

Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic

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The stomach contents of 2992 wild and 863 putative escaped farmed Atlantic salmon caught on floating long-lines in a Faroese research fishery in the late autumn (November–December) and winter (February–March) in the Northeast Atlantic (63–66°N and 1–10°W) during three consecutive fishing periods 1992/1993–1994/1995 were analysed. Hyperiid amphipods of the genus *Themisto*, euphausiids and mesopelagic shrimps are important sources of food for salmon in the autumn period and various mesopelagic fish as lantern fishes, pearlsides and barracudinas become equally important during the late winter period. The occasional presence in the stomachs of larger fish such as herring, blue whiting and mackerel is not considered to be evidence that these fish are a main source of food for salmon in the sea north of the Faroes. The proportion of stomachs containing food was significantly lower during autumn (53%) than during winter (78%). However, temperature-dependent evacuation rates could partly explain the apparent lower stomach content during the autumn, since the average ambient sea-surface temperature is 7°C in autumn compared to 3°C in winter. There was evidence of selective foraging. Fish were preferred over crustaceans, and amphipods were chosen over euphausiids. Large salmon (3+SW) tended to be more piscivorous than smaller fish. There was no difference in condition factor, number and weight proportions of prey, or in diet between wild and escaped farmed salmon, which suggests that escaped farmed salmon adapt well to the “wild” life in the ocean.

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Introduction

The abundance of Atlantic salmon (*Salmo salar* L.) has generally decreased during the last two decades (Parrish *et al.*, 1998; ICES, 1999). There are several reasons for this, including degradation of their freshwater habitats, pollution, the effects of parasites and diseases, and perhaps overfishing (see Parrish *et al.*, 1998; Mather, 1998). Furthermore, over the same period it has been observed that major changes in the distribution of sea-surface temperatures in the North Atlantic have taken place, and the effects of this have been suggested as contributing to increased post-smolt mortality (Reddin and Friedland, 1993; Friedland *et al.*, 1998).

Although more information about anadromous Atlantic salmon in their marine phase has been gained in

recent years (e.g. Mills, 1993), little is known about the food and feeding habits of salmon in the Northeast Atlantic (for review, see Hislop and Shelton, 1993). The few studies in the vicinity of the Faroes and in the Norwegian Sea mainly give a qualitative assessment of the importance of the various prey species for salmon (Struthers, 1970, 1971; Thurow, 1973; Hislop and Youngson, 1984; Hansen and Pethon, 1985). Salmon probably spend most of their time in the ocean close to the sea surface (Templeman, 1967; Reddin, 1985) preying on pelagic animals such as fish, crustaceans and squid.

The seaward migration of salmon smolts occurs in spring. The salmon normally spend one to three years, but occasionally up to five years, in the open ocean. One important feeding area for salmon in the Northeast

Atlantic during the autumn and winter months is in the central and southern Norwegian Sea, i.e. the area to the north of the Faroe Islands. This area is characterised by a front that separates warmer Atlantic water to the south from the colder and less saline Arctic water to the north (Hansen, 1985). Salmon are typically distributed in or close to the frontal areas (Jákupsstovu, 1988).

Since the development of large-scale fish farming in many areas of the Northeast Atlantic, significant numbers of fish farm escapees have been captured in the oceanic waters north of the Faroes (Hansen *et al.*, 1993, 1999). The fate of escaped salmon is poorly known, and we do not know how well they respond to the need to feed on wild prey items following their escape from culture.

Several authors have suggested that wild Atlantic salmon are opportunistic feeders (Hansen and Pethon, 1985; Reddin, 1988; Percy, 1992; Hislop and Shelton, 1993; Sturlaugsson, 1994). However, in the Atlantic there is no information that compares the stomach content of salmon at sea with the ranges of potential prey available. Although information from the literature on plankton and micronekton distributions in the Northeast Atlantic (e.g. Dunbar, 1964; Dalpadado *et al.*, 1998) might give a clue to the potential prey available to salmon, the insufficient temporal and spatial overlap of the data prevents any conclusion to prey selection and the feeding behaviour and foraging strategy of Atlantic salmon has been inferred only from indirect measures such as stomach analysis.

We test the hypothesis that Atlantic salmon that escape from fish farms are capable of exploiting wild prey in the same manner as wild fish in the same area by comparing stomach content of wild and escaped farmed salmon of different sea ages during autumn and winter in the sea north of the Faroes. In addition, we compared stomach contents with locally available prey to determine whether Atlantic salmon are selective or opportunistic feeders.

Materials and methods

Atlantic salmon were caught with floating long-lines in an experimental fishery in the Norwegian Sea (north of the Faroes) between 63–66°N and 1–10°W (Figure 1). Sampling took place during the autumn (November–December) and winter (February–March) in the three fishing periods 1992/1993, 1993/1994 and 1994/1995. The experimental fishery followed the general pattern of the commercial salmon fishery, which usually starts relatively close to the Faroes and, as the season progresses, moves gradually in a northeasterly direction (Figure 1). Normally there is a period of one to two months (late December to mid-February) separating the autumn and winter fisheries, when fishing is difficult due to bad weather.

The long-lines (on average 2000 hooks baited with sprat) were set at the surface early in the morning, before dawn. Hauling started approximately at noon and was completed between five and ten h later, depending on the weather conditions and complications, such as breaking of the line. Usually the first 50 salmon caught from each set were sampled for stomach analysis. The sea-surface temperature (SST) was measured four times a day, before and after setting and hauling of the long-line, respectively.

There was no indication that salmon regurgitate after capture. This cannot be completely verified, but neither the scientific staff onboard the research vessel nor the salmon fishermen noted any stomach contents on deck or in the water when hauling the line. Whether salmon regurgitate during hooking was not possible to determine.

Stomachs were removed and frozen immediately after capture. Fork length and gutted weight were measured and scales were collected from each fish. At 13 fishing locations, concurrent plankton samples were obtained (Figure 1, encircled points) using a modified Isaacs/Kidd midwater trawl (MIK), which is a circular framed 2-m diameter plankton net with a mouth opening of 3.1 m², with 2.5-mm meshes in the foremost 11 m and 0.5 mm in the hindmost 2 m. The net was towed at 2.5 knots for ten minutes at three depths; 5 m, 25 m, and 50 m, respectively. Plankton sampling was carried out in the morning (about 0700 and 0800 h) just after the long-lines had been set, except on the first station when the sample was taken at 1800 h.

Origin and sea age of salmon

Scales were used to identify the origin (i.e. wild or farmed) (Lund *et al.*, 1989; Lund and Hansen, 1991) and the sea age of the fish. The method used to identify farmed fish was developed by analysing Norwegian salmon of known origin, and the characters used were: estimated back calculated smolt size, the characteristics of the transition zone from fresh water to salt water, the position of sea winter bands, the number of summer checks, and the proportion of replacement scales at the marine stage. To be classified as reared at least two out of the six characters examined must indicate that the fish were of reared origin. This method has been shown to give good separation between farmed and wild salmon, but fish that escape at the smolt stage or were released as smolts for ranching or enhancement are difficult to detect accurately (Lund *et al.*, 1989). To minimise the bias in discriminating the salmon, fish that had been tagged or fin clipped, which is common for deliberate smolt releases, were excluded from the present analyses.

When no scale samples were available the origin of the fish was determined on the basis of discriminating external characters like fin erosion, which is common on

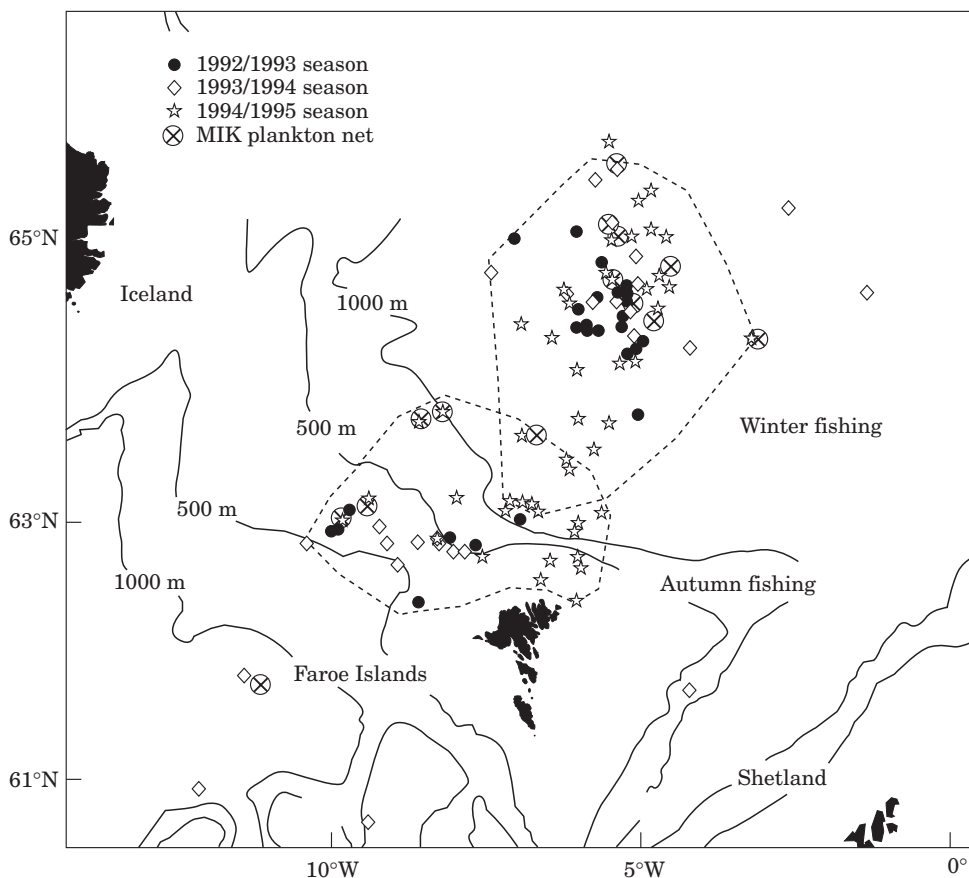


Figure 1. Fishing locations where 3855 stomachs of Atlantic salmon were sampled during the autumn (November–December) and winter (February–March) fishery in 1992/1993, 1993/1994, and 1994/1995 north of the Faroes. Plankton samples were taken on 15 locations in 1994 and 1995 (MIK plankton net). The main fisheries take place in the autumn closer to the Faroes than in the winter season (inside the stippled area). The 500 and 1000 m depth contours are shown.

reared salmon (Lund *et al.*, 1989). This method tends to be more conservative in that it underestimates the proportion of reared salmon that escape at an early stage, compared to the discrimination from the scale analysis. In this paper we consider the escaped farmed salmon as one group, irrespective of whether they have gained most of their weight in the wild or in a net pen prior to capture.

Salmon during their first winter in sea are termed one sea-winter (1SW) salmon. Salmon during their second winter in sea are termed two sea-winter (2SW) salmon, and similarly for 3SW and older salmon. The sea age of wild fish without scale samples was determined by applying a sea age/length relationship established from fish whose scales had been sampled [Figure 2(a)]. For farmed fish, however, a reliable sea age/length relationship could not be established from the examination of scales due to considerable overlap in length at various sea ages [Figure 2(b)]. However, to facilitate comparisons between different sea age groups of wild and

escaped farmed salmon in the analyses, it was decided to use the threshold lengths established for wild salmon in ageing the farmed fish without scale samples.

Stomach analysis

The identifiable stomach contents were separated by species and measured. Prey were weighed individually if possible, or divided into length groups, which were weighed and counted. The remaining food items were grouped, according to the degree of digestion, to genus, family or broad categories such as fish remains, crustacean remains or organic remains.

For quantitative analyses of the feeding habits of salmon, it is important that the number and corresponding weight of each prey species or prey group is available, to enable calculations of relative abundances. In 9% of the case (randomly scattered within the material) where either weights or lengths of prey could not be recorded due to advanced digestion, the corresponding

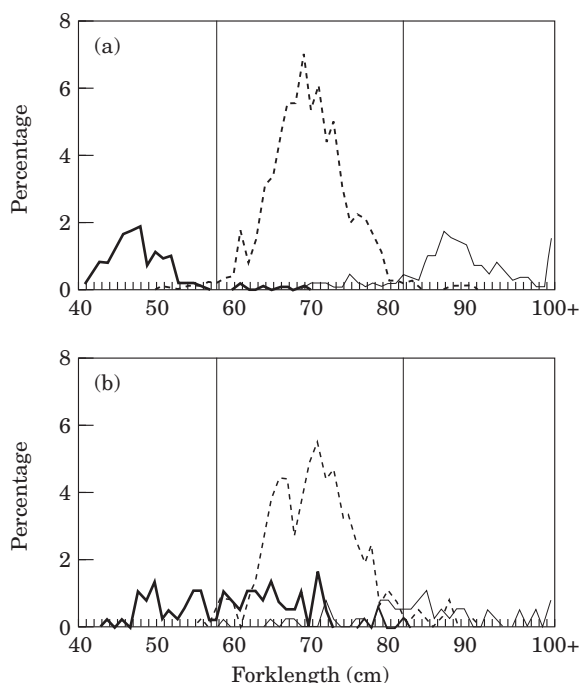


Figure 2. Size distribution (forklength) by sea age of wild salmon (a) and escaped farmed salmon (b) during 1992/1993–1994/1995 fishing seasons north of the Faroes (autumn and winter samples pooled). Sea age was determined by scale readings of 1112 wild and 369 farmed salmon, representing 37% and 43% of the total wild and farmed salmon caught, respectively. Threshold lengths separating wild salmon of sea age 1 and 2 (57 cm) and 2 and 3+ (81 cm) are shown as vertical lines on the graph. Bold line, 1SW; broken line, 2SW; solid line, 3+SW.

lengths or weights were estimated from a length/weight relationship established from less digested specimens. To minimise possible bias the length/weight relationship was obtained from other stomachs in the same long-line set. In the diet overlap calculations, where all prey items need to be enumerated, the stomachs containing unidentified prey were excluded. In doing so it was assumed that the distribution of prey species in the excluded stomachs was similar to that in stomachs with identifiable prey. The occurrence of stomachs with unidentified prey in the various categories in the analyses was on average 6% (range 2–13%).

Sprats that were obviously baits were observed in nearly half of the stomachs. Furthermore, bird feathers and inanimate material, such as nylon gut, sheets of plastic, flakes of paint etc. were also present in a few stomachs. Stomachs that contained only bait, feathers or inanimate material were categorised as empty.

For statistical analyses the data were grouped by several categories: season (autumn and winter), origin of salmon (wild and farmed) and sea age (1, 2, and 3+SW salmon). We also performed analyses by year (actually

by fishing period lasting from November–March) where data permitted such analyses, but unless otherwise stated all three years were pooled.

Condition

The condition factor (K) was calculated as $K = 10^5 w/l^3$, where w is gutted weight in kg and l is forklength in cm. When comparing categories, the condition factors were log transformed prior to ANOVA to normalise the data.

Feeding intensity and diet overlap

The feeding intensity was estimated from the proportion of empty stomachs in the total number of stomachs examined, as well as by the ratio of the average stomach content of prey (g) to body weight (kg). The data were log-transformed to ensure normality.

Relative abundance of each species in the stomachs was studied by use of three frequently used measures: (1) the percentage frequency of occurrence (%F), based on the number of stomachs in which each food item occurred in relation to the total number of stomachs sampled (including empty stomachs), (2) the percentage in number (%N) of each prey item in all stomachs in a sample, and (3) the weight percentages (%W) of each prey item in all stomachs in a sample.

The intraspecific diet overlap between wild and farmed salmon, sea ages of salmon, and seasons was investigated using the simplified Morisita overlap index (Horn, 1996) between predator j and k , $C_H = 2\sum p_{ij}p_{ik} / (\sum p_{ij}^2 + \sum p_{ik}^2)$, where p_{ij} and p_{ik} are the proportions (number or weight) of prey species i in the stomach contents of the predator j and k , respectively. The diet overlap was estimated for several pairs of predator groups, dependent on the problems addressed, i.e. between wild and farmed salmon, between sea ages, between autumn and winter samples. To assess the degree of diet overlap, the prey species (i) were split into ten groups, based on taxonomic adherence and size: 1=amphipods, 2=euphausiids, 3=shrimps, 4=other crustaceans, 5=pearlsides, 6=lanternfishes, 7=other small fish, 8=barracudinas, 9=other large fish, and 10=squids.

The overlap indices are critically dependent on the taxonomic resolution of the prey species groups (Krebs, 1989; Hansson *et al.*, 1996). A high degree of pooling gives a high overlap index. Because of this sensitivity, we do not consider the statistical significance of the results, but use them for descriptive purposes and discuss them in qualitative terms.

Prey availability and prey selection

The simplified Morisita overlap index was used to compare the MIK plankton samples and the salmon

Table 1. The salmon stomachs collected from 106 long-line sets in the Faroese research fishery during three fishing periods 1992/1993, 1993/1994, and 1994/1995. The number of salmon stomachs sampled by season, by putative origin (wild or farmed), and by sea aged (1, 2 and 3+ sea winters) are shown. Sea age 3+ includes some fish older than 3SW.

Fishing period	Season	Origin	1SW	Sea age 2SW	3+SW	Total
1992	Autumn	Farmed	6	15	4	25
		Wild	30	63	5	98
1993	Winter	Farmed	24	173	44	241
		Wild	26	549	341	916
Subtotal:			86	800	394	1280
1993	Autumn	Farmed	27	103	10	140
		Wild	27	260	23	310
1994	Winter	Farmed	25	85	11	121
		Wild	112	228	101	441
Subtotal:			191	676	145	1012
1994	Autumn	Farmed	19	120	1	140
		Wild	126	467	15	608
1995	Winter	Farmed	31	148	17	196
		Wild	48	506	65	619
Subtotal			224	1241	98	1563
Grand total:			501	2717	637	3855

stomach samples. However, large fish such as herring, barracudinas and the larger capelin (>50 mm) which may have been able to avoid the MIK plankton sampler, were excluded from the comparative analysis, as were jellyfish and remains of fish and crustaceans, that could not be enumerated.

Results

The numbers of stomachs sampled by season, putative origin and sea age are shown in Table 1. The overall proportion of farmed fish was estimated to be 863 fish (22.4%) of the 3855 fish sampled for stomach analyses. The threshold lengths separating 1 and 2SW and 2 and 3SW wild salmon were 57 cm and 81 cm, respectively [Figure 2(a)], with a misclassification of 6%. The same threshold lengths were used to age the farmed fish without scale samples, resulting in a misclassification of 22.5%. The number of 1SW farmed fish was underestimated and the number of 2 and 3SW farmed salmon was overestimated by this procedure [Figure 2(b)].

Of the 3855 stomachs collected, 1176 (31%) were empty or contained only bait, unidentified or inanimate material. On average, only half of the stomachs sampled in the autumn (53%) contained food while during winter 78% contained food. This difference was consistent over the three fishing periods. The frequency of fish containing food was significantly higher in farmed fish (85%) than in wild fish (76%) in winter samples ($\chi^2=18.74$, d.f.=1, $p<0.001$), but the difference was marginally non-significant in the autumn samples: 57% farmed and 51% wild ($\chi^2=3.61$, d.f.=1, $p=0.057$). There was no

conclusive trend with age in the proportion of empty stomachs.

Weight of stomach contents

From a regression analysis with log transformed data of the non-empty stomachs the average food content, s (g), was found to be proportional to the length, l (cm), of the fish, $s=3.153 \times 10^{-4} l^{2.238}$ ($r^2=0.58$, $p<0.001$, Figure 3). The value of the allometric exponent (2.238) suggests that neither the weight nor cube of the length would have standardised the data with respect to size of the fish. In our case since the weight (kg) of the salmon is proportional to the length of the fish, in that $w=3.542 \times 10^{-6} l^{3.22}$ ($r^2=0.95$, $p<0.001$), the stomach content/body weight ratio as a function of fish length would be $s/w=89.02 l^{-0.982}$, or approximately inversely related to fish length. Thus all quantitative comparisons of stomach contents were restricted to length or age groups to avoid ontogenetic dependencies.

Quantitative differences in stomach contents were observed between autumn and winter. A separate ANOVA by sea age of the logarithm of the stomach content/body weight ratio, $\ln(s/w)$, on season and type of salmon (Figure 4), showed no difference between wild and farmed salmon, but a significantly higher ratio in the winter than in the autumn for age groups 1 (1.966 vs. 0.599, $F_{1,276}=26.0$, $p<0.001$) and 2 (1.053 vs. 0.297, $F_{1,1913}=162.3$, $p<0.001$). The seasonal difference was non-significant for 3+SW salmon (0.416 vs. 0.215, $F_{1,478}=3.5$, $p=0.060$).

The increase in the average food content per salmon from autumn to winter was mainly due to a relative

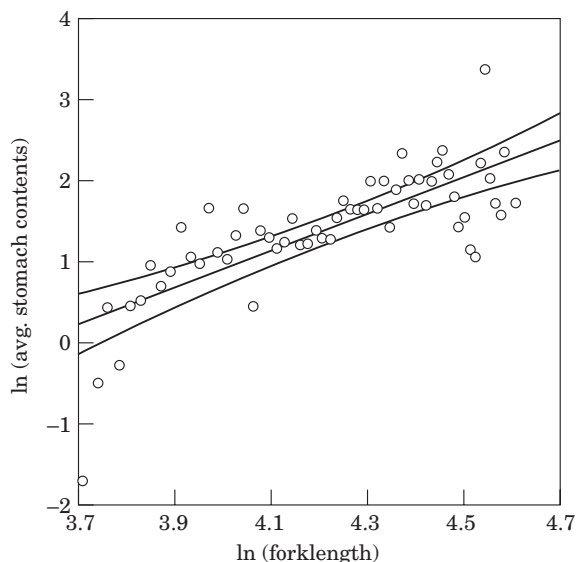


Figure 3. Double logarithmic regression of forklength (cm) on average stomach food content (g) per cm group, with 95% confidence bounds on the regression line. Data were obtained from 2679 non-empty salmon stomachs sampled during autumn and winter 1992/1993, 1993/1994, and 1994/1995 north of the Faroes.

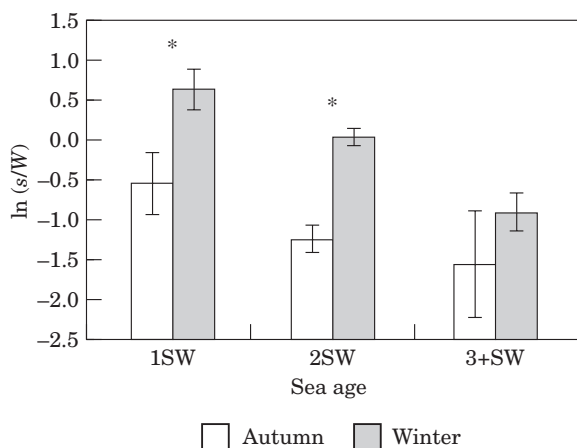


Figure 4. Average stomach content of prey (g)/body weight (kg) ratio (s/w) by sea age 1, 2 and 3+SW, respectively, grouped by season (autumn or winter). Wild and farmed salmon were pooled as there were no differences between them. Confidence intervals (95%) are indicated around the estimates and a star (*) indicates significant differences between seasons.

increase in mesopelagic fish (lanternfishes, pearlshades and barracudinas) in the diet (Tables 2 and 3).

Bait

Of the 3855 salmon caught and analysed, sprats that were obviously baits were observed in 1164 (30%) wild

and 390 (10%) farmed salmon. Of these, 78 (2%) wild and 36 (1%) farmed salmon, had taken more than one sprat, and a few salmon had even taken up to four baits prior to capture.

We anticipated that the frequency of fish that contained bait vs. no bait when caught would be independent of season, type of fish and size or age of fish. However, a significantly higher proportion of salmon contained bait during winter (43%) than during autumn (35%) ($\chi^2=27.3$, d.f.=1, $p<0.001$), and a significantly higher proportion of farmed salmon (45%) contained bait compared to wild salmon (39%) ($\chi^2=11.0$, d.f.=1, $p<0.001$). There were also significant differences in the proportions that contained bait vs. no bait among sea ages of salmon ($\chi^2=30.0$, d.f.=2, $p<0.001$), both during autumn and winter and for wild and farmed salmon. Bonferroni adjusted *a posteriori* tests showed that the proportion of the smaller 1SW (22%) salmon containing bait was significantly lower than for the larger 2 (41%) and 3+SW (52%) salmon, irrespective of season and type of fish ($\chi^2=77.2$, d.f.=1, $p<0.001$). The 2 and 3+SW salmon were not significantly different (average 43%).

The proportion of salmon that had taken two or more baits prior to capture vs. those containing only one bait was significantly higher during winter (9%) than during the autumn (3%) ($\chi^2=17.4$, d.f.=1, $p<0.001$), and this difference was highly significant for wild salmon: winter (2%) and autumn (8%) ($\chi^2=15.1$, d.f.=1, $p<0.001$). Although the same tendency was observed for farmed salmon, the results were non-significant: winter (5%) and autumn (11%) ($\chi^2=3.4$, d.f.=1, $p=0.064$). No differences were observed among sea ages of salmon in this respect.

Composition of the diet

The dietary importance of different food by seasons of wild and farmed salmon is shown in Tables 2 and 3. The most important crustaceans were amphipods (*Themisto libellula*, *T. compressa*, *T. abyssorum* and *Eusirus holmi*), shrimps (*Hymenodora glacialis*) and euphausiids (*Megamnyctiphanes norvegica* and *Thysanoessa inermis*). The most important fishes were pearlshades (*Maurollicus muelleri*), lanternfishes (*Benthosema glaciale* and *Notoscopeus kroeyeri*), barracudinas (*Notolepis rissoi kroeyeri*, *Paralepis coregonoides borealis*), blue whiting (*Micromesistius poutassou*), herring (*Clupea harengus*), capelin (*Mallotus villosus*), and mackerel (*Scomber scombrus*). There was no apparent difference in the prey species composition between wild and farmed salmon.

The abundances of the various prey species differed between seasons, but the differences were highly dependent on whether frequency of occurrence or percentages by number or weight was calculated. The occurrence and numerical representations favour the importance of

Table 2. Diet of wild salmon: frequency of occurrence (%F, including empty stomachs), number (%N), and weight percentages (%W) of prey items in salmon by autumn (A, November–December), winter (W, February–March) and in total. Values of 0 signify <0.1%. Data were collected from 2992 wild salmon stomachs of which 961 (32%) were empty.

Prey groups	%F			%N			%W		
	A	W	Total	A	W	Total	A	W	Total
Crustaceans:									
Hyperiid amphipods:									
<i>Themisto</i> spp.	16.1	14.9	15.3	22.6	21.6	22.2	11.6	4.0	5.3
<i>Themisto libellula</i>	14.6	26.7	22.6	5.2	27.8	14.1	4.2	6.6	6.2
<i>Themisto compressa</i>	23.2	19.4	20.7	70.3	19.8	50.2	31.5	1.4	6.7
<i>Themisto abyssorum</i>	1.0	3.3	2.5	0	0.3	0.1	0	0	0
Euphausiids:									
Euphausiidae	5.9	6.2	6.1	0.5	2.6	1.3	0.8	0.6	0.6
<i>Meganyctiphanes norvegica</i>	16.8	36.9	30.1	0.9	12.0	5.3	2.6	3.7	3.5
<i>Thysanoessa inermis</i>	0.7	2.2	1.7	0	0.4	0.2	0.1	0.1	0.1
<i>Thysanoessa longicaudata</i>	0.3	0.2	0.2	0	0	0	0	0	0
Shrimps:									
<i>Hymenodora glacialis</i>	2.7	23.0	16.1	0.1	2.4	1.0	0.8	4.5	3.8
<i>Sergestes arcticus</i>	0.4	0.2	0.3	0	0	0	0.1	0	0
<i>Pasiphaea tarda</i>	—	0.1	0	—	0	0	—	0	0
Other crustaceans:									
<i>Paraeucaeta norvegica</i>	0.3	—	0.1	0	—	0	0	—	0
Gammaridea	—	0.2	0.1	—	0	0	—	0	0
<i>Aristias tumidus</i>	0.1	—	0	0	—	0	0	—	0
<i>Eusirus holmi</i>	—	2.0	1.3	—	0.1	0.1	—	0.2	0.1
Crustacea remains:	2.4	17.7	12.5	0.1	1.1	0.5	0.5	4.0	3.4
Fishes:									
Pearlsides:									
<i>Maurollicus muelleri</i>	2.4	16.8	11.9	0.1	3.6	1.5	1.3	10.0	8.5
Baracudinas:									
Paralepidae	0.3	2.3	1.6	0	0.2	0.1	2.6	8.2	7.2
<i>Notolepis rissoi kroyeri</i>	0.1	0.9	0.6	0	0.1	0	0.5	3.9	3.3
<i>Paralepis coregonoides borealis</i>	0.4	0.2	0.3	0	0	0	2.5	0.9	1.2
Lanternfishes:									
Myctophidae	0.4	8.1	5.5	0	1.2	0.5	0.3	6.8	5.7
<i>Lampanyctus crocodilus</i>	—	0.1	0	—	0	0	—	0.1	0.1
<i>Notoscopelus kroyeri</i>	0.6	0.3	0.4	0	0	0	2.8	0.4	0.8
<i>Myctophum punctatum</i>	0.1	0.6	0.4	0	0.1	0	0.1	0.5	0.4
<i>Benthoosema glaciale</i>	0.9	10.3	7.1	0	1.7	0.7	0.9	10.1	8.5
Other fish:									
Ammodytidae	—	0.2	0.1	—	0	0	—	0	0
<i>Mallotus villosus</i>	—	0.2	0.1	—	0.1	0	—	0.9	0.8
Fry (mostly <i>Mallotus villosus</i>)	0.5	3.5	2.5	0.1	2.3	1.0	0.2	1.6	1.4
<i>Clupea harengus</i>	0.2	0.6	0.4	0	0	0	5.5	9.0	8.4
<i>Micromesistius poutassou</i>	0.7	—	0.2	0	—	0	18.5	—	3.3
<i>Onogadus argentatus</i>	—	—	—	—	—	—	—	—	—
<i>Lycenchelys</i> sp.	—	0.1	0	—	0	0	—	0.1	0.1
<i>Scomber scombrus</i>	0.3	0.1	0.1	0	0	0	7.3	0.5	1.7
<i>Belone belone</i>	—	0.1	0.1	—	0	0	—	0.6	0.5
<i>Gasterosteus aculeatus</i>	—	0.1	0.1	—	0	0	—	0.1	0.1
Fish remains:	6.1	34.4	24.8	0.1	2.2	1.0	4.2	17.1	14.8
Squid:									
Gonatidae	0.1	0.9	0.6	0	0.1	0	0	2.4	2.0
<i>Gonatus fabricii</i>	—	0.1	0	—	0	0	—	0.2	0.1
Inanimate remains:	2.2	2.8	2.6	0	0.2	0.1	1.1	1.2	1.2
Birds and bird remains:	0.3	0.4	0.3	—	0	0	—	0.2	0.1

numerous small and frequently occurring prey (e.g. crustaceans) whereas the weight representations favour the larger and often infrequent prey such as fish. Crustaceans including *Themisto* spp., euphausiids and pelagic

shrimps accounted for 95% of the food in number, but only about 30% by weight. By weight, 66% of the stomach content was fish, particularly mesopelagic fish such as lanternfishes, pearlsides and barracudinas, which

Table 3. Diet of putative farmed salmon: frequency of occurrence (%F, including empty stomachs), number (%N), and weight percentages (%W) of prey items in salmon by autumn (A, November–December), winter (W, February–March) and in total. Values of 0 signify <0.1%. Data were collected from 863 farmed salmon stomachs of which 215 (25%) were empty.

Prey groups	%F			%N			%W		
	A	W	Total	A	W	Total	A	W	Total
Crustaceans:									
Hyperiid amphipods:									
<i>Themisto</i> spp.	20.3	19.0	19.5	23.2	24.0	23.5	11.6	3.6	4.8
<i>Themisto libellula</i>	13.8	28.5	23.3	10.9	22.3	15.6	6.5	4.8	5.1
<i>Themisto compressa</i>	25.6	24.6	24.9	60.8	17.9	43.1	25.7	1.4	5.0
<i>Themisto abyssorum</i>	1.3	4.5	3.4	0.1	0.4	0.2	0.1	0	0.1
Euphausiids:									
Euphausiidae	7.5	8.2	8.0	3.1	4.1	3.5	5.2	0.7	1.4
<i>Meganyctiphanes norvegica</i>	21.6	43.2	35.6	1.4	14.7	6.8	4.0	3.9	3.9
<i>Thysanoessa inermis</i>	1.0	2.7	2.1	0	0.3	0.1	0.1	0.1	0.1
<i>Thysanoessa longicaudata</i>	1.0	0.2	0.5	0	0	0	0	0	0
Shrimps:									
<i>Hymenodora glacialis</i>	2.3	26.5	18.0	0.1	2.9	1.2	1.2	4.2	3.8
<i>Sergestes arcticus</i>	0.3	0.2	0.2	0	0	0	0.1	0.2	0.1
<i>Pasiphaea tarda</i>	—	—	—	—	—	—	—	—	—
Other crustaceans:									
<i>Paraeuchaeta norvegica</i>	0.7	—	0.2	0	—	0	0	—	0
Gammaridea	—	0.4	0.2	—	0	0	—	0	0
<i>Aristias tumidus</i>	—	—	—	—	—	—	—	—	—
<i>Eusirus holmi</i>	0.3	2.7	1.9	0	0.2	0.1	0.1	0.2	0.2
Crustacea remains:	20.3	19.0	19.5	0	1.3	0.6	0.7	4.8	4.2
Fishes:									
Pearlsides:									
<i>Maurollicus muelleri</i>	2.3	20.8	14.3	0.1	3.4	1.4	2.2	7.6	6.8
Baracudinas:									
Paralepidae	0.3	3.2	2.2	0	0.2	0.1	4.3	9.6	8.8
<i>Notolepis rissoi kroyeri</i>	—	0.7	0.5	—	0	0	—	2.0	1.7
<i>Paralepis coregonoides borealis</i>	—	0.4	0.2	—	0	0	—	0.6	0.5
Lanternfishes:									
Myctophidae	2.0	8.6	6.3	0.1	1.3	0.6	2.2	6.1	5.5
<i>Lampanyctus crocodilus</i>	—	—	—	—	—	—	—	—	—
<i>Notoscopelus kroeyeri</i>	—	0.2	0.1	—	0	0	—	0.4	0.4
<i>Myctophum punctatum</i>	—	0.4	0.2	—	0	0	—	0.6	0.5
<i>Benthoosema glaciale</i>	1.0	9.9	6.7	0	1.6	0.7	0.9	7.2	6.3
Other fish:									
Ammodytidae	—	—	—	—	—	—	—	—	—
<i>Mallotus villosus</i>	0.7	0.5	0.6	0	0	0	1.5	0.7	0.8
Fry (mostly <i>Mallotus villosus</i>)	0.3	4.1	2.8	0	2.3	0.9	0	1.4	1.2
<i>Clupea harengus</i>	0.3	0.7	0.6	0	0.1	0	6.7	10.8	10.2
<i>Micromesistius poutassou</i>	1.0	—	0.3	0	—	0	20.4	—	3.0
<i>Onogadus argentatus</i>	0.3	—	0.1	0	—	0	0.7	—	0.1
<i>Lycenchelys</i> sp.	—	—	—	—	—	—	—	—	—
<i>Scomber scombrus</i>	—	—	—	—	—	—	—	—	—
<i>Belone belone</i>	—	—	—	—	—	—	—	—	—
<i>Gasterosteus aculeatus</i>	—	—	—	—	—	—	—	—	—
Fish remains:	6.2	39.1	27.5	0.1	2.5	1.1	4.1	22.7	19.9
Squid:									
Gonatidae	—	1.6	1.0	—	0.1	0	—	2.3	1.9
<i>Gonatus fabricii</i>	—	—	—	—	—	—	—	—	—
Inanimate remains:	1.6	6.5	4.8	0	0.4	0.2	1.6	3.8	3.5
Birds and bird remains:	—	0.4	0.2	—	0	0	—	0.5	0.4

corresponded to only 5% in number. Some larger pelagic fish such as herring, blue whiting and mackerel were also present (0.1% by number and 13% by weight). Fish and crustacean prey accounted for 96% of the weight of all

prey taken, the remainder was equally divided between unidentified organic remains and squid. These figures were similar for wild and farmed salmon (Tables 2 and 3).

Table 4. ANOVA of condition factor ($K=10^5 w/l^3$) for 3855 salmon grouped by season (autumn or winter), type (wild or farmed) and sea age (1, 2 or 3+SW). ***=0.1% significance level.

Source of variation	Sum of squares	d.f.	Mean-square	F-ratio	p	Sign
Season	0.558	1	0.558	48.234	0.000	***
Type	0.027	1	0.027	2.325	0.127	
Sea age	0.033	2	1.517	131.103	0.000	***
Season \times Type	0.001	1	0.001	0.064	0.800	
Season \times Sea age	0.034	2	0.017	1.467	0.231	
Type \times Sea age	0.005	2	0.002	0.209	0.811	
Error	44.483	3845	0.012			

Condition

The multiple ANOVA revealed highly significant differences in K between season (autumn and winter) and sea age (1, 2 and 3+SW) but not between wild and escaped farmed salmon during their feeding phase in the sea (Table 4). The significant difference between the age groups was due to a large increase in K from the smaller 1 and 2SW salmon (which were not significantly different) to the larger 3+SW fish (Figure 5). Both 1 and 2SW salmon had significantly higher condition factors in autumn than in winter, but the condition of 3+SW salmon did not depend on season (Figure 5).

Prey type versus sea-surface temperature

Seasonal differences in temperature regimes were observed between the autumn and winter feeding areas (Figure 1), with a shift in the ambient sea-surface temperature (SST+s.d.) at the fish locations (sets) from 7°C ($\pm 1.6^\circ\text{C}$) ($n=48$) in the autumn to 3°C ($\pm 1.3^\circ\text{C}$) ($n=70$) in the winter.

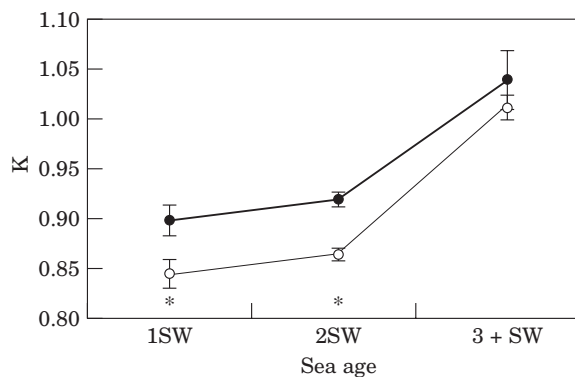


Figure 5. Condition factor ($K=w/10^5 l^3$, w is gutted weight in kg and l is forklength in cm) in 3855 salmon grouped by season (autumn or winter) and sea age (1, 2 or 3+SW). Wild and farmed salmon were pooled due to no difference in K . Confidence intervals (95%) are indicated around the estimates and a star (*) indicates significant differences between seasons. —●—, Autumn; —○—, winter.

The species composition of two of the three hyperiid amphipods of the genus *Themisto* found in the stomachs, i.e. *Themisto libellula* and *T. compressa* f. *compressa* [the “short-legged” form of *T. compressa* (Schneppenheim and Weigmann-Haas, 1986), a phenotype developing in warmer water than the “long-legged” form *T. compressa* f. *bispinosa* (Sheader, 1975)], showed an inverse relationship of abundance (number and weight) in the stomachs of both wild (Table 2) and farmed salmon (Table 3). When *T. compressa* f. *compressa* is present in large numbers, then the number of *T. libellula* is low and vice versa. Linear regressions of the natural logarithm of prey weight percentages of *T. libellula* and *T. c. f. compressa*, respectively on ambient SST (Figure 6), showed that the abundance of *T. libellula* was significantly positively related to ambient

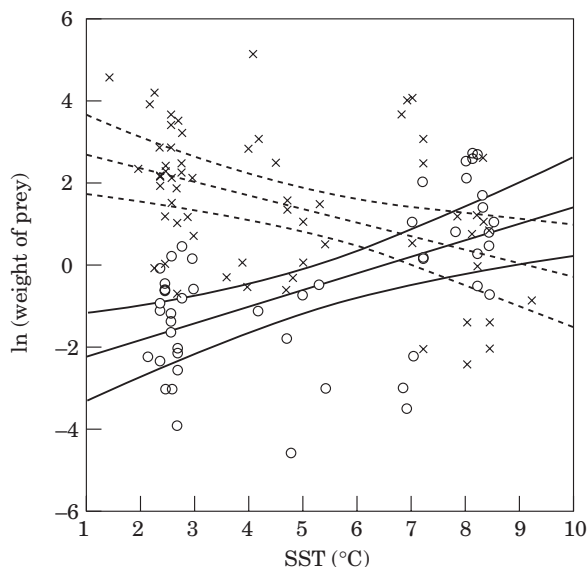


Figure 6. Percentage weight distribution of two hyperiid amphipods *Themisto libellula* and *T. compressa* f. *compressa*, respectively, in the salmon stomachs grouped by SST (sea-surface temperature) from the period 1993–1995. The 95% confidence intervals on the regression lines are indicated. ○ and —, *T. compressa* f.c.; × and —, *T. libellula*.

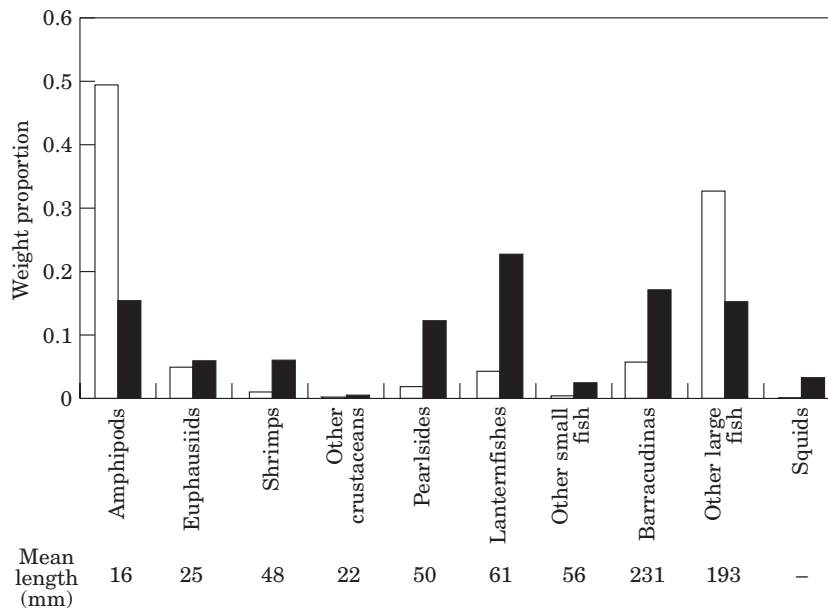


Figure 7. Diet of salmon (proportions by weight) in autumn (open) and winter (filled), for the ten prey groups defined and used in the calculation of diet overlap. Mean prey length (mm) is indicated below each prey group. Squid were not measured, but were juveniles.

SST ($F_{1,63}=14.8$, $r^2=0.196$, $p<0.001$) and the abundance of *T. c. f. compressa* was significantly negatively related to ambient SST ($F_{1,43}=21.6$, $r^2=0.315$, $p<0.001$). Thus, of the amphipods *T. libellula* dominated in the stomachs of salmon caught in the colder areas or periods while *T. c. f. compressa* dominated in salmon from the warmer areas.

Diet overlap

There was no difference in the diets of wild and farmed salmon; the simplified Morisita overlap index was 0.995, indicating a very high degree of overlap in choice of prey species or species groups. The high overlap was also evident between seasons (autumn, 0.994 and winter, 0.991) and sea age groups 1, 2, and 3+SW (0.876, 0.984, and 0.981, respectively). Thus we pooled wild and farmed salmon in the further analyses.

The seasonal index was 0.584, indicating a moderately low overlap in the stomach content between autumn and winter. The seasonal overlap within each age group was 0.706, 0.527, and 0.728 for sea age 1, 2, and 3+SW, respectively, indicating that the differences between seasons was mainly due to 2SW salmon, which is the main age group caught (72%). The seasonal differences in prey (Figure 7) show that mainly amphipods and the group “other large fish” were eaten during autumn, while the contribution to the weight percentages were more evenly distributed among lanternfishes,

barracudinas, pearlsides, “other large fish” and amphipods during winter.

A closer examination of the seasonal differences of the large fish prey, i.e. the groups barracudinas and “other large fish” show that mainly blue whiting, and to a lesser extent herring, and barracudinas (Tables 2 and 3) were eaten during autumn, while mainly barracudinas, herring, and some capelin fry were eaten during winter (Figure 8). Although the contribution in weight of the larger fish prey is high, only 136 salmon (3.5%) had taken these prey.

The 1 and 2SW salmon had a relatively high diet overlap (0.764). However, the moderate diet overlap between 2 and 3+SW salmon (0.648) and the low overlap between 1 and 3+SW (0.359) indicated a shift in prey composition among age (size) groups of salmon. The smaller 1SW salmon had mainly eaten amphipods and lanternfishes, and some barracudinas, while the larger 3+SW salmon had mainly eaten large fish, barracudinas and lanternfishes, and the 2SW salmon had eaten the various prey groups in intermediate proportions compared to the 1SW and 3+SW salmon (Figure 9). Thus, with increasing age (size) of the predator, the larger fish prey were preferred to smaller mesopelagic fish and crustaceans. The age distribution of salmon containing large prey (3% 1SW, 66% 2SW, and 31% 3+SW) was significantly larger than for the remaining fish (11% 1SW, 72% 2SW, and 17% 3+SW) (χ^2 , d.f.=2, $p<0.001$) and the difference between each proportion within each age was significant (χ^2 tests adjusted for

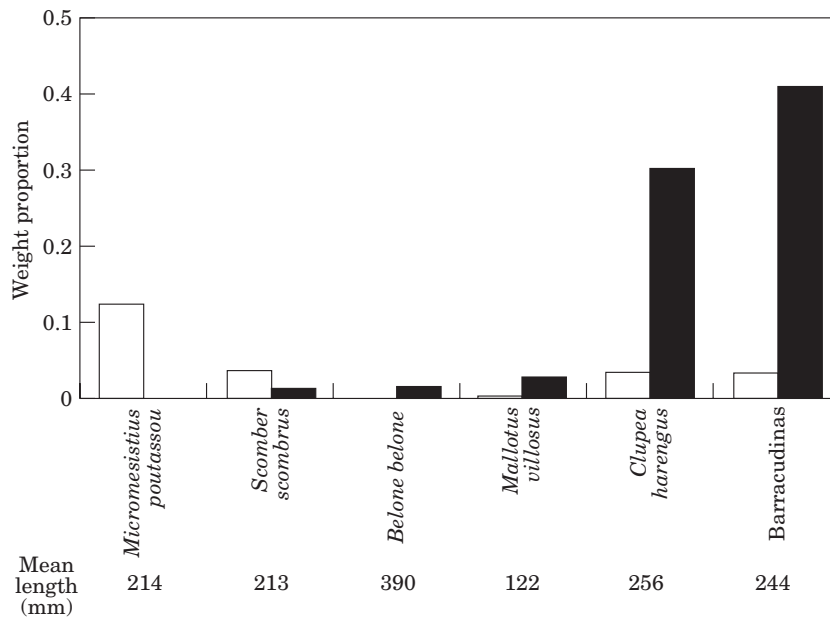


Figure 8. Proportion by weight of large fish prey taken by salmon in autumn (open) and winter (filled). Mean prey length (mm) is indicated below each prey group. Only one *Belone belone* was measured.

multiple comparisons). The reported age-specific changes towards fish with increasing age were evident both in the autumn and winter season.

Prey size to fish size

The relationships between average prey size and fish size for *Themisto libellula*, *Meganyctiphanes norvegica*, *Hymenodora glacialis* and *Mauroliticus muelleri* were examined. Generally the average prey size in the stomachs did not depend on fish size, except for *T. libellula*, where a significant positive relationship was observed ($r^2=0.039$, d.f.=426, $p<0.001$). The lengths of *T. libellula* were transformed to natural logarithms to assure that they were normally distributed. However, the regression had a very low explanatory value (4%).

Prey availability and prey selection

In total 319 non-empty salmon stomachs were observed at the 13 fishing stations where corresponding MIK plankton samples were available. The abundance of prey species and their weight percentages show that the plankton tows generally included the same species as found in the stomachs, i.e. the hyperiid amphipods, euphausiids, shrimps, lanternfishes and pearlsides (Table 5). However, *Sagitta* spp. and a few individuals of the small copepod, *Calanus finmarchius*, were observed in the plankton samples, but were absent from the stomachs. On the other hand, large fish such as herring, barracudinas and the larger capelin (>50 mm) found in

the salmon stomachs were not caught with the net, probably due to avoidance. The data set for calculating an overlap index was thus limited by excluding larger fish as well as jellyfish and remains of fish and crustaceans that could not be enumerated (Table 5). Although most of the species occurred in both data sets, their relative proportions differed greatly, resulting in a low overlap index (0.3). Atlantic salmon appeared to prefer small pelagic fish to crustaceans. Furthermore, they appeared to prefer amphipods (*Themisto* spp.) to euphausiids. On average, the salmon had taken twice as much amphipod as euphausiid prey while the plankton sampler caught 13 times more euphausiids than amphipods (Table 5). There were also great variations and low overlap between the two prey groups at the individual sampling stations, but the preference of amphipods to euphausiids was also evident at sampling station level (Figure 10). Of the euphausiids, it seems that salmon prefer the larger *Meganyctiphanes norvegica* to the smaller *Thysanoessa longicaudata* and *T. inermis*, suggesting size selective feeding (Figure 10).

To further explore possible selective feeding behaviour by salmon, the percentage length distributions of six species or groups were studied in more detail [Figure 11(a)–(f)]. The pearlsides, *Mauroliticus muelleri*; the amphipods *Themisto libellula*, *T. compressa*, including both forms, i.e. *T. c. f. compressa* and *T. c. f. bispinosa*, and *T. abyssorum*; the euphausiids *Meganyctiphanes norvegica*, and *Thysanoessa* spp., including both *T. inermis* and *T. longicaudata* were chosen due to available length distributions in both the plankton and the

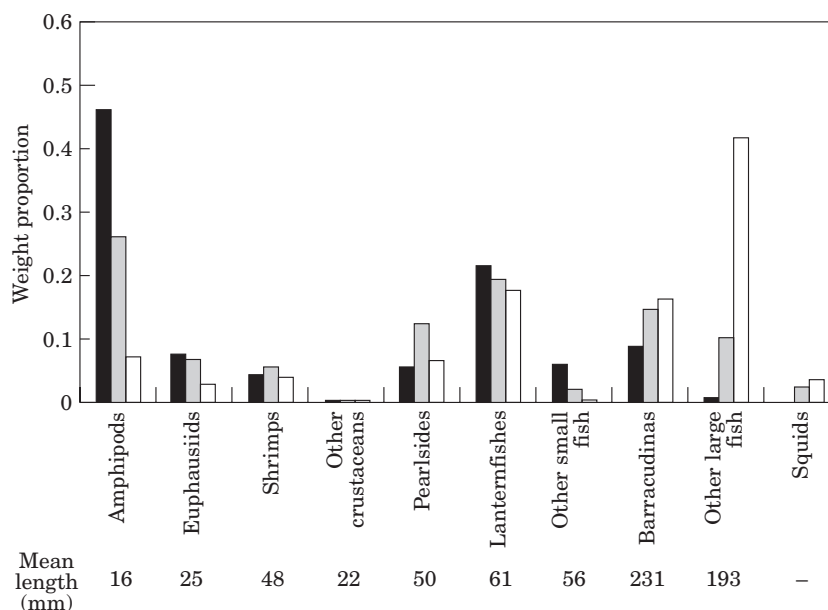


Figure 9. Diet of 1 (filled), 2 (hatched), and 3+SW (open) salmon (proportions by weight, in the ten prey groups defined and used in the calculation of diet overlap). Mean prey length (mm) is indicated below each prey group. Squid were not measured, but were juveniles.

stomach samples. For four of the six groups the size distribution of the prey eaten by salmon was larger than that of the animals caught in the corresponding plankton samples. This was especially true for *M. mülleri*, where the 1 and 2+ groups were eaten by salmon but only the 1 groups were caught in the plankton net [Figure 11(a)]. There was an almost perfect overlap between the length distributions in the stomach content and plankton samples of the amphipods *Themisto libellula* and *T. compressa* [Figure 11(b)–(c)], but all *T. abyssorum* taken by salmon were larger than those caught in the plankton sampler [Figure 11(d)]. Similarly, the euphausiids eaten were larger than those caught in the plankton net [Figure 11(e)–(f)].

Discussion

The classification of the salmon as wild or farmed based on scale samples was considered accurate to within approximately 8% (Lund *et al.*, 1989). The classification of the remaining fish without scale samples (62% of total) based on external discriminating characters resulted in a less effective discrimination of the reared component that escape as smolt or at the early marine stage (for a discussion, see Hansen *et al.*, 1999).

The ageing of wild salmon without scale samples (63% of the wild salmon) was fairly accurate while the ageing of the farmed fish without scale samples (57% of the farmed salmon) was less effective with a misclassification of 22.5%. The relatively large discrepancy between

length-at-age of the escaped farmed fish compared to the wild salmon is mainly due to the variable size at time of escape from sea cages at the coast, and the fact that reared salmon are larger at age than wild salmon due to the high growth rate under rearing conditions. Furthermore, the age of the farmed fish tend to be overestimated due to marks or checks in the scales being erroneously interpreted as winter bands (Lund *et al.*, 1989).

About 80–90% of the salmon (all sea ages) present in the area north of the Faroes are estimated to mature the following autumn (ICES, 1984; Youngson and McLay, 1985; Jákupsstovu, 1988), and are thus destined to leave this area sometime during late winter or spring, the timing being supposedly dependent on the distance to the home river (Jacobsen *et al.*, 2001). The relatively high proportion of mature fish in the sampling area makes comparisons among sea age groups less affected by the fact that some of the non-maturing fish might have different life history strategies than the maturing fish.

Stomach contents

The results of the present study revealed that crustaceans including *Themisto* spp., euphausiids and pelagic shrimp accounted for more than 95% of the food in number, but by weight 66% of the stomach content was fish, particularly lantern fishes, pearlsides and barracudinas. Some larger pelagic fish such as herring, blue whiting and mackerel were also present (0.1% by number and 13% by weight).

Table 5. Total wet-weight percentages of different prey groups in the salmon stomachs and in the MIK plankton samples from 13 corresponding fishing locations. Table entries marked with a dash (—), means that prey species/group were not found in the sample. Total wet-weights (g) of all samples are given at the bottom row in parentheses. Well digested crustacean and fish remains were found in the stomachs, while in the MIK samples the material was fresh and identifiable to species or family. To calculate the simplified Morisita overlap index between the prey species in the stomachs and in the MIK samples, the data set was reduced by excluding large fish that avoided the plankton net, and remains and jellyfish that could not be enumerated, i.e. the entries marked with a star (*) in the two right-hand columns.

Species/group	Category	Stomachs weight % ^a	MIK samples weight % ^b	Stomachs weight %	MIK samples weight %
Scyphozoa	Jellyfish	—	2.17	*	*
<i>Tomopteris</i> sp.	Polychaeta	—	0.05	—	0.05
Bivalvia	Mussels	—	0.01	—	0.01
<i>Sagitta</i> sp.	Chaetognatha	—	0.98	—	1.01
<i>Lepeophtheirus salmonis</i> ^c	Crustaceans	—	0.01	—	0.01
<i>Calanus finmarchicus</i>	Crustaceans	—	0.10	—	0.10
<i>Aristias tumidus</i>	Crustaceans	0.003	—	0.006	—
<i>Eusirus holmi</i>	Crustaceans	0.25	—	0.43	—
<i>Pareuchaeta norvegica</i>	Crustaceans	0.002	1.25	0.003	1.27
<i>Themisto</i> spp.	Crustaceans	16.37	6.82	31.85	6.97
Euphausiidae	Crustaceans	8.72	87.54	14.90	89.47
<i>Hymenodora glacialis</i>	Crustaceans	5.15	0.05	8.90	0.05
Crustacean remains	Crustaceans	5.62	—	*	*
<i>Gonatus fabricii</i>	Squid	0.02	0.03	0.03	0.03
<i>Maurolicus mülleri</i>	Fish-small	4.74	0.54	8.10	0.56
Myctophidae	Fish-small	18.25	0.03	31.17	0.03
<i>Mallotus villosus</i> ^d	Fish-small	2.70	0.44	4.61	0.44
<i>Mallotus villosus</i> ^d	Fish-large	0.44	—	*	*
Paralepididae	Fish-large	9.45	—	*	*
<i>Clupea harengus</i>	Fish-large	15.90	—	*	*
Fish remains	Fish	12.38	—	*	*
Total wet-weight (g)		(1 719)	(837)	(1 006)	(819)

^aTotal weight % in 319 non-empty salmon stomachs (of 481 sampled) from 13 fishing locations.

^bTotal weight % in the MIK plankton samples taken on the 13 fishing locations as above.

^cA few salmon lice have been found in salmon stomachs from other samples in the same area.

^dOnly capelin fry (<50 mm) was caught in the MIK samples while both fry and adult specimens were found in the salmon stomachs.

Hislop and Shelton (1993) proposed that the crustaceans were a much less important prey than fish in the North Atlantic. However, the extensive material studied here places more emphasis on crustacean prey in the Northeast Atlantic, particularly the hyperiid amphipods and to a lesser extent euphausiids. Even so, fish were twice as important as crustaceans in terms of weight. In the autumn salmon seemed to rely on amphipods as food. This is in contrast to the food of adult fish captured in net sets in coastal areas when returning to spawn (Blair, 1965; Grønvik and Klemetsen, 1987; Hislop and Webb, 1992), where fish totally dominate [with one notable exception where crustaceans were the main food (Neilson and Gillis, 1979)].

Condition

It appears that the condition factor, K, for salmon in the sea off the Faroes is relatively high, especially for 3+SW salmon, and is comparable to that of salmon in West

Greenland waters (Lear, 1972; Munro and Swain, 1980). It is also higher than the K observed experimentally with salmon fed *ad libitum* at comparable temperatures by Dwyer and Piper (1987), with levels of K around 0.82 and 0.85, respectively, compared to our respective estimates of 0.90 and 0.94.

If the condition factor is indicative of feeding performance in the area, then the significantly higher condition of 3+SW salmon than of the smaller salmon, irrespective of season, might be a reflection of higher tolerance (due to size) of low temperatures, greater potential to forage over a wide area and greater possibility to capture a wide range of prey. In addition, the feeding rate (stomach content/body weight ratio) of the larger 3+SW salmon is more independent of season than for the smaller salmon. It should be noted that any influence of maturity on the condition factors can be ruled out since the K was calculated from gutted weight.

There was no difference in condition between wild and farmed salmon, despite the likelihood that some of the

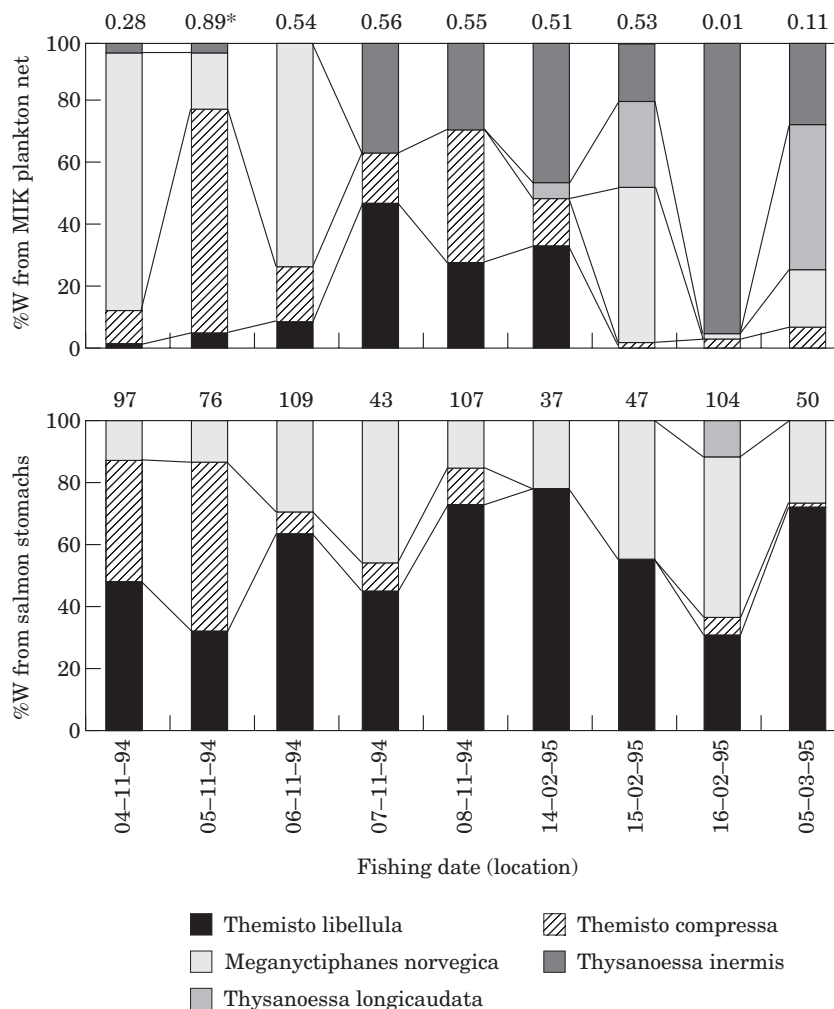


Figure 10. Relative weight distribution (%) of two *Themisto* species and three euphausiids species from MIK plankton net samples, 0–50 m depth (upper panel) and from corresponding salmon stomachs samples (lower panel), at nine of the 13 fishing locations with detailed species segregation of euphausiids and amphipods in both samples. Simplified Morisita overlap indices are shown on top of upper panel, a star indicates high overlap. Number of stomachs are labelled on top of lower panel.

reared fish might have escaped rather recently, as indicated by their higher load of salmon louse (*Lepeophtheirus salmonis*) compared to wild salmon (Jacobsen and Gaard, 1997), and might thus have gained most of their weight in culture prior to capture.

Feeding intensity

On the assumption that the proportion of empty stomachs is indicative of the intensity of feeding (Rae, 1967; Bowman and Bowman, 1980), salmon north of the Faroes feed more intensively in winter than in autumn, when nearly half of the stomachs were empty. Of the stomachs containing food, the weight of the stomach content increased from autumn to winter for the 1 and 2SW fish, but not for 3+SW salmon. The increase was

mainly due to higher proportions of fish in the winter diet, particularly of mesopelagic fish. The apparently low feeding rate in late autumn could be an indication of reduced food availability in the sea during this period. By comparison, salmon sampled in the Labrador Sea (Lear, 1980) had less food in their stomachs in the autumn than in the spring (3.1 g and 5.7 g food per kg of salmon, respectively) and were feeding less actively (28% and 8% empty stomachs, respectively). Lower feeding rates during winter were also observed in the Baltic (Thurow, 1966).

The higher condition factor of salmon in the autumn than winter seems to contradict the earlier statement that food availability is lower during autumn. This apparent ambiguity might be explained by the fact that the gastric evacuation rate is highly dependent on

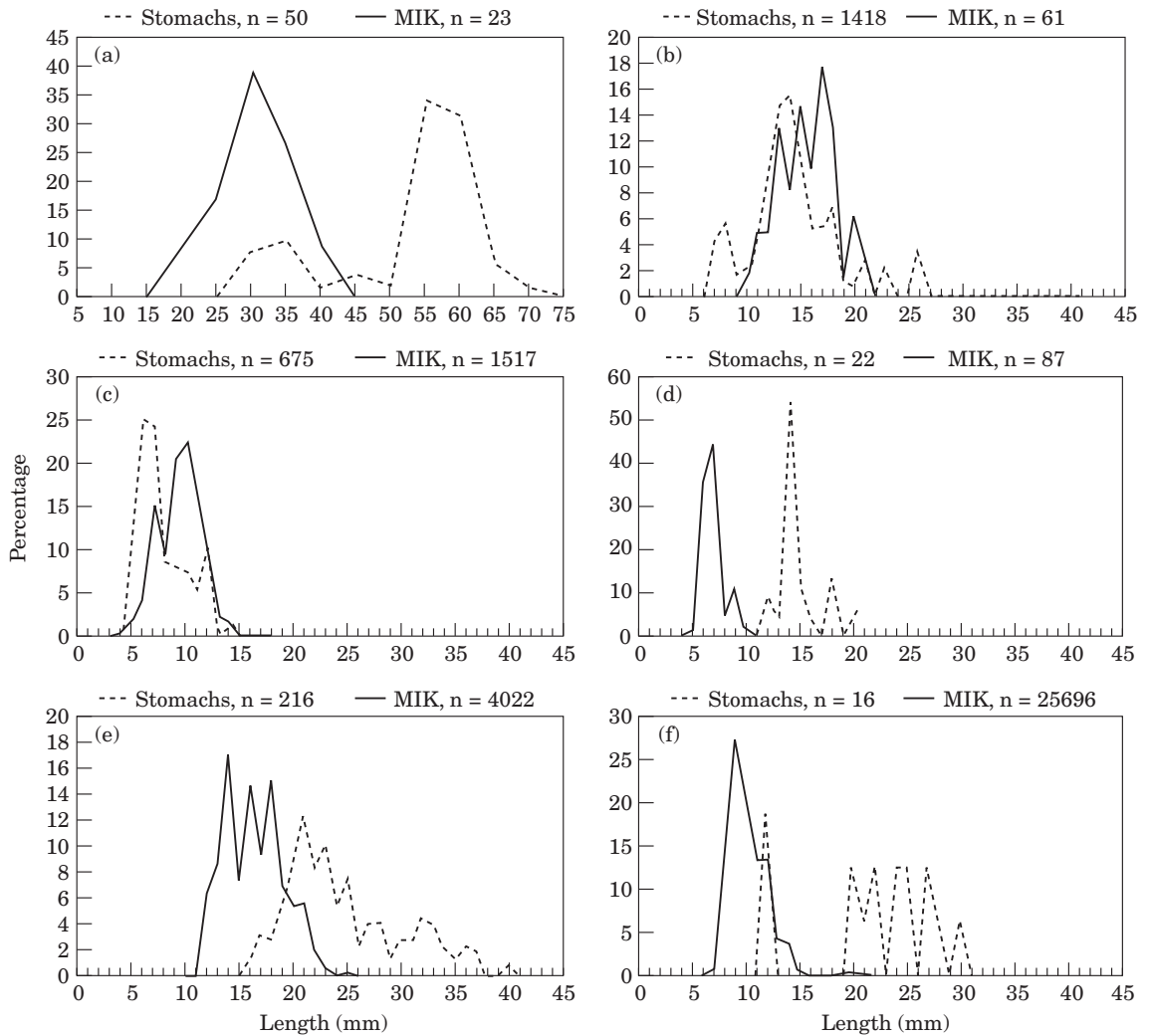


Figure 11. Length distribution of various prey from corresponding stomach samples and MIK plankton net samples (0–50 m depth), at nine of the 13 fishing locations with detailed species segregation of euphausiids and amphipods in both samples: (a) *Maurolicus mülleri*, (b) *Themisto libellula*, (c) *Themisto compressa*, i.e. *T. c. f. compressa* and *T. c. f. bispinosa*, (d) *Themisto abyssorum*, (e) *Meganyctiphanes norvegica*, and (f) *Thysanoessa* spp., i.e. both *T. inermis* and *T. longicaudata*.

temperature (Dos Santo and Jobling, 1991). The lower rate of emptying of the stomach during winter caused by lower ambient temperature would lead to fewer stomachs being empty and on average the non-empty stomachs would contain more food due to slow digestion.

We observed a significantly higher proportion of salmon containing bait during winter than in autumn, and a significantly higher proportion of salmon had taken two or more baits prior to capture during winter than in autumn. The biological significance of these observations is not clear, but this might indicate that the salmon have a greater appetite during the winter.

The observation that a higher proportion of escaped farmed fish contained bait than wild salmon is difficult

to explain. The probability that a salmon takes the bait probably depends on whether the bait and hook was approached and swallowed in one bout or the capture was a result of hooking without swallowing. Obviously some fish took the bait without being hooked. If the feeding behaviour of the escaped farmed fish, especially the more recent escapees, differed from that of wild salmon, it might result in a different proportion of farmed fish containing bait compared to wild fish. The escapees might be more eager, i.e. less cautious, when approaching and taking the bait. Furthermore, farmed salmon have been selected for fast and efficient growth for generations, which have resulted in a higher demand for energy (Thodesen *et al.*, 1999), and might thus have made farmed salmon a more aggressive feeder.

If the escaped farmed fish behave differently compared with wild salmon in the sea, either having problems to adapt to the wild environment or being more eager to feed than wild salmon, it might be expected that the condition factors of the two groups would be different. However, no difference in condition was observed between wild and escaped farmed salmon during the feeding phase in the sea. Neither were any differences observed in frequency, number or weight proportions of prey between wild and farmed salmon, nor in diet overlap. Furthermore, a higher proportion of farmed fish contained food than wild fish. This strongly suggests that fish farm escapees that survived until capture are well able to feed in the oceanic environment. Farmed salmon caught in Scottish coastal waters have also been observed to feed on natural prey (Hislop and Webb, 1992).

Prey availability and prey selection

The comparative material from the salmon stomachs and the plankton samples might contain several potential sources of bias, including avoidance of the MIK net, limited sampling range (0–50 m) and uncertainty over how accurately the stomach contents represent the relative abundance of prey when ingested (Kohler and Ney, 1982). The validity of the plankton samples as indices of prey availability could not be addressed. However, all but one of the MIK samples were taken in the morning between 0700 and 0800 h, between setting and hauling the long-line, thus minimising possible diurnal variations in the material and further ensuring that the plankton samples were obtained while the long-line was fishing, although not necessarily when the salmon was feeding.

Although the large fish species such as herring, barracudinas, and the larger capelin (>50 mm) were excluded prior to the comparative analysis, the resulting overlap index was low (0.3), which might indicate at least a partly selective feeding strategy of salmon. Judging from the fact that pearlsides up to 40 mm and capelin fry (40–50 mm) were caught in the plankton net, avoidance of the net by crustaceans (mainly <30 mm) should be negligible. We further assume no difference in avoidance behaviour between amphipods and euphausiids of similar size. Other researchers have reported that large zooplankton and fish (>45 mm) avoid the MIK and similar plankton sampling devices (Munk, 1988; Dalpadado *et al.*, 1998).

Even though most of the species occurred in both data sets, their relative proportion differed greatly. Our results suggest that fish were preferred over crustaceans, amphipods were preferred over euphausiids and, of the three species of euphausiids, the larger *Meganycitiphanes norvegica* was preferred over the smaller *Thysanoessa inermis* and *T. longicaudata*. Furthermore, within each of the three euphausiid species, the prey ingested were

larger than those in the plankton samples. The preference of fish to crustaceans, and of the larger *M. norvegica* over *Thysanoessa* spp. can be explained by size-selective feeding of salmon. However, the preference of amphipods to euphausiids seems more subtle, as the sizes of these groups in the plankton samples are comparable but in the stomachs the euphausiids were larger than the amphipods. The energetic content of euphausiids and amphipods might be different and/or the swimming and predatory escape behaviour of the two groups might be different. However, it is most likely that the large and heavily pigmented compound eye of amphipods make them more conspicuous than euphausiids (Zaret and Kerfoot, 1975). It further seems that, although on the evidence of the plankton data there are numerous *Thysanoessa* spp. available in the upper 50 m, this genus is hardly preyed upon by salmon. In the Pacific, Peterson *et al.* (1982) also found a preference for amphipods to similar sized stages of a copepod by juvenile coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) off the Oregon coast. The relatively low overlap between salmon diet and the available prey in our study, and the preference of amphipods to euphausiids and of the larger *Meganycitiphanes norvegica* to the smaller *Thysanoessa* spp. (both euphausiids), indicate that the Atlantic salmon is a selective feeder.

A shift in prey composition among age (size) groups of salmon was also indicated, the smaller 1SW salmon had taken higher proportions of amphipods compared to the larger 2+SW fish, while the proportion of fish prey, particularly barracudinas and other large fish, increased with age, indicating a higher degree of piscivory with age. Selective feeding was reported by Lear (1972) in the Northwest Atlantic, where salmon preferred herring to capelin, and large salmon contained significantly more herring than did small salmon.

Salmon north of the Faroes did not feed on *Sagitta* spp., which was found in the plankton samples, although it has been reported as food for salmon in the Pacific (Brodeur & Pearcy, 1990).

At least two year classes (1 and 2+ group) of pearlsides (*Maurolicus müelleri*) were present in the salmon stomachs, although only the smaller 1 group was present in the plankton samples. The larger pearlsides might have avoided the plankton sampler or been distributed below the sampling depth of 50 m. In some areas pearlsides has been reported to be separated into two depth strata during winter, with the older individuals occupying the lower stratum (Goodson *et al.*, 1995), and in the Norwegian Sea pearlsides are reported to be most numerous below 200 m (Dalpadado *et al.*, 1998). Thus salmon probably also feed deeper than 50 m depth. Salmon has been observed from acoustic tagging to make occasional descents from surface layers to depths of 150 m or more (Jäkupsstovu, 1988). Pacific salmon

also occasionally feed deeper than 150–200 m during the day (Pearcy *et al.*, 1988).

We conclude that crustaceans and particularly the hyperiid amphipods of the genus *Themisto*, euphausiids and mesopelagic shrimps are important sources of food for salmon in the autumn period and various mesopelagic fish as lantern fishes, pearlsides and barracudinas become equally important during the late winter period. The occasional presence in the stomachs of larger fish such as herring, blue whiting and mackerel is not considered to be evidence that these fish are a main source of food for salmon in the sea around the Faroes. We were not able to assess whether food is a limiting factor for salmon in the sea. We suggest that salmon feed opportunistically, however they tend to select the larger size range of available prey. Finally we conclude that escaped farmed salmon that survive until capture adapt well to the “wild” life in the ocean.

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