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Historical ecology of anadromous houting (*Coregonus oxyrinchus* / *C. lavaretus*) in the Rhine-Meuse delta

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ABSTRACT

Houting (*Coregonus oxyrinchus* / *C. lavaretus*) is a facultative anadromous fish species that gradually declined and finally extirpated from the Rhine-Meuse delta during the first half of the 20th century, together with several other migratory fish species. We examined > 10k multi-characteristic historic sources of potential information on houting, like paintings and newspaper articles, to reconstruct historic presence, abundance and environmental history of houting. Our results showed that houting was present in the Rhine-Meuse delta at least from the early 13th century and started to decline from the second half of the 19th century, decades earlier than stated in previous studies. The strong decline in houting abundance coincided with large morphological changes and intensifying river fisheries. This trend preceded the strong deterioration of the chemical water quality and the period in which river connectivity was lost by the building of barriers, like weirs and dams. The recent recovery of houting in the Netherlands coincided with a strong improvement of chemical water quality and restocking programs in NW-Europe. Since river fisheries are virtually absent to date, and the river morphology is still highly artificial, we argue that houting suffered mainly from fisheries in the period 1850–1940 and that its recovery was hampered by a poor chemical water quality and not by a loss of river connectivity. Our multi-source, single-species approach provided greater insight into the human induced impacts on the decline and recovery of a keystone migratory fish species. Our study supports the development of targeted, species-specific actions to address bottlenecks hindering the successful recovery of migratory fish populations in European rivers.

1. Introduction

Anthropogenic stressors like pollution, over-fishing, river regulation, and the creation of weirs and dams caused the decline and extinction of many migratory fish species worldwide (Dias et al., 2017; Limburg and Waldman, 2009; Ormerod, 2004). Present-day studies can rely on plentiful environmental data from monitoring programs to understand stressors that impact these fish

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populations (e.g. Dafforn et al., 2015; Reid et al., 2019; Sayer et al., 2025; Sun et al., 2025). However, many migratory fish species had their major decline before the intensive data collections started in the second half of the 20th century (Hall et al., 2011; Lenders, 2017; Mattocks et al., 2017; Waldman and Quinn, 2022). Therefore, it is difficult to point out the specific stressors that are responsible for the decline in stocks, and subsequently, it also remains uncertain which actions should be taken to relieve the bottlenecks for successful recovery of their populations (Hartgers and Buijse, 2002; Lenders et al., 2016).

This also relates to anadromous populations of houting which can be considered a keystone species for the group of anadromous migratory fish. Historically, an inconsistent variety of both scientific (*Coregonus oxyrinchus*, *C. lavaretus*) and common names (houting, North Sea houting, European whitefish) was used to indicate the anadromous population in the Rhine-Meuse delta (Kroes et al., 2023). In this study we use “houting” to refer to this population. Houting was abundant in the river Rhine before 1900 (de Groot, 2002; Lenders, 2017), but between 1916 and 1940, commercial fisheries reported strong declines in catches in the river Rhine (Kranenburg et al., 2002). During the late 1930's, anadromous houting even disappeared completely from all Northwest European rivers and estuaries, except from a few Danish rivers (de Groot, 2002; Borcharding et al., 2010; Jepsen et al., 2012). However, after a long period of absence, increasing number of records of houting in the Rhine delta were observed from the 1990's onwards showcasing the recovery of houting. In addition, Borcharding et al. (2014), (2010) and Kranenburg et al. (2002) provided proof of natural reproduction which indicates that currently a stable self-sustaining population is present.

The radical changes in presence and abundance of houting in the beginning of the 20th century in the Rhine delta coincide with manyfold changes in environmental conditions and management activities. For example, during this period the water quality of the river Rhine decreased dramatically due to industrial pollution (Beurskens et al., 1993; bij de Vaate et al., 2006), but also improved again because of measures taken in the framework of the Convention of the International Commission for the Protection of the Rhine (ICPR) in 1963, the Rhine Action Program in 1987 (Beurskens et al., 1994; van der Geest, 2001) and the European Water Framework Directive (European Commission, 2000). While during the peak of pollution massive fish kills occurred in the river Rhine (Lelek and Köhler, 1990), water quality is nowadays no longer an obstacle for many fish species to recover (Admiraal et al., 1993; Uehlinger et al., 2009). Besides these changes in water quality, other factors are addressed to the decline and recovery of houting as well, including fisheries and large changes in the hydrology, morphology and connectivity of the Rhine delta (de Groot, 2002). Also, several restocking programs were attempted to reintroduce houting in the Rhine delta from the remaining Danish populations (Borcharding et al., 2010, 2014; de Leeuw et al., 2005). But it remains unknown how these restocking events impacted local populations.

Historical ecological studies on comparable anadromous species gave insight in the causes of the decline of fish populations in the Rhine delta. For example, stocks of Atlantic sturgeon (*Acipenser sturio*) and Atlantic salmon (*Salmo salar*) were already in decline before the industrial revolution, intensive river regulation, and pollution. The intensified fisheries ended the remaining stocks in the 20th century (Brevé et al., 2022; Lenders, 2017). However, these studies only describe causes for the decline of fish populations, not for the recovery. They also predominantly use market data from fisheries for the reconstruction of species abundance through time and such data is only available for commercially and/or culturally important species. For houting, such abundance data is only available from limited time series (de Groot, 2002; Lenders, 2017; Quak, 2013). Moreover, monitoring data on environmental parameters from the period when anadromous fish disappeared from the Rhine delta are scarce (bij de Vaate, 2003) and available data were not used in previous historical ecological studies. Subsequently, it remains unclear which (combination of) factors in the Rhine delta caused the decline of anadromous fish in general and the decline and recovery of houting in particular.

Therefore, in this study we will take an historical ecological approach to fill this knowledge gap by including data from > 10k newspaper articles, books, paintings, survey reports, angler reports and specimens from natural history museums to describe the ecological history of houting in the Dutch part of the Rhine delta. Similar approaches were previously used to successfully study both marine and freshwater fish to examine the effects of human disturbance on aquatic ecosystems (Begossi and Caires, 2015; Haidvogel et al., 2014; Jackson et al., 2001; Poulsen, 2008; Tribot et al., 2021). By zooming in on local biodiversity and local disturbances over longer timescales using an historical ecological approach, we aim to gain a better understanding of the anthropogenic impact on ecosystems and resulting management actions. To achieve this, we:

- 1) determine the presence and abundance of houting from the early Middle Ages to present-day,
- 2) review the anthropogenic impact on the environmental history of the Rhine delta,
- 3) identify the changes in impact of different anthropogenic drivers during the decline and recovery of houting,
- 4) discuss limitations and usefulness of historic sources for previous and future studies on migratory fish.

2. Methods

2.1. Houting nomenclature

In the whitefish genus *Coregonus*, taxonomic confusion resulted in a number of nomenclatural issues (Himberg and Lehtonen, 1995; Freyhof and Kottelat, 2007; Østbye et al., 2005). Originally, the common whitefish *C. lavaretus* was considered a distinctive species with a different distribution in comparison to the North Sea houting, *C. oxyrinchus*. However, a recent phylogenetic study of Kroes et al. (2023) argued that the species distinction between *C. lavaretus* and *C. oxyrinchus* is incorrect and that the latter is a junior synonym. In this study, ‘houting’ is used to refer to both species concepts. In addition, a list of Dutch synonyms for the species was composed from written sources used in this study (newspapers, books, encyclopedia and historic dictionaries) until no new synonyms were found (see supplementary S.1). For written documents, only entirely Dutch texts were studied to limit linguistic errors.

2.2. Life-history traits

Adult houting are tapered fish that can grow up to 50–70 cm. Houting is able to adapt to a broad range of aquatic habitats. Traits like salinity tolerance, gill raker physiology and migration motivation vary between populations from different geographical areas (Kroes et al., 2023). Houting has limited swimming capacity, struggles to cross fish passages and is unable to cross weirs (Jepsen et al., 2012). The historical houting population in the Rhine-Meuse delta was probably anadromous. Nowadays both anadromous and potamodromous populations are present (Borcherding et al., 2008; 2010). However, spawning locations, spawning timing and larval development of houting in this region are unknown. The taxonomic ambiguity further complicates a strict description of its traits from other studies or databases like Fishbase.

2.3. Geographical study area

Houting populate both freshwater and marine habitats in Central and Northwest Europe (Kahilainen and Østbye, 2006). Anadromous houting is geographically limited to the Wadden Sea area and the coastal zones of the southern North Sea (Hansen et al., 2008). To zoom in on local biodiversity and local disturbances, this study only focused on observations of houting in the Dutch part of the deltas of the rivers Rhine, Meuse, including lake IJsselmeer, the Wadden Sea, river Scheldt estuary and the Dutch coastal zone (Fig. 1).

2.4. Houting data collection and database construction

Recognizing the potential risks of subjectivity, bias, and representativeness in individual sources, Haidvogel et al. (2014) recommend the use of diverse historical sources in historical ecology. Accordingly, to reconstruct the historical presence of houting in the Netherlands, a variety of sources was utilized, including artworks, written sources (newspapers, books, etc.), survey data, angler reports and specimens in natural history collections. These were compiled into a database of houting records, with the number of individuals recorded for each entry when available.

2.5. Art work

The artworks were selected from the two largest online collections of Dutch art: the RKD Images from the Netherlands Institute for



Fig. 1. Map of the study area with locations and names of waterways and constructions referred to in the text.

Art History (Rijksbureau voor Kunsthistorische Documentatie, RKD) and the Rijksstudio from the Amsterdam Rijksmuseum. Artworks from the RKD Images were selected by using the keyword “vis” (Dutch for “fish”). The Rijksmuseum API was used to select artworks in the Rijksstudio with the following selection criteria: time frame: 1500–1880; type of work: painting, drawing, etching or engraving; origin: Dutch; keywords: fishes, bony fishes, other fishes, deep sea fishes, eels, cartilaginous fishes, fishes (with NAME), and the Dutch keyword “vissen” (plural for fish). This resulted in a combined set of 2567 artworks. Duplicates and irrelevant images (e.g., fantasy creatures or scenes without clearly distinguishable fish) were removed by sorting on the title and visually judging the images. This resulted in a set of 2240 images; 379 from the Rijksmuseum and 1961 from the RKD (Table 1 and S.1).

The selected artworks were used in an online crowdsourcing project from the NWO program ‘A new history of fishes’. Citizens were asked to determine fish species from a random selection of pictures on <https://www.zooniverse.org/projects/anneoverduin/fishing-in-the-past>, which resulted in 197 artworks on which houting was identified. Expert judgment was done twice on the entire image data set to correct for false-positive and false-negative classifications from the crowdsourcing project. The body shape, and the presence of a distinct snout and an adipose fin were used as classification criteria. False-positive were determined in 196 out of 197 artworks. Additionally, 2 false-negative identifications were found, which resulted in the inclusion of 3 artworks in the database (Fig. 2). No quantitative data was used from the artworks. Qualitative data about the origin and composition of the artworks was noted for each record.

Image sources: A) Object number SK-A-1487 from the Rijksmuseum <https://id.rijksmuseum.nl/20027370>; B) Object number RP-P-1896-A-19046 from the Rijksmuseum <https://id.rijksmuseum.nl/200167518>; C) Object number RP-T-BR-2017-1-6-45 from the Rijksmuseum <https://id.rijksmuseum.nl/200707855>; D) Object number RP-P-1881-A-4580 from the Rijksmuseum <https://id.rijksmuseum.nl/200175485>

Table 1

Overview of all studied sources for artworks, writings, angler reports, survey data and specimens in natural history collections. For each source a short description was given, including the number of studied objects. For included records, oldest and latest record are dated. The number of records included for each source (N) is noted in the last column. ‘Total’ describes the time period with houting records (1400–2021) and the total number of houting records (1740) included.

	Source	Description	N studied object	First record (y)	Last record (y)	N records with houting data
Art	RKD Images	Digital database from the Nederlands Instituut voor Kunstgeschiedenis (Netherlands Institute for Art History, formerly known as Rijksbureau voor Kunsthistorische Documentatie, RKD) with 267,856 images of paintings, etchings and drawings from Dutch artists	1961	1485	2009	0
	Rijksstudio	Digital database from the Rijksmuseum with 796,904 images of paintings, etchings, drawings from Dutch artists	379	1556	1771	3
Writings	Delpher	Digital database with historic Dutch newspapers (6.1 M), books (164 K), magazines (432 K) and radio bulletins (1.5 M) from 1400-present	9704	1400	2018	1351
	DBNL	Digital library from the Digitale Bibliotheek voor de Nederlandse Letteren (DBNL) with books and texts from Dutch literature, linguistics cultural history with > 15 K books and magazines from the 9th century-present	31	1677	2008	10
	UBA	Collection of recipe books from the Universiteitsbibliotheek van Amsterdam (Amsterdam University Library, UBA)	43			0
Survey data	CLO	Compendium voor de leefomgeving (Compendium for the Living Environment, CLO) is an online database from four Dutch institutes that collect environmental data	37	1910	2006	37
	NIOZ	Monitoring data from continuous fyke monitoring by the Koninklijk Nederlands Instituut voor Onderzoek der Zee (Royal Netherlands Institute for Sea Research, NWO-NIOZ) in the Dutch Wadden Sea from 1959-present	6	2013	2019	6
	ATKB	Monitoring data from consultancy agency ATKB from annual fish surveys within the Water Framework Directive	99	2006	2020	99
	WMR	Monitoring data from Wageningen Marine Research (WMR) from freshwater surveys in large Dutch waterbodies	133	1991	2020	133
	Unpubl	Unpublished data from two studies on migratory fish in Westeinderplassen and Schellingwoude	13	2017	2019	13
Angler reports	Zeevisland	Website for written angler reports	2	2017	2020	2
	Mijn Vismaat	Android/iOS application from Sportvisserij Nederland for angler catch reports	37	2013	2021	32
Specimens from collections	Naturalis	Online database for the museum collection of Naturalis, the national research institute for biodiversity	28	1843	1998	17
	NHM	Online database for the museum collection of the Natural History Museum London (NHM)	3	1843	1998	3
	UvA	Online database from the Allard Pierson Museum, the archeological museum of the University of Amsterdam (UvA)	2	1818	1885	2
TOTAL			12,478	1400	2021	1708

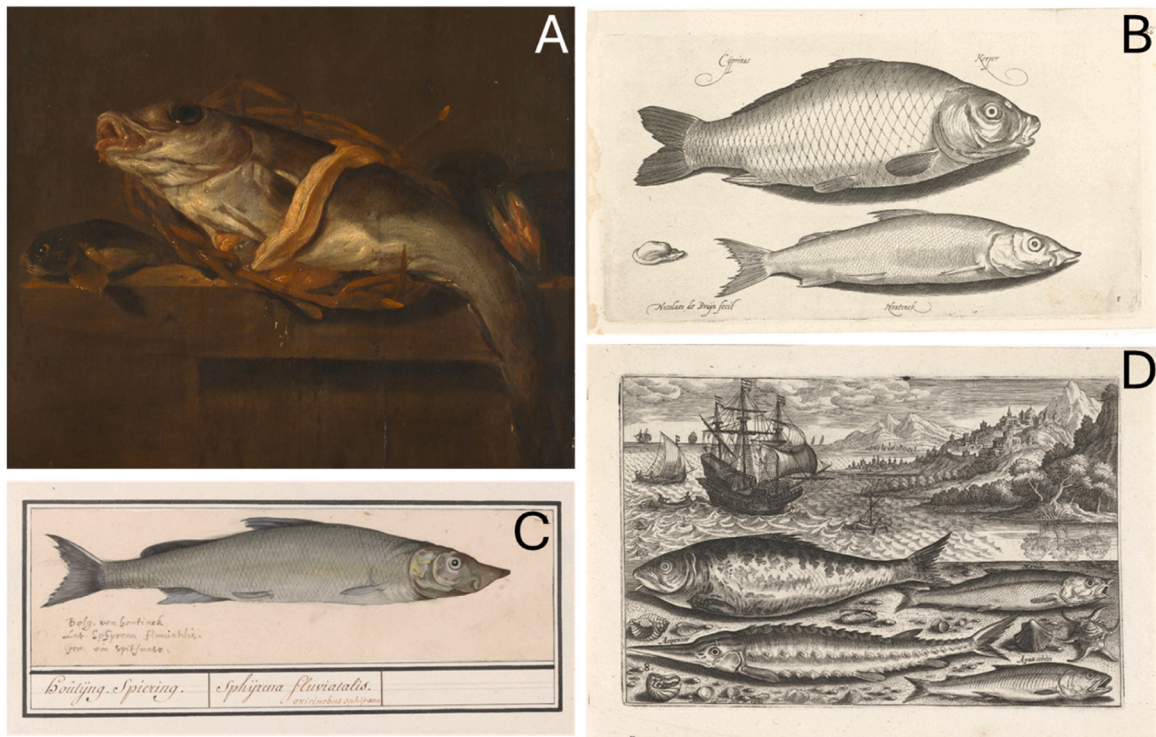


Fig. 2. Examples of historical artworks that were reported as depicting houting (*Coregonus* sp.). The selected works were part of an online crowdsourcing project within the NWO program A New History of Fishes. Citizens indicated houting in 197 out of 2240 artworks, which were then reviewed twice by experts to correct for misidentifications. Panel A shows a false-negative: the haddock (*Melanogrammus aeglefinus*) in Jan Vonck's painting "Visstilleven met schelvis en knorhaan" (1640–1662) was mistakenly identified as houting. Panels B–D illustrate cases where (some of) the depicted fish are houting: (B) "Karper en Houting" (1581–1656) by Nicolaes de Bruyn shows a carp (above) and a houting; (C) "Houtijng. Spiering" (1596–1610) by Anselmus Boetius de Boodt shows a houting. (D) "Vier vissen op het strand" (1598–1618) by Adriaen Collaert depicts an allis shad, houting, smelt, and sturgeon; This figure highlights that expert judgment, using morphological traits such as body shape, snout, and adipose fin, is essential to reliably distinguish houting in historical sources and to correct for false-positive and false-negative identifications from crowd-sourced data.

2.6. Written documents

Written documents were selected from three sources: the first was Delpher (<https://www.delpher.nl/>), a large digital database with historic Dutch newspapers (6.1 M), books (164 K) and magazines (432 K) from the 13th century to today. The second was the 'Digitale Bibliotheek voor de Nederlandse Letteren' (DBNL; <https://www.dbnl.org/>). DNBL is a digital library with books and texts from Dutch literature, linguistics cultural history with > 15 K books and magazines from the 9th century till present. The third was the digital library of the University of Amsterdam (<https://uba.uva.nl/>), containing scientific literature, zoologic reports and a collection of 43 historic fish recipe books (18th-20th century).

The following Dutch keywords were used: houting, houtingh, houtings, houtingen, coregonus, oxyrinchus, oxhyrinchus, oxyrhynchus, lavaret, lavaretus, adelvisch, blauwneus, houtinck, haltinckvisch, noordzeehouting, marene (NOT 'kleine marene'). Results were filtered for online publication date, only records published until December 5th, 2021 were used. All records were then individually examined to remove duplicates. Text with other subjects than fish (mainly person names, advertisements, wedding reports, obituaries), text with fish from outside the Netherlands, and false-positive results from spelling errors in the text or reading errors from the search engine were also excluded. This resulted in a set of 1390 individual written records arranged by the date of publication and if applicable, the year and place to which the observation of houting referred.

If available, a short description was noted for each record to interpret its context. For example, "houting catches started to pick up at Woudrichem", "each autumn, salmon, Allis shad and houting swim from sea into our rivers to spawn" or "new closed season for the next species is legislated". If stated, numbers of caught houting were also noted.

2.7. Survey data

Survey data for recent observations of houting in the Netherlands were obtained from five sources. The first was from the NWO-NIOZ Royal Netherlands Institute for Sea Research who performed a continuous fike net monitoring program in the Dutch Wadden Sea from 1959-present. The second was the 'Compendium voor de leefomgeving' (<https://www.clo.nl/>), a website with environmental

data from four Dutch institutes that collect environmental data. The third was ATKB, a Dutch consulting agency that performs annual fish monitoring for local and national governments within the Water Framework Directive. The fourth was Wageningen Marine Research (WMR), a research institute that performs surveys in large Dutch waterbodies. The final source was data from two yet unpublished studies about migratory fish from the University of Amsterdam (UvA). Both *C. lavaretus* and *C. oxyrinchus* and their Dutch synonyms were used to select data. Each survey date on which 1 or more houting was caught was included as a single record. 282 records from survey data were included, numbers of caught fish were noted for each record for quantitative analysis.

2.8. Angler reports

Angler reports were obtained from 'Mijn VISmaat' (<https://www.mijnvismaat.nl/>) and 'Zeevisland' (<https://zeevisland.com/>), two online platforms with catch reports of freshwater and marine anglers, from 2007-present and 2002-present, respectively. Both *C. lavaretus* and *C. oxyrinchus* and their Dutch synonyms were used as keywords. Reports without photo and catch location were excluded. After expert judgment, 34 out of 39 records of single fish were included.

2.9. Specimens from natural history collections

Data of museum specimens were obtained from the collections of Naturalis Biodiversity Center (<https://biportal.naturalis.nl/>), the Natural History Museum London (<https://data.nhm.ac.uk/>) and the University of Amsterdam from the Allard Pierson Museum (<https://lib.uva.nl/>). Both *C. lavaretus* and *C. oxyrinchus* and Dutch synonyms were used as keywords, as well as historic species name *Salmo oxyrinchus* (syntype name) and alternative spelling of 'oxyrinchus'. 22 specimen originating from the Netherlands were included in the database.

2.10. Data processing of houting records

In total, 12,478 individual sources were studied for records of houting in the Netherlands. After filtering and selecting for each source as described above, 1723 records with data on houting records remained (Table 1, S.3.). Qualitative data was used to indicate the presence of houting in the Netherlands over time. Short descriptions of records from artworks, writings and museum specimens were used for cultural interpretation, firstly to describe the cultural, nutritional and economical value of houting in the Netherlands, and secondly, to indicate possible over- or underrepresentation of houting records from other sources.

Quantitative data from angler reports, fisheries and surveys was used as a reference for the abundance of houting over time. Fisheries catch data was not only obtained from fisheries statistics data, but mainly from weekly reports on river fisheries in newspapers. For each decade from 1841, average annual catch was calculated by dividing the sum of catch per decade by the number of years with reported catch for that decade and plotted on a Log₁₀ scale. Numbers of annually caught houting were divided by the number of included records for those years and plotted on a Log₁₀ scale (catch/year/source) to correct for outliers caused by data availability. For sources that report catch weight or CPUE, numbers of caught houting were converted from weight to numbers by assuming that 1 kg represented 1 individual. Together with the description of the qualitative data, the plots were used to indicate trends in abundance of houting over time.

2.11. Historical environmental data

Since abundance and presence of houting was predominantly derived from observations from the rivers Rhine and Meuse, the environmental history of those rivers was reviewed. This was done by reviewing both scientific and secondary literature for anthropogenic changes in those rivers in the categories river morphology, barriers, fisheries, nutrients, organic load and pollutants (S. 2). For each stressor type, the main trends, relevant events and estimated maximum impact were dated and described. Since reliable quantitative data were absent before 1950 (bij de Vaate, 2003; Nienhuis, 2008), we did not use quantitative data. Instead a qualitative approach was used in which we searched for statements in relevant literature of strongest level of impact and no level of impact. Then we searched for statements on increasing and decreasing impacts. For example: "strong increase in salmon fisheries and dredging due to the use of steam engines in 1880" (Nienhuis, 2008) or "N- and P-load increase ca. nine fold in river Rhine from pre-industrial period to 1990" (de Jonge et al., 2002). This resulted in a qualitative list of key-events through time. The strongest level of impact for each stressor was dated first and used as a relative reference for impact in earlier and later periods. The dating of increasing or decreasing impact was used to construct an estimated trendline for impact over time.

Changes in river morphology were described based on the position of old-meanders and bifurcations, dredging activity in the river bed, the occurrence of new bifurcations and river connections, the relocation of river mouths, and the installation of river groynes and dykes. Changes in connectivity within the river system were described based on the construction year of dams, weirs, spillways, sluices, hydropower stations and storm surge barriers. Changes in fisheries were based on the size of salmon river fisheries fleet in the Rhine-Meuse estuary, since houting was caught by salmon fisheries, but was not a target species (van Drimmelen, 1987; de Groot, 1989; Quak, 2013). Changes in nutrient concentrations were only based on the Dissolved Inorganic Nitrogen (DIN) and PO₄³⁻ concentrations in the river Rhine. Changes in the organic load were based on Biological Oxygen Demand (BOD) measurements, the use of manure and fertilizers in Dutch agriculture, and descriptions of the transition from land-based cesspools to surface water-connected sewer overflows and wastewater treatment plants. Changes in pollutants were based on heavy metal measurements, only obtained from the river Rhine, and qualitative statements on the impact of developing industries in the upstream Ruhr area.

Drivers for decline and recovery of houting were discussed by comparing timing and sequence of stressors impact with timing of the changes in species abundance in the Netherlands.

3. Results

3.1. Presence and abundance of houting in The Netherlands

Two indirect sources from 1938 (history book) and 1944 (newspaper article) document houting in fisheries and their use as a food source dating back to at least the year 1400. However, the first direct historic sources were two etchings and a drawing of houting dated from the late 16th/early 17th century (Fig. 2). These pictures all were part of natural historic albums with common fish, frogs, shellfish and sea creatures from Dutch artists, indicating that houting was a common species at that time.

From the 17th, 18th and 19th century, 15 natural history books with historical descriptions of houting and other endemic fish in the Netherlands were found. Also, in 1699 the first record of 'houting' appeared in a Dutch dictionary. The first newspaper article on houting appeared in 1803, as part of an announcement on legislation for designated fishing tackle for river fisheries. From 1833 onwards, newspaper articles report on designated fishing tackle and minimum size legislation concerning houting for at least once a year. No houting was found on any of the studied oil paintings from Dutch masters that often displayed an excess of other freshwater and saltwater fish species in kitchen or market settings. Also, no recipes with houting were found in any of the studied fish recipe books.

Data density was relatively low for the period before the mid-19th century. Before 1950, houting was found in 47 records of which only one contained quantitative data (Fig. 3). From the second half of the 19th century, the number of houting records increased, predominantly caused by the increasing number of newspaper articles that report on houting. In these articles, many weekly catches of river fisheries were reported, among others reports of weekly market prices for other riverine fish, like salmon and shad. The articles included mainly appeared from October to December and reflected the season in which houting from the North Sea migrated upstream to spawn. Houting was landed in several villages and cities along the river Rhine, Meuse and IJssel, but mainly in the villages of Woudrichem and Gorinchem along the river Waal, the major bifurcation of the river Rhine. These cities were the center of Dutch river salmon fisheries. Houting was originally bycatch, but by the end of the 18th century, catch of houting (and allis shad among others) was used to compensate for decreasing salmon catches. Incidentally, landed houting from sea fisheries were also reported.

The first quantitative houting record was found in a weekly newspaper from 1844 in a fisheries catch report. Weekly catch reports increased strongly in the following decades and peaked at the transition from the 19th to the 20th century. From 1851 onwards, newspapers also published articles on the houting catch from an entire previous year in annual reports. Both weekly and annual reports could be used as quantitative reference for the number of caught or observed houting specimens, although the frequency of these reports varied per week and year (Fig. 4).

The highest annual catch ($N = 97,420$) from annual reports was reported in 1859. The highest annual catch that was calculated from weekly caught houting was reported in 1885 ($N = 25,871$). In newspaper articles from 1880 onwards, it was regularly reported that the Dutch river fisheries, including houting catch, showed an accelerating decline. From 1900 onwards, newspapers also reported about the deplorable state of the Dutch river fisheries. Corrected catch data endorse these observations, showing decreasing catches over time (Fig. 5). Remarkably, catch in annual reports from the national fisheries archives was outnumbered by a factor 3–38 by the

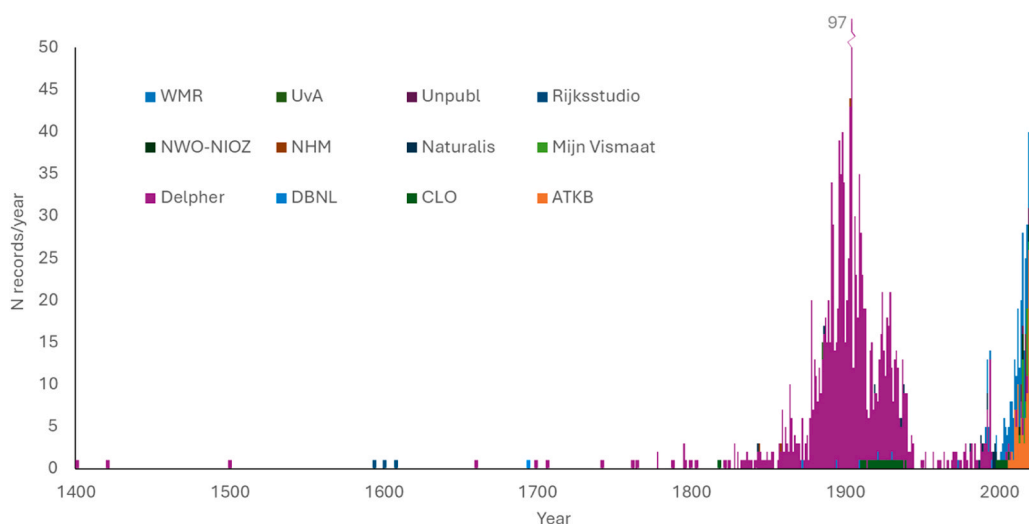


Fig. 3. Cumulative number of records per year per source. For the time period 1942–1977, the sources report about the absence of houting in Dutch waters or historic houting catch from before 1942. Note that the number of records do not directly reflect the total abundance since catch effort from different periods is incomparable. For full terms of the abbreviations, see Table 1.

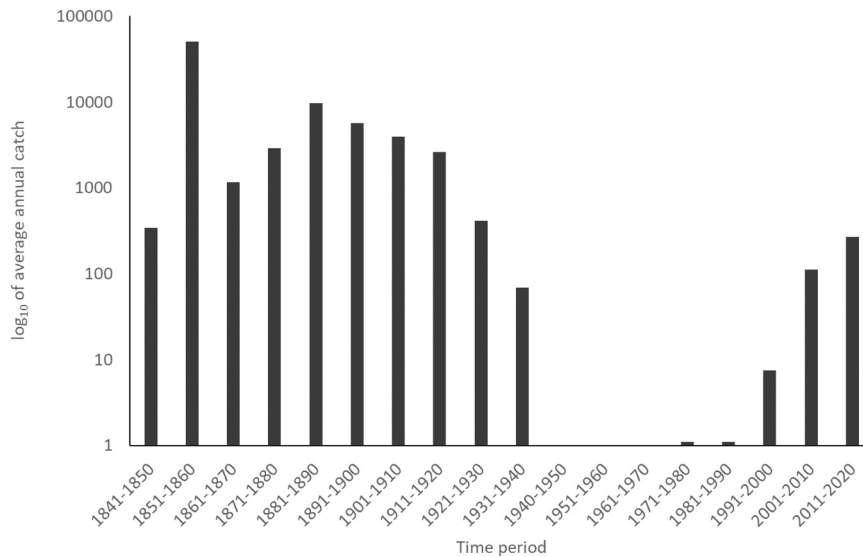


Fig. 4. Average annual catch of houting per decade (sum of catch / number of years with reported catch per decade) as calculated from the records that either refer to catches or to observations within the Netherlands. Some records contained catch reports from previous years. In those cases, the previous year is used for dating. For the periods 1971–1980 and 1981–1990, the value 1 was manually transformed into 1.1 to prevent invisibility on the log-scale.

calculated total yearly catch based on the weekly fishery reports in the years 1911, 1917, 1925, 1930 and 1933.

According to a reflecting newspaper article about the disappearance of Dutch river fisheries, published in 1960, the last houting was caught in 1942. Between 1943 and 1977, no houting observations were recorded. Later on, several newspaper articles reported on the disappearance of houting from the Netherlands or the absence in catch efforts or observations. Also, survey's, fisheries reports and nature historical newspaper articles reported the extinction or absence of houting for this period. Given the low stocks, the disappearance of intensive river fisheries after World War II and the records of re-occurring houting before recent anthropogenic restocking started, it remains uncertain whether houting was really absent in the Netherlands between 1942 and 1977.

After 35 years of observed absence, the re-occurrence of houting was first recorded in 1978 by one of the few remaining river fishermen. Systematic fish surveys in rivers started around 1964, reporting the first houting in 1998. Since, the numbers of recorded houting increased steadily (Figs. 4, 5), possibly because of natural recolonization, new hatching and restocking projects with houting from the Danish River Vidå between 1996 and 2005 (Borcharding et al., 2008, 2010) and/or improved chemical water quality in the large rivers. Surveys and anglers also report houting catches in the Wadden Sea and the shallow lakes. Although houting records increased over the last decades, present day catches from surveys and anglers are a fraction of the fisheries catches in the second half of the 19th century. However, catch effort between these periods is incomparable, since river fisheries are nowadays virtually absent in the Rhine delta.

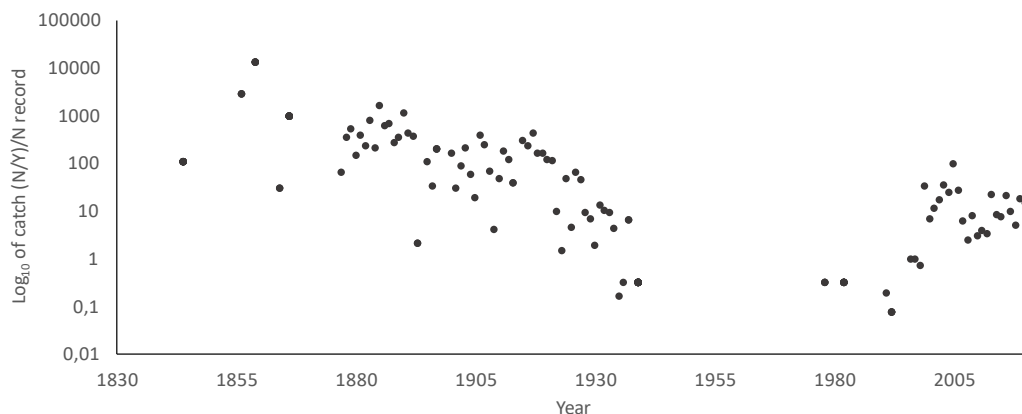


Fig. 5. Annual houting catch, corrected for the number of records presented on a Log₁₀-scale (number of reported individuals per year N/Y, divided by the number of included records N for the corresponding year). Some records contained catch reports from previous years. In those cases, the previous year is used for dating.

In summary, quantitative and qualitative data showed that houting was a common and abundant species for the Dutch river systems at least until the end of the 19th century. The data suggest that houting stocks already decreased from the second half of the 19th century. Between 1942 and 1977, houting was either extirpated or just undetected. By the end of the 20th century, houting recovered, although stock levels should be interpreted with care, since catch effort from different periods is incomparable.

3.2. Anthropogenic impact on environmental history of the Rhine delta

3.2.1. Morphology

Dutch rivers were used for fisheries, transport, irrigation and drinking water from ~3500 BC. The first river dykes, dams and sluices

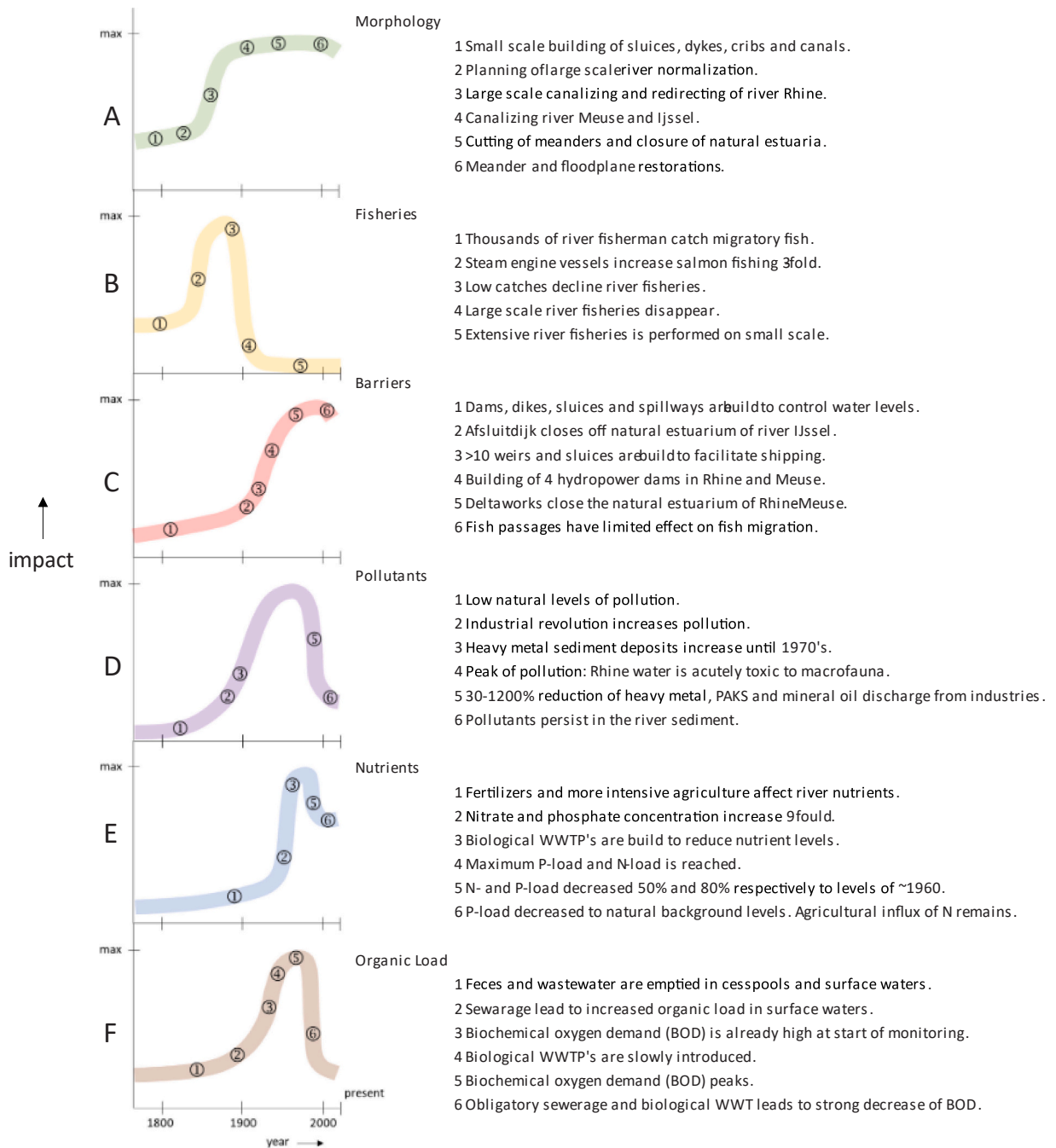


Fig. 6. Trends of relative impact from six stressors in river Rhine and river Meuse. The graphs represent the synthesis of qualitative and quantitative data, striking events per stressor are given in text next. S.2 contains a complete overview of the environmental data.

were built in the 10th and 11th century (Arts, 2010). In the 18th century, several connections between river Rhine and river Meuse were closed (ten Brinke, 2004). The building of the Pannerdens Kanaal in 1707 was the first large-scale measure to manipulate and divert the discharge of the river Rhine (Nienhuis, 2008). The impact of anthropogenic activities on the Dutch Rhine delta was relatively low until around 1850 (Fig. 6A). Although dykes, dams, sluices, bifurcation canals, and spillways had been constructed for centuries, natural phenomena such as flooding and sedimentation remained only partially controlled by these anthropogenic structures until the mid-19th century (ten Brinke, 2004; Nienhuis, 2008). From 1850 on the impact of anthropogenic activities exponentially increased (Fig. 6). National stability, economic prosperity and industrial revolution made it possible to radically change the meandering free-flowing river into straitened, canalized shipping routes (Broseliske et al., 1991; (de Nijs and Beukers, 2003); Nienhuis, 2008). Around the 1950's, the last changes were made on the course of river IJssel, altering the natural course of the main Dutch rivers to its current state (de Nijs and Beukers, 2003; ten Brinke, 2004; Nienhuis, 2008).

Only very recently, measures were taken to restore some of the natural morphology of the river Rhine and Meuse floodplain with the national program 'Ruimte voor de rivier' (<https://www.rijkswaterstaat.nl/water/waterbeheer/bescherming-tegen-het-water/maatregelen-om-overstromingen-te-voorkomen/ruimte-voor-de-rivieren>). Flood prevention shifted from dyke building to river bed enlargement, resulting in the relocation of several stretches of river dykes and restoration of parts of the floodplains (Nienhuis, 2008; Stoffers et al., 2021). However, large-scale restoration of the original meandering river course is blocked by anthropogenic use of both rivers and the surrounding land.

3.3. River fisheries

During the industrial revolution in the second half of the 19th century, the impact of river fisheries in the Rhine delta strongly increased (Fig. 6B). Fisheries statistics show that salmon river fisheries intensified three-fold from 1852 to 1880, since steam engines were used for vessels and seine net handling (van Drimmelen, 1987). From 1880, catches of river fish declined rapidly. Between 1912 and 1938, large-scale river fisheries entirely disappeared from the river Rhine and Meuse to date (van Drimmelen, 1987; de Groot, 1992).

3.4. Barriers

Several original connections between the rivers Rhine and Meuse were closed between 1727 and 1904 (van Drimmelen, 1987; ten Brinke, 2004; de Nijs and Beukers, 2003). The first barriers were built upstream, in Swiss, Germany, Belgium and France.

In the Dutch part of the Rhine-Meuse-Scheldt delta, the majority of barriers were built between 1930 and 1970 (van Drimmelen, 1987; de Nijs and Beukers, 2003; ten Brinke, 2004; Nienhuis, 2008) (Fig. 6C). The largest structure of this kind is likely the Afsluitdijk, completed in 1932, which enclosed the former Zuiderzee. This dam resulted in the formation of Lake IJsselmeer and established an abrupt barrier between the freshwater river system and the Wadden Sea (Nienhuis, 2008).

A storm flood in 1953 resulted in the building of the Delta Works which closed off large tidal areas and almost the entire Rhine-Meuse delta with dams and storm surge barriers to prevent future flooding. In 1970, the Haringvliet closed, which left an artificial canal (the Nieuwe Waterweg) as the only remaining open connection between the Dutch large rivers and the North Sea (ten Brinke, 2004).

The first fish passages in the river Meuse were built in the 1950's but the majority was built since 1988. Nowadays, the river Rhine has an open connection for migrating fish of approximately 700 km from the river mouth to the first weir at Iffezheim, Germany. Several measures were taken to further improve river-sea connectivity in the Dutch delta. For example, in 2019, the Haringvliet was partly reconnected with the North Sea by a fish-friendly sluice management of the storm surge barrier. In 2022, the building of the 'Fish Migration River' in the Afsluitdijk started, an artificial structure connecting the Wadden Sea with the river IJssel in the near future. However, the river Meuse and almost all Dutch tributaries and bifurcations of the river Rhine are still blocked by dams, sluices, hydropower plants and weirs.

3.5. Pollution

As part of the industrial revolution, steel production in the Ruhr area had started in 1849. Heavy metals and other chemicals from steel production and other upcoming industries were deposited in the Ruhr, a tributary of river Rhine in Germany and increasingly affected the river chemistry (Klink, 1989; Brüggemeier, 1994; Nienhuis, 2008; Havekes et al., 2021) (Fig. 6D). Furthermore, industries also started discharging wastewater. Historic data show that heavy metal concentrations started to increase from 1900 to peak around 1970 (van Broekhoven, 1987; Broseliske et al., 1991; Malle, 1996).

After this increase, heavy metal concentrations in river Rhine decreased again dramatically (ca. 90 %) from 1970 to 1992 (Malle, 1996), although this reduction is not measured for all heavy metals (Broseliske et al., 1991; Dendievel et al., 2022; van Broekhoven, 1987). In the 20th century, many spills from several disasters also caused acute and lethal toxicity for many organisms (van Broekhoven, 1987; Admiraal et al., 1993; Dieperink, 1998). Pollution of heavy metals and organic pollutants in river Meuse started earlier than in river Rhine because of mining activities (Nienhuis, 2008). Recovery from pollution will probably take a long time, since sediments remain loaded with a wide variety of persistent pollutants (Admiraal et al., 1993; Nienhuis, 2008). Moreover, improved monitoring techniques give increasing insights in the presence of over 350,000 anthropogenic chemicals that were previously undetected and can negatively impact aquatic ecosystems (Wang et al., 2020; Yang et al., 2021).

3.6. Nutrients and organic load

Until the mid-19th century, chemical water quality was predominantly and increasingly affected by human feces and wastewater that were for centuries deposited directly in the rivers or entered the rivers from cesspools via the groundwater (de Nijs and Beukers, 2003; Nienhuis, 2008; Havekes et al., 2021). Organic loads in the River Rhine began rising in the mid-19th century due to rapid population growth and the direct discharge of untreated sewage from cities along the river (Fig. 6F). The adoption of water closets, beginning around 1890 in Dutch cities, further accelerated the input of organic matter into surface waters, as rivers were used as natural sewage discharge systems (Broseliske et al., 1991; Havekes et al., 2021). In rivers systems, the organic load for a long time remained less problematic since the loads were low (dilution), the processes of self-purification and the relatively fast transport to the sea (Broseliske et al., 1991).

By the end of the 19th century, the rise in nutrients diminished the spatial gradient between nutrient-poor river floodplains and nutrient-enriched fields near farms (Nienhuis, 2008) (Fig. 6E). By 1900, elevated levels of phosphorus (P) and nitrogen (N) triggered diatom blooms during spring, which caused nutrient diffusion and increased phytoplankton productivity (de Jonge et al., 2002; van Bennekom et al., 1975; van Beusekom, 2018).

Systematic monitoring of total N and phosphate (PO₄) at Lobith (River Rhine) began in the 1950s, revealing significant concentration increases with a peak observed in the mid-1970s (Broseliske et al., 1991; van Dijk et al., 1996; Klink, 1989; <https://www.clo.nl/>). The construction of biological wastewater treatment plants from the 1970's onwards proved to be very effective in reducing the loads of nutrients and organic waste to the rivers and caused a strong decrease of BOD, nitrogen and phosphorus concentrations in the large rivers (van Lohuizen, 2006; <https://www.clo.nl/>) (Broseliske et al., 1991; Nienhuis, 2008). Today, diffuse sources are the primary contributors of phosphorus to large rivers, while nitrogen levels have remained steady since 2000, comparable to levels observed in the 1960s (van Ginneken et al., 2016; Havekes et al., 2021; Noordhuis et al., 2019; <https://www.clo.nl/>).

4. Discussion

We observed the presence of houting from at least the early fifteenth century to present-day and showed that houting was a common species for centuries in the Rhine-Meuse delta. The decline in catches reported in newspapers indicate that houting abundance decreased strongly from the 1880's at least. Between 1942 and 1978, houting was not detected in the Netherlands. Since, number of records increased, indicating the recovery of houting in the Rhine-Meuse delta.

Artworks and natural historic books about native species in the Dutch water wildlife did not provide quantitative data but were useful to show that houting was present in Dutch waters from at least the 1200's. The absence in recipe books and oil paintings that often display kitchen scenes with overwhelming amounts of Atlantic salmon, Atlantic cod, European eel and other species could indicate that houting was not a common species. However, houting is probably underrepresented in the works because of low cultural and nutritional value as indicated on the etching by Adriaen Collaert as 'fish for the poor' (Fig. 2) and by several newspaper articles that report about 'our tasteless freshwater fish'. These cultural observations underline the importance of alternative sources for reconstruction of ecological history of fish species. Especially for non-commercial fish species like houting, alternative sources are the only way to determine their presence in past times.

Our historical ecology study provided better insight in presence and abundance of houting. National fisheries archives only described houting catch from river fisheries between 1910 and 1939 and are often used to state that houting started to decline from 1916 (de Groot, 1989). However, our study revealed additional fisheries data from local market reports as early as 1844 which indicate that declines already started decades earlier. In addition, the weekly reports from river fisheries that were found in this study show that catch reports from houting in fisheries archives highly underestimate actual catch from fisheries. This nuance in dating and catch is crucial for the indication of main environmental changes that caused decline and extirpation of migratory fish.

4.1. Anthropogenic drivers for decline and recovery of houting

The information and data show that houting disappeared from the Dutch rivers before strong observed decreases in chemical water quality in the second half of the 20th century. Also, most of the barriers in the river Rhine and Meuse were built when houting abundance was already low. This indicates that overfishing and major changes in river morphology in the period 1850–1940 were most probably the main cause for the decline and temporal extirpation of houting from the Dutch rivers. Additional support is provided by the observation that in the Rhine-Meuse delta, the disappearance occurred at the same time as the disappearance of other migratory riverine fish species like Atlantic sturgeon, Allis shad and Atlantic salmon (Brevé et al., 2022; Lenders, 2017). Overexploitation from fisheries is widely accepted as a main driver for the loss of migratory fish in river systems, but other studies also indicate pollution and migration barriers (Segurado et al., 2015; Haidvogel et al., 2015; Lenders et al., 2017). For example, Merg et al. (2020) showed that the loss of migratory fish in a French river system was strongly correlated with river fragmentation from physical barriers. However, they used a model in which only the contemporary status of a limited set of environmental stressors in large French rivers was linked to the historical loss of taxon richness of diadromous fish. Since houting recovered in the Rhine delta before the majority of fish passages was built, physical barriers in the large rivers in the Netherlands are probably not an important factor for houting populations. Potentially, loss of habitat connectivity in smaller rivers and streams also affected houting populations in the Dutch rivers, but this effect is unknown, since the ecology of houting and its habitat use in the Netherlands has not been studied yet and environmental history of these small systems was not evaluated.

Unlike many other anadromous fish (Breteler et al., 2007; Brevé et al., 2022, 2024; Griffioen et al., 2024; van Rijssel et al., 2024),

houting shows strong signs of recovery in the Rhine delta in the last two decades. In this period, recovery of houting populations occurred in years after chemical pollution, organic load and eutrophication improved. We hypothesize that recovery of houting after river fisheries disappeared from the Dutch rivers was hampered by the sharply deteriorated chemical water quality from the 1940's. Currently, river morphology and connectivity is still highly managed and lacks effective habitat restoration measures (Cals et al., 1998; Griffioen et al., 2022). For example, Stoffers et al. (2021) showed that floodplain restoration only had positive effect on riverine fish for about 15 years until the current type of restoration has to be repeated. Since river fisheries are virtually absent to date, and the river morphology is still highly artificial, this underlines our observation that houting suffered mainly from fisheries in the previous centuries as stated by other authors for other fish species in both marine and freshwater systems (Jackson et al., 2001; Lenders, 2007).

Currently, the general assumption is that recovery of houting in The Netherlands was induced by a stocking programs in Germany and lake IJsselmeer in the late 1980's with anadromous houting from Denmark (Borcherding et al., 2008, 2010; Kranenborg et al., 2002). Unlike unsuccessful previous stocking programs between 1907 and 1927 (de Groot, 2002), houting records increased after the recent stocking programs (Borcherding et al., 2010, 2014). However, these programs were preceded by observations of houting in Dutch rivers in the late 1970's and early 1980's, as found in this study. This indicates that recolonization from natural stocks at least occurred, perhaps from retaining populations in Denmark (de Groot, 2002; Borcherding et al., 2010; Jepsen et al., 2012; Quak, 2013). However, the observed increase in records from 1995 might be a result of restocking efforts that started in that period nonetheless.

4.2. Usefulness of historical sources

Historical ecology studies on fish almost exclusively use sources from commercial exploitation. Although this data is useful, they suffer from bias because they often only describe commercially interesting fish species for restricted time periods and use economic data as a proxy for fish abundance (Haidvogel et al., 2014, 2015; Bennema and Rijnsdorp, 2015). In addition, historical data on fish and environmental conditions are generally scarce, fragmented and for a large part anecdotal (Swetnam et al., 1999; Szabó, 2015; Belliard et al., 2018; Merg et al., 2020).

To limit bias, both qualitative information and quantitative data from a wide variety of sources was used in the present study for the reconstruction of the historical ecology of houting. This was particularly important since houting was not a widely commercially exploited fish species, at least not for the local Dutch market. Pre-industrial media reflecting natural history were very useful to indicate presence of species like houting. Still, low data density before 1850 restricted the reconstruction of houting abundance in earlier centuries. Qualitative data for fish catch was found from 1844, but since catch effort was unknown, a catch per unit effort (CPUE) could not be calculated, hampering trend analyses on fish abundance. Also, increased media availability from 1850 might bias the number of houting recorded in that period. Low observed numbers of houting between 1861 and 1880 (Fig. 3) might be caused by relatively low numbers of market reports from that time. However, we also corrected catch data for the number of included media sources and observed steadily decreasing catch in a period with strong increasing media availability (Figs. 3–5).

The environmental history data from the pre-1950 period was mainly adapted from anecdotal sources. Systematic monitoring of water quality parameters in the Rhine-Meuse delta started from the 1950's, earlier monitoring data is only fragmentary documented (Nienhuis, 2008; bij de Vaate, 2003). Although historical environmental changes can explain the observed changes in houting records and subsequent assumptions on houting stocks, we emphasize that our findings are observational, not causal. We could not analyze but only interpret possible effects of changing environmental on houting abundance. Recent studies show how multiple stressors affect fish simultaneously, but can only be analyzed when sufficient data is available (Mueller et al., 2020; Zajicek et al., 2018). As a result, such multi-stress analyses cannot be performed on fish in historical ecology studies that predate the era of large-scale continuous monitoring.

Lastly, historical ecology studies are very time-consuming. We manually examined thousands of pictures and descriptions from houting and other marine and freshwater fish species in artwork, literature and newspaper archives. Automation could have helped, but van Erp et al. (2018) showed that automatic queries on animal names in the newspaper archive of Delpher were not flawless. Crowdsourcing for fish species in art works proved to be even more ineffective, as shown by the high number of incorrect species identification in present and other studies (Durso et al., 2021; Jones et al., 2018; Silvertown et al., 2015).

5. Conclusion

Our study indicates that houting was an abundant species in the Rhine-Meuse delta for ages and that decreased strongly from the 1880's, decades earlier than fisheries statics showed. Fisheries was indicated as the main driver for its decline and disappearance from the Dutch rivers. Between 1942 and 1978 houting was undetected in the Netherlands. Subsequent single observations indicate recolonization from a very small resident population in the North Sea basin. Restocking might have boosted houting to a steady, self-sustaining population. We argue that before its recovery since 1980's, houting abundance was limited by the deteriorated chemical water quality, and not by changed river morphology or migration barriers.

Relevance

The EU Water Framework Directive now mandates the ecological restoration of rivers across Europe. Migratory fish species, such as houting and others, play a crucial role in these restoration efforts. Effective protection and restoration measures for migratory fish populations require a comprehensive historical perspective on river ecosystem functioning, as relying solely on recent observations provides a limited understanding (Jackson et al., 2001). Identifying the primary stressors within a fluvial system is essential for

implementing appropriate conservation measures (Mueller et al., 2020) and without a clear understanding of the drivers behind changes in the abundance of target species, the effectiveness of conservation measures and the objectives of restoration projects can be compromised. For this reason, the IUCN Guidelines for reintroductions and conservation translocation of species were developed (Zlatanova, 2016).

Our findings demonstrate that a multi-source, single-species approach can provide valuable insights into the anthropogenic impacts on the decline and recovery of a keystone migratory fish species. Therefore, the general assumption that migratory fish in European rivers are affected by numerous stressors requires refinement. Depending on the species, the environment, the available data, and the time scale, more specific conditions needed for recovery can be identified. While houting has shown signs of recovery in the absence of fisheries pressure, other more ecologically demanding migratory fish species have not yet recovered, despite improvements in chemical water quality and restocking efforts (Waldman et al., 2016; van Puijenbroek et al., 2019). For these species, further advancements in chemical water quality, connectivity, or river morphology are necessary.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03823](https://doi.org/10.1016/j.gecco.2025.e03823).

Data availability

Data Link Provided

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