

Intraspecific food resource partitioning in Atlantic salmon (*Salmo salar*) parr in a subarctic river

Per-Arne Amundsen*, Heidi-Marie Gabler, Lars Sigvald Riise

Department of Marine and Freshwater Biology, Norwegian College of Fishery Science, University of Tromsø, N-9037 Tromsø, Norway

Received 24 October 2000; accepted 15 May 2001

Abstract – The food utilisation and partitioning between three age-groups of Atlantic salmon parr were studied in the subarctic river Tana (70° N, 27° E) by analysis of fish stomach contents and invertebrate composition in the three main lotic feeding habitats: bottom substratum, water column and surface. The salmon parr exhibited large seasonal variation in their food choice, but the different age-groups had a similar diet, dominated by mayfly and stonefly nymphs in May, flying insects and simuliid larvae and pupae in July, and caddis fly larvae in August and September. Some differences in the food resource use of the three age-groups were however also observed, mainly related to size-dependent differences in feeding abilities, but partly also to different use of feeding habitats. Small-sized stonefly and mayfly nymphs and simuliid larvae and pupae decreased in importance with increasing fish age, whereas Trichoptera larvae and flying insects increased. The low resource partitioning between the different age-groups of salmon parr suggests that intraspecific competition for food may occur. All age-groups mostly fed on prey types associated with the bottom habitat, and substantial drift feeding was only observed in July, probably due to low drift rates throughout most of the summer season in this subarctic river. © 2001 Éditions scientifiques et médicales Elsevier SAS

diet / food partitioning / benthos / drift / Atlantic salmon / subarctic

Résumé – Le partage intraspécifique des ressources alimentaires chez les tacons du saumon Atlantique (*Salmo salar*) dans un fleuve subarctique. L'utilisation et le partage de la nourriture entre trois groupes d'âge de tacons (stade « parr ») du saumon Atlantique du fleuve Tana (70° N, 27° E) ont été étudiés par analyse des contenus stomacaux et par la composition en invertébrés pour trois types d'habitats principaux : sur le fond, dans la colonne d'eau et en surface. Les tacons montrent une grande variation saisonnière dans leur choix de nourriture mais les différents groupes d'âge ont un régime alimentaire similaire, dominé par des nymphes d'insectes éphéméroptères et des nymphes de plécoptères en mai, des insectes volants et des larves et pupes de simuliidés en juillet, et des larves de trichoptères à fourreau, en août et septembre. Quelques différences dans l'usage des ressources alimentaires des trois groupes d'âge sont également observées, principalement relatives aux différences de taille dans la capacité alimentaire, mais aussi en partie liées aux différents types d'habitat. Les nymphes de plécoptères de petites tailles, et celles d'éphéméroptères et les larves et pupes de simuliidés diminuent en importance avec l'augmentation de l'âge, alors que les larves de trichoptères et les insectes volants augmentent. La faible partition des ressources entre les différents groupes d'âge des tacons montre que la compétition intraspécifique pour la nourriture peut se présenter. La plupart des groupes d'âge se nourrissent de proies associées à l'habitat situé sur le fond, et une alimentation substantielle basée sur des proies dérivant dans le courant est seulement observée en juillet, probablement due aux faibles taux de proies dérivant en été, durant la majeure partie de la saison estivale dans ce fleuve subarctique. © 2001 Éditions scientifiques et médicales Elsevier SAS

régime alimentaire / partition alimentaire / benthos / dérive / saumon atlantique / zone subarctique

1. INTRODUCTION

Atlantic salmon (*Salmo salar*) have a freshwater residential stage as parr, prior to smoltification and

seaward migration. This freshwater stage may be regarded as a feeding and growth stage preparing the fish for smoltification, and is of major importance in the completion of the life cycle. Fish will therefore

*Correspondence and reprints: fax: +47 77646020.
E-mail address: pera@nfh.uit.no (P.A. Amundsen).

seek to optimise the food intake during the freshwater stage (Wańkowski and Thorpe, 1979). The diet of salmon parr mostly consists of freshwater invertebrates (Allan, 1940, 1941; Egglisshaw, 1967; Stradmeyer and Thorpe, 1987; Thonney and Gibson, 1989). These invertebrates can be taken from the bottom, or as drift suspended in the water column or at the water surface (Wańkowski and Thorpe, 1979). Salmon parr is described as a visual predator (Higgins and Talbot, 1985), feeding mostly on drifting invertebrates (Keenleyside, 1962; Stradmeyer and Thorpe, 1987; Vignes, 1999; Wańkowski and Thorpe, 1979), or on invertebrates in motion (Rimmer and Power, 1978). Wańkowski (1979) demonstrated that salmon parr have a size restricted diet with a maximum, minimum and optimum prey size, which also may influence the prey choice of different size-classes of fish. Keeley and Grant (1997) and Vignes (1998) also found that prey size increased with increasing size of juvenile salmon. Observational studies have further shown that the oldest age-groups of salmon parr tend to use surface feeding more frequently than younger parr (Keenleyside, 1962; Peterson and Martin-Rubichaud, 1986; Stradmeyer and Thorpe, 1987). Except from these studies, little has been done to examine intraspecific differences in resource use of juvenile Atlantic salmon. The inter-cohort relationships may be particularly important in high-latitude rivers where several age-groups of salmon parr usually co-occur due to slow growth rates and late smoltification.

The objective of the present study was to investigate resource partitioning between different age-groups of salmon parr in a large subarctic river, particularly in relation to prey availability in the three main lotic feeding habitats: bottom substratum, water column and surface. The salmon parr were expected to feed primarily on drift suspended in the water column or at the surface, with the oldest age-groups using these feeding habitats more frequently than the younger. Seasonal variations in food availability and resource use of the salmon parr were also studied in expectation that resource utilisation and partitioning would change with changing food resources.

2. MATERIALS AND METHODS

The river Tana (Teno in Finnish) is located on the border between northern Norway and Finland (70° N, 27° E), and is the most important salmon river in both countries, as well as one of the most important Atlantic salmon producing rivers in the world. The total salmon catches vary from 100 to 200 tons a year. The river has a catchment area of 16 386 km² (Erkinaro, 1995), the average discharge is about 163 m³·s⁻¹, and the largest recorded discharge rate during spring flow is 3 544 m³·s⁻¹. The river is normally ice covered from the end of October to the beginning of May, and the spring flow usually occurs in late May or in June (figure 1). During the sampling season of 1995, the water temperature at the sampling site reached a

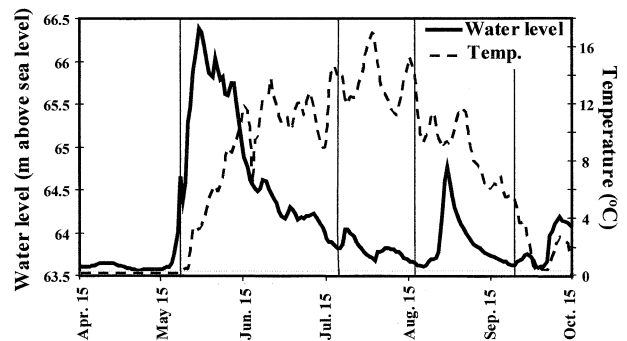


Figure 1. Water level (m above sea level) and temperature (°C) at the sampling locality in the river Tana during the summer season of 1995.

maximum of 17 °C in early August, but most of the summer, the temperature was below 14 °C (figure 1).

The present study was carried out on a 500-m homogeneous stretch in the main stem of the river situated about 150 km from the sea (69°54' N, 27°03' E). River width at the site was ca. 230 m, and sampling was done up to 25–50 m from the river bank down to approx. 1 m depth. The site has rapid water currents (predominantly 0.3–0.7 m·s⁻¹), and an unsettled bottom substratum dominated by small stones (8–10 cm diameter), but also sand, gravel and stones up to 50 cm in diameter. Sampling took place in four periods during the ice-free season of 1995; 22–23 May, 20–21 July, 18–19 August and 24–25 September. Salmon parr were caught by electrofishing, and the sampled fish were immediately preserved in 96 % alcohol. The abdomen of fish 8 cm and larger were opened to ensure complete conservation of the stomach contents. In the laboratory, fish were measured to the nearest millimetre (fork length) and scales were taken for age determination. The material primarily included fish from age 1+ to 3+. In May, some smolts (mostly 4+) were caught, and in August and September a few fry (0+), but these were excluded from the further analysis (table I).

The stomachs were opened and percent total fullness was qualitatively assessed, ranging from empty (0 %) to full (100 %). Food items were identified and counted, and their contribution to the stomach fullness estimated. Plecoptera and Ephemeroptera nymphs and Trichoptera larvae were identified to the species or genus levels, and other taxa usually to the family level. In the diet description, the contribution of each prey to the stomach content is described as percent prey abundance (A_i) (Amundsen et al., 1996):

$$A_i = 100 \sum_{i=1}^n S_i \left(\sum_{i=1}^n S_i \right)^{-1} \quad (1)$$

where S_i is stomach fullness of prey item i , and S_t is the total fullness of all prey categories.

Table I. Water temperature, and number and mean length of Atlantic salmon parr in each age-group from the different sampling periods in the river Tana. * Number of fish with empty stomachs. SD, Standard deviation.

Month	Water temp. (°C)	Age-group (year)	Number of fish (*)	Mean length (± SD) (cm)
May	0.2	1	33 (1)	4.4 (± 0.68)
		2	26 (3)	6.7 (± 0.85)
		3	16 (1)	10.3 (± 1.29)
July	14.0	1	40 (0)	5.8 (± 0.43)
		2	39 (2)	8.2 (± 0.71)
		3	39 (1)	11.0 (± 0.59)
August	13.5	1	39 (0)	6.1 (± 0.66)
		2	40 (2)	8.1 (± 0.82)
		3	38 (1)	10.9 (± 1.19)
September	6.0	1	39 (6)	6.6 (± 0.44)
		2	40 (6)	8.6 (± 0.68)
		3	40 (0)	11.4 (± 0.81)

Benthic and drift samples were collected at the same time periods as the fish were sampled. Benthic samples were collected using the kicking technique (Frost et al., 1971; Pollard, 1981; Williams and Feltmate, 1992), kicking for 3 min inside a metal frame embracing a fixed area (2.25 m²) and collecting the invertebrates in a 250-µm net positioned immediately downstream. Drifting invertebrates were collected with traps made from 30 cm long plastic tubes with an inner diameter of 10 cm and a 100-cm long conic net (mesh size 250 µm) attached around the downstream end. Sampling was performed in a 40 to 75-cm deep area of the river, and the tube traps were attached at different depths to vertical iron poles driven into the substratum. One or two submerged traps and one surface trap were attached to each pole. The lowermost traps were placed at a minimum of 10 cm above the bottom, whereas the uppermost traps were partly submerged at the surface. The drift sampling was carried out over 24-h periods, but the traps were emptied every 6 h. The drift rate (sensu Allan and Russek, 1985) was expressed as the mean number of animals passing through each drift trap per hour of sampling.

The percent similarity (or overlap) index was used to compare the similarity in invertebrate composition between different feeding habitats and between different age-groups of fish (Schoener, 1970; Krebs, 1989):

$$P_{xy} = 100 \left[\sum_{i=1}^n (\text{minimum } x_i, y_i) \right] \quad (2)$$

where x and y represent either feeding habitat x and y or age-group x and y of the fish, x_i is the proportion of invertebrate category i in x , y_i is the proportion of invertebrate category i in y , and n the total number of invertebrate categories. The similarity or overlap is considered to be significant when the index value exceeds 60 % (Wallace, 1981).

As a measure of diet width, the Levins index (W , Levins, 1968) was used:

$$W = \left(\sum_{i=1}^n p_i^2 \right)^{-1} \quad (3)$$

where p_i is the fraction of prey i in the diet, and n is the number of prey categories in the diet. W may range from 1 to n , where 1 is the minimum diet width and n the maximum.

To investigate the relative use of the bottom and the drift as feeding habitats for the fish, the different invertebrate taxa found in the stomachs were categorised as drifting or benthic prey according to their presence in the drift and benthos samples each sampling month. Invertebrates that occurred in the drift samples but were absent or rare (< 0.1 % numerical contribution) in the benthos were characterised as drift, whereas taxa that occurred in the benthos samples but were absent or rare in the drift are referred to as benthos. Prey taxa that occurred in both drift and benthos samples are referred to as 'drift or benthos', since it is unknown where they were consumed by the fish.

3. RESULTS

3.1. Prey availability

Both in the benthos and in the suspended and surface drift, the density of invertebrates was highest in July and lowest in May and September (figure 2). The drift rate was markedly higher at the surface than in the water column, the differences being highest in July and August, and lowest in May. A total of 51 different invertebrate taxa was recorded in the samples. The presence and relative composition of invertebrates differed between the three habitats, although there was a strong resemblance between the

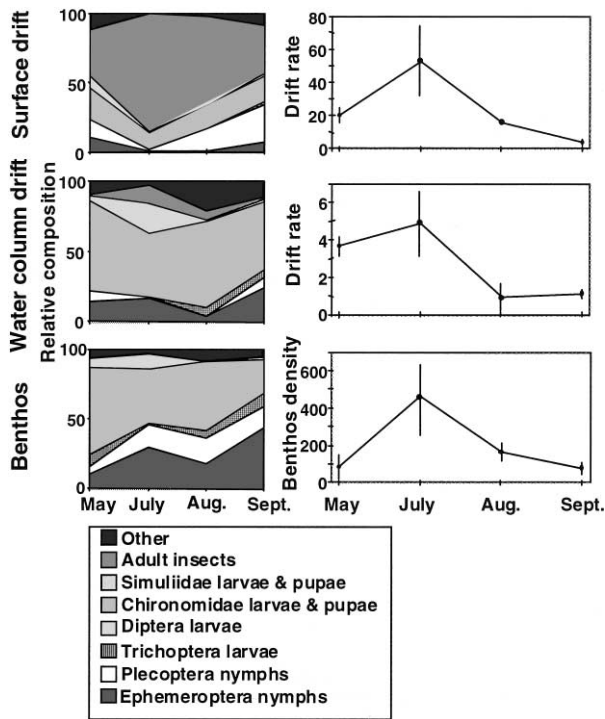


Figure 2. Seasonal variation in relative composition (percentage by number) and abundance (\pm SE; drift rate = mean No. trap⁻¹ h⁻¹; benthos density = mean No. m⁻²) of invertebrates in the three different feeding habitats.

Table II. Similarity (percent overlap index) in invertebrate composition between the three different feeding habitats.

	Surface vs. suspended drift	Surface drift vs. benthos	Suspended drift vs. benthos
May	51.9	41.0	82.4
July	27.7	12.6	63.0
August	26.3	26.1	58.8
September	44.9	44.6	63.9

suspended drift and the benthos (table II), mainly due to a dominance of chironomid larvae and pupae in both habitats. The benthos differed, however, somewhat from the suspended drift in having a higher proportion of mayfly and stonefly nymphs (figure 2). The surface drift differed from the suspended drift and the bottom fauna by a dominance of adult insects, which were more or less absent in the other two habitats.

Chironomid larvae dominated the bottom fauna, but mayfly and stonefly nymphs were also of primary importance from July to September. The dominant mayfly species were *Ephemera aurivillii* and *Baetis* spp./*Ameletus inopinatus*. The stonefly fauna was dominated by *Amphinemura borealis* in May, *Taeniopteryx nebulosa* and *Diura nanseni* in July, *D. nanseni* and *Capnia* spp. in August, and *D. nanseni*, *Capnia* spp. and *T. nebulosa* in September. Caddis larvae had in general low densities in the bottom samples, but the case-building *Apatania stigmatella* was important in August and September.

Chironomid larvae also dominated the suspended drift. Simuliid larvae and pupae were important in July, and mayfly nymphs (mainly *Baetis* spp./*A. inopinatus*) in all months except August. The surface drift was in contrast dominated by adult insects, mainly adult stoneflies in May, adult chironomids and other Diptera (almost exclusively adult simuliids) in July, and adult chironomids in August and September. The most common mayfly nymphs in the surface drift were *Baetis* spp./*A. inopinatus*, while several stonefly species were found drifting: *Capnia* spp. dominating in May, *D. nanseni* in July, *Capnia* spp. and *Leuctra* spp. in August, and *Capnia* spp. and *D. nanseni* in September.

3.2. Fish diet

A total of 47 prey taxa were recorded in the salmon parr stomachs. The diet consisted mostly of aquatic insects. Mayfly and stonefly nymphs, caddis larvae, simuliid larvae and pupae, and flying insects were the most important prey groups for all age-groups. The different age-groups had a similar diet, but there were some gradual dietary changes in resource use from the youngest to the oldest age-group (figure 3). Mayfly nymphs and simuliid larvae and pupae decreased in importance with increasing age of the fish, whereas

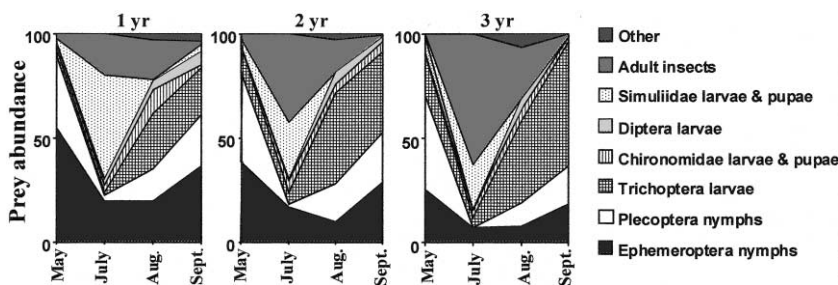


Figure 3. Seasonal variation in diet composition of the three age-groups of Atlantic salmon parr in the river Tana.

Trichoptera larvae and flying insects increased. More specifically, mayfly and stonefly nymphs were the dominant prey in May, but the contribution of mayfly nymphs decreased and stonefly nymphs increased with increasing fish age. In July, simuliid larvae and pupae as well as flying insects were dominant prey, but the proportion of simuliids decreased and flying insects

increased with increasing fish age. Similarly, in August and September, the proportion of caddis larvae increased and mayfly nymphs decreased with increasing fish age.

The most important mayfly nymphs in the diet were *E. aurivillii* and *Baetis* spp./*A. inopinatus* (figure 4a), the importance of the latter group decreasing with

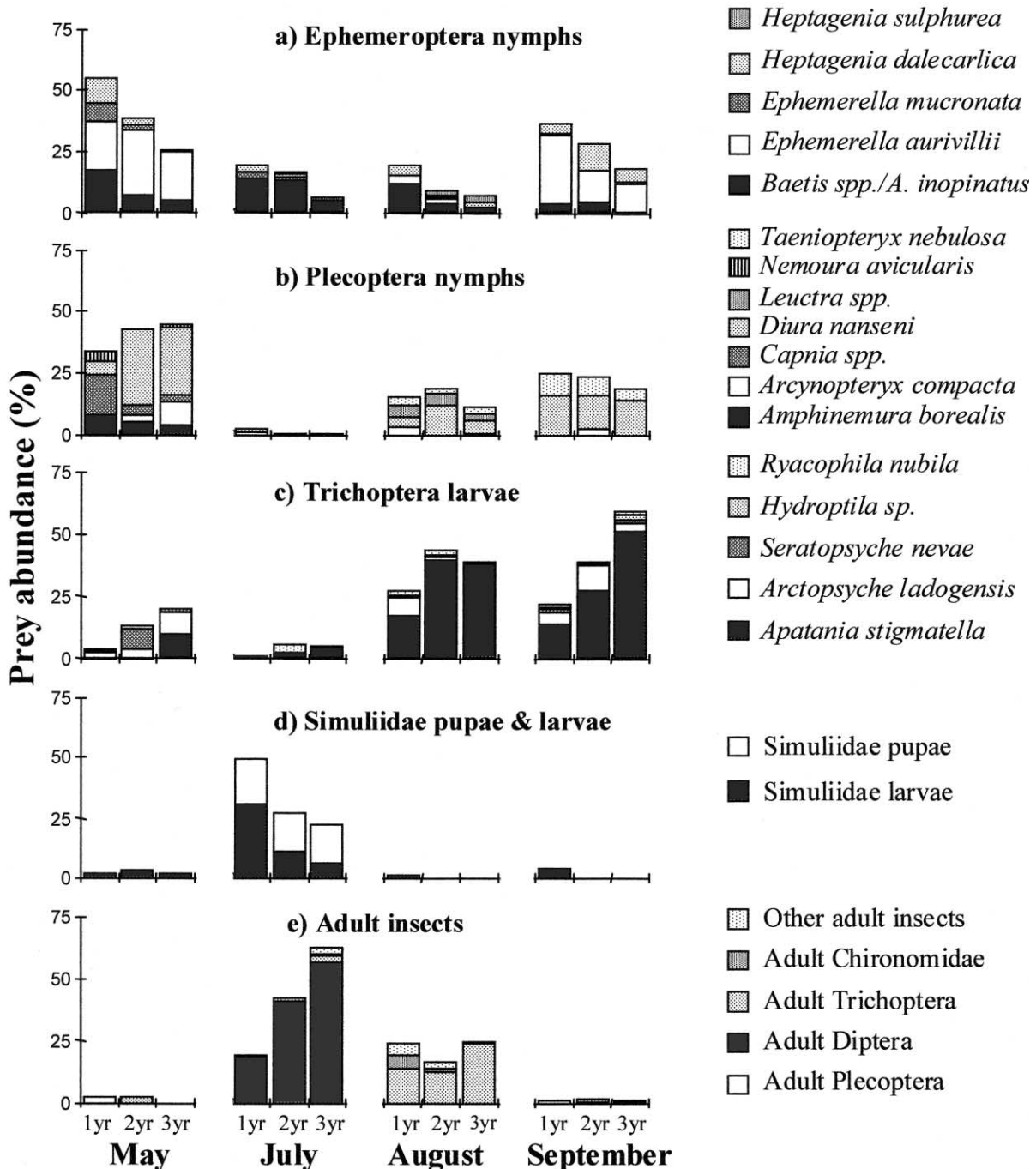


Figure 4. The composition of the main invertebrate groups in the diet of the three age-groups of Atlantic salmon parr in the river Tana.

increasing fish age. The most important stonefly nymphs were *Diura nanseni* (figure 4b). In May, however, the 1-year-old fish had consumed more of the small species *Amphinemoura borealis*, *Capnia* spp. and *Nemoura avicularis* than the other two age-groups, which in turn had eaten more of the two large species *D. nanseni* and *Arcynopteryx compacta*. The caddis larvae in the salmon diet were dominated by *Apatania stigmatella*, but in May only the 3-year-old fish ate this species (figure 4c). Simuliid larvae and pupae were important prey in July (figure 4d). The proportion of simuliid pupae was similar in all age-groups, while the importance of simuliid larvae decreased with increasing fish age. Adult insects in the fish diet were dominated by adult Diptera in July and adult Trichoptera in August (figure 4e). In August, 1-year-old fish also consumed adult chironomids.

3.3. Diet overlap and niche width

The 2- and 3-year-old salmon parr exhibited a significant (i.e. > 60 %) diet overlap in all months (table III). The 1- and 2-year-old fish had a significant overlap in all months except May, whereas the 1- and 3-year-old parr exhibited a significant overlap only in August. Thus, 2-year-old fish had a diet quite similar to the 3-year-old fish, while the 1-year-old fish differed more in diet compared to the other two age-groups, although overlapping quite extensively with the 2-year-old fish. The different age-groups had least in common in May, after which the diet similarity increased towards July and August and were slightly reduced again in September. The diet widths of the three salmon age-groups were in general most narrow in July (table IV). Throughout the season there was a general trend that the diet width decreased with increasing age of the fish.

3.4. Drift versus benthic feeding

In May, the salmon parr had mostly consumed benthic prey, although a large proportion of the diet could not be classified as either benthos or drift (figure 5). Drift was found to dominate the diet only in July, and in particular for the 2- and 3-year-old parr. The proportion of drift in the diet of salmon parr decreased rapidly towards autumn, and both in August and September, predominantly benthic prey had been consumed (figure 5).

The composition of invertebrates in the diet of salmon parr generally showed a positive correlation

Table III. Percent overlap in diet between the different age-groups of Atlantic salmon parr through the sampling season in the river Tana.

	Age-group (year)		
	1–2	1–3	2–3
May	51.2	43.4	69.3
July	69.7	52.7	77.1
August	65.6	61.7	79.9
September	65.2	56.6	70.5

Table IV. Diet width (Levins index) for the three age-groups of Atlantic salmon parr through the sampling season in the river Tana.

	Age-group (year)		
	1	2	3
May	7.9	5.3	6.6
July	5.4	4.9	3.3
August	11.2	5.0	4.7
September	6.8	6.9	3.2

with the composition in samples from benthos and surface and water column drift. However, strongest and significant rank correlations were mainly found between the diet and benthos, and only occasionally between diet and drift (figure 6).

4. DISCUSSION

There were large seasonal fluctuations in the abundance and relative composition of invertebrates in both benthos and drift, which appear to be a typical trait for lotic systems (Angermeier, 1982; Elliott, 1967). In all three lotic habitats, the invertebrate density was relatively low in May, highest in July and decreased to a minimum towards autumn. Both zoobenthos abundance and drift rates at the sampling site were low compared to densities found in tributaries to the river Tana (Erkinaro and Erkinaro, 1998). Flying insects made up the bulk of the surface drift, whereas chironomid larvae dominated both the suspended drift and the benthos, which has also commonly been observed in other subarctic rivers (Bergersen, 1989; Gabler et al., 2001; Huru, 1986).

The diet of the salmon parr exhibited large variations through the sampling season, and differed from the invertebrate composition in the environment. In

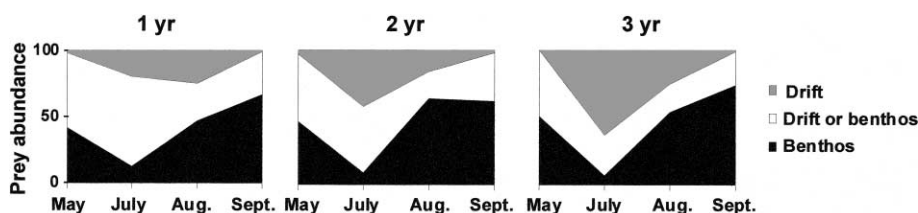


Figure 5. Seasonal variation in drift and benthos feeding of the three age-groups of Atlantic salmon parr in the river Tana.

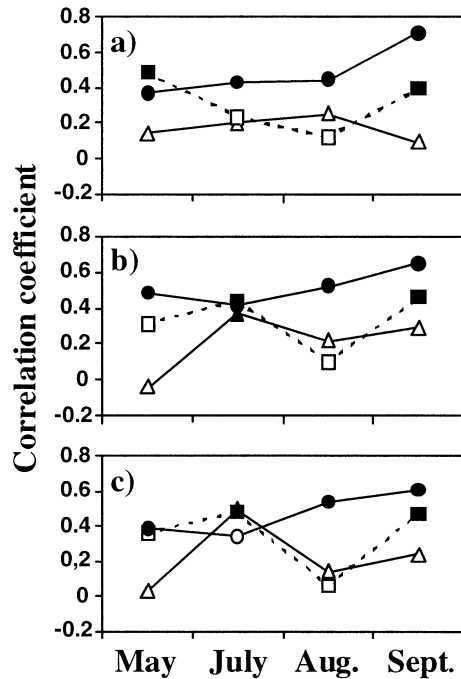


Figure 6. Spearman's rank correlation of percent composition of invertebrates in stomach samples of a) 1-, b) 2- and c) 3-year-old Atlantic salmon parr versus samples from surface drift (triangles), water column drift (squares) and benthos (circles). Closed symbols represent rank correlations that are significant ($P < 0.05$).

spring, mayfly and stonefly nymphs dominated in the stomachs, whereas surface insects and partly simuliid larvae were the most important prey types in July. Towards the autumn, Trichoptera larvae, in particular *A. stigmatella*, became increasingly important and dominated the diet, but mayfly and stonefly nymphs also made up a significant proportion. The three age-groups had in general a similar food resource use and the diet overlap was high, especially between the 2- and 3-year-old fish. Some differences could, however, also be seen between the 1- and 3-year-old parr.

In May, August and September, mayfly and stonefly nymphs and caddis fly larvae dominated the diets of all three age-groups. These prey groups occurred commonly in the environment samples, but were never dominant except in the bottom samples in September. Chironomid larvae, the group that generally dominated the zoobenthos and water column drift, were on the other hand not common in fish stomachs, even though other studies have shown that these larvae may constitute an important part of the salmon parr diet (e.g. Allan, 1940; Huru, 1986; Keeley and Grant, 1997). The dominant chironomid larvae in the environmental samples from the river Tana were small-sized, and may in light of Wańkowski's (1979) size experiments have been too small to be a valuable prey for the salmon parr. Wańkowski also pointed out that the optimum prey size changes with the size of the fish,

and even though the diet similarities between the different age-groups of the salmon parr in the river Tana were large, there were resource use patterns that suggested that some size-dependent diet segregation occurred. For example, large-sized caddis fly larvae increased in importance with increasing fish age, whereas the smaller mayfly nymphs and simuliid larvae and pupae decreased.

Other size-related differences in feeding behaviour between the different age-groups were apparent when taking the species level of invertebrate prey into account. In May, this could be best observed in the utilisation of stonefly nymphs. The 1-year-old fish had eaten all of the small stonefly species, very little of the larger *D. nanseni* and none of the big *A. compacta*. The older age-groups had in contrast concentrated on the two large species and not utilised the small stonefly nymphs. A similar size-related diet segregation could also be seen in the use of the large-sized larvae of the caddis fly *A. stigmatella*. In May, only the 3-year-old fish consumed this species. In September, all age-groups fed upon *A. stigmatella* larvae, but the abundance increased sharply with increasing age of the fish. An age-differentiated use of *A. stigmatella* larvae could also be seen in August, but not in the same degree as in May and September. These seasonal differences in the consumption of *A. stigmatella* were probably related to the life cycle of the species. In August, the larvae were in an early instar and small-sized. However, towards autumn and also during winter, they apparently grew rapidly and were found to be particularly large in early spring just before their emergence as adults. A similar life cycle of *A. stigmatella* has also been observed in streams in northern Sweden (Ulfstrand, 1968). Thus, in May and partly in September, these caged caddis fly larvae appeared to be too large to be efficiently preyed upon by the small salmon parr. The 1-year-old salmon parr therefore seemed to experience morphological limitations that excluded them from exploiting the largest prey types available, whereas the largest parr on the other hand appeared to avoid the smallest prey types (see also Keeley and Grant, 1997). As a result, some size-related diet segregation occurred between the different year-classes of salmon in the river Tana, and in particular between the 1- and 3-year-old parr.

In contrast to the other sampling months, both Trichoptera larvae and Plecoptera and Ephemeroptera nymphs were of minor importance in the diet of the salmon parr in July, and had been replaced by flying insects and simuliid larvae and pupae. The different age-groups had used these two prey categories in a different manner (figure 4d, e), but this diet pattern appeared not to be related to a size-restricted prey selection since these prey groups were relatively similar in size. The flying insects dominated the surface drift and was also the most important group in the July diet of the 3- and partly the 2-year-old fish, but less important with decreasing age. The simuliid larvae are on the other hand mostly associated with the

bottom, and this category was the dominant prey in the diet of the 1-year-old fish and became less important with increasing age. Thus, the dietary differences between the age-groups in July appeared to be related to a segregation in feeding habitat rather than being the result of a size-restricted prey selection. Large salmon parr have also in other studies been shown to take a larger proportion of their diet from the drift than the smaller fish (Stradmeyer and Thorpe, 1987; Thonney and Gibson, 1989).

July was the only month that drift feeding was found to be substantial for the salmon parr; in the other sampling months benthic feeding prevailed, in particular reflected by a large dietary contribution of the stone-cased caddis fly larvae *A. stigmatella*. This is surprising in light of the general view of salmon parr as a typical drift feeder (Keeley and Grant, 1997; Keenleyside, 1962; Stradmeyer and Thorpe, 1987; Vignes, 1999; Wańkowski and Thorpe, 1979), but extensive feeding from the bottom has also been demonstrated in other studies of juvenile salmon (Sosiak et al., 1979; Williams, 1981). Low drift feeding in the river Tana is also supported by the fact that the parr in late summer and autumn consumed most of their diet during the night (Amundsen et al., 2000). Salmon parr are known to have problems feeding from the drift when light levels are low, but are able to feed from the bottom even in complete darkness (Fraser and Metcalfe, 1997; Jørgensen and Jobling, 1992). The restricted drift feeding of the salmon parr in the river Tana may partly be related to low water temperatures. During sampling in May, the water temperature was only 0.2 °C, and at such low temperatures salmon parr are known to be unwilling to leave the bottom substrate to forage actively (Borgstrøm and Skaala, 1993). It has also been shown that drift feeding of salmon parr decreases towards autumn when the temperature decreases (Metcalfe et al., 1986; Stradmeyer and Thorpe, 1987). In the river Tana, however, drift feeding was less important than benthic feeding already in August, even though the temperature was almost as high as in July. The drift rates in the river Tana were generally low, but peaked in July. Apparently, the fish chose to feed from the drift only when the drift rates were high, and the availability of drifting prey seems to be a more important determinant for the incidence of drift feeding than the temperature. Similar results have also been found in studies of Dolly Varden charr (*Salvelinus malma*), where the fish changed from ambushing drifting invertebrates at fixed focal points to actively searching for and picking benthic invertebrates from the substratum when drift rates declined (Fausch et al., 1997; Nakano et al., 1999). Nislow et al. (1998) also found that age-0 Atlantic salmon reduced their drift foray rates and increased their benthic feeding when drift availability was experimentally reduced. The drift feeding feature of Atlantic salmon thus appears to be strongly dependent on the drift rates, and in subarctic rivers like the river Tana, the invertebrate production and drift rates

may be so low that drift feeding by salmon parr is feasible only during a short mid-summer period. Similar conclusions have also been reached in studies from other large subarctic rivers (Bergersen, 1989; Gabler and Amundsen, 1999; Amundsen et al., 2000; Gabler et al., 2001).

In conclusion, there was in general a high overlap in food resource utilisation between the different age-groups of salmon parr in the river Tana, although some diet segregation occurred, particularly between the 1- and 3-year-old fish. This segregation appeared to be related to size-dependent differences in prey choice and feeding abilities, but in July also to a different use of the drift and benthic feeding habitats. The low resource partitioning between the different age groups of salmon parr suggests that intraspecific competition for food may occur. All age-groups appeared to take most of their prey from the bottom, and substantial drift feeding only occurred in July. Restricted drift feeding of salmon parr may be a common feature of subarctic rivers due to low drift rates throughout most of the summer season.

Acknowledgements. Thanks are due to Trond Herfindal, Laina Dalsbø, Jan Evjen and Lisbeth Jørgensen for help and support during the course of the study. Financial support was provided by the Norwegian Directorate for Nature Management and the Governor of Finnmark County.

References

- Allan, J.D., Russek, E., 1985. The quantification of stream drift. *Can. J. Fish. Aquat. Sci.* 42, 210–215.
- Allan, K.R., 1940. Studies on the biology of the early stages of the salmon (*Salmo salar*) 1. Growth in the river Eden. *J. Anim. Ecol.* 9, 1–23.
- Allan, K.R., 1941. Studies on the biology of the early stages of the salmon (*Salmo salar*) 2. Feeding habits. *J. Anim. Ecol.* 10, 47–76.
- Amundsen, P.A., Gabler, H.M., Staldvik, F.J., 1996. A new method for graphical analysis of feeding strategy from stomach contents data. *J. Fish Biol.* 48, 607–614.
- Amundsen, P.A., Gabler, H.M., Herfindal, T., Riise, L.S., 2000. Feeding chronology of Atlantic salmon parr in subarctic rivers: consistency of nocturnal feeding. *J. Fish Biol.* 56, 676–686.
- Angermeier, P.L., 1982. Resource seasonality and fish diets in an Illinois stream. *Environ. Biol. Fish.* 7, 251–264.
- Bergersen, R., 1989. Zoobenthos and food of Atlantic salmon (*Salmo salar* L.) fry in Alta River, North Norway - and notes on the measurement of faunal resemblance. *Nordic J. Freshw. Res.* 65, 99–115.
- Borgstrøm, R., Skaala, Ø., 1993. Size-dependent catchability of brown trout and Atlantic salmon parr by electrofishing in a low conductivity stream. *Nordic J. Freshw. Res.* 68, 14–21.

- Egglisshaw, H.J., 1967. The food, growth and population structure of salmon and trout in two streams in the Scottish Highlands. *Freshw. Salmonid Fish. Res.* 38, 1–32.
- Elliott, J.M., 1967. Invertebrate drift in a Dartmoor stream. *Arch. Hydrobiol.* 63, 202–237.
- Erkinaro, H., Erkinaro, J., 1998. Feeding of Atlantic salmon, *Salmo salar* L., parr in the subarctic River Teno and three tributaries in northernmost Finland. *Ecol. Freshw. Fish* 7, 13–24.
- Erkinaro, J., 1995. The age structure and distribution of Atlantic salmon parr, *Salmo salar* L., in small tributaries and main stems of the subarctic River Tana, northern Finland. *Ecol. Freshw. Fish* 4, 53–61.
- Fausch, K., Nakano, S., Kitano, S., 1997. Experimentally induced foraging mode shift by sympatric charrs in a Japanese mountain stream. *Behav. Ecol.* 8, 414–420.
- Fraser, N.H.C., Metcalfe, N.B., 1997. The cost of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. *Funct. Ecol.* 11, 385–391.
- Frost, S., Hundi, A., Kershaw, W.E., 1971. Evaluation of a kicking technique for sampling stream bottom fauna. *Can. J. Zool.* 49, 167–173.
- Gabler, H.-M., Amundsen, P.-A., 1999. Resource partitioning between Siberian sculpin (*Cottus poecilopus* Heckel) and Atlantic salmon parr (*Salmo salar* L.) in a sub-Arctic river, North Norway. *Ecol. Freshw. Fish* 8, 201–208.
- Gabler, H.-M., Amundsen, P.-A., Herfindal, T., 2001. Diet segregation between introduced bullhead (*Cottus gobio* L.) and Atlantic salmon parr (*Salmo salar* L.) in a sub-Arctic river. *Arch. Hydrobiol.* 152 in press.
- Higgins, P.J., Talbot, C., 1985. Growth and feeding in juvenile Atlantic salmon (*Salmo salar* L.). In: Cowey, C.B., Mackie, A.M., Bell, J.G. (Eds.), *Nutrition and Feeding in Fish*. Academic Press, London, pp. 243–263.
- Huru, H., 1986. Diurnal variations in the diet of 0 to 3 years old Atlantic salmon *Salmo salar* L. under semiarctic summer conditions in the Alta River, northern Norway. *Fauna Norvegica Ser. A* 7, 33–40.
- Jørgensen, E.H., Jobling, M., 1992. Feeding behaviour and effect of feeding regime on growth of Atlantic salmon, *Salmo salar*. *Aquaculture* 101, 135–146.
- Keeley, E.R., Grant, J.W.A., 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 54, 1894–1902.
- Keenleyside, M.H.A., 1962. Skin-diving observations of Atlantic salmon and Brook trout in the Miramichi river, New Brunswick. *J. Fish. Res. Board Can.* 19, 625–634.
- Krebs, C.J., 1989. *Ecological Methodology*. Harper Collins Publ., New York.
- Levins, R., 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton.
- Metcalfe, N.B., Huntingford, F.A., Thorpe, J.E., 1986. Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). *Can. J. Zool.* 64, 2439–2446.
- Nakano, S., Fausch, K.D., Kitano, S., 1999. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. *J. Anim. Ecol.* 68, 1079–1092.
- Nislow, K.H., Folt, C., Seandel, M., 1998. Food and foraging in relation to microhabitat use and survival of age-0 Atlantic salmon. *Can. J. Fish. Aquat. Sci.* 55, 116–127.
- Peterson, R.H., Martin-Rubichaud, D.J., 1986. Aquatic insect histories and Atlantic salmon fry diets in the St. Croix River, New Brunswick, Canada. *Can. Tech. Rep. Fish. Aquat. Sci.* 1485, 1–26.
- Pollard, J.E., 1981. Investigator differences associated with kicking method for sampling macroinvertebrates. *J. Freshw. Ecol.* 1, 215–224.
- Rimmer, D.M., Power, G., 1978. Feeding response of Atlantic salmon (*Salmo salar*) alevins in flowing and still water. *J. Fish. Res. Board Can.* 35, 329–332.
- Schoener, T.W., 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51, 408–418.
- Sosiak, A.J., Randall, R.G., McKenzie, J.A., 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. *Can. J. Fish. Aquat. Sci.* 36, 1408–1412.
- Stradmeyer, L., Thorpe, J.E., 1987. Feeding behaviour of wild Atlantic salmon (*Salmo salar* L.) parr in mid- to late summer in a Scottish river. *Aquacult. Fish. Manage.* 18, 33–49.
- Thonney, J.P., Gibson, R.J., 1989. Feeding strategies of brook trout, *Salvelinus fontinalis*, and juvenile Atlantic salmon, *Salmo salar*, in a Newfoundland river. *Can. Field-Nat.* 103, 48–56.
- Ulfstrand, S., 1968. Benthic animal communities in Lapland streams. *Oikos Suppl.* 10, 1–20.
- Vignes, J.C., 1998. Relationships between size of Atlantic salmon parr (*Salmo salar*) and some characteristics of their prey. *Cybius* 22, 49–56.
- Vignes, J.C., 1999. Feeding rhythms of juvenile Atlantic salmon (*Salmo salar* L.) and trophic relationship with invertebrate drift. *Vie Milieu* 49, 293–300.
- Wallace, R.K., 1981. An assessment of diet-overlap indexes. *Trans. Am. Fish Soc.* 110, 72–76.
- Wańkowski, J.W.J., 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon (*Salmo salar* L.). *J. Fish Biol.* 14, 89–100.
- Wańkowski, J.W.J., Thorpe, J.E., 1979. Spatial distribution and feeding in Atlantic salmon (*Salmo salar* L.) juveniles. *J. Fish Biol.* 14, 239–247.
- Williams, D.D., 1981. The first diet of postemergent brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) alevins in a Quebec river. *Can. J. Fish. Aquat. Sci.* 38, 765–771.
- Williams, D.D., Feltmate, B.W., 1992. *Aquatic Insects*. CAB International, Wallingford.