hand, salmon that return to the river Sieg might have suffered from the stocking of non-local individuals as this can lead to hybrid vigour (i.e., heterosis) but also often to lower performances of hybrids relative to parental lineages (i.e., outbreeding depression; Fraser et al., 2008; Le Cam et al., 2015). Moreover, captive breeding may select, after only one generation, for maladaptive traits in the wild hence potentially affecting the fitness of wild populations (Araki et al., 2007; Le Cam et al., 2015; Milot et al., 2013). For instance, one of the reasons the Ätran strain was selected was because of its similar spawning time to the historical Sieg strain which is relatively early (Schneider, 2011). The Irish strain, which is still present in the Rhine catchment, spawns later than the Swedish strains. Spawning time has a strong genetic component in salmonids and is considered to be an adaptation to the temperature regime of the native river (Quinn et al., 2000; Webb & McLay, 1996) and it is known that translocated strains can keep their inherited spawning time in a new environment for several generations (Schneider, 2011). The strong genetic component of spawning time could be maladaptive in times of climate change with reduced discharges.

4.2.7 | Decreased body condition

Several studies have shown that the weight and body condition of returning salmon has decreased over the years in both Scottish and French waters (Bacon et al., 2009; Bal et al., 2017). The reasons for this remain obscure although it has been suggested that the environmental and food supply changes on the marine salmon feeding grounds (Jacobson et al., 2018; Jonsson et al., 2016; Renkawitz et al., 2015) might have resulted in these lower body conditions (Friedland et al., 2000; Jensen et al., 2011; Mccarthy et al., 2008; Peyronnet et al., 2007). In addition, (human-induced) genetic and evolutionary changes also have been hypothesized to have contributed to the decrease of salmon body condition (Garcia de Leaniz et al., 2007; Hard et al., 2008), as has infection with sea lice (Susdorf et al., 2018).

Although not significantly different, the body condition of non-detected salmonids was lower than it was for detected salmonids in the Netherlands (Bij de Vaate & Breukelaar, 2001), suggesting that fish with a higher body condition start their migration upstream and fish with a lower body condition deter from it. In a more recent study,

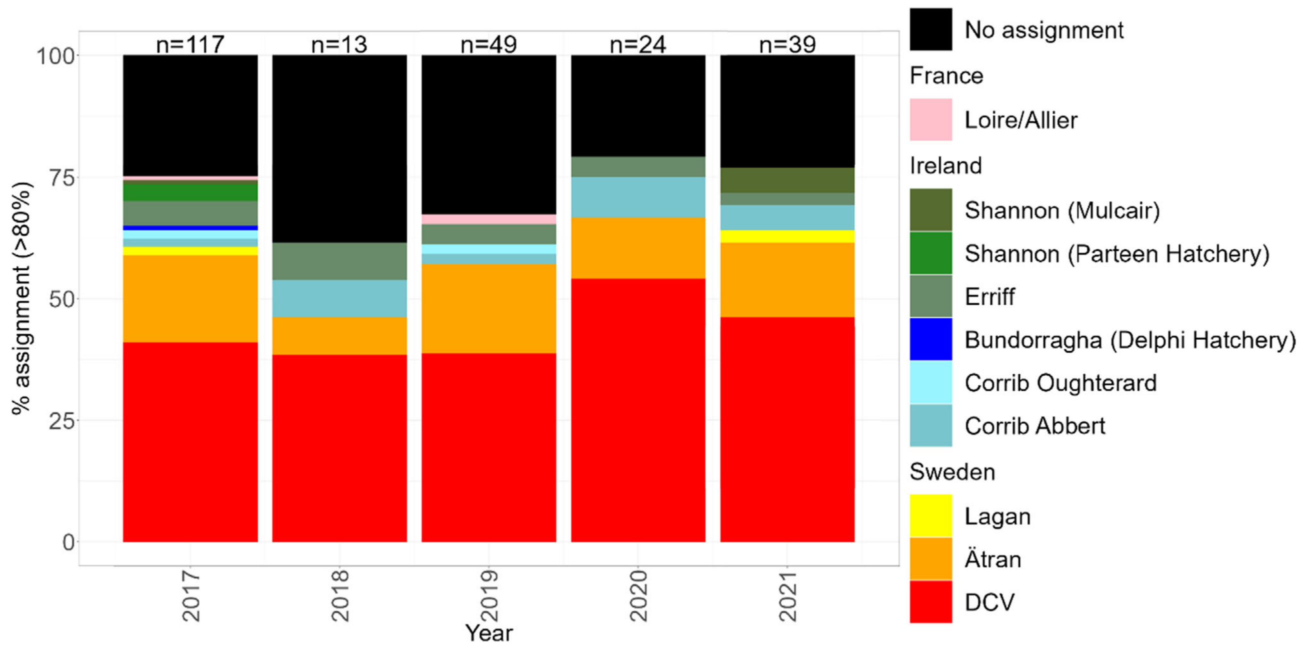

FIGURE 6 The distribution percentages of assigned samples from the Wildlachszentrum Rhein Sieg to the population Denmark Centre of Vildlaks (DCV, Vonlanthen & Kreienbühl, 2018b) and the reference populations from the Salsea-Merge panel (Gilbey et al., 2018) that were stocked in the Rhine in the past. The samples were taken from returnees in the Wildlachszentrum caught in the river Sieg (Buisdorf) and river Agger (Troisdorf). The analysis was done with the Software GeneClass2 (Piry et al., 2004). Assignments below the cut-off value of 80% are considered as 'no assignment'. [Color figure can be viewed at wileyonlinelibrary.com]

Hop and Vriese (2018) showed that tagged adult salmon in the 'Voordelta' (coastal zone in front of the Haringvliet sluices), had an average body condition of 0.87 while the detected salmon had a significant ($p = 0.0078$) higher average body condition of 1. It should be noted that a lower body condition during tagging does not necessarily mean a lower body condition during the start of the migration.

4.2.8 | Recreational fisheries

Recreational fisheries on salmon in Germany used to occur frequently in the river mouths of the Sieg and Saynbach and approximately 1–60 adult salmon were caught and extracted from the population on a yearly basis between 2007 and 2012 (Schneider & Seufert, 2021). Since 2014, however, the number of closed areas for both commercial and recreational fisheries including the estuaries of the Sieg and Saynbach reduced this number drastically to 1–3 fish per year (Schneider & Seufert, 2021). The number of salmon caught by Dutch recreational fishermen remains obscure. Estimates of salmonids caught at the Haringvliet sluices varied from 5 to 30 by Jansen et al. (2008) to hundreds on a yearly basis based on interviews (van Giels & Vriese, 2016). Although commercial and recreational fishermen are obliged by law to return caught salmonids since the year 2000, it is unclear what percentage of these fishermen actually comply with this requirement. It is known that there are several recreational fishermen that are targeting salmonids, however, it seems that these are few and that actually catching a salmon on the Dutch rivers is a rarity (source: Sportvisserij Nederland), although chances of catching one at the so-called hotspots Haringvliet and Maasvlakte (Nieuwe Waterweg) and IJmuiden (mainly sea trout) are thought to be higher.

4.2.9 | Commercial fisheries

There were no commercial freshwater/coastal fisheries targeting salmon after the reintroduction programme started. Hence, salmon could only have been bycaught in fisheries targeting other species. Commercial fisheries in the Dutch branches of the Rhine were mainly restricted to eel using fyke nets. Since 2011, these fisheries were banned due to high dioxin and PCB levels in eel. In the coastal zone, more types of fisheries occur, for example, gill-nets, trawling and fyke nets. Based on interviews, questionnaires, monitoring data and observations performed in 2018, van Rijssel et al. (2019) reported a rough (intermediate) estimate of 187 adult Atlantic salmon and 202 smolts being caught by commercial fishermen in the Netherlands on a yearly basis. It should be noted that, in the past 5 years, 2018–2022, the number of returning salmon to spawn is the lowest since 2000 (Figure 3, Armin Nemitz & Jörg Schneider, personal communication). As a result, the chances of commercial fishermen bycatching one are smaller than in previous years.

4.3 | Self-sustaining population?

The previously mentioned threats are likely all contributing to the low number of returning salmon. The average percentage of returning salmon over 2010–2021 is estimated to be 0.5%–0.6% of smolt equivalents. Recent estimates of returning stocked salmon based on monitoring data at station Buisdorf in the river Sieg (1998–2017 stocking data, 2000–2019 return data) showed a return rate of 0.1% with an estimated catch efficiency of 50%, which then results in an estimate of 0.2%. For wild salmon smolts, this was estimated to be between 0.6% and 0.8% (Armin Nemitz, personal communication). Our estimated average return rate (over 2010–2021) is in the same order of magnitude (0.5%–0.6%) indicating stocking remains a necessity besides the necessary Rhine system restoration efforts as these estimates are far from the 3% supposedly needed to maintain a self-sustaining population (Schneider, 2011). However, return rates of wild smolts of both European and North American 1SW stocks (1999–2008), which are self-sustaining (although declining), are often around or above this threshold, varying from 0.1% to 13% (Chaput, 2012). The same holds true for more recent data (2008–2014, 2018–2019) on return rates from Scottish and Irish rivers varying from 0.8% to 4.7% (Simmons et al., 2022). Return rates of hatchery-reared smolts are generally lower than those of wild smolts (Chaput, 2012) indicating that the desired return rate of 3% is a bare minimum.

5 | CONCLUSIONS AND MANAGEMENT IMPLICATIONS

After an initial increase since reintroduction started, the Atlantic salmon population of the river Rhine declined rapidly since 2010 with an estimated spawning population of only ~350–800 individuals. Based on a yearly amount of ~78,000–140,000 smolts starting to migrate (mainly stocked at different life stages), the return percentage ranges between 0.5%–0.6%, far from the 3% supposedly needed to maintain a self-sustaining population (Schneider, 2011). During their migrations, many individuals disappear, with the highest losses reported in the rivers (an estimated 86% for downstream migrating smolts and 94% for adult upstream migration), in contrast to the finding that for many stocks the highest numbers of salmon lost are at the marine stage (ICES, 2021; Olmos et al., 2020). The highest percentages of smolts are disappearing in the Dutch lower Rhine (71%) followed by the German tributaries (44%), which might be an overestimation caused by using hatchery reared smolts for tagging, which then leads to an underestimation of the open sea loss percentage. The percentage of disappearing adults is very high in both the Dutch and the German parts of the Rhine (74% and 78%, respectively). The causes of the decline per river section remain unclear. Our data suggest that there are high losses of smolts in the river Rhine, but also before they enter the river mouth, which might be caused by predation by both piscivorous birds and fish. Based on our data, high losses of smolts in the German tributaries cannot be attributed to upstream situated barriers as the tagged smolts were released downstream of these barriers in the tributaries and the main route downstream via Waal and Nieuwe Waterweg has no barriers. However, anecdotal evidence does suggest that high losses of smolts around barriers do occur. High losses of returning adult salmon in the Dutch and German parts of the river Rhine are probably due to the cumulated effects of the above-mentioned threats.

Marine mortality rates have a large influence on the number of adult salmon returning to spawn (Nieland et al., 2015). However, there is no evidence for compensatory mortality in the marine environment (Einum & Nislow, 2010; Milner et al., 2003). This means that any increase in the smolt output from a river is assumed to translate directly into an increase in the number of returning adults, assuming other factors influencing natural mortality in the ocean remain constant (Thorstad et al., 2021). In addition, marine survival rates are influenced by the condition and quality of the smolts when they leave fresh water (Russell et al., 2012). We therefore fully support the view of Thorstad et al. (2021) that a fundamental strategy should be to ensure that the highest number of wild smolts in the best condition leaves the river Rhine to the North Sea. There is great scope for water quality, river regulation, migration barriers and physical river habitat improvements, although these should be addressed adequately. Restoration efforts can fail when the causes of a decline are misidentified, and interventions do not address the right problem. For the Rhine, despite over €600 million being spent on restoration measures to improve water quality, habitat conditions and especially connectivity (ICPR, 2020a), the current ecological state of the Rhine system is still insufficient to support a viable salmon population throughout the species' original range within its catchment. In this case, the loss of habitat and sediment quality due to hydromorphological alternations were not addressed sufficiently (Lennox et al., 2021). In addition, van Puijenbroek et al. (2019) found that viable populations of Atlantic salmon occurred mainly in rivers that were at least 85% accessible. In rivers where the population was extinct or restocking of juvenile salmon was practiced, accessibility averaged only 25%. Restocking of Atlantic salmon in European rivers often occurs in high numbers and repeatedly over several years (HELCOM, 2011; ICPR, 2015; Wolter, 2015), just as is the case for the river Rhine. These results, together with ours, indicate that restocking the river Rhine might only result in a self-sustaining population with more ecological restoration than carried out so far along the highly regulated river course and associated high levels of predation and high intensity of shipping, and might be increasingly limited by future climate change.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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