On re-introducing sturgeons to the river Rhine and the North Sea

Niels Willem Paavo Brevé

Propositions

1. Two sturgeon species are native to the river Rhine and the North Sea, not one.
(this thesis)

2. *Ex situ* conservation precedes *in situ* conservation.
(this thesis)

3. The peer review system slows down the progress of science.

4. The distance of a horizontal jump is to be measured from the take-off point, not the take-off line.

5. The seaward expansion of the port of Rotterdam impedes water management at the Haringvliet sluices.

6. Democracy prevents governments from making long term commitments.

7. Fence removal saves wildlife.

Propositions belonging to the thesis, entitled:

On re-introducing sturgeons to the river Rhine and the North Sea

Niels Willem Paavo Brevé

Wageningen, 27 November 2024

On re-introducing sturgeons to the river Rhine and the North Sea

Niels Willem Paavo Brevé

Thesis committee

Promotors
Prof. Dr A.J. (Tinka) Murk
Professor, Marine Animal Ecology group
Wageningen University & Research

Prof. Dr A.D. (Tom) Buijse
Special Professor, Aquaculture and Fisheries group
Wageningen University & Research

Co-promotor
Dr L.A.J. (Leo) Nagelkerke
Assistant professor, Aquaculture and Fisheries group
Wageningen University & Research

Other members
Prof. Dr E.S. (Liesbeth) Bakker Netherlands Institute of Ecology (NIOO-KNAW)
Dr T. (Thomas) Friedrich BOKU-University, Institute for Hydrobiology and Aquatic Ecosystem Management, Vienna, Austria
Prof. Dr R. (Robert) Arlinghaus Humboldt-Universität zu Berlin, Germany
Dr P.A. (Paddy) Walker Nederlandse Elasmobranchen Vereniging, Engwierum

This research was conducted under the auspices of the Graduate School WIAS (Wageningen Institute of Animal Sciences)

On re-introducing sturgeons to the river Rhine and the North Sea

Niels Willem Paavo Brevé

Thesis
Submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr C. Kroeze
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Wednesday 27 November 2024
at 13 p.m. in the Omnia Auditorium

Niels Willem Paavo Brevé
On re-introducing sturgeons to the river Rhine and the North Sea
238 pages

Ph.D. Thesis, Wageningen University, Wageningen, the Netherlands (2024)
With references, with summary in English

ISBN/EAN: 978-94-6510-206-1
DOI: https://doi.org/10.18174/670690

Contents

PORT OF ROTTERDAM
& HARINGVLIET SLUICES
BYCATCH MORTALITY
INTERNATIONAL APPROACH
LONG TERM VISION
ACTION PLAN RHINE STURGEON
ALIEN STURGEONS
EXPERIMENTAL RELEASES
RE-INTRODUCING STURGEONS

ATLANTIC STURGEON

VULNERABLE

ARTIFICIAL REARING
***EX SITU* BROODSTOCK**

EUROPEAN STURGEON

CRITICALLY ENDANGERED

RELEASE EVENTS & MEDIA

NL-DE-BE-LU-FR-CH

RHINE

ACOUSTIC TELEMETRY

BRACKISH TRANSITIONAL ZONE

SPAWNING GROUNDS

LIFE INTERREG
DUTCH ZIP CODE LOTTERY

GOOD ECOLOGICAL STATUS

NORTH SEA

ICPR
HABITAT RESTORATION
HISTORICAL RECONSTRUCTION
BIODIVERSITY

Summary

Summary

Historically, the anadromous European sturgeon (*Acipenser sturio*) was found in all marine- and major river basins of north-western Europe. Unfortunately, this species, which has roamed the earth for 90 million years, disappeared in about 150 years as a result of overfishing, habitat degradation and loss of longitudinal connectivity in the natal rivers. Today, the European sturgeon is listed by the IUCN as critically endangered and on the brink of extinction. This endangered status calls for urgent conservation action, which, given the highly migratory nature of the species, must be taken at an international level.

Currently, the Rhine is considered a key river for the reintroduction of the species, in addition to the Garonne and Dordogne and the Elbe rivers. Climate change scenarios, the partially intact longitudinal connectivity of the Rhine, and recent international efforts to improve water quality, suggest that the species might be able to return. However, by-catch in the North Sea, introduction of alien sturgeon species (predation, competition) and specific local/regional pressures such as inland shipping and coastal infrastructure may prevent this. Therefore, a feasibility assessment should be carried out before reintroduction can take place to avoid wasting time, money and extremely rare individuals of a critically endangered species.

This thesis aimed to assess the feasibility of reintroducing the critically endangered European sturgeon (*Acipenser sturio*) to the river Rhine and the North Sea. The assessment provides a basis to define the critical boundary conditions for successful reintroduction and can advise whether it is useful to stop or continue the reintroduction effort, and if so what additional conservation measures are needed.

Four research question were answered to be able to perform the assessment:

- Is sufficient suitable habitat available for European sturgeon in the North Sea and the river Rhine?
- What are the potential threats from incidental bycatch in coastal and estuarine areas for successful sturgeon reintroduction and from the currently present alien (non-native) sturgeons?
- What other local and/or regional threats could hinder the sturgeon's return?
- What are possible strategies considering the potential reintroduction of two native sturgeon species?

These research questions were answered in four parts, 1) habitats, 2) threats, 3) tracking, and 4) alternatives, ultimately culminating in part 5) the overall reintroduction feasibility assessment as presented in the synthesis.

Part 1. Key habitats – sea, estuary, river - Chapters 2 and 3

Chapter 2 presents a reconstruction of the historical spatio-temporal distribution of sturgeon populations in Northwest Europe based on fisheries data from the 14th – twentieth century, consisting of > 5000 records of sturgeon landings and sales (c. 40,000 specimens) from the Netherlands, Belgium, Germany, Luxemburg, France and Switzerland. Sturgeons showed a strong preference for large river habitats and were mainly found in the estuary and lower reaches of the river Rhine. The adjacent rivers and tributaries of the Rhine were hardly used by sturgeons. Based on this historical information the study area was defined and seasonality of occurrence of specific life stages. In Chapter 3 a systematic literature review of critical factors for European sturgeon key habitats was used as basis for 1D and 2D modelling and GIS-based mapping of potentially suitable spawning and nursery areas. This study shows that the river Rhine offers sufficient spawning habitat for about 2,500 female European sturgeons located in the German state of North Rhine-Westphalia, while there is sufficient habitat for nursery in the Rhine delta in the Netherlands. This, however, may be an overestimation considering the impact of inland shipping and infrastructures that may limit the accessibility.

Part 2. Threats: bycatch and alien sturgeons – Chapters 2, 4 and 5

The historical study (chapter 2) revealed that estuarine and coastal fishing had increasingly decimated the sturgeon population until the last sturgeon was caught in the river Rhine in 1952. Since then, fishing pressure has only increased further. Unfortunately, fishers are currently experiencing difficult economic circumstances, and fear of further restrictions on their fishing area and gear makes them reluctant to report sturgeon by-catches. From interviews with fishers, scientists, environmental NGOs and authorities in France, Germany, the Netherlands and the UK (chapter 4) it became clear that all key conditions for good cooperation with fishers needed for endangered, threatened and protected species conservation (shared vision, clear roles, communication and trust), are seriously hampered. In addition to fishers' lack of trust, fuelled by the communication strategies of some NGOs that use iconic species to lobby for fishing restrictions, lack of government coordination hampers adequate conservation management of rare marine species. The study presented in chapter 5 shows that a total of 10 alien Acipenseriformes (nine sturgeons and one paddlefish) and their hybrids, plus the native Atlantic sturgeon (*A. oxyrinchus*) (see chapter 8), are widely cultivated and traded in the Netherlands, Belgium, and Germany. Over 2,500 individuals were reported in more than 60 isolated water bodies in the Rhine delta, and about 500 alien sturgeon individuals were found in hydrologically connected water bodies. Although alien sturgeons are ubiquitous in the study area, they do not pose an immediate threat to the reintroduction of the native sturgeon, as these fish do not reproduce in the wild. However, their presence does pose a risk as they could carry diseases and parasites.

Part 3. Tracking sturgeons to discover additional threats – Chapters 6 and 7

After an absence of 70 years, a total of 87 juvenile European sturgeons that had been aqua cultured in the *ex situ* brood stock in southern France, were experimentally released into the Rhine at the Dutch-German border in May and June 2012 and 2015. The fish, aged between 3 and 5 years, were tagged for radio telemetry. The tracking revealed the impact of inland shipping on the species (ship propeller strikes) and showed that the sturgeons migrated to the North Sea via the port of Rotterdam, neglecting the historic route (estuary) via the Haringvliet lake. Ten sturgeons were reported caught (and released) by shrimp fishers and gill-netters along the Dutch coast and in the Wadden Sea. Only after seven years did a female European sturgeon reproduce in captivity again enabling a next tracking study (chapter 7). A total of 74 juvenile sturgeons aged between 13 and 15 months, tagged for acoustic telemetry, were released into the Rhine delta in June and August 2023. Surprisingly, within a month the young fish also migrated to the North Sea via the port of Rotterdam instead of staying in the Rhine delta. Tracking showed significant predation losses in the impounded, slow-flowing parts of the river. Only seven fish reached the North Sea, five of which stayed close to the port of Rotterdam. The telemetry studies were of great value as the results could not have been predicted based on desk studies. Local and regional pressure factors were highlighted, i.e. losses from inland shipping (propeller strikes), coastal infrastructure obstructing migration pathways, predation in the slow-flowing, impounded parts of the estuary and the high bycatch risk (mortality) along the Dutch coast.

Part 4. Alternative reintroduction strategies – Chapter 8

In chapter 8 molecular research on museum specimens confirmed the presence of two native sturgeon species in the river Rhine and the North Sea into the twentieth century, namely the European sturgeon and the Atlantic sturgeon (*A. oxyrinchus*). This means that a reintroduction programme for the vulnerable (IUCN status 2024) *A. oxyrinchus* in North Sea rivers could be considered in addition to that for the much extremely rare *A. sturio*. A number of considerations may guide the choice of which species to reintroduce and where: (1) prioritising the restoration of only the critically endangered *A. sturio*; (2) maintaining a strict north-south division of reintroductions for the two species; and (3) restoring a 'mixed zone' of sympatric occurrences in Northwest Europe, particularly in North Sea rivers, like the Rhine. Given the rapid progress made with *A. oxyrinchus* re-introduction to the Baltic region, and the fact that sub-adults of both species already occur in sympatry in the North Sea, it is advised to further explore the pros and cons of scenario 3.

Part 5 Sturgeon reintroduction feasibility assessment – synthesis – Chapter 9

In chapter 9 the key pressures are discussed per life stage in the three distinguished areas (the North Sea, the Rhine delta and the Lower Rhine). Four major threats were identified that could derail an entire reintroduction effort: 1) coastal and estuarine bycatch, and a lack of data for full impact assessment of this threat; 2) coastal infrastructures that obstruct or seriously limit sturgeon migration routes and prevent permanent transitional, tidal zones (acclimatisation areas for sturgeons). In addition, the coastal infrastructures, 3) attract local aggregations of predatory species that massively prey on juvenile sturgeons. In the Lower Rhine, 4) inland shipping poses direct (wounding) and indirect (habitat reduction and noise pollution) to sturgeons. It is yet unknown to what extent the historical sediment pollution is reason for toxicological concern.

Overall it can be concluded that although the habitat assessment indicated sufficient spawning and nursery habitat in the study area, the reintroduction of native sturgeons is not yet appropriate based on the threats assessment.

It is, however, strongly recommended to continue experimental releases of telemetry tagged juvenile sturgeons, considering both native sturgeon species, the European sturgeon and the Atlantic sturgeon. Telemetry has proved to be an excellent method of habitat- and pressure assessment. In total, six recommendations were identified in chapter 9 that, once (full)filled, would support improved sturgeon conservation and reintroduction effort success (Table 9.3).

Table 9.3. Overview of recommendations per main area.

Area		Recommendation
North Sea	1	Include fishers in research, value their expertise.
Rhine delta	2	Water managers should be encouraged to carefully redirect river water towards the port of Rotterdam.
	3	Prevent introduction of alien sturgeons to natural waters and use their current presence to the advantage of reintroducing the native species.
Lower Rhine	4	Investigate innovations and measures to reduce impacts of inland shipping to sturgeons and diadromous fish in general.
Rhine river basin	5	Include all migratory fish in the ICPR's Master Plan Migratory fish, including sturgeons.
	6	Develop a plan and protocol to establish a Dutch or German rearing station using Atlantic sturgeon in addition to European sturgeon to increase numbers of fish that can be experimentally released.

Chapter 1

General introduction and thesis overview

Photo: Satellite image of the transition zone between the southern North Sea and the estuaries of the Rhine, Meuse and Scheldt rivers. Source: Rijkswaterstaat 2020. Former migration corridor of sturgeons. Due to the Dutch storm surge barrier system, only the port of Rotterdam (north, top) currently offers a direct route between the North Sea and the river Rhine. The Western Scheldt (south, bottom), is an open connection between river and sea, but of less interest to sturgeons as the Scheldt is a much smaller river compared to the Rhine.

1.1 The European sturgeon was almost lost

This thesis aims to assess the feasibility for reintroducing the critically endangered European sturgeon (*Acipenser sturio*) to the river Rhine and the North Sea. Based on the feasibility assessment a recommendation needs to be made: should reintroduction of the European sturgeon be considered for the Rhine?

European sturgeon (Fig. 1.1) is a historical textbook example of a species with traits that make them vulnerable for ecological changes and over-exploitation. The anadromous European sturgeon spends most of its (sub-)adult life at sea, and depends on large rivers and estuaries for its recruitment (Williot & Castelnaud, 2011). Around 1850, European sturgeon populations were still present in all marine basins and large catchments of northwestern Europe (Holčík et al., 1989; Kottelat & Freyhof, 2007). 150 years later all populations had disappeared due to overfishing, habitat degradation and -loss due to hydro-damming, diking and canalisation, and environmental pollution (Williot et al., 2002a).

Today, the European sturgeon is classified as *critically endangered* by the IUCN, the International Union for Conservation of Nature and natural resources (Gessner et al., 2010c). The species is protected under the legal systems of the Bern Convention, the Bonn Convention, the OSPAR Convention, the Rhine Convention, and the EU Habitats Directive. The European sturgeon is the most endangered, threatened and protected (ETP) species in Western Europe (Bastmeijer, 2019). Figure 1.2 depicts its current presence compared to the situation in 1850.

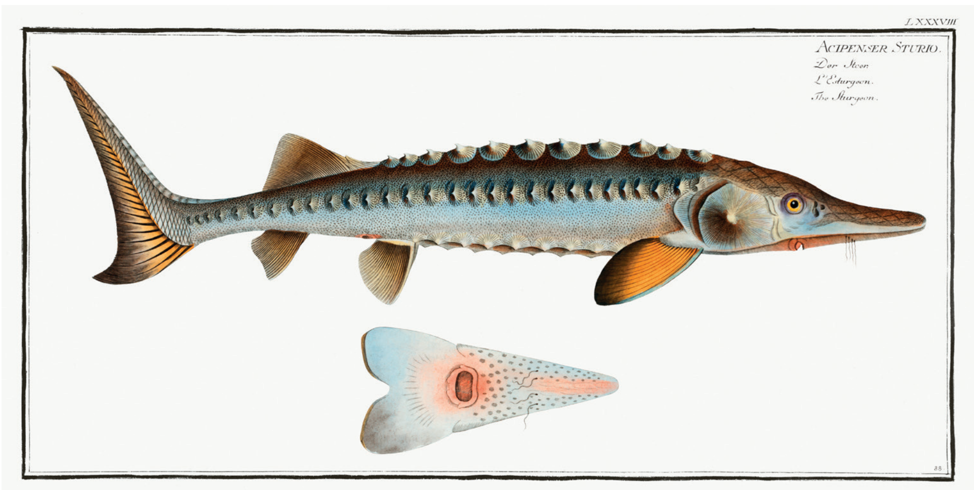


Figure 1.1. The European sturgeon (*Acipencer Sturio*). Derived from Bloch (1785–1797).

Unfortunately, the European sturgeon does not really benefit from this protected status. Restoring the populations and of the key aquatic environments is in conflict with economic interests and societal uses of these marine basins and large rivers. Moreover, most Northwestern European river basins can be considered 'lost' for the species due to habitat fragmentation caused by damming and canalisation (Puijenbroek et al., 2019). Only a few rivers and especially in the species´ former northern range of the northwest Atlantic and North Sea could still be suitable for re-introduction of the species.

The river Rhine (Fig. 1.3) is suggested to be a key-river for European sturgeon reintroduction, taking into account climate change scenarios (Lassalle et al., 2010), a good longitudinal connectivity across 850 river kilometres (Jakob, 1996; Nemitz, 2010; Winden et al., 2000), and recent international efforts to mitigate the rivers water quality (albeit not everywhere in the sediments) (Villamayor-Tomas et al., 2014). Evidence of the improved suitability of the Rhine for migratory fish species is found in the partial return of a number of the Rhine's previously extirpated diadromous species, including the Twaite shad (*Alosa fallax*), houting (*Coregonus oxyrinchus*), European river lamprey (*Lampetra fluviatilis*), and possibly even Allis shad (*Alosa alosa*) (Borcherding et al., 2010; Hundt et al., 2015; Winter et al., 2015). Moreover, subadult European sturgeon individuals, stocked in the river basins of the Garonne/Dordogne and the Elbe that have reportedly been caught (and released) in North Sea fisheries, currently appear in the southern North Sea, even in the outer estuary of the Rhine (Charbonnel & Acolas, 2022). The latter implies that the marine environment seems to offer sufficient foraging grounds for the species to thrive.

However, the Rhine and North Sea habitat currently holds several potential drawbacks for sturgeon reoccurrence, including intensive fisheries in the North Sea, coastal infrastructure (dykes and a storm surge barrier system) and large scale/intensive inland shipping (Winter et al., 2015). Before the species can be reintroduced to the Rhine, a feasibility assessment is of paramount importance - to prevent the potential loss of effort, time, money and precious individuals of an extremely rare species upon a potentially failing reintroduction.

As the European sturgeon is absent from the Rhine the technical term is 'reintroduction'. However, as European sturgeon from releases in France and Germany are already present in their former habitat in the North Sea, the technical term is 'reinforcement'.

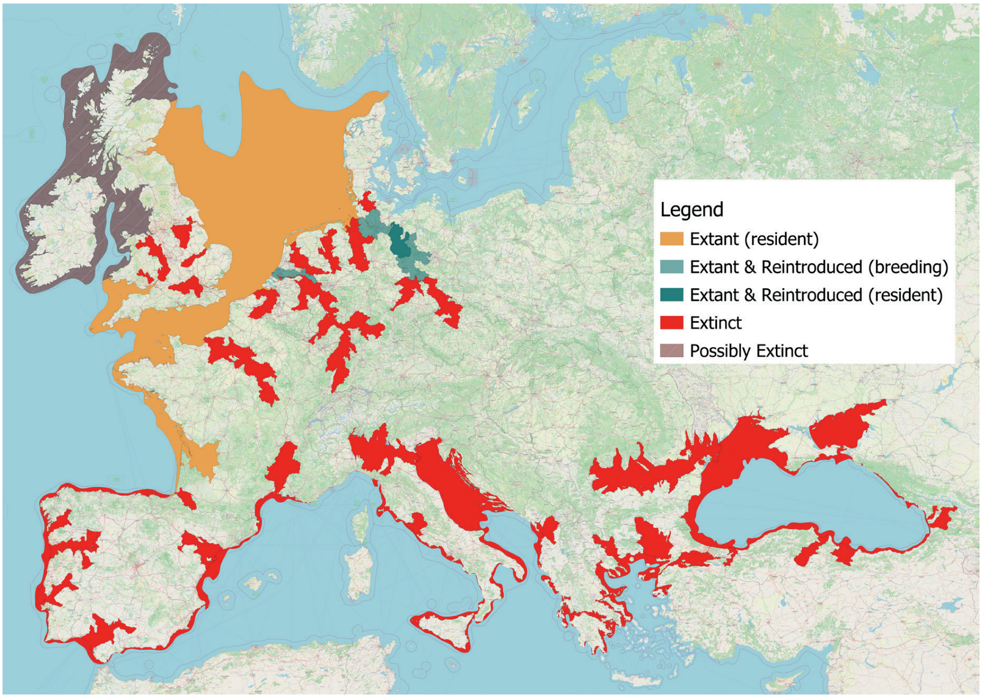


Figure 1.2. Status of European sturgeon (*Acipenser sturio*) in 2022. Derived from the IUCN Gessner et al. (2022).

Restoring the European sturgeon is a challenge. But it will also bring added value. Because of its critical traits, the European sturgeon is an excellent flagship species facilitating the restoration of co-occurring fish species (Caro, 2010; Council of Europe, 2018; Roberge & Angelstam, 2004). The restoration of the charismatic European sturgeon would be a strong demonstrator and advocate of how environmental policies - that aim to restore rivers to a good ecological status and combat biodiversity loss, can be successful, e.g. the European Water Framework Directive, the Habitats Directive and Nature 2000 (EEC, 1992; European Union, 2000; ICPR, 2018; Kallis & Butler, 2001). The restoration of the European sturgeon would be a major environmental and ethical achievement, and a remarkable sight: A majestic fish with its four long whisker-like barbels and five rows of diamond-shaped armoured plates (scutes, sturgeons have no scales) that could grow to a total length of 4 to 5 m and a total weight of 300 to 400 kg (Muus et al., 1968). A fish that has swum straight out of a palaeontologists, or rather ichthyologist textbook (Fig 1.1).

1.2 Ecological and biological traits, vulnerabilities and pressures

Good understanding of the specific ecological and biological traits and key habitats of the order of Acipenseriform fishes (25 sturgeons and 2 paddlefishes) is crucial to be able to judge what is required to restore their populations. Below this information is presented in two sections: 1) Sturgeons under pressure in the Anthropocene, and 2) a description of the complex life cycle of the European sturgeon.

1.2.1 Sturgeons under pressure in the Anthropocene

The order of Acipenseriform fishes first appeared in the fossil records of the Lower Jurassic period and only occurred in the northern hemisphere (Bemis & Kynard, 1997). Today, 85% of the species are critically endangered, four are considered extinct, and their decline has not been brought to a halt yet (Birstein et al., 1997a; Haxton & Cano, 2016; Pikitch et al., 2005; Zhang et al., 2020). For example, the Chinese paddlefish (*Psephurus gladius*), was declared extinct in 2020 (Xie, 2003; Zhang et al., 2020). Therefore, this is one of the oldest orders of extant actinopterygian fishes, and currently one of the most endangered, threatened and protected orders of fishes in the world (Bemis et al., 1997; Bemis & Kynard, 1997; Gardiner, 1984; Haxton & Cano, 2016).

Basically, the same ecological and biological traits that made Acipenseriform fishes survive for some 200 million years, currently make them vulnerable to anthropogenic pressures of overfishing, and habitat degradation and loss (Bemis & Kynard, 1997; Birstein et al., 2006; Boreman, 1997; Xie, 2003). Acipenseriform fishes are large, and long-lived creatures that only mature at a great age of 8-25 years (Birstein et al., 2006; Boreman, 1997). The oldest known sturgeon, a Lake sturgeon (*A. fulvescens*), was reported to be 152 years old (Anderson, 1954). Although there are some dwarf species known from the Aral sea area, most acipenseriform fishes rank amongst the largest fish in the world. Individuals of the Kaluga (*H. dauricus*) and the White sturgeon (*A. transmontanus*) can grow to over 5 m in length and weigh over 800 kg, while the largest freshwater fish in the world, the Great sturgeon or Beluga (*Huso huso*) can attain a length of over 7 m, weighing over 1 ton (Krykhtin & Svirskii, 1997; Scott & Crossman, 1973) (Figs. 1.4a and b). For example, a specimen caught in the Volga estuary in 1827 was 7.2 m long and weighed 1,571 kg (Wood, 1983). Another Great sturgeon of unknown length, caught in the Caspian Sea weighed 3,200 kg (Kottelat & Freyhof, 2007). Unfortunately, megafauna like these are sensitive to overfishing. The egg-bearing female sturgeons are sought after due to the extremely high value placed on their eggs, while males and juveniles have been continuously exploited for their meat (Pikitch et al., 2005). This resulted in mortality rates that could not be compensated by the sturgeon's natural recruitment (Boreman, 1997; Helfman et al., 2009).

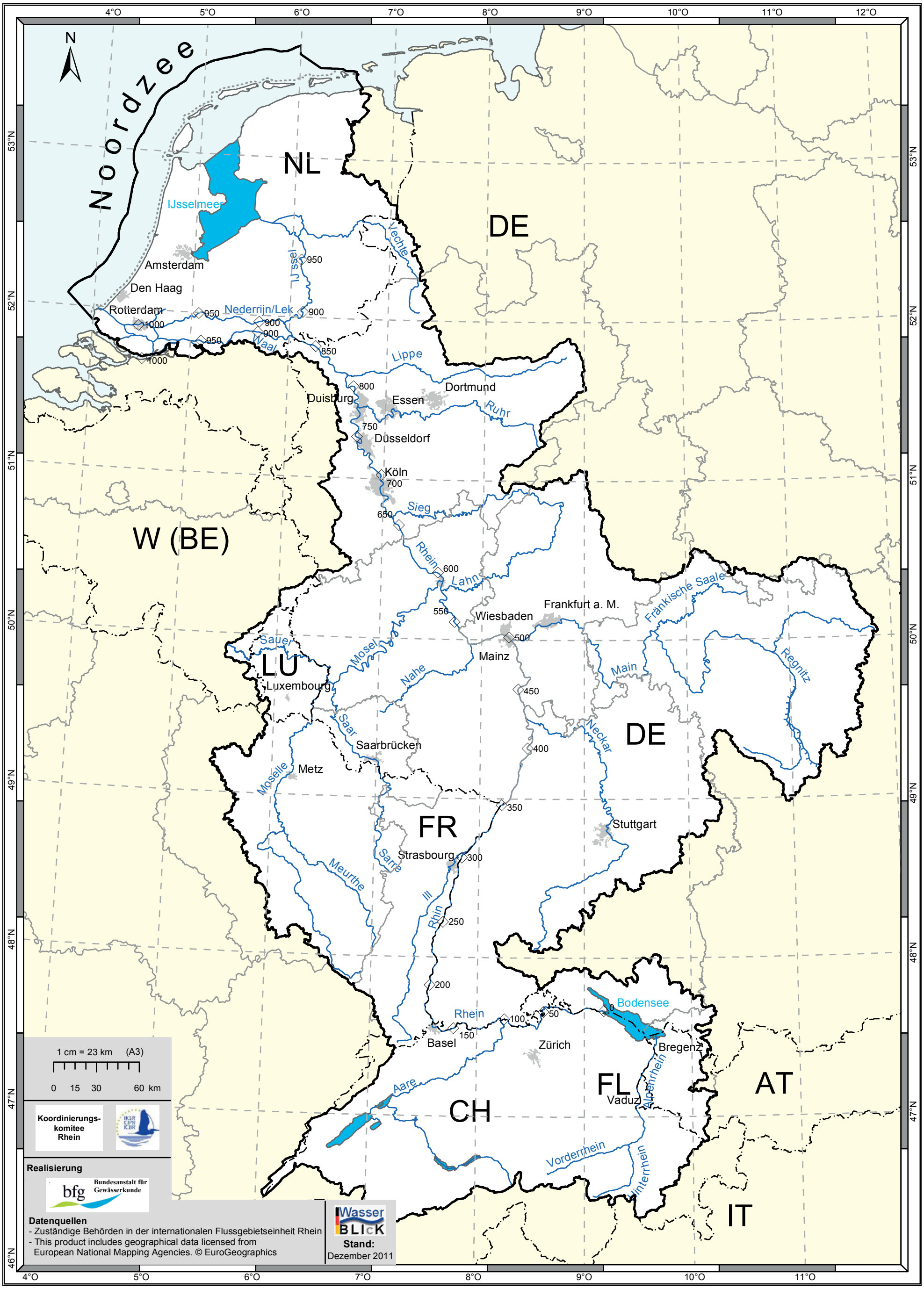


Figure 1.3. The river Rhine. Former stronghold of the European sturgeon (Kinzelbach, 1987).The abbreviations indicate the Rhine member states (n.b. FL = Fürstentum Liechtenstein). Derived from the ICPR (2022).

Figure 1.4. Historical captures of the Great sturgeon (*Huso huso*), beluga: (a) a 7.2 m long specimen weighing 1179,39 kg, caught in the Caspian Sea, Russia in 1910; (b) an approximately 7 m long specimen weighing 1224 kg, and two 'smaller' specimen, caught near the town Tetyushi (150 km from Kazan), on the upper River Volga in 1921. The source of these photographs is unknown.

Another persistent threat to Acipenseriform fishes is damming. Most species of this order are anadromous and require longitudinal connectivity between the sea and the lower and middle ranges of their natal rivers (Bemis & Kynard, 1997; Billard & Lecointre, 2000). Estuaries and rivers are crucial for sturgeon recruitment and contain the most vulnerable life stages of fertilized eggs and yolk-sac hatchlings (Bemis & Kynard, 1997). This reliance makes them vulnerable to a river basins' fragmentation, caused by migration obstructions, such as coastal infrastructure (storm surge barriers, dykes), and hydro-dams that result in the loss of spawning sites (Bemis & Kynard, 1997; Birstein et al., 2006; Birstein, 1993; Debus, 1997; Haxton & Cano, 2016; Puijenbroek et al., 2019; Williot et al., 2002a). For instance, figure 1.4b shows three Great sturgeons caught in the upper River Volga and landed in Tetyushi in 1921. The town is currently located on the banks of the Kuybyshevskoye Reservoir, Europe's largest reservoir created by the Zhiguli Hydroelectric Station dam built in the 1950's. Due to this dam, the Beluga's can no longer reach their spawning grounds in the upper Volga and have become extinct from this large part of the river.

1.2.2 The complex life cycle of the European sturgeon

The life cycle of the European sturgeon is summarized in fig 1.5. Subadults of the anadromous European sturgeon thrive in coastal areas and large estuaries, while mature individuals exhibit extensive homing behaviour to the natal rivers, and only few fish might stray (Acolas et al., 2011a; Castelnaud et al., 1991b; Charbonnel & Acolas, 2022; Magnin, 1962; Rochard et al., 1997a, 1997b; Thieren et al., 2016a). Once mature, the ripe broodfish aggregate in Spring and Summer months in the estuaries of especially large rivers (Acolas et al., 2011a). They cease feeding, use deep scour holes as resting habitats, and seek out highly oxygenated, clean and heterogeneous hard substrates to spawn (Acolas et al., 2011a; Magnin, 1962).

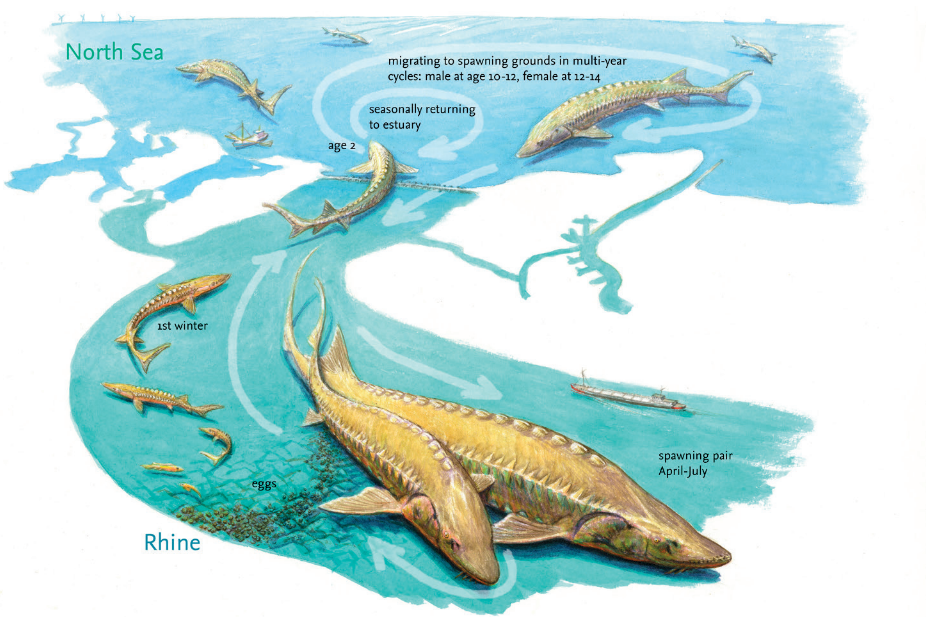


Figure 1.5. Sketch of the life cycle of the European sturgeon. Source: Jeroen Helmer / ARK Rewilding Nederland.

Although there are differences in observations for various river basins, it is suggested that during the spawning season more males appear in the river than females. This as a result of differentiation in both sexes spawning periodicity: while male sturgeons reach puberty at ages of 13 to 15 years and spawn approximately every other year, female sturgeons reach puberty between the ages of 15 and 22 years and spawn approximately every 3 to 5 years (Acolas et al., 2011a; Magnin, 1962; Williot et al., 1997; Williot et al., 2011b). The slow reproductive cycle of the female sturgeons is attributed to the physical effort required for egg development. This adds to the slow population recovery process that may take 30-50 years (Magnin, 1962; Sulak & Randall, 2002).

In autumn, most of the spent sturgeons have returned to the sea while the fertilized eggs hatch and the yolk-sac larvae hide within the interstitial spaces in the gravel beds (Williot et al., 2011b). Fertilized eggs are highly vulnerable to O_2 saturation levels below 70 % and embryonic survival is highest at a temperature of 20 °C (Delage et al., 2019). The upper tolerance limit is between 26 and 30 °C and the lower tolerance limit below 12 °C (Delage et al., 2019). Exogenous feeding of the benthic larvae begins between 9-11 days after hatching (Delage et al., 2019). The larvae gradually disperse downstream and already during their first winter most of the juvenile sturgeons reach the upper estuary where they settle in flow calm areas with soft substrates such as mud, silt, or fine sand, usually near banks and islands (Acolas et al., 2011a; Rochard et al., 2001). Here they develop best when feeding on small, soft-bodied prey, such as larval Oligochaetae and Chironomidae(Brosse & Elie, 2003; Brosse et al., 2000; Lepage et al., 2005).

Juvenile European sturgeon are capable of enduring higher salinities than juveniles of any other sturgeon species (Holčík, 1989). They can adapt their osmoregulation to seawater at an age as early as on average 15 months (Acolas et al., 2011a; Rochard et al., 2001). As a result, the juvenile sturgeons disperse widely across the estuary, whereby a variety of migration tactics to and from the sea can be observed: while some remain in the oligohaline area, others may rapidly move into the polyhaline area and the sea (Acolas et al., 2017; Acolas et al., 2012).

Another specific feature is that juvenile European sturgeons exhibit a circular, seasonal migration pattern, called in French the 'Mouvée de la Saint Jean' (Acolas et al., 2011a). European sturgeon juveniles may follow the adult fish on their spawning run upstream, from the lower estuary towards the upper estuary and back. European sturgeon juveniles continue to occupy the estuary until they are approximately seven years of age, whereafter they move more permanently into the sea, until they reach maturity and are in turn ready to spawn (Magnin, 1962).

In summary: The highly migratory, anadromous European sturgeon spends most of its subadult life at sea near coast (in the neritic zone), but strongly depends for its recruitment on estuaries and the lower and middle ranges of large northwestern European rivers.

1.3 International cooperation to save the European sturgeon

Considering the highly migratory nature of the European sturgeon and its former range across northwestern Europe, international cooperation is a necessity to restore the species and its key habitats. Before going into further details of the work to be performed for this thesis, I introduce (and acknowledge) below the diversity of European efforts by organisations pursuing a common goal: To save the European sturgeon from extinction and restore the sturgeon's populations across most of its former northern range.

French organisations involved in the conservation of the European sturgeon since the 1970s are the research institute INRAE (National Research Institute for Agriculture, Food and the Environment), and MIGADO (L'association MIGADO – Migrateurs Garonne Dordogne Charente Seudre), the organisation that manages the *ex-situ* brood stock in the rearing station located in St. Seurin sur l'Isle. Their activities are set in the French national European Sturgeon Action Plan (France Ministère de l'Écologie, 2020), and implemented under the auspices of the regional government DREAL d'Aquitaine, the department of the Ministère de la Transition Écologique et Solidaire and the prefect of the region.

The scientific staff of INRAE advised the 'Dutch' feasibility assessment since 2009 and organises quarterly meetings for international exchange of experiences since 2022. MIGADO provided juvenile European sturgeons for experimental releases in the Rhine in 2012, 2015 and 2023 (Fig. 1.6). Noticeably, information about the European sturgeon's life cycle is largely obtained from French literature, as mainly French biologists were able to study the species' last relict population that reproduced until 1994 in the basin of the Gironde estuary and Dordogne and Garonne rivers (Acolas et al., 2011a; Magnin, 1962; Trouvery et al., 1984; Williot et al., 1997; Williot et al., 2011a; Williot et al., 2011b).

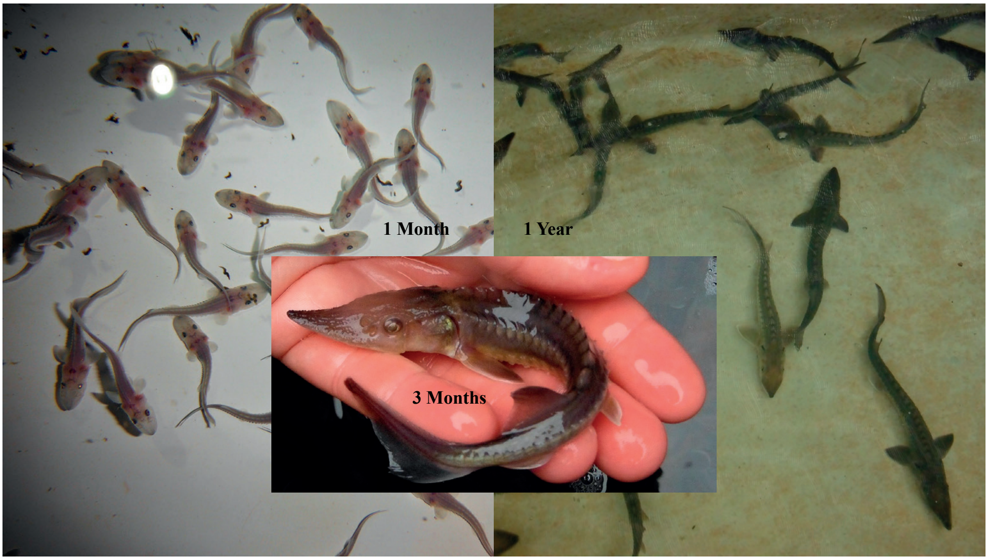


Figure 1.6. Extremely rare juvenile European sturgeons raised in MIGADO's hatchery to different ages, of which fish were provided for experimentally releases in the Rhine in 2012, 2015 and 2023. Photos: Vanessa Lauronce.

German organisations involved in the conservation of the European sturgeon since the 1990s are the "Gesellschaft zur Rettung des Störes" (Association for the Salvation of the Sturgeon), with their lead partner the Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB). IGB holds the second *ex-situ* brood stock of European sturgeon, in Berlin, and has activities up-and-running to reintroduce both European sturgeon and Atlantic sturgeon in different rivers and the marine basins of the North Sea and

Baltic Sea, respectively (Gessner et al., 2019). The Association's partners formulated the German National Action Plan for European Sturgeon (Gessner et al., 2011c), which was implemented under the auspices of the Ministerium für Umwelt, Landwirtschaft, Natur- und Verbraucherschutz des Landes Nordrhein-Westfalen (German Federal Ministry for Nature). IGB is in the lead for the Pan-European Action Plan for Sturgeons (Council of Europe, 2018), and has been a trusted source of advice for the Dutch partners.

Dutch organisations involved in European sturgeon reintroduction since 1999 (van Winden et al., 2000) for the river Rhine and North Sea, are ARK Rewilding the Netherlands, the World Wide Fund for Nature, and the Royal Dutch Angling Alliance (in Dutch: Koninklijke Sportvisserij Nederland), and more recently also the Rotterdam Zoo (Blijdorp). The Dutch alliance produced a multitude of desktop studies, technical reports and fieldwork, of which the outcomes were summarized and translated into advice for priority actions in the First Action Plan for reintroduction of the European Sturgeon (*Acipenser sturio*) for the Lower Rhine (Visser et al., 2020). The action plan was supported by the Dutch Ministry of Agriculture, Nature and Food Quality (Min LNV) between 2020-2024.

Today, the international conservation efforts for restoration of the European sturgeon to the Rhine and North Sea, is acknowledged by more than **30 stakeholders** of different nationalities, including the World Sturgeon Conservation Society (WSCS), French fisheries organisations CAPENA (Centre pour l'Aquaculture, la Pêche et l'Environnement de Nouvelle-Aquitaine) and Le Comité national des pêches maritimes et des élevages marins (CNPMEM), and the Dutch fisheries association (Nederlandse Vissersbond). Noticeably, European sturgeons in the wild are rarely observed and occur mainly as extremely rare, incidental bycatch coastal and estuarine fisheries. Some live European sturgeons are displayed for the public in Rotterdam Zoo and Breslau aquarium (Poland). The breeding stations of MIGADO (France) and IGB (Germany) are not open to the public.

Spanish organisations involved in repopulation of the river Ebro with European sturgeon and other migratory fish are IRTA (the Institute of Agrifood Research and Technology, based in Sant Carles de la Ràpita), and the Mediterranean Rivers Studies Centre (CERM). Other partners include the Institute for the Development of the Ebro Region (IDECE), the Fundació Catalunya - La Pedrera, and the Ministry of Agriculture, Livestock, Fisheries, Food and the Environment of the Government of Catalonia. The work is funded by the LIFE Nature Migrator Ebre project. A batch of 44 juvenile European sturgeons, obtained from MIGADO (France), were experimentally released in the Ebro in 2023.

Organisations in the **UK** involved in sturgeon conservation (European sturgeon and Atlantic sturgeon) are united in the UK Sturgeon Alliance, an NGO-coalition made up of the Blue Marine Foundation (BLUE), the Zoological Society of London (ZSL), the Institute of Fisheries Management (IFM), the Severn Rivers Trust, and Nature@ Work. The UK Sturgeon Alliance recently published a Strategy and Action Plan for Sturgeon Conservation (Colclough, 2021; McCormick et al., 2023). In 2023 and 2024, ZSL organised workshops in London Zoo to discuss important issues in sturgeon conservation to be resolved for the mutual benefit of the international sturgeon network. These activities include the prevention of bycatch mortality at sea, and to achieve an exchange of information on the historical occurrences (nativeness) of European sturgeon and Atlantic sturgeon in UK waters.

1.4 European sturgeon, main problem areas and required international approach

Although the European sturgeon has been saved from extinction through artificial rearing, fisheries managers, biologists and conservationists still face certain challenges to restore the natural populations. Table 1.1, summarizes the five main problem areas distinguished by the internation communities, the required international approach, plus an overview of implications for the feasibility assessment. This short summary of problems and required mitigation activities are more fully elaborated on in the French, German and Dutch action plans for the European sturgeon, and the Pan-European action plan for sturgeons as mentioned in paragraph 1.3 (Council of Europe, 2018; France Ministère de l'Écologie, 2020; Gessner et al., 2011c; Visser et al., 2020).

Problem area 1. Limited brood stocks and genetic erosion

The survival of the European sturgeon currently depends on artificial rearing. The species exists in just two *ex situ* brood stocks of extremely limited size, and the species is facing a major problem due to its reduced genetic variability (Debus, 1999; Holčík et al., 1989). Although European sturgeons have a high fertility rate, producing between 0.5 and 2.5 million eggs per female, female European sturgeons take 15-22 years to mature (Magnin, 1959; Magnin, 1962). Despite the stocking of 1.7 million European sturgeon larvae and juvenile sturgeons in France and Germany, the species' natural survival in the first year of life is only between 1% and 3% (Borodin, 1925). In the current situation of highly modified rivers in northwestern Europe the survival percentage may be significantly lower.

Currently the number of mature individuals living in the sea is estimated to be a maximum of 750 (Gessner et al., 2022). Even if natural reproduction were to occur in the near future, the low numbers of individuals may still result in a population collapse due to the Allee effect (Myers et al., 1995). This is caused by the too limited opportunities for finding mates for spawning in addition to the eroded genetic diversity which limits their ability to adapt to environmental changes (Myers et al., 1995). To improve the genetic diversity of the species, carefully designed and long-lasting breeding plans are implemented in France and Germany (Chebanov et al., 2011; Williot & Chevre, 2011; Williot & Kirschbaum, 2011). These plans are essential, but complex, requiring long-term planning for the extremely low number of genetic individuals available for brooding as well as the slow maturation (Williot and Chevre 2011; Williot et al. 2011b). The rarity of the species unfortunately limits the number of individual fish that can be used in experimentally releases (e.g. in the Rhine) to monitor the species survival, distributions and outmigration pathways to the sea.

Problem area 2. Incidental bycatch mortality

Since the 18th century, European sturgeon populations have been increasingly impacted by commercial fisheries. Developments in propulsions from sails to steam and diesel engines allowed fishers to tow bigger nets and move faster between ports and fishing grounds (Brevé et al., 2022d; Castelnaud et al., 1991a; Lenders, 2017; Letaconnoux, 1961; Mohr, 1952). By the end of the nineteenth century, sturgeons from the Rhine and the North Sea became increasingly scarce, while landings of the last big fish gained the interest of photographers (Fig. 1.7).

Figure 1.7. Historical sturgeon captures from the Rhine and the North Sea. Photo left: an approximately 3 m long sturgeon caught in industrial salmon fisheries during the closed season. Although the fish was released, it was caught a second time and brought into the town of Dordrecht, the Netherlands in 1917 (Zalmvisserij Volharding, vangst locatie: Krabbegors Dordrecht). Photo source: City Archive Dordrecht. Photo right: An approximately 2.5 m long sturgeon, weighing 175 kg, caught by a steam trawler in the North Sea and landed at the Dutch seaport IJmuiden in 1937. Photo source: City Archive IJmuiden.

Table 1.1. Five main problem areas to European sturgeon restoration and the required international approach, plus implications for a feasibility assessment for the reintroduction to the Rhine and North Sea.

Main problem areas	**Required international approach**	**Implications for the feasibility assessment**
1. Limited broodstock and genetic erosion. Restrictions to effectively reproduce due to extremely small size and wide dispersion of the remaining natural populations (**Allee effect**).	Stop the decline of the existing European sturgeon populations and secure genetic diversity. Establish *ex situ* living gene banks and release fish in natural waters from artificial rearing.	Use a minimum number of experimentally released fish to monitor their survival, dispersion and outmigration pathways across the study area.
2. Incidental bycatch, especially along coasts and in estuaries that causes mortality and impacts the scarce remaining populations. Further reducing the survival and mating probabilities.	Eliminate bycatch mortality of European sturgeon. Stop illegal landings, and create awareness amongst fishers to safeguard the fish's release. Continuous monitoring of the population development is essential.	Investigate into the willingness of fishers to participate in sturgeon conservation activities.
3. Further habitat degradation and loss in the natal rivers causes a multitude of problems, including reduced reproductive success due to **environmental pollution,** (hydro-) **damming,** changes hydrologic and hydrodynamic regimes in rivers and estuaries through **channelization** (diking, dredging, etc.), and **shipping**, that may cause harmful water movements, noise pollution, ship propeller strikes, etc.	Restore historic migration corridors. Identify and effectively protect existing reproductive habitats, while potential habitats are mapped, and restoration is ongoing. Address sources of pollution such as domestic, agricultural, and industrial wastes.	Investigate into the availability of spawning and nursery grounds, and identify priority pressures that negatively affect the species and its key habitats. N.B. Because it is exceptionally difficult to assess the cumulative effects of all (potential) pressures, it is advised to monitor the survival, spatiotemporal distributions and migration pathways of a limited number of experimentally released juvenile sturgeons, using telemetry.
4. **Alien sturgeon species** may host/transfer diseases and parasites, predate on native fauna, compete and potentially hybridize with native sturgeon species (outbreeding).	Stop introductions and spread of alien sturgeons in natural, hydrologically connected waters. Ensure sufficient monitoring of the alien sturgeon populations.	Assess the risks of introductions (and spread) of alien sturgeons on the native biodiversity.
5. Climate change may further impact on future performance characteristics of sturgeons and of the suitability of rivers.	Decide on which river basins are most suitable for sturgeon restoration, considering changes in temperatures, rainfall, and droughts. Bare in mind that other river characteristics may be of influence as well.	Investigate into the effects of increased temperatures, droughts, also in relation to other pressures that may cause cumulative effects. For example, during dry summer months fish and ships are forced into a narrowed channel.

Sources: (Council of Europe, 2018; France Ministère de l'Écologie, 2020; Gessner et al., 2011; Visser et al., 2020).

Although the European sturgeon is currently one of the most protected species in the world (Bastmeijer, 2019), the species is still threatened by coastal and estuarine bycatch (OSPAR Commission, 2021). Unintendedly caught fish may die, depending on gear, soaking time of the net, careless handling, or delayed release (Castelnaud et al., 1991b; Charbonnel & Acolas, 2022; Letaconnoux, 1961; Michelet, 2011; Rochard et al., 1997b). To further protect the last of the wild sturgeons, strict fisheries management measures are required, including the closure of fishing grounds and gear adaptations (Council of Europe, 2018; EEC, 1992). However, such measures may also give rise to opposition and significantly reduce the willingness of fishers to support the conservation effort. Bycatch reporting is needed to assess the species' population developments at sea. however, organising effective (fisheries) measures becomes very difficult without the registration of incidental bycatch reports. It is therefore unfortunate that such reports, that used to be common (figure 1.8), have recently strongly reduced as most fishers have refrained from reporting.

Figure 1.8. Photos of recent European sturgeon captures and releases at sea. Photo left: Aboard the trawler WR 12, fishing for shrimp in the Wadden Sea in August 2012. The juvenile sturgeon had previously been tagged for radio telemetry and was released in the river Rhine in June 2012. Photo right: Aboard the trawler LT 162 in 2017.

Problem area 3. Further habitat degradation and loss in the natal rivers

Habitat degradation and loss in the natal rivers and estuaries impacts the usability for sturgeon recruitment. According to the action plans (Table 1.1), main habitat problems are environmental pollution, (hydro-)damming and blockage of migration routes, changes in hydrologic and hydrodynamic regimes through channelization and inland navigation. Rivers serve as sinks of anthropogenic waste, including pesticides, pharmaceuticals, hydrocarbons, and heavy metals (Best, 2019; Wilkinson et al., 2022). After decades of heavy environmental pollution, the Rhine's water quality has improved considerably due to joint efforts of the Rhine member states, following European regulations and national policies on integrated water resources management (Dendievel et al., 2022; Mostert, 2009; Villamayor-Tomas et al., 2014). Still, in the sediments of the delta Rhine, historical pollution with persistent toxic compounds is present and accumulates in local organisms as has been shown for example in European eel (*Anguilla anguilla*) and Chinese mitten crab (*Eriocheir sinensis*) (Hoogenboom et al., 2006; Hoogenboom et al., 2015; Murk, 2024; Zafeiraki et al., 2019). Consequently, human consumption of eels and mitten crab from the Dutch Rhine is prohibited (Guhl et al., 2014; Haenen et al., 2010; van den Dungen et al., 2016) and freshwater fisheries in the estuary have been decimated. Environmental pollution thus implies a toxicological hazard, and a promise of reduced bycatch.

To fulfil its life cycle, the sturgeon depends on an open connection with brackish water area between the sea and the lower middle reaches of northwest Europe's largest rivers (Acolas et al., 2011; Trouvery et al., 1984; Williot, Rochard, et al., 2011; Williot, Rouault, et al., 2011). In most of these rivers, dams restrict the migration range of sturgeons across the river basin, often resulting in a permanent loss of spawning and nursery grounds by blocking the access (Assis, 1990; Best, 2019; Dadswell et al., 1986; Granada-Lorencio, 1991; McAdam et al., 2018). There are over 1.2 million instream dams in 36 European countries, and only one third of European rivers currently meet the criteria for a 'good ecological status' (Belletti et al., 2020). Only a few rivers in northwest Europe have a free-flowing mainstem facilitating viable migratory fish populations (Puijenbroek et al., 2019). Although the historical estuary of rivers Rhine and Meuse is obstructed by the Haringvliet sluices, the Rhine still has an open connection via the Nieuwe Waterweg between the sea and its middle reaches across 850 river km's (ICPR, 2018). Currently, the Dutch government is exploring the possibilities to gradually improve fish migration opportunities by opening the Haringvliet sluices.

Two other main threats to the restoration of (European) sturgeon populations are canalisation and inland navigation (shipping) (Mako & Galieriková, 2021; Sexton et al., 2024). Most western European rivers have been transformed into effective shipping lanes through extensive river engineering, hydro-damming, canalisation, the disconnection of (dis)tributaries and flood plains (Fig. 1.9) and continuous dredging of bed sediment (Brown & Murphy, 2010; Rochard et al., 1990; Schletterer et al., 2018; Williot et al., 1997). The far-reaching reduction of a rivers' natural morphology has led to a substantial loss of natural spawning and nursery habitats for sturgeons. Meanwhile, inland industrial shipping that is proposed to increase in the coming years, is associated with substantial loss of biodiversity (Sexton et al., 2024) because of harmful water movements, noise pollution (Spierts, 2016) and ship propeller strikes. Since the Rhine is one of the busiest shipping lanes in the world (Mako & Galieriková, 2021), intensive inland navigation probably poses significant direct risks to the sturgeons and its key habitats. In particular during increasingly dry summer months when the river's main channel is reduced in depth and width (Van de Ven, 2021) direct and indirect effects are to be expected.

Problem area 4. Introduction, spread and establishment of alien sturgeon species
About 100 years ago, the loss of natural sturgeon populations and the continued demand for caviar and their meat led to the development of sturgeon aquaculture industries across Eurasia and North America (Bronzi et al., 2011; Chebanov et al., 2011; Mims & Shelton, 2015). Sturgeon cultivation can reduce fishing pressure on natural populations. Artificial rearing ex situ brood stocks can facilitate reintroductions (Chebanov et al., 2011; Williot et al., 2001). However, active introductions and escapees of alien sturgeons and their hybrids to natural waters are also associated with predation, competition for food and reproductive habitat, hybridisation with the scarce native populations, and the introduction of diseases and parasites alien sturgeons may host (Ludwig et al., 2009a; Radosavljević et al., 2019; Shivaramu, 2019; Stachnik et al., 2021). The potential risks posed by alien sturgeon species should therefore be assessed, including their degree of introduction, spread and establishment in the area of concern.

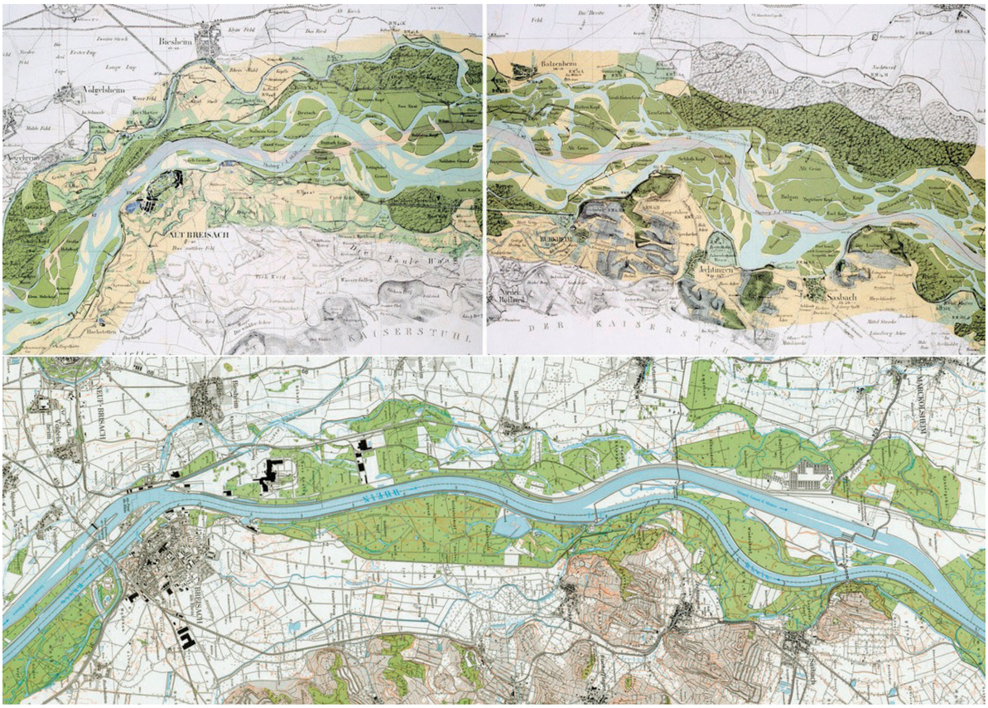


Figure 1.9. The morphology of the Rhine near Breisach in 1938 (top) and 1980 (bottom). Source: www.iksr.org.

Problem area 5. Climate change effects on the river basin conditions

Based on the habitat degradation and loss for sturgeons in the natal rivers, and despite ongoing restoration efforts, it is estimated that less than 10% of the historical watersheds of the European sturgeons former entire range can be repopulated (Gessner et al., 2009; Gessner et al., 2010c). The former core area of the species' historical *southern* range of the Mediterranean Sea, Adriatic Sea and Black Sea (fig. 1.2) is considered almost entirely lost. This is due to irreversible river engineering, while temperature increases due to climate change is increasingly negatively affecting these basins as habitat for sturgeons (Lassalle et al., 2010). In contrast, predicted shifts in temperatures and precipitation based on climate change scenarios, seem to favour the reintroduction of the European sturgeon to several rivers in its former *northern* range, including the Rhine (Lassalle et al., 2010).

1.5 Thesis overview

This study aimed to assess the feasibility of reintroducing the critically endangered European sturgeon (*Acipenser sturio*) to the river Rhine and the North Sea. The assessment provides a basis to define the critical boundary conditions for successful reintroduction and can advise whether it is useful to stop or continue the reintroduction effort, and if so what additional conservation measures are needed.

The results presented in this thesis include an assessment of the availability of sufficient suitable habitats for the European sturgeon to fulfil its complete life cycle across a chain of marine, estuarine and riverine habitats. In addition, the main anthropogenic threats to the species and to its critical habitats are assessed, and it is discussed to what extent these threats can be mediated to enable a successful reintroduction to the river Rhine and the North Sea.

Four research question were formulated:

- Is sufficient suitable habitat available for European sturgeon in the North Sea and the river Rhine?
- What are the potential threats from incidental bycatch in coastal and estuarine areas for successful sturgeon reintroduction and from the currently present alien (non-native) sturgeons?
- What other local and/or regional threats could hinder the sturgeon's return?
- What are possible strategies considering the potential reintroduction of two native sturgeon species?

These research questions were answered in four sections, 1) habitats, 2) threats, 3) tracking, and 4) alternatives, ultimately culminating in section 5) the overall reintroduction feasibility assessment as presented in the synthesis (Fig. 1.10).

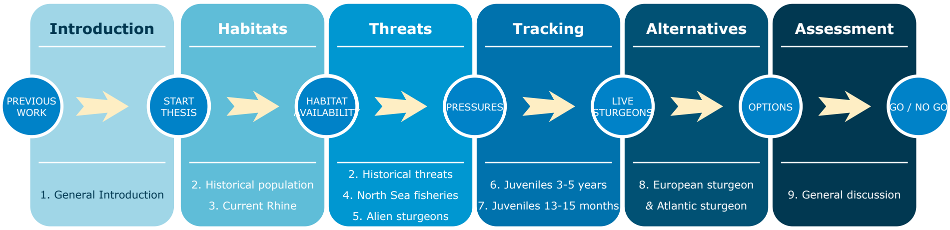


Figure 1.10. Thesis design.

Part 1: Key habitats

In **Chapter two,** the historical spatiotemporal distributions of the now extinct sturgeon populations in the river Rhine and the adjacent catchments of the rivers Ems, Meuse, and Scheldt are unveiled. This enables the determination of the study area and compares each river's importance for the species. This chapter was also used to assesses the contribution of historical anthropogenic activities to the extinction of sturgeon. The research is based on research in archives of the Royal libraries from the Netherlands, Belgium, Germany, France, and Switzerland. The dataset spans five countries and uses thousands of books, newspaper articles and manuscripts. The data will be stored in a publicly available data repository.

Chapter three presents the availability and localisation of the species' potential spawning and nursery grounds in the current river Rhine. This is achieved by a systematic literature review that identifies the species key habitat requirements for spawning and nursery, 1D and 2D modelling, and GIS-based mapping. This chapter also highlights the potential negative effects of coastal infrastructure and inland navigation on the species and its key habitats.

Part 2: Main threats

In **Chapter four** the perceptions and attitudes of fishers are studied, that may be the reasons that they avoid reporting sturgeon bycatch. Also, potential approaches are presented that could encourage them to report and cooperate in sturgeon conservation. Incidental bycatch mortality is considered one of the primary anthropogenic pressures to the extremely limited population at sea . Because monitoring the population development is extremely challenging due to the species highly migratory nature and technical limitations, obtaining data on the species occurrences at sea largely depends on fishers' willingness to report incidental bycatch. This qualitative research uses semi-structured interviews.

Chapter five assesses the potential risks that alien sturgeons may pose to their novel environment and to the local native biodiversity. Data used are obtained from the industry (sturgeon aquaculture, wholesalers, distributors), anglers (digital logbooks), commercial fishers, and research institutes to investigate the extent to which alien sturgeon species are cultivated in the delta of rivers Rhine and Meuse. The abundance of sturgeon species will be verified in hydrologically connected waters, unveiling the pathways of their introductions. The results will be mapped in a GIS to show the densities of alien sturgeon species in combination with the extent of the sturgeon industries in the studied area. The risks will be assessed using the online Harmonia$^+$ protocol, a first-line risk assessment protocol developed by the Belgian Biodiversity Platform (D'hondt et al., 2015) for potentially invasive plants, animals, and their pathogens. The data will be stored in a publicly available data repository.

Part 3: Tracking - telemetry to verify the species sensitivity to other threats
Chapter six presents the results of an experimental release to analyse the outmigration patterns of juvenile sturgeons aged 3-5 years (n=87) using the NEDAP Trail system (radio telemetry). At this age, sturgeon juveniles are capable of full osmoregulation making them ready and able to migrate along the river's main channel downstream into the sea (Brevé et al., 2013a). Fish were released into the Rhine at the German-Dutch border, in May and June of 2012 and 2015 to provide valuable information regarding the threats the animals encounter during their downstream migration, including shipping-related problems and incidental bycatch mortality at sea. This complements the desk top studies.

The survival and spatiotemporal distribution of 13-15 months old (younger) sturgeons are examined in **Chapter seven.** The animals (n=74) were tagged for acoustic telemetry and released in the Rhine at the bifurcation of rivers Rhine and Meuse (Biesbosch area) in 2023. A total of 79 acoustic receivers were installed in the Lower Rhine-Meuse delta and the coastal zone, including the port of Rotterdam, the historical estuary of the Rhine 'Haringvliet and Hollandsch Diep', as well as in the interconnective waterways. The released juvenile European sturgeons only just acquired the capability to full osmoregulation and therefore were expected to remain longer in the estuary than the cohort of older fish described in Chapter 6. The research presents the spatiotemporal habitat use of juvenile sturgeons, and identifies the local and regional pressures that affect their survival and the timing of their out-migration into the North Sea.

Part 4: Alternatives
Chapter eight delivers evidence of the historically presence into the twentieth century of two sturgeon species in the river Rhine and the North Sea, namely the European sturgeon and the Atlantic sturgeon (*A. oxyrinchus*). This is not commonly assumed, and this chapter discusses the benefits and drawbacks of strategies to reintroduce either a single or both sturgeon species, considering the current conditions, including climate change and a poleward (northward) shift in suitable river basins.

Part 5: Synthesis of the feasibility assessment
Chapter nine the General Discussion provides a synthesis of the thesis and has the conclusions. This chapter combines the results of the habitat feasibility assessment, identifies knowledge gaps, highlights future perspectives, and provides science-based advice (recommendations) about critical boundary conditions that should be secured for successful reintroduction of European sturgeon to the river Rhine and the North Sea.

Chapter 2

Historical reconstruction of sturgeon (*Acipenser* spp.) spatiotemporal distribution and causes for their decline in North-Western Europe

Part 1 & 2

Published as:

Brevé, N. W., Nagelkerke, L. A., Buijse, A. D., van Tuijn, T. J., Murk, A. J., Winter, H. V., & Lenders, H. R. (2022). Historical reconstruction of sturgeon (*Acipenser* spp.) spatiotemporal distribution and causes for their decline in North-Western Europe. Biodiversity and Conservation, 31(4), 1149-1173.

https://doi.org/10.1007/s10531-022-02381-1

Photo: Sturgeon caught in the Rhine, in 1917. Source: City Archive Dordrecht.

Abstract

This study aims to reconstruct the historical spatiotemporal distribution of the anadromous sturgeons, *Acipenser sturio* and *A. oxyrinchus,* in NW-Europe (especially in the Rhine, Meuse, Scheldt, and Ems rivers, and in the North Sea), in light of evaluating the possibilities for their reintroduction. It is based on fisheries data from the 14th-twentieth century, consisting of >5,000 records of sturgeon landings and sales (c. 40,000 specimens) from the Netherlands, Belgium, Germany, Luxemburg, France and Switzerland. Most data originate from fisheries in the Rhine-Meuse delta (c. 28,000 specimens, 98% of the Rhine catches). Further upstream, far fewer sturgeons (c. 600 specimens) were reported from the Rhine's mainstem and its principal tributaries, Mosel, Neckar and Main. Smaller tributaries and the Ems, Meuse, and Scheldt rivers seldom yielded sturgeons. This spatial pattern can be related to the species' preference for large-river habitat, combined with fisheries activities that were most intensive in the delta areas. Sturgeon catches began to dwindle in the late nineteenth century, at a time when river engineering first strongly affected the sturgeon's reproductive habitats in the Lower Rhine and delta areas. Also from then onwards, North Sea fishery pressure increased, as trawlers switched from sail to steam-powered propulsion. These sea fisheries harvested all age-classes of sturgeons year-round, including populations from other European rivers. The outcomes strongly suggest that NW-European sturgeon populations were initially impacted by intensive river fisheries, but especially by destruction of reproductive habitat, due to river regulation, and an intensified North Sea fishery, ultimately resulting in total population collapse.

2.1 Introduction

Sturgeons (order *Acipenseriformes*; sturgeons and paddlefish) only occur in the Northern Hemisphere (Billard & Lecointre, 2000). Most sturgeons are long-lived, large-bodied, late-maturing fish that undertake long-distance anadromous migrations through marine, estuarine and riverine habitats (Bemis & Kynard, 1997). Due to these life history characteristics and their anadromous nature, sturgeon populations are easily affected by (marine) overfishing and river engineering. This includes dredging, diking, canalisation, and barriers to upstream and downstream migration due to weirs, dams, sluices and hydropower plants, amongst others (Birstein et al., 1997a; Puijenbroek et al., 2019; Rochard et al., 1990). According to the IUCN Red Data List, at present 85% of all *Acipenseriformes* are endangered, making it the most threatened order of vertebrates in the world. This conservation status is a wake-up call to restore their populations, migration routes, and core habitats in their natal rivers and estuaries (for spawning, nursery, and salt/freshwater acclimatisation).

This study aims to reconstruct the historical spatiotemporal distribution of sturgeons in the river Rhine and in the adjacent Ems, Meuse and Scheldt rivers (Fig. 2.1). Two sturgeon species from the north Atlantic Ocean, the now critically endangered European sturgeon (*Acipenser sturio*) (Gessner et al., 2010c) and the near threatened Atlantic sturgeon (*Acipenser oxyrinchus*) used to display extensive homing behaviour to these rivers (Thieren et al., 2016a; Van Neer et al., 2012). These sturgeon species, that represent a separate clade distinct from all other *Acipenseriformes* (Thieren et al., 2015), were strongly impacted during the nineteenth and twentieth centuries. While Atlantic sturgeon populations survived on the North American side of the Atlantic Ocean, this species became extinct in Europe (Chassaing et al., 2016; Gessner et al., 2006; Williot et al., 2002a), but was recently reintroduced in the river Oder and the Baltic Sea (Gessner et al., 2010a; Kolman et al., 2011b). The European sturgeon, which only occurs on the European side of the Atlantic Ocean, was barely saved from global extinction during the 1990's, when 53 specimens were collected from a relict population in the Gironde basin in France (Williot & Castelnaud, 2011). These specimens were raised to build an *ex situ* brood stock in Bordeaux and another one in Berlin, for restocking fry and fingerlings in the Gironde and Elbe river basins (Williot & Kirschbaum, 2011).

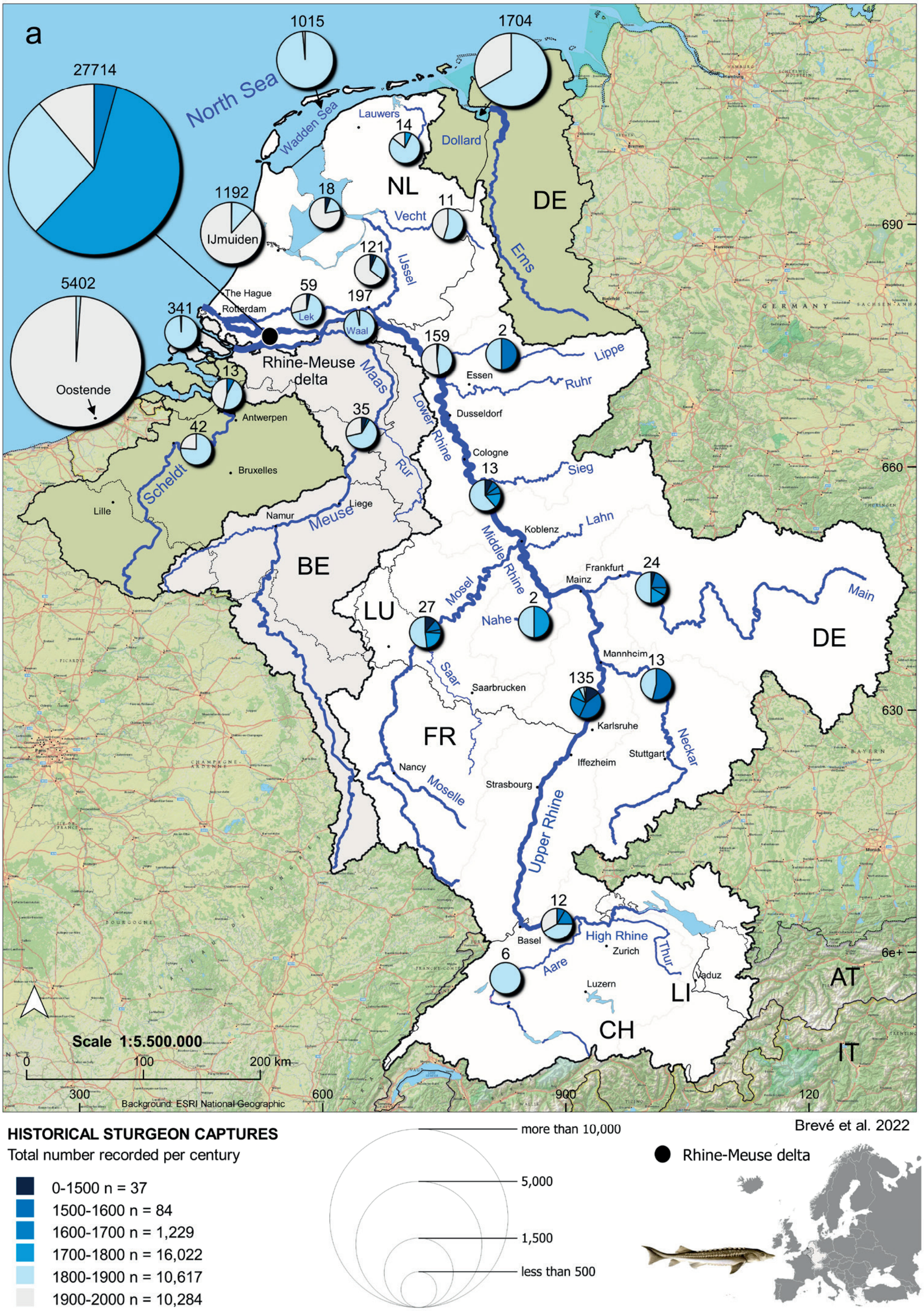
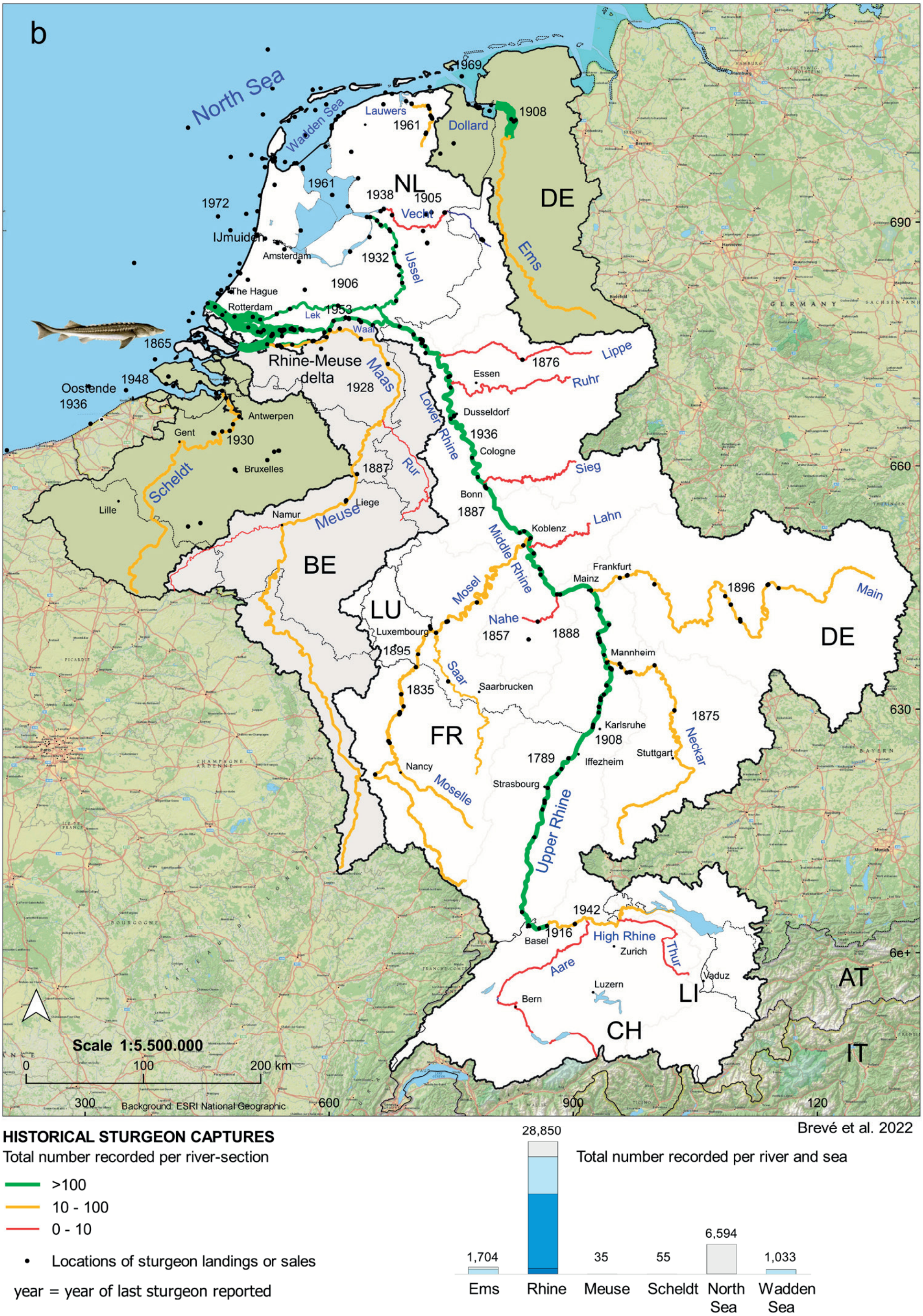


Figure 2.1. (a) Reported historical sturgeon landings and sales (fisheries reports) between 1300-2000 from the basins of the Rhine, Meuse, Scheldt and Ems rivers, the North Sea & the Wadden Sea. Pie-charts show total numbers reported per century, per river-section (Rhine-Meuse delta; Lower-, Middle-, Upper- and High Rhine, and tributary rivers, e.g., river Mosel, Neckar and Main).



(b) Traffic-light colours indicate historical abundances of sturgeons per river-section. The stacked bar-chart in Fig. 2.1b presents the total number of recorded sturgeons per century per river basin and sea. Labels with years (e.g. 1972) give the year for the last known sturgeon reported from that specific river-section or sea.

As a result of the restocking efforts, in recent years hundreds of European sturgeon juveniles and adolescents have been observed in neritic zones of the northeast Atlantic Ocean (Council of Europe, 2018; OSPAR Commission, 2021). Although the species' status is still critical, as no natural reproduction is yet observed, this gives rise to consideration of the expansion of restoration efforts. The species' core habitat in the Mediterranean (Chassaing et al., 2016) is almost completely lost due to substantial anthropogenic impacts, like dams and human-induced climate change (droughts, increased temperatures) (Lassalle et al., 2010; Williot et al., 2002a), making recovery virtually impossible. In contrast, the river Rhine (from now on: Rhine) has an intact longitudinal connectivity between the North Sea, the Port of Rotterdam, and the upper reaches, over 850 river kilometres upstream (ICPR, 2018). In addition, remediation of 18th-twentieth century industrial pollution (Villamayor-Tomas et al., 2014) has further improved the Rhine's carrying capacity for diadromous fishes (Borcherding et al., 2010; Hundt et al., 2015). To strengthen the conservation status in the species' northern range, the possibility of re-introducing the European sturgeon in the Rhine is currently under assessment, which includes experimental releases of tagged individuals (Brevé et al., 2019b; Brevé et al., 2013a). However, before actual restocking of this river can be implemented, a thorough habitat feasibility and risk assessment is paramount to reduce any risks to this critically endangered species (IUCN/SSC, 2013). For example, the Rhine's use as a major European shipping lane potentially poses serious threats to sturgeons (ship-propeller strikes, noise pollution, dredging, *etc*.).

A study of the historical spatiotemporal distribution and core habitat of sturgeons in the Rhine is an important starting point for evaluating the opportunities for their reintroduction. Historical fisheries data can be used as an indicator for long-term population distribution and abundance, with changes therein potentially linked to anthropogenic or climatological influences (Fortibuoni et al., 2017). Although historical fisheries data does not distinguish between the closely resembling *A. sturio* and *A. oxyrinchus* (Thieren & van Neer, 2016), historical biogeographical research can identify former core habitats and the species' seasonal distribution in the Rhine and adjacent catchments (Gessner et al., 2011b; Lenders, 2017; Paaver, 1999; Spratte, 2014; Williot & Castelnaud, 2011). This study therefore addressed the following research questions, using historical sturgeon fisheries landings data and sales from the Netherlands, Germany, Belgium, Luxemburg, France and Switzerland:

1. What were the spatiotemporal distribution patterns of the now extirpated sturgeon populations in NW-Europe, with an emphasis on the Rhine river basin, but including the adjacent catchments of the Ems, Meuse and Scheldt rivers?
2. Which historical anthropogenic activities most likely dictated the extirpation of sturgeon populations in these river systems?

2.2 Materials and methods

2.2.1 Study area

The river Rhine is the 9th largest Eurasian river. Its drainage basin covers 185,260 km^2, along a total length of 1,230 km, with an average discharge of about 2.200 m^3/s (Uehlinger et al., 2009) (Fig. 2.1). It flows to the north, from its origin in the Alps in Switzerland, through Germany, France and Luxemburg, to the lowlands in the Netherlands where it drains into the North Sea. The Rhine's mainstem is divided into the Alpine, High, Upper, Middle and Lower Rhine, based upon geomorphological characteristics (Uehlinger et al., 2009). Its largest tributaries are the Mosel, Main, Neckar and Aare rivers. In the Netherlands, the IJssel distributary of the Rhine drains c. 1/9 of the discharge to the north into the Wadden Sea. To the southwest, the Rhine's mainstem confluences with the river Meuse into a freshwater delta (from now on: Rhine-Meuse delta), an area renowned for its historical Atlantic salmon (*Salmo salar*), Allis shad (*Alosa alosa*), North Sea houting (*Coregonus oxyrinchus*) and sturgeon fisheries (Martens, 1992). Downstream, the combined Rhine and Meuse rivers share a delta with the river Scheldt. Historically these rivers continuously shifted course (Berendsen & Stouthamer, 2000). From the 18th century onwards, intensive river engineering that began upstream, shortened, and shaped these rivers into efficient shipping routes (Bloesch & Sieber, 2003). Currently, the Rhine is a major European shipping lane with the Port of Rotterdam as its terminal, while the Rhine-Meuse-Scheldt delta is marked by huge storm surge barriers and strong land reclamation (Steenhuis et al., 2016; Wolff et al., 1994). Because of the intricately interwoven geographical, hydrological and biogeographical connections between the river Rhine and its tributaries, the Meuse, Scheldt and Ems rivers, data were collected for all four of these river systems.

2.2.2 Data collection

Although there are several data series that span decades of sturgeon landings and sales for specific sites (De Jong et al., 1988; Martens, 1992; Mohr, 1952; Verhey, 1949), there are no high-quality, long-term time series for the four river basins. We therefore collected data from multiple sources and collated a comprehensive dataset and time series. Data on fish consumption, references to fish in culture (legends, plays), and anecdotal data, were collected, but we focused on fish trading sources (especially fish market sales lists), fisheries sources, and early scientific fish ecological surveys (for typology, see (Haidvogl et al., 2014) (Table 2.1). Most data stems from the nineteenth century and later, but we have also tried to collect many older sources, because disregarding such older sources could lead to a serious content bias, leaving relevant long-term causes and processes out of the picture (Hoffmann, 1996). Historical sturgeon data, including archival sources and handwritten documents obtained from many different institutes and professions, were previously collected by (Kinzelbach, 1978; Kinzelbach, 1997), whose data was rechecked and added to our dataset.

Table 2.1. Total number of records per source per country for sturgeons reported from the study area.

Typology*	Source type	Used in study?	Total number of records per source per country							Data collected from this source	General data quality	Period for most data	Data frequency	Data on price?	Fishing ground confirmed?	Species confirmed?
			NL	BE	DE	FR	LU	CH	sum							
b, c	Fisheries statistics (mainly fish market sales lists in newspaper articles)	yes	3138	678	70	1			3887	Location of fish market/auction, price per total individual count and/or total weight, and/or total price, either in 1/2 kg or kg	high	1875 - 1975	day, month, year	yes	indirect	no
a, b, c	Data on sturgeon landings, other than fisheries statistics	yes	537	715	219	32	4	14	1521	Fishing ground, individual count, length, weight, price	high	1300 - 1975	day, month, year	no	yes	no
b, c	Newspaper articles on large individual sturgeon captures, and (very rare) sightings	yes	528	1333	11	9		3	1884	Location, measurements or estimates of length, girth, weight (caviar), value (price paid or reward given)	high	1850 - 1950	random	yes	yes	no
d	Fish shop advertisements, abattoir notices	no	41	624					665	Prices either in 1/2 kg or kg, no data on individual count, sometimes for weight	medium	1845 - 1952	day, week	yes	no	no
b	Fishing rights, taxes, legislation	no	178	1	1				180	Fishing ground, season, minimum size, gear-type, mesh-size, owner, and tenant	medium	1300 - 1975	year	no	yes	no
e	Trivia	no	42	15	19	2		2	80	Legends, play's, stories, often indications of fishing ground and individual count	low	of all times	random	no	yes	no
a, b	Museum pieces, archaeological bottom finds	no	20	4	13	1			38	Bones, scutes, tissue, ancient DNA, estimates of individual count, length, weight, and age	high	of all times	random	no	no	yes

* Typology is based on classification of written historical sources: a = Early scientific fish ecological surveys, b = Fisheries sources, c = Fish trading, d = Fish consumption, e = Fish in culture (Haidvogl et al. 2014).

Google Scholar, Scopus and NSC ProQuest were searched, but contemporary reviewed literature yielded surprisingly little additional historical data for the study area. The database of the Global Biodiversity Information Facility (www.gbif.org) was downloaded (April 4, 2021) for *Acipenser sturio* and *Acipenser oxyrinchus,* and checked, which gave an additional 22 data entries. The dataset was further extended with data from historical books and handwritings, obtained through Google books and the Universities acknowledged. A major contribution to the dataset was achieved by searching digitised newspaper-articles via www.delpher.nl (1618-2005, National Library of the Netherlands), www.belgicapress.be (1814-1970, Royal Library of Belgium), www.europeana.eu (1618-1980, European newspapers from 20 countries) and www.e-newspaperarchives.ch (1692-2018, Swiss National Library). These platforms yielded substantial quantitative data on fisheries statistics (individual counts, weights, and prices) for the period 1845-1953.

The following search keywords were used in all platforms: sturgeon* (this includes the French 'esturgeon'), stör*, "*Acipenser sturio*", steur*; combined with Rijn, Rhin, Rhein, Maas, Meuse, Scheldt, Ems, Escaut. Searches for vernacular names and aberrant spellings like 'rombus' or 'fteur' yielded only 50 additional results. This search delivered nearly 150,000 hits that were sorted, filtered, and cleaned. Data on landings and sales could concern duplicates in the sense of 'repeated' records from different sources (mainly newspapers), and in the sense of 'summed' per week, month or year (mainly for fish auctions). Duplicate data were individually checked and, if applicable, marked in the dataset and filtered-out for data analysis. All data were sorted into predefined fields (such as year, month, week, numbers, weights, length, price per kg, per fish, source, URL). For sturgeon landings, and locations of fish auctions and markets, coordinates were found in historical maps provided by the Netherlands' Cadastre, Land Registry and Mapping Agency (Het Kadaster) *via* https://www.topotijdreis.nl, and verified with Google Maps https://maps.google.nl, adding an accuracy in km's when necessary (NA, 1, 2, 5, 10, 20, 50, 100, 200 km). The final dataset spans the 14^{th}–20^{th} centuries, it includes >5,000 unique data entries on landings and sales of approximately 40,000 sturgeons for the study area and is deposited in the repository DANS-EASY under a CC BY license (Brevé et al., 2022c); Table 2.1 for the overview).

2.2.3 Fisheries data analysis

For spatiotemporal analysis, total numbers of sturgeon landings and sales (i.e. individual counts, locations, weights, and prices) were summarised per century, river (section) or sea (North Sea and Wadden Sea) and mapped in QGIS 3.16. Total numbers of sturgeons were summarised in separate timelines for the Rhine's delta, the river's mainstem, and for the sea. Seasonal distributions were analysed for all sturgeon numbers that were traceable to the month of catch. To obtain a proxy for the species local or regional abundance or scarcity, price developments on freshwater and sea fish markets were calculated by averaging yearly and 5-yearly prices, numbers and weights. This is a valid approach for socio-economically stable periods in history (so, excluding wars or economic crises), when the price of products is strongly linked to their availability (Lenders et al., 2016; Lenders, 2017). Historical prices in Dutch Guilders were converted to equivalents in euros in 2016 via the consumer price index of the Institute of the Royal Netherlands Academy of Arts and Sciences (KNAW), based on Van Zanden (2013) (available for years 1450-2016); and from Belgian Francs to Euros in 2015 *via* the currency converter provided online http://www.historicalstatistics.org/Currencyconverter.html (Latest update 10 January 2016, available for years 1880-1950, except 1914-1920).

2.3 Results

2.3.1 Spatiotemporal distributions of sturgeon landings and sales

The historical distribution of sturgeons in the four river systems appears to be confined to the estuaries, the (freshwater) delta areas and the Rhine river's mainstem. Clearly, fewer sturgeons were reported for the tributary rivers, the High Rhine, and the Ems, Meuse, and Scheldt rivers. Most data were obtained from fisheries and fish auctions in the Rhine-Meuse delta in the Netherlands (27,714 specimens: 98% of all sturgeon capture reports from the river Rhine) (Fig. 2.1a). For the Rhine, the number of reported sturgeons diminished immediately upstream from this area. In total 590 (2%) sturgeons were reported from the Rhine's mainstem in the Netherlands, Germany, France, Luxemburg, and Switzerland; of which 319 originated from the Lower, Middle, Upper and High Rhine, and 70 from the main tributaries Mosel, Main, Neckar and Are, while all other (of the thirty-three) Rhine tributaries seldom yielded sturgeons.

From the Wadden Sea and the estuaries of the therein debouching rivers, sturgeons were only occasionally reported, yet these reports represent high numbers of fish. For example, 237 sturgeons in 1869 and 80 in 1870 were landed and sold at one seaport situated in the river Lauwers estuary; in 1896, 672 sturgeons were landed at hamlets in the north of the Netherlands. No weights or prices were mentioned. Because, in general, adult sturgeons were usually weighed, priced, and taxed, the sturgeons mentioned may have concerned smaller/younger specimens. From the river Ems, 40 sturgeons were reported, which is much lower than the total of 1,704 sturgeons captured in the Ems-estuary (named: Dollard). From the small river Lauwers-estuary and its tributaries, 14 mature sturgeons were reported between June and July. Although, according to anecdotal information, large numbers of sturgeons were captured in the Rhine's IJssel distributary and its freshwater delta in the Zuiderzee pre-1700 (Ennema, 1946), only a total of 121 sturgeons were reported from this region between 1321 and 1932.

For the North Sea, most sturgeon reports were obtained from the late 19th and early twentieth centuries. The decreasing river catches and increasing marine catches resulted in a yearly marine harvest in the Netherlands that, by 1910, exceeded that from the Rhine-Meuse delta. Belgian and Dutch sea-fisheries reported a total catch of 1,192 and 5,402 sturgeons respectively (see also Fig. 2.1a). Yields of trawl fisheries were registered by the Dutch and Belgian governments in annual reports. For the Netherlands the series spans 16 years (Hoek, 1894; Redeke, 1915), for Belgium 24 years (Zeevisscherij, 1912, 1936). These Belgian statistics specify propulsion type, seaport, and fishing ground for sturgeon harvests. For this period, almost 100% of sturgeons marketed in Belgium were landed by steam trawlers (not sail), sold at Belgium's main fish market in Oostende, and caught at both nearby fishing grounds (e.g. the Belgian coast and the English Channel), as well as from distant areas (e.g. the Bay of Biscay, Portugal, and the northern North Sea). Although there are many data gaps in the timeline (Fig. 2.2), the pattern for the 18th-twentieth century, and historical reports (e.g. Hoek 1910), suggests that the sturgeon's decline started in the late 19th century, around 1885. This was followed by approximately 35 years of rapid population decrease, until c. 1920 when the species effectively vanished from the river systems, followed by another 30-50 years of sporadic landings until the species total disappearance. The last sturgeon captured in the river Rhine dates from 1952, for the North Sea the year is 1974 (Fig. 2.1b).

2.3.2 Seasonal patterns

Seasonal analyses of summed-up catches of mature sturgeons over the years, showed a strong pattern. Catches of riverine sturgeon increased from March onwards, with a dominant peak in June, after which catches declined again until August (Fig. 2.3). Although there are very rare reports of sturgeon occurrences during winter months, i.e. one sighting in the Meuse in 1890 and four from the river Aare in 1895, in general, the mature spawners left the rivers between September and March. Catches ranged from 0 to 2500 specimens per month. Marine catches, that started around 1885, showed far less seasonal fluctuation, ranging from 50 to 150 per month, with a dip in the number of catches between May and September (Fig. 2.3). Maturity was based on the sturgeons' size (see also the mean weight in Fig. 2.4b).

2.3.3 Market developments

Remarkably, the dataset unveils a substantial trade in sturgeons from the Netherlands to Belgium. As early as the 15th century, fisheries and fish auctions from the Rhine-Meuse delta transported salmon, Allis shad and sturgeon (salted or pickled in barrels) towards Belgian and French cities (Leuven, Gent, Antwerp, Brussels, Liège, Paris, etc.). This was mentioned by, for example, Hoek (1910) and (Martens, 1992), and substantiated in this study by the collection of hundreds of newspaper articles from Brussels' 'Poissonneries' (fish shops), advertising sales of sturgeon 'from Holland' (Brevé et al., 2022c). Between 1742-1775, different fisheries delivered their harvests to the region's central Geertruidenberg fish auction, which sold on average 468 sturgeons per year from the Rhine-Meuse delta, while between 1895-1900 all fish auctions in the area reported a combined average of 521 sturgeon sales per year (Fig. 2.2a).

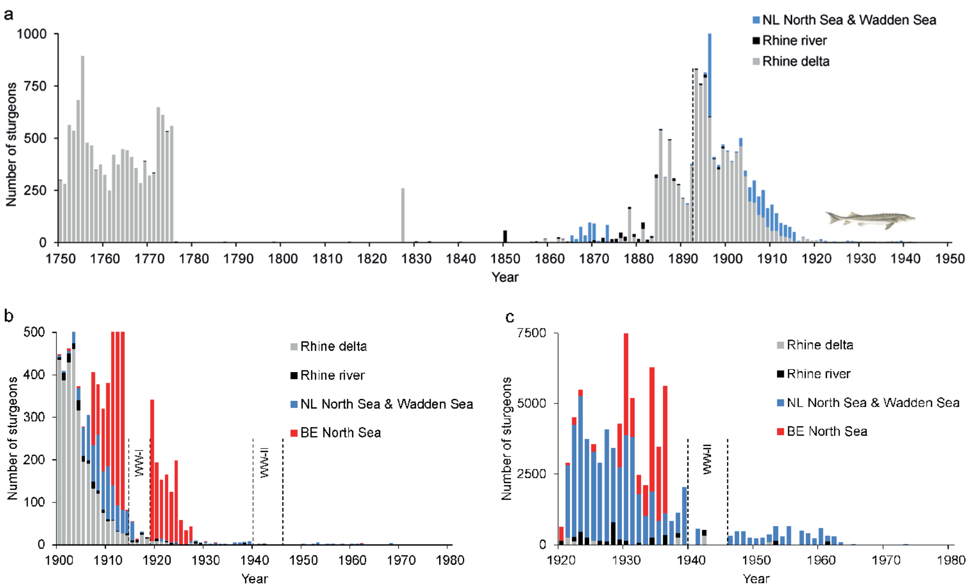


Figure 2.2. (a) Total numbers of reported sturgeon landings and sales per year between 1300-2000 from the river Rhine (black), Rhine-Meuse delta (grey), North Sea & Wadden Sea (blue). Excluded are data for the Ems, Scheldt and Meuse rivers. The 'peak' between 1742-1775 (shown in this graph from 1750 onwards) originates from the region's central, collective fish auction (Geertruidenberg) for six different fisheries in the Rhine-Meuse delta (Martens, 1992). Data between 1875-1931 originate mainly from other central fish auctions (Hardinxveld, Kralingsche Veer) and different fisheries in this area. Dotted line: start of the North Sea steam trawl fisheries. (b) Total numbers of sturgeons per year between 1900-1980 from the river (black) and all delta areas (grey), North Sea and Wadden Sea for the Netherlands (NL Sea, blue) and Belgium-Sea (BE Sea, red). (c) Idem, between 1920-1980, in total weights. N.B. From 1920 onwards fish auctions reported sturgeons in weights. Sometimes, both the numbers and total weights are available, enabling an estimate of the average weight of individual fish. Dotted lines: beginning and end of World Wars I and II.

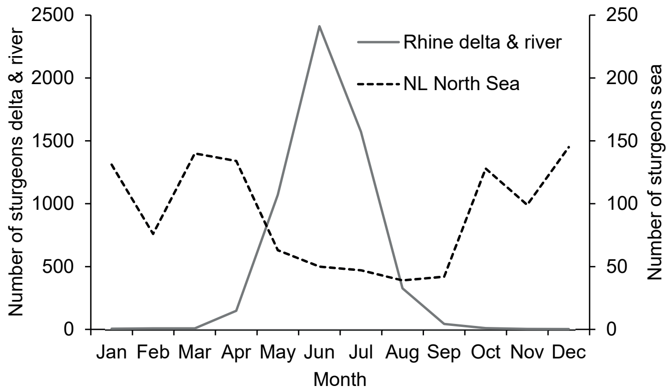


Figure 2.3. Summed catches over the year (in the period 1300-2000) of sturgeons from the Rhine river basin (n = 5656, grey line), and from the North Sea for The Netherlands (n = 1103, black dashed line).

Although exceptionally big sturgeons were landed from the sea (the largest on record had a total length of >5 m and weighed 350 kg (Brevé et al., 2022c), in general sturgeons from the sea were smaller than those harvested from the Rhine-Meuse delta (Fig. 2.4b). Figure 2.4b also provides some evidence of a diachronic change in sturgeon weights between 1895-1914. During this period, the average individual weight for sturgeons sold at fish auctions in the Rhine-Meuse delta increased from 60 to 90 kg, whilst numbers dropped by 90%. Simultaneously, sturgeons harvested from the sea decreased in average weight from 60 to 20 kg, whilst their numbers increased, after which these harvests also collapsed (Fig. 2.4b). Between 1895-1914, a sturgeon's value in the Netherlands, taken from the Rhine-Meuse delta, almost doubled from an equivalent of circa 10 euro per kg to 18 euro per kg (Figs. 2.4a-b). The largest sturgeons fetched the highest prices, even up to an equivalent of >1000 euro per fish (Fig. 2.4c). Prices continued to increase at a time when sturgeons became scarce between 1905-1914 (Fig. 2.4a). The data suggests that prices were influenced by World-War I when the Netherlands were neutral, while Belgium, Germany and so many other countries were at war. The war caused a decreasing demand, which led to prices dropping heavily from 1914 onwards, making clear that it was mainly an export market that drove Dutch Rhine and North Sea sturgeon fisheries.

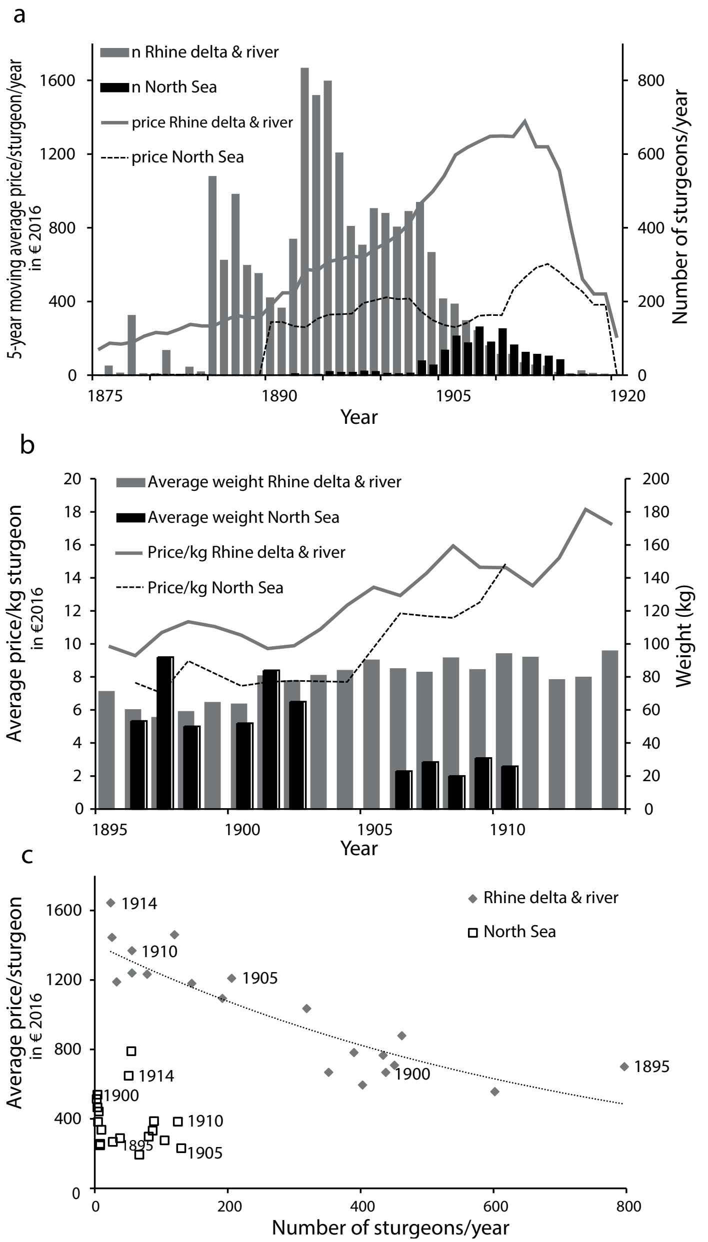


Figure 2.4. Price development for sturgeon at Dutch fish auctions, selling sturgeons from the river Rhine and North Sea. (a) 5-year moving averages in price per sturgeon between 1875-1920 and the total number sold per year (n/year). (b) Average price/kg and average weight per sturgeon between 1895-1914. Grey lines and symbols = sturgeons caught in the delta & river; black (dashed line) = sturgeons caught at sea. (c) Average price per sturgeon in relation to the total number of sold sturgeons per year (n/year) between 1895-1914. Original prices in Dutch guilders were converted to 2016 Euros (€). For the Rhine river the exponential relationship is statistically significant ($y=1408 \cdot e^{-0.00133x}$; $R^2=0.75$, $p=<.0001$, $n=20$), for the North Sea catches there is no statistically significant relationship ($R^2=0.06$, $p=0.298$, $n=19$).

2.4 Discussion

This study aims to identify the historical spatiotemporal distributions and core reproductive habitats of sturgeons from the river Rhine and neighbouring basins of the Ems-Dollard, Meuse and Scheldt rivers, as well as the principal factors behind the sturgeon's population decline and ultimate extirpation. From the Late Middle Ages onwards, sturgeons were claimed by, and given to, the central authorities of ecclesiastical and secular powers (Blackstone, 1830). Sturgeons were a welcome food source, and of general interest (put on display) to the public because of their size (Boddeke, 1971). Hence sturgeons were often numerically recorded, and taxed (Martens, 1992), yielding high prices in the Netherlands, Belgium, Germany, and other North Sea countries (Hoek, 1900; Mohr, 1952; Zeevisscherij, 1925). This strong interest suggests that sturgeons will have been fished for, wherever they occurred.

2.4.1 Historical data, use and limitations

A large dataset could be collected from historical books, handwritten notes, annual fisheries statistics and newspapers that included exceptional captures (big fish), fish shop advertisements, and frequent fisheries statistics for local or regional markets and auctions (Brevé et al., 2022c). Yet there are inevitably numerous data gaps and probably many historical statistical records have been lost. Searching digital (newspaper) archives is laborious, despite the availability of ever better digital filtering techniques (van Erp et al., 2018), and it is inevitable that some of the data is not found because some sources are still insufficiently accessible. Many libraries were damaged during the second World War (Van der Hoeven & Van Albada, 1996). Moreover, fewer catch records were obtained from small-scale fisheries than for fish expedited straight to markets abroad (Antwerp, Brussels) (Hoek, 1910). Catch- or market data could also have been underreported to avoid taxes (Haidvogl et al., 2014); and in general, most reports concern adult fish, not the younger sturgeons. Although most data collected originates from post 1850, the data collated from pre-1850 sources comprises >300 verified records. These long-term data also help in avoiding bias, since they offer insight into potentially relevant ecological and economical processes that may have influenced – in this case – sturgeon population developments. Thus, the findings of this study are supported by several lines of evidence, from spatiotemporal distributions and developments in numbers, weights and prices, which substantiate the identification and seasonality of the species' reproductive grounds; and from historical anthropogenic pressures affecting the historical sturgeon population in NW-Europe.

2.4.2 Reproduction grounds and season

One main finding is that a surprisingly high number of sturgeons were reported from the Rhine-Meuse delta in the Netherlands (c. 28,000 or 98% of the total river Rhine's catch). This is in strong contrast to the fraction of sturgeon landings and sales (c. 600 specimens) reported from all upstream river reaches, including the tributary rivers in Germany, Luxemburg, France, and Switzerland. This geographical distribution pattern is in accordance with previous reports for the Rhine and for other river basins, like the river Elbe where most sturgeons were also reported from the river's mouth (Holčík et al., 1989; Kinzelbach, 1978; Kinzelbach, 1997). However, this distribution in data raises the question as to whether the sturgeons' dominant occurrences in the Rhine-Meuse delta can be explained by their biology and ecology, an important part of their life cycle being spent in estuaries/delta areas (see e.g. Acolas et al. 2011), or by a strong regional fisheries effort, or by both. Answering this question is critical in identifying which river sections were key to sturgeons, because this is of paramount importance for sturgeon habitat restoration and protection.

2.4.3 Spawning season and main pathways upstream

This study shows that the sturgeons' spawning run peaked in June, around the longest day, at the start of the summer season when the Rhine is still fed by snowmelt from the Alps (Uehlinger et al., 2009). Notably, rivers fed merely by rain have a decreased discharge during dry summer months (e.g. rivers Meuse, Scheldt, and Ems), whilst rivers fed by rain and snowmelt (like the river Rhine) have a more continuous river discharge, even during dry summer months. The influence of snow melt is therefore discernible to the delta (Uehlinger et al., 2009) and the strongest freshwater current may have lured sturgeons towards the Rhine, instead of to the Meuse, Scheldt, and Ems. The sturgeons clearly preferred certain river systems and sections. Rare captures of mature sturgeons occurred in the tiny Lauwers river system and in the smallest of tributaries of the river Scheldt. These fish most probably strayed into these minor water courses, as these provide no suitable spawning habitat. There is also proof of occasional occurrences in the river Meuse near the Belgian cities of Visé and Liège, mostly before 1850 when the population was still at an average level, and often during and after rainfall (Brevé et al., 2022c). Supposedly, these fish used the risen water levels to enter the Meuse from the Rhine-Meuse delta and explored this river that normally carries much less water than the Rhine. These findings demonstrate that mature sturgeons could occur in all parts of the four river systems, even in the capillaries, however, the largest numbers occurred in the (largest) currents and delta areas.

2.4.4 Spawning grounds

Because of the sturgeon's abundance in the Rhine-Meuse delta, it was suggested by several authors that this particular area was used for spawning (Deelder & Huussen

Jr, 1973). Yet Hoek, the first prominent Dutch fisheries biologist, declared that no spawning activity was observed and suggested that this occurred further upstream in the deep sections of the river (Hoek, 1910). In 1949, Verhey writes that the entrepreneur of the 'Nieuwe Merwede' fisheries (salmon-seine fisheries located in the most upstream part of the Rhine-Meuse delta) had never seen a spent sturgeon. Verhey (1949) observed that sturgeons at this location were mainly captured during ebb periods in the deepest part of the delta, when the strongest and deepest currents occur. Because of this he suggested that sturgeons at this site were on their spawning run, moving further upstream. Current knowledge on sturgeons' biological cycles and morphological insight in the area seems to corroborate these findings. Both the Rhine and Meuse rivers confluence in this freshwater delta and continuously deposit part of their silty and muddy bedload. Continuous sedimentation, creating environments of swampy creeks and islands provides no suitable spawning habitat for the European sturgeon, because this species requires deep, oxygenated, heterogenous gravel beds (Jego et al., 2002). Moreover, the influx of brackish waters in the Rhine-Meuse delta would hamper the survival of larvae and young-of-the-year sturgeons that naturally move downstream and are unable to osmo-regulate in their first year (Acolas et al., 2011a). The area seems unsuitable for Atlantic sturgeon spawners as well, which prefer gravel for ease of attachment of the adhesive eggs and for the interstitial spaces providing refuge for the larvae, although they may use sandier or even siltier substrates, but not pure mud (Bain et al., 2000; Sulak et al., 2016). It thus becomes apparent that sturgeons, together with Atlantic salmon, Allis shad, and other diadromous fish aggregated 'en masse' within these funnel-shaped, shallow grounds (Martens, 1992), but none of these species spawned in the Rhine-Meuse delta (Huijbregt, 1984; Martens, 1992; Reekers, 1916).

As the spawning grounds were most probably further upstream, the question remains: how far upstream? Both sturgeon species can undertake long range spawning migrations. European sturgeons can even cover over 1,000 river kms (refs in Holčík 1989), with their migration distance being positively correlated with river discharge (Holčík et al., 1989). Sturgeons from the Rhine were occasionally reported at Strasbourg (Upper Rhine) (Baldner, 1666), but only exceptionally further upstream at Basel and Bern in Switzerland (High Rhine). This consistent pattern was previously reported by several authors (Brandt, 1833; Hartmann, 1827; Leuthner, 1877) and written down as early as in 1625: "Their migrations in the Rhine rarely extend beyond the lower Rhine, which is why its appearance in the middle Rhine is already rare. The sturgeon rises to Basel even more rarely and only as an exception." (Leuthner, 1877). This implies that sturgeons normally occurred between Bingen (river km 530) and the Port of Rotterdam (river km 1026), i.e. at a maximum distance of c. 500 km from the river mouth. Yet, mature sturgeons probably did not need to move far into Germany, as approximately 100 km in the upstream direction in the Lower Rhine in Nord Rhine-Westphalia (Germany) sturgeons encountered an abundance of deep, highly oxygenated, heterogenous gravel beds in strong currents, ideal spawning habitat for European sturgeons. Possibly, Atlantic sturgeons would spawn somewhat closer to the delta than European sturgeons, because of their preference for somewhat smaller sized substrates, but this cannot be substantiated from the collected dataset as no distinction could be made between the two species. This is consistent with observations that most mature sturgeons did not move far into Germany, something that was previously attested by (Hoek, 1910), (Verhey, 1949) and Kinzelbach (1987). Considering that the sturgeon's spawning run only lasted a couple of months, whereafter they left the river empty between September and March, and considering the energy costs and duration of up- and downstream migration over 1000 kilometres, it seems plausible that most sturgeons didn't move that far upstream. In comparison, most of the 27 mapped historical spawning sites in the Garonne and Dordogne rivers were located within 200-270 km from the Gironde estuary (Bismuth & Lauronce, 2019; Jego et al., 2002). In the river Elbe, sturgeons were found to spawn up to 400 kilometres upstream, but the main spawning areas were not that far upstream. We cite from (Jego et al., 2002): "*In the river Elbe the main spawning sites in the nineteenth century were in the lower part of the river between Brunsbuttel – only approximately 40 rkm – and Hamburg at 110 rkm* (Quantz, 1903)."

2.4.5 Nursery grounds

As nursery grounds are naturally located downstream from the spawning grounds (Acolas et al., 2011a), this suggests that the freshwater Rhine-Meuse delta in the Netherlands, and the IJssel distributary in the Wadden Sea (former Zuiderzee) would have been an important habitat for young-of-the-year sturgeons. There are indeed indications of large numbers (hundreds) of sturgeons captured over a period of weeks in these areas (Brevé et al., 2022c; Ennema, 1946), which needs further study.

2.4.6 Historical anthropogenic pressures

The decline of the Rhine's diadromous fishes is generally explained by a strong deterioration and loss of spawning and nursery habitat, caused by reduced water quality and extensive river-reconstruction, as well as overfishing (de Groot, 2002; Nemitz, 2010; Van Emmerik, 2004). In salmon, the decline could have started as early as during Early Modern Times (post 1500 AD), caused by the historical rise of water power in tributary rivers (Lenders et al., 2016). In sturgeon, the decline seems to have started at the earliest by the end of the 18th century (Lenders, 2017), which was confirmed by this present study. This raises the question: which anthropogenic activities impacted the sturgeons most, when and where?

2.4.7 Fisheries in the Rhine-Meuse delta

Historical information shows the existence of a thriving fisheries community in the Rhine-Meuse delta as early as 1421, which continued for centuries, as the area is well suited to large-scale fisheries for diadromous fish (Deelder & Huussen Jr, 1973; Martens, 1992; Verhey, 1949). Sturgeons were targeted with driftnets and other types of strong fishing gear (Brehm, 1900; Hoek, 1910; Mohr, 1952). Sturgeons became trapped in fykes and entangled in seine nets used in salmon and shad fisheries (Brehm, 1900; Brevé et al., 2022c). From c. 1870 onwards, fisheries in the Rhine-Meuse delta became industrialised, simultaneously with a reasonably well-developed fish auction system (Hoek, 1910; Martens, 1992), which is mirrored in the increased sales notifications from multiple markets in the Rhine-Meuse delta (aggregated in Fig. 2.4). This increase could partially be due to an underestimation of the true sales by under reporting in older sources, as by 1885 sturgeon yields were already in decline, which was described by (Hoek, 1910). When the actual decline began remains unclear, due to a substantial lack of older data. In 1908, fishers in the Rhine-Meuse delta tried to make their business more profitable by scaling up and further increasing mechanisation, to improve efficiency, which led to a short-lived increase in salmon and shad harvests, especially during World-War I. Their partnership 'Nieuwe Merwede' continued until 1931, after which they, and most other large seine fisheries, were forced to close their business due to a substantial decline in yields (Verhey, 1949).

2.4.8 Upstream fisheries

In upstream river sections, sturgeons have historically most probably always been rarer than in the downstream reaches (Quantz, 1903; Williot et al., 2011b). Although upstream fisheries may have been unevenly distributed, it is unlikely that German sturgeon captures from the 19th and 20th centuries were left completely unreported. Several indications for this exist. For instance, German fisheries in the Rhine successfully targeted salmon, and their sturgeon harvests were much lower than in the Netherlands (Böcking, 1988; Bürger, 1926). This finding is further supported by the fact that in 1886, a salmon treaty was signed between the German, Swiss, Luxembourg and Dutch governments (Von Boetticher, 1886). The reason for this treaty was a general decline in salmon yields. It prohibited the use of fishing methods which would block more than half of the breadth of the watercourse, prescribed closed seasons, minimum fish size, etc. However, this treaty did not consider sturgeons. The scarcity of sturgeon captures was confirmed by a study by colleagues from the Rheinische Fischerei Verband, who stress that that salmon fisheries were abundant in the mouths of tributary rivers (Sieg, Lippe, Mosel, etc.), yet hardly any sturgeons were recorded (Nemitz, 2010). Thus, all available sources point to a rather limited abundance of sturgeons in upstream fisheries, which cannot be exclusively explained by a lack of such fisheries in either the Lower, Middle, Upper or High Rhine in Germany, France, Luxemburg or Switzerland.

2.4.9 Fisheries at sea

As sturgeons spend most of their life at sea, and only migrate back into their spawning rivers at an advanced age, and for mature females only every 3-5 years (Acolas et al., 2011a; Bain, 1997), the risk of rapidly overfishing a population at sea is greater than in the river. River fisheries harvested a part of the mature spawners, but only seasonally, mostly in June when the sturgeon's spawning run peaked (Fig. 2.3). Between 1895 and 1914, freshwater fish auctions sold increasingly heavier sturgeons, and landed numbers further collapsed. In contrast, sturgeon harvests from the sea decreased in average weight during the same period. The rise in harvests from the North Sea fleet coincides with the introduction of steam engines to the fishery and the replacement of sail trawlers. Steam trawl fisheries developed in England and Scotland and expanded by the end of the 19th century. The construction of a steam trawler fleet in Britain was rapidly followed (with purchases in England) by Belgium (1884), Germany (1885), the Netherlands (1892), France (1894), and other sea faring countries (Sahrhage & Lundbeck, 2012). Compared to sail trawlers, steam trawlers towed larger gear, moved faster, fished in more distant waters, further offshore and in deeper grounds, and for longer periods (less influenced by the wind) (Engelhard, 2008). Consequently, the rise in steam trawlers impacted the marine populations year-round, targeting sturgeons of all age classes, including populations from multiple rivers debouching in the northeast Atlantic (possibly also from the Thames, Severn, Elbe, Loire-Allier, Gironde, etc.) (Demoll & Maier, 1940; Engelhard, 2008; Gessner et al., 2011b).

2.4.10 River engineering

Considering the natural distribution of sturgeon's reproductive areas in the lower courses of the river's mainstem, it is unlikely that sturgeon recruitment was fully limited by the pressure of deteriorating habitats in the tributary rivers, or upstream in the river's mainstem of the High- or Alpine Rhine in Germany, France or Switzerland. After the start of the Tulla corrections (straightening of the Rhine from 1814 onwards), undoubtedly a lot of fine-grained material was washed out in the High and Upper Rhine, possibly deposited on pebble/boulder substrate further downstream and deteriorating spawning and nursery habitat. Additionally, sand and gravel was dredged away for construction works. In the Garonne and Dordogne rivers dredging of gravel destroyed multiple historical sturgeon spawning grounds, an activity which is now banned (Williot & Castelnaud, 2011). However, even at present, and although it is partially impacted by the shipping lane, there is ample spawning habitat left in the Lower Rhine in Germany (Staas, 2017). Another anthropogenic stressor, the building of huge storm surge barriers in the Netherlands (in 1932 and 1970; (Steenhuis, 2015) affected all diadromous fish populations. Interestingly, these dams only appeared after sturgeons had already effectively vanished from the Rhine River system, which was around 1920. Moreover, at present, the river's mainstem and its broad, deep gravel beds are still partially intact and in open connection to the North Sea over a length of approximately 850 km. Therefore, habitat deterioration and loss alone cannot fully explain the sturgeon's extirpation from the Rhine. Loss of suitable spawning and nursery habitat in concert with intensified fisheries in the river and, especially, sea fisheries can.

2.4.11 Implications for sturgeon population restoration

This study provides evidence that the sturgeon's decline in NW-Europe at the end of the 19th century was impacted by reproductive habitat deterioration, industrialised fisheries in the delta, and strongly increased catches by marine steam trawl fisheries. The results from this historical study suggest that the minimum requirement to make the delta area and river Rhine suitable for sustaining a viable sturgeon population, should be for reproductive habitat restoration in the Rhine-Meuse delta in the Netherlands, and in the Lower Rhine in Germany, and not in upstream reaches or tributaries in Germany, Luxemburg, France or Switzerland. It is highly recommended to study the potential for this habitat restoration under the current conditions and anthropogenic influences, further drawing on lessons from the past.

Acknowledgements

The authors would like to thank Ria Derkx, Annemie Kersten and Joke Webbink from Wageningen University & Research – Library; Jaap Quak, Remko Verspui and Connie Kolfschoten from Sportvisserij Nederland; Herman van Dam from Gemeente Amsterdam Stadsarchief; and the libraries of Radboud University Nijmegen, the Flanders Marine Institute, and the Royal Netherlands Institute for Sea Research for their aid collecting the data; Mark van Leeuwen for his artwork; Igor Spierts and Arjan van Doorn for their comments on a first draft; Irene Verhagen and Hilda van der Pol from Wageningen University & Research's Research Data Management group for their aid in storing the data in a repository; Miranda Maybank for English language editing.

Availability of data and material: The datasets generated and analysed during the study are available in a DANS Easy repository as:

Brevé, N.W.P., Nagelkerke, L.A.J., Buijse, A.D., Van Tuijn, T., Murk, A.J., Winter, H.V., Lenders, H.J.R., 2022. Data underlying the publication: historical reconstruction of sturgeon (Acipenser spp.) spatiotemporal distribution and causes for their decline in North-Western Europe.

https://doi.org/10.17026/dans-xns-5c7c


VisAdvies

Chapter 3

Assessing potential spawning and nursery habitat availability in the river Rhine for the critically endangered European sturgeon

Part 1

Currently under review for *Aquatic Conservation:*

Brevé NWP, van Dieren DAJ, Weeber M, Mosselman E, Nagelkerke LAJ, Murk AJ & Buijse AD (2024) Assessing potential spawning and nursery habitat availability in the river Rhine for the critically endangered European sturgeon. *Aquatic Conservation.*

Photo: Release of juvenile European sturgeons tagged for acoustic telemetry in summer 2023. Source: Ernst Schrijver.

Abstract

Information about reproductive habitat and migration pathways is of paramount importance to restore migratory fish species. This study assesses the availability of spawning and nursery habitats for the European sturgeon (*Acipenser sturio*) in the delta and lower Rhine (covering over 350 river kilometres) as part of a larger feasibility assessment for a future restoration of this critically endangered species. The general approach has three steps: (1) the identification of the species' specific habitat requirements, based on a systematic literature review; (2) the collection and pre-processing of data from two countries, including the 1D and 2D modelling of water depths and flow velocities; and (3) GIS-based mapping of spawning and nursery habitat. Based on a HSI score of 1 we identify a total of 0.75 km^2 as minimal spawning habitat, potentially suitable for approximately 2,500 female European sturgeons (one spawning site would use ca. 300 m^2). This is sufficient, as currently only an estimated maximum number of 750 adults exist. Suitable spawning habitat is mainly located in the German state of North Rhine-Westphalia, while suitable nursery habitat is mainly located in the Netherlands. The availability is, however, significantly reduced by coastal infrastructure (damming) and inland navigation. The insights gained can be used to assess the current suitability of the river Rhine for the species' reintroduction and to identify opportunities for habitat restoration and protection for various life stages. The outcomes thus play an essential role in the conservation of the species. In addition, the modelling approach developed could be applied to other northwestern European rivers too. This broader application would allow inter-comparison and support decisions about which rivers are best suited for future reintroduction of the critically endangered European sturgeon.

3.1 Introduction

The European sturgeon is listed as *critically endangered* by the International Union for Conservation of Nature and natural resources (IUCN) (Gessner et al., 2022). The endangered status requires urgent action to save the species from going extinct in the wild. Possibly the river Rhine, a former stronghold of the species (Brevé et al., 2022d; Kinzelbach, 1987), may be suitable for its reintroduction as a third river basin, in addition to the basins of the Gironde estuary and the Garonne and Dordogne rivers in southern France (GGD river basin) and that of the river Elbe in Germany.

Historically, the anadromous European sturgeon (*Acipenser sturio*) occurred in all marine and large river basins of northwestern Europe (Williot et al., 2002a). Around 1850, the species' populations began to decline due to various human activities, in particular overfishing, damming, canalisation, and environmental pollution due to industrial effluent agricultural runoff and urban wastes (Debus, 1997; Holčík et al., 1989; Williot et al., 2002a). In the course of the twentieth century the European sturgeon became extirpated across its entire former range, but for one small relict population in the GGD river basin. At this site, the species naturally reproduced until 1994 (Williot & Castelnaud, 2011). The species was only saved from extinction by capturing the last individuals from the wild, which formed the basis of a programme of artificial reproduction (Williot & Castelnaud, 2011; Williot et al., 2002b).

Today, the European sturgeon still depends for its survival on *ex situ* artificial rearing and the release of offspring (stocking) in the GGD river basin (France Ministère de l'Écologie, 2020). Unfortunately, no natural reproduction has been observed in this river basin yet (status 2024) notwithstanding the *in situ* habitat restoration performed (Gessner et al., 2022). Since the 1990s, a second *ex situ* broodstock in Berlin is established for reintroduction of the species to the river Elbe (Gessner et al., 2011c), while the river Rhine is currently under consideration for a potential third reintroduction (De Nie & Ommering, 1998; Visser et al., 2020). However, before a decision can be made to translocate sturgeon offspring from the French hatchery to the Rhine, a thorough feasibility assessment is required. This, in order to prevent the potential waste of time, money, and individuals of this extremely rare species, on a potentially failing reintroduction (IUCN, 2012).

The Rhine potentially has certain advantages for restoring a population of its largest fish species. This is one of only a few large European rivers that still has an open connection between the sea and its middle and upper reaches across 850 river kilometres (Puijenbroek et al., 2019; Uehlinger et al., 2009). The Rhine has been subjected to major restoration efforts, cleaning up its historical industrial pollution (albeit not everywhere in the river bed) (Dieperink, 1998; Mostert, 2009; Van Dijk et al., 1995; Villamayor-Tomas et al., 2014). And following the objectives as set out in the European Water Framework Directive and the Habitats Directive (EEC, 1992; European Union, 2000; ICPR, 2018) the Rhine has seen a strong improvement of its water quality and ecological status. The latter is underlined by the partial recovery of several of the Rhine's migratory fish populations, such as river Lamprey (*Lampetra fluviatilis*) and Houting (*Coregonus oxyrinchus*), and there are initial signs of recovery of Allis shad (*Alosa alosa*) (Brevé et al., 2014a; Hundt et al., 2015; ICPR, 2018).

However, the Rhine also has several disadvantages for reintroducing its extinct migratory fish species. Although the Rhine's main stem is free from fish migration barriers and there is an open connection to the sea via the port of Rotterdam, a significant part of its delta in the Netherlands is obstructed by dikes and storm surge barriers that impair the fish migration routes (Bij de Vaate et al., 2003; Breukelaar et al., 2009; Brevé et al., 2019a; Brevé et al., 2013a; Verbiest et al., 2012). The Rhine is also one of the most intensively navigated rivers in the world (Mako & Galieriková, 2021; Uehlinger et al., 2009) and shipping may induce harmful water movements and mechanically damage (migratory) fish through ship propeller strikes (Brevé et al., 2019b; Spierts, 2016). As such, damming and shipping in the Rhine are still pressures of sufficient concern to include them in the feasibility assessment.

The feasibility assessment thus aims to estimate the impact of these disadvantages and if necessary design management activities to mitigate these, as is outlined in the "First Action Plan for the European sturgeon (*Acipenser sturio*) for the Lower Rhine" (Visser et al., 2020). Unfortunately, the feasibility assessment lacks vital information about the availability of the species' spawning and nursery grounds. As the Rhine's sturgeon population became already virtually extinct in the 1920s, at a time when fisheries biologists were unaware of the species' complex life-cycle, no historical information was collected of the historical spawning and nursery grounds in the Rhine (Hoek, 1910; Verhey, 1949, 1963). The present study therefore aims to address an important part of the feasibility assessment, by answering the question: Where, and how much suitable spawning and nursery habitats of the European sturgeon can be found in the river Rhine? Answering this question will support a science-based go/no-go decision for reintroduction of the species into this large, heavily modified European river.

3.2 Materials and methods

3.2.1 Study area

The study area is based on the European sturgeon's historical spatiotemporal occurrences of capture reports of sturgeons, as described in Brevé et al. (2022d). From this study it was deduced that adult sturgeon on their spawning run occurred in the Rhine from the end of April to mid-August, with a clear peak during the last week of June. Approximately 95% of the historical sturgeon catches were collected from the delta of the rivers Rhine and Meuse in the Netherlands and from the Rhine's main stem within 250 river km from the sea (Brevé et al., 2022d). So, to include most of the catches, presumably aligning the localisation of the historical spawning sites, the study area comprises the Rhine in the Netherlands and the German state of North Rhein-Westphalia (NRW), i.e. from the port of Rotterdam to Bad Honnef (a town near Bonn, see Fig. 3.1). For comparison: in the GGD river basin in southern France European sturgeon also spawned between May and August, whereby these spawning grounds were mainly located upstream of the tidal zone between river km 170 and 245. That is, for the Dordogne between Pessac and Bergerac and for the Garonne between Meilhan and Agen (Bismuth & Lauronce, 2019; Jego et al., 2002).

3.2.2 General approach

The general approach consists of three main steps: (1) a systematic literature review to identify the species' abiotic requirements for spawning and nursery; (2) the collection of data from the study area, and pre-processing of water depths and flow velocities using 1D and 2D modelling techniques; and (3) GIS-based mapping of spawning and nursery grounds for European sturgeon in the river Rhine. Noticeably, in the discussion section we evaluate the outcomes and discuss the potential negative effects of damming and shipping, as these may reduce the suitability and hamper the sturgeon migration pathways to and from the spawning and nursery habitats.

3.2.3 Step 1. Systematic literature review

The systematic literature review, used to identify key abiotic parameters for spawning and nursery of European sturgeon was conducted through the platforms of the Natural Science Collection ProQuest (https://www.proquest.com/products-services/natural_science.html) and Scopus (www.elsevier.com/solutions/scopus). The following *query string* was applied in 'advanced search' in Titles, Abstracts and Summaries (* = wildcard): ("*Acipenser sturio*" *or* "*Acipenser oxyrinchus*") *and* (egg *or* yolk *or* embryo *or* larv* *or* depth *or* discharge *or* juvenile *or* oxygen *or* O^2 *or* pH *or* nursery *or* salinity *or* spawn* *or* substrate *or* sediment *or* temperature *or* tide *or* tidal *or* turbidity *or* sediment *or* velocity *or* current). After eliminating duplicate information, scanning all abstracts and further snowballing (citation tracking), in total 142 documents (articles, book chapters, reports, theses) remained that were of interest to this study (for references, see Supporting Information, Appendix A)

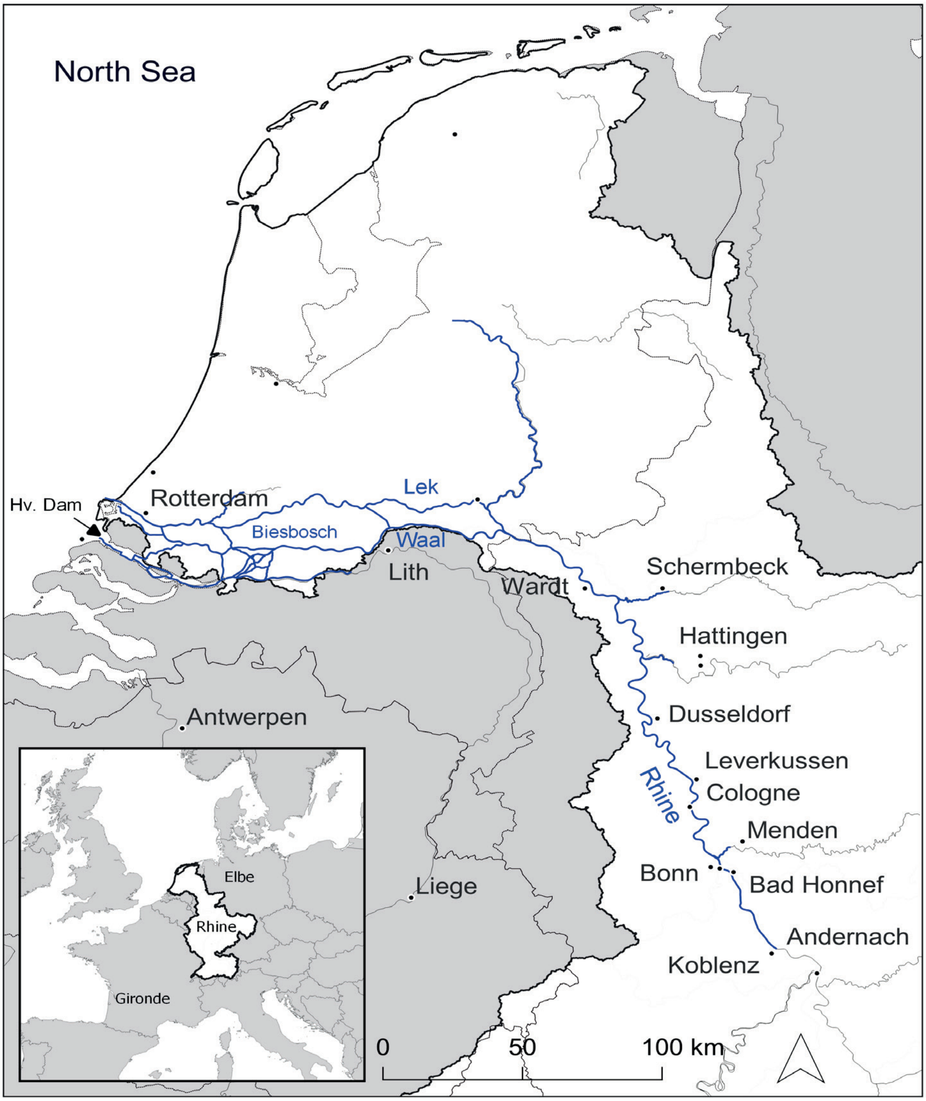


Figure 3.1. Map overview of the study area. In white: the delta and lower river part of the Rhine river basin. In blue: three combined SOBEK models (see Table 3.1), whereby modelling of the Rhine was done for the Netherlands and the German state of North Rhine-Westphalia (from the North Sea until Bad Honnef). Hv. Dam = Haringvliet Dam.

3.2.4 Step 2. Data collection and modelling (pre-processing)

Based on the systematic literature review we identified the ranges of values for key abiotic parameters for European sturgeon spawning and nursery habitats, which can be divided into: (a) parameters that hardly change during one spawning season: river morphology (digital elevation model, DEM), and substrate composition (sediment type, grain size and sorting); and (b) parameters that fluctuate on a daily basis in a highly dynamic riverine environment of the Rhine: river discharge, water depth, flow velocity, water temperature, oxygen saturation, and Ph. Most data were obtained from several Dutch and German governmental agencies (see Table 3.1). However, water depths and flow velocities were derived from a hydrodynamic model because these data are not measured on a scale with enough detail to enable the identification of potential spawning and nursery sites.

Among existing models, only 1D models covered the full study area from the port of Rotterdam in the Netherlands to Bad Honnef (near Bonn) in Germany. We therefore merged three SOBEK models into a single hydrodynamic model that covered the full study area (Fig. 3.1). SOBEK's partial models (for references see Table 3.1) simulate complex flows and water-related processes, with hydrodynamic 1D and 2D simulation and robust computational methods at any scale.

We used the resulting SOBEK model to calculate water levels along the Rhine river basin for discharges in June-August according to a dry, mean, and wet scenario: P10, P50, and P90 respectively, whereby 10, 50 and 90 are percentile occurrences. The corresponding main inflow river discharges to the SOBEK model were 23, 35, and 73 m^3/s at Hattingen; 10, 21, and 49 m^3/s at Menden; 1301, 1976, and 2499 m^3/s at Andernach; 20, 23, and 36 m^3/s at Schermbeck; and 82, 135, and 245 m^3/s at Lith (for locations see Fig. 3.1). These discharges were derived from time series for years 1964 -2020.

The 1D outputs for water levels were translated into 2D water depths by using the bed levels of a DEM that cover the area between the winter dikes (see Table 3.1, NL: RWS Baseline; De: WSV Digitales Geländemodell). The water depth d_k was calculated for each grid cell k by subtracting the local bed level z_k from the water level h at the nearest SOBEK *observation point* (river kilometre): $d_k = h - z_k$. Flow velocities were calculated for the *reaches* (trajectories) between consecutive observation points, by deriving water depths from water levels at these observation points and bed levels according to the DEM and representative SOBEK cross-sections for the reaches. So, we calculated depth for observation points and flow velocities for reaches. We divided each cross-section into 150 *bins j* (vertical strips) with equal width ΔB. Applying the Chézy (1776) equation and the definition of discharge, the flow velocity at each bin was calculated under the assumption of steady uniform flow by

Table 3.1. Data collection sources.

Data type (unit)	The Netherlands	North Rhine-Westphalia, Germany
Digital Elevation Model (DEM), 1x1 m^2 resolution grid cells derived from DEM and multibeam sonar bathymetric survey data.	RWS Baseline https://iplo.nl/thema/water/applicaties-modellen/watermanagementmodellen/baseline/	WSV; Digitales Geländemodell, 1m: https://www.opengeodata.nrw.de/produkte/geobasis/hm/dgm1_xyz/dgm1_xyz/
Sediment grain size (diameter) in D10, D50, and D90 for every 500 m, albeit with some data gaps (largest = 11 km).	RWS; Fugro (2002) https://data.4tu.nl/datasets/c6e7c1ff-44e6-46f9-9b30-e010e91a97dd	Staas (2017); BafG https://geoportal.bafg.de/ggina-portal/
Rhine water level (m above NAP)	RWS Waterinfo https://waterinfo.rws.nl/#/nav/bulkdownload	WSV https://www.pegelonline.wsv.de/gast/start
River discharge (m^3/s)		BafG https://portal.grdc.bafg.de/applications/public.html?publicuser=PublicUser#dataDownload/Stations
Water temperature (°C), O^2 saturation (%), pH		LANUV https://www.opengeodata.nrw.de/produkte/umwelt_klima/wasser/oberflaechengewaesser/gues/
SOBEK models	Deltares, reference websites for the models: *sobek-rmm-vzm-j15_5-v4 (Rhine-Meuse Estuary, https://iplo.nl/thema/water/applicaties-modellen/modelschematisaties/zuidwestelijke-delta/), sobek-rijn-j22_6-v1a1_rwsos (NL Rhine branches), and sobek-rijn-j17_5-v2-rwsos_merge (DE Rhine to Andernach): https://iplo.nl/thema/water/applicaties-modellen/modelschematisaties/rivieren/* sobek-rijn-j22_6-v1a1_rwsos (NL Rhine branches), and sobek-rijn-j17_5-v2-rwsos_merge (DE Rhine to Andernach).	
Water depths (m) and Flow velocities (m/s)	Obtained from hydrodynamic modelling, using SOBEK.	

Data sources: For the Netherlands: Rijkswaterstaat, the executive agency of the Ministry for Infrastructure and Water Management (RWS) and Deltares. For the German state of North Rhine-Westphalia: the Bundesanstalt für Gewässerkunde (BafG), Wasserstraßen und Schifffahrtsverwaltung des Bundes (WSV), Das Landesamt für Natur, Umwelt und Verbraucherschutz (LANUV), Wasser- und Schifffahrtsamt Duisburg-Rhein (WSA), and Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen (LANUV).

$$u_j = \frac{Q}{\Delta B}\frac{d_j^{1/2}}{\left(d_1^{3/2} + d_2^{3/2} + .. + d_{150}^{3/2}\right)}$$

where Q denotes the total discharge through a cross-section. We compared initial results with those from a 2D hydrodynamic model of the Dutch Rhine branches (dflowfm2d-rijn-j22_6-v1a; (Kosters, 2022)) for a 10 km long test area. This revealed that the 1D results *overestimated* flow velocities in shallow areas (< 4 m) and *underestimated* flow velocities in deep areas (> 4m). We used this to introduce a depth-dependent correction factor in our method. Furthermore, the formula *overestimated* flow velocities in deep areas outside the main channel, such as lakes and harbours, where virtually no water flows in the months June-August (dry summer months). Grid sells in such areas were therefore set to a low flow velocity of 0.1 m/s.

Sediment grain size was superimposed on the DEM grid based on observational data. We used sediment grain size data (grain diameter, see Table 3.2) from measurements to determine the minimum, medium and maximum D_{50} grain size. For the Netherlands these grain sizes are available for every kilometre, on the left, in the centre and on the right side of river. For Germany only one set of grain sizes is available per cross-section, every 500 m with gaps up to a river stretch of 11 km. Data on sediment grain size were not measured in the estuary of the Rhine and Meuse rivers in the Netherlands, but were assumed to be approximately 1 mm based on Fugro (2002).

3.2.5 Step 3. GIS-based mapping of spawning and nursery habitats

Using the Habitat Evaluation Procedure (HEP) (U.S. Fish and Wildlife Service, 1980) we mapped the Habitat Suitability Index (HSI) and the limiting variables for spawning and nursery areas for European sturgeon (HSI maps). These HSI maps were created by confronting the derived species' criteria (see Table 3.2) with the modelled values of water depth, flow velocity and sediment grain size (sedmax, sedmed, sedmin) for the Rhine, for three scenarios (P10, P50, P90). We then estimated the total sum of suitable spawning and nursery sites for the river Rhine in km^2 for these criteria and scenarios (see Table 3.3).

For this method, we chose to apply pre-determined suitability categories and based the suitability value on the minimum value methodology (Zhang et al., 2016), resulting in a hard cut-off between classes instead of a gradual fuzzy logic approach. We used D-Eco Impact (Weeber et al., 2024), to map spawning and nursery areas within the study area, based on the modelled values of parameters water depth, flow velocity and sediment grain size.

The results of the modelled values in addition to the suitability mapping exercise were presented in QGIS (version 3.28.2).

Table 3.2. Parameter-setting for GIS-mapping of spawning and nursery habitat for European sturgeon (*Acipenser sturio*). This is a summary of data from the literature review. For the full dataset see Supp. Info. App. A.

Habitat		**Spawning and hatching**	**Nursery**
Life-stage		**Fertilized-eggs & Yolk-sac larvae**	**Larvae (< 50 mm) & juveniles 0^+ (< 300 mm)**
Location in river basin		River main stem, mainly within 250 river km.	River main stem, lower reaches, and estuary.
Main season		June - August	June - March
Total length		Yolk-sac larvae ca. 15 mm.	15-300 mm.
Age		Hatching after 3-7 days.	0-11 months old.
Parameter	**Classification (category)**	**Parameter-setting for modelling**	
Water depth	0 - 2 m (shallow)	0.25	0.75
	2 - 4 m (moderately deep)	1	1
	4 - 6 m (deep)	0.75	1
	> 6 m (very deep)	0.5	0.75
Flow velocity	0 - 0.5 m/s	0.5	1
	0.5 - 1.0 m/s	1	0.5
	1.0 - 1.5 m/s	0.75	0.25
	1.5 - 2.0 m/s	0.5	0
	> 2.0 m/s	0	0
Grain Ø (substrate composition in ASTM grid D50) Eggs will not be deposited in sediment-rich areas.	< 0.075 mm (silt and mud)	0	1
	0.075 - 2 mm (sand)	0	0.75
	2 - 16 mm (gravel fine)	0	0.25
	16 - 31.5 mm (gravel medium)	1	0
	> 31.5 mm (gravel and large rock)	0.75	0
Water temperature Embryonic survival peaks at 20 °C. Larvae upper tolerance limit is between 26 and 30 °C, and lower tolerance limit < 12 °C.	< 15°C	0	0.5
	15 - 17°C	0.25	0.75
	17 - 19°C	0.75	1
	19 - 21°C	1	1
	21 - 23°C	0.5	0.5
	> 23°C	0.25	0
O^2 saturation Oxygen depletion induces sublethal effects at 70% O2 sat.n and lethal effects at 50% O2 sat.	< 50%	0	0
	50 - 70%	0	0.5
	70 - 90%	0.5	0.75
	> 90%	1	1
pH Minimum 5.5 Median 7.6 Maximum 8.7	< 5	0	0
	5 - 6	0	0
	6 - 7	0.5	0.5
	7 - 8	1	1
	8 - 9	0.5	0.5
	> 9	0	0

3.3 Results

3.3.1 Abiotic parameters that identify spawning and nursery habitats

The literature study was used to specify the ranges (i.e. minimum, optimum, and maximum values) of key habitat abiotic parameters that identify spawning and nursery habitats for the European sturgeon (see Supplementary Information Appendix A). The HSI parameter-setting for modelling is scaled along a simple gradient ranging from unsuitable to suitable, with values 0, 0.25, 0.50, and 1 (Table 3.2) estimated based on the literature review. Consequently, in our HSI modelling the suitable reproductive habitats are limited by parameter values lower than 1 (Fig. 3.2).

3.3.3. Mapping spawning and nursery habitats, using HSI scores

GIS-based mapping using HSI scores revealed that the main suitable spawning and nursery sites in the Rhine are roughly divided over the two countries: spawning in NRW-Germany and nursery in the Dutch Delta. Examples can be seen in Fig. 3.2, where the top and bottom panels show spawning and nursery areas respectively, and the left and right panels show suitable and unsuitable areas respectively. The currently suitable *spawning* sites in the Rhine are mainly located in NRW-Germany because of the high scores (>0.75) for water depth, flow velocity and grain diameter. Unsuitable spawning sites in this area are limited by water depth (too shallow), flow velocity (too low), and partially grain size (too fine). The currently suitable *nursery* sites are mainly located in the Netherlands. In NRW-Germany the availability of suitable nursery sites is mainly limited by flow velocity (too high). For the Dutch Delta, the suitability of spawning habitat is mainly limited by grain size (too fine), while some limitations are caused by combined qualities of flow velocity, water depth, and grain size. Notably, an HSI score of 1 for nursery sites was never obtained because the average and minimum of grain size do not reach the required P50 minimum value of 0.075 mm (Table 3.2).

Table 3.3. Available area (in km2) of potentially suitable habitat for spawning and nursery of European sturgeon (Acipenser sturio) in the river Rhine. The data are obtained through modelling of the ranges of water depth, flow velocity, sediment grain size, and overall (combined). See Table 3.2 for the parameter settings. HSI scenario's use water level (P10, P50, and P90) and sediment grain size. Notably, we use sedmed and sedmax for spawning sites as mature European sturgeons prefer coarse substrates; and sedmed and sedmin for nursery sites as juvenile European sturgeons prefer finer grain sizes. Colour indications range from red to green and indicate the quality from unsuitable to suitable.

		Parameter	**Water depth**					**Water velocity**					**Sediment (grain size)**					**Overall**				
		Setting	**0**	**0,25**	**0,5**	**0,75**	**1**	**0**	**0,25**	**0,5**	**0,75**	**1**	**0**	**0,25**	**0,5**	**0,75**	**1**	**0**	**0,25**	**0,5**	**0,75**	**1**
Habitat use	**Sediment type**	**HSI**																				
spawning	**sedmed**	**P10**	0	110	146	124	118	2	0	405	36	55	433	0	0	15	50	436	12	38	12	0,69
		P50	0	110	163	143	96	8	0	417	34	53	446	0	0	16	51	453	9	43	5	0,75
		P90	0	110	194	123	95	26	0	399	35	62	452	0	0	17	53	476	9	30	5	0,96
	sedmax	**P10**	0	110	146	124	118	2	0	405	36	55	415	0	0	55	28	418	15	45	20	0,81
		P50	0	110	163	143	96	8	0	417	34	53	427	0	0	58	28	435	12	55	9	0,76
		P90	0	110	194	123	95	26	0	399	35	62	432	0	0	61	29	459	11	43	8	0,76
nursery	**sedmed**	**P10**	0	0	0	254	239	35	35	55	0	367	63	74	0	355	0,05	67	77	42	305	0
		P50	0	0	0	273	239	52	34	53	0	373	67	80	0	365	0,05	77	85	43	307	0
		P90	0	0	0	304	218	61	35	62	0	364	71	83	0	368	0,05	86	86	52	297	0
	sedmin	**P10**	0	0	0	254	239	35	35	55	0	367	24	103	0	365	1,31	45	90	45	311	0,72
		P50	0	0	0	273	239	52	34	53	0	373	26	109	0	376	1,32	61	91	45	314	0,72
		P90	0	0	0	304	218	61	35	62	0	364	27	114	0	380	1,32	70	93	55	303	0,72

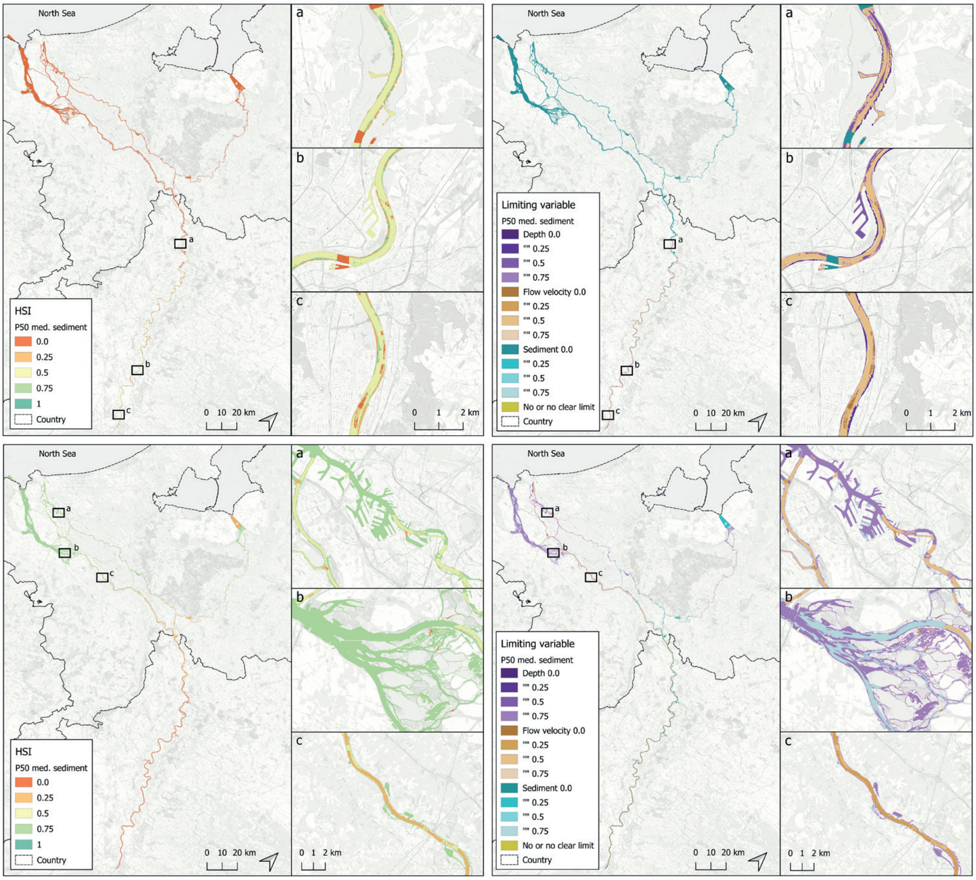


Figure 3.2. Potential areas in the river Rhine for European sturgeon *spawning* (top) and *nursery* (bottom), obtained through GIS-based mapping. Inlay maps (a, b and c) show examples in more detail. Names are those of towns (e.g. Wardt and Bonn; for locations also see Fig. 3.1). Left and right panels show sites that are either *suitable* (habitat suitability index determined for scenario P50, medium sediment suitability) and *unsuitable* (limiting variables), respectively. top: a = Wardt (effect of sediment cut-off), b = Cologne (highly suitable), c = Bonn (effect of modelling / changes in flow velocity through calibration). bottom: a = the port of Rotterdam (suitable, however sediments are not fine enough), b = Biesbosch freshwater delta (idem as a), c = the river branch Waal.

3.3.4 Availability of spawning and nursery habitat for European sturgeon in the Rhine

Based on a HSI overall score of 1 and sedmed P50, the Rhine comprises 0.75 km^2 habitat suitable for spawning and 0 km^2 suitable for nursery. The latter is because of the strict limitations set for sediment grain size (< 0.075 mm, see Table 3.2). As a result, hardly any location in the Rhine scored an overall HSI of 1 for spawning, and none for nursery (see Table 3). The choice of the parameter values are based on the systematic literature review and possibly our settings were too strict. It cannot be excluded, however, that currently no suitable nursery habitat is available anymore. When for the HSI an overall score of 0.75 and sedmed P50 are accepted, the Rhine provides 5.75 km^2 (5 + 0.75) for spawning (mainly located in NRW Germany) and 307 km^2 (307 + 0) as nursery habitat area (mainly located in the Netherlands) (see Table 3.3, indicated with the two black frames).

So, how many female European sturgeons could probably spawn in the Rhine? According to Gessner and Bartel (2000), the carrying capacity of European sturgeon spawning grounds can be estimated based on the density of incubation (Derzhavin, 1947). With an average fertility of one million eggs and an optimum density of 1,000-3,500 eggs/m^2, the average spawning site size for one female would be approximately 300 m^2 (Jakob, 1996). Therefore, 0.75 km^2 of suitable spawning sites would provide 2.500 female European sturgeons with suitable spawning habitat (see Table 3.4).

Table 3.4. Number of female European sturgeons that could theoretically be provided with suitable spawning habitat based on a 300 m^2 requirement. This is based on presence of area with certain characteristics, no other limiting factors were taken into account. HSI 0 = unsuitable, HSI 1 = optimal.

Habitat use	Sediment type	HSI	>=0.25	>=0.5	>=0.75	1
Spawning	sedmed	P10	208,967	168,967	42,300	2,300
		P50	1925,00	162,500	19,167	2,500
		P90	149,867	119,867	19,867	3,200
	sedmax	P10	269,367	219,367	69,367	2,700
		P50	255,867	215,867	32,533	2,533
		P90	212,500	175,833	32,500	2,500

3.4 Discussion

3.4.1 Limitations in underlying data availability

As the European sturgeon has been extinct in the Rhine since 1953 (Verhey, 1963), our assessment had to be based upon (historical) literature information and our modelling cannot be validated. Part of the required data was lacking for the study area and no 2D model is available for the North Rhine-Westphalia Rhine basin in Germany. The spawning and nursery habitat requirements had to be estimated from a limited set of parameters as compiled from the systematic literature review. We have shown that the Rhine comprises sufficient habitat for approximately 2,500 to 19,000 female European sturgeons to spawn, depending on a HSI of 1.0 or 0.75 respectively. This would be sufficient for the estimated maximum of 750 (sub)adult European sturgeons alive in the wild (Gessner et al., 2022). However, it is important to consider the potential negative effects of climate change, consequences of inland navigation on physical habitat quality and safe migration, as well as adverse impacts on migration from coastal flood protection infrastructure. The latter would imply an overestimation in the modelling, but there is also the possibility of an underestimation.

3.4.2 Underestimation in the modelling

The use of average parameter values and hard cut-off values for parameter settings (Table 3.2) may *underestimate* habitat suitability. European sturgeon is naturally capable of coping with a variety of environmental conditions during migrations up – and downstream (Staaks et al., 1999). Furthermore, the real spatial variation in flow velocities is larger than the values from the 1D model in the GIS maps. The water depths in the model are approximately 20 cm larger than the measured values due to the conversion from a 1D to a 2D model. This could be improved by calculating more observation points in the SOBEK model through linear interpolation between existing observation points. Finally, sturgeons might seek out suitable spawning sites further upstream river, in case there isn't enough to be found in the Lower Rhine.

3.4.3 Overestimation in the modelling

In contrast, our neglect of the effects of temperature, oxygen saturation, pH and the physical influence of damming and shipping might have led to *overestimating* habitat suitability. Adult European sturgeons are late-spring and summer spawners (main season: May-August). They can cope with various microclimates during their migrations (Staaks et al., 1999) and are tolerant to oxygen deficiencies (Holčík, 1989). The youngest life stages of fertilized eggs and yolk sac larvae, however, are sensitive to aberrant temperatures and O_2 saturation, and to a lesser extent to variations in pH (Delage et al., 2014; Delage et al., 2019; Delage et al., 2015). Embryonic survival is highest at a temperature of 20 °C with a range of 17-22 °C, which currently still is the normal temperature range in the river Rhine during summer months. The upper tolerance limit is between 26 and 30 °C (Delage et al., 2019). Due to anthropogenic thermal effluents and climate change, the measured summer water temperature at Koblenz increased by over 2 °C between 1978 and 2011 and the number of days per year with water temperatures above 22 °C increased as well (ICPR, 2013). Future projections diverge (Lassalle et al., 2010; Lassalle & Rochard, 2009); Hardenbicker et al. (2017). The decommissioning of German nuclear power plant units has recently reduced the thermal effluents (ICPR, 2013; Zavarsky & Duester, 2020). Oxygen levels below 6 mg/L are harmful for embryo's (references in van Winden et al. (2000)(also see Supporting Information, Appendix A), whilst pH levels are optimal between a pH of 7 to 7.8 and should not go below 5.5 or above 8.7 (Delage et al., 2019; Williot et al., 2009b). Thanks to improved water quality, the Rhine's O_2 levels were already at safe levels in 2009 at approximately 9-10 mg/L (Uehlinger et al., 2009). The mean annual pH (1995–2004) varied between 7.9 and 8.3, and decreases downstream (Uehlinger et al., 2009). Therefore, water temperature, oxygen saturation and pH in the Rhine do not seem to pose an issue to European sturgeon reintroduction.

The Rhine is one of the most intensively navigated rivers in the world (Mako & Galieriková, 2021). The adult European sturgeons preferably swim in the deep and fast flowing river sections and may use the river's scour holes as resting and hiding places during their spawning migration (see Appendix A, Supporting Information). They have to swim occasionally to the surface to inflate their swim bladder, which makes this species vulnerable to collisions with passing vessels or ship propeller strikes (Spierts, 2016). This could become aggravated when summer river levels decrease due to climate change. Moreover, river bed erosion, and continuous dredging and nourishment (augmentation) of bed sediment within the river's deepest parts to maintain the shipping lane (Frings, 2015) is known to reduce the availability and quality of spawning and nursery sites for the Atlantic sturgeon (*A. oxyrinchus*), sister species of European sturgeon (Balazik et al., 2020; Barber, 2017; Nellis et al., 2007). In the Rhine main river stem, especially between the towns of Nijmegen and Cologne, shipping intensity portrays an almost permanent disturbance (Staas, 2017; Van de Ven, 2021). Passing ships create waves and water displacement which may affect egg and yolk-sac larvae survival at the spawning sites (Gabel et al., 2017; Spierts, 2016). If turbulence, water displacement, ship propeller strikes, and waves are harmful, they could seriously impair the quality of the Rhine for the European sturgeon's youngest life phase.

The main stem of the Rhine is open between the port of Rotterdam and the first hydropower plant at Iffezheim at river km 334, but the Haringvliet Dam between the North Sea and the historical estuary of the rivers Rhine and Meuse (see Fig. 3.1) forms a major barrier to fish migration (Bij de Vaate et al., 2003; Bij de Vaate et al., 2001; Breukelaar, 2017; Brevé et al., 2019a; Brevé et al., 2019b). The dam is open for high river discharges to the sea. It was envisaged to enable fish migration through a small opening at low river discharges too, but this has remained limited or absent to prevent salinization of the freshwater reservoir (Noordhuis, 2017). This hampers safe and accessible migration to and from habitats. European sturgeon on their downstream migration avoided the Haringvliet route altogether and migrated towards the North Sea via the port of Rotterdam that carries much more river discharge (Brevé et al., 2019b). This limits the possible migration routes. The present study shows that damming of the former estuary of the rivers Rhine and Meuse also resulted in unsuitable nursery habitat.

3.4.4 Opportunities to increase habitat suitability and further research

This study has identified the availability and quality of spawning and nursery habitats for sturgeons in the Rhine. The results could also provide advice on opportunities for active habitat restoration and protection from the harmful effects of inland navigation and coastal infrastructure (damming). One of the most promising adjustments would be to split the main single channel into two parallel channels as has been done in the Room for the River pilot 'longitudinal training dam'. Over a stretch of 10 km such dams significantly reduce the impact of passing ships (Collas et al., 2018). Also side channels without navigation could fulfil such roles when they are sufficiently large. Other options for passing key spawning habitats could be a reduced speed and lower rates per minute for reducing harmful water displacements and the chance of ship propeller strikes. But the efficacy is unknown and thus quite uncertain. Sheltering and resting places such as scour holes near spawning areas could be spared from sediment fills. For the Haringvliet sluices only a change in management towards using them as a storm surge barrier allowing a permanent estuarine gradient with a reinstatement of the tidal amplitude is expected to restore the suitable habitat conditions. This would have such drastic consequences for the freshwater supply in the region that it is not considered to be a realistic scenario in the near future. Given the extreme endangered status and rareness of the European sturgeon and availability of its offspring we recommend to carefully monitor the effects using small cohorts and telemetry. The results can be used to validate and improve the assessment model we developed, and fine-tune the parameter values.

3.4.5 Implications for conservation

The insights from the current study on spawning and nursery habitat requirements of the European sturgeon can be used to assess the current suitability of the river Rhine for the species' reintroduction and to identify opportunities for habitat restoration and protection for various life stages. The outcomes thus play an essential role in the conservation of the species. In addition, the modelling approach developed to map spawning and nursery habitats for the Rhine could be applied to other northwestern European rivers too. This broader application would allow inter-comparison and support decisions about which rivers are best suited for future reintroductions of the critically endangered European sturgeon.

Acknowledgments

We gratefully acknowledge the constructive input from many organisations and colleagues, for delivery of their data collection from the Rhine-Meuse delta in the Netherlands and the Niederrhein in Germany. We thank Stefan Staas and Mark Groen for their reports on spawning and nursery habitat suitability for European sturgeon. We thank Julia Bleser, Willem Ottevanger, Anna Koster and Victor Chavarrias (Deltares) for modelling support and collecting data for the Rhine from different Dutch and German sources, Martin Brinkmann (LANUV) for supplying data on water levels, Nils Holman (Wasser- und Schifffahrtsverwaltung des Bundes, WSV) for supplying data on water depth, and Dr. Schumacher (Bundesanstalt für Gewässerkunde, BfG) for supplying sediment data. We are grateful to Marie-Laure Acolas, Jörn Gessner, Eric Rochard and Vanessa Lauronce for their verification of ranges in abiotic variables of *A. sturio* spawning and nursery sites. We thank Peter Tamas for his course on systematic review, and the Library of Wageningen University and Research for their help in collecting literature.

Data availability

The data that support the findings of this study are available online, see Table 3.1 for URL's.

Funding

This study has been co-financed by the MERLIN project (EU Horizon 2020 grant agreement No 101036337).

Supplementary material

Supplementary material associated with this article can be found in the online version at *URL will be made available after publication*: Appendix A: systematic review on reproductive habitat for the European sturgeon. Appendix B: (Hydrodynamic) translation and Deriving the Habitat Suitability Index.

Chapter 4

Fishers' willingness to report incidental bycatches of endangered, threatened and protected fish species: The case of European sturgeon in the Northeast Atlantic Ocean

Part 2

Published as:

Brevé, N. W., Urbanovych, K., Murk, A. J., van Zwieten, P. A., Nagelkerke, L. A., & Kraan, M. (2024). Fishers' willingness to report incidental bycatches of endangered, threatened and protected fish species: The case of European sturgeon in the Northeast Atlantic Ocean. Marine Policy, 162, 106056.

https://doi.org/10.1016/j.marpol.2024.106056

Photo: Aboard HD 36, sturgeon of 134 cm (caught and released) in the North Sea, 60 miles west from Sylt, in 2019. Source: skipper Mick Zijlstra, mariner Bob Slot.

Abstract

Incidental fisheries bycatch contributes to the dire situation of endangered, threatened and protected (ETP) species. Few published estimates of the severity of fisheries impacts exist as incidental bycatch is difficult to monitor, and reporting can be a sensitive matter for fishers. This paper addresses these sensitivities, the reasons for non-reporting, and possible solutions, using bycatch of the critically endangered European sturgeon (*Acipenser sturio* L.) in the Northeast Atlantic fisheries as a case study. This study comprises 36 interviews with fishers, fisher representatives, environmental non-governmental organizations (NGOs), researchers, and governments involved in European sturgeon conservation from four countries: France, Germany, the Netherlands, and the United Kingdom. Fishers experience difficult economic circumstances, while fear of restrictions in their fishing area and gear makes them reluctant to report such rare bycatch. Adequate management of the European sturgeon and other marine ETP species is worsened by a lack of governmental coordination, and trust issues fuelled by some NGOs' communication strategies using iconic species to lobby for fishing restrictions. This paper discusses solutions to strengthen fishers' cooperation in ETP species research. This would need to include developing a shared vision, clear role separation between stakeholders, communication and trust building.

Fishers' willingness to report incidental bycatches of endangered, threatened and protected fish species: the case of European sturgeon in the Northeast Atlantic Ocean

Niels Brevé*, Kateryna Urbanovych, Tinka Murk, Paul van Zwieten, Leopold Nagelkerke & Marloes Kraan

Highlights

- Fishers' reporting of bycatches are crucial for management of ETP species.
- Fishers fear that bycatch reports of ETP fish species will be used against them.
- All core aspects for fishers' cooperation for bycatch reporting are hampered.
- European sturgeon conservation activities are driven by NGOs and scientists.
- More involvement of governmental bodies would strengthen the action plans.

4.1 Introduction

Incidental fisheries bycatches and associated post-release mortality contribute to the dire situation of endangered, threatened and protected (ETP) species. The magnitude of the impact of incidental bycatch and associated mortality is however, unclear as few estimates are reported. This is partly due to the inherently rare nature of ETP species interactions with fisheries, and because incidental bycatch reports rely largely on voluntary action of fishers, as it is difficult to design observer programs to effectively monitor (extremely) rare ETP species bycatch (Babcock et al., 2003). As a consequence, inaccuracies in bycatch recordings cause uncertainty in population assessments (Babcock et al., 2003; Gray & Kennelly, 2018). If fishers decide to report incidental ETP species bycatches, this will help us to gain insights into the spatiotemporal distributions and the localisation of key habitats of ETP fish species (e.g. spawning, nursery, foraging, and wintering grounds), and strengthen the design, implementation and monitoring of best-practice measures (Lutchman, 2014). Improving fishers' participation in reporting incidental, rare marine bycatches is therefore of paramount importance for (monitoring) the conservation of ETP species populations.

One ETP species of which the population assessment at sea largely depends on voluntary bycatch reports is the anadromous European sturgeon (*Acipenser sturio* L., 1758). Today, IUCN lists the European sturgeon as critically endangered (facing a high risk of extinction), and it is protected under the legal systems of the Bern Convention, the Bonn Convention, the OSPAR Convention, the Rhine Convention, and the EU Habitats Directive (Bastmeijer, 2019; Williot & Castelnaud, 2011). This makes European sturgeon currently one of the most endangered, threatened, and protected fish species in Northwest Europe (Bastmeijer, 2019).

Historically, the 'common sturgeon' occurred in all Northwest European marine systems and major river basins (Williot & Castelnaud, 2011). Around 1850, the species' was still widespread, but 150 years later, the species had almost entirely vanished due to overfishing and degradation and loss of spawning grounds in the natal rivers (Acolas et al., 2011a; Brevé et al., 2022d; Lenders, 2017). In the 1990s, only one relict population survived in the watersheds of the Garonne and Dordogne rivers and the Gironde estuary (Gironde river basin from now on) in southern France. From this basin, approximately 50 European sturgeon individuals were captured and raised to build two *ex situ* brood stocks to save the species from extinction: one in France and one in Germany (Williot et al., 2007). Artificial reproduction of European sturgeons was challenging (Williot et al., 2007); it succeeded once in 1995, and later between 2007 and 2015, and again in 2022. In total 1.7 million larvae and juveniles were released in the Gironde river basin and 20,000 in the Elbe river system (Chèvre et al., 2019; Jatteau, 2015), while a total of 161 individual juveniles were experimentally released in the Rhine river system (Brevé et al., 2019b). As a result, currently, European sturgeon occur in nearshore areas and form marine aggregations near the mouths of river systems (Charbonnel & Acolas, 2022). Even though the numbers of fish released may seem high, the species' survival rate during the first year of life is naturally low (Acolas et al., 2011a). Although the stocked European sturgeon individuals are nearing maturity, no natural spawning has been observed yet. In fact, the last observed natural reproduction was reported in 1994 (OSPAR Commission, 2021; Williot et al., 2002b).

As any additional mortality due to anthropogenic stressors will greatly impact the species' chances of recovery these should be reduced as much as possible (OSPAR Commission, 2021). Therefore, even the rare, incidental bycatch, as currently reported for the different fisheries along the Northeast Atlantic coast (Fig. 3.1), may already further reduce the number of subadult specimens (Gessner et al., 2010c; OSPAR Commission, 2009, 2021). European sturgeons live at sea for the greatest part of their life (Acolas et al., 2011a), but monitoring the sturgeon population's development at sea is challenging, given the large extent of the species' home range and the low catch rate (Charbonnel & Acolas, 2022; Charbonnel et al., 2022). Although migration patterns of European sturgeon juveniles in rivers and estuaries have been studied using biotelemetry techniques (Abecasis et al., 2018; Acolas et al., 2017; Brevé et al., 2019b), these techniques have not yet been used to study the species' movements in the marine environment. This is largely due to the required investments in time, money and effort related to such techniques, and to the extremely limited availability of (sub)adult individuals of this critically endangered species (Gessner et al., 2022). Therefore, systematic incidental bycatch reporting by fisheries (including any mark-recaptures) would greatly contribute to obtaining accurate knowledge about the developments of the population of European sturgeon.

Since the 1950s, fisheries across the Northeast Atlantic have provided data showing declining numbers of European sturgeon populations (Castelnaud et al., 1991b; Letaconnoux, 1961; Rochard et al., 1997b). Fishers continued to declare (part of) their bycatch between 2007 and 2020 (Charbonnel & Acolas, 2022), which demonstrated that the French-German stocking efforts resulted in more sturgeon occurrences at sea (France Ministère de l'Écologie, 2020). However, reporting suddenly stopped in 2020, in particular in France and the Netherlands. Officers from the Centre pour l'Aquaculture, la Pêche et l'Environnement de Nouvelle-Aquitaine (CAPENA), who represent the fishers from the Gironde estuary were consulted, and confirmed that fishers indeed refrained from reporting. In addition, the Dutch environmental NGO ARK Nature reported that they had not received any sturgeon bycatch reports since 2020, and now experienced a reluctance in reporting from fishers.

Reporting European sturgeon bycatch clearly has become a sensitive topic, while it previously was much less of an issue, in particular with French fishers who have a long record of reporting their sturgeon bycatch (Castelnaud, 1988). As this reluctance of reporting negatively affects the international conservation and restoration efforts, the current study aims to understand the reasons for this, by inquiring about the perceptions of fishers and other stakeholders on the need and consequences of bycatch reporting. The main questions are: what has caused fishers to stop reporting sturgeon bycatch, and what is needed to restore their willingness to report again? European sturgeon is one of the longest studied ETP species in the northeast Atlantic, is highly migratory, and highly vulnerable to overfishing. This case study therefore exemplifies many of the problems and challenges in ETP species conservation management and provides a basis for reflection on a better understanding of bycatch reporting in conservation efforts for marine ETP species in general (Gerring, 2004; Leedy & Ormrod, 2005).

4.2 Materials and methods

4.2.1 Study area

The case study area covers the current distribution area of European sturgeon. Sturgeon were reported from the Gironde river basin and along the coastal regions of the Bay of Biscay, the English Channel, and the southern North Sea, including the marine territories of France, Belgium, and the Netherlands, and to a lesser extent those of the United Kingdom, Germany, and Denmark (Fig. 4.1).

4.2.2 General approach

This study used semi-structured interviews (Barriball & While, 1994) to assess what drives or hinders fishers from reporting sturgeon bycatch (and other marine ETP species), and investigates the complexity of interpretations, values, attitudes, and insights of sturgeon conservation among all stakeholders, i.e. fishers, fisher representatives, researchers, governments and environmental non-governmental organisations (NGOs).

4.2.3 Research population

The research population for this study was selected from the four countries (FR, NL, DE, UK) in two steps. **Step 1** listed all fishers that had reported European sturgeon bycatches in previous years. From that group the author team identified fisheries métiers that were prone to catching sturgeon based on target species, gear, area fished, and seasonality (Ulrich et al., 2012). As the European sturgeon belongs to the same clade as the very similar, Atlantic sturgeon (*Acipenser oxyrinchus* Mitchill, 1815) (Peng et al., 2007), which is regularly caught in bottom trawl and gill-net fisheries (Beardsall et al., 2013), we focussed on this fishing gear(Charbonnel & Acolas, 2022).

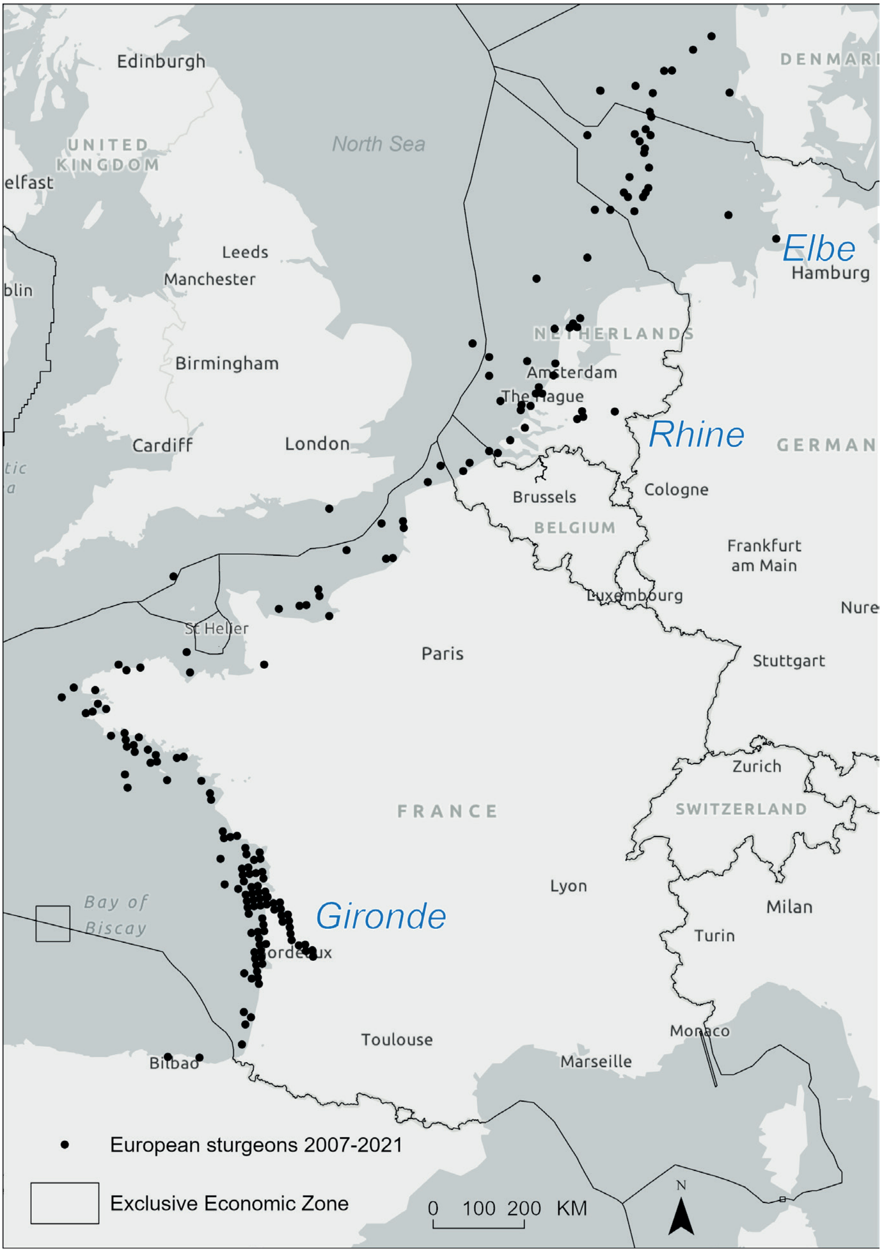


Figure 4.1. Study area. Black dots indicate the distribution of European sturgeon bycatch, reported between 2007 and 2021. European sturgeon have been stocked in the Gironde (1.7 million), Elbe (20,000) and Rhine (161 individuals) river basins, and this maps shows that the sturgeon mainly occurred in the Gironde estuary and along the coasts of the Bay of Biscay, English Channel and North Sea. Dotted lines indicate the Exclusive Economic Zones (EEZ). The interviewed Dutch fishers mainly fished the North Sea and English Channel, while interviewed French fishers mainly fished the Bay of Biscay and the Gironde estuary. Data was collected by the institutes of INRAE, CAPENA, IGB and ARK Nature, and collated to make this figure.

We further concentrated the research on France and the Netherlands, because data on sturgeon bycatch mainly originated from within their Exclusive Economic Zones (EEZ) (Fig. 4.1), and it is within these countries that the sudden drop in reports occurred. Fishers involved in reporting were mainly French and Dutch. The French fishing in the Bay of Biscay using various types of trawl gear, and the Gironde estuary seasonally targeting meagre (*Argyrosomus regius*, Sciaenidae) using drift nets (gill-nets) (Rochard et al., 1997b; Williot & Kirschbaum, 2011). The Dutch, fishing the southern North Sea and English Channel, i.e. fishers who predominantly employ various types of beam trawl gear (Schadeberg et al., 2021). CAPENAS' officers assisted in the interviews with French fishers, because this topic was very sensitive and finding willing fishers to be interviewed was difficult. In the Netherlands, the snowball sampling technique (Atkinson & Flint, 2001) was used, whereby recommendations were given from interviewed fishers to find new fishers. This clearly aided to acquisition of access to most interviewees. An article was posted in the digital newsletter of the Nederlandse Vissersbond in June 2022, through the help of a fishers' representative, but this did not yield any responses. Fishers organisations interviewed were CAPENA, the National Maritime Fisheries Committee (CNPMEM), the Nederlandse Vissersbond (NVB), Eendracht Maakt Kracht (EMK), the Institute of Fisheries Management (IFM), the Marine Management Organization (MMO), and the Royal Society of Fish (RSF).

Step 2 identified the different stakeholder groups, involved in sturgeon conservation in each country (FR, NL, DE, UK). Involved NGOs were the Défense des Milieux Aquatiques (DMA), ARK Nature, and the Blue Marine Foundation (BMF). Involved research institutes were the National Research Institute for Agriculture, Food and the Environment (INRAE), Wageningen Marine Research (WMR), and the Leibniz Institute for Freshwater Ecology and Inland Fisheries (in German: IGB). Involved government departments were the French DREAL Nouvelle-Aquitaine (régional Directory of de l'État relevant des Ministères de la Transition écologique et de la Cohésion des territoires et de la Transition énergétique), and the Dutch Ministry of Agriculture, Nature and Food Quality.

4.2.4 Interview guide, interviews and saturation

To ensure consistency whilst working with multiple interviewers, all interviews were based on an interview guide, which touched on four themes: (1) sturgeon captures (if any); (2) pros and cons of reporting rare marine fish bycatches; (3) interactions between stakeholder groups; and (4) awareness and criticism of the sturgeon programme. The guide was tested during two interviews and subsequently translated, resulting in English, French, Dutch, and German versions (see Supplementary material A for the English version). Before the interview, each interviewee was informed of the purpose, method and intended use of the interview, and was asked to give consent through either a confirmation e-mail or a signed consent form (Supplementary material B). Although face-to-face interviewing was preferred (Bailey, 2008; Barriball & While, 1994), due to Covid-19, the majority (27 out of 36) of the interviews were conducted via Microsoft Teams, Zoom or telephone. Interviews lasted between 30 and 60 minutes. After the interview a brief written note was made of the first impression of the interview and its context to be used in the analysis (Barriball & While, 1994). All interviews were audio-recorded, transcribed verbatim and shared with the interviewees. The interviewees consisted of a total of 18 fishers and five fisher representatives. The fishers and their representatives were selected by purposeful sampling (described in 2.3) and interviewed until no further variation of the main themes occurred, i.e. saturation was reached, meaning that no new information was discovered, resulting in qualitative representativeness and no further interviews were therefore deemed necessary (Fusch Ph D & Ness, 2015; Glaser & Strauss, 1967; Guest et al., 2006). The other interviewees were selected from the different organisations (research institutes, NGOs, government departments per country) involved in European sturgeon conservation (Table 4.1). We ensured that a diversity of roles and countries was reached.

4.2.5 Anonymisation, transcription and thematic analysis

A list of interviewee codes was created to anonymise the data, using two capital letter country codes, three letter stakeholder group codes, and a serial number, e.g. NLfre1 = interview with Dutch fisher representative #1 (Table 1 and Supplementary material C). The interviews were transcribed and translated into English, imported into a qualitative data analysis software ATLAS.ti. (2022), and coded. Coding used the different themes of the interview guide.

Table 4.1. Number of interviewees per stakeholder group per country.

Country	Fishers (fis)	Fisher representatives (fre)	Researchers (res)	NGO representatives (ngo)	Governmental representatives (gov)
France (FR)	5	2	2	1	1
The Netherlands (NL)	12	3	2	3	1
United Kingdom (UK)	1	0	1	1	
Germany (DE)	0	0	1	0	
	18	5	6	5	2

4.3 Results

For fluent reading quotes from the interviewees that support the results are given separately per paragraph.

4.3.1 Pros of reporting rare bycatch

The pros and cons for reporting incidental bycatches of marine ETP fish species are summarized in Table 4.2. Pros are related to: (1) fishers interest in rare, iconic species; and (2) fishers wanting to express their responsibility towards good stewardship for marine resources.

First, catching a sturgeon is generally perceived by fishers as a rare and impressive event. For some it is even seen as a "party moment" (NLfis3). Fishers interviewed found an interest to share their extremely rare (sturgeon) bycatch throughout their social networks and were (in principle) certainly willing to report it as they realise that otherwise scientists would be unable to find them. Fishers and all other stakeholders claim sturgeon capture reports to be an essential and instrumental source of data that is extremely difficult to obtain otherwise.
Second, fishers feel that reporting is a sign of 'good stewardship' for marine life as it underlines a connection between the quality of the ecosystem and its users. Reporting sturgeon bycatch showcases fishers' sense of responsibility for the sturgeon population.

- Sturgeon is a very emblematic, very beautiful fish that doesn't look like a fish from our time. (FRfis1)
- Since you catch something special, you just report it… If no one brings these fish up, the scientists will be unable to find them. (NLfis1)
- That's our job, not only catching the fish, it's also caring for nature. (NLfis2)
- Bycatch reports of rare fish are a very good indicator of the relationship, the bond, you [i.e. other stakeholders] create with the fisher. (FRfre1)
- Fishers are partners in the [sturgeon restoration] programme. They contribute to the monitoring of sturgeon in the natural environment and provide all relevant knowledge for the evaluation of the programme and more generally for the evaluation of the sturgeon population… Reporting sturgeon bycatch could be a great opportunity to do some good PR [for fishers], by disseminating it widely when someone catches a sturgeon. (FRgov1)

4.3.2 Cons of reporting rare bycatch

The interest fishers have in sturgeon and other rare iconic species is a good basis for reporting the rare bycatch (and release). However, there are also four reasons for fishers to not report the bycatch of sturgeon, which surfaced from the interviews: (1) a lack of (financial) interest; (2) a lack of time; (3) a lack of understanding (awareness) of how important the information about the species is for the species conservation management; and (4) the trust (or lack thereof) that fishers have in the other stakeholders involved, plus concerns about how the information might be used to result in more regulations, such as closed areas and/or technical measures to reduce bycatch.

First, most fishers commented that such reports do not carry any inherent (economical) benefit for themselves. The critically endangered European sturgeon is protected, and it is illegal to land and sell.

Second, Fishers explained that sharing photographs and footage of incidental bycatch through social media is done often and can be done quickly. Reporting, however, requires measuring the fish, writing down the coordinates and sending out an accurate report, which takes time and interferes with their regular work. Interestingly, several French fishers previously did not find it so much of a problem to report sturgeons and had often done so.

- So we take a photo of [the sturgeon], we weigh it, we measure it if we have the means and we take the GPS position, so that's all we do, so we can't say that it's very difficult… I'm interested in seeing sturgeon again. Financially, it doesn't bring me anything, but… it's not a constraint at all, I don't see who couldn't comply with it. (FRfis3)

Third, we reasoned that fishers willingness to report sturgeon bycatch would be higher if they were aware of how important the information about the species is for the species conservation management, but this is not *per se* true. In France, researchers promoted the sturgeon restoration through an awareness campaign (Michelet, 2011), while fishers are currently informed about the sturgeon restoration through regular updates from CAPENA and CNPMEM (FRres2). In France, even though well informed, fishers suddenly stopped reporting in 2020 (see §3.2). In the Netherlands, fishers were informed about the European sturgeon re-introduction through several articles in fisheries newsmagazines. Fishers were rewarded 100 euro per confirmed European sturgeon capture report and given a flag with a printed sturgeon on it. This information helped to collect data, but certainly did not reach all fishers. Several fishers were not interested in such a reward, nor the conservation activities. In the Netherlands sturgeon reports had also stopped by 2020. In Germany, information meetings with fishers are the preferred method of communicating official action plans (DEres1). Still, DEres1 stressed a lack of general knowledge about sturgeon restoration among fishers and the general public. In the United Kingdom, UKfis1, when contacting the Marine Management Organization, was not offered any instructions on what to do with his rare sturgeon report. Support was offered after contacting the Blue Marine Foundation through the website 'Save the sturgeon'. This illustrates how rare sturgeons are around the British Isles and that the sturgeon restoration programme is not well known among fisher organisations in the UK.

- Most people should be aware of the release of these baby sturgeons [but they are not]. (FRfre1)
- I know it [sturgeon] is back and for me that was an indication that the North Sea is doing better. I didn't know that it was because of a programme, or some hatchery or whatever. (NLfis3).
- I do think that at some point there could be some kind of professionalization towards the wider public… that could be the final push for such a project [sturgeon restoration programme] to succeed. (NLgov1)
- Despite multiple news items it is plausible that a large part of the general public [and fishers] in Germany is still mostly unaware of the sturgeon rehabilitation programme. (DEres1)
- Sturgeon is preferably seen as the source of caviar, not as a flagship species that represents the restoration of an aquatic ecosystem. (UKres1)

Fourth, the fishing industry is faced with difficult economic circumstances, including high fuel costs. Fishers have experienced a sharp decline in the number of operational fishing vessels. For most interviewed fishers it has become a challenge to remain economically viable. Fishers are highly concerned about the loss of space at sea due to closures of Natura 2000 areas and of wind farms, and other no-go areas where fisheries are restricted like the 'plaice box' in the Netherlands.

- In the 1980s there were around 240 beam trawlers, now we have 80, and more are going, I think 30 or 40. (NLfis5)
- The local fishermen are extremely threatened, because their numbers are declining over the last 30 years. So, we initially started out with around about 1200 fishermen. And in the meantime, there's like 10% of them who are still active. (DEres1)
- If they say: 'Oh, it's like the panda of the ocean and we should make a no-go area'. Yeah, then it's obviously worrying. (NLfis3)
- We [fishers] want to cooperate in everything, except closed areas. (NLfis5)
- The ocean and North Sea is getting taken from us, from the fishermen, as we feel, by wind farms. (NLfis2)
- The [government] have already closed 40,000 km2 of the North Sea for the big fishing ships. It's called the plaice box. And that's why the fishermen say we don't want to close anything anymore, because it doesn't have an effect. (NLfre2)

Fishers also worry about forced gear adaptations to reduce bycatch risks. This fear reduces fishers' willingness to report rare bycatch. They have experience that such information could be used by NGOs to lobby for further restrictions of fishing opportunities. Dutch fishers refer to the ban on pulse fishing (Haasnoot et al., 2016; Kraan et al., 2020), but in other countries fishers also express a fear of gear restrictions. For example, DEres1 explained how his research team worked on adapting the settings of gill-nets, these being the predominant gear used in German nearshore coastal waters. These nets rest on the bottom and reach up 2.5 m into the water column. Through sections of rope the researchers lifted the nets 30 cm off the ground, which reduced sturgeon bycatch by 90%, as the sturgeons move along the bottom. This researcher had organised three meetings with fishers to ask them if they would be willing to test this adaptation in gear-setting, to see whether the numbers of fish that they would catch (target fish as well as bycatch) would differ between those two different net settings. However, it never came to anything, as the researchers were threatened during the first meeting by the fishers and removed from the property. German fishers were not willing to comment, but fishers interviewed from the Netherlands were quite clear. Fishers feel misunderstood and that they should be considered and hired as experts to design solutions to reduce rare bycatch, not constantly be told what to do.

- The boss of the cooperative told us that if we wouldn't get off his property within the next 10 minutes, they would certainly arrange for beating up. (DEres1)
- I know you can report it [sturgeon and other rare fish bycatch], but [fishers] are pretty careful about that… That's how a fisherman thinks! Everything you say is used against you!... You cannot change the whole fleet [adapt gear] for only two or three sturgeons. (NLfis1)
- [Researchers and NGOs] are working too little with fishermen even if it's fishermen who know a lot about the sea… I'm often treated like a criminal [by NGOs], but I never did something else than providing food… We [fishers] don't see the future that positive anymore… We are really afraid that another negative development will come, based on what [researchers and NGOs] find in the data we deliver. Speech is silver, silence is golden. (NLfis4, a third-generation fisherman who recently had to put his two trawlers on a chain and find another job.)

Notably, some interviewees claimed that there is a general, substantial lack of sturgeon bycatch reporting. FRres2 explained how the French research institutes survey the Gironde estuary for sturgeons every two months and how they capture (measure, check the tag and release) far more sturgeon than the numbers of sturgeon bycatch reported by individual fishers, fishing the same area, using the same fishing gear. In addition, it is important to mention that non- or underreporting does not *per se* means that fishers do not support the presence of rare species. Several fishers interviewed claim that they do release their rare bycatch alive.

- Even if a report is not produced, this does not mean that the bycaught fish [sturgeon] is treated badly or injured. Sturgeons are released alive, without reporting. (NLfis4)

Table 4.2. Summary of perceived pros and cons of fishers reporting incidental sturgeon bycatch, per stakeholder group.

Stakeholders' perceptions	Fishers	Fishers organisations	NGOs	Research institutes	National governments
Pros	Sturgeon reports are of interest to fishers' and their social network. Reporting expresses 'Good stewardship' of the marine environment.	Indication of the bond between fishers and other stakeholders. Good PR.	Shows that fishers are taking responsibility for a healthy ecosystem. Increase of public awareness.	Essential data for population assessment and monitoring spatiotemporal distributions.	Useful for making management decisions. Lack in bycatch reports hampers making management decisions.
Cons	No inherent economic profit. Takes time (costs money). May create severe problems for fishers, such as closed areas and forced gear adaptations and restrictions.		Lacking declarations of dead sturgeons are misleading.	No cons.	No cons.

4.3.3 Sudden drop of reporting

In France, the number of bycatch reports decreased substantially in 2020, then stopped. The French fishers' reason was, that one of the NGO's - active in sturgeon management in the Gironde area - had gone to court aiming to force the French administration to enforce Habitat Directive, article 12 (EEC, 1992). The article prohibits any form of capture, disturbance or intentional killing in the wild of the species listed in Annex IV (including European sturgeon) and *obliges* fishers to release and report such species bycatch. The reason for the court case was that the NGO suspected the French government of using the bycatch reports to suggest that fisheries have no negative impact on sturgeons, thereby undermining effective sturgeon management. According to the French NGO the best solution to conserve sturgeon is therefore, to ban fishing in the Gironde. French researchers stated that since then French fishing organizations are far less open to collaboration and fishers have stopped reporting sturgeon bycatch. Remarkably, in the Netherlands sturgeon bycatch reports stopped as well in 2020, but interviewees expressed no link between the French and Dutch situation.

- The government uses bycatch reports to assure that the bycatches are not fatal for the fish, since dead sturgeons are never reported… Catch declarations are as useful as they are misleading! (FRngo1).
- This [court case] had the effect of a bomb in the [Gironde] region, resulting in fishers to become very hesitant to report anything as they feel that everything they [fishers] do in terms of transparency ultimately backfires… They don't want to inform that in a certain area [Gironde] they [fishers] catch a lot of sturgeon because they don't want to have restrictions to access to this area. (FRres2)

4.3.4 Interviewee suggested solutions to improve reporting

The interviewees also mentioned examples that improved reporting may improve sturgeon conservation. In France, tag readers were handed out (as most stocked juvenile European sturgeons are chipped) and visits to the rearing station were organised. Fishers' involvement and willingness improved when they participated in the programmes' research. This was underlined by FRfre1, "My main advice would be to create a trust relationship with fishers to involve them. And to put them at the same level as scientists… I think that's the main key to the success of the reintroduction programme". In the Netherlands, fishers and their representatives also expressed a wish to participate in research. It was stressed by all stakeholders that the researchers needed to be fully transparent towards fishers about the ways in which bycatch reports would be used.

- Fishers can be an arm of the scientists, because we're on the water all the time. (FRfis2)
- Involve [fishers] above all in the research, involve them as researchers! (NLfre3)
- Research should create a clear feedback loop between what is reported and what is achieved from these reports. (NLres2)
- I think it would be a good idea in itself if [government and organizations managing the sturgeon action plan] could sit around the table with [fishers] more often. That [fishers] know what is happening in the action plan, and what might come their way. (NLgov1)

4.3.5 Perceptions of sturgeon management

All interviewees were asked to reflect on the sturgeon action plans, as these are managed differently across the four countries (Table 4.3). In France, the government officially controls the action plan whilst the activities are carried out by researchers (France Ministère de l'Écologie, 2020). French researchers explained the strength of the governments' legal, administrative and financial help. In contrast, the French NGO expressed a strong dissatisfaction and underlined that the French government is not actively involved. In Germany, the sturgeon action plan is also driven by research, yet without any governmental involvement (Gessner et al., 2011c; Kirschbaum & Gessner, 2000). The German researchers explained how most of the implementation work (including fund raising) is being carried out by volunteers, which is less than optimal. In the Netherlands, the Dutch action plan was initiated and has also been run by NGOs, since 1995. The NGOs also finance research on a feasibility assessment of reintroducing the species in the river Rhine. NGOs developed the required sturgeon action plan, which was offered to the government (Visser et al., 2020). The government partially supports this plan, financially. Yet, the NGOs sketched the necessity for a stronger, long-term governmental collaboration. In the United Kingdom, sturgeon reintroduction is in its initial phase, and governmental resistance was experienced in accepting European sturgeon as a native species. Only after an evidence report was produced and enough pressure from researchers and NGOs did the UK government started taking notice of the possibility of the rehabilitation of sturgeon.

- The French Action Plan is t*he last hope for the species*. (FRgov1)
- The [French] administration does not want to protect nature and only takes decisions that create an illusion of improving the situation. (FRngo1)
- In Germany the government is not involved in the rehabilitation. But it should be. Bring authorities together to implement changes that were requested in the action plan. (DEres1)
- By putting people on the project, putting out the actions, and getting more involvement from the fishers. (NLngo3)
- I don't think UK authorities were really taking this [sturgeon's return to UK waters] seriously. (UKres1)

Outside France and the Netherlands, other administrations of European member states are not directly involved in the sturgeon action plans. European sturgeon conservation in Germany and the United Kingdom (and partially in the Netherlands) is left to project-based funding. As a consequence, overall, coordinated tasks are driven by NGOs and researchers. No other countries are involved, even though the species occurs within their EEZ (e.g. Spain, Portugal, Belgium, Denmark, Ireland). The interviewees see this lack of European and national governmental involvement as a source of problems, as this causes gaps in international engagement, continuity in long-term funding, coordination of actions, monitoring of fisheries measures, and consistent application of legal documents to assure mitigation of anthropogenic pressures and sturgeon protection (e.g. mitigation of bycatch mortality). The challenge is that EU member states are responsible for (fisheries) management measures in their inland and coastal waters, whereas management at sea is agreed upon at EU level. By default therefore coordination is required, but currently this is not the case for the European sturgeon and other marine ETP species.

Table 4.3. Stakeholder groups' relevance to bycatch reporting and their (current) role in European sturgeon conservation.

Stakeholder group	Reports on sturgeon bycatches	Current role in sturgeon conservation
Fishers	Fishers bycatch reports are highly useful to researchers and policy makers. Good handling of the fish on deck (and careful release) will save individuals of a rare species.	Eyes and ears (and hands) at sea. Potentially impacted by restrictions determined by the sturgeon conservation. Not directly involved in sturgeon Action Plans.
Fisher organisations	Main communication channel to and from fishers. Represent the interests of fishers. May inform fisheries-management on bycatch mitigation of ETP species.	Manage eventual restrictions determined by the sturgeon conservation. Voice to evaluate the fisheries management measures from a fishers' perspective. Not directly involved in sturgeon Action Plans.
Research institutes	Collect, collate and analyse bycatch data. May use data to assess ETP species' populations, spatiotemporal distributions, and advice on sustainable fisheries management measures.	Main drivers of sturgeon conservation in France (since 1980) and Germany (since 1990).
NGOs	Use bycatch data and research outcomes in their respectful (to other actors involved) communication strategies to lobby for adaptations in fisheries management measures.	Main drivers of sturgeon conservation in the Netherlands (since 2010) and the United Kingdom (since 2015).
National governments	Use bycatch data and research outcomes and translates advice into fisheries management measures in collaboration with other countries to rehabilitate these ETP fish species in European waters.	Responsible for the restoration of ETP species and therefore of the (sturgeon) conservation programme. Only in France actively involved in European sturgeon conservation. European collaboration and coordination would be extremely helpful for the national governments involved.

4.4 Discussion

In recent years fishers have been increasingly challenged by reduced space to fish and are competing for space with an increasing amount of other users (Van Hoof et al., 2020). This comes on top of a history of increased fisheries management interventions, reduced fishing opportunities and rising fuel costs (Parker & Tyedmers, 2015). Fishers perceive that others (researchers, policy makers, NGOs) are, both directly and indirectly limiting their fishing opportunities for different reasons. These issues make them extra sensitive about disclosing information that they perceive could worsen their situation (Van Hoof et al., 2020). In consequence of the sensitivities, finding willing interviewees was challenging. For example, the French fishers interviewed were approachable only through mediation by their organisations. Yet, fishers sharing information is key to the management of ETP species and thus fishers' cooperation could be instrumental in species conservation.

4.4.1 Core aspects of successful cooperation with fishers

A vast body of literature exists on fishers and researchers cooperating in data gathering (Johnson, 2011; Johnson & van Densen, 2007; Kraan et al., 2013; Steins et al., 2020; Steins et al., 2022; Stephenson et al., 2016). Reported core aspects of successful cooperation are: 1.a shared vision; 2.a clear role separation; 3.communication and 4.trust. However, this study shows that all these core aspects of cooperation are seriously hampered. It is governments who are legally responsible for European sturgeon conservation (Bastmeijer, 2019) and other ETP species. Apart from in France, the management of European sturgeon action plans is not carried out by governments but by researchers and/or NGOs. Several countries where the species occurs within the EEZ are not even involved in European sturgeon conservation and rehabilitation. The interviewees see this lack of an international shared vision and approach as a source of problems, as it impairs consistent international collaboration, coordination, optimized approaches and long-term finance.

In addition, there are issues of communication and trust of fishers in the intentions of NGOs and (vice versa) trust of NGOs in data gathered by fishers, and neither of these are unique to this case (Steins et al., 2022). There is a strong trend of environmental NGOs, emphasizing scientific evidence for the negative effects of fishing in lawsuits, to obtain strengthened ecosystem and species protection (Hilborn, 2007). NGOs and fishers often have different forms of causal reasoning from available data and observations, information, and knowledge, e.g. scientific vs. lay reasoning, and differences in knowing what is really going on at sea, and thus diverging points of view (Verweij et al., 2010). They have different perceptions. Where NGOs demand fishers to take more responsibility for the state of the marine resources, fishers perceive themselves to act responsibly for 'their' resources and feel connected to the sea itself. While fishers indicate that fishing is essential as it feeds the human population, NGOs point to the negative effects of fishing on marine ecosystems and fish habitats (Auster & Langton, 1999; Jennings & Kaiser, 1998). NGOs call for preserving and closure of marine ecosystems opposes the interests of commercial fishers who demand the continued access to space and resources (Baker, 2000; Hilborn, 2007; Voyer et al., 2014, 2015). The observed conflict and different objectives can be summarized as one between preservation (NGOs) versus utilization (fisheries) (Hilborn, 2007). The experiences in France demonstrate that when this difference is not bridged, dispute will arise and the much-needed cooperation with fishers will come to an end.

4.4.2 Ways forward

The interviewees explained how three pragmatic solutions may aid to improve fishers cooperation potential (thus touching on the four core aspects listed in 4.1): (1) involve fishers in sturgeon conservation activities and research, make clear what is in it for fishers, and thus build trust between fishers and researchers; (2) improve completeness, accuracy and speed in fishers reporting incidental bycatch through technological means and social media; and (3) solve trust issue between fishers and NGOs.

First, fishers need to perceive much more benefit (including intrinsic rewards) and value in declaring ETP species bycatch. The interviewees stated that this can be achieved by fishers cooperation in research. Fishers show (in principle) willingness to participate in such research, and contribute data and experiential knowledge (Steins et al., 2022). Those that currently participate may do so out of their own interest or understanding of the importance. For fishers to fully collaborate in research, it is required that they be acknowledged for their knowledge, expertise and skills (Yochum et al., 2011). However, no fisher is likely to report on ETP species if the information could be used to advise on, or lobby for closed areas or forced gear adaptations. Researchers are interested in facilitating the participation of fishers in cooperative research as it has multiple benefits, such as improving (rare) fish population assessments, improved relevance of research to fisheries management, and improved relationships and trust between fishers, researchers, and managers (Johnson & van Densen, 2007; Pustelnik & Guerri, 2000). Motivating each group of actors and including them in a collective project can help to achieve the goals of the European sturgeon restoration action plans. Fishers are more likely to trust researchers if: (1) they are allowed to participate in the research project formulation (National Research Council, 2003); (2) understand how scientific reporting works (Johnson & van Densen, 2007); and (3) understand what the consequences of their data delivery could be. With good role separation fishers can also see that science is responsible for data analysis and advice based on the data, and that policy is responsible for making decisions based on different sources of information. Research cooperation is also useful as it often takes place in projects in which the settings and rules of engagement can be made clearer (Yochum et al., 2011). Research cooperation opens up the ability to address trust issues between fishers and researchers, and can do so, much faster than by depending on voluntary reporting of bycatch by fishers alone. This approach implies that researchers must work on improved relations, i.e. deliver positive feedback on capture reports, and on a regular basis via social and fishers' corporate media. Inviting fishers to visit rearing stations, as done in France, in addition to handing out tag readers is a good idea as it gives fishers an idea of the purpose of their work. Increased communication can also minimize negative relationships between fishing communities and management agencies (refs in Yochum et al., 2011).

Second, bycatch reports must be collected in ways that are acceptable to fishers (also in terms of time and money spent). Researchers wish to facilitate fishers' self-sampling studies (Kraan et al., 2013), including training and strengthened communication. This approach would imply that fishers aid scientists to develop protocols on how to minimize handling time on deck and could result in fishers licensed to tag fish (Beardsall et al., 2016; Doddema et al., 2020). It should be carefully assessed how such tasks can be designed to consume minimal time and effort on the part of the fishers (see for example Doddema et al. (2020)). Data declaration and collection could also be facilitated by internationally standardized monitoring methodologies to improve speed, accessibility, accuracy and anonymisation (Gray & Kennelly, 2018; Savoca et al., 2020; van Helmond et al., 2020). However, certainly not all fishers are interested in implementing electronic monitoring techniques (van Helmond et al., 2020). The data collection should be acceptable for the users of the data by making use of accepted quality assurance frameworks (Steins et al., 2022).

Third, ideally, obtaining fishers cooperation must be based on trust and willingness, not on constant monitoring as this may be ineffective as fishers could feel victimised (Ford & Stewart, 2021). Trust issues between fishers and NGOs are often based on differing interpretations and opinions of species conservation, and such interpretations depend heavily on specific social, cultural, and historical contexts (Auster et al., 2022). Obtaining fishers' and NGOs cooperation to the European sturgeon Action Plans can therefore be characterised as a complex, or a "wicked problem" (Jentoft & Chuenpagdee, 2009) in the sense that the problem is difficult to define, delineates from other and bigger problems, and tends to reappear.

For comparison purposes: the (successful) rehabilitation of the beaver (*Castor fiber*) in Scotland was described by Coz and Young (2020) to be an example of such a "wicked problem". In this case, conflicts and trust issues existed between NGOs and farmers or landowners, as such groups held different views on the beaver's return (Coz & Young, 2020). By engagement in effective discussions all stakeholders came to agree on a shared vision and clear role division, resulting in a broad and long-term conservation plan. Gradually, issues were finally set aside, which led to successful rehabilitation in certain designated areas in Scotland (Coz & Young, 2020). Another successful example can be found in Canada, where an imperilled population of Atlantic salmon (*Salmo salar*) in the Northwest river rapidly and sustainably recovered, after managers decided to turn to an adaptive management approach with fishers based on local cooperation and transparency (Cote et al., 2021). Both examples show how important it is to involve local users. In the case of European sturgeon restoration and conservation, this means strongly improving the cooperation with local fishing communities fishing in the European sturgeon's essential habitats, e.g. the Gironde (estuary), and fishers from the town of Urk (currently the largest Dutch fishing fleet using bottom trawls), and shrimpers fishing the Belgian, Dutch and German shallow coastal zones of the North Sea (Brevé et al., 2013a). This also requires that the local NGOs (that are already involved) understand the difficulties of data acquirement of ETP species at sea, and how their communication campaigns may raise unwanted conflicts, even work in a counterproductive manner as they may push fishers further away from conservation activities.

4.5 Concluding remarks

Because of the Endangered, Threatened and Protected status, the management of the European sturgeon and any other ETP fish species must be at the top of the agenda of Europe's fisheries management. However, under-reporting of these species bycatch (and mortality) is still left largely unaddressed. Apart from France and partially in the Netherlands, governments are not recognizing the European sturgeon conservation activities. Researchers and/or NGOs lead the activities. This holds true for France, Germany, the Netherlands, and the United Kingdom. Other countries where the species occurs within their EEZ are not even involved. The interviewees see this as a main source of problems, as it impairs consistent international collaboration, coordination, optimized approaches and long-term finance.
This study also shows that all core aspects for fishers' cooperation in ETP species conservation (a shared vision, a clear role separation, communication and trust) are seriously hampered. Fishers feel a responsibility for the sea and its natural resources, and are inclined to report rare bycatch, but most have stopped doing so since 2020 for many reasons. Fishers experience difficult economic circumstances and feel that the sea is taken from them through closure of fishing grounds (e.g. wind farms, natura 2000 areas). Fishers feel misunderstood as their knowledge and expertise is not recognized and they are not involved in planning. Fishers feel threatened by NGOs who use iconic species in their communication strategies to reduce fishing possibilities.

To solve the issue, all interviewed stakeholder groups pointed to the required national and international, governmental uptake of European sturgeon conservation. Another solution is to involve fishers in research, improve communication and build trust. This could be done by training fishers to participate in the scientific data collection (e.g. self-sampling of data and fin-clipping for molecular biology studies), and by organisation of participatory workshops involving all the stakeholders, whereby fishers would be encouraged to propose specific mitigation measures. The latter also implies that NGOs need to understand that they should not be dominant in the debate about what needs to be done to improve sturgeon bycatch reporting and subsequent protection. It also implies that researchers keep fishers in a constant feedback loop and explain what their data is used for.

If the shared goal is to express 'good stewardship' of the marine environment, then all stakeholder groups involved should develop best practice methods, and solve any issue that might hamper the restoration and conservation of marine ETP fish species. We therefore invite the fishery management councils, in which member states come together (e.g. the Scheveningen Group for the North Sea), to put the subject of reporting rare marine fish species on their agendas.

Acknowledgements

We thank all anonymous interviewees for their time and expertise given during the interviews. A special 'thank you!' goes out to: Tom Buijse for his comments on a first draft of this manuscript; Bart van Woerden for conducting interviews amongst ten Dutch fishers; Ingmar Rondeel, Luuk Wilbers and Laura Zirnheld for translating French interviews into English; two anonymous reviewers; and Nigel Gardiner-Harvey for copy editing the reviewed manuscript throughout.

Data availability

Interview descriptions and survey results are available from the corresponding author, upon reasonable request, and under condition that all names are anonymized.

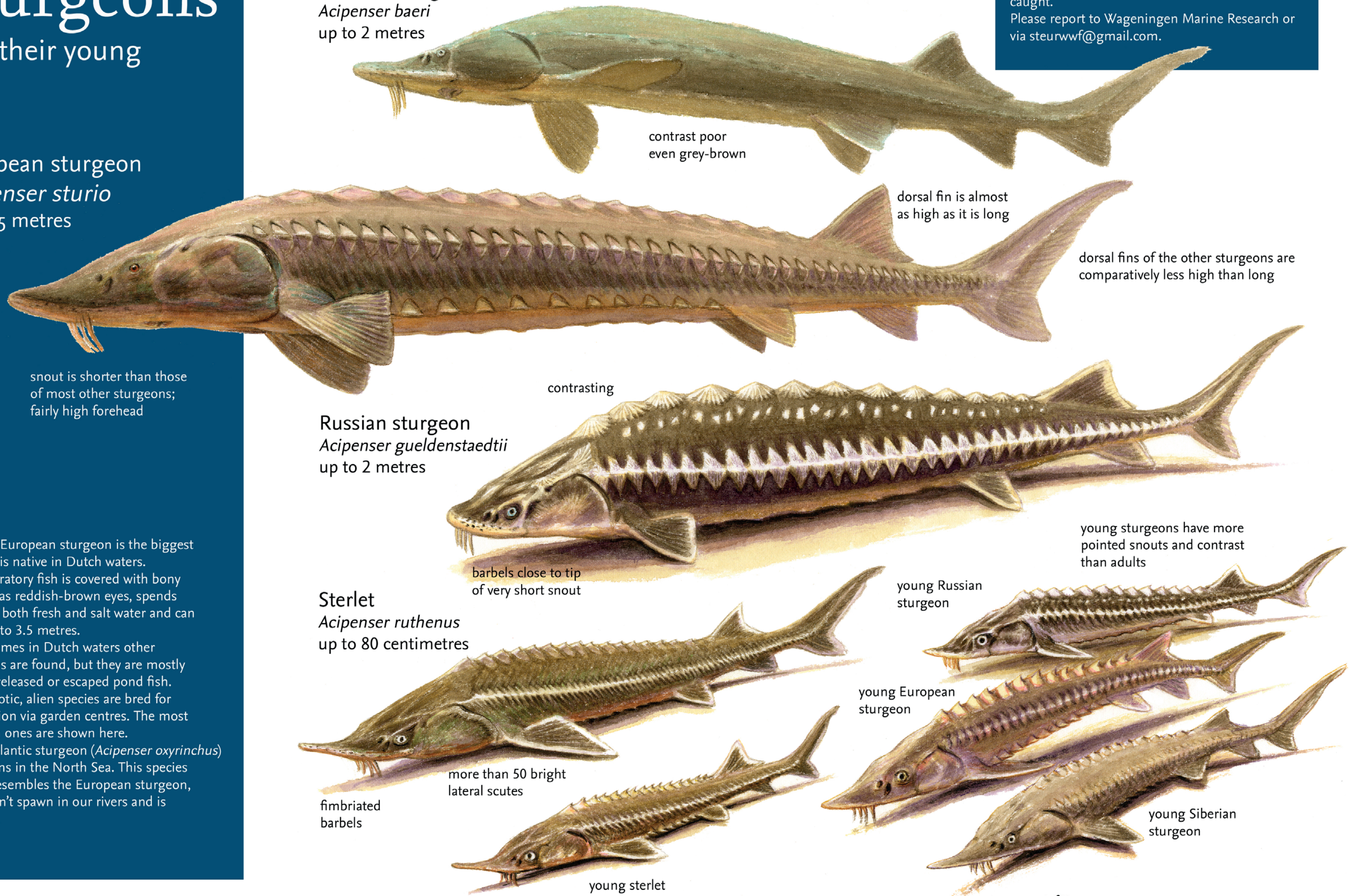
Supplementary material

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.marpol.2024.106056: Appendix A provides the Interview Guide in English; Appendix B the Informed consent form in English; Appendix C an overview of the organisations' acronyms, 2 letter country codes & 3 letter stakeholder codes.

Sturgeons

and their young

The European sturgeon is a protected species and has to be released as soon as possible after being caught.
Please report to Wageningen Marine Research or via steurwwf@gmail.com.



The rare European sturgeon is the biggest fish that is native in Dutch waters. This migratory fish is covered with bony scutes, has reddish-brown eyes, spends its life in both fresh and salt water and can grow up to 3.5 metres.

Sometimes in Dutch waters other sturgeons are found, but they are mostly illegally released or escaped pond fish. These exotic, alien species are bred for distribution via garden centres. The most common ones are shown here.

The Atlantic sturgeon (*Acipenser oxyrinchus*) also swims in the North Sea. This species closely resembles the European sturgeon, but doesn't spawn in our rivers and is less rare.

www.ark.eu/steur
© Jeroen Helmer / ARK Nature

Chapter 5

The conservation paradox of critically endangered fish species: Trading alien sturgeons versus native sturgeon reintroduction in the Rhine-Meuse river delta

Part 2

Published as:

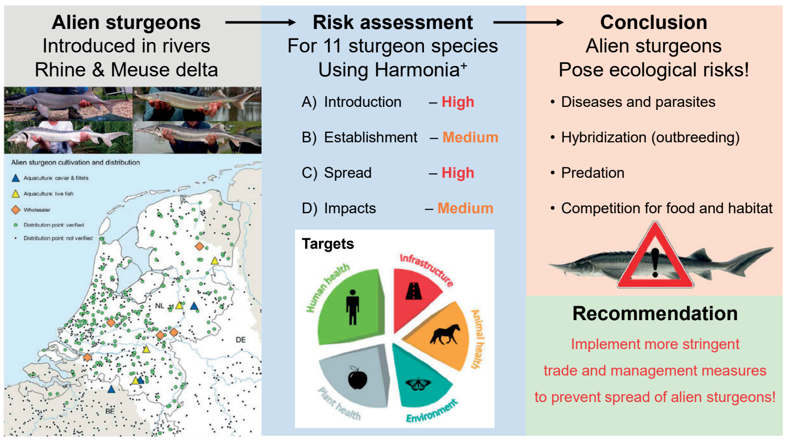
Brevé, N. W., Leuven, R. S., Buijse, A. D., Murk, A. J., Venema, J., & Nagelkerke, L. A. (2022). The conservation paradox of critically endangered fish species: Trading alien sturgeons versus native sturgeon reintroduction in the Rhine-Meuse river delta. Science of the Total Environment, 848, 157641.

https://doi.org/10.1016/j.scitotenv.2022.157641

Poster: Sturgeons and their young, representing the native European sturgeon and three alien sturgeons for the Rhine delta. Source: Jeroen Helmer / ARK Rewilding Nederland.

Abstract

Sturgeons rank among the most endangered vertebrates in the world. Yet, the dwindling of wild sturgeon populations stands in stark contrast to their thriving status in aquaculture. Moreover, through the exotic pet trade, sturgeons are introduced outside their natural ranges where they may compete and hybridize with native species and transmit parasites and diseases. Here, we present an in-depth inventory of alien sturgeons in the delta of the rivers Rhine and Meuse, because several countries consider reintroduction of the native, critically endangered European sturgeon (*Acipenser sturio*). Our study is based on (a) an inventory of the industry of sturgeon cultivation; (b) reports on spread of alien sturgeons; (c) an analysis of pathways for introduction and spread; and (d) a risk assessment using the Harmonia+ protocol. In total, 11 alien Acipenseriformes (sturgeons and paddlefishes) were traded across an intricate network of >1000 distribution points in the Netherlands, Belgium, and Germany. Circa 2500 alien sturgeons were reported from 53 angling ponds and 64 other lakes and ponds, whereas circa 500 alien sturgeons were reported widespread across hydrologically connected waters. Species that posed the highest risk of introduction, establishment and spread are Siberian sturgeon (*A. baerii*), Russian sturgeon (*A. gueldenstaedtii*) and Sterlet (*A. ruthenus*). We recommend to implement stringent trade regulations and practical solutions to prevent spread of alien sturgeons. Measures must preferably be taken at the spatial scale of river basins.



Highlights

- Endangered sturgeons are widely used in aquaculture, garden- and angling ponds.
- 11 alien sturgeons are traded across an intricate distribution network.
- Three alien sturgeon species potentially pose ecological risks in the study area.
- Risks comprise diseases and parasites, hybridization, predation, and competition.
- Implementing trade and management measures prevents spread of alien sturgeons.

5.1 Introduction

Biodiversity loss is one of the biggest problems facing our planet today (Cardinale et al., 2012; Piccolo, 2017). At present, the order of Acipenseriformes (25 sturgeons and two paddlefishes) is the most threatened order of vertebrae in the world (Pikitch et al., 2005). According to the International Union for Conservation of Nature and natural resources (IUCN), four Acipenseriform species are recently considered extinct, including the Chinese paddlefish (*Psephurus gladius*) (Zhang et al., 2020), while of the remaining 23 species 85 % is endangered (Birstein et al., 1997a; Haxton & Cano, 2016; Pikitch et al., 2005). The historical decline in Acipenseriformes ('sturgeons' from now on) is generally explained by overfishing and ecological change that impacted sturgeon's natal rivers for the past 150 years (Birstein, 1993; Debus, 1997).

The endangered status of sturgeons is a wake-up call to restore the wild populations. However, the endangered status of the wild populations stands in stark contrast to their thriving status in aquaculture. Approximately 100 years ago, the extirpation of the wild populations prompted the development of sturgeon aquaculture, as a means for artificial propagation for reintroduction, and for production of the highly valued black caviar and meat (Havelka & Arai, 2018). During the second half of the 20th century, the industry of sturgeon aquaculture steadily expanded. Market demands had farmers switch from using specific sturgeon species producing high quality caviar, mainly Russian sturgeon (*Acipenser gueldenstaedtii*), Great sturgeon or Beluga (*Huso huso*) and Starry sturgeon (*A. stellatus*) (Williot et al., 2001), to highly productive hybrids, such as the 'Bester': Great sturgeon × Sterlet (*A. ruthenus*). Whereas recently, several other, even more profitable crosses were bred (Arndt et al., 2002; Bronzi et al., 1999; Bronzi et al., 2011; Wei et al., 2004; Williot et al., 2001). In consequence of the developments in sturgeon aquaculture, more species are exploited, and a large portion of caviar production is attributed to farmed hybrids. Moreover, at present, sturgeon aquaculture has become an economically important industry that increasingly includes the production of live fish for the exotic pet trade and for sport fishing (Lockwood et al., 2019).

Even though sturgeon cultivation saves certain sturgeon species from becoming extinct and potentially reduces the pressure on natural populations (Jarić et al., 2018), sturgeon cultivation also impedes sturgeon conservation in the wild. Net pens in rivers are occasionally flooded during storms and because of accidental escapes, and intentional or unwanted releases, sturgeons and their hybrids are introduced in waters outside their native ranges (Arndt et al., 2000; Gessner et al., 1999; Hanel et al., 2011; Maury-Brachet et al., 2008; Spratte, 2014; Wei et al., 2004). Alien sturgeons, i.e. sturgeons belonging to any (sub)species introduced outside their natural range that might survive and subsequently reproduce (European Commission, 2014), may impose three categories of threats to their novel environments and native biodiversity: hybridisation with native sturgeons, distribution of diseases and parasites, and predation and aggressive behaviour. A major threat in sturgeon conservation is the potential interspecies hybridisation leading to genetic deviation through outbreeding (Birstein & Bemis, 1997; Birstein et al., 1997b; Ludwig et al., 2009a). Sturgeons are prone to introgressive hybridisation because all sturgeons are polyploids, and even intergeneric hybrids can be fertile and survive in the wild (Birstein et al., 1997a; Havelka et al., 2011). In such cases, introgression, thus movement of genes from one species to another, can occur, threatening vulnerable native populations. Another persistent risk of introducing cultured fish, and a consequence of intensive rearing operations, is the transmission of associated diseases and parasites that may spread to new hosts in the receiving area (Barber et al., 2000; Bauer et al., 2002; Spikmans et al., 2020; Welcomme, 1988). Several pathogens are associated with cultivated sturgeons, such as Viral haemorrhagic septicaemia and Infectious haematopoietic necrosis (Bauer et al., 2002; European Union, 2018). In such cases the actual threat may be the pathogen, not the host. However, the main problems attributed to invasive alien species (IAS) are predation and aggressive behaviour. In general, competition for prey and reproduction grounds has caused numerous reductions and collapses of native fish populations before (Lehtonen, 2002; Van der Veer & Nentwig, 2015) and may happen among alien and native sturgeon species.

Notably, several sturgeon species rank among the largest predatory fish on the planet. For example, both the Great sturgeon and the White sturgeon (*A. transmontanus*) can grow over 5 m in total length and over 1000 kg in weight (Kottelat & Freyhof, 2007; Page & Burr, 2011). Still, due to sturgeons' laggard life cycles and their vulnerability to anthropogenic pressures, they cannot be considered as typical IAS. Normally their introductions will fail (Maury-Brachet et al., 2008; US Fish and Wildlife Service, 2018d). On the other hand, as long as introductions, escapes and releases continue, the risks that alien sturgeons and their hybrids may pose to their novel environments and native biodiversity will also persist.

The present study analyses the environmental risk that alien sturgeons may pose, as countries consider reintroducing European sturgeon (*A. sturio*) in the rivers Rhine and Meuse. Two native sturgeon species from the north Atlantic Ocean, that represent a separate clade distinct from all other Acipenseriformes (Birstein & Doukakis, 2000), used these rivers to spawn: the now critically endangered European sturgeon and the near threatened Atlantic sturgeon (*A. oxyrinchus*) (Gessner et al., 2010b; St. Pierre & Parauka, 2006; Thieren et al., 2016a; Van Neer et al., 2012). Historically, the Rhine sturgeon populations started to dwindle at the end of the 19th century, and the last sturgeon from these rivers was captured in 1952 (Brevé et al., 2022d; Verhey, 1963). In recent decades, however, the improved water quality and the largely restored longitudinal connectivity resulted in a partial return of the Rhine's diadromous fish (Bij de Vaate et al., 2006; Borcherding et al., 2010; De Groot, 1992; Mostert, 2009). Moreover, at present, adolescent European sturgeons occur in the northeast Atlantic Ocean, even in the outer estuary of the river Rhine (OSPAR Commission, 2021). Their renewed presence is a result of ongoing stocking efforts in French and German rivers (Williot & Kirschbaum, 2011), and as such promising for a future reintroduction of the native sturgeon species in the river Rhine.

The reappearances of migratory fish triggered ARK Nature, the World Wide Fund for Nature and Sportvisserij Nederland, to initiate a reintroduction programme of this iconic species in the river Rhine (Brevé et al., 2013a). However, with the current improved water conditions, alien sturgeons may also survive and establish in this river and their presence may pose a conflict with the reintroduction efforts. Thus, before the native sturgeon species can be reintroduced, a risk assessment is of paramount importance, and recommended by the French, German and Dutch action plans for the European sturgeon, and the Pan-European Action Plan for Sturgeons (Council of Europe, 2018; France Ministère de l'Écologie, 2020; Gessner et al., 2011c; MEDDTL, 2011; Visser et al., 2020). Such a risk assessment will prevent the potential loss of money, time and individuals of the endangered European sturgeon.

The research questions that will be addressed here are: what is the extent of alien sturgeon introductions, what are potential risks these could pose for the environment, and for the reintroduction of the European sturgeon in the rivers Rhine and Meuse? It was hypothesized that alien sturgeons pose an environmental risk related to their hybridisation, predation, competition, diseases and parasites, even though they may also be a good indicator of restored environmental quality of the rivers Rhine and Meuse. To answer the research questions we quantified the distribution network of sturgeon cultivation and of introduced alien sturgeon species. We also analysed the pathways for their introduction and spread, and assessed the environmental risks. Only with this knowledge, decision makers and stakeholders can be informed and urged to stop the unwanted releases and spreading of alien sturgeons.

5.2 Materials and methods

5.2.1 Study area

The area of concern for the risk assessment comprises the main geographical distribution area of the historical native Atlantic sturgeon and European sturgeon populations in the delta of the rivers Rhine and Meuse (Brevé et al., 2022c, 2022d) (Fig. 5.1). The area covers three neighbouring countries in northwest Europe: the Netherlands, Belgium, and Nord-Rhine Westphalia in Germany. The study included regional sturgeon aquaculture and trade of all alien sturgeon and paddlefish species.

5.2.2 Data collection

We collected data from multiple sources to obtain two complete datasets. The first comprised the industry of sturgeon aquaculture, including data from commercial and non-commercial angling ponds as these locations also hold alien sturgeon species for (non-) commercial purposes. The second dataset comprised reported catches and sightings of free-living alien sturgeons introduced to the study area.

5.2.3 Inventory of sturgeon aquaculture and angling ponds

We performed an inventory of hatcheries, farms, wholesalers, importers, retailers (e.g., garden centres and pet shops), and consumers of alien sturgeon species. This dataset was collected by the following four methods: (a) an online Google search for sturgeon farms producing sturgeon caviar and meat, and live fish for the exotic pet trade; (b) merging and unifying lists provided by all three Dutch wholesalers that delivered live sturgeons to their distributors in the Netherlands, Germany and Belgium; (c) a search for other online distribution points via www.marktplaats.nl and www.eBay.com. Key words used were “steur”, “sturgeon”, “esturgeon” and “Stör”, which resulted in a list of over 50 web shops; and finally, by (d) screening anglers’ logbooks, dive websites, and biodiversity databases for any other locations in-field where sturgeons are commercially or non-commercially fished or observed during diving. This dataset was validated by querying all entrepreneurs in the Netherlands. We asked if they sold sturgeons and which species, first by e-mail, and then by telephone for non-respondents. Entrepreneurs in Belgium and Germany were not contacted because the Netherlands covers the largest part (ca. 80 %) of the Rhine-Meuse delta and already included over 350 verified addresses.

5.2.4 Inventory of catches of free-living alien sturgeons

We also collected data on capture reports and sightings from research institutes, commercial fishers, anglers (digital logbooks), biodiversity databases, dive websites and social media. The collected data were sorted per country and water type, either in isolated waters (ponds or lakes) or hydrologically connected waters (rivers or canals) in the period 1990–2021. For the Netherlands, the sources were obtained from (a) VAART software B.V., digital anglers logbook Sportvis Vangsten Registratie (n = 1180); (b) Sportvisserij Nederland, digital anglers logbook MijnVISmaat (n = 1791); (c) Sportvisserij Nederland, field inventory system Piscaria (n = 26); (d) ARK Nature, sturgeon recapture reports from commercial fishers (n = 37, mostly European sturgeon in the North Sea); (e) Wageningen Marine Research (WMR), sturgeons captured in fyke fisheries (n = 289, mostly unidentified sturgeon species); and (f) RAVON, sturgeons captured with landing nets (n = 50).

Notably, Belgium and German fisheries research institutes do not provide online anglers' logbooks, nor do they collect data on alien sturgeon captures or sightings. This was confirmed by colleagues working at the Rheinischer Fischereiverband and INBO Research Institute for Nature and Forest. Therefore, we carried out a search via Google, which yielded additional data for both countries (n = 100). Finally, data on alien sturgeons was downloaded from GBIF.org (24–05–2021) GBIF Occurrence Download (https://doi.org/10.15468/dd.fjuaer) (Brevé et al., 2022a). This database included 10,576 data-entries worldwide but was reduced to 349 records after filtering 'human observations' within the study area. The full dataset was validated by the authors for species and locations by checking photographs, coordinates in Google Maps, and through local knowledge. Data with validated species but non-validated location were not used. Unidentifiable sturgeon species or hybrids were named Acipenser spp. Data without validated species and without validated location were excluded from analysis. As a result, this dataset has unified and double validated species and location data.

5.2.5 Data quality control

The datasets on aquaculture, angling ponds, catches and sightings were sorted, filtered, summed per sturgeon species, year, and water type. Distribution patterns of the industry and of the free-living sturgeons were mapped and assessed through simple point pattern analysis in QGIS 3.16. The datasets, assessments, tables, and figures are stored in the data repository underlying this publication (Brevé et al., 2022a).

5.2.6 Risk assessment

The risk assessment followed two steps: (a) An analysis of pathways for introduction and spread of alien sturgeons using the classification system that was developed within the framework of the Convention on Biological Diversity (Harrower et al., 2018); (b) A risk assessment using the internet-based Harmonia+ protocol that was developed by the Belgian Biodiversity Platform (D'hondt et al., 2015; Vanderhoeven et al., 2015), to screen the environmental risks for 10 sturgeon and one paddlefish species introduced in the Rhine-Meuse delta. Harmonia+ is a first-line risk assessment protocol for potentially invasive plants, animals, and their pathogens. This protocol includes all invasion stages (Leung et al., 2012), concerns all environmental impacts (Verbrugge et al., 2010) and separates the likelihood from magnitude of these impacts (Kumschick & Richardson, 2013). The general structure of the Harmonia+ protocol and its key elements are described in D'hondt et al. (2015). The full protocol and detailed explanations for the assessments can be consulted online at http://ias.biodiversity.be/harmoniaplus. The assessment consisted of 41 questions grouped into six categories: 1) context, 2) introduction, 3) establishment, 4) spread, 5) impact categories (environment, plant cultivation, animal production, human health, infrastructural and ecosystem services), and 6) future effect of climate change (Fig. 5.2). The risk analysis was thus interpreted for the potential (risk of) survival under current and future climate conditions in the Rhine-Meuse delta. As recommended by D'hondt et al. (2015), we first performed the assessments individually, based on literature and best professional knowledge. This allowed for assigning individual risk scores and confidence levels to all questions for each species.

We then plenary discussed differences in environmental risk scores and assigned confidence levels to elucidate whether these apparent disagreements could be traced to epistemic or linguistic uncertainties or persisted as different expert opinions. This process generally yields consensus on final risk scores and increases the level of confidence for all assessed species (Leung et al., 2012). The Harmonia+ risk classification yielded an invasion score, impact score and overall risk score, by calculating the arithmetic mean and maximum score for each risk category. The numerical analysis allows for ranking of species overall risks and can be used both for prioritization schemes of already-present species and for horizon scanning of emerging species (D'hondt et al., 2015). All risk assessments can be found in (Brevé et al., 2022a).

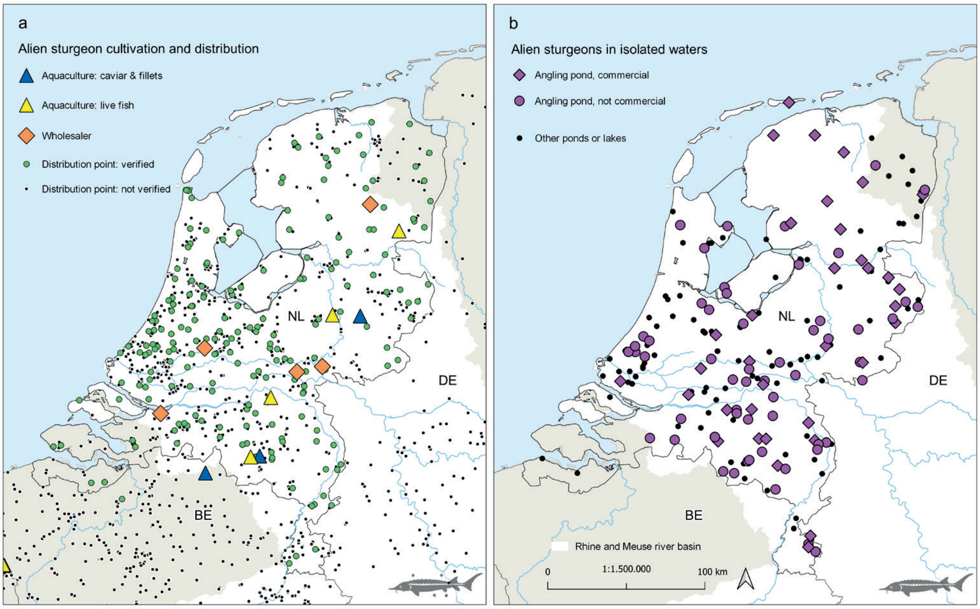


Figure 5.1. The industry of alien sturgeon cultivation in 2021: locations of (a) aquaculture, wholesalers, and distribution points (e.g., garden centres and pet shops) in the Rhine-Meuse delta ('verified' = confirmed after querying by e-mail and phone; 'not verified' = known distribution point from wholesaler dataset but not queried in-person); and (b) angling ponds, and other ponds or lakes with live alien sturgeons in the Netherlands. BE: Belgium; DE: Germany; NL: The Netherlands.

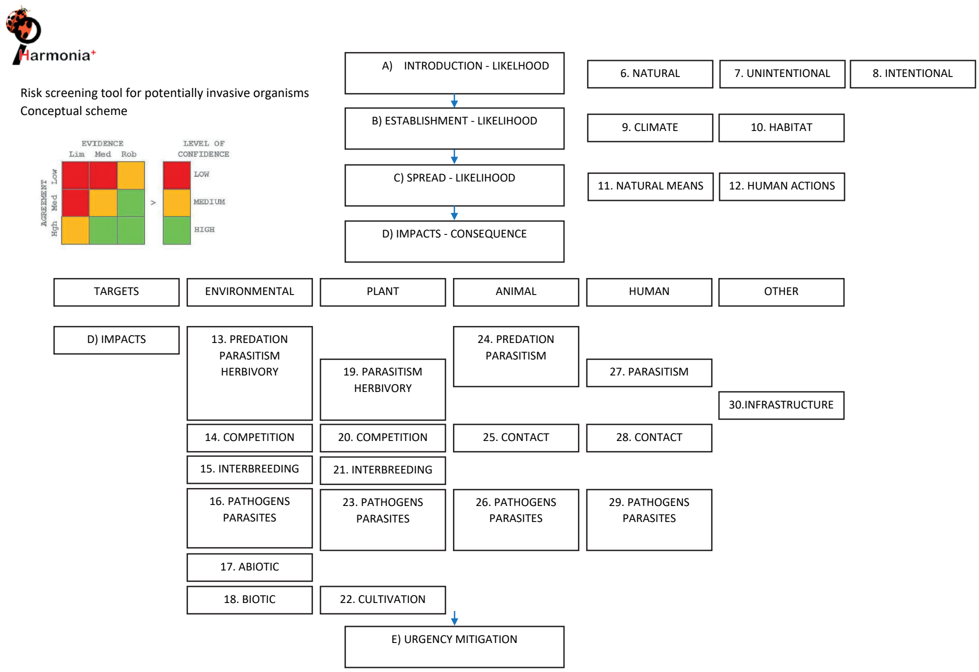


Figure 5.2. Conceptual scheme: general structure of the Harmonia+ assessment tool.

5.3 Results

5.3.1 Distributions of alien sturgeons

Based on the dataset on distribution of sturgeon aquaculture, we localized 26 hatcheries, caviar farms and wholesalers that sold live sturgeons in 2021. Wholesalers distributed their fish over an intricate network of >1000 distribution points such as garden centres, pet shops and fishing tackle shops with aquarium and/or pond facilities. We verified over 350 distribution points (entrepreneurs) who all responded to our questions about sturgeons (Fig. 5.1a). In turn, these distribution points sold sturgeons to numerous customers, such as garden pond owners, aquarists, angling clubs, and dive centres all of which released sturgeons in isolated waters, such as angling ponds, recreational lakes, city park ponds, and (flooded) quarries. While little data exists on sturgeons obtained by these customers, we localized 53 commercial and 64 non-commercial angling ponds and lakes that were stocked with alien sturgeons (Fig. 5.1b). Based on the catch and sightings dataset, we also localized the presence of 10 alien sturgeon and one paddlefish species in the study area, of which eight sturgeon species were stocked in commercial angling ponds (Fig. 5.3).

Figure 5.3. Photographs with examples of (sub)adult alien sturgeon individuals introduced in the Rhine-Meuse delta, caught (and released) by anglers: (a) *Acipenser baerii*, (b) *A. gueldenstaedtii*, (c) *A. naccarii*, (d) *A. oxyrinchus* (which is a native species), (e) *A. ruthenus*, (f) *A. stellatus*, (g), *A. transmontanus* and (h) *Huso huso*. In 2021, other Acipenseriformes, also kept in aquaculture in the Rhine-Meuse delta were not reported in hydrologically connected waters, especially *Polyodon spathula*, *Scaphirhynchus platorynchus*, *A. brevirostrum* and *A. nudiventris*.

All water types, that is isolated and hydrologically connected waters, were dominated by three sturgeon species: Siberian sturgeon (*A. baerii*), Russian sturgeon (*A. gueldenstaedtii*) and Sterlet, and their hybrids. All other seven alien sturgeon species and the paddlefish composed <10 % of total number of individuals (Fig. 5.4, Fig. 5.5). These other species were found across the study area in three main settings: (a) Mississippi paddlefish (*Polyodon spathula*), Shortnose sturgeon (*A. brevirostrum*), and Shovelnose sturgeon (*Scaphirhynchus platorynchus*) were confined to aquaculture and garden ponds; (b) Adriatic sturgeon (*A. naccarii*), Atlantic sturgeon (which is a native species), and White sturgeon, were confined to aquaculture and commercial angling ponds; (c) Stellate sturgeon and Great sturgeon were confined to aquaculture and multiple commercial angling ponds, but also occurred sporadically in hydrologically connected waters (Fig. 5.4d).

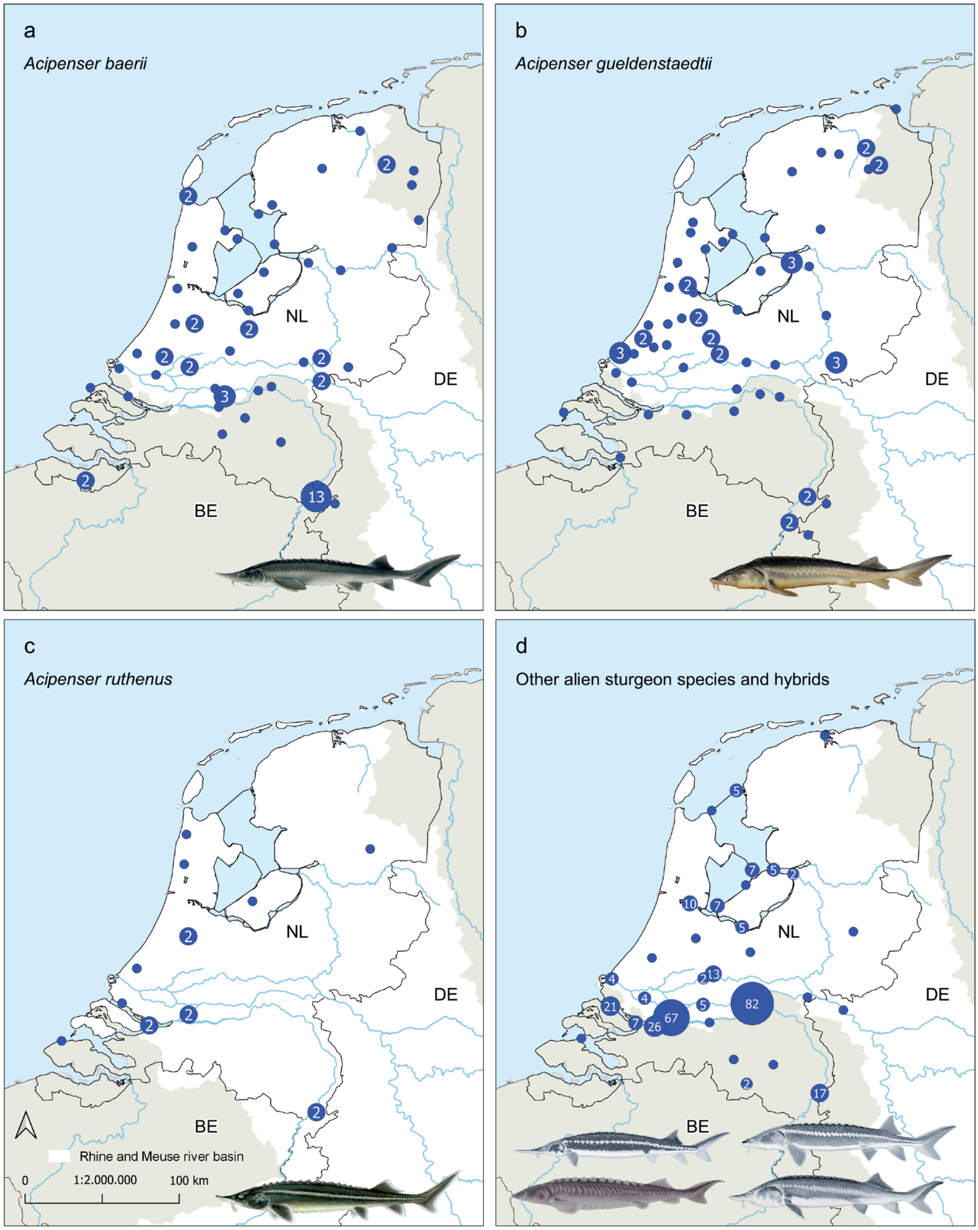


Figure 5.4. Verified records of alien sturgeon individuals, free-living in hydrologically connected waters (river or canal) in the Rhine-Meuse delta in the years 1990–2021 for the three most captured (and released) species: (a) *Acipenser baerii*, (b) *A. gueldenstaedtii* and (c) *A. ruthenus*, and (d) other alien sturgeon species and hybrids.

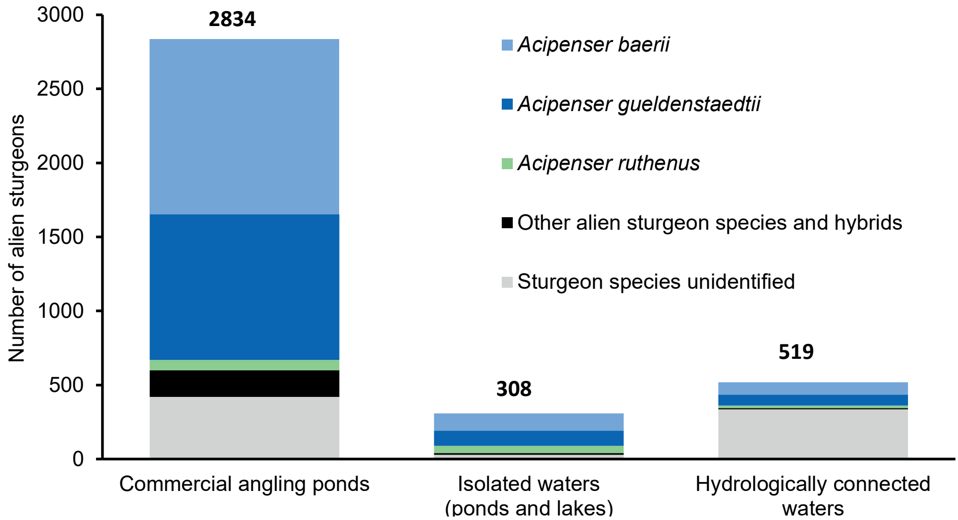


Figure 5.5. Reported number of alien sturgeons (n) distributed over commercial angling ponds, other hydrologically isolated waters (pond or lake), and connected waters (river or canal).

5.3.2 Free-living alien sturgeons

Between 1990 and 2021, 519 sturgeons were recorded from hydrologically connected waters (Fig. 5.5). We found no proof of alien sturgeon establishment in our data, that is no sightings of eggs, nor sightings of young-of-the-year sturgeon juveniles. In total 336 individual sturgeons were not identified. From the identified 182 sturgeons, 175 (96 %) concerned the three species Siberian sturgeon, Russian sturgeon and Sterlet (Fig. 5.4, Fig. 5.5). The first capture of a free-living alien sturgeon concerned one Sterlet in 1944 (Fig. 5.6). All other alien sturgeons were only recorded after the start of sturgeon cultivation in the Rhine-Meuse delta from 1990 onwards. The total number of alien sturgeons was <10 % of the mean yearly numbers of native sturgeons that were reported around 1900 (Fig. 5.6).

5.3.3 Assessments of introduction, establishment, spread and risks

Using the Harmonia+ protocol (Fig. 5.2), we focussed risk assessments on alien sturgeons that occurred in hydrologically connected waters. Based on the arithmetic mean scores the three most frequent species Siberian sturgeon, Russian sturgeon and Sterlet scored a high risk for introduction (confidence level, cl: high) and establishment (cl: medium) (Table 5.1). These three species also scored a high overall risk of invasion but a low overall risk for impacts (Table 5.2). The other sturgeons, Starry sturgeon and Great sturgeon, that were reported sporadically in hydrologically connected waters (<10 in a decade), scored a low risk of introduction (cl: high) and a medium risk of establishment (cl: medium).

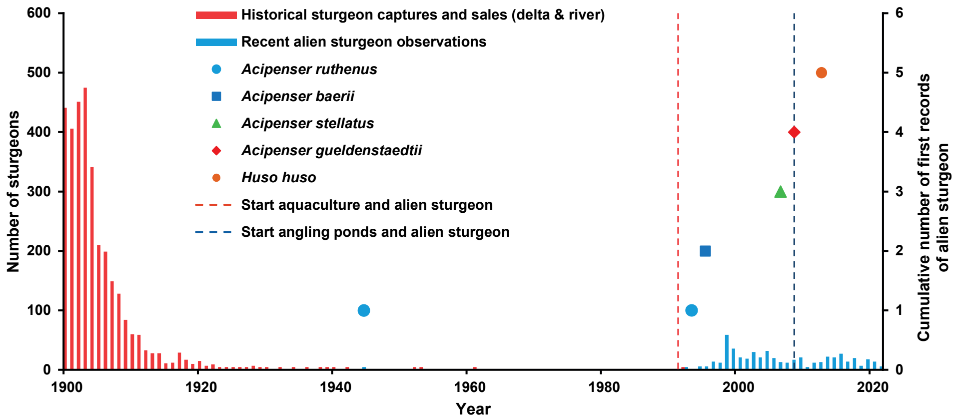


Figure 5.6. Timeline of reported number of captures (n) of native sturgeons (*Acipenser sturio* and *A. oxyrinchus*) (red bars) and alien sturgeons (blue bars), and the first reports of alien sturgeon species (various symbols) free-living in hydrologically connected waters (river or canal) in the Rhine-Meuse delta in the years 1900–2021. The first capture of one free-living *A. ruthenus* was reported in 1944 (blue dot*).

Due to sturgeons' highly migratory nature, all 11 sturgeon species assessed scored a high risk of spread (cl: high). Moreover, all 11 sturgeon species scored medium impacts on environmental and animal targets (cl: medium), with the exception of the predatory Great sturgeon that attained a high risk for environmental impacts (cl: medium). All 11 sturgeons scored low impacts on plant, human and other targets (cl: high). Species that were not reported in hydrologically connected waters were: Mississippi paddlefish, Shortnose sturgeon, Adriatic sturgeon, Ship sturgeon (*A. nudiventris*), White sturgeon and Pallid sturgeon (*Scaphirhynchus albus*). The risks related to these species were not described in detail here, but all individual sturgeon assessments are available in Brevé et al. (2022a).

Table 5.1. Aggregated risk assessment of recorded alien Acipenseriformes for the Rhine-Meuse delta, using Harmonia+

Acipenseridae	**Species**	*Polyodon spathula*		*Acipenser baerii*		*Acipenser brevirostrum*		*Acipenser gueldenstaedtii*		*Acipenser naccarii*		*Acipenser nudiventris*		*Acipenser ruthenus*		*Acipenser stellatus*		*Acipenser transmontanus*		*Huso huso*		*Scaphirhynchus platorynchus*	
Module	**Risk category**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**	**Risk**	**Confi-dence**
Average	*Introduction*	0,333	0,67	0,667	0,83	0	0,67	0,667	0,67	0	0,83	0	0,67	0,667	0,83	0	1,00	0	1,00	0	1,00	0	0,67
	Establishment	1	0,50	0,75	0,50	0,75	0,50	0,75	0,50	0,75	0,50	0,75	0,50	0,75	0,50	0,75	0,50	0,5	0,50	0,75	0,50	0,75	0,50
	Spread	1	1,00	1	1,00	1	1,0	1	1,00	1	1,00	0,75	0,75	1	1,00	1	1,00	1	1,00	1	1,00	1	1.0
	Impacts: environmental targets	0,333	0,58	0,458	0,75	0,083	0,50	0,5	0,58	0,417	0,75	0,167	0,50	0,542	0,67	0,458	0,50	0,375	0,67	0,667	0,67	0,083	0,50
	Impacts: plant targets	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00
	Impacts: animal targets	0,167	0,50	0,25	0,67	0,167	0,50	0,333	0,67	0,167	0,67	0,333	0,50	0,25	0,67	0,25	0,67	0,167	0,83	0,25	0,83	0,083	0,50
	Impatcts: human targets	0	0,50	0	0,50	0	0,50	0	0,50	0	0,50	0	0,50	0	0,50	0	0,25	0	0,25	0	0,25	0	0,50
	Impacts: other targets	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00
Maximum	*Introduction*	0,5	1,00	1	1,00	0	1,00	1	1,00	0	1,00	0	1,00	1	1,00	0	1,00	0	1,00	0	1,00	0	1,00
	Establishment	1	0,50	1	0,50	1	0,50	1	0,50	1	0,50	1	0,50	1	0,50	1	0,50	0,5	0,50	1	0,50	1	0,50
	Spread	1	1,00	1	1,00	1	1,00	1	1,00	1	1,00	1	1,00	1	1,00	1	1,00	1	1,00	1	1,00	1	1,00
	Impacts: environmental targets	0,5	0,50	1	1,00	0,25	0,50	0,75	1,00	0,5	1,00	0,5	0,50	1	1,00	0,75	1,00	1	1,00	1	1,00	0,25	0,50
	Impacts: plant targets	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00
	Impacts: animal targets	0,5	0,50	0,75	1,00	0,5	0,50	0,75	1,00	0,5	1,00	0,75	0,50	0,75	1,00	0,75	1,00	0,5	1,00	0,75	1,00	0,25	0,50
	Impatcts: human targets	0	0,50	0	1,00	0	1,00	0	0,50	0	1,00	0	1,00	0	1,00	0	0,50	0	0,50	0	0,50	0	1,00
	Impacts: other targets	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00	0	1,00

Legend for colour schemes used in tables produced with Harmonia+

Risk score*	**Category**	**Risk**	**Confi-dence**
<0.33	Low		
0.33 ≤ RS ≤ 0.66	Medium		
>0.66	High		

*: Arbitrary cut-off values

Table 5.2. Summary of risk assessments (average and maximum scenario's) of 11 alien Acipenseriformes introduced in the Rhine-Meuse delta, using Harmonia+.

Species	Risk category	Overall risk score according to Harmonia+ protocol		Potential (risk of) survival under current climate conditions in the Rhine-Meuse delta *	Supporting material in data repository
		Average	Maximum		
Polyodon spathula	invasion	0,69	0,79	+	Table 3
	impact	0,10	0,50		
	overall risk score	0,07	0,40		
Acipenser baerii	invasion	0,79	1,00	++	Table 4
	impact	0,14	1,00		
	overall risk score	0,11	1,00		
Acipenser brevirostrum	invasion	0,00	0,00	+	Table 5
	impact	0,05	0,50		
	overall risk score	0,00	0,00		
Acipenser gueldenstaedtii	invasion	0,79	1,00	++	Table 6
	impact	0,17	0,75		
	overall risk score	0,13	0,75		
Acipenser naccarii	invasion	0,00	0,00	+	Table 7
	impact	0,12	0,50		
	overall risk score	0,00	0,00		
Acipenser nudiventris	invasion	0,00	0,00	+	Table 8
	impact	0,10	0,75		
	overall risk score	0,00	0,00		
Acipenser ruthenus	invasion	0,79	1,00	++	Table 9
	impact	0,16	1,00		
	overall risk score	0,13	1,00		
Acipenser stellatus	invasion	0,00	0,00	-	Table 10
	impact	0,14	0,75		
	overall risk score	0,00	0,00		
Acipenser transmontanus	invasion	0,00	0,00	-	Table 11
	impact	0,11	1,00		
	overall risk score	0,00	0,00		
Huso huso	invasion	0,00	0,00	-	Table 12
	impact	0,18	1,00		
	overall risk score	0,00	0,00		
Scaphirhynchus platorynchus	invasion	0,00	0,00	+	Table 13
	impact	0,03	0,25		
	overall risk score	0,00	0,00		

* ++ can certainly survive, + is likely to survive, 0 unknown, - is unlikely to survive, -- cannot survive

5.4 Discussion

5.4.1 Intricate distribution network

Alien sturgeons have been cultivated in the Rhine-Meuse delta since 1990. In total, 10 sturgeon species, one paddlefish and their various hybrids were introduced in hatcheries and commercial farms. From these farms live sturgeons were distributed across an intricate network of over 1000 localities in The Netherlands, Germany and Belgium. Although not all localities were verified by us (via e-mail or telephone), they were advertised by wholesalers as sturgeon sales points online. Hence, it became clear that the sturgeon distribution network is omnipresent across the study area and most probably across north-western Europe. This is a major finding as no other previous study showed the intensity of this distribution network of alien sturgeons.

Another major finding concerns the occurrence of 11 alien sturgeon species across the study area, as 85 % of all acipenseriform fishes are listed as critically endangered by the IUCN, including those in the study area. However, from the 11 species, only three were reported frequently, that is Siberian sturgeon, Russian sturgeon and Sterlet. Most sturgeons were stocked in isolated ponds and lakes, but also >500 individuals were reported free-living in rivers and canals in the Rhine-Meuse delta between 1990 and 2021. Of these sturgeons, the majority (>300 fishes) were not identified to the species level by the fishers, nor were photos available. However, it is highly unlikely that these were European sturgeons. The species spend their adolescent and most of their adult life at sea (Acolas et al., 2011a) and European sturgeon larvae and juveniles from the French and German sturgeon programmes stocked between 2007 and 2015 had not reached maturity in 2021 (OSPAR Commission, 2021). Still, the non-identifications severely affected our analysis of trends in sturgeon occurrences at the species level. We therefore emphasize that sturgeons need to be identified to the species level and pictures of all individual sturgeons should be taken for expert verification purposes. Moreover, when alien sturgeon identification is certain, then commercial fishers could even be allowed to land these alien species.

5.4.2 Assessments of pathways for introduction and spread

The pathways for sturgeons' introductions are (a) import, and (b) sturgeons moving in from surrounding areas via river corridors, or coastal waters. Most probably import is the main pathway, as naturally occurring sturgeon species are extremely rare in the study area and in surrounding waters. For example, Sterlet has a native range in the Danube, a river that is connected to the river Rhine through the Rhine-Main-Danube canal. This canal acted as invasion corridor for a multitude of AIS into the river Rhine (Leuven et al., 2009). However, at present the Danube Sterlet population is endangered and there are multiple migration barriers in the river Danube restraining fish migration (Friedrich, 2018; Friedrich et al., 2019). Therefore, this species will not likely disperse to the river Rhine via this corridor and must have been introduced, then spread. Still, Sterlet poses a high risk of establishment due to the optimal climate it encounters in the river Rhine.

The pathways for spread of alien sturgeons within our area of concern are (a) intentional releases, (b) unintentional escape from confinement, and (c) unaided, through natural dispersal via interconnected canals, rivers and coastal waters within the Rhine and Meuse river systems. Sturgeons are highly migratory species (Bemis & Kynard, 1997). Therefore, once introduced, they can disperse over hundreds of kilometres, unless barriers and impoundments limit this (Puijenbroek et al., 2019). Escape from confinement is not possible as open net pen facilities do not exist in the study area. However, escapes from garden ponds and angling ponds are likely because some ponds were flooded during recent high river discharges. Finally, intentional release into the wild by anglers, garden pond owners and aquarium keepers is also plausible because sturgeons can attain unexpected large size and longevity, and there is no take-back obligation for sellers, nor do pet rescue centres for these fish exist. Thus, plausible explanations for sturgeons' presence in hydrologically connected waters are escapes during floods and/or intentional releases.

Three patterns in sturgeon sales explain the dominant occurrences among the sturgeons of Siberian sturgeon, Russian sturgeon and Sterlet: 1) These three sturgeon species are widely available at over >1000 distribution points, and even online through web shops and platforms such as www.marktplaats.nl and www.ebay.com; 2) these sturgeon species are sold at reasonable prices of €25.- to €75.- each. The other eight species are rare and expensive, ranging from €250.- for Shortnose sturgeon to €5200.-. for an exceptionally rare 2.5 m White sturgeon; 3) these three sturgeon species are sold without restrictions, while the rarer species are mostly chipped and registered. To prevent impulsive purchases it would be helpful to create more awareness about the size and longevity that these fish can attain. In addition, all sturgeon sales could be restricted to only registered, certified, and chipped sturgeons. This will prevent alien sturgeon farming outside certified, controlled aquaculture. Moreover, chipping all alien sturgeons' will aid to identify their origin and monitor species first appearances, survival, and potential establishment when fish end up in hydrologically connected waters.

5.4.3 Risk assessments of introduction, establishment, spread and impacts

We carried out a risk assessment with the Harmonia+ protocol for all 10 reported alien sturgeon and one paddlefish species, although our priority was the three sturgeons most frequently occurring in hydrologically connected waters. The risk assessment for these three species consequently showed a high risk of introduction, establishment and spread with a high confidence level. Considering their establishment, until now, none of the species was able to reproduce successfully in the Rhine-Meuse delta and to establish viable populations. Yet, their spawning periods and spawning grounds are comparable to those of the native European sturgeon and Atlantic sturgeon. The three alien and two native sturgeon species all spawn in spring and summer months in the rivers' mainstream over gravelly substrates, and under comparable ranges of water temperature, water depths and flow velocities (Acolas et al., 2011a; Brevé et al., 2022a; Gessner & Bartel, 2006; US Fish and Wildlife Service, 2018a, 2018b, 2018c; Van Eenennaam et al., 1996). Therefore, these alien sturgeons might compete and hybridize with the native species. Even though we found no proof of alien sturgeons' reproduction and establishment of viable populations in the Rhine-Meuse delta, this does not imply that they will not achieve to do so in the future when habitats and connectivity would be improved. As long as the introductions continue, the numbers of these animals will increase also without reproduction. Importantly, as sturgeon releases continue, risk of spread of their diseases and parasites also continues and this might pose a high risk for the rivers Rhine and Meuse environment and potentially introduced native sturgeons and other fish species (European Union, 2018; Mugetti et al., 2020; Radosavljević et al., 2019).

Several risk assessments of Siberian sturgeon and Sterlet have been performed before for other areas of concern in Europe (Almeida et al., 2013; Verbrugge et al., 2019; Vilizzi et al., 2019) and North America (Wyman-Grothem, 2019). Although a variety of protocols and risk score systems were used, the results of these assessments are in line with our scores for environmental impacts and overall risks. Siberian sturgeon even classified for the German-Austrian black-list of invasive alien species (Essl et al., 2011; Nehring et al., 2010).

5.4.4 Measures to mitigate introductions and spread

Based on the outcomes of the Harmonia+ risk assessments and the other risk assessments we can confirm the recommendations of the French, German, Dutch and Pan-European sturgeon action plans, that is to use caution in sturgeon cultivation and introductions of alien sturgeons (Council of Europe 2018; France Ministère de l'Écologie 2020; Gessner et al. 2011; Rosenthal 2008; Visser et al. 2020). Not surprisingly, the legal framework to stop the introductions and spread of invasive species and of related diseases and parasites is already in force. Yet sturgeons are not easily recognized as potential IAS, nor are the restrictions of their introductions and spread enforced. While invasions of alien species, in general, can be stopped at an early stage, they are difficult and even impossible to stop after the invasion is well underway (Navid, 1989) and thus, there is an urgency to act. We therefore recommend to assess whether specific alien sturgeon species could be placed on the list of invasive species of EU concern, according to the Regulation on prevention and management of IAS (European Parliamant, 2014). This regulation would imply that import, trade, containment, distribution, and release of specific sturgeon species are banned throughout the European Union. The advantage would be that the risk related to their introductions would be mitigated at the highest possible international legislative level in Europe. The disadvantage would be a commercial loss, especially to the sector involved in the exotic pet trade. If the latter is not acceptable, then another option would be to implement more stringent trade regulations for specific sturgeon species that apply on a scale of (interconnected) river basins, such as the Rhine and Danube rivers. This would imply that the Rhine and Danube member states must follow the examples given by the German-Austrian black-list of invasive alien species (Essl et al., 2011; Nehring et al., 2010). This means that mitigation measures (like the stop of intentional release) prevail instead of immediate action and eradication, in Germany and Austria.

5.4.5 The paradoxical status between sturgeon cultivation and sturgeon conservation

For three decades sturgeon aquaculture steadily increased while sturgeon conservation struggled to achieve success. The contrast could hardly be more evident. On the one hand, there is a general ease with which rare, endangered sturgeons can be traded, cultivated, multiplied, hybridized and distributed outside their natural range. Thus, without restrictions to a clientele that is hardly aware of the related risks. On the other hand, sturgeon conservation follows strict rules and guidelines for conservation translocations of endangered native sturgeons species (IUCN/SSC, 2013), which comes at great costs and efforts. We therefore suggest to develop a more critical view on the industry of sturgeon cultivation and balance the activities with Europe’s main policies on river restoration and biodiversity goals. The minimum requirement to achieve this would be to imply more stringent trade regulations that apply to specific species, preferably on the scale of river basins, and chip all sturgeons that are sold across the exotic pet trade.

Acknowledgments

We thank the associate editor Sergi Sabater and two anonymous reviewers for their critical remarks and suggestions to improve our paper. We also gratefully acknowledge the constructive input from many organisations and colleagues, commercial fishers, anglers and divers for their data collection on alien sturgeon occurrences in the Rhine-Meuse delta; especially Olvin van Keeken from Wageningen Marine Research for supplying governmental data collected from commercial fyke fisheries; Paul Wijmans and Remko Verspui for their data collected from digital anglers' logbooks (Piscaria and MijnVISmaat); Ernst Schrijver for data on *Acipenser sturio* occurrences from the North Sea fisheries, collected by ARK Nature; Martin Hoorweg, Pieter Beelen, Pascal Rommelaere and Frank Habets for their photographs of alien sturgeons; Jörn Gessner for identifying sturgeon species in our collection of over 1,000 photographs; the Library of Wageningen University and Research for their aid in collecting literature; Peter Griffith for his comments on several drafts; and Laura Zeeman and Rita Hoving for their help in preparing the dataset and submission in a DANS-EASY data repository.

Data availability

The datasets generated and analysed during the study are available in a data repository:

Brevé, N.W.P., Leuven, R.S.E.W., Buijse, A.D., Murk, A.J., Venema, J. & Nagelkerke, L.A.J. (2022): Data underlying the publication: The conservation paradox of critically endangered fish species: trading alien sturgeons versus native sturgeon reintroduction in the Rhine-Meuse river delta. DANS.

https://doi.org/10.17026/dans-28u-x3w3

Chapter 6

Outmigration pathways of stocked juvenile European sturgeon (*Acipenser sturio* L., 1758) in the Lower Rhine River, as revealed by telemetry

Part 3

Published as:

Brevé, N. W., Vis, H., Houben, B., Breukelaar, A., & Acolas, M. L. (2019). Outmigration pathways of stocked juvenile European sturgeon (*Acipenser sturio* L., 1758) in the Lower Rhine River, as revealed by telemetry. Journal of Applied Ichthyology, 35(1), 61-68.

https://doi.org/10.1111/jai.13815

Photo: Researcher Marie-Laure Acolas surgically implanting a NEDAP transponder in a young European sturgeon at the breeding station in France in 2015.

Abstract

Working towards a future Rhine Sturgeon Action Plan the outmigration pathways of stocked juvenile European sturgeon (*Acipenser sturio* L., 1758) were studied in the River Rhine in 2012 and 2015 using the NEDAP Trail system. A total of 87 sturgeon of 3 to 5 years old (n = 43 in 2012, n = 44 in 2015) were implanted with transponders and released in May and June in the river Rhine at the Dutch-German border, ap- proximately 160 km from the sea. In total three sturgeons (3%) were found dead on river banks within seven days after the release. Based upon their wounds these sturgeons were likely hit by ship-propellers. Tracking results were obtained from 57 (66%) of the sturgeons, of which 39 (45%) indicated movement into the Port of Rotterdam. Here the sturgeons remained for an average of two weeks, which suggests they spent time to acclimatize to higher salinities before entering the North Sea. Of the 45 (52%) sturgeons that were confirmed to have entered the North Sea, ten (22%) were recaptured (mainly by shrimpers and gill-nets) close to the Dutch coastline; nine were alive and were released. From the results we obtained the preferred outmigration pathways, movement speeds and an indication of impacting factors (i.e. ship propellers and bycatch). Bycatches provided also localisations information in the coastal area. A next step to complete this work would be to assess habitat selection in freshwater and downstream migration of young of the year (YOY sturgeons) in the Lower Rhine.

6.1 Introduction

Around 1900 the European sturgeon (*Acipenser sturio* L. 1758) still spawned in all main European rivers (Holčík et al., 1989). However, at present the species faces a high risk of extinction according to the IUCN (Gessner et al., 2010c); the species has nearly disappeared from all rivers including the Rhine basin (Rhine) (De Nie & Ommering, 1998). The last European population is originated from the Gironde basin in France and stocking in Europe is currently supported by national action plans in the Gironde in France (MEDDTL, 2011) and in the Elbe in Germany (Gessner et al., 2011c).

6.1.1 Towards a Rhine sturgeon action plan

A possible re-establishment of European sturgeon in the Rhine could support the attempts towards effective prevention of extinction and recovery of the species in its Northern range. However, as a prerequisite for a possible rehabilitation in the Rhine, a sound scientific assessment of the suitability of its current state of habitat is paramount: cited from (Kirschbaum et al., 2009) "Natural populations can be established only if the most important factors that contributed to the decline of the species are no longer present in the rivers chosen for the re-introduction measures." As a result of water quality improvements and under the current scenarios for climate change the Rhine is suggested to provide again a potentially suitable basin for the species (Lassalle et al., 2010; Williot et al., 2011a). Based upon this assessment, a political commitment and a realistic Rhine Sturgeon Action Plan within the catchment has to be reached that includes the potential countermeasures to circumvent adverse conditions for the species before actually considering to implement a reintroduction (Acolas et al., 2011b; de Groot, 2002). Due to certain biological features (e.g. females mature at 14–15 years old [yo] (Magnin, 1962) the population recovery is a long-term process with an estimated minimum timeframe of 30–50 years (Jarić & Gessner, 2013).

Considering a future Rhine Sturgeon Action Plan, as is out- lined in several studies (Gessner et al., 2011c; Nemitz, 2010; Williot & Kirschbaum, 2011), there are key aspects that need to be addressed:

1. Determination of the outmigration pathways of the species (if possible under different hydrological regimes) and the (adverse) impacting factors upon the species.
2. Assessment of availability, size/extent, stability and quality of critical habitats, such as spawning habitat and the identification of area for saltwater acclimatization.
3. Determination of the interference with navigation (current practice as well as the future development options). The Rhine is in- tensely navigated and the propulsions of these vessels cause strong and possible harmful water movements.

4. Monitoring the habitat use of juvenile sturgeons in the southern North Sea and investigating the effects and impacts of fisheries.
5. Assess the cooperation potential of fisheries.
6. Assess the usage of potential nursery areas in the Rhine in Germany.
7. Evaluate the effects of the temporal opening of the Haringvliet discharge sluices on sturgeon behaviour. This will only be possible after actual installed remediation management in 2018.

The outcomes of these assessments could provide the baseline information to verify the necessity and intensity of future habitat improvements and to help develop and deploy international cooperation on those subjects as is advised in related studies (Bölscher et al., 2013; IKSR-CIPR-ICBR, 2009).

6.1.2 Experimental releases

Within the project of a Rhine sturgeon action plan the present study focuses on key question 1, i.e. characterising the outmigration pathways in the lower Rhine, but some elements for questions 3, 4 and 5 were also acquired. Considering the configuration of this part of the Rhine, a complex network of channels and the Haringvlietdam that blocks the access to the sea at one stretch, it is important to identify if juvenile sturgeons are capable to reach the sea to fulfil their life cycle.

In the summers of 2012 and 2015 two tracking studies were carried out with marked juvenile European sturgeons to answer this question. The specimens were obtained from the French captive stock within intra-governmental agreement for a limited number of sturgeon for experimental releases. The results obtained in 2012 have been published in Brevé et al. (2013a), the results obtained in 2015 and a comparison between both field studies are given in the present paper.

6.2 Materials and methods

6.2.1 Study area

The study area covers the Lower Rhine in the Netherlands, a mix of channels and natural habitats that are strongly modified by hydraulic engineering (Figure 6.1a and b). This includes the port of Rotterdam the terminus of all Rhine navigation, and some of the largest storm surge barriers in the world i.e. the Haringvlietdam and Afsluitdijk. During the study, the water temperature varied between 18 and 24°C for both years. The average Rhine flow velocity is estimated by RWS to be approximately 1 m/s at discharges of 2,000 m3 /s. In 2015, the average Rhine discharge in the first week after the release was 1,868 m3 /s and in 2012 it was 2,000 m3 /s in May and 2,443 m3 /s in June (Figure 6.2a and b).

6.2.2 Sturgeon tagging and release

In 2012, 43 juvenile *A. sturio* from 3 to 5 yo (76 ± 4.4 cm in total length (TL), 1.65 ± 0.25 kg) were released in the Rhine on May 10 (n = 13) and June 21 (n = 30) (Figure 6.1a). In 2015, on June 10, 44 conspecifics (4 yo, 80.9 ± 10.2 cm TL, 2.39 ± 0.9 kg) were released 15 km higher upstream at the Dutch/German border (Figure 6.1b) to identify if they would choose the Waal or the Pannerdensch channel to migrate downstream. In 2012 the tracking lasted 171 days and in 2015 97 days.

All sturgeons originated of a controlled reproduction of the French broodstock (Williot & Chevre, 2011). Notably, the three to five yo sturgeons were physically able to support the salinity of the sea (Acolas et al., 2011a). All sturgeons had been implanted into the abdominal cavity with transponders for the NEDAP TRAIL system® (Breukelaar et al., 1998). The telemetry system has detection stations installed at each main weir in the Rhine and Meuse Rivers in the Netherlands (Figure 6.1a and b). Surgery took place at the Irstea French experimentation station and the method of tagging and recuperation, transportation to the Netherlands and acclimatisation of the sturgeon to Rhine water followed the procedure described in Brevé et al. (2013a). The transponders are contained within a shell of surgical glass (26.5 g in air; Ø: 15 mm; length: 70 mm; battery life of approximately 4 years). Their weight was less than 2% of the total weight of the lightest sturgeon which is an acceptable ratio for studies in underwater biotelemetry (Winter, 1983). WOT-tags were inserted on all released individuals at the base of their dorsal fin to provide external recognition.

The involvement of commercial fisherman was obtained by inviting their representatives at the release events and by providing a handling protocol, an Id-card and a 100 euro reward for reported re- captures. News during the study's progress (tracking and recaptures) was published in magazine Visserijnieuws.

6.2.3 Data analysis

Outmigration pathways were plotted in ArcMAP according to registrations (detections, finds and recaptures at sea) of the sturgeon. The downstream movement speed in m/s of individual sturgeon and the average speed for all sturgeons (net ground speed of the sturgeon downstream + average river flow velocity) was calculated for the river stretch between the release site and the first station Waal_Brakel, whereby the distance was measured in Google maps along the midst of the river and the time between the release moment and the first detection at this station. Detection rate of two Nedap stations (Waal_Brakel and Beneden_Merwede_Sliedrecht, Table 6.1) was estimated by the number of sturgeon detected divided by the total number that should have been detected according to additional registrations downstream. Both calculations were not made for other river stretches nor other stations since there are many bifurcations further downstream thus possible detours.

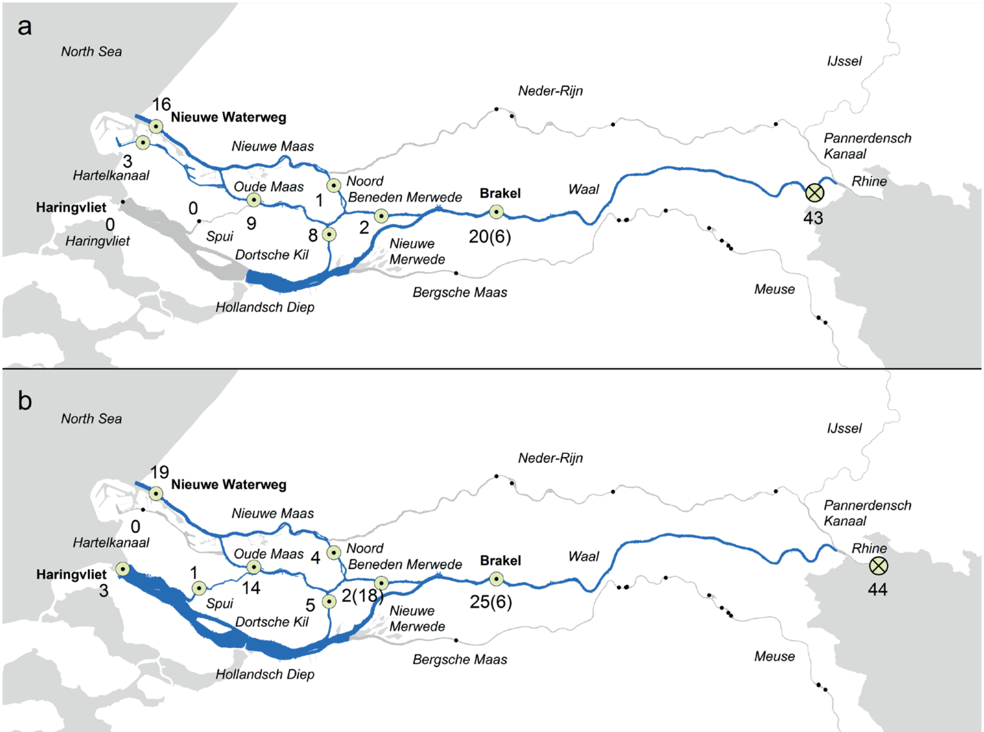


Figure 6.1. Study area and outmigration pathways (blue lines and areas). (a) 2012, (b) 2015. Yellow circles with crosses = release locations; black dots = NEDAP trail stations with no detections; white dots with black centres = stations with detections; numbers = detections of individual sturgeons (n); numbers between brackets = other individual sturgeons that passed this station without being recorded as deduced from detections collected further downstream.

6.3 Results

6.3.1 Outmigration pathways

The outmigration pathways were mapped (Figure 6.1a and b) based upon detections derived from 63 (72%) of the sturgeon (Table 6.1); additional data was obtained from finds on river banks and recaptures in the North Sea (Table 6.2, Figure 6.3). No sturgeon was detected upstream of the release sites. Considering the release site in 2015, the sturgeon reached the first bifurcation 9.5 km downstream (Figure 6.1b) between the Pannerdensch kanaal (channel) which carries approximately a third in river discharge and the Waal (river) carrying two third of the discharge. All sturgeons detected followed the maximum river discharge. At the first station ("Waal_Brakel", Figure 6.1a and b) 20 and 25 sturgeons were detected in 2012 and 2015, respectively. But by back-tracking of individuals detected at stations further downstream and by additional recaptures from the North Sea that were previously undetected, it was deduced that more sturgeons must have passed station Brakel undetected i.e. 29 and 32, respectively; the same principle applies to station “Beneden Merwede Sliedrecht” (Table 6.2, Figure 6.1a and b). At 102/117 km downstream from the release location there is a second bifurcation between the Nieuwe Merwede and the Oude Merwede (Figure 6.1a and b). From this bifurcation two main routes lead towards the North Sea, via the discharge sluices of the Haringvlietdam or via the Port of Rotterdam (Nedap stations “Nieuwe Waterweg” and “Hartelkanaal”, Table 6.1). In 2012 the sturgeons preferred the route Nieuwe Merwede → Hollandsch diep → Dordtsche Kil → Oude Maas → Nieuwe Waterweg (Figure 6.1a). In 2015 the sturgeons preferred the route Beneden Merwede → Oude Maas →Nieuwe Waterweg (Figure 6.1b).

Both years, most sturgeons migrated towards the station “Nieuwe Waterweg” which corresponds to the Port of Rotterdam (Table 6.2, Figure 6.1a and b). The number of detections collected at this station differed between both years: in 2012 the station collected 99% of all detections, in 2015 this proportion was 78% of all detections (Table 6.1) and for both years it corresponds to the most frequented area (169 and 95 days of detections).

In 2012, the migration from the release site towards the Nieuwe Waterweg took between 2.5 and 48 days (n = 16), with an average of seven days. Three sturgeon were detected in the Hartelkanaal (Port of Rotterdam), but no sturgeon was detected at the Haringvlietdam. In 2015, the migration to the Nieuwe Waterweg took between 3 and 52 days (n = 19), with an average of 13 days. In 2015 sturgeon were also detected along the route towards the Haringvlietdam which took between 8 and 13 days (n = 3), with an average of 11 days. Two sturgeons passed the Haringvlietdam immediately after their arrival, whereas a third sturgeon was delayed for 5 days. One sturgeon was detected in the channel Noord (Figure 6.1b) which most likely reached the North Sea through the Nieuwe Waterweg. Thus, in both years at least 50% of the sturgeons were confirmed to have reached the North Sea (Table 6.2).
In 2012 the average movement speed downstream was 1.2 m/s (106 km/day) and the fastest sturgeon moved 1.6 m/s (142 km/day). In 2015, 1.1 m/s (96 km/day) and 1.5 m/s (127 km/day), respectively.

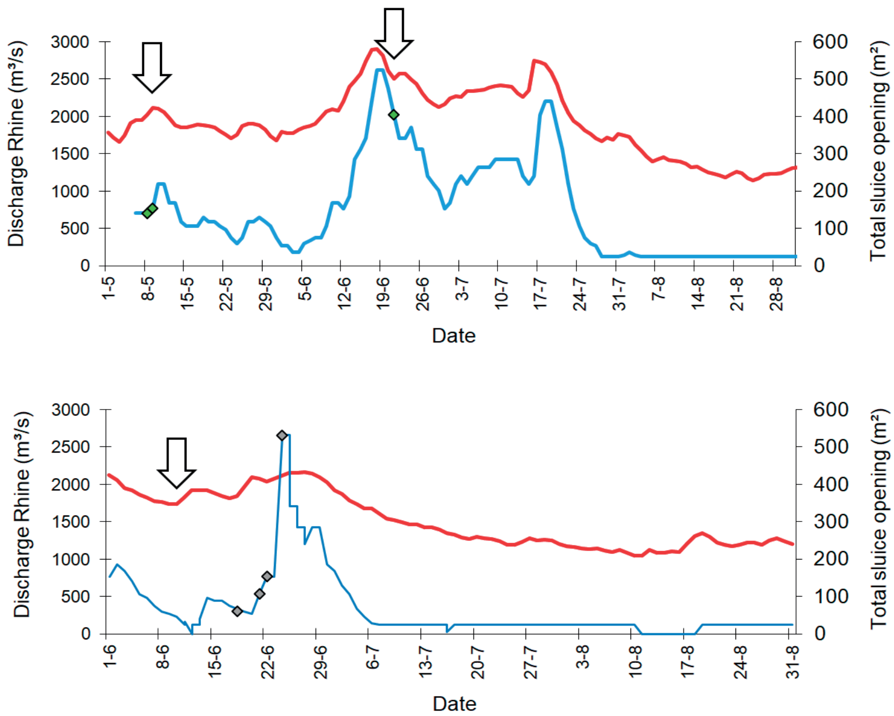


Figure 6.2. (a) 2012 and (b) 2015 Rhine River discharge (red line), total opening of the sluices of the Haringvlietdam (blue line), release moments (arrows), and sturgeon detections at the Haringvlietdam in 2015 (green squares). Source: RWS Operationele bedieningsstaat Haringvlietdam.

Table 6.1 Detections collected by the NEDAP Trail system in 2012 and 2015.

	Kekerdom		**Spijk**	
Release site and month =>	**May/June 2012 (*n* = 43)**		**June 2015 (*n* = 44)**	
Name NEDAP stations W	***n*[a]**	***n*(%)**	***n*[a]**	***n*(%)**
Water location	**sturgeons**	**sturgeons**	**sturgeons**	**sturgeons**
Waal Brakel	20 (6)	20	25 (6)	47
Beneden Merwede Sliedrecht	2	2	2 (18)	13
Dordtsche Kil s'Gravendeel	8	8	5	6
Noord Kinderdijk	1	1	4	5
Spui Zuidland	-	-	1	2
Oude Maas Spijkenisse	9	14	14	18
Hartelkanaal Port of Rotterdam	3	5	-	-
Nieuwe Waterweg Port of Rotterdam	16	5,412 (99%)	19	365 (78%)
Haringvliet dam	-	-	3	9
Total detected	26	5,426	31	465

[a] Missed detections as recalculated from detections downstream.

6.3.2 Interactions between sturgeons, ship propellers and fishermen from the north sea

In total three sturgeons were found dead on river banks by pedestrians (Table 6.1, Figure 6.3), all within seven days after their release. Based upon the decomposition of the bodies they were dead for several days. None of the dead sturgeon were detected. Two were found between the release site and station Brakel, nearly decapitated with sharp cuts perpendicular to the body. A third sturgeon was found at 102 km from the release site but the transponder was broken, the sturgeon had a broken tail, a broken dorsal spine, and a sharp but shallow cut at the beginning of the belly.

Ten sturgeons were reported in coastal waters, representing 11% of all sturgeons released (n = 87) and 22% of the sturgeons that were confirmed to have reached the North Sea (n = 45) (Table 6.2). Nine sturgeons were released alive and one died in 2012 due to a stone that was picked up by the net. In 2012, six sturgeons (three not detected) were recaptured by beam trawlers (Figure 6.3). Five were caught between July 19 and August 20, thus within 1 month after the release. During this period shrimpers were licensed to fish without sieve net (to omit abundant sea weed), a provision to reduce by catch (Polet et al., 2004). In 2015, four sturgeons, all detected by the Nedap system, were recaptured between June 28 and December 31. Two were caught in a gill net, one by a beam trawler and one by an angler on December 19 in the Oosterschelde (Figure 6.3). Until present (April 2018) no further re- captures were reported of tagged sturgeon from this study. In total the observed mortality (finds and recaptures) was 5% (n = 4). Sturgeons with unknown fate represented in 2012 25% (n = 11) of the released sturgeons and 36% (n = 16) in 2015 (Table 6.2).

6.4 Discussion

6.4.1 Function of the Nedap trail system

In total 65% (n = 57) of the sturgeons were detected which resulted in 5,927 detections collected by nine stations (Table 6.1). In 2012 the stations in the Beneden Merwede and in the Haringvlietdam were malfunctioning, both were repaired in that year. The other stations were functional during the study period, but there were still non-detections and back-tracking was done to receive a better image of the outmigration pathways. In a similar study with Atlantic salmon smolts (*Salmo salar*) the overall percentage of non-detections was 13.6% (unpublished data). Possible reasons for non–detections are: (a) the signal is interrupted when a transponder is less than 10 cm to the hull of a vessel; (b) when the transponder is parallel to the antennae the chance of non-detection becomes higher (Ensing & Breukelaar, 2017).

6.4.2 Outmigration pathways

Both years, most sturgeon reached the Port of Rotterdam within 2 weeks. The overall downstream movement speed was approximately 100 km/day which is about 20 km/day faster than the estimated speed of the river. A close look at the outmigration patterns shows that the sturgeons probably followed the routes with the highest river dis- charge. In 2015, at the first bifurcation all sturgeon took the route over the Rhine/Waal, which carries approximately 2/3 of river discharge. At the second bifurcation Beneden-/Nieuwe Merwede the same principle applies, although a bit less obvious, which can be explained as follows: the sluices of the Haringvlietdam are used to redirect river water in the Lower Rhine network to facilitate navigation and to prevent excessive salt water intrusions in the Port of Rotterdam. When the river discharge is below 1,100 m3 /s the sluices are closed and most river water flows into the Port of Rotterdam and out into the North Sea. At higher river discharges the redundant river water is discharged during ebb tides under free fall into the North Sea via a measured opening of the sluices of the Haringvlietdam. This starts at a river discharge of between 1,100 and 1700 m3 /s (RWS, 1984) and at higher discharges consequently more water is directed via the Nieuwe Merwede towards the Haringvlietdam. In 2015, the sturgeon preferred the route through the Beneden Merwede. In the first week after their release the average river discharge was 1868 m^3 /s and the average sluice opening of the Haringvlietdam was 65 m^2 . Three sturgeons were detected at the Haringvlietdam. However, in 2012, the sturgeons preferred the route through the Nieuwe Merwede. In the first seven days after the release the average river discharge was somewhat higher than in 2015: 2,000 m^3/s and 2,443 m^3/s and the average sluice opening of the Haringvlietdam was 164 m^2 and 314 m^2 . No sturgeon was detected at the Haringvlietdam but this station was out of order in that year. In 2012 three sturgeons not previously detected were recaptured at sea, and this is an indication that probably more sturgeons entered the North Sea through the Haringvlietdam.

Nevertheless, most sturgeons were detected at station Nieuwe Waterweg, a location with a high influx of the sea, characterized by a dynamic salt-fresh water gradient (Dankers et al., 2006). Here the sturgeon stayed on average 14 and 22 days, and probably this is an expression of acclimatization behaviour to salt water. Notably, sturgeon that passed the Haringvlietdam did have no time to adapt to salt water, they went from Lake Haringvliet immediately into the North Sea and this could have been a problem for their wellbeing or even survival. Given the high average movement speed and the uniformity with which the sturgeons migrated downstream it is not very likely that any sturgeon stayed in the river. In addition, no sturgeon was detected during the year after the last detection observed in 2015.

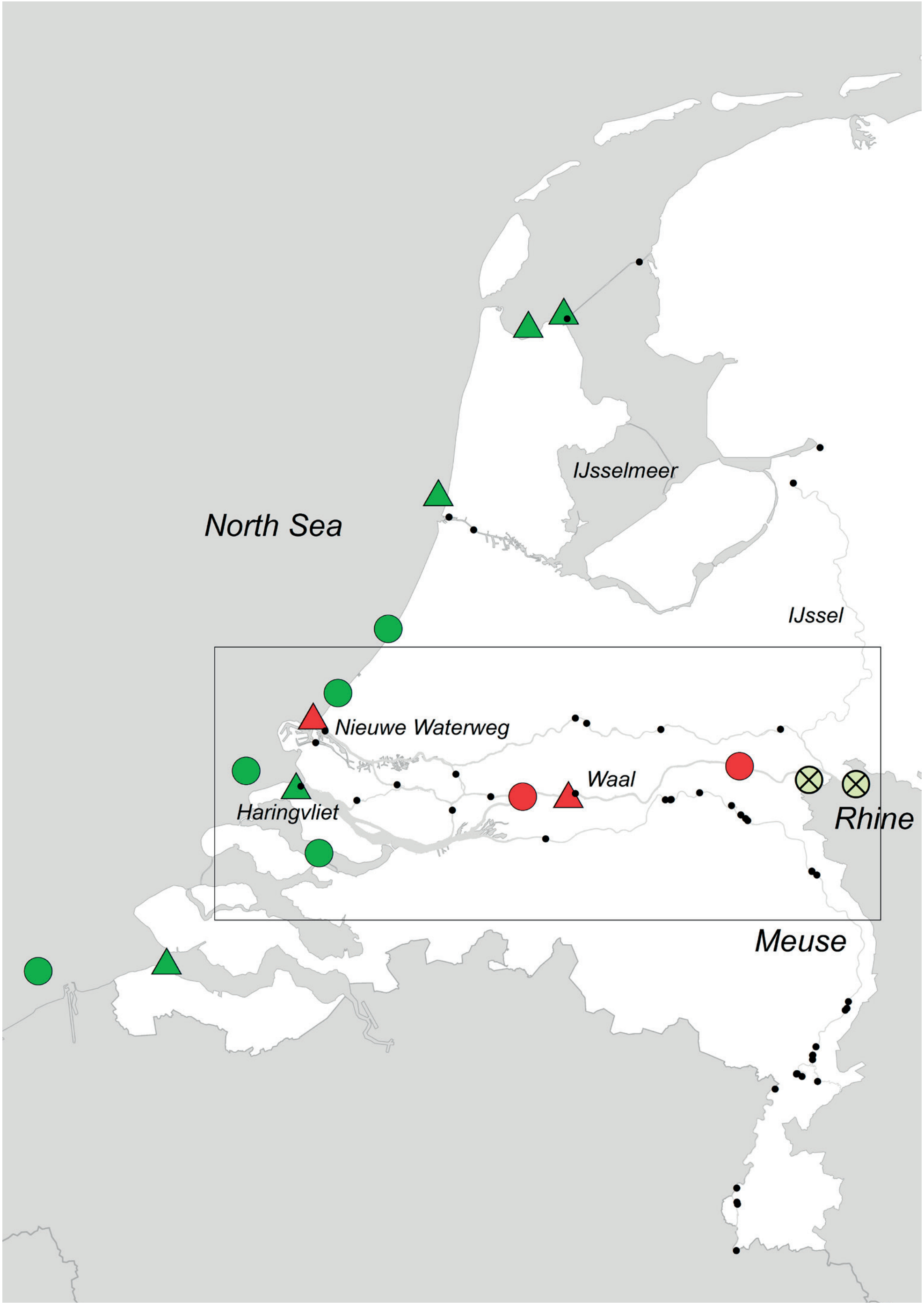


Figure 6.3. Locations of release locations (two circles with crosses), sturgeons found on river banks (red) and of reported recaptures (green). Circles = 2012, triangles = 2015.

6.4.3 Sturgeons found on river banks, recaptures from north sea and mortality rates

Three sturgeons were found dead along a 100 km shoreline. In this river stretch, the banks are not easily reached by foot, limiting the number of possible encounters. It is likely that not all sturgeons that died washed ashore, nor were discovered but the exact number remains unknown due to the non-detections. Several studies describe the loss of Atlantic sturgeon (*Acipenser oxyrinchus*) due to collisions with ships and propellers in the Delaware and James rivers, USA (Balazik et al., 2012; Brown & Murphy, 2010). No direct evidence was collected, but the wounds described and shown in pictures resemble those of the finds in the Rhine.
Mortality was not only observed in the river but also at sea. The reported recapture rate was quite high from 14% to 9% according to years but the mortality declared by fishermen was low (10%). The Dutch coast is intensively fished by demersal fisheries such as gill-netting and beam trawling (e.g. Bergman & Hup, 1992) and this probably hampers future sturgeon rehabilitation when fishing gear is not fine-tuned to minimize the bycatch. Commercial fishers were willing to report their catch. In 2012, five out of six sturgeons were caught within one month when shrimpers were allowed to fish without sieve nets. A sieve net reduces bycatch in beam trawling, most round fish will then be released under water (e.g. Polet et al., 2004). In 2015, only one sturgeon was caught by a shrimper. By that time sieve nets were obligatory and it seems from the reduced number of bycatch that sieve nets may work for sturgeon. The other gear types mentioned are impossible to facilitate with comparable escape routes for round fish. Thus other measures would be necessary to reduce possible mortality and it is therefore recommended to aid commercial fishermen and anglers by delivering good id-cards and handling protocols.

The estimation of overall mortality lies between n = 4 and 28 (4 confirmed dead, 24 unknown fate) i.e. 5%–32% (Table 6.2). It is difficult to interpret what happened with the undetected sturgeons. Considering the variability of the Nedap system detection efficiency, some could have reached the North Sea without being detected, and some could have died either due to ship propellers or due to difficulties to adapt to the natural environment. Notably, the sturgeons were raised in a protected environment for many years and released into a main European River that is intensely navigated and with high current velocity. Although the sturgeons were acclimatized to river water, most likely the sturgeons encountered difficulties in adapting their behaviour immediately after the release, and this could have caused extra mortality in comparison to wild sturgeons of the same age that would be more adapted to the River environment.

6.4.4 Towards a Rhine sturgeon action plan

Considering the first key question as mentioned in the introduction section, it seems that the outmigration pathways in the Lower Rhine are available and the Port of Rotterdam corresponds to the main entrance at sea. However, when regarding the extremely slow growth of an European sturgeon population and the long generation time, any source of mortality amongst individual sturgeons caused by mankind (i.e. ship propellers and by-catch) may continue to hamper current and future efforts to restore the population, as is outlined for a close relative, the Atlantic sturgeon *Acipenser oxyrinchus* (Boreman, 1997; Gross et al., 2002). Considering the ship propellers injuries observed in this study as well as the rate of by-catch, the overall estimated mortality being between 5% and 32%, the key questions 3 (interference with navigation) and 5 (cooperation with fishermen) are prior questions to be assessed in the project of a Rhine sturgeon action plan.

To complete the present study carried out on sturgeons >3 year old, studies on YOY sturgeon survival and behaviour (habitat selection, downstream migration) in freshwater and transitional waters would be relevant. Such a study should preferably be carried out during 2019–2020 (see key question no. 7) when a new management scheme of the discharge sluices of the Haringvlietdam will be implemented to improve fish migration between the natural estuary of Rhine and Meuse Rivers and the North Sea, and includes the recovery of a semi-permanent salt-fresh water transitional zone in this estuary (Paalvast, 2016). However, considering the actual availability of YOY in the French captive stock it may not happen before 2021. When the assessment of experimental release of YOY in the Rhine will be possible, a comparison with the behaviour described in the Gironde (Acolas et al., 2017), and the habitat assessment in the Elbe (Gessner et al., 2014), or a joined study would make sense to help find data gaps, differences in survival, growth parameters and spatial and temporal distribution.

Acknowledgements

Co-finance was obtained in 2012 via the Living North Sea pro- gramme (funded by Interreg IVB) and in 2015 by the Nationale Postcode Loterij Dream fund. Licenses were obtained from the Ministère de l'écologie, du développement durable et de l'énergie, Les directions régionales de l'environnement, de l'aménagement et du logement (DREAL) (GA/LM-15.012801-no 132) and the Dutch Government (FF/75A/2011/066 and FF/75A/2014/049). The telemetry was carried out under license no. AVD223000002015110, provided by the Dutch Commission for the Control of Animal Experiments.

Chapter 7

Surviving young European sturgeons *Acipenser sturio* go with the flow

Part 3

Currently under review for *Journal of Fish Biology:*

Brevé NWP, Vis H, Verspui R, Lauronce V, Veenstra A, Buijse AD, Murk AJ & Nagelkerke LAJ (2024). Surviving young European sturgeons *Acipenser sturio* go with the flow. Journal of Fish Biology

Photo: Deployment of a buoy and attached acoustic antenna in the Haringvliet lake, on board the ship 'Merwestroom', Rijkswaterstaat.

Abstract

Seventy-four European sturgeons *Acipenser sturio*, aged 13-15 months, were tagged for acoustic telemetry and released into the freshwater estuary of the Rhine and Meuse rivers. Significant losses occurred within one month in the dammed, slow-flowing waters within seven km of the release site (n=31, 42%). Lower losses occurred in the free-flowing parts towards the North Sea, up to 66 km from the release site (n=36, 49%). Only seven fish reached the North Sea. We suspect that predation caused the losses and recommend future releases in free-flowing river sections, at night.

Brief communication

This study is part of a feasibility assessment for the reintroduction of the critically endangered, anadromous European sturgeon *Acipenser sturio* into the river Rhine. In a previous study, carried out in 2012 and 2015, 3-5 year old juvenile sturgeon, tagged for radio-telemetry, were released into the Rhine (n = 43 and n = 44 respectively) (Breve et al., 2019). Tracking data obtained from 57 fish (66%) revealed the species' downstream migration pathways through the Rhine delta, of which 39 (68% of fish detected, and 45% of total fish released) moved into the Port of Rotterdam where they spent two weeks, supposedly acclimatizing to seawater, before entering the North Sea. The study highlighted two problems: ship propeller strikes, as three fish (3%) with visible sharp wounds were found dead on the shores within seven days after their release; and bycatch at sea, as of the 45 fish (52%) confirmed to have reached the North Sea, ten (22%) were caught near the coast by shrimpers and gillnetters, of which nine fish were released alive and one died (Brevé et al., 2018).

One possible explanation for what was considered to be a reduced survival was that these 87 juvenile sturgeon came straight from the hatchery, so they may have been naive to a natural environment, and more susceptible to predation and human pressures than wild fish. Furthermore, as these 'older' juveniles were already able to adjust their osmoregulation to the salinity of seawater, they swam straight into the North Sea. The combined studies provided insight into the migration pathways and potential associated problems, but limited insight into the species' natural behaviour, survival, and habitat use in the estuary of the Rhine and Meuse rivers.

The present study used acoustic-telemetry to track younger juvenile European sturgeons (13 - 15 months of age, Table 7.1). Acoustic telemetry requires smaller tags than the used radio-telemetry, allowing the tracking of smaller and younger fish: in this case, fish >100g, using tags of 2g, following the 2% rule of thumb (Smircich & Kelly, 2014). Sturgeons were provided by MIGADO from the same *ex situ* broodstock in southern France, as those from the previous radio-telemetry study. It was assumed that these younger fish would remain in the estuary for at least one to three months, as juvenile European sturgeon become tolerant to salinity fluctuations after approximately 15 months of age (Rochard et al., 2001).

We used InnovaSea's VUE tag model V8-4x-BLU-1, IDs A69-1604-17036 / 17110. These tags have a mass of 2.0 g, are 8 mm in diameter, 20.5 mm long and can optionally be set to a power output of 144 or 147 dB (low or high). The V8-4x tags were configured in three steps. In step 1, the tags were turned on for one hour at low power with a minimum delay of 40 s to allow tag-checking during surgical implantation (all tags worked). See Brevé et al. (2013) for the surgical protocol. In step 2, the tags were turned off for 23 days. During this period, fish were quarantined at the hatchery for two weeks, adapted to river currents, transported to the Netherlands during one night in an 800 L tank with adjustable oxygen supply and manually checked every two hours. Hereafter, the fish were kept for one week in a holding vessel with river Rhine water (this vessel has a reservoir with perforated screens) to allow the sturgeons to acclimatise to the local water conditions. The fish were fed twice daily with krill and bloodworms provided by MIGADO. In step 3, tags were set to on, with a delay ranging from 40 to 190 seconds, and a high power output level of 147 dB, based on range tests carried out in the Port of Rotterdam and at the Haringvliet Dam (Fig. 7.1). Tag-life was estimated to be approximately 148 days.

On 2 June, and 11August 2023, a total of 74 juvenile sturgeon were released in the 'Biesbosch' (Fig. 7.1 and Table 7.1). This freshwater estuary has a history of seasonal sturgeon aggregations (Brevé et al., 2022) and provides abundant food sources for juvenile sturgeon (Van de Ven, 2020). The study area included the port of Rotterdam and the dammed freshwater Haringvliet reservoir, which was historically an open estuary of the Rhine and an important fish migration route, until it was closed by the Haringvliet Dam in 1970. The route via the port of Rotterdam is currently the only open and free-flowing connection between the Rhine and the North Sea. The sluices in the Haringvliet Dam form a coastal migration barrier and an abrupt transition between freshwater and seawater, and negatively affect fish migration, especially during dry summer months (Breukelaar et al., 2009).

The study used a telemetry network of 79 InnovaSea VR2W-69 kHz and VR2Tx receivers mounted on buoys. The receivers were provided by Wageningen Marine Research and the Royal Dutch Angling Alliance (Sportvisserij Nederland), while the buoys were maintained by Rijkswaterstaat, the executive agency of the Ministry for Infrastructure and Water Management. In the estuary, the receivers were placed in arrays, spaced no more than 400 metres apart. At sea, the receivers were mounted further apart on buoys that define the shipping lane along the coast.

Forty-three juvenile sturgeons (61%) were identified by the telemetry network. The tracking data revealed that the juvenile sturgeons typically left the Biesbosch within 2-4 days. A total of 31 fish were not detected and may not have left the area. They were also not found during a dedicated search in the Biesbosch, using a V100 mobile antenna on 26 June and 4 October in 2023 (24 and 54 days after release, respectively) at seven locations within an individual distance of approximately 1 km, between the release site and the main exit to the south (Fig. 7.1). While it is possible that the tagged fish found one other, very narrow, alternative route out of the Biesbosch to the north, it is more likely that these fish were lost due to predation by fish or birds that may have moved beyond the detection range. Furthermore, of the 43 juvenile sturgeon identified by the telemetry network at the main exit of the Biesbosch, only 7% were not detected further downstream. And the two receivers covering the main exit of the Biesbosch continuously detected each other every day throughout the study, indicating full coverage of this migration route. Therefore, the telemetry system seems to have functioned adequately, making it highly unlikely that tagged sturgeon leaving the Biesbosch would not be detected by antennas further downstream.

The 43 fish that migrated from the Biesbosch mainly followed the free-flowing route towards the North Sea, taking the route Dortsche Kil, Oude Maas, Nieuwe Waterweg (see Fig. 7.1a). Thirty-four fish (79%) were last detected within 30 days (batch 1: 9 out of 18 and batch 2: 21 out of 25). The tagged sturgeons actively avoided the mostly dammed and slow flowing parts of the estuary. Only seven fish reached the North Sea, batch 1 (n=5) between 3-9 days and batch 2 (n=2) between 4 and 79 days (see Fig 7.1b). These fish swam towards the Haringvliet, but returned on their tracks to enter the free-flowing Dortsche Kil. Five of these seven fish stayed at the seaward side of the Haringvliet Dam. Notably, this migration pattern is consistent with the routes used by the sturgeons in 2012 and 2015, when also most fish found the North Sea via the port of Rotterdam (Brevé et al., 2018).

The study shows that the juvenile European sturgeons suffered significant losses in the dammed and slow flowing sections of the estuary (Hollandsch Diep and Haringvliet, see fig. 7.1) compared to relatively lower losses in the free-flowing sections. For future experimental releases of juvenile sturgeons, it is recommended that they be released in flowing river conditions, preferably in the middle of the river and at night, on the assumption that this will minimize predation. This method could reduce the hunting success of predatory birds and fish that rely on vision. In order to verify the suspected predation problem, we recommend to repeat the experimental release at the exit of the Biesbosch area, but only with a minimum number of sturgeon (n=30), using predation tags (e.g. model V7D-2x) and a more closely spaced receiver network at this site in particular in the direct vicinity of the release site.

Table 7.1. Dates of hatch, tagging, and release of 74 juvenile European sturgeons, released in the estuary of Rhine and Meuse rivers, and estimated end of tag life.

Batch	Number of fish	Hatched	Tagging	Release	Age of fish in days	Age of fish in months	Days between tag and release	Estimated end of tag life (148 days)
1	29	24-5-2022	9-5-2023	2-6-2023	375	13	24	28-10-2023
2	45	24-5-2022	17-7-2023	11-8-2023	445	15	25	6-1-2024

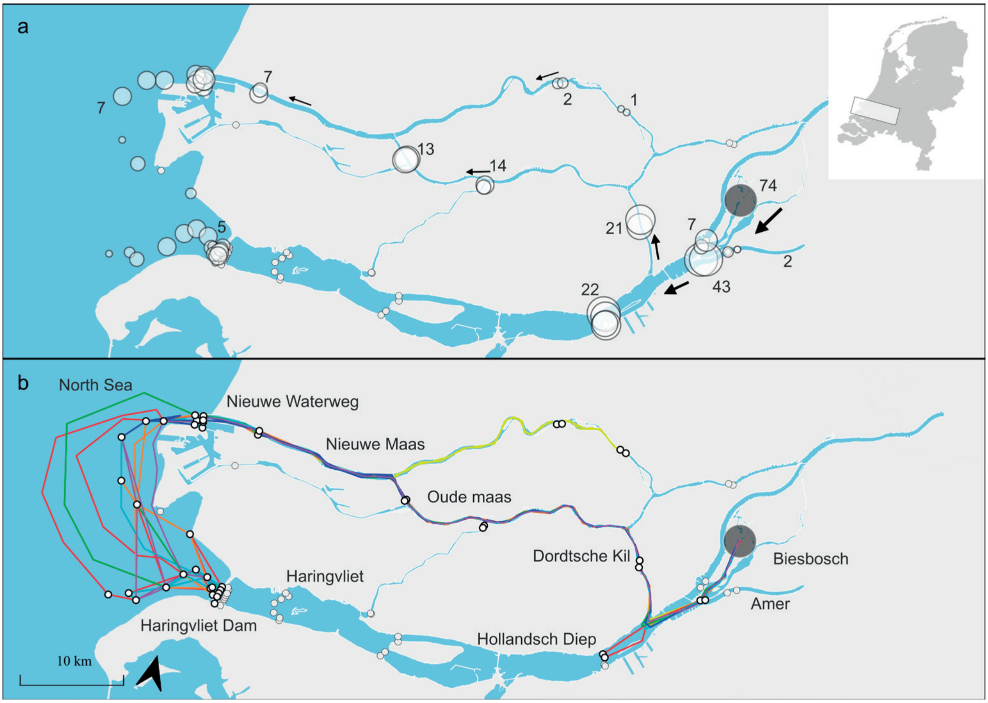


Figure 7.1. Observed migration patterns of European sturgeon *Acipenser sturio* in the age of 13-15 months, released in the estuary of rivers Rhine and Meuse. Fish were tagged for acoustic telemetry. Grey dot = release site in the Biesbosch area. (a) Map overview showing the locations of 79 antennas (white dots) and number of individual fish detected, as well as the route choices of juvenile European sturgeons, released on 2 June and 11 August in 2023 (n=29 and n=45, respectively). The arrows show the main migration route taken by the fish, which is also the main river discharge, and the main route taken by the juvenile European sturgeons in the age of 3-5 years, in 2012 and 2015. (b) The migration route of the seven tagged juvenile sturgeon that reached the North Sea. Fish did not enter the dammed, slow flowing waters of Hollandsch Diep and Haringvliet, but showed some searching behaviour in the area, before choosing to the free-flowing migration route towards the North Sea. Thereafter, five fish remained at the seaward side of the Haringvliet Dam during the full study period.

Acknowledgements

We are grateful to the staff of INRAE, Eric Rochard and Marie-Laure Acolas for providing their expertise in the telemetry studies, and to the staff of MIGADO, William Bouyssonie, Damien Filloux, Baptiste Henri, Quentin Buisson and Alexandre Daronnat for writing the French project plan, providing and tagging the sturgeons, and the CITES permit. We thank the staff of VisAdvies, Robin Blokhuijzen and Marnix van Schaik, for organising the transport of the fish, renting and placing the holding vessel, feeding the sturgeons during their stay in the Netherlands, and for their work during the release event. We thank ARK Rewilding the Netherlands, especially Bram Houben, Ernst Schrijver and Iris Roggema, and colleagues from the World Wide Fund for Nature, especially Maarten Bruns, for organising and chairing the sturgeon release event on 2 June 2023. We thank Melanie Meijer Zu Schlochtern of Wageningen Marine Research, and Robert Weijman, Paul Wijmans, and Marcus de Boer of Sportvisserij Nederland, and the staff of Rijkswaterstaat, especially Arjen Ponger, for collecting the data from the receiver network on two occasions, in October 2023 and January 2024. We thank Menno de Ridder and Donné Slangen of LNV and Niels Houben from Sportvisserij Zuidwest Nederland, for providing licences for the study.

Chapter 8

Europeans or Americans? Towards an optimized strategy for reintroducing sea sturgeons (*Acipenser sturio* and *A. oxyrinchus*) to Europe

Part 4

Currently under review for *Biodiversity and Conservation:*

Brevé NWP, Nagelkerke LAJ, Buijse AD, Murk AJ, Philipsen P, Nijland R & Lenders HJR (2024) Europeans or Americans? Towards an optimized strategy for reintroducing sea sturgeons (*Acipenser sturio* and *A. oxyrinchus*) to Europe. *Biodiversity and Conservation.*

Photo: Researcher Reindert Nijland looks at the 'wet' collection of juvenile sturgeons at the Naturalis Biodiversity Center, Leiden.

Abstract

The aim of this paper is to identify an optimized strategy for the reintroduction of two anadromous sturgeon species to Europe: the critically endangered European sturgeon (*Acipenser sturio*) and the vulnerable Atlantic sturgeon (*A. oxyrinchus*). Restoration efforts began in 1991 with artificial rearing and stocking (release) of *A. sturio* in rivers of the French Atlantic coast and North Sea, followed in 2006 by the stocking of *A. oxyrinchus* in Baltic Sea rivers. This approach is based on the most recent geographical occurrences of both species, but may no longer be a viable strategy. We deliver evidence that both species spawned in North Sea rivers into the 20th century by analysing acipenserid remains, and argue that additional factors need to be considered to determine which species has to be reintroduced where. Factors include poleward (northward) shifts in suitable habitats due to climate change; the scarcity of *A. sturio* that limits stocking possibilities, monitor population developments and evaluate (fisheries) management measures; and the risk of hybridisation and outbreeding of the genetically eroded *A. sturio*. This paper analyses the various factors and re-evaluates three alternative, theoretical strategies to determine their advantages and disadvantages: (1) prioritising the restoration of only the critically endangered *A. sturio*, (2) maintaining a strict north-south division of reintroductions for the two species, and (3) restoring a 'mixed zone' of sympatric occurrences in Northwest Europe, particularly in North Sea rivers. This re-evaluation emphasis the significance of scientific communities in Europe to closely collaborate in reintroducing these species.

8.1 Introduction

Insights may change as scientific knowledge expands across multiple disciplines (Marg & Theiler, 2023). After decades of efforts to conserve and restore the European sturgeon (*Acipenser sturio*) (Williot & Castelnaud, 2011), studies of acipenserid remains revealed that not one, but two closely related anadromous sturgeon species had existed in Europe: *A. sturio* and the Atlantic sturgeon (*A. oxyrinchus*) (Ludwig et al., 2002). This insight influenced the reintroduction strategy. Between the 1970s and 2002, conservation measures focussed solely on *A. sturio* by tag-recapture studies and later artificial rearing and stocking offspring in the Gironde, Garonne and Dordogne (GGD) river basin in France, home to the last relict population of the species (Williot et al., 2009b). The river Elbe in Germany was selected as a backup option with the implementation of a second *ex situ* broodstock with sturgeon derived from the French broodstock in 1996 (Williot & Kirschbaum, 2011). While, from 2000 onwards, the river Rhine in the Netherlands, Germany, France and Switzerland, became the subject of a feasibility assessment for a potentially third reintroduction effort (Brevé et al., 2019b; France Ministère de l'Écologie, 2020; Visser et al., 2020; Williot & Kirschbaum, 2011).

Rivers in *Acipenser sturio*'s former southern range, in the Mediterranean, Adriatic, and Black Seas, were not considered for reintroduction due to the severe environmental degradation caused by damming, canalisation, intensive fisheries, and pollution (Almaca & Elvira, 2000; Bacalbaşa-Dobrovici & Holčík, 2000; Economidis et al., 2000; Jarić et al., 2010; Kolman & Zarkua, 2002; Ludwig et al., 2011; Ninua, 1976; Puijenbroek et al., 2019; Williot et al., 2002a), and because of climate change. According to Lassalle et al. (2010), climate change will render the species' former southern range less habitable, while increasing the suitability of historic areas such as the North Sea, as well as additional northern areas, such as Icelandic or Norwegian rivers.

From 2002 onwards, a study of historical acipenserid remains in the Baltic region, led to the reintroduction of *A. oxyrinchus* from a genetically comparable Canadian source to Baltic Sea rivers. Experimental releases were effectuated in 2006 in the Oder and Vistula rivers in Poland and Germany, and participation of other Baltic countries subsequently increased over time (Gessner et al., 2019; Kolman et al., 2016; Purvina & Medne, 2018; Ruban, 2020).

Consequently, *A. sturio* is reintroduced in two rivers of its former northern range, but not in its original southern range, while *A. oxyrinchus* is reintroduced in a growing number of Baltic rivers. However, this strategy may not necessarily provide a solid foundation for the sustainable conservation of both species, for five main reasons described below.

(1) Hybridisation is common in sturgeon species (Birstein et al., 1997b) and fertile offspring is produced in most sturgeon crossbreeding (Shivaramu, 2019). Hybridisation and introgression between *A. sturio* and *A. oxyrinchus* has occurred in the past (Birstein, 2002; Chassaing et al., 2018; Chassaing et al., 2011b; Fontana et al., 2008; Popović et al., 2014; Thieren et al., 2016a) and may occur in the future, which could pose a problem for their conservation in Europe, in particular for the genetically eroded *A. sturio*. Although both sturgeons express homing behaviour to their natal rivers (Bemis & Kynard, 1997) they are also highly migratory species that spend most of their lifespan in estuaries and coastal waters. Both species are known to partially stray, colonize adjacent rivers, and expand their range (Ludwig et al., 2002; Nikulina & Schmölcke, 2018). Currently, both species are stocked in geographically separated rivers, but catches of tagged subadult *A. oxyrinchus* stocked in Baltic Sea rivers have already been reported from the marine environment, off the coasts of Norway, Cornwall, and from the Loire River mouth; meanwhile, *A. sturio* stocked in the Gironde and Elbe rivers occur along the French Atlantic coast (including the Bay of Biscay and English Channel), and in the North Sea and the Western Baltic Sea (Charbonnel & Acolas, 2022; McCormick et al., 2023). Thus, subadults of both species already occur in sympatry in their marine habitat, and because of a process of straying and colonisation it may be difficult, if not impossible, to maintain a strict north-south separation of both species for the medium and long term to prevent hybridisation.

(2) There is a clear difference between the two species' Red List status and consequently between the urgency and potential (availability) to take restoration measures. The International Union for Conservation of Nature (IUCN) lists *A. sturio* as critically endangered (CR) with less than 750 mature individuals estimated to exist (Gessner et al., 2022). In contrast, *A. oxyrinchus* is listed as vulnerable (VU), and although the species is extinct in Europe, populations are increasing worldwide. Currently, the number of mature *A. oxyrinchus* individuals has been assessed to be approximately 10,000 specimens in North America (Hilton & Fox, 2022). The scarcity of *A. sturio* and its current limited genetic diversity (Ludwig et al., 2004) emphasizes the need for strong conservation efforts. However, obviously, the restricted reproductions and intermittent supply of *A. sturio* offspring has hindered conservation efforts, including stocking opportunities, monitoring population development at sea, and assessing the effectiveness of fisheries management measures (Charbonnel & Acolas, 2022; Charbonnel et al., 2022). In contrast to the limited availability of *A. sturio*, *A. oxyrinchus* is widely available from aquaculture (Brevé et al., 2022b; Waldman et al., 2002). Using *A. oxyrinchus* for restoration in the French Atlantic coast and North Sea could lead to faster progress than solely focusing on *A. sturio*. In that case, the potential hybridisation risk would be accepted (see point 1).

> "Acipenser sturio *is so scarce that each specimen is precious; thus, it is risky to experiment with them. But given the similarities between the two species, those seeking to restore* A. sturio *should be able to adapt much of the information learned from managers of* A. oxyrinchus." (Waldman, 2000), p. 237.

(3) The current reintroduction programmes are primarily based on the last known historical geographical occurrences of both species during the 19th and 20th centuries. However, insights have recently changed and are still developing. There is still some debate over whether *A. sturio* 'outcompeted' *A. oxyrinchus* in the French Atlantic coast and North Sea, or whether both species coexisted in the region during the early 20th century (Nikulina & Schmölcke, 2016a, 2016b; Nikulina & Schmölcke, 2018; Thieren et al., 2016a; Van Neer et al., 2012). Moreover, samples from the 19th and 20th century only provide insight into the situation immediately before the extinction (Ludwig et al., 2002). According to IUCN/SSC (2013), useful anchoring dates for species reintroductions are 1500 (pre-European expansion) and 1750 (pre-industrialization). For example, if reintroduction were to commit to 1750 as anchoring date, a different strategy should be considered. Both species coexisted in rivers along the French Atlantic coast and in North Sea rivers for approximately 6,000 years before 1750 (Nikulina & Schmölcke, 2016b; Nikulina & Schmölcke, 2018; Thieren et al., 2016a).

(4) Most of the anthropogenic threats that caused the extinction of the two sturgeon species in Europe have increased in intensity *thereafter*. Thus, "*The last place in which a species/population was found may not be the best habitat for returning the species.*" (IUCN/SSC, 2013), p. 8. Fisheries intensity has significantly increased in the past century, and currently incidental bycatch mortality is considered a main threat to *A. sturio* conservation in the Northeast Atlantic (OSPAR Commission, 2009, 2021; Sahrhage & Lundbeck, 2012). Most European rivers have been transformed into effective shipping lanes through canalisation, and hard river engineering, and fish migration routes between the sea and the rivers' lower and middle ranges have been lost due to diking, hydro-damming, and the building of storm surge barriers (Eigaard et al., 2017; Mako & Galieriková, 2021; Puijenbroek et al., 2019; Sahrhage & Lundbeck, 2012). So, not only have the chances of survival at sea decreased, but also the quality of suitable spawning habitat in the natal rivers across the species entire former range.

And lastly (5), there is ongoing international interest in sturgeon restoration, which has consequences for a much-needed Pan-European strategy. These include the efforts for the Rhine, the development of a sturgeon action plan for the UK (Colclough, 2021; McCormick et al., 2023), and the experimental release of *A. sturio* juveniles in the river Ebro in Spain in 2023. The latter illustrates that even though there are strong arguments against *A. sturio* restoration in its former southern range (climate change, habitat degradation and loss) there are still some 'southern' rivers that may offer potential for the species reintroduction, including the Minho in Portugal, the Ebro in Spain, the Po in Italy, the Danube in Hungary, and the Rioni in Georgia (Bacalbaşa-Dobrovici & Holčík, 2000; Kolman & Zarkua, 2002; Ninua, 1976). Restoration of *A. sturio* to these rivers would omit potential conflicts of hybridisation between the two species, since *A. oxyrinchus* was historically absent from *A. sturio*'s southern range.

> "*As habitats vary over space and time, species' ranges are dynamic. Environmental conditions will continue to change after species extinction. It is invalid to assume that former range will invariably provide suitable habitat."* (IUCN/SSC, 2013), p. 13.

This study re-assesses the reintroduction strategies for *A. sturio* and *A. oxyrinchus* in Europe, by asking whether a preferential strategy can be identified for reintroducing both species. This paper, therefore, distinguishes three distinct theoretical strategies to discuss and identify the advantages and disadvantages of the resulting measures: (1) a priority focus on restoring only the critically endangered *A. sturio*; (2) aiming to maintain a strict north-south division of reintroductions; and (3) inducing a 'mixed zone' of sympatric occurrences in Europe and in particular in North Sea rivers.

8.2. Methods

8.2.1 Literature study

This study is partly based on a literature search, conducted through the platforms of Scopus (www.elsevier.com/solutions/scopus) and Natural Science Collection ProQuest (https://www.proquest.com/products-services/natural_science.html). The following query string was applied in 'advanced search' in Titles, Abstracts and Summaries: "*Acipenser sturio*" or "*Acipenser oxyrinchus*" and "Europe*" (* = wildcard). After eliminating duplicate information, scanning all abstracts and further snowballing (citation tracking), a total of 117 articles were selected that were considered of direct relevance to this study. These articles were used to identify all factors that could potentially affect the different reintroduction strategies.

8.2.2 Species check for the Rhine

The Rhine is currently considered for reintroduction of *A. sturio*. As this river basin is located in the middle of the 'mixed zone' of both species historical occurrences in North Sea rivers, we investigated whether *A. oxyrinchus* occurred and spawned in the Rhine during the 19^{th} and 20^{th} centuries, using two methods. First, we verified both species' occurrences in the archaeological data from Thieren et al. (2016a), who state that *A. oxyrinchus* has been the dominant species for the North Sea rivers, including the

Rhine, for records that date to the Modern era. The authors of the latter study provided their unpublished data for this present study, detailed per river and era. Secondly, to verify the results for the Rhine, we additionally identified ten acipenserid specimens, dated between 1840-1905, to the species level. The specimens are present at the Dutch Naturalis Biodiversity Centre: six in the wet collection (bottled fish < 45 cm TL) and four in the dry collection (stuffed specimens and skeletons >100 cm TL). Specimens from the wet collection were identified through genome skimming, as described in Trevisan et al. (2019), and by mapping the corresponding DNA sequences to publicly known mitochondrial DNA. Specimens from the dry collection were identified based on a visual evaluation of the surface pattern of their bony plates (scutes). Although both sturgeon are morphologically very similar, especially in their early life stages, they can be identified to the species level based on the presence of alveolar or tubercular patterns on their bony plates. The different patterns are diagnostic for *A. oxyrinchus* and *A. sturio* respectively, but only for individuals of over one meter in total length (Thieren et al., 2016b); Thieren et al. (2015).

8.2.3 Synthesis of information

In the results and discussion section, we use the literature review to describe both past and present reintroduction strategies for both sturgeon species in Europe. We present the results of the data analyses of archaeological and museum specimens for the Rhine and link these to a general discussion of which of the two sturgeon species is native to which geographical area. The discussion continues with a description of the potential consequences of ongoing climate change on shifts in geographical ranges, and the consequences of hybridisation and competition between the two species. Finally, we discuss what these factors mean for three theoretical reintroduction strategies, with their respective advantages, disadvantages and knowledge gaps, and highlight what is realistically feasible, taking into account reintroduction efforts already underway.

8.3. Results and discussion

8.3.1 Sturgeon colonisation of the Northeast Atlantic, the North Sea and the altic Sea

Before 2002, it was an accepted theory that the two sea sturgeons had been separated by the Atlantic Ocean for 60 million years (Bemis & Kynard, 1997). While the American coast from Labrador to Florida was inhabited by *A. oxyrinchus*, *A. sturio* was assumed to have a wide distribution in Europe, including the marine basins and large rivers of the Black Sea, Mediterranean Sea, Adriatic Sea, French Atlantic coast, North Sea, and Baltic Sea (Billard & Lecointre, 2000). However, the picture changed (particularly for the Baltic Sea) when morphological, genetic and archaeological evidence proved that both species' spatiotemporal distributions were affected by the transition from the Weichselian glaciation to the current interglacial period (Ludwig et al., 2002; Ludwig et al., 2009b; Peng et al., 2007).

In 2002, Ludwig et al. (2002) stated that *A. oxyrinchus* had 'swam east' during the Middle Ages and immigrated from North America into the Baltic Sea, where it replaced the native *A. sturio* there. From later studies, more detailed, additional information became available about the exact timing of when and where *A. oxyrinchus* colonised Europe, and how the species spread. The up until now oldest known finds of *A. oxyrinchus* are from the site of the Yangtzehaven (Rotterdam, the Netherlands, mouth of the river Rhine) and date between 7000 and 6500 BC (Thieren et al., 2016a). Archaeological finds of *A. oxyrinchus* are reported along the Northeast Atlantic coast of France and Great Britain, the North Sea, the Baltic Sea, and Lake Ladoga in Russia (Arndt et al., 2006; Chassaing et al., 2013; Galimova et al., 2015; Gessner et al., 2007; Nikulina & Schmölcke, 2016b; Popović et al., 2014; Thieren et al., 2016a; Tiedemann et al., 2007). Archaeological finds of *A. sturio* show that this species' populations colonized the French Atlantic coast and the North Sea roughly from 6,000 BC onwards, originating from Mediterranean and Iberian waters (Chassaing et al., 2011a; Chassaing et al., 2013; Desse-Berset, 2009; Desse-Berset & Williot, 2011; Nikulina & Schmölcke, 2016b; Popović et al., 2014; Thieren et al., 2016a). However, no self-sustaining population of *A. sturio* seems to have occurred in the Baltic Sea; only *A. oxyrinchus* and *A. oxyrinchus x A. sturio*, the latter probably through hybridisation in more southerly North Sea and Atlantic rivers and subsequent colonisation northwards (Chassaing et al., 2011a; Galimova et al., 2015).

8.3.2 Different interpretations of last appearances for the southern North Sea

For the southern North Sea, the historical presence of both species is accepted, but there is less agreement as to when each of the two species dominated or last occurred in the area. Nikulina and Schmölcke (2016b) concluded that *A. oxyrinchus* was the dominant sturgeon species of the southern North Sea between 6,000-1,000 years ago, after which *A. oxyrinchus* was thought to have been gradually replaced, and possibly outcompeted, by *A. sturio*. This conclusion was drawn from an analysis of 438 archaeological acipenserid remains from the Rhine, Ems, Weser, Elbe and Eider rivers. In contrast, Thieren et al. (2016a) showed that *A. oxyrinchus* continued to dominate in the North Sea well into the 20th century. This study analysed over 7,000 acipenserid bones collected from the catchments of the Ems, Rhine, Meuse, Scheldt and Thames rivers. The authors of the latter study provided their unpublished data for this present study (Table 8.1). The table shows that both species have been present for millennia in the southern North Sea and that *A. oxyrinchus* has been the dominant species. For the Modern Era the number is small but indicative: *A. oxyrinchus* and *A. sturio* both occurred in the rivers Thames (n = 4 and 1 respectively) and Scheldt (n= 1 and 2 respectively) (Table 8.1). For the Naturalis collection for the Rhine and Meuse rivers, three out of six acipenserid remains, previously labelled as *A. sturio*, were identified as *A. oxyrinchus*, including a 20 cm long specimen caught in the Rhine in November 1905 (Table 8.2). As *A. oxyrinchus* (and *A. sturio*) of this size are not yet able to adapt their osmoregulation to seawater (Acolas et al., 2011a; Acolas et al., 2012; Allen et al., 2014; McCord et al., 2007; Rochard et al., 2001), this specimen is evidence of *A. oxyrinchus* spawning in the Rhine in the summer of 1904.

Due to the difficulties in identifying acipenserid remains to the species level, it is possible that previous identifications were inaccurate. Sturgeon skeletons are primarily cartilaginous, only partially ossified, and their remains are often strongly eroded (Panagiotopoulou et al., 2014; Thieren et al., 2015). Still, on the basis of both small datasets we can conclude that both species were native to the southern North Sea and the rivers Thames, Scheldt, Rhine and Meuse, and that *A. oxyrinchus* spawned in the Rhine into the 20th century. Based on the historical evidence, there is no objection to consider both species for reintroduction to southern North Sea rivers.

8.3.3 Decline in sturgeon populations

Although both sturgeon species coexisted along the French and UK Atlantic coast, from the Bay of Biscay to the southern North Sea, from approximately 7,000 BC onwards (Thieren et al., 2016a), their populations began to decline and disappear in the late 19th century (Brevé et al., 2022d; Lenders, 2017; Thieren et al., 2016a; Van Neer et al., 2012). The last natural reproductions for *A. sturio* were documented in the Gironde basin (France) in 1980, 1988, and 1994 (Ludwig et al., 2004). No last reproductions were documented for *A. oxyrinchus*, but last catches were reported from the Baltic Sea in the second half of the 20th century (Kolman et al., 2011a), and a catch was reported from the North Sea off the coast of Grimsby (UK), in 1986 (Thieren et al., 2016b).

8.3.4 Acipenser sturio restoration in Northwest Europe

During the 20th century, *A. oxyrinchus* vanished from Europe, while for *A. sturio* only one relict population remained in southern France. This population became the subject of a restoration program that was planned as early as the 1970's by the National Research Centre for Agricultural and Environmental Engineering (CEMAGREF, currently INRAE) (Castelnaud, 1988; Castelnaud et al., 1991b; Williot & Castelnaud, 2011). The strategy was formulated as a four-point approach: (1) gain in-depth insight into the species' biological and ecological characteristics, such as through tag-recapture studies (Castelnaud et al., 1991a; Letaconnoux, 1961); (2) sustain the relict population through restocking from an *ex situ* broodstock, using wild-caught spawners to artificially reproduce offspring (Charlon & Williot, 1978; Williot & Castelnaud, 2011; Williot et al., 2002b); (3) acquire knowledge from the Siberian sturgeon (*A. baerii*) to avoid adverse effects of research on the relict *A. sturio* population (Williot et al., 2018); and (4) create awareness amongst stakeholders (fishers) and the public about the dwindling population and the extinction risk (Michelet, 2011).

Table 8.1. Number of zooarchaeological sturgeon remains from North Sea rivers and coasts per archaeological/historical period. Numbers represent specimens identified with near-certainty to the species level on the basis of splanchnocranium or scute pattern of sturgeon with a reconstructed length > 1 meter (*A. sturio*: tubercular pattern; *A. oxyrinchus*: alveolar pattern). Numbers between brackets represent scutes of sturgeon with a reconstructed length < 1 meter or of sturgeon of unknown length. Archaeological and historical periods are defined as follows: Mesolithic c. 11000–7300 BP; Neolithic 7300–4000 BP; Bronze Age 4100–2800 BP; Iron Age 2800–2057 BP; Roman Period 2057–1600 BP; Middle Ages 1500–500 BP; Modern Era 400–200 BP. Data kindly provided by Els Thieren.

Era	**North Sea Rivers**	**Coast**	**Ems**	**IJsselmeer Wadden Sea**	**Laak Coast**	**Rhine-Meuse**	**Orne**	**Scheldt**	**Somme**	**Thames**	**Trent**
Mesolithic	*A. oxy.*					1 (1)					
	A. sturio										
Neolithic	*A. oxy.*	(37)				346 (10)		1			
	A. sturio	(8)				57 (4)					
Bronze Age	*A. oxy.*					5 (1)					
	A. sturio										
Iron Age	*A. oxy.*	(2)		(1)							
	A. sturio	(1)									
Roman	*A. oxy.*					61 (15)			(3)		
	A. sturio					7 (3)					
Middle Ages	*A. oxy.*		(1)		1	2	(1)	2		4 (1)	(5)
	A. sturio				1					2	(6)
Modern Era	*A. oxy.*							1		4	
	A. sturio							2		1	
Total	*A. oxy.*	(39)	(1)	(1)	1	410 (27)	(1)	4	(3)	8 (1)	(5)
	A. sturio	(9)			1	64 (7)		2		3	(6)

Table 8.2. Selection of acipenserid remains from the Naturalis collection verified to the species level. Specimens from the dry collection (all > 100 cm TL) were identified on the basis of morphological characteristics; specimens from the wet collection (all < 45 cm TL) were identified on the basis of DNA-analysis. All specimens were previously identified as *Acipenser sturio*. Verification showed that at least three fish were *A. oxyrinchus*. NL = the Netherlands.

Collection	Location	Date	Length (cm)	Live stage	Verified species identification	Naturalis Registration
Dry (> 1 m TL)	NL		125	adolescent	*Acipenser sturio*	RMNH.PISC.D.2715
	North Sea, NL		100	adolescent	*Acipenser sturio*	RMNH.PISC.D.2730
	North Sea, NL		129	adolescent	*Acipenser sturio*	RMNH.PISC.D.2734
	NL	Sept. 1840	107	adolescent	*Acipenser oxyrinchus*	RMNH.PISC.S.302
Wet (< 45 cm TL)	Meuse, NL			juvenile	Uncertain	ZMA.PISC.123532
	Rhine, NL Nieuwe Maas, Rotterdam	29 Nov. 1905	20	juvenile	*Acipenser oxyrinchus*	ZMA.PISC.123533
	North Sea, NL, Noordwijk			juvenile	Uncertain	RMNH.PISC.4053
	North Sea, NL	30 Apr. 1873	50	juvenile	*Acipenser oxyrinchus*	RMNH.PISC.4565
	Rhine, NL, IJsselmonde,			juvenile	Uncertain	RMNH.PISC.8930
	North Sea, NL Texel			juvenile	Uncertain	RMNH.PISC.27159

However, due to a continued deterioration of the species' population, the restoration strategy changed and included the development of a breeding plan for conservation of genetic variability (Ludwig et al., 2004), and an action plan for careful management of the population and the species' critical habitats (France Ministère de l'Écologie, 2020; Kirschbaum et al., 2000; Williot et al., 2009a). Unfortunately, the French hatchery broodstock of *A. sturio* has a low genetic variability. When it was established in 1991, it used 38 wild-caught individuals from the 1980s, and in addition 29 from 1994, the last year of natural reproduction, whereafter more fish were obtained through artificial rearing of an incidentally caught pair of adult spawners in 1995 (Ludwig et al., 2004; Williot et al., 2000; Williot & Chevre, 2011; Williot et al., 2002b). All specimens from 1994 and 1995 are full siblings and have the same genetic value for artificial reproduction (Ludwig et al., 2004). The breeding plan uses forced disassortative mating, i.e., mating of any reproducing female with a genetically distantly related male, facilitated by cryoconservation of sperm, in order to maintain the genetic variability and minimize inbreeding (Tiedemann et al., 2011). A first success was achieved in 1995 (Williot et al., 2000), again between 2007 and 2014 (Williot & Chevre, 2011), and most recently in 2022 and 2023.

In 1996, a second broodstock was established in collaboration with the Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB in Berlin, Germany) to spread the risk of losing the species. These sturgeons were derived from the French brood stock whenever there was a surplus of offspring (Council of Europe, 2018; Williot & Kirschbaum, 2011; Williot et al., 2007), and were used to reintroduce *A. sturio* to the river Elbe (Williot & Kirschbaum, 2011). Currently, the French-German sturgeon cooperation is still ongoing. To date, a total of 1.7 million *A. sturio* larvae and juveniles have been released intermittently in the Gironde basin and 20,000 in the Elbe basin (Charbonnel & Acolas, 2022). In addition, a total of 161 tagged sturgeon juveniles were experimentally released in the river Rhine in 2012, 2015 (Brevé et al., 2019b), and 2023. As a result of stocking, (sub)adult *A. sturio* have been reported from incidental bycatch captures from the French Atlantic coast, English Channel and southern North Sea (Charbonnel & Acolas, 2022; Charbonnel et al., 2022). Natural reproduction has not been observed to date.

The same holds true for reintroduced (stocked) *A. oxyrinchus* to Baltic Sea rivers. Fertilised eggs, larvae, and fry were obtained from the population of the Saint John River in Canada (Gessner et al., 2006; Gessner et al., 2010a; Kolman et al., 2011c). Broodstocks have been established in German and Polish facilities, and the first offspring was obtained in 2010. As of 2022, approximately 6.5 million specimens have been released into the Oder, Vistula, Nemunas, Venta, and Narwa rivers in Poland, Germany, Latvia, Estonia, and Lithuania as part of a marine basin-wide approach coordinated by the Helsinki Convention (Gessner et al., 2019; Kolman et al., 2016; Purvina & Medne, 2018). Although the fish are approaching maturity as evidenced by reported incidental bycatch in Baltic and North Sea fisheries, no natural reproduction of *A. oxyrinchus* has yet been observed.

8.3.5 Climate change and distribution ranges

Climate change is an important factor to be taken into consideration for both species´ restoration and geographical reintroductions. Because of the long-term commitment required it is important to assess the historical spatiotemporal shifts of their ranges, and of potential *additional* shifts under current climate change, since, "*an ecological benchmark is a moving target*" Lyman (2006).

The historical occupation of the Baltic Sea by *A. oxyrinchus* is generally attributed to its slightly higher tolerance to colder climates compared to *A. sturio* (Chassaing et al., 2013; Ludwig et al., 2002; Ludwig & Gessner, 2007; Ruban, 2020). Kolman et al. (2018) estimated the optimal temperature for *A. oxyrinchus* egg incubation to be 16°C, while Delage et al. (2019) estimated it to be close to 20°C for *A. sturio*. However, populations of both species have been found in both temperate and subtropical zones (Bemis &

Kynard, 1997). It is possible that these may represent different genetically adaptations to local environmental circumstances, still, temperature alone cannot fully explain the changes in historical distribution patterns (Nikulina & Schmölcke, 2016b). We therefore suggest that the observed patterns are due to differences in temperature *and* the osmoregulatory capacity of juveniles between the two species, with salinity being the determining factor.

Acipenser sturio can adjust its osmoregulation to higher salinities at an earlier life stage than any other sturgeon species (Holčík et al., 1989). Juvenile *A. sturio* spend their first years in brackish estuarine waters with salinities of 5-25‰, and at approximately 15 months of age they are able to migrate to seawater with a salinity level of 33‰ (Rochard et al., 2001). In contrast, juvenile *A. oxyrinchus* have the physiological ability to move between different salinity habitats, but they grow much faster at low salinities (0-10‰) than at marine conditions (33‰) (Allen et al., 2014; McCord et al., 2007; Niklitschek & Secor, 2010). The combination of temperature *and* salinity may therefore explain why *A. sturio* thrived in the extreme saline (38-39‰) warm Mediterranean Sea (Economidis et al., 2000), while *A. oxyrinchus* thrived in the low saline cold Baltic Sea.

Historic large-scale ice melt, which has lowered the temperature and salinity of Northeast Atlantic coastal waters since about 10,000 BC, could explain the timing of *A. oxyrinchus* colonisation of Northwest European waters. The flux of meltwater peaked during deglaciation, after which the ice sheet persisted until approximately 8,000 BC (Mauri et al., 2015; Siegert & Dowdeswell, 2002; Strandberg et al., 2022). Due to ice-cap melting and increased precipitation during a large part of the Holocene, salinities and temperatures decreased significantly. As a result, conditions in the Northeast Atlantic, North Sea and specifically in the Baltic Sea may have become more suitable for *A. oxyrinchus*, but less so for *A. sturio*.

Currently, there is a noticeable difference in salinity levels across the entire historical range of both sturgeon species. Surface salinities in the Mediterranean Sea reach 38-39‰, while along the French Northeast Atlantic coast, it is 37‰. In the German Bight, it is 32‰, and in the Baltic Sea, surface salinities range between 8-17‰ (Dormann, 2023; Sammartino et al., 2022). In Northwest Europe, salinity may decrease due to the melting of the polar ice caps, increased precipitation and subsequent freshwater discharge into the sea. Climate change predictions show a strong latitudinal gradient, with a temperature rise and decreased precipitation in the southern part of Europe, and an increased precipitation in the northern part of Europe (Milly et al., 2005; Teuling et al., 2019). According to the IPCC, the Mediterranean region is expected to experience a greater increase in sea temperature compared to the Northwest region (e.g. North Sea) (Masson-Delmotte et al., 2021; Philipsen, 2023).

In conclusion, under current climate change scenarios, the Mediterranean, Adriatic and Black Seas may become less suitable for *A. sturio*, due to further temperature increases. However, the Northeast Atlantic, Bay of Biscay, English Channel and North Sea, and even the coastlines of Island and Norway may become (more) suitable for both species (Lassalle et al., 2010; Lassalle et al., 2009; Lassalle & Rochard, 2009).

8.3.6 Hybridisation and competition

The conservation of *A. sturio* currently relies on *ex situ* management and meticulous genetic characterisation to safeguard the remaining genetic diversity in the long-term (Council of Europe, 2018; France Ministère de l'Écologie, 2020; Gessner et al., 2011c). The species is highly endangered and unsuitable for experimental hybridisation. Although both species naturally exhibit extensive homing to their natal rivers (Ludwig et al., 2002; Waldman, 2000), it is important to note that they have hybridised in the past (Thieren et al., 2016b). This implies that both species can – at least partially – use the same spawning grounds. As both species are currently stocked rather than born in rivers, their imprinting and homing behaviour may not be well developed. This could lead to greater straying and colonisation than under natural conditions. If both species colonise the same rivers, *A. oxyrinchus*, which is stocked in much higher quantities, may do so before *A. sturio* has the opportunity, or more frequently. The presence of a larger number of *A. oxyrinchus* compared to *A. sturio* may increase the likelihood of hybridisation and potentially lead to the disappearance of *A. sturio* as a distinct species. However, any hybridisation or competition is only likely to occur in the medium to long term. The generation interval for each species is approximately 14 years (FishBase, 2020a, 2020b) and it takes approximately 50-150 years for sea sturgeon to build multi-generational populations (Acolas et al., 2011a; Waldman et al., 2019).

8.3.7 Alternative strategies for reintroductions

Based on the different determining factors or drivers that could guide the reintroductions of *A. sturio* and *A. oxyrinchus* to Northwest Europe, we have identified three distinct, alternative theoretical reintroduction strategies (see Table 8.3): 1) prioritising the restoration of only the critically endangered *A. sturio*, (2) maintaining a strict north-south division of reintroductions for the two species, and (3) restoring a 'mixed zone' of sympatric occurrences in Northwest Europe, particularly in North Sea rivers. Notably, all strategies depend on *ex situ* broodstocks and artificial rearing. Table 8.4 has an overview of the aim, advantages and disadvantages of each strategy.

Table 8.3. Historical geographical distribution of *A. oxyrinchus* (*Ao*) and *A. sturio* (*As*) across Northwest Europe, and three theoretical reintroduction strategies. N.B. historically, *A. oxyrinchus* was absent in the Mediterranean, Adriatic and Black Seas; *A. sturio* was absent in the Baltic Sea, but there were *A. oxyrinchus* x *A. sturio* hybrids.

Range	Marine basin, and large rivers debouching therein	Historical reference (before 1750)	Current strategy (2024)	Alternative reintroduction strategies		
				Strategy 1 Focus only on *As*	Strategy 2 North: *Ao* South: *As*	Strategy 3 *Ao* and *As* plus 'Mixed' zone
North	Baltic Sea	*Ao and Ao x As*	*Ao*	-	*Ao*	*Ao*
	North Sea	*Ao, As and Ao x As*	*As*	*As*	-	*Ao and As*
	French Atlantic coast, including Bay of Biscay & English Channel	*Ao, As and Ao x As*	*As*	*As*	*As*	*Ao and As*
South	Mediterranean Sea Adriatic Sea Black Sea	*As*	The southern range, former stronghold of *As*, is currently considered lost for the species' and reintroduction may become even less suitable due to climate change.			

8.3.8 Theoretical strategy 1: Focus on solely reintroducing the critically endangered *A. sturio*

The aim of this strategy is to prevent the global extinction of *A. sturio*. Therefore, efforts are exclusively focused on the restoration of *A. sturio* populations. Due to climate change, rivers in the species' northern range are primarily considered. The reintroduction of *A. sturio* into unsuitable rivers is not recommended (IUCN/SSC, 2013) and may even be illegal (Bastmeijer, 2019) as it carries a risk of losing individuals of this critically endangered species in a potentially unsuccessful reintroduction effort. To make progress, feasibility assessments of rivers that may still offer opportunities for *A. sturio* reintroduction could be conducted by other countries than France and Germany. This strategy has already been implemented for the Rhine in the Netherlands, the Severn in the UK, and for the last stretch of the Ebro in Spain. This approach could be further extended to other rivers and countries (Gessner et al., 2011c; McCormick et al., 2023; Visser et al., 2020). One advantage of this strategy is that it helps to develop a common approach to save the critically endangered *A. sturio*. However, a disadvantage - that comes from the species critically endangered status - is the limited broodstock and as a consequence the limited possibilities for raising large quantities of fish for stocking and addressing the genetic erosion of the species. Although *A. sturio*'s capacity to evolve in response to different environmental changes cannot be assessed, it may be extremely low and not representative of the past intraspecific diversity (Ludwig et al., 2004). This means that the artificially reared *A. sturio* from a single relict source population may be ill equipped both genetically and phenotypically to survive and adapt to rivers outside than the GGD river basin or to environmental changes. To counteract the issue, additional *ex situ* broodstocks could be built using imprinting of river water from other basins. To improve the chances of settlement of *A. sturio* and eliminate any possibility of competition and hybridisation, it may be considered to discontinue the reintroduction of *A. oxyrinchus* to Europe. As *A. oxyrinchus* populations are not endangered in North America, there is no urgent need for action in Europe. However, if the current reintroduction effort of *A. oxyrinchus* in the Baltic Sea area proves successful with natural reproduction - as 6.5 million individuals are already stocked - discontinuing the effort would be impossible.

8.3.9 Theoretical strategy 2: Maintain a strict north-south division between both species' reintroductions

This strategy aims to maintain a clear division between the reintroduction of the two species, with *A. oxyrinchus* being reintroduced to multiple Baltic Sea rivers and *A. sturio* to the GGD river basin in southern France. To avoid any potential negative impact of competition and hybridisation on *A. sturio* restoration, in this strategy all activities for North Sea rivers should be discontinued to increase a geographical distance between both species reintroductions. This includes the feasibility assessments for the Rhine and Severn, and of the reintroduction of the species to the river Elbe. However, discontinuation of *A. sturio* restoration already underway would meet strong opposition from Germany, the Netherlands and the UK. In addition, it is questionable whether a strict north-south division can be maintained in the long term, as the two highly migratory species already mix in the North Sea. Many individuals originate from fish that moved northward from the GGD river system, and possibly, due to climate change, *A. sturio* may lose its livelihood in the GGD river basin, and find more suitable rivers poleward.

8.3.10 Theoretical strategy 3: Reintroduce both species and allow for sympatry

The aim of this strategy is to reintroduce *A. oxyrinchus* not only to Baltic Sea rivers, but also to other areas where the species was native, including the French and UK Atlantic coast and North Sea rivers,(Chassaing et al., 2013), and in addition to the current reintroductions of *A. sturio*. This strategy ignores the potential risk of hybridisation, as *A. oxyrinchus* could establish in the middle of the range of a critically endangered species, potentially leading to the loss of genetically 'pure' *A. sturio*. The advantage would be to boost sea sturgeon presence, regardless of conservation status and achieve faster progress in sturgeon restoration, particularly for the North Sea area, than what has been achieved since the 1970s. This strategy allows for rapid progress by stocking large quantities of readily available *A. oxyrinchus*. Information on *A. oxyrinchus* can be obtained regarding incidental bycatch mortality, migration patterns, population development, and the monitoring of the effects of fisheries management measures. This information can be used to construct models of translocation strategies and outcomes, and to gain a better understanding of any pressures occurring to sturgeons.

> "*Where knowledge is limited, the best available information should be used, and further subsequent information used to confirm or adjust management.*" (IUCN/SSC, 2013) Annex 5.1.

8.5 Conclusions

The knowledge gained over the last twenty years allows for a reassessment of the main strategy to restore *A. sturio* and *A. oxyrinchus* in Europe. This paper discusses three potential alternative strategies, each based on fundamentally different preferences and troubled by several uncertainties. The appropriate strategy depends on the criteria deemed important, such as the preservation of *A. sturio* and the recovery of both sturgeon species throughout their former range.

Before a strategy can be chosen, it is necessary to address at least three main knowledge gaps: Firstly, what are the factors that inhibit natural reproduction? Secondly, how does climate change (including temperature and salinity shifts) influences the geographical ranges of both species? Finally, to what extent will introduced specimens of *A. oxyrinchus* influence the survival and genetic composition of *A. sturio* in river basins primarily intended for *A. sturio* introduction?

Notably, the risk of competition and hybridisation between *A. oxyrinchus* and *A. sturio* varies between the strategies employed. It could be minimised in strategy 1, but only if the current stocking of *A. oxyrinchus* to Baltic Sea rivers is halted (which is highly unlikely). It will increase in strategy 2 with the ongoing reintroductions of *A. oxyrinchus* to Baltic Sea rivers, unless a larger north-south separation is effectuated by halting *A. sturio* reintroduction to the river Elbe (also highly unlikely). In strategy 3, where both species are reintroduced into the same North Sea rivers the issue could become even more pronounced.

Table 8.4. Objectives, advantages and disadvantages of three strategies for sturgeon reintroduction to Northwest Europe.

Theoretical Strategy, Aim	**Advantages**	**Disadvantages**
1. Prioritising the restoration of only the critically endangered *A. sturio*. Considering the discontinuation of reintroducing *A. oxyrinchus* to Baltic Sea rivers.	Further development of a wider European commitment based upon a shared vision and a priority focus to save the critically endangered species would help to gain improved progress, involving more countries, assess the potential of more rivers for *A. sturio* reintroductions, and build additional *ex situ* broodstocks.	Mainly rivers in the species northern range are considered due to climate change. The extremely limited brood stock of *A. sturio* negatively affects the possibilities to obtain progress in stocking and experimental releases for feasibility assessments. The genetic erosion of the species may imply a low adaptability to reintroduction to rivers other than the GGD river basin. Discontinuation of *A. oxyrinchus* reintroduction to Europe, would eliminate a risk of possible competition and hybridisation, but would also meet strong opposition.
2. Maintaining a strict north-south division of reintroductions for the two species. Considering the continued reintroduction of *A. oxyrinchus* to Baltic Sea rivers, and of *A. sturio* to the GGD river basin in southern France. As well as the discontinuation of the reintroduction of *A. sturio* to North Sea rivers.	Discontinuing the reintroduction of *A. sturio* to North Sea rivers would increase the geographical distance between the reintroduction of both species, preventing competition and hybridisation.	Maintaining a clear north-south division between highly migratory species reintroductions, particularly in the North Sea where both species already mix, seems rather impossible. Reintroducing *A. sturio* to North Sea rivers would face strong opposition. The effects of climate change may threaten the livelihood of *A. sturio* in the GGD river basin.
3. Restoring a 'mixed zone' of sympatric occurrences in Northwest Europe, particularly in North Sea rivers. Considering the reintroduction of *A. oxyrinchus* to rivers in the Baltic Sea and North Sea.	Increasing the presence of sea sturgeon, regardless of the species and the conservation status, has advantages in terms of gaining a better understanding of all the pressures that affect the two sturgeon populations. Stocking large quantities of *A. oxyrinchus* can lead to fast progress in this regard. The presence of *A. oxyrinchus* can provide valuable insights into population development and the effects of fisheries management measures. Furthermore, the conservation of *A. sturio* could benefit from avoiding the risk of losing individuals of this critically endangered species.	Allowing a conspecific to establish within the middle of a critically endangered species range may potentially lead to the loss of pure *A. sturio*.

Given the critical status of *A. sturio* and the need to prevent the species extinction, the pursuit of current activities while addressing knowledge gaps appears to be the most effective approach. However, it is important to set a deadline due to the pressing time constraints, especially for the critically endangered *A. sturio*. A feasible deadline could be 2030, when all sturgeon stocked since 2006 and 2007 should have matured and had the opportunity to reproduce naturally. The strategy can then be adjusted based on the results of whether or not natural reproduction has occurred.

The main outcome of this paper is that it outlines the need for a playing field for both species' recovery in Europe. All stakeholders need to closely collaborate - be open to discuss the newest findings about the historical and current situation as well as underlying motivations - to develop a harmonized Pan-European strategy for both sturgeons´ rehabilitation and conservation. This strategy should consider the ecological responses of the two sturgeon species to changing environmental conditions, previous conservation efforts, and ethical principles, i.e., respect for the specimens that have already been released, an the great responsibility for the future-proof conservation of *A. sturio* in particular.
We hope that our analysis can help the development of a common strategy based on the knowledge and opportunities outlined. Given the nature of the two sturgeon species of which one is on the verge of extinction, there is a need for all stakeholders (national governments, NGOs and the scientific community) to collaborate across political boundaries to restore both native sturgeon populations. This work can be linked to the National Biodiversity Action Plans being developed in the wake of Montreal and/or the EU Biodiversity Strategy and Nature Restoration Plans.

Acknowledgements

We would like to express our gratitude to Wim van Neer and especially Els Thieren of the Royal Belgian Institute of Natural Sciences, for providing and reworking their data of Holocene acipenserid remains from the Rhine and other North Sea rivers for this study and for independently checking our own morphological identifications. We thank the staff of the Naturalis Biodiversity Centre: Esther Dondorp, Hannco Bakker, Elza Duijm, and Marina Ventayol, for granting us access to the dry and wet collections and allowing us to take tissue samples of acipenserid remains. We thank Jörn Gessner of the Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Eric Rochard of the French National Institute for Agriculture, Food, and Environment (INRAE), and Steve Colclough of the Institute of Fisheries Management (IFM) for thought-provoking discussions and the exchange of ideas. We thank Daniël van Berkel of the WUR Gen-lab for his mtDNA analysis of the Naturalis collection.

Chapter 9

General Discussion

Part 5

Photo: A young girl is interviewed by NOS Jeugdjournaal (Dutch national television for youth) about her opinion on the release of sturgeons into the river Rhine.

9.1 Introduction

This study aimed to assess the feasibility of reintroducing the critically endangered European sturgeon (*Acipenser sturio*) to the river Rhine and the North Sea. The assessment provides a basis to define the critical boundary conditions for successful reintroduction and can advise whether it is useful to stop or continue the reintroduction effort, and if so what additional conservation measures are needed.

The results presented in this thesis include an assessment of the availability of sufficient suitable habitats for the European sturgeon to fulfil its complete life cycle across a chain of marine, estuarine and riverine habitats. In addition, the main anthropogenic threats to the species and to its critical habitats are assessed, and it is discussed to what extent these threats can be mediated to enable a successful reintroduction to the river Rhine and the North Sea.

Four research question were formulated:

- Is sufficient suitable habitat available for European sturgeon in the North Sea and the river Rhine?
- What are the potential threats from incidental bycatch in coastal and estuarine areas for successful sturgeon reintroduction and from the currently present alien (non-native) sturgeons?
- What other local and/or regional threats could hinder the sturgeon's return?
- What are possible strategies considering the potential reintroduction of two native sturgeon species?

These research questions were answered in four sections, 1) habitats, 2) threats, 3) tracking, and 4) alternatives, ultimately culminating in section 5) the overall reintroduction feasibility assessment as presented in the synthesis (Fig. 9.1, Tables 9.1 and 9.2).

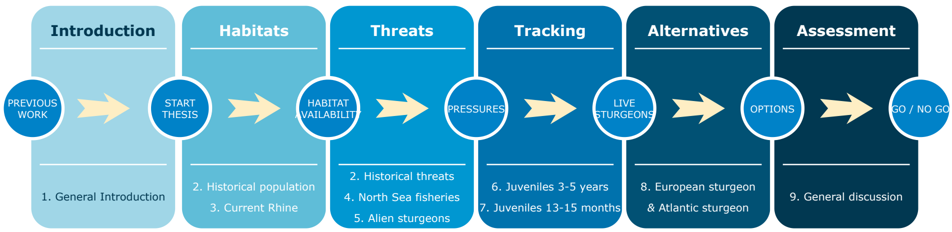


Figure 9.1. Thesis design.

9.2 Part 1. Key habitats – sea, estuary, river - Chapters 2 and 3

Main findings: The North Sea and the river Rhine provide sufficient habitat for the European sturgeon to complete its entire life cycle. The Rhine provides spawning habitat for around 2,500 female European sturgeon. However, the results may be an overestimate given the impact of inland shipping and coastal infrastructure, and probably also toxicological safety issues for juvenile sturgeon in the Rhine delta.

An assessment of foraging and overwintering habitats for European sturgeon in the North Sea has already been carried out in 2015, using dynamic energy budget (DEB) modelling and benthic food production data for shallow marine habitats (Winter et al., 2015). The results are supported by the survival of subadult fish that were released in the Garonne and Dordogne rivers, between 2007 and 2015, which invariably swim northwards into the southern North Sea and are occasionally observed along the Dutch coast (Charbonnel & Acolas, 2022; Charbonnel et al., 2024).

This thesis study into the availability of suitable habitat for European sturgeon in the river Rhine and the North Sea, began by reconstructing the historical seasonal and geographical distribution of sturgeons within the Rhine and the adjacent basins of rivers Ems, Meuse, and Scheldt (Brevé et al., 2022d). More than 98% of historical sturgeon reports originate from the Rhine-Meuse delta in the Netherlands and the Lower Rhine in the German state of North Rhine-Westphalia, and mainly between May and mid-August (Chapter 2)(Brevé et al., 2022d). Historically, sturgeons have sporadically been observed far upstream the river Rhine (Holčík et al., 1989), even 1,000 km from the North Sea in the tributary river Aare in Switzerland and also during winter months (Brevé et al., 2022c). Mature sturgeons clearly preferred the main stem of the Rhine above all other adjacent river basins and upstream tributaries such as the Main, Mosel, Neckar, etc. (Chapter 2, Figs. 2.1a and b). This geographical distribution pattern can be explained by the sturgeon's preference to spawn in deep, wide gravel beds in strong currents (Chapter 3, Supporting Information, Appendix A).

Subsequent 1D and 2D modelling and GIS based mapping of the *current* river Rhine habitat in Chapter 3 showed that potential nursery areas for sturgeons are mainly located in the Dutch Rhine delta, an area with an abundance of potential prey (Van de Ven, 2020). Moreover, the main stem of the Rhine in the German state of North Rhine-Westphalia offers approximately 0.75 km^2 of potential spawning areas, suitable for approximately 2,500 mature female European sturgeon to spawn. This is sufficient, as currently no more than 750 sub-adult European sturgeons exist (status 2021) (OSPAR Commission, 2021). However, the carrying potential of the current river Rhine for sturgeon and the species' recruitment potential, is reduced by other pressures such as impact of inland shipping and coastal infrastructure. Another potential threat is contamination of the water sediments with high levels of persistent, accumulating toxic compounds. This toxicological risk is the reason why eel fisheries and eel consumption in this area is banned (van den Dungen et al., 2016). The toxicological safety of the Rhine delta for sturgeons is a knowledge gap that requires further study (Tables 9.1 and 9.2).

9.3 Part 2. Threats: bycatch and alien sturgeons – Chapters 2, 4 and 5

Main findings: Coastal and estuarine bycatch always had a strong impact on the sturgeon population. A research complicating issue is that fishers currently refrain from reporting bycatch, as they suspect it will be used against them. The alien (non-native) sturgeons that are omnipresent in the study area, do not seem to pose an immediate threat to the reintroduction of the native sturgeon (considering predation or competition) as these fish do not seem to reproduce in the wild. Still, their presence is associated with a risk of introduction and spread of diseases and parasites.

9.3.1 Bycatch and fishers' unwillingness to support sturgeon conservation

With legal commercial sturgeon fisheries banned in Europe, unintended bycatch could be a main factor that is impairing sturgeon population recovery (Bastmeijer, 2019; OSPAR Commission, 2021). Also, when fishers do not release the Endangered, Threatened and Protected (ETP) species immediately, it is no longer considered an incidental bycatch but an act of poaching.

Anadromous sturgeons are particularly vulnerable to become incidental bycatch victims in shallow marine areas and estuaries where they congregate during feeding and spawning migrations (Charbonnel & Acolas, 2022; Rochard et al., 1997a). Unfortunately, since the Industrial Revolution, North Sea fisheries have further intensified (Sahrhage & Lundbeck, 2012). This resulted in a shift in harvests of sturgeons from spring and summer spawning aggregations in the estuaries to additional harvests of younger/smaller fish in coastal marine waters throughout the year (Chapter 2)(Brevé et al., 2022d; Hoek, 1910). Fisheries developments thus depleted the sturgeons stocks. Since then, estuarine and coastal fisheries have intensified further (Sahrhage & Lundbeck, 2012; Winter et al., 2015). Of the experimentally released fish in the Rhine, all reported sturgeon by-catches were made by small beam trawlers targeting shrimp (Chapter 6). By-catch mortality could be prevented and reduced by a number of measures, including more discriminating fishing gear (Chapter 6), awareness raising of sturgeon conservation, and having fishers involved in research on sturgeon conservation. Unfortunately, at present fishers refrain from reporting incidental bycatch and they are insufficiently involved in sturgeon conservation. Chapter 4 provides insights in this, and it explains why it is paramount to achieve a good understanding and what is required to obtain fishers' cooperation.

From the interviews held among fishers, researchers, and staff from environmental NGO's and the authorities in France, the Netherlands, Germany and the UK (mainly FR and NL) (Chapter 4), it became clear that there are four reasons why fishers do not report sturgeon bycatch: (1) lack of (financial) interest; (2) lack of time; (3) lack of understanding (awareness) of how important the information on the species is for conservation management; and (4) the trust (or lack thereof) that fishers have in other involved stakeholders, as well as concerns about how the information might be used to lead to more regulations, such as closed areas and/or technical measures to reduce bycatch. Fishers literally say that reporting rare species can and will be hold against them. They are not wrong: This study (Chapter 4) also shows that all key aspects of fisher's cooperation in ETP species conservation (a shared vision, a clear division of roles, communication and trust) are seriously hampered. Solutions are difficult to find, as there is no general consensus on the approach. One solution is to incorporate fishers in sturgeon conservation research, which requires a commitment of researchers as to acknowledging fishers as experts to prevent and reduce bycatch (Chapter 4).

It was also made clear by the interviewees that the work on sturgeon conservation is limited by its dependence on *ad hoc* initiatives and -funding gathered by staff from research institutions and/or environmental NGOs in different settings for different countries. The responsible authorities generally refrain from species-specific conservation and focus on habitat restoration and *ex situ* instead of *in situ* conservation which is needed to save the species (Chapter 4). In case of the European sturgeon, *ex situ* conservation precedes *in situ* conservation. If it had been done the other way around, the species would have already been lost.

9.3.2 Alien sturgeon introductions and spread

The current presence and spread of introduced alien (non-native) sturgeon species is another potentially serious threat to the reintroduction and conservation of European sturgeon population (France Ministère de l'Écologie, 2020; OSPAR Commission, 2021; Visser et al., 2020).

Chapter 5 presents an inventory of sales points, biodiversity datasets, and fishers' and anglers' logbooks, showing that a total of 10 alien Acipenseriformes (nine sturgeon and one paddlefish species) and their hybrids, plus the native *A. oxyrinchus*, are widely cultivated and traded in the Netherlands, Belgium, and Germany. Over 2,500 individuals were reported in more than 60 isolated water bodies in the Rhine delta, and about

500 alien sturgeon individuals were found in hydrologically connected water bodies (status 2022). The latter group mainly concerns three species: the Siberian sturgeon (*A. baerii*), the Russian sturgeon (*A. gueldenstaedtii*) and the Sterlet (*A. ruthenus*). This confirms previous research from neighbouring countries that those three species have the most likeliness to establish in north-western European countries (Arndt et al., 2000; Arndt et al., 2002). Following the publication of Chapter 5 as a paper (Brevé et al., 2022b) dozens of reports of sightings and catches of alien sturgeon arrived at our office, including from a beach on the island of Texel and from fishers using fykes outside the Haringvliet sluices. These reports mainly concerned sub-adult Siberian sturgeon. Although omnipresent, no newborn alien sturgeons were reported for the study area, suggesting that their population expansion at present does not pose a serious threat. In contrast, however, the potential transmission of diseases and parasites is of serious concern (Barber et al., 2000; Bauer et al., 2002; Radosavljević et al., 2019; Spikmans et al., 2020) (Tables 9.1 and 9.2). E.g. in the 1980s, escapes of the imported Asian eel (*Anguilla japonica*) into European waters led to the introduction and spread of *Anguillicoloides crassus*, a parasitic nematode of the swim bladder. The nematode has since infested eel populations throughout Europe since, while the alien host has long since disappeared (Peters & Hartmann, 1986).

It is therefore prudent to implement stricter trade regulations and practical solutions to prevent the release of alien sturgeons into the wild. This requires raising awareness in the aquaculture industry, garden centres, pet shops and the angling community (Chapter 5) (Brevé et al., 2022b). This proves to be effective, as communicating the results of this study to a total of 160 garden centres and fishing pond owners in 2023 plus publication of a laymen story in the corporate magazine VISionair of Sportvisserij Nederland resulted in cessation by several garden centres in the Netherlands of selling sturgeon.

9.4 Part 3. Tracking sturgeons to discover additional threats – Chapters 6 and 7

Main findings: Tracking of experimentally released juvenile sturgeons revealed local and regional pressure factors related to inland shipping, coastal infrastructure, and predation, especially in flow inhibited (slow-flowing, impounded) parts of the Rhine delta.

9.4.1 Inland shipping

Inland shipping will increase in the coming years as it is proposed low-carbon transportation (Sexton et al., 2024). Unfortunately, shipping is also associated with significant loss of fish and macroinvertebrate taxonomic richness, diversity and trait richness (Sexton et al., 2024), and poses a threat to sturgeons and other (migratory) fish

(Spierts, 2016; Staas, 2017; Van de Ven, 2021). With an annual average of over 100,000 ship movements in the Waal and Lower Rhine and the port of Rotterdam as its terminal, the Rhine is one of the busiest shipping lanes in the world (Mako & Galieriková, 2021; Van de Ven, 2021) and potentially leading to massive loss of ecological value such as it negatively affects habitat, provides noise pollution and the risk of seriously wounding fish. In 2012 and 2015, three juvenile sturgeons, released in the Rhine at the Dutch-German border were found dead on the river banks with sharp cuts across their bodies (Chapter 6). All fish were previously acclimatized to Rhine river water and healthy and fit upon release and there were no hydroelectric power stations or pumping stations between the release sites and the sites found. It is therefore suspected that the fish were hit by ship propellers as has been shown for eel, especially in late summer when water levels are low (Brevé et al., 2019b).

A literature review also supported the hypothesis that sturgeon are damaged and killed by ship propellers (Balazik et al., 2012; Spierts, 2016). Sturgeons' habitat use coincides with that of inland shipping, both occupying the rivers main stem. Sturgeons are relatively sensitive to ship movements due to the fish's large body size, its preference for deep and fast-flowing river sections, and their reliance on inhaling air at the surface to inflate their swim bladder (refs. in Spierts (2016)).

Ships in the Rhine cause strong wave action on the gravel beds and along the river banks (Spierts, 2016). During dry summer months, when fish and ships are forced into a narrower and shallower shipping lane, the largest vessels start to adjust their depth position (reduce cargo) and increase sailing hours (Van de Ven, 2021). Ships may occasionally touch the bottom, while the full river discharge passes through these propellers several times (Van de Ven, 2021), which further increases the likelihood of fish being struck by propellers or entrained by the ship´s hull (Spierts, 2016; Staas, 2017; Van de Ven, 2021).

Noticeably, noise pollution, related to inland shipping may also impact sturgeons. It is suggested that sturgeons can detect sounds between 100 Hz to perhaps 1,000 Hz (Meyer and Popper, unpublished). Sturgeons may use sound for different purposes, such as predator avoidance and prey detection, acoustic communication, and use of the 'soundscape' to learn about the environment. Noise pollution may cause disturbance and deterrence in sturgeon distributions, mask communication (range reduction and information loss), predator-prey interactions (avoidance, interference and community effects), and decrease survival and fitness (reduced growth and reproduction) (Slabbekoorn et al., 2010).

In conclusion: It is likely that sturgeons may be harmed by inland shipping in the Rhine, although the evidence is not conclusive.

9.4.2 Coastal infrastructure and the importance of the port of Rotterdam for fish migration

The Rhine delta is highly modified. Currently, there are two potential outmigration routes for sturgeons from the Lower Rhine into the North Sea: the Haringvliet sluices and the Port of Rotterdam. Of those two options, telemetry studies from Chapters 6 and 7 showed that most of the juvenile sturgeons strongly prefer to swim downstream following the main branch of the Rhine, omitting the distributary branches IJssel and Nederrijn and further downstream lake Haringvliet the former Rhine estuary. In 2012 and 2015, 45% of 3 to 5 years old fish, released at the Dutch-German border, migrated through the port of Rotterdam to the North Sea (Brevé et al., 2019b). In 2023, of all sturgeons in the age of 13 to 15 months old, all fish that reached the North Sea also did so via the port of Rotterdam (chapter 7). The results therefore underline the limitations of the current water management at the Haringvliet sluices for diadromous fish in general and sturgeon conservation specifically that need much greater water flows through the sluices than now is enabled.

9.4.3 Predation pressure

The outcomes of the telemetry studies raised concern about the influence of predation on sturgeon survival. The greatest losses of the youngest batch of juvenile sturgeons were mainly observed in the flow inhibited (slow-flowing, impounded) estuarine parts (Chapter 7). The area is known for populations of predatory fish and birds, in particular pike (*Esox lucius*), pikeperch (*Sander lucioperca*), perch (*Perca fluviatilis*), European catfish (*Silurus glanis*) and great cormorant (*Phalacrocorax carbo*) (Brevé et al., 2014b; Copp et al., 2009; Vejřík et al., 2019), while Grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) aggregate at the seaside of the Haringvliet sluices (Brevé et al., 2014b; Fijn et al., 2022; Kranenbarg, 2018; van Rijn & van Eerden, 2022).

The problem of increased predation near migration barriers and fish passages in the Rhine delta is well known (Brevé et al., 2014b; Brevé et al., 2013b; van Rijssel et al., 2024). It is a dilemma that recovery of one species (e.g. cormorants) can negatively affect the recovery of another species (e.g. salmon). Consequently, only a few solutions remain to reduce impacts of predation on the rare diadromous fish. For sturgeons, one strategy could be to rear and release fish at an adolescent size/age, which makes them more resistant to predation (Kirschbaum & Williot, 2011). The other strategy would be to rear and release higher numbers (hundreds, possibly even thousands) of young-of-the-year sturgeons.

9.5 Part 4. Alternative reintroduction strategies

Main findings: The discovery of the historical presence of A. oxyrinchus in the Baltic region (Ludwig et al., 2002) led to its reintroduction in the Oder, Vistula, and other rivers since 2009 (Gessner et al., 2019). Our confirmation of the historical occurrence of two sturgeon species in the Rhine and the North Sea even into the twentieth century, namely the European sturgeon (A. sturio) and the Atlantic sturgeon (A. oxyrinchus), could support the choice for a reintroduction of A. oxyrinchus to North Sea rivers. It would require the North Sea and Rhine member states to realise that A. oxyrinchus actually is a native species first.

Our data confirmed that two sturgeon species historically spawned in the Rhine and populated the North Sea during the Holocene (Thieren et al., 2016a) and even into the twentieth century, namely the European sturgeon (*Acipenser sturio*) and the Atlantic sturgeon (*A. oxyrinchus*) (Fig. 9.2) (Chapter 8). As both species have very similar life cycles and morphology, and are sensitive to similar pressures (Gessner et al., 2022; Hilton & Fox, 2022; Thieren et al., 2016b), the assessment has value for the conservation strategies of both species.

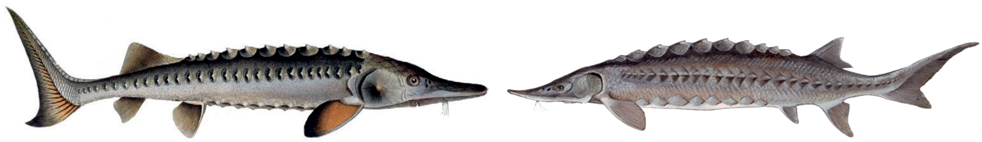


Figure 9.2. Historical drawings of mature anadromous sturgeons (of unknown size): (left) *Acipenser sturio* and (right) *Acipenser oxyrinchus*. Derived from: Bloch (1785–1797) and USFWS National Digital Library.

Chapter 8 introduced three potential strategies to discuss and identify the advantages and disadvantages of the resulting actions: (1) a priority focus to restoring only the critically endangered *A. sturio*, aimed at preventing the global extinction; (2) a strategy aimed at maintaining a strict north-south division of reintroductions between the two species, to avoid any potential negative effects of competition and hybridisation; and (3) the induction of a 'mixed zone' of sympatric occurrences in Europe, and particularly in the North Sea rivers. This means reintroducing *A. oxyrinchus* to all areas where the species was native, ignoring the potential risks of hybridisation and competition.

Given the rapid progress made with *A. oxyrinchus* in the Baltic region (Gessner et al., 2019), and the fact that sub-adults of both species already occur in sympatry in the North Sea, it seems logical to explore the pros and cons of the not yet generally accepted scenario 3.

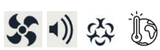
9.6 Part 5 Sturgeon reintroduction feasibility assessment - synthesis

Main findings: Although the carrying capacity of the river Rhine and the North Sea is greatly reduced compared to historical conditions, there still appears to be sufficient habitat in the study area to support all life stages of the European sturgeon. The threats assessment, however, indicates that sturgeon reintroduction is not yet a good idea until these are mitigated. Telemetry offers an excellent method to unveil critical locations and threats as well as the effectiveness of both habitat restoration and pressure mitigation. Also because it keeps momentum going in sturgeon conservation, it is recommended to continue the experimental release of tagged juvenile sturgeon.

9.6.1 Overall assessment of habitat qualities and pressures

Overall, there is sufficient habitat for sturgeons across the study area. However, the threats assessment indicates that there are pressures that still need remediation before sturgeon re-introduction can be considered and effectuated. Per distinct area, the North Sea, the Rhine delta and the Lower Rhine, the key pressures on the European sturgeon are summarized in Table 9.1. The habitat and pressure assessments are presented in some detail in Table 9.2.

Table 9.1. Aggregated overview of confirmed pressures and known unknowns for sturgeon restoration, per area of concern. Further study may improve the feasibility assessment. Source of (most) icons: OSPAR (2021).

Area of concern	Pressures (confirmed)	Pressures (known unknowns)
North Sea		 (unfortunately not reported anymore)
Rhine delta		
Lower Rhine		

Explanation of the icons: Incidental bycatch; Migration barriers ; Loss of brackish areas; Habitat loss; Habitat degradation; Hydrological changes; Introduction of di[illegible] and parasites via alien species; Predation; Inland shipping; Underwater noise; Environmental pollution; Contamination of prey species; Climate change (for the river Rhine: increased occurrences of extremely low and high water flows and increased water temperatures).

Table 9.2. Assessment of habitat availability and pressure factors for sturgeon restoration in the river Rhine (Rhine delta and Lower Rhine) and the North Sea. The assessment is based on social, biological, and technical studies and expertise as described in Chapters 2 to 8. **Assessment:** The habitat suitability and main threats are summarized per life stage where the three colours indicate whether currently for that specific life stage the habitat suitability is considered suitable (green), unsuitable (red) or somewhat suitable (orange), NA = Not Applicable. **Method of assessment**: Numbers in the colours indicate whether the assessment is: (1) (mainly) based on this thesis, (2) reports by others, (3) or own expert judgement. mo = months old.

Area	Adults	Eggs & larvae	Juveniles <13 mo	Juveniles > 13 mo	Argumentation	Main references
North Sea	2, 3	NA	NA	2, 3	High quality foraging opportunities for sturgeons occur in the southern North Sea.	Winter et al. (2015) Charbonnel and Acolas (2022)
	1, 2, 3	NA	NA	1, 2, 3	Coastal and estuarine bycatch is a main pressure. Monitoring of impact on the population and trends is hampered by a lack of bycatch reports.	OSPAR (2021) Ch. 4.
Rhine delta	NA	NA	1, 2		Sufficient nursery grounds (abiotic conditions) and ample foraging opportunities are available in the Rhine delta.	Ch. 3. Van de Ven (2020)
	1, 3	NA	1, 3		The port of Rotterdam is a major fish migration corridor in contrast to the Haringvliet sluices.	Ch. 6 and 7. Winter et al. (2015)
	3	NA	1, 2, 3		Coastal infrastructure reduces the quality and connectivity of the Rhine delta for diadromous fish. Increased aggregations of predatory fish, birds and seals in flow inhibited (slow-flowing, impounded) areas.	Ch. 6 and 7. van Rijssel et al. (2024)
	3	NA	2,3		There is reason for concern about the toxicological safety of the sediments.	Murk (2024)
	1, 2, 3	NA	1, 2, 3		Alien sturgeons pose a risk as a host of parasites and diseases.	Ch. 5.
Lower Rhine	1	1	1	NA	The water quality of the river Rhine has greatly improved.	ICPR (2018)
	1, 3	1, 3	NA	NA	Sturgeon spawning grounds are mainly found in the Lower Rhine in the German state of North Rhine-Westphalia, suitable for appr. 2,500 female European sturgeons.	Ch. 2 and 3.
	2	2	1, 2	NA	Habitat diversity is reduced by river normalisation, dredging and filling of scour holes (resting places for fish). Inland shipping is a concern as ships can damage or kill sturgeons and produce intense underwater noise.	Ch. 6. Refs in Spierts (2016) Van de Ven (2021)
Rhine river basin	2	2	2		According to climate change scenarios, the river Rhine is considered suitable, although there are concerns considering temperatures and late summer river levels and droughts.	Lassalle et al. (2010) Ch. 8.

The key pressures differ per distinguished area: At least four major threats could derail an entire reintroduction effort. For the survival in the marine environment, 1) a major threat is coastal and estuarine bycatch of especially bottom trawling, and mitigation is hampered by a lack of data for full impact assessment of this threat. For the Rhine delta, a serious threat is posed by, 2) coastal infrastructures that obstruct or seriously limits sturgeon migration routes and prevent permanent transitional, tidal zones between the sea and river (brackish water for sturgeon's to acclimatise during their migration up- or downstream). In addition, the coastal infrastructures, 3) attract local aggregations of predatory species that massively prey on juvenile sturgeons. In the Lower Rhine, 4) inland shipping poses direct (wounding) and indirect (habitat reduction and noise pollution) to sturgeons. It is yet unknown to what extent the historical sediment pollution is reason for toxicological concern.

Of course habitat suitability and impact of threats greatly depend on the life stage of the animals as they have different traits. Therefore, based on chapters 2 to 8 in this thesis, the habitat suitability and main threats are summarized per life stage in table 9.2. With three colours it is indicated whether currently for that specific life stage the habitat suitability is considered suitable (green), unsuitable (red) or somewhat suitable (orange).

9.6.2 Recommendations for sturgeon conservation and reintroduction

Based on the results presented in this thesis and subsequent overall assessment of habitat qualities and pressures, the following six recommendations were identified that, once (full)filled, would improve sturgeon conservation and reintroduction effort success. The recommendations are sorted per main area (Table 9.3).

Table 9.3. Overview of recommendations per main area.

Area		**Recommendation**
North Sea	1	Include fishers in research, value their expertise.
Rhine delta	2	Water managers should be encouraged to carefully redirect river water towards the port of Rotterdam.
	3	Prevent introduction of alien sturgeons to natural waters and use their current presence to the advantage of reintroducing the native species.
Lower Rhine	4	Investigate innovations and measures to reduce impacts of inland shipping to sturgeons and diadromous fish in general.
Rhine river basin	5	Include all migratory fish in the ICPR's Master Plan Migratory fish, including sturgeons.
	6	Develop a plan and protocol to establish a Dutch or German rearing station using Atlantic sturgeon in addition to European sturgeon to increase numbers of fish that can be experimentally released.

Recommendation 1: Include fishers in research, value their expertise.

Fishers can be involved in conservation of rare species in at least three significant ways to increase monitoring results and reduce sturgeon bycatch. (1) Campaigns that raise awareness about the importance of species conservation and the impacts of bycatch have greatly helped to improve acceptance of conservation measures and receive more/better bycatch reports (Arndt et al., 2000; Lepage & Rochard, 2011). (2) Establish an officially recognised database to record bycatch and its characteristics to support bycatch prevention and reduction. Despite the legal obligation for such a system, among others stemming from Article 12 of the European Habitats Directive (EEC, 1992), such a system is still lacking. Neither are logbooks systematically retrieved and analysed. Fortunately, a database was developed within the project 'Sturwild France' based on voluntary fishers reports, which proved to be an important asset for studies on the species marine distributions and habitats. Ideally, this database would be made applicable to other countries and further developed upon. Of course this requires effort to increase trust and participation. (3) Bycatch avoidance is the best solution to prevent bycatch mortality. Based on their field-experience, fishers could play an important role in development of approaches to omit bycatch of ETP species through sharing best practices, supporting research and innovation in selective fishing gear (Bahn, 2010). Omitting unwanted bycatch is of interest to fishers as it saves them time, effort and money. For a review on bycatch reducing fishing gear, see Jenkins et al. (2023).

Recommendation 2: Water managers should be encouraged to carefully redirect river water towards the port of Rotterdam.

Diadromous fish require a permanent, high-volume directional current (open migration route) and a permanent tidal zone between the Rhine and the North Sea. Although the Haringvliet sluices (part of a storm surge barrier system in the Netherlands) currently has the so-called 'kier', an opening in the sluices to allow international fish migration to (and from) the Rhine, this does not benefit sturgeon migration (Chapters 6 and 7). Not only is the water flow too limited when the sluices are open, but the Haringvliet sluices are also closed during dry periods to keep seawater out of the Haringvliet lake (the historic estuary of the Rhine). This is harmful because it facilitates excessive predation on sturgeons and other diadromous fish in the flow-inhibited (slow-flowing, impounded) areas and at the Haringvliet sluices. This means that the route through the port of Rotterdam is crucial for the recovery of migratory diadromous fish populations. Water management should include supporting safe and effective fish migration in the Rhine delta, also taking into account the nature compensation area in the area southwest of

Maasvlakte II. This also means that the fish migration facilities at the Haringvliet sluices should be made more permanent, including a permanent brackish tidal zone, which can possibly be achieved by moving the freshwater inlet (at Middelharnis that prevents this) further upstream.

Recommendation 3: Prevent introduction of alien sturgeons to natural waters and use their current presence to the advantage of reintroducing the native species.

As alien sturgeons may host parasites and diseases that are deleterious for their novel environment and for reintroduced native sturgeons, it is important to limit alien sturgeon introductions to natural waters as much as possible. Solutions investigated into with the aquaculture industry should include: (1) Imply more stringent regulations in alien sturgeon trade, preferably on the scale of river basins. (2) Chip all sturgeons (PIT-tag) that are sold across the exotic pet trade in order to be able to trace and address the source. (3) Continue to raise awareness in the aquaculture industry, garden centres, pet shops and the angling community. Still, the currently present alien sturgeons can be used to identify important sturgeon aggregation grounds by application of mark-recapture or acoustic telemetry techniques (Brownscombe et al., 2022). In addition, the alien sturgeons present can be used as a proxy to investigate the accumulation and effects of sediment-bound environmental pollution in the Rhine delta. Because alien sturgeons, like *A. baerii*, generally live in the same estuary and feed on the same prey as *A. sturio* (Maury-Brachet et al., 2008), estimation of exposure location and resulting body burdens may help to assess toxicological safety for native sturgeons and possibly help to specify priority locations for clean-up measures.

Recommendation 4: Investigate innovations and measures to reduce impacts of inland shipping to sturgeons and diadromous fish in general.

The main adverse impacts of inland shipping are direct injury, habitat degradation and noise pollution. Therefore, the following mitigation measures are proposed to reduce the impact of inland shipping on diadromous fish, which should be investigated in close cooperation with the shipping industry: (1) Re-route ships to avoid important spawning grounds. The designated shipping channel is about 150 m, which is about 50% (annual average) of the total channel width in the Lower Rhine (Staas 2017). (2) Maintain a sufficient height of the water column between the river bottom and a ship's hull and propellers, e.g. by reducing the ship's load. (3) Reduce ship speed and propeller speed in certain river sections to reduce the risk of collision. (4) Develop “fish friendly” propellers. (5) Install longitudinal training dams for ecological rehabilitation. If they are designed to meet the needs of sturgeon, they will be safer and there will be less noise pollution. Other species, such as eels, are also likely to benefit from these longitudinal training dams.

Recommendation 5: Include all migratory fish in the ICPR’s Master Plan Migratory fish, including sturgeons.

The International Commission for Protection of the Rhine (ICPR) uses Atlantic salmon (*Salmo salar*) and European eel (*Anguilla anguilla*), “to represent all migrating fish species, including endangered species according to IUCN and species exclusively migrating in inland waters (potamodromous species)” (ICPR, 2018), p.5. The traits of these species, however, differ strongly from the sturgeons as well as from other endangered, threatened and protected diadromous fish species of the Rhine (Fig. 9.3). Moreover, several of those species show indications of recovery, e.g. the river lamprey (*Lampetra fluviatilis*), houting (*Coregonus oxyrinchus*), Twait shad (*Alosa fallax*), and Allis shad (*Alosa alosa*) (van der Hammen et al., 2021; van Rijssel et al., 2024), while salmon and eel populations are at an all-time low (Hundt et al., 2015; van der Hammen et al., 2021; van Rijssel et al., 2024). The other species mentioned do not depend on such long distance migrations (salmon) or moving in such capillaries (eel), so “The ecological guild approach blurs species-specific needs” (Stoffers, 2022). A more trait-based approach, including distance and timing of migration, and monitoring, will help to gain a better in-depth insight into local/regional spatiotemporal distributions of species population developments and of the effects of local/regional pressures and restoration activities. An approach based on the diversity of traits will be an important basis for a basin-wide view of where restoration and remediation of specific stressors is urgently needed and where a good situation has been achieved.

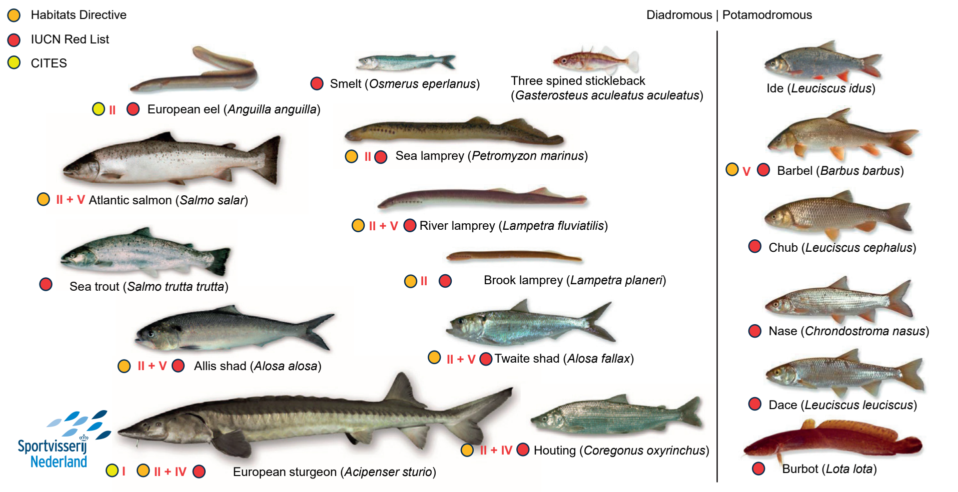


Figure 9.3. Migratory fish of the river Rhine and their status in 2024 according to the European Habitats Directive, the IUCN red list and CITES. Noticeably, the Atlantic sturgeon (*A. oxyrinchus*) is not depicted here, as this species is not officially acknowledged as a native species of the Rhine.

Recommendation 6: Develop a plan and protocol to establish a Dutch or German rearing station using *A. oxyrinchus* in addition to *A. sturio* to increase numbers of fish that can be experimentally released.

Experimental releases of telemetry tagged juvenile sturgeons have proved to be an excellent method of assessing habitat- and pressure management (Chapters 6 and 7), and it is strongly recommended that this be continued.

This recommendation aims to improve the re-introduction efforts and is based on the following six arguments: (1) Although not (yet) officially recognized, there is strong supportive evidence that both species are native to the Rhine into the twentieth century (Chapter 8). (2) The point of no return for potential hybridisation is already past, considering the presence of both species in the North Sea, and their capacity to stray and colonize adjacent river basins (Thieren et al., 2016a). (3) In other river basins multiple sturgeon species lived in sympatry, with *A. sturio*, like in the Danube (Friedrich, 2018). (4) If *A. oxyrinchus* were to be used for a reintroduction into the Rhine, there are several additional genetically different donor populations available - other than *A. oxyrinchus* sourced from a Canadian river currently used for the Baltic area (Gessner et al., 2011a) – including from the US with a strong environmental match, more closely resembling the reintroduction site in the river Rhine (Crandall et al., 2000). (5) The genetic diversity of

A. sturio is low despite intensive breeding plans and it is questionable whether *A. sturio* derived from a French source will survive and display homing behaviour in the Rhine. (6) Given their comparable traits, *A. oxyrinchus* can be used as sentinel species for *A. sturio* in telemetry studies. However, due to lacking artificial rearing in the *ex situ* brood stock in France (which is simply due to the extreme scarcity of the species) of *A. sturio* between 2015 and 2022, sturgeon conservation activities for the Rhine lost momentum. When fish became available, telemetry studies provided crucial insights about local/regional threats that would not be obtained from desktop studies (Chapters 6 and 7). Furthermore, national media coverage of the releases of live fish gained momentum for the sturgeon conservation. It helped to obtain additional funding, hire biologists, develop the First Action Plan for Sturgeon in the Lower Rhine (Visser et al., 2020), and brought sturgeon conservation to the table of the Dutch Ministry of Agriculture, Nature and Food Quality and the ICPR expert group FISH.

9.7 Concluding remarks

The re-introduction of lost species can only be successful if the key factors that contributed to their decline are no longer present, and if other anthropogenic or natural developments in the areas since their disappearance do not create critical problems for the re-introduction.

This thesis reveals that for the river Rhine and the North Sea there are still too many threats/problem areas that need to be mitigated and critical knowledge gaps that need to be investigated further. Although promising, the river Rhine and the North Sea are not yet suitable for sturgeon re-introduction. Most of the pressures on the species and its key habitats occur in the river Rhine. By-catch is the main pressure in the North Sea, and the active participation of fishers in reporting would be a great help in the assessment of the development of the sturgeon population at sea.

While the river Rhine, which provides key habitats for sturgeon recruitment, will continue to be restored to a good ecological status in line with current European environmental policy, stocking (releases of) European sturgeon offspring in the French and German river basins will help to rebuild several generations of sturgeon at sea. Experimental releases in the river Rhine, using telemetry techniques, will provide us with information on habitat and pressure status and will also keep the momentum for conservation efforts going. For a future sturgeon population in the river Rhine, the governments of the Netherlands and the German state of North Rhine-Westphalia should take the lead, ideally coordinating the efforts of all stakeholders.

Ein Stör, ist ein rechter Meer fisch, kompt auß der Niderländischen See, doch seindt derselben in 20. Jahren, drey bey vns gefangen worden, die haben ein fleisch hart vnd grob, hornichte schupen, daß maul haben sie vnden her, der letste von diesen dreyen, so Anno. 1624. gefangen, war 9. werckschuh lang, vnd ist der fischer stub alhie gezeigt worden.

Anno. 1654. den 2. Januarij. ist in dem Mistener bann abermal ein Stör gefangen, vnd ist der fischer stub gezeigt worden, der war 8. werckschuh lang.

Anno. 1655, den 3. Maij. ist ein Stör in dem Altenheimer bann gefangen worden, der war 6. schuh lang, die Männlin oder die gemilchten haben ein kürtzern auch dickern kopff alß die weiblin, auch haben die weiblin ein schwartzen rogen.

Anno. 1657. den 6. Maij. ist ein Stör bey Stattmatt gefangen worden, der war 8½. werck schuh lang.

Anno. 1663. den 14. Maij. ist widrumb ein Stör gefangen worden im Escharer Rhein, der war 8. schuh vnd 2. zoll lang, Es hatt ein jeder Stör so lang gedärm, so lang er ist, vnd wird man allzeit in seim magen ein steinel find.

References

Photo: Baldner, L. (1666). Das Vogel-Fisch-und Thierbuch des Strassburger Fischers. Historical report of sturgeons caught in the Rhine in Germany. Free translation of the first sentence: The sturgeon is a true fish of the sea, comes from the sea in the Netherlands, but over the past 20 years has also been caught in Germany.

References

Abecasis, D., Steckenreuter, A., Reubens, J., Aarestrup, K., Alós, J., Badalamenti, F., Bajona, L., Boylan, P., Deneudt, K., Greenberg, L., Brevé, N., Hernández, F., Humphries, N., Meyer, C., David Sims, D., Thorstad, E., Walker, A., Whoriskey, F., & Afonso, P. (2018). A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. *Animal Biotelemetry*, *6*(1), 1-7. https://doi.org/https://doi.org/10.1186/s40317-018-0156-0

Acolas, M. L., Castelnaud, G., Lepage, M., & Rochard, E. (2011a). Biological cycles and migrations of *Acipenser sturio*. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758* (pp. 147-152). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_10

Acolas, M. L., Gessner, J., & Rochard, E. (2011b). Population conservation requires improved understanding of in situ life histories. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758* (pp. 585-592). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_44

Acolas, M. L., Le Pichon, C., & Rochard, E. (2017). Spring habitat use by stocked one year old European sturgeon *Acipenser sturio* in the freshwater-oligohaline area of the Gironde estuary. *Estuarine, Coastal and Shelf Science*, *196*, 58-69. https://doi.org/10.1016/j.ecss.2017.06.029

Acolas, M. L., Rochard, E., Le Pichon, C., & Rouleau, E. (2012). Downstream migration patterns of one-year-old hatchery-reared European sturgeon (*Acipenser sturio*). *Journal of Experimental Marine Biology and Ecology*, *430*, 68-77. https://doi.org/10.1016/j.jembe.2012.06.026

Allen, P. J., Mitchell, Z. A., DeVries, R. J., Aboagye, D. L., Ciaramella, M. A., Ramee, S. W., Stewart, H. A., & Shartau, R. B. (2014). Salinity effects on Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus* Mitchill, 1815) growth and osmoregulation. *Journal of Applied Ichthyology*, *30*(6), 1229-1236. https://doi.org/http://dx.doi.org/10.1111/jai.12542

Almaca, C., & Elvira, B. (2000). Past and present distribution of *Acipenser sturio* L., 1758 on the Iberian Peninsula. *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA*, *16*(1/4), 11-16.

Almeida, D., Ribeiro, F., Leunda, P. M., Vilizzi, L., & Copp, G. H. (2013). Effectiveness of FISK, an invasiveness screening tool for non-native freshwater fishes, to perform risk identification assessments in the Iberian Peninsula. *Risk Analysis*, *33*(8), 1404-1413. https://doi.org/https://doi.org/10.1111/risa.12050

Anderson, A. (1954). A 152-year-old lake sturgeon caught in Ontario. *Commercial Fisheries Review*, *18*, 28.

Arndt, G., Gessner, J., Anders, E., Spratte, S., Filipiak, J., Debus, L., & Skora, K. (2000). Predominance of exotic and introduced species among sturgeons captured from the Baltic and North Seas and their watersheds, 1981-1999. *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA*, *16*(1/4), 29-36.

Arndt, G., Gessner, J., & Raymakers, C. (2002). Trends in farming, trade and occurrence of native and exotic sturgeons in natural habitats in Central and Western Europe. *Journal of Applied Ichthyology*, *18*(4/6), 444-448. https://doi.org/https://doi.org/10.1046/j.1439-0426.2002.00415.x

Arndt, G. M., Tiedemann, R., Bartel, R., & Kirschbaum, F. (2006). Remediation measures for the Baltic sturgeon: Status review and perspectives. *Journal of Applied Ichthyology/Zeitschrift fur angewandte Ichthyologie*, *22*(Suppl.), 23-31. https://doi.org/https://doi.org/10.1111/j.1439-0426.2007.00925.x

Assis, C. A. (1990). Threats to the survival of anadromous fishes in the River Tagus, Portugal. *Journal of Fish Biology*. https://doi.org/https://doi.org/10.1111/j.1095-8649.1990.tb05046.x

Atkinson, R., & Flint, J. (2001). Accessing hidden and hard-to-reach populations: Snowball research strategies. *Social research update*, *33*(1), 1-4.

ATLAS.ti. (2022). *Scientific Software Development GmbH [ATLAS.ti 22 Windows]. https://atlasti.com/.* In

Auster, P. J., & Langton, R. W. (1999). The effects of fishing on fish habitat. In American Fisheries Society Symposium (Vol. 22, No. 150-187).

Auster, R. E., Barr, S. W., & Brazier, R. E. (2022). Renewed coexistence: learning from steering group stakeholders on a beaver reintroduction project in England. *European Journal of Wildlife Research*, *68*(1), 1-22. https://doi.org/10.1007/s10344-021-01555-6

Babcock, E. A., Pikitch, E. K., & Hudson, C. G. (2003). *How much observer coverage is enough to adequately estimate bycatch?* Pew Institute of Ocean Science Miami, FL.

Bacalbaşa-Dobrovici, N., & Holčík, J. (2000). Distribution of *Acipenser sturio* L., 1758 in the Black Sea and its watershed [Article]. *Boletin - Instituto Espanol de Oceanografia*, *16*(1-4), 37-41. https://www.scopus.com/inward/record.uri?eid=2-s2.0-0034443998&partnerID=40&md5=83427952a68e0a1dd915843779dd66a5

Bahn, R. A. (2010). *Bycatch of shortnose sturgeon in the commercial shad fishery of the Altamaha River, Georgia* Doctoral dissertation, University of Georgia].

Bailey, K. (2008). *Methods of social research*. Simon and Schuster.

Bain, M., Haley, N., Peterson, D., Waldman, J., & Arend, K. (2000). Harvest and habitats of Atlantic sturgeon *Acipenser oxyrinchus* Mitchill, 1815 in the Hudson River estuary: lessons for sturgeon conservation. *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA*, *16*(1/4), 43-54.

Bain, M. B. (1997). Atlantic and shortnose sturgeons of the Hudson River: A common and divergent life history attributes. *Environ. Biol. Fish.*, *48*(1-4), 347-358. https://doi.org/https://doi.org/10.1023/A:1007325814893

Baker, B. (2000). Fisheries management faces many challenges. *BioScience*, *50*(8), 652-652. https://doi.org/DOI:10.1641/0006-3568(2000)050[0652:FMFMC]2.0.CO;2

Balazik, M., Barber, M., Altman, S., Reine, K., Katzenmeyer, A., Bunch, A., & Garman, G. (2020). Dredging activity and associated sound have negligible effects on adult Atlantic sturgeon migration to spawning habitat in a large coastal river. *PloS one*, *15*(3), e0230029. https://doi.org/https://doi.org/10.1371/journal.pone.0230029

Balazik, M. T., Reine, K. J., Spells, A. J., Fredrickson, C. A., Fine, M. L., Garman, G. C., & McIninch, S. P. (2012). The potential for vessel interactions with adult Atlantic sturgeon in the James River, Virginia. *North American Journal of Fisheries Management*, *32*(6), 1062-1069. https://doi.org/10.1080/02755947.2012.716016

Baldner, L. (1666). Das Vogel-Fisch-und Thierbuch des Strassburger Fischers Leonhard Baldner. In.

Barber, I., Hoare, D., & Krause, J. (2000). Effects of parasites on fish behaviour: a review and evolutionary perspective. *Reviews in fish biology and fisheries*, *10*(2), 131-165. https://doi.org/https://doi.org/10.1023/A:1016658224470

Barber, M. R. (2017). Effects of Hydraulic Dredging and Vessel Operation on Atlantic Sturgeon Behavior in a Large Coastal River. https://doi.org/https://doi.org/10.25772/KPFH-Z425

Barriball, K. L., & While, A. (1994). Collecting data using a semi-structured interview: a discussion paper. *Journal of Advanced Nursing*, *18*, 328-335. https://doi.org/10.1111/j.1365-2648.1994.tb01088.x

Bastmeijer, K. (2019). *De Juridische Status van de Europese Steur (Acipenser sturio) en de Positie van Nederland (The Legal Status of the European Sturgeon (Acipenser sturio) and the Position of the Netherlands (with English summary)): Een onderzoek in opdracht van ARK Natuurontwikkeling en het Wereldnatuurfonds Nederland*. https://research.tilburguniversity.edu/en/publications/de-juridische-status-van-de-europese-steur-acipenser-sturio-en-de

Bauer, O., Pugachev, O., & Voronin, V. (2002). Study of parasites and diseases of sturgeons in Russia: a review. *Journal of Applied Ichthyology*, *18*(4-6), 420-429. https://doi.org/https://doi.org/10.1046/j.1439-0426.2002.00422.x

Beardsall, J. W., McLean, M. F., Cooke, S. J., Wilson, B. C., Dadswell, M. J., Redden, A. M., & Stokesbury, M. J. (2013). Consequences of incidental otter trawl capture on survival and physiological condition of threatened Atlantic sturgeon. *Transactions of the American Fisheries Society*, *142*(5), 1202-1214. https://doi.org/https://doi.org/10.1080/00028487.2013.806347

Beardsall, J. W., Stokesbury, M. J. W., Logan-Chesney, L. M., & Dadswell, M. J. (2016). Atlantic sturgeon *Acipenser oxyrinchus* Mitchill, 1815 seasonal marine depth and temperature occupancy and movement in the Bay of Fundy. *Journal of Applied Ichthyology*, *32*(5), 809-819. https://doi.org/http://dx.doi.org/10.1111/jai.13175

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., Van de Bund, W., Aarestrup, K., & Barry, J. (2020). More than one million barriers fragment Europe's rivers. *Nature*, *588*(7838), 436-441. https://doi.org/https://doi.org/10.1038/s41586-020-3005-2

Bemis, W. E., Findeis, E. K., & Grande, L. (1997). An overview of Acipenseriformes. *Environmental Biology of Fishes*, *48*(1), 25-71. https://doi.org/10.1023/A:1007370213924

Bemis, W. E., & Kynard, B. (1997). Sturgeon rivers: An introduction to Acipenseriform biogeography and life history. *Environmental Biology of Fishes*, *48*(1-4), 167-183. https://doi.org/https://doi.org/10.1023/A:1007312524792

Berendsen, H. J., & Stouthamer, E. (2000). Late Weichselian and Holocene palaeogeography of the Rhine–Meuse delta, the Netherlands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *161*(3-4), 311-335. https://doi.org/https://doi.org/10.1016/S0031-0182(00)00073-0

Best, J. (2019). Anthropogenic stresses on the world's big rivers. *Nature Geoscience*, *12*(1), 7-21. https://doi.org/https://doi.org/10.1038/s41561-018-0262-x

Bij de Vaate, A., Breukel, R., & Van der Velde, G. (2006). Long-term developments in ecological rehabilitation of the main distributaries in the Rhine delta: fish and macroinvertebrates. *Hydrobiologia*, *565*(1), 229-242. https://doi.org/https://doi.org/10.1007/s10750-005-1916-4

Bij de Vaate, A., Breukelaar, A., De Laak, G., & Dijkers, C. (2003). Sea trout migration in the Rhine delta. *Journal of Fish Biology*, *63*(4), 892-908. https://doi.org/https://doi.org/10.1046/j.1095-8649.2003.00198.x

Bij de Vaate, A., Breukelaar, A., de Laak, G., Vriese, T., Dijkers, C., & Pakes, U. (2001). *De migratie van zeeforel in Nederland.* (2001.046). (Rijksinstituut voor Integraal Zoetwaterbeheer & Afvalwaterbehandeling, Issue.

Billard, R., & Lecointre, G. (2000). Biology and conservation of sturgeon and paddlefish. *Reviews in fish biology and fisheries*, *10*(4), 355-392. https://doi.org/http://dx.doi.org/10.1023/A:1012231526151

Birstein, V. (2002). Sturgeon species and hybrids: can hybrids produce caviar. *Environmental Policy and Law*, *32*(vol. 32, no. 5), 210-214.

Birstein, V., & Bemis, W. (1997). How many species are there within the genus Acipenser? *Environmental Biology of Fishes*, *48*(1-4), 157-163. https://doi.org/10.1023/A:1007354827093

Birstein, V., Bemis, W., & Waldman, J. (1997a). The Threatened Status of Acipenseriform Fishes: A Summary. *Environmental Biology of Fishes*, *48*(1), 427. https://doi.org/https://doi.org/10.1007/0-306-46854-9_33

Birstein, V., & Doukakis, P. (2000). Molecular analysis of *Acipenser sturio* L., 1758 and *Acipenser oxyrinchus* Mitchill, 1815: A review. *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA*, *16*(1/4), 61-74.

Birstein, V., Hanner, R., & DeSalle, R. (1997b). Phylogeny of the Acipenseriformes: cytogenetic and molecular approaches. In *sturgeon biodiversity and conservation* (pp. 127-155). Springer. https://doi.org/https://doi.org/10.1007/0-306-46854-9_6

Birstein, V., Waldman, J., & Bemis, W. (2006). *Sturgeon biodiversity and conservation* (Vol. 17). Springer Science & Business Media.

Birstein, V. J. (1993). Sturgeons and paddlefishes: threatened fishes in need of conservation. *Conservation Biology*, *7*(4), 773-787. https://doi.org/https://doi.org/10.1046/j.1523-1739.1993.740773.x

Bismuth, A., & Lauronce, V. (2019). *Les frayères potentielles d'esturgeons européens Acipenser sturio L. 1758, dans le bassin Garonne-dordogne, une problématique majeure aujourd'hui pour préparer les repeuplements de demain*.

Blackstone, W. (1830). *Commentaries on the Laws of England* (Vol. 2). Collins & Hannay.

Bloch, M. E. (1785–1797). *Ichtylogie, ou Histoire naturelle: génerale et particuliére des poissons (1785–1797)*.

Bloesch, J., & Sieber, U. (2003). The morphological destruction and subsequent restoration programmes of large rivers in Europe. *Large Rivers*, 363-385. https://doi.org/https://doi.org/10.1127/lr/14/2003/363

Böcking, W. (1988). So fischte man am Niederrhein: die einstigen Fangmethoden von Emmerich bis Neuss; Bilder eines alten Handwerks.

Boddeke, R. (1971). Vissen & vissen: ervaringen van een visserijbioloog en sportvisser. In (pp. 169-175).

Bölscher, T., Van Slobbe, E., Van Vliet, M. T., & Werners, S. E. (2013). Adaptation turning points in river restoration? The Rhine salmon case. *Sustainability*, *5*(6), 2288-2304. https://hal.science/hal-04217026/

Borcherding, J., Heynen, M., Jäger-Kleinicke, T., Winter, H., & Eckmann, R. (2010). Re-establishment of the North Sea houting in the River Rhine. *Fisheries Management and Ecology*, *17*(3), 291-293. https://doi.org/https://doi-org.ezproxy.library.wur.nl/10.1111/j.1365-2400.2009.00710.x

Boreman, J. (1997). Sensitivity of North American sturgeons and paddlefish to fishing mortality. In *Sturgeon biodiversity and conservation* (pp. 399-405). Springer. https://doi.org/https://doi.org/10.1007/0-306-46854-9_28

Borodin, N. (1925). Biological observations on the Atlantic sturgeon (*Acipenser sturio*). *Transactions of the American Fisheries Society*, *55*(1), 184-190. https://doi.org/https://doi.org/10.1577/1548-8659(1925)55[184:BOOTAS]2.0.CO;2

Brandt, J. F. J. T. C. R. (1833). *Medizinische Zoologie oder getreue Darstellung und Beschreibung der Thiere die in die Artzneimittellehre in Betracht kommen is systematischer Folge herausgegeben.* (Vol. Zweiter Band). Hirschwald.

Brehm, A. E. (1900). *Het leven der dieren. Derde deel. Kruipende dieren - Visschen - Insecten - Lagere dieren.* Van Belkum.

Breukelaar, A. (2017). Downstream Migration of Silver Eel and Salmon Smolts in the Rivers Rhine and Meuse with Special Attention to Effects of Passing Hydropower Stations and Weirs. In 147th Annual Meeting of the American Fisheries Society. AFS.,

Breukelaar, A., Ingendahl, D., Vriese, F., De Laak, G., Staas, S., & Klein Breteler, J. (2009). Route choices, migration speeds and daily migration activity of European silver eels *Anguilla anguilla* in the River Rhine, north-west Europe. *Journal of Fish Biology*, *74*(9), 2139-2157. https://doi.org/https://doi.org/10.1111/j.1095-8649.2009.02293.x

Breukelaar, A. W., bij de Vaate, A., & Fockens, K. T. (1998). Inland migration study of sea trout (*Salmo trutta*) into the rivers Rhine and Meuse (The Netherlands), based on inductive coupling radio telemetry. *Hydrobiologia*, *371*(0), 29-33. https://doi.org/https://doi.org/10.1023/A:1017058718334

Brevé, N., Buijse, A., Kroes, M., Wanningen, H., & Vriese, F. (2014a). Supporting decision-making for improving longitudinal connectivity for diadromous and potamodromous fishes in complex catchments. *Science of the Total Environment*, *496*, 206-218. https://doi.org/10.1016/j.scitotenv.2014.07.043

Brevé, N., Leuven, R., Buijse, A., Murk, A., J, V., & Nagelkerke, L. (2022a). *Data underlying the publication: The conservation paradox of critically endangered fish species: Trading alien sturgeons versus native sturgeon reintroduction in the Rhine-Meuse river delta* (https://doi.org/https://doi.org/10.17026/dans-28u-x3w3

Brevé, N., Leuven, R., Buijse, A., Murk, A., Venema, J., & Nagelkerke, L. (2022b). The conservation paradox of critically endangered fish species: Trading alien sturgeons versus native sturgeon reintroduction in the Rhine-Meuse river delta. *Science of the Total Environment*, *848*, 157641. https://doi.org/https://doi.org/10.1016/j.scitotenv.2022.157641

Brevé, N., Nagelkerke, L., Buijse, A., van Tuijn, T., Murk, A., Winter, H., & Lenders, H. (2022c). *Data underlying the publication: Historical reconstruction of sturgeon (Acipenser spp.) spatiotemporal distribution and causes for their decline in North-Western Europe* (https://doi.org/https://doi.org/10.17026/dans-xns-5c7c

Brevé, N., Nagelkerke, L., Buijse, A., Van Tuijn, T., Murk, A., Winter, H., & Lenders, H. (2022d). Historical reconstruction of sturgeon (Acipenser spp.) spatiotemporal distribution and causes for their decline in North-Western Europe. *Biodiversity and Conservation*(31), 1149–1173. https://doi.org/https://doi.org/10.1007/s10531-022-02381-1

Brevé, N., Verspui, R., de Laak, G., Bendall, B., Breukelaar, A., & Spierts, I. (2014b). Explicit site fidelity of European catfish (*Silurus glanis*, L., 1758) to man-made habitat in the River Meuse, Netherlands. *Journal of Applied Ichthyology*, *30*(3), 472-478. https://doi.org/https://doi.org/10.1111/jai.12410

Brevé, N., Vis, H., & Breukelaar, A. (2019a). Escape from the North Sea: the possibilities for pikeperch (*Sander lucioperca* L. 1758) to re-enter the Rhine and Meuse estuary via the Haringvlietdam, as revealed by telemetry. *Journal of Coastal Conservation*, *23*(1), 239-252. https://doi.org/10.1007/s11852-018-0654-5

Brevé, N., Vis, H., Houben, B., Breukelaar, A., & Acolas, M. (2019b). Outmigration pathways of stocked juvenile European sturgeon (*Acipenser sturio* L., 1758) in the Lower Rhine River, as revealed by telemetry [Article]. *Journal of Applied Ichthyology*, *35*(1), 61-68. https://doi.org/https://doi.org/10.1111/jai.13815

Brevé, N., Vis, H., Houben, B., de Laak, G., Breukelaar, A., Acolas, M., de Bruijn, Q., & Spierts, I. (2013a). Exploring the possibilities of seaward migrating juvenile European sturgeon *Acipenser sturio* L., in the Dutch part of the River Rhine. *Journal of Coastal Conservation*, *18*(2), 131-143. https://doi.org/https://doi.org/10.1007/s11852-013-0281-0

Brevé, N., Vis, H., Spierts, I., de Laak, G., Moquette, F., & Breukelaar, A. (2013b). Exorbitant mortality of hatchery-reared Atlantic salmon smolts *Salmo salar* L., in the Meuse river system in the Netherlands. *Journal of Coastal Conservation*, *18*(2), 97-109. https://doi.org/https://doi.org/10.1007/s11852-013-0237-4

Bronzi, P., Rosenthal, H., Arlati, G., & Williot, P. (1999). A brief overview on the status and prospects of sturgeon farming in Western and Central Europe. *Journal of Applied Ichthyology*, *15*(4-5), 224-227. https://doi.org/https://doi.org/10.1111/j.1439-0426.1999.tb00239.x

Bronzi, P., Rosenthal, H., & Gessner, J. (2011). Global sturgeon aquaculture production: an overview. *Journal of Applied Ichthyology*, *27*(2), 169-175. https://doi.org/https://doi.org/10.1111/j.1439-0426.2011.01757.x

Brosse, L., & Elie, P. (2003). *Caracterisation des habitats des juveniles d'esturgeon europeen, Acipenser sturio, dans l'estuaire de la Gironde: Relations trophiques, hierarchisation et vulnerabilite des habitats* Universite Toulouse 3, Toulouse (France)]. Natural Science Collection.

Brosse, L., Lepage, M., & Dumont, P. (2000). First results on the diet of the young Atlantic sturgeon *Acipenser sturio* L., 1758 in the Gironde estuary. *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA*, *16*(1/4), 75-80. https://doi.org/https://hal.inrae.fr/hal-02579645

Brown, J., & Murphy, G. W. (2010). Atlantic Sturgeon Vessel-Strike Mortalities in the Delaware Estuary. *Fisheries*, *35*(2), 72-83. https://doi.org/http://dx.doi.org/10.1577/1548-8446-35.2.72

Brownscombe, J. W., Griffin, L. P., Brooks, J. L., Danylchuk, A. J., Cooke, S. J., & Midwood, J. D. (2022). Applications of telemetry to fish habitat science and management. *Canadian Journal of Fisheries and Aquatic Sciences*, *79*(8), 1347-1359. https://doi.org/https://doi.org/10.1139/cjfas-2021-010

Bürger, F. (1926). Die Fischereiverhältnisse im Rhein im Bereich der preußischen Rheinprovinz. *Zeitschrift für Fischerei*, *24*, 217-398.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., & Wardle, D. A. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59-67. https://doi.org/https://doi.org/10.1038/nature11148

Caro, T. (2010). *Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species*. Island Press.

Castelnaud, G. (1988). *The sturgeon tagging programme in the Gironde estuary (France): A European dimension*. ICES, COPENHAGEN (DENMARK). https://doi.org/https://hal.inrae.fr/hal-02604456

Castelnaud, G., Rochard, E., Jatteau, P., & Lepage, M. (1991a). *Data on Acipenser sturio biology in the Gironde Estuary.* [Donnees actuelles sur la biologie d'*Acipenser sturio* dans l'estuaire de la Gironde]. https://doi.org/https://hal.inrae.fr/hal-02575987

Castelnaud, G., Rochard, E., Jatteau, P., & Lepage, M. (1991b). Données actuelles sur la biologie d'*Acipenser sturio* dans l'estuaire de la Gironde. *Acipenser. Cemagref, Antony*, 251-275. https://doi.org/https://hal.inrae.fr/hal-02575987

Charbonnel, A., & Acolas, M. (2022). *Identification des habitats marins utilisés par l'esturgeon européen* *et fréquentation des aires marines protégées, projet MOMIE MOuvements MIgratoires de l'Esturgeon européen Acipenser sturio : habitats en mer et retour des géniteurs en fleuves. Rapport final Tâche 1, contrat de recherche et développement INRAE/OFB 2019-2022. 117p.*

Charbonnel, A., Lambert, P., Lassalle, G., Quinton, E., Guisan, A., Mas, L., Paquignon, G., Lecomte, M., & Acolas, M.-L. (2022). Developing species distribution models for critically endangered species using participatory data: The European sturgeon marine habitat suitability. *Estuarine, Coastal and Shelf Science*, 108136. https://doi.org/https://doi.org/10.1016/j.ecss.2022.108136

Charbonnel, A., Lassalle, G., Lambert, P., Quinton, E., Geßner, J., Rochard, E., Colclough, S., Brevé, N., & Acolas, M.-L. (2024). Travelling away from home? Joining global change and recovery scenarios to anticipate the marine distribution of diadromous fish. *Ecological Indicators*, *160*, 111762. https://doi.org/https://doi.org/10.1016/j.ecolind.2024.111762

Charlon, N., & Williot, P. (1978). Elevage d'esturgeons de repeuplement et de consommation en URSS.

Chassaing, O., Desse-Berset, N., Duffraisse, M., Piquès, G., Hänni, C., & Berrebi, P. (2011a). Palaeogeographic patterns of *A. sturio*. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758* (pp. 117-129). Springer.

Chassaing, O., Desse-Berset, N., Hänni, C., Hughes, S., & Berrebi, P. (2016). Phylogeography of the European sturgeon (*Acipenser sturio*): a critically endangered species. *Molecular phylogenetics and evolution*, *94*(Pt A), 346-357. https://doi.org/https://doi.org/10.1016/j.ympev.2015.09.020

Chassaing, O., Desse-Berset, N., Duffraisse, M., Hughes, S., Hänni, C., & Berrebi, P. (2013). Palaeogenetics of western French sturgeons spotlights the relationships between *Acipenser sturio* and *Acipenser oxyrinchus*. *Journal of Biogeography*, *40*(2), 382-393. https://doi.org/https://doi.org/10.1111/j.1365-2699.2012.02785.x

Chassaing, O., Desse-Berset, N., Hänni, C., Hughes, S., & Berrebi, P. (2018). Microsatellite diversity of a critically endangered sturgeon, *Acipenser sturio* L. 1758, assessed from museum and archaeological tissue remains. *Journal of Biogeography*, *45*(5), 1043-1053. https://doi.org/10.1111/jbi.13187

Chassaing, O., Hänni, C., & Berrebi, P. (2011b). Distinguishing species of European sturgeons *Acipenser* spp. using microsatellite allele sequences. *Journal of Fish Biology*, *78*(1), 208-226. https://doi.org/https://doi.org/10.1111/j.1095-8649.2010.02852.x

Chebanov, M., Rosenthal, H., Gessner, J., Van Anrooy, R., Doukakis, P., Pourkazemi, M., & Williot, P. (2011). *Sturgeon hatchery practices and management for release. Guidelines*. FAO, Ankara (Turkey), [mailto:publications-sales@fao.org]. https://doi.org/https://www.fao.org/3/i2428e/i2428e.pdf

Chèvre, P., Goncharov, B. F., & Rochard, E. (2019). European sturgeon (*Acipenser sturio*) mass propagation. *Journal of Applied Ichthyology*, *35*(1), 94-102. https://doi.org/http://dx.doi.org/10.1111/jai.13694

Chézy, A. (1776). Formule pour trouver la vitesse de l'eau conduit dan une rigole donnée. Dossier 847 (MS 1915) of the manuscript collection of the École Nationaldes Ponts et Chaussées, Paris. Reproduced in: Mouret, G.(1921). Antoine Chézy: histoire d'une formule d'hydraulique. Annales des Ponts et Chaussées,

Colclough, S. (2021). *The Common or European Sturgeon Acipenser sturio (L., 1758). An evidence report of the history and status of the species in Great Britain*.

Collas, F., Buijse, A., Van den Heuvel, L., Van Kessel, N., Schoor, M., Eerden, H., & Leuven, R. (2018). Longitudinal training dams mitigate effects of shipping on environmental conditions and fish density in the littoral zones of the river Rhine. *Science of the Total Environment*, *619*, 1183-1193. https://doi.org/https://doi.org/10.1016/j.scitotenv.2017.10.299

Copp, G. H., Robert Britton, J., Cucherousset, J., García-Berthou, E., Kirk, R., Peeler, E., & Stakėnas, S. (2009). Voracious invader or benign feline? A review of the environmental biology of European catfish *Silurus glanis* in its native and introduced ranges. *Fish and Fisheries*, *10*(3), 252-282. https://doi.org/https://doi.org/10.1111/j.1467-2979.2008.00321.x

Cote, D., Van Leeuwen, T., Bath, A., Gonzales, E., & Cote, A. (2021). Social–ecological management results in sustained recovery of an imperiled salmon population. *Restoration Ecology*, *29*(5), e13401. https://doi.org/https://doi.org/10.1111/rec.13401

Council of Europe. (2018). *Pan-European Action Plan for Sturgeons*. Strasbourg: European Union

Coz, D. M., & Young, J. C. (2020). Conflicts over wildlife conservation: learning from the reintroduction of beavers in Scotland. *People and Nature*, *2*(2), 406-419. https://doi.org/https://doi.org/10.1002/pan3.10076

Crandall, K. A., Bininda-Emonds, O. R., Mace, G. M., & Wayne, R. K. (2000). Considering evolutionary processes in conservation biology. *Trends in ecology & evolution*, *15*(7), 290-295. https://doi.org/https://doi.org/10.1016/S0169-5347(00)01876-0

D'hondt, B., Vanderhoeven, S., Roelandt, S., Mayer, F., Versteirt, V., Adriaens, T., Ducheyne, E., San Martin, G., Grégoire, J.-C., & Stiers, I. (2015). Harmonia+ and Pandora+: risk screening tools for potentially invasive plants, animals and their pathogens. *Biological Invasions*, *17*(6), 1869-1883. https://doi.org/https://doi.org/10.1007/s10530-015-0843-1

Dadswell, M. J., Rulifson, R. A., & Daborn, G. R. (1986). Potential Impact of Large-Scale Tidal Power Developments in the Upper Bay of Fundy on Fisheries Resources of the Northwest Atlantic. *Fisheries*, *11*(4), 26-35. https://doi.org/http://dx.doi.org/10.1577/1548-8446(1986)011-0026:PIOLTP>2.0.CO;2

Dankers, N., Texel, A., & Steenbergen, J. (2006). *Geleidelijke zoet-zout overgangen in Nederland. Alterra Texel, RIVO Yerseke. Programma 418 proj nr 230243-06.*

De Groot, S. (1992). Herstel van riviertrekvissen in de Rijn een realiteit? 6. De steur. *De Levende Natuur*, *93*(1), 14-18.

de Groot, S. (2002). A review of the past and present status of anadromous fish species in the Netherlands: is restocking the Rhine feasible? In *Hydrobiologia* (Vol. 478, pp. 205-218). Kluwer Academic Publishers. https://doi.org/https://doi.org/10.1007/978-94-017-1335-1_11

De Jong, D., Parel, P., Verdonk, J., Den Breejen, P., & Van der Esch, J. (1988). *Hardinxveld en de riviervisserij*.

De Nie, H. W., & Ommering, G. (1998). *Bedreigde en kwetsbare zoetwatervissen in Nederland: Toelichting op de Rode Lijst*.

Debus, L. (1997). *Sturgeons in Europe and causes of their decline* Occas. Pap. IUCN Species Survival Commission,

Debus, L. (1999). Meristic and morphological features of the Baltic sturgeon (*Acipenser sturio* L.). *Journal of Applied Ichthyology*, *15*(4-5), 38-45. https://doi.org/https://doi.org/10.1111/j.1439-0426.1999.tb00203.x

Deelder, C., & Huussen Jr, A. (1973). Opmerkingen betreffende de kuilvisserij op de voormalige Zuiderzee, voornamelijk in de zestiende eeuw. *Holland*, *5*(5), 221-242.

Delage, N., Cachot, J., Rochard, E., Fraty, R., & Jatteau, P. (2014). Hypoxia tolerance of European sturgeon (*Acipenser sturio* L., 1758) young stages at two temperatures. *Journal of Applied Ichthyology*, *30*(6), 1195-1202. https://doi.org/10.1111/jai.12609

Delage, N., Couturier, B., Jatteau, P., Larcher, T., Ledevin, M., Goubin, H., Cachot, J., & Rochard, E. (2019). Oxythermal window drastically constraints the survival and development of European sturgeon early life phases. *Environmental Science and Pollution Research International*, 1. https://doi.org/http://dx.doi.org/10.1007/s11356-018-4021-8

Delage, N., Rochard, E., & Cachot, J. (2015). *Experimental study of environmental conditions effects (temperature, oxygen, pollutants) on survival, development and behaviour of European sturgeon, Acipenser sturio, embryo-larval stages*.

Demoll, R., & Maier, H. (1940). *Handbuch der Binnenfischerei Mitteleuropas* (Vol. vol III. B.).

Dendievel, A.-M., Grosbois, C., Ayrault, S., Evrard, O., Coynel, A., Debret, M., Gardes, T., Euzen, C., Schmitt, L., & Chabaux, F. (2022). Key factors influencing metal concentrations in sediments along Western European Rivers: A long-term monitoring study (1945–2020). *Science of the Total Environment*, *805*, 149778. https://doi.org/https://doi.org/10.1016/j.scitotenv.2021.149778

Derzhavin, A. (1947). Restoration of sturgeon fishes.(OT: Vosproizvodstvo zapasov osetrovykh ryb). *Izd. Akad. Nauk. Azerbaidzhanzkoi SSR, Baku.[In Russian]*, 243.

Desse-Berset, N. (2009). First archaeozoological identification of Atlantic sturgeon (*Acipenser oxyrinchus* Mitchill 1815) in France. *Comptes Rendus Palevol*, *8*(8), 717-724. https://doi.org/https://doi.org/10.1016/j.crpv.2009.06.001

Desse-Berset, N., & Williot, P. (2011). Emerging questions from the discovery of the long term presence of *Acipenser oxyrinchus* in France. *Journal of Applied Ichthyology*, *27*(2), 263-268. https://doi.org/https://doi.org/10.1111/j.1439-0426.2010.01649.x

Dieperink, C. (1998). From open sewer to salmon run: lessons from the Rhine water quality regime. *Water policy*, *1*(5), 471-485. https://doi.org/https://doi.org/10.1016/S1366-7017(99)00010-0

Doddema, M., Spaargaren, G., Wiryawan, B., & Bush, S. R. (2020). Fisher and trader responses to traceability interventions in Indonesia. *Society & Natural Resources*, *33*(10), 1232-1251. https://doi.org/https://doi.org/10.1080/08941920.2020.1739358

Dormann, W. (2023). The Surface Salinity of the North Sea and Baltic Sea Area. In *Terrestrial Coastal Ecosystems in Germany and Climate Change* (pp. 67-73). Springer. https://doi.org/https://doi.org/10.1007/978-3-031-12539-3_7

Economidis, P. S., Koutrakis, E. T., & Bobori, D. C. (2000). Distribution and conservation of *Acipenser sturio* L., 1758 and related species in Greek waters. In *Boletin - Instituto Espanol de Oceanografia* (Vol. 16, pp. 81-88).

The Habitats Directive, (1992). https://ec.europa.eu/environment/nature/legislation/habitatsdirective/

Eigaard, O. R., Bastardie, F., Hintzen, N. T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G. E., Egekvist, J., Fock, H. O., & Geitner, K. (2017). The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. *ICES Journal of Marine Science*, *74*(3), 847-865. https://doi.org/10.1093/icesjms/fsw194

Engelhard, G. H. (2008). One hundred and twenty years of change in fishing power of English North Sea trawlers. In *Advances in fisheries science* (Vol. 50, pp. 1-25).

Ennema, J. H. P. (1946). *Heemscutseire Kampen* (Vol. 47) [Book series]. Allert de Lange.

Ensing, D., & Breukelaar, A. (2017). *Genetic structure and tracking of sea trout (Salmo trutta L.) in the Rhine and Meuse estuary in the Netherlands (pp. 253–266) Sea Trout: Sience & management. Proceedings of the 2nd International Sea Trout Symposium 20–22 October 2016 Dundalk: Ireland. ISBN: 978 1788035 354.*

Essl, F., Nehring, S., Klingenstein, F., Milasowszky, N., Nowack, C., & Rabitsch, W. (2011). Review of risk assessment systems of IAS in Europe and introducing the German–Austrian Black List Information System (GABLIS). *Journal for Nature Conservation*, *19*(6), 339-350. https://doi.org/https://doi.org/10.1016/j.jnc.2011.08.005

European Parliamant. (2014). *Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species*. Retrieved from http://data.europa.eu/eli/reg/2014/1143/oj

European Union. (2000). *Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy*. Retrieved from https://eur-lex.europa.eu/eli/dir/2000/60/oj

European Union. (2018). *Commission Implementing Regulation (EU) 2018/1882 of 3 Decem ber 2018 on the application of certain disease prevention and control rules to categories of listed diseases and establishing a list of species and groups of species posing a considerable risk for the spread of those listed diseases. Off. J. Eur. Union 61, 21–29 ISSN 1977-0677.*: Official Journal of the European Union Retrieved from https://eur-lex.europa.eu/eli/reg_impl/2018/1882/oj

Fijn, R. C., De Jong, J. W., Adema, J., Van Horssen, P. W., Poot, M. J., Van Rijn, S., Van Eerden, M. R., & Boudewijn, T. J. (2022). GPS-tracking of Great Cormorants *Phalacrocorax carbo sinensis* reveals sex-specific differences in foraging behaviour. *Ardea*, *109*(3), 491-505. https://doi.org/https://doi.org/10.5253/arde.v109i2.a19

FishBase. (2020a). *Acipenser oxyrinchus*. FishBase. Retrieved 13-01-2020 from http://www.fishbase.us/summary/SpeciesSummary.php?ID=2593&genusname=Acipenser&speciesname=oxyrinchus&AT=acipenser+oxyrinchus&lang=English

FishBase. (2020b). *Acipenser sturio*. FishBase. Retrieved 13-01-2020 from http://www.fishbase.us/summary/SpeciesSummary.php?ID=2066&genusname=Acipenser&speciesname=sturio&AT=acipenser+sturio&lang=EnglishFontana, F., Lanfredi, M., Kirschbaum, F., Garrido-Ramos, M. A., Robles, F., Forlani, A., & Congiu, L. (2008). Comparison of karyotypes of *Acipenser oxyrinchus* and *A. sturio* by chromosome banding and fluorescent in situ hybridization. *Genetica*, *132*(3), 281-286. https://doi.org/https://doi.org/10.1007/s10709-007-9171-4

Fortibuoni, T., Libralato, S., Arneri, E., Giovanardi, O., Solidoro, C., & Raicevich, S. (2017). Fish and fishery historical data since the 19th century in the Adriatic Sea, Mediterranean. *Scientific data*, *4*(1), 1-13. https://doi.org/https://doi.org/10.1038/sdata.2017.104

France Ministère de l'Écologie. (2020). *Plan National d'Actions Esturgeon Européen 2020-2029*.

Friedrich, T. (2018). Danube sturgeons: past and future. In *Riverine ecosystem management: science for governing towards a sustainable future* (Vol. 8, pp. 507-518).

Friedrich, T., Reinartz, R., & Gessner, J. (2019). Sturgeon re-introduction in the Upper and Middle Danube River Basin. *Journal of Applied Ichthyology*, *35*(5), 1059-1068. https://doi.org/https://doi.org/10.1111/jai.13966

Frings, R. M. (2015). Sand and gravel on the move: Human impacts on bed-material load along the Lower Rhine River. In *Geomorphic approaches to integrated floodplain management of lowland fluvial systems in North America and Europe* (pp. 9-26).

Fugro. (2002). *Laboratoriumresultaten Betreffende Morfologisch Modelleren (Datarapport) (No. Opdrachtnummer H-4086).*

Fusch Ph D, P. I., & Ness, L. R. (2015). Are we there yet? Data saturation in qualitative research. https://nsuworks.nova.edu/tqr/vol20/iss9/3

Gabel, F., Lorenz, S., & Stoll, S. (2017). Effects of ship-induced waves on aquatic ecosystems. *Science of the Total Environment*, *601*, 926-939. https://doi.org/https://doi.org/10.1016/j.scitotenv.2017.05.206

Galimova, D. N., Askeyev, I. V., Askeyev, O. V., Popović, D., & Panagiotopoulou, H. (2015). *A study of the fish bones from the medieval town-Staraya Ladoga* Fishing through time. Archaeoichthyology, Biodiversity, Ecology and Human Impact on Aquatic Environments. 18th Fish Remains Working Group International Council for Archaeozoology. 28th September-3rd October,

Gardiner, B. G. (1984). Sturgeons as living fossils. In *Living fossils* (pp. 148-152). Springer. https://doi.org/10.1007/978-1-4613-8271-3_15

Gerring, J. (2004). What is a case study and what is it good for? *American political science review*, *98*(2), 341-354. https://doi.org/https://doi.org/10.1017/S0003055404001182

Gessner, J., Arndt, G.-M., Andrzej Kapusta, S., Gushin, A., Pilinkovskij, A., Povliūnas, J., Medne, R., Purvina, S., Tambets, M., & Möller10, P. R. (2019). HELCOM-Action Plan.

Gessner, J., Arndt, G.-M., Fredrich, F., Ludwig, A., Kirschbaum, F., Bartel, R., & von Nordheim, H. (2011a). Remediation of Atlantic sturgeon *Acipenser oxyrinchus* in the Oder River: background and first results. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758: The Reunion of the European and Atlantic Sturgeons* (pp. 539-559). https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_41

Gessner, J., Arndt, G. M., Ludwig, A., & Kirschbaum, F. (2007). *Remediation of Atlantic Sturgeon in the Baltic Sea: Background, Status, and Perspectives*.

Gessner, J., Arndt, G. M., Tiedemann, R., Bartel, R., & Kirschbaum, F. (2006). Remediation measures for the Baltic sturgeon: status review and perspectives. *Journal of Applied Ichthyology*, *22*, 23-31. https://doi.org/https://doi.org/10.1111/j.1439-0426.2007.00925.x

Gessner, J., & Bartel, R. (2000). Sturgeon spawning grounds in the Odra River tributaries: a first assessment. *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA*, *16*(1/4), 127-138.

Gessner, J., & Bartel, R. (2006). Characteristics and availability of spawning habitat for Baltic sturgeon in the Odra River and its tributaries. *Journal of Applied Ichthyology/Zeitschrift fur angewandte Ichthyologie*, *22*(Suppl.), 172-181. https://doi.org/https://doi.org/10.1111/j.1439-0426.2007.00947.x

Gessner, J., Chèvre, P., & Rochard, E. (2009). *Remediation of the European Atlantic sturgeon (Acipenser sturio)* 2nd International Conference on Progress in Marine Conservation Europe 2009, Germany, 2-6 November 2009.

Gessner, J., Debus, L., Filipiak, J., Spratte, S., Skora, K., & Arndt, G. (1999). Development of sturgeon catches in German and adjacent waters since 1980. *Journal of Applied Ichthyology*, *15*(4-5), 136-141. https://doi.org/https://doi.org/10.1111/j.1439-0426.1999.tb00223.x

Gessner, J., Fredrich, F., Arndt, G. M., & Von Nordheim, H. (2010a). Conserving and reintroducing the

Atlantic sturgeon in North and Baltic Sea tributaries [Article]. *Natur und Landschaft*, *85*(12), 514-519. https://doi.org/https://doi.org/10.17433/12.2010.50153053.514-519

Gessner, J., Spratte, S., & Kirschbaum, F. (2011b). Historic overview on the status of the European Sturgeon (*Acipenser sturio*) and its fishery in the North Sea and its tributaries with a focus on German waters. In *Biology and Conservation of the European SturgeonAcipenser sturioL. 1758* (pp. 195-219). Springer.

Gessner, J., Tautenhahn, M., Spratte, S., Arndt, G., & von Nordheim, H. (2011c). Development of a German Action Plan for the restoration of the European sturgeon *Acipenser sturio* L.–implementing international commitments on a national scale. *Journal of Applied Ichthyology*, *27*(2), 192-198. https://doi.org/ https://doi.org/10.1111/j.1439-0426.2011.01697.x

Gessner, J., Tautenhahn, M., von Nordheim, H., & Borchers, T. (2010b). *Nationaler Aktionsplan zum Schutz und zur Erhaltung des europäischen Störs (Acipenser sturio)* (Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit (BMU), Bundesamt für Naturschutz (BfN). Silber Druck, Niestetal, Issue.

Gessner, J., Williot, P., Rochard, E., Freyhof, J., & Kottelat, M. (2010c). *Acipenser sturio*. The IUCN Red List of Threatened Species 2010: e.T230A13040963. https://doi.org/https://dx.doi.org/10.2305/IUCN.UK.2010-1.RLTS.T230A13040963.en.

Gessner, J., Williot, P., Rochard, E., Freyhof, J., & Kottelat, M. (2022). *Acipenser sturio*. The IUCN Red List of Threatened Species 2022: e.T230A137215851. https://doi.org/https://dx.doi.org/10.2305/IUCN.UK.2022-1.RLTS.T230A137215851.en

Gessner, J., Zahn, S., Jaric, I., & Wolter, C. (2014). Estimating the potential for habitat restoration and connectivity effects on European sturgeon (*Acipenser sturio* L. 1758) population rehabilitation in a lowland river - the Havel, Germany. *Journal of Applied Ichthyology*, *30*(6), 1473-1482. https://doi.org/10.1111/jai.12613

Glaser, B. G., & Strauss, A. L. (1967). *The discovery of grounded theory: Strategies for qualitative research*. Aldine Pub. Co. https://doi.org/https://doi.org/10.4324/9780203793206

Granada-Lorencio, C. (1991). The effect of man on the fish fauna of the River Guadalquivir, Spain. *Fisheries research*, *12*(2), 91-100. https://doi.org/http://dx.doi.org/10.1016/0165-7836(91)90034-D

Gray, C. A., & Kennelly, S. J. (2018). Bycatches of endangered, threatened and protected species in marine fisheries. *Reviews in fish biology and fisheries*, *28*(3), 521-541. https://doi.org/https://doi.org/10.1007/s11160-018-9520-7

Gross, M. R., Repka, J., Robertson, C. T., Secor, D. H., & Van Winkle, W. (2002). Sturgeon conservation: insights from elasticity analysis. American Fisheries Society Symposium,

Guest, G., Bunce, A., & Johnson, L. (2006). How many interviews are enough? An experiment with data saturation and variability. *Field methods*, *18*(1), 59-82. https://doi.org/10.1177/1525822X05279903

Guhl, B., Stürenberg, F.-J., & Santora, G. (2014). Contaminant levels in the European eel (*Anguilla anguilla*) in North Rhine-Westphalian rivers. *Environmental Sciences Europe*, *26*, 1-16. https://doi.org/https://doi.org/10.1186/s12302-014-0026-1

Haasnoot, T., Kraan, M., & Bush, S. R. (2016). Fishing gear transitions: lessons from the Dutch flatfish pulse trawl. *ICES Journal of Marine Science*, *73*(4), 1235-1243. https://doi.org/https://doi.org/10.1093/icesjms/fsw002

Haenen, O., Lehmann, J., Engelsma, M., Stürenberg, F.-J., Roozenburg, I., Kerkhoff, S., & Breteler, J. K. (2010). The health status of European silver eels, *Anguilla anguilla*, in the Dutch River Rhine Watershed and Lake IJsselmeer. *Aquaculture*, *309*(1-4), 15-24. https://doi.org/https://doi.org/10.1016/j.aquaculture.2010.08.026

Haidvogl, G., Lajus, D., Pont, D., Schmid, M., Jungwirth, M., & Lajus, J. (2014). Typology of historical sources and the reconstruction of long-term historical changes of riverine fish: a case study of the Austrian Danube and northern Russian rivers. *Ecology of Freshwater Fish*, *23*(4), 498-515. https://doi.org/https://doi.org/10.1111/eff.12103

Hanel, L., Plesník, J., Andreska, J., Lusk, S., Novák, J., & Plíštil, J. (2011). Alien fishes in European waters. *Bulletin Lampetra*, *7*, 148-185.

Hardenbicker, P., Viergutz, C., Becker, A., Kirchesch, V., Nilson, E., & Fischer, H. (2017). *Water temperature increases in the river Rhine in response to climate change* (1436-3798). (Regional Environmental Change, Issue.

Harrower, C., Scalera, R., Pagad, S., Schonrogge, K., & Roy, H. (2018). *Guidance for interpretation of CBD categories on introduction pathways*.

Hartmann, G. L. (1827). *Helvetische Ichthyologie: oder ausführliche Naturgeschichte der in der Schweiz sich vorfindenden Fische*. Orell, Füssli und Company.

Havelka, M., & Arai, K. (2018). Hybridization and polyploidization in sturgeon. *Sex Control in Aquaculture*, 669-687. https://doi.org/https://doi.org/10.1002/9781119127291.ch34

Havelka, M., Kašpar, V., Hulák, M., & Flajšhans, M. (2011). Sturgeon genetics and cytogenetics: a review related to ploidy levels and interspecific hybridization. *Journal of Vertebrate Biology*, *60*(2), 93-103. https://doi.org/https://doi.org/10.25225/fozo.v60.i2.a3.2011

Haxton, T. J., & Cano, T. M. (2016). A global perspective of fragmentation on a declining taxon-the sturgeon (Acipenseriformes). *Endangered Species Research*, *31*(1), 203-210. https://doi.org/10.3354/esr00767

Helfman, G., Collette, B. B., Facey, D. E., & Bowen, B. W. (2009). *The diversity of fishes: biology, evolution, and ecology*. John Wiley & Sons.

Hilborn, R. (2007). Defining success in fisheries and conflicts in objectives. *Marine Policy*, *31*(2), 153-158. https://doi.org/https://doi.org/10.1016/j.marpol.2006.05.014

Hilton, E., & Fox, D. (2022). *Acipenser oxyrinchus*. The IUCN Red List of Threatened Species. https://dx.doi.org/10.2305/IUCN.UK.2022-1.RLTS.T245A2785934.en

Hoek, P. P. C. (1894). *Mededeelingen over visscherij; maandblad in overleg met het College voor de Zeevisscherijen* (Vol. 1). De Boer.

Hoek, P. P. C. (1900). *Mededeelingen over visscherij; maandblad in overleg met het College voor de Zeevisscherijen* (Vol. 7). De Boer.

Hoek, P. P. C. (1910). De achteruitgang der steurvisscherij onzer benedenrivieren. *Mededeelingen over Visscherij maandblad met gebruikmaking van officieele bescheiden*, *17*.

Hoffmann, R. C. (1996). *Economic development and aquatic ecosystems in medieval Europe* (Vol. 101).

Holčík, J. (1989). *The Freshwater Fishes of Europe: General Introduction to Fishes. Acipenseriformes*. Aula-Verlag.

Holčík, J., Kinzelbach, R., Sokolov, L., & Vasil'ev, V. (1989). *Acipenser sturio* Linnaeus, 1758. In *The freshwater fishes of Europe* (Vol. 1, pp. 367-394).

Hoogenboom, R., Bovee, T., Traag, W., Hoogerbrugge, R., Baumann, B., Portier, L., van de Weg, G., & de Vries, J. (2006). The use of the DR CALUX® bioassay and indicator polychlorinated biphenyls for screening of elevated levels of dioxins and dioxin-like polychlorinated biphenyls in eel. *Molecular nutrition & food research*, *50*(10), 945-957. https://doi.org/https://doi.org/10.1002/mnfr.200600061

Hoogenboom, R. L., Kotterman, M. J., Hoek-van Nieuwenhuizen, M., van der Lee, M. K., Mennes, W. C., Jeurissen, S. M., & van Leeuwen, S. P. (2015). Dioxins, PCBs and heavy metals in Chinese mitten crabs from Dutch rivers and lakes. *Chemosphere*, *123*, 1-8. https://doi.org/https://doi.org/10.1016/j.chemosphere.2014.10.055

Huijbregt, P. J. (1984). De Zalmzegenvisserij in de Lek bij Ammersloot. In J. E. A. Boomgaard (Ed.), *Holland, Regionaal-historisch tijdschrift 16e jaargang, nummer 3-4. juni-augustus 1984* (Vol. 16, pp. 200-206).

Hundt, M., Scharbert, A., Weibel, U., Kuhn, G., Metzner, K., Jatteau, P., Pies, A., Schulz, R., & Gergs, R. (2015). Chapter VII: First evidence of natural reproduction of the Allis shad *Alosa alosa* (L. 1758) in River Rhine following reintroduction measures. *Aquaculture, conservation and restoration of anadromous fish populations of River Rhine with particular regard to the re-introduction of the Allis shad Alosa alosa.*, *87*(2), 37. https://doi.org/https://doi.org/10.1111/jfb.12721

ICPR. (2013). *Development of Rhine water temperatures based on validated temperature measurements between 1978 and 2011* (978-3-941994-36-2).

ICPR. (2018). *Master Plan Migratory Fish Rhine 2018*.

IKSR-CIPR-ICBR. (2009). *Master plan migratory fish Rhine. Koblenz: International Commission for the Protection of the Rhine (p. 32). ISBN 978-3-941994-09-6*.

IUCN. (2012). *Red List categories and criteria: Version 3.1.* (Second edition. ed., Vol. iv). IUCN.

IUCN/SSC. (2013). *Guidelines for Reintroductions and Other Conservation Translocations.* (978-2-8317-1609-1).

Jakob, E. (1996). Das Potential des Unteren Niederrheins als Laich-und Bruthabitat des europäischen Störs *Acipenser sturio*. *LÖBF (Landesanstalt für Ökologie, Bodenverordnung und Forsten Nordrhein Westfalen). Kirchhundem, Duitsland*.

Jarić, I., Ebenhard, T., & Lenhardt, M. (2010). Population viability analysis of the Danube sturgeon populations in a Vortex simulation model. *Reviews in fish biology and fisheries*, *20*(2), 219-237. https://doi.org/http://dx.doi.org/10.1007/s11160-009-9151-0

Jarić, I., & Gessner, J. (2013). A life-stage population model of the European sturgeon (*Acipenser sturio*) in the Elbe River. Part I: general model outline and potential applications. *Journal of Applied Ichthyology*, *29*(3), 483-493. https://doi.org/https://doi.org/10.1111/jai.12235

Jarić, I., Riepe, C., & Gessner, J. (2018). Sturgeon and paddlefish life history and management: Experts' knowledge and beliefs. *Journal of Applied Ichthyology*, *34*(2), 244-257. https://doi.org/10.1111/jai.13563

Jatteau, P. (2015). *Programme de recherche et de conservation de l'esturgeon européen Acipenser sturio* (Publication Number Etude N° 187) Irstea]. Bordeaux. https://hal.inrae.fr/hal-02596673

Jego, S., Gazeau, C., Jatteau, P., Elie, P., & Rochard, E. (2002). Spawning grounds available for the European sturgeon *Acipenser sturio* L. 1758 in the Garonne-Dordogne basin. Methods used, present status and prospects [Les frayeres potentielles de l'esturgeon europeen *Acipenser sturio* L. 1758 dans le bassin Garonne-Dordogne. Methodes d'investigation , etat actuel et perspectives]. *Bulletin francais de la peche et de la pisciculture*(365-366), 487-505.

Jenkins, L. D., Eayrs, S., Pol, M. V., & Thompson, K. R. (2023). Uptake of proven bycatch reduction fishing gear: perceived best practices and the role of affective change readiness. *ICES Journal of Marine Science*, *80*(3), 437-445. https://doi.org/https://doi.org/10.1093/icesjms/fsac126

Jennings, S., & Kaiser, M. J. (1998). The effects of fishing on marine ecosystems. In *Advances in marine biology* (Vol. 34, pp. 201-352). Elsevier. https://doi.org/https://doi.org/10.1016/S0065-2881(08)60212-6

Jentoft, S., & Chuenpagdee, R. (2009). Fisheries and coastal governance as a wicked problem. *Marine Policy*, *33*(4), 553-560. https://doi.org/https://doi.org/10.1016/j.marpol.2008.12.002

Johnson, T. R. (2011). Fishermen, scientists, and boundary spanners: cooperative research in the US Illex squid fishery. *Society and Natural Resources*, *24*(3), 242-255. https://doi.org/https://doi.org/10.1080/08941920802545800

Johnson, T. R., & van Densen, W. L. (2007). Benefits and organization of cooperative research for fisheries management. *ICES Journal of Marine Science*, *64*(4), 834-840. https://doi.org/https://doi.org/10.1093/icesjms/fsm014

Kallis, G., & Butler, D. (2001). The EU water framework directive: measures and implications. *Water policy*, *3*(2), 125-142. https://doi.org/https://doi.org/10.1016/S1366-7017(01)00007-1

Kinzelbach, R. (1978). Veränderungen der Fauna des Oberrheins. *Beih. Veröff. Naturschutz Landschaftspflege Baden-Württemberg*, *11*, 291-301.

Kinzelbach, R. (1987). Das ehemalige Vorkommen des Störs, *Acipenser sturio* (Linnaeus, 1758), im Einzugsgebiet des Rheins (Chondrostei: Acipenseridae). *Zeitschrift für angewandte Zoologie*, *74*(2), 167-200. https://doi.org/http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=7600720

Kinzelbach, R. K. (1997). The sturgeon (*Acipenser sturio* L. 1758) in Europe. *Zeitschrift für Ökologie und Naturschutz*, *6*, 129-135.

Kirschbaum, F., & Gessner, J. (2000). Re-establishment programme for *Acipenser sturio* L., 1758: The German approach. In *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA* (Vol. 16, pp. 149-156).

Kirschbaum, F., Gessner, J., & Williot, P. (2000). Restoration of *Acipenser sturio* L., 1758 in Germany: Growth characteristics of juvenile fish reared under experimental indoor conditions. In *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA* (Vol. 16, pp. 157-166).

Kirschbaum, F., & Williot, P. (2011). Ontogeny of the european sturgeon, *Acipenser sturio*. In *Biology and Conservation of the European SturgeonAcipenser sturioL. 1758* (pp. 65-80). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_5

Kirschbaum, F., Wuertz, S., Williot, P., Tiedemann, R., Gerd-Michael, A., Anders, E., Krüger, A., Bartel, R., & Gessner, J. (2009). Prerequisites for the Restoration of the European Atlantic Sturgeon, *Acipenser sturio* and the Baltic Sturgeon (*A. oxyrinchus*× *A. sturio*) in Germany. In *Biology, conservation and sustainable development of sturgeons* (pp. 385-401). Springer. https://doi.org/https://doi.org/10.1007/978-1-4020-8437-9_24

Kolman, R., Gushchin, A., & Lysanskii, I. (2016). *Possibility of restoring the population of the sharp-nosed sturgeon Acipenser oxyrinchus oxyrinchus Mitchill in the Neman River basin* Proceedings of the Third Scientific and Practical Conference with International Participation "Environmental Safety of NPP, Kaliningrad.

Kolman, R., Kapusta, A., & Duda, A. (2011a). Re-establishing the Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus* Mitchill) in Poland. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758: The Reunion of the European and Atlantic Sturgeons* (pp. 573-581). https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_43

Kolman, R., Kapusta, A., Duda, A., Szczepkowski, M., Wiszniewski, G., & Sakowicz, S. (2011b, 2017-04-18). Recovery of Baltic sturgeon *Acipenser oxyrinchus* Mitchill in Poland: Sturgeon restocking programme gives positive results. *EUROFISH magazine*, (5), 47-48.

Kolman, R., Kapusta, A., Duda, A., & Wiszniewski, G. (2011c). Review of the current status of the Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus* Mitchill 1815, in Poland: principles, previous experience, and results. *Journal of Applied Ichthyology*, *27*(2), 186-191. https://doi.org/10.1111/j.1439-0426.2011.01680.x

Kolman, R., Khudyi, O., Kushniryk, O., Khuda, L., Prusinska, M., & Wiszniewski, G. (2018). Influence of temperature and *Artemia* enriched with ω-3 PUFAs on the early ontogenesis of Atlantic sturgeon, *Acipenser oxyrinchus* Mitchill, 1815. *Aquaculture research*, *49*(5), 1740-1751. https://doi.org/http://dx.doi.org/10.1111/are.13629

Kolman, R., & Zarkua, Z. (2002). Environmental conditions of common sturgeon (*Acipenser sturio* L.) spawning in River Rioni (Georgia). *Electronic Journal of Polish Agricultural Universities. Series Fisheries*, *2*(05). https://doi.org/http://www.ejpau.media.pl/

Kosters, A., Visser, T., . (2022). *Jaarlijkse actualisatie modellen Rijn 2022 : Baseline en D-Hydro j22_6. Rapport voor Rijkswaterstaat Water, Verkeer en Leefomgeving.*

Kottelat, M., & Freyhof, J. r. (2007). *Handbook of European freshwater fishes*. Publications Kottelat.

Kraan, M., Groeneveld, R., Pauwelussen, A., Haasnoot, T., & Bush, S. R. (2020). Science, subsidies and the politics of the pulse trawl ban in the European Union. *Marine Policy*, *118*, 103975. https://doi.org/https://doi.org/10.1016/j.marpol.2020.103975

Kraan, M., Uhlmann, S., Steenbergen, J., Van Helmond, A., & Van Hoof, L. (2013). The optimal process of self-sampling in fisheries: lessons learned in the Netherlands. *83*(4), 963-973. https://doi.org/https://doi.org/10.1111/jfb.12192

Kranenbarg, J. (2018). Haringvlietsluizen op een kier: kansen voor vissen. *RAVON*, *20*(2), 20-23.

Krykhtin, M. L., & Svirskii, V. G. (1997). Endemic sturgeons of the Amur River: kaluga, *Huso dauricus*, and Amur sturgeon, *Acipenser schrenckii*. *Environmental Biology of Fishes*, *48*(1), 231-239. https://doi.org/https://doi.org/10.1023/A:1007358027263

Kumschick, S., & Richardson, D. M. (2013). Species-based risk assessments for biological invasions: advances and challenges. *Diversity and Distributions*, *19*(9), 1095-1105. https://doi.org/https://doi.org/10.1111/ddi.12110

Lassalle, G., Crouzet, P., Gessner, J., & Rochard, E. (2010). Global warming impacts and conservation responses for the critically endangered European Atlantic sturgeon. *Biological Conservation*, *143*(11), 2441-2452. https://doi.org/https://doi.org/10.1016/j.biocon.2010.06.008

Lassalle, G., Crouzet, P., & Rochard, E. (2009). Modelling the current distribution of European diadromous fishes: an approach integrating regional anthropogenic pressures. *Freshwater Biology*, *54*(3), 587-606. https://doi.org/http://dx.doi.org/10.1111/j.1365-2427.2008.02135.x

Lassalle, G., & Rochard, E. (2009). Impact of twenty-first century climate change on diadromous fish spread over Europe, North Africa and the Middle East. *Global change biology*, *15*(5), 1072-1089. https://doi.org/http://dx.doi.org/10.1111/j.1365-2486.2008.01794.x

Leedy, P. D., & Ormrod, J. E. (2005). *Practical research* (Vol. 108). Pearson Custom Saddle River, NJ, USA.

Lehtonen, H. (2002). Alien freshwater fishes of Europe. In *Invasive aquatic species of Europe. Distribution, impacts and management* (pp. 153-161). Springer. https://doi.org/https://doi.org/10.1007/978-94-015-9956-6_17

Lenders, H., Chamuleau, T., Hendriks, A., Lauwerier, R., Leuven, R., & Verberk, W. (2016). Historical rise of waterpower initiated the collapse of salmon stocks. *Scientific Reports*, *6*(1), 1-9. https://doi.org/https://doi.org/10.1038/srep29269

Lenders, H. R. (2017). Fish and fisheries in the Lower Rhine 1550–1950: A historical-ecological perspective. *Journal of environmental management*, *202*, 403-411. https://doi.org/https://doi.org/10.1016/j.jenvman.2016.09.011

Lepage, M., & Rochard, E. (2011). Fishery by-catch of European Sturgeon in the Bay of Biscay. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758: The Reunion of the European and Atlantic Sturgeons* (pp. 335-342). https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_22

Lepage, M., Taverny, C., Piefort, S., Pumont, P., Rochard, E., & Brosse, L. (2005). Juvenile sturgeon (*Acipenser sturio*) habitat utilization in the Gironde estuary as determined by acoustic telemetry. In M. T. Spedicato, G. Lembo, & G. Marmulla (Eds.), (pp. 9-177). FAO/COISPA, Rome (Italy). https://doi.org/https://www.fao.org/4/y5999e/y5999e00.htm

Letaconnoux, R. (1961). Note sur la fréquence de la distribution des captures d'esturgeons (*Acipenser sturio* L.) dans le Golfe de Gascogne. *Revue des Travaux de l'Institut des Pêches Maritimes*, *25*, 253-261.

Leung, B., Roura-Pascual, N., Bacher, S., Heikkilä, J., Brotons, L., Burgman, M. A., Dehnen-Schmutz, K., Essl, F., Hulme, P. E., & Richardson, D. M. (2012). TEASIng apart alien species risk assessments: a framework for best practices. *Ecology Letters*, *15*(12), 1475-1493. https://doi.org/https://doi.org/10.1111/ele.12003

Leuthner, F. (1877). *Die mittelrheinische Fischfauna mit besonderer Berücksichtigung des Rheins bei Basel: nebst einer mit kurzen diagnosen versehenen systematischen Uebersicht zur Bestimmung der rheinischen Fische*. H. Georg.

Lockwood, J. L., Welbourne, D. J., Romagosa, C. M., Cassey, P., Mandrak, N. E., Strecker, A., Leung, B., Stringham, O. C., Udell, B., & Episcopio-Sturgeon, D. J. (2019). When pets become pests: the role of the exotic pet trade in producing invasive vertebrate animals. *Frontiers in Ecology and the Environment*, *17*(6), 323-330. https://doi.org/https://doi.org/10.1002/fee.2059

Ludwig, A., Debus, L., Lieckfeldt, D., Wirgin, I., Benecke, N., Jenneckens, I., Williot, P., Waldman, J. R., & Pitra, C. (2002). When the American sea sturgeon swam east. *Nature*, *419*(6906), 447-448. https://doi.org/https://doi.org/10.1038/419447a

Ludwig, A., & Gessner, J. (2007, 2007). *What Makes the Difference?--Sea Sturgeon on Both Sides of the Atlantic Ocean*

Ludwig, A., Lippold, S., Debus, L., & Reinartz, R. (2009a). First evidence of hybridization between endangered sterlets (*Acipenser ruthenus*) and exotic Siberian sturgeons (*Acipenser baerii*) in the Danube River. *Biological Invasions*, *11*(3), 753-760. https://doi.org/10.1007/s10530-008-9289-z

Ludwig, A., Makowiecki, D., & Benecke, N. (2009b). Further evidence of trans-Atlantic colonization of Western Europe by American Atlantic sturgeons. *Archaeofauna*, *18*, 185-192.

Ludwig, A., Morales-Muniz, A., & Roselló-Izquierdo, E. (2011). Sturgeon in Iberia from past to present. In *Biology and Conservation of the European SturgeonAcipenser sturioL. 1758* (pp. 131-146). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_9

Ludwig, A., Williot, P., Kirschbaum, F., & Lieckfeld, D. (2004). Genetic variability of the Gironde population of *Acipenser sturio*. *Species differentiation and population identification in the sturgeons Acipenser sturio L. and Acipenser oxyrinchus*, *101*, 54-72. https://doi.org/https://hal.inrae.fr/hal-02583188

Lutchman, I. (2014). *A review of best practice mitigation measures to address the problem of bycatch in commercial fisheries* (Marine Stewardship Council Science Series, Issue.

Lyman, R. L. (2006). Paleozoology in the service of conservation biology. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *15*(1), 11-19. https://doi.org/https://doi.org/10.1002/evan.20083

Magnin, E. (1959). Détermination de l'âge et croissance de l'*Acipenser sturio* L. de la Gironde. *Bulletin Français de Pisciculture*(193), 152-159.

Magnin, E. (1962). *Recherches sur la systématique et la biologie des Acipensérid és Acipenser sturio L'Acipenser oxyrhynchus Mitchill, Acipenser fulvescens Raf* Imprimerie nationale].

Mako, P., & Galieriková, A. (2021). Inland navigation on the Danube and the Rhine waterways. *Transportation Research Procedia*, *55*, 10-17. https://doi.org/https://doi.org/10.1016/j.trpro.2021.06.002

Marg, O., & Theiler, L. (2023). Effects of transdisciplinary research on scientific knowledge and reflexivity. *Research Evaluation*, rvad033. https://doi.org/https://doi.org/10.1093/reseval/rvad033

Martens, P. J. M. (1992). De zalmvissers van de Biesbosch: een onderzoek naar de visserij op het Bergse Veld, 1421-1869.

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., & Gomis, M. (2021). *Climate change 2021: the physical science basis* (Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change, Issue.

Mauri, A., Davis, B., Collins, P., & Kaplan, J. O. (2015). The climate of Europe during the Holocene: a gridded pollen-based reconstruction and its multi-proxy evaluation. *Quaternary Science Reviews*, *112*, 109-127. https://doi.org/https://doi.org/10.1016/j.quascirev.2015.01.013

Maury-Brachet, R., Rochard, E., Durrieu, G., & Boudou, A. (2008). The 'Storm of the Century'(December 1999) and the accidental escape of Siberian sturgeons (*Acipenser baerii*) into the Gironde estuary (Southwest France). *Environmental Science and Pollution Research*, *15*(1), 89-94. https://doi.org/https://doi.org/10.1065/espr2007.12.469

McAdam, S. O., Crossman, J. A., Williamson, C., St-Onge, I., Dion, R., Manny, B. A., & Gessner, J. (2018). If you build it, will they come? Spawning habitat remediation for sturgeon. *Journal of Applied Ichthyology*, *34*(2), 258-278. https://doi.org/10.1111/jai.13566

McCord, J. W., Collins, M. R., Post, W. C., & Smith, T. I. J. (2007). Attempts to Develop an Index of Abundance for Age-1 Atlantic Sturgeon in South Carolina, USA. *In American Fisheries Society Symposium (Vol. 56, p. 397). American Fisheries Society.*

McCormick, H., Murray, J., Colclough, S., Gessner, J., Greenslade, J., Reynolds, L., Hedges, S., Philipsen, P., & Debney, A. (2023). *UK Sturgeon Conservation Strategy and Action Plan 2023 –2033* (Online: 978-0-900881-96-1 In print: 978-0-900881-97-8).

MEDDTL. (2011). *Plan national d'actions en faveur de l'esturgeon européen Acipenser sturio.* Bordeaux: Ministère de l'écologie du développement durable des transports et du logement. France

Michelet, N. (2011). Why, how and results from an awareness campaign within marine professional fishermen for the protection of large migratory fish, the European sturgeon *Acipenser sturio*. In *Biology and Conservation of the European SturgeonAcipenser sturioL. 1758* (pp. 489-498). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_37

Milly, P. C., Dunne, K. A., & Vecchia, A. V. (2005). Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, *438*(7066), 347-350. https://doi.org/https://doi.org/10.1038/nature04312

Mims, S. D., & Shelton, W. L. (2015). *Paddlefish aquaculture*. John Wiley & Sons.

Mohr, E. (1952). *Der Stör*. Geest & Portig.

Mostert, E. (2009). International co-operation on Rhine water quality 1945–2008: An example to follow? *Physics and Chemistry of the Earth, Parts A/B/C*, *34*(3), 142-149. https://doi.org/https://doi.org/10.1016/j.pce.2008.06.007

Mugetti, D., Pastorino, P., Menconi, V., Pedron, C., & Prearo, M. (2020). The old and the new on viral diseases in sturgeon. *Pathogens*, *9*(2), 146. https://doi.org/https://doi.org/10.3390/pathogens9020146

Murk, A. (2024). *Toxicological safety assessment for sturgeons in the Rhine-Meuse Delta after sturgeon population establishment Risk estimation and critical knowledge gaps*.

Muus, B., Dahlström, P., & Terofal, F. (1968). BLV Bestimmungsbuch Süßwasserfische–Europas. *Farben abgebildet und beschrieben Biologie, Fang, wirtschaftliche Bedeutung. BLV Verlagsgesellschaft, München, Germany*.

Myers, R., Barrowman, N., Hutchings, J., & Rosenberg, A. (1995). Population dynamics of exploited fish stocks at low population levels. *science*, *269*(5227), 1106-1108. https://doi.org/DOI: 10.1126/science.269.5227.11

National Research Council. (2003). *Cooperative research in the national marine fisheries service*. National Academies Press.

Navid, D. (1989). The international law of migratory species: the Ramsar Convention. *Nat. Resources J.*, *29*, 1001.

Nehring, S., Essl, F., Klingenstein, F., Nowack, C., Rabitsch, W., Stöhr, O., Wiesner, C., & Wolter, C. (2010). Schwarze Liste invasiver Arten: Kriteriensystem und Schwarze Listen invasiver Fische für Deutschland und für Österreich. *BfN-Skripten*, *285*, 185.

Nellis, P., Senneville, S., Munro, J., Drapeau, G., Hatin, D., Desrosiers, G., & Saucier, F. J. (2007). *Tracking the Dumping and Bed Load Transport of Dredged Sediment in the St. Lawrence Estuarine Transition Zone and Assessing Their Impacts on Macrobenthos in Atlantic Sturgeon Habitat*.

Nemitz, A. (2010). *Perspektiven für eine Wiederansiedlung des Europäischen Störs (Acipenser sturio L., 1758) im Einzugsgebiet des Rheins* (Unveröffentlichte Studie des Rheinischen Fischereiverbandes von 1880 e.V., Issue.

Niklitschek, E. J., & Secor, D. H. (2010). Experimental and field evidence of behavioural habitat selection by juvenile Atlantic *Acipenser oxyrinchus oxyrinchus* and shortnose *Acipenser brevirostrum* sturgeons. *Journal of Fish Biology*, *77*(6), 1293-1308. https://doi.org/http://dx.doi.org/10.1111/j.1095-8649.2010.02748.x

Nikulina, E. A., & Schmölcke, U. (2016a). Archaeogenetic evidence for medieval occurrence of Atlantic sturgeon *Acipenser oxyrinchus* in the North Sea. *Environmental Archaeology*, *21*(2), 137-143. https://doi.org/https://doi.org/10.1179/1749631415Y.0000000022

Nikulina, E. A., & Schmölcke, U. (2016b). Reconstruction of the historical distribution of sturgeons (Acipenseridae) in the eastern North Atlantic based on ancient DNA and bone morphology of archaeological remains: Implications for conservation and restoration programmes. *Diversity and Distributions*, *22*(10), 1036-1044. https://doi.org/https://doi.org/10.1111/ddi.12461

Nikulina, E. A., & Schmölcke, U. (2018). Historische Verbreitung von Europäischem Stör (*Acipenser sturio*) und Atlantischem Stör (*Acipenser oxyrinchus*) in West- und Mitteleuropa. *Beiträge zur Archäozoologie und Prähistorischen Anthropologie*, *11*, 37–44.

Ninua, N. (1976). *Atlantic sturgeon from the Rioni River* [Atlanticheskij osetr reki Rioni]. Metsniereba, Tbilisi (USSR).

Noordhuis, R. (2017). *Het Haringvliet na de Kier: Samenvatting van hydrologische prognoses ten behoeve van effectinschattingen op vis en vogels*. Deltares.

OSPAR Commission. (2009). *Background Document for the Common sturgeon - Acipenser sturio* (ISBN 978-1-906840-57-0). (Biodiversity Series, Issue.

OSPAR Commission. (2021). *BDC2020/European or Common sturgeon*. Retrieved from https://oap.ospar.org/en/ospar-assessments/committee-assessments/biodiversity-committee/status-assesments/european-or-common-sturgeon/

Paalvast, P. (2016). *Monitoringsplan Ecologie Project Kierbesluit*.

Paaver, T. (1999). Historic and recent records of native and exotic sturgeon species in Estonia. *Journal of Applied Ichthyology*, *15*(4-5), 129-132.

Page, L. M., & Burr, B. M. (2011). *Peterson field guide to freshwater fishes of North America north of Mexico*. Houghton Mifflin Harcourt.

Panagiotopoulou, H., Baca, M., Popovic, D., Weglenski, P., & Stankovic, A. (2014). A PCR-RFLP based test for distinguishing European and Atlantic sturgeons [Article]. *Journal of Applied Ichthyology*, *30*(1), 14-17. https://doi.org/10.1111/jai.12328

Parker, R. W., & Tyedmers, P. H. (2015). Fuel consumption of global fishing fleets: current understanding and knowledge gaps. *Fish and Fisheries*, *16*(4), 684-696. https://doi.org/https://doi.org/10.1111/faf.12087

Peng, Z., Ludwig, A., Wang, D., Diogo, R., Wei, Q., & He, S. (2007). Age and biogeography of major clades in sturgeons and paddlefishes (Pisces: Acipenseriformes). *Molecular phylogenetics and evolution*, *42*(3), 854-862. https://doi.org/https://doi.org/10.1016/j.ympev.2006.09.008

Peters, G., & Hartmann, F. (1986). *Anguillicola*, a parasitic nematode of the swim bladder spreading among eel populations in Europe. *Diseases of aquatic organisms*, *1*(3), 229-230.

Philipsen, P. (2023). *Potentieel Ecologische Waarde Zuidwestelijke Delta in 2050 en 2150. Langetermijnperspectief 2150 inclusief klimaatverandering en middellangetermijnperspectief 2050 met advies streefbeeld PAGW.* https://open.rws.nl/open-overheid/onderzoeksrapporten/@258651/potentieel-ecologische-waarde/

Piccolo, J. J. (2017). Intrinsic values in nature: Objective good or simply half of an unhelpful dichotomy? *Journal for Nature Conservation*, *37*, 8-11. https://doi.org/https://doi.org/10.1016/j.jnc.2017.02.007

Pikitch, E. K., Doukakis, P., Lauck, L., Chakrabarty, P., & Erickson, D. L. (2005). Status, trends and management of sturgeon and paddlefish fisheries. *Fish and Fisheries*, *6*(3), 233-265. https://doi.org/DOI 10.1111/j.1467-2979.2005.00190.x

Polet, H., Coenjaerts, J., & Verschoore, R. (2004). Evaluation of the sieve net as a selectivity-improving device in the Belgian brown shrimp (Crangon crangon) fishery. *Fisheries research*, *69*(1), 35-48. https://doi.org/https://doi.org/10.1016/j.fishres.2004.04.007

Popović, D., Panagiotopoulou, H., Baca, M., Stefaniak, K., Mackiewicz, P., Makowiecki, D., King, T. L., Gruchota, J., Weglenski, P., & Stankovic, A. (2014). The history of sturgeon in the Baltic Sea. *Journal of Biogeography*, *41*(8), 1590-1602. https://doi.org/https://doi.org/10.1111/jbi.12307

Puijenbroek, P. J. T. M., Buijse, A. D., Kraak, M. H. S., & Verdonschot, P. F. M. (2019). Species and river specific effects of river fragmentation on European anadromous fish species. *River Research and Applications*, *35*(1), 68-77. https://doi.org/https://doi.org/10.1002/rra.3386

Purvina, S., & Medne, R. (2018). Reintroduction of sturgeon, *Acipenser oxyrinchus*, in the Gulf of Riga, East-Central Baltic Sea. *Archiwum Rybactwa Polskiego = Archives of Polish Fisheries*, *26*(1), 39-46. https://doi.org/http://dx.doi.org/10.2478/aopf-2018-0005

Pustelnik, G., & Guerri, O. (2000). Analysis of partnership and conservation requirements for a threatened species, *Acipenser sturio* L., 1758: Towards the implementation of a recovery plan. In *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA* (Vol. 16, pp. 209-216).

Quantz, H. (1903). Störfischerei und Störzucht im Gebiet der deutschen Norseeküste [Sturgeon fishery and sturgeon reproduction in the area of the German North sea coast]. *Mitteilungen des Deutschen Seefischerei-Vereins, 19 (6): 176-204*.

Radosavljević, V., Milićević, V., Maksimović-Zorić, J., Veljović, L., Nešić, K., Pavlović, M., Pelić, D. L., & Marković, Z. (2019). Sturgeon diseases in aquaculture. *Archives of Veterinary Medicine*, *12*(1), 5-20. https://doi.org/https://doi.org/10.46784/e-avm.v12i1.34

Redeke, H. C. (1915). *Mededeelingen over Visscherij maandblad met gebruikmaking van officieele bescheiden uitgegeven door Dr. H. C. Redeke*.

Reekers, F. (1916). *Verslag van de Staatscommissie voor het Zalmvraagstuk / Deel I*.

Roberge, J. M., & Angelstam, P. (2004). Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology*, *18*(1), 76-85. https://doi.org/10.1111/j.1523-1739.2004.00450.x

Rochard, E., Castelnaud, G., & Lepage, M. (1990). Sturgeons (Pisces: Acipenseridae); threats and prospects. *Journal of Fish Biology*, *37*, 123-132.

Rochard, E., Lepage, M., Dumont, P., Tremblay, S., & Gazeau, C. (2001). Downstream Migration of Juvenile European Sturgeon *Acipenser sturio* L. in the Gironde Estuary. *Estuaries*, *24*(1), 108-115. https://doi.org/https://doi.org/10.2307/1352817

Rochard, E., Lepage, M., & Meauzé, L. (1997a). Identification and characterisation of the marine distribution of the European sturgeon *Acipenser sturio*. *Aquatic Living Resources*, *10*(2), 101-109. https://doi.org/10.1051/alr:1997011

Rochard, E., Lepage, M., & Meauzé, L. (1997b). Identification et caractérisation de l'aire de répartition marine de l'esturgeon européen *Acipenser sturio* ā partir de déclarations de captures. *Aquatic Living Resources*, *10*(2), 101-109. https://doi.org/https://doi.org/10.1051/alr:1997011

Ruban, G. (2020). History of Baltic Sea Sturgeon Fauna Formation. *Russian Journal of Biological Invasions*, *11*(4), 372-378. https://doi.org/https://doi.org/10.1134/S207511172004013X

RWS. (1984). *Bedieningsprogramma Haringvlietsluizen (LPH '84). Rijkswaterstaat, directie benedenrivieren, maart 1984.*

Sahrhage, D., & Lundbeck, J. (2012). *A history of fishing*. Springer Science & Business Media.

Sammartino, M., Aronica, S., Santoleri, R., & Buongiorno Nardelli, B. (2022). Retrieving Mediterranean Sea Surface Salinity Distribution and Interannual Trends from Multi-Sensor Satellite and In Situ Data. *Remote Sensing*, *14*(10), 2502. https://doi.org/https://doi.org/10.3390/rs14102502

Savoca, M. S., Brodie, S., Welch, H., Hoover, A., Benaka, L. R., Bograd, S. J., & Hazen, E. L. (2020). Comprehensive bycatch assessment in US fisheries for prioritizing management. *Nature Sustainability*, *3*(6), 472-480. https://doi.org/https://doi.org/10.1038/s41893-020-0506-9

Schadeberg, A., Kraan, M., & Hamon, K. G. (2021). Beyond métiers: social factors influence fisher behaviour. *ICES Journal of Marine Science*. https://doi.org/https://doi.org/10.1093/icesjms/fsab050

Schletterer, M., Kuzovlev, V., Zhenikov, Y., Tuhtan, J., Haidvogl, G., Friedrich, T., Górski, K., & Füreder, L. (2018). Fish fauna and fisheries of large European rivers: Examples from the Volga and the Danube. *Hydrobiologia*, *814*(1), 45-60. https://doi.org/https://doi.org/10.1007/s10750-017-3370-5

Scott, W. B., & Crossman, E. J. (1973). *Freshwater fishes of Canada*. Fisheries and Marine Service. https://archive.org/details/freshwaterfishes0000scot_d4d2

Sexton, A. N., Beisel, J.-N., Staentzel, C., Wolter, C., Tales, E., Belliard, J., Buijse, A. D., Martínez Fernández, V., Wantzen, K. M., & Jähnig, S. C. (2024). Inland navigation and land use interact to impact European freshwater biodiversity. *Nature Ecology & Evolution*, 1-11. https://doi.org/https://doi.org/10.1038/s41559-024-02414-8

Shivaramu, S. (2019). *Hybridization of sturgeons* (Publication Number ISBN 978-80-7514-095-1) PhD Thesis, University of South Bohemia in České Budějovice, Czech Republic].

Siegert, M., & Dowdeswell, J. (2002). Late Weichselian iceberg, surface-melt and sediment production from the Eurasian Ice Sheet: results from numerical ice-sheet modelling. *Marine Geology*, *188*(1-2), 109-127. https://doi.org/https://doi.org/10.1016/S0025-3227(02)00277-3

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., & Popper, A. N. (2010). A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends in ecology & evolution*, *25*(7), 419-427. https://doi.org/https://doi.org/10.1016/j.tree.2010.04.005

Smircich, M. G., & Kelly, J. T. (2014). Extending the 2% rule: the effects of heavy internal tags on stress physiology, swimming performance, and growth in brook trout. *Animal Biotelemetry*, *2*(1), 1-7. https://doi.org/https://doi.org/10.1186/2050-3385-2-16

Spierts, I. (2016). *The effects of ship propellers on migratory fish species, with empahsis on the European sturgeon (Acipenser sturio), a literature study.* ATKB.

Spikmans, F., Lemmers, P., op den Camp, H. J., van Haren, E., Kappen, F., Blaakmeer, A., van der Velde, G., van Langevelde, F., Leuven, R. S., & van Alen, T. A. (2020). Impact of the invasive alien topmouth gudgeon (*Pseudorasbora parva*) and its associated parasite *Sphaerothecum destruens* on native fish species. *Biological Invasions*, *22*(2), 587-601. https://doi.org/https://doi.org/10.1007/s10530-019-02114-6

Spratte, S. (2014). *Störe in Schleswig-HolsteinVergangenheit – Gegenwart - Zukunft* (978-3-937937-74-8).

St. Pierre, R., & Parauka, F. (2006). *Acipenser oxyrinchus* (errata version published in 2016). The IUCN Red

List of Threatened Species 2006: e.T245A107249015. https://doi.org/https://doi.org/10.2305/IUCN.UK.2006.RLTS.T245A13046974.en

Staaks, G., Kirschbaum, F., & Williot, P. (1999). Experimental studies on thermal behaviour and diurnal activity rhythms of juvenile European sturgeon (*Acipenser sturio*). *Journal of Applied Ichthyology*, *15*(4-5), 243-247. https://doi.org/https://doi.org/10.1111/j.1439-0426.1999.tb00243.x

Staas, S. (2017). *Evaluation of potential reproductive habitats of European Sturgeon in the Lower Rhine River in Germany*.

Stachnik, M., Matras, M., Borzym, E., Maj-Paluch, J., & Reichert, M. (2021). Emerging viral pathogens in sturgeon aquaculture in Poland: Focus on Herpesviruses and Mimivirus detection. *Viruses*, *13*(8), 1496. https://doi.org/https://doi.org/10.3390/v13081496

Steenhuis, M. (2015). The Deltaworks: heritage and new space for a changing world. In *Water & heritage. Material, conceptual and spiritual connections. Sidestone Press, Leiden* (pp. 331-350).

Steenhuis, M., Voerman, L., Swart, S., & Emmerik, J. (2016). *De Deltawerken*. Nai010 uitgevers.

Steins, N. A., Kraan, M. L., van der Reijden, K. J., Quirijns, F. J., van Broekhoven, W., & Poos, J. J. (2020). Integrating collaborative research in marine science: Recommendations from an evaluation of evolving science-industry partnerships in Dutch demersal fisheries. *Fish and Fisheries*, *21*(1), 146-161. https://doi.org/https://doi.org/10.1111/faf.12423

Steins, N. A., Mackinson, S., Mangi, S. C., Pastoors, M. A., Stephenson, R., Ballesteros, M., Brooks, K., Mcisaac, J., Baker, M., & Calderwood, J. (2022). A will-o'-the wisp? On the utility of voluntary contributions of data and knowledge from the fishing industry to marine science. *Frontiers in Marine Science*, 2420. https://doi.org/https://doi.org/10.3389/fmars.2022.954959

Stephenson, R. L., Paul, S., Pastoors, M. A., Kraan, M., Holm, P., Wiber, M., Mackinson, S., Dankel, D. J., Brooks, K., & Benson, A. (2016). Integrating fishers' knowledge research in science and management. *ICES Journal of Marine Science*, *73*(6), 1459-1465. https://doi.org/https://doi.org/10.1093/icesjms/fsw025

Stoffers, T. (2022). *Surviving and growing in dynamic floodplains: Habitat heterogeneity drives communities of young fish in the lower river Rhine* Wageningen University and Research].

Strandberg, G., Lindström, J., Poska, A., Zhang, Q., Fyfe, R., Githumbi, E., Kjellström, E., Mazier, F., Nielsen, A. B., & Sugita, S. (2022). Mid-Holocene European climate revisited: New high-resolution regional climate model simulations using pollen-based land-cover. *Quaternary Science Reviews*, *281*, 107431. https://doi.org/https://doi.org/10.1016/j.quascirev.2022.107431

Sulak, K., & Randall, M. (2002). Understanding sturgeon life history: enigmas, myths, and insights from scientific studies. *Journal of Applied Ichthyology*, *18*(4-6), 519-528. https://doi.org/https://doi.org/10.1046/j.1439-0426.2002.00413.x

Sulak, K. J., Parauka, F., Slack, W. T., Ruth, R. T., Randall, M. T., Luke, K., Mettee, M. F., & Price, M. E. (2016). Status of scientific knowledge, recovery progress, and future research directions for the Gulf Sturgeon, *Acipenser oxyrinchus* desotoi Vladykov, 1955. *Journal of Applied Ichthyology*, *32 Suppl S1*, 87-161. https://doi.org/http://dx.doi.org/10.1111/jai.13245

Teuling, A. J., De Badts, E. A., Jansen, F. A., Fuchs, R., Buitink, J., Hoek van Dijke, A. J., & Sterling, S. M. (2019). Climate change, reforestation/afforestation, and urbanization impacts on evapotranspiration and streamflow in Europe. *Hydrology and Earth System Sciences*, *23*(9), 3631-3652. https://doi.org/https://doi.org/10.5194/hess-23-3631-2019, 2019

Thieren, E., Ervynck, A., Brinkhuizen, D., Locker, A., & van Neer, W. (2016a). The Holocene occurrence of Acipenser spp. in the southern North Sea: the archaeological record. *Journal of Fish Biology*, *89*(4), 1958-1973. https://doi.org/https://doi.org/10.1111/jfb.13094

Thieren, E., Ottoni, C., Popović, D., & van Neer, W. (2016b). Inter- and intraspecific variation in the surface pattern of the dermal bones of two sturgeon species. *Journal of Applied Ichthyology*, *32*(4), 609-628. https://doi.org/https://doi.org/10.1111/jai.13091

Thieren, E., & van Neer, W. (2016). Scutes for sturgeon size reconstruction: traditional and geometric morphometric techniques applied to *Acipenser sturio* and *A. oxyrinchus*. *Archaeofauna*, *25*(1). https://doi.org/https://doi.org/10.15366/archaeofauna2016.25

Thieren, E., Wouters, W., & Van Neer, W. (2015). Guide for the identification of archaeological sea sturgeon (*Acipenser sturio* and *A. oxyrinchus*) remains [Article]. *Cybium*, *39*(3), 175-192. https://doi.org/https://doi.org/10.26028/cybium/2015-393-002

Tiedemann, R., Moll, K., Paulus, K. B., Scheer, M., Williot, P., Bartel, R., Gessner, J., & Kirschbaum, F. (2007). Atlantic sturgeons (*Acipenser sturio*, *Acipenser oxyrinchus*): American females successful in Europe. *Naturwissenschaften*, *94*(3), 213-217. https://doi.org/https://doi.org/10.1007/s00114-006-0175-1

Tiedemann, R., Schneider, A., Williot, P., & Kirschbaum, F. (2011). Genetic variability of cultured European sturgeon *Acipenser sturio*. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758* (pp. 455-464). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_34

Trevisan, B., Alcantara, D. M., Machado, D. J., Marques, F. P., & Lahr, D. J. (2019). Genome skimming is a low-cost and robust strategy to assemble complete mitochondrial genomes from ethanol preserved specimens in biodiversity studies. *PeerJ*, *7*, e7543. https://doi.org/10.7717/peerj.7543

Trouvery, M., Williot, P., & Castelnaud, G. (1984). *Biology and ecology of Acipenser sturio. Study of fishery.*

U.S. Fish and Wildlife Service. (1980). HEP. In *Habitat Evaluation Procedures*. https://www.fws.gov/policy-library/870fw1

Uehlinger, U. F., Wantzen, K. M., Leuven, R. S., & Arndt, H. (2009). *The Rhine river basin*. http://nbn-resolving.de/urn:nbn:de:bsz:352-opus-75190

Ulrich, C., Wilson, D. C., Nielsen, J. R., Bastardie, F., Reeves, S. A., Andersen, B. S., & Eigaard, O. R. (2012). Challenges and opportunities for fleet-and métier-based approaches for fisheries management under the European Common Fishery Policy. *Ocean & Coastal Management*, *70*, 38-47. https://doi.org/https://doi.org/10.1016/j.ocecoaman.2012.06.002

US Fish and Wildlife Service. (2018a). *Russian Sturgeon (Acipenser gueldenstaedtii) Ecological Risk Screening Summary*.

US Fish and Wildlife Service. (2018b). *Siberian Sturgeon (Acipenser baerii) Ecological Risk Screening Summary*.

US Fish and Wildlife Service. (2018c). *Sterlet (Acipenser ruthenus) Ecological Risk Screening Summary*.

US Fish and Wildlife Service. (2018d). *White Sturgeon (Acipenser transmontanus) Ecological Risk Screening Summary*.

Van de Ven, M. (2020). *Voedselbeschikbaarheid voor europese steur (Acipencer sturio) in de Nederlandse rijntakken en benedenrivieren*.

Van de Ven, M. (2021). *Scheepvaart en aalsterfte in de Nederlandse Rijntakken*.

van den Dungen, M. W., Kok, D. E., Polder, A., Hoogenboom, R. L., van Leeuwen, S. P., Steegenga, W. T., Kampman, E., & Murk, A. J. (2016). Accumulation of persistent organic pollutants in consumers of eel from polluted rivers compared to marketable eel. *Environmental Pollution*, *219*, 80-88. https://doi.org/https://doi.org/10.1016/j.envpol.2016.09.019

van der Hammen, T., Soudijn, F., Volwater, J., van Rijssel, J., Griffioen, A., Chen, C., & Winter, H. (2021). *European Eel (Anguilla anguilla) stock size, anthropogenic mortality and silver eel escapement in the Netherlands 2006-2020*.

Van der Hoeven, H., & Van Albada, J. (1996). *Lost memory: libraries and archives destroyed in the twentieth century*. UNESCO.

Van der Veer, G., & Nentwig, W. (2015). Environmental and economic impact assessment of alien and invasive fish species in Europe using the generic impact scoring system. *Ecology of Freshwater Fish*, *24*(4), 646-656. https://doi.org/https://doi.org/10.1111/eff.12181

Van Dijk, G., Marteijn, E., & Schulte-Wülwer-Leidig, A. (1995). Ecological rehabilitation of the River Rhine: plans, progress and perspectives. *Regulated Rivers: Research & Management*, *11*(3-4), 377-388. https://doi.org/https://doi.org/10.1002/rrr.3450110311

Van Eenennaam, J. P., Doroshov, S. I., Moberg, G. P., Watson, J. G., Moore, D. S., & Linares, J. (1996). Reproductive conditions of the Atlantic sturgeon (*Acipenser oxyrinchus*) in the Hudson River. *Estuaries*, *19*(4), 769-777. https://doi.org/https://doi.org/10.2307/1352296

Van Emmerik, W. (2004). *Kennisdocument Atlantische steur, Acipenser sturio (Linnaeus, 1758)*.

van Erp, M., de Does, J., Depuydt, K., Lenders, R., & van Goethem, T. (2018). *Slicing and dicing a newspaper corpus for historical ecology research* European Knowledge Acquisition Workshop,

van Helmond, A. T., Mortensen, L. O., Plet-Hansen, K. S., Ulrich, C., Needle, C. L., Oesterwind, D., Kindt-Larsen, L., Catchpole, T., Mangi, S., & Zimmermann, C. (2020). Electronic monitoring in fisheries: lessons from global experiences and future opportunities. *Fish and Fisheries*, *21*(1), 162-189. https://doi.org/https://doi.org/10.1111/faf.12425

Van Hoof, L., Steins, N., Smith, S., & Kraan, M. (2020). Change as a permanent condition: A history of transition processes in Dutch North Sea fisheries. *Marine Policy*, *122*, 104245. https://doi.org/https://doi.org/10.1016/j.marpol.2020.104245

Van Neer, W., Thieren, E., & Brinkhuizen, D. (2012). 19 Identification of a 19th century sturgeon from North-East Friesland. *A bouquet of*, 195.

van Rijn, S., & van Eerden, M. R. (2022). Food choice and prey selection by Great Cormorants *Phalacrocorax carbo* in a shallow coastal zone in the Dutch delta area: importance of local flatfish stocks. *Ardea*, *109*(3), 507-528. https://doi.org/https://doi.org/10.5253/arde.v109i2.a20

van Rijssel, J., Breukelaar, A., de Leeuw, J., van Puijenbroek, M., Schilder, K., Schrimpf, A., Vriese, F., & Winter, H. (2024). Reintroducing Atlantic salmon in the river Rhine for decades: Why did it not result in the return of a viable population? *River Research and Applications*. https://doi.org/https://doi.org/10.1002/rra.4284

van Winden, A., Overmars, W., Bosman, W., & Klink, A. (2000). *De Atlantische steur*.

Van Zanden, J. L. (2013). Prices and wages and the cost of living in the western part of the Netherlands, 1450-1800. *Visited online at the International Institute of Social History, www. iisg. nl*. http://www.iisg.nl/scripts/print.php?language=en&url=www.iisg.nl%2Fhpw%2Fbrenv.php

Vanderhoeven, S., Adriaens, T., D'hondt, B., Van Gossum, H., Vandegehuchte, M., Verreycken, H., Cigar, J., & Branquart, E. (2015). Information Management A science based approach to tackle invasive alien species in Belgium – the role of the ISEIA protocol and the Harmonia information system as decision support tools. Manag. Biol. Invasions 6 (2), 197–208. https://doi.org/0.3391/mbi.2015.6.2.10

Vejřík, L., Vejříková, I., Kočvara, L., Blabolil, P., Peterka, J., Sajdlová, Z., Jůza, T., Šmejkal, M., Kolařík, T., & Bartoň, D. (2019). The pros and cons of the invasive freshwater apex predator, European catfish *Silurus glanis*, and powerful angling technique for its population control. *Journal of environmental management*, *241*, 374-382. https://doi.org/https://doi.org/10.1016/j.jenvman.2019.04.005

Verbiest, H., Breukelaar, A., Ovidio, M., Philippart, J. C., & Belpaire, C. (2012). Escapement success and patterns of downstream migration of female silver eel *Anguilla anguilla* in the River Meuse. *Ecology of Freshwater Fish*, *21*(3), 395-403. https://doi.org/https://doi.org/10.1111/j.1600-0633.2012.00559.x

Verbrugge, L., de Hoop, L., Aukema, R., Beringen, R., Creemers, R., van Duinen, G., Hollander, H., de Hullu, E., Scherpenisse, M., & Spikmans, F. (2019). Lessons learned from rapid environmental risk assessments for prioritization of alien species using expert panels. *Journal of environmental management*, *249*, 109405. https://doi.org/https://doi.org/10.1016/j.jenvman.2019.109405

Verbrugge, L., Leuven, R. S., & Velde, G. (2010). *Evaluation of international risk assessment protocols for exotic species*.

Verhey, C. (1949). Het voorkomen van de Steur (*Acipenser sturio* L.) in de Nieuwe Merwede tussen 1900 en 1931. *De Levende Natuur*, *52*(8), 152-159. http://natuurtijdschriften.nl/search?identifier=492727

Verhey, C. (1963). Het voorkomen van de Steur (*Acipenser sturio* L.) in Nederland na 1941. *De Levende Natuur*, *66*(1), 15-16.

Verweij, M. C., Densen, v. W. L. T., & Mol, A. P. J. (2010). The tower of Babel: Different perceptions and controversies on change and status of North Sea fish stocks in multi-stakeholder settings. *Marine Policy*, *34*(3), 522-533. https://doi.org/https://doi.org/10.1016/j.marpol.2009.10.008

Vilizzi, L., Copp, G. H., Adamovich, B., Almeida, D., Chan, J., Davison, P. I., Dembski, S., Ekmekçi, F. G., Ferincz, Á., & Forneck, S. C. (2019). A global review and meta-analysis of applications of the freshwater Fish Invasiveness Screening Kit. *Reviews in fish biology and fisheries*, *29*(3), 529-568. https://doi.org/https://doi.org/10.1007/s11160-019-09562-2

Villamayor-Tomas, S., Fleischman, F. D., Ibarra, I. P., Thiel, A., & van Laerhoven, F. (2014). From Sandoz to Salmon: Conceptualizing resource and institutional dynamics in the Rhine watershed through the SES framework. *International Journal of the Commons*, *8*(2), 361-395. https://doi.org/https://doi.org/10.18352/ijc.411

Visser, S., De Bruijne, W., Houben, B., Roels, B., & Brevé, N. (2020). *First Action Plan for the EuropeanSturgeon (Acipenser sturio) for the Lower Rhine*.

Von Boetticher, W. (1886). Lachsvertrag NL-DE. In *Reichs Gesetzblatt* (pp. 224). Berlin.

Voyer, M., Gladstone, W., & Goodall, H. (2014). Understanding marine park opposition: the relationship between social impacts, environmental knowledge and motivation to fish. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*(4), 441-462. https://doi.org/https://doi.org/10.1002/aqc.2363

Voyer, M., Gladstone, W., & Goodall, H. (2015). Obtaining a social licence for MPAs–influences on social acceptability. *Marine Policy*, *51*, 260-266. https://doi.org/https://doi.org/10.1016/j.marpol.2014.09.004

Waldman, J. (2000). Restoring *Acipenser sturio* L., 1758 in Europe: lessons from the *Acipenser oxyrinchus* Mitchill, 1815 experience in North America. In *BOLETIN-INSTITUTO ESPANOL DE OCEANOGRAFIA* (Vol. 16, pp. 237-244).

Waldman, J., Alter, S. E., Peterson, D., Maceda, L., Roy, N., & Wirgin, I. (2019). Contemporary and historical effective population sizes of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*. *Conservation Genetics*, *20*(2), 167-184. https://doi.org/10.1007/s10592-018-1121-4

Waldman, J. R., Grunwald, C., Stabile, J., & Wirgin, I. (2002). Impacts of life history and biogeography on the genetic stock structure of Atlantic sturgeon *Acipenser oxyrinchus oxyrinchus*, Gulf sturgeon *A. oxyrinchus desotoi*, and shortnose sturgeon *A. brevirostrum* [Article]. *Journal of Applied Ichthyology*, *18*(4-6), 509-518. https://doi.org/10.1046/j.1439-0426.2002.00361.x

Weeber, M., Elzinga, H., Schoonveld, W., De Vries, C., Klapwijk, M., Mischa, I., Rodriguez Aguilera, D., Farrag, M., Ye, Q., Markus, A., Van Oorschot, M., Saager, P., & Icke, J. (2024). *D-Eco Impact (v0.3.0)*.

Wei, Q., He, J., Yang, D., Zheng, W., & Li, L. (2004). Status of sturgeon aquaculture and sturgeon trade in China: a review based on two recent nationwide surveys. *Journal of Applied Ichthyology*, *20*(5), 321-332. https://doi.org/https://doi.org/10.1111/j.1439-0426.2004.00593.x

Welcomme, R. (1988). *International Introductions of Inland Aquatic Species* (M-44 ISBN 92-5-102664-5). https://www.fao.org/3/x5628e/x5628e00.htm

Wilkinson, J. L., Boxall, A. B., Kolpin, D. W., Leung, K. M., Lai, R. W., Galbán-Malagón, C., Adell, A. D., Mondon, J., Metian, M., & Marchant, R. A. (2022). Pharmaceutical pollution of the world's rivers. *Proceedings of the National Academy of Sciences*, *119*(8), e2113947119. https://doi.org/https://doi.org/10.1073/pnas.2113947119

Williot, P., Arlati, G., Chebanov, M., Gulyas, T., Kasimov, R., Kirschbaum, F., Patriche, N., Pavlovskaya, L., Poliakova, L., Pourkazemi, M., Kim, Y., Zhuang, P., & Zholdasova, I. (2002a). Status and management of Eurasian sturgeon: an overview. *International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology*, *87*(5-6), 483-506. https://doi.org/https://doi.org/10.1002/1522-2632(200211)87:5/6<483::AID-IROH483>3.0.CO;2-K

Williot, P., Brun, R., Pelard, M., & Mercier, D. (2000). Induced maturation and spawning in an incidentally caught adult pair of critically endangered European sturgeon, *Acipenser sturio* L. *Journal of Applied Ichthyology*, *16*(6), 279-281. https://doi.org/https://doi.org/10.1046/j.1439-0426.2000.00238.x

Williot, P., & Castelnaud, G. (2011). Historic overview of the European sturgeon *Acipenser sturio* in France: surveys, regulations, reasons for the decline, conservation, and analysis. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758* (pp. 285-307). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_20

Williot, P., & Chevre, P. (2011). Reproduction of the cultured brood fish. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758* (pp. 439-448). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_32

Williot, P., & Kirschbaum, F. (2011). The French–German cooperation: the key issue for the success of the preservation and restoration of the European sturgeon, *Acipenser sturio*, and its significance for other sturgeon issues. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758* (pp. 499-513). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_38

Williot, P., Nonnotte, G., Vizziano-Cantonnet, D., & Chebanov, M. (2018). *The Siberian Sturgeon (Acipenser baerii, Brandt, 1869) Volume 1-Biology*. Springer. https://doi.org/https://doi.org/10.1007/978-3-319-61664-3

Williot, P., Rochard, E., Castelnaud, G., Rouault, T., Brun, R., Lepage, M., & Elie, P. (1997). Biological characteristics of European Atlantic sturgeon, *Acipenser sturio*, as the basis for a restoration program in France. In *Sturgeon Biodiversity and Conservation* (pp. 359-370). Springer. https://doi.org/https://doi.org/10.1007/0-306-46854-9_24

Williot, P., Rochard, E., Desse-Berset, N., Kirschbaum, F., & Gessner, J. (2011a). *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758: The Reunion of the European and Atlantic Sturgeons*. Springer Science & Business Media.

Williot, P., Rochard, E., Rouault, T., & Kirschbaum, F. (2009a). *Acipenser sturio* recovery research actions in France. In *Biology, conservation and sustainable development of sturgeons* (pp. 247-263). Springer. https://doi.org/https://doi.org/10.1007/978-1-4020-8437-9_15

Williot, P., Rouault, T., Brun, R., & Gessner, J. (2011b). Characteristics of the reproductive cycle of wild *Acipenser sturio*. In *Biology and Conservation of the European Sturgeon Acipenser sturio L. 1758* (pp. 165-175). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-20611-5_12

Williot, P., Rouault, T., Brun, R., Pelard, M., & Mercier, D. (2002b). Status of caught wild spawners and propagation of the endangered sturgeon *Acipenser sturio* in France: a synthesis. *International Review of Hydrobiology: A Journal Covering all Aspects of Limnology and Marine Biology*, *87*(5-6), 515-524. https://doi.org/https://doi.org/10.1002/1522-2632(200211)87:5/6<515::AID-IROH515>3.0.CO;2-%23

Williot, P., Rouault, T., Pelard, M., Mercier, D., & Jacobs, L. (2009b). Artificial reproduction and larval rearing of captive endangered Atlantic sturgeon *Acipenser sturio*. *Endangered Species Research*, *6*(3), 251-257. https://doi.org/http://dx.doi.org/10.3354/esr00174

Williot, P., Rouault, T., Pelard, M., Mercier, D., Lepage, M., Davail-Cuisset, B., Kirschbaum, F., & Ludwig, A. (2007). Building a broodstock of the critically endangered sturgeon *Acipenser sturio*: problems and observations associated with the adaptation of wild-caught fish to hatchery conditions. *Cybium*, *31*(1), 3-11. https://doi.org/https://hal.inrae.fr/hal-02589274

Williot, P., Sabeau, L., Gessner, J., Arlati, G., Bronzi, P., Gulyas, T., & Berni, P. (2001). Sturgeon farming in Western Europe: recent developments and perspectives. *Aquatic Living Resources*, *14*(6), 367-374. https://doi.org/10.1016/S0990-7440(01)01136-6

Winden, A. v., Overmars, W., Bosman, W., & Klink, A. (2000). *De Atlantische steur: Terugkeer in de Rijn* (Wereld Natuur Fonds/Stichting ARK, Issue.

Winter, H., Teal, L., van de Wolfshaar, K. E., Griffioen, A., Houben, B., & Breve, N. (2015). *Desk-study on habitat quality for the European Sturgeon in the Dutch Rhine and southern North Sea*.

Winter, J. (1983). Underwater biotelemetry. *In: Nielsen LA, Johnson DL, editors. Fisheries techniques. Bethesda: American Fisheries Society*, 371–395.

Wolff, W., Dankers, N., Dijkema, K., Reijnders, P., & Smit, C. (1994). Biodiversity of the Wadden Sea (Denmark, Germany, The Netherlands): recent changes and future projections. In *Biodiversity, Temperate Ecosystems, and Global Change* (pp. 337-355). Springer. https://doi.org/https://doi.org/10.1007/978-3-642-78972-4_18

Wood, G. (1983). The Guinness Book of Animal Facts and Feats, S terling Pub Co. *Inc., New York*.

Wyman-Grothem, K. (2019). Update on USFWS risk assessment activities.

Xie, P. (2003). Three-Gorges Dam: risk to ancient fish. *science*, *302*(5648), 1149-1151. https://doi.org/10.1126/science.302.5648.1149b

Yochum, N., Starr, R. M., & Wendt, D. E. (2011). Utilizing fishermen knowledge and expertise: keys to success for collaborative fisheries research. *Fisheries*, *36*(12), 593-605. https://doi.org/https://doi.org/10.1080/03632415.2011.633467

Zafeiraki, E., Gebbink, W. A., Hoogenboom, R. L., Kotterman, M., Kwadijk, C., Dassenakis, E., & van Leeuwen, S. P. (2019). Occurrence of perfluoroalkyl substances (PFASs) in a large number of wild and farmed aquatic animals collected in the Netherlands. *Chemosphere*, *232*, 415-423. https://doi.org/https://doi.org/10.1016/j.chemosphere.2019.05.200

Zavarsky, A., & Duester, L. (2020). Anthropogenic influence on the Rhine water temperatures. *Hydrology and Earth System Sciences*, *24*(10), 5027-5041. https://doi.org/https://doi.org/10.5194/hess-24-5027-2020

Zeevisscherij, J. (1912). *Eerste jaarverslag der Commissie van Zeevisscherij*.

Zeevisscherij, J. (1925). *Negende jaarverslag der Commissie van Zeevisscherij*.

Zeevisscherij, J. (1936). *Bestuurlijk Jaarverslag over de Zeevisscherij 1936*.

Zhang, H., Jarić, I., Roberts, D. L., He, Y., Du, H., Wu, J., Wang, C., & Wei, Q. (2020). Extinction of one of the world's largest freshwater fishes: Lessons for conserving the endangered Yangtze fauna. *Science of the Total Environment*, *710*, 136242. https://doi.org/https://doi.org/10.1016/j.scitotenv.2019.136242

Zhang, H., Sun, T., Shao, D., & Yang, W. (2016). Fuzzy logic method for evaluating habitat suitability in an estuary affected by land reclamation. *Wetlands*, *36*, 19-30. https://doi.org/https://doi.org/10.1007/s13157-014-0606-2


Sportvisserij
Nederland

Acknowledgements

Photo: Release of young European sturgeon at Museumeiland Biesbsosch, the Netherlands, summer 2023. Together with the sturgeon team of ARK Rewilding the Netherlands, the World Wide Fund for Nature and Sportvisserij Nederland. Source: Arthur de Bruin | Blikonderwater producties.

Acknowledgements

I would like to acknowledge and express my sincere appreciation to the following people that have helped me to carry out the research for this thesis and the sturgeon conservation.

Tinka Murk, we first met in Utrecht at the thornback ray hatchery, and it was an instant 'click'. Thank you so much for offering me the opportunity to study and be part of the Faculty of Marine Animal Ecology. It has been a wonderful learning experience. I appreciate your calm, knowledgeable explanations and our friendly discussions. You have been a helping hand, a listening ear, and a trusted source of advice to me. I absolutely enjoyed the warm atmosphere at 'your' part of the Wageningen campus. Thank you for being my promotor.

Tom Buijse, your clear guidance has changed my 'line of thought', and the readability of my writing. You made me 'kill my darlings' and as a result I left a trail of murdered sentences, paragraphs, propositions, and ideas, which was good. Thank you for providing access to the Deltares facilities and for finding additional funding for the habitat study. Thank you for sharing your thoughts when times turned somewhat difficult. I find it amazing to see how you manage such a heavy workload, travelling around the world, and still seem to find time for the occasional social chat. Thank you for being a good, knowledgeable, strong promotor.

Leo Nagelkerke, your prompt and accurate responses to a myriad of queries have greatly improved the quality of the research for this thesis. You have helped me to supervise a dozen students while at the same time supervising me. I have never met anyone (in more than 25 years of schooling and more than 50 years of life) with such a flexible and sincere attitude to teaching. I would like to let you know 'officially' that I have greatly appreciated your daily supervision. Thank you very much! And I hope we can do some more research together. Be it on sturgeons, perch, sharks or any other 'species' or topic that 'catches' our attention.

Colleagues from Sportvisserij Nederland (including federations):
I would like to take this opportunity to express my appreciation and thanks to my colleagues who supported, and/or encouraged and/or participated in the study for this thesis: Joop Bongers, Fred Bloot, Rosetta Kooistra, Jan Kamman, Simone van den Essenburg, Onno Terlouw, Remko Verspui, Paul Wijmans, Connie Kolfschoten, Willy van Emmerik, Pieter Beelen, Marco Kraal, Robert de Wilt, Joran Bal, Mark Pijnappels, Robert Weijman, Maikel Stegeman, Jaap Quak, Gerard de Laak, Annika van Dam, Marcus de Boer, Gerrit van Eck, Lindsay de Haan, Michaéla van Driel, Frank Bosman,

Danny Bok, Niels Houben, Michelle Sibeijn. And to all other colleagues not specifically mentioned here: You all have my gratitude and respect.

ARK Rewilding Nederland:
Bram Houben, Esther Blom, Karsten Reiniers, Ans ter Voert, Gijs van Zonneveld, Petra Souwerbren Iris Roggema, Thijmen van Heerde, Jos Rademakers, Ernst Schrijver, Réanna Stegeman, Sabine Wolters, the sturgeon reintroduction programme/project has been a priority aim of ARK Rewilding Nederland for over a decade. You have funded sturgeon studies, commissioned technical reports, supported the hatchery in France, built sturgeon statues… You even had a 7 m long plastic sturgeon barged down the Rhine towards Dordrecht. You searched for a girl (now in her seventies) who had witnessed the landing of the last of the Rhine sturgeons. You made a 'Kiertje' film and organised release events. Without ARK Rewilding Nederland, hardly anyone in the Netherlands would have known about sturgeons. Jeroen Helmer, thank you for the beautiful illustrations! I'd especially like to thank **Bram Houben, without your enthusiastic dedication, none of this work on sturgeon conservation would have been possible.**

World Wide Fund for Nature:
Bas Roels, Maarten Bruns, Johan van de Gronden, Kirsten Schuijt, Monique van de Water, Eveline Meltzer, thank you for being a strong member of the sturgeon team. Thank you for your long-term commitment and your clear and proud words, like these: "*Rarely is conservation work more concrete than the release of a locally extinct species. (…) It is a tremendously important signal to the general public: nature can be restored and, under certain circumstances, locally extinct species can, with a little help, become established again*". Johan van de Gronden.

Rotterdam Zoo, Diergaarde Blijdorp:
Mark de Boer and Ron Bernhard, thank you for hosting three sturgeons at the North Sea Aquarium and bringing sturgeons to the attention of millions of people. Public aquariums play a vital role in raising awareness and without in situ conservation, a critically endangered species would have been lost. I urge everyone to come to Rotterdam and see what a zoo can do for the conservation of species like the European sturgeon.

Ministry of Infrastructure and Water Management, Rijkswaterstaat (RWS):
André Breukelaar, Pieter Beeldman, Aniel Balla, Koen Workel, Karin Stone, I am grateful to have been granted access to the NEDAP Trail System®. I enjoyed our meetings in Stellendam at the 'Klankbordgroep Kier', and I thank you for your work at the Haringvliet sluices to improve international fish migration. *RWS Centrale Informatie Voorziening* Arjen Ponger, thank you so much for implementing the acoustic telemetry network

in the estuary of rivers Rhine and Meuse. *RWS Oost Nederland*. Margriet Schoor, Luc Jans, Roland van Aalderen, Leon van den Berg, Barbara Lugthart, and Marco Tijnagel, thank you for taking the lead in the Interreg VI-A Deutschland-Nederland project, De Rijn Verbindt. Thank you for your research on the rare migratory fish populations of the Rhine and for your work to combat plastic pollution and improve the water quality of the Rhine.

Ministry of Agriculture, Nature and Food Quality, Ministerie van Landbouw en Voedselkwaliteit (LNV): Donné Slangen, Menno de Ridder, and colleagues. I'd like to take this opportunity to express the gratitude of the Dutch Sturgeon Team for your support to the First Action Plan for the European Sturgeon (*Acipenser sturio*) for the Lower Rhine.

Visser Water Management: Steven Visser, and *OAK:* Wilco de Bruijne, thank you for writing this action plan, which has become a milestone in Dutch sturgeon conservation.

B2Consultancy: Bernadette Botman, thank you for your skilful project management on two different INTERREG projects, the De Groen Blauwe Rijn Alliantie and De Rijn Verbindt.

WUR Marine Animal Ecology: Reindert Nijland and Daniël van Berkel, your eDNA studies have been instrumental in solving so many of our sturgeon and shark queries. We now know that two sturgeon species were native to the river Rhine, that there are three males (no female) sturgeons in Rotterdam Zoo, and that there is only one population of *Mustelus asterias* in the North Sea, not two. You even provided evidence that a 'very dead' European sturgeon found on the banks of the Hartelkanaal, was actually a Siberian sturgeon. This made it to Vara's Vroege Vogels radio. Ronald Osinga, Edwin Foekema, Saskia Oosterbroek, Lara Jansen, Annemiek Hermans, Valentin Bordoux, Danielle Carmiggelt, Lisette Bourquin, Paddy Haripersaud and to all colleagues from MAE not specifically mentioned here: Please know: The MAEsocial app is my favourite app.

WUR Aquaculture and Fisheries (AFI): Geert Wiegertjes, I highly appreciate that you provided me access to the Aquaculture and Fisheries chair group. I enjoy your way of communicating. Your personal style and tone in emails are not only interesting, they are enlightened with clarity, friendly patience and light-hearted humour. If only everybody could write like this our digital world would be a much nicer place to live in. Jan Jaap Poos and Paul van Zwieten, It was a valuable experience to be able to share a room with you. This helped me to find a good working place at the campus. Annet Hage Willink, thank you for introducing me to the university-facilities and for your explanations on how things work at the campus. It saved me a lot of time and effort.

WUR - Library: Ria Derkx, Annemie Kersten and Joke Webbink I wish to express my gratitude for the courses on EndNote and how to review a scientific paper. *WUR - Data Management group*: Laura Zeeman, Rita Hoving, Irene Verhagen and Hilda van der Pol, I would like to express my gratitude for your help in preparing two large datasets for DANS-EASY. *WUR - Research Methodology* Peter Tamas I have greatly enjoyed participating in your course on systematic reviews. It helped to deliver two reviews for this thesis. Thanks!

Wageningen Marine Research (WMR): Erwin Winter, Pieke Molenaar, Olvin van Keeken, I thank you for our shark tag-recapture programme. Melanie Meijer Zu Schlochtern, thank you for installation of the telemetry system in the port of Rotterdam and the estuary of rivers Rhine and Meuse. Marloes Kraan, thank you so much for co-authoring our paper and help in guiding students. Erwin, I highly appreciated our interesting discussions, your clear and humoristic approach. If you want we can still go for a paper on stingrays.

Radboud University Nijmegen (RUN): Rob Lenders, I am grateful for your supervision, which succeeded us to publish a paper on the spatiotemporal distributions of the Rhine sturgeon populations from the past. I absolutely enjoyed our chats, and I think back with great pleasure to our visits to Naturalis, the Heimans and Thijsse Stichting. Your motivation to dive into archives was so contagious that it turned me into a monk for almost two years. Yet it was absolutely worth it! Rob Leuven, I would like to express my gratitude to you for sharing your expertise on alien species introductions. I found your accurate and friendly way of teaching extremely helpful. Thank you for your explanation on how to use Harmonia^{+}.

Tilburg University: Kees Bastmeijer, your report on the European sturgeon's legal status has been a fundamental reference in our sturgeon restoration programme. Thank you for this!

De Nederlandse Vissersbond/CPO Nederlandse Vissersbond, EMK Eendracht Maakt Kracht, fishers are ′our′ eyes and ears at sea. Your expertise in fish and fisheries is greatly appreciated. Sturgeon conservation will only succeed with your cooperation. Thank you for reporting sturgeon recaptures. These are much appreciated and of high value to the conservation of sturgeons and other rare species. *Visserijbedrijf Frans Komen & Zn*, I am grateful for your help at the sturgeon release events in the Waal. I enjoyed our chats wherein you shared so much of your working experience. *Klop Visserij BV*, thank you very much for renting-out the keep ship. It allowed us to store the juvenile sturgeons and made the handling and transportation of fish so much easier.

Biesbosch Museum Eiland, Peter van Beek, Annemarie de Stigter, Henk Kruithof, Jan Abbring, and colleagues, thank you for helping to organise the sturgeon release event at your premises on 2 June 2023.

VisAdvies: Jan Kemper, Hendry Vis, Robin Blokhuijzen, Marnix van Schaik, Arno Veenstra, thank you for your field work, e.g. at the Waal, the Biesbosch Museum, Woudrichem and Millinger Waard. Thank you for your field work, professional advice and your excellent technical reports. VisAdvies has become an incredibly important, strong and valuable partner in our telemetry studies and an asset for sturgeon conservation. Your cooperation for over a decade has greatly improved the quality of the work on telemetry and sturgeon conservation.

Van Leeuwen – vijvervissen: Kaz van Leeuwen, Thank you for taking care of the transportation of sturgeon in the dark of the night, from southern France to the Biesbosch.

RAVON: Jan Kranenbarg, Jelger Herder, Mark Groen, Jeroen Tummers, Jesper Berndsen, Martijn Schiphouwer, you produced technical reports on sturgeon conservation. It is because of your expertise that you have become a frequent member of the sturgeon project team. I hope that RAVON and Sportvisserij Nederland can work even closer together in the future. Thank you so much for the technical reports, field work and help with guiding students.

Blik Onder Water: Arthur de Bruijn, thank you for all the footage you provided (and we could use some more).

Sander Boer Fotografie, hartelijk bedankt voor de leuke portretfoto!

AT-KB: Igor Spierts, Tim Vriese, Max van de Ven, Rob Kroes, Benjamin Peters, thank you for three technical reports on shipping, migratory fish, and food availability for European sturgeon in the Rhine. Thank you for organising the VIE tagging of silver eels in Cologne.

Naturalis Biodiversity Center Leiden: Esther Dondorp, Elza Duijm, Marina Ventayol, Annet Westbroek, and Hannco Bakker, thank you for allowing us access to the ‘wet’ and ‘dry’ collections. Thank you for sequencing the sturgeon tissue samples, including PCR for barcoding and the protocol for preparing ancient DNA libraries.

Deltares and the Technical University Delft: Marc Weeber, Erik Mosselman, Debora van Dieren, Julia Bleser, Willem Ottevanger, Anna Koster and Victor Chavarrias, thank you for your work on the habitat study for the European sturgeon in the Rhine. Thank you for collecting data from different Dutch and German sources, 1D and 2D modelling and GIS based mapping. Thank you for organising meetings at the offices in Delft and Utrecht.

Nature@Work: Peter Philipsen, thank you for organising the Vismigratie Rijn-West meetings. I always enjoy our in-depth discussions, wherever we meet: at the Utrecht Central Station, the Wageningen campus, London Zoo. Please continue the good work!

Gemeente Amsterdam Stadsarchief, Heimans en Thijsse Stichting: Herman van Dam, many thanks for the historical information on sturgeon fisheries. Thank you for the round trip at the premises in Amsterdam.

VAART software B.V.: Jorrit, thank you for your help with the alien sturgeon study!

To the students who worked with great enthusiasm and dedication: Tim van Tuijn, Annemijn Sandig, Bart van Woerden, Benjamin Peters, Eleanor Greenway, Mark van Leeuwen, Monika Bačinić, Olaf Bensink, Sam Minekus, Silas Nagtzaam, Daniël van Berkel, Willem Bouw, Ingmar Rondeel, Kateryna Urbanovych, Lotte Pohl, Debora van Dieren, Lars Essink, Jeroen Verveld, Lisette Rabenberg, you have gone to incredible lengths to support the studies on sharks and rays, broken silver eels, and sturgeons. You all went the extra mile. Some of you literally when you walked hundreds of miles along the banks of the Rhine looking for mechanically damaged fish. Others of you carried out extensive literature searches, provided a dataset of thousands of sales and catches of historical sturgeon landings, or carried out dozens of interviews with fishers, scientists and staff of NGO's and governmental departments. You found native French speakers to translate the interviews, and supported the study with modelling and GIS mapping. Thank you all. It was a honour and a pleasure to help you with your thesis and internships.

INRAE: France's National Research Institute for Agriculture, Food and Environment:
Eric Rochard, Marie-Laure Acolas, and colleagues, I am very appreciative for your shared insights and expertise. You helped interviewing French fishers, organised quarterly international meetings online, and contributed as a co-author the radio telemetry study. We have known each other for over ten years. It has been an absolute pleasure.
L'association MIGADO – Migrateurs Garonne Dordogne Charente Seudre:
Vanessa Lauronce, William Bouyssonie, Damien Filloux, Baptiste Henri, Quentin Buisson and Alexandre Daronnat, and colleagues, on behalf of the Dutch sturgeon

team, I would like to take this opportunity to thank you for providing juvenile sturgeons to the Dutch studies, for writing the French project plan and for arranging permits, like those for CITES. We highly regard your work.

CAPENA and CNPMEM Lise Mas and Marie Lecomte, thank you so much for your help in interviewing French fishers from the Gironde estuary.

Zoological society of London: Hannah McCormick, Thalassa McMurdo Hamilton, Alison Debney, many thanks for organising the workshops in Londen. I hope that we may have the opportunity to join you in the near future during a release of tagged juvenile sturgeons in the UK. *Institute of Fisheries Management (IFM):* Steve Colclough, I was surprised to discover that you also spend years on an archival research on sturgeons. It was an honour to meet you at the sturgeon release event in the Netherlands in 2023, much appreciated!

Leibniz-Institut für Gewässerökologie und Binnenfischerei (IGB): Jörn Gessner, you had our back for years in our sturgeon adventures. Thank you for sharing your expertise and in-depth knowledge and for advice given. I remember so much of wherever we met. Like the wonderful event when we (Bram and I) joined you, and released 6,000 juvenile sturgeons in the river Oder. The image of those tiny fish that vanished in the dark waters with yellow T-bars was a beautiful sight. Hopefully we can do this more often in more European rivers.

The International Commission for Protection of the Rhine (ICPR): Christa Groshart, Laura Poinsot, Mark de Rooy, Michelle Zülich, Nikola Livrozet, and colleagues. On behalf of Sportvisserij Nederland, I would like to express our gratitude for the opportunity to participate as an observer in the EG FISH. We are grateful for the ICPR's invaluable work to restore the Rhine to a good ecological status. I hope that the ICPR will consider including all migratory fish in the Master Plan Migratory Fish and we are happy to discuss the options.

Ministerium für Umwelt, Landwirtschaft, Natur- und Verbraucherschutz des Landes Nordrhein-Westfalen: Peter Beeck and colleagues, we were delighted to have you with us at the release events for Allis shad larvae and juvenile European sturgeons to the Rhine in the Netherlands. Your speeches given at the sturgeon release events were well received. *Der Rheinische Fischereiverband von 1880 e.V.:* Andreas Scharbert, Armin Nemitz, and colleagues, thank you for your efforts to restore populations of salmon, shad, sturgeon and other migratory fish of the river Rhine. We are honoured to work together, be it in studies for Interreg, or any other work that further strengthens our bond. *Firma LimnoPlan:* Stefan Staas, your technical report on the habitat assessment for sturgeon in the Rhine has found much appreciation amongst the sturgeon project team. I thank you so much for this exquisite work.

University of Cologne: Frank Nitsche, we highly appreciate you for giving us the opportunity to work at the facilities of the Ecological Rhine Station of the University of Cologne in October and November 2023. This allowed us to keep 1,200 silver eels in flow-through Rhine river water and perform VIE tagging in perfect conditions. *Struktur- und Genehmigungsdirektion Nord (SGD):* Roland Mauden, thank you for bringing us into contact with the fishers from Rhine and Mosel who provided silver eels for our tagging programme. *LANUV* Martin Brinkmann, thank you for the data on water levels. *Wasser- und Schifffahrtsverwaltung des Bundes, WSV* Nils Holman, thank you for the data on water depth. *Bundesanstalt für Gewässerkunde, BfG* Dr. Schumacher, thank you for the sediment data.

Royal Belgian Institute of Natural Sciences. Wim van Neer and Els Thieren, I would like to express my gratitude to you for reworking your data on Holocene acipenserid remains from the Rhine and other North Sea rivers.

To our highly esteemed guests: Princess Laurentien, Jan Terlouw, and Professor Pieter van Vollenhoven. On behalf of the sturgeon project team, I thank you for your invaluable contributions to the success of the sturgeon release events in 2012, 2015 and 2023.

To the media: I would like to take this opportunity to express my sincere gratitude to the diversity of interested and positively critical journalists and reporters who have dedicated their time and interest to produce their impressive articles on the radio, TV, in magazines, online and newspapers. It helped to draw attention to sturgeon conservation, you created awareness, and by doing so you have greatly improved the chances of sturgeons to return. Thank you so much for your work!

I would like to extend my gratitude to Miranda Maybank and Peter Griffith for their assistance with the English language editing of two papers. I am particularly indebted to my English teacher, Nigel Gardiner-Harvey. Thank you, Nigel, for your thoughtful guidance and support, for checking some of the texts in this manuscript. You have greatly improved my English language skills.

Wim, Mizzi, Ivor, Anneke, Otto, Dominique, het is mooi om een kleine maar fijne familie te hebben. Het voelt goed en vertrouwd. Dank voor jullie steun, en gezelligheid. Corry en Lottie en iedereen in deze mooie familie: Hartelijk bedankt voor het meedenken en de gezelligheid!

Pedro, Pierrette, Esi, Marc, Margriet, Berend Lieke, Gerard, John, Gijs, Wim, André, Mirjam, André, Mechteld, Walter, Jannita, Gerben, Ingrid, Titia, Jørgen, Maaike, Memet, Handan, Arjen, Susanna, Ceciel, Steven, Christina, Pia, Ron, Guido, Cinderella, Yvo, Priscilla, Gerard, Petra, jullie vriendschap heeft enorm geholpen om werk, PhD studie en het privé leven te scheiden, en zo in goede banen te leiden. Zonder onze uitstapjes, feestjes, wandelingen en natuurwerkdagen zou het leven maar een saaie boel worden.

Inge, het is fijn dat je mij mijzelf laat zijn. Je hebt mij gesteund om deze studie tot een goed einde te brengen. In de nu al twintig jaar dat wij elkaars partner zijn hebben we al heel wat van de wereld gezien, en van elkaar. Dat zal alleen maar meer worden. Ik houd van jou.

Curriculum Vitae

About the author

Niels Willem Paavo Brevé was born in Amsterdam on 15 May 1966. He graduated from the Faculty of Earth Sciences at the Vrije Universiteit Amsterdam on 11 May 1994. His passion for angling, fish, and their environment led him to apply for a job at the Organisatie ter Verbetering van de Binnenvisserij in 2001, now Sportvisserij Nederland.

Niels has a broad interest in people and their relationship with nature conservation. He has used his work experience and network of contacts to attract substantial funding and international cooperation for his research. The feasibility assessment for the European sturgeon commenced in 2009 as part of a collaboration between the Dutch organisations of ARK Rewilding Nature, the World Wide Fund for Nature, Sportvisserij Nederland and Rotterdam Zoo (Blijdorp). This project gained further support from international partners INRAE and MIGADO in France, IGB in Germany and several other partners in the UK and Spain. The project was also acknowledged by the Dutch Ministry of Agriculture, Nature, and Food quality, and more than 30 stakeholders of different nationalities, including fisheries organisations and the World Sturgeon Conservation Society (WSCS). This collaboration also formed a strong basis for the research of this thesis, which Niels started in 2019 at Wageningen University, in a collaboration between the chair groups Marine Animal Ecology and Aquaculture and Fisheries.

Niels had to overcome several additional challenges in order to continue fieldwork during the COVID-19 pandemic. These included the telemetry study for Chapter 7, but also work-related fieldwork, in particular a mark-recapture study on sharks and rays along the Dutch coast ('Sharkatag') and a study on silver eels, which are often found mechanically damaged along the banks of the Rhine. Niels participated in and supervised the technical reports (see list of publications) and was pleased to have the help of 20 students. Journalists and reporters were particularly interested in the release of juvenile European sturgeon in the Rhine. As a result, his research was broadcast on national television, radio, newspapers and magazines. Niels managed to complete his PhD part-time (2 days a week) in five and a half years.

Contact: niels.breve@gmail.com, 0031-625591607

Publications

(Status June 2024)

Peer reviewed articles

- Niels W.P. **Brevé**, Debora A.J. van Dieren, Marc Weeber, Erik Mosselman, Leopold A.J. Nagelkerke, AlberTinka J. Murk & Anthonie D. Buijse (2024 in prep.). Modelling reproductive habitat availability of the critically endangered European sturgeon in a highly modified European river.
- Niels W.P. **Brevé**, Hendry Vis, Remko Verspui, Vanessa Lauronce, Arno Veenstra, Anthonie D. Buijse, AlberTinka J. Murk & Leopold A.J. Nagelkerke (2024 in prep.). Surviving young European sturgeons *Acipenser sturio* go with the flow.
- Niels W.P. **Brevé**, Leo A.J. Nagelkerke, Anthonie D. Buijse, AlberTinka J. Murk, Peter Philipsen, Reindert Nijland & H.J. Rob Lenders (2024 in prep.). Europeans or Americans? Towards an optimized strategy for reintroducing sea sturgeons (*Acipenser sturio* and *A. oxyrinchus*) to Europe.
- **Brevé**, N. W., Urbanovych, K., Murk, A. J., van Zwieten, P. A., Nagelkerke, L. A., & Kraan, M. (2024). Fishers' willingness to report incidental bycatches of endangered, threatened and protected fish species: The case of European sturgeon in the Northeast Atlantic Ocean. Marine Policy, 162, 106056. https://doi.org/10.1016/j.marpol.2024.106056
- Charbonnel, A., Lassalle, G., Lambert, P., Quinton, E., Geßner, J., Rochard, E., Colclough, S., **Brevé**, N. & Acolas, M. L. (2024). Travelling away from home? Joining global change and recovery scenarios to anticipate the marine distribution of diadromous fish. Ecological Indicators, 160, 111762. https://doi.org/10.1016/j.ecolind.2024.111762
- **Brevé**, N.W.P, Leuven, R.S.E.W., Buijse, A. D., Murk, A. J., Venema, J., & Nagelkerke, L. A. (2022). The conservation paradox of critically endangered fish species: Trading alien sturgeons versus native sturgeon reintroduction in the Rhine-Meuse river delta. Science of the Total Environment, 848, 157641. https://doi.org/10.1016/j.scitotenv.2022.157641.
- **Brevé**, N.W.P., Leuven, R.S.E.W., Buijse, A.D., Murk, A.J., Venema, J. & Nagelkerke, L.A.J. (2022): **Data** underlying the publication: The conservation paradox of critically endangered fish species: trading alien sturgeons versus native sturgeon reintroduction in the Rhine-Meuse river delta. DANS. https://doi.org/10.17026/dans-28u-x3w3
- **Brevé**, N. W. P., Nagelkerke, L. A. J., Buijse, A. D., Van Tuijn, T., Murk, A. J., Winter, H. V., & Lenders, H. J. R. (2022) Historical reconstruction of sturgeon (*Acipenser* spp.) spatiotemporal distribution and causes for their decline in North-Western Europe. Biodivers Conserv 31, 1149–1173 (2022). https://doi.org/10.1007/s10531-022-02381-1.
- **Brevé**, N. W. P., Nagelkerke, L. A. J., Buijse, A. D., Van Tuijn, T., Murk, A. J., Winter, H. V., & Lenders, H. J. R. (2022). **Data** underlying the publication: Historical reconstruction of sturgeon (*Acipenser* spp.) spatiotemporal distribution and causes for their decline in North-Western Europe. https://doi.org/10.17026/dans-xns-5c7c.

Peer reviewed articles (continued)

- **Brevé**, N.W.P., Winter, H.V., Wijmans, P.A.D.M., Greenway, E.S.I. & Nagelkerke, L.A.J. (2021): **Data** underlying the publication: Sex differentiation in seasonal distribution of the starry smooth hound Mustelus asterias. DANS. https://doi.org/10.17026/dans-22d-j6yx.
- **Brevé**, N.W.P., Winter, H. V., Wijmans, P. A., Greenway, E. S., & Nagelkerke, L. A. (2020). Sex differentiation in seasonal distribution of the starry smooth-hound Mustelus asterias. Journal of Fish Biology, 97(6), 1870-1875. https://doi.org/10.1111/jfb.14548.
- **Brevé**, N.W.P., Vis, H., Houben, B., Breukelaar, A., & Acolas, M. L. (2018). Outmigration pathways of stocked juvenile European sturgeon (*Acipenser sturio* L., 1758) in the Lower Rhine River, as revealed by telemetry. Journal of Applied Ichthyology, 35(1), 61-68. https://doi.org/10.1111/jai.13815.
- **Brevé**, N. W. P., Vis, H., & Breukelaar, A. W. (2019). Escape from the North Sea: the possibilities for pikeperch (*Sander lucioperca* L. 1758) to re-enter the Rhine and Meuse estuary via the Haringvlietdam, as revealed by telemetry. Journal of Coastal Conservation, 23(1), 239-252. https://doi.org/10.1007/s11852-018-0654-5.
- David Abecasis, Andre Steckenreuter, Jan Reubens, Kim Aarestrup, Josep Alós, Fabio Badalamenti, Lenore Bajona, Patrick Boylan, Klaas Deneudt, Larry Greenberg, Niels **Brevé**, Francisco Hernández, Nick Humphries, Carl Meyer, David Sims, Eva B. Thorstad, Alan M. Walker, Fred Whoriskey & Pedro Afonso (2018). A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. Animal Biotelemetry, 6(1), 1-7. https://doi.org/10.1186/s40317-018-0156-0.
- **Brevé**, N. W. P., Winter, H. V., Van Overzee, H. M. J., Farrell, E. D., & Walker, P. A. (2016). Seasonal migration of the starry smooth-hound shark *Mustelus asterias* as revealed from tag-recapture data of an angler-led tagging programme. Journal of Fish Biology, 89(2), 1158-1177. https://doi.org/10.1111/jfb.12994.
- Brevé, N. W. P., Verspui, R., de Laak, G. A. J., Bendall, B., Breukelaar, A. W., & Spierts, I. L. Y. (2014). **Explicit** site fidelity of European catfish (*Silurus glanis*, L., 1758) to man-made habitat in the River Meuse, Netherlands. Journal of Applied Ichthyology, 30(3), 472-478. https://doi.org/10.1111/jai.12410.
- **Brevé**, N.W.P., Buijse, A. D., Kroes, M. J., Wanningen, H., & Vriese, F. T. (2014). Supporting decision-making for improving longitudinal connectivity for diadromous and potamodromous fishes in complex catchments. Science of the Total Environment, 496, 206-218. https://doi.org/10.1016/j.scitotenv.2014.07.043.
- **Brevé**, N.W.P., Vis, H., Spierts, I., de Laak, G., Moquette, F., & Breukelaar, A. (2014). Exorbitant mortality of hatchery-reared Atlantic salmon smolts *Salmo salar* L., in the Meuse river system in the Netherlands. Journal of coastal conservation, 18(2), 97-109. https://doi.org/10.1007/s11852-013-0237-4.
- **Brevé**, N. W. P., Vis, H., Houben, B., de Laak, G. A. J., Breukelaar, A. W., Acolas, M. L., & Spierts, I. (2014). Exploring the possibilities of seaward migrating juvenile European sturgeon *Acipenser sturio* L., in the Dutch part of the River Rhine. Journal of coastal conservation, 18(2), 131-143. https://doi.org/10.1007/s11852-013-0281-0.

Oral presentations

- **Brevé** N.W.P. (2024) Lessons learned from telemetry: How climate change affects pathways of migratory fish in one of Europe's largest river basins. Free Flow Conference (FFC) April 15-17, 2024, Oosterpoort, Groningen, The Netherlands Freeflowconference.eu.
- Niels **Brevé** (Sportvisserij Nederland) (2024) – Overleving en routekeuzes van juveniele Europese steur in de Rijn (akoestische telemetrie). Vissennetwerk. Biesbosch museum eiland. Werkhoven.
- Niels **Brevé** (2024) – Herintroductie van de steur. Biesbosch. Dordrecht.
- Niels **Brevé** (2024) – Herintroductie van de steur. De Rijn Verbindt. De Bastei, Nijmegen.
- **Brevé**, N.W.P., Buijse, A. D., Leuven, R. S. E. W., Murk, A. J., Venema, J., & Nagelkerke, L. A. J. (2022). Risks of alien sturgeon species in the River Rhine basin for the reintroduction success of the endangered native European sturgeon. In Program and abstracts 22nd International Conference on Aquatic Invasive Species (ICAIS): Global Climate Change Amplifies Aquatic Invasive Species Impacts (pp. 73-73). April 18-22, 2022, Oostende, Belgium.
- Houben, B., **Brevé**, N.W.P., The Rhine Sturgeon Project: a brief overview and a look into the future. 8th International Symposium on Sturgeon (ISS8), 10-15 of September 2017, Vienna, Austria.
- **Brevé**, N.W.P., Houben, B., Breukelaar, A., and Vis, H. (2017) Survival and downstream migration of juvenile European sturgeon in the Rhine River, Netherlands, as revealed by telemetry. 8th International Symposium on Sturgeon (ISS8), 10-15 of September 2017, Vienna, Austria.
- **Brevé**, N.W.P., Vis, H., Houben, B., de Laak, G., Breukelaar, A., Acolas, Marie-Laure, de Bruijn, Q.A.A. & Spierts, I. Is the River Rhine ready for the European sturgeon? ISS7, 7th International symposium on sturgeon, Sturgeon, science and society at the crossroads: meeting the challenges of the 21st century, Jul 2013, Nanaimo, Canada. pp.1, 2013. https://hal.inrae.fr/hal-02607396.

Magazine articles

- **Brevé**, N.W.P.; Nagelkerke, L.A.J., Lenders, H. J. R., Leuven, R.S.E.W. (2022) Vreemde steuren bedwingen. VISionair: het vakblad van Sportvisserij Nederland (66). p. 16-19.
- **Brevé**, N.W.P., Houben, B. (2020) Europeanen versus Amerikanen: De juiste steur in het juiste water. VISionair: het vakblad van Sportvisserij Nederland (58). p. 28-31.
- **Brevé** N.W.P., and Houben B. (Oktober 2019) Meer steur in Europa via het lab. AQUAculture (19), p. 19-24
- **Brevé** N.W.P. & Houben B. (September 2019) Steuren uit het lab. VISionair: het vakblad van Sportvisserij Nederland (53). p. 9-11.
- **Brevé**, N.W.P., de Laak, G., Houben, B., Reiniers, K., van Zonneveld, G., Blom, E., & Vis, H. (2015). Terug naar de oertijd: herintroductie van de Atlantische steur in de Rijn. Visionair: het vakblad van Sportvisserij Nederland, 10(38), 4-7.
- **Brevé N.WP.** VISionair, Steur terug in Nederland, nr. 30 – december 2013.
- **Brevé N.WP.** VISionair, Steur terug in de Rijn, nr. 24 – juni 2012.
- **Brevé N.WP.** 2011 Posters and flyer : Zet bedreigde vissen altijd terug! Distributed amongst 850 angling tackle shops in the NL.

Technical reports

- Groen, M., J. Kranenbarg, B. Houben & **Brevé**, N. W. P. (2022). Naar een totaalbeeld van de actuele geschiktheid van de Rijn voor de Europese steur (*Acipenser sturio*). Bruikbaarheid informatiebronnen en aanbevelingen. RAVON, Nijmegen. Rapport nr. 2021.213.
- Visser, S., De Bruijne, W., Houben, B., Roels, B., & **Brevé**, N.W.P. (2020) First Action Plan for the European Sturgeon (*Acipenser sturio*) for the Lower Rhine. Report pp 72.
- Groen, M, Kranenbarg J, Houben, B & **Brevé**, N. W.P., 2019. GIS analyse habitat voor Europese steur. Beschikbaar habitat voor de voortplanting en opgroei in de Nederlandse Rijntakken bovenstrooms van het zoetwatergetijdengebied. RAVON, Nijmegen. Rapport nr. 2018.152.
- Kranenbarg J., Houben, B., & **Brevé**, N.W.P. (2018). Voorstudie Rijn actieplan Europese steur. Noodzakelijke acties en actoren met het oog op een herintroductieprogramma in de Rijn. RAVON, Nijmegen. Rapport nr. 2017.146.
- Council of Europe (2018) Pan-European Action Plan for Sturgeons. In: Committee S (ed). European Union, Strasbourg, p 85 (contributor).
- Spierts, I.L.Y., Kampen, J., Vriese, F.T., **Brevé**, N.W.P. (2018) The effects of ship propellers on migratory fish species, with emphasis on the European sturgeon (*Acipenser sturio*), a literature study.
- Winter, H. V., Teal, L. R., van de Wolfshaar, K. E., Griffioen, A. B., Houben, B., & **Brevé**, N. W. P. (2015). Desk-study on habitat quality for the European Sturgeon in the Dutch Rhine and southern North Sea (No. C044/15). IMARES.

Media outreach

(status June 2024)

Television interviews

- Offringa, E. (30/05/2023) Nieuwsuur https://nos.nl/nieuwsuur/video/2477135-de-steur-terug-in-nederland. https://twitter.com/Nieuwsuur/status/1663644195641257986?t=CCegebgQoqkSuHIFejhLAQ&s=08
- (05/06/2023) RTV Dordrecht https://www.rtvdordrecht.nl/nieuws/zeldzame-vissoort-de-steur-na-70-jaar-weer-thuis-in-de-biesbosch
- Jamaine van der Vegt (12/09/2018) RTV Rijnmond Stroom https://www.rijnmond.nl/tv/programma/113/Stroom/aflevering/14121.
- De Jong, M. (20/04/2018) RTV Rijnmond Nieuws – World Fish Migration Day - Geef trekvissen de ruimte! Steur in beeld. The preview was shown on Nature Today: https://www.naturetoday.com/nl/nl/nature-reports/message/?msg=24252.

Radio interviews

- NPO 1 (3 June 2024) F. Wallenburg Nieuws & Co Het lot van 70 steurtjes. https://www.nporadio1.nl/uitzendingen/nieuws-en-co/9bd0c6ae-855e-4286-ba89-378915f94777/2024-06-03-nieuws-en-co
- NPO 1 (1 april 2024) F. Wallenburg Nieuws & Co Beroepsvissers melden bijzondere bijvangsten zelden nog. 'Zwijgen is goud' https://www.nporadio1.nl/podcasts/nieuwsenco/105545/uitzending-van-2-april-2024 (vanaf 16:55 minuten)
- NPO 1 EenVandaag (01/07/2023) Feit of fictie: is de steur zeldzamer dan de reuzenpanda? https://www.nporadio1.nl/fragmenten/eenvandaag/f7bc95d5-fcb3-45c7-91c0-dff4c9a74174/2023-06-01-feit-of-fictie-is-de-steur-zeldzamer-dan-de-reuzenpanda
- Rijnmond (01/09/2022) Eric viste naar snoekbaars maar vond het stinkende karkas van een verdwenen vis https://www.rijnmond.nl/nieuws/1545066/eric-viste-naar-snoekbaars-maar-vond-het-stinkende-karkas-van-een-verdwenen-vis.
- NPO 1 (11/09/2022) Komt Europese steur terug in Nederlandse wateren? – BNNVARA https://www.nporadio1.nl/nieuws/preview/a34d2492-fe00-4fc9-bd2b-61659f51ecca?x-craft-preview=L5rQZddAJ5.
- NPO 1 (26/07/2022) Over steuren in Nederland https://www.nporadio1.nl/uitzendingen/nos-radio-1-journaal/5950439a-a8d7-4558-897d-537c99914084/2022-07-26-nos-radio-1-journaal.
- Tijn, L. Buitengewoon Radio (13/06/2021) Rivierharing keert terug om zich hier met veel herrie voort te planten. Ook meterslange steur keert terug. Steur heeft eigen meldpunt. (Omroep Gelderland) https://www.rn7.nl/9363-rivierharing-keert-terug-om-zich-hier-met-veel-herrie-voort-te-planten.

Articles in newspapers and news sites

- Van der Linde I. De Groene Amsterdammer (5 mei 2024) Keert de oervis de steur terug naar onze rivieren?
- Buiter R. Trouw (1 april 2024) Beroepsvissers melden bijzondere bijvangsten zelden nog. 'Zwijgen is goud' https://www.trouw.nl/duurzaamheid-economie/beroepsvissers-melden-bijzondere-bijvangsten-zelden-nog-zwijgen-is-goud~bd617435/?referrer=https://duckduckgo.com/
- NTR Wetenschap, Focus (07/07/2023) https://www.instagram.com/reel/CuXNAIEombC/?igshid=MTc4MmM1YmI2Ng==
- RTV Dordrecht (05/06/2023) Zeldzame vissoort 'de steur' na 70 jaar weer thuis in de Biesbosch https://www.rtvdordrecht.nl/nieuws/zeldzame-vissoort-de-steur-na-70-jaar-weer-thuis-in-de-biesbosch
- Sportvisserij Nederland (05/06/2023) Steur na 70 jaar terug in Nederland https://www.sportvisserijnederland.nl/actueel/nieuws/26343/Steur%20keert%20na%2070%20jaar%20terug%20in%20Nederland%20(video).html
- Omroep Brabant (02/06/2023) Na 70 jaar is de steur terug in het Brabantse water https://www.omroepbrabant.nl/nieuws/4286087/na-70-jaar-is-de-steur-terug-in-het-brabantse-water
- NOS Nieuws & Omroep Brabant (29/04/2023) De steur krijgt een nieuwe kans in de Biesbosch https://nos.nl/artikel/2473245-de-steur-krijgt-een-nieuwe-kans-in-de-biesbosch

- Cartens, R. (28/04/2023) Omroep Brabant. Joekels van oervissen krijgen kans in de Biesbosch: tot 5 meter en 400 kilo https://www.omroepbrabant.nl/nieuws/4267748/joekels-van-oervissen-krijgen-kans-in-de-biesbosch-tot-5-meter-en-400-kilo
- Zwartbol, A. (18/11/2022) Nederlands Dagblad. Hij komt. Of toch niet? De terugkeer van een oervis. https://www.nd.nl/leven/leven/1151460/hij-komt-of-toch-niet-ligt-hij-te-wachten-in-de-noordzee-de-ter.
- Kleis, R. (10/04/2022) Resource-online. The return of the sturgeon https://www.resource-online.nl/index.php/2022/04/10/the-return-of-the-sturgeon/?lang=en.
- Kamer, L. (05/01/2022) Kijk op Bodegraven-Reeuwijk. https://www.kobr.nl/nieuws/human-interest/28883/steur-in-de-reeuwijkse-plassen.
- Havermans, O. (07/06/2021) Trouw. De triomfantelijke terugkeer van de zo gewilde trekvis https://www.trouw.nl/duurzaamheid-economie/de-triomfantelijke-terugkeer-van-de-zo-gewilde-trekvis~bdf42e8d/.
- Van Der Vleuten, O., (23/02/2018). Steur keert terug in de Schelde | Zeeuws nieuws | pzc.nl https://www.ad.nl/zeeland/steur-keert-terug-in-de-schelde~a92ddaac/.

Magazine articles

- ARK (02/06/2024) Sluizen open voor de steur. https://www.naturetoday.com/intl/nl/nature-reports/message/?msg=32379
- Hét VISblad (31/08/2023) Opnieuw jonge steuren uitgezet in de Biesbosch
- WWF Nederland (26/05/2023) Nature Today, Na zeventig jaar keert bijna uitgestorven steur terug naar Biesbosch https://www.naturetoday.com/intl/nl/nature-reports/message/?msg=30829
- Moons, K. BioNieuws (26/11/2022) Zenderonderzoek. Het spoor bijster. Vissen op het droge https://bionieuws.nl/article/1276250/het_spoor_bijster.
- Van Emmerik, W. Kijk op Exoten, nr. 41 (December 2022) Exotische steuren in Nederland https://natuurtijdschriften.nl/pub/1019957.
- Rijnmond (12/09/2022) Gevonden visskelet blijkt geen Europese steur, maar een 'ontsnapte' exoot en dat is een groot probleem https://www.rijnmond.nl/nieuws/1550093/gevonden-visskelet-blijkt-geen-europese-steur-maar-een-ontsnapte-exoot-en-dat-is-een-groot-probleem.
- Noordhollands Dagblad (30/08/2022) Michel heeft de vangst van zijn leven: een 'uitgestorven' steur van een meter lang https://www.noordhollandsdagblad.nl/cnt/dmf20220830_55562963.
- **Brevé**, N.W.P., Schuitemaker, A. (14/07/2022) Nederlandse Vissersbond De toekomst van de steur in de Noordzee: jouw mening telt! https://www.vissersbond.nl/de-toekomst-van-de-steur-in-de-noordzee-jouw-mening-telt/.
- Wageningen University (02/03/2022) Nature Today Nederland veel belangrijker voor steur dan altijd is gedacht https://www.naturetoday.com/intl/nl/nature-reports/message/?msg=28863.
- ARK, WNF, SVNL (09/02/2022) Nature Today Levensloop van steuren in beeld https://www.naturetoday.com/intl/nl/nature-reports/message/?msg=28761.

- **Brevé**, N.W.P., Houben, B., Roels, B., Helmer, J., Herder, J. (24/07/2022) Nature Today Langverwacht broedsucces van Europese steur https://www.naturetoday.com/intl/nl/nature-reports/message/?msg=29499.
- Vanderheyden, M. Na 2030 moeten Europese steuren opnieuw in de Rijn zwemmen EOS (September 2021) p. 45-49.
- **Brevé**, N.W.P. (19/01/2021) Sportvisserij Nederland De Kier is een mooi begin https://www.sportvisserijnederland.nl/actueel/nieuws/21382/De%20kier%20is%20een%20mooi%20begin.html.
- **Brevé** N.W.P. (14/12/2020) Sportvisserij Nederland Actieplan Europese steur https://www.sportvisserijnederland.nl/actueel/nieuws/21328/Actieplan%20Europese%20steur.html.

Training and Education

Name PhD candidate	Drs. N.W.P. Brevé
Project title	On re-introducing sturgeons to the river Rhine and the North Sea
Group	MAE / AFI
Supervising team	**Name**
Promotor	Prof. Dr A.J. Murk
Promotor	Prof. Dr Ir. A.D. Buijse
Co-promotor / daily supervisor	Dr Ir. L.A.J. Nagelkerke
Project term	From January 1, 2019 until December 31, 2024

A. The Basic Package	Year	Credits
Personal effectiveness (Schouten & Nelissen)	2003	
Ethics in Animal Sciences course	2020	
Introduction Day	2021	
WGS Scientific Integrity course	2023	
		3
B. Disciplinary Competences		
Writing of PhD research proposal	2019	
Use of ArcGIS Pro (ESRI, the Netherlands)	2021	
Introduction to R and R Studio	2023	
		8
C. Professional Competences		
Effective & relaxed speaking for groups (Schouten & Nelissen)	2004	
Project management project leader skills (Schouten & Nelissen)	2008	
Fast reading (Schouten & Nelissen)	2009	
Presenting skills (Schworks)	2009	
Communicate and influence effectively (Doomernik Training & Coaching)	2011	
Effective Meetings (NCOI)	2016	
Systematic approaches to reviewing literature	2019	
Searching and Organising Literature	2020	
Research Data Management	2020	
Brain Training	2020	
Reviewing a Scientific Manuscript	2021	
Last Stretch Of The PhD Programme	2021	
Writing propositions for your PhD	2021	
Managing your - scientific - network	2021	
Scientific Writing	2022	
Introduction to LaTeX	2022	
Intensive writing week	2023	
WIAS The Final Touch: Writing the General Introduction and Discussion	2023	
		13

D. Societal Relevance		
Press & Media (buitendelijntjescommunicatie.nl)	2017	
Communication with the Media and the General Public	2022	
Writing technical reports and magazine articles on sturgeon conservation	2015-2022	
Communicating research on the radio, television, in newspapers and magazines	2018-2024	
		6
E. Presentation Skills		
Oral presentations	2019-2024	
		4
F. Teaching Competences		
Supervising MSc major and minor thesis students	2019-2024	
Supervising BSc thesis students	2019-2024	
Supervising internship students	2019-2024	
		6
TOTAL (*One ECTS credit equals a study load of appr.28 hours*)		**41**

Colophon

The research described in this thesis was financially supported by Sportvisserij Nederland, ARK Rewilding Nederland, het Wereld Natuur Fonds, the Dutch Zip code Lottery 'Dream fund' grant (Nationale Postcode Loterij, Droomfonds) (2015-2022), the Dutch Ministry of Agriculture, Nature and Food Quality (Ministerie van Landbouw, Natuur en Voedselkwaliteit, LNV) (2020-2024), Interreg IV-B the Living North Sea programme (2012), Interreg V-A Deutschland-Nederland the Green & Blue Rhine Alliance project (2014-2020), Interreg VI-A Deutschland-Nederland De Rijn Verbindt project (2023-2026), and the MERLIN project (EU Horizon 2020 grant agreement No 101036337).

Financial support from Wageningen University for printing this thesis is gratefully acknowledged.

The funding bodies had no role in the design of the thesis studies, or in the analysis and interpretation of data.

Cover design by: Jeroen Helmer / ARK Rewilding Nederland, Annemarie van Amerongen and Niels Brevé
Layout by: Bregje Jaspers | ProefschriftOntwerp.nl and Niels Brevé
Printed by: ProefschriftMaken | www.proefschriftmaken.nl