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The food of Atlantic salmon *Salmo salar* L. and brown trout *Salmo trutta* L. smolts during migration in the Orkla river, Norway

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Stomach analyses were carried out on 286 Atlantic salmon smolts and 163 brown trout smolts during migration in the river Orkla, Central Norway (63°N, 10°E), from 1982 to 1984. Empty stomachs comprised less than 18,4% for salmon and 25,4% for trout. The food composition of both species varied little from year to year. The dominant food items of Atlantic salmon smolts were Trichoptera larvae and nymphs of Plecoptera and Ephemeroptera, each comprising from 17,7 to 31,2% of the stomach volume. These three insect orders were also the main food of brown trout smolts in addition to Diptera pupae, varying from 17,4% to 32,3% in volume for each food item.

The volume of Trichoptera larvae in the smolt stomachs decreased during the migration, while the importance of Ephemeroptera and Plecoptera nymphs as food for the smolts increased. There was a significant overlap in diet between salmon and brown trout smolts both in the different years and during the migration period in 1984.

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INTRODUCTION

Several authors have studied the food composition of Atlantic salmon and brown trout parr (Allen 1940, Frost 1950, Mc Cormack 1962, Thomas 1962, Maitland 1965, Egglishaw 1967, Lillehammer 1973). The general trend is that both species feed mainly on drifting larvae and nymphs of larger benthic insects and on terrestrial insects. Despite well documented literature on the food of juvenile salmon and trout, less information exists on the feeding relationships of the two species during smolt migration (Baglinière 1980). This may be attributable to the fact that sampling of smolts during their descent in spring is difficult, especially in large rivers with high water discharge (Mitans 1970).

The downstream movement of smolts is mainly a passive displacement (Tytler et al. 1978, Thorpe et al. 1981) and smolts usually follow the main current in the river (Hesthagen and Garnås in press). The start of the run may either be connected with water temperature (Elson 1962, Mills 1964, Jessop 1975, Solomon 1978) or with water discharge (Baglinière 1976, Hesthagen and Garnås in press) when the smolts have become physiologically fitted for life in the sea. One would not expect the smolts to feed heavily during the descending period, because the passive displacement of smolts in fast turbid water currents would make feeding difficult. This paper gives further information on the feeding relationships of Atlantic salmon and brown trout smolts during downstream migration.

MATERIAL AND METHODS

The Orkla river is situated in Central Norway (63°N, 10°E) and is about 170 km long. The river is about 60 m wide, with an average discharge before the regulation in 1983 of about 30 m^3/sec. Spring runoff may however exceed 300 m^3/sec. Atlantic salmon and migrating brown trout travel some 92 km up the river to spawn.

The sampling of smolts was carried out during a three year period from 1982 to 1984 from April 20th to June 15th. The smolts were captured using a trap consisting of a 1 x 1 m steel frame with a net pouch of mesh size 10 mm. The trap was lowered into the river with wire and winch at Meldal bridge situated some 40 km from the sea (Hesthagen and Garnås, in press). The major part of the smolts in the Orkla river migrate in the darkest period of the night (Hest-

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hagen and Garnås, in press). Thus the traps were operated in a six hours period between 2100 and 0300 and emptied every third hour.

The smolts were measured to the nearest mm, and their age was determined from the otoliths. The stomachs were preserved in 70% ethanol. In 1982 and 1983 stomach analyses were carried out on smolts caught at random during the migration period. In 1984 the smolts were sampled in four periods to see if there were any differences in food composition during the smolt run.

The amount of food in the stomach was classified according to a six point scale of 0%, 20%, 40%, ... and 100% of stomach fullness. The food items in each stomach were identified to different taxonomic levels. To express the relative importance of each food category, frequency of occurrence and percent contribution of the total stomach volume were used (c.f. Hynes 1950).

In order to ascertain the degree, if any, of overlap in food between Atlantic salmon and brown trout smolts, Schoener's index of diet overlap (Schoener 1970) was calculated according to the formula

$$a = 1 - 0.5 \left(\sum_{i=1}^{n} |p_{xi} - p_{yi}| \right)$$

where p_{xi} and p_{yi} are the volume of food category i of species x and y respectively, and n is the number of food categories. The index ranges between 0 and + 1. There is a significant degree of overlap in diet when the index exceeds 0,6 (Wallace 1981).

RESULTS

The diet of Atlantic salmon and brown trout smolts in the Orkla river during migrations from 1982 to 1984 is listed in Table 1. The mean amount of food in the stomachs varied from 38% to 68% of the stomach fullness and empty stomachs comprised less than 18.4% for salmon and 25.4% for trout (Table 2). The amount of food increased and the number of empty stomachs decreased during the smolt run.

The dominant food items of Atlantic salmon smolts were Trichoptera larvae, and nymphs of Plecoptera and Ephemeroptera. These three food categories made up from 17.7% to 31.2% each of the stomach volume, with frequencies from 25.9% to 57.7%. With the exception of Diptera pupae in 1982, other food items made up less than 10 percent volume.

The stomach contents of brown trout smolts consisted mainly of Trichoptera larvae in spring 1982. Plecoptera nymphs and Diptera pupae varied from 17.4% to 32.3% in volume and 18.5% to 25.9% in frequency. In 1983 and 1984 the Diptera pupae were replaced by Ephemeroptera nymphs, revealing a brown trout diet similar to that of Atlantic salmon. The volume of Trichoptera larvae and nymphs of Plecoptera and Ephemeroptera comprised from 14.7% to 22.8%, and the frequencies varied between 31.4% and 61.5%. Fish remains were observed in the stomachs of both species.

Figure 1 shows seasonal variation in diet during the migration in spring 1984. Among Atlantic salmon smolts the volume of Trichoptera and Chironomidae larvae decreased during the

Table 1. Stomach contents of Atlantic salmon and brown trout smolts during migration in the Orkla river in spring 1982 to 1984. F = Frequency, V = Volume (%).

	ATLANTIC SALMON						BROWN TROUT					
	1982		1983		1984		1982		1983		1984	
Food item	F	V	F	V	F	V	F	V	F	V	F	V
Trichoptera larvae	53.3	25.9	44.2	20.4	40.2	18.2	25.4	24.7	61.5	21.5	43.7	24.1
Ephemeroptera nymphs	51.7	17.7	57.7	24.5	54.9	21.8	18.5	5.5	61.5	14.7	31.4	15.9
Plecoptera nymphs	40.0	20.2	48.1	23.3	46.5	31.2	22.2	17.4	61.5	20.6	54.3	22.8
Chironomidae larvae	20.0	3.6	23.1	4.3	30.5	9.3	7.0	0.4	38.5	2.3	17.1	1.9
Chironomidae pupae	1.7	0.1	3.8	0.2	4.8	0.6	3.7	0.2			2.5	1.2
Diptera pupae	25.0	14.7	5.7	0.8	10.3	2.8	37.0	32.3	30.8	13.1	12.1	6.0
Megaloptera larvae			3.8	2.3	4.9	1.5			7.7	2.7	4.3	1.1
Dytiscidae larvae			5.8	2.2	3.3	1.2					4.0	1.8
Lamellibranchiata					0.5	0.1			7.7	4.6	3.2	0.6
Lumbricidae			1.9	1.5	3.4	1.9					11.8	8.4
Pisces			1.9	1.4	1.3	0.6					1.3	0.5
Terrestrial insects	1.7	0.1	9.6	0.8	3.6	0.7	11.1	13.8	30.8	3.9	7.9	3.0
Unidentified	40.0	17.7	46.2	18.3	32.9	10.1	14.8	5.7	53.8	16.6	34.5	12.7

Table 2. Smolt age, mean length, stomach fullness and Schoener's index of diet overlap (a) of Atlantic salmon and brown trout smolts captured during migration in the Orkla river from 1982 to 1984. N = Number of smolts, S = Atlantic salmon, T = Brown trout, L = length (mm), Sd = standard deviation (mm), Sf = stomach fullness, Est = empty stomachs.

Year		N	Smolt age (year)	L	Sd	Sf (%)	Est %	a
1982	S	60	3.1	126	12	56	13.3	0.70*
	T	27	2.6	128	17	40	25.1	
1983	S	52	3.0	123	11	—	0	0.81*
	T	13	2.8	134	24	—	0	
1984	S	174	3.1	120	9	54	12.1	0.79*
	T	123	2.8	140	26	58	10.6	
1984:								
April 26—May 5	S	49	3.1	121	12	42	18.4	0.64*
	T	31	2.7	133	22	38	22.6	
May 6—May 11	S	35	3.1	121	10	50	17.1	0.77*
	T	18	2.7	127	23	68	5.6	
May 14—May 22	S	50	3.1	120	7	66	6.0	0.65*
	T	40	3.1	147	30	62	7.5	
May 25—May 31	S	40	3.1	120	15	60	7.5	0.77*
	T	34	3.0	148	26	62	8.8	

* = $p < 0.05$

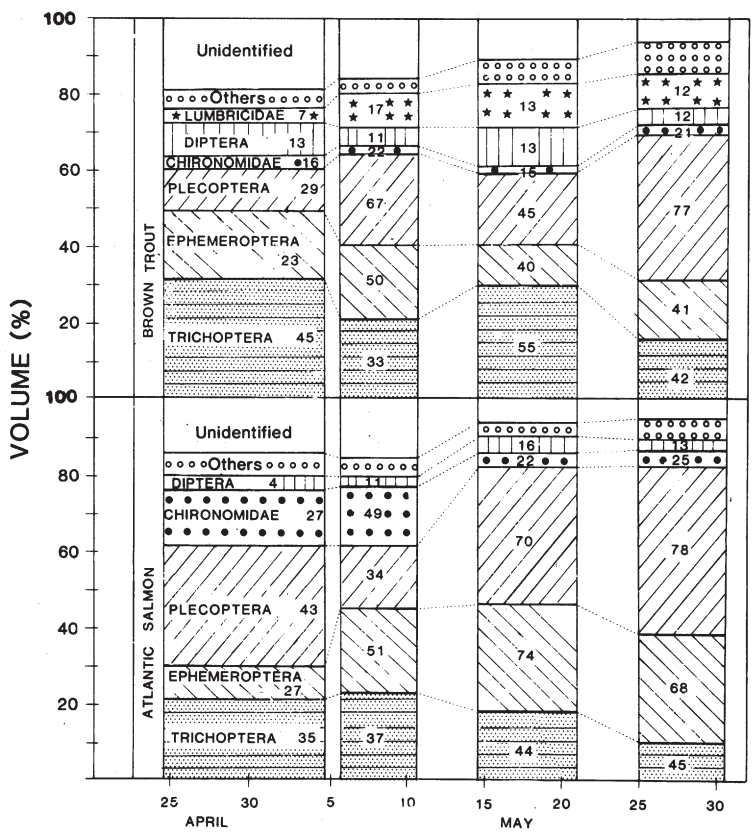

Fig. 1. The food of Atlantic salmon and brown trout smolts during the migration period in spring 1984 in the Orkla river. The number in each column represents the frequency of each food category.

season from 20.9% and 15.1%, to 10.8% and 3.2% respectively.

Plecoptera and Ephemeroptera nymphs simultaneously increased in volume from 32.7% and 8.1% at the end of April to 43.8% and 27.4% at the end of May. The frequencies for these two food categories were as high as 68% and 78% at the end of the migration period.

The volume of Trichoptera larvae was also reduced in the stomachs of brown trout smolts during their descent period, from 31.1% to 15.2%. Ephemeroptera nymphs made up from 11.7 to 18.7% of the volume during the migration, while Plecoptera nymphs increased from 10.4% at the start of the season to 37% at the end of May. At this time the frequency of Plecoptera was as high as 77%.

There was a significant overlap in diet between salmon and brown trout smolts both in the different years ($a > 0.70$, $p < 0.05$), and during the migration period in 1984 ($a > 0{,}64$, $p < 0.05$) (Table 2).

DISCUSSION

Smolts of both Atlantic salmon and brown trout in the Orkla river fed actively during migration. Empty stomachs comprised less than twenty five percent of the sample, and the stomach contents usually made up more than fifty percent of stomach volume. The diet was mainly dominated by Trichoptera larvae, Ephemeroptera nymphs and Plecoptera nymphs. These insect groups are, in addition to Chironomidae larvae, also the main food categories of Atlantic salmon and brown trout parr (Allen 1940, Frost 1950, Mills 1964, Egglishaw 1967).

Active feeding during the smolt run has also been reported elsewhere (Mills 1964, Södergren and Österdahl 1966, Mitans 1970, Bakshtansky et al. 1976, Baglinière 1980). The common prey items in these studies were mostly the same as those found in the Orkla river, with varying dominance of Trichoptera larvae, Plecoptera and Ephemeroptera nymphs. Baglinière (1980) suggests that the differences between rivers in the diet of smolts, merely are a result of differential timing of the spring migration. The differences in the diet of smolts are therefore due to the fact that the smolts feed on whatever is available in the river at the time of migration. Active feeding has also been documented for Pacific salmon smolts with diets similar to that found in the Orkla (Churikov 1975, Lofthus and Lenon 1977).

Parr of Salmonids in running water usually feed on organisms suspended in the water column. This drift feeding is far more common than bottom feeding (Hynes 1970, Bachman 1984). However, during migration, smolts probably engage in a more benthic oriented feeding behaviour. Heavy smolt predation on *Gammarus pulex* found by Mitans (1970), and observations of snails in smolt stomachs by Södergren and Österdahl (1966) are both indications of benthic feeding, as neither of these food categories usually occurs in drift. In the Orkla river smolts descend during the night and at high water discharges during the spring runoff (Hesthagen and Garnås in press). It is reasonable to assume that during the day smolts stay near the bottom where they feed on benthic fauna. Drift feeding at this time is difficult because of fast water currents (2—3 m/sec.). This is supported by the fact that chironomid larvae were of little importance during the most intense smolt run in May. Chironomid larvae are frequent in the drift column (Tippets and Moyle 1978) and are important as food for both Atlantic salmon and brown trout parr (Egglishaw 1967). Kalleberg (1958) showed experimentally that smolts during migration stopped in order to feed. Mitans (1970) found a drop in feeding activity at night, because migration prevented intense feeding. However, feeding started up again when the smolts rested in pools during the day.

The significant overlap in diet between Atlantic salmon and brown trout smolts in the Orkla river, indicates that the two species have a similar diet during the smolt run. The food relationship between Atlantic salmon and brown trout smolts seems therefore to be similar to that found for salmon and trout parr (Frost 1950, Kalleberg 1958, Maitland 1965, Egglishaw 1967, Pedley and Jones 1978). The two species have been considered as competing for food (Frost 1950, Thomas 1962, Mills 1964); however competition between two species exists only when food resources are limited. We have no information on available food resources for migrating smolts in the Orkla. It is therefore not possible to evaluate the existance or significance of competition between the two species during the migration period. However it is most likely that the diets of both Atlantic salmon and brown trout smolts are simply an expression of which food items are available in the microhabitats where the smolts rest in order to feed during migration.

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