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Semelparous whitefish *Coregonus lavaretus:* do they exist?

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The life history of the whitefish *Coregonus lavaretus* population in the eutrophic Lake Temse, Southern Norway, was studied in 1985 and 1986. Growth was intermediate compared to other populations, whitefish attained 13 and 21 cm first and second winter, respectively. The population was dominated (91%) by the age groups 0, 1 and 2. Oldest aged male and female whitefish were 6 and 4 years, respectively. Fishing pressure and emigration could not explain the observed age structure and age at sexual maturity, but evolution towards semelparity and optimal age at sexual maturity could. Restricted spawning areas are suggested as being the principal factor in the development of semelparity in the population of whitefish studied.

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INTRODUCTION

The majority of teleost fishes spawn more than once and are designated iteroparous. This life history strategy evolves when fertility and post-breeding survival and growth are concave functions of reproductive effort (defined as the proportion of available resource allocated to breeding) (Schaffer 1974). Conversely, when these characteristics are strictly convex functions of reproductive effort semelparity will usually evolve.

A species is usually either semelparous (spawning only once), as in Pacific salmon *Oncorhynchus* (Scott & Crossman 1973), or iteroparous, as in most species. However, in five populations of American shad *Alosa sapidissima* on the Atlantic coast of North America, Leggett and Carscadden (1978) have described a gradient from a strictly semelparous southern population to iteroparous northern populations. This variation appears to be a result of variability in the thermal regimes of the home rivers which influences egg and larval survival.

Much interest has been paid to whitefish *Coregonus lavaretus,* mainly concerning systematics (Svärdson 1979). Most studies on population dynamics of whitefishes have demonstrated iteroparity, and in Scandinavian populations extreme iteroparity, with fish apparently spawning more than ten times, is fairly common (e.g. Ausen 1976, Svärdson 1979, Sandlund et al. 1981, Qvenild & Skurdal 1983). The present study describes a population of whitefish where particularly the females seem to be largely semelparous.

MATERIALS AND METHODS

Lake Temse (surface 64 ha; maximum depth 10 m) is a eutrophic lake in the River Nidelva watersystem, Southern Norway (58° 23'N, 8°37'E), situated 16 m above sea level and 3.70 m above River Nidelva. The lake receives a high imput of nutrient-rich water from agricultural areas. The specific conductivity is about 90 μs/cm, pH = 6.8 and colour 20 mg Pt/1 (Boman & Andreassen 1981). Lake Temse is situated at the Ra moraine, a distinct ridge of glacial material which was deposited at the end of the Weichselian period. The fish fauna is numerically dominated by perch *Perca fluviatilis.* Less abundant species are whitefish, pike *Esox lucius* and eel *Anguilla*

anguilla. The yearly yield of whitefish is approximately 0.2 kg/ha.

During May — November 1985 and November 1986, we caught 178 whitefish using multipanel gill nets (8—55 mm bar mesh, 2—9 mm mesh increment) both in the pelagial and littoral zones. The whitefish were measured (natural tip length (Ricker 1979)) to the nearest 0.1 cm, and sex and degree of sexual maturity were determined. The number of gillrakers on the first left gill arch was counted in a random sample of whitefish. All whitefish were aged using the otoliths (Skurdal et al. 1985) The von Bertalanffy growth curves were fitted to length data using Gulland's (1969) method for obtaining the estimates of the parameters L_∞, k and T_0 in the equation $L = L_\infty (1-e^{-k(T-T_0)})$.

RESULTS

The age distribution of whitefish caught in 1985 and 1986 were not significantly different (Kolmogorov-Smirnov, $p>0.05$), and the material was pooled. The population of whitefish in Lake Temse is skewed in favour of young individuals (Table 1). The three youngest age groups made up approximately 90% of the catch. Males were significantly older than females ($\chi^2 = 13.86$, d.f. = 3, $p<0.01$), the oldest aged male and female whitefish were 6 and 4 years, respectively.

The population was significantly dominated by males (Table 1). Female surplus occurred only, but not significantly, in the youngest age group ($p>0.05$). This indicated that females experience higher mortality than males during sexual maturity and spawning activity.

In both sexes one third reached sexual maturity in the second year of life, and the following year the spawning stock was fully recruited (Table 1). The median age at maturity is 1.2 years in both sexes, assuming that the frequency of mature fish among all fish aged fits a sigmoid curve (Bell et al. 1977). Age distribution and maturity indicate that whitefish, and particularly females, only spawn once.

There were no significant differences between empirical lengths of males and females in age groups where n > 10 (t-test, p>0-05). and the material was pooled. The growth was substantial during the first year of life, the mean empirical length was 13.6 cm the first winter (Table 2). The following years the yearly length increment was reduced, and whitefish reached approximately 30 cm in their fourth year. The growth rate of whitefish in Lake Temse is described by the equation $1_t = 34.9 (1\text{-}0.313^{\,t-2.14})$.

Table 1. Sexual maturity (%), cumulative age structure (%) and sex ratio given as per cent males. Number of samples in brackets (ns = $p>0.05$, * = $p<0.05$. ** = $p<0.01$)

Age	Sexual maturity Males	Sexual maturity Females	Cumulative age structure	Sex ratio
0	0 (27)	0 (29)	31.5	48 ns
1	33 (40)	33 (21)	65.7	66 *
2	100 (30)	100 (15)	91.0	67 *
≥3	93 (15)	100 (1)	100.0	94 **
Total	112	66		63 **

Table 2. Mean empirical lengths with standard deviation of whitefish caught in Lake Temse in 1985 and 1986. Number of samples in brackets. (ns = $p>0.05$, ** = $p<0.01$)

Age group	August	November/May	Difference between groups
0	12.7±0.42 (10)	13.6±0.58 (46)	**
1	19.8±0.35 (11)	21.0±0.83 (50)	**
2	25.3±1.18 (19)	25.7±1.52 (26)	ns
3	0	29.2±1.70 (10)	
4	33.3 (1)	34.0±0.00 (2)	
5	0	32.0±0.71 (2)	
6	0	33.5 (1)	

Mean empirical lengths of age group 0 and 1 were significantly shorter in August than corresponding lengths in November/May (Table 2). At the age when all whitefish were sexually mature, i.e. in age group 2, no such difference was observed. This demonstrates that after the attainment of maturity the main part of the food consumed by the fish is used not for growth but for the ripening of the gonads.

The mean number of gillrakers in whitefish inhabiting Lake Temse was 35.0 (95% C.I.: 0.58). This was compared with the mean number of gillrakers in whitefish inhabiting River Nidelva 2 km downstream from Lake Temse (38.5 ± 2.05). These two values are significantly different (t = 5.75, d.f. 43, $p<0.001$).

DISCUSSION

Gill nets are selective (Hamley 1975), and underrepresentation of the youngest age groups will usually occur. The selectivity curves of nylon nets of the mesh sizes used in the present study indicate, however, that catches of whitefish longer than approximately 20 cm will be representative (Qvenild & Skurdal 1981). Thus, the whitefish population in Lake Temse is extremely skewed in favour of the youngest age groups. The method of age determination applied in this study excludes the possibility of underestimating ages of older fish (Barnes & Power 1984, Skurdal et al. 1985). This bias in favour of young individuals in a whitefish population is in contrast to previously described whitefish populations (e.g. Dahr 1947, Svärdson 1950, Bagenal 1970, Ausen 1976, Lethonen 1981, Qvenild & Skurdal 1983). This may be due to environmental conditions, significant fishing mortality, or intrinsic factors such as emigration or a high extent of semelparity.

In Lake Temse the yearly yield of whitefish is low (approximately 0.2 kg/ha) compared to other Norwegian lakes (1—55 kg/ha (Ausen 1976, Qvenild 1981, Qvenild & Skurdal 1983, Sandlund & Næsje 1986). The low yield is due to low effort and few fishermen. The whitefish fishing takes place in late autumn at the spawning areas. According to Lindroth (1957) and Bagenal (1970) the males occupy the spawning grounds in advance of the females and remain there for a long time. Although we have no data, we assume that the spawning behaviour in whitefish do not vary significantly among populations. Thus, in Lake Temse males experience higher fishing mortality than females, which would increase the proportion of mature females in the older part of the population. The reverse was observed in Lake Temse which is in contrast to other populations of whitefish (Qvenild & Skurdal 1983) and lake whitefish (Bell et al. 1977). This difference may be due to the considerably shorter life span of whitefish in Lake Temse. Thus, the fishing pressure can explain neither the significant reduction of whitefish in older age groups, nor the annual change in sex ratio with age.

A significant emigration of sexually mature whitefish from Lake Temse would leave a population dominated by young immature individuals. Emigrating whitefish would probably intermingle and spawn with the downstream population of whitefish in River Nidelva. If the emigrants significantly increased the spawning stock in River Nidelva, differences between the populations in genetic and meristic characters would be eliminated (cf. Svärdson 1979). The small altitudinal difference (<4m) makes upstream exchange of whitefish possible in heavy floods (Helland 1904). The mean number of gillrakers in the population of whitefish in Lake Temse is significantly lower than the mean number of gillrakers in the population of whitefish in River Nidelva. Thus, the hypothesis that any significant exchange of sexual mature whitefish occurs between Lake Temse and River Nidelva does not seem likely.

Consequently, we suggest that the whitefish in Lake Temse are semelparous or in a state of evolution towards semelparity. Semelparity, existing in Pacific salmon (Scott & Crossman 1973), American shad (Leggett & Carscadden 1978) and the aphyine genera of gobies (Miller 1984), has not been previously observed in Coregonids, although cisco *Coregonus albula* with life spans less than 3 years are reported in several Swedish and Finnish localities (review Svärdson 1966). The ages of individuals in these populations of cisco may, however, have been underestimated due to the use of scales in ageing. Aass (1972) demonstrated in cisco that beyond otolith age 3, otolith age was higher than scale age in nearly all cases of disagreement. Therefore, the population of whitefish in Lake Temse seems to be an exception among described coregonid populations.

We can think of one factor that explains the observed breeding age and early sexual maturity in the whitefish population in Lake Temse. Whitefish spawning areas consist of stones and pebbles to which the eggs adhere (Fabricius & Lindroth 1954). In the eutrophic Lake Temse accessible spawning areas are restricted due to heavy sedimentation of organic matter. Underwater springs may, however, supply restricted satisfactory spawning areas where incubation capacity is small. As individual fecundity increases with fish size, there is in this case no reproductive profit in being big.

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