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RESEARCH ARTICLE

Changes in age and maturity of anadromous whitefish (*Coregonus lavaretus*) in the northern Baltic Sea from 1998 to 2014

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Abstract – The maturation of anadromous whitefish (*Coregonus lavaretus*) was analysed from samples taken from commercial coastal fishing in 1998–2014 in the Gulf of Bothnia. Whitefish matured at a younger age from year to year. The proportion of older (5–12 sea years) mature males decreased from 79% to 39% in the northern Gulf of Bothnia (66°N–64°N) and from 76% to 14% in southern (64°N–60°30'N) during the study period. At the same time, the proportion of young males (2–4 sea years) increased. Whitefish matured younger: the proportion of mature fish at age four increased in both the north and south among females (13% → 98%; 6% → 85%) and males (68% → 99%; 29% → 89%). The catch length of four-year-old fish increased during the study period in both sexes. In contrast, the length of six-year-old females decreased from year to year. Sea surface temperatures increased during the study period, and were possibly associated with a decrease in the age of maturation and faster growth.

Keywords: Anadromous whitefish / maturation / temperature / Baltic Sea

1 Introduction

The maturation and growth rate of anadromous whitefish (*Coregonus lavaretus*) varies between local stocks in Finnish coastal areas (Lehtonen, 1981; Heikinheimo and Mikkola, 2004; Aronsuu and Huhmarniemi, 2004). This variation may either be due to an evolutionary adaptation to local conditions (Säisä et al., 2008; Olsson et al., 2012; Hägerstrand et al., 2017) or partly or entirely due to phenotypic plasticity (Price et al., 2003). The age structure of the spawning stock may be wide, rangingin fish from 2 to 12 years of age (Lehtonen, 1981; Czerniejewski and Rybczyk, 2010).

Fishing of European whitefish has changed considerably during last seven decades in the Finnish coastal waters in the Baltic Sea. The most important fishing gears in the 1950s were trap nets in the Gulf of Bothnia. Caught whitefish weighted 1–3 kg, and mesh sizes in trap nets and gillnets were usually between 50 and 65 mm (Lehtonen and Jokikokko, 2002). Pelagic drift net fishing of migrating anadromous whitefish was started in the 1960s. In the 1990s the mesh size in gill nets has decreased, being 40–55 and 30–35 mm in the southern and northern part of Gulf of Bothnia, respectively and harvested whitefish weighted 0.4–0.8 kg (Lehtonen and Jokikokko, 2002). The mesh size of gill nets in commercial whitefish fishing in 1998–2011 was mainly 40–45 and 25–39 mm in the southern and northern Gulf of Bothnia, respectively (Kallio-Nyberg et al., 2018).The average length-at-size of old anadromous whitefish entering to their home rivers in the Gulf of Bothnia has decreased since 1980s (Lehtonen and Jokikokko, 2002) and mean weight of mature anadromous whitefish in the River Tornionjoki has had a decreasing trend from 1980 to 2019 (Jokikokko and Huhmarniemi, 2014; Jokikokko et al., 2020).

Whitefish stocks have undergone large-scale changes since the 1950s in Finnish coastal waters (Urho, 2011). Many original stocks have been lost and natural production has decreased (Kaukoranta et al., 2000), and the sea catch has decreased since the 1990s to nearly fourth part of top level (Urho, 2011; OSF, 2020). The commercial whitefish catch in

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Finnish coastal waters in 2017 was 476 tonnes, and 81% of the catch was taken in the Gulf of Bothnia (GoB) (OSF, 2020). The loss of natural production has been compensated for fisheries with large-scale stockings in Finland (Jokikokko et al., 2002; Jokikokko and Huhmarniemi, 2014). The level of stockings was highest in the 1980s when over 15 million fingerlings were released to the coastal area (Salojärvi, 1986). Recently, the fingerling stockings have decreased substantially and are approx. 7 million fingerlings annually (ICES, 2018). Also newly hatched larvae are stocked, and the quantities have decreased from level of 40–90 million larvae in 1990s (Jokikokko et al., 2002) to approx. 30 million annually (ICES, 2018). Most of the releases are done with anadromous whitefish fingerlings or larvae in rivers running to the northern Gulf of Bothnia (Jokikokko and Huhmarniemi, 2014). Whitefish larvae or fingerlings disperse to feeding migration immediately after hatching or release (Lehtonen et al., 1992), and return to home river as mature fish (Kallio-Nyberg et al., 2019). Stockings likely have a strong impact on spawning stock and catches (Leskelä et al., 2004; Jokikokko and Huhmarniemi, 2014).

Gillnet fishing has been shown to affect the life history traits of exploited stocks (Lehtonen and Jokikokko, 2002; Nusslé et al., 2009; Uusi-Heikkilä et al., 2015). In commercial fishingin the Gulf of Bothnia approx. 80% of whitefish are caught with gillnets and the rest with trapnets (OSF, 2020). Gill-net fishing effectively removes the largest individuals (Heikinheimo and Mikkola, 2004) and puts anadromous whitefish under selective fishing (Lehtonen and Jokikokko, 2002; Aronsuu and Huhmarniemi, 2004). It has e.g. been observed that the length of the six-year-old anadromous females has decreased in the commercial catches of the Gulf of Bothnia in 1998–2014 (Kallio-Nyberg et al., 2019). The decreased size and age at maturation in an intensive harvested pikeperch (*Sander lucioperca*) stock in the southern Gulf of Bothnia was likely a consequence of the selective gill net fishing (Kokkonen et al., 2015).

Temperature is known to play a significant role in the growth rate, survival, year-class strength, distribution and maturation of fish species (Jonsson and Jonsson, 2009; Pankhurst and Munday, 2011; Audzijonyte et al., 2020) and effect of annual environmental temperature variation on life-history traits of fish species can be seen also in the Baltic Sea (Jutila et al., 2005; Kallio-Nyberg et al., 2006; Pekcan-Hekim et al., 2011; Heikinheimo et al., 2014). Several documents suggest that the observed body-size reduction is a universal response to global warming (Gardner et al., 2011). Many fish species has shifted their distribution northward with climate warming (Perry et al., 2005). Global temperature has increased, and most scenarios concerning the Baltic Sea area predict an increase in the sea temperature and a shorter period of ice cover in winter (Meier et al., 2004; Mackenzie et al., 2007; Räisänen, 2017).

The aim of this study was to analyse the maturation and growth trends of anadromous whitefish during a time period when the sea temperature increasedand fishing was concentrated more and more on larger anadromous whitefish instead of local sea spawning whitefish, partly due to collapse of southern sea spawning whitefish stocks (Veneranta et al., 2013). This smaller whitefish was in earlier years a target for intensive fishing thus balancing the effort towards anadromous form (Jokikokko et al., 2018; Kallio-Nyberg et al., 2020). Special attention is placed on the effect covariation of climate data such as the North Atlantic Oscillation (NAO) and the local sea surface temperature (SST) with the age of maturation.

2 Material and methods

2.1 Whitefish samples

Whitefish samples were collected as part of the EU Data Collection Framework (DCF) by Natural Resources Institute Finland. The DCF whitefish sample is an unbiased sample of the Finnish commercial whitefish fishery from 1998 to 2014. The samples used in this and earlier studies (Kallio-Nyberg et al., 2018, 2019) represent commercial whitefish fishing in the GoB both spatially and temporally. Samples were from fish quarterly bought from unselected catch of fishermen along the coast of the GoB and covering all fishing methods. For the analyses the GoB was split into the northern part (the northern Bothnian Bay), covering ICES rectangles 1–16 (between 66°N and 64°N), and the southern part (the southern Bothnian Bay and the Bothnian Sea), covering ICES rectangles 17–47 (64°N–60°30'N; Fig. 1). The northern and southern samples were analysed separately, because the fishing and growth rate of anadromous whitefish differ between these areas (Lehtonen, 1981; Hägerstrand et al., 2017; Kallio-Nyberg et al., 2019). The median mesh size used in the gill net fishing for all whitefish forms is smaller (28 mm from knot to knot) in the northern than in the southern GoB (40 mm) in the unbiased sample from the commercial catch in the Gulf of Bothnia in 1998–2011 (Kallio-Nyberg et al., 2018). The southern anadromous stocks migrate only in the southern part of Gulf of Bothnia, but northern stocks migrate in the both, southern and northern sea areas (Leskelä et al., 2002; Leinonen et al., 2020).

In the Finnish coastal area, two forms of whitefish (*Coregonus lavaretus*) occur, namely anadromous and sea-spawning forms (Kallio-Nyberg et al., 2019). These two forms were separated from each other by gill raker counts, growth rate, size and maturation and spawning place (Lehtonen, 1981; Himberg et al., 2015). The mean gill-raker number for anadromous whitefish was 29.6 ($n = 11799$, SD = 2.1, min = 21, max = 43). From anadromous whitefish 33% and 67% were caught in the northern and southern GoB, respectively. Mature whitefish totalled 4944 and 6021, respectively, at the age of 2–12 years. Their sex was also determined (Tab. 1).

The whitefish stocks from the rivers of the Bothnian Bay migrate to feed even as far as to the Bothnian Sea in the south (Leskelä et al., 2002), but a proportion of northern anadromous whitefish remain in the Bothnian Bay near their home rivers (Lehtonen and Jokikokko, 2002; Hägerstrand et al., 2017; Jokikokko et al., 2018). For most whitefish the gillrakers were counted and the age, sex, maturation, total length (mm) and weight (g) were determined. Ageing of fish was based on otoliths which were cut and grinded to show the growth rings and the reading was made with a microscope. Based on the maturation state, the anadromous whitefish were divided into immature fish with no sign of maturation in the ovarian, and mature fish, which were identified as being able to spawn in the catch year according to Kesteven (1960). The first sea year for whitefish was considered to be the next whole year after the year of hatching or release (1–12 months). The whitefish were aged and their form and maturation was identified by professional personnel in LUKE.

The fishermen reported the fishing site, date and the gear used. The whitefish samples were caught with trap nets (34%) and gillnets (66%). The most important fishing months were August (18.9%) and September (24.8%) in the southern GoB and June (19.4%) and September (33.8%) in the northern GoB, when all male and female whitefish were included in the study (south: $n = 11\ 578$; north: $n = 6045$).

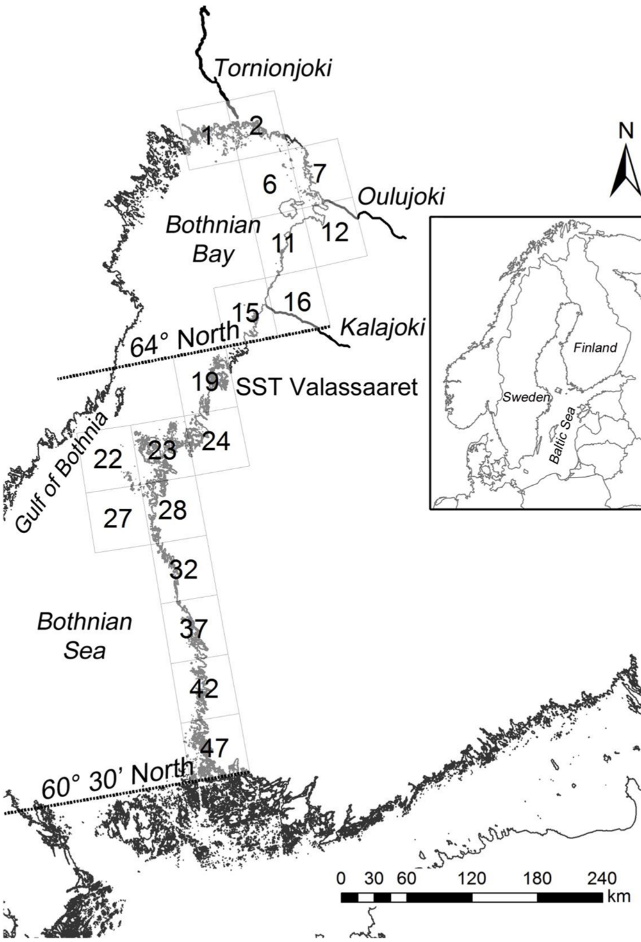

Fig. 1. The northern Gulf of Bothnia, covering ICES rectangles 1–16 (between latitudes 66°N and 64°N), and the southern Gulf of Bothnia, covering ICES rectangles 17–47 (between latitudes 64°N and 60°30'N). The whitefish (*Coregonus lavaretus*) samples were collected in the indicated rectangles in 1998–2014. Rivers: 1 = Tornionjoki, 2 = Oulujoki, 3 = Kalajoki. Sea surface temperature measurement site: Valassaaret station.

2.2 Statistics

The age distributions of mature female and male anadromous whitefish caught in both the northern and southern GoB were calculated and the differences between sexes and areas were tested using the χ^2 test during 1998–2014. Age groups were excluded from the χ^2 test if their sample size was under 5. The median age for the sexes in the south and north was calculated and the differences were tested using the Kruskal-Wallis test. Also the mean age for sexes was calculated and the normality of age distribution was tested using Kolmogorov-Smirnov –test andnon-parametric testing was applied due to the lack of normality.The younger age groups (2, 3, 4, 5, 6, 7 years) were separate and older (8–12 years) age groups were pooled in age distribution during 1998–2014, and the proportion of the mature fishin these seven groups were calculated separately. All mature fish in the sample independent from the catch months were included.

The change in the mean catch age with time (1998–2014) was analysed using linear regression, and the sexes were analysed separately for the northern and southern GoB (Results in Appendix: Mean age of whitefish in relation to catch year; Fig. A.1).

Changes in the proportions of the young (2–4 years, $n = 4620$) and old (5–12 years, $n = 6345$) age groups were explained by year (1998–2014, continuous variable), sex, and area (northern and southern GoB) in a binomial regression model as applied in Saloniemi et al. (2004). The two-year-old fish were the youngest fish in the sample, and halving the data to groups 2–4 and 5–12 years old gave close to equal number of fish in both age groups and four- and five-year-old fish were the most common the data (Appendix: Proportion of old mature fish and maturation rate at age group, Tab. A.1).

Trends of maturation age by year (1998–2014) were analysed by calculating the proportion of mature individuals in 4- and 5-year-old fish in the northern and southern GoB. The probability of anadromous whitefish being mature (binomial mature vs. immature) at the age of four or five years was analysed according to binomial regression models, when sex, sea area (southern and northern) and year, and their

Table 1. Age distribution (%) and median age (md) with quartiles (q1–q3) and mean age of mature anadromous male (M) and female (F) whitefish (*Coregonus lavaretus*) in the northern and southern Gulf of Bothnia in 1998–2014.

Area	Sample	Age (%)							Age	Age
Sex	*n*	2	3	4	5	6	7	8–12	md (q1–q3)	mean (std)
North (M)	3156	0.1	3.9	35.0	32.7	18.1	6.9	3.3	5 (4–6)	5.0 (1.2)
North (F)	1788	0.0	0.8	16.7	37.1	26.1	11.9	7.4	5 (5–6)	5.6 (1.2)
South (M)	3351	0.4	12.9	45.2	32.8	7.3	1.0	0.4	4 (4–5)	4.4 (0.9)
South (F)	2670	0.4	10.5	30.9	37.1	16.2	3.9	1.0	5 (4–5)	4.7 (1.1)

Number of fish = n. The P-value of the goodness-of-fit test (Kolmogorov-Smirnov-test) for normal distribution for each four groups was $P < 0.010$.

Table 2. The proportion of mature anadromous whitefish (%; *Coregonus lavaretus*) in different sea age groups amongmales (M) and females (F) in the northern and southern Gulf of Bothnia in 1998–2014.

Area	Immature	Mature	Proportion (%) of mature whitefish in age groups						
Sex	*n*	*n*	2	3	4	5	6	7	8–12
North (M)	241	3156	40.0	75.6	94.1	94.4	92.4	93.6	94.6
North (F)	319	1788	0	20.6	76.1	87.7	89.1	94.7	97.1
South (M)	2041	3351	28.0	49.2	62.8	67.6	67.4	73.3	92.3
South (F)	1969	2670	28.2	41.2	45.4	69.1	82.2	90.5	96.3

The age groups 8–12 years are pooled. Number of fish = *n*.

interactions were used as predictors (Appendix: Proportion of old mature fish and maturation rate at age group, Tab. A.2). Only fish caught in June–December were included, because whitefish spawn in late autumn (Lehtonen, 1981).

The increase in length was analysed as a function of age (in months) and sex for both study periods. At first, the sample was divided to two periods: early (1996–2002) and later (2003–2009), because we wanted to study first the change separately in both periods. To account for non-linear trends, the time spent at sea was also included in the squared form (month*month) in the models. The individual fish aged 3–6 sea years (25–72 months) caught in the GoB (rectangles 17–47) were included, and the body length of whitefish was log-transformed to normality (Appendix: Growth of anadromous whitefish, Tab. A.3). Next the increase in size was also analysed by including the period as a separate predictor in the previous model (Appendix: Growth of anadromous whitefish, Tab. A.4).

Associations between the mean age of mature fish of year class and environmental factors experienced by this year class was analysed using Spearman correlation. The annual environmental factors were the mean sea surface temperature (SST) in June measured weekly (4–5 times per month)in Valassaaret (63°44’N, 21°07’E) and the seasonal NAO index in June to August (Hurrell and National Center for Atmospheric Research Staff, 2016). The year class experienced the annual SST average in June in third sea year (25–36 months at sea). Linear regression was also used to test if the June SST (in the third summer of the year class) and NAO index (in the second summer of the year class) predicted the age of the mature females of the year class.

Valassaaret station is located in the middle of the feeding areas of several anadromous whitefish stocks (Koljonen et al., 2019; Leinonen et al., 2020). SST has increased in the Baltic Sea in last decades (Jylhä et al., 2009). During positive seasonal NAO index westerly winds and a mild marine climate are dominant in summer, while during negative seasonal NAO index, east winds and continental climate dominates in Europe (Hurrell and National Center for Atmospheric Research Staff, 2016). Here it was used NAO index in June to August, which the year class was experienced in their second sea year (13–24 months at sea; January–December) The NAO index in the summer months is used in this research, because the growth of whitefish is highest in summer. NAO index in the early sea-migration period, in the second summer of the year class was used, since the maturation of the year-class begins at this point. All statistical analyses were conducted with SAS 9.4 software package (SAS Institute Inc, Cary, North Carolina).

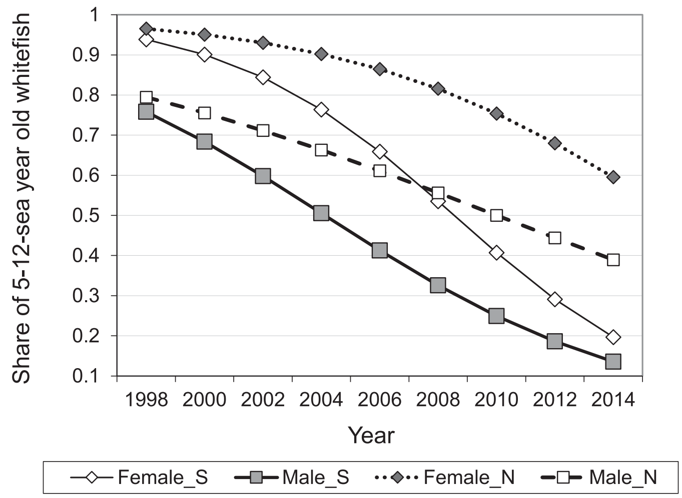

Fig. 2. The predicted share of 5–12-year-old mature female and male anadromous whitefish (*Coregonus lavaretus*) in the catch in the northern (N) and southern (S) Gulf of Bothnia (GoB) in relation to the catch year (1998–2014). The response variable was classified as young (age 2–4) or older (age 5–12 years) fish. The age group, sex and area are predictors (model Tab. A.1). Sample sizes for young and old fish 4620 and 6345 in GoB, respectively.

3 Results

During the study period, 1998–2014, most mature whitefish were four or five years old in the GoB (Tab. 1). Fish were younger in the south compared to the north (Kruskal-Wallis; median length: males: df = 5, $\chi^2 = 544.9$, $P < 0.001$; females: df = 5, $\chi^2 = 468.9.1$, $P < 0.001$ [Tab. 1]). The youngest age in the catch was two both in the north and south, and even some of them were mature (see Tab. 2).

The share of older whitefish (5–12 sea years) among the mature stock decreased from year to year in 1998–2014, whereas the proportion of younger fish (2–4 sea years) increased in the sea catch in the southern and northern Gulf of Bothnia (Fig. 2). The proportion of older (5–12 sea years) mature females in the stock near the home rivers in north decreased from 97% to 60% and that of males from 79% to 39% from the beginning of the study period in 1998 until the end in 2014 (Fig. 2; models shown in Tab. A.1).

At the same time, the proportion of mature fish among young age groups increased. The proportion of mature whitefish at the age of four increased among fish caught in

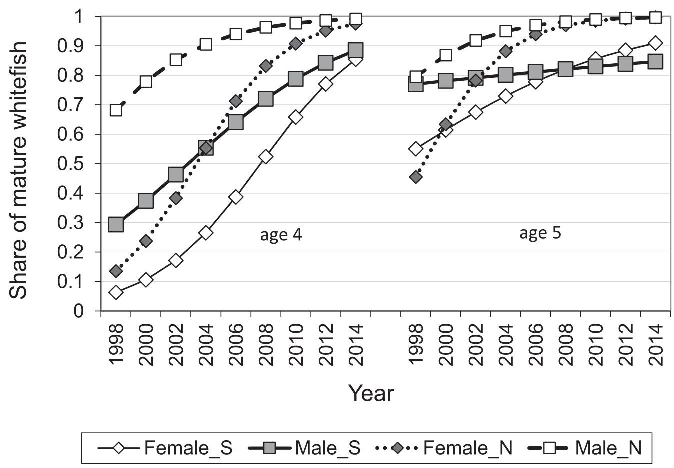

Fig. 3. The predicted proportion of mature female and male anadromous whitefish (*Coregonus lavaretus*) in relation to the catch year (1998–2014) among four- (age 4) and five-year-old (age 5) mature and immature fish caught in June–December in the southern (S) and northern (N) Gulf of Bothnia (models, Tab. A.2). Sample sizes for mature and immature fish 3479 and 1668 at age 4 and 3260 and 644 at age 5, respectively.

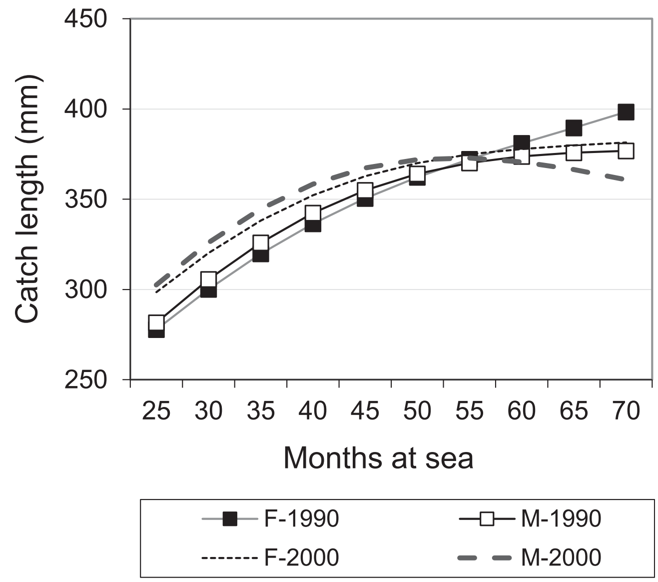

Fig. 4. Predicted length of individual anadromous female (F) and male (M) whitefish (*Coregonus lavaretus*) in relation to time (months) spent at sea in two year-class periods (1996–2002, 2003–2009; symbols: 1990 and 2000, respectively) in the Gulf of Bothnia according to linear regression model. The whitefish captured by trap and gill nets in the third-sixth sea year (25–72 months; 25–36 months = the third year; 37–48 = the fourth year, 49–60 = the fifth year, 61–72 = the sixth year) are included (sample size = 12653). The length is log-transformed (natural) in the model, but transformed back to linearity in the figures. Sample size for earlier and later periods, $n = 6151$ and $n = 6516$, respectively (Tab. A.4).

June–December in the GoB. The proportion of mature four-year-old females increased from 13% to 98% and that of males from 68% to 99% in the northern sea area from year to year in 1998–2014, i.e., practically all four-year-old fish were mature at the end of study period (sex: $P < 0.001$; catch year: $P < 0.001$; model: Appendix: Tab. A.2 [Fig. 3]). In the southern GoB, the proportion of mature fish increased more among females (6% → 85%) than males (29% → 89%), with a significant difference between the sexes (sex*catch year: $P < 0.001$). The same trend is seen among five-year-old fish (Fig. 3).

Growth was modelled using age (25–72 months) and sex as predictors (Appendix Tab. A.3) and finally by including the year period as a separate predictor in the previous models (Fig. 4; Appendix Tab. A.4). The catch length of sexes was different in both year-class periods, the difference between sexes was larger in the later period (Fig. 4; Tab. A.4). The young fish grew faster in the period 2003–2009 than in the period 1996–2002. In contrast, the growth of old fish declined in the later period (Tab. A.5). The period was statistically significant when it was included in the model (Tab. A.4).

There was a significant negative correlation between the mean age of mature whitefish of the year class and the SST (Valassaaret station, June) experienced by this year class in its third sea summer (Fig. 5; Tab. 3). In addition, there was a significant positive correlation between the mean age of mature whitefish of the year class and the seasonal NAO index in June to August in the second summer of the year class (Tab. 3), meaning that the marine climate in summer months (NAO high) was associated with the higher age of mature anadromous whitefish.

The mean sea surface temperature in June in the third sea year of the year class was used to predict the sea age of the mature females of the year class in the southern Gulf of Bothnia (Linear regression model: Age (year) = 7.77–0.280 × SST, $F_{(1,12)} = 23.11$, $P < 0.001$, $R^2 = 0.658$ [Fig. 6]). High summer SST was associated with a younger mean sea age of the year class. If the NAO index was added to the same model too, only SST explained the sea age of females of the year class.

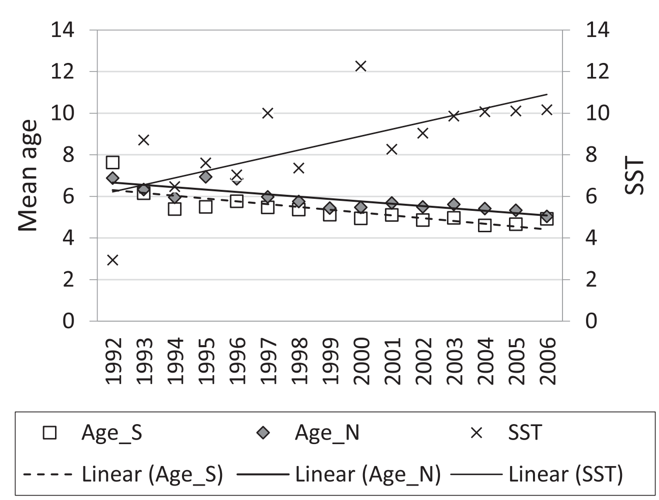

Fig. 5. The mean age of anadromous female whitefish (*Coregonus lavaretus*) in the southern (Age_S) and northern (Age_N) Gulf of Bothnia in the year classes 1992–2006 in their third sea year and sea surface temperature (SST) at the Valassaaret station. The linear trends of the mean age and SST are shown. Correlation between the mean age and SST: north: $P = 0.003$; south: $P = 0.004$.

Table 3. Spearman correlation coefficient (*r*) between the mean age of anadromous *Coregonus lavaretus* year class and the annual sea surface temperature (SST) or between the seasonal (June–August) NAO index in the northern and southern Gulf of Bothnia.

Area	Sex	Correlation between mean age and SST at Valassaaret			Correlation between mean age and NAO index		
		r	*P*	*n*	*r*	*P*	*n*
North	Male	−0.662	0.005	16	0.507	0.037	17
North	Female	−0.688	0.003	16	0.613	0.008	17
South	Male	−0.538	0.058	13	0.395	0.116	17
South	Female	−0.723	0.004	14	0.574	0.016	17

Number of years = *n*. Significance = *P*. The SST in June was measured in the third sea year of the year class and the NAO in June to August was measured in the second sea year of the year class.

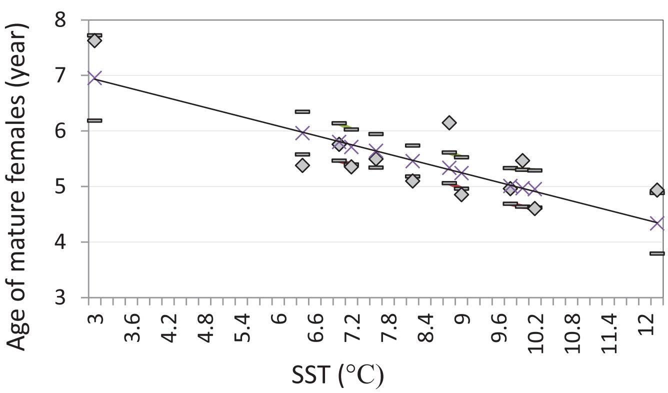

Fig. 6. Model for the dependence of the mean age of mature whitefish on sea surface temperature (SST) in June in Valassaaret. The model predicts a linear trend (continuous line) between the mean age of mature females of the year class and June SST in the third summer of the year class. The 95% confidence limits of the mean (broken lines) and observations (diamond) are presented.

4 Discussion

The age of mature fish, maturation at a specific age, and the growth rate of the anadromous whitefish changed dramatically in the GoB during 1998–2014, and these age changes were likely linked to climatic changes and fishing.The used data was temporally and spatially unbiased sample from the GoB whitefish fishing (Kallio-Nyberg et al., 2018, 2019), thus the decreased proportion of the old (6+ and older) mature whitefish in the northern GoB, near the home rivers of the anadromous whitefish stocks suggest that the age distribution of spawning stocks have changed. A decreasing trend in the whitefish catch size during upstream migration has been observed in the Kalajoki and Tornionjoki rivers (Aronsuu and Huhmarniemi, 2004; Jokikokko and Huhmarniemi, 2014), suggesting also that spawners are younger and smaller than earlier. In this study, the sea age of mature anadromous whitefish decreased with time, and in the same period sea surface temperature increased in the GoB. Increased environmental temperature has reported to be an indirect or direct influence on developmental rate and maturation (Jonsson and Jonsson, 2009; Pankhurst and Munday, 2011). The climatic conditions and temperature experienced by fish in their development affect their later life history phase (Jonsson et al., 2005) and even traits in next generation (Jonsson and Jonsson, 2016). Here, it was used only June SST in the third summer in the analysis between temperature and age of mature females, but is likely that temperature has increased also in other phases of the year class over time. Fish species have optimum temperature and thermal limits for growth and increase of warming within lowest thermal limit and optimum temperature usually increases growth rate (Elliot and Elliot, 2010) and when growth rate is in interaction with maturation; then climatic-induced increased growth usually tends to lead to earlier maturation (Neuheimer and Grønkjær, 2012).

However, the selective effect of gill-net fishing on the age of mature fish cannot be excluded. Selective fishing has been shown to be the most important driving factor favouring early maturation (Jørgensen et al., 2009), for instance, in pikeperch (Kokkonen et al., 2015). Earlier studies on the anadromous whitefish in the GoB have provided evidence of both selective fishing (Lehtonen and Jokikokko, 2002; Heikinheimo and Mikkola, 2004) and annual and long-term changes in the sea water temperature (Mackenzie et al., 2007; Siegel and Gerth, 2017). Kallio-Nyberg et al. (2019) reported a link between the improved growth of young and small whitefish and increasing air temperature in the GoB. This same whitefish catch data shows that the growth of the fast-growing anadromous whitefish and slow-growing sea-spawning whitefish differed between 1998 and 2014 in the GoB. The catch size-at-age of the small sea-spawning whitefish was increasing, but the large anadromous whitefish was decreasing, which suggests selective fishing against fast growth rate, large size of spawners and late maturation (Kallio-Nyberg et al., 2019). Also here the growth rate of old anadromous whitefish decreased from year class period 1996–2002 to period 2003–2009 (Fig. 4). Age and age-specific size has decreased also in the spawning stock of the anadromous whitefish in the River Kemijoki (Kallio-Nyberg et al., 2020).

On average, males reached sexual maturity one year earlier than females among all mature whitefish in this study (1998–2014). During 1999–2002, mature females were mainly aged five and six and males were aged four and five in the Bothnian Bay (Leskelä et al., 2004). The shift in the maturation rate differed between the sexes: the proportion of maturating 4–5 year-old whitefish increased faster among females than males, and the size of six-year-old females decreased, which suggests that the present selection pressure is stronger in the life-history traits of females compared to males. The female fecundity and egg size increase with body size (Szczepkowski et al., 2010).

Thus, an earlier allocation of resources to reproduction instead of growth reduces the proportion of larger and older females in the spawning stock, which probably decreases the fitness of the stock (Birkeland and Dayton, 2005). Regarding the whitefish, the decreasing size of female spawners, which has already happened (Kallio-Nyberg et al., 2020), likely leads to decreasing reproductive capacity of the natural stocks.

The gill net is a selective item of fishing gear that effectively takes the fastest growing, largest individuals, thus affecting the size and sea-age distribution of the stock (Heikinheimo and Mikkola, 2004). The most anadromous whitefish in GoB are caught by selective gill nets (Jokikokko et al., 2020), and e.g., in commercial fishing approx. 80% from catch is from gillnet fishing and 20% from fyke-net fishing. The mesh size in gill nets decreased in the Bothnian Bay during 1998–2011 (Kallio-Nyberg et al., 2018), which likely increased selective effect of this gear. It is probable that this has targeted fishing on relatively late-maturing, large and old females in the GoB, and small individuals have had a higher probability of reproducing than late-maturing fish. Known responses to gill-net fishing include earlier maturation (Kokkonen et al., 2015) and a decreased growth in older whitefish (Heikinheimo and Mikkola, 2004; Aronsuu and Huhmarniemi, 2004; Kallio-Nyberg et al., 2019). The age structure and maturity stages observed here in whitefish are likely to be responses to the combined effects of fishing and climate-induced changes. Selective fishing increases the proportion of small and likely young fish in the spawning stock (see Jokikokko et al., 2018), while a warming climate increases the growth rate and leads to maturation at a younger age. When the size-at-age increases, the fish are recruited at a younger age for fishing.

Simultaneous selective fishing and increasing temperatures may compensate each other. In many cases, the effects of fishing-induced changes may lead to the under estimation of the effect of global warming. An increasing SST increases the growth rate, independent of the time spent at sea, but this fast growth rate is not realised in older age groups due to the counteracting effects of selective fishing. However, new data from Koljonen et al. (2019) and Leinonen et al. (2020) indicates that whitefish fishing targets mixed anadromous whitefish stocks. Thus, the change in the vitality of stocks and variation in stocking numbers may also interact with observed changes in the growth pattern. Stockings are done annually and mainly with anadromous whitefish stocks for compensatory purposes in dammed rivers running to the northern Gulf of Bothnia but not anymore for common-good as in 1960s–1980s (Jokikokko and Huhmarniemi, 2014).

The changes in fish species size and maturation due to fishing or climate-induced evolution can have major ecological, genetic and economic consequences (Daufresne et al., 2009; Sheridan and Bickford, 2011; Uusi-Heikkilä et al., 2015). Larger fish species, in particular, decrease in abundance and size (Todd et al., 2008; Genner et al., 2010). The whitefish catches in commercial fishing have decreased during this century in the GoB, but part of this decrease is probably due to changes in fishing and a reduction in stocking (Jokikokko and Huhmarniemi, 2014). Other factors, such as the low price and decreasing demand for small sea spawning whitefish, increasing number of seals that both consume whitefish and disturb fishing (Hansson et al., 2017; Tverin et al., 2019), or fishing regulations, have reduced the profitability and hence the intensity of gill-net fishing (Söderlind, 2004; Jokikokko et al., 2018).

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Appendix: A

A.1 Mean age of whitefish in relation to catch year

The annual mean age of male and female whitefish decreased over the years (1998–2014) both in the northern and southern Gulf of Bothnia (GoB; Fig. A.1). The annual mean age of female and male fish covaried in both areas (northern GoB: $r = 0.784$, $n = 17$, $P < 0.001$, and southern GoB: $r = 0.836$, $n = 17$, $P < 0.001$).

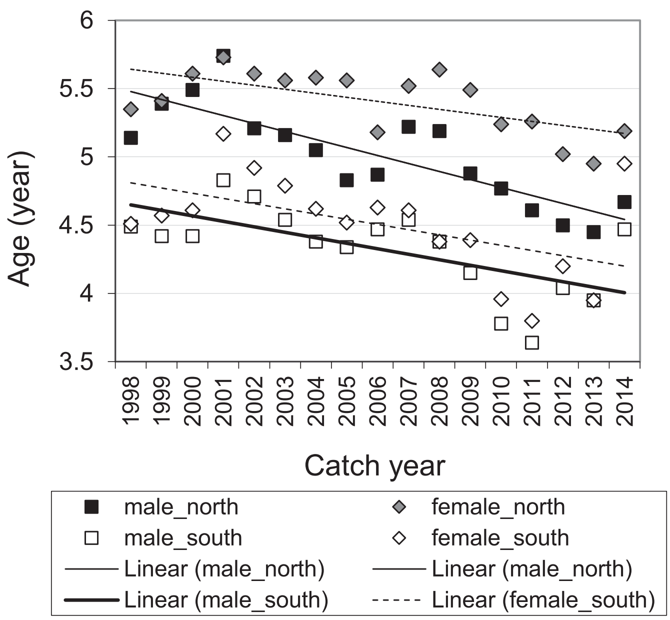

Fig. A.1. The annual mean age of anadromous male and female whitefish (*Coregonus lavaretus*) age classes in the catch years 1998–2014 in the northern (north) and southern (south) Gulf of Bothnia. The mean annual age decreased over 1998–2014 (regression for males in north: mean age = 122.382 – 0.058 × year, $F_{1,15} = 32.23$, $P < 0.001$, $r^2 = 0.661$; females in north: mean age = 64.824 – 0.029 × year, $F_{1,15} = 11.01$, $P = 0.005$, $r^2 = 0.423$; males in south: mean age = 84.170 – 0.039 × year, $F_{1,15} = 10.22$, $P = 0.006$, $r^2 = 0.405$; and females in south: mean age = 80.801–0.038 × year, $F_{1,15} = 5.59$, $P = 0.032$, $r^2 = 0.272$).

A.2 Fishing season and sample time

The fishing season within the period from June–December started earlier in the northern GoB (month = 33.051 – 0.012 × catch year; $F_{1,1569} = 2.50$, $P = 0.001$) and in the southern GoB (month = 36.127 – 0.014 × year; $F_{1,2331} = 4.12$, $P = 0.001$) when five-year-old fish were included. The median sample month in the northern GoB for five-year-old males was 9 (= September; quartiles: 8–9) ($n = 917$) and that for females was 9 (7–9; $n = 654$). In the southern GoB, this was 8 both for males and for females ($n = 1281$, $n = 1052$, respectively) when June–December sample sizes were included in the models.

A.3 Proportion of old mature fish and maturation rate at age group

Table A.1. Predicted share of the 5–12-year-old mature whitefish in the northern and southern Gulf of Bothnia in relation to the catch year and sex.

Effect	DF	F-value	*P*	AIC
Sex	1	37.67	<0.001	12651.8
Area	1	46.08	<0.001	
Year	1	766.98	<0.001	
Sex*area	1	16.65	<0.001	
Sex*year	1	37.13	<0.001	
Area*year	1	46.76	<0.001	

The response variable was classified as young (age 2–4) and older (age 5–12 years). The fish caught in January-December included.

Table A.2. Model for the proportion of mature four- and five-year-old whitefish in the Gulf of Bothnia during 1998–2014.

Group	Effect	DF	F value	*P*	AIC
Age 4	Sex	1	26.24	<0.001	3124.7
	Sea area	1	5.30	0.0214	
	Year	1	408.02	<0.001	
	Sex*area	1	13.45	0.000	
	Sex*year	1	25.83	<0.001	
	Area*year	1	5.44	0.019	
Age 5	Sex	1	16.52	<0.001	4894.0
	Sea area	1	56.91	<0.001	
	Year	1	49.07	<0.001	
	Sex*area	1	5.16	0.023	
	Sex*year	1	16.41	<0.001	
	Area*year	1	57.22	<0.001	

The probability of anadromous whitefish being mature (binomial mature vs. immature) at age four or age five according to binomial regression models, when sex, sea area (southern and northern) and year and their interactions (*) were used as predictors. Sample sizes for mature and immature fish were 3479 and 1668 at age 4 and 3260 and 644 at age 5, respectively. Fish caught in June-December included.

A.4 Growth of anadromous whitefish

Table A.3. Growth models for 3-6-year-old whitefish in the GoB separately in two year-class periods.

Period	Response	Effect	DF	F value	*P*	AIC
1996–2002	Length	Sex	1, 6145	749.09	<0.001	−11338.1
		Month	1, 6145	36.78	<0.001	
		Month^2	1, 6145	20.24	<0.001	
		Month*month^2	1, 6145	13.51	<0.001	
		Month^{2*}sex	1, 6145	92.07	<0.001	
2003–2009	Length	Sex	1, 6510	1266.46	<0.001	−12328.2
		Month	1, 6510	28.75	<0.001	
		Month^2	1, 6510	11.64	<0.001	
		Month*month^2	1, 6510	4.26	0.039	
		Month^{2*}sex	1, 6510	41.87	<0.001	

Type 3 test of fixed effects for linear regression models for size-at age of individual anadromous male and female whitefish in relation to months spent at sea separately for the year class 1996–2002 and year-class period 2003–2009 in the GoB. Mature and immature whitefish which had spent 25–72 months at sea (3–6 years) were included.
*Interaction between variables.

Table A.4. Growth models for 3–6-year-old whitefish in the GoB.

Response	Effect	DF	F value	*P*	AIC
Weight	Year-class period	1, 13000	311.26	<0.001	7526.5
	Sex	1, 13000	0.76	0.3843	
	Month	1, 13000	81.00	<0.001	
	Month^2	1, 13000	46.55	<0.001	
	Month*sex	1, 13000	5.10	0.0239	
	Month*month^2	1, 13000	29.93	<0.001	
	Month^{2*}period	1, 13000	265.51	<0.001	
	Month^{2*}sex	1, 13000	14.09	<0.001	
Length	Year-class period	1, 13000	329.67	<0.001	−23722.3
	Sex	1, 13000	2.18	0.1397	
	Month	1, 13000	70.99	<0.001	
	Month^2	1, 13000	34.27	<0.001	
	Month*sex	1, 13000	8.17	0.0043	
	Month*month^2	1, 13000	18.35	<0.001	
	Month^{2*}period	1, 13000	237.61	<0.001	
	Month^{2*}sex	1, 13000	17.54	<0.001	

Type 3 test of fixed effects for linear regression models for size-at age of individual anadromous male and female whitefish in relation to months spent at sea in the two time periods (year classes 1996–2002; 2003–2009) in the GoB. Mature and immature whitefish spent 25–72 months at sea (3–6 years) were included.
*Interaction between variables.

Table A.5. Age-specific median (Md) weight (g) of anadromous male and female whitefish in two class periods (1996–2002; 2003–2009) in the Gulf of Bothnia.

Sex	Age	Period 1996–2002		Period 2003–2009		K-S
		N	Md (q1–q3)	*N*	Md(q1–q3)	*P*
Male	3	185	292 (250–346)	589	338 (287–392)	<0.001
	4	1415	382 (321–473)	1781	417 (354–516)	<0.001
	5	1358	440 (359–536)	1051	412 (348–520)	<0.001
	6	534	434 (351–552)	283	391 (328–466)	<0.001
Female	3	153	284 (231-321)	438	335 (287–372)	<0.001
	4	821	362 (309–427)	1183	391 (334–495)	<0.001
	5	1089	451 (359–617)	908	428 (352–601)	0.025
	6	603	507 (392–715)	298	413 (347–558)	<0.001

Whitefish captured by trap and gill nets in the third-sixth sea year are included. Differences in age-specific weights between periods were tested using the Kolmogorov-Smirnov test (K-S). Quartiles = q1; q3.