Hydrobiologia 478: 205–218, 2002.
P.H. Nienhuis & R.D. Gulati (eds), Ecological Restoration of Aquatic and Semi-Aquatic Ecosystems in the Netherlands (NW Europe).

A review of the past and present status of anadromous fish species in the Netherlands: is restocking the Rhine feasible?

S.J. de Groot[1]
Netherlands Institute for Fisheries Research (RIVO-DLO), P.O. Box 68, 1970 AB IJmuiden, The Netherlands
[1]*Present address: Brederoodseweg 49, 2082 BS Santpoort-Zuid, The Netherlands*

Key words: anadromous fish, Rhine, decline, extinction, restocking, feasibility

Abstract

The paper reviews the past, present and future of eight anadromous fish species inhabiting the Lower Rhine (The Netherlands), viz. -sturgeon (*Acipenser sturio*), whitefish and houting (*Coregonus lavaretus*, C. oxyrinchus), smelt (*Osmerus eperlanus*), allis and twaite shad (*Alosa alosa*, A. fallax), sea trout (*Salmo trutta*) and salmon (*Salmo salar*). All species are under threat or became extinct (e.g. sturgeon, allis shad). It is not possible to single out a specific factor for the decline or disappearance. A combination of factors is responsible, as the degradation of the spawning and nursery areas, river correction for shipping, building of sluices and hydropower dams, extraction of sand and gravel and river pollution. The likelihood that a species will return via natural recovery, or restocking is assessed. The return of the sturgeon is unlikely. Present observations of sturgeon can be attributed to releases of unwanted sturgeon hybrids. A natural stock of coregonids in Dutch waters seems not feasible any more due to irreversible habitat degradation. Present day catches originate from German releases. The anadromous smelt, heavily reduced in numbers, still inhabits some of our waters, the non-migratory smelt is still very common. The allis shad is extinct and unlikely to recover. The species never spawned in the Dutch part of the Rhine. Twaite shad, declining in numbers, are still observed in the lower reaches of Rhine and Meuse. Sea trout is presumably still present in the same varying numbers as before. Spawning in our waters has not been documented. The salmon, once fished in large numbers, is now the subject of restocking programmes in Germany. Observations of individuals can partly be attributed to these programmes but also to straying salmon. Restocking programmes should be considerably improved before noticeable success is to be met.

Introduction

The anadromous fish species of the Rhine were economically valuable species, especially the salmon, the coregonids (whitefish, houting), allis shad and sturgeon. However, sea trout, smelt and twaite shad were also commercially exploited. The life history stages of anadromous fish require several ecosystems to thrive, both marine and freshwater habitats. These habitats are severely impacted by humans. A number of factors, alone or in combination, can be held responsible for the decline of anadromous fish populations: destruction of spawning habitat by deepening the river, and sand and gravel extraction, habitat fragmentation and degradation, resulting from the building of locks, construction of hydropower stations and river pollution and overfishing. Even if it will be possible to restore a small stock of salmon in the Rhine system, the interaction between fish from hatcheries and wild fish may give rise to other unanticipated problems.

This review summarizes the status of eight anadromous fish species of the river Rhine-system. All of them have declined in numbers or became extinct (allis shad, sturgeon), and likely causes for their decline will be indicated. At present, no successes of restocking programmes can be recorded, but perhaps in the case of the salmon there is some light at the horizon. Potential problems arising from such restoration projects will be reviewed.

Sturgeon (*Acipenser sturio*, Linnaeus, 1758)

Sturgeons (Acipenseridae) are confined to the northern hemisphere on both sides of the Atlantic and Pacific. There are 27 species, most of them are endangered, threatened by extinction or, in case of some species and populations, already extinct. The European sturgeon (*Acipenser sturio*, Linnaeus, 1758) which inhabits the Northern European coasts and rivers, is extinct in large parts of its range primarily due to overfishing (Lelek, 1987; Rochard et al., 1990; Anonymous, 1994; Billard, 1995). In north-western Europe, the sturgeon is only present in the river system of the Gironde–Garonne, Dordogne (France). Since the mid 1980s, a restocking programme was initiated in this river system (Castelnaud & Trouvery, 1984). It is unlikely that stocks from the Gironde system will recolonize the river Rhine system.

Historical distribution

In this paper, sturgeon is only discussed in relation to the river Rhine system. From the Iron Age (700–300 BC) and Roman times (57 BC–406 AD), it is known that the sturgeon inhabited Dutch waters. This was demonstrated by Prummel (1989), who excavated fragments of a dermal plate and of spina pectoralis on the former island of Voorne-Putten, dating back to the Iron Age. Moreover, Brinkhuizen (1989) described remains of a 1-m long sturgeon found near Velsen (North Sea coast), and early Middle Ages (600–1200) sturgeon remains are known from the area near Oldenburg (Germany) (Prummel, 1991). Kinzelbach (1987) carried out a reconstruction of the now extinct population of the sturgeon in the river Rhine-system. He based his study on records from the 15th century. Sturgeon were common in the Delta and in the Lower Rhine until about 1910, becoming extinct as a breeding species in 1942. Kinzelbach (1987) described in detail the sturgeon distribution higher up in the river systems and stated that the species was more common higher up the river than was formerly assumed. Nevertheless, about two thirds of the sturgeon population stayed in the Lower Rhine and Delta and about one third swam up to the Middle and Upper Rhine (up to 850 km upstream) and their tributaries. It is estimated that about 3000–4000 sturgeons lived in the Rhine from perhaps 1440 until 1900. The stock was larger in the middle and at the end of the 16th century.

It is unknown where sturgeon nurseries existed in the river Rhine. It is assumed that spawning took place in the deeper parts of the river, mainly between May and August. Minimum water depth requirements for spawning are 3 m, although spawning can occur in depths up to 20 m (Jakob, 1996). The so-called 'pits' in which sturgeons were observed (e.g. Mohr, 1952) in the river Eider, north Germany are in fact refugia for fish to rest for a while during the spawning process. Deelder & Huussen (1973) and Lobregt & van Os (1977), indicate that sturgeon spawn in very shallow water, however, on what grounds this statement is based is unclear. Spawning of sturgeon has never been observed in Dutch waters. The smallest sturgeons mentioned in the literature in comparable German waters (Eider, Elbe-river system) were 40–60 cm, or at least 1–2 years old. Hence, there has been no indication of a spawning area at all (Hoek, 1910).

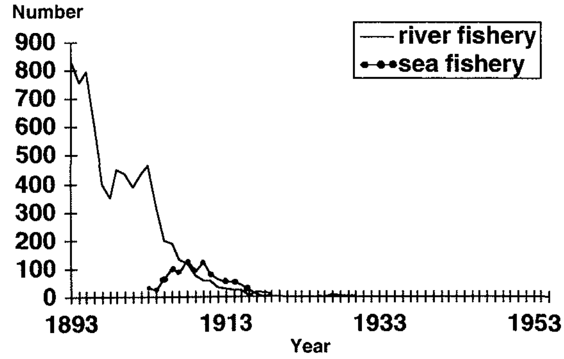

Figure 1. Number of sturgeon (*Acipenser sturio*) caught in the Lower Rhine and North Sea; data from Fisheries Inspection (Anonymous, 1920) and Verhey (1961).

After spawning the adults migrate rapidly to the sea, where they remain before returning to spawn again. The juveniles leave the freshwater area and move into the estuary. They may migrate for a while into the sea and then return to the estuary. The fact that sturgeon males require about 8 years to reach sexual maturity, and females even 14 years, makes them especially vulnerable to fishing. Verhey (1949, 1961, 1963) analysed the sturgeon fishery of the Lower Rhine, with an emphasis on the period from 1900 to 1931. In the year 1749, 8.999 sturgeons were caught in the Lower Rhine and landed at Dordrecht fish market. Between 1824 and 1852, an average of 3000 sturgeons per year were caught. Complete reliable fishery statistics of sturgeon date from the end of the 19th century. Figure 1 is based on data collected by the Dutch Fishery-inspectorate (Anonymous, 1920), augmented with Verhey's data. Also added to this figure are catch data of sturgeon by the North Sea fishing fleet (1903–1919) (Anonymous, 1920). After a strong decline of river caught sturgeon, sea catches exceeded the river catches during a short period, but after 1960 no river catches of sturgeon in the Lower Rhine were reported. Sturgeons, approximately 1 m in length, were occasionally caught in the North Sea or washed ashore on the beaches (Nijssen & de Groot, 1987).

After 1992, however, juvenile sturgeons have been reported from the Lower Rhine and adjacent waters (Volz & de Groot, 1992). The first individual (8-2-1992) from the river Merwede (Rhine-estuary) proved to be a juvenile *Acipenser sturio*; the body was mutilated, perhaps by a propeller of a ship. Since then, occasional small sturgeons have been reported (e.g. Hartgers et al., 1998). After careful examination, they proved to be hybrids, with many features of the Russian sturgeon (*A. gueldenstaedti*, Brandt, 1833) and stellate sturgeon (*A. stellatus*, Pallas, 1811). The reported revival of the sturgeon in the Rhine can not be taken seriously, as the specimen collected are likely originating from accidental releases of aquarium fish.

Causes of decline

What are the causes of the decline and ultimate extinction of the sturgeon in the Rhine? Kinzelbach (1987), assuming that the fisheries took about 30% of the sturgeons in the Rhine, calculated that around the turn of the 19th century, the stock of the Middle- and Upper Rhine was 100–1000 sturgeons. In the Lower Rhine and Delta, the stock was about 2400 sturgeons. He concluded that the decline of the sturgeon started in the mid 19th century and that the species became extinct in the thirties of the 20th century. The most likely cause was the overfishing, and the destruction of spawning grounds, due to canalisation and the construction of dams and weirs. For a restoration endeavour the following requirements are essential: a gravel bottom (1.7–6.5 cm gravel), with a water velocity of 1 m s^1 and a water temperature of 15–20 °C, needed for spawning. Oxygen concentrations of $\geq$6 mg l^{-1}, water depths of 3–20 m, and a spawning area per female of about 300 m^2 are also required for successful reproduction.

Increased fishing pressure proved to be as destructive as the deterioration of the spawning areas. The river fisheries caught far too many adult specimens, the sea fisheries finished off the immature and remaining adults (Steinert, 1951; Mohr, 1952). Birstein (1993) and Shagaeva et al. (1993) described serious changes in the structure of gonads of sturgeon and their larvae in the Volga due to water pollution. As for most of the world's sturgeons, the combination of river pollution, river regulation, and overfishing brought about the eventual collapse of a once abundant population (reviewed in Barannikova, 1987).

Table 1. Dutch coregonid catches 1910–1939 (data in the archive of RIVO-DLO, IJmuiden)

Year	Landings (kg)	Year	Landings (kg)
1910	2769	1925	65
1911	3586	1926	597
1912	1665[a]	1927	534
1913	1241[a]	1928	115
1914	3170[a]	1929	140
1915	14 682[a]	1930	24
1916	3298	1931	109
1917	4737	1932	139
1918	1175	1933	129
1919	1644	1934	53
1920	720	1935	1
1921	972	1936	2
1922	130	1937	46
1923	25	1938	0
1924	690	1939	3

[a] Underestimate.

Coregonids

Depending upon the taxonomic system selected, either two or three anadromous coregonid species inhabit, or have inhabited the Rhine: *Coregonus lavaretus* (Linnaeus, 1758) (whitefish); *C. oxyrinchus* (Linnaeus, 1758) (houting); and *C. albula* (Linnaeus, 1758) (vendace). Vendace have been caught only a few times in the Rhine (the last time in 1927), but it is most likely that the fish were simply incorrectly identified when caught. At the turn of the century, whitefish were caught in all large rivers such as the Rhine, IJssel and Meuse, houting was very common in the Wadden Sea (Redeke,1934). At present only a small original population of houting still exists in the Danish Wadden Sea, with a proven spawning ground in the river Vidå near Tønder. Since the discovery of the existence of this spawning ground, houting has been released in the Baltic Sea, in German and Danish waters, and also in the German river Eider (Grøn, 1987; Grøn et al., 1988; Jäger, 1999; Scheffel, 1999).

Coregonid fishing occurs from August to November. Prior to 1910, catch data are difficult to trace because fish were sold directly by the fishermen at local markets. However, it was possible to obtain data for 1910–1939 (Table 1). Although the fishery was never large, the obvious decline between 1916 and 1920 is remarkable. In 1917, the catch was still around

Table 2. Overview of releases of fry and juvenile coregonids in The Netherlands. (Reuter, 1966; Nijssen & de Groot, 1987)

Year	Numbers	Age	Location
1907	50 000	fry	Meuse/IJssel
1908	400 000	4 weeks	Meuse/IJssel
1922	60 000	6 weeks	?
1923	22 000	fry	Meuse
1924	–	–	–
1925	500 000	fry	Meuse/IJssel
1926	2121 000	4 weeks	Meuse/IJssel
1927	2442 000	fry	Meuse/IJssel
	1000	6 months	Reeuwijkse plassen
	1000	6 months	Amstel
1928	50 000	3–4 weeks	Meuse
	175 000	3–4 weeks	Meuse
	400 000	fry	Gelderse IJssel
	1625 000	1 year	Meuse
	900 000	1 year	Gelderse IJssel
	9220	1 year	Meuse
1929	500 000	fry	Meuse
	500 000	fry	IJssel
	150 000	fry	Meuse
	749	1 year	Meuse/Reeuwijkse plassen
1930	5150	1 year	Meuse
1931	1000 000	fry	Meuse
1937	50 000	fry	Reeuwijkse plassen
	50 000	fry	Bergumermeer
	50 000	fry	Binnen Maas
	50 000	fry	Alkmaardermeer
	50 000	fry	Beulakerwijde
	700 000	fry	Lake IJsselmeer
	1800	6 months	Reeuwijkse plassen/Binnen
1938	failed	–	Meuse/Alkmaardermeer
1939	–	–	–

5000 kg: the decline was therefore far quicker than that observed for salmon (de Groot, 1992). The dramatic downward trend and near-extinction of the species was reason for great concern by government authorities. Artificial rearing was tried, for the first time in 1907, and a restocking programme with eggs, 1-month and 1-year-old whitefish, imported from Peipus Lake, Russia, was initiated. In Dutch inland waters, a total of nearly 119 million larval or juvenile whitefish were released between 1907 and 1939 (Table 2); however, there were no increases in abundance.

There is a growing concern in Germany for the preservation of coregonids. Non-migratory stock in German alpine lakes are threatened by pollution,

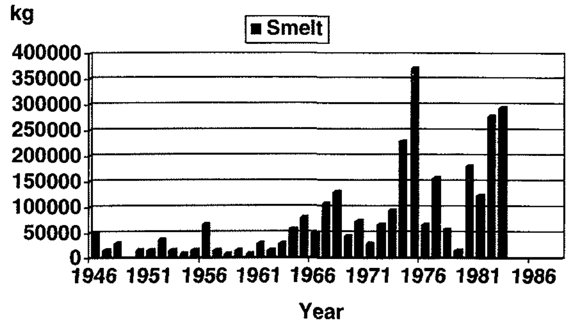

Figure 2. Smelt (*Osmerus eperlanus*) catches in Hollands Diep and Haringvliet between 1946 and 1988.

hence, extensive annual restocking operations are carried out in large lakes created by barrages (so called 'Talsperre'). Coregonids are released mainly in the States of Nordrhein-Westfalia and Hessen. It is assumed that the present increase in the Rhine, as well as in the Dutch Lake IJsselmeer, must originate from these Danish/German restocking attempts (de Groot & Nijssen, 1997; Hartgers et al., 1998).

Coregonid populations have not recovered in Dutch inland waters. Migratory forms of coregonids are unable to enter the inland waters owing to the disappearance of suitable tidal inlets. The houting spawned in the Netherlands, very likely in the northern province of Groningen, adjacent to the Wadden Sea, up to the beginning of the 20th century. However, the rivers and waterways of Groningen have been changed from 1870 to 1977, and the tidal movement still observed in the harbour of the town of Groningen disappeared. Channels were deepened, the surrounding land was better irrigated and exploited, and sluice systems were built to prevent the inlet of seawater during flood tide. At present, plans to regulate the water level in Lake Lauwersmeer, a former inlet of the Waddensea, will definitely close off the entry of the houting into inland waters in the northern part of the Netherlands. This blockade between the small rivers and the sea is exacerbated owing to subsidence of the land mass caused by the exploitation of natural gas, disturbing the natural run off of water from land to sea. All these factors make the return of houting for spawning in Dutch inland rivers a remote possibility.

(Osmerus eperlanus **Linnaeus, 1758)**

Smelt (*Osmerus eperlanus*) in Dutch waters are present in both migratory (anadromous) and land-

Table 3. Lake IJsselmeer smelt catches 1980–1998 (data Fisheries Directorate, The Hague)

	Landings (kg)
1980	157 000
1981	160 000
1982	2309 000
1983	1235 000
1984	1305 000
1985	1357 000
1986	1881 000
1987	2317 000
1988	3319 000
1989	1982 000
1990	1481 000
1991	2504 000
1992	1517 000
1993	586 000
1994	1402 000
1995	2345 000
1996	856 000
1997	1032 000
1998	327 000

Table 4. Smelt catches in Holland's Diep and Haringvliet 1914–1919 (data Fisheries Directorate, The Hague)

Year	Total (kg)
1914	140 771
1915	109 366
1916	225 955
1917	101 097
1918	176 055
1919	146 275

locked (non-migratory) forms. The migratory form is known in the estuaries, the Wadden Sea and the lower reaches of the large rivers. Migratory smelt have essentially vanished from Dutch coastal waters (Fig. 3) owing to the construction of the large Delta works project, the Haringvlietdam, a safety scheme against flooding, completed in 1970, and virtually sealing off the estuary from the sea. The non-migratory form is found in large quantities in the Lake IJsselmeer (Table 3), the Frisian lakes and in the provinces of North and South Holland (Table 4, Fig. 2).

Migratory smelt reach a length of up to 30 cm in 8 years (Mohr, 1941). Non-migratory smelt of the IJssel Lake, a large freshwater body, reach lengths of 19

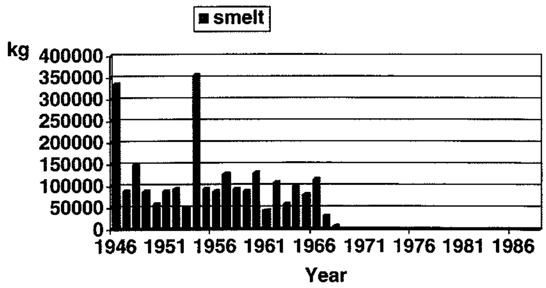

Figure 3. Smelt (*Osmerus eperlanus*) catches in the Dutch Wadden Sea between 1946 and 1988.

cm in their fourth year (first year: 6 cm, second year: 12 cm; third year: 14 cm), but these large individuals are, however, uncommon (Redeke, 1907, 1914, 1922; Havinga, 1928, 1954). Redeke (1914) indicated that migratory smelt spawned in the lower reaches of the Rhine and in the freshwater tidal areas of Hollands Diep, between Moerdijk-bridges and Willemstad. The migratory smelt was always rare near Arnhem and Nijmegen in the upper Rhine reaches of the Netherlands (van den Ende, 1847). The non-migratory smelt spawn in both lakes and rivers from February to April when water temperatures are between 4 and 12 °C. The eggs are ellipsoidal and average fecundity is 40 000 eggs. The eggs adhere to stones, gravel, or water plants, but never to silt bottoms. Average egg density is 6 eggs cm^{-2}, but sometimes eggs are also found in layers. The larvae hatch between temperatures of 18–20 °C.

One reason for the decline of the river Rhine smelt is the building of extensive coastal defence constructions, which prevent migration of fish to their spawning habitats. An additional cause of the decline is the deposition of enormous amounts of river borne silt, following the closure of the Haringvliet estuary (Anonymous, 1987). Silt-covered and heavily polluted river bottoms are unsuitable for egg survival.

Allis shad (*Alosa alosa* Linnaeus, 1758) and twaite shad (*A. fallax* Lacépède, 1803)

The allis shad and the twaite shad both belong to the riverine Clupeidae, and supported considerable commercial fisheries in the past. Historically, the catches of the allis shad were rather important, but the twaite shad has gained some importance concurrently with the disappearance of allis shad.

Table 5. Allis shad (*Alosa alosa*) landings at Kralingseveer, Rotterdam (1869–1894) (after Hoek, 1894)

Year	Number	Year	Number
1869	42 217	1882	141 542
1870	79 184	1883	103 746
1871	94 786	1884	84 170
1872	79 322	1885	184 209
1873	69 851	1886	179 439
1874	116 033	1887	167 966
1875	85 181	1888	148 846
1876	71 431	1889	128 837
1877	67 495	1890	123 233
1878	91 998	1891	53 568
1879	91 232	1892	43 915
1880	65 707	1893	34 289
1881	122 398	1894	35 500

Allis shad

In the past, adult fish were caught by the Dutch river fisheries between the third week of March and the first week of June. In good years, the catch made up about 20% of the annual income for the local fishermen, and salmon comprised the remaining 80%. The decline in allis shad over the years is striking (Fig. 4, Table 5). Landings averaged 207 423 (1881–1890), 54 685 (1891–1900), 39 701 (1901–1910), 1249 (1911–1920) and finally 13 (1931–1936) individuals (Redeke, 1938). Nationally as well as internationally, protective fishery measures were difficult to agree upon. The reasons were simple: restricting allis shad fishing from March to June would also have had repercussions on salmon fishing. Hence, the main reason for the sharp decline in stocks was probably overfishing.

The allis shad entered rivers to spawn when the water was about 11–12 °C. Males arrived in small schools a few weeks earlier in the season than females. Allis shad was commonly caught in the Rhine from March to June, and the spawning period was May to June. Actual spawning never took place in Dutch waters, but rather in the higher reaches of the Rhine, near Koblenz; the Mosel, near Trier; and the Neckar, between Neckarsteinach and Hirschhorn. Spawning took place mainly at night in the upper water column, and over a gravely bottom. During spawning the fishes could be heard splashing through the surface waters, a sound described by the late Roman Ausonius in his poem 'Moselia'. The best known description of this spawning was given by Vincent (1894). Parental fish leave the river after spawning. The eggs are fertilized in mid-water and then sink to the bottom, where they enter the interstices of the gravel. A female produces about 50 000 eggs per kg body weight. Depending on the water temperature, larvae emerge within 4–8 days (22–24 °C). Larvae and juveniles are transported downriver into the tidal zone. Vertical diurnal activity, rhythmically synchronized with water ebb and flow, permits them to remain in the estuary for over 1 year.

River alterations (e.g. deepening, barrages, etc.) have negatively effected the spawning areas of allis shad. Nevertheless, Lelek (1987) stated that "poor water quality is probably chiefly responsible for the decline and extinction in many European rivers". This seems less true for the Rhine, where overfishing and destruction of spawning habitat can be considered as the main factors leading to extinction. Pollution combined with physical difficulties for anadromous fish species to enter into the Rhine-Scheldt estuary will certainly hamper future reintroduction efforts. In the past the lower reaches of the river Rhine acted as a nursery. Due to the construction of large flood defence works (Delta works), juvenile fish of both allis and twaite shad can no longer thrive throughout the year in the lower river reaches, because the complex system of vertical migration combined with the tidal movement for species maintenance no longer exists.

The theory presented by Redeke (1938), based on earlier observations of Hoek (1894, 1899) that the hybridisation of allis and twaite shad played an important role in their disappearance, is supported by recent electrophoretic work (Boisneau et al., 1992); this would explain the disappearance of the allis shad from the relatively clean Rhône river (Rameye et al., 1976). As far as the river Rhine population is concerned, even if this process had occurred, the effect would have been insignificant because the spawning areas of both species were geographically well separated.

Twaite shad

Twaite shad spawned under conditions similar to those of the allis shad. However, the twaite shad stayed in the freshwater tidal zone, spawning mainly in the Dutch part of the Rhine river, whereas the allis shad moved further upstream. Because the twaite shad had a shorter distance to move upstream, the entry period and the length of the stay of the adult fish in the area were much shorter than that of the allis shad. April and May were the months of river

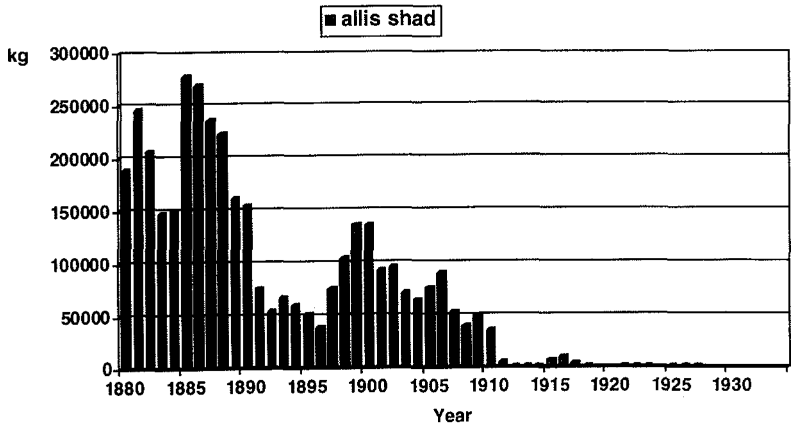

Figure 4. Allis shad (*Alosa alosa*) landings in the Netherlands between 1880 and 1934.

entry and spawning, with actual spawning occurring over 3 weeks. Well known spawning areas were in the Merwede (near Woudrichem) and in the Bergse Maas (near Genderen), but actual spawning sites were never identified. After spawning, the adult twaite shad left the river but the juveniles remained in the lower reaches together with young allis shad. The fish reached maturity within 3 years (Hoek, 1899).

As twaite shad were considered inferior during the days when allis shad were plentiful, no catch data were kept. Only when allis shad catches were declining did this fish become of interest, leading to a fishery between 1933 and 1944 (Figs 5 and 6). Records in early years certainly underestimate true catches; however, it is obvious that catches peaked in 1934–1939. Although the statistics during World War II (1940–1945) underestimate catches, the decline in landings are obvious. In 1950, catches increased to some extent, but since 1966 when Hollands Diep and Haringvliet were virtually cut off from the sea by the Delta works, catches dropped to zero in the lower Rhine river reaches. Twaite shad are currently found in very small numbers in several locations close to the coast of the Netherlands. Observations in Lake IJsselmeer do not coincide with the spawning period, and justified the assumption that the fish enter Lake IJsselmeer unintentionally or only for a short period of time (Hartgers et al., 1998).

Decline of the twaite shad in the Rhine was probably caused by several factors, not only overfishing. River regulation works destroyed several spawning habitats, and pollution and silting up may also have played a role in the stock depletion. Closing off of the river, thereby changing the freshwater tidal system in the estuary into a river with a one-way flow, has likely been the fatal blow for the population. However, the introduction of a new sluicing regime in the Haringvliet (Delta works) is being reconsidered, to allow part of the former tidal movement (Anonyous, 1998), and this may lead to a partial recovery of the twaite shad population in the south-west of the Netherlands.

Sea trout (*Salmo trutta* Linnaeus, 1758)

The life cycle of the sea trout resembles that of other anadromous fish such as the salmon. However, an important difference is that both sexually mature and immature trout ascend the river together in autumn on their return from the sea (Shearer, 1955). Trout can reproduce several times over their life-span, with the eggs being laid in gravel beds in the upper reaches of the river (Stuart, 1953; Frost & Brown, 1967). Sea trout hybridise with brown trout, and are rarely found in rivers with currents in excess of 60 cm s^{-1}.

In contrast to salmon, sea trout generally remain closer to the coast; most of the trout leaving Dutch waters head northwards (Svärdson & Fagerström, 1982) and stay within 100–350 km of the coast. Compared with salmon catches, the numbers of sea trout caught in the river Rhine were relatively small and had an average length of 50 cm and weighed approximately 1 kg.

The fact that a significant proportion of sea trout that are landed, never appear in the fisheries statistics is not new. As early as 1920, officials noted that many of the sea trout caught were not sold at market and therefore not included in the catch statistics. Nevertheless, using information from Hoek (1893) and catch figures from the Fisheries Inspectorate, which

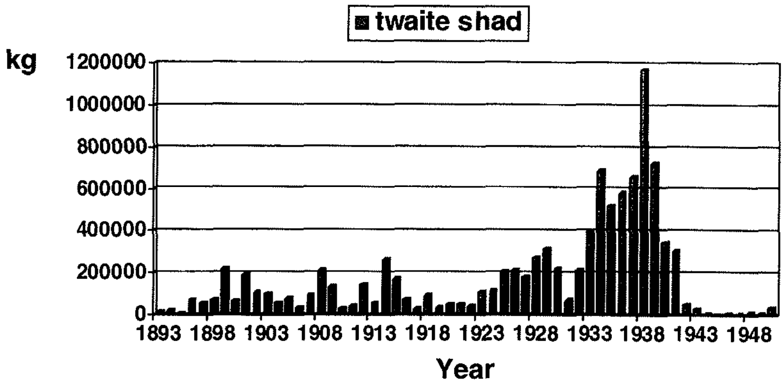

Figure 5. Twaite shad (*Alosa fallax*) landings in the Netherlands between 1893 and 1950.

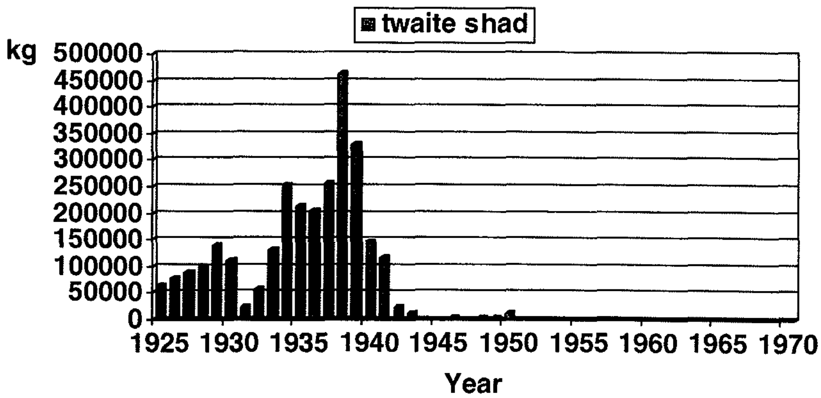

Figure 6. Twaite shad (*Alosa fallax*) landings in the Netherlands (Hollands Diep and Haringvliet) between 1925 and 1970.

later became known as the Fisheries Division and the Department of Fisheries, estimates can be made of the number of trout landed between 1886 and 1986 (Fig. 7). Annual trout catches over this period varied considerably, but no evidence can be found to suggest that there has been a systematic decline in numbers (de Groot, 1989b). Reports from professional fishermen are too infrequent to allow firm conclusions to be drawn about trout stocks, but do provide an indication of the continuing presence of trout in the river.

The action that has most affected the sea trout and other migratory fish in the Rhine is the closure of the sea inlets in the south-west of the Netherlands. The presence of sea trout in the IJsselmeer could be due to trout entering via the rivers Rhine and IJssel. However, it is also plausible that sea trout enter via the sluices in the Barrier Dam at Kornwerderzand and Den Oever. The fact that trout are mainly caught in the lake and not in the rivers is not sufficient justification for assuming that trout are only present in large numbers in Lake IJsselmeer and that this serves as a catchment area for trout. Thorpe's (1990) hypothesis about the archetypal life history strategy comprising specific physiological and morphological adaptations of trout to the freshwater environment, places the occurrence of sea trout in the Rhine and Meuse in a different light. Sightings of silver-coloured trout in Nordrhein-Westfalen or in the Meuse can no longer be taken as proof that trout have swum upstream from the sea. These fish could equally well originate from brown trout populations and have been forced to leave their environment because of insufficient food supplies or inadequate conditions. Similarly, the presence of sea trout in the lower reaches of the rivers Meuse, Lek, Merwede or in the Rhine-Meuse-Scheldt estuary can not be viewed as conclusive evidence that these fish are intending to ascend the river. In contrast to the behaviour of the salmon, young sea trout often undertake what are known as 'dummy runs'. Sexually immature trout that inhabit coastal waters often accompany their sexually mature counterparts a short distance up the river before returning to the sea. Although it is generally agreed that trout enter Dutch rivers from the sea, it is difficult to establish to what extent this occurs. The

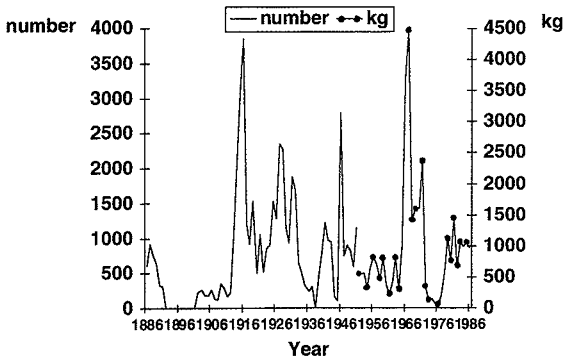

Figure 7. Catches of sea trout (*Salmo trutta*) over the period 1886–1986; data not available for 1892–1901 (source RIVO-data).

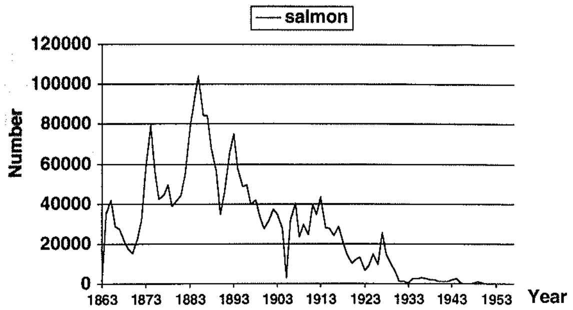

Figure 8. Dutch salmon (*Salmo salar*) catches 1863–1957 (source RIVO-data).

irregular catch statistics merely provide an indication of such movements.

Salmon (*Salmo salar* Linnaeus, 1758)

The history of the Dutch fishing industry can be traced back to the oldest inhabitants of the Netherlands, although it is difficult to specify exactly when salmon fishing began. The first written evidence to suggest that salmon were being caught in reasonable numbers dates back to 1100. However, proper statistics describing the number of salmon caught in the Netherlands at that time are not available. Similarly, few details are to be found about domestic consumption or export. Due to the lack of data, it is impossible to give precise estimates of the number of salmon caught in the Dutch, German, French and Swiss sections of the Rhine basin on an annual basis. The most detailed historical records (1863–1957) that were kept concern the salmon caught in the Dutch part of the Rhine (Fig. 8).

The end of the 1920s witnessed a major decline in salmon catches in the Rhine. In subsequent years, the numbers of salmon landed in the Dutch section was stabilised at about 1000–2000 fish per year, up to 1944. However, these figures would probably have been higher, had organised salmon fishing not ceased in Dutch waters in 1933. To rehabilitate the Rhine salmon population, experiments began as early as 1861 releasing salmon fry which had been reared under controlled conditions. These activities assumed greater importance after the ratification of the Salmon Convention in 1886. Enormous numbers of fry and parr were released into the Rhine at the end of the 19th and the beginning of the 20th centuries. Restocking operations in Switzerland and Germany between 1879 and 1912, to which the Netherlands contributed, involved about 160 million young salmon. In addition, about 13 million young salmon were released into the Rhine in the Netherlands over the period 1861–1897. Throughout the period that serious restocking operations were carried out, most observers were convinced of the positive effect of this policy. It was felt that without such action the decline in salmon numbers would have been even more rapid. However, in 1947, a report on the effect of restocking operations on salmon catches concluded that no clear statistical evidence could be found to support such a link from the available data (de Groot, 1989a, 1992).

A number of factors is hold responsible for the disappearance of the salmon from the Dutch coastal area and the large rivers. De Jonge & de Jong (2002) and Nienhuis et al. (2002) devote an extensive discussion to the anthropogenic disturbances that have led the deterioration of surface waters in the Netherlands. In the following paragraphs, a brief survey will be given of the main factors behind the decline of the once important salmon fishery in the Netherlands.

Canalisation and flood control

The Rhine is basically a glacier stream that receives an important supply of water during the summer months. As a consequence, the difference between seasonal high and low water levels in the Rhine is less marked than in a river fed by rainwater, such as the Meuse. This feature makes the Rhine particularly attractive to shipping. The move towards greater industrialization in the 19th century led to deepening of the navigation channel and, where necessary, the construction of weirs and locks. The fact that canalisation of the Rhine proceeded at a more rapid pace than, for instance, that of the Meuse, reinforced the natural superiority of the Rhine as a major inland shipping route. It is not only the presence of locks and weirs along the Rhine that are preventing the return of salmon. The condition of the many streams and rivulets that traditionally formed the spawning grounds for these fish has also changed by human intervention (van de Ven, 1976). Moreover, simply restoring a few tributaries of the Rhine – which is suggested by certain parties as a potential solution – would not guarantee the return of the salmon on a permanent basis, as a variety of habitats will be required.

At present, the Nieuwe Waterweg offers the only open link with the sea in the Netherlands. However, the intensity of shipping along this route could discourage salmon migration. Since the construction of the 'Afsluitdijk' (Barrier Dam), which closed off the Zuiderzee, salmon have been hampered from using their once traditional route to re-enter the Rhine via the river IJssel. Sluices are not forming an absolute barrier, and a few salmon entered the freshwater via the sluices in the Afsluitdijk and those of the North Sea Canal (IJmuiden) (Larsson, 1984). This was recently demonstrated by the first record of an Arctic charr (*Salvelinus alpinus* Linnaeus, 1758) in the Netherlands. The fish was caught (6-7-1999) in a fykenet near Breezand. The total length was 26.7 cm, the weight: 90 g.

Sand and gravel extraction

Sand and gravel extraction activities in Dutch rivers are not thought to have had a serious impact on salmon stocks, mainly because salmon only pass through the Netherlands, either on their way to the sea as smolts or kelts, or in ascending the river as grilse, 2-sea-winter, or multi-sea-winter salmon. Sand and gravel extraction operations in the smaller German rivers and streams will have had a much more dramatic effect on the salmon population since these areas were historically used as spawning grounds. The increase in silt levels in the river and subsequent sedimentation on the spawning grounds make these spots unsuitable for reproduction purposes.

Waste water discharges

As early as the beginning of this century, discharges of polluted waste water were identified as one of the possible reasons for the decline in the salmon population in the Rhine (Hoek, 1916b). Hoek was convinced that the Rhine, as a large fast-flowing river, would have had an inherent capacity to 'clean itself'. Although large quantities of waste water were discharged into the Rhine, he pointed out that after relatively short distances, the effects were hardy noticeable due to ample dilution. Hoek concluded that: "Although the effects of local pollution on the salmon population of the Rhine should not be ignored, care should be taken not to overestimate the extent of the damage caused". Some 10 years later, Redeke (1927) was requested by the International Council for the Exploration of the Sea to summarize the impact of river pollution on fisheries. In general, it can be said that by 1927 domestic and industrial waste waters were considered to pose a far greater threat to the fish population than had been thought possible less than 25 years before. The number of fish kills had increased dramatically. However, it was often difficult or even impossible to give precise explanations for such events, in spite of the fact that a large number of potential causes could be identified (van Brummelen, 1989).

An exception is the effect of acidity on smolt development. It has been shown that acid (and acid plus aluminium) exposures that have little effect on survival and growth of parr or smolts in freshwater, completely destroy the function of the gill in saltwater (Staurnes et al., 1996). The smolt inhabit the main stream of rivers and estuaries, which are more heavily impacted by pollutants then high elevation tributaries where fry and parr live. Pollutants may also, intervene with the development of olfactory imprinting (Bardach & Case, 1965; Holl, 1965; Bardach, et al., 1965, 1967; Holl et al., 1970).

The impact of the fishing industry on salmon stocks

With the advantage of hindsight, it can clearly be said that the fishing industry has had a negative effect on salmon stocks in the Rhine. However, in the final analysis, economic forces dictate that the fishing industry often can not fish a particular species to extinction. The loss of income as the size of the catch declines can bring such activities to a natural end, as was the case with the Rhine. The Dutch salmon fishing industry effectively ceased to exist after 1933 and that of the Germans after 1950.

Feasibility of restocking operations for salmon

At present, salmon catches in the entire North Atlantic are declining. (1970 – 10 735 ton; 1980 – 10 127 ton; 1990 – 4943 ton; 1995 – 3625 ton; 1996 – 3132 ton; 1997 – 2377 ton; 1998 – 2401 ton; ICES, 1999). Many fisheries, both commercial and recreational, have already been closed. Fishing seasons are shortened, and more and more anglers are returning their caught fish to the river. The situation is quite serious. This is particularly true at the southern limit of the salmon distribution range in Portugal, Spain and the United States e.g. the American Government has decided to list the wild salmon in eight rivers as 'endangered' under the Endangered Species Act (Information NASCO, Edinburgh). The effects of Global Warming become manifest, just as with the cod (*Gadus morhua* Linnaeus, 1758) in the North Sea. Even though a number of excellent salmon rivers are still to be found in countries around or near the North Sea, salmon catches (rod catches) in these rivers are on the decline as well. Salmon culture on the contrary flourishes. In 1998, the production of Norway was 360 536 tons and in Scotland 110 917 tons. If attempts to halt the decline are successful, the purity of the original species will have been affected by interbreeding with non-indigenous or cultivated salmon (Gross, 1998) Experience from France and Spain has shown that eggs recovered from indigenous fish are more suitable for rearing and eventual release than imported eggs from Scotland and Norway. It is, therefore, clear that restocking the tributaries of the Rhine will be a slow and arduous process.

Migration behaviour of stocked fish may also be impaired. It is not clear whether certain smells that are characteristic of the spawning grounds are still discernible to salmon that have passed through rivers rich in detergents (Holl, 1965; Holl et al., 1970). A further complication is that none of the rivers in the vicinity of the Rhine can serve as alternative entry points for salmon returning from sea. Rivers such as the Ems, Weser and Elbe, which once had relatively small salmon populations, now can not be regarded as true salmon rivers. The latter also applies to the Meuse and river Scheldt. Consequently, factors such as straying and infiltration, which play an important role in populating remote rivers, are likely to be of little significance in the Rhine basin.

It should be possible, however, for river systems along the main stream of the Rhine to be recolonized by salmon, and hence to increase the size of the spawning grounds. It is, therefore, essential that a wealth of spawning streams be made available for salmon in the Rhine. However, creating the right conditions is no guarantee of success. Salmon interbreed with trout (Refstie & Gjedrem, 1975), and this may endanger restocking programmes. In 1992, 43% of the salmonid fry in the German river Sieg (Rhine – river system), where a restocking programme was conducted, consisted of hybrids of salmon and trout (Schreiber et al., 1994). A natural hesitation exists to kill the trout in a river system before carrying out restocking with salmon. However this would be the best solution, as trout also prey on salmon. Only when a salmon stock has established itself, trout should be allowed to return.

The limited success of establishing spawning stocks in German tributaries of the river Rhine system by simply releasing fry obtained from all over Europe (Norway, Scotland) might be explained by the work by Youngson & McLaren (1998), who concluded that restocking a river with naturally spawned salmonid ova resulted in a far better survival ratio then using fry from hatchery reared salmonids. If the Rhine is to be rehabilitated as a salmon river, it is essential that the water quality of the river should meet the requirements for salmon rivers as laid down in the relevant EC Directives. Finally, it can be concluded that establishing a natural population of salmon in the Rhine without outside help will certainly not be realized within the foreseeable future (10–20 years). After all, the Rhine is still one of the most polluted rivers in Europe and it suffers from the added disadvantages that it contains a large number of locks and weirs that restrict fish access to traditional habitats.

To conclude

At the end of the 19th century, the once important freshwater fisheries, mostly those on the large rivers forming the Rhine-Meuse estuary, were declining rapidly. The decline in catches of salmon and allis shad became the reason for great concern, but so did the declining catches of far less important species such as sea trout, and the coregonids (houting and whitefish), sturgeon, twaite shad and smelt. The reason for the decline of these species must be found in the rapidly changing abiotic conditions resulting from river regulation works, the construction of numerous barrages and sluice systems to improve shipping on the rivers, dredging away the gravel of the spawning beds, increasing turbidity, and the impact of various chemical pollutants, and changes in oxygen content and temperature. In the early days of the 20th century, it was thought that mass releases of fertilized eggs or juvenile stages would counteract the negative effects of river development. This was unsuccessful in all cases for the salmonids. Restocking the waters with eggs of the allis shad was abandoned after a few experiments. It was never tried to restock the sturgeon in the river Rhine. Hybridisation might also explain anadromous fish disappearance from clean rivers, for example in France. The mixing of salmon escaped from hatcheries with wild salmon, will lead to genetic, behavioural and ecological interactions. As a rule, these interactions are likely to be negative in their effect on the viability of wild populations (Youngson & Verspoor, 1998).

To place much emphasis on recent observations of an odd salmon, houting, whitefish is, in fact, misleading. Many of the declines of anadromous species mentioned above can not be attributed to a single factors, such as the construction of dams, pollution, dewatering of streams or sand and gravel extraction. It is better not to single out a culprit as the reason of decline, as most factors do not act singly, but rather in concert.

References

Anonymous, 1920. Jaarverslag Visscherij inspectie 1919 (4): 77–81 (in Dutch).

Anonymous, 1987. Vervuilde baggerspecie is groot aandachtsgebied van overheid. Land en Water 27: 60–61 (in Dutch).

Anonymous, 1994. Sturgeons, urgent action is needed. IUCN-Vorschlag für die 9 Vertragstaaten konferenz zum Washingtoner Artenschutzübereinkomen – Bundesamt für Naturschutz, 9 August 1994, Bonn: 15pp.

Anonymous, 1998. Vierde Nota Waterhuishouding Regeringsbeslissing Min. Verkeer en Waterstaat, Den Haag: 49–59 (in Dutch).

Barannikova, I. A., 1987. Review of sturgeon farming in the Soviet Union. Vopr. Ichthiol. 27 (5): 735–746.

Bardach, J. E. & J. Case, 1965. Sensory capabilities of the modified fins of squirrel hake (*Urophycis chuss*) and searobins (*Prionotus carolinus* and *P. evolans*). Copeia 1965: 194–206.

Bardach, J. E., M. Fujiya & A. Holl, 1965. Detergents: effects on the chemical senses of the fish *Ictalurus natalis* (le Sueur). Science 148: 1605–1607.

Bardach, J. E., M. Fujiya & A. Holl, 1967. Investigations of external chemoreceptors of fishes. In Hayaski, T. (ed.), Olfaction and Taste. 11th. Proc. Sec. Int. Symp. Tokyo, Sept. 1965. Pergamon Press, Oxford: 647–665.

Billard, R., 1995. Elements sur la biologie des esturgeons. Pêche Marit. 74 (1): 33-47.

Birstein, V. J., 1993. Sturgeons and paddlefishes: threatened fishes in need of conservation. Conserv. Biol. 7: 773–787.

Boisneau, P., C. Mennesson-Boisneau & R. Guyomard, 1992. Electrophoretic identity between allis shad, *Alosa alosa* (L.) and twaite shad, *A. fallax* (Lacépède). J. Fish Biol. 40: 731–738.

Brinkhuizen, D. C., 1989. Ichthyo-archeologisch onderzoek: methoden en toepassing aan de hand van Romeins vismateriaal uit Velsen (Nederland), PhD Thesis University of Groningen: 312 pp. (in Dutch).

Castelnaud, G. & M. Trouvery, 1984. Premiers résultats de trois années de marquage de l'esturgeon *Acipenser sturio* dans le bas estuaire de la Gironde. CEMAGREF/AGEDRA, Etude No. 18–Ser. Esturgeon 2: 1–25.

De Groot, S. J., 1989a. Literature survey into the possibility of restocking the River Rhine and its tributaries with Atlantic Salmon (*Salmo salar*). Publs. Reps. Ecol. Rehab. Rivers Rhine and Meuse 11: 1–56.

De Groot, S. J., 1989b. Literature survey into the possibility of restocking the River Rhine and its tributaries with sea trout (*Salmo trutta trutta*). Reps. Ecol. Rehab. Rivers Rhine and Meuse 12: 1–14.

De Groot, S. J., 1992. Decline and fall of the salmon fisheries in the Netherlands: is restocking the Rhine a reality. Aquaculture. Fish Managem. 23: 253–264.

De Groot, S. J. & H. Nijssen, 1997. The North Sea houting, *Coregonus oxyrinchus*, back in the Netherlands (Pisces, Salmoniformes, Salmonidae). Bull. Zool. Mus. Univ. Amsterdam 16: 21–24.

De Jonge, V. N. & D. J. de Jong, 2002. Ecological restoration in coastal areas in the Netherlands: concepts, dilemmas and some examples. Hydrobiologia 478/Dev. Hydrobiol. 166: 7–28.

Deelder, C. D. L. & A. H. Huussen Jr., 1973. Opmerkingen betreffende de kuilvisserij op de voormalige Zuiderzee, voornamelijk in de zestiende eeuw. Holland 5(5): 221–242 (in Dutch).

Frost, W. E. & M. E. Brown, 1967. The Trout, New Naturalist, vol. 21, London, Collins: 286 pp.

Grøn, P., 1987. Saving the North Sea houting. In: Proc. 5th Int. Wadden Sea Symp. Sept. 29th–Oct. 3rd 1986, Esbjerg, Denmark: 146–159.

Grøn, P., B. Møller. M. B. Nielsen, M. Ejbye-Ernst & L. K. Larsen, 1988. Snaeblen – en truet fiskeart. Ribe Amtsrad, Sonder jylands Amtsrad, Tonder, Ribe: 31 pp.

Gross, M. R., 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. Can. J. Fish. aquat. Sci. 55 (supl. 1): 131–144.

Hartgers, E. M., A. D. Buijse & W. Dekker, 1998. Salmonids and other migratory fish in Lake IJsselmeer Publs. Reps. Ecol. Rehab. Rivers Rhine and Meuse 76: 1–41.

Havinga, B., 1928. De spiering in de Zuiderzee. Meded. Zuiderzee Comm. 1: 1–18 (in Dutch).

Havinga, B., 1954. Vissen. In: de Beaufort, L. F. (ed.), Veranderingen in de Flora en Fauna van de Zuiderzee (thans IJsselmeer) na afsluiting in 1932. Den Helder, Neth. Zool. Soc.: 253–267 (in Dutch).

Hoek, P. P. C., 1893. Über die Meerforelle des Rheingebietes. Z. Fisch. 1: 3–20.

Hoek, P. P. C., 1894. De elft op onze rivieren. Meded. Vissch. 1: 49–54, 65–69, 81–86 (in Dutch).

Hoek, P. P. C., 1899. Neuere Lachs- und Maifish studien. Tijdschr. Ned. Dierk. Ver. 2 Ser. 6: 156–242.

Hoek, P. P. C., 1910. De achteruitgang der steurvisscherij onzer beneden-rivieren. Meded. Vissch. 17: 103–109, 118–124 (in Dutch).
Hoek, P. P. C., 1916a. Rapport over de beteekenis der zalmvisscherÿ op de Maas. In Versl. Staatscomm. Zalmvraagstuk 2: 159–172.
Hoek, P. P. C., 1916b. Rapport over den Rÿn als zalmrivier. In versl. Staatscomm. Zalmvraagstuk 2: 173–238.
Holl, A., 1965. Vital staining by trypan blue: its selectivity for olfactory receptor cells of the brown trout bullhead, *Ictalurus natalis*. Stain Technol. 40: 269–273.
Holl, A., E. Schulte & W. Meinel, 1970. Funktionelle Morphologie des Geruchsorgans und Histologie der Kopfanhänge der Nasenmuräne , *Rhinomuraena ambonesis* (Teleostei, Anguilliformes). Helgoländer. wiss. Meeresunters. 21: 103–125.
ICES, 1999. Report of the Working Group on North Atlantic Salmon. ICES CM 1999/ACFM 14: 1–288.
Jäger, T., 1999. Die Wiedereinbürgerung des Nordseeschnäpels. In: Der Nordseeschnäpel. Offenbach, Verband Deutscher Sportfischer e.V: 3–11.
Jakob, E., 1996. Das Potential des Unteren Niederrheins ab Laich- und Bruthabitat des europaïschen Stör *Acipenser sturio*. Das Land NRW – Landesanstalt für Ökologie, Bodenordnung und Forsten/Landesamt für Agrarordnung NRW, Dezernate für Fischerei, Albaum, Köln: 45 pp.
Kinzelbach, R., 1987. Das ehemalige Vorkommen des Störs, *Acipenser sturio* (Linnaeus, 1758), im Einzugsgebiet des Rheins (Chondrostei: Acipenseridae). Z. angew. Zool. 74: 167–200.
Larsson, P. O., 1984. Remote straying of salmon (*Salmo salar* L.) from the Swedish west coast and possible effects on sea ranching operations. Aquaculture 38: 83–87.
Lelek, A., 1987. The Freshwater Fishes of Europe – Vol. 9. Threatened Fishes of Europe, AULA-Verlag, Wiesbaden: 42–45, 58–61.
Lobregt, P. & J. van Os, 1977. De laatste riviervissers, Heerewaarden: 131 pp. (in Dutch).
Mohr, E., 1941. Stint (*Osmerus artedi*). In Demoll, R. & Maier (eds), Hndb. Binnenfisch. Mitteleuropas: Vol. 3 (7a): 1–11, 504–526.
Mohr, E., 1952. Der Stör: Die neue Brehm-Bücherei. 84. Akad. Verlagsgesellschaft Geest und Portig K.G, Leipzig: 66 pp.
Nienhuis, P. H., A. D. Buijse, R. S. E. W. Leuven, A. J. M. Smits, R. J. W. de Nooij & E. M. Samborska, 2002. Ecological rehabilitation of the lowland basin of the river Rhine (NW Europe). Hydrobiologia 478/Dev. Hydrobiol. 166: 53–72.
Nijssen, H. & S. J. de Groot, 1987. De vissen van Nederland, Kon. Ned. Natuurh. Ver., Publ. 42: 224 pp. (p. 67–68) (in Dutch).
Prummel, W., 1989. Iron Age animal husbandry, hunting, fowling and fishing on Voorne-Putten (the Netherlands) Palaeohistoria 31: 235–265.
Prummel, W., 1991. Kapitel 12- Haus- und Wildtiere, in Starigard/Oldenburg. In Müller-Wille, M. (ed.), Ein slawischer Herrschersitz des frühen Mittelalters in Ostholstein. Karl Wachholtz Verlag, Neumünster: 299–306.
Rameye, L., A. Kiener, C. P. Spillmann & J. Biousse, 1976. Aspects de la biologie de l'alose du Rhône. Pêche et difficultes croissantes de ses migrations. Bull. Fr. Piscic. 49: 50–76.
Redeke, H. C., 1907. De spiering (*Osmerus eperlanus*). In Redeke, H. C. (ed.), Rapport over onderzoekingen betreffende de visscherij in de Zuiderzee ingesteld in de jaren 1905 en 1906. Min. Landbouw, Nijverheid en Hand's. Gravenhage: 79–81 (in Dutch).
Redeke, H. C., 1914. De spiering en de spieringvisscherij. Meded. Vissch. 21: 51–54, 70–74, 83–85 (in Dutch).
Redeke, H. C., 1922. Visschen. In Flora en Fauna der Zuiderzee. Den Helder, Nederlandse Dierkundige Vereeniging: 426–442 (in Dutch).
Redeke, H. C., 1927. River pollution and fisheries. Rapp. P.-v. Reun. Cons. perm. int. Explor. Mer 43: 1–50.
Redeke, H. C., 1934. Über den Rheinschnäpel, *Coregonus oxyrhynchus* L. Verh. int. Ver. Limnol. 6: 352–357.
Redeke, H. C., 1938. Uber den Bastard Clupea alosa finta Hoek. Arch. Néerld. Zool. Suppl. 3: 148–158.
Refstie, T. & T. Gjedrem, 1975. Hybrids between Salmonidae species. Hatchability and growth rate in the freshwater period. Aquaculture 6: 333–342.
Reuter, J. H., 1996. Houdt de houting. Visserij-Nieuws 19: 206–210 (in Dutch).
Rochard, E, G. Castelnaud & M. Lepage, 1990. Sturgeons (Pisces: Acipenseridae); threats and prospects. J. Fish Biol. 37 (Supplement A): 123–132.
Scheffel, H. J., 1999. Biologie des Nordseeschnäpels. In: Der Nordseeschnäpel. Offenbach, Verband Deutscher Sportfischer e.V.: 12–37.
Schreiber, A., M. Schenk, J. Lehmann & F. J. Stürenberg, 1994. Genetische Untersuchungen an Meerforellen- und Lachswildfängen aus dem Rheinsystem in Nordrhein-Westfalen. Fischer und Teichwirt. 2: 52–53.
Shagaeva, V. G., M. P. Nikolskaya, N. V. Akimova, K. P. Markov & N. G. Nikolskaya, 1993. A study of the early ontogeny of Volga sturgeon (Acipenseridae) subjected to human activity, J. Ichthyol. 33(6): 123–141.
Shearer, W. M., 1955. 'Homing Instinct' in Sea Trout. Nature 176: 171–172.
Staurnes, M., F. Kroglund & B. O. Rosseland, 1996. Water quality requirement of Atlantic salmon (*Salmo salar*) in water undergoing acidification or liming in Norway. Wat. Air Soil Poll. 85: 347–352.
Steinert, H., 1951. Kaviar in der Fischkinderklinik? Orion 6 (18): 713–716.
Stuart, T. A., 1953. Spawning migration, reproduction and young stages of Loch Trout (*Salmo trutta* L.) Sci. Invest. Freshw. Fish. Scot. 5: 1–39.
Svárdson, G. & A. Fagerström, 1982. Adoptive differences in the long-distance migration of some trout (*Salmo trutta* L.) stocks. Inst. Freshw. Res. Drottningholm Rep. 60: 51–80.
Thorpe, J. E., 1990. Sea trout: an archetypal life history strategy for *Salmo trutta* L. In Piggins, D. J. & W. M. Shearer (eds), Sea Trout in Scotland. Symp. Scot. Mar. Biol. Ass. Oban, Scotland, June 1987: 1–4.
Van Brummelen, T. C., 1989. Chemicals affecting the spawning migration of anadromous fish by causing avoidance responses or orientational disability, with special reference to concentrations in the River Rhine – Study Institute for Inland Water Management and Waste Water Treatment (BDW/RIZA) – University of Utrecht, Section Aquatic Toxicology: 77 pp.
Van den Ende, W. P., 1847. Eenige bijzonderheden betreffende den spiering op den IJssel. Versl. werkzh. Ver. tot bevord. Inl. Ichthyol. 1: 55–55, 69–76 (in Dutch).
Van de Ven, G. P., 1976. Aan de wieg van de Rijkswaterstaat. Wordingsgeschiedenis van het Pannerdens Kanaal. Walburg Pers, Zutphen: 1–438 (in Dutch).

Verhey, C. J., 1949. Het voorkomen van de steur (*Acipenser sturio* L.) in de Nieuwe Merwede tussen 1900 en 1931. De Levende Natuur 52: 152–159 (in Dutch).

Verhey, C. J., 1961. De vissen en de visvangst. In Verhey, C. J. (ed.), De Biesbosch, land van het levende water. W.J. Thieme, Zutphen: 142–146; 249–250 (in Dutch).

Verhey, C. J., 1963. Het voorkomen van de steur (*Acipenser sturio* L.) in Nederland na 1931. De levende Natuur 66: 15–16 (in Dutch).

Vincent, P. B., 1894. Notes sur l'alose. Bull. Pêche. Marit.: 427–441, 465–477, 525–534.

Volz, J. & S. J. de Groot, 1992. Erster Nachweis des Störs (*Acipenser sturio*) im niederiändischen Rhein seit 40 Jahren. Fischökologie 6: 3–6.

Youngson, A. F. & I. S. MacLaren, 1998. Relocation of naturally spawned salmonid ova as a countermeasure to patchiness in adult distribution at spawning. Scot. Fish. Res. Rep. 61: 12 pp.

Youngson, A. F. & E. Verspoor, 1998. Interactions between wild and introduced Atlantic salmon (*Salmo salar*). Can. J. Fish. aquat. Sci. 55 (suppl. 1): 153–160.