Variation within and between rivers in adult size and sea age at maturity of anadromous brown trout, *Salmo trutta*

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Variation within and between Rivers in Adult Size and Sea Age at Maturity of Anadromous Brown Trout, *Salmo trutta*

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L'Abée-Lund, J. H. 1991. Variation within and between rivers in adult size and sea age at maturity of anadromous brown trout, *Salmo trutta*. Can. J. Fish. Aquat. Sci. 48: 1015–1021.

I compared adult size and sea age at sexual maturity among nine populations of anadromous brown trout, *Salmo trutta*, in two Norwegian rivers to determine the extent of inter- and intrariverine variations. Variation in the mean length of spawners and in the mean sea age at sexual maturity were mainly dependent on the variations found within rather than between rivers. Mean lengths and mean age at maturity of males increased significantly with increasing altitude of the spawning area and with migration distance in freshwater. In females, positive significant correlations were found with mean lengths and altitude of the spawning area and with mean sea age at maturity and both spawning site altitude and migration distance. Mean lengths and ages of males and females were not significantly correlated with the rate of water discharge in the streams during spawning. The size of gravel substrate for spawning was of minor importance in explaining interpopulation variation in mean female size. The increase noted in mean length and in mean sea age at maturity of both males and females is probably an adaptation to greater energy expenditure to reach the uppermost natal spawning areas.

On a comparé la taille à l'âge adulte le temps passé en mer à la maturité sexuelle de truites brunes, *Salmo trutta*, anadromes appartenant à neuf populations vivant dans deux rivières de la Norvège afin d'étudier les variations dans une même rivière et entre rivières. On a constaté que la variation de la longueur moyenne des reproducteurs et du temps moyen passé en mer à la maturité sexuelle dépendent essentiellement des variations dans une même rivière plutôt qu'entre rivières. La longueur moyenne et le temps moyen à la maturité chez les mâles augmentaient dans une mesure significative en fonction de l'altitude du lieu de fraye et de la distance de migration en eau douce. Chez les femelles, on a constaté des corrélations positives significatives entre la longueur moyenne et l'altitude du lieu de fraye de même qu'entre le temps moyen en mer à la maturité et l'altitude du lieu de fraye ainsi que la distance de migration. Chez les mâles et les femelles, il n'est pas apparu de corrélation significative entre la longueur moyenne et le temps passé en mer et le débit des cours d'eau durant la fraye. La granulométrie du gravier de fraye s'est révélé n'avoir qu'une influence mineure sur la variation de la taille moyenne des femelles d'une population à l'autre. L'augmentation de la longueur moyenne et du temps moyen passé en mer à la maturité constatée tant chez les mâles que chez les femelles est probablement une adaptation découlant de ce qu'il faut une dépense énergétique est plus importante pour atteindre les eaux de fraye d'origine les plus élevées.

Interriverine variation in size of Atlantic salmon, *Salmo salar*, has been related to environmental factors such as the migratory distance in freshwater to the natal spawning areas and the rate of water discharge (Schaffer and Elson 1975; Thorpe and Mitchell 1981; Scarnecchia 1983). As migration distance and river discharge determine the energy used to reach the spawning ground, Schaffer and Elson (1975) suggested that long, large rivers would favor selection for larger sized fish with greater energy reserves. One consequence of this could be that within rivers the larger fish may spawn in the upper part and the smaller fish further downstream. Glebe and Leggett (1981) demonstrated in American shad, *Alosa sapidissima*, a higher energy cost of migration in smaller fish. However, in several anadromous fish species (American shad, Atlantic salmon, and coho salmon, *Oncorhynchus kisutch*) and the results are contrary to Schaffer and Elson's (1975) prediction (Carscadden and Leggett 1975; Scarnecchia 1983; Fleming and Gross 1989). In a recent study of 34 populations of anadromous brown trout, *Salmo trutta*, L'Abée-Lund et al. (1989) found no significant correlation of adult fish length with river length and water discharge. However, it was pointed out that such relationships may nevertheless exist because the precise spawning areas for many of the populations were unknown. The homing behavior of brown trout for its natal spawning area (Stuart 1957; Hindar et al. 1991) is of great importance to maintain any intrariverine variation in adult size and sea age at sexual maturity.

Salmonids are selective in choosing the substrate for spawning by avoiding areas with silt and clay. Reiser and Bjornn (1979) stated that in salmonids the suitability of a particular size gravel substrate depended mostly on fish size. However, Ottaway et al. (1981) demonstrated that the grain size of brown trout redds was not related to the fish length.

In this paper I compared the variation in sea age at sexual maturity and size of adult anadromous brown trout from nine populations, whose spawning areas were known, in two rivers. The null hypotheses was that (1) the sea age at sexual maturity and adult size were independent of increasing migration distance, spawning site altitude, and mean water discharge during the spawning season in the spawning area and (2) the length of females was not related to the grain sizes within redds.

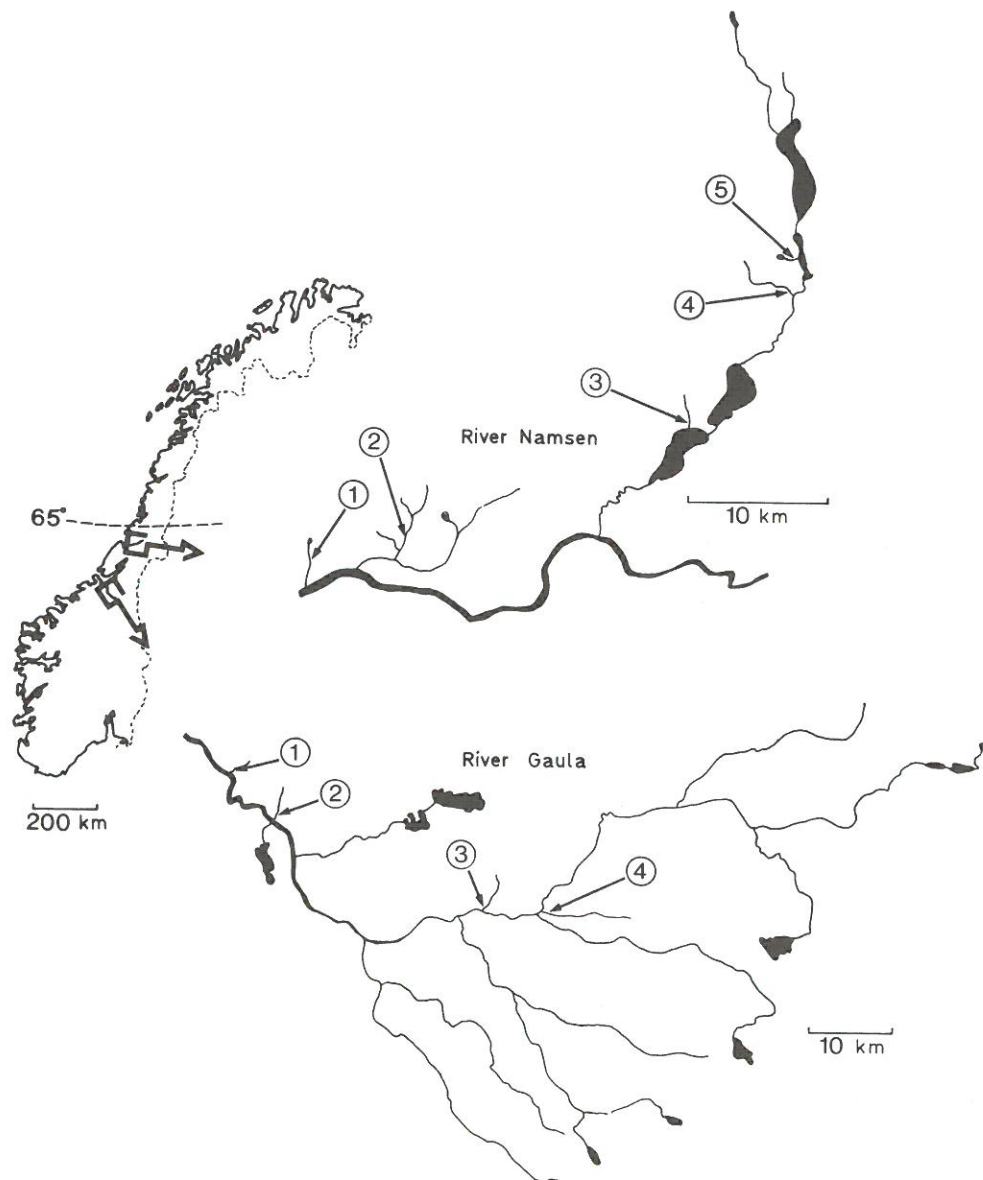*Can. J. Fish. Aquat. Sci., Vol. 48, 1991*

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FIG. 1. Locations of the nine tributary streams of the two Norwegian rivers in which the populations of anadromous brown trout were studied. Tributary names are shown in Table 1.

Materials and Methods

Sampling

Anadromous brown trout were investigated in nine tributaries of two Norwegian rivers, the River Gaula and the River Namsen, situated at $63°20'N$ and $64°28'N$, respectively (Fig. 1). The distance between tributaries along the main river varied from approximately 4 to 44 km (Table 1). Fish were sampled during the spawning season, i.e. September–October, by electrofishing. Fish were caught while spawning, as all males had running milt, and most females had running roe or were spent. The remaining females were almost ready to ovulate. Local homing in brown trout has been found when it was looked for (e.g. Stuart 1957; Halvorsen and Stabell 1990; Hindar et al. 1991). Thus, I define the individuals spawning within each stream to form a population (Mayr 1970).

Traits

Each fish was measured (total length) to the nearest millimetre and sex and degree of sexual maturity were recorded (Dahl 1917). Ages were determined from scales (Jonsson 1985). Determination of age at sexual maturity was based on scale readings (Dahl 1910). Comparisons of mean age and size at smolting revealed that the two uppermost populations in both rivers smoltified at a significantly (Scheffé procedure on means, $P < 0.05$) greater age and size than those in the lowermost populations (Table 2). Within populations, no significant differences ($P > 0.05$) were found in smolt age and size between sexes. Thus, to reduce the effect of freshwater history, age at sexual maturity was expressed as the number of summers spent at sea before reaching sexual maturity.

Environmental Parameters

In each of the four tributaries of the River Gaula, two to seven samples of gravel substrate (3227 – 11 687 g) were analysed. If possible, redds were sampled. Samples were dry screened through three sieves (2, 6.3 and 20.0 mm), and the structure of spawning substrate within tributaries are expressed as mean frequency of different grain sizes.

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TABLE 1. Tributary streams sampled, migration distance (distance from the sea to the tributary), spawning site altitude, mean rate of water discharge (minimum–maximum) in the tributaries during spawning season, and sampling period for nine populations of anadromous brown trout from two Norwegian rivers.

Location	Migration distance (km)	Altitude (m)	Water discharge (m^3/s)	Sampling period
River Gaula				
1. Loddbekken	9.9	20	0.16 (0.03–0.38)	1986–88
2. Bortna	22.1	40	0.16 (0.02–0.38)	1986–88
3. Malma	59.2	135	0.27 (0.03–0.90)	1989
4. Herjåa	67.6	170	0.92 (0.11–3.13)	1988–89
River Namsen				
1. Mølleelven	0.6	10	0.18 (0.03–0.42)	1989
2. Norddalselven	6.9	10	1.24 (0.17–2.96)	1989
3. Vikabekken	51.0	10	0.27 (0.04–0.61)	1986
4. Almåselven	70.0	40	0.49 (0.07–1.12)	1986–89
5. Skeitjørnbekken	73.9	65	0.15 (0.02–0.33)	1986

TABLE 2. Smolt age and size (arithmetic means ± 95% C.L. and ranges) for nine anadromous brown trout populations from two Norwegian rivers.

Location	Age (yr)			Size (cm)		
	n	Mean	Range	n	Mean	Range
River Gaula						
1. Loddbekken	64	3.0 ± 0.18	2–5	64	15.1 ± 0.92	8–24
2. Bortna	56	2.8 ± 0.14	2–4	56	13.8 ± 0.97	8–26
3. Malma	15	3.6 ± 0.41	2–5	15	17.5 ± 1.88	12–24
4. Herjåa	28	3.7 ± 0.26	3–5	30	16.2 ± 1.04	12–26
River Namsen						
1. Mølleelven	33	2.6 ± 0.22	2–4	34	12.3 ± 1.08	8–17
2. Norddalselven	32	2.8 ± 0.23	2–4	32	13.4 ± 1.05	7–19
3. Vikabekken	22	3.5 ± 0.36	2–5	22	17.8 ± 1.55	12–22
4. Almåselven	59	3.8 ± 0.21	2–6	61	20.0 ± 0.99	7–30
5. Skeitjørnbekken	23	3.6 ± 0.45	2–6	23	18.7 ± 2.18	11–28

TABLE 3. Lengths of adult fish and sea ages at sexual maturity (arithmetic means ± 95% C.L. and ranges) for nine anadromous brown trout populations from two Norwegian rivers. Asterisks indicate significant ($P < 0.05$) differences in length and age between sexes within populations.

Location	Males			Females		
	n	Length (cm)	Age (summers at sea)	n	Length (cm)	Age (summers at sea)
River Gaula						
1. Loddbekken	48	36.7 ± 2.14 (25–56)	2.0 ± 0.11 (1–3)	16	43.0 ± 4.10 (31–59)*	2.4 ± 0.33 (1–3)*
2. Bortna	42	36.6 ± 2.12 (24–50)	2.0 ± 0.14 (1–3)	14	42.7 ± 3.70 (32–53)*	2.6 ± 0.43 (2–4)*
3. Malma	8	47.6 ± 7.30 (29–56)	2.6 ± 0.62 (2–4)	7	53.2 ± 6.36 (43–63)	2.7 ± 0.45 (2–3)
4. Herjåa	12	52.7 ± 5.58 (41–69)	2.9 ± 0.50 (2–4)	18	53.3 ± 3.12 (41–61)	3.3 ± 0.29 (2–4)
River Namsen						
1. Mølleelven	24	33.5 ± 2.21 (24–45)	2.1 ± 0.19 (1–3)	12	36.2 ± 3.13 (31–46)	2.3 ± 0.29 (2–3)
2. Norddalselven	22	37.7 ± 2.97 (25–48)	2.5 ± 0.31 (2–4)	13	42.3 ± 2.75 (36–52)*	2.5 ± 0.31 (2–3)
3. Vikabekken	9	35.5 ± 3.81 (27–41)	2.1 ± 0.46 (i–3)	13	38.8 ± 4.82 (24–51)	2.0 ± 0.53 (1–4)
4. Almåselven	42	41.3 ± 1.70 (28–59)	2.8 ± 0.34 (1–4)	25	41.9 ± 2.00 (35–57)	2.9 ± 0.32 (2–4)
5. Skeitjørnbekken	18	43.9 ± 2.18 (34–51)	2.5 ± 0.39 (2–4)	5	42.8 ± 8.29 (36–50)	2.6 ± 0.68 (2–3)

The climatic differences between the two rivers (i.e. water temperature, precipitation, and photoperiod) are probably small due to their relatively close proximity. The rate of water discharge (cubic metres per second) in each spawning area during the spawning season was estimated. This was done by estimating the drainage area of each tributary from topographic maps and relating this to the total drainage area of the river and the water discharge measured by the Norwegian Water and Electricity Board, Hydrological Department, in the river's catchment basin during the spawning season. Mean water discharge during spawning season varied among tributaries from 0.15 to 1.24 m^3/s (Table 1). Migration distance (kilometres) is the distance that the brown trout of each population have to migrate in freshwater from the sea to the natal spawning trib-

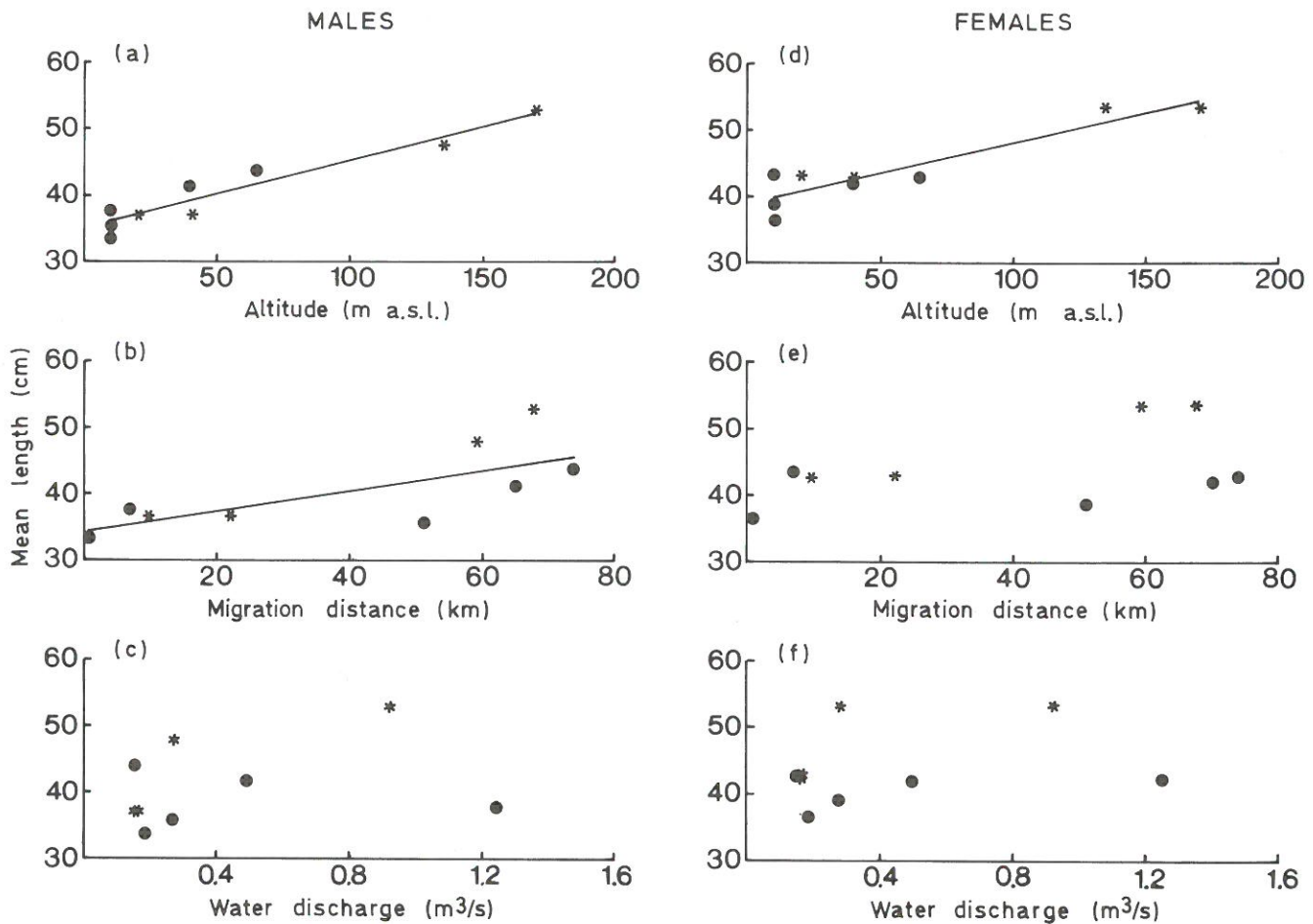*Can. J. Fish. Aquat. Sci., Vol. 48, 1991*

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FIG. 2. Relationships between spawning site altitude, distance of freshwater migration, and mean water discharge during spawning and mean size of mature males and females for nine populations of anadromous brown trout in the River Gaula (asterisks) and the River Namsen (solid points).

TABLE 4. Linear regression statistics for the least-squares regression lines in Fig. 2 and 3 based on nine measurements of mean adult length (cm) and mean maturity sea age (summers at sea) as dependent variables (Y) and spawning site altitude (m a.s.l.), and migration distance in freshwater (km) as independent variables (X) yielded $Y = a + bX$; r = regression coefficient. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Group	a	b	r
Length vs. spawning site altitude			
Males	34.8	1.034	0.96***
Females	38.9	0.909	0.92***
Length vs. migration distance			
Males	34.3	1.546	0.73*
Age vs. spawning site altitude			
Males	2.2	0.0042	0.72*
Females	2.4	0.0042	0.81**
Age vs. migration distance			
Males	2.1	0.0080	0.70*
Females	2.3	0.0074	0.73*

utary, and it varied from 0.6 to 73.9 km. The brown trout spawned in the tributaries about 100–500 m from the main river. The altitudes of the spawning areas were estimated from topographic maps.

Statistical Analysis

Interriverine analysis of adult length and sea age at maturity were carried out with analysis of covariance (ANCOVA) only when the dependent and independent variables met the assumptions of this model. In this study, these assumptions were significant linearity of each relation between Y and X and homogeneity in slopes (Sokal and Rohlf 1981). Intrariverine analysis of traits were carried out with analysis of variance (ANOVA). Linear least-squares regression models were developed (SPSS/PC) for mean length and mean age at sexual maturity on spawning site altitude and migration distance.

Results

Length of Male and Female Fish

Females were generally larger than males but the difference was significant in only three populations (Table 3). The mean lengths of males increased significantly ($P < 0.05$) with increasing altitude and migration distance (Fig. 2a and 2b; Table 4), but not with mean water discharge in the streams (Fig. 2c). When computing the linear least-squares multiple regression of mean lengths of males on spawning site altitude and migration distance (the latter two variables were significantly uncorrelated (Pearson's $r = 0.619$, $n = 9$)), the latter did not significantly improve the coefficient of determination of mean lengths of males and spawning site altitude. This indicates that elevation was of major importance in determining length of male trout. Interriverine differences

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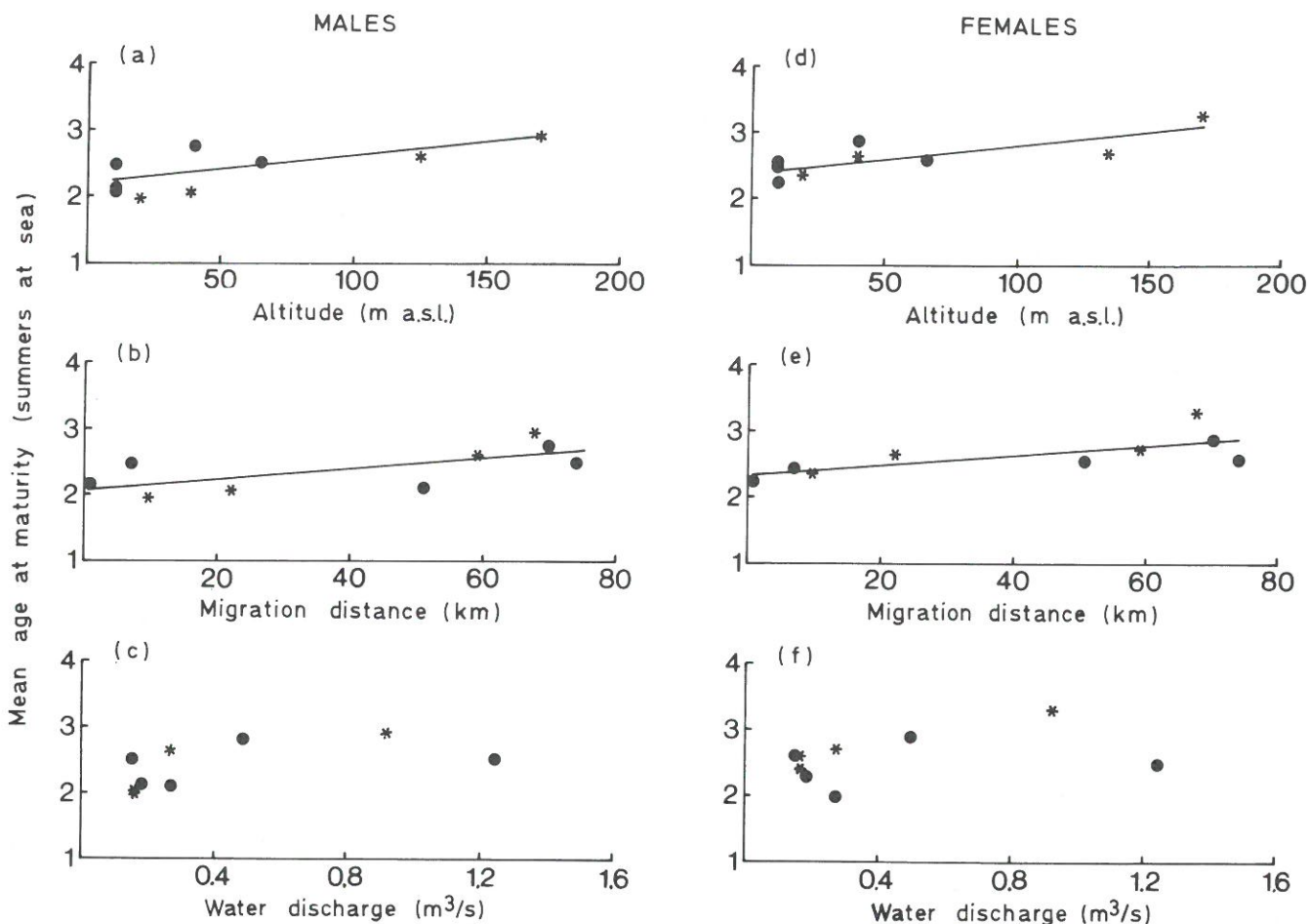Can. J. Fish. Aquat. Sci., Vol. 48, 1991

FIG. 3. Relationships between spawning site altitude, distance of freshwater migration, and mean water discharge during spawning and mean age at sexual maturity of males and females for nine populations of anadromous brown trout in the River Gaula (asterisks) and the River Namsen (solid points).

TABLE 5. Frequency (arithmetic means ± 95% C.L. and ranges) of redd grain sizes from four tributaries into the River Gaula.

		Grain size (mm)			
Tributary	n	<2.0	2.0–6.3	6.3–20.0	>20.0
1. Bortna	3	1.9 ± 4.47 (0.6–4.0)	4.5 ± 3.97 (3.3–6.3)	13.8 ± 8.45 (11.2–17.7)	79.9 ± 6.96 (77.9–83.1)
2. Loddbekken	7	6.1 ± 6.38 (0.2–14.6)	7.9 ± 4.81 (2.2–15.6)	21.0 ± 7.40 (12.1–33.8)	65.0 ± 15.91 (43.1–85.6)
3. Malma	3	7.7 ± 3.23 (6.4–8.9)	9.7 ± 3.73 (8.4–11.4)	23.3 ± 12.17 (19.3–28.8)	59.4 ± 17.14 (52.1–65.9)
4. Herjåa	2	1.2 ± 7.19 (0.6–1.7)	1.8 ± 0.90 (1.7–1.8)	7.1 ± 46.72 (3.4–10.8)	89.8 ± 35.94 (86.9–92.6)

did account for a significant portion of the variation in mean lengths of males after the effect of spawning site altitude was accounted for (ANCOVA, $P < 0.05$).

The mean lengths of females increased significantly ($P < 0.05$) with spawning site altitude (Fig. 2d; Table 4), but not with migration distance or water discharge (Fig. 2e and 2f). When computing the linear least-squares multiple regression of mean lengths of females on spawning site altitude and migration distance, the latter did not significantly improve the coefficient of determination of mean lengths of females and spawning site altitude. This indicates that elevation was of major importance in determining the length of female trout.

Analysis of the variability of fish length within the rivers showed that a significant degree of heterogeneity existed within sexes among the different populations ($P < 0.05$). Spawners of both sexes in the two uppermost tributaries of the River Gaula

were significantly larger than those in the two lowermost tributaries (Scheffé procedure on means, $P < 0.05$). Males in the uppermost tributary in the River Namsen were significantly larger than the males of the populations in the three lowermost tributaries ($P < 0.05$), and males in Almåselven (population No. 4) were also significantly larger than males of the lowermost population. No two groups of females were significantly different ($P > 0.05$) in the River Namsen.

Age at Sexual Maturity

Females were generally sexually mature at an older sea age than males, but the difference was significant in only two populations (Table 3). The mean age at sexual maturity of males increased significantly ($P < 0.05$) with migration distance and spawning site altitude (Fig. 3a and 3b; Table 4), but not with water discharge (Fig. 3c). When computing the linear least-

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squares multiple regression of mean age of males on spawning site altitude and migration distance, the latter did not significantly improve the coefficient of determination of mean age of males and spawning site altitude. Interriverine difference was significant for male age at maturity when migration distance was a covariate (ANCOVA, $P < 0.05$).

The mean age at sexual maturity of females increased significantly ($P < 0.05$) with spawning site altitude and migration distance (Fig. 3d and 3e; Table 4), but not with water discharge (Fig. 3f). When computing the linear least-squares multiple regression of mean age of females on spawning site altitude and migration distance, the latter significantly improved the coefficient of determination from $R^2 = 0.648$ to $R^2 = 0.734$. Interriverine difference was significant for female age at maturity with migration distance as covariate (ANCOVA, $P < 0.05$).

The ages at maturity of both sexes (treated separately) among the populations in the River Gaula were significantly different (ANOVA, $P < 0.001$), but those in the River Namsen populations were not ($P > 0.05$). Comparison of means revealed that males and females of the two uppermost populations of the River Gaula matured sexually at a significant older age than those in the two lowermost populations ($P < 0.05$).

Grain Size of Redds

The variation in redd structure was approximately the same within as among tributaries (Table 5). The fraction >20.0 mm made up more than 50% of the gravels in the redds. The largest mean lengths and oldest sea age at maturity of brown trout populations were found in the tributaries with the lowest (Malma) and the highest (Herjåa) values of the largest grain fraction. This indicates that there is no selection for large brown trout to spawn on coarse gravel.

Discussion

For all the nine populations of anadromous brown trout studied, the length of the spawners and their sea age at maturity were significantly correlated with the migration distance and spawning site altitude. ANCOVA revealed that the interriverine differences accounted for only a minor part of the overall variation in these particular life-history traits. Interriverine effects were recorded only in mean length of males with spawning site altitude as the covariate and in sea age at maturity of males and females with migration distance as the covariate. Neither mean water discharge in the tributaries during spawning nor that in the main river (L'Abée-Lund et al. 1989) had any influence on these life-history traits. This contrasts with the observation made by Jonsson (1985) that adult brown trout size was related to the rate of water discharge of the tributary in which the fish spawned. Because the migration distance and spawning site altitudes were identical for all three of Jonsson's (1985) populations, his study provided a more appropriate test for the significance of water discharge alone.

Differences in fish length among populations could be due to differences in size of gravel substrate, as the suitability of a particular size gravel substrate depends mostly on fish size (Reiser and Bjornn 1979). However, analysis of the mean grain size of brown trout redds in four streams into the River Gaula revealed no relationship with mean length of female brown trout. This is in accordance with a more detailed study on the structure of brown trout redds (Ottaway et al. 1981). Thus, the size of gravel substrate for spawning is of minor importance in explaining interpopulation variation in mean brown trout size.

Second, in the present study, the uppermost populations in both rivers have to overcome stretches of rapids before reaching their natal areas to spawn. However, the two lowermost populations in both rivers encounter no rapids during their migration from the sea to their natal tributaries. This implies that the energy requirement during the spawning migration will be greater for the populations spawning further upriver than that for the downriver populations. An increased energy requirement can be compensated for by an increase in body size, since power loading and body size are positively correlated (Bonner 1965). Glebe and Leggett (1981) showed that the energy cost of migration was higher in small American shad than in larger ones. An intraspecific variation in body size of the dark-eyed junco, *Junco hyemalis* (Ketterson and Nolan 1976), and of the red deer, *Cervus elaphus* (Langvatn and Albon 1986), has been found to be positively correlated with the distance of migration. Studies of the energetics of migration of the American shad and of several salmonid species have shown that a large body size provided a greater range of those swimming speeds over which the absolute energy requirement was minimal (Weaver 1963; Leggett and Trump 1978). Thus, energy requirement is probably a factor selecting for larger sized individuals in upriver fish populations. Because fish growth decreases after sexual maturity (Nikolsky 1963), the fish achieves larger length by delaying sexual maturity. This was observed in the present study. In the populations with the largest individuals, these individuals attained sexual maturity at an older age than fish in the smaller sized populations. This suggests that environmental severity might have a considerable influence on certain life-history traits of anadromous brown trout populations. In coregonines, freshwater migration is also an important factor, responsible for the different reproductive patterns exhibited by anadromous species (Lambert and Dodson 1990a, 1990b).

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