Long-term variation in piscivory in a brown trout population: Effect of changes in available prey organisms

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J. H. L'Abée-Lund
Norwegian Water Resources and Energy Directorate

Harald Sægrov
Rådgivende Biologer AS

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Abstract – The piscivorous behaviour in a brown trout (*Salmo trutta* L.) population was studied in four discrete periods over seven decades (1917–94) in the hydroelectric reservoir Tunhovdfjord in Norway established in 1919. Piscivorous brown trout were extremely scarce prior to the introduction of two fish species Arctic charr (*Salvelinus alpinus* L.) and European minnow (*Phoxinus phoxinus* L.) in the 1920s. Brown trout started eating minnow at 17 cm and Arctic charr at 22 cm of length. In the 1950s, the brown trout predated extensively (60% of analysed trout) on Arctic charr and minnow. During the next four decades, the incidence of piscivorous brown trout declined to 15%, whereas the frequency of brown trout eating Arctic charr remained constant at 10%. The growth pattern, expressed as back-calculated length, demonstrated similarity in three periods (1920s, 1960s and 1990s) and improved growth in the 1950s. The improvement was addressed the impoundment of a reservoir upstream. We did not find any marked change in growth rate due to piscivority, but coefficient of variance of back-calculated lengths indicated significant variation in individual growth in age group ≥6 years from 1950 onwards. We accredit this variation to the rise of piscivorous brown trout.

J. H. L'Abée-Lund[1]*, P. Aass[2], H. Sægrov[3]
[1]Department of Biology, University of Oslo, P.O. Box 1050, Blindern, N-0316 Oslo, Norway, [2]Zoological Museum, University of Oslo, P.O. Box 1172, Blindern, N-0318 Oslo, Norway, [3]Rådgivende Biologer AS, Bredsgården, Bryggen, N-5003 Bergen, Norway
*Present address: Norwegian Water Resources and Energy Directorate, P.O. Box 5091, Majorstuen, N-0301 Oslo, Norway

Key words: minnows; introductions; piscivory; salmonids; diet

Jan Henning L'Abée-Lund, Department of Biology, University of Oslo, P.O. Box 1050, N-0316 Oslo, Norway; fax: +47 22 95 90 02; e-mail: lbl@nve.no

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

The impacts of piscivores on prey fish have been widely investigated since the study of Popova (1967). A common factor in these predator–prey studies has been the focus on the effects of the predator on the prey fish. Piscivores have been documented to be a major structuring agent in fresh water fish communities. The effects may be due primarily to two mechanisms, namely selective feeding (Tonn et al. 1992; Brönmark et al. 1995; Macchi et al. 1999; Findlay et al. 2000) and involvement of behavioural traits (Werner et al. 1983; Fraser & Gilliam 1992; Eklöv & Persson 1995). Selective piscivorous feeding may act among and within prey species. Findlay et al. (2000) showed that introduction of piscivores may be harmful to some minnow communities, whereas others were unaffected. Within prey species, size selectivity by predators is evident (e.g., Tonn et al. 1992). The presence of a predator may significantly affect the habitat use of the prey species, leading to more frequent use of low-risk areas (e.g., Werner et al. 1983).

The growth of fishes is flexible and indeterminate (Wootton 1990). Several factors are important for the size achieved by individuals such as physical habitat constraints (e.g., Sandlund et al. 1992), habitat use due to predation risk (e.g., Werner et al. 1983), onset of sexual maturation (Alm 1959), and prey size (Kerr 1971). The modelling work by Kerr (1971) showed that sustained growth in fish required increasingly larger prey organisms. The growth pattern of piscivorous brown trout

(*Salmo trutta* L.) illustrates this by the distinct change in growth rate when the predator shifts to fish diet (Aass et al. 1989; Jonsson et al. 1999).

The influence of native or introduced piscivores has been inferred from negative correlations between the intensity of piscivory and richness or abundance of potential prey species, such as cyprinids (e.g., Tonn & Magnusson 1982; Robinson & Tonn 1989; Persson 1997; Findlay et al. 2000). Less attention has been paid to the effect of an introduction of potential prey fish on facultative piscivorous fish species. Accidental or strategic introduction of fish species as prey may cause changes in the native fish communities. Changes and their relationships should be most conspicuous in communities with few fish species. Brown trout is an eminent experimental organism to test the effect of introduction of fish species. As adult, brown trout may demonstrate great variability in food consumption, from being almost exclusively zooplankton (Klemetsen 1967) or fish eater (Aass et al. 1989), to demonstrate a wide range of organisms eaten (Langeland et al. 1991). The diet of piscivorous brown trout changes according to the availability and biomass of the prey species exposed to predation by brown trout (L'Abée-Lund et al. 1992). The study by Andersen & Vøllestad (1996) illustrates the plasticity of the piscivorous behaviour in brown trout. Historically, a phenotype of the brown trout in Lake Selura was feeding on Arctic charr *Salvelinus alpinus* (L.). The piscivorous phenotype disappeared as the Arctic charr population declined dramatically due to acidification. However, after liming of the lake, the charr population increased in number and the piscivorous phenotype reappeared shortly afterwards.

A data set on brown trout diet covering a period of more than seven decades from a Norwegian reservoir makes it possible to test how a brown trout population reacts to a rapid and dramatic reduction in original food organisms and a subsequent colonisation by two potential fish prey species namely Arctic charr and European minnow (*Phoxinus phoxinus* L.). We examined the data to determine if the brown trout population responded to the altered prey base by changing its feeding habit and increasing the incidence of piscivory, and whether this resulted in increased growth.

Materials and methods

Study site

The Tunhovdfjord reservoir (60°19′N, 8°56′E) in central Norway (hereafter Tunhovdfjord) consisted of three small lakes prior to impoundment in 1919. Construction of the hydroelectric reservoir resulted in an elevated water level and annual water fluctuation of 18 m (736–718 m a.s.l.). The reservoir area fluctuates annually between 14 and 25 km^2. Tunhovdfjord is oligotrophic (secchi disc transparency 10 m) and 70 m deep, but temperature stratification seldom occurs due to wind exposure.

Construction of the dam destroyed brown trout spawning areas in the outlet and in the river reaches connecting the three lakes. A second dam, creating Pålsbufjord reservoir in the main inlet some 500-m upstream of Tunhovdfjord in 1946, further reduced available spawning areas. To compensate for these impacts, stocking of brown trout has been carried out since the establishment of the reservoir. Brown trout alevins of non-native origin were stocked during the first years (Dahl 1926). From 1964 onwards, however, only native F1-juveniles have been stocked, alternating between young-of-the-year (4–6 cm), yearlings (8–12 cm) and 2-year-old fish (14–28 cm). The compensation programme uses fish of both sexes generally larger than 35 cm, caught in the major inlet during the spawning run. Since 1958, 860 000 juveniles have been released after been marked by cutting the adipose fin and/or maxilla or by tagging with Carlin tags (Carlin 1955).

Originally brown trout was the only fish species in Tunhovdfjord. In the 1920s, Arctic charr and European minnow immigrated into the lake as a result of releases further upstream. No data exist regarding the development of the population of Arctic charr and minnow in Tunhovdfjord during the first decades after introduction. However, Huitfeldt-Kaas (1935) reported that large number of Arctic charr was observed at the outlet of the Pålsbufjord in 1929, and in 1949, both species existed in high numbers in Tunhovdfjord (P. Aass, unpublished data).

Data collection

This study relies on data of the brown trout collected from four time periods that extend over seven decades. Sampling site and sampling techniques remained constant throughout the entire study. Each of the four periods consisted of 2–5 consecutive years of sampling throughout a 6-month season (May–October). Personnel responsible for the sampling during 1950–69 and for most of 1989–94 remained constant.

The first period (1917–31) consists of data prior to and right after the reservoir came into use and was published by Dahl (1926) and Huitfeldt-Kaas (1935). During the periods in the 1950s, 1960s and 1990s, all brown trout collected were individually recorded by length, date of capture, and the stomachs preserved. From 1966 onwards, each fish was classified as wild or hatchery reared based on the presence or absence of tags. Trout were collected with epibenthic gill nets (bar mesh 26, 35 and 40 mm) during May–October at the same locality used by Dahl (1926). To supplement these samples during 1989–94, multimesh gill nets (10, 12.5, 16, 19.5, 24, 29 and 35 mm) were used in both pelagic and epibenthic areas. The supplementary data comprise, however, only a minor part (5.0%) of the overall data from that period.

From May–October 1917–94, a total of 3884 brown trout were sampled of which 3265 were used for stomach analysis (287 from 1917–31, 191 from 1950–52, 347 from 1966–69 and 2440 from 1989–94) and 1651 for growth analysis (300 from 1917–31, 387 from 1950–52, 231 from 1966–69 and 753 from 1989–94). The periods are subsequently denoted as the 1920s, 1950s, 1960s, and 1990s, respectively.

Data analysis

Undigested fish in stomach contents were measured, counted and identified to species. For digested fish, the presence of pharyngeal teeth or otoliths was used for species identification. Zooplankton was identified to species, whereas other aquatic organisms were taken to higher taxonomic groups. The following major food categories were used for invertebrates found in stomachs: (i) zooplankton (*Bythotrephes longimanus*, *Holopedium gibberum*, *Bosmina longispina*, *Daphnia* sp., *Heterocope saliens*), (ii) littoral crustaceans (*Eurycercus lammelatus*, *Gammarus lacustris*), (iii) *Lepidurus arcticus*, (iv) Chironomidae, (v) other zoobenthos, and (vi) surface insects.

The stomach contents were divided into three categories: empty, those containing invertebrates (zooplankton, aquatic and terrestrial insects), and those containing fish. A brown trout was defined as piscivorous when fish remains were found in the stomach content. Naturally produced (wild) and hatchery-reared (stocked) brown trout could be distinguished in the 1960s and 1990s due the tagging procedure of stocked fish. Ages were determined by scales (Jonsson 1976) and corresponding lengths were estimated by back-calculation (Lea 1910). Fish sampled in the 1920s were aged by Knut Dahl whereas the remaining fish were aged by one of the authors (PA). Coefficient of variation (CV (%) = 100 × SD/mean) of age-specific lengths were computed within each period. Presentation of mean lengths and CV in Fig. 7 are expressed only when the number of fish exceeds five individuals.

Logistic regression analyses were carried out to test differences in occurrence of piscivory among the four time periods. Differences in stomach contents among time periods were tested by testing for heterogeneity (G_H-test) (Sokal & Rohlf 1981). The *t*-tests were performed to test for between-group differences of age-specific back-calculated lengths.

Results

Piscivory

The brown trout demonstrated significant changes in diet over the four study periods ($G_H = 325.0$, $P < 0.001$). Piscivory was reported only once (0.3%) in the 1920s (Dahl 1926). About 30 years after the introduction by minnow and Arctic charr, the diet of trout consisted mostly of fish as approximately 60% of the brown trout had consumed fish. However, in the following periods, a significant ($P < 0.001$) decline in the fraction of piscivores took place, reaching 15% in the 1990s (Fig. 1).

Wild and stocked brown trout showed similar pattern in piscivory indices within the 1960s and 1990s (Fig. 2); thus, the two groups of fish were pooled. The incidence of Arctic charr in the total data set of brown trout stomachs remained surprisingly constant from the 1950s to the 1990s, varying between 10.4 and 12.8%. This implies that the decline in the frequency of piscivorous brown trout from the 1950s and 1960s to the 1990s was due to reduced intake of minnows. The piscivorous brown trout in the 1990s ate proportionately ($\chi^2 = 158.3$, $P < 0.001$) more Arctic charr than brown trout in the previous decades (Fig. 3).

Brown trout started feeding minnow at a length of 17 cm and Arctic charr at a length of 22 cm (Fig. 4). Very few brown trout ate minnow after attaining a length of 40 cm. In the overlapping length interval of piscivorous brown trout, minnows were most frequently found in the stomach of brown trout smaller than 33 cm, whereas Arctic charr dominated in larger Arctic charr. Despite considerable overlap in length of brown trout eating minnow or Arctic charr, we found that individual trout were remarkable conservative in choosing fish prey species. We were able to determine the species of the fish eaten by 501 brown trout of which 314 and 183 had consumed Arctic charr or minnow, respectively, and only three brown trout had consumed both species. In 1923, the one piscivorous brown trout reported (Dahl 1926) had eaten one conspecific. At that time brown trout was the only fish species present.

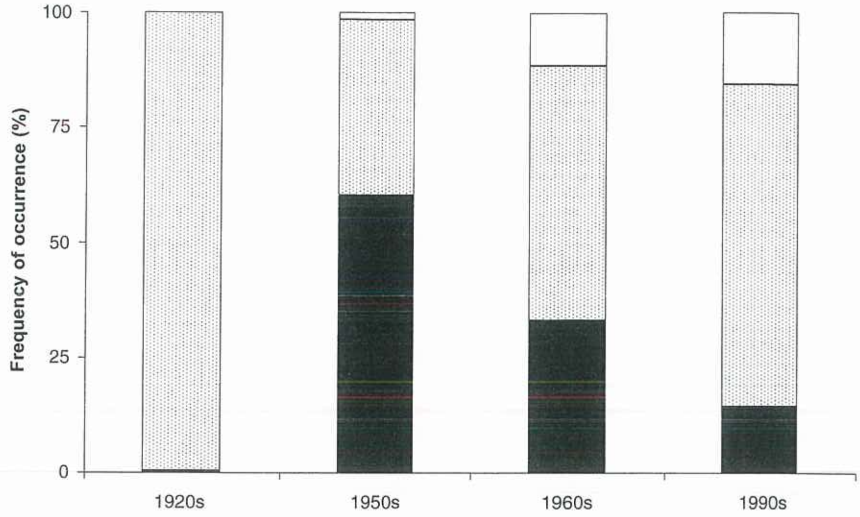

Fig. 1. The frequency of different contents found in stomach of brown trout caught in Tunhovdfjord 1917–94. Shaded = fish; stippled = invertebrates; open = surface insects.

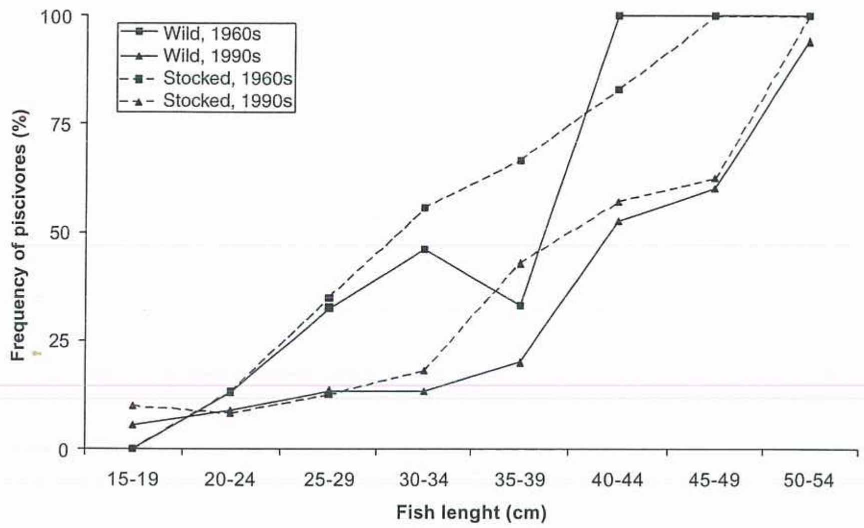

Fig. 2. The incidence of piscivory in wild and stocked brown trout in Tunhovdfjord in 1960s and 1990s. Solid and dotted lines show wild and hatchery-reared individuals, respectively; and squares and triangles show 1960s and 1990s, respectively.

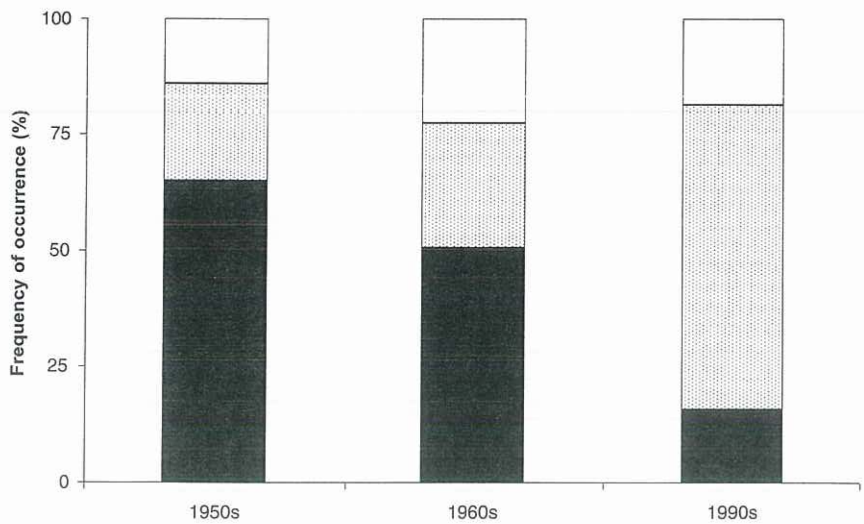

Fig. 3. Distribution of different fish categories in piscivorous brown trout stomachs. Shaded = minnow; stippled = Arctic charr; open = fish remains of undetermined origin.

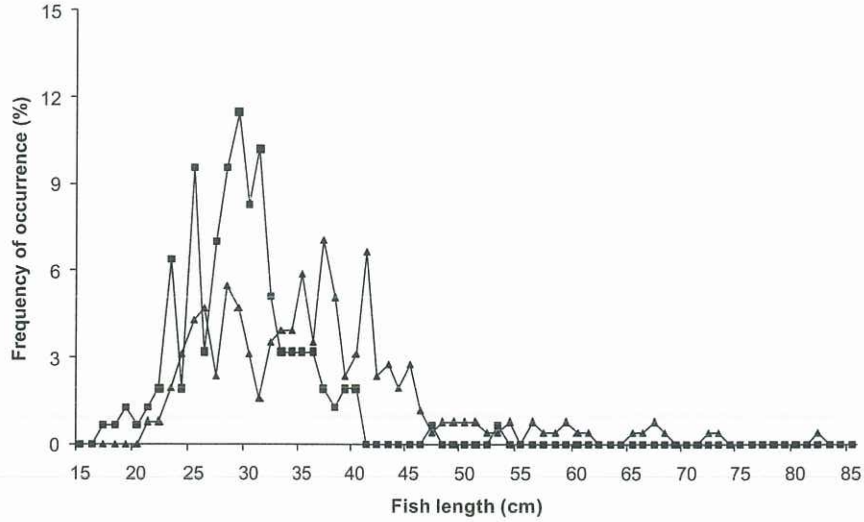

Fig. 4. The frequency of brown trout stomachs containing minnow (■) and Arctic charr (▲) in different brown trout length intervals given that the stomach had food contents.

Since the introduction of minnow and Arctic charr populations, cannibalism has not been recorded.

The indices of piscivory changed significantly ($P < 0.001$) among periods (Fig. 5). Brown trout started feeding on fish at smaller lengths in the 1990s than in the two previous periods. Obligate piscivory was achieved at somewhat smaller length in the 1950s and 1960s (40–45 cm) than in the 1990s (>50 cm).

Invertebrate food items

Analysis of invertebrates found in brown trout stomachs revealed that brown trout mainly feed on the same group of food organisms in the study period (Fig. 6). Zooplankton was a major food item in the 1920s but showed reduced importance afterwards, being partly replaced by surface insects. Stomachs from the 1950s showed that littoral crustaceans and *Lepidurus arcticus* were eaten at a negligible rate. Although the group zoobenthos were found in numerous brown trout stomachs in all periods, the group showed a reduction in number of taxonomic groups. In the 1920s, Planorbidae, Ephemeroptera, Trichoptera, Coleoptera and midges were the dominating groups, whereas Trichoptera and Planorbidae were almost exclusively eaten in the 1960s and 1990s. In the 1950s, Ephemeroptera, Trichoptera and Planorbidae were the dominating taxonomic invertebrates among zoobenthos.

Growth

Growth based on back-calculated length, remained remarkable stable throughout the entire study period (Fig. 7). It is noteworthy that age-

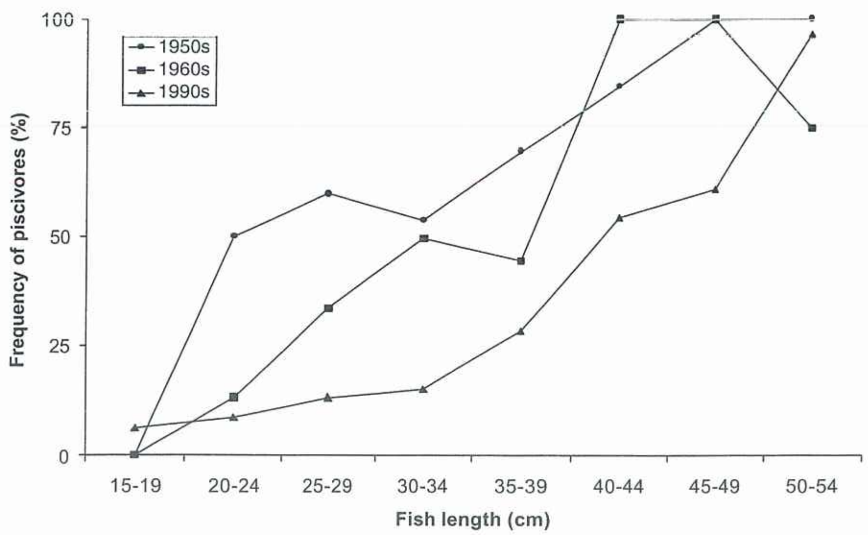

Fig. 5. The incidence of piscivorous brown trout in Tunhovdfjord 1950s–1990s.

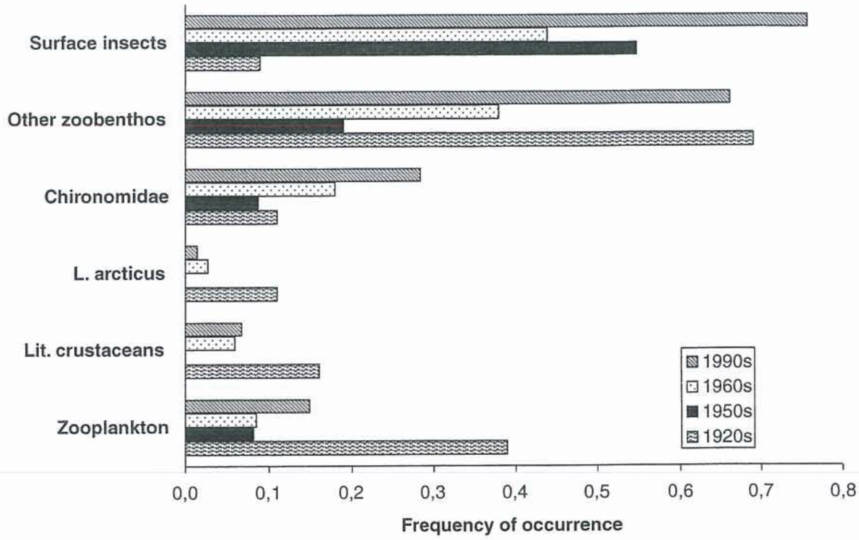

Fig. 6. Frequency of the different invertebrate food items of brown trout caught in Tunhovdfjord 1917–94.

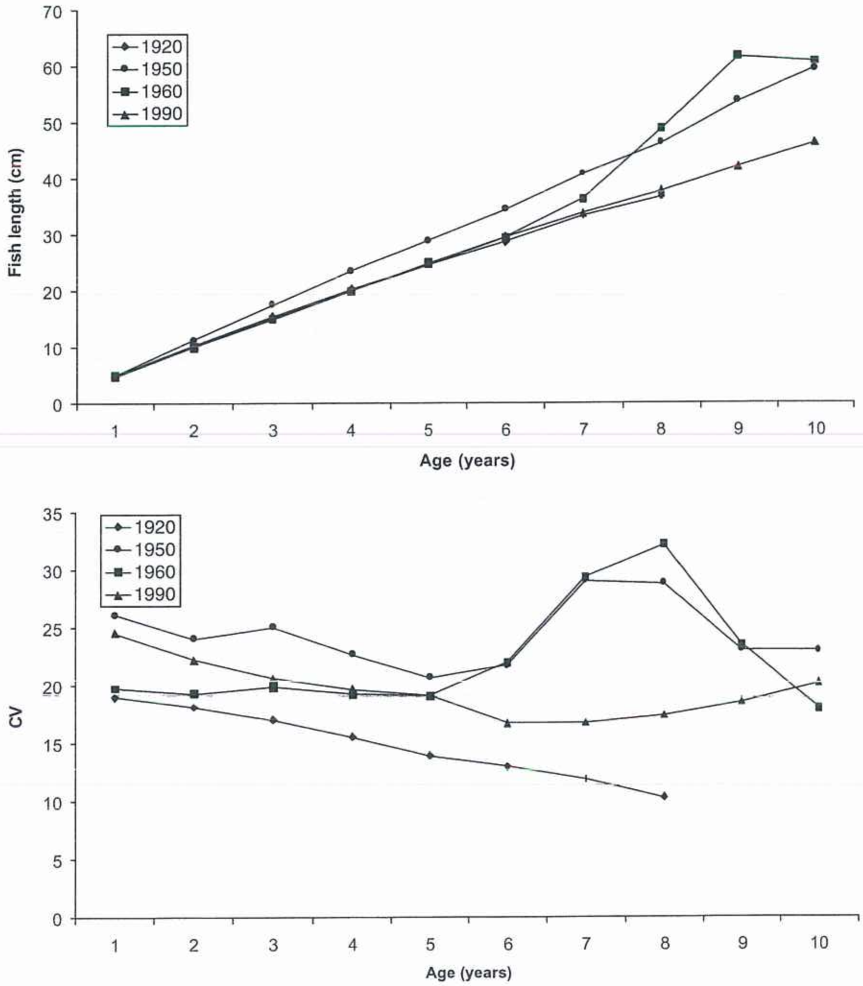

Fig. 7. Growth of brown trout in Tunhovdfjord 1917–94: upper panel, back-calculated length; and lower panel, coefficient of variation of age-specific back-calculated lengths.

specific lengths of brown trout from 1920s, 1960s and 1990s were identical until 6 years of age. At higher ages, brown trout from the 1920s and 1990s continued to grow at nearly the same rate, whereas in the 1960s, brown trout improved their growth and achieved significantly (*t*-tests, $P < 0.05$) larger size as 8- and 9-year-old compared to brown trout from the 1950s. Brown trout caught in the 1950s demonstrated for age groups 2–7 years significantly (*t*-tests, $P < 0.001$) larger size than fish caught both earlier and later. Moreover, the growth pattern for all periods did not show any marked increase in growth rate, indicating no significant growth improvement in the population due to piscivory.

On the other hand, the coefficient of variance of age-specific lengths demonstrated great variability (Fig. 7). Back-calculated lengths of fish caught in the 1920s demonstrated the lowest CV values for all ages in addition to a gradual decline from age 1. The other periods also demonstrated a decline in the CV in the younger age groups, but contrary to the 1920s they demonstrated an increase in CV at some age (age 5 in 1950s and 1960s and age 6 in the 1990s).

Discussion

Long-term data series can be invaluable in understanding changes in population dynamics. One problem with such series is, however, that methodology often varies during the study. However, in our data set, sampling site and sampling techniques remained constant. In addition, the same persons were responsible for the sampling throughout 1950–69 and for most of the data sampled in 1989–94. These factors improve the consistency of the total data set.

Our study, covering a >70-year time span, demonstrates two major results. We found significant changes in the degree of piscivory of the brown trout after the introduction of suitable fish prey species. Secondly, we did not find any corresponding increase in the mean growth rate in the population.

The change in diet took place and a brown trout population relying on fish as the main food item was established within 20–30 years. The time needed by an introduced fish species to build up a strong and viable population may depend on local conditions. In Norwegian mountain lakes, about 10 years seems necessary for Arctic charr (Sømme 1933) and European minnow (Borgstrøm et al. 1996). As a food resource for predaceous brown trout, these two species complement each other both in size and availability. After attaining the size (about 15 cm) that makes piscivority possible in brown trout (L'Abée-Lund et al. 1992; this study), brown trout start feeding on minnow which form shoals in shallow waters. At this size, brown trout are restricted to use the littoral zone (Haraldstad & Jonsson 1983; this study unpublished data). As juvenile Arctic charr are restricted to deep epibenthic strata (Hindar & Jonsson 1982; Sandlund et al. 1992), small brown trout are not able to find and predate on them. However, by increasing length brown trout utilise both pelagic habitat and deeper strata of the epibenthic zone (Haraldstad & Jonsson 1983; this study unpublished data). This ontogenetic habitat shift makes them able to utilise similar habitat as juvenile Arctic charr, and feed upon them. Thus, we don't expect to find Arctic charr in the stomach of the smallest brown trout. Length distributions of piscivorous brown trout caught in Tunhovdfjorden lend support this hypothesis.

The incidence of piscivorous brown trout in Tunhovdfjord is comparable with other piscivorous brown trout populations. The highest incidence of piscivory (50–100%) is found in lakes supporting a diverse or dense fish community of small-sized species such as smelt (*Osmerus eperlanus* L.), vendance (*Coregonus albula* L.), perch (*Perca fluviatilis* L.) and three-spined stickleback (*Gasterosteus aculeatus* L.), in combination with larger fish species such as whitefish (*Coregonus lavaretus* L.) and Arctic charr (Skurdal et al. 1992; Næsje et al. 1998; Niva 1999). The situation in Tunhovdfjord in the 1950s and 1960s resembled such ecosystems with dense forage fish populations, and the incidence of piscivory in Tunhovdfjord was the highest ever recorded (approximately 60%) in the lake. Then, the minnow population declined as a result of the reservoir impoverishment and so, the incidence of piscivorous brown trout reached values comparable to lakes supporting only brown trout and Arctic charr (<10%) (L'Abée-Lund et al. 1992; Damsgård & Langeland 1994; Per Aass unpublished data). The coefficient of variation of the age-specific back-calculated lengths lend support to this change in the feeding regime in the 1950s and 1960s compared to 1990s. The high proportion of minnow feeding brown trout in 1950s and 1960s resulted in a marked increase in the CV of length in the age group ≥6 years. We found no such marked change in the data set from the 1990s probably due to the small fraction of piscivores.

During the first decades after the impoundment of Tunhovdfjord, the drawdown zone was littered with remnants of trees and woody debris. In the 1990s, the zone consisted mostly of sand and boulders, and woody debris was restricted to the upper shoreline and chiefly in shallow bays. Habitat structure in the area inhabited by minnows thus changed greatly during the study period. Tree stumps, branches and twigs provided shelter and breeding conditions for the minnows in the early phase. We have no quantitative data on the minnow population at that time, but assume the situation resembled the postimpoundment period of the Pålsbufjord reservoir, situated 500-m upstream of the Tunhovdfjord. In 1946, Pålsbufjord was raised 12.5 m thereby damming

$7.2 km^2$. The minnow population increased remarkably and became easily available to brown trout. Three and 4 years after impoundment of Pålsbufjord, fish constituted 94–99% by mass of the brown trout diet (Aass 1953). In spring and early summer, minnows dominated the stomach contents and numbers of fish found in an individual trout could surpass 90. This impoundment effect lasted about 10 years, then the minnow population declined and Arctic charr became increasingly more important as brown trout food (Aass 1973).

The presence of the cold stenotherm crustacean *Lepidurus arcticus* Pallas in the brown trout stomachs may be used as an indirect measurement of variations in the minnow population. Minnows are efficient predators on the early stages of the *L. arcticus* (Borgstrøm et al. 1985), and after the introduction of minnow into Tunhovdfjord in the late 1920s, *L. arcticus* disappeared as brown trout food. The species reappeared in the 1960s (and 1990s) when the positive regulation effect on the minnow had vanished (Andersen et al. 1994). The highest incidence of trout feeding on minnow was found in the 1950s (48.4% of nonempty stomachs) compared to 26.9 and 5.0% in the 1960s and 1990s, respectively. These observations at least indicate a reduction in the minnow population. We are unfortunately not able to quantify the past and present importance of minnow as a stepping stone for brown trout in the change to a fish diet, and thus, the consequences for piscivority in the brown trout population.

Despite the formidable hydrological and environmental changes in Tunhovdfjord, the growth pattern of brown trout have remained strikingly unchanged during the last 70 years. Similar conservative trend has also been documented in another piscivorous brown trout population subjected to considerable environmental changes due to human encroachments (Aass et al. 1989). We expected to find, however, marked changes in growth pattern of the population among years, as by changing to a fish diet the brown trout are documented to speed up their growth (Aass et al. 1989; Jonsson et al. 1999). Whereas population means in our study are nearly identical among periods, coefficients of variance of age-specific lengths indicate changes in individual growth pattern. Lowest coefficients of variation of age-specific lengths were found in the 1920s and prior to the appearance of piscivory. The high CV values especially in age groups ≥ 6 years in the 1950s and later, demonstrate increased variation in individual growth pattern. This implies increased number of both slow and fast growers. Increased fraction of slow growers is most probably a consequence of reduced diversity and amount of important invertebrate food organisms due to the impoundment. After the first winter with low water level, Dahl (1926) showed that the biomass and diversity of benthic invertebrates had decreased. He further confirmed this change in the invertebrate community in his studies 3 years later. The significant change and reduction in benthic invertebrate community and the consequences for brown trout have been documented in several reservoirs with fluctuating water level (Grimås 1961, 1962; Nilsson 1961, 1964).

We see no other plausible explanations than the increased fraction of fast growers must be a consequence of the change in diet and the appearance of piscivorous brown trout in the population in the 1950s and later. The growth model of Kerr (1971) and empirical data (Aass et al. 1989; Jonsson et al. 1999) lend support to this explanation.

The growth pattern demonstrated in the 1950s was higher than the other periods for most age groups. The impoundment of the upstream Pålsbufjord reservoir in the late 1940s led to a positive regulation effect and a temporary surplus of food organisms, especially minnows, and the growth rate of brown trout and Arctic charr improved greatly (Aass 1953). Due to the fact that the nearby Pålsbufjord reservoir empties into our study lake, we suggest that also the fish population in Tunhovdfjord gained from this temporary surplus of nutrient and food organisms. We find no other plausible explanations for increased growth of the young age groups in the 1950s compared to the other periods.

In conclusions, this study provides a specific example of the effect of changed food abundance (i.e., reduced zoobenthos diversity and introduction of potential prey fish) for the growth pattern of brown trout. The trout responded to these changes by becoming piscivorous. The high incidence of piscivory in the population, however, did not result in any marked change in growth as the back-calculated age-specific lengths remained almost unchanged through the study period of >70 years.

Resumen

1. El comportamiento piscívoro de la población de *Salmo trutta* del embalse de Tunhovdfjord (Noruega, establecido en el año 1919) fue estudiado en 4 periodos de tiempo discretos a lo largo de 7 decadas (1917–94). Las truchas piscívoras eran extremadamente escasas antes de la introducción, en los años 20, de dos especies: *Salvelinus alpinus* and *Phoxinus phoxinus*. Las truchas comienzan a alimentarse de *Ph. Phoxinus* a los 17 cm y *S. alpinus* a los 22 cm de longitud. En los años 50, las truchas predaban extensivamente (60% de las truchas analizadas) sobre *S. alpinus* y *Ph. Phoxinus*. Durante las siguientes 4 decadas la incidencia de las truchas piscivoras decayó al 10%

2. El patrón de crecimiento expresado como longitudes retro-calculads demostró ser similar en las decadas de los años 20, 60 y 90, mientras que mejoró en los años 50, relacionado con un nuevo embalse aguas arriba. No encontramos cambios marcados en la tasa crecimiento debidos a la piscivoria pero el coeficiente de variacíon de las longitudes retro-calculadas indicaron variaciones significativas en el crecimiento individual en los grupos de edad >6 años a partir de los años 50. Acreditamos que esta variación se debe al aumento de truchas piscivoras.

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