

Life History Patterns of Freshwater Resident and Sea-Run Migrant Brown Trout in Norway

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Abstract

Brown trout *Salmo trutta* in Vangsvatnet Lake, Norway, include freshwater residents that mature sexually without any sea run and migrants that smoltify and migrate between fresh water and the sea one or more years before maturing. Migrants leave Vangsvatnet Lake during spring and move in coastal waters up to 100 km from the lake outlet before they return to their home river in summer or autumn; older migrants return earlier than younger migrants, sexually mature fish before immatures. Both residents and migrants spawn together in tributaries to Vangsvatnet Lake. Young brown trout (parr) grow in the tributaries and lake; lake dwellers grow faster than stream dwellers. Parr that become migrants at age 2 grow faster than parr that become residents, but parr that become migrants at age 4 and older grow more slowly than those that become residents. Parr that smoltify or mature at a young age grow faster than parr that do so later. Resident males are 2-8 years of age, and 13-47 cm in tip length, resident females 3-10 years and 21-45 cm. Smolts are 2-7 years old and 14-29 cm long. Mature migrants are 3-9 years old; males are 29-67 cm and females 34-67 cm long. Sex-ratios were in favor of males among residents, in favor of females among migrants.

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Many populations of diadromous salmonids feature heterogeneous phenotypes; some individuals live in the sea for one or more growth seasons before they mature sexually (termed migrants here), whereas others mature without migrating to the sea (termed residents here). Freshwater individuals are smaller than their migrating counterparts; they may be precocious males only, as in Atlantic salmon *Salmo salar* (Jones 1959), or both sexes as in Arctic char *Salvelinus alpinus* (Nordeng 1961, 1983) and sockeye salmon *Oncorhynchus nerka* (Ricker 1938; McCart 1970).

Population structures of brown trout *Salmo trutta* are not well known, but there is some evidence that stocks can consist of both residents and migrants. Precocious males have been reported (Svårdson and Anheden 1963; Campbell 1977). According to Frost and Brown (1967), progeny of resident brown trout from the Lake Windermere, England, transplanted to New Zealand and the Falkland Islands, have given rise to migrant brown trout. Furthermore, Rounsefell (1958) gave circumstantial evidence for that both residents and migrants have developed from releases of brown trout in North American rivers, whether the donor stocks consisted of either res-

idents or migrants. Among other salmonids like sockeye salmon and Arctic char, both residents and migrants have been reared from the same parental type (Foerster 1947; Nordeng 1983). But there is a genetic basis for the smoltification of salmonids (Landgrebe 1941), the process that physiologically adapts fish for sea life, and there are inherited differences in tendency to migrate among brown trout stocks (Jonsson 1982; Svårdson and Fagerström 1982).

Here, I describe the life history of resident and migrant brown trout spawning in tributaries of Vangsvatnet Lake, Norway. To determine whether or not the resident and the migrant forms are members of the same demes, I measured migration, age distribution, age at sexual maturity, growth, and fecundity for both groups. These data were then synthesized in a schematic model describing the life history of the brown trout.

Methods

Study Area

Vangsvatnet Lake is a part of the Voss River (Fig. 1). The spawning streams for brown trout are the Dyrvo, Rekveselva, Mossafinnelva, and Vosso; the latter arises from confluence of the Strandaelva and Raundalselva rivers upstream of the lake. The Strandaelva (average discharge $23 \text{ m}^3 \cdot \text{s}^{-1}$), Raundalselva ($30 \text{ m}^3 \cdot \text{s}^{-1}$), and Vos-

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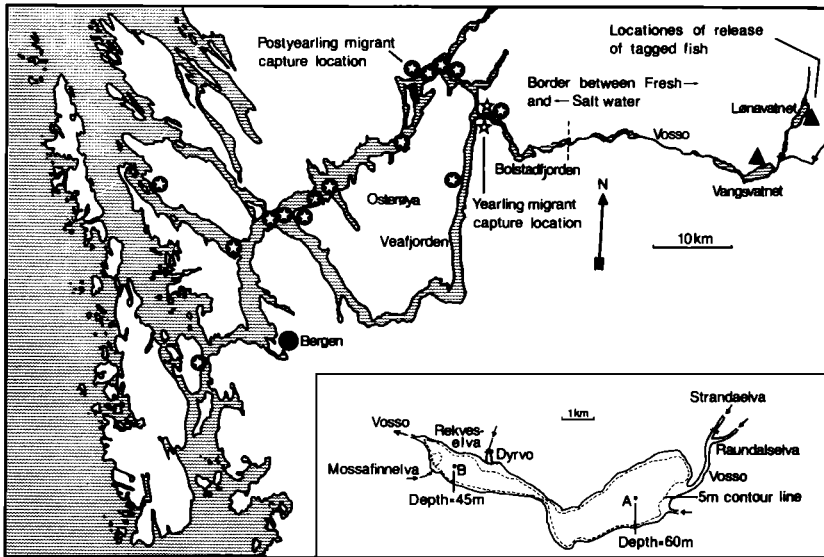


FIGURE 1.—Voss River and coastal waters of western Norway. Definitions of the brown trout phenotypes are given in Table 1. Inset: Vangvatnet Lake. Pelagic net stations are located at A and B. Spawning areas of brown trout are located in the named tributaries.

so were too large to sample for spawning brown trout. Thus, spawning was studied in the other tributaries. The Dyrvo ($1.5 \text{ m}^3 \cdot \text{s}^{-1}$) is the largest of these; its water depths are about 25 cm in the spawning areas and downstream. In the Rekveselva and Mossafinnelva, the corresponding water depths were about 20 and 15 cm. Because the Strandaelva, Raundalselva, and Vosso are large and remain open for most of the winter, brown trout can winter there. Ice and snow make the smaller streams unsuitable for wintering brown trout. Vangvatnet Lake is usually ice-covered from December to April, but it is an appropriate habitat for wintering brown trout.

Data Collection and Analysis

Brown trout were collected ($N = 4,939$) from Vangvatnet Lake and the Strandaelva, Dyrvo, Rekveselva, and Mossafinnelva rivers from October 1976 to October 1979. Parr and smolts ($N = 1,282$) larger than 12 cm were tagged with Carlin's tag (Carlin 1955) after having been anaesthetized with tricaine (MS 222 Sandoz). The fish were tagged at a water temperature of about 5°C between November 1976 and May 1978. After being tagged, they were kept in a hatchery for 1 month of observation. Fish hurt by the handling were removed. The tagged fish were released in Lønavatnet ($N = 638$) and Vangs-

vatnet ($N = 644$) lakes (Fig. 1). The rest of the brown trout ($N = 3,657$) were killed for registration of phenotype, size, age, sex, degree of sexual maturity, and fecundity.

In Vangvatnet Lake, monthly samples were taken through 1 year by beach seine (bar mesh 7.8 mm) and bottom and pelagic gill nets with a large range of mesh sizes (10–52 mm, 2–7 mm in bar-mesh increment). Sampling techniques are described by Haraldstad and Jonsson (1983). These nets catch all sizes of brown trout between 18 and 45 cm with similar efficiencies (Jensen 1977). In the Strandaelva, at the point where it joins the Raundalselva, monthly electrofishing was done for a year in an area of about $1,500 \text{ m}^2$. In the other tributaries, brown trout were electrofished during all seasons of the year, but were killed for biological analysis only during the spawning period (October–November).

Brown trout were differentiated into four general groups, some of these having subcategories (Table 1). Fish lengths (to 0.1 cm) were measured from the tip of the snout to the outer lobes of the tail as the tail lay in a natural position (natural tip length sensu Ricker 1979); sex and degree of sexual maturity were determined (Frost and Brown 1967). Egg number in 106 females (maturity stage 4, lengths 21–60 cm) and diameters of 10 eggs (measured to nearest 0.1 mm) of 83

TABLE 1.—*Brown trout life history stages in Norway.*

Stage	Characteristics
1. Stream-dwelling parr	Sexually immature with dark coloration, living in lotic environments
Lake-dwelling parr	Sexually immature with light coloration, living in lentic environments
2. Resident	Sexually mature in fresh water; signs of a dark spawning dress usually can be seen throughout the year
3. Smolt	Silver-colored and pelagic during the first run to the sea
4. Migrant	Sexually immature or mature fish from the moment they reach the estuary until death
Yearling migrant	One growth season in the sea
Postyearling migrant	Two or more growth seasons in the sea

females (maturity stage 5, lengths 21–62 cm) were recorded (Määr 1950). Ages were determined from scales and otoliths (Jonsson 1976). Parr were aged by both methods, whereas residents were aged by otoliths, scales often being unreadable. Migrants were aged by scales, which were easier to read than otoliths. Age at smolting and the number of repeat spawnings of migrants were determined from scales (Frost and Brown 1967). Growth of parr, smolts, and residents, was back-calculated by use of otoliths (r_1 : Jonsson and Stenseth 1977). The least-squares linear regression of body lengths, evenly distributed between 2.3 cm and 33 cm (L , cm), on otolith radius (X_o , mm) was

$$L = 15.6X_o - 1.9; N = 2,166; \\ r = 0.95; P < 0.0001. \quad (1)$$

Sea growth was back-calculated by use of scales, as fish length of migrants was more highly correlated with scale radius ($r = 0.91$) than with otolith radius ($r = 0.72$). The regression of body length of migrants, evenly distributed between 22.5 and 67 cm, on scale radius (X_s , mm) was

$$L = 16.9X_s + 0.4; N = 703; P < 0.0001. \quad (2)$$

Results

Migration

Of the 1,282 brown trout tagged in 1976–1978, 142 (11.1%) were recaptured during 1977–1984. Ninety-three of these were recaptured as parr and smolts, the stage at which they had been tagged, or residents (both sexes) in the lakes of release. Sixteen were captured as smolts downstream of

the lakes of release, 17 as migrants in coastal waters, and 16 as migrants in the Voss River. Brown trout were recaptured as far as 100 km from the outlet of Vangsvatnet Lake (Fig. 1). Migrants developed from both sexes of parr that had been released among resident brown trout in Lønavatnet Lake or among migrants in Vangsvatnet Lake. No tagged brown trout were captured in fresh water other than in the Voss River.

Monthly catches in Vangsvatnet Lake indicated that migrants ($N = 609$) left the lake for coastal waters during April–May; the smolts ($N = 331$) left during April–August. Sexually mature migrants returned mainly in August, immature postyearling migrants in August–September, and yearling migrants in September–October. These differences in time of return were significant (August–October: $\chi^2 = 37.88$; $df = 4$; $P < 0.001$), although there was quite a lot of overlap among the various phenotypes. Both immature and sexually mature migrants stayed in coastal waters during summer, but spent the winter in the Voss River.

Spawning

The ratio of resident to migrant spawners differed little among years within each tributary (Table 2), but varied among tributaries ($\chi^2 = 19.35$; $df = 2$; $P < 0.001$). The largest stream, Dyrvo, had the smallest proportion of resident spawners, whereas the smallest stream, Mossafinnelva, had the largest proportion. Migrants in the Dyrvo were significantly larger than those in the other streams sampled in 1977 (both sexes combined: $t = 3.39$; $P < 0.01$), but not in 1979, so this may have been a random event. None of the other biological variables differed significantly among tributaries (Table 2). I sampled only a few resident females in the tributaries, so they were omitted from Table 2. At the redds, most females, whether migrant or resident, were tended by one or two migrant males and several resident males. On a few occasions, migrant females were tended by resident males only. I could never observe which male actually fertilized the eggs, but the attendance of both female phenotypes by both male phenotypes suggests that the two phenotypes are parts of the same demes.

Distribution, Age, and Sex

The density of stream-dwelling parr in the Strandaelva River was highest during summer, reaching a peak in August (0.11 individuals $\cdot m^{-2}$).

TABLE 2.—Life history variables of resident and migrant brown trout spawning in tributaries to Vangsvatnet Lake, Norway, during the period 10 October–20 November 1977–1979; 95% confidence limits are given when $N > 5$. Lengths are tip lengths.

Year	N	Ratio, residents : mi- grants	Resident males		Migrant males				Migrant females			
			Length (cm)	Age (years)	Length (cm)	Smolt age (years)	Sea age (years)	Repeat spawn- ings	Length (cm)	Smolt age (years)	Sea age (years)	Repeat spawn- ings
Dyrvo River												
1977	126	1.8	23.5 ±0.8	3.6 ±0.2	44.0 ±1.8	2.5 ±0.3	2.9 ±0.3	1.3 ±0.2	48.2 ±2.4	2.8 ±0.4	3.6 ±0.3	1.8 ±0.4
1978	85	2.0	23.9 ±0.7	3.5 ±0.4	43.3 ±2.0	3.0 ±0.3	2.5 ±0.3	1.2 ±0.1	53.9 ±3.6	3.0 ±0.8	4.3 ±0.7	2.0 ±0.4
1979	137	1.9	22.0 ±0.7	3.6 ±0.4	39.5 ±1.6	2.9 ±0.2	2.1 ±0.2	1.0 ±0.1	53.0	3.0	3.6	1.5
Rekveselva River												
1977	38	4.4	23.3 ±1.3	3.5 ±0.3	38.0	2.3	2.5	1.0	44.4	3.0	3.7	1.3
1979	43	5.1	20.6 ±1.0	3.4 ±1.0	35.6	3.3	2.0	1.0	46.0	3.0	3.0	1.0
Mossafinnelva River												
1977	16	15.0	22.7 ±1.5	3.8 ±0.9	35.8	3.0	2.0	1.0				
1979	57	7.1	22.8 ±0.8	3.7 ±0.5	41.4 ±4.8	3.3 ±0.8	2.3 ±0.4	1.0 ±0.0				

During autumn, brown trout moved from the river to the lake; in January no brown trout were observed in the sampling area. That month, therefore, I sampled elsewhere in the river for brown trout. A few wintering parr were found between boulders and under ice along the shore. Parr recolonized the Strandaelva River from March through June. The Dyrvo, Rekveselva, and Mossafinnelva streams were empty of brown trout from December through May, but were re-

colonized in June concurrently with the emergence of brown trout alevins from the gravel. Males dominated numerically in age-groups 0 and 1 of stream-dwelling parr (Table 3; binomial test: $z = 3.41$; $P < 0.001$). At older ages, the sex ratio approached 1.0. The reason for this is that many stream-dwelling males, but not females, 2 years and older were sexually mature and counted as residents.

Lake-dwelling parr 1–4 years of age were abun-

TABLE 3.—Age and percentage of male brown trout in different life history stages caught in Vangsvatnet Lake and its tributaries.

Age (years)	Stream-dwelling parr		Lake-dwelling parr		Smolts		Residents			
							Tributaries		Lake	
	N	%	N	%	N	%	N	%	N	%
0	120	60.8	22	45.5						
1	113	61.9	600	54.3						
2	59	47.5	730	46.7	27	44.4	42	100.0	35	100.0
3	12	50.0	249	55.0	54	42.6	93	98.9	106	96.2
4	4	50.0	107	36.4	40	42.5	86	95.3	149	76.5
5			12	50.0	8	25.0	37	89.2	76	46.1
6	1	0.0	5	0.0			10	100.0	21	66.7
7			2	50.0			6	100.0	7	100.0
8			1	0.0					3	33.3
≥9							2	50.0	4	50.0

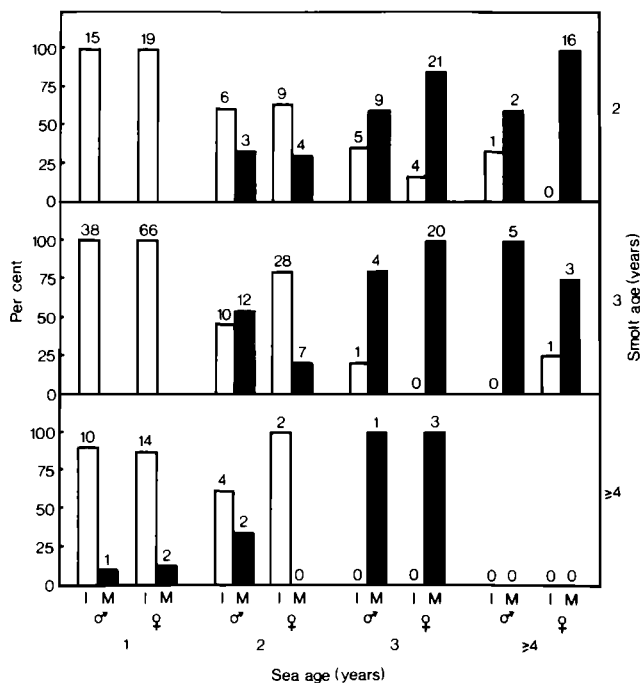


FIGURE 2.—Percentage and number of sexually immature (I) and mature (M) male and female migrant brown trout with smolt ages of 2–4+ years and sea ages of 1–4+ years. Numbers above the bars are sample sizes. The fish were caught with nets in the Vangsvatnet Lake during 1–8 October 1977 and December 1977 through April 1978.

dant in Vangsvatnet Lake (Table 3). The sex ratio was 1.0 averaged over all age groups, but varied among the age groups. Resident males significantly outnumbered females in Vangsvatnet Lake ($z = 10.9$; $P < 0.001$), and numerical dominance of males was even greater in the streams ($z = 15.35$; $P < 0.001$).

Most migrants smolted at age 3 (Table 3). This result was verified from scales of the migrants ($N = 703$). Smolt ages varied from 2 to 7 years; 35.5% of the sample had smolted at age 2, 53.0% at age 3, and 11.5% at age 4 years and older. Among both smolts and migrants, about 60% were females ($z = 4.27$; $P < 0.001$). Most migrant females matured sexually during their third sea run; males matured at a more variable age than females (Fig. 2). This difference between the sexes was significant ($\chi^2 = 10.25$; $df = 4$; $P < 0.05$). Once they were mature, the migrants seemed to spawn every year during the rest of their lives. Judged from the scales, significantly more migrants maturing at sea-age 2 (34%; $N =$

99) than at sea-age 3 (23%; $N = 171$) survived and became repeat spawners ($\chi^2 = 4.18$; $df = 1$; $P < 0.05$). Twenty percent of the mature males and 29% of the mature females were repeat spawners, but this difference was not significant ($P = 0.09$).

Growth and Size

Judged from the zone formation in scales and otoliths (Jonsson 1976, 1977), parr grew in length between May and October and residents between June and September. According to the Bonferroni inequality (Lienert 1973)

$$P(\text{global}) \leq \sum_{i=1}^r P(\text{simultaneous}),$$

lake-dwelling parr were larger overall than stream-dwelling parr ($P < 0.01$; Fig. 3). Resident females were significantly larger than resident males in age-group 4 ($t = 2.44$; $P < 0.05$), but

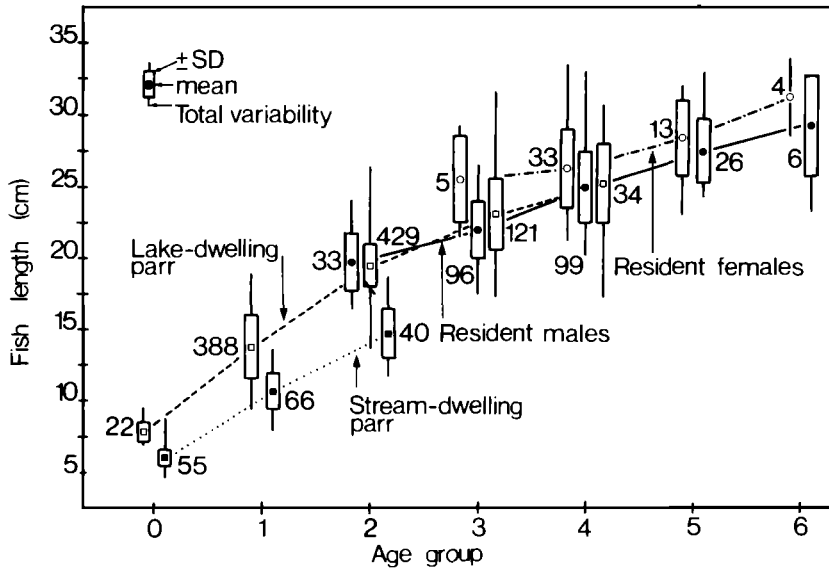


FIGURE 3.—Tip lengths at age for brown trout parr caught during October–April, and residents caught during September–April 1976–1978 in the Vangsvatnet Lake and tributaries. Sample sizes are next to data points.

not in any other age group. The length variations of resident males and females (all ages) were, respectively, 13–47 cm and 21–45 cm; their respective mean lengths \pm SD were 23.5 ± 3.8 cm and 26.8 ± 2.8 cm. These mean lengths were significantly different ($t = 8.08$; $P < 0.001$).

Back-calculation of growth of parr (equation 1) showed that the fastest-growing parr became smolts at age 2 and that slower-growing parr had successively older smolt ages (Table 4). Among

migrants, there were no significant differences in growth rate between the sexes, which were pooled. Mean growth of male parr that developed into residents fell between those that smolted at ages 2 and 4; mean growth of corresponding female parr were between those that smolted at 2 and 3 years of age. Older age groups of residents may include some repeat spawners.

Mean lengths \pm 95% confidence limits (cm) of 2–5-year-old smolts caught during spring and

TABLE 4.—Back-calculated growth (mean tip length, cm, \pm 95% confidence limits) during the parr stage of resident and migrant brown trout from otolith measurements (equation 1). The last column of each age group corresponds to winter length the year before smolting (migrants) or sexual maturity (residents).

Age (years)	Phenotype	N	Annulus number				
			1	2	3	4	5
2	Migrant	233	7.2 \pm 0.2	15.4 \pm 0.2			
	Resident ♂	32	6.7 \pm 0.5	14.0 \pm 0.6			
	Resident ♀	0					
3	Migrant	361	6.1 \pm 0.2	12.9 \pm 0.2	18.7 \pm 0.2		
	Resident ♂	96	6.1 \pm 0.2	13.1 \pm 0.4	18.1 \pm 0.4		
	Resident ♀	11	7.0 \pm 0.9	14.8 \pm 1.1	21.0 \pm 2.0		
4	Migrant	51	5.7 \pm 0.4	11.8 \pm 0.6	16.8 \pm 0.6	21.2 \pm 0.6	
	Resident ♂	96	5.9 \pm 0.2	13.2 \pm 0.4	18.5 \pm 0.4	22.0 \pm 0.4	
	Resident ♀	40	6.8 \pm 0.5	14.2 \pm 0.6	19.3 \pm 0.6	23.1 \pm 0.6	
5	Migrant	12	5.4 \pm 0.6	10.9 \pm 1.6	14.6 \pm 1.7	19.6 \pm 1.7	23.7 \pm 1.9
	Resident ♂	26	5.7 \pm 0.6	12.3 \pm 1.1	17.4 \pm 1.1	21.5 \pm 1.1	24.3 \pm 0.8
	Resident ♀	38	6.5 \pm 0.5	13.7 \pm 0.8	18.8 \pm 0.8	22.4 \pm 0.8	25.2 \pm 0.8

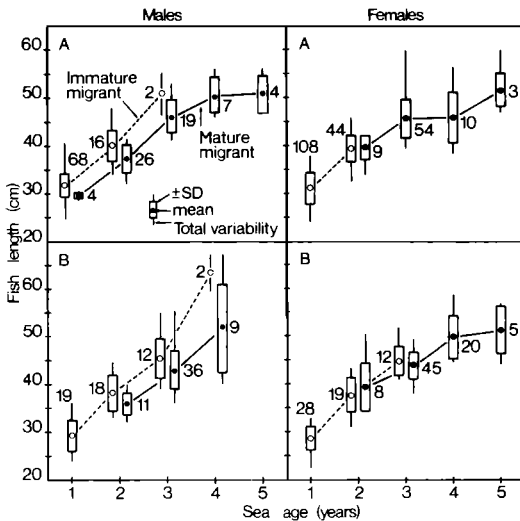


FIGURE 4.—Tip lengths at age for migrant brown trout with smolt ages 3 (A) and 2 (B) years, caught from October 1976 through April 1978 in the Vangsvatnet Lake and tributaries. Sample sizes are next to data points.

summer (sample sizes in Table 3) were, respectively, 16.1 ± 0.4 , 19.5 ± 0.5 , 24.4 ± 0.7 , and 25.0 ± 1.3 . The measured smolts were caught in the growth season, so their lengths are larger than the estimated winter lengths of smolts (Table 4).

Migrants with smolt age 2+ were, according to the Bonferroni inequality, shorter than those with smolt age 3+ during the first 3 years at sea ($P < 0.05$; Fig. 4). The sizes of immature males and females of the same age did not differ significantly ($P > 0.05$). Mature females with sea age 3 years and younger were generally smaller than corresponding males, but the difference was only significant for those with smolt age 3 years and sea age 2 years ($t = 2.59$; $P < 0.05$). Among older migrants, there were no significant differences in size between the sexes, except that females with smolt age 3 and sea age 4 years were smaller than males of the same age ($t = 2.11$; $P < 0.05$). The length variations of sexually mature migrant males and females (sea ages 1–7) were, respectively, 29–67 cm and 34–67 cm; their respective mean lengths \pm SD were 43.3 ± 7.4 cm and 45.8 ± 5.7 cm.

Back-calculation of sea growth (equation 2) showed that immature migrants grew significantly faster than mature migrants of the same age. Mean yearly growth \pm 95% confidence lim-

its (cm) of immatures with sea ages 1–3 years were, respectively, 13.0 ± 0.4 ($N = 236$), 10.3 ± 0.5 ($N = 107$), and 7.8 ± 1.0 ($N = 29$). The corresponding yearly growth of mature fish with sea ages 2–5 years were, respectively, 5.4 ± 0.6 ($N = 58$), 3.5 ± 0.3 ($N = 137$), 3.4 ± 0.7 ($N = 25$), and 2.8 ± 1.2 ($N = 11$). The growth rates of the two sexes did not differ significantly ($P > 0.05$).

Fecundity

Individual fecundity increased with body length for both residents and migrants (Table 5). Analysis of covariance gave a significant heterogeneity in slopes between residents, first-time-spawning and repeat-spawning migrants ($F_{2,100} = 29.3$; $P < 0.0001$). The egg diameter increased significantly with body length for all fish combined, but the fit was not very good. The regression coefficients of residents, or repeat-spawning migrants alone, did not differ significantly from 0 ($P > 0.05$).

Discussion

Population Structure

Resident and migrant brown trout are parts of the same demes. The two morphs spawn together in tributaries to Vangsvatnet Lake. Sex ratios of the morphs are uneven, but males are surplus among residents and females among migrant. Both morphs develop from monomorphic lake-dwelling parr that were tagged and released in two different lakes in the Voss River. Observations by Rounsefell (1958) and Frost and Brown (1967) implied that polymorphism could exist in brown trout populations, but few explicit descriptions of polymorphic brown trout stocks exist. However, populations consisting of migrants and residents have been documented for sockeye salmon in British Columbia (Ricker 1938; McCart 1970) and Arctic char in Russia (Savvaitova 1973, 1980) and Norway (Nordeng 1983).

Both genetics and environment influence whether salmonids become residents or migrants. The genetic influence is suggested by the very existence of resident and migrant fish within the species (Frost and Brown 1967), as well as within stocks of the species. Svårdson and Fagerström (1982) reared and released brown trout smolts from various stocks; stock differences in tendency to migrate were maintained when the fish were released together. Svårdson and Fagerström's (1982) results are supported by results from the Voss River (Jonsson 1982). Brown trout

TABLE 5.—Regressions of fecundity (f) and egg diameter (d) on fish tip length (L , cm) of brown trout. All F values are significant at $P < 0.0001$.

Phenotype	Regression	r	F
Residents	$\log_{10}f = 2.688 \log_{10}L - 1.324$	0.80	43.8
First-time spawning migrants	$\log_{10}f = 2.340 \log_{10}L - 0.634$	0.82	106.8
Repeat spawning migrants	$\log_{10}f = 2.731 \log_{10}L - 1.383$	0.81	47.4
All phenotypes	$d = 0.022L + 4.26$	0.51	29.0

from Vangsvatnet and Lønavatnet lakes differ in their tendency to migrate. This difference has probably evolved during the last 6–7 thousand years, as the two stocks have been separated by a waterfall since that time. Inherited between-stock variations in tendency to migrate also exist in other salmonid species such as rainbow trout *Salmo gairdneri* (Neave 1944; Northcote 1969), sockeye salmon (Ricker 1972), and Arctic char (Nordeng 1983).

Environmental influence on the tendency to become resident or migrant has been demonstrated in rearing and releasing experiments with Arctic char. By changing feeding intensity, Nordeng (1983) was able to vary the proportion of residents versus migrants. Changes in temperature during early ontogeny of the fish affect the life history of salmonids in a similar way as changes in feeding intensity (Balon 1980b, 1983). As I explain later, the reason for this may be that food and temperature strongly influence fish growth (Alm 1959; Elliott 1976, 1982), and thereby affect fish fitness.

The "decision" whether parr develop to residents or migrants is closely connected with age at smolting and age at sexual maturity. Both these traits are themselves influenced by genetics and environment (Alm 1959; Schaffer and Elson 1975; Refstie et al. 1977; Thorpe and Morgan 1978; Bailey et al. 1980; Nævdal 1983; Saunders et al. 1983; Jonsson et al. 1984). Life history variables probably are adapted to the environment through natural selection (Fisher 1930; Stearns 1976, 1980). Reproductive success is determined largely by growth rate and survival of the fish (Jonsson et al. 1984; Roff 1984). Growth rates and survival rates differ among brown trout living in different rivers; thus, life histories of adapted fish will differ. Within one stock, growth rates also will vary among individuals. This partly may be due to genetics (Refstie and Steine 1978), but occurs mainly because different individuals happen to find different amounts of food (Alm 1959). The optimal life history pat-

terns vary accordingly. Therefore, a flexible life history pattern that accommodates differences in growth rate can be a better adaptation for fish than a rigid genetically fixed pattern. Besides brown trout, growth-related flexibility in life history patterns has been demonstrated for several fish species (Ricker 1938; Alm 1959; Fryer and Iles 1969; Jonsson and Hindar 1982; Stearns 1983; Jonsson et al. 1984; Roff 1984).

Little is known about genetic mechanisms regulating life history patterns. Allendorf et al. (1983) found a phosphoglucosylase locus (*Pgm-1*) in the liver of rainbow trout that had pronounced phenotypic effects. Rainbow trout with liver *Pgm-1* expression hatched earlier, matured younger, and achieved a size advantage that was maintained until sexual maturity compared with those without liver *Pgm-1* expression. Allendorf et al. (1983) maintained that the relative success of rainbow trout with and without liver *Pgm-1* depends on environmental conditions at the time of hatching. One might expect that similar genetic polymorphism could explain the presence of migrants and residents within the present stock of brown trout, because there were differences in size between parr that became smolts and parr that became residents. But experiments with other salmonids indicate that smolting and age at sexual maturity vary with changes in the habitat of immature fish and not only with habitat differences during early development (Lundqvist and Fridberg 1982; Nordeng 1983). Thus, genetic polymorphism as described by Allendorf et al. (1983) cannot alone explain environmental regulation of life history traits. Another possibility is that fish might possess switching genes (Mayr 1970) that release or suppress a particular process (such as smoltification or maturation) according to the nature of a given stimulus (such as growth rate). Molecular mechanisms controlling the flexibility of life history responses to environmental variations are not well known (Britten and Davidson 1969; MacIntyre 1982; Allendorf et al. 1983), and further research is

needed to reveal the genetics of life history variations.

Differences between Sexes

The sexes varied in several life history traits. Males predominated among stream-dwelling parr and residents, females among the migrants. Resident males matured, on average, younger than resident females. Migrant males matured at more variable ages than migrant females. These differences in sex ratio and maturation age resulted in sexually mature males being, on average, smaller and more variable in size than mature females. Such size differences between the sexes have been observed for other stocks of brown trout (Stuart 1957; Jonsson and Sandlund 1979) as well as for other salmonids (Jones 1959; Gross 1984).

Whatever causes more male than female brown trout to establish residence in the Voss system, habitat affects growth rate as the life history patterns develop. Stream dwellers grow more slowly than lake dwellers, and lake dwellers grow more slowly than migrants feeding in coastal waters. These differences are independent of genetics. The two sexes grow equally fast when they feed in the same habitat. Furthermore, Alm (1959) showed that offspring of slow-growing stream dwellers grow as well as progeny of fast-growing lake dwellers when reared under the same conditions.

The differing sizes at sexual maturation between male and female brown trout may be related to fertility. Female fertility increases with body size (Bagenal 1973), whereas both small and large males seem to have relatively high fertility (Schroder 1982; Gross 1985). Large males are usually the principal spawners (Jones and Ball 1954), but small males (satellites) may dart in and fertilize some of the eggs of females that are spawning primarily with large males (Jones and King 1952; Schroder 1982; Gross 1984, 1985). In addition, observations from the Voss River indicate that resident males become principal spawners when migrant males are absent. Early-maturing, smaller males doubtless are selected for under some circumstances.

Life History

I have summarized the life history of brown trout that spawn in four tributaries to Vangsvatnet Lake in Fig. 5. The tributaries are nursery areas for parr from spring through autumn. Most

stream dwellers are 0–2 years of age, although individuals as old as 6 years occur. The majority of the stream dwellers leave running water during autumn, and spend the winter in the lake. Some of them move back to the tributaries the following spring and the rest become lake dwelling parr. The spring invasion into the tributaries coincides with the emergence of brown trout alevins from the gravel. Stuart (1957) suggested that parr enter streams in spring to feed on alevins but I cannot support this idea after 10 years of intensive observations and analysis of hundreds of stomachs from stream dwelling parr. Some stream dwelling male parr mature sexually and become residents, whereas few corresponding females mature at this time.

Most lake dwelling parr are 0–4 years of age, although individuals as old as 8 years may be found. The sex ratio differs between various age groups, but the overall sex ratio is not significantly different from 1.0. Some lacustrine parr mature sexually and became residents, most of these being males. Others, mostly females, become smolts and migrate. (Female surplus among migrants has been observed in other brown trout studies: Alm 1959; Pemberton 1976. Smolt ages and sizes observed in the present study are well within the range observed elsewhere: Järvi 1940; Jensen 1968a.)

Residents stay in fresh water throughout their life span, and their biology parallels that described for landlocked brown trout (Frost and Brown 1967; Jonsson 1977). Migrants complete one sea run every year, leaving the Voss River in spring and returning in autumn. The migrants feed in coastal waters up to 100 km from the outlet of Vangsvatnet Lake, which is approximately the same migration distance reported for migrant brown trout elsewhere in Norway (Jensen 1968b). Sexually mature migrants return earlier in the autumn than immatures; postyearlings return earlier than yearlings. (The tendency of both immature and mature migrants to spend the winter in fresh water occurs also in other salmonids, such as cutthroat trout *Salmo clarki* [Johnston 1982], Arctic char [Nordeng 1977; Johnson 1980], brook trout *Salvelinus fontinalis* [Power 1980], and Dolly Varden *Salvelinus malma* [Armstrong and Morrow 1980].) A few yearlings attain sexual maturity, but most of them stay immature until the second or third year in the sea. After spawning, both migrants and residents leave the tributaries and winter in Vangs-

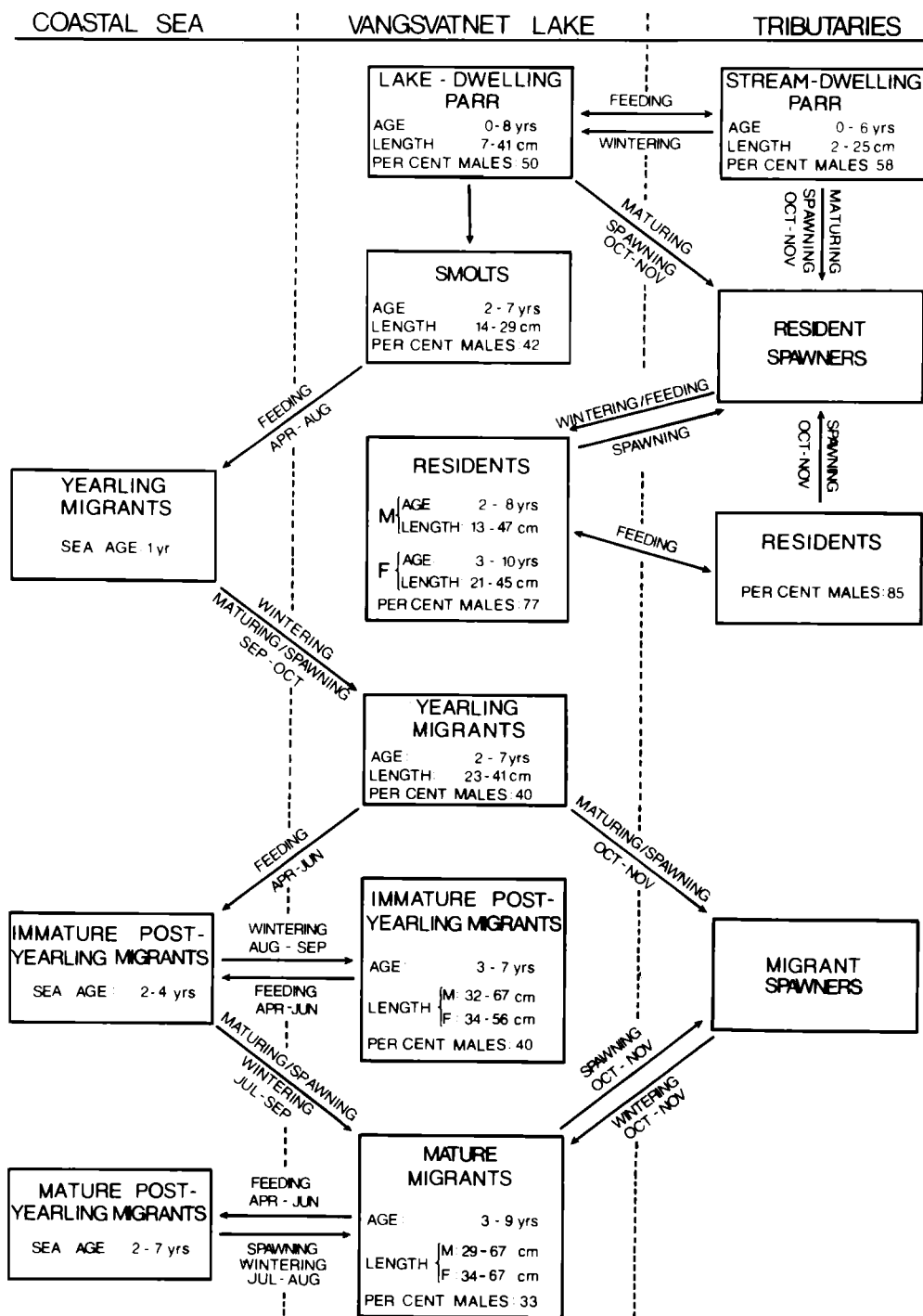


FIGURE 5.—Schematic model for the life history of resident and migrant brown trout spawning together in tributaries of Vangsvatnet Lake, Norway.

vatnet Lake. Mean length of mature migrants is about 45 cm in length, which may be about average for migrant brown trout in Norway (Jensen 1968a; personal observations).

The present study gives an example of how a stock of brown trout can exploit both fresh water and the sea. Both survival and growth conditions differ markedly between the habitats, but there is probably no definite selective advantage for either residents or migrants. The dichotomous population structure observed may be quite common in coastal populations of brown trout with free access to the sea, although little has been known about this up to now.

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