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Growth of different year classes of smelt *Osmerus eperlanus* L. in Lake Tyrifjorden, Norway

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Smelt *Osmerus eperlanus* L. were collected during spawning run in May in Lake Tyrifjorden in southern Norway. Age determination was carried out by otoliths. Fish length (Y) and otolith radius (X) were correlated (r = 0.954). Calculation of growth was carried out for 610 mature smelt of age 1 + to age 6 +, by using the regression model Y = 81.39 X + 17.95.

Females were significantly longer than males, except those of age 4 + and 5 +. The smelt grew about 60 mm in first year and from 20—30 mm in second and third year of growth. Then the growth decreased gradually. The eldest smelt caught were five smelt of age 7 +. Back-calculation of growth indicated differences in growth rates between the year classes, with an apparent steady decrease in yearly growth rate of younger year classes. Natural mortality caused by strong size selective predation from other fish species, is considered to be the cause for this growth pattern.

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INTRODUCTION

Smelts *Osmerus* spp (Osmeridae) are fresh and brackish water fishes found in the northern hemisphere. Different species populations are known to vary in growth rate and body size (Rupp & Redmond 1966, Belyanina 1969). As in many fish species, also intraspecific differences in growth rate exist between year classes and between the sexes. Females usually grow faster and attain larger body size than males (Huitfeldt-Kaas 1927, McKenzie 1958, Belyanina 1969, Bergaust 1972). The main purpose of this investigation was to study the growth pattern of the population of smelt in Lake Tyrifjorden.

Calculation of growth depends on correct age determination. Previously age determination of smelts has mainly been carried out by using the scales (Masterman 1913, McKenzie 1958, Rembiszewski 1970). However Bergaust (1972) found otoliths to be more reliable for age determination of elder smelt. Investigations upon other fish species have also shown that otoliths are more reliable for determination of age (Nordeng 1961, Aass 1972, Ausen 1976, Jonsson 1976, Six & Horton 1977). In order to find the best method for age determination of smelt in Lake Tyrifjorden, a comparison between scales and otoliths was carried out on a selected material.

MATERIAL AND METHODS

Lake Tyrifjorden is situated in the south-eastern part of Norway (59° 53'—60° 08' N, 10°—10° 21'E). The lake has a surface area of 134.1 km^2 and lies at an altitude of 64 m. Maximum depth recorded is 295 m, and mean depth 114 m. The limnology of the lake has been studied by Strøm (1932), Nyhagen (1959) and Holtan (1970). In summer metalimnion lies at a depth of 15—20 m. The temperature in epilimnion varies between 8°C and 17°C during most of the summer. There is little variation in pH, which lies about 7.0. The ecological condition of the lake may be interpreted as incipient eutrophication (Langeland 1974). Twelve fish species have been recorded from the lake.

In May 1977 866 smelt between 79—182 mm were caught during the spawning run by using a seine in the part of the lake called Nordfjorden. The seine was used in late evening and early night, because smelt are known to be present on the spawning grounds at this time (Belyanina 1969). In 1976 54 smelt from 26—31 mm were collected in July and 20 smelt between 50—60 mm were caught in October using a fine meshed net.

To find the best method for age determination, 82 smelt collected in May were randomly picked and the scales were examined according

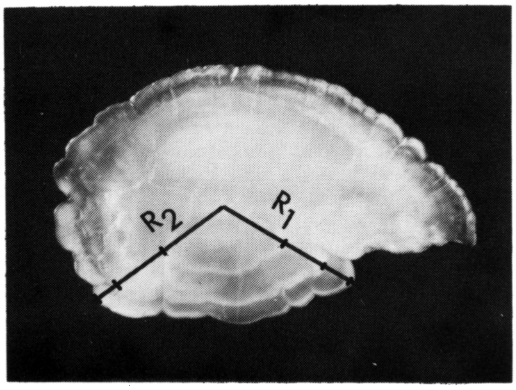


Fig. 1. Otolith from a three year old smelt, showing the two measured radii (R_1, R_2) correlated with fish length. The hyaline zones (winter zones) are seen (x 20).

to Masterman (1913). The otoliths were examined in immersion oil (refraction index 1.515) using a stereoscopic microscope and reflected light. The hyaline zones (winter zones) were counted. When comparing the number of winter zones in otoliths and scales of fish with more than tree winter zones on the otolith, the scales nearly always showed fewer zones than the otoliths. Only in smelts with one or two winter zones on the otolith did the data from scales and otoliths agree. The use of scales thus underestimates the age of smelt in Lake Tyrifjorden. Further age determinations and growth calculation were therefore based on the otolith data.

In order to make correct calculations of growth, a relationship had to be established between fish length and some dimension of the otolith. Two radii (Fig. 1, R_1 and R_2) were measured on the otolith and correlated with corresponding fish length for the 886 smelts between 50—182 mm. Radius R_1 was best correlated with corresponding fish length ($r = 0.954$, $P < 0.0001$), giving a linear regression between fish length (Y) and otolith radius (X) of $Y = 81.39 X + 17.95$. Calculation of growth was carried out by using this regression model.

RESULTS

All smelt caught in May were mature, while the smelt collected in July and October were immature. Fig. 2 shows the age and length distribution of the smelt caught during the spawning run. Smelt of age 2 + and 6 + were most numerous. Only five specimens of age 7 + were caught while the youngest fishes were of age 1 +. Except in age group 3 + and 4 + there were significantly more males than females among the mature smelt ($P < 0.05$. Sign-test).

The five smelt of age 7 + varied from 143—182 mm. Overlap in length was observed in all age groups. Except for smelt of age 4 + and 5 +, the females were significantly longer than the males ($P < 0.05$ Mann-Whitney U-test).

Fig. 3 and 4 show back-calculated growth of 610 smelt from age 1 + to 6 +. Because of high numbers of smelt in age groups 2 +, 3 + and 6 +, a number of 55—87 males and females respectively were randomly picked in each age category. In July and October in the first year of life, the smelt were according to the catches about 30 and 50 mm. Smelt at the end of the first year of growth were not caught, but according to back-calculation they are then about 60 mm. Second and third mean growth increment were 20—30 mm, fourth year of life about 12—14 mm and fifth and sixth year 8—9 mm and 6 mm respectively.

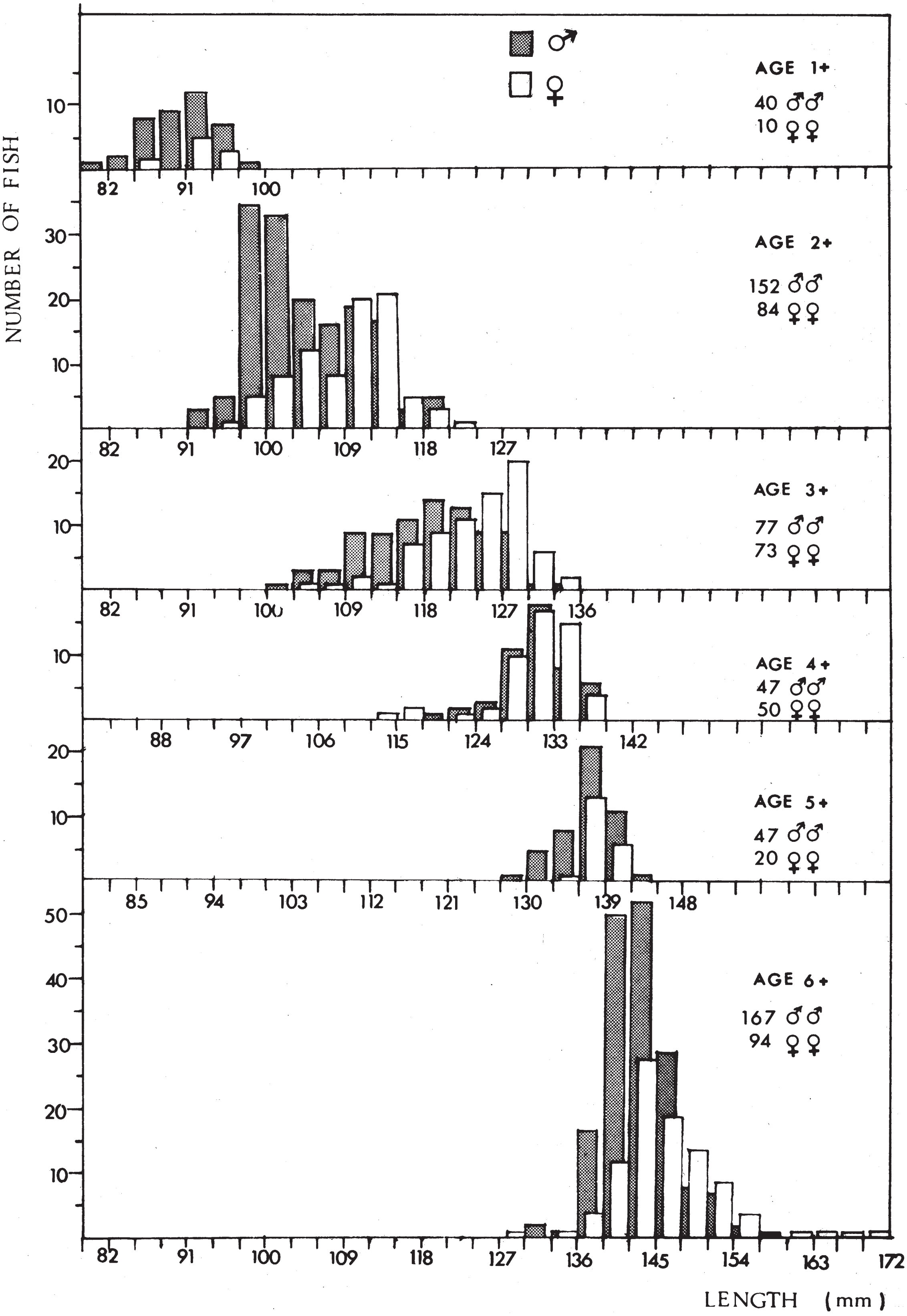
According to the growth pattern in Fig. 3 and 4, the elder smelt have grown faster than younger smelt in corresponding year of life after the first year of growth. The only exception were females of the year class 1973. These differences between the year classes in calculated growth at each age, were significant except between males in year class 1972 and 1973 at age 2, and between males in year class 1971 and 1972 at age 2, 3 and 4 ($P < 0.05$. Mann-Whitney U-test).

DISCUSSION

The results of the present investigation indicate dominance of males and of two year classes in the spawning run. Because the data are based on only one spawning season, it is not possible to say if this is a general trend in Lake Tyrifjorden. However Sandlund et al. (1980) found different strength of the year classes of smelt in Lake Mjøsa, and according to Belyanina (1969) males are more numerous than females in younger year classes.

Mature smelt of age 1 + were present at the spawning grounds in Lake Tyrifjorden. They were however less numerous than the elder

Fig. 2. Length distribution of 861 mature smelt caught in Lake Tyrifjord during spawning run i May. The number of males and females in each year class are given.



NUMBER OF FISH
♂
♀
AGE 1+
40 ♂♂
10 ♀♀
AGE 2+
152 ♂♂
84 ♀♀
AGE 3+
77 ♂♂
73 ♀♀
AGE 4+
47 ♂♂
50 ♀♀
AGE 5+
47 ♂♂
20 ♀♀
AGE 6+
167 ♂♂
94 ♀♀
LENGTH (mm)

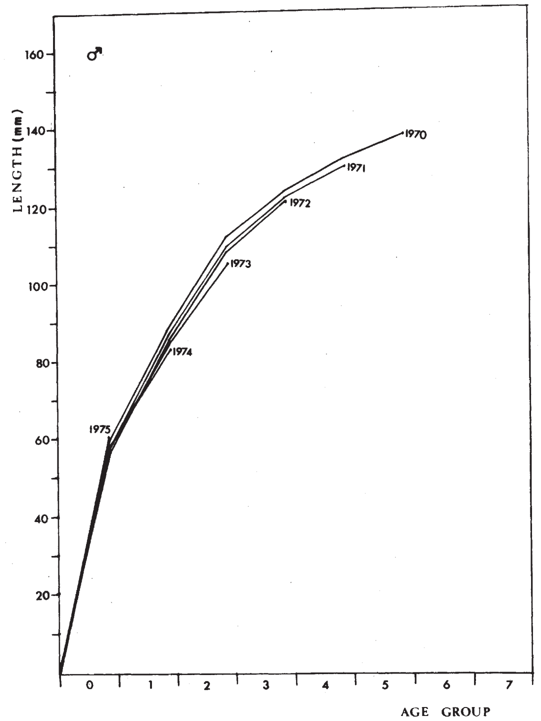


Fig. 3. Calculated mean growth of different year classes of smelt (males) caught in Lake Tyrifjord in May.

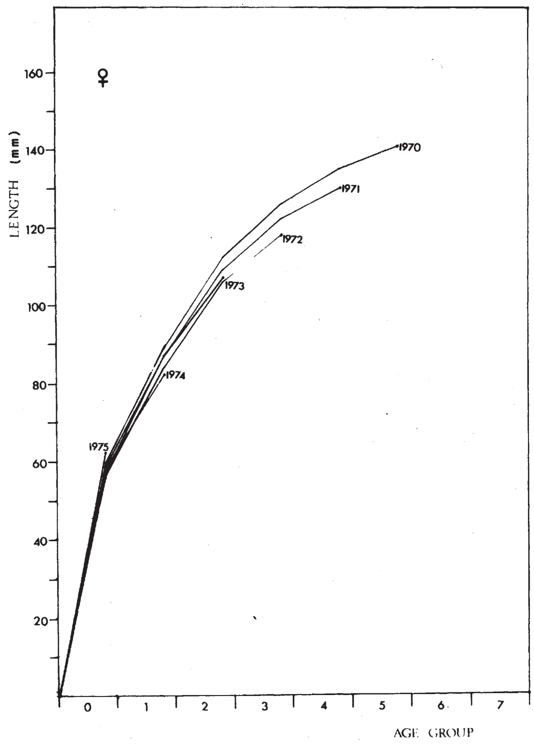


Fig. 4. Calculated mean growth of different year classes of smelt (females) caught in Lake Tyrifjord in May.

smelt, and most of them were males. This may be a result of different strength of the year classes, but it may also be caused by different age of maturity within the population. Some of the smelt, mostly males, are mature after two years, while the main part become mature during the third year as found in other smelt populations (Nordquist 1910, Lillelund 1961, Rembiszewski 1970, Bergaust 1972, Sandlund et al. 1980).

The results of the growth calculations indicate that linear growth of smelt in Lake Tyrifjorden is similar to that found in most other European lakes (Nordquist 1910, Alm 1917, Willer 1926, Huitfeldt-Kaas 1927, Belyanina 1969) during the first years, but somewhat smaller from age four to seven. In Polish lakes however, smelt grow about 10—20 mm more during the first year than in Lake Tyrifjorden (Leskien 1942, Czeczuga 1959, Rembiszewski 1970). As found in many smelt populations (Belyanina 1969), females were growing faster than males also in Lake Tyrifjorden.

The causes for varying growth and body size of different smelt populations are according to Rupp & Redmond (1966) not genetic variations between the populations, but differences in abiotic and biotic factors of the lakes. Temperature differences between the lakes during the growth season may result in different growth rates of the smelt populations (Nikolsky 1963, Belyanina 1969). However, quantity and quality of food are considered to be the main causes for the differences in growth rates of smelt populations (Willer 1926, Rupp & Redmond 1966, Belyanina 1969). In Lake Tyrifjorden the main food in most of the year is zooplankton dominated by cladocerans (Garnås 1978), while in shallow lakes benthic evertebrates play a more important part in the smelts diet (Bergaust 1972, Hakkari 1978). The smelt of Lake Steinsfjorden (Bergaust op. cit) grew 20—40 mm more during second year than the smelt of Lake Tyrifjorden. Competition for food from char *(Salvelinus alpinus)* and whitefish *(Coregonus lavaretus)* may also have influence on the growth rate of the smelt in Lake Tyrifjorden.

Difference in diet and interspecific competition do not, however, explain the different growth rates between the year classes, with an apparent steady decrease in yearly growth rate of younger year classes. A similar growth pattern has also been found for female smelt in lake Mjøsa (Sandlund et al 1980). Differences in growth rate of year classes can be caused by population density (Abrosov & Agapov 1957, Lillelund 1961, Belyanina 1969). Due to increased competition for food, strong year classes will show slower growth than year classes of lower density. Delayed spawning caused by unfavourable spawning conditions may also lead to different growth rate between year classes. Smelt hatched in years with delayed spawning will attain smaller size after one year due to shorter growing season. Temperature during the season of growth can also have influence on the growth of a year class. Smelt are known to grow faster in warm summers than in colder summers (Belyanina 1969). This will lead to the largest differences in length between year classes, if low water temperatures occur during the first year of life, when growth is fastest.

It is however not probable that any of the above mentioned factores are the main cause for the growth pattern of smelt in Lake Tyrifjorden. Occasional variations in the surroundings would not have given such a gradual decrease in growth rate from older to younger year classes in corresponding year of life. According to meteorological data there has neither been a gradual decrease in summer temperatures from 1970 to 1975. Natural selective mortality appears to be a more probable explanation for the kind of growth that was found for smelt in Lake Tyrifjorden. Within a year class there will always be individual differences in growth. The first year these may be due to different hatching date or physiological differences at birth (Ricker 1958), which later intraspecific competition for food may maintain. Those individuals within a year class with the best growth rate will be better protected against predators, because the predation pressure is always heaviest on the smallest individuals in a fish population (Ricker 1958, Lindström 1962, Tesch 1971).

Smelts are generally exposed to strong predation from fish species like perch *(Perca fluviatilis)*, pike-perch *(Stizostedion lucioperca)*, burbot *(Lota lota)*, char *(Salvelinus alpinus)* and trout *(Salmo trutta)*(Alm 1917, Belyanina 1969, Milbrink 1973, Nilsson 1974). Also in Lake Tyrifjorden smelt were found in the stomachs of perch, char, trout and pike *(Esox lucius)*. Natural mortality caused by size selective predation will therefore have significant influence on the survival pattern of smelt year class populations, because the bigger fishes in each year class survive on average longer than the smaller ones. This «survival of the biggest» explains the growth pattern found in Lake Tyrifjorden smelt.

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