

Life history variables of resident Brown trout *Salmo trutta* L. in a coastal stream in northern Norway

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This study focused on the population structure and life history of resident Brown trout in the lower parts of a coastal stream in northern Norway. An uneven age distribution was strongly evidenced by the low number of young fish. There was a high frequency of sexually mature males, while only a few females were sexually mature. Males mature sexually at ages between 2—8 years, compared with 4—5 years for females. Females had a significantly higher mortality rate than males, and were fewer in number amongst older fish. There were no differences between the sexes in growth rates or in the length/weight relationship.

It is suggested that the low number of spawning females, as well as density-independent mortality in young stages caused by environmental catastrophes, are important factors affecting the present structure of the Brown trout population in the study area. The population is probably maintained by immigration of older specimens into the area.

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INTRODUCTION

Small streams in temperate regions are typically unstable environments for aquatic life because of extreme, often unpredictable fluctuations in their physical characteristics (Moyle & Vondracek 1985). The population structure of stream-dwelling Brown trout (*Salmo trutta*) in such habitat may vary, depending on the relative importance of endogenous and exogenous sources of recruits (Milner et al. 1979). Several studies have demonstrated quite distinct and self-maintaining stocks of Brown trout (Schunk 1945, Allen 1951, Egglisshaw & Shackley 1977, Mortensen 1977a, 1977b). In contrast, unbalanced age distribution and considerable immigration by all age-classes into trout populations have been documented in other streams (Horten 1961, Solomon & Templeton 1976, Milner et al. 1978, 1979, Jonsson & Sandlund 1979). Great fluctuations in recruitment and population figures also occur commonly among Brown trout in different stream habitats (Needham et al. 1945, Burnet 1959, Mann 1971, Crisp et al. 1975, Mense 1975, Jonsson & Sandlund 1979).

The numerical changes and population regulation in lotic fish stocks may either be

due to density dependent or density independent factors (Le Cren 1973, Egglisshaw & Shackley 1977, 1982, Mortensen 1977a, 1977b, Elliott 1984, 1985). An analysis made by Elliott (1987a) showed density-dependent regulation for Brown trout in a high density stream, while extremes of flow were chiefly responsible for changes in population numbers in a low density stream. Jonsson & Sandlund (1979) also emphasize the importance of density-independent mortality (environmental «catastrophes») for Brown trout reproducing in unstable habitats. Floods have been stated to be a large source of mortality in stream-dwelling salmonids by several authors (Allen 1951, McFadden & Cooper 1962, Elwood & Waters 1969, Seegrist & Gard 1972, Nelson 1986).

Growth, survival and maturation patterns vary among Brown trout living in different habitat, and thus life history of adapted fish will differ (Jonsson 1985). Reproductive success is determined largely by the growth rate and survival of fish (Jonsson et al. 1984, Roff 1984, Jensen 1985, Stearns & Koella 1986). Stunting and maturation at an early age is advantageous for fish populations li-

ving in unstable habitats (Fryer & Illes 1969). Variation in reproductive life span is associated with age at maturity (Roff 1981), and fish mature at an age which maximizes their overall lifetime reproductive potential (Jonsson et al. 1984). Several studies indicate that changes in age and size at maturity as well as in growth are associated with changes in mortality (Ware 1980, 1982, Jensen 1981, 1985, Roff 1981, 1984, Jonsson & Hindar 1982, Pauly 1982).

The chief objective of the present work was to study aspects of the life history of Brown trout occupying the lower parts of a coastal stream in northern Norway. Special attention will be paid to population structure, growth rate and maturation pattern.

THE STUDY AREA

The study was carried out in the lower part of Tverrelva, a stream near Tromsø in northern Norway (69°45'N, 19°15'E, Fig. 1). Tverrelva is 3.4 km long and originates in the Movikvatn lake, which supports a population of Brown trout. The stream drains into the river Tønsvikelva about 1 km from the sea. Tverrelva has an average width and depth of 3–4 m and 10–30 cm, respectively,

and the river bed consists of stones from 5–30 cm in diameter. In addition to Brown trout, Tverrelva supports a small population of European eel, *Anguilla anguilla* L.. The lower and upper part of the study area (Area I and Area II) were stocked with Atlantic salmon *Salmo salar* L. fry in the springs of 1976 and 1977, respectively (Heggberget & Hesthagen 1981). Therefore these two stretches were inhabited by 1+ and 2+ aged salmon when the study was conducted in 1977.

There are great variations in the amount of rain during fall in the study area as shown for

Table 1. Monthly rainfall (mm) during May–October from 1972–1977 measured at Tromsø, about 10 km from the study area (Source: Norwegian Institute for Meteorology. The values from May and October also include some amounts of snow).

Year	May	June	July	Aug.	Sept.	Oct.
1972	13	54	90	100	202	152
1973	56	73	35	193	61	169
1974	21	18	76	64	121	17
1975	80	72	85	105	160	155
1976	30	17	67	92	151	46
1977	64	70	73	79	62	91

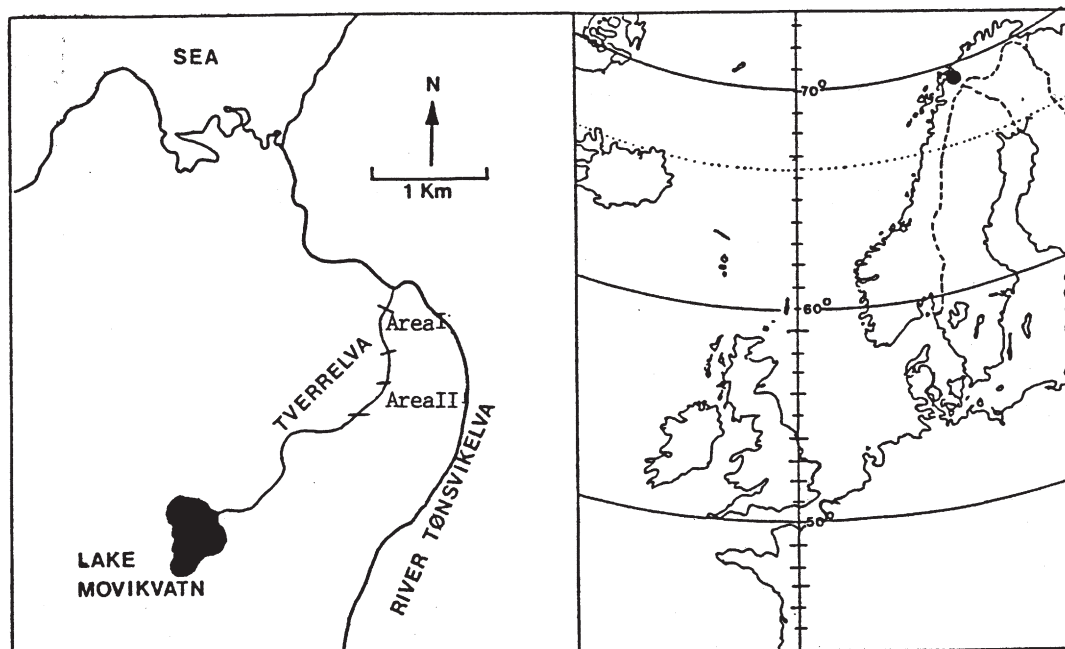


Fig. 1. Geographic location and the sampling area of Tverrelva.

the period 1972—1977 (Table 1). On the other hand, the amounts of rain during spring and summer are generally low. The water flow in Tverrelva is high during spring snowmelt due to a thick snow cover in the watershed.

METHODS

Brown trout from two stretches of the stream were sampled during the period 14—20 september 1977. The first stretch covered a length of 345 m (1326 m², Area I, Fig. 1) and the second of 593 m (1753 m², Area II). Fish were caught with an electrofishing apparatus (1600 V, DC unloaded). Five successive fishing runs were carried out at Area I, and an additional run and rotenon treatment were conducted five days later (Heggberget & Hesthagen 1979). Area II was sampled during three successive electrofishing runs. The collected fish were frozen, and total length (0.1 cm), weight (1.0 g) and sexual maturity (Dahl 1917) were determined later. Age was determined by using otoliths (Jonsson 1976). The instantaneous mortality rate (*Z*) was estimated for age groups which were fully represented in the population by the equation: $Z = -\ln N_{t+1} + N_t$, where N_{t+1} and N_t = the number of fish in age group $t+1$ and t , respectively (Ricker 1975). Estimation of the growth parameters by von Bertalanffy's growth equation was carried out according to Gulland (1969).

The weight/length relationships in fish can be expressed by the formula: $W = a l^b$, or by

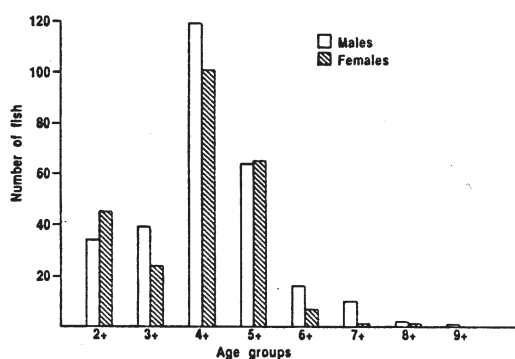


Fig. 2. Age distribution of males and females of Brown trout from Tverrelva in autumn 1977 (Data on fry are omitted, cf. Table 2).

logarithmic transformation: $\log W = \log a + b \log l$, where W = weight, l = total length, a = constant and b = exponent.

RESULTS

The uneven age distribution of Brown trout in Tverrelva is evidenced by low numbers of fish aged 0+ to 3+ compared with older fish (Fig. 2). No one-year-old trout were registered in the two study areas, and the number of 2+ age trout was low compared with that of 3+. Fish in age group 4+ were most abundant, and the annual instantaneous mortality rates (*Z*) for the sexes were estimated for age groups 4+ through 9+:

Table 2. Mean length ($\bar{x}L$, mm), mean weight ($\bar{x}W$, g), standard deviation (SD), and percent of mature specimens (% M) in each age group of male and female Brown trout in Tverrelva. N = number of fish.

Age	Males						Females					
	$\bar{x}L$	SD	$\bar{x}W$	SD	N	% M	$\bar{x}L$	SD	$\bar{x}W$	SD	N	% M
0+	43	3.3	—	—	50*	—	43	3.3	—	—	50*	—
2+	86	8.3	7	2.3	34	2.9	86	6.8	7	2.1	45	0.0
3+	110	6.7	15	3.0	39	20.5	113	8.7	16	3.8	24	0.0
4+	128	8.8	25	5.7	119	47.1	129	8.6	25	5.3	101	0.0
5+	143	8.3	36	7.0	64	64.1	141	8.0	32	5.1	65	3.1
6+	151	12.3	43	9.4	16	81.3	154	8.6	40	6.1	7	42.9
7+	168	4.8	59	6.1	10	100.0	166	—	56	—	1	0.0
8+	183	16.3	70	7.1	2	100.0	170	—	55	—	1	0.0
9+	222	—	117	—	1	100.0	—	—	—	—	—	—

*The number of fry was estimated by a mark-recapture experiment in Area I. I assume that sex ratio did not differ significantly from unity, and that mean lengths were the same for both sexes.

Males:
0.99 (S.E. = 0.07), $F_{1,4} = 233.1$ $P < 0.0001$, $R^2 = 0.98$

Females:
1.34 (S.E. = 0.22), $F_{1,3} = 36.1$ $P < 0.01$, $R^2 = 0.92$

The female mortality rate was significantly higher than that for males (analysis of covariance, $P < 0.05$).

Brown trout in Tverrelva grew slowly, and reached a length of 151–168 mm and a weight of 40–59 g at the age of six to seven years (Table 2). The annual length increment from 2+ to 7+ ranged from 8 to 27 mm. Mean length of males and females in the various age groups varied less than 3 mm, which was not significantly different (Student t-test, all $P < 0.05$).

Based on average length for both sexes in each age group, the growth pattern could be fitted into von Bertalanffy's model for linear growth: $F_{1,4} = 14.0$, $P < 0.05$, $R^2 = 0.78$.

The growth coefficient (K) and the asymptotic length (L_{max}) in this equation were estimated at 0.16 and 228 mm, respectively.

The slopes and intercepts in the length-weight relationship did not differ significantly between the sexes (Table 3, analysis of covariance, $P < 0.001$). The regression coefficient was significantly different from 3.0 (allometric growth) for both sexes.

Sex ratio (M/F) of age groups 2–5 (1.09) did not differ significantly from unity ($\chi^2 = 0.90$, $df = 1$, $P > 0.05$). However, there was a significant surplus of males among older fish (M/F = 3.22, $\chi^2 = 5.80$, $df = 1$, $P < 0.05$). Among mature specimens, males were highly dominant (M/F ratio was 27:1, $\chi^2 = 117.73$, $P < 0.0001$).

Male Brown trout in Tverrelva matured at a younger age than females (Table 2). For the number of mature specimens in age groups 2+/3+, 4+, 5+, 6+ and $\geq 7+$, $\chi^2 = 13.10$, $df = 4$, $P < 0.05$. Males matured gradually from age 2 upwards, and 100% maturity was reached at age 7. Of 285 male trout examined, 132 (46%) were mature. Female trout attain-

ned maturity at age 5, but the sample size was small ($N = 5$, 2% of total). Within different age-groups, mean lengths of mature and immature specimens of both sexes did not differ significantly (Student t-test, $P > 0.05$).

DISCUSSION

The age distribution of Brown trout from the lower part of Tverrelva was uneven and the number of young fish was low compared with older ones. In stable self-maintaining populations, the abundance of age classes typically decreases with increasing age (Milner et al. 1978). This distribution has often been recorded in streams in which stratified sampling covers a wide range of habitat types, including nursery areas (Allen 1951, Burnet 1959, Crisp et al. 1974, Egglshaw & Shackley 1977, Mortensen 1977a, 1977b). Therefore, age frequency data may be misleading if sampling is restricted to small sections of a stream because the results might then describe *statistical populations* rather than *biological populations* in an entire stream (Crisp et al. 1974). However, the present age distribution is not thought to be due to sampling error as a relatively large part of the stream was included in the investigation. Further, repeated electrofishing surveys and the use of rotenon are thought to yield a reliable picture of the population structure.

The low and uneven number of Brown trout younger age groups (0+ to 3+) indicated great annual fluctuations in Brown trout recruitment in Tverrelva. Such population changes seem to be evident in unstable habitat, where abiotic factors (environmental «catastrophes» like extremes in waterflow, erosion by ice and freezing) are regarded as important factors for changes in Brown trout stocks (Jonsson & Sandlund 1979, Elliott 1987a). Changes in population number due to abiotic factors were also found by Allen (1951) and McFadden & Cooper (1962) where nearly total reproduction failure and a

Table 3. Values of slope (b) and intercept (a) with standard error (SE) in the weight/length relationship $W = aL^b$ for male and female Brown trout in Tverrelva.

Sex	b	(SE)	a	(SE)	F value	R^2
Male	3.15	0.033	In -12.09	0.331	$F_{1,283} = 9088.3$	0.97
Female	3.18	0.034	In -12.28	0.341	$F_{1,241} = 8727.3$	0.97

strong reduction in the number of fingerling Brown trout coincided with the occurrence of the most severe winter floods. Great annual variation in the recruitment of Brown trout in small streams in New Zealand was also correlated with great fluctuations in water flow (Burnet 1959). In the Beaverhead River in Montana (USA), floods during or prior to peak spawning for Brown trout appear to have hindered reproduction and hence influenced recruitment (Nelson 1986), which he associated with disruption of spawning. This abiotic factor may in one way or another influence reproduction and recruitment for Brown trout in Tverrelva as well. The amount of rain in the area during the spawning period for Brown trout (September/October) showed great annual variation for the years 1972—1977 (Table 1).

In unstable habitats, adapted populations usually exhibit rapid development and early sexual maturation, which in turn ensure that a large part of the population becomes sexually mature (Fryer & Iles 1969). Among Brown trout in Tverrelva, the operation of this strategy was evident for males, as they matured at a low age and at a variety of ages (2+ — 8+). On the other hand, the population only included a few mature females, which were significantly older than males and belonged to two year-classes only (4+ and 5+). Females also had a higher mortality rate than males in Tverrelva. A similar maturation pattern for stream-dwelling Brown trout has also been observed elsewhere (Stuart 1957, Jonsson & Sandlund 1979, Jonsson 1985). The number of females is more limiting to the number of offspring than that of males, as female abundance dictates the number of eggs produced, and one male may fertilize several females (Jonsson 1977, 1985). In populations where spawning females only belong to a few year-classes, the failure of a year class due to environmental catastrophes will have a much more conspicuous effect than in populations where mature females belong to many year-classes (Elliott 1987a). With the present number of mature females in Tverrelva, the population seems unsustainable.

The male/female sex ratio among mature specimens in Tverrelva was extremely high (27:1) compared with that exhibited by other Brown trout stocks. Campbell (1977) found that a corresponding ratio approximated 6:1 for resident Brown trout in the River Tweed, which also harbours migrant Brown trout. In

tributaries of the Vangsvatnet lake, the number of mature resident females seems to be low compared to that of resident males and migrant females (Jonsson 1985). The smallest stream had the largest proportion of resident spawners (Jonsson op. cit.). The sex ratio among migrants in the River Tweed and in tributaries of the Vangsvatnet lake was skewed in favour of females. Jonsson (1985) observed resident and migrant Brown trout of both sexes at the same spawning grounds, and suggested that both phenotypes are part of the same demes. This assumption is also supported by observations of spawners made by Campbell (1977). Thus, the interaction between these two phenotypes may be an important aspect of the maintenance of Brown trout stocks in coastal streams with free access to the sea. The hypothesis is supported by observations made by Egglisshaw & Shackley (1982). In the absence of sea trout, juvenile Brown trout often occurred in low densities in Scottish streams, probably as a result of the low number of spawning adults. Migrant Brown trout have been observed in Tverrelva in the 1960's, but not in more recent years (H. Jenssen personal communication).

Besides a great variation in annual survival, the Brown trout stock in Tverrelva is characterized by a slow growth rate, the asymptotic length being estimated at 228 mm. McFadden & Cooper (1962) found great variations in annual survival for various age groups for six Brown trout populations under a wide range of environmental conditions. From their study it appears that the high average survival rate which is required to maintain a Brown trout population of low fecundity rate in a stationary state is either achieved through high survival during the early months of life or during the adult period or both. In many cases, it seems evident that there are small yearly variations in growth rate *within* a stream-living population of Brown trout, which might tend to compensate for changes in population density, compared with the range of potential variability in growth (McFadden & Cooper 1964). However, they state that differences in growth *among* populations are known to be great. Thus, it seems evident that mortality rates of Brown trout in unstable stream habitat are more susceptible to changes than growth rates. It is generally assumed that an increase in juvenile mortality rates accelerates maturation.

tion. However, Stearns & Koella (1986) predicted that increases in juvenile mortality rates result in delayed maturity. Schaffer (1974) stated that there seems to be no justification for assuming that environmental uncertainty necessarily selects for increased reproductive output. He pointed out that while increased density-independent mortality may select for reduced reproductive effort, it is the age-specificity of the mortality, constant or fluctuating, that determines the adaptive response.

The low number of mature females in Tverrelva prior to the spawning season may be caused by fish from the main river (Tønsvikelva) migrating into the stream to spawn (cf. Jonsson & Sandlund 1979). However, no such migration or vice versa could be registered through electrofishing surveys.

The number of young Brown trout in the stream may to some extent be related to interspecific competition with juvenile Atlantic salmon (age 1+ and 2+), although some habitat segregation between these two species seems to exist (Hesthagen 1988). However, the age-classes 0+ to 3+ were underrepresented in this population. Hence, these age groups should be less influenced by the salmon stockings in the stream. Further, low numbers of young trout (<10 cm) were registered throughout most reaches of Tverrelva during the study period.

An uneven age structure in fish stocks may occur when nursery areas are spatially separated from habitat for older and mature specimens. Solomon & Templeton (1976) and Milner et al. (1978) found that Brown trout populations could be largely maintained through immigration from nursery areas located in upper stream stretches. Such a recruitment process implies upstream spawning migration, as found by these authors and others (Schunk 1945, Stuart 1953, Horton 1961). However, mature Brown trout in Tverrelva did not undertake any spawning migration in the fall (Hesthagen 1988). Presumably, this reflects the fact that stretches of the stream which are suitable for fish in all stages, are in close proximity to each other (Needham et al. 1945, Stuart 1953).

However, offspring from outlet spawning Brown trout stock in Movikvatn (Fig. 1) may represent such immigrants. I caught a relatively high number of spawners at the outlet of the lake and about 150 m downstream during the study period. Extensive movements of

Brown trout fry shortly after they emerge have been recorded elsewhere (Le Cren 1973, Elliott 1966, Mortensen 1977a, Elliott 1986, 1987b). However, the dispersal of fish within a stream seems to be a continuous process. The fact that there was a peak in abundance of 4+ fish in the lower part of Tverrelva, indicated that any immigration to this area occurs among older fish. The Brown trout stock in the stream consists of a large sedentary and a small mobile component (Hesthagen 1988). Further, I found a positive correlation between population density of Brown trout in different sections of Tverrelva and movement rates. Thus, migration as well as density dependent movement may act as important mechanisms for attaining population stability and distribution for Brown trout stocks subjected to great fluctuations in recruitment and population numbers in an unstable stream habitat such as Tverrelva.

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