The growth of whitefish in relation to water quality and fish species composition

J. Raitaniemi*, T. Malinen†, K. Nyberg‡ and M. Rask§
*University of Helsinki, Department of Ecological and Environmental Sciences, Niemenkatu 73 C, FIN-15210 Lahti, Finland; †University of Helsinki, Department of Ecological and Environmental Sciences, Niemenkatu 73 C, FIN-15210 Lahti, Finland; ‡University of Helsinki, Department of Limnology and Environmental Protection, Viikki (E-building), FIN-00014 Helsinki, Finland and §Finnish Game and Fisheries Research Institute, Evo Fisheries Research, FIN-16970 Evo, Finland

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Water quality in 16 Finnish lakes did not affect directly densely gill-rakered whitefish growth, except possibly in an acid (pH 4.9) lake, Iso Lehmälampi, where acidity may have retarded the growth of whitefish. The density of roach affected whitefish growth in the second year of life: highest growth rates were in lakes without a roach population and lowest growth rates in lakes having strong roach populations. Competition by vendace also retarded the growth of young whitefish. The efficient mass removal of roach from a eutrophic lake was considered to have increased the growth rate of young whitefish. It is suggested that an examination of the fish species composition and relative abundance, as well as the growth of whitefish, can be used as an aid in predicting the success of stocking with whitefish.

Key words: whitefish; growth; roach; vendace; water characteristics, acidity.

INTRODUCTION

The only native whitefish species in Finland, Coregonus lavaretus (L.), is important in both commercial and recreational fisheries (Railo et al., 1995; Heikinheimo et al., 1997). Restocking with one-summer-old whitefish fingerlings is carried out frequently to increase the fisheries value of the waters (Westman et al., 1984; Salojärvi, 1992). Whitefish stocks with high gill raker numbers (45–60, also called C. l. pallasii) are used commonly for stocking in inland waters because of the good growth of the fish (Bergstrand, 1982; Miinalainen & Heikinheimo, 1998). In small lakes, whitefish do not reproduce naturally, but can grow quickly, and are easy to catch with gillnets commonly used in Finland in recreational fishing. In large waters, whitefish stocking is often carried out to compensate for losses to fisheries caused by environmental changes like water level regulation, damming and dredging of the spawning river, etc. (Huhmarniemi et al., 1985; Heikinheimo-Schmid & Huusko, 1988; Salojärvi &

One major factor affecting the profitability of stocking is the growth of the stocked fish. Slow growth due to competition has probably led to failures of some stockings (Salojärvi & Ekholm, 1990). Environmental changes may also affect whitefish growth (Heikinheimo-Schmid, 1985; Rask et al., 1988; Tammi et al., 1997).

The purpose of this study was to clarify the factors that affect whitefish growth by examining growth in environments with different water characteristics and fish species compositions. We concentrated on whitefish growth in 16 lakes or basins with different acid-related water characteristics and fish species composition; in a single lake before and after the collapse of a strong vendace Coregonus albula (L.) population; and in a eutrophic lake basin after the mass removal of roach Rutilus rutilus (L.).

THE LAKES AND WHITEFISH OF THE STUDY

Most of the whitefish material for the study was from lakes that had been included in earlier studies—11 oligotrophic, small lakes (area <100 ha) in southern Finland that were used in the acidification studies (HAPRO) in the 1980s (Tuunainen et al., 1991; Rask et al., 1995). In addition, the data for three large lakes and two large basins (area >1000 ha) were included. The lakes Lappajärvi, Evijärvi, and Alajärvi are located in Ostrobothnian area and the basins of Vesijärvi, Enonselkä and Kajaanselkä, in southern Finland (Fig. 1).

In the samples from all lakes but one, the C. lavaretus individuals represented a morph which has a mean gill raker number ≥ 50. In Vesijärvi, the majority of the samples consisted of whitefish with typically 42–45 gill rakers and an equal growth rate with whitefish having an average of 55 gill rakers.

Lappajärvi is a regulated lake, in which some remarkable changes in the fish stocks have been observed since the end of the 1980s, including the collapse of a strong vendace population, increase in the smelt Osmerus eperlanus (L.) population, and the successful reintroduction of zander Stizostedion lucioperca (L.). About 95% of the whitefish are stocked.

In the 1980s, before the mass removal of fish from the eutrophic Enonselkä basin of Vesijärvi (Horppila & Peltonen, 1994), Enonselkä suffered from severe blooms caused by cyanobacteria, and fishing there was unpopular. Whitefish was a rare species in test gillnets, but some whitefish were caught by fishermen (Hanski, unpubl.). In the other basin, Kajaanselkä, problems of this magnitude have not occurred and no biomanipulation has been conducted. Due to the mass removal by intensive trawling in Enonselkä in 1989–1993, the roach biomass decreased from 172 to c. 50 kg ha⁻¹ (Horppila & Peltonen, 1994) and smelt biomass from 75 to 12 kg ha⁻¹ (Horppila et al., 1996). The total phosphorus concentration decreased from 45 to <30 µg l⁻¹, the biomass of cyanobacteria decreased from 1·4 to <0·4 g m⁻³, and transparency increased from 1·5 to 3·5 m (Horppila et al., 1998). Enonselkä has been stocked regularly with whitefish (two to three individuals ha⁻¹ year⁻¹); in addition, a strong year class born in 1994 was found in the seine and trawl catches in 1997.
MATERIAL AND METHODS

SAMPLING

Samples for water chemistry from the 11 oligotrophic small lakes and the two basins of Vesijärvi were taken at the time of summer stratification (20–100 cm depth), excluding nitrogen and phosphorus contents that were taken during the autumn turnover, which lasts about 2 months in Finland (Ruuhiälä, 1974), or spring turnover. The Ostrobothnian lakes were sampled during the autumn turnover. The Finnish standard methods for water analysis (SFS standards) were applied. The laboratory of the Finnish Game and Fisheries Research Institute analysed the samples from the small lakes, the laboratories of the Finnish Environment Institute analysed the nitrogen and phosphorus contents and the samples from the Ostrobothnian lakes, and the Lahti Research Laboratory the two basins of Vesijärvi (Table I).

Fig. 1. Locations of the studied lakes in Finland.
### Table I. Surface area, water properties, and number of fish species in the lakes and basins of the study

<table>
<thead>
<tr>
<th>Lake or basin</th>
<th>Area (ha)</th>
<th>pH (mmol l(^{-1}))</th>
<th>Alk. (mg Pt(^{-1}))</th>
<th>Colour (mg Pt(^{-1}))</th>
<th>Conductivity (mS m(^{-1}))</th>
<th>Ca(^{2+}) (mmol l(^{-1}))</th>
<th>COD (mg l(^{-1}))</th>
<th>Fe (µg l(^{-1}))</th>
<th>N tot. (µg l(^{-1}))</th>
<th>P tot. (µg l(^{-1}))</th>
<th>Number of species</th>
<th>Roach density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lappajärvi</td>
<td>14 200</td>
<td>6.7</td>
<td>0.16</td>
<td>56</td>
<td>10</td>
<td>0.11</td>
<td>—</td>
<td>287</td>
<td>599</td>
<td>23</td>
<td>18</td>
<td>18</td>
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<tr>
<td>Kajaanselkä</td>
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<td>7.8</td>
<td>0.54</td>
<td>10</td>
<td>10.5</td>
<td>0.20</td>
<td>4.0</td>
<td>—</td>
<td>380</td>
<td>15</td>
<td>19</td>
<td>19</td>
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<tr>
<td>Evijärvi</td>
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<td>0.16</td>
<td>70</td>
<td>5.9</td>
<td>0.10</td>
<td>—</td>
<td>466</td>
<td>605</td>
<td>21</td>
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<td>16</td>
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<td>7.8</td>
<td>0.54</td>
<td>15</td>
<td>11.5</td>
<td>—</td>
<td>4.9</td>
<td>35</td>
<td>450</td>
<td>20</td>
<td>19</td>
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<td>0.14</td>
<td>185</td>
<td>5.1</td>
<td>0.11</td>
<td>—</td>
<td>564</td>
<td>1101</td>
<td>57</td>
<td>12</td>
<td>12</td>
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<td>Saarijärvi</td>
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<td>5.6</td>
<td>0.04</td>
<td>10</td>
<td>3.4</td>
<td>0.06</td>
<td>2.7</td>
<td>67</td>
<td>170</td>
<td>2</td>
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<td>1</td>
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<tr>
<td>Siikajärvi</td>
<td>88</td>
<td>5.2</td>
<td>0.03</td>
<td>15</td>
<td>2.3</td>
<td>0.03</td>
<td>5.1</td>
<td>59</td>
<td>290</td>
<td>5</td>
<td>4</td>
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<td>Iso-Melkutin</td>
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<td>7.6</td>
<td>0.37</td>
<td>10</td>
<td>5.3</td>
<td>0.15</td>
<td>2.2</td>
<td>16</td>
<td>300</td>
<td>7</td>
<td>5</td>
<td>5</td>
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<td>Alinenjärvi</td>
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<td>5.3</td>
<td>0.02</td>
<td>35</td>
<td>4.4</td>
<td>0.08</td>
<td>6.6</td>
<td>298</td>
<td>200</td>
<td>10</td>
<td>6</td>
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<td>5.8</td>
<td>0.04</td>
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<td>0.05</td>
<td>0.8</td>
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<td>350</td>
<td>3</td>
<td>5</td>
<td>0</td>
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<td>Sahajärvi</td>
<td>27</td>
<td>6.1</td>
<td>0.04</td>
<td>5</td>
<td>2.6</td>
<td>0.05</td>
<td>3.8</td>
<td>7</td>
<td>—</td>
<td>—</td>
<td>4</td>
<td>0</td>
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<td>Valkeinen</td>
<td>27</td>
<td>5.8</td>
<td>0.05</td>
<td>5</td>
<td>2.8</td>
<td>0.03</td>
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<td>0</td>
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<td>6.6</td>
<td>0.07</td>
<td>70</td>
<td>3.9</td>
<td>0.11</td>
<td>9.2</td>
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<td>590</td>
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<td>0</td>
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<td>0.01</td>
<td>30</td>
<td>3.0</td>
<td>0.05</td>
<td>3.8</td>
<td>45</td>
<td>300</td>
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<td>1</td>
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<tr>
<td>Iso Lehmälampi</td>
<td>5</td>
<td>4.8</td>
<td>0.02</td>
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<td>1.7</td>
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<td>130</td>
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<td>6.6</td>
<td>0.22</td>
<td>25</td>
<td>5.1</td>
<td>0.14</td>
<td>2.5</td>
<td>51</td>
<td>510</td>
<td>4</td>
<td>6</td>
<td>2</td>
</tr>
</tbody>
</table>

Classes of roach density: 0, absent; 1, sparse population; 2, normal population; 3, dense population.
From the small HAPRO lakes, the whitefish were caught with a gillnet series including 12-, 15-, 20-, 25-, 30-, 35-, 45-, and 60-mm bar mesh. The fish from the Ostrobothnian lakes were caught by fishermen who used either gillnets or pound nets or both. The whitefish from Vesijärvi were caught with seine, trawl, and gillnets.

In the acidification studies of the 1980s (HAPRO lakes), only scales were taken from the whitefish for back-calculation of growth. The number of individuals in the samples was 10–23 in nine lakes and six to nine in four lakes. In the Ostrobothnian samples, the growth of the fish was determined from opercular bones (Lappajärvi, 1990: n = 238, 1993: n = 500, Evijärvi: n = 90, Alajärvi: n = 6), though scales and otoliths were also used in age determination. In the Vesijärvi sample, scales and otoliths were taken from 181 individuals and scales, otoliths, and the opercular bone from 232 individuals. Different individuals took the samples; some scales were taken from the site between the tips of the pelvic fins and the rest from the flank between the lateral line and the anus. Two persons aged separately all individuals in the Vesijärvi scale–otolith sample (n = 181). The ageing method was based on the validation in Raitaniemi (1997) and Raitaniemi et al. (1998).

**THE BACKCALCULATION OF GROWTH**

The total lengths of the whitefish at earlier ages were backcalculated using Monastyrsky’s (1930, in Bagenal & Tesch, 1978) formula. The growth of 50 individuals from the Vesijärvi sample was backcalculated from both scales and opercular bones. A paired samples t-test did not show significant differences between the yearly growth based on opercular bones and scales in age groups 2–5 (t = −0.99–1.08, d.f. = 12–48, P = 0.196–0.775).

The value of b for opercular bone (L = aS^b, where L = length of fish, S = radius of opercular bone) was calculated from the Vesijärvi sample, where different sizes of whitefish were well represented (b = 1.045, r^2 = 0.97). There were not enough whitefish of different sizes to calculate the value of b for those Vesijärvi whitefish whose growth was backcalculated from scales. Therefore, the size backcalculated from opercular bones was used to produce b for scales in these fish. The value of b used for the scales between the tips of the pelvic fins was 0.634 and for the scales taken from the flank 0.525 and 0.614 (two measurers used a slightly different line in the measurements). In the backcalculation from the scales of small samples, the values of b based on the Vesijärvi material were used.

In the opercular bone material, the body proportional backcalculated lengths (BPH) were systematically 1–4 mm greater in each age group than scale-proportional lengths (SPH; Francis, 1990). Although the differences in scale material were probably greater, it was considered that real growth differences could still be detected. In a group of 40 whitefish from the Kajaanselkä basin, statistically significant differences between the yearly growth of males and females were found only in the growth in the third year (t-test, second year: t = 0.73, d.f. = 33, P = 0.470; third year: t = 2.24, d.f. = 33, P = 0.032, (the growth increment of males 1 cm longer than that of females); fourth year: t = 0.64, d.f. = 27, P = 0.526; fifth year: t = 1.21, d.f. = 25, P = 0.237).

The growth rates after the fifth year of age were not compared, because scales were the only calcified structures available from most of the lakes and scales are not reliable in ageing old and slow growing whitefish (Skurdal et al., 1985; Raitaniemi et al., 1998).

**THE EXAMINATION OF THE DATA**

The relationships between backcalculated yearly increase in length of whitefish and water chemistry (pH, alkalinity, colour, conductivity, Ca^2+, Fe, N_{tot}, P_{tot}) were examined, as well as relationships with the most common fish species, perch *Perca fluviatilis* L., roach, and ruff *Gymnocephalus cernuus* (L.). As fully comparable quantitative catch data were available only from the test-netted small lakes (n = 11), the density of roach in all lakes was grouped in four classes: 0, not present; 1, sparse population; 2, normal population; 3, dense population (Table I). In moderately acidified lakes (alkalinity ≤ 0.05 mmol l^{-1}), in which the mean weight of roach was >70 g, roach populations were considered to be sparse (in normal populations mean weight 40–51 g). As an acid-sensitive species, roach has an increased mean weight in populations where the
number of roach has decreased because of unsuccessful reproduction (Rask et al., 1995). In Alajärvi, the roach population was regarded as dense because of the observations of the fishermen, slow growth of roach, and high nutrient status of the water (Horppila et al., 1998). For lakes in which nothing exceptional in the roach had been discovered, the population was interpreted as normal.

Variables such as the number of fish species, or in 11–14 lakes, for which fairly comparable test-netting data were available, the numbers of perch, roach, or ruffe in a test gillnetting catch were also included.

The associations among the abiotic and biotic variables were examined using correlation tests (mostly Pearson correlation and Spearman with the grouped roach density). In these, the two samples from Lappajärvi (periods of dense and sparse vendace population) were treated as if they were from different lakes. Abiotic variables (excluding pH and Ca content), the number of species, the numbers of roach and ruffe, and the mean weight of roach in the gillnet catch were log transformed to normalize the distributions. Partial correlation and stepwise regression were used to analyse the influence of different factors on whitefish growth. The first year of growth was not included in the tests, because in most cases the lakes had been stocked with one-summer-old fingerlings, reared in artificial ponds. The differences in the second year growth between the lakes were tested with one-way analysis of variance (ANOVA) and Tukey’s test. Repeated-measures ANOVA and Tukey’s test (Raitaniemi et al., 1995) were used in testing the differences in growth rates of different year classes from Lappajärvi. In cases where two groups were compared, t-test was used.

**RESULTS**

The second-year growth of whitefish differed from the growth in the other years; it was correlated clearly with a number of biotic and abiotic factors. The clearest was the negative correlation with roach density (Fig. 2), and the relationship with the catch of roach in the gillnet fishing was also significant, as well as the negative correlation with the number of fish species (Table II).

Negative relationships were also found with the following abiotic variables: conductivity, Ca, P$_{\text{tot}}$, pH, alkalinity, and colour. Among the variables, conductivity and number of fish species had the highest correlation with roach density ($r=0\cdot83$ in both cases), and the others also correlated with roach density ($r=0\cdot48–0\cdot78$). Of the chemical variables, conductivity, Ca, pH, and alkalinity correlated with each other ($r=0\cdot76–0\cdot90$), as did colour, P$_{\text{tot}}$, and N$_{\text{tot}}$ ($r=0\cdot66–0\cdot87$), and conductivity correlated with P$_{\text{tot}}$ ($r=0\cdot68$).

The negative correlations between the second year growth of whitefish and roach density remained significant when the chemical variables or the number of fish species were held constant (partial correlation, each variable held constant separately, $r=−0\cdot68–−0\cdot84$, 14–17 lakes, $P<0\cdot001–0\cdot01$), but the correlations between the second year growth and the chemical variables became non-significant when roach density was kept constant. Correspondingly, the correlations between the growth and the catch of roach in number remained ($r=−0\cdot60–0\cdot67$, 14 lakes, $P<0\cdot01–0\cdot05$), and the relationships with alkalinity, pH, and colour were not significant. However, partial correlation was not successful in distinguishing the effects of different variables when testing the catch of roach with conductivity, Ca, P$_{\text{tot}}$, and the number of fish species.

In a stepwise regression, roach density was the only variable among Ca, P$_{\text{tot}}$, and colour affecting the second year growth of whitefish ($r^2=0\cdot66$, $n=15$,
In ANOVA, the differences in the second year growth were clearest when comparing lakes without roach with lakes inhabited by normal or dense roach populations ($F=111.19$, d.f.$=16$, $P<0.001$; Tukey’s test, Fig. 3).

The growth of whitefish during the fifth year had a significant positive relationship with the number of species, lake area, and conductivity of the water (Table II), which all correlated clearly with each other.

In Lappajärvi, the growth rate of whitefish increased when vendace catches collapsed (repeated-measures ANOVA, age $\times$ year class $F=20.05$, d.f.$=12$, $P<0.001$). The clearest differences between the whitefish year classes were in the growth in the second year (Tukey’s test; Raitaniemi et al., 1995; Fig. 4). Among the lakes and basins, the fastest growth of whitefish during the fourth year of life was observed in the biomanipulated Enonselkä basin of Vesijärvi. The growth of whitefish in Enonselkä was significantly faster than in the Kajaanselkä basin of the same lake during the second, third and fourth year of life ($t$-test: $t=7.95$, d.f.$=348$, $P<0.001$; $t=6.22$, d.f.$=238$, $P<0.001$; $t=7.15$, d.f.$=159$, $P<0.001$, respectively), but not in the fifth year ($t=−1.44$, d.f.$=52$, $P=0.157$).
The correlation coefficients ($r$) between the average growth of whitefish in their second, third, fourth, and fifth growing season and different biotic and abiotic factors. Pearson correlation is used except with roach density that is a grouped variable (Spearman correlation).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Second year growth $r$</th>
<th>n</th>
<th>Third year growth $r$</th>
<th>n</th>
<th>Fourth year growth $r$</th>
<th>n</th>
<th>Fifth year growth $r$</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roach density</td>
<td>-0.87***</td>
<td>17</td>
<td>-0.04</td>
<td>16</td>
<td>0.31</td>
<td>12</td>
<td>0.53†</td>
<td>12</td>
</tr>
<tr>
<td>Cond. (mS m$^{-1}$)</td>
<td>-0.74***</td>
<td>17</td>
<td>-0.22</td>
<td>16</td>
<td>0.52†</td>
<td>12</td>
<td>0.74*</td>
<td>12</td>
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<tr>
<td>Catch of roach (n)</td>
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<td>14</td>
<td>-0.01</td>
<td>13</td>
<td>0.44</td>
<td>9</td>
<td>0.39</td>
<td>9</td>
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<tr>
<td>Ca$^{2+}$ (mmol l$^{-1}$)</td>
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<td>-0.28</td>
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<td>11</td>
<td>0.51</td>
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<tr>
<td>$P_{tot}$ (µg l$^{-1}$)</td>
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<td>-0.30</td>
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<td>Alk. (mmol l$^{-1}$)</td>
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<td>0.07</td>
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<td>0.37</td>
<td>12</td>
<td>0.56†</td>
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<td>Colour (mg Pt l$^{-1}$)</td>
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<td>-0.51*</td>
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<td>-0.06</td>
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<tr>
<td>$N_{tot}$ (µg l$^{-1}$)</td>
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<td>-0.30</td>
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<td>-0.05</td>
<td>11</td>
<td>0.23</td>
<td>11</td>
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<tr>
<td>Fe (µg l$^{-1}$)</td>
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<td>-0.63*</td>
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<td>11</td>
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<td>COD (mg l$^{-1}$)</td>
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<td>16</td>
<td>0.42</td>
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</tbody>
</table>

***$P<0.001$, **$P<0.01$, *$P<0.05$, †$P<0.10$. 


In Iso Lehmälampi, the most acidic lake with pH<5, perch were practically absent and there were no fish in 1986, when the lake was stocked with whitefish. The whitefish of moderately acidic Sahajärvi, which lacks roach, grew faster during their second year than the individuals in Iso Lehmälampi (Fig. 3, 1990 Evijärvi Lappajarvi 1993 Alajarvi Iso-Melkutin Kajaanselka Syrjanalunen Alinenjärvi Enonselkä Lappajarvi 1993 500 Enonselkä 103 Alinenjärvi 11 Syrjänalunen 8 Kajaanselkä 113 Iso-Melkutin 16 Alajärvi 6 Lappajarvi 1990 238 Evijärvi 90 Fig. 3. Differences between lakes in the increase in length of whitefish during the second growing season (Tukey’s test, P<0.05). Lakes with no significant difference are combined with the line.


In Iso Lehmälampi, the most acidic lake with pH<5, perch were practically absent and there were no fish in 1986, when the lake was stocked with whitefish. The whitefish of moderately acidic Sahajärvi, which lacks roach, grew faster during their second year than the individuals in Iso Lehmälampi (Fig. 3,
DISCUSSION

INTERSPECIFIC COMPETITION AND ACIDITY

The indirect relationship between the second-year growth of whitefish and acidity-related water characteristics resembles the relationship found with perch that grow well in some highly acidic lakes due to decreased competition for food (Almer, 1974; Raitaniemi et al., 1988). In perch, intraspecific competition, in particular, has decreased, because the reproduction of perch largely fails, and the few survivors have abundant food resources. In the case of whitefish, acidity reduces the survival of roach (Rask et al., 1995). When an effective planktivore like roach (Langeland & Nøst, 1995) disappears, the competition for zooplankton resources decreases and whitefish as more acid-resistant fish are able to increase their growth rate.

Some examples of roach–whitefish relationship have been documented. The introduction of roach into a Norwegian lake inhabited by pike Esox lucius L., and whitefish only was followed by a great decline in the whitefish population (Langeland & Nøst, 1994). In a Swedish lake undergoing eutrophication, cyprinids increased and whitefish decreased, and the growth of whitefish was inhibited (Bergstrand, 1990). In southern Finland, both C. lavaretus and C. peled grew more slowly in a lake with large numbers of cyprinids than in a lake without cyprinids (Pruuki & Pursiainen, 1984).

Stress caused by acidity may have retarded whitefish growth in the most acid lake, Iso Lehmälampi. Although the growth in the second year was comparatively fast, it was slower than in the less acid Sahajärvi or the other lakes without roach. However, in most of the other lakes, the stocking density of whitefish was lower than in Iso Lehmälampi. According to Rask et al. (1992), the growth of

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**Table III**

The second-year growth and mean annual stocking density of whitefish in some lakes or basins

<table>
<thead>
<tr>
<th>Lake or basin</th>
<th>Second-year growth (cm)</th>
<th>Stocking density, (ind. ha⁻¹)</th>
<th>Roach density</th>
<th>Vendace density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>s.d.</td>
<td>n</td>
<td></td>
</tr>
<tr>
<td>Alajärvi</td>
<td>6·3</td>
<td>0·6</td>
<td>6</td>
<td>20</td>
</tr>
<tr>
<td>Enonselkä basin</td>
<td>9·1</td>
<td>1·8</td>
<td>103</td>
<td>2 (0–9)</td>
</tr>
<tr>
<td>Evijärvi</td>
<td>7·1</td>
<td>2·0</td>
<td>90</td>
<td>11</td>
</tr>
<tr>
<td>Iso Lehmälampi</td>
<td>11·3</td>
<td>1·9</td>
<td>18</td>
<td>100 (only 1 year)</td>
</tr>
<tr>
<td>Kajaanselkä basin</td>
<td>7·6</td>
<td>1·7</td>
<td>113</td>
<td>9</td>
</tr>
<tr>
<td>Lappajärvi 1990</td>
<td>7·0</td>
<td>1·6</td>
<td>238</td>
<td>13 (1985 35-5)</td>
</tr>
<tr>
<td>Lappajärvi 1993</td>
<td>10·2</td>
<td>1·8</td>
<td>500</td>
<td>13</td>
</tr>
<tr>
<td>Sahajärvi</td>
<td>14·8</td>
<td>3·2</td>
<td>15</td>
<td>72</td>
</tr>
<tr>
<td>Siikajärvi</td>
<td>16·3</td>
<td>1·5</td>
<td>17</td>
<td>23</td>
</tr>
<tr>
<td>Valkjärvi</td>
<td>20·8</td>
<td>1·6</td>
<td>6</td>
<td>about 14 (only 1 year)</td>
</tr>
</tbody>
</table>

Roach and vendace densities: 0, absent; 1, sparse population (in vendace fishing unprofitable); 2, normal population; 3, dense population. Significant natural reproduction of whitefish is probable in the basins Enonselkä and Kajaanselkä.

Table III), although Sahajärvi had a normal perch population and a higher stocking density of whitefish (Table III).

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whitefish in Iso Lehmälampi was faster than in two less acid lakes. In the more neutral of these, higher intraspecific competition than in Iso Lehmälampi was possible. The concentrations of plasma Na\(^+\) and Cl\(^-\) were 10–15% lower in the whitefish in Iso Lehmälampi and the other lake than in the fish from the most neutral lake, which indicated acid stress. Thus, although the retardation of whitefish growth by acid stress has been shown in laboratory (Rask et al., 1988), in nature the possible effects of acidity are easily masked by biotic factors.

The presence or density of perch did not seem to affect whitefish growth; rather the density of perch was related negatively to roach density (Sumari, 1971; Persson, 1986). Neither did ruffe seem to affect whitefish growth; however, the gillnets with 12-mm bar mesh did not catch small ruffe and the catches may not have indicated the real densities of ruffe. As a bentos feeder, ruffe probably does not compete directly for food with densely gill rakered, pelagic whitefish (Marttinen, 1983).

In large lakes, the species’ relations may differ from those in small lakes. The competition between whitefish and vendace, described earlier by Svärdson (1976), seems to be the reason for the increased growth rate of stocked whitefish in Lappajärvi after the collapse of vendace (Fig. 3). Corresponding reflections in the growth of pelagic whitefish from changes in vendace density have been observed by Heikinheimo-Schmid (1992) and Haakana et al. (1997). They noted that in the indigenous whitefish, the response to the change in vendace density was clearest in the growth in the first year, but still noticeable in the second year. In Lappajärvi, the change in the growth rate was clearest in the second year of life, which was the first year in the lake.

In addition to increased whitefish growth in Lappajärvi, the collapse of vendace was accompanied by the rise of smelt and perch. The increase in smelt population was detected by the fishermen in seine catches and echosoundings. Whitefish and smelt may compete for food (Marttinen, 1983; Sandlund et al., 1987). Even after the collapse of vendace, whitefish in Lappajärvi did not grow as fast during the second year as in the small lakes without roach. As the stocking density in Lappajärvi was low, there was still competition for food between whitefish and one or several other species, possibly smelt and/or roach. In Kurtinjärvi, several hundred kilometres to the north-east of Lappajärvi, faster whitefish growth than that in Lappajärvi was attained after efficient fishing of perch, roach, and whitefish (Lehtinen et al., 1996). This shows that at the latitude of Lappajärvi, whitefish has the capacity for faster growth.

INTRASPECIFIC COMPETITION

High density of whitefish can lead to intraspecific competition and retarded growth (Salojärvi, 1988). The retardation of growth due to intraspecific competition possibly differs from the retardation caused by competition with roach or vendace. While vendace and roach affect whitefish growth especially in the first years of life, probably by competing for the same zooplankton food that the young whitefish eat (Sarvala et al., 1988; Horppila, 1994; Langeland & Nøst, 1994; Miinalainen & Heikinheimo, 1998), intraspecific competition may often be the main reason for the retardation of growth in all age groups or at older age. Growth rate has been found frequently to increase after a fall in population density in whitefish populations (Amundsen, 1988; Brown & Scott, 1994). Klein
observed the increase in all age groups and as did Salonen et al. (1997), in two C. peled populations; Valkeajärvi (1992) detected the increase in growth rate at greater age.

The lake size and, further, the complexity of the ecosystem (number of fish species) may also affect the growth rate of older and larger specimens (Fig. 2, Table II), since they have more diverse chances to shift from plankton to larger prey like amphipods, mussels, etc., when compared with small lakes with simpler systems (Odenwall, 1927; Nilsson, 1979).

THE BIOMANIPULATED ENONSELKA BASIN

The high growth rate of whitefish in the biomanipulated Enonselkä basin is possibly a consequence of the mass removal of roach that lived earlier at high densities in both pelagic and littoral zones (Horppila & Peltonen, 1994). It is likely that the high roach density, and perhaps also smelt, retarded the growth of young whitefish. The roach may have prevented the successful reproduction of coregonines, by indirectly affecting water quality (Müller, 1992) or by species interactions (Salojärvi, 1991; Langeland & Nøst, 1994), since both whitefish and vendace appeared in larger numbers in the catches of Enonselkä after some years of biomanipulation. In 1994, a substantial year class of both species was born (Malinen & Peltonen, unpubl.). When compared with whitefish growth in Enonselkä, the slower growth in the Kajaanselkä basin was probably related not only to roach or smelt density, but also to vendace density. If vendace or whitefish density increased greatly or roach and smelt recovered to earlier densities in Enonselkä in the future, whitefish growth rate may also decrease as competition increased.

PROFITABILITY OF STOCKING

The comparison of our results with those of Salojärvi & Ekholm (1990) reveals that the examination of whitefish growth can be used as an aid in predicting the profitability of whitefish stocking. The most successfully stocked lakes in their study were the ones where the proportion of perch or perch, pike, and burbot in the catches was high, and the poorest results were obtained from lakes where the catches of roach, roach and vendace, or whitefish were high. The decrease in the catch of whitefish and vendace and the profitability of stocking with them was coupled with an increase in cyprinids in a Polish lake undergoing eutrophication (Wolos et al., 1998).

Salojärvi & Ekholm (1990) stressed the effect of predators and especially pike on the success of whitefish stocking. By decreasing competition, predators surely improve the conditions for whitefish, but the abundance of other species is also important. At the time of the test fishing, the local fishermen at Siikajärvi suggested that there was no pike in the lake, nor was it caught in the test gillnettings. The growth of whitefish was fast, because roach was also absent and only perch and ruffe were abundant. In Evijärvi, pike accounted for 34–39% of the total catch in 1989–1993, perch 18–22%, roach 10–15%, and bream 24–31% (Raitaniemi et al., 1995). Although the catches of pike were even higher than in the lakes of Salojärvi & Ekholm (1990), the results of whitefish stocking were disappointing and the growth of whitefish was among the poorest in this study. According to test gillnettings, bream and roach were the most common fish
species in the lake, suggesting that the competition with cyprinids was the main reason for the poor performance of whitefish.

Fish species composition is important when considering how whitefish will grow or how many whitefish fingerlings should be stocked into a lake. If roach and vendace are absent and perch or ruff is the most abundant species, even a large number of stocked whitefish fingerlings can, in Finnish conditions, exceed 35 cm in total length and 400 g in weight in 2–3 years. If roach or vendace are abundant, special attention should be paid to avoid overstocking. In the case of roach, efficient removal can improve the conditions of coregonines and foster their good growth.

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