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Challenges in mixed-stock fishery management: The case of the European whitefish in Kvarken, northern Baltic Sea

Topi K. Lehtonen^{a,*,1} , Lari Veneranta^{b,2}, Oliver Bitz^{c,3}, Daniel Fischer^{c,4}, Miika Tapio^c, Tuomas Leinonen^{d,5}

^a Natural Resources Institute Finland, Oulu, Finland

^b Natural Resources Institute Finland, Vaasa, Finland

^c Natural Resources Institute Finland, Jokioinen, Finland

^d Natural Resources Institute Finland, Helsinki, Finland

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ABSTRACT

Fisheries management units—i.e. 'stocks'—frequently match poorly with biological variation. This mismatch poses a management challenge particularly when within-species units differ in their resilience to harvesting. It is therefore essential to both identify the distinct biological units and adjust fishing pressure accordingly. In the northern Baltic Sea, the European whitefish (*Coregonus lavaretus*) has two ecotypes, anadromous and sea-spawning, harvested primarily with gillnets. The former is endangered due to river connectivity issues and fishing pressure, while the latter is faring better. However, the key elements of effective management, accurate stock component identification and stock-component-specific fishing pressure adjustment, have not been assessed in this mixed-stock fishery. To address this knowledge gap, we compared ecotype identification methods and examined how fishing depth, season, and gillnet mesh size influence the whitefish catch composition. First, we assessed how well the ecotypes could be identified using phenotypic traits (gill rakers and growth) and genetic data (SNP genotyping). While both approaches were useful, many individuals exhibited intermediate characteristics and were not reliably identified, with phenotypic and genetic identification approaches agreeing only moderately. The prevalence of individuals with intermediate traits may reflect past stocking practices, habitat degradation, or inherently inconsistent homing behaviour. Nevertheless, we caught a higher share of sea-spawner-like individuals from deeper waters, earlier in the season, and with gillnets of smaller mesh size. The fact that it was possible to markedly affect the catch composition suggests that spatial and temporal fishing regulations have potential in the management of whitefish mixed-stock fisheries.

1. Introduction

In fisheries, a management unit, commonly referred to as a 'stock', is typically treated as a large, homogeneously distributed population, which is typically defined by administrative or political boundaries rather than real biological units (Stephenson, 1999; Reiss et al., 2009; Svedäng et al., 2010; Cadrin, 2020; Lindegren et al., 2022). This common approach is problematic because many commercially exploited fish

species exhibit substantial genetic, morphological, behavioural, or life-history variation across various spatial and temporal scales (Hilborn et al., 2003; Schindler et al., 2010; Benson et al., 2015). When such biological diversity is overlooked in fisheries assessment or management decisions, some intraspecific units, such as distinct populations or ecotypes, may become overexploited, even if the overall species-level fishing pressure seems sustainable (Hilborn et al., 2003; Sterner, 2007; Cope and Punt, 2011; Ciannelli et al., 2013; Kerr et al., 2017). Indeed,

* Correspondence to: Topi K. Lehtonen, Paavo Havaksen tie 3, Oulu 90570, Finland.

E-mail address: topi.lehtonen@luke.fi (T.K. Lehtonen).

¹ <https://orcid.org/0000-0002-1372-9509>

² <https://orcid.org/0000-0001-5074-0822>

³ <https://orcid.org/0009-0003-4572-3448>

⁴ <https://orcid.org/0000-0002-7513-683X>

⁵ <https://orcid.org/0000-0002-3328-229X>

intraspecific units may differ in their sensitivity to fishing pressure or changes in environmental conditions (Morrongiello et al., 2014; Momigliano et al., 2019; Villanueva et al., 2022), and sometimes the sustainability of a fishery may depend less on the total abundance of the target species and more on the ability of the fishery management to adjust to the variable needs of different within-species components (Benson et al., 2015; Hilborn et al., 2015). Hence, the presence of biologically distinct within-species units represents a challenge for effective management and conservation of fish species under fishing pressure.

Given these challenges, reliably identifying the different within-species components in catches is often a necessary step toward implementation of appropriate management measures. Traditionally, such identification has relied on external tags (Hall, 2014; Vollset et al., 2020) or morphological traits (Campana and Casselman, 1993; Rawat et al., 2017), and more recently increasingly also on life-history-related chemical signatures (Kerr and Campana, 2014; Tzadik et al., 2017; Walther, 2019) and genetic data (Bernatchez et al., 2017; Dahle et al., 2018; Quintela et al., 2020). However, some of these methods are effective only when the stock components correspond closely to reproductively relatively isolated units (Waples and Gaggiotti, 2006), which

is not always the case. Another key challenge in fisheries management is to determine appropriate spatial boundaries for management efforts and to account for ecological heterogeneity within these areas; like many other biological processes, fish movement patterns and spatial orientation can vary substantially over time and space (Hilborn et al., 2020; Bekkevold et al., 2023; Cadrin et al., 2023).

These mixed-stock fishery challenges are relevant in the case of the two ecotypes of the European whitefish (*Coregonus lavaretus*, also known as *C. maraena*), hereafter simply 'whitefish', in the Baltic Sea. Individuals of the anadromous ecotype undertake long feeding migrations that can span several hundreds of kilometres, before returning to spawn, typically in the same coastal river from which they originated (Lehtonen, 1981; Lehtonen and Himberg, 1992; Leskelä et al., 2002; Aronsuu and Huhmarniemi, 2004). Individuals originating from (or restocked into) the rivers of the northernmost part of the Baltic Sea, the Bothnian Bay (Fig. 1), have been recorded feeding as far south as the waters around Åland Island and the central Baltic Sea coast of Sweden (Lehtonen and Himberg, 1992; Leskelä et al., 2002; Hägerstrand et al., 2017). Because whitefish are targeted by both commercial and recreational fisheries throughout the coasts of Finland, anadromous

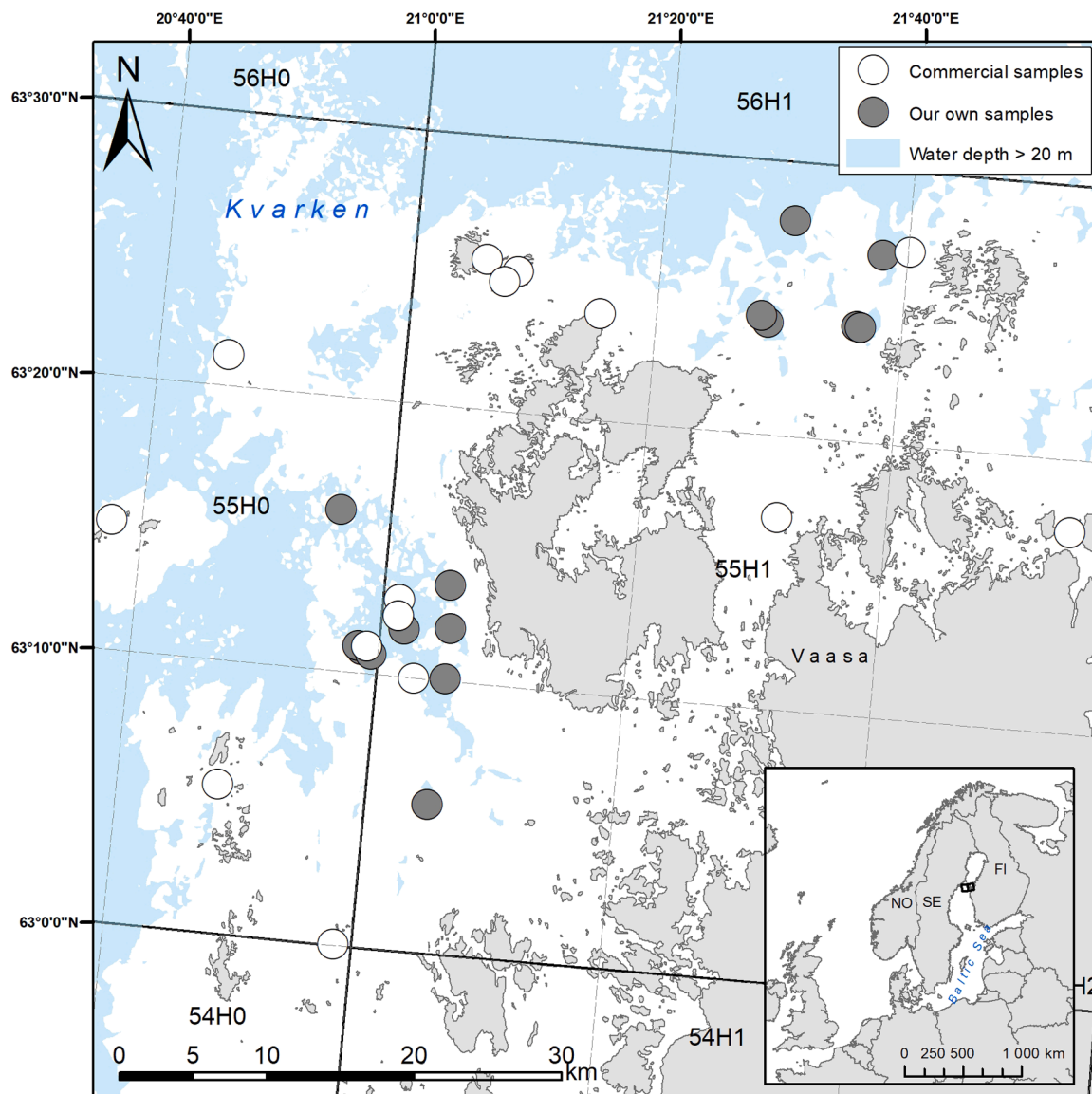


Fig. 1. Study area in Kvarken, northern Baltic Sea. Circles indicate the sites from which we obtained samples for the study. We obtained our own catch samples from 12 sampling trips, in 3 of which we had gillnets in two adjacent sites, resulting in 15 grey circles.

individuals caught in a given area, for example the Kvarken region (Fig. 1), may originate from nearby rivers or from rivers located significantly farther away. The other ecotype, sea-spawning whitefish, inhabits the same coastal waters, but it typically exhibits more limited movement patterns along the coast (Lehtonen, 1981; Lehtonen and Himberg, 1992), potentially forming distinct (sub)populations in different parts of it. As a result, catches from any given coastal area may consist of individuals from multiple populations and both ecotypes.

The reproduction of anadromous individuals has been severely compromised by anthropogenic changes to river environments; the vast majority of Finnish coastal rivers have been dammed, resulting in very low levels of natural, unassisted reproduction (Leskelä et al., 1991; Jokikokko and Huhmarniemi, 1998; Finnäs et al., 2020). As a consequence, the anadromous ecotype is currently classified as endangered both nationally (Urho et al., 2019) and at the level of the Baltic Sea (HELCOM, 2025). To compensate for some of the impacts of the river construction, extensive restocking programmes have been implemented for decades, so that the disrupted life cycle is artificially completed in hatcheries (Jokikokko and Huhmarniemi, 1998, 2014; Jokikokko et al., 2007). These practices rely primarily on broodfish captured downstream of river dams, meaning that these fish have been subject to natural selection during their feeding migration. In the Gulf of Bothnia, ~7 million one-summer-old juveniles and ~30 million newly hatched larvae are released annually (ICES, 2018). Such restocking practices have been considered to provide reasonably good returns relative to their costs, in terms of sustaining the fishery (Leskelä et al., 2004). In the Kvarken region (Fig. 1), whitefish restocking has involved both migratory whitefish and a local subpopulation of relatively fast-growing sea-spawning whitefish (Veneranta and Harjunpää, 2021). However, the number of individuals released in the region has not been particularly high, ~0.1 million one-summer-old juveniles per year.

Despite the disconcerting conservation status of the anadromous ecotype, restocking efforts to boost its numbers have enabled the whitefish to remain one of the commercially most important fish species along the Finnish coast. In recent decades, however, both annual stocking rates and coastal whitefish catches have been declining (Larsson et al., 2013; Jokikokko and Huhmarniemi, 2014; Verliin et al., 2013; Berkström et al., 2021). In fact, commercial catches in coastal areas have recently dropped to their lowest levels since the start of the detailed catch records, i.e. the year 1980 (Fig. 2). In addition to the decline in natural reproduction and reduction in stocking efforts, other contributing factors are likely to include environmental changes, declining fisher numbers, and intensifying conflicts between fisheries and quickly recovering seal populations (Anneville et al., 2015; Berkström et al., 2021; Veneranta et al., 2021; Suuronen et al., 2023). Fishing pressure also continues to have a significant effect on whitefish populations, particularly when fishing-related mortality is biased

towards anadromous individuals before they have had a chance to return to their natal river to spawn (Heikinheimo and Mikkola, 2004; Jokikokko et al., 2007; Kallio-Nyberg et al., 2019; Berkström et al., 2021). In that regard, the gillnet-dominated commercial and recreational fisheries target larger individuals in relatively shallow waters (<10 m), which are thought to be predominantly of the anadromous ecotype (Leskelä et al., 2002; Kallio-Nyberg et al., 2019).

While coastal waters are also subject to anthropogenic pressures, natural reproduction of the sea-spawning ecotype, which is sometimes considered a distinct subspecies or species *C. widegreni* (Lehtonen, 1981; Mehner et al., 2018; Kallio-Nyberg et al., 2019; HELCOM, 2025), takes place in areas with a sufficiently clean seabed (Veneranta et al., 2013). This ecotype is nationally classified as vulnerable rather than endangered (Urho et al., 2019). Its current fishing pressure is assumed to be sustainable, as judged for instance by the presence of healthy numbers of old individuals in catches (Veneranta et al., 2021). Therefore, presuming that whitefish harvesting continues, the fishery would probably be more sustainable if, in addition to any overall reductions in effort, fishing pressure were shifted from the endangered anadromous ecotype toward the sea-spawning ecotype, which has locally healthy populations despite the vulnerable status at the scale of the entire Finnish coast. Consequently, there has recently been a growing interest in managing the coastal mixed-stock whitefish fishery in a way that reduces fishing pressure on the endangered anadromous ecotype, while maintaining reasonable catches but with a considerably higher share of the less threatened sea-spawning ecotype. However, achieving such a management goal presents two key challenges typical of mixed-stock fisheries: first, how to reliably identify the different stock components (here: ecotypes), and second, how to implement effective measures that alter catch composition in the desired fashion.

We set out to address these two general challenges in mixed-stock fisheries management—which also represent key knowledge gaps for the Baltic Sea whitefish fishery—by focusing on the Kvarken region in the northern Baltic Sea (Fig. 1). Of these, our main objective was to assess the identification of the two ecotypes that are difficult to distinguish reliably by their appearance. Sea-spawning whitefish typically grow more slowly and attain a smaller size at any given age than anadromous whitefish (Lehtonen, 1981; Kallio-Nyberg et al., 2019; Veneranta et al., 2021). Differences in size and growth have therefore been used in identification of the ecotypes (Lehtonen, 1981; Kallio-Nyberg et al., 2019), while the traditional default method has been based on gill raker counts (Lehtonen, 1981; Himberg et al., 2015). The gill raker number has been linked to ecological differentiation in coregonids, with lower counts generally associated with a more benthic life style and diet (Amundsen et al., 2004; Kahilainen et al., 2011). This is also true for the two northern Baltic Sea ecotypes, with reported mean gill raker numbers of ~27 for the sea-spawning and ~30 for the anadromous ecotype (Lehtonen, 1981; Himberg et al., 2015). However, the distributions are known to substantially overlap between the two ecotypes (Lehtonen, 1981; Himberg et al., 2015), which limits the reliability of this trait alone as an individual-level ecotype identification method. Consequently, there is a clear need for additional identification approaches, such as genetic methods. Previous studies from more southern Baltic Sea coastal areas have reported very low genetic differentiation between the two ecotypes, albeit with potential for ecotype identification (Ozerov et al., 2015, 2016). Thus far, these methods have not been applied in the context of management efforts in the northern Baltic Sea whitefish fishery.

Accordingly, we evaluated the utility of phenotypic traits (gill raker counts and length-at-age) and a genetic approach (Single nucleotide polymorphism markers, hereafter ‘SNP’) for distinguishing between the anadromous and sea-spawning ecotypes. Regarding the latter, given the ecologically relevant phenotypic differences between the two Baltic Sea whitefish ecotypes (growth, size, and gill raker number), we sought to identify genetic markers that could be linked to ecotype identity. To this end, we first used double-digest Restriction site Associated DNA

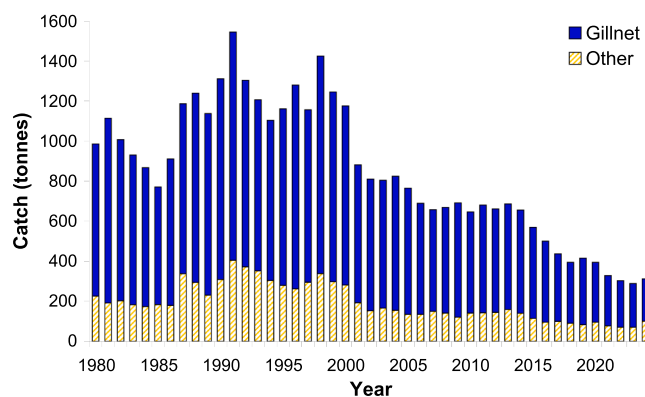


Fig. 2. Commercial European whitefish catches in Finnish coastal waters. The ‘other’ category includes all other fishing gears besides gillnets. The anadromous and sea-spawning ecotypes are not differentiated in the catch statistics.

(ddRAD) sequencing to identify SNPs that differed between the ecotypes. We then used these discriminating SNPs to construct a genetic baseline comprising populations representing the two Baltic Sea ecotypes, which we subsequently applied to estimate the ecotype composition of whitefish catches from the Kvarken region. In addition, we investigated whether (or not) this mixed-stock fishery could be managed using seasonal, fishing depth, or gillnet mesh size adjustments so that the catch composition would shift toward the sea-spawning ecotype.

2. Methods

2.1. Sample collection and variables of interest

We collected whitefish catch samples during the open water season (May–November) of 2023 in the Kvarken area, Finnish coast of the Baltic Sea (between 63°N and 63.5°N), within ICES rectangles 55H0 and 55H1 (Fig. 1). The 27 catch samples came from two different sources. In 15 cases, we bought a commercial whitefish fisher's entire gillnet catch, or a catch subsample that represented all of the nets they had used that day ($N = 795$ whitefish individuals). In addition, we conducted 12 gillnet fishing trips, which boosted whitefish catch coverage from deeper water areas, most of which were not commonly targeted by the commercial fishery ($N = 369$ whitefish). Each whitefish individual provided the following information: total length (mm), weight (g), gill raker count, sex, maturity class (1–8), catch sample ID, date of capture, geographic coordinates (WGS 84) of the fishing site, fishing depth (m), length of the fishing period (i.e. the time the nets were in water), gillnet length, gillnet height, and mesh size (as bar length, measured knot-to-knot). We also collected otoliths that were later used for assessing each individual's age in years and scales for extracting DNA for genetic analyses (see below for details).

In recent decades, the local whitefish fishery has mostly targeted whitefish in relatively shallow (<5 m) water using gillnets, typically with mesh sizes of ~40 mm (bar length). In addition to these typical commercial catches, we requested, for the benefit of the current study, fishers to target also deeper water areas, resulting in 5 out of the 15 commercial catches being from 20 m or deeper (Table 1). The commercial fishers used nets with the mesh size of either 40 mm or 43 mm (Table 1). Regarding the additional 12 fishing trips that the Institute of Natural Resources Finland conducted to collect additional data, we always had gillnets of three different mesh sizes: 38 mm, 40 mm, and 45 mm. The total length of the 40 mm nets was, during all fishing trips, considerably higher than that of the other two mesh sizes (Table 1). All these additional catches were from deeper water (19–30 m; Table 1) over soft seabed substrate, on which whitefish are, based on the local knowledge of fishers, assumed to forage on the benthic amphipod *Monoporeia affinis*, similarly to for instance *C. clupearformis* foraging on *Diporeia* deep water amphipods in the North American Great Lakes (Rennie et al., 2009).

Our first task was to identify the ecotypes of the whitefish in the catches. We used three different approaches, two phenotypic and one genetic.

2.2. Phenotypic identification

We focused on gill raker number and length-at-age (growth) as phenotypic traits, because these have previously been associated with ecotype identity (Lehtonen, 1981; Himberg et al., 2015; Kallio-Nyberg et al., 2019). Of the 1164 whitefish individuals in our samples, 5 had damaged gills and another 4 were missing readable otolith samples (used in the age assessment), leaving 1155 individuals with complete phenotypic data. We took two separate phenotypic approaches to identify the ecotypes.

First, we drew upon previous reports showing that the sea-spawning ecotype typically has fewer gill rakers (~27) than the anadromous (~30) ecotype (Lehtonen, 1981; Himberg et al., 2015), and that the

Table 1

The whitefish catch samples collected during the study (in 2023). Mesh size refers to the gillnet's bar length (measured knot-to-knot), net length indicates the overall length of gillnets used at the fishing site, and fishing depth represents the average depth at the site where the nests were set.

Date	Mesh size (mm)	Gillnet length (m)	Fishing depth (m)	# of whitefish
May 14	43	1050	2	48
June 6	40	180	4	50
June 19	40	2430	26	50
June 27	40	5100	26	81
June 28	43	180	4	49
July 11	40	2700	11	59
July 31	40	2700	25	47
August 4	38, 40, 45	360, 1680, 360	19–22	5, 8, 0
August 10	38, 40, 45	360, 1680, 360	24–28	40, 34, 0
August 23	38, 40, 45	360, 1680, 360	22–26	30, 27, 2
August 23	40	900	3	50
September 3	40	990	3	44
September 8	38, 40, 45	360, 1680, 360	24	13, 42, 1
September 10	40	750	3	49
September 11	40	1350	25	50
September 15	38, 40, 45	360, 1680, 360	21	6, 25, 3
September 18	38, 40, 45	360, 1680, 360	24	7, 22, 3
September 18	40	900	3	49
September 24	38, 40, 45	360, 1680, 360	21	4, 6, 0
October 3	38, 40, 45	360, 1620, 360	30	4, 21, 0
October 3	40	1500	20	52
October 4	38, 40, 45	360, 1620, 360	23	1, 19, 4
October 9	38, 40, 45	360, 1620, 360	24	3, 19, 0
October 10	38, 40, 45	360, 1620, 360	22	2, 0, 0
October 17	38, 40, 45	360, 1620, 360	19	3, 15, 0
October 21	40	1200	3	66
November 8	40	2400	16	52

anadromous ecotype generally grows faster and attains a larger size at a given age (Lehtonen, 1981; Kallio-Nyberg et al., 2019; Veneranta et al., 2021). Here, we considered gill raker numbers below 27 as a strong indicator towards the sea-spawning ecotype, 27–28 gill rakes as a weak indication towards sea-spawning ecotype, 29–30 gill rakers as a weak indication towards the anadromous ecotype, and gill raker numbers over 30 as a strong indication of the anadromous ecotype. We also drew upon the putative difference in the ecotypes' growth, with cut-off assignment values suggested by Lehtonen (1981), originally for whitefish in Finnish coastal waters (Pori region) ~200 km south of the current study area. The cut-off values were the following: 315 mm at 3 years, 345 mm at 4 years, 385 mm at 5 years, 400 mm at 6 years, 440 mm at 7 years, 480 mm at 8 years, and 500 mm at 10 years, with individuals shorter than the cut-off identified as the sea-spawning ecotype and longer ones as the anadromous ecotype (Lehtonen, 1981). We subjectively considered a divergence of > 10 % from each cut-off value as a strong enough signal of the ecotype identity that it overruled a weak gill raker evidence (as detailed above), due to the reported overlap in gill raker numbers between the ecotypes (Lehtonen, 1981; Himberg et al., 2015). In other cases of conflicting evidence regarding the two phenotypic traits, we were not confident to categorise the individual to either ecotype, and we considered it as 'unidentified'.

Second, we applied a mixture distribution approach that enabled automated categorisation of individuals into two distinct stock components based on gill raker counts and length-at-age data. No confidence threshold was imposed, and all 1155 individuals were therefore allocated to one of the two stock components (i.e. ecotypes).

2.3. Genetic identification

For genetic identification of the two ecotypes, we used 66 SNP (single nucleotide polymorphism) markers. These specific SNP markers were chosen and developed from a pool of 5951 SNPs obtained through Genotyping-by-Sequencing (GBS) of 690 individuals that represented the six whitefish ecotypes (Svärdson, 1979) occurring in Finland (Table S1). Four of these ecotypes are found exclusively in freshwater, whereas the two assessed here, the anadromous and sea-spawning ecotype, inhabit the Baltic Sea. At this stage, we included all six ecotypes, because the ecological traits that distinguish them (growth, adult size, gill raker number) are shared between inland waters and the Baltic Sea. The GBS approach utilised double-digest Restriction-site Associated DNA (ddRAD) sequencing, as described in detail in Supplementary material. We excluded markers with missing 10 % genotypes overall or 35 % within a population, as well as those where F_{IT} deviated more than 2.5 standard deviations from the mean. We used differentiation (based on fixation index and PCA) and diversity measures to generate several shortlists of SNP candidates for testing. These shortlists were iteratively used to include and exclude markers in the candidate list, using five-fold cross-validation resampling and prioritising markers, with consistent improvement to genetic assignment of whitefish genotypes (see below). Limited success in transitioning the shortlisted 107 markers into routine genotyping reduced the number of markers used in subsequent stages.

To produce a genetic baseline against which to compare the catch samples, a total of 217 anadromous and sea-spawning whitefish from 15 populations were genotyped with the chosen 66 SNPs using Fluidigm EPI (Standard BioTools Inc.). These samples included the anadromous and sea-spawning whitefish used in the GBS and samples from an additional four anadromous and eight sea-spawning populations. Further details on the calibration of the genotypic assignment are provided in the Supplementary material. Of the 1155 phenotypically assessed individuals in the catch samples, 527 were also genotyped, and their ecotype was determined by comparing their genotype to the genetic baseline. This subset was deliberately selected to include an increased proportion of phenotypically unidentified individuals (i.e. not successfully assigned by phenotypic cut-off values) and to represent five complete catch samples (i.e. fishing trips).

2.4. Catch ecotype composition, catch size and whitefish body size

Once individuals had been assigned both phenotypically and (a subset) genotypically, we assessed the extent to which the mixed stock whitefish fishery could be shifted toward the sea-spawning ecotype and away from the more endangered anadromous ecotype by adjusting fishing season, depth, and gillnet mesh size. We also assessed overall catch, as most fishers' (economic) interests relate more directly to their total catch (per unit effort) than to ecotype composition. Although larger whitefish are economically more valuable, the mesh sizes used in this study restricted the size range, and we approximated catch as the number of whitefish individuals. Finally, we examined how body size of the caught whitefish was influenced by the fishing variables of interest, season, depth, and mesh size.

2.5. Statistical analyses

We performed all statistical analyses in R 4.2.2 (<https://www.r-project.org/>) using the *mclust* v. 6.1.2 (Scrucca et al., 2023), *adegenet* v. 2.1.10 (Jombart, 2008; Jombart and Ahmed, 2011), *rubias* v. 0.3.4 (Moran and Anderson, 2019), and *glmmTMB* v.1.1.4 (Brooks et al., 2022) analysis packages. These were used to assign the individuals to ecotypes using phenotypic traits and genotypes, as well as to assess the composition and size of whitefish catches, as detailed below.

To assign individuals into two distinct stock components (here: ecotypes) based on gill raker counts and growth per year, we used two approaches. First, we assigned individuals manually using literature-

based cut-off values. Second, we applied mixture modelling using the *mclust* package (Scrucca et al., 2023), in which we defined the number of subpopulations as two. Besides these two phenotypic approaches, we also used a genotypic assignment approach. Here, we first trialled combining phenotypic assignment with genetic classification of phenotypically unidentified individuals and constructed calibration curves, which we compared with the posterior probabilities obtained from discriminant analysis of principal components (hereafter DAPC). The calibration curves closely matched the DAPC posterior probabilities (see Supplementary material for details). We therefore proceeded with assessing the anadromous and sea-spawning ecotypes in the reference data with the DAPC and Bayesian genetic stock identification (hereafter GSI), as implemented in the *adegenet* 2.1.11 (Jombart, 2008; Jombart and Ahmed, 2011) and *rubias* packages (Moran and Anderson, 2019), respectively. In DAPC, individual posterior probabilities for assigning individual fish as the sea-spawning ecotype were based on clustering with the ecotypes in the reference populations. The ecotype population clusters were identified using hierarchical complete-linkage clustering, excluding three populations (Supplementary material), in which the genetic clustering disagreed with phenotypic population assignment. These populations spawn in estuaries and are intermediate in their life history and ecotype characteristics. Clustering was performed using correlation-derived distances based on Euclidean distances, which allowed us to slightly emphasise the co-variation of the distances, rather than their absolute values, thus increasing the weight of diagnostic markers. The posterior probabilities were based on seven sea-spawning sampling locations (assumed populations) and eight anadromous populations (Supplementary material).

We compared correlations between individual-level DAPC posterior probabilities of being a sea-spawner and our fish origin and phenotypic trait values. In addition, to compare the ecotype distributions provided by the three assignment methods, we conducted pairwise two-proportion z-tests. These comparisons only included individuals that were successfully assigned to an ecotype and hence excluded individuals that remained unassigned, i.e. unidentified.

To investigate the factors that might influence the relative occurrence of the two ecotypes in the catch, we used all 27 gillnet catches (Table 1). We analysed the counts of individuals assigned to the two ecotypes. We did this separately for the counts provided by the three ecotype identification methods (two phenotypic and DAPC). Note that for the two approaches with unidentified individuals, the results would have been similar if we had used sea-spawners versus all other whitefish in the catch, an approach which would have assumed most of the unidentified individuals to be of the anadromous ecotype. We combined the counts of individuals of the two ecotypes in the catch (per mesh size) using the 'cbind' command and used the combination as the response variable. We then fitted a binomial generalized linear mixed model (hereafter GLMM), with mesh size (bar length: 38/40/43/45 mm), fishing depth (m), and month (5–11) as explanatory variables, using the *glmmTMB* package (Brooks et al., 2022). Whenever more than one mesh size had been in use (Table 1), the fish of each mesh size were used as a separate datapoint and we therefore added catch sample number (hereafter Sample ID) as a random effect [i.e. ecotype shares \sim mesh size + fishing depth + month + (1|Sample ID)].

To assess factors affecting whitefish numbers in the catch, we applied a GLMM with a negative binomial distribution using the *glmmTMB* package. The response variable was the total number of whitefish in the catch (both ecotypes included). We fitted the model with the following explanatory variables: mesh size, month, net length, and length of fishing time (per fishing trip). Net length and fishing time were included to account for the fishing effort, making the approach as close to a catch per unit effort (CPUE) analysis as feasible. We again added Sample ID as a random effect.

Finally, we investigated the factors affecting the body size of whitefish individuals in the catch. For this purpose, we assessed the individual-level data (N = 1155 individuals). After discovering that the

length data (at the accuracy of 1 mm) were not normally distributed, we applied a GLMM with a negative binomial distribution, with fish length (in full mm) as the response variable, and mesh size (38/40/43/45 mm), fishing depth (m), month (5–11), and sex (male/female) as explanatory variables. To account for the effect of fishing trip (i.e. Sample ID) on the results, we included it as a random effect. The conclusions are qualitatively the same if weight instead of length is used as the response variable. We again used the *glmmTMB* package.

3. Results

3.1. Ecotype distributions based on phenotypic and genotypic assignments

Of the 1155 individuals assigned based on reported gill raker number and growth values, 53 % (617) were deemed to be of the sea-spawning ecotype, 27 % (309) of the anadromous ecotype, while 20 % (229) were not successfully assigned into either group (Table 2). The automated assignment by mixture modelling assigned ~50 % of the individuals to each ecotype (sea-spawning: 581, anadromous: 574; Table 2), and for the subset of 527 genotyped (DAPC) individuals, the proportions were sea-spawning 39 % (207), anadromous 41 % (216) and unidentified 20 % (104) (Table 2).

The DAPC calibration curve indicated that intermediate posterior probabilities had low reliability in the dataset (Figure S1). Nevertheless, the posterior ecotype probabilities showed clear peaks corresponding to the two ecotypes (Fig. 3). Overall, these results support the existence of two ecotypes, but with intermediate individuals and probable mixing between them (Fig. 3). The posterior ecotype probability approach also allows fine-tuned assessment of variation in affinity to the ecotypes.

When the ecotypes were assigned by mixture modelling (Fig. 4), sea-spawning fish had fewer gill rakers (sea-spawning: 26.6 ± 2.1 [mean \pm SD], $N = 581$; anadromous: 28.9 ± 2.2 , $N = 574$), were shorter (sea-spawning: 344 ± 23 mm, $N = 581$; anadromous: 360 ± 30 mm, $N = 574$) and older (sea-spawning: 7.0 ± 1.9 years, $N = 581$; anadromous: 3.8 ± 0.8 years, $N = 574$) than fish assigned to be anadromous. When the ecotypes were assigned by genotyping, the two were very similar in their gill raker numbers (sea-spawning: 28.3 ± 2.4 , $N = 207$; anadromous: 28.4 ± 2.1 , $N = 216$), differed moderately in length (sea-spawning: 35.0 ± 2.6 cm, $N = 207$; anadromous: 35.9 ± 3.1 cm, $N = 216$), and sea-spawning individuals were again older (sea-spawning: 5.8 ± 2.5 years, $N = 207$; anadromous: 4.2 ± 1.6 years, $N = 216$).

3.2. Comparisons of ecotype distributions based on the different assignment methods

We first compared the DAPC posterior probabilities of being a sea-spawner to variables related to fish phenotype and origin. Here, phenotypic assignments to be a sea-spawner, based on the cut-off value method overall as well as growth cut-off values (Fig. 4) separately, were clearly associated with the estimated posterior probability of being a sea-spawner, while phenotypic assignment based on gill rakers alone

was not significantly correlated (Fig. 5). Of additional individual level categorical variables, maturity index and sex also covaried with the estimated posterior probability (Fig. 6). Besides these, some additional fish and catching site characteristics correlated with the DAPC ecotype probability. In particular, sea-spawning ecotype probability had positive correlations with fish age, catching site longitude, catching site latitude, and fishing depth, and negative correlations with fish weight and length (Fig. 6). In contrast, the body condition score, number of gill rakers, and month of fishing did not show any significant trends (Fig. 6).

Direct pairwise ecotype distribution comparisons between the three assignment methods indicated moderate agreement (Table 2). By considering only the individuals that were assigned as either sea-spawning or anadromous, we found that the distribution of ecotypes as assigned phenotypically based on published cut-off values (sea-spawning/anadromous: 130/116) and the distribution provided by the DAPC genetic method (140/106) did not significantly differ from each other (two-proportions z-test, $\chi^2 = 0.6649$, $df = 1$, $p = 0.41$). The two phenotypic approaches also provided similar (published cut-off values method, sea-spawning/anadromous: 617/309; mixture distribution analysis: 558/368; Table 2), albeit statistically different (two-proportions z-test, $\chi^2 = 7.832$, $df = 1$, $p = 0.0051$) distributions. The ecotype distributions provided by DAPC (207/216) and mixture distribution (129/294) were significantly different (two-proportions z-test, $\chi^2 = 29.27$, $df = 1$, $p < 0.0001$), having unbalanced match accuracies regarding identities of the two ecotypes (Table 2).

3.3. Factors that affect ecotype distribution in the catch

Based on both phenotypic assessments, the proportion of the sea-spawning-like individuals in the catch increased with fishing depth (cut-off value assignment: GLMM: $\beta \pm SD = 0.08849 \pm 0.03118$, $z = 2.838$, $p = 0.0045$; mixture distribution assignment: GLMM, $\beta \pm SD = 0.08534 \pm 0.02910$, $z = 2.910$, $p = 0.0036$) (Fig. 7) and decreased with the progress of the open water season (cut-off values, month effect: GLMM, $\beta \pm SD = -0.6543 \pm 0.1949$, $z = -3.357$, $p = 0.0008$; mixture distribution: GLMM, $\beta \pm SD = -0.3961 \pm 0.1811$, $z = -2.187$, $p = 0.029$) (Fig. 7). Consequently, the proportion of the sea-spawning ecotype was the highest in deep water areas during the summer months (catch samples from >10 m from June to August, cut-off values: 317/373, 85 %), whereas in shallower water the anadromous ecotype tended to be dominant. In addition, the share of sea-spawners tended to be smaller when larger mesh sizes were used (cut-off-value identification: GLMM, $\beta \pm SD = -0.3273 \pm 0.1135$, $z = -2.883$, $p = 0.0039$; mixture distribution: GLMM, $\beta \pm SD = -0.1516 \pm 0.0892$, $z = -1.700$, $p = 0.089$) (Fig. 7).

Using the subset of individuals that were genotyped, the proportion of the sea-spawning ecotype increased with depth (GLMM: $\beta \pm SD = 0.03551 \pm 0.01554$, $z = 2.284$, $p = 0.022$) (Fig. 7), while the effects of season (GLMM: $\beta \pm SD = -0.07051 \pm 0.09673$, $z = -0.729$, $p = 0.47$) and mesh size (GLMM, month: $\beta \pm SD = -0.1461 \pm 0.0887$, $z = -1.647$, $p = 0.10$) were, while non-significant, to the same direction as when the

Table 2

The pairwise incidences of matching and non-matching whitefish ecotype assignments by three identification methods. For instance, of the 207 individuals identified as sea-spawning by the DAPC method, 101 (49 %) were identified sea-spawning also by using phenotypic cut-off values. The bold numbers show matching identifications. Note that the same comparisons appear both horizontally and vertically in the table.

		DAPC			Cut-off values			Mixture distribution	
		Anadromous	Sea-spawning	Unidentified	Anadromous	Sea-spawning	Unidentified	Anadromous	Sea-spawning
DAPC	Anadromous				77 (36 %)	29 (13 %)	110 (51 %)	194 (90 %)	22 (10 %)
	Sea-spawning				39 (19 %)	101 (49 %)	67 (32 %)	100 (48 %)	107 (52 %)
	Unidentified				32 (31 %)	24 (23 %)	48 (46 %)	77 (74 %)	27 (26 %)
Cut-off values	Anadromous	77 (52 %)	39 (26 %)	32 (22 %)				308 (100 %)	1 (0.3 %)
	Sea-spawning	29 (19 %)	101 (66 %)	24 (16 %)				60 (10 %)	557 (90 %)
	Unidentified	110 (49 %)	67 (30 %)	48 (21 %)				206 (90 %)	23 (10 %)
Mixture distribution	Anadromous	194 (52 %)	100 (27 %)	77 (21 %)	308 (54 %)	60 (10 %)	206 (36 %)		
	Sea-spawning	22 (14 %)	107 (69 %)	27 (17 %)	1 (0.2 %)	557 (96 %)	23 (4 %)		

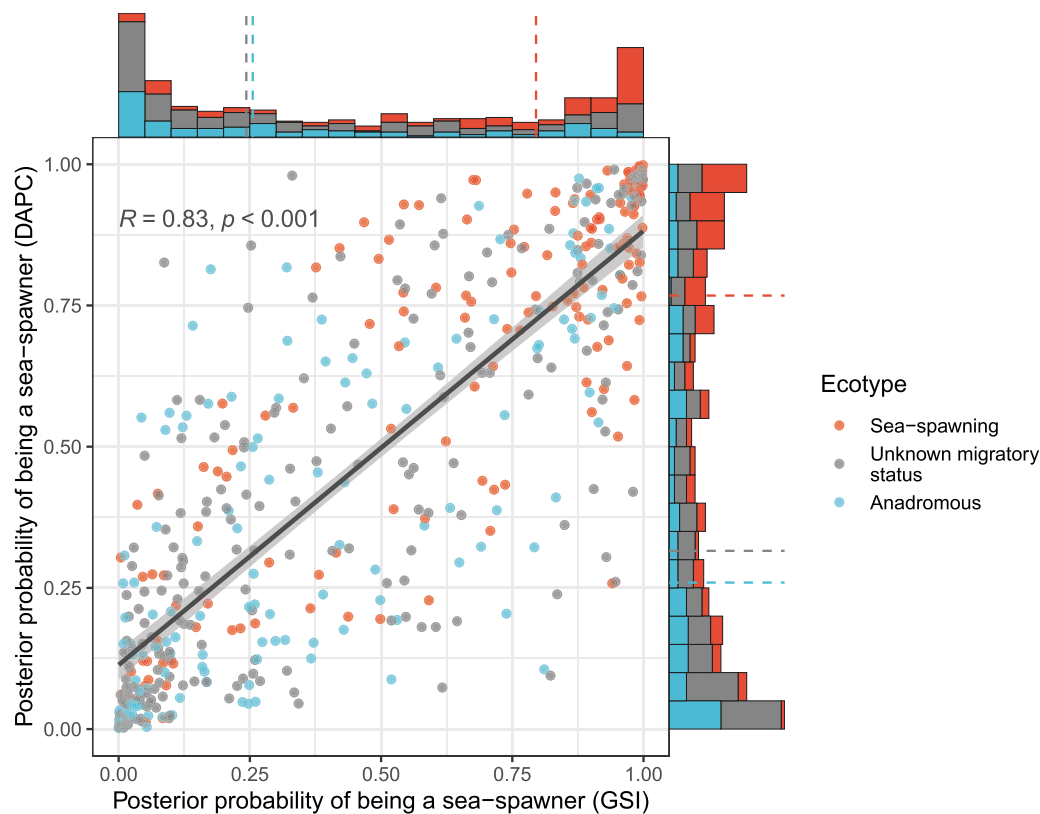


Fig. 3. Relationship between genotypic posterior probabilities and phenotypic ecotype categorisation based on published cut-off values. The scatter plot and fitted correlation line demonstrate the relationship between genetic assignments with DAPC and GSI. Histograms on the top and right margins show the distribution of phenotypically assigned ecotype categories. Dashed lines in the margins indicate medians for these distributions.

assignment was based on the phenotype (Fig. 7).

3.4. Factors that affect the number and size of whitefish in the catch

When whitefish catches were assessed as numbers of individuals (irrespective of the ecotype), more fish were caught in shallow than deep water (GLMM: $\beta \pm SD = -0.06424 \pm 0.01342$, $z = -4.786$, $p < 0.0001$) (Fig. 8). The progress of the season did not significantly affect the catches (GLMM, month: $\beta \pm SD = -0.1124 \pm 0.0912$, $z = -1.231$, $p = 0.21$) (Fig. 8). Instead, the catches were smaller when larger mesh sizes were used (GLMM: $\beta \pm SD = -0.2185 \pm 0.0569$, $z = -3.838$, $p = 0.0001$) (Fig. 8). Regarding our proxies of the fishing effort, longer nets caught more whitefish (GLMM: $\beta \pm SD = -0.0005247 \pm 0.0001219$, $z = 4.303$, $p < 0.0001$), whereas the effect of fishing time (i.e. the number of hours the net was in water that day) did not have a significant independent effect (GLMM: $\beta \pm SD = 0.0006493 \pm 0.0007332$, $z = 0.886$, $p = 0.38$).

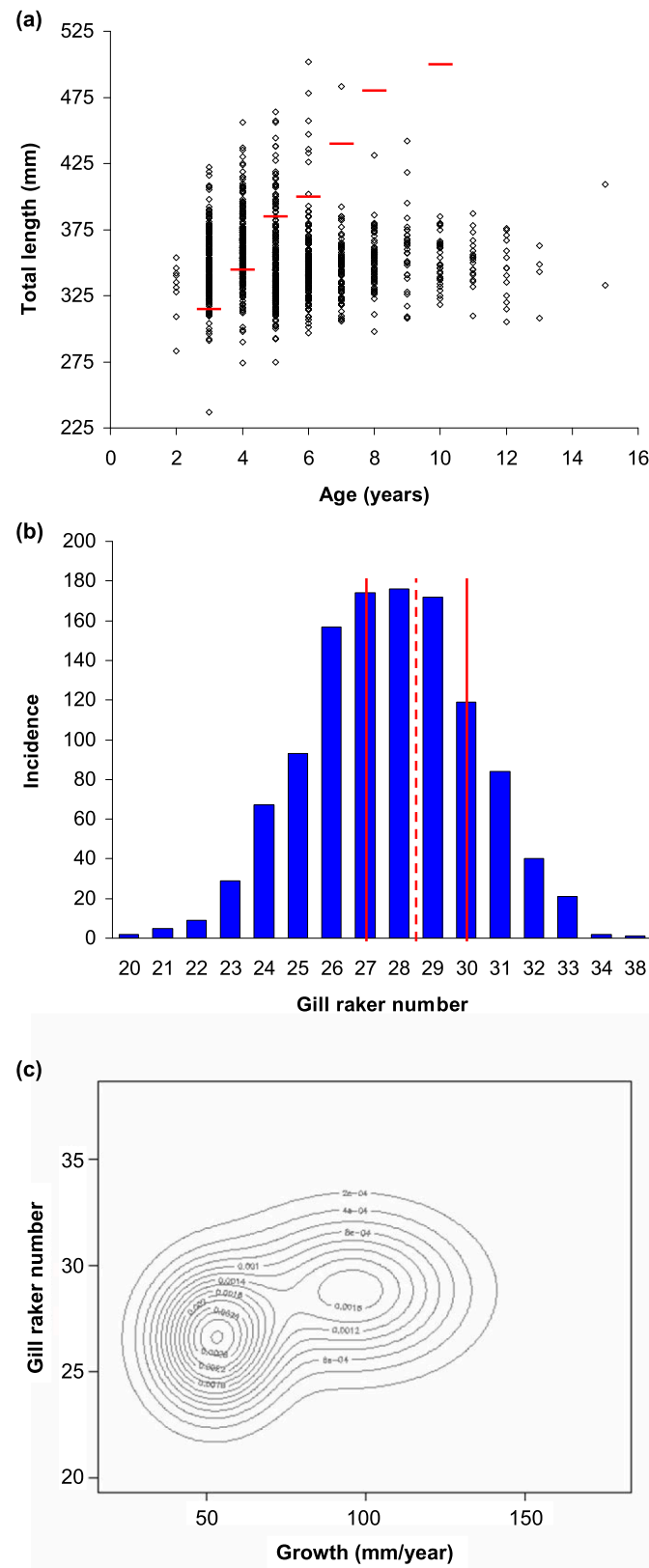
Regarding the size (total length) of the whitefish caught, depth did not have a significant effect (GLMM: $\beta \pm SD = 0.0002123 \pm 0.0006282$, $z = 0.34$, $p = 0.74$) (Fig. 8). Fish caught later in the year were larger (GLMM, month: $\beta \pm SD = 0.01049 \pm 0.00386$, $z = 2.72$, $p = 0.0065$) and nets of larger mesh size caught larger whitefish (GLMM: $\beta \pm SD = 0.02407 \pm 0.00241$, $z = 11.73$, $p < 0.0001$) (Fig. 8). Females were on average slightly larger than males (GLMM: $\beta \pm SD = 0.008747 \pm 0.00393$, $z = 2.22$, $p = 0.026$).

4. Discussion

Central challenges in many mixed-stock fisheries include the reliable identification of the different intraspecific stocks or stock components in the catch and the adjustment of fishing pressure in relation to these (Hilborn et al., 2015; Moore et al., 2021). In the current study, we

addressed both these challenges in the context of the whitefish fishery in the Kvarken region on the Finnish west coast of the Baltic Sea. This was relevant especially because the two whitefish ecotypes, anadromous and sea-spawning, differ in conservation status, with the anadromous ecotype being more severely threatened, particularly by river construction and relatively high fishing pressure. However, distinguishing between the two ecotypes proved to be challenging. We used two phenotypic approaches (both based on gill raker counts and length-at-age) that agreed relatively well. However, of these, the approach based on previously published cut-off criteria resulted in ~20 % of the individuals unassigned due to conflicting phenotypic features. Similarly, genotyping with SNP markers identified a substantial number of intermediate individuals, again with ~20 % not assigned to either ecotype. Overall, concordance between the three assignment methods was merely moderate: about two-thirds of the individuals phenotypically identified as sea-spawning were also genotyped the same, with the remainder classified as anadromous or intermediate (unidentified). The presence of phenotypic and genotypic intermediates highlights the challenge of assigning individuals to ecotypes in mixed-stock catches, especially under real-world fishing conditions. Therefore, as a management measure, we propose the implementation of fishing regulations that affect the catch component (here: ecotype) shares without requiring the identification of the captured individuals. Such regulations should be based on prior investigations of their effectiveness, with the present study providing initial steps toward this goal for the northern Baltic Sea whitefish fishery.

When assessing the scope for implementing such fishing regulations, we found that by adjusting spatial or temporal aspects of the fishing effort, it was possible to influence the fishing pressure regarding the ecotypes, especially when they were assigned by phenotypic traits. Fish from greater depths were more often sea-spawners, independent of the method by which they were identified. Moreover, fishing earlier in the



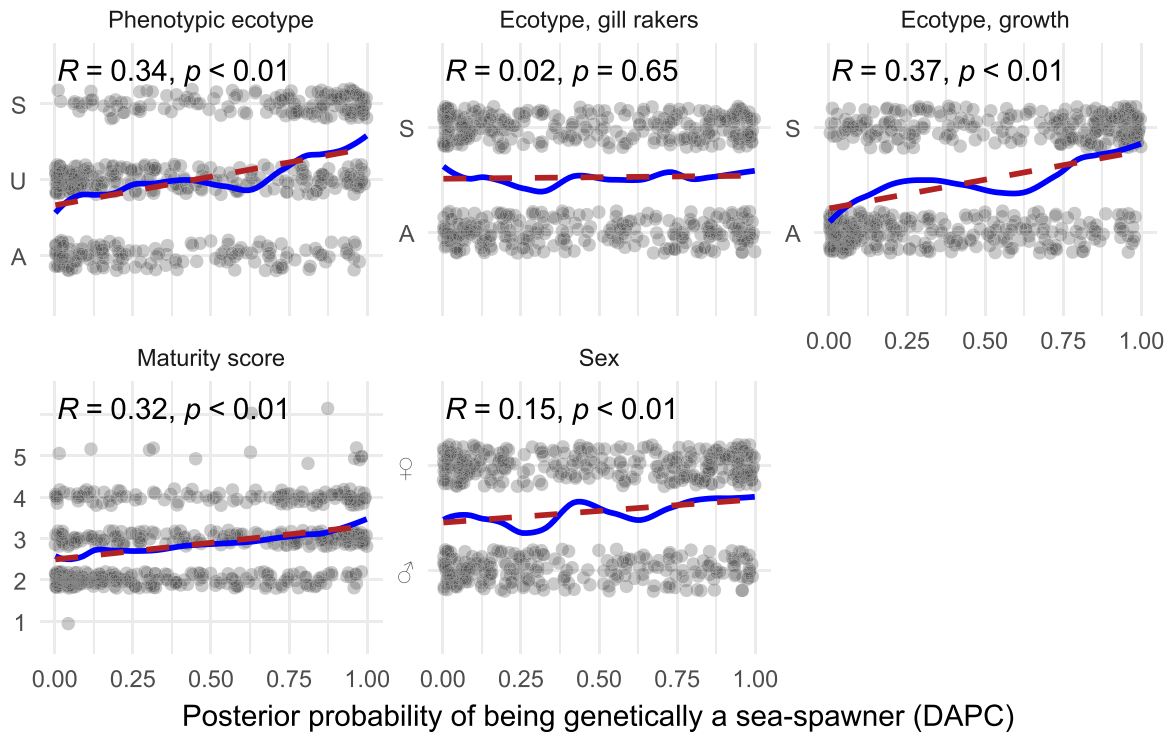


Fig. 5. Scatter plots of qualitative fish and catching site characteristics against the posterior probabilities of genotype-based (DAPC) ecotype categorisation. Each scatter plot shows a locally estimated scatterplot smoothing line (solid blue) and a linear regression line (dashed red). The correlation coefficient and its P-value are shown on the top part of each panel. Categories are represented as pseudo quantitative traits, because they either have only two categories or a natural order. Phenotypic ecotype refers to the cut-off value assignment. S = sea-spawning, A = migratory/anadromous, U = phenotypically unidentified ecotype.

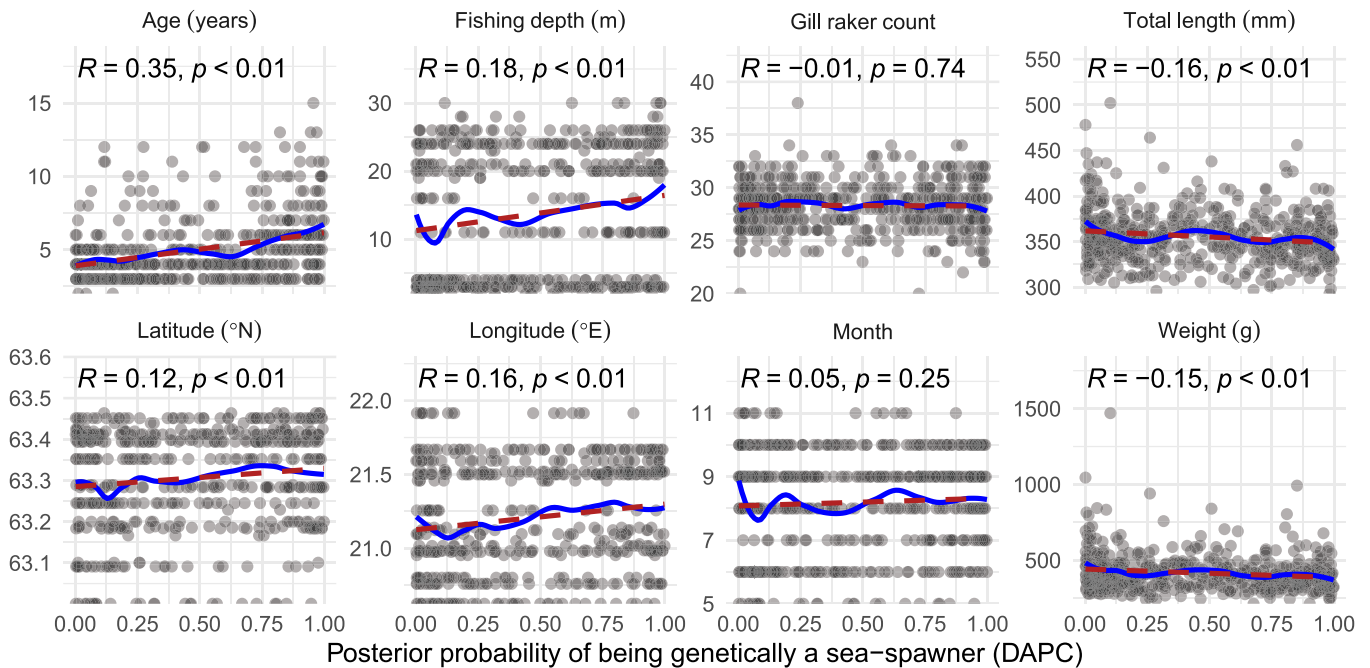


Fig. 6. Scatter plots of quantitative fish and catching site characteristics against the posterior probabilities of the genotype-based (DAPC) ecotype categorisations. Each scatter plot shows a locally estimated scatter plot smoothing line (solid blue) and linear regression line (dashed red). The correlation coefficient and its p-value are written on the top part of each panel.

open-water season and using smaller mesh sizes resulted in higher proportions of individuals displaying phenotypic characteristics typical of sea-spawning whitefish: slower growth combined with lower gill raker number. While the trends for season and mesh size for genetically assigned fish were towards the same direction as those observed in the

phenotypic assessments, they were not statistically significant. This discrepancy may be partly explained by the smaller number of individuals available for the genetic analysis due to logistic constraints. In addition, it is possible that phenotypic traits more directly influence an individual's behaviour, movement patterns and habitat use than its

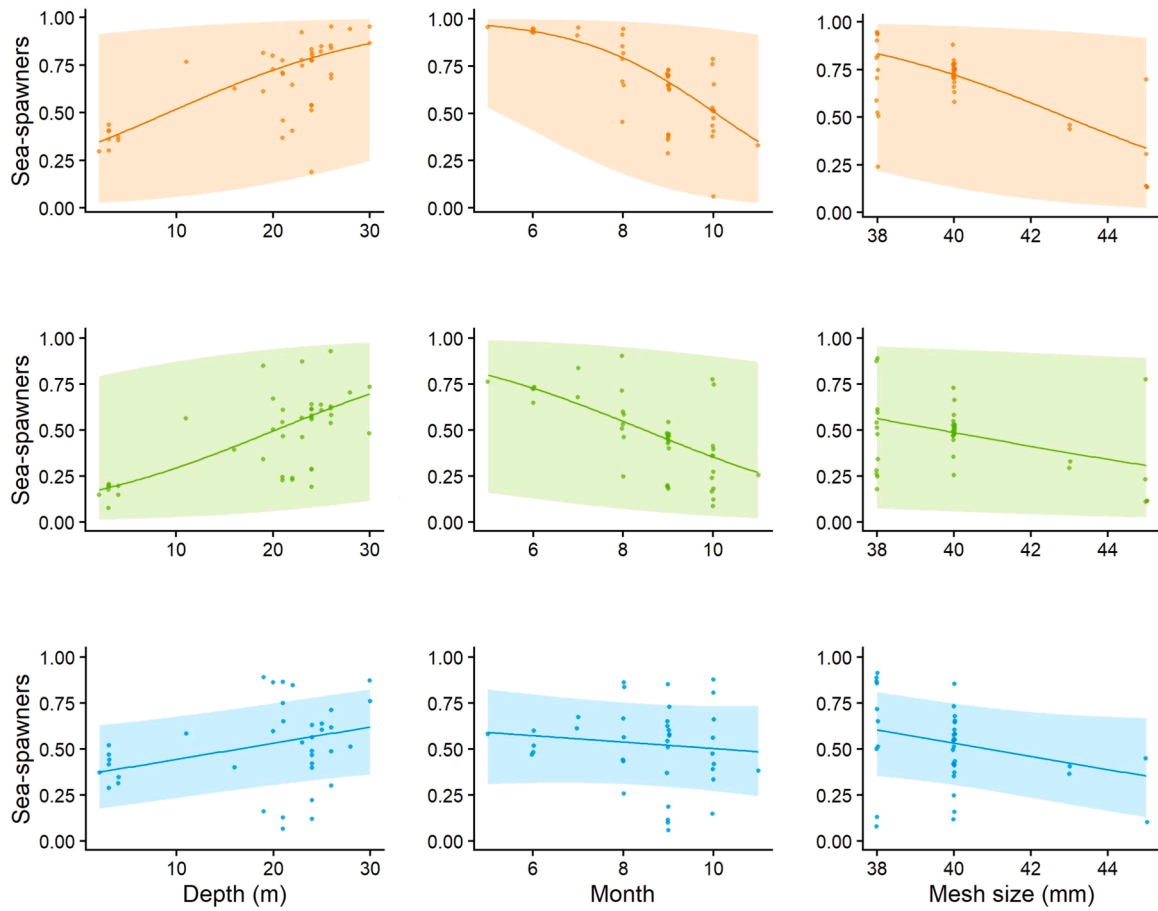


Fig. 7. Model-predicted proportions of individuals categorised as ‘sea-spawning’ in relation to fishing depth, month of capture, and gillnet mesh size (bar length). The three rows show results based on our different categorisation methods; upper row (orange): phenotypic assignment based on published cut-off values, middle row (green): phenotypic assignment with mixture distribution analysis, and lower row (blue): genotypic assignment. Shaded areas indicate 95 % confidence intervals and dots represent residuals from the model fits.

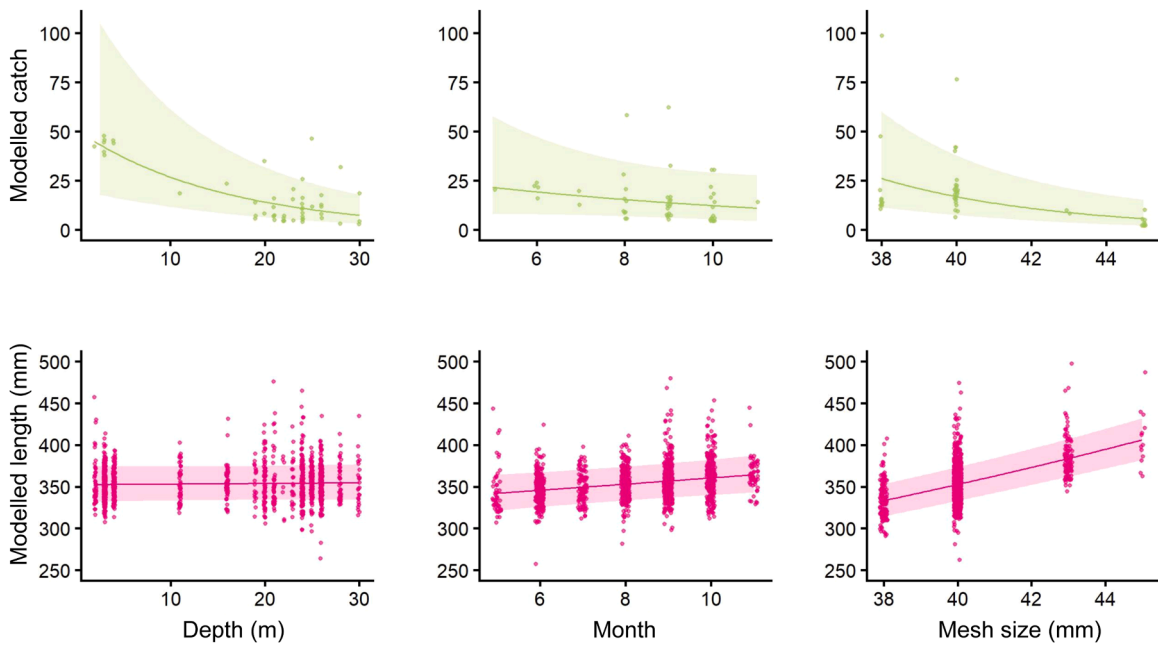


Fig. 8. Upper row (green): model-predicted whitefish catch, expressed as the number of individuals standardised for fishing effort. Lower row (pink): model-predicted total length of whitefish in the catch. Both are shown in relation to fishing depth, month of capture, and gillnet mesh size (bar length). Shaded areas indicate 95 % confidence intervals and dots represent residuals from the model fits.

ecotype-related genetic background. Such phenotype-environment link could help to explain why the temporal pattern in ecotype catches was more pronounced when the ecotypes were identified phenotypically. Environmental factors may also play a direct role in shaping the phenotype: for example, if individuals consistently forage near the substrate in deeper waters, their propensity to migrate may be affected (Chapman et al., 2012) or their phenotype may plastically develop towards traits typically associated with the more benthic sea-spawning ecotype. Previously, cranial shape (Borovikova et al., 2020) and gill rakers (Lindsey, 1981) have been found to be phenotypically plastic, supporting the role of plasticity when genetic and phenotypic classifications of whitefish ecotypes (or populations) mismatch (Østbye et al., 2005).

Although the above results suggest that, with currently available tools, the two ecotypes cannot always be reliably identified, possibly because the ecotypes are not sufficiently distinct (at least in the Kvarken area), they nevertheless represent biologically meaningful entities. Some individuals follow an anadromous life history, migrating to rivers to spawn after growing in the sea, while others reproduce in coastal habitats and presumably never enter rivers. Our genetic data support this interpretation, as the genotype distributions differed clearly between ecotypes, although with some overlap (Fig. 3). The results, however, raise important questions: why do so many individuals have intermediate genetic or conflicting phenotypic features, and why the concordance between the assignment methods was only moderate?

Several non-exclusive explanations are possible. First, our findings are consistent with previous studies from more southern coastal areas of the Baltic Sea, which suggested very low genetic differentiation between the two ecotypes (Ozerov et al., 2015, 2016), with clearer isolation by distance (Olsson et al., 2012). This raises the possibility that some individuals may retain the capacity to spawn either in rivers or in the sea, potentially depending on environmental factors. However, the extent and significance of such life history flexibility remains uncertain and warrants further research to determine whether phenotypic traits, such as growth rate, could influence the life history strategy an individual ultimately adopts.

The second ecological explanation for the lack of clearer differentiation between the ecotypes in our study area, despite previous studies detailing phenotypic ecotype differences (Lehtonen, 1981; Lehtonen and Himberg, 1992; Himberg et al., 2015; Kallio-Nyberg et al., 2019; Lindén et al., 2019; Veneranta et al., 2021), is that ecotype distinctions may have eroded relatively recently. Decades of restocking programmes have primarily used anadromous parent fish (caught in rivers) and to a lesser extent sea-spawning individuals that have sometimes originated from different water bodies than into which the hatchery-reared progeny have later been released (Rohtla et al., 2017). In the Kvarken region, stocking is done by rearing juveniles in fish ponds and then releasing them as one-summer-old directly to the coastal waters. Some of these practices may be detrimental to local populations because of their high potential to introduce genotypes adapted to other environments due to artificial mixing of populations and to cause inbreeding or outbreeding depression (Ward, 2006), which can break down population structures and life history patterns.

Third, eutrophication (Vonlanthen et al., 2012) and other ecosystem changes (Bhat et al., 2014; Reid et al., 2017; Haase et al., 2025) may also have exerted homogenising effects. We also acknowledge the possibility that these complications may have affected the baseline reference material used in our genetic assignment. Nonetheless, even allowing such uncertainties, our results emphasise the substantial overlap between the ecotypes in their traits and the high prevalence of individuals exhibiting intermediate or conflicting features. Future identification efforts may benefit from a larger number of genetic markers and from considering that the European whitefish possesses a largely duplicated genome (Pokharel et al., 2025). Although the SNPs used in the present study were derived from on genome-wide ddRAD sequencing and proved useful in ecotype identification, the potential of plasticity in ecotype

formation remains unresolved. Integrating whole-genome sequencing with individual tagging or otolith microchemistry could provide a clearer understanding of the links between genotypes and life history and enable an assessment of plasticity, which has previously been shown to contribute to differences between whitefish ecotypes (Ohlund et al., 2020). Such an integrated approach would also allow a more rigorous evaluation of the representativeness of baseline samples, which, given the current methods and any whitefish population, may include individuals with genotypic and phenotypic ecotype signals that do not align. A related, albeit logistically very challenging, approach to attain life-history-relevant samples would involve tagging a large number of individuals followed by recapture by (river) fisheries (see Lehtonen and Himberg, 1992).

Our results demonstrate that although identification of the ecotypes in the Kvarken area was challenging, the phenotypic composition of a whitefish catch can be influenced with temporal and spatial regulations, while maintaining reasonable overall catches. This implies potential for management measures based on phenotypic characteristics and, under certain conditions, the associated ecotypes. In particular, we found a higher proportion of sea-spawning individuals in catches from deeper waters and, when based on phenotypic assessment, also during the summer season (June to August). These patterns in the catch composition may reflect differences in migratory patterns between the two ecotypes, or individuals with different feeding habits or growth rates. Seasonal trends in ecotype proportions, as judged by the phenotypes in whitefish catches, have also been reported in a more southern region of the Finnish Baltic Sea (Lindén et al., 2019), supporting the idea of utilising seasonal movement patterns in management.

Our results also indicate a potential role for mesh size regulations in the management of mixed-stock fisheries of whitefish and similar species. As expected, gillnets with larger mesh sizes caught fewer but larger fish. Similarly, the proportion of phenotypically identified sea-spawners decreased with increasing mesh sizes, a trend that was a similar, although less clear, when ecotypes were assigned based on their genotypes. However, changes in size selectivity may have unintended consequences particularly if smaller mesh sizes are used. Changes in size-selectivity and the populations' size distributions are linked, potentially necessitating additional regulatory adjustments over time. At the other end of the spectrum, the use of larger mesh sizes to reduce fishing pressure on smaller individuals also presents challenges: overall whitefish catches were very low when we used the largest mesh size (45 mm bar length), indicating that such nets may not be well suited for the current size distribution of whitefish in the Kvarken area. Regarding spatial variation, overall whitefish catches were larger in shallower waters, which could be partly explained by more detailed local knowledge on the shallower water fishing sites. It also aligns with the presumed habitat preference of the anadromous ecotype. In contrast, depth did not significantly explain variation in whitefish size. In all depths, most of the whitefish caught in the present study were sexually mature. The implications of this finding may differ between ecotypes: judging by age distributions, anadromous individuals caught in coastal gillnet fisheries are likely on their first spawning migration towards rivers, whereas sea-spawning individuals caught, on average, at a higher age (as observed here and in Kallio-Nyberg et al., 2019) may have had opportunities to reproduce in previous years before being harvested. This difference underscores the presumably greater reproductive cost of the current harvest patterns to anadromous individuals.

While our results offer valuable insights for the management of the whitefish fishery and generate hypotheses relevant to other similar mixed-stock fisheries, it is important to acknowledge the spatial and temporal limitations of the current study. Our sampling was restricted to the Kvarken area and included very few samples from the 5–20 m depth range. Moreover, the early phase of the open-water season, following melting of the sea ice, was represented by only a single catch sample from May, and all data were collected within a single year (2023). To determine long-term applicability of spatial or temporal management

measures, such as shifting fishing effort towards deeper waters or summer months, multi-year catch monitoring will be needed. Such extended monitoring is necessary to assess whether these management strategies reliably reduce the proportion of anadromous whitefish in the catch in longer term. Additional studies are also needed to evaluate whether the relatively high proportion of intermediate individuals, identified both phenotypically and genotypically in the current study, is a localised phenomenon or a broader pattern within the species' range in the Baltic Sea.

To conclude, identifying distinct populations or their catch components in mixed-stock fisheries is often challenging, as demonstrated by the case of the whitefish fishery in the Kvarken region in the northern Baltic Sea. Both phenotypic and genetic assignment methods involved uncertainty in classifying individuals into ecotypes. Several ecological processes may contribute to this ambiguity, including interbreeding between ecotypes, past and ongoing stocking practices, and the possibility of a degree of phenotypic plasticity in the determination of life history strategies. In this context, our results highlight the need for greater caution in stocking programs for the endangered anadromous whitefish, particularly with respect to using broodstock originating from the appropriate local populations (Ward, 2006). The results also question the practical reliability of relying on widely used phenotypic traits, growth, and especially gill raker number, in ecotype identification (in a management context). Nevertheless, our results also suggest that it is possible to adjust fishing mortality in a desired manner by exploiting behavioural and ecological differences between individuals. Specifically, our catch data indicate that fishing with smaller mesh sizes (38 or 40 mm bar length) during summer months (June–August) in deep water areas resulted in a higher proportion of sea-spawners or sea-spawner-like individuals in the catches. If these findings are to be applied in fisheries management, long-term catch monitoring will be essential to verify the stability of the intended catch composition biases.

CRedit authorship contribution statement

Miika Tapio: Writing – review & editing, Visualization, Formal analysis. **Tuomas Leinonen:** Writing – review & editing, Visualization, Resources, Methodology, Funding acquisition, Formal analysis. **Daniel Fischer:** Writing – review & editing, Software. **Lari Veneranta:** Writing – review & editing, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Oliver Bitz:** Writing – review & editing, Formal analysis. **Topi K. Lehtonen:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Formal analysis, Data curation.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2026.107648](https://doi.org/10.1016/j.fishres.2026.107648).

Data availability

Data will be made available on request.

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