Environmental Biology of Fishes **34**: 247–255, 1992.

Effects of siltation on resource utilization and dynamics of allopatric brown trout, *Salmo trutta*, in a reservoir

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Received 27.11.1990 Accepted 16.5.1991

Key words: Regulated lake, Turbidity, Zooplankton, Fish

Synopsis

The water level of the old hydroelectric Ringedal Reservoir in western Norway was unusually low during 1985, resulting in severe erosion and siltation. The secchi disc transparency was 18 m in July 1984, decreased to 0.3 m in July 1985, and increased to 13 m in July 1986 after a rise in the water level. The abiotic changes induced major effects in the zooplankton community, with a strong reduction in occurrence of Cladocera (*Holopedium gibberum* and *Bosmina longispina*). The allopatric population of brown trout, *Salmo trutta,* which mainly fed on zooplankton before the siltation, fed predominantly on surface insects during the summer of high siltation. The food consumption was lower than in the pre- and post-siltation years, resulting in reduced k-values, reduced number of spawners, and increased mortality of mature fish.

Introduction

In general, brown trout, *Salmo trutta* L., utilize zoobenthos and surface insects as food in littoral areas (Dahl 1918, Olstad 1925, Nilsson 1955, 1960, 1961, Lien 1978). At high population densities and low abundance of zoobenthos, however, brown trout feed to a great extent upon zooplankton (Dahl 1917, Klemetsen 1967, Aass 1969, Haraldstad & Jonsson 1983, Brabrand & Saltveit 1988).

After impoundment of lakes, brown trout are often observed to use zooplankton and pelagic areas more extensively. This is typical both in allopatric populations (Aass 1969), and in populations coexisting with perch, *Perca fluviatilis,* and minnow, *Phoxinus phoxinus* (Brabrand & Saltveit 1988). Under such conditions, a reduction in zooplankton availability might be expected to seriously affect food consumption and, consequently, have a negative effect upon the population dynamics.

The present study describes resource utilization and the dynamics of an allopatric brown trout population in an old reservoir, where an increased lowering of the water level resulted in heavy siltation and decreased abundance of cladocerans.

Methods

Study area

The Ringedal Reservoir in western Norway (Fig. 1) was regulated in 1908. Until 1984, the water level amplitude was allowed to vary between 465 and 418 m a.s.l., while by a new allowance it was pos-

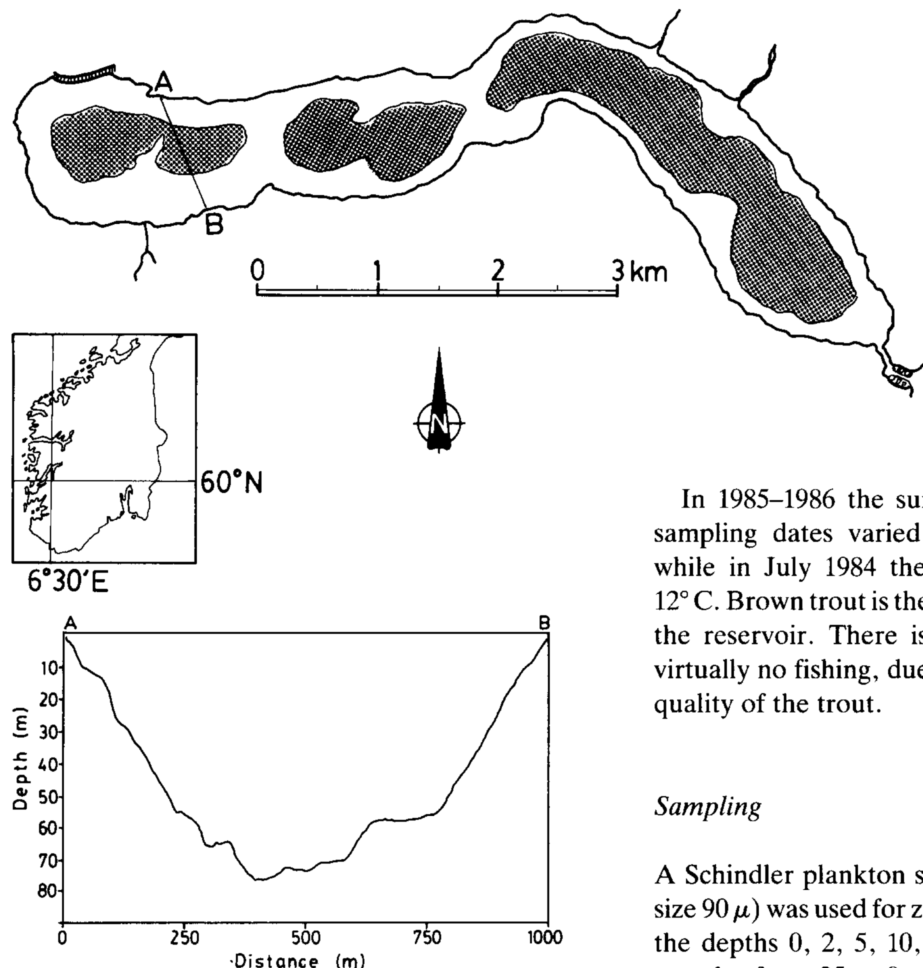

Fig. 1. The geographic position of the Ringedal Reservoir, western Norway. Area at minimum water level indicated by hatching. The depth contour in transect A–B is within the sampling locality.

sible to lower the reservoir to 371 m a.s.l. At maximum water level, the surface area is 4.5 km^2, with a maximum water depth of 144 m. A depth transect of the reservoir at the sampling site is given in Figure 1. In 1985 the reservoir was lowered to 413 m a.s.l., and the water level during spring and summer this year was much lower than in preceding years (Fig. 2). This led to considerable erosion of the exposed bottom areas. Secchi-disc transparency was reduced from approx. 18 m in July 1984 to 0.3 m in July 1985. During 1986, the water level increased, and the Secchi disc transparency returned to the pre-erosion level (Fig. 3).

In 1985–1986 the surface temperatures on the sampling dates varied between 8° C and 14° C, while in July 1984 the surface temperature was 12° C. Brown trout is the only fish species present in the reservoir. There is no stocking of fish, and virtually no fishing, due to the small size and poor quality of the trout.

Sampling

A Schindler plankton sampler (volume 15 l, mesh size 90 μ) was used for zooplankton sampling, from the depths 0, 2, 5, 10, 15 and 20 m. In addition, samples from 25 to 0 m were taken by a plankton net (diameter 25 cm, mesh size 90 μ). Fish were captured by monofilament gill nets, 25 m long and 1.5 m deep, set on the bottom in the littoral zone from a depth of approximately 2 m to 8 m, and floating gill nets, 25 m long and 6 m deep, in the pelagic zone. The floating gill nets were set in lines, each consisting of three nets, at depths 0–6 m and 6–12 m, at least 75 m from the shore. Each sampling lasted for either one or two hours, at six-hour intervals throughout a 24 or 48 hour period. Both types of gill nets had the mesh sizes 16, 19.5, 21 and 22.5 mm (knot to knot measure).

Treatment of the material

The contents of the oesophagus and stomach were removed and immediately frozen. After counting

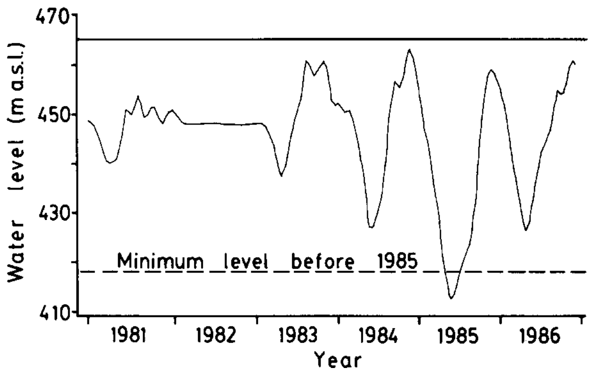

Fig. 2. Monthly water levels in Ringedal Reservoir from 1981 to 1986.

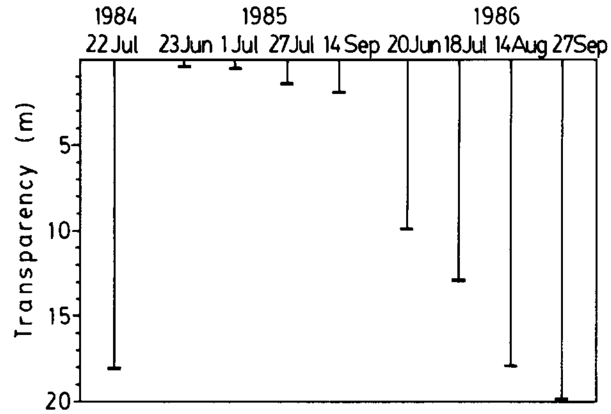

Fig. 3. Secchi disc transparencies from July 1984 to September 1986 in the Ringedal Reservoir.

and identification, the food items were dried for 48 hours at 65° C and weighed. Fish length was measured in mm and weighed to the nearest gram. Gonadal development was recorded as described by Dahl (1917). Otoliths were used for age determination. The otoliths were cut in half through the centre, burnt as described by Christensen (1964), and examined under a binocular microscope.

When large within-sample variation in the weight of stomach contents occurs, Amundsen & Klemetsen (1986) concluded that the Eggers (1979) modification of the Bajkov (1935) method was likely to give more robust estimates of food consumption than the method of Elliott & Persson (1978). In the material from Ringedal Reservoir the within-sample variation was high, with a high number of empty stomachs, and large differences in the weight of stomach contents. The daily food consumption (C_{24}) was therefore estimated according to the equation:

$$C_{24} = 24\,S \star R,$$

where S is the mean stomach content over the 24 h period, and R is the instantaneous gastric evacuation rate (Eggers 1979). R is estimated according to the equation $R = a \star e^{bT}$ given by Elliott (1972), where a and b are constants, and T temperature in °C. In the calculations of R the values $a = 0.053$ and $b = 0.112$ in Elliott (1972) were used for chironomids and zooplankton, while Elliott's values for *Protonemura*, $a = 0.049$ and $b = 0.107$, were used for terrestrial and benthic insects except chironomids.

Results

The zooplankton community

As evident from the Schindler samples (Fig. 4) and net plankton hauls (Table 1), major changes in density and diversity of zooplankton occurred from 1985 to 1986. Throughout the summer of 1985, with extremely high turbidity, the zooplankton community was dominated by calanoid copepods, especially *Arctodiaptomus laticeps* and *Mixodiaptomus laciniatus*. *Holopedium gibberum* was absent, while *Bosmina longispina* occurred in September. The following year *A. laticeps* still dominated, but *H. gibberum* and *B. longispina* were more abundant, with an increased abundance and frequency of *H. gibberum* from June to September. In July 1984, the zooplankton was not sampled, but *H. gibberum* occurred frequently in the brown trout diet and dominated the stomach contents, confirming its presence in the reservoir.

Habitat utilization

The captured trout had lengths between 12.0 and 24.9 cm. No significant differences in length fre-

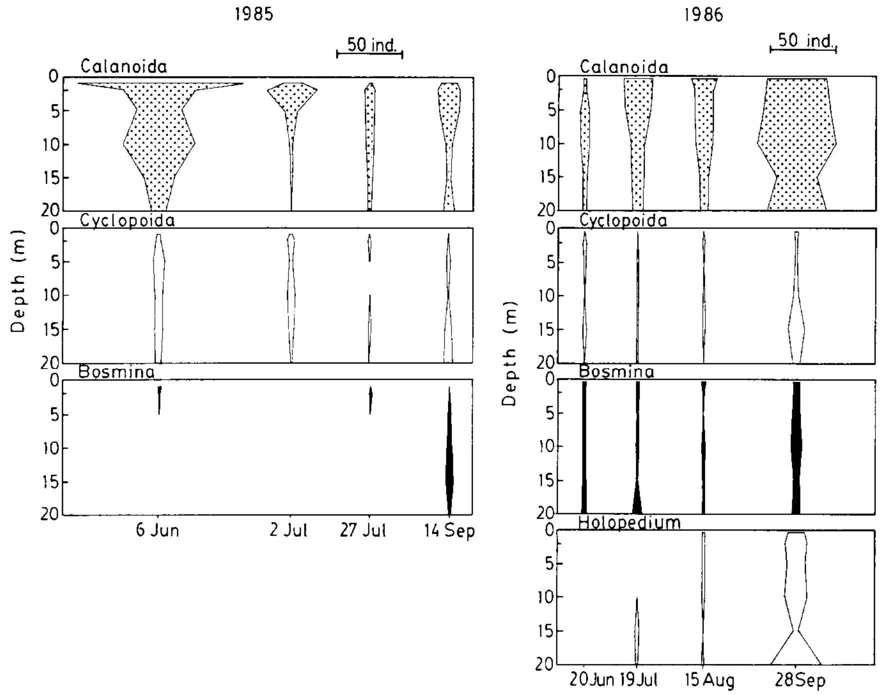

Fig. 4. Number of Calanoida, Cyclopoida and Cladocera per 15 l in Schindler sampler from depths between 0 and 20 m, in Ringedal Reservoir during the period June-September 1985 and 1986.

quency distributions between catches in littoral and pelagial gill nets were found (Kolmogorov-Smirnov test, $p = 0.99$).

The higher catch per unit effort (CPUE) in littoral gill nets compared to the floating gill nets (Fig. 5) suggests a higher density of fish in the littoral than in the pelagic zone. However, because the volume of the pelagic zone in the depth interval 0–12 m is about ten times larger than the littoral zone down to 12 m (Fig. 1), the catches indicate that the majority of the population utilized the pelagic zone.

From 1984 to 1985 the CPUE for both littoral and floating gill nets increased (Fig. 5). During the most turbid period (June-July 1985), fish were only captured in the depth interval 0–2 m in pelagic nets. In 1986, the pelagic CPUE was lower than in 1984 and 1985, but showed a small increase from June to September, concurrent with a decrease in the littoral CPUE.

Table 1. Frequency (%) of copepod and cladoceran species in net plankton samples from Ringedal Reservoir, June–September 1985–1986.

Species	1985				1986			
	6 Jun	2 Jul	27 Jul	14 Sep	20 Jun	19 Jul	15 Aug	28 Sep
Cyclops scutifer	40.3	1.3	8.4	4.9	23.1	12.3	9.6	10.2
Arctodiaptomus laticeps	41.9	74.0	37.3	32.0	53.4	41.3	47.8	55.0
Heterocope saliens	9.6	4.3	3.1	9.7	2.7	1.5	4.7	
Mixodiaptomus laciniatus	8.3	19.6	51.3	27.4	6.0	5.4	8.7	1.2
Bosmina longispina		0.4		25.3	14.3	36.8	19.3	20.4
Holopedium gibberum		0.2		0.6	0.6	2.8	9.8	13.3

Food consumption and daily food rations

In July 1984, *H. gibberum* and chironomids occurred frequently in the stomach contents, with *H. gibberum* as the dominant food item by weight. Larvae and pupae of chironomids were also important contributors to the weight of stomach contents, while terrestrial insects and copepods were of minor importance (Fig. 6).

From June to September 1985, during the most severe siltation, terrestrial insects were the only food item of importance, both by weight and frequency of occurrence. *H. gibberum* was not found in the stomach contents this year. Calanoid copepods, however, were eaten in all months of 1985, but they made up only a small part of the total stomach content by weight.

In 1986, terrestrial insects still had a high frequency of occurrence, and were the main food item by weight from June to August. Compared to 1985, the weight of copepods and chironomids in the diet increased. In September, *H. gibberum* reappeared in the diet, and was the most common food item by weight.

In 1985 and 1986, terrestrial insects were the main contributors to the estimated daily food rations. In July 1984, however, terrestrial insects were quite insignificant (Fig. 7a). In June-September 1985, the estimated daily rations made up of food items produced in the reservoir (crustaceans, chironomids and other benthic invertebrates) were much smaller than in June–September 1986 and in July 1984 (Fig. 7b), resulting in low total daily rations, which varied between 1.1 g in June and 4.7 g dry weight g^{-1} fish wet weight in September.

Population dynamics

Fish older than 2 winters showed low annual growth rates, with an average annual length increment of less than 1 cm from age 2 to age 16. Moreover, in all sampling periods the condition factors (k) declined with increasing fish lengths (Fig. 8). Even before the siltation, in July 1984, trout with total lengths ≥ 20.0 cm had k-values ≤ 0.80. In June 1985 the condition factors were approximately as in July 1984, but they declined during the summer. In July and September, all length classes ≥ 19 cm had k-values < 0.80, with minimum values close to 0.50 for some fish. In June 1986, a further decline had taken place, and all length classes > 14 cm had k-values ≤ 0.80. During the 1986 season, however, a considerable increase in k-values was observed, along with a decrease in water turbidity. In September, the k-values for the length classes 15–20 cm were ≥ 0.95, and only length classes above 22 cm had k-values < 0.80 (Fig. 8).

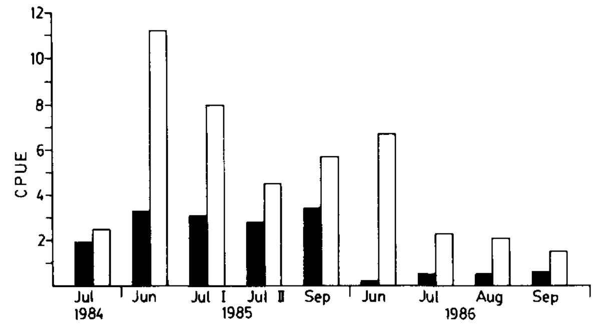

Fig. 5. Average number of brown trout captured per hour per 100 m^2 net area (CPUE) in littoral (open columns) and pelagic (black columns) gill nets in Ringedal Reservoir, July 1984–September 1986.

In September 1985, only females 7 years and older developed mature eggs. The age groups 11–13 winters (8 females) consisted of fish not undergoing a maturation cycle. In September 1986, the proportion of maturing fish had increased significantly relative to 1985 (Fig. 9).

The annual mortality rates for the year-classes 1971–1978, obtained from the catch curves, were 0.266 ($p < 0.01$, $r^2 = 0.94$) in 1985 and 0.344 ($p < 0.01$, $r^2 = 0.72$) in 1986. The increase in estimated mortality rate for the same year-classes, from 1985 to 1986, indicates that the loss of older fish was proportionally higher than for the younger age-classes.

Discussion

Siltation and habitat use

In general, the amount and distribution of avail-

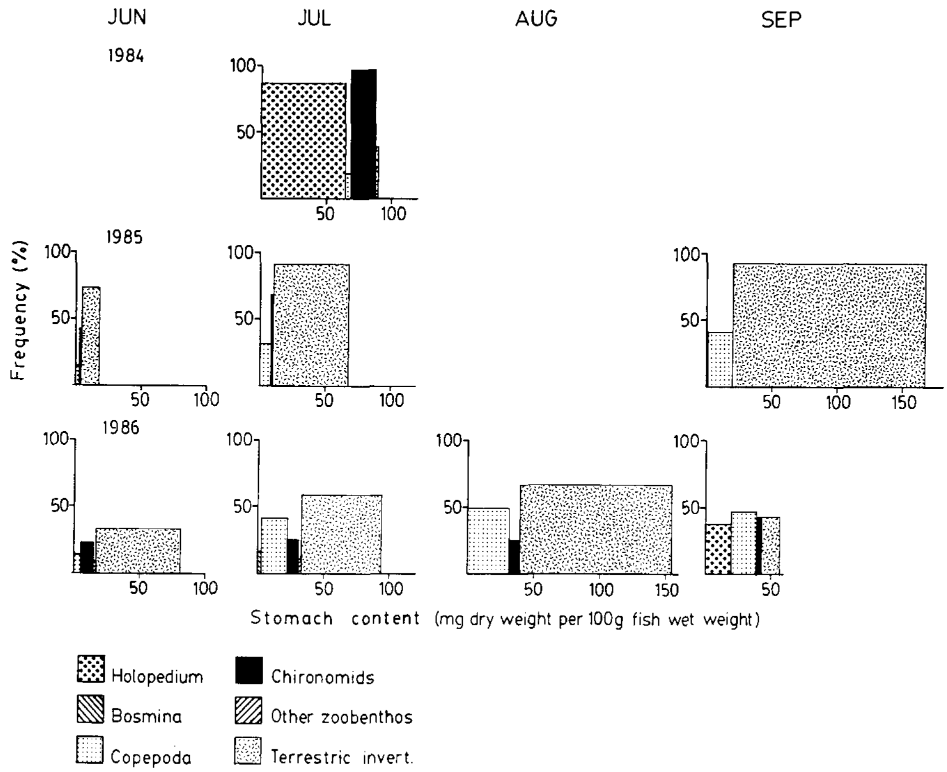

Fig. 6. Milligram dry weight of stomach contents per 100 gram of trout, and frequency of occurrence of food items in brown trout from Ringedal Reservoir.

able food resources is of decisive importance for habitat utilization in fish, and several fish species have been demonstrated to shift habitat after a change in food availability (Werner & Hall 1976, 1977, Langeland 1982, Persson 1983a, b, 1986, 1987). In the absence of arctic charr and whitefish, the decline of zoobenthos after impoundment of natural lakes usually results in a shift from benthivory/surface insect feeding to planktivory/surface insect feeding by brown trout (Aass 1969, Brabrand & Saltveit 1988). Furthermore, the zoobenthic biomass and production are low in reservoirs with large water level amplitudes (Grimås 1961, 1962). Thus, the only food resources of importance in Ringedal Reservoir will be zooplankton and terrestrial insects. The extensive use of the pelagic habitat by all length classes of trout, during pre- and post-siltation, as well as during the siltation period, suggests that utilization of pelagic food resources is the most profitable strategy under such conditions. These findings further indicate that the size-dependent habitat segregation usually found in other brown trout populations, with the smaller

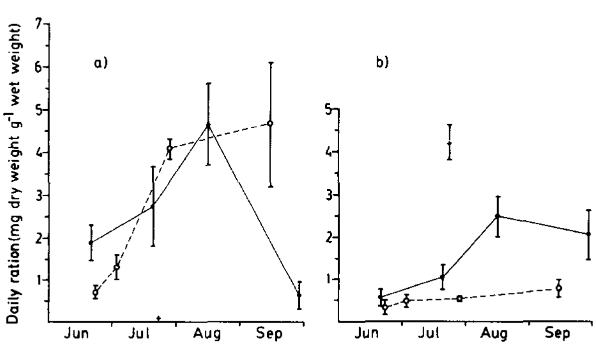

Fig. 7. Estimated daily rations in mg dry weight g^{-1} fish wet weight for brown trout in Ringedal Reservoir: a – Daily rations composed of terrestrial insects, and b – Daily rations of food items produced in the reservoir (crustaceans, chironomids and other benthic invertebrates). + 1984, ○ 1985, ● 1986. Vertical lines denote standard error of the means.

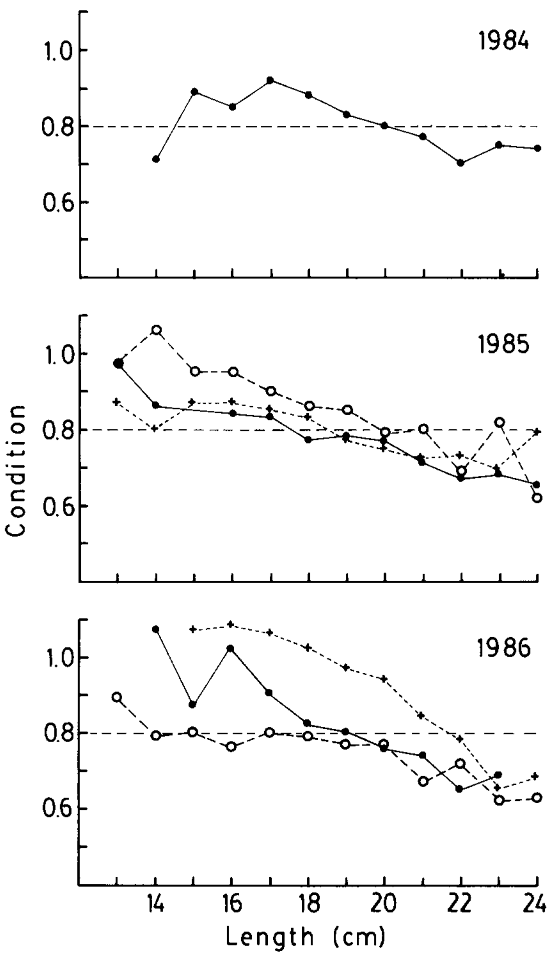

Fig. 8. Average values of Fultons condition factor for each cm-class of brown trout, in July 1984, and June–September 1985 and 1986, in the Ringedal Reservoir. June O---O, July ●——●, September +---+.

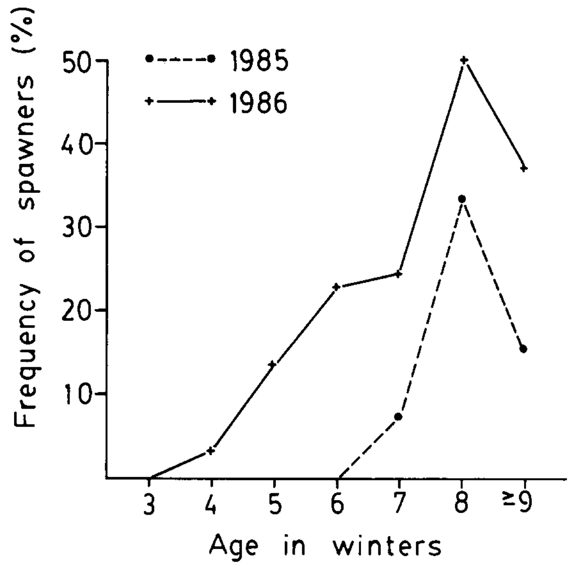

Fig. 9. Frequency of females with mature eggs in each year-class of brown trout captured in September 1985 and 1986.

The high CPUE during this period probably also reflects the high concentration of trout near the surface, and the reduced ability of trout to detect the gill nets in silted water. A similar situation was observed after heavy silting of the reservoir Mårvatn where the brown trout were concentrated in the clear water near the main inlet (Borgstrøm 1973).

fish inhabiting the shallow littoral zone, and the larger fish utilizing the pelagial and deep waters (Thorpe 1974, Haraldstad & Jonsson 1983, Jonsson 1989), may be determined by available resources.

Turbidity and reduced light intensities reduce the reactive distance and feeding rates of visual predators (Vinyard & O'Brien 1976, Confer et al. 1978, Gardner 1981, Berg & Northcote 1985, Henderson & Northcote 1985). Thus, the increased turbidity of the reservoir during 1985 may have adversely affected the visual ability of brown trout to detect prey, and is likely to be the reason why trout were concentrated to the upper 2 meters of the water column during the most silted period.

Food consumption and population dynamics

In some high mountain lakes influenced by glacial ooze, a high abundance of rotifers and copepods has been observed, while the filtering cladocerans were absent or recorded in low numbers (Blakar & Jakobsen 1979, Elgmork & Eie 1989). Thus, increased turbidity caused by mineral particles can change zooplankton abundance and community structure; accordingly, the disappearance of *H. gibberum* and *B. longispina* during the period with high turbidity may be a direct effect of the high ooze concentration.

The estimated daily food rations, especially during the most severe siltation, are far below values given by Elliott (1975) for maintainance rations of brown trout at temperatures in the range of 10–14°C. As the per cent fat, protein, and energy values of brown trout all decrease with decreasing ration size (Elliott 1976), the marked decline in weight from July 1984 to September 1985, and the following increase during the 1986 season, is therefore likely to be a result of changes in ration size and energy intake.

The high age and small size of brown trout in the reservoir demonstrate that trout can survive for several years on food rations which give little or no energy surplus for somatic growth. The energy loss connected with spawning, which might amount to nearly 50% both for male and female brown trout (Lien 1978), is normally regained the next summer (Sømme 1941). In Ringedal Reservoir, however, this energy loss was not replaced, as the condition factor, growth rate, and the reproductive potential decreased with increasing age, even before the siltation. The rapid decline in condition of the fish during the siltation period, and the increased mortality of old fish documented in our study, indicate that the fish under these extreme conditions were no longer able to balance the energy deficits by using their own body tissues for maintainance energy. Reimers (1957) found that starved trout generally died when the condition factor fell below 0.55–0.60, which is close to the values observed for brown trout in the reservoir.

We suggest that increased lowering of the water level, resulting in erosion of exposed bottom areas with fine sediments, will generally cause a substantial reduction in diversity of zooplankton, with disappearance of cladocerans. This disappearance will adversely affect planktivorous fish, resulting in rapid weight and energy loss and accordingly, lower reproductive potential and increased mortality. Continued siltation, lasting for several years, may thus completely change the basis for fish production.

Acknowledgements

We acknowledge the financial support given by the Norwegian Fund for River Regulation Licensing Fees, the Directorate for Nature Management, AS Tyssefaldene, and the Agricultural University of Norway. We also want to thank Sigrid Jøsendal, Per Jan Sandven and Odd Inge Tvedt for their field assistance, Jan Heggenes, Howard Parker, and two unknown referees for critizing drafts of this paper, and Linda Hjeljord for correcting the English.

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