

International Council for
the Exploration of the Sea

M74- Syndrome and similar Reproductive
Disturbances in Marine Animals
CM 1999/U:09

**Yolk-sac-fry mortality (M74) in Baltic Sea salmon (*Salmo salar* L.):
Analyses of its relation to the diet**

by

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Abstract

In recent years, Baltic Sea salmon (*Salmo salar*) have suffered reproduction difficulties, due to high mortality during the larval phase (the M74 disease). Analyses of long term mortality records (1928-98) from two salmon hatcheries indicate that M74 did not occur or was infrequent before the 1970s. The disease can be cured by thiamine treatment and this indicates that the mortality results from a thiamine deficiency. The frequency of M74 is strongly correlated to the abundance of sprat (*Sprattus sprattus* (L.)) and it has been suggested that M74 results from changes in the food web. To study the possible role of diet changes in relation to M74, we have compared stomach content in salmon collected 1959-62 and 1994-97. Sprat, herring (*Clupea harengus* L.) and threespined stickleback (*Gasterosteus aculeatus* L.) dominated the diet in both periods. The average size of consumed sprat and herring was significant smaller in the 1994-97 compared to 1959-62. The results also indicate that herring, and to some extent also threespined stickleback, has increased in the diet of salmon. This suggests that sprat constituted a smaller part of the salmon diet in 1994-97. It is thus difficult to explain the M74 with its positive correlation to the sprat population alone. The ultimate cause of M74 and the thiamine deficiency is not known, but our hypothesis is still that it is related to foodweb changes. Possible causes includes: changes in thiamine or thiaminase content in forage fish (related to the decreased size of these fish in the diet or their decreased growth/condition), increased growth rate and winter-feeding of salmon and general changes in thiamine synthesis in the Baltic Sea (potentially influenced by eutrophication).

Introduction

In 1974, yolk-sac salmon (*Salmo salar* L.) fry died in unusually large number in the Bergforsen salmon hatchery (Bengtsson *et al.* 1999). After this first recording of mortality, observations of dying fry increased and were reported from many other hatcheries around the Baltic. In 1993, almost 80% of all female Baltic salmon in Swedish hatcheries produced offspring that died at the yolk-sac stage (Bengtsson *et al.* 1999). There are indications that naturally spawning salmon (Karlström, 1999) and possibly also brown trout (*Salmo trutta* L., Landergren *et al.* 1999) have suffered from similar mortalities.

By the time this salmon mortality was detected, some other top predators in the Baltic ecosystem suffered from recruitment problems that were caused by toxic substances (Olsson *et al.* 1992; Koistinen *et al.* 1997). Because of this, and high concentrations of such substances in Baltic Sea salmon (e.g., Koistinen, 1990), many assumed that the mortality was caused by pollutants. The salmon fry mortality was named the M74 syndrome, where M is an abbreviation of the Swedish word "miljörelaterad" ("environmentally related") and 74 for the year it was first documented. However, no clear link between M74 and environmental pollutants has been found (Anonymous, 1999).

Almost at the same time as M74 was detected and became a problem in the Baltic, similar reproduction disturbances occurred in salmonids in the North American Great Lakes (the early mortality syndrome, EMS) and in the New York Finger Lakes (the Cayuga syndrome, Anonymous, 1998). A common denominator for fish suffering from the M-74, EMS and the Cayuga syndrome is that the eggs have very low thiamine concentrations and that the mortality can be dramatically reduced by thiamine treatment (Honeyfield *et al.* 1998). The three syndromes also shows several similarities in their clinical signs, while non of them show clear correlations to known toxic substances (Bengtsson *et al.* 1999; Fitzsimons *et al.* 1999).

From the North American Great Lakes, Fitzsimons *et al.* (1999) report negative correlations between the EMS frequency in salmonids and the abundance of one of their common prey, the clupeid *Alosa pseudoharengus* (Wilson). The opposite, a positive correlation, is found between M74 and another clupeid species, the Baltic Sea sprat (*Sprattus sprattus* (L.)), Karlsson *et al.* 1999). These findings indicate that the salmonid fry mortalities, and the thiamine deficiencies, are caused by changes in the food web. The correlations between mortality frequencies and prey abundances must not necessarily, however, reflect causal relationships. The actual food web changes that may have caused the fry mortalities are still unknown. In this paper, we will try to shed some light on this by comparing gut content data of Baltic Sea salmon from two periods, 1959-62 and 1994-97. We will also present analyses of mortality records from two salmon hatcheries, which shows that there was no indication of M74 during the first period while the M74 frequency was ~65% during the latter period.

Material and methods

To follow the long-term development of M74, mortality data from 1928-98 in the salmon hatcheries in the rivers Dalälven and Mörrumsån (Fig. 1) were analysed. The characteristics of these data vary substantially over time. During 1928-63, the

hatcheries were operated to deliver newly hatched and un-fed fry for immediate stocking in streams. The data from this period consist of summaries of the number of eggs or fry in the hatchery, summed figures of mortality, release or transferral of fish, as well as daily records of the rearing water temperature. It is often noted when hatching started and finished. As mortality during pre- and post-hatch was not normally separated, we summed the mortality occurring in the period from the middle point between start and end of hatching and until 300 degree-days had been achieved after hatching. Summing from the start and end of hatching gave maximum and minimum estimates of the annual mortality. The 300 degree-days limit for terminating mortality counts was based on Amcoff *et al.* (1999) whom found that the M74 mortality develops well before this stage. Sometimes fry were removed from the hatchery before 300 degree-days had passed, but only seldom before 250 degree-days. If the proportion removed before 300-degree-days exceeded 40% of the total number of hatched larvae, or if no mortality data existed after 300 degree-days, these annual values were deleted. For 1964-84, estimates of M74 were obtained from the total mortalities in the relevant period after hatching, subtracted by identified non-M74 sources of mortality. Between 1985-98, frequencies are based on actual identifications of M74. In this period the mortality is given as the percentage of females whose offspring suffered of M74.

Stomachs have been analysed from almost 8000 salmon, of which 6710 contained food. The fish were collected in two periods, 1959-62 (number of fish (n) = 3157) and 1994-97 (n=4802). Most of the salmon were >60 cm and from the commercial offshore drift net (mesh size 160 mm stretched) and long line fisheries. Drift nets are used under ice-free conditions and long lines mainly during winter. To get smaller salmon (30-60 cm), fishing was also done with a mesh size of 100 mm in 1996-97. Data from salmon caught in drift nets and on long lines were merged in diet composition analyses, since there are no gear dependent differences in stomach content composition (Karlsson *et al.* 1999). Salmon from coastal areas of the Gulf of Riga and the Gulf of Bothnia, were collected from various trap nets. These fish were mainly individuals on their spawning run.

After each fish was removed from the gear its total length was measured. In data from 1959-62, this length data is often missing, but these fish were generally >60 cm (O. Christensen, unpubl.). Recorded length data from this period does not differ significantly from the 1994-97 data (Mann-Whitney U-test: $Z=-1.85$, $p>0.05$; average length 1959-62: 80 cm, 1994-97: 78 cm). Each fish was gutted, and the stomach frozen or stored in alcohol or formaldehyde. The salmon included in this paper were collected in different research programme, with slightly different sampling and analysis procedures. In 1959-62, the length of relatively intact prey fish was documented but no prey weights were recorded. Both the length and weight of prey were recorded in 1994-97. Intact and almost intact prey fish had their length determined as the "actual length", while the size of partly digested prey was estimated from what was left and classified as the "approximate length". When weight data were missing, it was estimated from the length (L, cm) to weight (W, g) relationships found for intact and almost intact prey (herring: $W=0.0094 \times L^{2.78}$, sprat: $W=0.0032 \times L^{3.20}$, threespined stickleback $W=0.0046 \times L^{3.26}$). Most (~95%) of the prey fish were identified to species, and only 0.2% were classified as "unknown fish" (remaining fish were classified to the genus level).

Further information on sampling and analyses of stomach content are in Karlsson *et al.* (1999).

Since we have no prey weight data from 1959-62, comparisons between the two sampling periods are based mainly on diets calculated from the number of different prey:

$$\%prey_{N,i} = \frac{100 \times prey_{N,i}}{prey_N} \quad (\text{eq. 1})$$

where $\%prey_{N,i}$ is the proportion (by number) of prey i in the diet. The total number of prey i in the analysed stomachs is $prey_{N,i}$ and the total number of prey in these stomachs is $prey_N$.

Diet compositions based on prey numbers probably overestimate the bioenergetic importance of small prey. To derive diets that reflect the food consumption more accurately, we also used weight data ($\%prey_{W,i}$):

$$\%prey_{W,i} = \frac{100 \times prey_{W,i}}{prey_W} \quad (\text{eq. 2})$$

where $prey_{W,i}$ is the weight of prey i in the analysed stomachs and $prey_W$ is the total weight of prey in these stomachs.

Data from 1994-97 were also used to calculate a stomach fullness index (fi) for each salmon:

$$fi = \frac{\text{total weight of stomach content(gram)}}{\text{salmon weight(kg)}} \quad (\text{eq. 3})$$

Since field conditions made it impossible to collect weight data from all sampled salmon, the *salmon weight* used to calculate fi was derived from length and our empirically found relationship $\text{weight(kg)} = 5.6 \times 10^{-6} \times \text{length(cm)}$.

If nothing else is stated, statistical analyses were done with SPSS 9.0 for Windows.

Results

In the first period from which we have fry mortality estimates (1928-63), values were normally below 10% (Fig. 2). Some higher figures (10-30%) in the late 1950s and early 60s in the river Dalälven hatchery were not paralleled by increases in the Mörrumsån hatchery. In the early 1990s, the M74-induced mortality was 50-90% in both hatcheries. There is thus a drastic difference in mortality estimates between the two periods from which we have diet data.

The first step in the analysis will be to describe the salmon diet in general terms, and then to describe diet differences between fish of different size, from different areas and seasons. From these results, we will create groups of fish with relatively homogenous diets and use these to compare stomach contents 1959-62 and 1994-97.

In the Baltic proper (ICES subdivisions, SD, 24-28 excluding the Gulf of Riga, Fig. 1), diet of salmon was dominated by sprat (*Sprattus sprattus* (L.)), herring (*Clupea harengus* L.) and threespined stickleback (*Gasterosteus aculeatus* L.). Sprat decreased or even disappeared in the diets from the Gulf of Bothnia (SD 30-31) and the Gulf of Riga. When sprat decreased in the diet, much of it was replaced by herring, but also

stickleback and other species increased (perch, smelt, sandeel, bream and eelpout (*Perca fluviatilis* L., *Osmerus eperlanus* (L.), *Ammodytes* sp., *Abramis brama* L., *Zoarces viviparus* L.), Fig. 3).

The size of consumed prey appeared surprisingly independent of the salmon size (Fig. 4). These data were analysed by a linear regression of prey size in cm (*prey*, only data on "actual length" used) versus salmon size in cm (*salmon*) and using sampling period (1959-62 and 1994-97) as a dummy variable (the approach described in Chatterjee and Price, 1991, pp 107-116). The predator-prey size relationships differed significantly between the periods ($F_{2,13379}=20.3$, $p<0.001$), both in slope ($t=2.11$, $p<0.05$) and intercept ($t=2.72$, $p<0.01$). For 1959-62, the relation could be described as $prey=14.3-0.038\times salmon$ and for 1994-97 as $prey=10.6-0.004\times salmon$. The larger salmon thus tended to eat smaller prey, and this was statistically significant in the earlier period ($t=2.78$, $p<0.01$) and close to significant in the 1990's ($t=1.78$, $p<0.08$). A simple comparison between prey sizes in the two periods showed significantly larger prey in 1959-62 (t-test, $t=7.00$, $p<0.001$).

An analysis of the correlation between salmon and prey size was also done separately for sprat. The correlation was significantly different between the periods ($F_{2,10631}=83.8$, $p<0.001$), both with regards to slopes ($t=3.18$, $p<0.001$) and intercepts ($t=4.41$, $p<0.001$). For 1959-62, the relation could be described as $sprat=13.5-0.027\times salmon$ and for 1994-97 as $sprat=9.8+0.005\times salmon$. The sprat that were consumed in 1959-62 were on average 1.1 cm larger than those consumed in 1994-97 ($t=13.4$, $p<0.001$).

We had "actual length" data from only 42 herring from the period 1959-62, but yet the periods were significantly different in the relationship between the size of salmon and consumed herring ($F_{2,1397}=3.51$, $p<0.05$). It was not possible, however, to determine if the differences were in slopes, intercepts or both. The relationship between salmon length and herring length can be described as $herring=6.1+0.128\times salmon$ for 1959-62 and $herring=10.3+0.063\times salmon$ for 1994-97. The consumed herring were on average 1.8 cm larger in 1959-62 ($t=3.62$, $p<0.001$).

The relationship between salmon size and the size of consumed threespined stickleback also differed significantly between the two periods ($F_{2,1058}=3.44$, $p<0.05$), and both in slopes ($t=2.44$, $p<0.02$) and intercepts ($t=2.38$, $p<0.02$). For 1959-62, the relationship between the lengths of salmon and sticklebacks was $stickleback=11.6-0.064\times salmon$ and for 1994-97 $stickleback=5.0+0.009\times salmon$. There was no difference between the periods in the average length of consumed sticklebacks ($t=0.93$, $p>0.3$)

Analyses of the effects of salmon size on the diet's species composition can be biased if there are size differences in the salmon analysed from different areas or seasons, in particular if sample sizes also differ substantially. In an effort to avoid effects of such imbalances, we estimated the average proportions (by weight, eq. 2) of herring, sprat and stickleback in 10 cm wide size classes of salmon, separately for each year, month and ICES subdivision. We included only mean values based on five or more salmon in the same size class. Within each year \times month \times SD combination, we correlated length to the average proportion of a prey species and recorded the Spearman rank

correlation coefficient. These correlation coefficients were then analysed in a second step. If there was no effect of salmon size on the proportion of a prey, the same frequency of positive and negative Spearman coefficients is expected. Under this assumption, the probability of an observed frequency and all more extreme frequencies is:

$$2 \times 0.5^a \times \sum_{i=0}^b \frac{a!}{i! \times (a-i)!} \quad (\text{eq. 4})$$

where a is the total number of Spearman rank correlation coefficients and b is the smallest of the number of positive and the number of negative coefficients.

These analyses (Fig. 5) showed that the proportion of sprat decreased, while herring and threespined stickleback increased with salmon size. The diet shift appears continuous, but once a size of 60 cm is reached, the diet composition is relatively stable. All diet changes were statistically significant (p-values in Fig. 5), but it must be recalled that the three analyses are not independent of each other. Changes in the consumption of one prey type necessarily results in changes also in the proportion of at least one other food component. Only data from 1994-97 were included in these analyses, since we had no prey weight data from 1959-62. There is, however, nothing in the data from the earlier period that contradicts the conclusions drawn from the later period.

In an earlier analysis of data from 1994-97 (Karlsson *et al.* 1999), we found diet differences particularly between seasons (Jan.-April, May-Aug, Sept-Dec.) and not to the same extent between the southern (SD 25 and 26) and the eastern (SD 28, excl. Gulf of Riga) Baltic. Sprat strongly dominated the diet in the beginning of the year (85-90% of the stomach content), but was partly replaced by herring and threespined stickleback as the year proceeded. The latter prey constituted 40-50% and 8-15% respectively in September-December.

Because of the effects of salmon size, season and to some extent capture area, on the diet of salmon, comparisons between the periods 1959-62 with 1994-97 had to be stratified. Furthermore, since no data on prey weight were recorded during the first study period, comparisons are based on prey numbers (eq. 1). All fish from 1959-62 were included in the analyses (very few <60 cm), while only salmon ≥ 60 cm were included for 1994-97. The procedure taken was the following:

For each month and ICES subdivision (excl. the Gulf or Riga), we estimated two sets of %prey_N values for herring, sprat and threespined stickleback. In the first set of values, all sampling years were merged, producing month \times SD specific values. The second set of values was calculated for each year (year \times month \times SD values). Separately for all month and SD combinations, each year \times month \times SD value then was classified as "higher" or "lower" than corresponding month \times SD value. The frequency of observations classified as "higher" and "lower" during the two periods was compared with χ^2 -statistics. SD \times month combinations that had only observations from one of the two periods (1959-62 and 1994-97) were excluded. These analyses indicated that herring, but to some extent also threespined stickleback, constituted a larger proportion of the diet of salmon in 1994-97 (Tab. 1).

These changes in diet between the two periods are also seen when the diet composition is estimated; herring and threespined stickleback appears to have increased while sprat and "other fish" have decreased from the first to the second period (Fig. 6). The high proportion of "other fish" in January-April 1959-62 was caused by 155 salmon that were caught within one week in February 1961 and which contained 420 sandeel. If this single sample is excluded from the analysis, the diets during the two periods are still somewhat different, although in both periods the diets are entirely dominated by three prey (sprat, herring and threespined stickleback).

The diet changes described above are relatively small when the diet composition is calculated from prey numbers. However, the difference become more pronounced if the size of different prey are taken into account. The average weight of herring, sprat and threespined stickleback consumed 1994-1997 was 22, 7.0 and 1.9 gram respectively. With the larger size of herring and sprat in 1959-62 (see above), the expected weights of these species during the earlier period were estimated to 29.1 and 9.7 gram. If these weights are multiplied with corresponding percentages in Fig. 6 (excluding other prey than these three fish species), weight based diets can be calculated. These calculations indicate that the diet change from the period 1959-62 to 1994-97 (decrease in sprat and increase particularly in herring) is rather substantial (Fig. 7). In the period 1994-97, there was a decrease over the year in the proportion of sprat in the diet (Karlsson *et al.* 1999) but this was not seen in data from 1959-62.

Using prey weights that were estimated from prey length allowed a third comparison between diets. Such weights could be calculated for only about ¼ of the samples from the first sampling period, but from all prey the second period. The differences between 1959-62 and 1994-97 are less clear in this analyses (Fig. 7) than in the two previous comparisons, although tendencies are the same (more herring and less sprat consumed in the latter period).

Another aspect of variation in diet composition between the periods and among seasons is differences in the size distribution of different prey. There were no clear seasonal dynamics in prey sizes, while differences between periods occurred as discussed above (Fig. 8).

It was difficult to compare stomach fullness indexes (f_i) between the two periods, since no prey weights were recorded in 1959-62. Based on the numbers of herring, sprat and threespined stickleback per stomach and their assumed weights (see above), it was however possible to estimate approximate f_i values. When comparing the two periods, salmon caught in drift nets and on long lines had to be separated, as the former had generally more stomach content ($t=22.4$, $p<0.001$, f_i values in salmon from 1994-97). Despite f_i values could be calculated only from some months from the earlier period (because of missing salmon size information), the results indicate that they had more stomach contents in 1994-97 (Fig. 9). This indicates higher food consumption and is consistent with a faster growth during this period (Karlsson *et al.* 1999).

Discussion

Data from the salmon hatcheries indicate that there was no serious M74 outbreak during the period 1928-63 (Fig. 2). It should be noted, however, that recordings from

this period only covered the first 300 degree-days after hatching. In the 1990s, M74 was manifested within this period after hatching, but it is possible that larvae during the first half of the century had higher concentrations of thiamine and that M74 mortality occurred at a later stage and passed unrecognised. It seems likely, however, that something that resembled M74 occurred before 1974, without being detected at least sometime, recorded as mortality and reported by the hatchery manager. Even if a low frequency of M74 occurred in the first period from which we have stomach content data (1959-62), there is no doubt that the frequency was substantially higher during the second period (1994-97). Furthermore it seems as if the situation in the Baltic Sea in the 1990s was uniquely well suited for development of M74, as nothing similar was recorded in the period 1928-1974.

In the late 1970's and early 1980's, Baltic cod produced some very rich year-classes, and the cod fishery almost doubled (Hansson and Rudstam, 1990). These years of successful cod reproduction was, however, followed by a long period of deep-water stagnation and poor recruitment (Vallin *et al.* 1999), and since the fishery was insufficiently restricted the cod stock dropped rapidly. As a response to this reduced cod population, the predation pressure on sprat decreased and this population increased rapidly (Köster and Möllmann, 1997) and their growth rate decreased (Raid and Lankov, 1995). The other main prey of cod, herring, did not increase in abundance to the same extent as sprat, but their growth rate and condition (the length/weight relationship) decreased (Raid and Lankov, 1995). This decrease in herring growth has been related to changes at lower trophic levels (Flinkman *et al.* 1998). During the period in which M74 has been recorded, there has thus been substantial dynamics in the upper trophic levels in the Baltic Sea ecosystem, at the same time as lower trophic levels have been influenced by eutrophication (Rosenberg *et al.* 1990).

The significant correlation between M74 and the sprat population biomass (Karlsson *et al.* 1999) indicates the M74 syndrome is caused by changes in the food web. However, the larger proportion of sprat in the salmon diet during 1959-62, compared to 1994-97, suggests that the causal explanation is not one of an unbalanced diet due to a too rich sprat population. More likely explanations are physiological unbalances caused by substantial winter feeding (Fig. 9) or decreased thiamine concentrations in the food. It is possible that decreased thiamine concentrations could be coupled to the shift to herring and sprat of smaller size, and the decreased growth and condition of these prey. The latter conditions could also result from changes at lower trophic levels like changes in the diet of herring and sprat (Raid and Lankov, 1995; Flinkman *et al.* 1998), see also Fitzsimons *et al.* 1999 and Karlsson *et al.* 1999).

Acknowledgements

This study was partly funded by the FiRe project at the Swedish Environmental Protection Agency; National Board of Fisheries (Sweden); Council for Forestry and Agricultural Research (Sweden); Ministry of Agriculture and Forestry (Finland); Finnish Game and Fisheries Research Institute; Nordic Council of Ministers and the Latvian Fisheries Research Institute. Special thanks to the Fisheries Research Station in Älvkarleby and the Fish Hatchery in Mörrum, and their former managers, for keeping good order of their hatchery journals.

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Table 1. Results of a comparison of the diet proportions (based on numbers) of sprat, herring and threespined stickleback during the periods 1959-62 and 1994-97.

Species	χ^2 -value (df=1);	p-value	Comment
Sprat	0.55;	>0.45	no change over time
Herring	17.30;	<0.001	clearly more in 1994-97
Threespined stickleback	3.78;	<0.06	indicates more in 1994-97

Fig. 1. The Baltic Sea with ICES subdivisions.

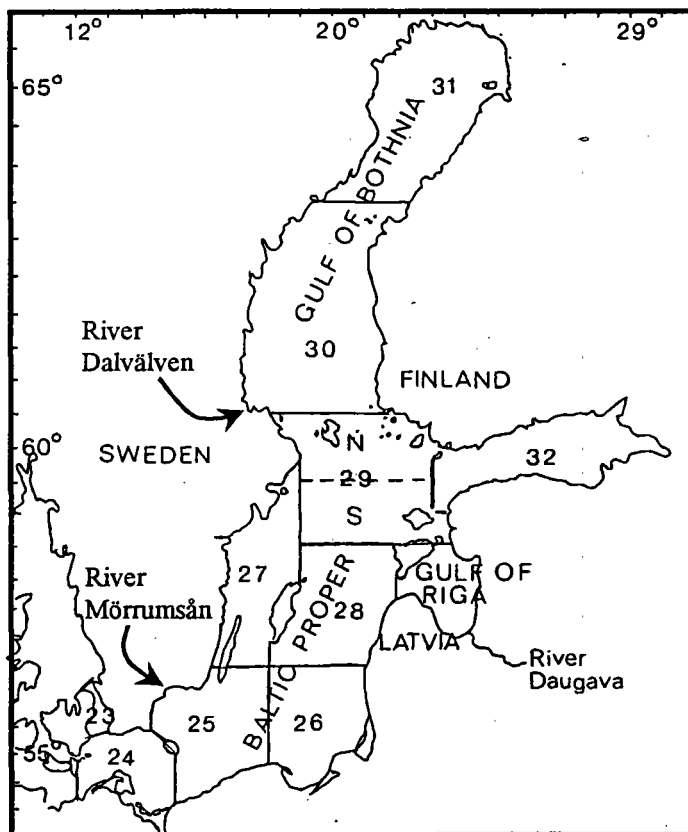


Fig. 2. Recorded annual mortality of post-hatching salmon larvae in two rearing stations in 1928-98 (year of hatching). The dotted lines separate three periods from which different types of data are available (for details see text). The bars in data from 1928-63 show estimated min and max values.

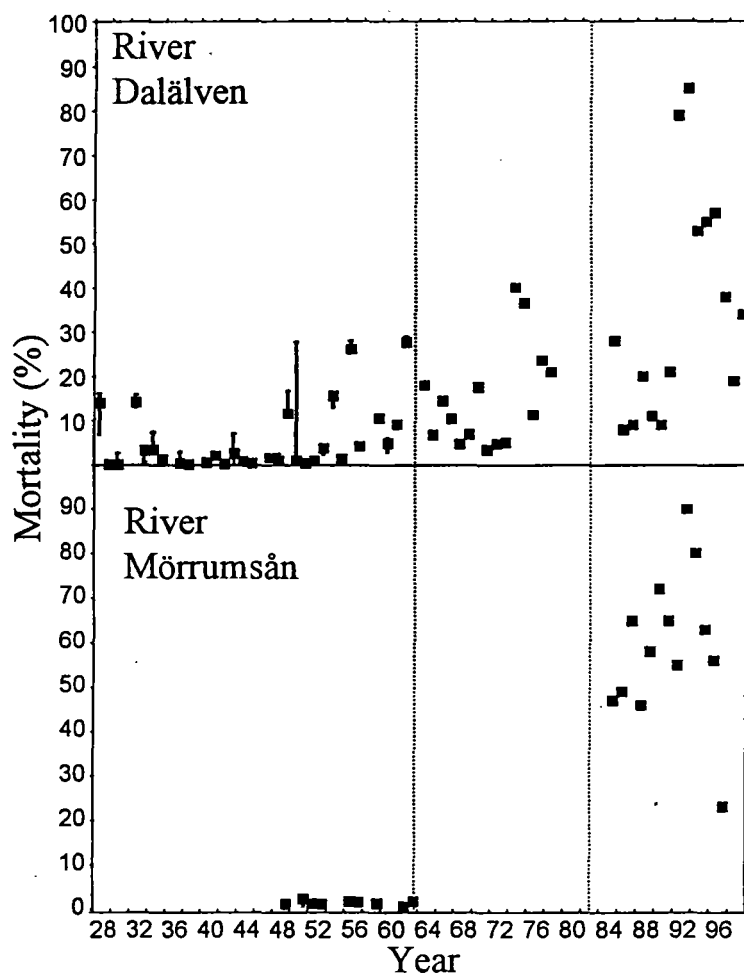


Fig. 3. Salmon diet in the Baltic Sea 1994-97, estimated from the weight of their stomach content (eq. 2). Fish from the open sea were caught in drift nets and on long lines, while coastal salmon were caught in different types of traps. 'n' shows the number of fish with stomach content.

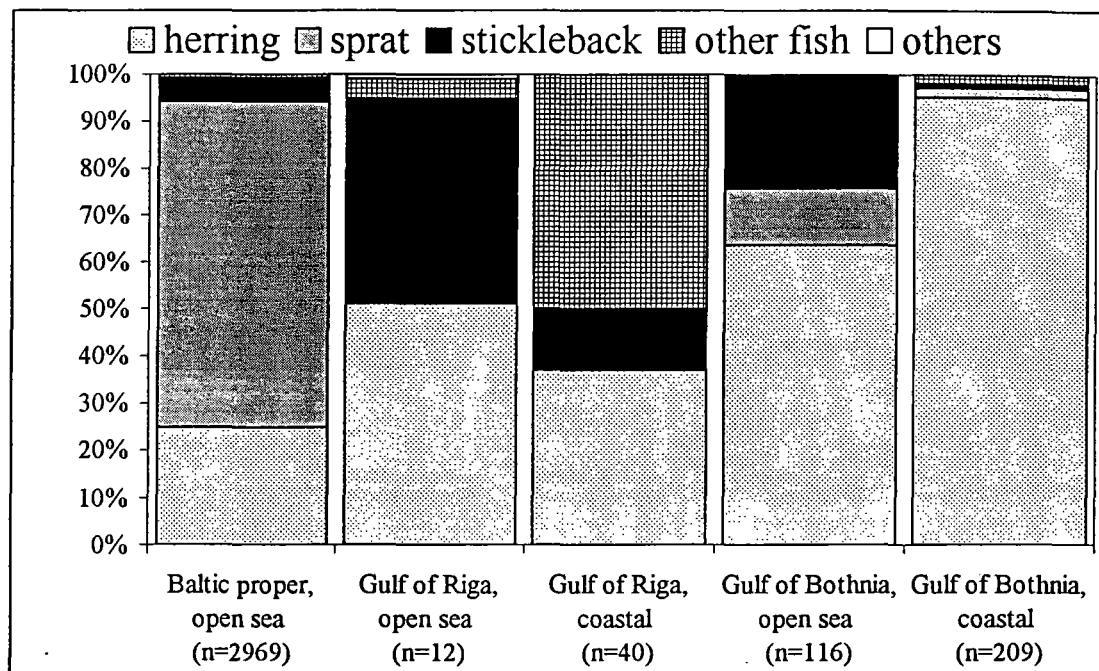


Fig. 4. The relationship between salmon size and the size ("actual length") of consumed prey fish. Based on data from 1994-97.

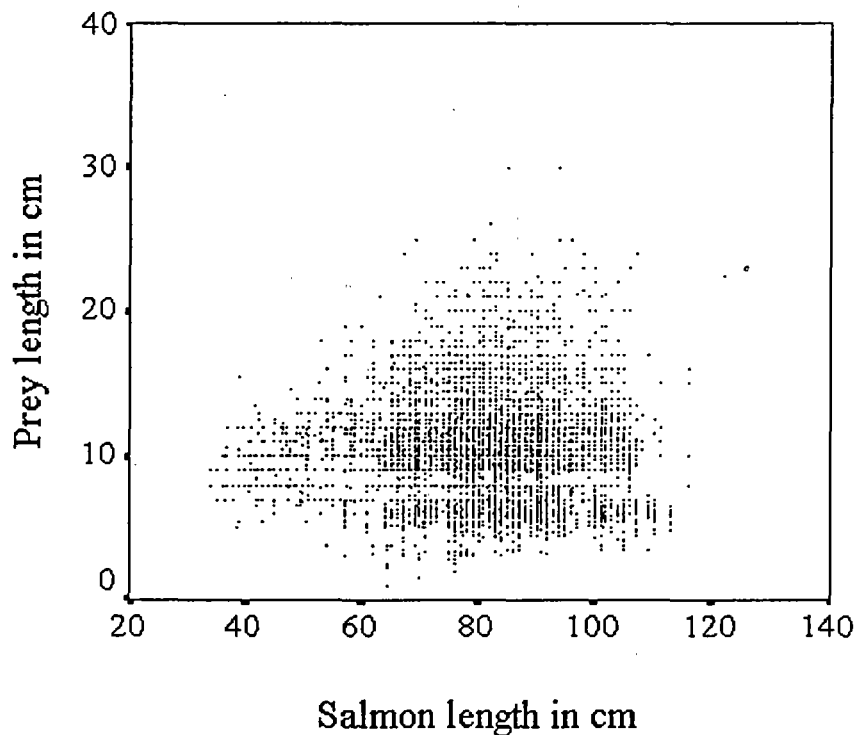


Fig. 5. Proportions (by weight) of sprat, herring and threespined stickleback in different sized salmon. Each point represent at least 5 salmon stomachs, collected the same year, month and in the same one ICES subdivision. The p-values given in the graphs were calculated with eq. 4.

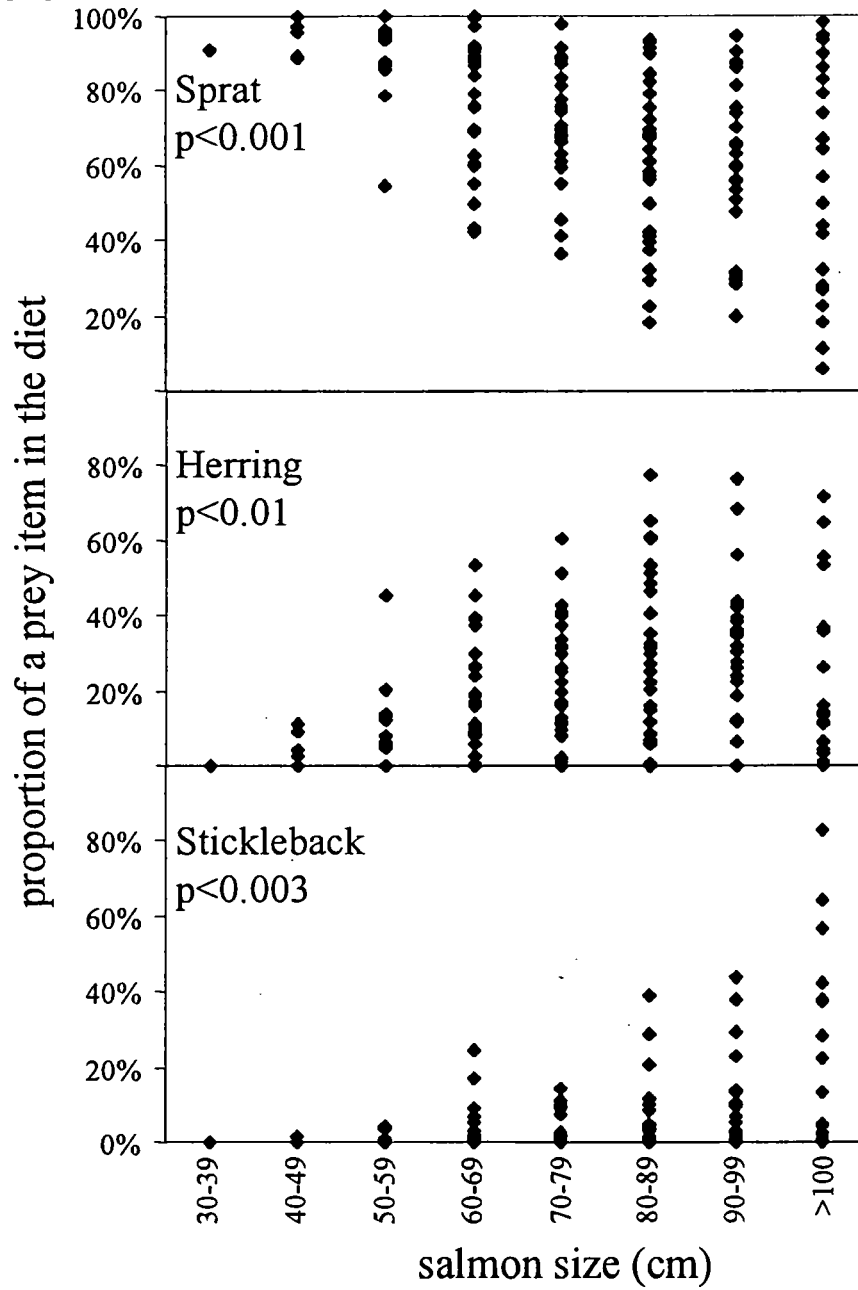


Fig. 6. The diet composition of salmon during the periods 1959-62 and 1994-97 (only fish ≥ 60 cm), estimated from the number of prey (eq. 1). Based on fish from ICES subdivisions 25, 26 and 28, excluding the Gulf of Riga. Two alternative data are presented for Januari-April 1959-62, one that includes all data and one that excludes 155 salmon caught within one week, with altogether 420 sandeels in their stomachs. Numbers of salmon with stomach content (n) is given in each bar.

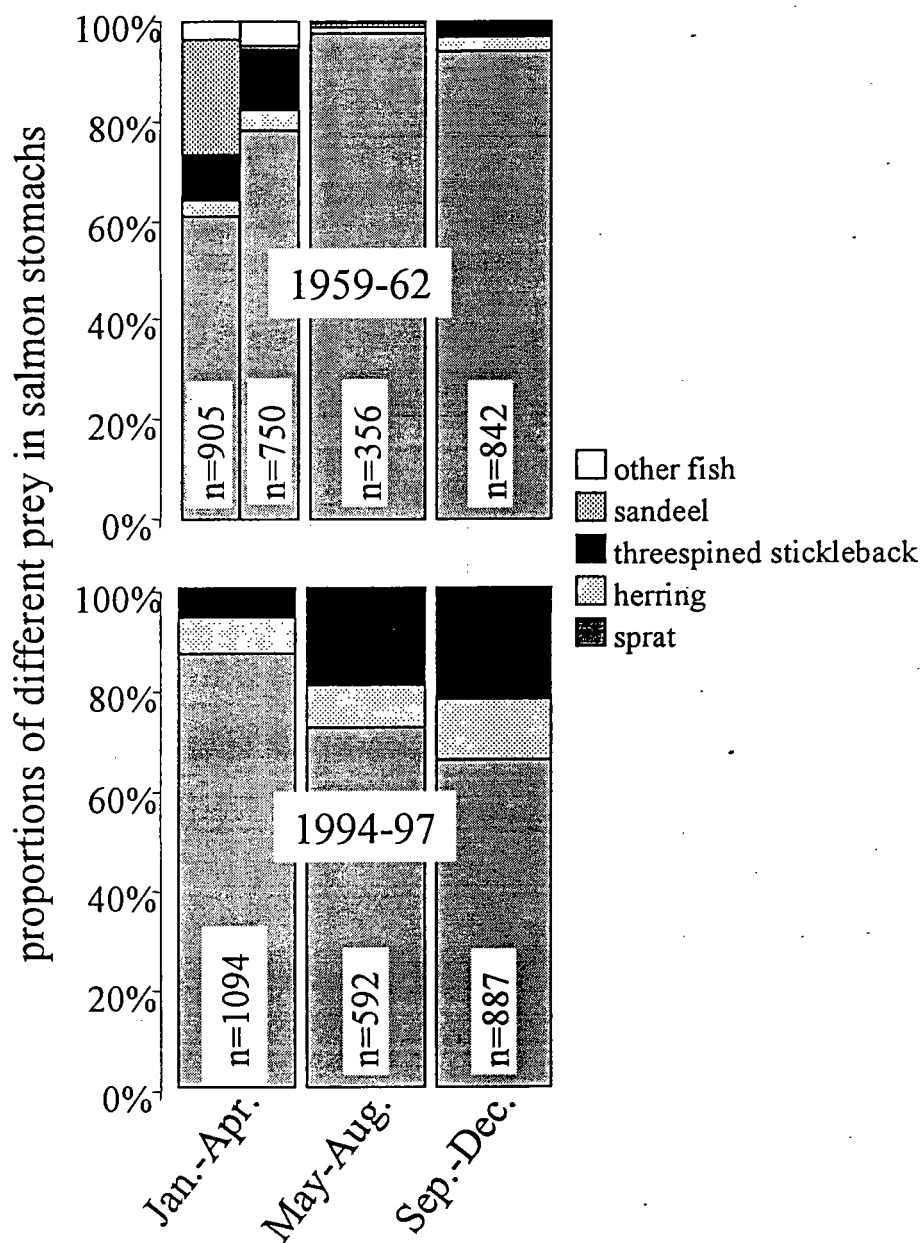


Fig. 7. The diet composition (by weight) of salmon during the periods 1959-62 and 1994-97. Diets the left column (a) were derived from compositions by prey numbers (Fig. 6) and the assumption that individual weights of sprat herring and threespined sticklebacks are 22, 7.0 and 1.9 gram respectively. In the right column (b), diets were calculated from prey weights that were derived from the length of all individual prey. Note that for the period 1959-62, the prey size had been determined only in some samples, reducing the number of salmon included in the analysis by about 3/4. The graphs are based on salmon $\geq 60\text{cm}$ and from ICES subdivisions 25, 26 and 28, excluding the Gulf of Riga. Of the two alternative diets presented for January-April 1959-62 in Fig. 6, this graph is based on data that excludes 155 salmon caught within one week in February 1961. Numbers of salmon with stomach content (n) is given in each bar.

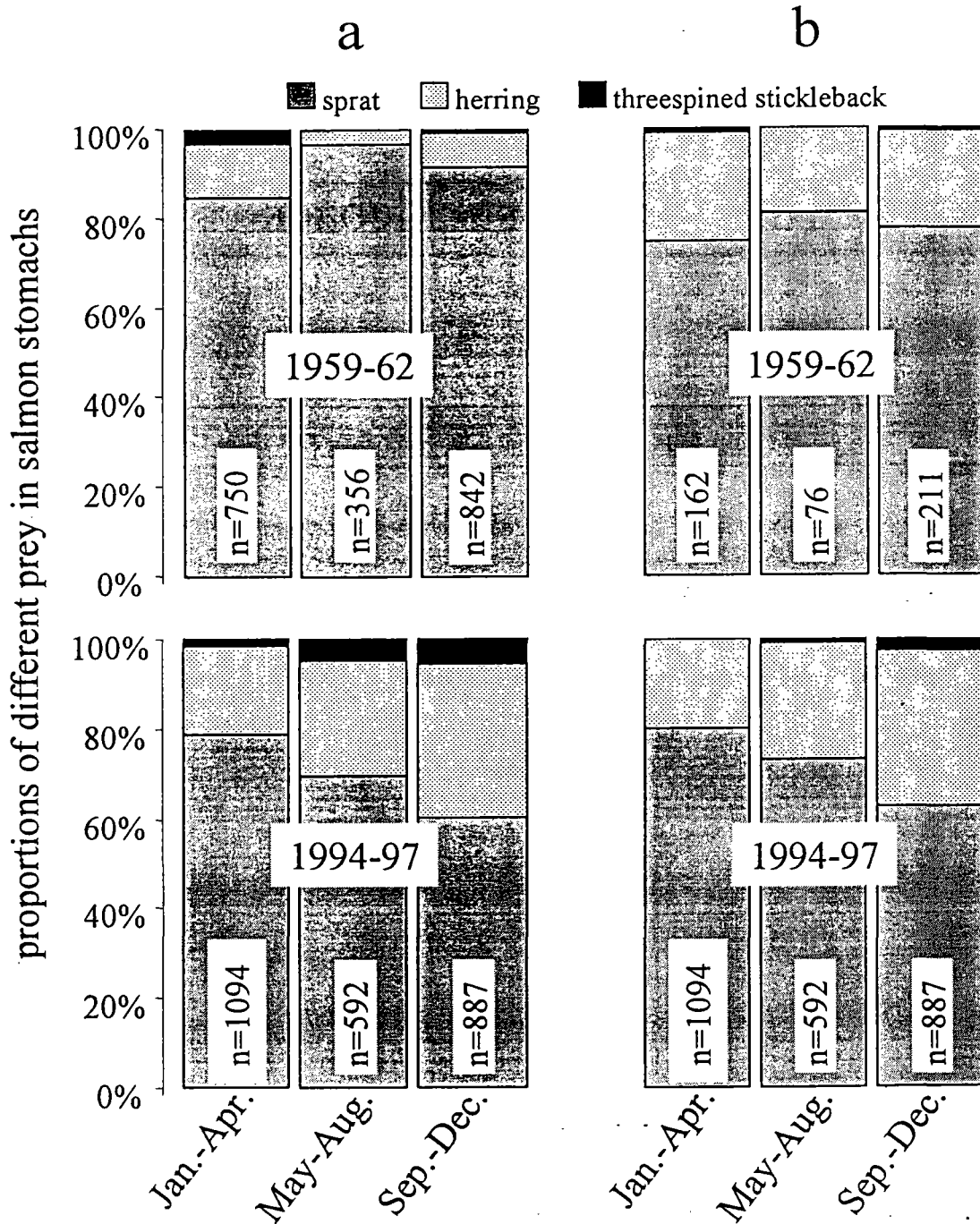


Fig. 8. Monthly averages of the size of prey consumed by Baltic Sea salmon.

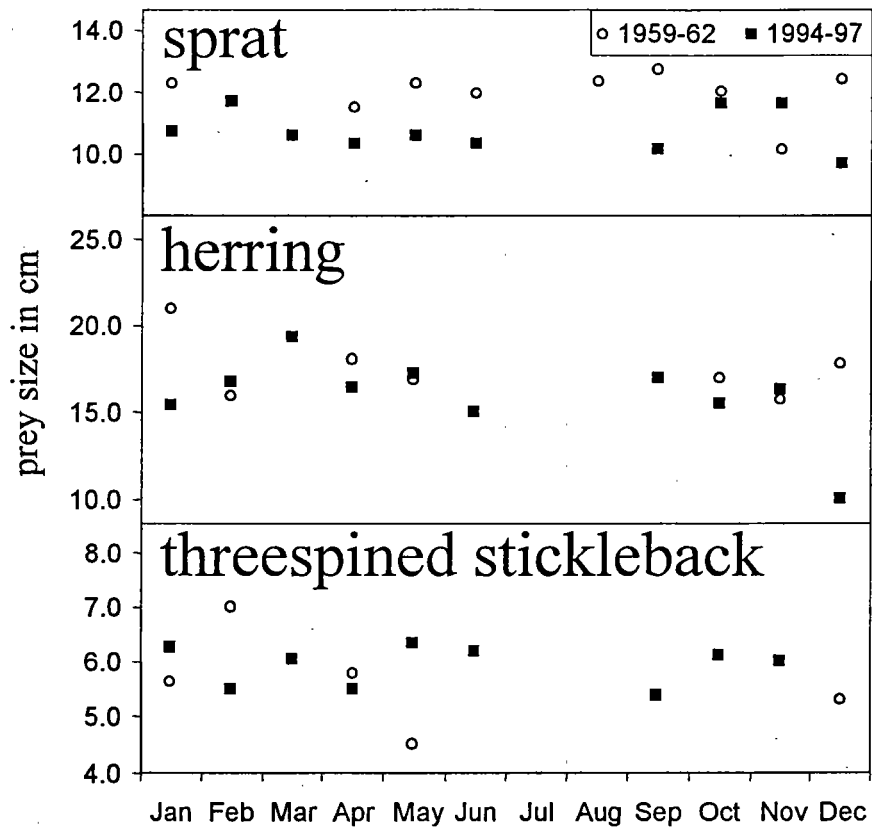


Fig. 9. Stomach fullness index (f_i , see eq. 3) in salmon caught on long lines and in drift nets. Data from the Baltic proper, excluding the Gulf of Riga.

