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Interpopulation variation in reproductive traits of anadromous female brown trout, *Salmo trutta* L.

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We studied reproductive traits in nine anadromous brown trout, *Salmo trutta* L., populations in seven Norwegian rivers. Within populations we found a positive significant correlation between fish length and fecundity in all populations, and between fish length and egg diameter in five populations. There were significant differences in these relationships between populations from different rivers, and between populations from different locations within rivers. When adjusted for variation in fish length, mean fecundity and mean egg diameter showed a negative significant correlation among populations. The ratio of gonadal weight to somatic weight (gonadosomatic index) varied significantly among populations but was not associated with variation in fish length. Comparatively few large eggs were found in brown trout populations co-existing with several other fish species.

Key words: *Salmo trutta*; local populations; fecundity; egg diameter; gonadosomatic index.

I. INTRODUCTION

Geographical variation in fecundity has been found in several fish species (review Bagenal, 1978). Variation in egg size is usually small even over quite large distances (Bagenal, 1971), but geographical variation in egg size has been shown for e.g. stone loach, *Nemacheilus barbatulus* (L.), (Mills & Eloranta, 1985) and coho salmon, *Oncorhynchus kisutch* (Walbaum), (Fleming & Gross, 1990).

Part of the variation in fecundity and egg size between populations results from interpopulation differences in body size, due to the positive association between fish length and both fecundity and egg size (Bagenal, 1978; Hislop, 1984; Mann *et al.*, 1984). Life-history theory has been used to explain additional interpopulation variation in these reproductive traits. It suggests that egg size is favoured over egg number in habitats with stable environmental conditions, high size-selective predation on small offspring and/or scarcity of food for the young (Stearns, 1976).

In the present study of female reproductive traits in anadromous populations of brown trout, *Salmo trutta* L., we examined to what extent differences in fish length could explain intra- and inter-population variation in fecundity, egg size and reproductive allocation. Additionally, we tested whether certain environmental conditions (fish community, migration distance) could explain variation in these reproductive traits after having adjusted for variation in fish length among populations. Specifically, we hypothesized that species-rich fish communities should lead to few, larger eggs, and that a long migration distance in fresh water should lead to a lower total reproductive allocation (Svärdson, 1949; Stearns, 1976; Leggett & Carscadden, 1978).

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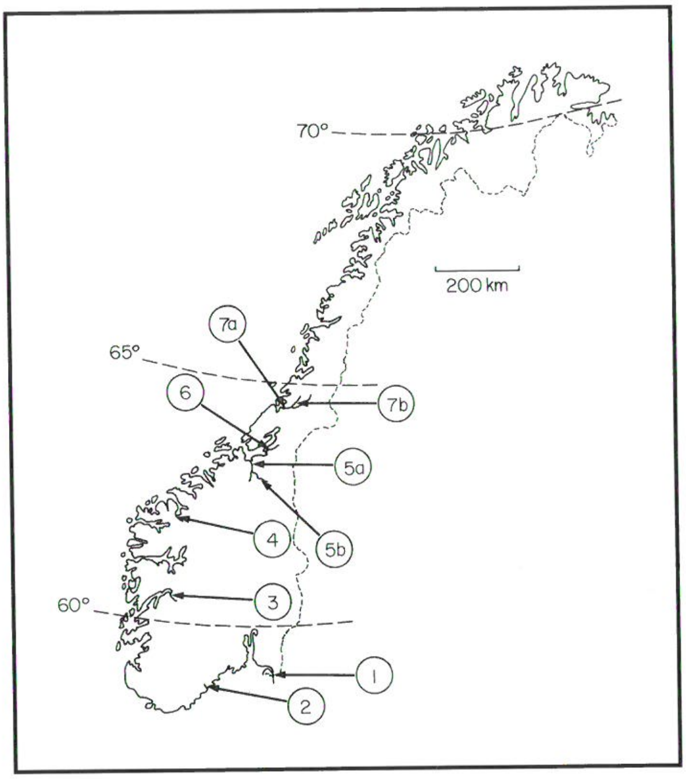

FIG. 1. Locations of the rivers studied. 1, R. Enningdalselva; 2, R. Langangselva; 3, R. Eio; 4, R. Korsbrekkelva; 5a, R. Gaula lower; 5b, R. Gaula upper; 6, R. Fættenelva; 7a, R. Namsen lower; 7b, R. Namsen upper.

II. MATERIALS AND METHODS

Mature anadromous female brown trout ($n=206$) were sampled by electrofishing in the spawning areas in seven Norwegian rivers, 1983–1989 (Fig. 1). The rivers are situated from 58°30′N to 64°28′N, and the spawning areas are situated between 1 to 70 km from the sea.

Anadromous brown trout were usually distinguished from co-existing resident brown trout by their larger body size. In addition, anadromous brown trout were recognized by their scale pattern, showing a contrast between river and sea growth (see e.g. Frost & Brown, 1967; Fahy, 1985). Fish length (0·1 cm), weight (W, g), and degree of sexual maturity (Dahl, 1943) were recorded for each fish. Mean length of the populations studied varied from 36·8 to 52·9 cm and mean age varied from 3·3 to 8·5 years (Table I). Ages were determined from scales (Jonsson, 1985). Individual fecundities were recorded as number of eggs of females in maturity stage 4–6. The mean egg diameter was determined by measuring 10 ripe eggs of females in maturity stage 5 to 6 to the nearest 0·1 mm. There were no significant (ANOVA, $P>0{\cdot}05$) differences in egg diameter between maturity stages within populations. Gonadosomatic index (GSI, %) of females in stage 5 to 6 was estimated as ovarian weight (OW, g) on somatic weight:

$$\text{GSI} = 100{*}OW/(W - OW) \qquad (1)$$

In all instances we $\log_{10}$-transformed fish length and fecundity, but not egg diameter before analysis. Tests for significant differences within and between populations were carried out by using the analysis of covariance (ANCOVA) with length as a co-variate in the BMDP package (Dixon, 1983). The model assesses the variation in slope and the variation

TABLE I. Lengths, ages (arithmetic means ± 95% confidence limits and ranges) and sampling period of mature anadromous female brown trout from seven Norwegian rivers

Map code	River	No. of fish	Length (cm)		Age (yr)		Period
			Mean	Range	Mean	Range	
1	Enningdalselva	22	40·3±4·10	25–63	3·3±0·42	2–6	1983–86
2	Langangselva	19	36·8±2·98	25–51	3·4±0·33	2–4	1984
3	Eio	18	42·4±4·48	29–59	5·6±0·66	3–9	1982–89
4	Korsbrekkelva	16	50·6±6·16	33–77	6·4±0·78	5–10	1986
5a	Gaula lower	29	43·7±2·54	31–59	5·4±0·56	3–10	1986–88
5b	Gaula upper	28	52·9±2·50	40–63	8·5±0·90	5–14	1988–89
6	Fættenelva	14	42·1±3·15	34–53	4·7±0·73	3–7	1986–89
7a	Namsen lower	23	39·9±2·37	32–49	5·8±0·38	4–7	1989
7b	Namsen upper	37	41·5±1·96	24–57	6·6±0·44	4–10	1986–89

TABLE II. Fecundity ($\log_{10}$-transformed) by fish length (cm, $\log_{10}$-transformed) of anadromous female brown trout from seven Norwegian rivers

Map code	River	No. of fish	Linear regression		Correlation coefficient
			Slope	Intercept	
1	Enningdalselva	21	2·565	−0·933	0·97***
2	Langangselva	18	2·220	−0·520	0·89***
3	Eio	11	2·396	−0·710	0·94***
4	Korsbrekkelva	16	2·265	−0·435	0·97***
5a	Gaula lower	21	2·518	−0·853	0·89***
5b	Gaula upper	14	2·010	0·004	0·84***
6	Fættenelva	9	2·340	−0·518	0·86**
7a	Namsen lower	8	2·673	−1·143	0·92**
7b	Namsen upper	17	2·764	−1·492	0·99***

**$P<0·01$; ***$P<0·001$.

in elevation, calculated as adjusted means. We used Gabriel's approximate test (Sokal & Rohlf, 1981) to visualize the differences in adjusted means between populations that did not differ in slope.

From the 206 females collected, data were obtained on fecundity and fish length from 135, egg diameter and fish length from 184, and gonadosomatic index (GSI) and fish length from 110.

III. RESULTS

FECUNDITY

Fecundity increased significantly ($P<0·05$) with fish length within all populations (Table II). There were no differences among populations in the slope of the

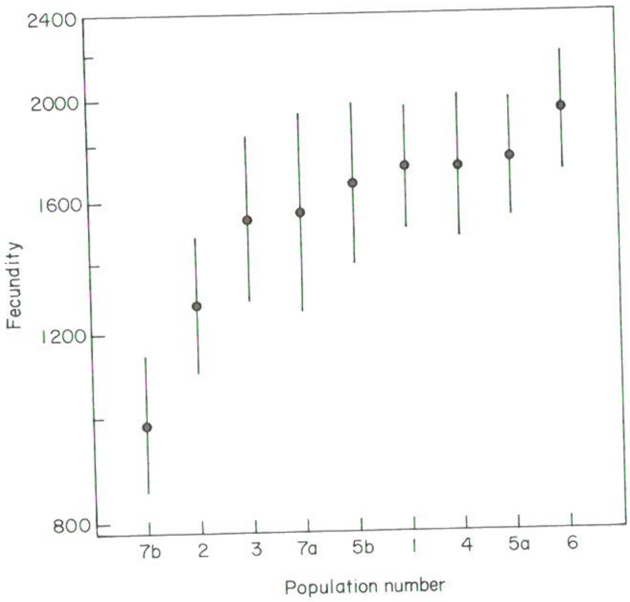

FIG. 2. Adjusted mean fecundity with 95% 'comparison limits' (log scale). Populations with non-overlapping 'comparison limits' are significantly different ($P<0·05$). The population numbers are: 1, R. Enningdalselva; 2, R. Langangselva; 3, R. Eio; 4, R. Korsbrekkelva; 5a, R. Gaula lower; 5b, R. Gaula upper; 6, R. Fættenelva; 7a, R. Namsen lower; 7b, R. Namsen upper.

relationship between fecundity and fish length (ANCOVA, $P>0·05$). On the other hand, the populations differed significantly ($F_{8,124}=16·97$, $P<0·001$) in adjusted mean fecundity (Fig. 2). The population in the upper R. Namsen (7b) had a significantly lower adjusted mean fecundity than all other populations except the R. Langangen (2) population. The latter population had significantly lower adjusted mean fecundity than population no. 1, 5a, and 6. The highest adjusted mean fecundity was found in the R. Fættenelva (6) population, but it only differed significantly ($P>0·05$) from the R. Langangen (2) and the upper R. Namsen (7b) populations.

A considerable difference in adjusted mean fecundity was found between the two populations studied in the R. Namsen (7), but not in the R. Gaula (5). In both rivers adjusted mean fecundity was lower in the upper populations (5b, 7b) than in the lower populations (5a, 7a). The intrariverine difference was, however, only significant in the R. Namsen (7).

It was possible on the basis of scale characters and growth to distinguish between first-time and repeat spawners. We did not find any significant effect of spawning history on fecundity after having accounted for the effects of length and locality (ANCOVA, $P>0·05$).

EGG SIZE

Egg diameter increased with fish length in all populations, and significantly so ($P<0·05$) for five of eight populations studied (Table III). The data are not sufficient to compare regressions of egg size on fish length of fish of comparable ages. However, the partial correlation coefficients of age and fish length in multiple

TABLE III. Egg diameter (mm) by fish length (cm, $\log_{10}$-transformed) of anadromous female brown trout from six Norwegian rivers

Map code	River	No. of fish	Linear regression		Correlation coefficient
			Slope	Intercept	
1	Enningdalselva	17	3·165	0·018	0·76**
2	Langangselva	19	1·790	2·642	0·44ns
3	Eio	17	2·170	1·924	0·74**
5a	Gaula lower	29	4·037	−1·251	0·74**
5b	Gaula upper	28	1·368	3·243	0·33ns
6	Fættenelva	14	3·498	−0·743	0·68*
7a	Namsen lower	23	2·120	1·822	0·41ns
7b	Namsen upper	37	2·804	1·041	0·59**

ns, $P>0·05$; $^*P<0·05$; $^{**}P<0·01$.

regression analysis revealed that age was not significantly ($P>0·05$) correlated with egg size. Age explained less than 9% in addition to fish length (11–58%) of the intrapopulation variation in egg size.

There were no differences among the populations in the slope of the relationship between egg diameter and fish length (ANCOVA, $P>0·05$), but the adjusted mean egg diameter differed significantly ($F_{7,174}=15·04$, $P<0·001$) among populations (Fig. 3). The highest (5·61 mm) and lowest (4·94 mm) adjusted mean egg diameter were found in the R. Langangen (2) and the R. Fættenelva (6), respectively. As for fecundity, we found no significant difference in egg diameter between first-time and repeat spawners after having accounted for the effects of length and locality (ANCOVA, $P>0·05$).

A significant difference in adjusted mean egg diameter was found between the two populations studied in the R. Namsen (7), where the adjusted mean egg diameter was larger in the upper population (7b) than in the lower population (7a). In the R. Gaula (5) the upper and lower populations had quite similar adjusted mean egg diameter.

Among populations, adjusted mean egg diameter and adjusted mean fecundity showed a negative significant correlation (Kendall's rank correlation coefficient $\tau=-0·71$, $n=8$, $P<0·05$).

GONADOSOMATIC INDEX (GSI)

The GSI [equation (1)] did not vary significantly ($P>0·05$) with fish length within populations. The GSI, however, varied significantly ($F_{7,102}=5·88$, $P<0·001$) among populations (Table IV). The significant variation was due to the low GSI in the R. Langangselva (2) and in the upper R. Namsen (7b), because when these populations were omitted from the analysis there was no significant variation among the remaining populations (ANOVA, $P>0·05$).

ENVIRONMENTAL VARIABLES AND REPRODUCTIVE TRAITS

The highest number of fish species (five including brown trout) was found in the R. Langangen (2) and the R. Namsen (7). These populations had few, large eggs

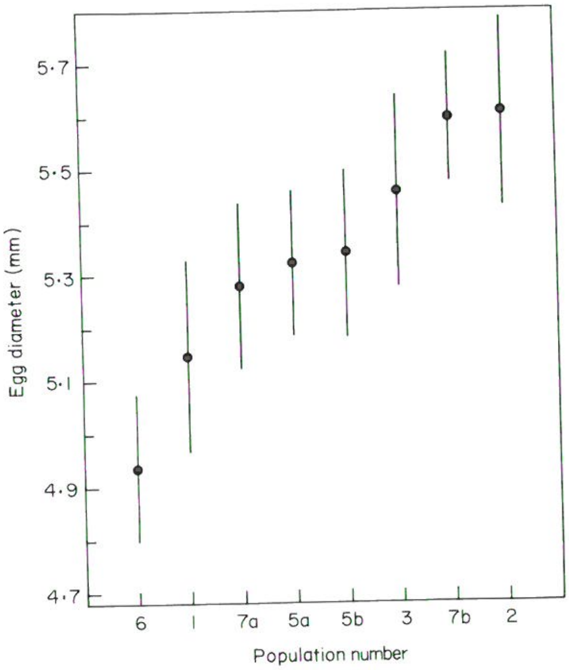

FIG. 3. Adjusted mean egg diameter (mm) with 95% 'comparison limits'. Populations with non-overlapping 'comparison limits' are significantly different ($P<0{\cdot}05$). The population numbers are: 1, R. Enningdalselva; 2, R. Langangselva; 3, R. Eio; 5a, R. Gaula lower; 5b, R. Gaula upper; 6, R. Fættenelva; 7a, R. Namsen lower; 7b, R. Namsen upper.

TABLE IV. Gonadosomatic index (mean ± 95% confidence limits and range) of anadromous female brown trout in six Norwegian rivers

Map code	River	No. of fish	Mean	Range
1	Enningdalselva	14	20·0±2·17	11·4–27·4
2	Langangselva	18	18·5±1·74	8·7–23·4
3	Eio	9	24·6±2·33	20·2–28·4
5a	Gaula lower	21	21·1±2·54	13·2–30·9
5b	Gaula upper	14	25·6±2·66	17·3–36·8
6	Fættenelva	9	20·0±3·05	15·9–26·6
7a	Namsen lower	8	20·5±3·20	14·3–27·4
7b	Namsen upper	17	17·6±2·03	8·6–25·5

compared with the remaining populations. The association between egg size and number of fish species was significant among the populations studied (Kendall's $\tau=0{\cdot}59$, $n=8$, $P<0{\cdot}05$).

TABLE V. Ranking of population specific reproductive traits [adjusted mean fecundity (Fec), adjusted mean egg diameter (Dia), and mean GSI], number of co-existing species (Sp), and distance migrated by spawners in fresh water (Md)

Map code	River	Rank				
		Fec	Dia	GSI	Sp	Md
1	Enningdalselva	4	7	5	3	9
2	Langangselva	8	1	7	1	4
3	Eio	7	3	2	3	6
4	Korsbrekkelva	3			6	8
5a	Gaula lower	2	5	3	6	3
5b	Gaula upper	5	4	1	6	2
6	Fættenelva	1	8	5	9	7
7a	Namsen lower	6	6	4	3	5
7b	Namsen upper	9	2	8	1	1

The upper R. Namsen (7b) population had the longest migration distance in fresh water and the lowest GSI compared with the other populations, but we did not find a significant association between GSI and migration distance in the total material ($P>0{\cdot}05$).

In summary, the results showed a relationship between fish length and the number and size of eggs produced, and demonstrated significant variation in these relationships between populations from different rivers, and between two populations from the same river. At one extreme in this study was the R. Fættenelva (6) population which had relatively many, small eggs (Table V). At the other extreme were the populations from the R. Langangen (2) and the upper R. Namsen (7b), which had relatively few, large eggs. The latter two populations also had the lowest mean GSI values recorded in this study. The highest mean GSI was found among populations having intermediate egg diameters and fecundities, e.g. the populations from the R. Eio (3) and the upper R. Gaula (5b). Moreover, populations inhabiting areas with many co-existing fish species had larger eggs than populations co-existing with few species (Table V).

IV. DISCUSSION

The individual trade-off between few, large eggs and many, small eggs has consequences for fitness in fish species. Variation in fecundity and egg size among populations may be directly caused by variation in feeding conditions (Scott, 1962; Wydoski & Cooper, 1966; Bagenal, 1969; Nikolskii, 1969; Thorpe *et al.*, 1984) and indirectly by variation in selective pressures among different environments (Stearns, 1977; Fleming & Gross, 1990).

Our results demonstrated significant relationships between fish length and the number and size of eggs produced; length explained 71–98% of the intrapopulation variation in fecundity, and 11–58% of the intrapopulation variation in egg diameter. Including age in a multiple regression model of egg diameter did not significantly increase the coefficient of determination. This suggests that much of the variation in egg size within populations must be attributed to other factors than length, age or maturity stage of the female. However, the fish length in brown trout explained as much of the variation in egg size within populations as does length in Atlantic salmon, *S. salar* L., (53%; Thorpe *et al.*, 1984) and coho salmon (3–78%; Fleming & Gross, 1990).

Our results also showed significant variation in the number and size of eggs produced, and in reproductive allocation between populations from different rivers, and between two populations from the same river. The variation in reproductive traits was mainly due to the extreme values of three populations; the R. Langangen (2), the R. Fættenelva (6) and the upper R. Namsen (7b). No single factor could explain the position of these populations.

Our results suggest that differences in composition of the fish community may account for some of the observed interpopulation variation in fecundity and egg diameter. The populations studied experienced different fish communities, partly due to habitat variation. Rivers with lakes as nursery areas for anadromous brown trout support more fish species than rivers without lakes. Therefore, predation risk and competition for food should be more pronounced in rivers with lakes than in other rivers. Natural selection favours larger eggs in such environments, as larger fry emerge from larger eggs and larger fry have better survival chances towards food competitors and predators (Brown, 1946; Stearns, 1976).

In the present study the populations with few, large eggs were found in relatively species-rich habitats. We cannot say whether there is a straightforward relationship between egg size and the number of co-existing species, as both predation and competition for food change with the species co-existing with brown trout. Other salmonids co-existing with anadromous brown trout in Norway (Atlantic salmon in population nos. 1, 3, 4, 5 and 7; Arctic charr, *Salvelinus alpinus* (L.), in population no. 7b) are food competitors (Kalleberg, 1958; Nilsson, 1963), whereas perch, *Perca fluviatilis* L., and pike, *Esox lucius* L., in population no. 2 are also predators (Vøllestad *et al.*, 1986).

We did not find significant correlations between reproductive traits and either latitude (between 59° and 64° N) or migration distance in fresh water (between 1 and 70 km). Such correlations have been reported for stone loach (Mills & Eloranta, 1985), American shad, *Alosa sapidissima* (Wilson), (Leggett & Carscadden, 1978), and coho salmon (Fleming & Gross, 1989, 1990), and may also be present in anadromous brown trout. However, with a limited number of populations studied, we did not expect to detect other than strong associations between reproductive traits and environmental variables. The relatively small variation in egg size is in agreement with Bagenal's (1971) contention that egg size varies little over quite large distances.

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