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The ecology and fishery of the vendace (*Coregonus albula*) in the Baltic Sea

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Abstract

Brackish water ecosystems often have high primary production, intermediate salinities, and fluctuating physical conditions and therefore provide challenging environments for many of their inhabitants. This is especially true of the Baltic Sea, which is a large body of brackish water under strong anthropogenic influence. One freshwater species that is able to cope under these conditions in the northern Baltic Sea is the vendace (*Coregonus albula*), a small salmonid fish. Here, we review the current knowledge of its ecology and fishery in this brackish water environment. The literature shows that, by competing for resources with other planktivores and being an important prey for a range of larger species, *C. albula* plays a notable role in the northern Baltic Sea ecosystem. It also sustains significant fisheries in the coastal waters of Sweden and Finland. We identify the need to better understand these *C. albula* populations in terms of the predator–prey interactions, distributions of anadromous and sea spawning populations and other putative (eco)morphs, extent of gene exchange between the populations, and effects of climate change on their future. In this regard, we recommend strengthening *C. albula*-related research and management efforts by improved collaboration and coordination between research institutions, other governmental agencies, and fishers, as well as by harmonization of fishery policies across national borders.

KEYWORDS

environmental change, fishing, phenotypic plasticity, population, salinity, Salmonidae

1 | INTRODUCTION TO BRACKISH WATER ENVIRONMENTS

This review covers the current knowledge of the ecology and fishery of a freshwater salmonid fish, the vendace (*Coregonus albula* L. 1758), in the brackish waters of the northern Baltic Sea. We place this topic within a more general framework of fish communities and fisheries in brackish waters, and the challenges that such environments induce to

freshwater fish in general and *C. albula* in particular. The aim is also to elucidate the current state of these *C. albula* populations and their fisheries, and to form predictions about their future by covering relevant literature and official fishery statistics. This information is useful, for example, when deciding on how to adjust management measures in response to the expected environmental changes. For the readers' convenience, we also provide a glossary (Table 1) with explanations of the key terms and geographic areas of this review.

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TABLE 1 Glossary

Anadromous	A fish migrating from the sea to a river to spawn
Baltic Sea	Relatively shallow brackish water sea, a component of the Atlantic Ocean and enclosed by the land masses of Denmark, Estonia, Finland, Germany, Latvia, Lithuania, Poland, Russia, and Sweden
Bothnian Bay	The northernmost part of the Gulf of Bothnia (see below), north of ~63°32'N (Finland) / ~63°59'N (Sweden), see Figure 1
Brackish water	Often defined as water with salinity between 0.5 and 30 ppt
By-catch	Individuals of an aquatic species caught unintentionally while targeting other species or sizes of aquatic wildlife
Coregonid	A fish of the subfamily Coregoninae in the family Salmonidae (see below)
Demersal	Living (or taking place) near the bottom of a body of water
Discard	The part of a catch that is not retained on board during commercial fishing
Eutrophication	The process by which a water body becomes progressively enriched with nutrients, particularly nitrogen and phosphorus, resulting in increased phytoplankton productivity
Fishery	The enterprise of harvesting (or raising) fish and other aquatic life
Gulf of Bothnia	The northernmost part of the Baltic Sea, between ~59°50'N and 65°54'N, consisting of the Bothnian Bay and Bothnian Sea, see Figure 1
Gulf of Finland	The easternmost extension of the Baltic Sea, with Finland to the north, Estonia to the south and Russia to the east, see Figure 1
Hypoxia	The state of a low or depleted oxygen in a water body
ICES Statistical Rectangles	A latitude-longitude based area mapping system that covers the north-east Atlantic, including the Baltic Sea, developed by the International Council for the Exploration of the Sea (ICES)
PSU	Practical Salinity Unit: a standardised way of measuring salinity of a water sample at 15 °C that, under most conditions, is nearly identical with salinity measures 'ppt', '‰' and '0.1‰'
Salmonid	A fish of the family Salmonidae, including trout, chars, whitefishes, graylings, taimens and lenoks
TAC	Total Allowable Catch: a control measure that limits the maximum overall quantity of the catch of one or multiple target species during a set timeframe
Vendace species complex	<i>Coregonus albula</i> and its closest relatives that some authors consider as conspecifics, including <i>C. sardinella</i> , <i>C. vandesius</i> , <i>C. trybomi</i> , <i>C. fontanae</i> and <i>C. lucinensis</i>
Year-class strength	Usually defined as the number of fish spawned or hatched in a given year

Brackish waters are often defined by their medium levels of salinity (Table 1). These aquatic environments can be found around the globe, typically where waters from sources of low and high salinity meet (Elliott & McLusky, 2002; Pérez-Ruzafa, Marcos, Pérez-Ruzafa & Pérez-Marcos, 2011). Such conditions in, for example, river deltas, lagoons, and estuaries, frequently promote high primary productivity (Correll, 1978; Houde & Rutherford, 1993; Pérez-Ruzafa, Marcos & Pérez-Ruzafa, 2011). Indeed, many brackish waters function as nursery areas or otherwise sustain large biomasses of fishes that tolerate their varying environmental conditions (Houde & Rutherford, 1993; Whitfield, 2016), commonly supporting fisheries (Table 1) of high socioeconomic importance (Costanza et al., 1997; Joyeux & Ward, 1998; Lamberth & Turpie, 2003; Pérez-Ruzafa & Marcos, 2012). Nevertheless, only a few species live solely in brackish water environments. Instead, these waters are commonly inhabited by a mix of freshwater, marine, and anadromous (Table 1) taxa and are typically dominated by a low number of species, often of marine origin (Beaudreau et al., 2022; Cabrera-Páez et al., 2021; Dyldin et al., 2020; Thiel et al., 2003; Whitfield, 1999). The abundance and diversity of marine species tend to increase, and those of freshwater species to decrease, along gradients of increasing salinity (Guo et al., 2022; Kindong et al., 2020; Morin et al., 1992; Thiel et al., 1995; Whitfield, 1999).

Because of the pronounced gradients of, and fluctuations in, physical and chemical conditions of brackish waters, they are considered to be naturally highly stressed ecosystems (Elliott & Quintino, 2007; Teichert

et al., 2017). In addition, low average depths and close connectivity to the adjacent terrestrial ecosystems have made many brackish waters and their fish populations vulnerable to over-fishing (Haimovici & Cardoso, 2017; Jackson et al., 2001; Ulman et al., 2020), climate change (Kashkooli et al., 2017; MacKenzie et al., 2007), eutrophication (Karadurmuş & Sari, 2022; Soria et al., 2022; Table 1), pollution (Barletta et al., 2019; Islam & Tanaka, 2004), and species invasions (Daskalov & Mamedov, 2007; Feyrer et al., 2003). These anthropogenic impacts have, in recent decades, resulted in significant declines of economically and ecologically important brackish water fish populations in, for instance, the Black Sea (Demirel et al., 2020; Oguz, 2017), Caspian Sea (Daskalov & Mamedov, 2007), Marmara Sea (Demirel et al., 2022), brackish lakes and lagoons (Haimovici & Cardoso, 2017; Mohanty et al., 2009), and certain major river estuaries (Shan et al., 2013; Zhou et al., 2019). Hence, many of these brackish water areas (and their fisheries) are in urgent need of effective recovery and management plans and actions.

2 | THE BALTIC SEA AS AN ENVIRONMENT FOR FRESHWATER FISH

The Baltic Sea (Figure 1; Table 1) is one of the world's largest brackish water areas, and it shares many challenges with other major brackish water bodies. Notably, it is among the most human-

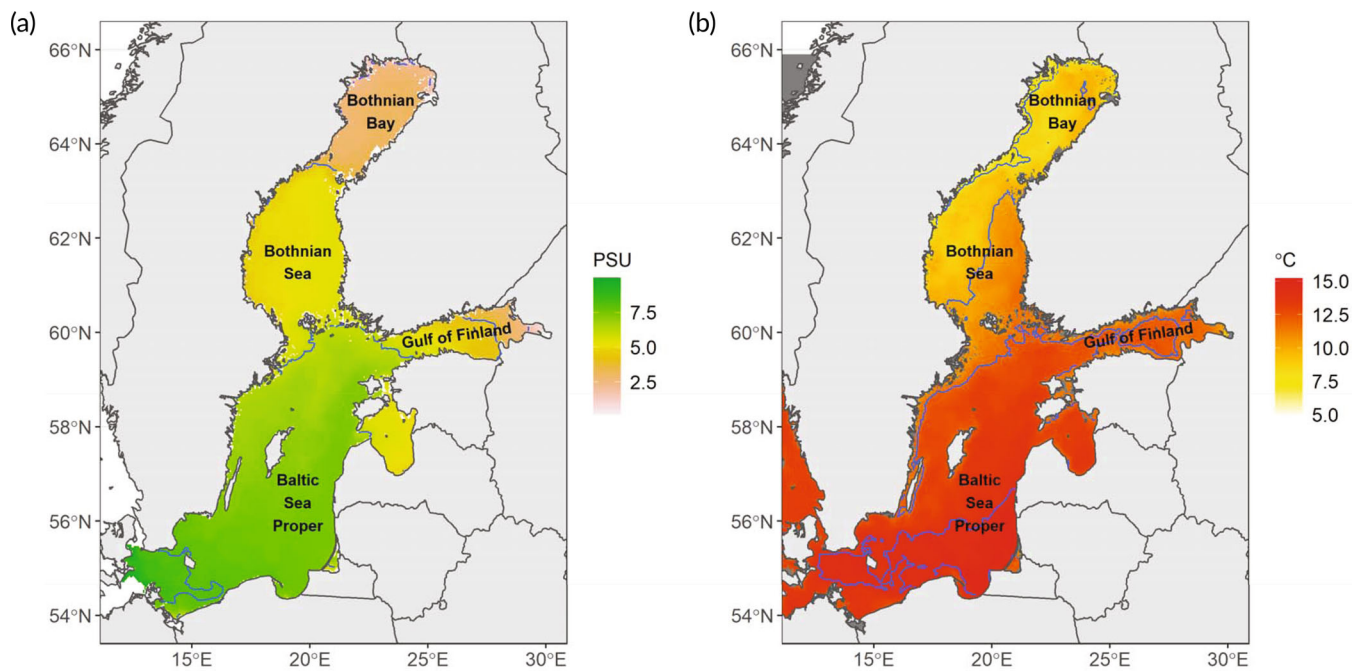


FIGURE 1 (a) October 2021 mean salinity (PSU) in the Baltic Sea. Here, salinity is bounded to ≤ 10 PSU to clarify its gradient. Blue contours highlight salinities of 2, 4, 6, and 8 PSU. (b) October 2021 mean temperature (degrees Celsius) at 1.5 m depth. The contours highlight 8, 10, 12, and 14°C. The different parts of the Baltic Sea, the Baltic Sea Proper in the south, the Gulf of Finland in the east, and the Bothnian Sea and Bothnian Bay in the north (the latter two being collectively called the Gulf of Bothnia) are also shown. The salinity and temperature data originate from the Swedish Meteorological and Hydrological Institute and have been modeled for the entire Baltic Sea by the ice-ocean model NEMO-Nordic (<https://doi.org/10.48670/moi-00013>).

influenced and stressed seas in the world (Aps & Lassen, 2010; Elmgren et al., 2015; Fleming-Lehtinen et al., 2015; Leppäkoski et al., 2002; Möllmann et al., 2009; Viitasalo & Bonsdorff, 2022). It is connected to the marine waters of the North Sea only through relatively narrow and shallow passages at its south-western corner, making it, in essence, a very large estuary, if not for its lack of significant tides (McLusky, 1999; Pérez-Ruzafa, Marcos, Pérez-Ruzafa & Pérez-Marcos, 2011). The influx of marine water to the sea is variable and the overall turnover of its water mass is slow, resulting in a pronounced salinity gradient and challenges related to eutrophication and hypoxic (Table 1) conditions (Fleming-Lehtinen et al., 2015; Viitasalo & Bonsdorff, 2022; Winsor et al., 2001). The salinity of the sea stays mostly below 10 PSU (Table 1) and as low as at 2–3 PSU in the Bothnian Bay and eastern Gulf of Finland (Figure 1; Table 1).

The relatively low and challengingly variable salinity levels of the Baltic Sea have resulted in low species richness, yet a fish fauna that consists of a unique mix of freshwater and marine species (MacKenzie et al., 2007; Ojaveer & Kalejs, 2005; Olsson, 2019). The salinity varies both among and within coastal locations, affecting fish distributions so extensively that general models linking fish species diversity and salinity have been based on the Baltic Sea data (Whitfield et al., 2012). Indeed, many of the Baltic Sea fish populations live at the physiological limit of their range (MacKenzie et al., 2007) and experience multiyear fluctuations in abundance, which are, at least partly, triggered by changes in environmental conditions or competitive interactions (Casini et al., 2009; Lehtonen et al., 1993; MacKenzie et al., 2007; Ojaveer

et al., 2010). Interestingly, despite the young geological age of the Baltic Sea (Björck, 1995), some of its inhabitants show signs of genetic adaptation to its environmental conditions or divergence between populations occupying different parts of the sea (Hill et al., 2019; Johannesson & André, 2006; Leder et al., 2021; Wennerström et al., 2017). For instance, in the southern Baltic Sea, European flounder (*Platichthys flesus* L. 1758) spawn pelagially (Table 1), whereas most of those in the north spawn demersally (Table 1), with the two forms showing a strong enough genetic divergence and reproductive isolation (Momigliano et al., 2017) that the latter was recently described as a separate species, *Platichthys solemdali* (Momigliano, Denys, Jokinen & Merilä 2018).

Besides their intriguing ecological features, Baltic Sea fish populations support several viable fisheries (Aps & Lassen, 2010; MacKenzie et al., 2007; Zeller et al., 2011). The subfamily Coregoninae and other salmonids (Table 1) are one such fish group, which has sustained recreational and commercial fisheries of high socioeconomical importance, while being particularly vulnerable to anthropogenic change (Dahlke et al., 2020; Smialek et al., 2021). The Baltic Sea has both anadromous and resident (i.e., sea spawning) salmonids (in genera *Coregonus*, *Salmo*, and *Thymallus*), most of which have been important targets of fishing for hundreds of years, if not for millennia (Lajus et al., 2013). While these fish have been found to develop local differences in salinity tolerance (Fraser et al., 2011; Larsen et al., 2008), the individuals that live outside their optimal salinity (Arnesen et al., 1993) or temperature (Griffiths et al., 1992) ranges may grow slowly and experience increased mortality.

3 | THE VENDACE IN THE BALTIC SEA

Coregonus albula is a small-sized (total length rarely exceeding 20 cm), schooling planktivore that prefers cold water and matures early (Bøhn et al., 2004; Gregersen et al., 2011; Lehtonen, 1981). Although both juveniles and adults dominantly forage on zooplankton (Northcote & Hammar, 2006; Sandlund, 1992; Viljanen, 1983), their diet is flexible, with adults opportunistically preying on benthic crustaceans, insect larvae, mollusks, and small fish, including conspecifics (Strelnikova & Berezina, 2021; Urpanen et al., 2012). Their typical, but not exclusive, living environments are large oligotrophic lakes in northern Europe,

including parts of Denmark, Estonia, Finland, Germany, Norway, Poland, Russia, and Sweden. Both anadromous (Bogdanov et al., 2021) and sea spawning (Björkvik et al., 2021; Enderlein, 1989; Veneranta et al., 2013) populations reside the low-salinity waters of the northern Baltic Sea (Gulf of Finland and Gulf of Bothnia; Figures 1 and 2). Locally, the species may also be found, or was previously found, in more southern parts of the sea (Lehtonen, 1981; Smitt, 1895). Similarly in lakes and the Baltic Sea, *C. albula* spawn along the shores when the water has cooled in October and November. The eggs then hatch the following spring around the time the ice cover melts (Karjalainen et al., 2016; Koho et al., 1991; Nyberg et al., 2001; Urpanen et al., 2005). The spawning is

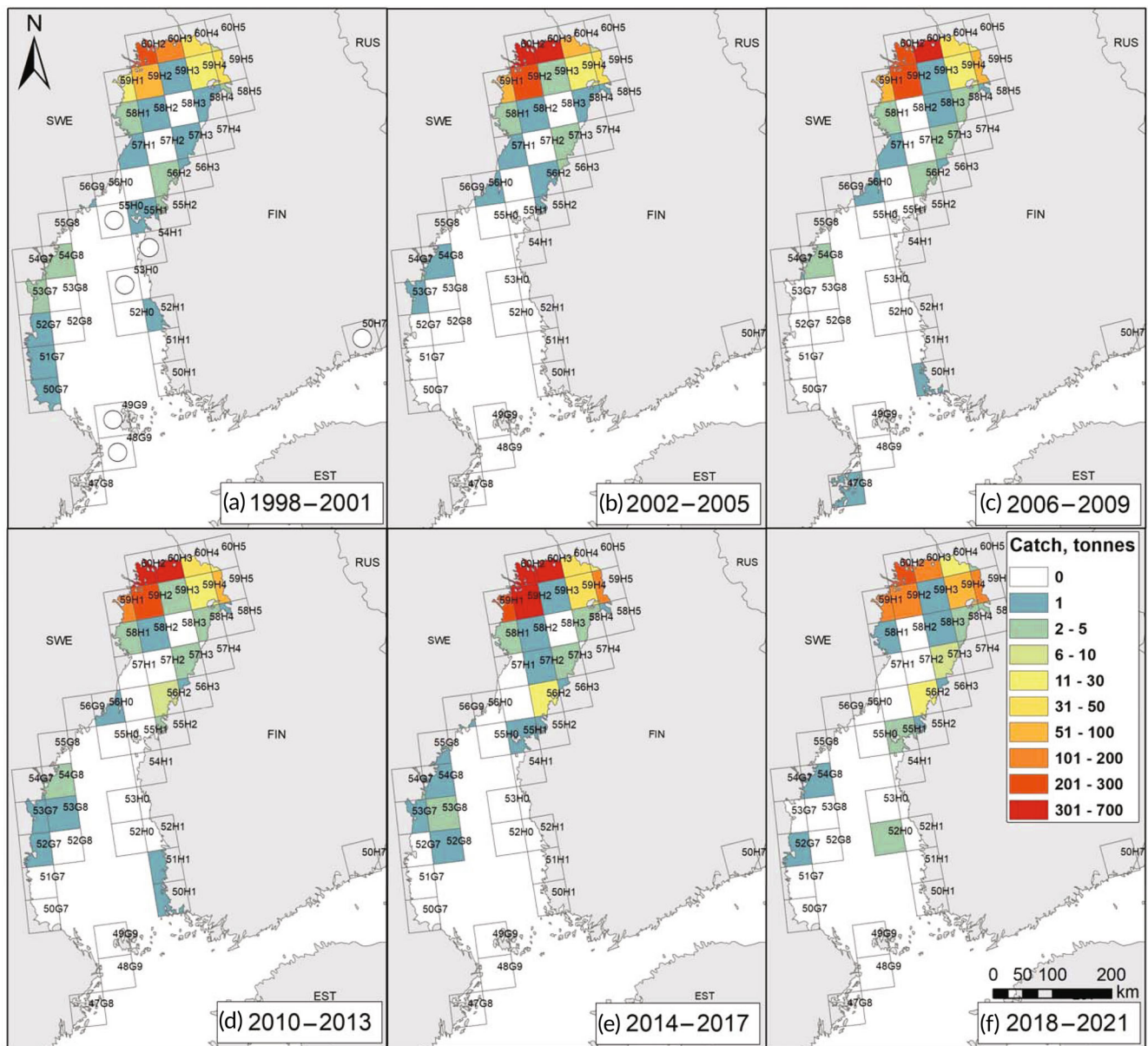


FIGURE 2 *Coregonus albula* catches in different parts of the Swedish and Finnish waters of the Baltic Sea since 1998. (a) 1999–2001 (white dots indicate additional Finnish coastal water areas where *C. albula* were commercially caught in 1980–1997), (b) 2002–2005, (c) 2006–2009, (d) 2010–2013, (e) 2014–2017, and (f) 2018–2021. Colors indicate the yearly average commercial *C. albula* catch within each 50 × 50 km ICES Statistical Rectangle (see Table 1) during the period stated in the panel. Note that in the Swedish fishery, effort and catch regulations (i.e., TAC, see Table 1) affect the catches and therefore they do not necessarily correlate well with the abundance of the species.

not concentrated within particular sites but takes place widely across suitable areas (Björkvik et al., 2021; Karjalainen et al., 2018; Veneranta et al., 2013). In the Bothnian Bay, important sites for reproduction are located in both Swedish and Finnish coastal areas and river mouths, where the fry are likely to remain for the first weeks of their lives after hatching (Veneranta et al., 2013). Tagging experiments conducted in the area suggest that *C. albula* return each year to the same region to spawn, and then during summertime spread around wider areas to feed (Enderlein, 1989). The typical maximum range of these migrations, however, seems to be only tens of kilometers (Enderlein, 1989).

Pronounced variability in year-class strength is typical of *C. albula* populations, both in lakes (Karjalainen et al., 2000; Marjomäki, Auvinen et al., 2021) and the Baltic Sea (Bergenius et al., 2013; Lehtonen, 1981). This variation has been observed both as cyclic fluctuations (Marjomäki, Auvinen et al., 2021) and more irregular alternations between strong and weak year-classes (Axenrot & Degerman, 2016; Sarvala et al., 2020). The postulated drivers of these oscillations include density-dependent survival of the youngest cohort, competition for food between cohorts, as well as other intraspecific interactions (Hamrin & Persson, 1986; Marjomäki Valkeajärvi et al., 2021). However, evidence also suggests that fishing mortality (Sarvala et al., 2020), environmental factors (Auvinen et al., 2004; Marjomäki et al., 2004), and interspecific interactions (see below for details) can markedly affect the variation in population abundance. Significant intraspecific and external factors are not mutually exclusive but can have simultaneous and interacting effects on the pronounced variation in *C. albula* abundance (Axenrot & Degerman, 2016; Bergenius et al., 2013; Helminen & Sarvala, 1994), while high plasticity in growth and fecundity probably dampen these fluctuations in the longer term (Karjalainen et al., 2016).

Being a freshwater species, the spatial range of *C. albula* in the Baltic Sea is presumably restricted by salinity more than any other single factor (Enderlein, 1989; Lehtonen, 1981). Laboratory experiments have shown that larvae are sensitive to salinities exceeding 5 PSU (Jäger et al., 1981). Although larger juveniles and adult fish survive in higher salinities (Jäger et al., 1981), the egg development is likely to require even lower salinities (Veneranta et al., 2013). The presence of additional physiological and ecological factors, such as temperature variation (Bergenius et al., 2013; Nyberg et al., 2001), eutrophication (Veneranta et al., 2013), intense intra- and interspecific competition (Enderlein, 1981; Hansson, 1984), and predation pressure, may also reduce the species' spatial range in the sea. Indeed, these factors, together with the physiological challenges of adapting to salinity, are among the typical limitations to freshwater fish diversity in brackish water environments (Whitfield, 2015).

Despite having only been able to establish within a limited spatial range in the Baltic Sea, *C. albula* exhibits a significant potential to adapt to local conditions. Sympatric forms that occupy different niches with respect to the timing of spawning (Delling & Palm, 2019; Schulz & Freyhof, 2003; Sendek, 2021), spawning migrations (Bogdanov et al., 2021), body size and growth (Reshetnikov et al., 2020; Strelnikova & Berezina, 2021), and diet (Strelnikova & Berezina, 2021) have been documented both in lakes and the Baltic Sea. For example,

Strelnikova and Berezina (2021) reported the existence of small and large-sized *C. albula* forms in the Gulf of Finland, with the latter occupying areas of deeper water. Moreover, while *C. albula* caught in the Gulf of Finland are likely to be predominantly anadromous (Bogdanov et al., 2021), those spawning in coastal waters seem to be dominating in the Gulf of Bothnia (Enderlein, 1989; López et al., 2022; Veneranta et al., 2013). However, significant genetic differences between fish from different parts of the Bothnian Bay indicate the potential presence of local anadromous *C. albula*, besides coastal spawners (López et al., 2022). The occurrence of newly hatched *C. albula* fry in the lower reaches of the river Tornionjoki that runs into the northernmost part of the Bothnian Bay (Natural Resources Institute Finland, unpublished data) could also indicate the presence of anadromous spawners in that river.

While the coastal spawners on the Swedish and Finnish sides of the bay may be demographically separated (López et al., 2022), current knowledge of population boundaries and spawning migrations is very limited and, as such, insufficient for the needs of knowledge-based management plans. Therefore, additional spatial and temporal sampling coverage is needed to better understand the distributions of separate *C. albula* (sub)populations and the extent of gene exchange between them. Interestingly, another species in the *C. albula* species complex (Mehner et al., 2021; Sendek et al., 2013; Sendek, 2021; Table 1), the closely related least cisco (*Coregonus sardinella* Valenciennes 1848), which inhabits many North American and Siberian freshwaters, can successfully occupy estuary waters of varying salinities up to 32 PSU (Craig, 1984). The populations assigned to each of these two *Coregonus* species are not monophyletic and are so much alike that some researchers argue that they constitute just one species (Borovikova et al., 2013; Borovikova & Artamonova, 2021), further suggesting a high potential for significant population-specific local adaptations within the *C. albula* species complex (potentially including the Baltic Sea populations). After having been introduced, *C. albula* have also been able to rapidly invade new northern European river and lake systems (Amundsen et al., 1999; Bøhn & Amundsen, 2001; Kahilainen et al., 2011).

Coregonus albula is an important node in the Baltic Sea food web because of its interactions with other species (and their fisheries). It competes with other planktivores (e.g., young whitefish, *Coregonus lavaretus* L. 1758, Baltic herring, *Clupea harengus* L. 1758, and smelt, *Osmerus eperlanus* L. 1758) for food, with such competitive interactions having potential to significantly affect the condition, and even survival, of both *C. albula* and its competitors, especially during periods of low food availability (Bøhn et al., 2008; Bøhn & Amundsen, 2001; Enderlein, 1981; Hamrin & Persson, 1986; Nyberg et al., 2001). Occasionally planktivorous fish (Miller et al., 1988), including *C. albula* (Strelnikova & Berezina, 2021), can also be significant predators of fish fry, which may, at least locally, affect the levels of recruitment. Moreover, *C. albula* is an important prey of commercially important predatory fish, including larger salmonids (Heikinheimo, 2001; Hyvärinen & Huusko, 2005), and therefore, when high in abundance, it has a positive effect on the survival of these culturally and economically important species in the northern Baltic Sea (Kallio-Nyberg et al., 2006). In the Gulf of Bothnia, it is also prey to

gray seals (*Halichoerus grypus* Fabricius 1791) (Suuronen & Lehtonen, 2012) and ringed seals (*Pusa hispida* Schreber 1775) (Kauhala et al., 2019; Suuronen & Lehtonen, 2012). Indeed, in the Baltic Sea, predation on *C. albula* by ringed seals can exceed the fishery catches, potentially having a significant impact on the *C. albula* populations (Gilljam et al., unpublished; Hansson et al., 2018). Predation by the European perch (*Perca fluviatilis* L. 1758) is also intense enough to impact fluctuations of *C. albula* populations at least in a lake environment (Valkeajärvi & Marjomäki, 2004) and given that this predator is predicted to benefit from climate change (Jeppesen et al., 2012; Kokkonen et al., 2019) and has been increasing in commercial catches (Official Statistics of Finland, 2023), its impact on *C. albula* in the Baltic Sea may increase in the future. In contrast, if future trends also include a continued decrease in salinity, *Clupea harengus* is likely to be negatively affected (Polte et al., 2021), which can release additional ecological space for *C. albula*.

4 | VENDACE FISHERIES IN THE BALTIC SEA

4.1 | History of vendace fisheries in the Baltic Sea

Although relatively old records of *C. albula* fishery in the Baltic Sea's brackish waters exist, the records are patchier than, for example, those of the congeneric *C. lavaretus* (Bogdanov et al., 2021). The reasons for the patchiness relate to a lower market value and extensive abundance variations of *C. albula* (Bogdanov et al., 2021). Records nevertheless show that it was a significant target species in the eastern Gulf of Finland in the 19th century (Bogdanov et al., 2021; Lajus et al., 2013). Later, by the 1930s, this *C. albula* fishery had been considerably reduced, presumably due to a decreased abundance, as a result of (natural) changes in environmental variables, especially temperature and salinity (Lajus et al., 2013). Starting from the latter part of the 1940s, the importance of the *C. albula* fishery in the eastern Gulf of Finland once again grew, with the Russian catches in this area being as high as 1000 tonnes by the late 1950s (Bogdanov et al., 2021; Lajus et al., 2013). The catches were still at a relatively high level in the early 1970s, but have since then much decreased, probably reflecting another period of a lower abundance due to both anthropogenic pressures and natural changes in local conditions (Bogdanov et al., 2021; Lajus et al., 2015).

Coregonus albula has, for decades, also been one of the most important target species of commercial fisheries in the Gulf of Bothnia in Sweden (Axenrot, 2021; Bergenius et al., 2018; Björkvik et al., 2020) and Finland (Lehtonen, 1981; Official Statistics of Finland, 2023). The utilization of these northern stocks increased rapidly with the use of commercial trawls, starting at the beginning and end of the 1960s in Sweden (Enderlein, 1978) and Finland (Lehtonen, 1981, 1983), respectively. The catches first peaked in the early 1970s (Bothnian Bay: >1500 tonnes per year; Figure 3) and then decreased, especially in Finland (Hildén et al., 1984; Lehtonen & Jokikokko, 1995; Figure 3). Anecdotal reports (Lehtonen, 1981) suggest that during this

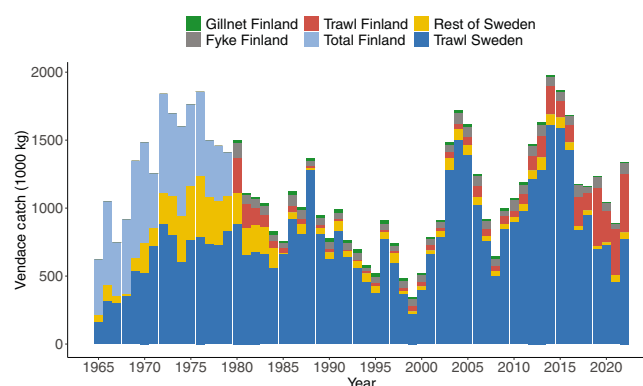


FIGURE 3 *Coregonus albula* catches from the Gulf of Bothnia. Total Finland data (1965–1979) are based on Lehtonen and Jokikokko (1995). The 1980–2022 Finnish data are according to the Official Statistics of Finland (2023). The Swedish data are according to Lövgren et al. (2022).

peak period the species was more widely distributed and harvested in Finnish coastal waters than it has been since then. In Sweden, the *C. albula* catches have remained at relatively high, albeit variable, levels during most of the past 50 years (Figure 3), sustaining an economically important fishery for roe (Bergenius et al., 2018; Björkvik et al., 2020).

4.2 | The current status of the Baltic Sea vendace fisheries

In recent years, *C. albula* catches in the Russian part of the Gulf of Finland have stayed at relatively stable but low (~10 tonnes) levels (Bogdanov et al., 2021). On the Finnish side of the gulf, the commercial fishing effort has in recent decades been between low and non-existent (Figure 2). In the Gulf of Bothnia, in turn, the current *C. albula* fisheries operate mostly north of the N 63° latitude (Figures 1 and 2). On the Swedish side of the Gulf of Bothnia, the catches reached almost 1700 tonnes in 2014–2015, which is the highest since modern fishery started, but have decreased to less than 1000 tonnes during the last few years (Bergenius, 2021; Figure 3). Catches in Sweden have been intense enough to have a measurable effect on *C. albula* recruitment, yet the impact of fishing on the population has been smaller than that of the winter water temperature and salinity combined (Bergenius et al., 2013). On the Finnish side, the commercial *C. albula* catches have recently been increasing, reaching the highest level since the 1970s, >500 tonnes, in 2022 (Figure 3).

In recent decades, trawling has been by far the most important fishing method used by commercial *C. albula* fisheries in the northern Baltic Sea (Finland ~75%, Sweden ~95%), followed by fish traps (fyke nets) and gillnets (Figure 3). Gillnets dominate recreational *C. albula* catches (>95% in Finland, Official Statistics of Finland, 2023). In Sweden, *C. albula* are caught mainly for their highly valued roe, and only a small proportion of the catch is consumed as fish meat. In particular, after roe extraction, the remaining fish carcasses are either burned or used as animal feed. In Finland, the catch is used in a large part for human

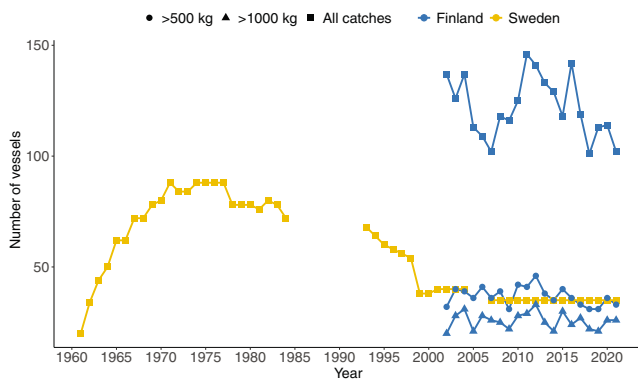


FIGURE 4 Approximate number of active vessels fishing for *Coregonus albula*. The Swedish vessel numbers are based on the licenses for a 5-week *C. albula* fishing season in Bothnian Bay. In Finland, the number of vessels is not restricted. The three Finnish datasets are for vessels with any reported commercial *C. albula* catches (including also small side catches when mainly targeting other species) any time of the year anywhere on the Finnish coast (squares), vessels with annual *C. albula* catches exceeding 500 kg (circles), and vessels with catches exceeding 1000 kg (triangles). The Finnish vessels are relatively small, with 89% and 3% of those reporting *C. albula* catches in 2021 being <10m and >14 m, respectively (Statistics Database Natural Resources Institute Finland, 2023).

consumption as fish meat and increasingly also for roe and animal feed. The current Baltic Sea *C. albula* fishery in Sweden is restricted to 40 trawl fishing licenses (Figure 4) and a fishing period of 5 weeks prior to the spawning peaking in October. In addition, the Swedish Agency for Marine and Water Management sets an annual catch quota after considering the biological advice provided by the Swedish University of Agricultural Sciences (Bergenijs, 2021). Swedish gear restrictions to the Baltic Sea *C. albula* fishery include a trawl modification requirement, which prevents the catching of too-small individuals, and the size of trawling vessels is limited to a maximum of 14 m. The allowed fishing area is also restricted. Parallel with these general regulations, self-regulation, such as additional area and time restrictions, is also encouraged. In contrast, in the Finnish waters of the Baltic Sea, the *C. albula* fishing effort is currently not regulated. The profitability of the Finnish *C. albula* fishery has had an increasing trend (Official Statistics of Finland, 2023), while the highest trawling effort to date was reached in 2022 (Figure 5). Overall, a relatively large number of small vessels participate in the Finnish fishery (Figure 4). The recreational *C. albula* fishery in the Baltic Sea is important only locally, being much smaller than the one in freshwaters (in recent years in Finland <50 tonnes per year versus 700–2500 tonnes, respectively; Official Statistics of Finland, 2023). Note that the official catch statistics, reported above and in Figures 2–6, are based on obligatory monthly catch reports by commercial fishers. The fishers are required to report, among other things, the gear they used, date and hours of fishing, fishing area (ICES Statistical Rectangle, see Table 1) and the catch per species in kilograms. Data on recreational catches are gathered less systematically and their estimates are therefore more tentative. In absolute terms, the official statistics may underestimate actual catches or have other inaccuracies, if the

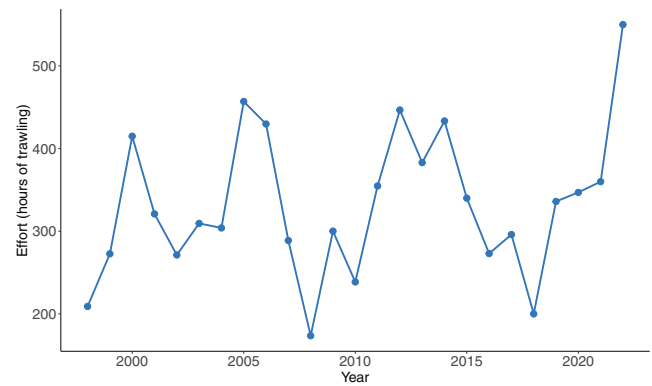


FIGURE 5 Yearly fishing effort of commercial *Coregonus albula* trawlers in Finnish coastal waters in 1998–2022 (Statistics Database Natural Resources Institute Finland, 2023). Note the scale of the y-axis.

catches are not duly reported by all fishers. We nevertheless expect the statistics to capture temporal and other relative changes reasonably accurately.

Regarding the ecological effects of the current fishery, it is also relevant to consider the by-catch (Table 1), especially that of commercial trawling (Figure 6), which is a key concern in fisheries management and policy (Davies et al., 2009; Kennelly & Broadhurst, 2021). The numbers of anadromous or sea-spawning ecotypes of *C. lavaretus* caught as a by-catch of *C. albula* trawling can, at least occasionally, be significant, warranting further assessment and monitoring (Leskelä & Lehtonen, 1992; Marjomäki et al., 2016). Young individuals of other larger species may also get caught by *C. albula* trawls (Jurvelius et al., 2000). For example, sea trout (*Salmo trutta* L. 1758) smolts, especially those that are reared in hatcheries to boost the threatened populations of the Baltic Sea catchment area, may be vulnerable to fishing practices that target other coastal species, including the sprat (*Sprattus sprattus* L. 1758) and *C. harengus* (Degerman et al., 2012; Kallio-Nyberg et al., 2007). Nevertheless, trout smolt mortality due to the current commercial *C. albula* fishery seems to be low (Statistics Database Natural Resources Finland, 2023; Figure 6). By-catch and discard (Table 1) issues aside, as a fishing method, bottom trawling can be very destructive to benthic habitats (Hiddink et al., 2017; Thrush & Dayton, 2002). *Coregonus albula* fisheries, however, typically use trawls over rocky habitats within restricted areas.

4.3 | The future of the Baltic Sea vendace

In the future, increasing temperatures in the Baltic Sea region are likely to be particularly challenging to cold-adapted species, such as *C. albula* and other native salmonids (Elliott & Bell, 2011; Graham & Harrod, 2009; Karjalainen et al., 2014; Kumar et al., 2013). It is possible, albeit not certain, that the salinity of the Baltic Sea surface waters will continue its recent declining trend with the warming climate (Lehmann et al., 2022), which would stress the ecosystem (Lehmann et al., 2022), but potentially benefit some freshwater species,

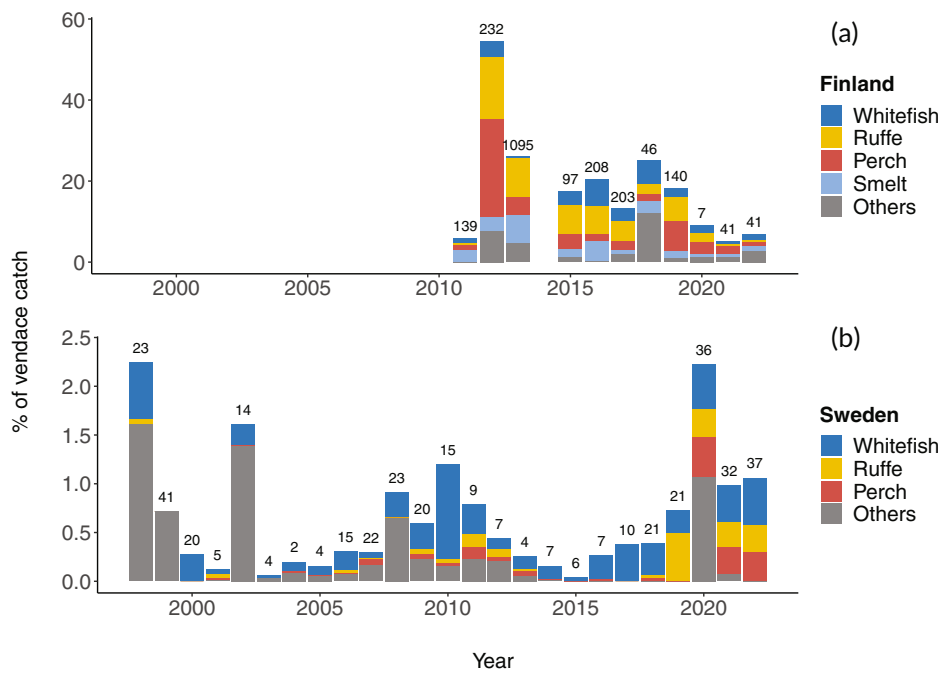


FIGURE 6 By-catches of the *Coregonus albula* fishery in (a) Finland and (b) Sweden. The percentage of the most important by-catch species compared to the catch of the target species *C. albula*. 'Others' refers to all other species. The percentages for the most important by-catch, the Baltic herring (*Clupea harengus*), are given as numbers above the bars. Note that for some fishers, especially in Finland, the herring catches were a desired by-product when *C. albula* was reported as the main target species. The Finnish by-catch data are based on limited samples of the *C. albula* fishery. The Swedish data are based on the trawl fishery, which constitutes over 95% of the total *C. albula* catch. Note the very different scales for Finland and Sweden.

including *C. albula* (Pekcan-Hekim et al., 2016). However, because the whole food web would be affected (Lehmann et al., 2022; Pekcan-Hekim et al., 2016) and the projections for the changes in salinity, stratification, and oxygen levels remain uncertain (Lehmann et al., 2022; Viitasalo & Bonsdorff, 2022), the consequences for future aquatic communities and their fish populations cannot be predicted with any high level of certainty (Viitasalo & Bonsdorff, 2022). Because *C. albula* populations in the Gulf of Bothnia and Gulf of Finland live at the margin of their distributions, the increasing environmental variation may well impact them more (either positively or negatively) than many other fish populations (Bergenius et al., 2013; Pekcan-Hekim et al., 2016). Given these uncertainties, and the demonstrated effects of environmental factors and fishing effort on *C. albula* recruitment (Bergenius et al., 2013; Huusko & Hyvärinen, 2005), future management measures should be set with caution to ensure that *C. albula* catches stay within sustainable levels. In this respect, fish populations are oblivious to national boundaries, highlighting the value of collaboration between neighboring countries in research and management efforts. This is especially important given that the current knowledge of the population structure of the Baltic Sea *Cor. albula*, including the extent of gene exchange between the Finnish and the Swedish parts of the Bay, is incomplete (López et al., 2022).

5 | CONCLUSIONS AND RECOMMENDATIONS

Our literature review shows that the fish fauna in the brackish waters of the Baltic Sea are vulnerable to human impact, including eutrophication, increasing temperatures (which could be coupled with decreasing salinity), overexploitation, and habitat degradation (Elmgren et al., 2015; MacKenzie et al., 2007; Viitasalo & Bonsdorff, 2022).

Commercially important species in the Baltic Sea include both anadromous and resident salmonids. One of these, *C. albula*, occupies the least saline parts of the Baltic Sea. While the species' distribution is limited by salinity in combination with other factors (Bergenius et al., 2013; Jäger et al., 1981), it also exhibits remarkable local adaptations and even sympatric forms that occupy slightly different niches (Reshetnikov et al., 2020; Strelnikova & Berezina, 2021). The vendace fishery is economically important on the Swedish side of the Bothnian Bay, recovering on the Finnish side (Figures 2 and 3), and much smaller in volume and predominantly recreational in the Gulf of Finland. Since projections of future changes to the Baltic Sea area are considerably uncertain, research efforts are needed to ensure appropriately adjusted fisheries management measures.

Another pertinent research need is to understand the extent to which the *C. albula* populations in the Baltic Sea (Gulf of Bothnia and Gulf of Finland) are able to exchange genes with the adjacent freshwater populations, especially given that, in most rivers, dams block access to the sea. In the same vein, we endorse unraveling the extent to which the different *C. albula* populations migrate to rivers to reproduce (i.e., are anadromous) versus completing their entire life cycle in the sea. The two life-history strategies can be expected to differ in the likelihood of gene exchange with other populations in the Baltic Sea and the adjacent freshwaters. More investigations are also needed on the extent to which the *C. albula* fisheries of the different nations surrounding the Gulf of Bothnia and Gulf of Finland are targeting shared versus separate breeding populations (see López et al., 2022). Earlier work assumed that the Swedish coast of the Bothnian Bay would be a significant source for adult *C. albula* on the Finnish side (Hildén et al., 1984), whereas a subsequent tagging assessment suggested more localized breeding populations (Enderlein, 1989). Further research is still needed to map the coastal spawning areas, as well as levels of philopatry and gene exchange by distance. Indeed, the current knowledge of the

species' population genetic structure in the Baltic Sea is still at best patchy, despite the importance of such knowledge for informed management and sustainable harvesting actions (Allendorf et al., 2008; Laikre et al., 2005; Palsbøll et al., 2007; Wennerström et al., 2013). The effects of the Bothnian Bay's planned wind power plant structures on the *C. albula* and its fishery represent a related, timely knowledge gap.

Research, management, and policy-making parties should also take into account that *C. albula* does not face environmental changes in isolation but instead in interaction with other species and, in many cases, their fisheries. In this regard, we endorse further research on by-catches of the Baltic Sea fisheries. The research efforts could, for instance, focus on whether *C. lavaretus* by-catches of the *C. albula* fisheries are substantial enough to negatively affect the various *C. lavaretus* populations and what practices could be adopted to further reduce by-catch levels and mitigate their effects. Such assessments should also be a part of the qualification process of sustainable fishery certifications (Agnew, 2019; Björkvik et al., 2020; Pappila & Tynkkynen, 2022; Pierucci et al., 2022). More generally, we need a better understanding of the relative impacts of the changing climate, eutrophication, habitat degradation, and fishing mortality. To attain these research and management goals, we encourage intensified collaboration and coordination efforts between fishers, research institutions, fisheries management, and other governmental agencies, as well as harmonization of fishery policies among the countries surrounding the northern Baltic Sea.

AUTHOR CONTRIBUTIONS

Topi K. Lehtonen conceived the study and wrote the first draft of the manuscript. David Gilljam, Lari Veneranta, and Topi K. Lehtonen designed the visualizations. All authors provided edits and additions to the manuscript. All authors reviewed and accepted its final version.

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