

Effect of selective gill-net fishing on the length distribution of European whitefish (*Coregonus lavaretus*) in the Gulf of Finland

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The Finnish sea area is inhabited by migratory and sea-spawning forms of the European whitefish (*Coregonus lavaretus* (L.)). In the Gulf of Finland, these forms have overlapping gill-raker counts but differing growth rates. The whitefish are heavily exploited with gill nets, so an age-and-length structured model was constructed to study the effects of fishing effort and alternative mesh size restrictions. The results show that the gill-net fishing effectively removes the largest individuals from the four- and five-year-old whitefish and thus strongly affects the length distribution, decreasing the mean length of the surviving population. Consequently, the share of slowly-growing individuals increases in mature age groups. In naturally-reproducing whitefish, this might be reflected in the genetic characteristics of the population. The strength of the selective effect on different age groups depends on the fishing effort and the mesh sizes used.

Introduction

In addition to the direct effects of intensive fishing on the reproduction and yield of fish stocks, fishing selectivity may also have indirect and complicated effects that are not easily detectable (e.g. Law 2000). In theory, as in the selective breeding of fish, a genetic change in the stock can be generated over time by the repeated removal of a given kind of individuals (Policansky 1993). Fishing is practically always non-random, mostly with respect to individual size but in some cases to spatial distribution, migratory or feeding habits, or maturity. Phenotypic changes in such traits as, for instance, size-at-age or age-at-maturation, are known to take place in exploited fish stocks (e.g. Handford *et al.* 1977,

Law 2000). However, such effects of fishing are generally difficult to distinguish from the plastic responses of the fish stock to environmental or biotic factors, for instance density-dependent growth (Policansky 1993, Reznick 1993). The prerequisites for fishing-induced evolution are that the phenotypic variation in the affected trait has a partly genetic basis and that fishing causes differential reproduction of the different genotypes (Policansky 1993).

Gill nets are the most common gear type in European whitefish (*Coregonus lavaretus* (L.)) fishing in Finland. Gill nets are highly selective with respect to fish size and the fishing effort is high in the Finnish sea area where there are two whitefish forms, i.e. the migratory whitefish (*C. lavaretus lavaretus*) and the sea-spawning

whitefish (*C. lavaretus widegreni*). In the Gulf of Bothnia, these two forms can be distinguished on the basis of their gillraker counts and growth rates (Lehtonen & Jokikokko 2002), although in the Gulf of Finland these features largely overlap (Raitaniemi *et al.* 1996).

In the Gulf of Bothnia, the gill-net effort has increased during the 1990s while the mean size-at-age has been decreasing in the spawning populations of migratory whitefish (Lehtonen & Jokikokko 2002, Aronsuu & Huhmarniemi 2003). The size of a whitefish in the catch from the sea area has also declined, because of which the fishermen tend to shift to smaller and smaller mesh sizes to maintain their catches (Jokikokko *et al.* 2001). Consequently, concern has arisen that the selective effect of fishing could be involved in the observed changes in the local river-spawning whitefish stocks (Jokikokko *et al.* 2001, Aronsuu & Huhmarniemi 2003), and that this could eventually lead to permanent changes in the genetic characteristics. In the Gulf of Bothnia, the whitefish catch comprises both migratory and sea-spawning whitefish, with varying growth rates. During their long migrations the migratory whitefish are vulnerable to gill-net and trap-net fisheries with regionally differing mesh sizes (27–45 mm bar length).

The indigenous river-spawning whitefish stocks of the Gulf of Bothnia have been classified as threatened (Kaukoranta *et al.* 2000). Spawners are caught annually from the rivers and their eggs used to produce new stocking material and brood stocks that are maintained at fish culture stations. The possibility of evolutionary changes imposed by fishing is therefore worthy of concern. Fingerlings originating from these brood stocks were earlier also commonly used for stocking in the Gulf of Finland, although currently the stocking material is mostly from local spawners.

The whitefish fishery in the Gulf of Finland is less complicated. There are no original river-spawning stocks left and so the fishery is maintained by intensive stocking with one-summer-old fingerlings. The whitefish catch is taken predominantly by recreational fishermen with gill nets of mesh sizes from 45–50 mm bar length. Growth overfishing of the stocked migratory whitefish has been reported (Raitaniemi *et*

al. 1996). The sea-spawning stocks are not well-examined but have local significance, and have also been used for stocking in the sea area near to Helsinki (Jokikokko *et al.* 2001).

The most effective methods in studying the potential evolutionary effects of selective fishing are experiments and simulation (Policansky 1993). We used the data from the Gulf of Finland to examine the mechanism of selective gill-net fishing and potential effects on the length-at-age of whitefish. An age-and-length structured model was constructed to simulate the effect of fishing, using the observed growth and mortality rates and a selectivity model (Kurkilahti 1999) to estimate the catchability of each length class.

The aim of the study was to address the following questions: (1) What is the effect of selective gill-net fishing on the length distribution of the whitefish forms with the current fishing effort and mesh sizes? (2) Would a proposed larger minimum mesh size (shift from 45 mm bar length to 50 mm) moderate the effects of gill-net fishing on the whitefish?

The whitefish stocks in the Gulf of Finland

The migratory whitefish was abundant in the Gulf of Finland in the 1950s, but natural reproduction ceased during the 1960s because of damming of rivers and deteriorations in water quality (Salojärvi *et al.* 1985). Extensive stocking has produced good results and catches have risen beyond even pre-collapse levels (Raitaniemi *et al.* 1996). The spawning areas of the sea-spawning whitefish have also diminished, but there are still naturally reproducing stocks in different parts of the Gulf of Finland, for instance in the eastern archipelago off Kotka and in the sea area off Hanko at Bengtsår. However, these sea-spawning stocks make up a minor part of the catch (Jokikokko *et al.* 2001).

Migratory whitefish have been stocked into the Gulf of Finland since the beginning of the 1980s, mainly to the mouths of the Kymijoki and Vantaanjoki rivers, as one-summer-old fingerlings. The number of annually stocked fingerlings reached a peak of 1.5 million in the 1990s. Stocking is partly made in compensation for the

adverse effects of city wastewaters, and partly for maintaining the fish stocks and fishery in the sea area. According to the stocking register of the Uusimaa Employment and Economic Development Centre, stocking with the sea-spawning Bengtsår whitefish started in the sea area off the Uusimaa county in the early 1990s, and between 1994 and 1997 it comprised about one third of the total amount of whitefish fingerlings released in this area. In recent years the share of the sea-spawning whitefish has been only 5% to 9% of the stocked fingerlings.

The commercial whitefish catch from the Gulf of Finland rose from 20 to 57 tonnes during the latter half of the 1990s (Söderkultalahti 2001). However, most of the whitefish catch is taken by recreational fishers. The estimates of whitefish catch from recreational fishing in the Gulf of Finland varied between 126 and 262 tonnes between 1998 and 2001 (Anon. 2000, 2002, Toivonen *et al.* 2003). Although most of the catch (88% in 2001) is taken with gill nets (Toivonen *et al.* 2003), whitefish angling in early spring has recently become popular on the coast of the Gulf of Finland, especially in the vicinity of population centres. The anglers' share of the whitefish catch in the sea area off Helsinki rose to 28% in 2000 (Vaajakorpi 2002), but was below 10% in the whole Gulf of Finland in 2001 (Toivonen *et al.* 2003).

The minimum mesh size allowed for gill nets in the sea area of Helsinki and Espoo is 45 mm bar length. Currently, whitefish are caught with both 45 mm and 50 mm mesh sizes in the study area (Vaajakorpi 2002).

Material and methods

The study area comprised the coastal waters of the Gulf of Finland off Uusimaa County, where the large cities of Helsinki and Espoo are located (60°N, 25°E). Material was sampled from the migratory whitefish that come to spawn at the rivermouth of the Vantaanjoki in Helsinki, and from gill-net fishing under ice in winter in the sea area off Espoo from 1995 to 2001. From 2000 to 2002, the anglers' catch was sampled in early spring. In addition, the spawning population of the sea-spawning whitefish was sampled

at Bengtsår in the sea area off Hango (60°N, 23°E) in 1998.

Total length and weight of the whitefish were measured, sex was determined and scales for age determination were taken from between the ventral fins and from the abdomen above the lateral line. In addition, whenever possible, the operculum bones and otoliths were also taken.

Age was determined primarily from scales and operculum bones, and in uncertain cases also from the otoliths. The distances of annuli were measured from the operculi using a binocular microscope with a 10× magnification. Monastyrsky's method was used for the back-calculation of lengths at earlier ages (Bagenal & Tesch 1978).

The instantaneous total mortality in the completely-recruited age groups of migratory whitefish was calculated using the catch curve method (Hilborn & Walters 1992) from the age structure of the spawning population. The samples were caught with a series of gill nets of 45, 50, and 55 mm bar length, with an equal number of nets of each mesh size. In 1999, samples were taken with a trap net by the personnel of the Sports Department of the City of Helsinki. The spawning stock of the sea-spawning whitefish was caught with 45 mm gill nets only and these samples were not suitable for the calculation of mortality because of bias caused by the strong selectivity of the gear.

Length-and-age-structured model

The model was constructed for each whitefish form separately. The model starts from three-year-old individuals, the first age-group to recruit to the gill-net fishery. The mean length and standard deviation in this age group, based on the back-calculations, were used to calculate the initial frequency in each 1-cm length class, assuming a normal distribution. An equilibrium state was assumed with constant annual recruitment, growth and mortality rates.

The number of fish that die from fishing was calculated according to the equation

$$C_{a,L} = F_L(F_L + M)^{-1}N_{a,L}[1 - \exp(-F_L - M)] \quad (1)$$

and the number of surviving fish that are moved

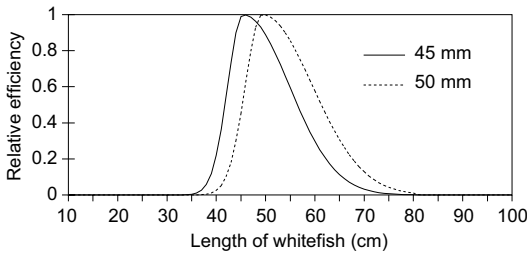


Fig. 1. Selectivity curves of gill nets with 45 and 50 mm mesh sizes (bar length) for the whitefish from the Gulf of Finland, according to the model by Kurkilahti (1999).

to the next age group ($a + 1$) to length classes ($L + g$) was calculated according to the equation

$$N_{a+1,L+g} = N_{a,L} \exp(-F_L - M) \quad (2)$$

where $C_{a,L}$ = catch in numbers from age group a and length class L , $N_{a,L}$ = number of individuals in age group a and in length class L in the beginning of the year, g = growth or length increment from age a to age $(a + 1)$ (discretized normal distribution), F_L = annual instantaneous rate of fishing mortality in length class L and M = annual instantaneous rate of natural mortality

The normal distributions of the length increments were calculated from the mean and SD in each age group, and assigned to 1 cm classes for the model. The surviving three-year-olds were then moved to the next age group and simultaneously to new length classes, according to the distribution of length increments. This procedure was repeated for successive age groups.

The fishing mortality in each length class was calculated as $F_L = q_L F$, where F = annual instantaneous rate of fishing mortality in fully recruited length classes, and q_L = catchability of the length class L , calculated with the selection model. The natural mortality (M) was assumed to be constant over the length classes.

Selection model

The selection model by Kurkilahti (1999) was used to calculate the relative efficiency of each gill net mesh size for different length classes (catchability of the length classes) of whitefish:

$$P_{ij(1)} = \exp(-\pi((m_j^*/m_i) - 1)^2 k_1^2),$$

$$(m_j^*/m_i) \leq 1 \quad (3a)$$

$$P_{ij(2)} = \exp(-\pi((m_j^*/m_i) - 1)^2 k_2^2), \quad (m_j^*/m_i) > 1 \quad (3b)$$

where m_i = size of mesh i (bar length) in millimetres, P_{ij} = relative efficiency of m_i for fish of size class j with constraint that $\max(P_{ij}) = 1$, m_j^* = optimum mesh size for fish length class j , k = factor to determine steepness of the net selectivity curve (k_1 for the ascending left limb of the curve, and k_2 for the descending right limb of the curve).

The optimum mesh size was determined on the basis of fish length using the equation

$$m_j^* = a + bL \quad (4)$$

where L = fish length in centimetres and a and b are constants.

The parameter values for the whitefish in the Gulf of Finland were $a = -13.84$; $b = 1.29$; $k_1 = 5.43$ and $k_2 = 1.81$. The resulting selectivity curves are shown in Fig. 1. In the length-age-structured model an average of these curves was used to represent the current situation, where both 45 and 50 mm mesh sizes are being used.

Results

Age distributions, growth, and mortality of the whitefish in the Gulf of Finland

In the winter gill-net fishing, the most common whitefish age groups in 45 mm mesh sizes were four and five and in 50 mm mesh sizes five and six. Older whitefish were very rare. Anglers' catches in spring included age groups from three to nine, with ages from four to six occurring most frequently and even 12-year-old specimens being caught occasionally.

The growth rates of both whitefish forms, based on back-calculated lengths from the spawning stocks, were almost equal until age three, but after that the growth of the sea-spawning whitefish decelerated so that in age groups seven and eight the difference in mean lengths was about 10 cm (Fig. 2). However, the variability of growth rate was large in both forms and no conclusions

could be drawn about the possible dependence of length increment on the starting length in each age group, in part because the material was particularly scarce in older age groups.

The annual instantaneous rate of total mortality (Z) of the migratory whitefish calculated from the spawning population sampled at the mouth of the Vantaanjoki in 1996, 1997 and 1999 varied from 1.0 to 1.4.

Modelling results

Simulation with current fishing effort and mesh sizes

The model was first run using the average selection curve for 45 and 50 mm bar lengths in gill nets and with different values of fishing mortality (F) in completely-recruited length classes, and values of 0.05 and 0.1 for natural mortality (M) (Table 1). According to the simulations, all input values (1.5 to 2.5) of F gave realistic mortalities for the migratory whitefish, and consistent values were received from the age compositions of the simulated catch and the simulated population. The mortalities of the sea-spawning whitefish were lower, due to the slower growth, which resulted in their recruitment being more gradual than that of the migratory whitefish. The difference in the mortality estimates from the simulated catch and the simulated population show that recruitment was still incomplete at the

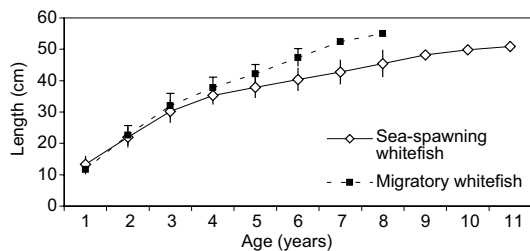


Fig. 2. Average lengths-at-age, with standard deviations, of the two whitefish forms in the Gulf of Finland: stocked migratory whitefish from the Vantaanjoki ($N = 40$) and sea-spawning whitefish from Bengtsår ($N = 32$). Lengths were back-calculated from operculum bones.

age of six years, which means that the mortality of the sea-spawning whitefish would be underestimated from catch samples.

The age compositions produced by the model were then compared with those in gill-net samples. All values of F produced an age composition in moderate accordance with the real catches. However, the age composition in the samples from gill-net catches varied annually, depending on the stocking numbers and survival of the stocked fingerlings in different year classes. On the basis of the comparisons of data and simulations, the input mortality values $F = 2.0$ (in completely-recruited length classes) and $M = 0.1$ were chosen to be used in further simulations to represent the current mortality.

The length distributions in the simulated gill-net catch and population, with the mortality values above and with one third of the recruits

Table 1. Total mortalities according to the model simulations with different input values of instantaneous fishing mortality F (in completely-recruited length classes) and natural mortality M . The real value of instantaneous total mortality Z is calculated from the simulated age composition of the population, the estimated mortality from the simulated age composition of the catch. The values of the total mortality estimates were calculated from age groups 5 to 8. For the sea-spawning whitefish, the values from age groups 6 to 8 are in parentheses.

Input parameter values in the simulation		Real value of total mortality (Z) in simulation (calculated from the population)		Total mortality (Z) estimated from the simulated catch	
F	M	Migratory	Sea-spawning	Migratory	Sea-spawning
1.5	0.05	0.94	0.67	0.97	0.43 (0.56)
2	0.05	1.19	0.74	1.16	0.53 (0.66)
2.5	0.05	1.40	0.80	1.30	0.60 (0.73)
1.5	0.1	0.99	0.72	1.02	0.47 (0.61)
2	0.1	1.24	0.80	1.21	0.58 (0.71)
2.5	0.1	1.45	0.85	1.34	0.65 (0.78)

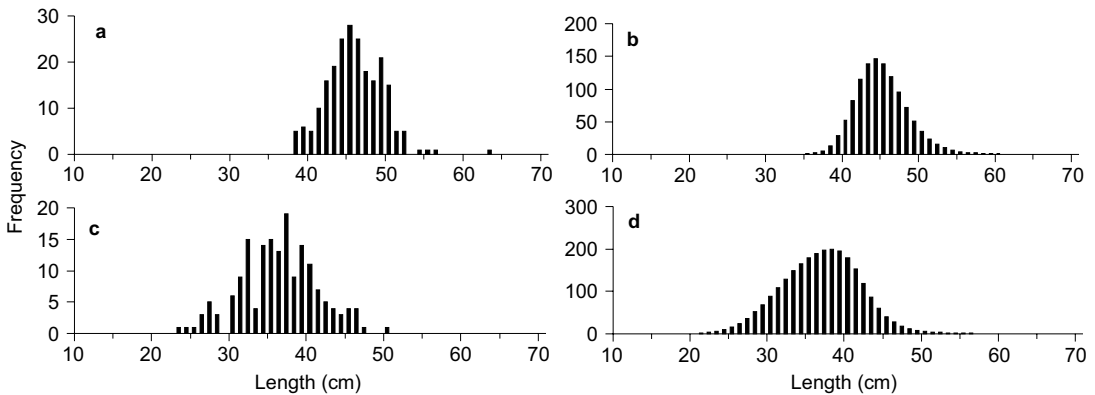


Fig. 3. Length distributions of whitefish from the catch samples and from simulations with current fishing mortality and mesh sizes, with annual recruitment of 1000 three-year-old migratory whitefish and 500 sea-spawning whitefish. — **a:** Gill-net catch (45–50 mm mesh sizes) from the Espoo sea area, $N = 223$. — **b:** Simulated gill net catch (age groups 3–8). — **c:** Anglers' catch from the Espoo sea area ($N = 172$). — **d:** Simulated population (age groups 3–8).

comprising sea-spawning whitefish, were compared with those in the real catches assuming that the angling catch represents the population in the sea (ages from three to eight). The length distribution in the gill-net catches from 1995 to 2001 from the Espoo sea area (mean length $45.4 \text{ cm} \pm \text{SD } 3.7 \text{ cm}$) was similar to the simulated gill-net catch ($44.8 \pm 3.5 \text{ cm}$) (Fig. 3). Similarly, the length distribution in the anglers' catch ($36.0 \pm 4.9 \text{ cm}$) resembled closely the simulated distribution in the whitefish population ($36.6 \pm 5.2 \text{ cm}$).

Effect of fishing on the length distribution of the whitefish

The simulation with the current fishing effort and gill nets of 45 and 50 mm mesh sizes revealed an effective removal of the larger individuals from the length distribution of the migratory whitefish, starting from age three (Fig. 4). Only a minor part of the recruits survived until their length exceeded the range of selection of the gill nets. As a consequence, the mean length of the whitefish was about 9 cm lower in the population than in the gill-net catch.

To study the effect of fishing effort and a proposed mesh size restriction (smallest allowed bar length 50 mm) on the length distribution in the population, the model was run using different values of F , with the selectivity pattern for 45 and 50 mm, and exclusively 50 mm gill nets, and the mean lengths in each age group were considered. The gill-net fishing affected the mean length of

the age groups from four to eight, i.e. the spawning stock, of both whitefish forms (Fig. 5). With the current fishing mortality (input value $F = 2$) the decrease in length compared to the unfished population was 3 to 8 cm (7% to 15%) in the age groups four to eight of the migratory whitefish, and 1 to 8 cm (4% to 16%) in the sea-spawning whitefish (Fig. 6).

The scheduled restriction with a minimum mesh size of 50 mm (bar length) would make the fishing affect the length of the age groups seven and eight of the migratory whitefish more than the current fishing (decrease in length 14% to 17%), in age group six there would be only a slight difference, and the younger age groups would be favoured by the restriction (Fig. 6). In the sea-spawning whitefish, in all age groups from four to eight the decline in mean length would be smaller (2% to 13%) with the 50 mm minimum mesh size.

Lowering the fishing effort would counteract the decline in mean length more effectively than the mesh size restriction, especially with the migratory whitefish (Fig. 5).

Discussion

Effects of selective fishing

The simulation results showed that the gill-net fishing is able to cause a drastic effect on the mean lengths-at-age of the mature whitefish at

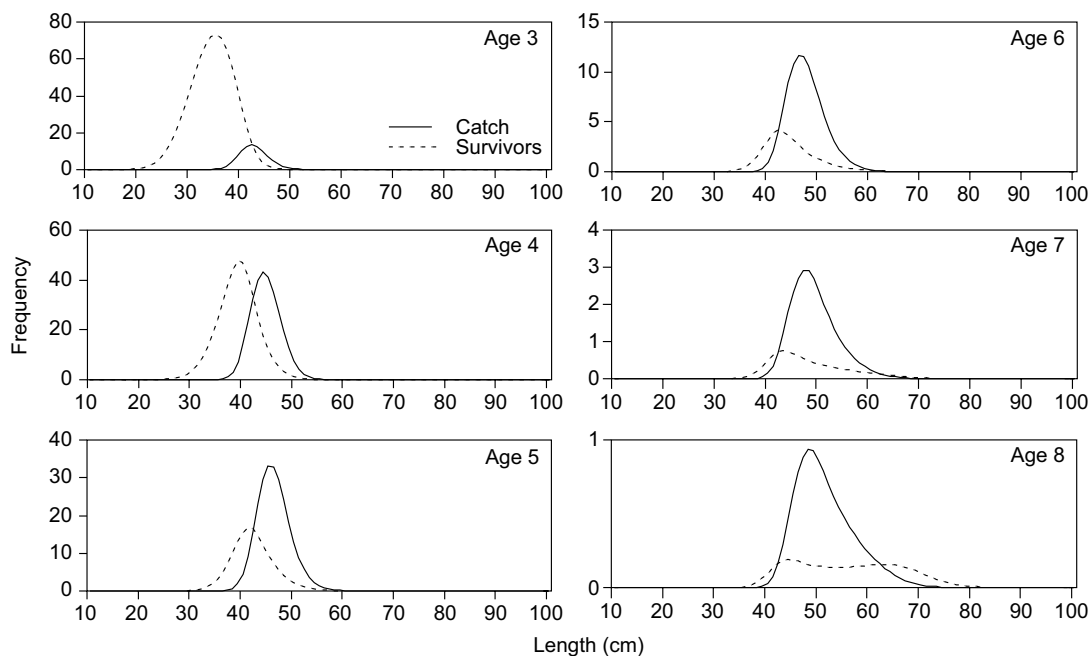


Fig. 4. Simulated length distributions by age of the migratory whitefish selected with gill nets (45–50 mm bar length, current fishing mortality) and of those that survive, starting from 1000 three-year-old recruits. Note the different scales of the y-axes.

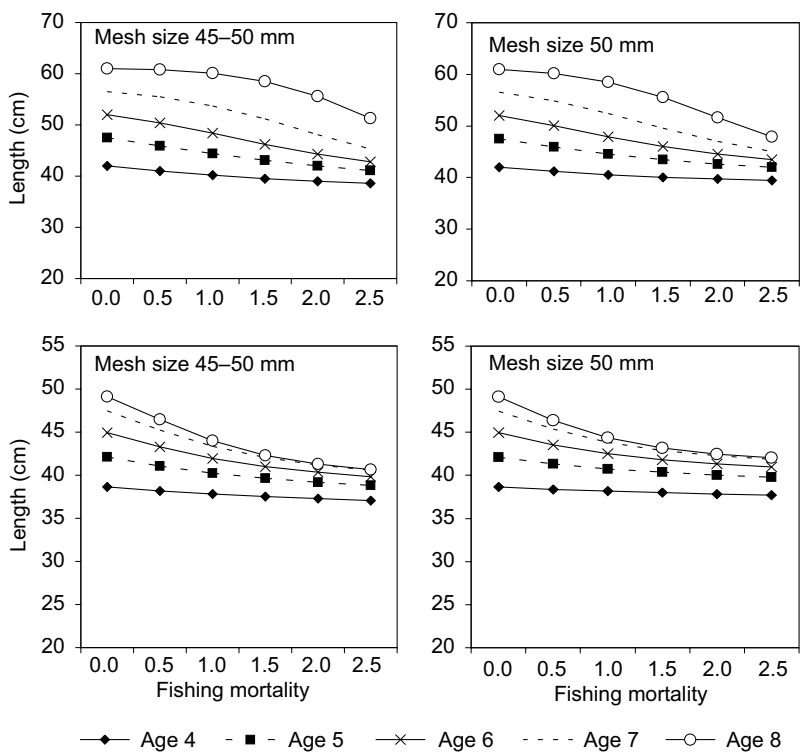


Fig. 5. The effect of fishing mortality (F) on the mean lengths of migratory whitefish (upper panels) and sea-spawning whitefish (lower panels), with the current gill-net mesh sizes (45–50 mm) and with exclusively 50 mm mesh size, according to simulation. The value 2 for F in completely recruited length classes represents the current rate of fishing.

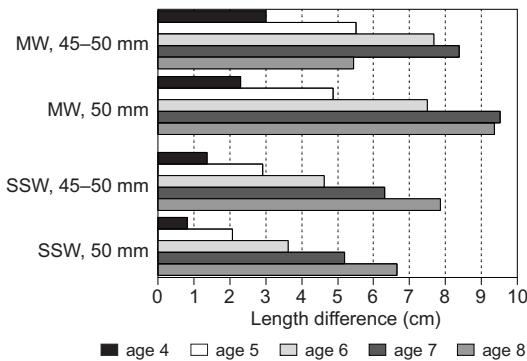


Fig. 6. Decrease in mean lengths-at-age of whitefish caused by gill-net fishing with the current fishing mortality in the Gulf of Finland for two mesh size options (45–50 and 50 mm), according to simulation. MW = migratory whitefish, SSW = sea-spawning whitefish.

the current level of fishing mortality in the Gulf of Finland. The changes caused by selection (i.e. selection differentials) were considerably larger than, for instance, corresponding effects on cod (*Gadus morhua* L.) in the North Sea reported by Law and Rowell (1993). The planned change in the minimum mesh size from 45 mm to 50 mm bar length would cause a shift in the effects of selection to older age groups in the migratory whitefish, and moderate the selection differentials in the sea-spawning whitefish.

Changes in growth and maturation in major commercially-exploited fish stocks over time have been demonstrated in several cases, and the argument that fishing could cause phenotypic evolution is widely recognized (Handford *et al.* 1977, Policansky 1993, Reznick 1993, Heino 1998, Law 2000). Generally, fishery-imposed evolutionary changes are difficult to detect and measure in wild fish stocks because they are often masked by physical and biotic environmental effects, or phenotypic responses to exploitation, such as compensatory growth (Policansky 1993, Reznick 1993).

The size-at-age in a fish population could decrease for several reasons, for instance because of a change in temperature regime, food resources, population density or interspecific competition, or fishing. In most cases it will not be possible to distinguish the environmentally-based changes from genetically-based ones (Policansky 1993). However, using the information collected routinely for stock assessment and

fisheries management purposes, it is feasible to construct approximate models to examine the underlying mechanisms and thus to estimate the strength of selection (Law 2000). The model can then be used to consider the effects of different management options.

Selective gill-net fishing can principally cause selection for slow growth only when the maturity is age-dependent, as in the simulation by Kirkpatrick (1993). Then, because the rapidly growing individuals will recruit earlier to the fishery, a smaller share of them will reach maturity compared to the slow-growing individuals. In such a situation, with high fishing effort, most spawners will be slow-growing individuals. When we consider a fish stock with purely size-dependent maturity, the same proportion of slow- and fast-growing fish would be caught before maturity, or the fast-growing individuals might even be favoured because they would be exposed to fishing or other predators for a shorter time before maturity.

In the whitefish stocks off the Finnish coast, maturity seems to be partly age-dependent and partly size-dependent, and the maturation size seems to be stock-specific. For instance, from the migratory whitefish stocked at the mouth of the Vantaanjoki, only the largest individuals from the youngest age groups migrate to spawn. The maturation age in males is 3 to 5 and in females 4 to 6. The three-year-old spawners are on average 40 cm in length and 500 g in weight in samples taken with electric fishing (O. Heikinheimo & J. Mikkola unpubl. data). According to the back-calculated lengths from the spawning population, the mean length of the age group three is about 35 cm. The more slow-growing migratory whitefish in the northern Gulf of Bothnia mature at 4 to 7 years (E. Jokikokko pers. comm.), and in the Kalajoki a little earlier as in the Gulf of Finland, starting from 3-year-old males (Aronsuu & Huhmarniemi 2003). The size-at-age in four-, five- and six-year-old spawners has decreased significantly in the Kalajoki during the study period 1984–2000 (Aronsuu & Huhmarniemi 2003). A similar development has been found in several other migratory whitefish stocks in the rivers flowing to the northern Gulf of Bothnia (Lehtonen & Jokikokko 2002).

The age- and size-at-maturity of the sea-

spawning whitefish in the Gulf of Finland seem to be similar to those of the migratory whitefish, but our spawning stock samples were caught with gill nets of 45 mm bar length which may have excluded small-sized spawners. In the northern part of the Gulf of Bothnia, the maturing age of the sea-spawning whitefish is the same as in the stocks mentioned above but the maturing length is only 20–25 cm (A. Huhmarniemi pers. comm.).

Large selection differentials alone are insufficient to cause evolution. In addition, there must be genetic differences between the fish caught and those that escape (Policansky 1993, Law 2000). Heritability (h^2) is defined as the proportion of trait variance in parents inherited by offspring (Conover & Munch 2002) and for body size in fish varies from 0.2 to 0.3 (McAllister *et al.* 1992, Law 2000, Conover & Munch 2002). Heritabilities of this magnitude have been sufficient to permit a rapid and substantial selection response in selective breeding of salmonids for aquaculture, and there is evidence that heritability values are of the same order in wild and farmed fish (Law 2000). Although the plasticity in the growth rate of whitefish is large, evidence for genetically-based differences has been found (Leskelä & Kucharczyk 1995, Kirchhofer & Lindt-Kirchhofer 1998).

Implications for fisheries management

There is already wide agreement on the need to protect original fish stocks, such as the river-spawning migratory whitefish, from extinction, but this thinking should be extended to protection of the genetic characteristics of the stock. The possible negative effects of selection on the fitness-determining traits of cultured fish stocks and of stocking material are well known (e.g. Jonsson 1997), but corresponding effects of selective fishing have been mostly ignored (Conover & Munch 2002). However, awareness of this issue is increasing and the current evidence is convincing enough to be considered in the fisheries management (Kirkpatrick 1993, Policansky 1993), especially when the precautionary approach is adopted. Genetic changes caused by fishing will not be readily reversed by altering, for instance, the patterns of fishing (Law 2000).

When applied to the whitefish fishery in the Finnish sea area, the above considerations mean that the fishing should be restricted to allow even the most fast-growing parts of the naturally-reproducing whitefish stocks to spawn at least once. Otherwise, the fishing may cause irreversible changes in the genetic composition of the stock by removing the fast-growing genotypes and favouring slow growth. Because the stocking material originates from the same wild stocks, the effect will also be transmitted to the stocked whitefish and influence the productivity of stocking. In addition, selective fishing affects the age and size composition of the spawning stocks and thus changes in the mean fecundity or quality of the offspring are also possible (Law 2000, Conover & Munch 2002).

Conover and Munch (2002) showed experimentally that somatic growth in fish (Atlantic silverside, *Menidia menidia*) evolves in directions opposite to the size bias of harvest. The mean size of small-harvested fish increased, while that of large-harvested fish decreased. Conover and Munch (2002) suggest that maximum size limits (i.e. all fish above a given size are protected) instead of minimum size restriction might offer some important advantages in terms of selection because fast-growing genotypes would thus be favoured.

Concerning the whitefish fishery in the Finnish sea area, this kind of thinking would lead to negative effects. Fishing with small-mesh gill nets and current effort would cause both growth overfishing and severe recruitment overfishing in the migratory whitefish stocks, and thus the existence of naturally-reproducing stocks would be threatened. Our results emphasize the need for larger mesh sizes in the areas with naturally-reproducing migratory whitefish, or alternatively, a considerably lower fishing effort. Regulation of the mesh sizes will be in this case more feasible than restricting the fishing effort. The minimum mesh size that would ensure spawning at least once among the fast-growing part of the migratory whitefish stocks depends on the stock-specific growth rates and will be smaller in the northernmost part of the Gulf of Bothnia. Evidently, some part of the original genetic variation in the whitefish stocks may have been lost already. In fisheries management research, potential evolu-

tionary effects of selective fishing should also be considered in the context of other fish species that are exposed to intensive gill-net fisheries.

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References

- Anon. 2000: Recreational fishing 1998. — *SVT Agriculture, Forestry and Fishery* 2000:1. Finnish Game and Fisheries Research Institute.
- Anon. 2002: Recreational fishing 2000. — *SVT Agriculture, Forestry and Fishery* 2002:54. Finnish Game and Fisheries Research Institute.
- Aronsoo, K. & Huhmarniemi, A. 2004: 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. — *Ann. Zool. Fennici* 41: 195–204.
- Bagenal, T. B. & Tesch, F. W. 1978: Age and growth. — In: Bagenal, T. (ed.), *Methods for assessment of fish production in fresh waters*: 10–136. Blackwell, Oxford.
- Conover, D. O. & Munch, S. B. 2002: Sustaining fisheries yields over evolutionary time scales. — *Science* 297: 94–96.
- Handford, P., Bell, G. & Reimchen, T. 1977: A gillnet fishery considered as an experiment in artificial selection. — *J. Fish. Res. Bd. Canada* 34: 954–961.
- Heino, M. 1998: Management of evolving fish stocks. — *Can. J. Fish. Aquat. Sci.* 55: 1971–1981.
- Hilborn, R. & Walters, C. J. 1992: *Quantitative fisheries stock assessment. Choice, dynamics and uncertainty*. — Chapman & Hall, New York and London.
- Jokikokko, E., Leskelä, A. & Heikinheimo, O. 2001: Merialueen siika. — In: Böhling, P. (ed.), *Kalavarat 2001 — Fiskresurser 2001*: 34–37. SVT Agriculture, Forestry and Fishery 2001:59. Finnish Game and Fisheries Research Institute.
- Jonsson, B. 1997: A review of ecological and behavioural interactions between cultured and wild Atlantic salmon. — *ICES J. Mar. Sci.* 54: 1031–1039.
- Kaukoranta, M., Koljonen, M.-L., Koskiniemi, J., Pennanen, J. T. & Tammi, J. 2000: *Atlas of Finnish fishes. English summary*. — Finnish Game and Fisheries Research Institute, Helsinki.
- Kirchhofer, A. & Lindt-Kirchhofer, T. J. 1998: Growth and development during early life stages of *Coregonus lavaretus* from three lakes in Switzerland. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 50: 49–59.
- Kirkpatrick, M. 1993: The evolution of size and growth in harvested natural populations. — In: Stokes, T. K., McGlade, J. M. & Law, R. (eds.), *The exploitation of evolving resources*: 145–154. Lecture notes in biomathematics 99. Springer-Verlag, Berlin.
- Kurkilahti, M. 1999: *Nordic multimesh gillnet — robust gear for sampling fish populations*. — Ph.D. thesis, Department of Biology, University of Turku and Finnish Game and Fisheries Research Institute, Helsinki.
- Law, R. 2000: Fishing, selection, and phenotypic evolution. — *ICES Journal of Marine Science* 57: 659–668.
- Law, R. & Rowell, C. A. 1993: Cohort-structured populations, selection responses, and exploitation of the North Sea cod. — In: Stokes, T. K., McGlade, J. M. & Law, R. (eds.), *The exploitation of evolving resources*: 155–173. Lecture notes in biomathematics 99. Springer-Verlag, Berlin.
- Lehtonen, H. & Jokikokko, E. 2002: Responses of anadromous European whitefish, *Coregonus lavaretus* (L.) to fishing in the Gulf of Bothnia. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 57: 669–676.
- Leskelä, A. & Kucharczyk, D. 1995: Effect of temperature on the growth of three forms of European whitefish (*Coregonus lavaretus* L.) larvae. — *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 46: 147–152.
- McAllister, M. K., Peterman, R. M. & Gillis, D. M. 1992: Statistical evaluation of a large-scale fishing experiment designed to test for a genetic effect of size-selective fishing on British Columbia Pink Salmon (*Oncorhynchus gorbuscha*). — *Can. J. Fish. Aquat. Sci.* 49: 1294–1304.
- Policansky, D. 1993: Fishing as a cause of evolution in fishes. — In: Stokes, T. K., McGlade, J. M. & Law, R. (eds.), *The exploitation of evolving resources*: 2–18. Lecture notes in biomathematics 99. Springer-Verlag, Berlin.
- Raitaniemi, J., Heikinheimo, O. & Mikkola, J. 1996: Vael-lussiika. Uudenmaan rannikon tuottoisa istutuskala [Whitefish. Successful stocking on the coast of the province of Uusimaa]. — *Kalaturkimuksia-Fiskundersökningar* 105. Finnish Game and Fisheries Research Institute. [In Finnish with English abstract].
- Reznick, D. N. 1993: Norms of reaction in fishes. — In: Stokes, T. K., McGlade, J. M. & Law, R. (eds.), *The exploitation of evolving resources*: 72–90. Lecture notes in biomathematics 99. Springer-Verlag, Berlin.
- Salojärvi, K., Ikonen, E. & Rahkonen, R. 1985: Possibilities for increasing the whitefish catch through stocking in the Gulf of Finland. — *Finnish Fish. Res.* 6: 127–133.
- Söderkultalahti, P. 2001: Commercial marine fishery. — In: *Finnish fishery time series*: 14–44. SVT Agriculture, Forestry and Fishery 2001:60. Finnish Game and Fisheries Research Institute.
- Toivonen, A.-L., Moilanen, P., Stigzelius, J. & Railo, E. 2003: Suomi kalastaa 2001. Lajisaaliit. — *Kala- ja riis-taraportteja* 283. Helsinki. Finnish Game and Fisheries Research Institute.
- Vaajakorpi, H. 2002: *Helsingin merialueen kalataloudellinen tarkkailututkimus vuosina 2000–2001*. — Vesihydro Oy. Helsingin kaupungin liikuntavirasto. [Mimeo].