



OSPAR
COMMISSION

*Protecting and conserving the
North-East Atlantic and its resources*

Background Document for Houting - Wadden Sea population of *Coregonus oxyrinchus*



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OSPAR Convention

The Convention for the Protection of the Marine Environment of the North-East Atlantic (the "OSPAR Convention") was opened for signature at the Ministerial Meeting of the former Oslo and Paris Commissions in Paris on 22 September 1992. The Convention entered into force on 25 March 1998. The Contracting Parties are Belgium, Denmark, the European Union, Finland, France, Germany, Iceland, Ireland, Luxembourg, the Netherlands, Norway, Portugal, Spain, Sweden, Switzerland and the United Kingdom.

Convention OSPAR

La Convention pour la protection du milieu marin de l'Atlantique du Nord-Est, dite Convention OSPAR, a été ouverte à la signature à la réunion ministérielle des anciennes Commissions d'Oslo et de Paris, à Paris le 22 septembre 1992. La Convention est entrée en vigueur le 25 mars 1998. Les Parties contractantes sont l'Allemagne, la Belgique, le Danemark, l'Espagne, la Finlande, la France, l'Irlande, l'Islande, le Luxembourg, la Norvège, les Pays-Bas, le Portugal, le Royaume-Uni de Grande Bretagne et d'Irlande du Nord, la Suède, la Suisse et l'Union européenne.

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Background Document for Houting – Wadden Sea population of *Coregonus oxyrinchus*

Executive Summary

This background document on houting, the Wadden Sea population of *Coregonus oxyrinchus*, has been developed by OSPAR following the inclusion of this species on the OSPAR List of threatened and/or declining species and habitats (OSPAR agreement 2008-6). The document provides a compilation of the reviews and assessments that have been prepared concerning the Wadden Sea population of this species since the agreement to include it in the OSPAR List in 2003. The original evaluation used to justify the inclusion of houting in the OSPAR List is here followed by an assessment of the most recent information on key threats included in the background document, which was prepared during 2019. Chapter 7 provides proposals for the actions and measures that could be taken to improve the conservation status of the population. In agreeing to the publication of this document, Contracting Parties have indicated the need to further review these proposals. Publication of this background document does not, therefore, imply any formal endorsement of these proposals by the OSPAR Commission. On the basis of the further review of these proposals, OSPAR will continue its work to ensure the protection of the houting, where necessary in cooperation with other competent organizations. This background document may be updated to reflect further developments or further information on the status of the population as this becomes available.

Récapitulatif

Le présent document de fond sur le Corégone oxyringue, population de la mer des Wadden, a été élaboré par OSPAR à la suite de l'inclusion de cette espèce dans la liste OSPAR des espèces et habitats menacés et/ou en déclin (OSPAR accord 2008-6). Ce document comporte une compilation des revues et des évaluations concernant le Corégone oxyringue (population de la mer des Wadden) qui ont été préparées depuis qu'il a été convenu de l'inclure dans la Liste OSPAR en 2003. L'évaluation d'origine permettant de justifier l'inclusion du Corégone oxyringue dans la Liste OSPAR est suivie d'une évaluation, préparée en 2019, des informations les plus récentes sur les menaces clés contenues dans le document de fond. Le chapitre 7 fournit des propositions d'actions et de mesures qui pourraient être prises afin d'améliorer l'état de conservation de la population de cette espèce. En se mettant d'accord sur la publication de ce document, les Parties contractantes ont indiqué la nécessité de réviser de nouveau ces propositions. La publication de ce document ne signifie pas, par conséquent, que la Commission OSPAR entérine ces propositions de manière formelle. A partir de la nouvelle révision de ces propositions, OSPAR poursuivra ses travaux afin d'assurer la protection du Corégone oxyringue, le cas échéant avec la coopération d'autres organisations compétentes. Ce document de fond pourra être actualisé pour tenir compte de nouvelles avancées ou de nouvelles informations qui deviendront disponibles sur l'état de la population de cette espèce.

Background information

Threat and Link to human activities

Houting are vulnerable to habitat modifications and the obstruction by weirs and barrages across their migratory routes. The mature adult houting enters rivers adjacent to the Wadden Sea area during autumn and probably spawn from mid-November to mid-December. Only rivers with free passage can be used for spawning, as even small weirs and dams block the migration of houting to upriver spawning areas. Fish ladders and small or steep bypass streams do not seem to work for the houting, and there is no evidence of spawning upstream of even small obstacles. Houting are also affected by poor chemical and physical water quality in the spawning habitat. In the Netherlands, a considerable part of the houting population does not migrate between the Wadden Sea and Lake IJsselmeer but stay, spawn and reproduce in Lake IJsselmeer (De Leeuw et al., 2005; Borcharding et al., 2008; Borcharding et al., 2014).

In February-March the eggs hatch and the approx. 10 mm long houting larvae drifts more or less passively down-stream the river system where it enters areas with standing water like flooded meadows, large meanders or lakes, the so-called nursery areas. If nursery areas are not present, the larvae will enter the ocean before being able to survive the high salinity and perish (Jensen et al. 2015).

In the long run most natural stocks are in severe risk of becoming extinct, due to small populations sizes. This might also happen in Germany if stocking programmes are terminated. The large majority of houting in Lake IJsselmeer originates from natural reproduction and not from stocking (Borcharding et al. 2010). There is an urgent need to improve habitat quality of the rivers (e.g. developing and incorporating appropriate measures to mitigate habitat destruction and blocking of migratory routes by weirs and dams). Threats to the successful reintroduction of houting, is the bycatch in static gears e.g. gill nets and traps. Estimations of houting bycatch in the Netherlands (mainly Lake IJsselmeer) are thousands to ten thousands on an annual basis (van Rijssen et al 2019). Until a good scientific reason for the declines are found, stocking may in some form prevent population collapse in German rivers. Also, having more than one viable population is essential as one catastrophic event (e.g. pollution), can wipe out the entire breeding stock.

Relevant human activities from the JAMP List (OSPAR Agreement 2014-2)

- Fisheries
- Coastal defence

Relevant pressures from the JAMP List (OSPAR Agreement 2014-2)

- Barrier to species movement
- Nutrient enrichment
- Organic enrichment
- Introduction or spread of non-indigenous species

A summary of the key activities which can cause impacts on houting carried out in inland waters is given in Table 2.

Table 2: Summary of key threats and impacts to houting

Cause of threat	Type of impact	Comment
Building of weirs and dams at	Obstacles blocking	Features such as weirs and dams may impede migration to spawning grounds. In comparison to many other migratory fish

Cause of threat	Type of impact	Comment
freshwater fish farms and hydroelectric power stations	access to spawning grounds	species, houting seem to be relatively poor at ascending obstacles to migration and are frequently restricted to the lower reaches of rivers.
Loss of suitable habitats and increased water velocity	Habitat modification	Poor physical diversity in the river reduces the area of feasible houting habitat in the rivers and young houting come in risk of being washed out by increased water currents to the sea before osmoregulatory functions adaptations for saltwater are evolved.
Land reclamation	Embankment	Especially in the lower parts of the rivers wetlands and larger areas with stagnant water that are thought to have functioned as "nursery areas" has disappeared due to land reclamation projects. The building of dikes and sluices disturbs natural run-off regime and water exchange with the sea.
Development and navigational maintenance Uses: coastal forestry/farming	Management of aquatic and bank vegetation for drainage purposes	Since it is thought that an important proportion of the life cycle of houtings is spent in wetlands and larger areas with stagnant water in the river, special attention must be paid to these (not normally considered as an important fish habitat). Also, the impact on spawning gravel must be considered when proposing development on a river.
By-catch in gill and fyke nets	Fishery	Probably the most important fishing related mortalities are caused by fish traps in estuarine waters in localities where houting concentrate before their upstream spawning migrations. Although historically the houting has been commercially fished throughout its European range, nowadays it is much reduced (Jensen et al. 2003). Accidental capture during trawling in marine waters seems to be very rare. In the Netherlands, bycatch of houting by gill nets and fykes is estimated to be in the order of 1000s-10,000s mainly caught in Lake IJsselmeer (van Rijssel et al 2019).
Fishfarm and power stations water intake	Juvenile mortality	The newly hatched houting are particularly vulnerable to passage pumps and other moving machinery. At fish farms fry may drift passively into the production ponds where they are eaten by the fish.
Pollution: sewage, pesticides/herbicides, heavy metals, ochre	Poor water quality	Houting need well-oxygenated freshwater in all stages of life.
Maintenance of riverbed, weed cutting	Loss of substrate for spawning	Weed cutting in rivers favours annual water plants like bur-reed <i>Sparganium</i> sp. which withers off in the late autumn instead of perennial winter-green submerged macrophytes. Also maintenance of riverbeds removes suitable substrate like gravel and stone.
Cormorant <i>Phalacrocorax carbo</i>	Predation	Entering of houting into freshwater in autumn coincides with high number of cormorants over-wintering and feeding in freshwaters of northern Europe. In Danish River Vidå, of the total natural mortality of 26%, cormorant predation accounted for at least 30% of this (Jensen et al. 2017). During population counts, more than 20% of the fish have injuries originating from predation

Existing management measures

The houting is listed on Annex IIa and IVa (as *Coregonus oxyrinchus* – anadromous populations in certain sectors of the North Sea) of the EC Habitats Directive and Annex III of the Bern Convention (since 1988). In Denmark the houting has been protected by a total ban on fishing since 1983.

Freyhof & Schöter (2005) claimed that the houting (*Coregonus oxyrinchus*) from the Rhine, Meuse and Scheldt rivers is a different species than that from the Danish Wadden Sea, and based on this was classified as Extinct by IUCN in 2008. They considered the houtings that live today to be a distinct evolutionary unit of the species *C. maraena*, with e.g. special adaptations to high salinity. However, the taxonomy of coregonids to date remains controversial and this view is not widely accepted by other scientists (Hansen *et al.* 2008; Volanthen *et al.* 2012, Winter 2017). Regardless of taxonomic discussions, there is agreement that it represents a unique taxonomic unit that merits consideration as an independent conservation unit (Hansen *et al.* 2008).

In 2005 an ambitious restoration project with a total project budget of 13.4 million euros was initiated in Denmark. The project was co-financed by the EU Life Programme with a grant of 8 million euros. The project focused on addressing the lack of adult upstream passage and lack of juvenile rearing habitat. In Denmark, only a few small-scale hydroelectric power plants block the rivers, but several hundred traditional trout farms are located along the rivers, and use weirs to divert water flow into the production ponds, thus blocking upstream and to some degree downstream migration of most fish species.

The overall project objective was to restore and maintain a favorable conservation status for houting in 4 Danish river systems: Vidaa, Varde, Ribe and Sneum. Weirs and dams have been removed to facilitate up and downstream migration. Two hydroelectric power plants and 11 other weirs at fish farms have been removed. Channelized river sections have been reengineered (e.g. by addition of natural channel elements such as meanders) and supplied with gravel and pebbles, creating new spawning areas. A combination of changes in hydrology and construction works created new flooded nursery areas for fry adjacent to the river. To summarize, the projects that have been carried out are intended to: enable houting to reclaim 120 km of river habitats by the removal of 13 man-made obstacles in 3 river systems; establish 470 ha of new nursery area; re-engineer 21 km of heavily modified river; remove fish farms to improve survival of drifting fry in 75 km of spawning habitat (formerly upstream of the fish farms); and if necessary, use supportive breeding to safeguard the total gene pool and ensure a viable population until it becomes self-sustaining.

The many projects have undoubtedly benefitted the houting, but the effects on population sizes in the different rivers have yet to be seen. Only in River Vidaa, there is still a self-sustaining population, and also in river Ribe there is still some natural reproduction. The latest estimate of the size of the breeding population from Denmark was only around 3.500 fish (Søgaard *et al.* 2015). The reasons for this are uncertain and further research in houting biology and habitat requirements is needed.

However, the project has had a profound and positive effect on numerous other components of the river ecosystems. Other rare species in the rivers have benefitted considerably from the improvements, including otter (*Lutra lutra*), salmon (*Salmo salar*) and sea trout (*Salmo trutta*).

Management needs and actions to be taken by OSPAR

Evidence

Further and more thorough research into the basic biology of the population is recommended. The population in Danish rivers have not responded significantly to the restoration project conducted here – despite removal of e.g. weirs and dams. Only when the biology is more thoroughly investigated new

management plans should be implemented here. It is relevant to investigate exactly where the spawning grounds/nursery areas are in especially River Vidaa, but also other rivers where houting has been reintroduced, and describe them, to find out exactly where the fry takes residence prior to migration to the sea and also telemetry studies of the adults migration could be of great interest, as almost nothing is known about the behaviour and habitat at sea. Further research in adult mortality in the coastal and marine environment, including through fisheries bycatch, is needed. Finally, genetic research could try to resolve the taxonomy; especially it would be of interest to carry out genomic analyses of DNA from the type material of *Coregonus oxyrinchus* to compare with contemporary houting.

Measures

OSPAR could recommend that relevant Contracting Parties (i.e. those having rivers which host or have historically hosted populations of houting) should take into account the need for the protection of the populations in the development and application of river basin management policies and plans with a view to:

Maintaining access to spawning grounds for adults and safe passage for juveniles on the outmigration of houting;

Maintaining the following habitat features in rivers hosting or having historically hosted houting:

- Silt free spawning gravels and areas with perennial winter-green submerged macrophytes to ensure that the eggs do not suffocate;
- Areas of reduced currents/backwaters as these are thought to be the preferred habitat of the juveniles in fresh and estuarine waters;
- Providing special protection including sufficient management (e.g. fisheries regulations to avoid bycatch) to sanctuary areas important for the persistence or recolonization of the population.

Also stocking could be necessary until scientific studies has given a more precise idea of why the diadromous populations in German rivers seem to be unable to survive on its own. In the Netherlands houting populations are self-sustaining and expanding their range, e.g. recently also a spawning run on the River Vecht was discovered.

Awareness raising

OSPAR could communicate the status of houting to stakeholders and other international competent authorities.

Table 3: Summary of key threats and existing protection for houting

Key threats	Encountered in inland waters: habitat alteration, pollution, predation Encountered in marine waters: By-catch in commercial fishing
Relevant Contracting Parties	Denmark, Germany, the Netherlands
Other responsible authorities	European Union
Already protected? Measures adequate?	<p>Habitat Directive Annex IIa and IVa (anadromous populations in certain sectors of the North Sea) Bern Convention Annex III. IUCN Red List Ex (Extinct) – this applies for the original populations houting of the Southern North Sea basin: Schelde, Rhine and Meuse drainages. The Danish houting populations are threatened.</p> <p>The protection is adequate, but unfortunately this is probably not sufficient to save the population in the long run, since numbers seem to drop drastically, when stocking is terminated. More research in the basic biology is needed.</p>

Annex 1. Overview of data and information provided by Contracting Parties

Contracting Party	Feature occurs in CP's Maritime Area	Contribution made to the assessment (e.g. data/information provided)	National reports References or weblinks
Netherlands	Y	Y	<p>Borcherding, J., Pickhardt, C., Winter, H.V., Becker, J.S. 2008. Migration history of North Sea houting (<i>Coregonus oxyrinchus</i> L.) caught in Lake IJsselmeer (The Netherlands) inferred from scale transects of Sr-88 : Ca-44 ratios. <i>Aquatic Sciences</i> 70, 47-56.</p> <p>Borcherding, J., Heynen, M., Jäger-Kleinicke, T. & Winter, H.V., Eckmann R. 2010. Re-establishment of the North Sea houting in the River Rhine. <i>Fish Management Ecology</i> 17: 291-293.</p> <p>Borcherding, J., Breukelaar, A.W., Winter, H. V. & König, U. 2014. Spawning migration and larval drift of anadromous North Sea houting (<i>Coregonus oxyrinchus</i>) in the River IJssel, the Netherlands. <i>Ecology of Freshwater Fish</i> 23: 161-170.</p> <p>Borcherding, J., C. Pickhardt, H.V. Winter & J.S. Becker (2008). Migratory history of North Sea Houting <i>Coregonus oxyrinchus</i> (L.) caught in Lake IJsselmeer (The Netherlands) inferred from scale transects of 88Sr:44Ca ratios. <i>Aquatic Sciences</i> 69: 47-56.</p> <p>De Leeuw, J.J., Tulp, I., de Boois, I.J., van Willigen, J., Westerink, H.J. 2005. Zeldzame vissen in het IJsselmeergebied. Jaarrapport 2007. IMARES rapport C024/07.</p> <p>Winter, H.V. 2017. Taxonomische status van houting in Nederlandse wateren. WUR rapport C115/17.</p>
Germany	Y	Y	<p>Freyhof, J. & Schöter, C. 2005. The houting <i>Coregonus oxyrinchus</i> (L.) (Salmoniformes: Coregonidae), a globally extinct species from the North Sea basin. <i>Journal of Fish Biology</i> 67: 713-729.</p> <p>Brunke, M., Dierking, J. & Eizaguirre, C. 2013: Untersuchungen zur Biologie und Status einer Wandermaräne, dem</p>

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			<p>Nordseeschnäpel. Deutsche Gesellschaft für Limnologie (DGL). Erweiterte Zusammenfassungen der Jahrestagung 2012 (Koblenz), Hardegsen 2013: 185-189.</p> <p>Dierking, J., Phelps, L., Præbel, K., Ramm, G., Prigge, E., Borchering, J., Brunke, M. & Eizaguirre, C. 2014. Anthropogenic hybridization and commercially harvested stationary whitefish taxa (<i>Coregonus</i> spp.). <i>Evolutionary applications</i> 7: 1068-1083.</p>
Denmark	Y	Y	<p>Jensen, A.R., Nielsen, H.T. & Ejbye-Ernst, M. 2003. National management plan for the Houting. Ministry of the Environment, Forest and Nature Agency, County of Southern Jutland and County of Ribe, Ribe.</p> <p>Jepsen, N., Deacon, M. & Koed, A. 2012. Decline of the North Sea Houting: Protective measures for an endangered anadromous fish. <i>Endangered Species Research</i> 16: 77-84.</p> <p>Hansen, M.M., Fraser, D.J., Als, T.D. & Mensberg, K.L.D. 2008: Reproductive isolation, evolutionary distinctiveness and setting conservation priorities: the case of European lake whitefish and the endangered North Sea houting (<i>Coregonus</i> spp.). <i>BMC Evolutionary Biology</i> 8: 137.</p> <p>Søgaard, B., Wind, P., Bladt, J.S., Mikkelsen, P., Wiberg-Larsen, P., Galatius, A. & Teilmann, J. 2015. Arter 2014. NOVANA. Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi. Videnskabelig rapport fra DCE - Nationalt Center for Miljø og Energi nr. 168.</p> <p>Jacobsen, M.W., Hansen, M.M., Orlando, L., Bekkevold, D., Bernatchez, L., Willerslev, E. & Gilbert, T.P. 2012. Mitogenome sequencing reveals shallow evolutionary histories and recent divergence time between morphologically and ecologically distinct European whitefish (<i>Coregonus</i> spp.). <i>Molecular Ecology</i> 21: 2727-2742.</p> <p>Jensen, L.F., Thomsen, D.S., Madsen, S.S., Ejbye-Ernst, M., Poulsen, S.B. & Svendsen, J.C. 2015. Development of salinity tolerance in the endangered anadromous North Sea houting <i>Coregonus oxyrinchus</i>: implications for conservation measures. <i>Endangered Species Research</i> 28: 175-186.</p>

			Jensen, L.F., Rognon, P., Aarestrup, K., Bøttcher, J.W., Pertoldi, C., Thomsen, S.N., Hertz, M., Winde, J. & Svendsen, J.C. 2017. Evidence of cormorant-induced mortality, disparate migration strategies and repeatable circadian rhythm in the endangered North Sea houting (<i>Coregonus oxyrinchus</i>): A telemetry study mapping the postspawning migration. Ecology of Freshwater Fish: 1-14.
<i>Belgium</i>	N	Y	No recent cases of houting reported in Belgium and no new information seems available. Since 2014 houting reappeared in the Scheldt estuary (J.Breine INBO, pers. Comm).
<i>United Kingdom</i>	N	Y	Houting are considered extinct in UK waters (where it most likely has only been observed as a guest). No new information seems available.

Summaries of country-specific information provided

Netherlands: The diadromous populations in the Netherlands (where part of the population remains in Lake IJsselmeer, Borcharding et al 2008) are primarily based on stocking in the German Rhine which ceased in 2006 (Borcharding et al. 2010), where after the populations were self-sustaining through natural reproduction (e.g. Borcharding et al 2014). In the Netherlands, self-sustaining populations of houting are present in Lake IJsselmeer, the lower Rhine branches and more recently also Meuse and probably the Vecht rivers. Of these populations, at least part does not migrate between the Wadden Sea and Lake IJsselmeer but migrates from Lake IJsselmeer to upstream rivers such as the IJssel thereby excluding the saltwater phase in their life cycle (De Leeuw et al 2005, Borcharding et al 2008, Borcharding et al. 2014). There is also evidence of another self-sustaining population in the Dutch Westeinderplassen system (de Bruin et al 2017).

Germany: The population in Germany is primarily based on and sustained by supportive breeding measures although successful natural reproduction has been recorded.

Denmark: In River Vidaa, there is a self-sustaining population, and in river Ribe there is some natural reproduction. The latest estimate of the size of the breeding population from Denmark was only around 3.500 fish (Søgaard et al. 2015). The EU LIFE projects have undoubtedly benefitted the houting, but the positive effects on population sizes in the different rivers are yet to be seen. The reason for this is uncertain and will require further research in houting biology and habitat requirements.

Belgium: No recent cases of houting reported in Belgium and no new information seems available. Since 2014, houting reappeared in the Scheldt estuary as shown by ongoing fish monitoring programmes (J.Breine INBO, pers.comm).

United Kingdom: There is reason to believe that Scottish, Welsh and Northern Irish waters never were part of its range, and most likely houting has only come to the United Kingdom as just a guest. There are no plans to “re-introduce” houting but there is interest in the possibility of seeing whether it recolonises naturally in Southern UK waters, following reintroductions on the continent.

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Annex 3 Other information

Name of species

The taxonomy and nomenclature of the whitefish genus *Coregonus* are complicated and have been debated for centuries. The lack of a general consensus is probably the result of the complicated evolutionary history of the genus, with repeated isolations, ongoing postglacial speciation, phenotypic plasticity and morphological convergence.

Some researchers (mainly fisheries biologists and population biologists, e.g. Evens et al. (2014) and Berg (2012) continue to use the old, conservative names *Coregonus lavaretus* (Linnaeus, 1758) for most European whitefish populations, and most use *Coregonus oxyrinchus* (Linnaeus, 1758) for populations in Wadden Sea rivers and estuaries (e.g. Jacobsen et al. 2012; Jensen et al. 2017) – known as houting or North Sea houting. The extinct populations of houting from rivers Rhine, Schelde and Meuse (Rhine holotype) are by some regarded as a separate species, the original houting, *C. oxyrinchus*. Several ichthyologists have suggested the name *Coregonus maraena* (Bloch, 1779) for most of the regions' *Coregonus* populations including the one still present in the southern North Sea tributaries (Freyhof & Schöter 2005; Kottelat & Freyhof 2007; Kullander & Delling 2012). The name *C. lavaretus* should according to Freyhof & Kottelat (2008a) only be used for the endemic populations in Lakes Bourget (France) and Geneva (Switzerland, France). Instead, they argued that the name *C. maraena* should be used, since the type material for this name is from northern Poland and examined morphological traits do not differ significantly from those in the Wadden Sea population (Freyhof & Schöter 2005). More recent studies have shown that the Danish Wadden Sea houting are not belonging to *C. maraena* (Jakobsen et al. 2012). Therefore, here we follow the nomenclature *C. oxyrinchus* as this has historically been used.

The current Wadden Sea population also known as the North Sea houting (*C. oxyrinchus*) has evolved recently. A recent, as yet unpublished, DNA based estimate of divergence time between houting and other whitefish populations (*C. lavaretus*) estimates that the split happened between 6,000 and 20,000 years ago, which implies that the two species separated either before or in connection with the last glacial retreat and the formation of the Wadden Sea. Previous genetic estimates based on more restricted genetic markers (with lower statistical power and employing more simplified statistical methods) concur with the two species splitting and having been effectively reproductively isolated for several thousand years (Hansen et al. 1999, Hansen et al. 2008, Jakobsen et al. 2012), although estimates of time since species separation were somewhat lower in those studies (~3,000 years). As such, it is one among many recently evolved, unique lineages in *Coregonus* (Hansen et al. 2008). The genetic difference between the Wadden Sea population and other whitefish populations is, however, not at the level typically expected between different species (Hansen 1997, Hansen et al. 2008, Jakobsen et al. 2012).

Analyses based on genetic methods show that houting and whitefish are able to hybridise (mate and produce viable offspring) (Hansen et al. 2008, Dierking et al. 2014). Hybridisation has also been demonstrated between other *Coregonus* species, such as whitefish and vendace (*Coregonus albula*) (Kahilainen et al. 2011) and the species complex seems to be generally capable of hybridisation. However, in *Coregonus*, hybridization is often associated with human interference such as hatchery stocking programmes or non-native introductions (Hansen et al. 2008, Kahilainen et al. 2011, Jakobsen et al. 2012, Dierking et al. 2014, Huuskonen et al. 2017, Feulner et al. 2019) and hybrid populations may not be viable on longer time scales, including in Houting (Dierking et al. 2014).

Morphological analyses have shown, that the current Wadden Sea population does not resemble the type material of the original Rhine holotype *C. oxyrinchus*, as the former has a much lower number of gill-rakers (26-35 vs. 38-46 on the first gill arch), which on the other hand are similar to the counts of other populations of *C. maraena* in the region (Freyhof & Schöter 2005; Jacobsen et al. 2012; Berg 2012). Freyhof & Schöter (2005), who compared these gill racks and snout length between museum specimens of *C. oxyrinchus* from the river Rhine collected in the 1940's and whitefish from outside this area, as well as Danish river Vidå Houting (the Wadden Sea population), then concluded that the holotype Rhine houting was extinct and that

all remaining sea-migrating populations belonged to the species whitefish (*C. lavaretus*). Controversy subsequently arose, because both of the examined traits used to classify species in their study are known to be highly plastic and may not reliably be used to determine species within a phylogenetic species context (Etheridge et al. 2012), including in whitefish (Ostbye et al. 2005). The IUCN nonetheless adopted the conclusion of Freyhof and Schöter that houting is extinct, albeit with the notation “Needs updating”(IUCN 2019). The causes of extinction are not known, but are suspected to be pollution and habitat destruction (Freyhof & Kottelat 2008b, Freyhof & Schöter 2005).

The original Rhine *C. oxyrinchus* lived in estuaries and brackish water in the Southern North Sea basin. Tracking studies have demonstrated that the current Wadden Sea population, in contrast to other whitefish, are capable of migrating under high-salinity conditions (Jensen et al. 2018), and physiological analyses show that juvenile and adults are capable of tolerating much higher salinity conditions than any tested whitefish, including whitefish from brackish populations (Jensen et al. 2015, Hertz et al. *in press*). Although this is not a “character” commonly used in fish taxonomy, it indicates that the Wadden Sea houting is functionally divergent from whitefish. On the other hand, in the Netherlands, a self-sustaining population of houting is present in Lake IJsselmeer, which originates from German restocking programmes. Of this population, a considerable part does not migrate between the Wadden Sea and Lake IJsselmeer but migrates from Lake IJsselmeer upstream to rivers such as the IJssel thereby excluding the saltwater phase in their life cycle (De Leeuw et al., 2005; Borcharding et al., 2008; Borcharding et al., 2014).

A recent study (Mehner et al. 2018) analysed a low number of genetic markers in 14 historical museum specimens of the original Rhine *C. oxyrinchus*, and compared genetic profiles with those of a number of whitefish populations. Samples also represented fish from the German river Treene, which had been stocked using Danish river Vidaa broodstock i.e. presumably representing the contemporary Danish (Wadden Sea) population. Inspection of the museum specimens showed that their gene profiles were not conclusive as to origin, as they generally simultaneously corresponded with multiple whitefish populations. A few specimens showed relatively closest genetic relationship with contemporary river Treene (Wadden Sea population) profiles, in those cases pointing to close genetic relationships between contemporary and historical houting samples. However, due to low statistical power, the results cannot be considered conclusive with regards to taxonomic relationships between houting and whitefish. Nonetheless, genetic marker based analyses are otherwise in full agreement and show that houting with pure (such as in the Danish river Vidaa and Ribe) and mainly-pure (such as re-stocked populations in the German rivers Rhine and Treene) genetic origin, can be identified and distinguished from any other whitefish, including Baltic Sea ‘houting’, with high statistical certainty (Hansen et al. 2008, Dierking et al. 2014, Bekkevold & Hansen 2018).

Determining whether a specific biological unit, such as the Wadden Sea population, is a species can be notoriously difficult, as several different scientific definitions can be adopted to determine what is required to elicit species status. For houting this is further complicated by the houting/whitefish genus *Coregonus* (i.e., group of evolutionary closest related species) showing tremendous ecological, morphological and behavioural variation within and between species, and has for this reason been used as a scientific model for studying speciation processes in real time (Bernatchez et al. 2010).

Although the current Wadden Sea houting population may or may not represent an endemic species, available scientific evidence points to that the Wadden Sea houting displays marked ecological and genetic divergence from whitefish, indicative of important evolutionary adaptations that are unique compared to any whitefish population. Hence, it represents a unique taxonomic unit that merits consideration as an independent conservation unit (Hansen et al. 2008).

Species ecology and breeding ecology

Adult houting reaches a length up to just over 60 cm and weighs between 2.5 and 3 kg with females being the largest. The houting is known to be a multiple spawner, spawning every year from the time they reach maturity. The eggs are small, but the number is high. A mature female houting contains 20.000-30.000 eggs

pr. kilogram bodyweight. Individual marking of adult fish has shown that some females may spawn up to 8-9 times in their lifetime.

The diadromous mature adult houting enters the major rivers adjacent to the Wadden Sea area during autumn and probably spawn from mid-November to mid-December. Only rivers with free passage can be used for spawning, as even small weirs and dams block the migration of houting to upriver spawning areas. Fish ladders and small or steep bypass streams do not seem to work for the houting, and there is no evidence of spawning upstream of even small obstacles.

Most authors mention that the classic spawning grounds is found in the lower or middle part of the watercourses, on stretches with a width of 5-6 meters, good water quality, a reasonable current, a ground substrate consisting of gravel and stone with the occurrence of perennial, wintergreen macrophytes such as the common water-crowfoot. The eggs are spawned freely into the water column and after fertilization they become adhesive and attach themselves to gravel and stone in the bottom or the perennial water plants. In February-March the eggs hatch and the approx. 10 mm long houting larvae drifts more or less passively down-stream the river system where it enters areas with standing water like flooded meadows, large meanders or lakes, the so-called nursery areas. If nursery areas are not present, the larvae will enter the ocean before being able to survive the high salinity and perish (Jensen et al. 2015). Much of this information needs confirmation from scientific investigations.

During the spring months the diadromous houting fry feed on zooplankton e.g. water fleas and in May-June the now 35-55 mm long houting fingerlings leave freshwater and enter the Wadden Sea. Males return for their first spawning after 2-3 years in the sea and female houting have their first spawning season after 3 or most often 4 years in the sea and the life-cycle is completed. Once they reach sexual maturity, houting grow relatively slowly (mean: 2.55 cm yr⁻¹, ranging from 0 to 13.8 cm yr⁻¹) and can reach an age of 10 to 12 yr. Catch-recapture experiments year after year indicates low mortality for adult fish (Jepsen et al. 2012; Jensen et al. 2017).

Population (current trends/future prospects)

When the Danish stocking programme was stopped after 1992 the situation gradually returned to the previous state and has remained stable at low numbers. From 2005 to 2013, large restoration projects were carried out in Danish rivers to improve habitat quality. Other species like salmon and trout has responded positively, but a response in the houting population has yet to be seen. Predation by cormorants *Phalacrocorax carbo* is now considered to be one of the main threats to the population in Danish rivers (Jensen et al. 2017). In the Netherlands, numbers of diadromous houting started to increase during the early 2000s up to 2010 (mainly caught at Kornwerderzand, the sluice between Lake IJsselmeer and the Wadden Sea). From 2010 onwards, there was a decline and numbers seem to be similar as before the 2000s. Monitoring by trawling and gillnets in Lake IJsselmeer showed that the residential houting is being caught on a regular basis, which is also true for the river IJssel (and more recently the river Vecht) where the majority of the Lake IJsselmeer population is believed to spawn.

In the long run most stocks are in severe risk of becoming extinct, due to small populations sizes. This might happen for diadromous populations in Germany if stocking programmes are terminated and to a lesser extent in Dutch rivers where stocking has ceased in 2006 and self-sustaining populations are present. Here, there is an urgent need to improve habitat quality of the rivers (e.g. developing and incorporating appropriate measures to mitigate habitat destruction and blocking of migratory routes by weirs and dams). Threats to the reintroduction of houting, is the bycatch in static gears e.g. gill nets and traps (1,000s-10,000s in the Netherlands, mainly in Lake IJsselmeer (van Rijssel et al. 2019).

Until a good scientific reason for the declines are found, stocking may in some form prevent population collapse in German rivers. Also, having more than one viable population is essential as one catastrophic event (e.g. pollution), can wipe out the entire breeding stock.

Conclusion on overall status

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The houting population in the Wadden Sea is still in severe danger of becoming extinct and remaining stocks are extremely vulnerable. In Denmark, only one viable, self-reproducing stock exists (in River Vidaa, Denmark). Other stocks in Denmark are low in numbers and in severe risk of being unable to survive for the future. Houting stocks in Germany are based on and sustained by supportive breeding measures, although successful natural reproduction has been recorded. The houting in the Netherlands is not supported by stocking which ceased in 2006 and hence, appear to be self-producing. In Netherlands two, possibly three self-reproducing stocks exist (Lake Ijsselmeer, possibly the Westeinderplassen system).



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