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Relationships between juvenile salmon, *Salmo salar* L., and invertebrate densities in the River Tana, Norway

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Abstract – Juvenile salmon density was related to invertebrate density in 13 streams within the River Tana, northern Norway. There were only small, nonsignificant, differences in benthic density between streams with and without juvenile salmon. All streams with a high density of juvenile salmon had low benthic densities at the stream mouth. Juvenile salmon were not found, or were in very low densities, in streams where the benthic density at the stream mouth was as high or higher than that in the stream. A multiple regression model showed that parr density was related negatively to benthic density at the stream mouth, water velocity and pH, and positively to benthic density within the stream and the proportion of the substratum covered by moss. The amount of overhanging cover in the different streams explained 93% of the variation in the drift density of terrestrial invertebrates in August. The highest densities of juvenile salmon were found in streams with riparian vegetation, and were thus associated with an abundant supply of drift food, especially terrestrial invertebrates.

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

The freshwater residential phase of the life cycle of Atlantic salmon (*Salmo salar* L.) is the feeding and growth stage prior to the parr becoming smolts and migrating to the sea. Foraging theory predicts that individuals should maximise their net energy gains by foraging in patches with high densities of preferred prey (Stephens & Krebs 1996). Efficient exploitation of available food resources is thus necessary.

Juvenile salmon migrate into many small-sized tributaries in the Tana river system in the summer (Erkinaro 1997; Johansen et al. 2005). Such migrating fish generally show enhanced growth compared with their counterparts in the larger tributaries and main river (Erkinaro & Niemelä 1995). However, the degree to which different streams are utilised by juvenile salmon differs greatly. In a comparative study of juvenile salmon density in 20 streams throughout the

Tana, Johansen et al. (2005) found that 0+ salmon parr were absent from seven streams, present at the mouth of 11 streams, and present within only two streams, both of which were probably spawning streams. In contrast, older parr migrated upstream into most streams and their highest densities were usually found in streams flowing directly into the spawning habitat in the three largest tributaries of the Tana or the river itself. Juvenile salmon were sparse or absent in streams flowing into the smallest tributaries.

These differences in salmon density were related to environmental variables. Twelve environmental variables were measured: stream width and depth, water velocity, four categories of substratum size, moss cover, instream cover, overhanging cover, pH and conductivity. As some of these variables were correlated, principal component analysis was used to identify the major variables and was followed by multiple regression, using a ridge regression analysis

to remedy the potential problems caused by colinearity. A more detailed account of these methods is given in Johansen et al. (2005). Four variables (stream width, overhanging cover, water velocity, pH) were significant enough to be included in a multiple regression model that explained 65% of the variation in salmon parr density across 80 sites in the 20 streams. Parr density was related positively to stream width and the amount of overhanging cover, and negatively to water velocity and pH. Therefore, 35% of the variation in parr density was due to other factors. The fish community in all streams consisted almost exclusively of salmon and brown trout, *Salmo trutta* L., with negligible numbers of other species (Johansen et al. 2005). It was possible that trout density could have affected salmon density, but no significant relationships could be found. It was therefore concluded that trout density was not responsible for even part of the remaining 35% of the variation in salmon density. One important factor not included in these earlier analyses was the density of invertebrates that provided potential food for the juvenile salmon. Therefore, the main objective of the present study was to relate the differences in the density of juvenile salmon to the density of invertebrates providing their food.

There are two different feeding regimes available for stream-dwelling fish: invertebrate benthos and drift (invertebrates drifting downstream on the water surface and in the water column). Fish can be chiefly benthic feeders, or benthic and drift feeders that take prey on the bottom, in the water column and at the water surface (Waters 1972). Juvenile salmon are opportunistic feeders, with some studies reporting that drift feeding is the predominant method of food acquisition (Wankowski & Thorpe 1979), whilst others note that benthic feeding is also frequently used (Keenleyside & Yamamoto 1962; Vignes 1999). Salmon parr feed relatively more from the benthos than brown trout (*Salmo trutta* L.) (Thomas 1962), and it has been proposed that juvenile brown trout are more capable of maintaining position in the water current than juvenile salmon (Shurov & Shustov 1989). Brown trout are also more aggressive than salmon (Heggenes et al. 1995, 1999).

The riparian zone is an important part of the stream landscape, affecting both the stability and productivity of a stream. Streamside forests affect food quality and quantity for macroinvertebrates directly through inputs of particulate food (leaf litter, soils, wood, etc.) and indirectly by affecting the structure and productivity of the microbial (algae, bacteria) food web through shading and modifying the levels of dissolved organic carbon and nutrients (Hynes 1975; Décamps 1996). Presence of overhanging riparian vegetation is also important for the amount of terrestrial invertebrates

falling into the stream (Wipfli 1997; Kawaguchi & Nakano 2001; Allan et al. 2003). The present study therefore examines the relationships between salmon density and invertebrate density in the benthos and drift, and evaluates the effects of riparian vegetation.

Methods

Study area

The present study was carried out in the large subarctic river Tana (Teno in Finnish) on the border between Norway and Finland (Fig. 1). Catchment area is 16 386 km^2. The Tana supports the largest fishery of Atlantic salmon in Europe, with mean annual catches of 200 metric tonnes in the river and 200 metric tonnes in the sea outside the river outlet (Moen 1991). In addition to the main river, there are over 30 tributaries with distinct spawning stocks of salmon (Moen 1991). At least 100 first, second and third order tributaries are known in which adult salmon do not spawn but juveniles enter from the main stems (Erkinaro 1997).

Samples were taken in 13 second, third and fourth order streams flowing either into the main Tana river or into major tributaries of the Tana. Four different categories of riparian vegetation are found in the Tana catchment: (A) willow (*Salix* spp.), (B) birch (*Betula pubescens* Ehrhart), (C) a mixture of birch and pine (*Pinus sylvestris* L.) and (D) nonforested alpine. The streams chosen for sampling were three in category A, five in B, three in C and two in D so that they were distributed in two groups, one in a downstream section up to about 100 m from the river mouth and the other in an upstream section about 200 m from the mouth (Fig. 1, Table 1). The sampling design was the same as that used in the previous study (Johansen et al. 2005). There were four sampling sites in each stream, one at the stream mouth where it joined the main river, and three within the stream, so that there was a total of 52 sampling sites. The sample at the stream mouth enabled comparisons to be made between densities of both fish and benthos within the stream and immediately outside the stream at its mouth. The distances between the three sites within the stream increased with the length of the stream and are provided in the previous study. The sites were sampled for fish and benthos in August and October 2000, 2001 and 2002. Johansen et al. (2005) describe the environmental characteristics of the streams in detail.

Sampling

The fish samples were the same as those used in the previous study (Johansen et al. 2005). Juvenile fish were caught by electrofishing using a pulsed DC
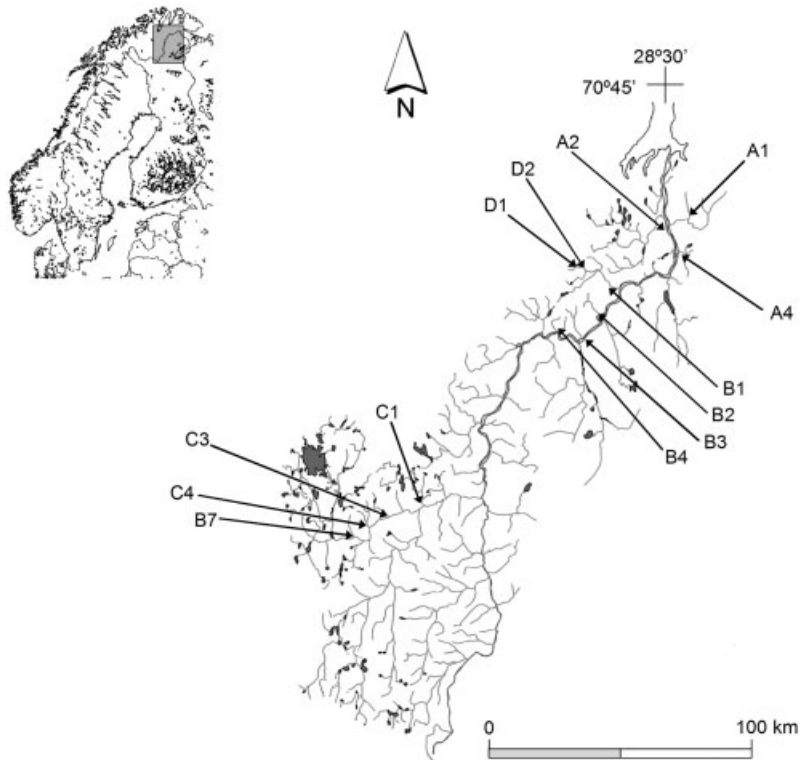
Fig. 1. Locations of the 13 streams sampled in the subarctic Tana river system; riparian vegetation was willow (streams A1, A2 and A4), birch (streams B1-B4 and B7), mixed birch and pine (streams C1, C3 and C4), and nonforested alpine (D1-D2).

Table 1. General characteristics of the 13 streams sampled.

	Name	Order	Length (km)	Gradient (m km^{-1})	Altitude of mouth (m)
A1	Govdagåljohka*	3	9.7	24.7	30
A2	Nuorttit Mohkkeveajjohka*	3	6.0	28.7	10
A4	Ruossajohka	3	12.0	15.0	15
B1	Marssajohka	2	5.7	23.7	105
B2	Galbajohka	4	15.0	17.5	60
B3	Levsejohka*	3	13.0	17.6	70
B4	Vuolit Vidis*	3	9.8	21.7	80
B7	Cærrugæsjohka	3	8.4	12.6	270
C1	Geaimmejohka*	4	18.4	10.4	135
C3	Ravdojohka*	3	7.0	25.3	195
C4	Jerguljohka	3	13.0	15.5	230
D1	Cagnajohka*	3	5.5	10.0	260
D2	Bihtusjohka*	3	12.4	6.8	245

Codes A1 to D2 correspond to those in Fig. 1.
*Streams that were drift sampled.

backpacker apparatus (current output 150–900 V; Geomega AS, Trondheim, Norway). The anode was a wand-mounted ring; the copper wire cathode lay on the stream bottom. A low voltage was used (300 V), thus reducing the effects of positive galvanotaxis (Heggenes et al. 1990). The sampling sites were fished once in an upstream direction, each site being combed carefully with 2-m anode strokes in a downstream direction after which 0.5 m sideways steps were taken. The sampling effort was thus standardised so that it was similar at each site. The sampling area at each site

was usually 100 m^2, but in a few cases a slightly larger area of 120 or 140 or 160 m^2 (only once) was used (Table 2). All fish densities were expressed as numbers per 100 m^2. Most sites were only accessible by walking for several hours on foot. Block nets are commonly used in electrofishing studies, but because of the difficult logistics of the present study, electrofishing was carried out without block nets. Recent studies have also indicated that block nets are often unnecessary (Bohlin et al. 1989). All the fish were returned to the site alive after measuring length to the nearest millimetre. The fish were divided into approximate age classes on the basis of their length distributions in the pooled samples from August and October (Johansen et al. 2005).

Five benthos samples from each site were collected using a Hess-Waters sampler (Waters & Knapp 1961), which samples a bottom area of 0.089 m^2. Mesh size of the sampler was 390 μm. The sampler was pushed into the substratum with the collecting bag facing downstream. The substratum inside the cylinder was then disturbed, while larger stones were handpicked and wiped clean. The current carried the invertebrates into the collecting bag. The samples were spaced out randomly in each site. Benthic densities were expressed as numbers per m^2 (with SE).

Drifting organisms were sampled in eight streams in August and October 2003 (Table 1), using floating drift nets with a mesh size of 430 μm (for a detailed

Table 2. Mean density (numbers per 100 m^2) (SE in parenthesis) of salmon (split into 0+ fry and 1+ and older parr) caught at each site in the 13 streams sampled in August 2000, 2001, 2002. Area sampled (m^2) for each site are also given.

	Site 0					Site 1					Site 2					Site 3				
	Area	0+ (Aug)	≥1+ (Aug)	0+ (Oct)	≥1+ (Oct)	Area	0+ (Aug)	≥1+ (Aug)	0+ (Oct)	≥1+ (Oct)	Area	0+ (Aug)	≥1+ (Aug)	0+ (Oct)	≥1+ (Oct)	Area	0+ (Aug)	≥1+ (Aug)	0+ (Oct)	≥1+ (Oct)
A1	140	9.0 (8.2)	9.3 (2.0)	2.4 (0.7)	5.2 (1.2)	100	0	0	0	0	100	0	0	0	0	120	0	0	0	0
A2	100	0	0	0	0	100	0	22.7 (5.6)	0	18.0 (2.1)	100	0	7.0 (1.0)	0	3.0 (1.0)	100	0	4.3 (1.2)	0	3.7 (0.9)
A4	120	15.3 (6.5)	3.3 (1.5)	5.6 (1.9)	4.2 (1.7)	100	0	15.0 (2.1)	0	6.7 (2.1)	100	0	10.7 (3.0)	0	6.7 (1.7)	120	0	9.7 (2.0)	0	0
B1	120	0	10.0 (2.3)	0	4.4 (0.9)	100	0	0.7 (0.7)	0	0	100	0	0	0	0	100	0	0	0	0
B2	120	7.8 (4.1)	9.2 (3.5)	5.8 (2.6)	8.1 (4.1)	100	0	1.7 (0.9)	0	1.7 (1.7)	120	0	2.5 (0.1)	0	1.7 (0.6)	120	0	1.9 (0.3)	0	0.6 (0.7)
B3	140	29.0 (17.1)	7.6 (3.5)	17.1 (11.0)	10.5 (4.5)	100	0	5.0 (1.0)	0	4.0 (1.7)	100	0	6.0 (0.6)	0	3.3 (0.9)	100	0	2.3 (0.9)	0	0
B4	120	47.5 (18.1)	44.2 (4.0)	36.9 (1.5)	33.1 (1.9)	100	0	24.0 (2.5)	0	11.3 (4.1)	120	0	10.0 (1.7)	0	5.6 (0.9)	120	0	9.2 (2.1)	0	1.9 (0.9)
B7	100		11.7 (2.8)	0	4.7 (0.3)	140	0	1.7 (0.9)	0	0	160	0	0	0	0	100	0	0	0	0
C1	100	12.0 (3.8)	3.7 (0.3)	12.0 (2.0)	5.0 (1.0)	120	10.6 (5.0)	17.8 (1.5)	11.1 (4.4)	17.8 (3.4)	120	18.6 (4.9)	30.8 (6.7)	16.7 (4.5)	21.4 (3.5)	140	0	12.4 (2.6)	0	7.9 (3.2)
C3	120	29.2 (10.6)	13.9 (1.3)	18.6 (5.8)	17.5 (3.5)	100	0	26.7 (3.4)	0	19.7 (5.8)	100	0	13.2 (2.2)	0	6.0 (1.5)	100	0	0	0	0
C4	100	0	0	0	0	100	0	1.7 (1.7)	0	0.7 (0.7)	140	0	0.5 (0.5)	0	0	140	0	0	0	0
D1	100	0	11.7 (3.8)	0	4 (0.8)	100	0	0.3 (0.3)	0	0.3 (0.4)	120	0	0	0	0	120	0	0	0	0
D2	100	37.0 (14.0)	20.3 (2.0)	12.7 (9.8)	14.7 (2.4)	140	0	2.6 (0.7)	0	0.7 (1.2)	100	0	0.7 (0.3)	0	0	100	0	0	0	0

Numbers A1 to D2 correspond to those in Fig. 1.

description see Elliott 1967). Three nets were used at each site. Each net sampled the water column from the surface down to a depth of 6 cm. Total submerged area was 288 cm^2. The nets sampled for 1 h every 3 h throughout one day and one night. At the beginning and end of each 1 h sample, a miniature current meter was used to measure water velocity at the middle of the net mouth. The volume of water filtered was estimated from the product of the submerged area, current velocity and duration of sampling. Flow through the nets was used to calculate drift density as the number of drifting invertebrates per 100 m^3 sampled (Elliott 1970; Allan & Russek 1985).

Both benthos and drift samples were preserved in 70% ethanol and later sorted in the laboratory at 6× magnification. All invertebrates were handpicked, identified and counted.

Statistical analysis

To relate salmon density to environmental variables and benthic densities, a multiple regression analysis was performed with salmon density as the dependent variable and the remaining factors as the independent variables. In choosing the best model, a procedure using all possible regressions was employed. This requires fitting of every possible regression equation associated with each possible combination of k independent variables. The statistic Mallow's C_p was used as the main criterion in selecting the best subset of independent variables, and a ridge regression analysis was performed to remedy the potential problems caused by colinearity (Neter et al. 1989). Ridge regression involves the arbitrary selection of a ridge constant c_r which controls the extent to which ridge estimates differ from least squares estimates. A ridge trace procedure was used to select c_r. With this method, parameter estimates were computed for several values of c_r. Values for Mallow's C_p were calculated for each c_r, and the value of c_r corresponding to the minimum value of C_p was selected.

Results

Benthos and fish density

Electrofishing showed that, with the exception of stream C1, 0+ fry were found only at the stream mouth sites (Table 2). Therefore, in the following analyses, the density of 0+ fry was related only to benthic density at the stream mouth, while density of 1+ and older parr was related to a suite of environmental factors in addition to benthic density both in the stream and at the stream mouth.

The mean density (±SE) per m^2 for the total benthos within each of the 13 sampled streams was

4520 ± 371 in August and 5025 ± 471 in October (Tables 3 and 4). There was no significant difference in benthic density between streams flowing into the main Tana river, into large-sized tributaries and into small-sized tributaries (single-factor ANOVA, August: $F = 0.69$; October: $F = 0.49$, both $P > 0.05$). Therefore, there were only small, non-significant differences in benthic density between streams with and without juvenile salmon, the latter being A1, B1 and B7 (Table 2).

Mean benthic density at the stream mouth was low for streams flowing into the main Tana river (A2, A4, B2, B3, B4) (August: 538 ± 128 per m^2, October: 511 ± 75), slightly higher for streams entering large-sized tributaries (B7, C1, C3, C4) (August: 1698 ± 393 per m^2, October: 1716 ± 243), and highest for streams entering small-sized tributaries (A1, B1, D1, D2) (August: 3065 ± 260 per m^2, October: 2526 ± 596) (Tables 3 and 4). The latter densities were often comparable with benthic density within the streams. The difference between benthic densities at stream mouth sites from streams flowing into the main Tana river, into large-sized tributaries and into small-sized tributaries was statistically significant (single-factor ANOVA, August: $F = 23.67$, $P < 0.001$; October: $F = 9.13$, $P < 0.01$).

Regression equations relating benthic and salmon densities at the stream mouth in both August and October were not significant for 0+ fry, or for 1+ and older parr ($P > 0.05$; $N = 13$). However, the regression of the density of 1+ and older parr within the streams on benthic density at the stream mouth was significant, and R^2 values indicated that the negative relationship explained 39% of the variation in parr density within streams in August and 29% in October (both $P < 0.05$, $N = 13$).

Therefore, all streams with a high density of juvenile salmon had low benthic densities at the stream mouth in both August and October (A2, A4, B4, C1, C3 in Fig. 2a,b). Juvenile salmon were not found, or found only in very low densities, in streams where the benthic density at the stream mouth was as high or higher than that in the stream (A1, B1, B7, C4, D1, D2 in Fig. 2b, c). Juvenile salmon at high and low densities occurred over a wider range of benthos densities within streams (Fig. 2d,e,f).

Twelve environmental factors (see Introduction) together with benthic density, both at the mouth and in the streams, were included in a regression analysis. Five variables emerged as significant enough to be included in the following multiple regression models that explained 90% of the variation in salmon parr density in August ($R^2 = 0.90$, $P < 0.01$, $N = 13$) and 67% in October ($R^2 = 0.67$, $P < 0.05$, $N = 13$):

$$\text{Parr density} = a + b_1 * \text{benthos}_{\text{stream}}$$
$$- b_2 * \text{benthos}_{\text{mouth}} + b_3 * \text{moss cover} \quad (1)$$
$$- b_4 * \text{water velocity} - b_5 * \text{pH}$$

where estimates (±SE) of the parameters a, b_1, b_2, b_3, b_4 and b_5 are given in Table 5 together with the partial correlation coefficients for b_1–b_5.

Therefore, parr density was related positively to benthic density in streams and the proportion of moss cover on the substratum (for assessment methodology, see Johansen et al. 2005), and negatively to benthic density at the stream mouth, water velocity and pH.

Drift and fish density

Mean values (±SE) for total drift density varied considerably between streams (Table 6). Benthic density and drift density of aquatic invertebrates for the eight streams correlated positively, although they were estimated in different years (August: $R = 0.73$; October: $R = 0.78$). Therefore, streams with high benthic densities also had high drift densities. There were some significant differences in drift of aquatic invertebrates between vegetation categories. Highest densities were found in streams A1 and C1 in August and October (Table 6). The difference between densities in categories A and C was not significant ($t = 0.85$, $P > 0.05$), and densities in A and C were significantly higher than B and D ($P < 0.001$). Therefore, the highest densities of aquatic invertebrates in the drift were found in streams with dense riparian vegetation, either chiefly willow (category A) or a mixture of birch and pine (C). A regression between drift density of aquatic invertebrates and the amount of overhanging cover for the eight streams was not significant in August or October (both $P > 0.05$; $N = 8$). Therefore, overhanging cover did not influence the number of benthic invertebrates entering the drift.

The highest densities of terrestrial invertebrates in August and October were found in the streams with dense riparian vegetation (category A in Table 6). Category A had a significantly higher density than categories B, C and D (all $P < 0.001$). B and C were also significantly higher than D (all $P < 0.001$). A regression between drift density of terrestrial invertebrates and the amount of overhanging cover was positive and explained 93% of the variation in drift in August and 65% in October (both $P < 0.05$; $N = 8$). Terrestrial invertebrates were found in much lower densities in October (Table 6). Category A was significantly higher than B, C and D (all $P < 0.001$). The differences in drift density of terrestrial invertebrates for the other three vegetation categories were

Table 3. Benthic densities per m² (mean values ± SE) of the invertebrates caught in 13 streams in August 2000, 2001, 2002.

	A1		A2		A4		B1		B2		B3	
	m	st	m	st	m	st	m	st	m	st	m	st
Ephemeroptera (SE)	438 (32)	1286 (146)	–	1181 (75)	–	1287 (67)	520 (55)	959 (86)	–	1031 (66)	222 (34)	372 (25)
Plecoptera (SE)	435 (26)	1290 (84)	–	610 (56)	–	1060 (49)	185 (19)	449 (32)	–	363 (21)	90 (8)	203 (14)
Diptera (SE)	2253 (224)	3880 (253)	66 (20)	1781 (147)	135 (25)	1306 (95)	1206 (111)	2712 (191)	210 (33)	1548 (140)	156 (27)	782 (61)
Coleoptera (SE)	47 (7)	5 (1)	–	18 (3)	–	46 (6)	22 (3)	28 (6)	–	8 (2)	–	7 (2)
Trichoptera (SE)	105 (12)	170 (15)	–	141 (11)	–	178 (12)	154 (16)	112 (9)	–	79 (7)	49 (5)	54 (5)
Hydracarina (SE)	32 (8)	179 (23)	–	67 (10)	–	181 (17)	132 (18)	117 (14)	–	41 (6)	26 (6)	43 (5)
Oligochaeta (SE)	197 (40)	235 (25)	102 (14)	94 (9)	135 (25)	101 (10)	102 (14)	277 (30)	124 (23)	323 (32)	32 (7)	167 (18)
Other (SE)	3 (1)	26 (5)	101 (21)	8 (1)	120 (15)	–	15 (2)	59 (10)	126 (15)	33 (4)	26 (5)	7 (2)
Total (SE)	3510 (249)	7069 (342)	269 (25)	4373 (178)	360 (32)	4157 (157)	2336 (132)	4713 (278)	460 (47)	3425 (208)	602 (57)	1633 (76)

st, samples taken from sites 1–3 in the stream; m, samples taken from the stream mouth.

Table 4. Benthic densities per m² (mean values ± SE) of the invertebrates caught in 13 streams in October 2000, 2001, 2002.

	A1		A2		A4		B1		B2		B3	
	m	st	m	st	m	st	m	st	m	st	m	st
Ephemeroptera (SE)	773 (63)	1755 (110)	–	1362 (91)	–	1312 (70)	693 (65)	1397 (87)	–	1410 (88)	244 (22)	897 (64)
Plecoptera (SE)	555 (46)	1493 (69)	–	1208 (46)	–	1352 (60)	164 (12)	317 (26)	–	325 (20)	66 (12)	350 (22)
Diptera (SE)	2404 (228)	4139 (244)	195 (42)	2347 (116)	129 (29)	2657 (121)	1720 (214)	2777 (140)	72 (18)	2194 (145)	350 (32)	1918 (111)
Coleoptera (SE)	78 (10)	208 (15)	–	216 (19)	–	240 (20)	31 (6)	65 (7)	–	61 (7)	–	17 (2)
Trichoptera (SE)	184 (11)	206 (15)	–	218 (15)	–	232 (16)	59 (7)	49 (4)	–	53 (4)	35 (5)	18 (2)
Hydracarina (SE)	11 (4)	41 (4)	–	53 (6)	–	46 (6)	8 (2)	33 (4)	–	26 (3)	7 (3)	27 (3)
Oligochaeta (SE)	87 (19)	170 (14)	114 (17)	180 (16)	134 (24)	196 (21)	19 (5)	58 (7)	122 (26)	77 (7)	19 (4)	414 (53)
Other (SE)	45 (5)	67 (7)	131 (15)	38 (5)	155 (18)	51 (6)	13 (3)	2 (1)	112 (16)	–	22 (4)	2 (1)
Total (SE)	4138 (260)	8080 (293)	439 (49)	5620 (175)	417 (39)	6085 (158)	2707 (224)	4700 (195)	333 (32)	4146 (192)	744 (47)	3644 (176)

st, samples taken from sites 1–3 in the stream; m, samples taken from the stream mouth.

not significant from each other. Therefore, in contrast to aquatic invertebrates in the drift, overhanging cover had a strong influence on the number of terrestrial invertebrates entering the drift.

Of the eight drift-sampled streams, juvenile salmon were found in high densities in four (A2, B4, C1, C3), low densities in three (B3, D1, D2) and not found in one (A1) (Fig. 3). All four streams with high salmon density were streams with a corresponding high benthic density and high drift density (both aquatic and terrestrial invertebrates). The streams with low salmon density had either low instream benthic density (B3) or low drift densities combined with high benthic densities at the stream mouths (D1 and D2). The stream A1 without salmon had both high benthic densities (Tables 3 and 4) and high drift densities (Table 6, Fig. 3). It also flowed into a small-sized tributary of the Tana with a high density of benthic invertebrates at the stream mouth (Tables 3 and 4). Therefore, the highest densities of juvenile salmon were found in streams with riparian vegetation, and were thus also associated with an abundant supply of drift food, including terrestrial invertebrates. The only discrepancy was stream A1 and possible reasons for this will be discussed later. Exclusion of this stream from further analyses reduced the number of streams to only seven and therefore it was not possible to fit a multiple regression model that included the 12 environmental variables (see Introduction), benthic density and drift density.

Discussion

The samples of benthos, fish and drift were taken in August and October, but, for logistic reasons, the drift samples were obtained in 2003, 1 year later than the fish and benthic samples of 2000, 2001 and 2002. In spite of this sampling discrepancy, there were close correlations between benthic and drift densities, probably because of the absence of significant differences between years for benthic densities in the same stream and month. Therefore, mean densities of benthos and drift in either August or October probably remained fairly constant between years within each stream.

The most common way of estimating fish abundance in streams is to use a three-pass removal sampling electrofishing method (Bohlin et al. 1989). This method is labour intensive and costly when applied to many areas, and tests show that a single-pass removal method can give a useful indication of fish abundance (Lobón-Cerviá & Utrilla 1993; Kruse & Hubert 1998). Catch probability is influenced by several factors, fish size (Randall 1990) and water flow

B4		B7		C1		C3		C4		D1		D2	
m	st	m	st	m	st	m	st	m	st	m	st	m	st
212 (32)	1052 (62)	809 (65)	927 (67)	271 (21)	1499 (117)	280 (17)	912 (72)	570 (29)	1614 (99)	474 (45)	658 (51)	535 (54)	701 (50)
22 (4)	333 (27)	213 (16)	338 (28)	99 (8)	272 (35)	148 (21)	621 (47)	170 (20)	244 (32)	46 (6)	139 (12)	102 (8)	307 (47)
377 (42)	4182 (298)	1454 (132)	3517 (232)	439 (49)	2619 (334)	523 (68)	2066 (173)	796 (104)	1961 (143)	2378 (173)	3221 (293)	1949 (181)	1714 (173)
12 (3)	163 (17)	40 (7)	121 (12)	–	258 (56)	–	128 (11)	–	69 (6)	12 (3)	14 (2)	108 (16)	281 (41)
77 (9)	169 (12)	155 (15)	108 (8)	66 (14)	126 (10)	62 (8)	196 (11)	86 (14)	115 (12)	93 (10)	195 (14)	27 (7)	141 (11)
71 (13)	182 (19)	13 (4)	133 (15)	13 (3)	190 (45)	12 (3)	126 (13)	12 (4)	42 (7)	108 (22)	182 (30)	212 (29)	299 (39)
57 (14)	159 (22)	73 (11)	176 (22)	68 (15)	264 (29)	73 (14)	91 (10)	90 (14)	183 (23)	36 (5)	51 (11)	38 (9)	69 (9)
173 (24)	55 (9)	7 (2)	28 (4)	94 (15)	16 (3)	67 (10)	57 (7)	85 (10)	10 (2)	210 (30)	103 (14)	86 (10)	93 (19)
999 (67)	6295 (315)	2766 (166)	5348 (294)	1049 (55)	5243 (468)	1165 (71)	4197 (255)	1810 (123)	4238 (230)	3357 (201)	4563 (304)	3058 (201)	3606 (261)

B4		B7		C1		C3		C4		D1		D2	
m	st	m	st	m	st	m	st	m	st	m	st	m	st
130 (16)	1203 (69)	650 (73)	752 (51)	390 (37)	1116 (64)	360 (18)	1487 (81)	644 (34)	1240 (74)	473 (56)	1036 (80)	327 (27)	1478 (102)
51 (6)	1049 (60)	120 (12)	781 (51)	138 (17)	393 (20)	135 (14)	514 (22)	178 (17)	518 (23)	94 (9)	238 (11)	128 (9)	185 (10)
309 (37)	3473 (158)	1274 (121)	2951 (166)	744 (121)	3089 (168)	718 (91)	3871 (206)	1070 (112)	3107 (164)	936 (117)	1670 (110)	765 (109)	1621 (112)
–	357 (43)	25 (3)	108 (10)	–	27 (4)	–	71 (9)	–	44 (5)	22 (5)	79 (10)	25 (4)	63 (9)
27 (4)	90 (8)	67 (8)	99 (9)	19 (3)	79 (7)	22 (5)	138 (7)	50 (5)	100 (6)	55 (8)	76 (9)	86 (17)	29 (3)
18 (4)	34 (4)	11 (3)	38 (5)	9 (2)	42 (5)	11 (2)	93 (9)	15 (3)	79 (7)	15 (5)	27 (4)	65 (14)	29 (5)
58 (12)	405 (63)	76 (12)	142 (14)	10 (2)	235 (22)	13 (3)	358 (30)	49 (10)	309 (30)	48 (11)	71 (8)	47 (11)	80 (10)
27 (7)	78 (5)	13 (4)	61 (7)	16 (4)	20 (2)	17 (2)	25 (4)	19 (5)	20 (3)	89 (14)	–	82 (8)	–
620 (49)	6688 (220)	2237 (168)	4933 (227)	1327 (138)	5002 (212)	1277 (97)	6557 (201)	2025 (132)	5418 (197)	1732 (144)	2131 (249)	1525 (92)	2323 (263)

(Jensen & Johnsen 1988) are usually the most important. Reported values of catch probability vary, but are usually estimated in the range 0.4–0.7 (e.g. Jensen & Johnsen 1988; Saksgård & Heggberget 1990). The estimates of fish density given in this study from the Tana river system should thus be handled with care. Many of the sampled streams are difficult to reach, and the main priority when choosing a sampling method was to obtain density estimates that were comparable between streams. The imprecision can be considerable, and therefore only very clear differences in density between streams are discussed here.

There were differences in food availability between different habitats available for juvenile salmon in the Tana river system. Sites sampled in the main river and in the three major tributaries had very low benthic densities, while sites in the smaller tributaries and in streams had high benthic densities. Earlier studies (Erkinaro 1997; Johansen et al. 2005) demonstrated that salmon migrate into streams during the summer and that the migrating fish generally showed enhanced growth compared with their counterparts in the main stems of the river. One conclusion from the present study was that the streams chiefly utilised by salmon were those with a low benthic density at the stream mouth. Juvenile salmon were absent or sparse in streams with a high benthic density at the stream mouth and there was a clear negative relationship between parr density within the streams and benthic density at the mouth. The multiple regression model explained 90% of the variation in salmon parr density in August and 67% in October. It also identified five key factors out of a possible 14, with the parr density being related negatively to benthic density at the stream mouth, water velocity and pH, and positively to benthic density within the stream and the proportion of the substratum covered by moss. The latter is a good indicator of the degree of substratum stability (Johansen et al. 2005).

Growth and survival of juvenile salmonids are variable and studies suggest that invertebrate biomass, production and drift are responsible for some of this variation (Cada et al. 1987; Filbert & Hawkins 1995). Studies of Atlantic salmon have shown positive correlations between prey abundance in streams and salmonid growth rates (Erkinaro & Niemelä 1995) and biomass (Egglishaw 1967; Gibson & Galbraith 1975). Benthic densities in the main Tana river are very low (Lax et al. 1993), and the benthos is mainly composed of invertebrates that are little used as food (chironomids, oligochaetes and nematodes). The corresponding low growth rates in juvenile salmon (Erkinaro & Niemelä 1995) suggest that they experience food limitation. Density-dependent growth of salmon in
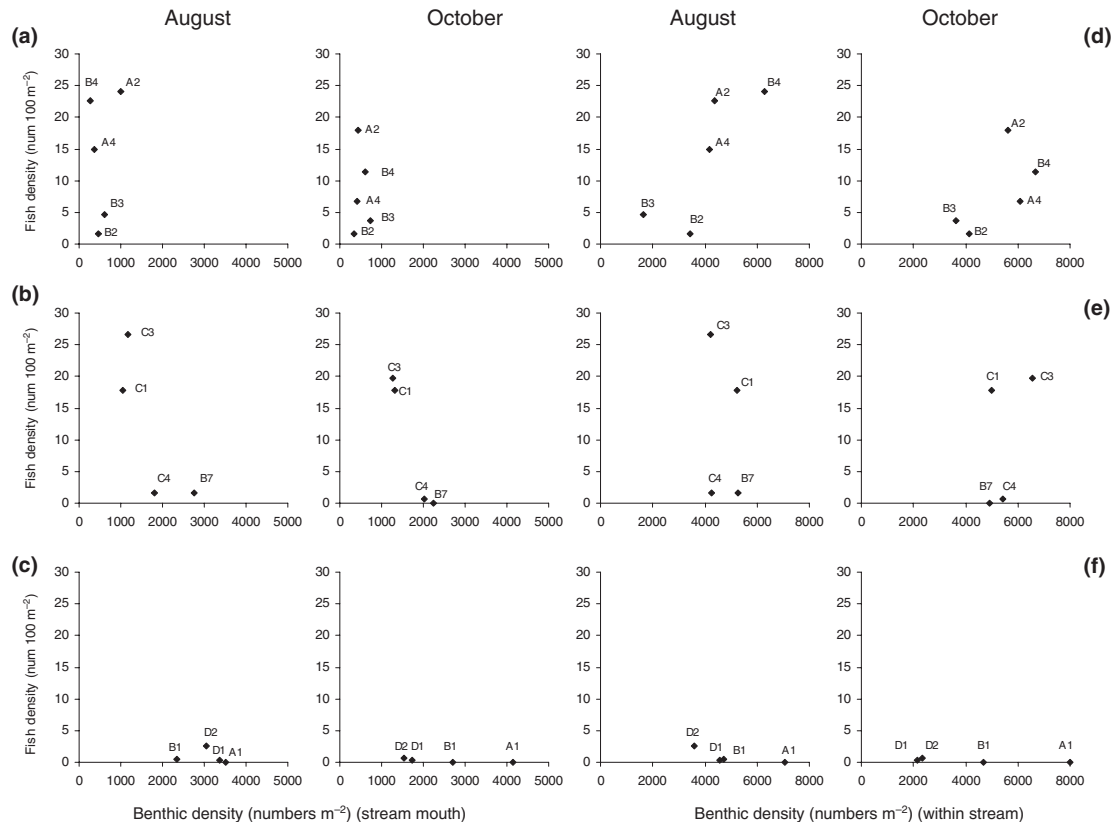
Fig. 2. Relationship between salmon density (numbers per 100 m^2) and benthic density (numbers per m^2) at the stream mouth (a,b,c) and within the stream (d,e,f) in August and October for: (a) streams flowing into the main Tana river; (b) streams flowing into the large-sized tributaries Karasjohka, Iesjohka and Anarjohka; (c) streams flowing into small-sized tributaries.

Table 5. Estimates (±SE) for the August and October samples of the parameter estimates a, b_1, b_2, b_3, b_4 and b_5 in eqn 1 together with partial correlation coefficients (r_p) for b_1-b_5.

	a	b_1	r_p	b_2	r_p	b_3	r_p	b_4	r_p	b_5	r_p
August	135.0 (70.0)	0.0029 (0.0009)	0.77	0.0072 (0.0011)	−0.92	0.30 (0.078)	0.83	75.8 (33.7)	−0.65	16.1 (10.4)	−0.51
October	51.7 (46.0)	0.0021 (0.00094)	0.64	0.0037 (0.0015)	−0.50	0.20 (0.090)	0.64	26.3 (40.0)	−0.24	6.87 (10.30)	−0.24

other parts of Norway also suggests that food limitation can occur (Bergheim & Hesthagen 1990; Heggenes & Borgstrøm 1991).

It was concluded that the presence of juvenile salmon had no detectable effect on the density of the benthos. The evidence for a significant effect of fish predators on the density and biomass of stream benthos is equivocal. Studies examining the effects of fish predation on benthos indicate that salmonids have few or no effects on prey density (Culp 1986; Schofield et al. 1988), while other kinds of fish can reduce prey populations significantly (Flecker 1984; Gilliam et al. 1989). Most publications report field experiments using enclosures and different densities of fish. There have been four meta-analyses of these results. Cooper et al. (1990; 14 studies) found a highly significant decrease in the magnitude of

predatory effects on invertebrate prey as the mesh size of the enclosures/exclosures increased. In contrast, Wooster (1994; 20 studies) and Dahl & Greenberg (1996; 10 studies) could not detect a relationship between predator effects and mesh size. Finally, Englund et al. (1999; 41 studies) summarised studies on the effects of fish and invertebrate predators on benthic invertebrates and emphasised the importance of the criteria used to select data for the meta-analysis. They illustrated the complexity of the relationships, leading to contradictory conclusions. In some experiments, the predators had no effect on the density of benthic invertebrates, whilst in other experiments there was a significant effect which was usually negative but occasionally positive, leading to an increase in benthic density. Some of these analyses also showed that prey selection can

Table 6. Drift densities per 100 m³ (mean ± SE) of the aquatic, adult aquatic and terrestrial invertebrates caught in eight streams flowing through different vegetation categories in August and October 2003.

	August								October							
	A1	A2	B3	B4	C1	C3	D1	D2	A1	A2	B3	B4	C1	C3	D1	D2
Aquatic inv. (SE)	**241 (18)**	**138 (12)**	**116 (9)**	**183 (15)**	**256 (15)**	**205 (14)**	**205 (18)**	**162 (16)**	**375 (34)**	**308 (31)**	**168 (18)**	**284 (28)**	**336 (31)**	**299 (29)**	**236 (19)**	**220 (19)**
Ephemeroptera (SE)	24 (3)	14 (2)	12 (1)	18 (2)	40 (5)	20 (3)	14 (2)	11 (2)	78 (12)	108 (13)	52 (8)	96 (13)	107 (16)	85 (13)	80 (13)	95 (15)
Plecoptera (SE)	21 (2)	11 (1)	7 (1)	19 (2)	9 (1)	12 (1)	8 (1)	6 (1)	76 (11)	55 (6)	32 (4)	44 (6)	48 (7)	56 (8)	6 (1)	5 (1)
Diptera (SE)	158 (15)	88 (9)	75 (8)	114 (13)	164 (13)	149 (3)	159 (17)	126 (15)	188 (18)	122 (15)	72 (9)	118 (13)	134 (13)	133 (13)	127 (13)	101 (11)
Coleoptera (SE)	1 (0)	6 (1)	5 (1)	7 (1)	14 (1)	6 (0)	3 (0)	2 (0)	6 (0)	3 (0)	2 (0)	4 (0)	11 (1)	4 (0)	3 (0)	3 (0)
Trichoptera (SE)	6 (1)	3 (1)	3 (0)	4 (1)	5 (0)	5 (0)	4 (0)	3 (0)	9 (1)	8 (1)	5 (0)	11 (1)	9 (1)	9 (1)	3 (0)	3 (0)
Adult aq. inv. (SE)	**160 (12)**	**155 (12)**	**137 (11)**	**118 (9)**	**126 (10)**	**147 (12)**	**140 (13)**	**139 (13)**	**20 (3)**	**12 (2)**	**6 (1)**	**12 (2)**	**21 (4)**	**12 (2)**	**18 (3)**	**15 (3)**
Diptera (SE)	157 (12)	151 (11)	131 (11)	118 (9)	123 (9)	145 (12)	137 (13)	136 (13)	19 (3)	11 (2)	6 (1)	11 (2)	20 (3)	11 (2)	17 (3)	14 (2)
Other (SE)	3 (0)	4 (1)	6 (0)	6 (0)	3 (0)	3 (0)	3 (0)	3 (0)	1 (0)	1 (0)	+	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)
Terrestrial inv. (SE)	**242 (16)**	**236 (19)**	**140 (14)**	**150 (16)**	**123 (12)**	**141 (14)**	**68 (6)**	**63 (6)**	**74 (6)**	**64 (6)**	**36 (3)**	**43 (4)**	**35 (3)**	**52 (4)**	**39 (3)**	**34 (3)**
Collembola (SE)	39 (4)	25 (3)	22 (2)	25 (4)	23 (3)	27 (5)	29 (3)	20 (2)	20 (2)	14 (2)	10 (2)	13 (2)	20 (2)	14 (2)	20 (2)	18 (2)
Diptera (SE)	23 (2)	28 (2)	11 (1)	12 (1)	17 (1)	12 (1)	9 (1)	13 (1)	3 (0)	3 (0)	1 (0)	2 (0)	1 (0)	2 (0)	7 (1)	6 (1)
Hemiptera (SE)	157 (12)	149 (18)	91 (11)	94 (13)	68 (9)	79 (11)	14 (2)	11 (2)	41 (4)	40 (4)	21 (3)	24 (2)	19 (2)	29 (3)	12 (2)	9 (2)
Hymenoptera (SE)	10 (1)	20 (3)	12 (2)	14 (2)	10 (2)	16 (3)	12 (2)	14 (3)	3 (0)	2 (0)	1 (0)	1 (0)	1 (0)	2 (0)	+	+
Lepidoptera (SE)	10 (1)	8 (1)	1 (0)	1 (0)	+	+	+	1 (0)	1 (0)	1 (0)	+	1 (0)	1 (0)	1 (0)	−	+
Other (SE)	3 (1)	5 (1)	4 (1)	4 (1)	5 (1)	7 (1)	3 (1)	3 (1)	6 (1)	5 (1)	2 (0)	2 (0)	3 (0)	4 (0)		−
Total (SE)	**644 (36)**	**528 (27)**	**394 (26)**	**450 (29)**	**505 (28)**	**494 (29)**	**413 (29)**	**363 (26)**	**469 (30)**	**384 (27)**	**210 (17)**	**339 (25)**	**392 (27)**	**363 (26)**	**293 (19)**	**268 (18)**

affect the size distribution of the surviving prey, species dominance and benthos diversity. Given this complexity, it is not surprising that it is almost impossible to detect predator effects in natural streams, such as the Tana system.

The importance of riparian vegetation was illustrated by the present study. It provides overhead cover, inputs of allochthonous material and shade. Temperature measurements show that water temperatures in the main Tana river can exceed 20 °C during the summer (data from the Norwegian Water Resources and Energy Directorate), while temperatures in shaded streams (Johansen et al. 2005) and tributaries (M. Johansen, unpublished data) are lower than 15 °C. Temperature directly regulates metabolic rate in salmonids (Elliott 1994), and the water temperature in the Tana exceeds the upper temperature for maximum food consumption (Forseth et al. 2001). High temperature combined with low food availability probably is a stress factor for juvenile salmon living in the main Tana and therefore juvenile fish escape by migrating into cooler streams with higher food availabilities.

Another conclusion was that there were also differences in food availability between streams flowing through different vegetation categories. Streams flowing through dense riparian vegetation (especially willow sites) had a higher drift density of terrestrial invertebrates than high mountain streams without any riparian tree vegetation. Other workers have found that the input of terrestrial invertebrates as fish food is influenced by riparian vegetation (Mason & MacDonald 1982; Allan et al. 2003). Salmon are commonly described as visual predators that feed on drifting invertebrates (Wankowski 1981; Stradmeyer & Thorpe 1987; Keeley & Grant 1997). It has been shown experimentally that changing the drift rate triggers a higher rate of benthic feeding (Nislow et al. 1998). Aerial invertebrates (terrestrial and adult aquatic invertebrates) can contribute up to 91% of trout prey (Kelly-Quinn & Bracken 1990). Salmon probably feed less on aerial prey than trout because of differences in the behaviour and feeding positions of the two species (Egglishaw 1967), but studies from Scotland and Newfoundland show that aerial invertebrates can be important in their diet (Gibson & Cunjak 1986; Bridcut 2000). The life cycles of many benthic insects in streams with dense riparian vegetation are synchronised with the input of leaves during the autumn. Growth of these species occurs during autumn and winter, and adults emerge in spring and early summer. As a result, the biomass of benthic insects is at its lowest point during summer, coinciding with the period when water temperatures are high and salmon metabolism is at its maximal level (Hunt 1975; Cada et al. 1987). This probably increases
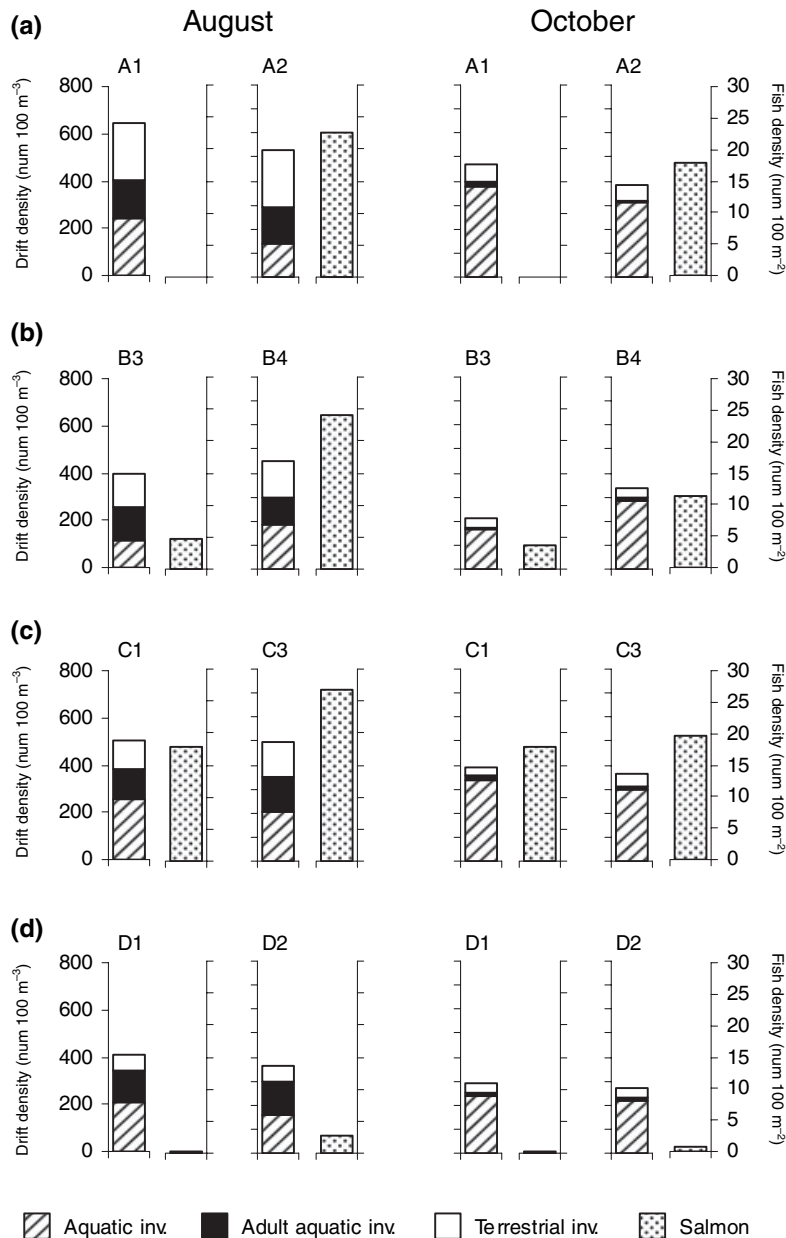
Fig. 3. Mean drift densities (numbers per 100 m³) and salmon densities (numbers per 100 m²) in streams with riparian vegetation consisting mainly of (a) willow; (b) birch; (c) birch and pine; (d) nonforested alpine.

the importance of the riparian input of terrestrial invertebrates as a readily available food for juvenile salmon.

Obtaining better food resources and thereby achieving higher growth rate is one possible cause of migration (Northcote 1984). An alternative view, supported by the present study, is that migration is a fundamental biological response to adversity (Taylor & Taylor 1977). This theory has been applied successfully to salmonid populations by Thorpe (1989). The juvenile salmon in the main Tana river and its large-sized tributaries face an environment with possible food limitations and therefore benefit from the higher food availability found in associated small streams. However, juvenile salmon living in the

smaller sized tributaries already live in an environment with relatively high benthic density, and the benefit of migrating to smaller streams in terms of food is thus smaller.

Finally, it is intriguing that a stream such as A1 was not utilised by juvenile salmon, in spite of its high benthic and drift densities. This suggests the existence of other factors besides food availability controlling migration or, more simply, that the juvenile salmon have not yet reached these streams. An obvious experiment would be to stock these streams with juvenile salmon to see if they could survive. If such an experiment was successful, then it would provide one method for increasing the nursery habitat for juvenile salmon in the Tana River.

Resumen

1. El principal objetivo fue relacionar la densidad de juveniles de *Salmo salar* con la densidad de invertebrados a lo largo del Río Tana (norte de Noruega). Los juveniles de *S. salar* fueron cuantificados con pesca eléctrica. Los invertebrados fueron muestreados en cuatro localidades de 13 ríos (una localidad en la boca del río y tres localidades aguas arriba) en Agosto y Octubre de los años 2000, 2001, y 2002. Muestreos de deriva fueron tomados en 8 ríos en Agosto y Octubre del año 2003.

2. Aparecieron solamente diferencias pequeñas y no significativas en la densidad de bentos en ríos con y sin *S. salar*. Todos los ríos con densidad alta de juveniles de *S. salar* tuvieron densidad bénticas bajas en las bocas de los ríos. Los juveniles de *S. salar* no fueron encontrados (o fueron encontrados en muy bajas densidades) en ríos donde la densidad de bentos en las bocas fue tan alta como, o mayor que, las densidades en los ríos. Un estudio previo mostró que los juveniles mayores de un año migran desde los hábitats de nacimiento en ríos mayores hacia los ríos más pequeños. Este estudio mostró que este movimiento está asociado con menores densidades de alimento de invertebrados en las bocas de los ríos, i.e., los juveniles se movieron desde áreas de baja a áreas de alta densidad de invertebrados. Una regresión múltiple explicó el 90% de las variaciones en la densidad entre ríos mostradas por los juveniles de *S. salar* en Agosto y un 67% en Octubre. Este estudio identificó 5 factores claves de un total de 14 factores posibles: la densidad de juveniles estuvo relacionada negativamente con la densidad de bentos en la boca de los ríos, la velocidad del agua y el Ph y positivamente con la densidad de bentos en los ríos aguas arriba y con la proporción de sustrato cubierto por vegetación, siendo este último factor, un indicador de la estabilidad del sustrato.

3. La densidad de la deriva de invertebrados fue mayor en ríos que fluyen sobre áreas con vegetación riparia densa que en áreas sin esta vegetación debido a la gran cantidad de invertebrados terrestres que caen al río desde la vegetación de los alrededores (la cantidad de cubierta vegetal en los ríos explicó en 93% de las variaciones en la densidad de la deriva de invertebrados terrestres). Las mayores densidades de juveniles fueron encontradas en ríos con vegetación riparia y estuvieron por ello asociados al abundante alimento en forma de deriva, especialmente de invertebrados terrestres.

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