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Changes in the European whitefish (*Coregonus lavaretus* (L.)) population of the Kalajoki — potential consequences of the alterations of fishing patterns in the Gulf of Bothnia

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The migration and catching areas of Carlin-tagged anadromous European whitefish (*Coregonus lavaretus lavaretus*) as well as the changes in the mean size, growth and age composition of stocked whitefish migrating to spawn in the Kalajoki, a river in Finland, were studied between the late 1970s and early 2000s. After spawning, whitefish migrate to the south, mostly to the Northern Quark and the Bothnian Sea. The proportion of tagged fish caught during January–June in the southern part of the migration route increased during the study period. At the same time the mean size and growth of whitefish entering the Kalajoki was reduced. In the late 1980s and early 1990s the mean age of whitefish declined rapidly. After that, it has increased gradually. The changes in whitefish growth and age composition were connected to the increased fishing effort and the reduction of the mesh size of gill nets in the Gulf of Bothnia.

Introduction

European whitefish (*Coregonus lavaretus* (L.)) is the second most important commercial fish in the Gulf of Bothnia. The professional catch of whitefish in the late 1990s was 1100–1400 tonnes per year (about 3 million EUR) (Anon. 2001). Anadromous whitefish (*Coregonus lavaretus lavaretus*) made up 70%–80% of the catch during that time period. In addition, the recreational catch of whitefish was estimated to be 600–800 tonnes per year (Anon. 1998, 2000).

The annual catch of anadromous whitefish off the Kalajoki shore decreased after the 1950s from 45 000–60 000 kg to 8000–10 000 kg in the 1970s (Tuikkala & Pirttijärvi 1976). As in the other areas of the Bothnian Bay, the decrease was due to the collapse of natural production mainly caused by stream regulation and declined water quality (Tuomi-Nikula 1981, Hildén *et al.* 1985, Huhmarniemi & Aronsuu 2001). In the early 1980s, the stocking of one-summer-old whitefish was increased to compensate for the loss of natural production. In 1981–2000, an average of 173 000 (range 62 000–400 000) one-summer-old whitefish were stocked annually into the Kalajoki. Since 1992, larval whitefish have also been stocked into the river. In spite of stocking, the total catch of anadromous whitefish in the sea area off the Kalajoki shore remained at

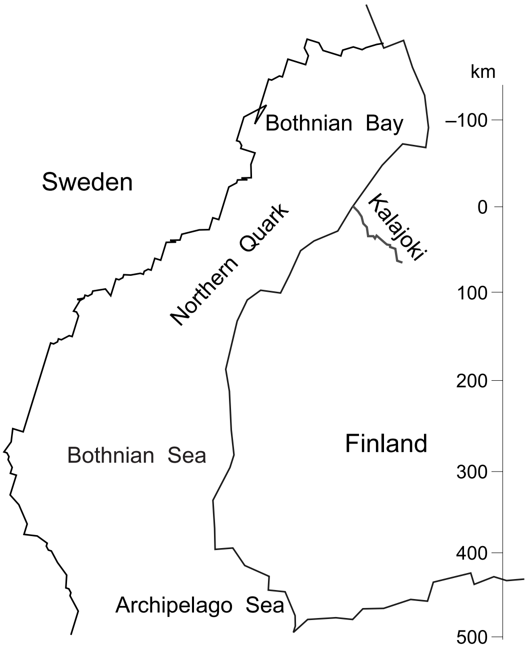

Fig. 1. A map of the study area showing the location of the Kalajoki and the north-south distance from the estuary of the Kalajoki.

the same level as in the 1970s (Huhmarniemi & Aronsuu 2001).

The fishing methods and equipment for catching whitefish in the sea developed gradually between the 1950s and late 1970s (Pirttijärvi & Ahvenniemi 1983), but in the late 1970s, fishing methods and areas in the Gulf of Bothnia began to change rapidly. Especially trap net, hooked net and gill net (bar length 37–45 mm) fishery increased in the Northern Quark between the years 1977 and 1985, while at the same time the catch in the Bothnian Bay decreased (Lehtonen & Böhling 1988). Between 1989 and 1991, the number of trap nets more than doubled in the Gulf of Bothnia (Kiuru 1995) and remained elevated until the early 2000s (Anon. 2000). The fishing effort of gill nets did not change as much as the fishing effort of trap nets, but since the late 1980s, the mesh size of bottom and surface gill nets was clearly reduced (Huhmarniemi & Salmi 1999). These alterations in fishing patterns have been assumed to cause the changes in growth rate and age structure in populations of anadromous whitefish in the Bay of Bothnia (Leskelä *et al*. 2000, Lehtonen & Jokikokko 2002).

We studied the migration and changes in the catching areas of whitefish tagged between 1977 and 1995. Furthermore, we investigated development of the mean size, growth and age composition of stocked whitefish migrating to spawn in the Kalajoki between 1984 and 2001. The changes in the catching areas, mean size, growth and age composition were linked to the modification of fishing patterns in the Gulf of Bothnia.

Materials and methods

Study area

The Kalajoki enters the Bothnian Bay at 64°16´N, 23°55´E (Fig. 1). The total length of the river is 130 km and the mean slope is 0.08%. The average annual discharge (MQ) is 29 $m^3\ s^{-1}$ (MHQ 239 $m^3\ s^{-1}$ and MNQ 4.0 $m^3\ s^{-1}$).

Stream regulation has had a negative impact on the Kalajoki. Between the 1950s and 1980s, large scale dredgings and embankments were made and hydropower dams and reservoirs were constructed. In the late 1970s, flow regulation was started mostly for hydropower and flood control purposes. During the same time period, the water quality of the Kalajoki declined mainly due to loading from agriculture and forestry. The Kalajoki is eutrophic (total phosphorus content 114 $\mu g\ l^{-1}$) and the content of suspended solids is considerably high (in April–May 30 mg l^{-1} and in other months 10 mg l^{-1}). Water pH is generally below seven and rarely drops below six.

Migration and catching areas

Migration and catching area of whitefish were studied in 1977–1995 by tagging 2185 fish entering the Kalajoki with Carlin-tags. A total of 422 specimens were tagged in 1977–1978, 1474 in 1981–1986, and 289 in 1993–1995. Tagged fish were released into the river or into the sea near the river mouth. In total, 707 tags with adequate information were returned. The number of recaptures of the fish tagged in the 1970s, 1980s and 1990s were 127, 481 and 99, respectively.

The north–south distance of the catching site from the mouth of the Kalajoki of each recaptured fish was estimated to the nearest 1 km. A fish caught south of the Kalajoki was given a positive and a fish caught north of the Kalajoki a negative value. To study migration routes fish were grouped according to the catching month (one to three months per group) and catching year (tagging year or after tagging year). Minimum, maximum, quartile and median values were calculated for each group.

The mean recapture distance from the Kalajoki was calculated to study changes in catching areas of fish tagged in different decades. The fish were also grouped into three catching periods according to the recapture month (January–June, July–August and September–December). The Kruskal-Wallis test followed by Tukey's multiple comparisons were used to compare the recapture distances in different decades. The same tests were used to study the differences in recapture distances in the catching period January–June between different decades. Nonparametric tests were used because the assumption of normal distribution was not fulfilled and data contained extreme outliers. To study the null hypothesis that the proportion of fish caught during different catching periods did not change through decades, a two dimensional 3×3 contingency table was formed and the null hypothesis was tested using chi-square test. Only fish recaptured after the tagging year were included in the above mentioned tests. The numbers of recaptures in the 1970s, 1980s and 1990s were 46, 194 and 41, respectively. The numbers of recaptures in the catching period January–June in the same decades were 13, 75 and 26.

Age, size and growth

In 1984–2001, length and age were determined for 3214 male and 1274 female whitefish caught by a fyke net in the estuary of the Kalajoki during the spawning migration from early September to late October. The same fyke net was used throughout the whole study period. The diameter of the trap hoops was 2.2 m and the mesh sizes of the nets were: fence 70 mm, wings 45 mm, and throats and enclosure 35 mm. In 1987 and 1992, trapping was prevented and in 1991 and 1998 interrupted by flood. In 1984–1997, scales were used for determining the age. In 1998–2001, otoliths were used in addition to scales.

To determine the trends of mean length at age through year classes, first the mean length at age was calculated for each year class for males and females at ages of four, five and six years. Six separate Spearman rank correlations using mean length at age and year class as variables were performed. Year classes with less than five fish at age were not included in the tests.

The differences in the mean lengths of males and females entering the Kalajoki between the catching periods of 1984–1989 and 1990–2001 were tested with a two-sample *t*-test. The Mann-Whitney test was used to compare the mean age of females between catching periods of 1984–1989 and 1990–2001. A nonparametric test was used because of the highly skewed distribution of the data. Two separate Spearman rank correlations using yearly mean age and year of catch as variables were performed to determine the trends in the mean age of males and females entering the Kalajoki between 1990 and 2001.

To determine the difference between changes in male and female subpopulations we first calculated the yearly ratio of mean length of females to that of males entering the Kalajoki. A yearly ratio was also calculated for the mean age of females to that of males. Furthermore, the ratio of mean lengths at ages four, five and six of females to those of males was calculated for each year class. Five separate Spearman rank correlations using the ratios were performed to test if there was a trend through time.

Fishing effort and catches

We used data from commercial fishing in the Northern Quark and the Bothnian Sea to indicate the changes in fishing effort and catches in the migration route of the whitefish population of the Kalajoki. The fishing effort and whitefish catch in trap nets, gill nets (bar length 36–60 mm), drift nets, and hooked nets were derived from unpublished data compiled by the Finnish Game and Fisheries Research Institute.

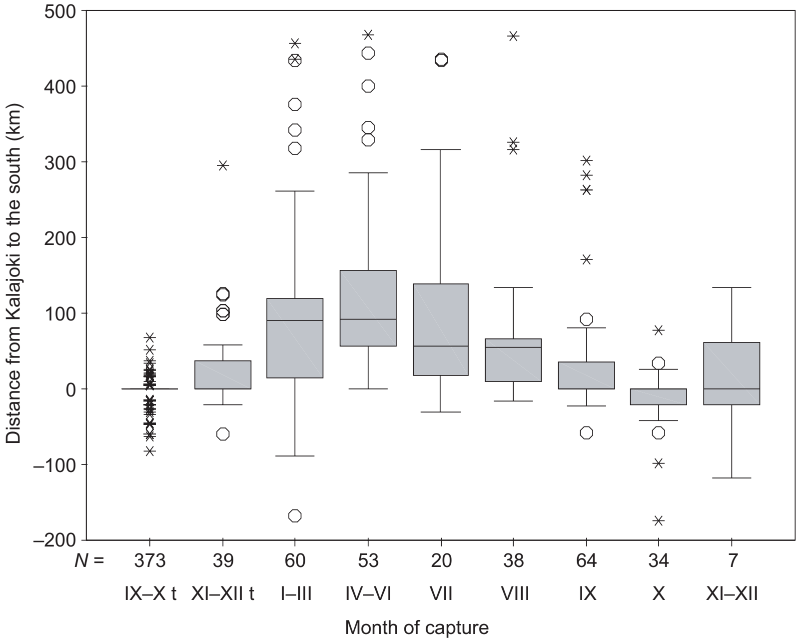

Fig. 2. Median (horizontal line), 25th percentile (the lower edge of the box) and 75th percentile (the upper edge of the box) of the recapture distance from the Kalajoki in different catching periods. Vertical lines represent the highest and lowest recapture distances that are not outliers. Outliers indicated with circles (o) are cases with values between 1.5 and 3 box lengths from the upper or lower edge of the box. Extremes indicated with asterisks (*) are cases with values more than 3 box lengths from the upper or lower edge of the box. *N* = number of returned tags, *t* = tagging year.

Results

Migration and recapture areas

The majority (60%) of the recaptured fish was caught in the Kalajoki or near the Kalajoki shore between September and December in the tagging year. Between January and June fish were mainly in their feeding grounds in the southern part of their migration route in the Northern Quark (Figs. 1 and 2). The median recapture distance of the fish was approximately 90 km south of the Kalajoki (Fig. 2). However, in April–June a few fish were captured in the Bothnian Bay adjacent to Kalajoki and some fish were caught almost 500 km south from the releasing site in the Archipelago Sea showing a wide variation in migration routes among individuals. In July and August tagged fish were caught further north than in the early summer due to the migration back to the spawning river. In September and October tagged fish were caught mainly in the Kalajoki or off the Kalajoki shore.

The average recapture distances of fish tagged in the 1970s (33 km), 1980s (74 km) and 1990s (85 km) differed significantly between all decades (Kruskal-Wallis test: $n = 241$, $H = 18.72$, $p < 0.001$, Tukey's multiple comparisons, $p < 0.001$). Also the proportion of recaptured fish in different catching seasons varied significantly between decades (chi-square test: df = 4, $\chi^2 = 18.21$, $p < 0.001$). The proportion of tagged fish caught in the southern part of the migration route in January through June increased, but decreased during the spawning migration in September–December (Fig. 3).

The average distances of recaptures during the time period January–June did not differ between decades (Kruskal-Wallis test: $n = 114$, $H = 0.616$, $p = 0.74$).

Age, size and growth

The mean size of whitefish entering the Kala-

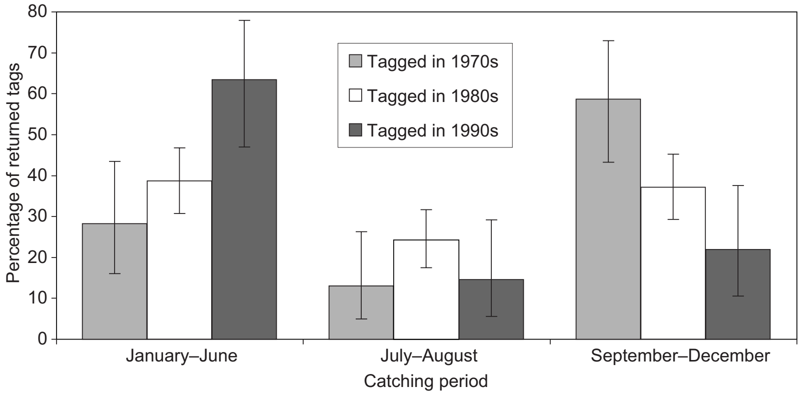

Fig. 3. The proportions (± 95% confidence interval) of recaptured fish in different catching periods in the 1970s, 1980s and 1990s.

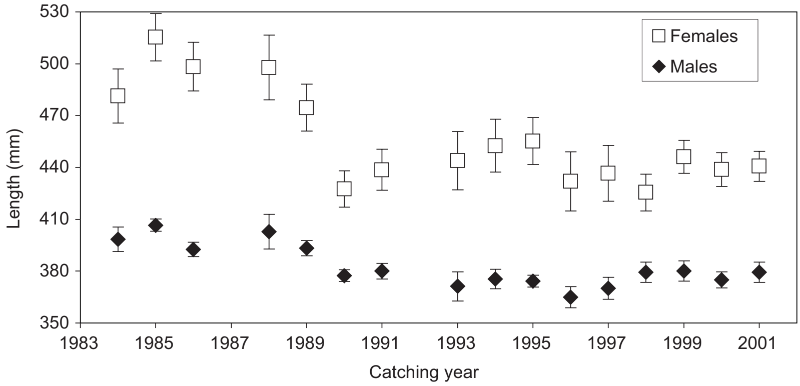

Fig. 4. The mean length (± 95% confidence interval) of female and male whitefish caught by the fyke net in the estuary of the Kalajoki during the study period.

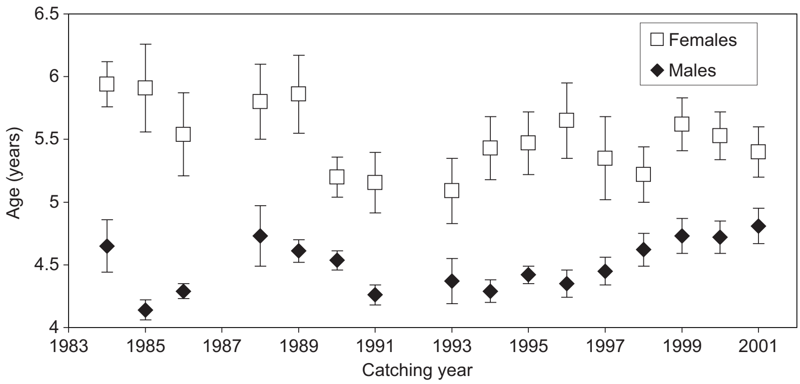

Fig. 5. The mean ages (± 95% confidence interval) of female and male whitefish caught by the fyke net in the estuary of the Kalajoki during the study period.

joki was reduced during the study period (Fig. 4). The mean length ± SD of females entering the river in 1984–1989 was 495 ± 66 mm and decreased to 440 ± 56 mm in 1990–2001. The decrease in length was highly significant (t test: df = 612, t = 13.98, $p < 0.001$). Also, the mean length ± SD of males was significantly higher in 1984–1989 (398 ± 38 mm) than in 1990–2001 (376 ± 34 mm) (t test: df = 2105, t = 16.17, $p < 0.001$).

The males entering the Kalajoki were mostly four or five and females five or six years old. Older individuals, especially large females, were observed mainly in the beginning of the study period. The mean age ± SD of females was statistically higher in the catching period of 1984–1989 (5.8 ± 1.4 years) than in the catching period 1990–2001 (5.4 ± 1.0 years) (Mann-Whitney test: n = 1274, U = 200649, $p < 0.001$, Fig. 5). In 1990–1993 the mean age

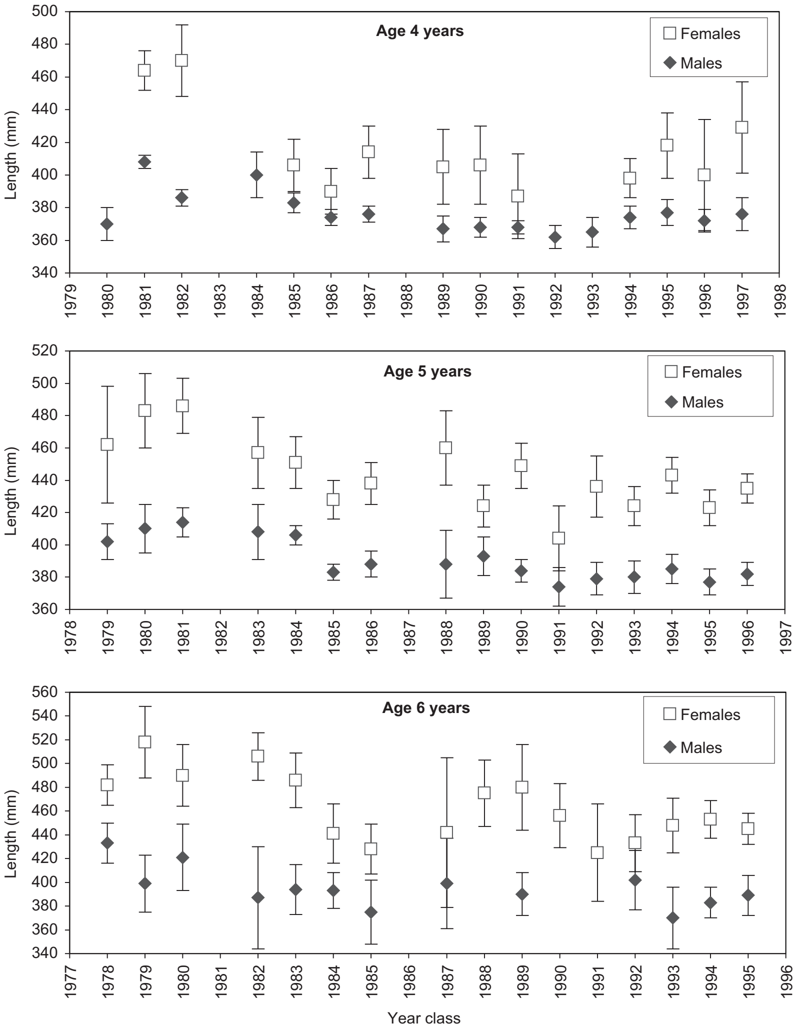

Fig. 6. The mean length (± 95% confidence interval) of females and males entered to the Kalajoki at the ages of 4, 5 and 6 years.

of females was only 5.1 (± 0.9) years. Between 1990 and 2001 the mean age of males entering the Kalajoki increased significantly (Spearman rank correlation: $n = 11$, $r_s = 0.755$, $p < 0.001$). In addition, the mean age of females showed a positive trend after 1990, but the trend was not statistically significant (Spearman rank correlation: $n = 11$, $r_s = 0.564$, $p > 0.05$).

The growth rate of whitefish decreased during the study period (Fig. 6). The mean lengths of males and females at ages 5 and 6 declined significantly during the study period (Spearman rank correlations: $p < 0.05$). The mean lengths of males and females at age 4 did not show a statistically significant trend ($n = 16$, $r_s = -0.385$, $p > 0.05$ and $n = 12$, $r_s = -0.280$, $p > 0.05$, respectively).

The ratio of the mean length and the mean age of females to those of males decreased significantly during the study period (Spearman rank correlations: $n = 16$, $r_s = -0.653$, $p < 0.01$ and $n = 16$, $r_s = -0.641$, $p < 0.01$, respectively), but the ratio of the length at ages four, five and six of females to those of males did not show any trend through time (Spearman rank correlations: $p > 0.5$).

Fishing effort and catches

The fishing effort of trap nets in the Northern Quark and the Bothnian Sea more than doubled between the years 1989 and 1991 (Fig. 7). In

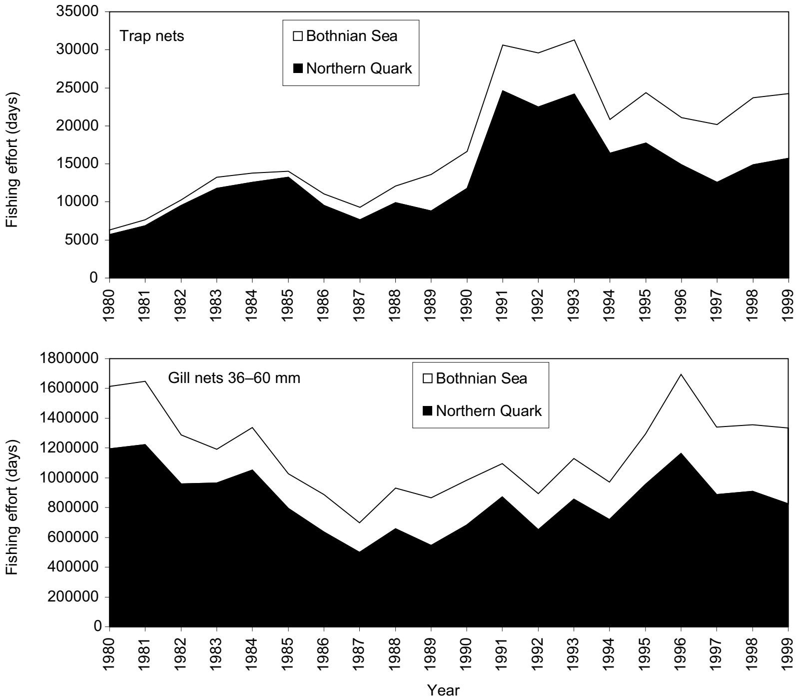

Fig. 7. The effort (days) of the commercial trap net and gill net (bar length 36–60 mm) fishing in the Northern Quark and the Bothnian Sea between 1980 and 1999.

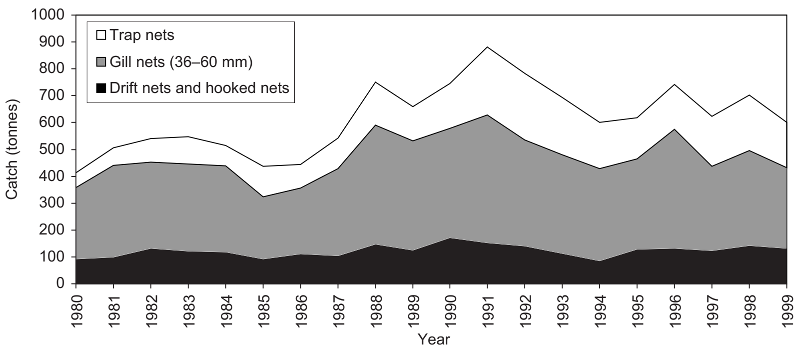

Fig. 8. The commercial catch of anadromous whitefish with trap nets, gill nets (bar length 36–60 mm), drift nets and hooked nets in the Northern Quark and the Bothnian Sea between 1980 and 1999.

the 1980s, less than 20% of the anadromous whitefish were caught with trap nets, while in the 1990s, the proportion was approximately 30%. The effort of gill net (mesh size 36–60 mm) fishing has shown an increasing trend since the late 1980s. In the early 1980s, the commercial catch of anadromous whitefish in the Northern Quark and the Bothnian Sea was on average 490 tonnes. The catch began to increase by the late 1980s and it peaked in 1991 with the total catch over 880 tonnes (Fig. 8). Later in the 1990s the commercial catch ranged between 600 and 785 tonnes.

Discussion

Post-spawned fish spend more than half of the year in their southern feeding grounds situated mainly in the Northern Quark, where the growing season is longer and the abundance and quality of food items, such as macrobenthos, is much higher compared to the Bothnian Bay (Lehtonen & Himberg 1992). Most of the one-summer-old whitefish stocked into the Bothnian Bay migrate to the southern feeding areas during the following summer after stockings and stay there several years before their first spawning migration at the ages of four to six years (Leskelä *et al*. 2002). Our results from taggings showed that the proportion of the post-spawned fish caught in their southern feeding grounds in the Northern Quark and the Bothnian Sea in the first half of the year has increased during the last two decades. In the 1970s anadromous whitefish were mostly caught in August and September during the spawning migration in the Northern Quark and the Bothnian Bay with trap net and large-meshed gill nets (Lehtonen & Böhling 1988).

We suggest that the main reason for the changes found in the whitefish population of the Kalajoki were alterations in the fishing patterns. It is likely that the strong increase in the fishing effort, especially in the numbers of trap nets in the late 1980s and early 1990s reduced the proportion of older individuals, thus, causing the mean size and age of whitefish entering the Kalajoki to decrease. All the equipment used for catching whitefish is size selective by nature and there is considerable variation in growth rate among individual fish of a given age. The increased fishing effort in the 1990s provided both the means and the opportunity for efficient selective removal of fast growing fish and depression of the population mean length at age. Furthermore, the mesh size of bottom and surface gill nets used for catching anadromus whitefish in the Gulf of Bothnia has been clearly reduced since the late 1980s (Huhmarniemi & Salmi 1999). That led fish to recruit earlier to the fishery and to be exposed to fishing for a longer time before the first spawning migration. In 2000, approximately 50% of the commercial catch of anadromus whitefish in the Gulf of Bothnia was captured by gill nets with 36–45 mm bar length (Anon. 2000).

By using an age-and-length structured model, Heikinheimo and Mikkola (2004) have shown that the current gill net fishing effort in the Gulf of Finland effectively removes the largest anadromous whitefish individuals, and consequently, the proportion of slow-growing individuals increases in mature age groups. The selective fishing has also affected the populations of other fish species. For example, the mean growth rate of fish in the highly exploited Atlantic cod (*Cadus morhua*) populations has decreased because of size-selective fishing mortality (Hanson & Chouinard 1992, Kristiansen & Svåsand 1998). The size-selective fishing has also been connected to the changes in populations of plaice (*Pleuronectes platessa*) (Millner *et al*. 1995) and long rough dab (*Hippoglossoides platessoides*) (Fossen *et al*. 1999).

Whitefish females are more vulnerable to fishing than males. Immature anadromous whitefish recruit to gill net fishing at the age of three to five years (Leskelä *et al*. 2002). Females recruit to fishing earlier than males due to their higher growth rate. Furthermore, females are on average one year older than males during their first spawn, and, therefore, exposed to fishing for a longer period before their first spawning migration. In our study, the relative mean length of females entering the Kalajoki decreased more than that of males. There was no significant difference in the relative decrease in growth rate between females and males, but rather the reason for more profound reduction in the relative mean length of entering females was the decrease of proportion of old females. We conclude that the current fishing pressure is so high that a smaller proportion of females is capable of avoiding fishing mortality and surviving over the age of six than in the 1980s. By the end of the study period the mean age of males gradually returned to the same level as in the beginning of the study. It seems that in the late 1990s the male population responded to the fishing pressure mainly by reduced growth rate. However, it is noteworthy that the growth and age structure in the mid 1980s had already been affected by earlier fishing (*see* Lehtonen & Böhling 1988).

Since the mid-1980s, the characteristics of the anadromous whitefish populations have also changed in the rivers Kemijoki, Oulujoki, and Tornionjoki entering the northern part of the Bothnian Bay. The mean size of whitefish entering these rivers has been reduced and the mean age has increased (Jokikokko *et al*. 1999). Lehtonen and Jokikokko (2002) concluded that changes in the anadromous whitefish populations of these rivers and in that of the Kalajoki were a result of the increased fishing effort in the southern part of the Gulf of Bothnia. They assumed that the changes were mainly due to increases in the proportion of non-migrating (slow-growing) fish in the spawning population while fishing reduced more of the migratory (fast-growing) proportion of the cohort. The numbers of recaptures of tagged fish depends on fishing effort, which seems to have increased more in the southern part of the migration route. However, large increases in numbers of sedentary, non-migratory fish should be observed as decreases in recapture distances. Our tagging data did not show significant changes in recapture distances through decades in January–June, when fish are supposed to be in their feeding grounds. This indicates that there was no major increase in the proportion of non-migratory fish in the population of the Kalajoki. However, individuals of the population in the Kalajoki showed variability in their migration behavior, which may lead to structural changes in the population when fishing effort and growth rate are variable in different areas (*see* Lehtonen & Jokikokko 2002).

In the northern part of the Gulf of Bothnia, slow-growing sea spawning whitefish (*Coregonus lavaretus widegreni* Malmgren) are caught with small mesh size gill nets and fyke nets and a high number of immature anadromous whitefish are caught as a by-catch (Lehtonen & Böhling 1988, Huhmarniemi & Aronsuu 2001). Fishing of the sea spawning whitefish has not changed much during the last two decades suggesting it has not affected the changes we found in the anadromous whitefish population. However, fishing of the sea spawning whitefish has a continuous negative impact on anadromous whitefish populations and complicates its exploitation (Lehtonen & Böhling 1988, Huhmarniemi & Aronsuu 2001).

The current fishing patterns exploit anadromous whitefish inefficiently. Most of the growth potential remains unexploited and spawning stocks remain at low levels when fish are caught as small and young in their southern feeding grounds and as by-catch of the sea spawning whitefish (*see* Jokikokko *et al*. 1997, Leskelä *et al*. 2000). It is also possible that size-selective fishing alters populations genetically by favoring slow-growing genotypes leading to lower productive capacity (Law 2000). Furthermore, the lower mean size of females leads to the lower mean fecundity. Enlarging the mesh size of gill nets used for catching anadromous whitefish would be likely to increase a total catch, the number of fish migrating to the river and also the mean size of mature fish (*see* also Leskelä *et al*. 2000).

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