

Relationships between fish stock changes in the Baltic Sea and the M74 syndrome, a reproductive disorder of Atlantic salmon (*Salmo salar*)

Jaakko Mikkonen¹, Marja Keinänen^{1*}, Michele Casini², Jukka Pönni³, and Pekka J. Vuorinen¹

¹Finnish Game and Fisheries Research Institute, PO Box 2, FI-00791 Helsinki, Finland

²Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, PO Box 4, 45321 Lysekil, Sweden

³Finnish Game and Fisheries Research Institute, Sapokankatu 2, FI-48100 Kotka, Finland

*Corresponding Author: tel: +358 40 7539893; fax: +358 205 751201; e-mail: marja.keinanen@rktl.fi.

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The M74 syndrome of Baltic salmon (*Salmo salar*), which appears as increased yolk-sac fry mortality (YSFM), impairs the reproduction of salmon stocks. Changes in the prey stocks of Baltic salmon in its two feeding areas, the southern Baltic Proper (BPr), where sprat (*Sprattus sprattus*) was the main prey species during the high incidence of M74, and the Bothnian Sea, where herring (*Clupea harengus*) is the dominant species, were analysed in relation to salmon growth and size and in relation to the incidence of M74. The high condition factor (CF > 1.05) of prespawning salmon predicted high YSFM. From the various stock factors of sprat and herring in the southern BPr, the biomass of sprat had the strongest positive relationships with the CF of prespawning salmon, and the total prey biomass with YSFM. It is concluded that the ample but unbalanced food resources for salmon in the BPr, primarily sprat, induce M74. By reducing the fishing pressure on cod (*Gadus morhua*) and by more effectively managing the sprat fishery in years when the cod stock is weak, the incidence of the M74 syndrome could be reduced and even prevented.

Keywords: Atlantic salmon, Baltic Sea, growth, herring, M74 syndrome, sprat, yolk-sac fry mortality.

Introduction

The M74 syndrome is a reproductive disorder of Atlantic salmon (*Salmo salar*) feeding in the Baltic Sea (hereafter Baltic salmon or salmon), and it appears as increased yolk-sac fry mortality (YSFM; Bengtsson *et al.*, 1999; Keinänen *et al.*, 2000). A low concentration of vitamin B1 (thiamine) in eggs is a correlate of high YSFM caused by M74 (Börjeson *et al.*, 1999; Lundström *et al.*, 1999; Vuorinen and Keinänen, 1999; Koski, 2004), similar to the early mortality syndrome (EMS) in salmonids in the Great Lakes of North America (Fitzsimons *et al.*, 1999) and the Cayuga syndrome in the Finger Lakes (Fisher *et al.*, 1996). After being first described in 1974, the incidence of M74 remained low until the early 1990s, whereupon it increased strongly in Sweden and Finland, affecting all the salmon stocks of the Gulf of Bothnia (GoB; Karlsson and Karlström, 1994; Keinänen *et al.*, 2008; ICES, 2010). The negative impact of high levels of M74 was also manifested in low densities of young-of-the-year salmon in rivers of the GoB (Figure 1), such as the Rivers Tornionjoki and Kalixälven (Karlström, 1999; Romakkaniemi *et al.*, 2003), from which most wild salmon in the Baltic Sea originate. Released salmon from the stocks of dammed rivers, e.g. the River Kemijoki, after the feeding migration in the Baltic Sea, likewise produce M74 offspring (Keinänen *et al.*, 2008; ICES, 2010).

The main feeding regions of salmon stocks from GoB rivers are in the Baltic Proper (BPr), but a smaller and highly variable proportion of salmon remain to feed in the Bothnian Sea (BS; Aro,

1989; Salminen *et al.*, 1994; Niva, 2001; Ikonen, 2006), depending on smolt production and the level of recruitment of herring (*Clupea harengus membras*; Kallio-Nyberg *et al.*, 1999). The diet of adult salmon in the BPr consists almost exclusively of sprat (*Sprattus sprattus*) and herring, and in addition of a small proportion of three-spined stickleback (*Gasterosteus aculeatus*; Karlsson *et al.*, 1999; Hansson *et al.*, 2001). Sprat has, however, dominated the diet in the BPr and herring in the BS. In the years 1994–1997, salmon diet in the BS also included small quantities of sprat (Karlsson *et al.*, 1999; Hansson *et al.*, 2001), but the species was absent from the diet from 1990 to 1993 (Salminen *et al.*, 2001).

The diet of salmon that have reached a total length of 60 cm is relatively stable; they most often prey on fish of length 4–15 cm and only rarely on fish >20 cm (Hansson *et al.*, 2001). Baltic sprat can reach a total length of 14–16 cm, remaining smaller than herring, which depending on the area can attain a length of ca. 30 cm (Parmanne, 1990). Therefore, all age groups of sprat, but only the youngest age groups of herring, are suitable prey for salmon. However, as a result of their slow growth rate, older herring in the 1990s than in previous decades were of a suitable size for salmon to consume (Keinänen *et al.*, 2000).

M74-induced mortalities were highest during the years when the growth rate, indicated as the body weight, of Baltic salmon was most rapid (Karlsson and Karlström, 1994; Karlsson *et al.*, 1999), and it has statistically been related to a high total biomass

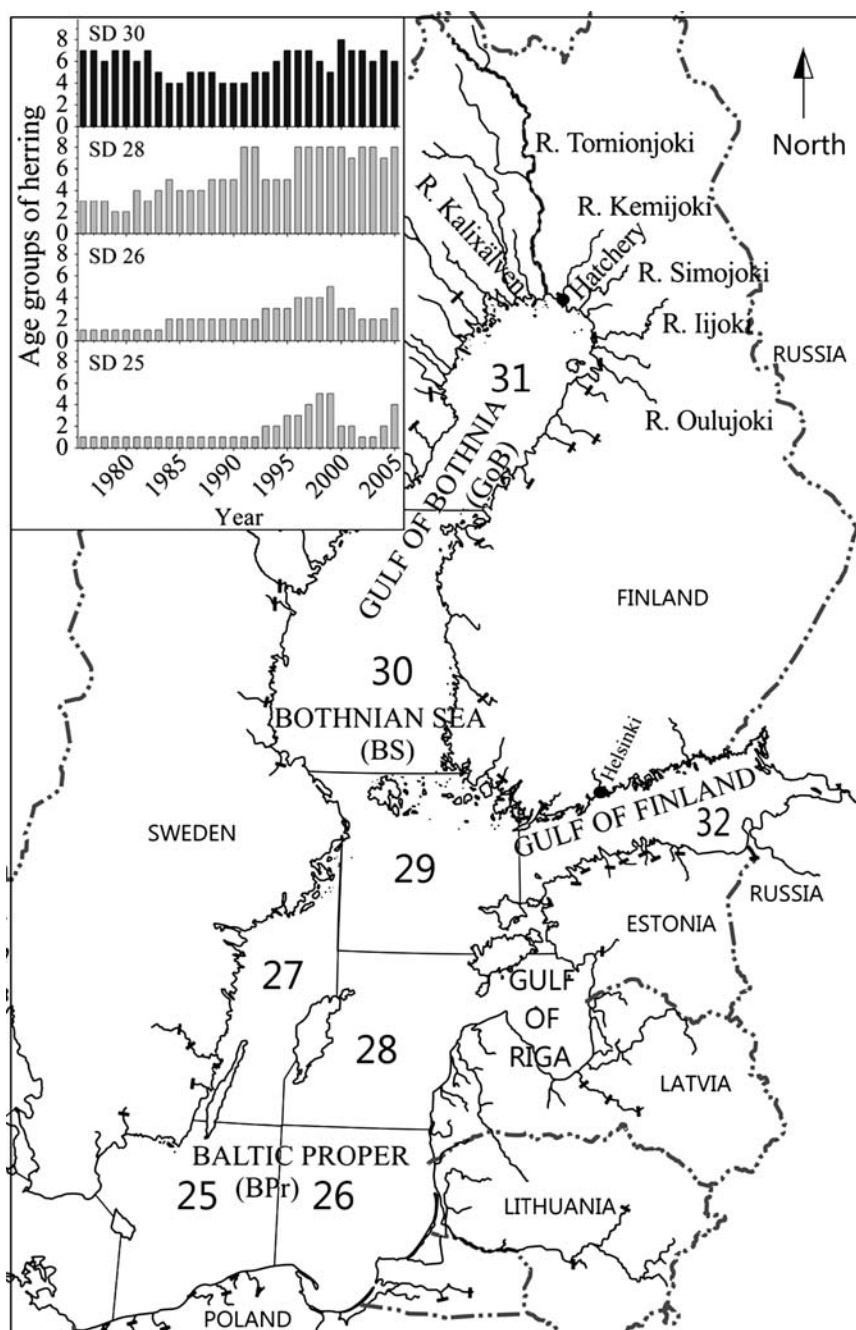


Figure 1. Locations of the salmon rivers of the GoB included in the study, and the important feeding areas of salmon from those rivers: ICES SDs 25, 26, and 28 in the BPr and SD 30 in the BS. Inset, age groups of herring with an average length < 19 cm estimated to be suitable prey for salmon in different years in ICES SDs 30, 28, 26, and 25. Calculated using datasets from ICES (2006a, b).

of sprat and a low weight of sprat in the Baltic Sea (Karlsson *et al.*, 1999). Moreover, an increase in the concentrations of particular organochlorines in salmon muscle, coincident with the outbreak of M74 at the start of the 1990s, was concluded to have resulted from enhanced feeding on sprat, which contained these pollutants in high concentration in all age groups, and in higher concentrations than in 1- to 3-year-old herring (Vuorinen *et al.*, 2002).

The aim of this study was to explore from new perspectives, and in more detail than in the investigation of Karlsson *et al.* (1999), how the M74 syndrome and the size or growth rate of salmon

are related to changes in the fish stocks of the Baltic Sea, focusing on the two main feeding areas of salmon from the rivers of the northeastern GoB.

Material and methods

Fish stocks and prey fish

The study focused on ICES Subdivisions (SDs) 25, 26, and 28, which are part of the BPr, and SD 30, which covers the BS part of the GoB (Figure 1). Data on the biomass of cod as well as the

biomass, number of specimens (or abundance), and mean weight-at-age of sprat and herring in the BPr during 1976–2005 were obtained from the database of the ICES Study Group on Multispecies Assessment in the Baltic (SGMAB; ICES, 2006b), and from the report of the Baltic Fisheries Assessment Working Group (WGBFAS; ICES, 2006a). Because according to Hansson *et al.* (2001), salmon only seldom prey on fish with a total length exceeding 20 cm, only age groups with a mean length of <19 cm were included in the calculations of herring biomass in each year. The SGMAB data included no information on herring or sprat length, so the length–weight curve was constructed for SDs 25, 26, and 28 from data provided by the Institute of Marine Research of the Swedish Board of Fisheries (IMR), and the SGMAB data were used to calculate the annual biomasses of the age groups of herring suitable as prey for salmon (Figure 1, inset).

For the BS, the annual biomasses for each age group of herring were calculated from the abundance and mean weight-at-age data of the WGBFAS. The length-at-age of herring in the BS was available from biological data, collected from commercial trawl and trapnet catches by the Finnish Game and Fisheries Research Institute (FGFRI), for calculating the annual biomasses using the same procedure as for the BPr. As no information was available on the biomass and number of sprat in the BS, they were estimated from the relative annual quantities of herring and sprat in the professional catch data of the BS (pelagic trawl dragged near the seabed) provided by the commercial marine fishing statistics of the FGFRI (2010).

The oldest herring with a total length of <19 cm are 1–5 years old in SDs 25 and 26, 2–8 years old in SD 28, and 4–8 years old in the BS (Figure 1, inset). All age groups of sprat were included in this analysis, because they are all of a suitable size for salmon to consume. Zero-year-old sprat during the final months of the year and herring during late summer already attain lengths (Salminen, 2002; data from IMR and FGFRI) that are appropriate for them to be prey for salmon. However, that age group was not included in the calculations of the biomass of available prey fish for salmon, because data on its abundance were lacking in the ICES database.

The condition factors (CFs) of sprat and herring in the BPr and BS were calculated ($CF = 100 \times \text{body weight} \times L_T^{-3}$, in which body weight is in grammes and L_T is the total length in centimetres) from data provided by the IMR and biological data collected from commercial trawl catches by the FGFRI for annual stock assessment purposes, respectively. Length and weight data were lacking for some years (sprat and herring in the BPr in 1991, 1993, 1995, and 1997, and sprat in the BS in 1991), so the respective CFs were also not available.

Growth and size of prespawning salmon

Tag-recovery data from the FGFRI were utilized to provide growth and size data on salmon. The data included tagged fish recaptured by fishers operating fykenets from May to August of 1971–2007 on the eastern side of the GoB in ICES SDs 30 and 31, so were therefore most probably prespawning salmon on their spawning migration towards the northern rivers of the GoB (Ikonen, 2006). These wild (trapped when descending during the smolt run) or hatchery-reared salmon of the GoB Rivers Simojoki and Tornionjoki and reared salmon, released at the mouth of the dammed Rivers Iijoki, Kemijoki, and Oulujoki (Figure 1), were tagged (Carlin tag) as smolts in the years 1969–2005. Only

salmon that had grown at sea for two growth seasons and having a CF between 0.70 and 1.50 were included in the calculations. The growth rate (cm year^{-1}) of these 2nd sea-year salmon (for a definition, see Salminen *et al.*, 1994) was calculated from their total length at tagging and on recapture. Although salmon do not grow uniformly during the 2 years, the length increment was divided by two to make interannual growth comparisons possible, and in calculating annual mean growths, the annual length increment of each salmon was taken into account for both feeding years.

M74 and the size of female salmon

Salmon ascending the rivers of the northeastern GoB (Figure 1) have been caught to maintain broodstocks and additionally to monitor offspring mortality at a hatchery of the FGFRI since 1985. After having been caught at the mouth or in the lower course of the rivers in late June–early July, salmon were weighed and their total length measured, then tagged with Carlin tags. Scales were removed for age determination. Salmon were kept until spawning (October) in the hatchery in basins supplied with water from the River Kemijoki. Before the stripping of eggs, salmon were measured again and weighed, and this weight was used in the present calculations of the size of spawning females. However, for the years 1998 and 2001–2006, salmon body weight on capture in the fykenet at the river mouth was also available for comparative size calculations. Eggs of each female were fertilized separately and incubated over winter in the hatchery, where mortalities were recorded until the end of the yolk-sac phase. Brood fish and their offspring were reared appropriately according to standard hatchery practice. All salmon were anaesthetized with MS-222 before handling.

Female-specific monitoring for ascending salmon from 1993 on has been performed in the laboratory of the FGFRI in Helsinki, allowing symptoms of M74 in yolk-sac fry to be more specifically observed and M74-related mortality to be recorded. The incidence of M74 in this study was determined as the annual average YSFM (%; Keinänen *et al.*, 2008; ICES, 2010). Monitoring results from the Rivers Simojoki (1985 on), Tornionjoki (1993 on), and Kemijoki (2005 on) were combined, because in those rivers, the trend and the intensity of M74 syndrome have been similar (Keinänen *et al.*, 2008; ICES, 2010). Only female spawners of the 2nd sea-year, the most abundant age group, with a CF between 0.70 and 1.50 were included in the analyses. Age data were missing for salmon captured in 1993, so the data for that year were not included in the analysis. The concentrations of thiamine components in unfertilized eggs have been measured since 1994 according to the method of Brown *et al.* (1998), modified by Vuorinen *et al.* (2002). In this study, the concentration of free (i.e. unphosphorylated) thiamine (hereafter, THIAM) was examined, because it has been used in thiamine-based prognoses of the incidence of M74 for the Baltic Salmon and Trout Working Group of ICES (ICES, 2006c), and it correlated better with YSFM than the total thiamine concentration of eggs, as also observed with EMS (Brown *et al.*, 2005).

Calculations and statistics

The two main feeding areas of salmon from the GoB rivers in the Baltic Sea, the BPr and the BS (SD 30), were treated separately, and in the BPr, only the areas where salmon mainly feed (SDs 25, 26, and 28), according to tag recoveries, were included in the analysis. The focus was only on prey fish that, taking into account the

abundance of each year class of sprat and herring and the size of herring preferred by salmon, were actually available as prey for salmon. Because of the non-normal distribution of some variables, non-parametric Spearman correlation analysis was applied always, and Bonferroni adjustment was used to control the risks of erroneous decisions of significance in multiple simultaneous comparisons. Statistical analyses were performed with the Statistical Analysis System (SAS) version 9.2 (SAS Institute Inc.), and figures were drawn with Origin version 8.1 (OriginLab Co.).

The annual mean CF values of herring and sprat were obtained by weighting the mean CF-at-age according to the proportion of the respective biomass. The correlations of the annual mean CF of herring and sprat and the weight of 1-year-old herring and 2-year-old sprat with the total biomass of clupeids were calculated for the two sea areas to compare herring and sprat status in relation to the biomasses of salmon prey. These age groups were selected because they are on average the most abundant within each year that were suitable as salmon prey. A delay of 1 year for prey fish factors was applied in testing their impact, because 2nd sea-year salmon have been feeding during the whole year before the year of capture.

Correlation analysis was applied in comparing the biomass of cod and the CF and growth rate of prespawning salmon with the biomass of herring and sprat, as well as with their combined biomass, and to compare the biomass of cod with the growth rate and CF of prespawning salmon. Because of the low sample size in some years, a 3-year moving average of the CF of prespawning salmon was used in statistical analyses. Correlation analysis was also applied to compare the THIAM of eggs and YSFM with the size and CF of female parent salmon, and with the prey biomass factors and the CF of prey fish. The interannual differences in the body weight and CF of female parent salmon were compared with analysis of variance (ANOVA) plus Tukey's test at $p < 0.05$.

The relationship between the CF or growth rate of prespawning salmon and food biomasses in the BPr and the BS was analysed by linear regression, and the relationship between the CF of these salmon and YSFM was examined with a non-linear model. Stepwise regression analysis was also applied to examine the relationships of various prey biomass parameters and the CF of herring and sprat from the BPr with the growth rate and CF of prespawning salmon, YSFM, and the THIAM of eggs.

Results

Changes in fish stocks

The biomass of cod in the BPr was greatest during the years 1978–1983, then decreased sharply up to the early 1990s, after which it remained low (Figure 2). The biomass of sprat varied inversely to that of cod. The biomass of herring of a size preferred by salmon as prey followed a declining trend in the BPr during the years 1976–2005. The biomass of sprat and the total biomass of clupeids correlated negatively with cod biomass ($r = -0.724$, $p < 0.001$, $n = 30$; $r = -0.653$, $p < 0.001$, $n = 30$; respectively), whereas the biomass of herring correlated positively with it ($r = 0.651$, $p < 0.001$, $n = 30$). In the BS, the biomass of herring was lowest at the start of the 1980s, but at the same time it was highest in the BPr. By the early 2000s, the situation had reversed (Figure 2). The annual abundances of sprat in the BS and BPr correlated positively ($r = 0.477$, $p < 0.05$, $n = 26$), but the abundances of herring correlated negatively ($r = -0.486$, $p < 0.01$,

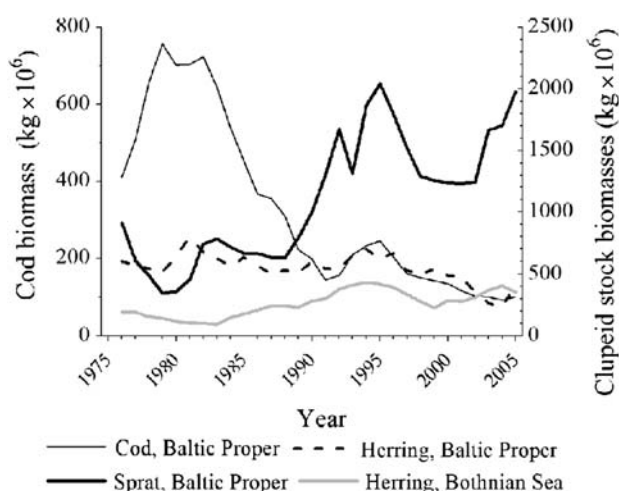


Figure 2. The biomasses of cod, sprat, and herring (<19 cm) in the BPr (ICES SDs 25, 26, and 28), and the biomass of herring (<19 cm) in the BS (ICES SD 30) in 1976–2005. Calculated using datasets from ICES (2006a, b).

$n = 30$) between the areas. However, no significant correlation was found between the respective biomasses.

The sprat biomass as a proportion of the clupeid food potentially available for salmon varied between 36 and 88% during the period 1976–2005 in the BPr (Figure 3a). The proportion was lowest in 1980, increasing to >50% after 1983 and to >60% after 1989. In the BS, herring accounted for >90% of the biomass of potential clupeid prey for salmon in the years 1980–2005. Sprat appeared in commercial catches in the BS for the first time in 1995 (Figure 3a). The total biomass of prey fish available to salmon correlated strongly and positively between the BPr and the BS (Figure 3b).

In the BPr, the mean body weight of 1-year-old herring followed a decreasing trend from 1976 to 2005, being highest in the first years of that period and lowest around and after the mid-1990s (Figure 4a). This variation in the growth rate was also generally seen in the age of herring that were of a size preferred by salmon as prey in all three SDs, 25, 26, and 28; before the mid-1980s, herring were on average youngest, and after the mid-1990s, they were oldest (Figure 1, inset). In the BS, the mean weight of 1-year-old herring had no clear trend (Figure 4a). The mean body weight of 2-year-old sprat in the BPr followed an increasing trend until the turn of the 1990s, then dropped sharply during the 1990s and temporarily increased after the turn of the century.

In the BPr in 1986–2005, the mean CF of sprat was at its highest at the end of the 1980s and lowest around and after the mid-1990s (Figure 4b). The mean CF of herring was highest during the 1980s, and lowest around and after the mid-1990s (Figure 4b). In the BS, the mean CF of herring in the years 1976–2005 varied less; on average, it increased until the mid-1990s, then decreased to its lowest values by the turn of and the first years of the new century. The mean CF of sprat in the BS was highest before the mid-1990s and lowest thereafter.

Salmon total food biomass in the BPr in 1976–2005 correlated negatively with the body weight of 1-year-old herring ($r = -0.718$, $p < 0.001$, $n = 30$), the body weight of 2-year-old sprat ($r = -0.488$, $p < 0.01$, $n = 30$), and the mean CF of herring ($r = -0.668$, $p < 0.01$, $n = 16$), but the negative

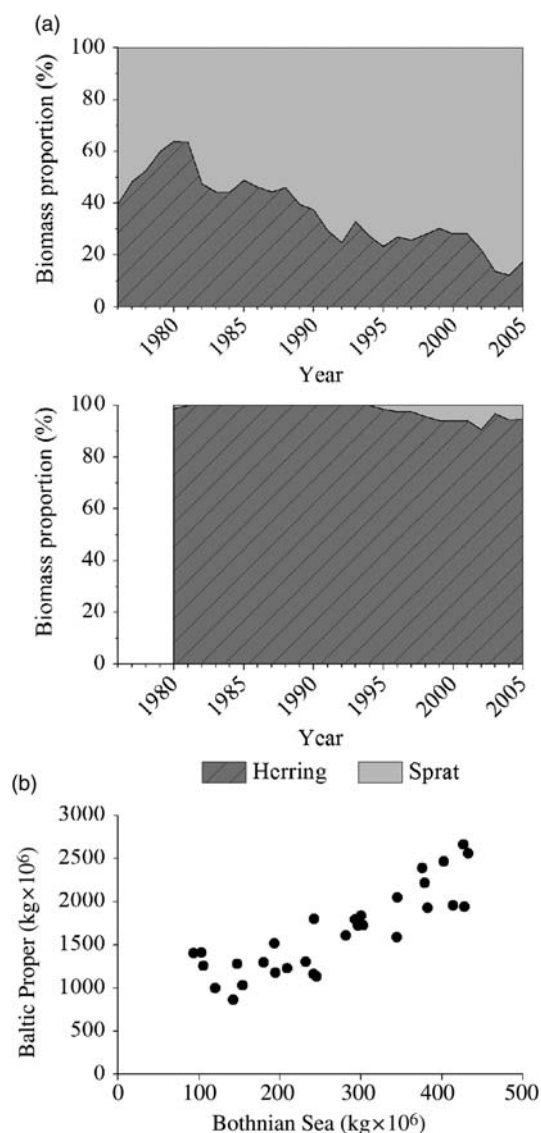


Figure 3. Proportion of the total clupeid biomass accounted for by herring (<19 cm) and sprat: (a, above) in the BPr (ICES SDs 25, 26, and 28) and (a, below) in the BS (ICES SD 30), and (b) Spearman correlation between the annual biomasses of salmon prey in the BPr and the BS in the years 1976–2005 ($r = 0.836$, $p < 0.001$, $n = 30$, number of years). Calculated using datasets from ICES (2006a, b), with estimation of sprat for the GoB from Finnish catch statistics (FGFRI, 2010).

correlation with the mean CF of sprat was not significant. In the BS, neither the body weight nor the mean CF of either prey species correlated with total salmon food biomass.

Size of prespawning salmon in relation to changes in prey fish stocks

The annual mean weight of 2nd sea-year prespawning salmon caught between 1971 and 2007 varied from 2.8 to 7.5 kg, and the length from 61 to 85 cm (data not shown). The CF was lowest (0.91) in the early 1980s, and taking into account the large interannual variation relating to sample size, started to increase strongly from the mid-1980s on, and further during the

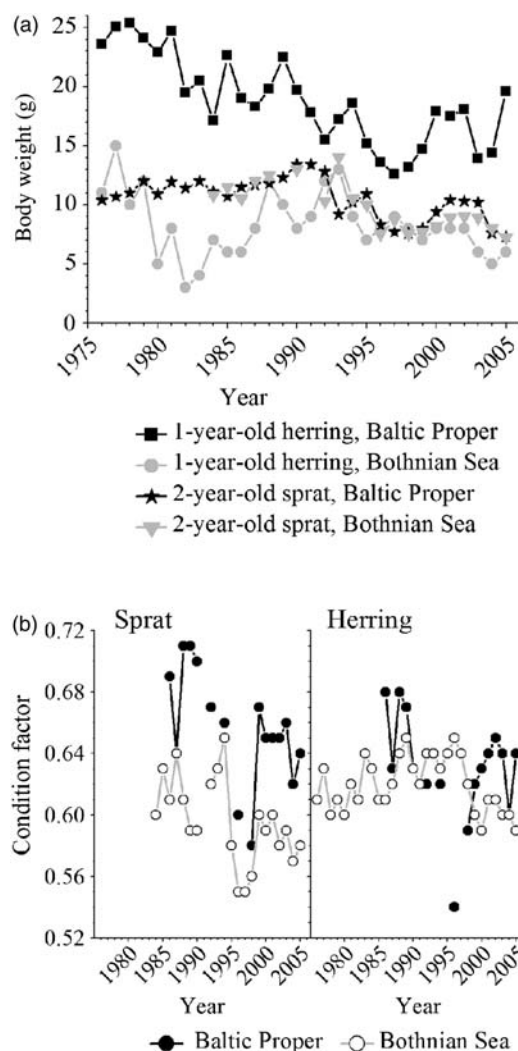


Figure 4. (a) Annual mean body weight of 1-year-old herring and 2-year-old sprat in the BPr and the BS, and (b) the annual mean CFs of herring (<19 cm) and sprat in the BPr and in the BS, 1976–2005. Data for CFs of herring and sprat are lacking from the BPr for the years 1976–1985, 1991, 1993, 1995, and 1997, and for sprat from the BS in 1976–1983 and 1991. The BPr consists of ICES SDs 25, 26, and 28 and the BS of ICES SD 30. Herring and sprat body weights were derived using datasets from ICES (2006a, b).

1990s, up to 1.20 (Figure 5a). The mean CF reached the values of the early 1970s at the start of the 1990s, and was highest thereafter.

The annual mean CF of prespawning 2nd sea-year salmon correlated negatively with the biomass of cod in the BPr ($r = -0.659$, $p < 0.001$, $n = 30$) and positively with the biomasses of total prey fish and of various age group combinations of sprat, but not with the biomass of herring in the BPr (Table 1). For the BS, the correlations were significant between the CF of salmon and the biomass of herring and total prey fish biomass (Table 1).

The mean growth rate of prespawning salmon varied from 23.8 to 32.3 cm year⁻¹ in the period 1971–2006. Growth was slower from the mid-1970s to the early 1980s. Thereafter it increased, and was greatest in the latter part of 1990s and in the 2000s. The growth rate had a negative correlation with the biomass of

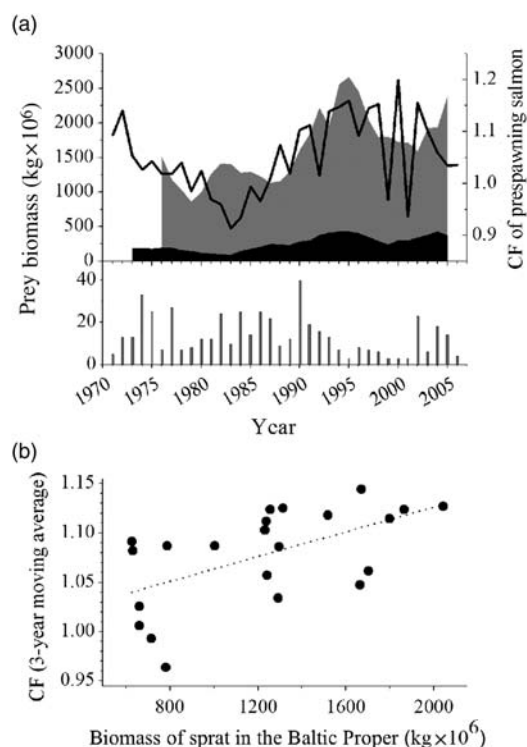


Figure 5. (a) The annual mean CF of prespawning 2nd sea-year salmon caught during their spawning migration from May to August from the GoB (black line), and the annual mean total prey biomass (age groups with herring < 19 cm and all age groups of sprat) in the BPr (ICES SDs 25, 26, and 28, grey area; $\text{CF} = 9.01 \times 10^{-11} \text{ biomass} + 0.90$, $r^2 = 0.514$, $p < 0.001$, $n = 30$) and in the BS (ICES SD 30, black area; $\text{CF} = 4.65 \times 10^{-10} \text{ biomass} + 0.93$, $r^2 = 0.730$, $p < 0.001$, $n = 33$). Columns in the lower part indicate annual numbers of salmon for the calculation of CFs. (b) CF (as a 3-year moving average) of these salmon in relation to the biomass of sprat in ICES SDs 25, 26, and 28 in the BPr. Salmon were assumed to have fed mainly during the year preceding their capture, i.e. a 1-year shift in biomasses was applied. Datasets from ICES (2006a, b) were used in the calculation of prey biomass, with the estimation of sprat for the GoB from Finnish catch statistics (FGFRI, 2010), and salmon data were from the tag-recovery dataset of the Finnish Game and Fisheries Research Institute.

cod ($r = -0.884$, $p < 0.001$, $n = 30$). From among the stock factors of prey fish in the BPr, growth of salmon had the strongest positive correlation with the biomass of sprat (Table 1). The growth rate also correlated significantly with the biomass of the young age groups of sprat and the total biomass of prey, but not with the biomass of herring in the BPr. Moreover, salmon growth correlated positively with the biomasses of sprat and herring for the BS, as well as with prey total biomass, but not with the young age groups of herring (Table 1).

The growth of prespawning salmon had a positive linear relationship with the biomass of prey fish in both feeding areas, in the BPr (growth = $3.52 \times 10^{-9} \text{ biomass} + 22.2$, $r^2 = 0.389$, $p < 0.001$, $n = 30$) and in the BS (growth = $1.81 \times 10^{-8} \text{ biomass} + 23.2$, $r^2 = 0.554$, $p < 0.001$, $n = 33$), and the same relationship was observed for the CF of salmon (Figure 5a). In a stepwise regression analysis, the total biomass of sprat from among various combinations of biomasses of prey fish in the BPr (Table 1) was the main explanatory for salmon growth, and

the biomass of herring had some additional effect (Table 2). However, most of the variation in the CF of prespawning salmon was explained by fluctuations in the biomass of sprat (Table 2), with which there was a linear relationship (Figure 5b).

M74 and the size of salmon

The relationship between the annual mean growth of 2nd sea-year prespawning salmon and the THIAM of eggs of the M74-monitored females or the YFSM of their offspring was not significant. However, YFSM had a positive non-linear relationship with the CF of prespawning salmon (Figure 6a), indicating that when the CF of salmon during the spawning migration was > 1.05 , the rate of YFSM among salmon offspring increased.

The annual mean length of 2nd sea-year female spawners, which were included in M74 monitoring, ranged from 72.6 to 94.3 cm during the years 1985–2006. The average body weight (range 3.4–8.6 kg) varied between years, so that in every year, it differed significantly from at least one other year. The mean CF of female salmon (range 0.84–1.03) was highest in 1990 and 1991, i.e. when the incidence of M74 increased notably, and in those years was significantly higher (ANOVA, Tukey's test, $p < 0.05$) than in 1986, 1988, 1989, 1994, and 1996–2006 (Figure 6b). The average YFSM ranged from 1 to 79% during the same period, being highest in the offspring of river ascendants from the early to the mid-1990s and lowest in the offspring of females that ascended in the 1980s, and again in the offspring of females that ascended from 2002 to 2004 (Figure 6b). Hence, the changes in the mean CF of female salmon and in YFSM roughly paralleled each other. Because of the interannual differences in the mean body weight and CF, the relationships between body weight, length, and CF of female salmon and the incidence of M74 (indicated as the THIAM of eggs or YFSM) were tested within years.

The THIAM in eggs correlated negatively with the size of females in 1998 (L_T : $r = -0.465$, $p < 0.01$; weight: $r = -0.406$, $p < 0.01$; $n = 47$) and 1999 (L_T : $r = -0.489$, $p < 0.01$; weight: $r = -0.525$, $p < 0.01$; $n = 27$), when the incidence of M74 was relatively high. There was also a negative correlation with the CF of female salmon in 1994 ($r = -0.642$, $p < 0.05$, $n = 10$), when the THIAM of eggs was analysed for the first time and when YFSM was still very high. Positive correlations between the egg THIAM and fish size were found in 1997 (L_T : $r = 0.773$, $p < 0.001$; weight: $r = 0.678$, $p < 0.01$; $n = 18$), when YFSM was at its lowest level of the 1990s, and with fish weight in 2004 ($r = 0.471$, $p < 0.05$, $n = 18$), when M74-related mortality was not significant.

The average YFSM correlated positively with the size of female salmon in 1998 (YFSM 56%; L_T : $r = 0.379$, $p < 0.01$; weight: $r = 0.361$, $p < 0.05$; $n = 49$) and with the CF in 1994 (YFSM 69%; $r = 0.654$, $p < 0.05$, $n = 14$), and in 1987 (YFSM 7%; $r = 0.677$, $p < 0.05$, $n = 10$), when symptoms of M74 had not yet been observed in the laboratory. A negative correlation between YFSM and the size of female salmon was detected in 1997 (YFSM 21%; L_T : $r = -0.490$, $p < 0.05$; weight: $r = -0.502$, $p < 0.05$; $n = 22$), and with the CF in 2005 (YFSM 17%; $r = -0.386$, $p < 0.05$, $n = 42$).

M74 and changes in prey fish stocks

In the BPr in 1994–2006, from among the prey fish stock factors tested, the biomass of herring (< 19 cm) correlated negatively with the THIAM of eggs produced by 2nd sea-year salmon (Table 3).

Table 1. Spearman correlation coefficients (r) between the various biomass variables of herring (<19 cm) and sprat in the BPr (ICES SDs 25, 26, and 28) and in the BS (SD 30) in the years 1985–2006, and the growth rate and CF (as a 3-year moving average) of salmon.

Factor	Mean growth rate of salmon (cm year ⁻¹)			Mean CF of salmon		
	r	p -value	n	r	p -value	n
Baltic Proper						
Biomass of herring	−0.313	n.s.	22	0.226	n.s.	22
Biomass of sprat	0.702	<0.01	22	0.579	<0.05	22
Total biomass	0.579	<0.05	22	0.587	<0.05	22
Biomass of 1- to 2-year-old sprat	0.604	<0.05	22	0.561	<0.05	22
Biomass of 2-year-old sprat	0.586	<0.05	22	0.560	<0.05	22
Biomass of 1- to 3-year-old sprat	0.662	<0.01	22	0.567	<0.05	22
Bothnian Sea						
Biomass of herring	0.647	<0.01	22	0.654	<0.01	22
Biomass of sprat	0.661	<0.01	22	0.012	n.s.	22
Total biomass	0.577	<0.05	22	0.616	<0.05	22
Biomass of 1-year-old herring	0.010	n.s.	22	0.338	n.s.	22
Biomass of 1- to 2-year-old herring	0.365	n.s.	22	0.333	n.s.	22
Biomass of 1- to 3-year-old herring	0.397	n.s.	22	0.432	n.s.	22
Biomass of 1- to 4-year-old herring	0.326	n.s.	22	0.481	n.s.	22

Growth was measured and the CF calculated from 2nd sea-year prespawning salmon caught on their spawning migration in SDs 30 and 31 from May to August.

n.s., non-significant, i.e. $p > 0.05$; n , number of years.

Herring and sprat biomasses were derived using datasets from ICES (2006a, b) with the estimation of sprat for the GoB from Finnish catch statistics (FGFRI, 2010), and salmon growth and CF from tag-recovery data held by the Finnish Game and Fisheries Research Institute.

Table 2. Coefficients of determination (r^2), F -values, and significances for the sprat and herring variables in the BPr that in the stepwise regression analysis best explained the growth and CF (as a 3-year moving average) of 2nd sea-year prespawning salmon caught during their spawning migration from May to August of the years 1985–2006 in ICES SDs 30 and 31, and combined YFSM of salmon from the Rivers Tornionjoki, Simojoki, and Kemijoki (for other data sources, see Table 1 and text).

Variable	Partial r^2	r^2	F	p -value
Growth of salmon				
Biomass of sprat	0.571	0.571	26.6	<0.001
Biomass of herring	0.084	0.655	4.62	<0.05
CF of salmon				
Biomass of sprat	0.327	0.327	9.73	<0.01
YFSM				
Total biomass	0.303	0.303	5.66	<0.05

In the BS, the biomass of sprat correlated positively with the THIAM in eggs (Table 3). The YFSM in the years 1985–2006 only correlated positively with total prey biomass and the biomass of sprat in the BPr (Table 3). YFSM did not correlate with any prey factor in the BS (Table 3).

In stepwise regression analysis including various biomass factors (Table 1) and the CF of prey fish in the BPr, there were no significant relationships between the THIAM in the eggs of salmon and any of the prey fish factors for the years 1994–2006. However, the total biomass of salmon prey best explained YFSM during the period 1985–2006 (Table 2).

Discussion

M74 and changes in fish stocks

The incidence of M74 was most clearly related to the total biomass of salmon prey in the BPr. In that feeding area, however, sprat was the dominant prey species of salmon in years of high YFSM. The

clear correlation between the incidence of M74 and the biomass of sprat is therefore consistent with the results of Karlsson *et al.* (1999). In Lake Michigan, EMS of coho salmon (*Oncorhynchus kisutch*) was also connected to variations in the abundance of its main prey species, the alewife (*Alosa pseudoharengus*; Fitzsimons *et al.*, 1999).

A marked collapse of the cod stock in the Baltic Sea preceded the sudden increase in sprat stock size and the strengthening of M74. The cause of the decrease in the cod stock was poor recruitment attributable to environmental changes such as reduced salinity and dissolved oxygen concentration in the spawning areas, a change in zooplankton species composition, and high fishing mortality (Vallin *et al.*, 1999; Köster *et al.*, 2005; ICES, 2006a; Heikinheimo, 2008). Since the collapse, persistent heavy fishing mortality combined with predation on cod eggs by sprat and food competition between sprat and young-of-the-year cod has inhibited cod recovery (Köster *et al.*, 2005; ICES, 2006a; Casini *et al.*, 2009).

The sprat biomass as a proportion of the available clupeid food for salmon in the BPr was <50% from the late 1970s to the early 1980s, when the cod stock was at its maximum. Thereafter, the proportion increased concomitant with the decline in cod (ICES, 2006a), and it was 70–80% in the 1990s, when the incidence of the M74 syndrome was at its highest. The biomass of herring of appropriate size as salmon prey declined on average from the early 1980s to the early 2000s, mainly through a decrease in the herring stock in the central Baltic Sea post-1974 (ICES, 2006a). The changes in the total sprat stock have, however, been manifold (ICES, 2006a), and the increase in the proportion of sprat in the total biomass of salmon prey is therefore mainly attributable to prominent changes in the size of that stock.

The inverse relationship between the THIAM of eggs and the biomass of herring as salmon prey in the BPr during the years 1994–2006 evidently only reflects the coincident decline in herring biomass in the Baltic Sea (ICES, 2006a), and the average decline in the incidence of M74. No data on egg THIAM exist

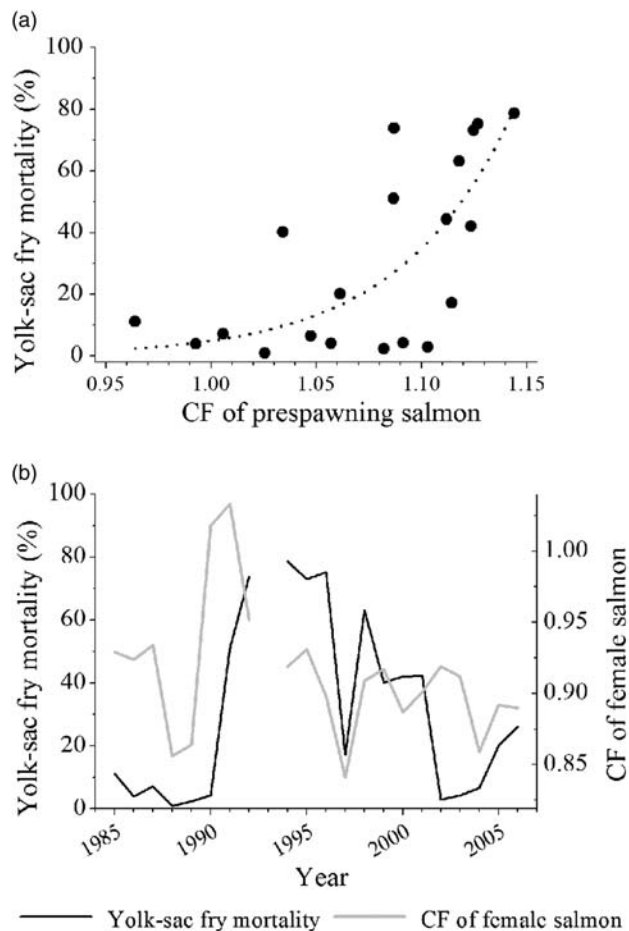


Figure 6. The annual mean YSFM (%) among offspring of 2nd sea-year salmon spawners from the Rivers Simojoki, Tornionjoki, and Kemijoki (a) in relation to CF (as a 3-year moving average) of 2nd sea-year prespawning salmon caught from the GoB during their spawning migration ($y = 4.38 \times 10^{-12} \times (1 + x)^{40.04}$, $r^2 = 0.475$, $p < 0.001$, $n = 20$, number of years), and (b) with the mean CF of 2nd sea-year female salmon used for M74 monitoring during 1985–2006 (data for the year 1993 are unavailable). Prespawning salmon data were from the tag-recovery dataset of the Finnish Game and Fisheries Research Institute.

before the outbreak of M74 or from the very first years with a high M74 incidence at the start of the 1990s. Data on thiamine concentrations in Baltic salmon prey species are also currently limited. In samples taken between October 1994 and January 1995, the concentration of thiamine was higher in herring than in sprat (Vuorinen *et al.*, 2002), but in both species, it was several times higher than the nutritional guideline value for the growth of salmonids (Woodward, 1994). Thiamine deficiency has been suggested to be induced by feeding on herring, in which higher thiaminase activity has been recorded than in sprat (Wistbacka and Bylund, 2008). Herring in the BPr have, however, only formed a minor part of total salmon food biomass, specifically during the period 1994–2005. From the late 1970s to the end of the 1980s, when M74 was not a problem, the proportion of herring was almost equal to that of sprat, and in some years even higher.

In the BS, sprat appeared in salmon diet (Hansson *et al.*, 2001; Salminen *et al.*, 2001) and commercial catches (FGFRI, 2010) only

Table 3. Spearman correlation coefficients (r) between the concentration of THIAM in unfertilized eggs (1994–2006) and offspring YSFM of 2nd sea-year salmon monitored for M74 (1985–2006), and the biomass and mean CF of herring (< 19 cm) and sprat, and their total biomass in the BPr (ICES SDs 25, 26, and 28) and the BS (SD 30).

Factor	Baltic Proper			Bothnian Sea		
	r	p -value	n	r	p -value	n
THIAM						
Biomass of herring	−0.754	<0.05	13	−0.311	n.s.	13
Biomass of sprat	−0.455	n.s.	13	0.839	<0.01	13
Total biomass	−0.499	n.s.	13	−0.345	n.s.	13
CF of herring	0.549	n.s.	10	−0.471	n.s.	13
CF of sprat	−0.099	n.s.	10	−0.449	n.s.	13
YSFM						
Biomass of herring	0.378	n.s.	21	0.526	n.s.	21
Biomass of sprat	0.622	<0.05	21	−0.134	n.s.	21
Total biomass	0.706	<0.01	21	0.528	n.s.	21
CF of herring	−0.607	n.s.	15	0.129	n.s.	21
CF of sprat	−0.132	n.s.	15	−0.137	n.s.	20

n.s., non-significant, i.e. $p > 0.05$; n , number of years.

Herring and sprat biomasses were derived from the datasets in ICES (2006a, b).

after the first years of high M74 incidence. The increase in sprat in the BS is most likely a consequence of the spillover of the species from the BPr, because the salinity in the BS is too low for sprat reproduction (Aro, 1989). The dispersal of sprat into the BS and the increase in its abundance there simultaneously with the decline in M74 were reflected in the positive relationship between the THIAM of salmon eggs and sprat biomass in the BS, without actual relevance. As sprat accounted for <5–10% of the biomass of clupeid salmon prey in the BS during the 1990s–2000s (see also Hansson *et al.*, 2001), it was not apparently an important prey species for salmon in the area during the highest incidence of M74.

Retarded growth of prey fish has been speculated to be a possible cause of M74; older, leaner prey fish may have a lower nutritional value than young ones. However, the low CF of clupeids was not associated with the incidence of M74, but in the BPr, it was related to abundance. As sprat and smaller herring feed on the same zooplankton species (Casini *et al.*, 2004; Möllmann *et al.*, 2004), the growth rate of herring that are of suitable size for salmon as prey is most evidently influenced by increased food competition with sprat, and the growth rate of sprat by increased intraspecific competition (Möllmann *et al.*, 2005; Casini *et al.*, 2006). Therefore, the cause of the retarded growth of prey fish has been the increase in the size of the sprat stock in the BPr and the consequent reduction in food availability (Casini *et al.*, 2006).

Although the average CF of clupeids in the BPr decreased most conspicuously during the outbreak of M74, the mean CF of both species in the BPr was at its lowest in the mid-1990s, whereas YSFM peaked at the beginning of the 1990s. Despite the retarded growth of clupeids and of older herring of suitable size as prey for salmon in the BPr, young sprat were most abundant coincidentally with the highest incidence of M74 at the start of the 1990s. This was evidenced by the clear positive relationships between the CF of prespawning salmon and the biomass of the youngest age groups of sprat, as well as high YSFM. The decrease by 1.5 cm in the average length of sprat consumed by salmon from the early

1960s to the mid-1990s (Hansson *et al.*, 2001) is apparently related to the abundance of young sprat.

Unlike in the BPr, the body weight and mean CFs of herring and sprat in the BS declined slightly only after the mid-1990s, when the incidence of M74 was not as high as earlier in that decade. Moreover, contrary to the BPr, the body weight of herring during the whole research period (1975–2005) was at its lowest in the 1980s. Although the abundance of herring in the BS increased concurrently with a decrease in its abundance in the BPr, the increase in the biomass of herring in the BS coincided with an increase in the stock size of sprat in the BPr, resulting in a correlation of the total prey biomasses between these two feeding areas.

Fish stock changes and salmon size

The weight-at-sea age of salmon from the GoB rivers had started to decrease in the early 1940s and remained low until the 1980s (Karlsson and Karlström, 1994; Karlsson *et al.*, 1999). Salmon growth began to accelerate again from the 1980s on, concomitantly with the decrease in the cod stock. At that time, Larsson (1984) presented a hypothesis that cod would compete with salmon for food in the Baltic Sea, with a resulting negative impact on salmon growth. The results of the present study, and those of Niva (2001) on the body weight of 2nd sea-year salmon ascending the GoB rivers to spawn, support that hypothesis.

In addition to the annual growth rate, the CF of prespawning salmon was inversely related to the size of the cod stock. In the early 1970s, the mean CF of prespawning salmon was as high as in the 1990s. The cod stock increased rapidly, almost threefold from 1974, i.e. the year when M74 was detected for the first time, to the early 1980s, when the CF of salmon was at its lowest. The cod stock apparently enlarged because of favourable salinity and oxygen conditions (Köster *et al.*, 2005; ICES, 2006a; Heikinheimo, 2008). As the ratio of the biomass of salmon to that of cod has been 1:100 in the Baltic Sea, cod has been the only predator of note on clupeids (Börjeson and Norrgren, 1997). Coincidentally with the decline in the cod stock since 1982, and following the consequent reduction in predation pressure, the sprat stock increased rapidly, and salmon therefore had more food available to them and grew faster, resulting also in a high CF.

Karlsson *et al.* (1999) concluded that the sprat and herring biomass of the Baltic Sea were predictors of salmon growth. However, no significant correlation in the present study was detected between either the CF or the growth rate of salmon and the biomass of herring in the BPr. Instead, the abundance of young age groups of sprat in the total prey biomass seemed to explain salmon growth in the correlation analysis. Although in the stepwise regression analysis here the biomass of herring influenced the growth rate of salmon along with the impact of sprat biomass, the increase in the CF of salmon was only related to the increase in sprat biomass in the BPr.

Despite the growth rate and CF of prespawning salmon correlating positively with the abundance of prey in both the BPr and BS, they were most clearly related to the sprat biomass in the BPr. In both regions, the biomass of salmon prey has increased notably since the early 1980s, and at the same time, salmon growth has accelerated. In the BS, the total biomass of salmon prey has, however, remained clearly less than in the BPr, probably also resulting in slow salmon growth there (Salminen *et al.*, 1994; Niva, 2001). Hence, the positive relationship between the growth

rate of Baltic salmon and the biomass of herring in the BS evidently resulted from the simultaneous strengthening of the herring stock in the BS and the increase in the sprat stock in the BPr since the 1980s.

M74 and the size of salmon

The positive relationships between high YFSM and a large size or high CF of mature female salmon or a high CF of prespawning salmon suggest that the M74 syndrome results from salmon feeding excessively on an unbalanced diet. Correspondingly, a low egg THIAM resulting in a high EMS mortality was related to a high body weight of Atlantic salmon feeding in Lake Michigan in North America (Werner *et al.*, 2006).

In the study by Backman (2004), the mean YFSM correlated positively with the annual mean growth rate of 2nd sea-year salmon when the years 1985–2000 were included in the analysis. During the 2000s, the growth rate of salmon was even greater in some years, but the YFSM did not increase in parallel. The reason for this was probably the reduced intensity of driftnet fishing from the late 1990s, which allowed faster-growing salmon a better chance of survival (Karlsson *et al.*, 1999). Apparently for this reason, no significant relationship was found in the present study between salmon growth and the THIAM of eggs or YFSM when the whole period from 1985 (YFSM) or 1994 (THIAM) to 2006 was included in the analysis.

The enhanced salmon growth rate was also concluded to have resulted from increased winter feeding during mild winters (Karlsson *et al.*, 1999). In the latter study, the diet in winter from January to April tended to consist of a larger proportion of sprat than during the rest of the year. Therefore, mild winters with a concomitant more-frequent intake of food, along with feeding more on sprat over the whole year (see also Karlsson *et al.*, 1999), in addition to an abundant food biomass (mainly sprat), may have contributed to the faster salmon growth rate. However, this result and the non-linear relationship between the CF of prespawning salmon and YFSM indicates that the high growth rate of salmon was not as such the cause of M74, but that the abundance of prey and its quality was responsible.

Evidently, because of great interannual variation in the growth rate, neither YFSM nor the THIAM of eggs of female River Simojoki salmon correlated with fish size when the data from the study years 1994–2001 were combined (Backman, 2004). Analysing the relationships between weight, length, or CF of parent female salmon and YFSM or the THIAM of eggs within years, a low egg THIAM was related to a large weight and length of females in the years 1998 and 1999, when the rate of YFSM was ca. 40–60%. In 1998, when the number of females, and, respectively, of offspring groups, in M74 monitoring was highest, YFSM also had a positive relationship with the length and weight of female salmon. Among the years studied, these results were most reliable, because of the large number of observations and the proportion of M74 females being ~50%. A low egg THIAM and high YFSM were also related to the high CF of female salmon in 1994, when most offspring groups still exhibited M74, a large proportion of them even having a mortality rate of 100%.

The negative relationship between the incidence of M74 and the size of female salmon in 1997, when YFSM and fish size and CF were at their lowest since the outbreak of M74 at the start of the 1990s, seems to be related to a large and rapid decrease in the biomass of salmon prey in the BPr. The connection was

especially clear between the total sprat stock of the Baltic Sea from 1995 on, and the resulting decrease in salmon growth (Backman, 2004). Respectively, the negative relationship between the incidence of M74 and the size of females in 2004 and 2005 reflects more-favourable nutritional conditions at the time when the sprat stock in the main feeding area of the BPr was at its smallest since the start of the 1990s. Among the offspring of salmon females that ascended to spawn in 2002–2004, M74 mortality was not significant for the first time since the early 1990s.

When the correlations between YFSM or the egg THIAM and the body weight, length, or CF were calculated based on body size data from M74 monitoring of females captured on arrival at the spawning river, they were somewhat better than when using the size values at the time of spawning. Salmon reduce their food intake when approaching their spawning river, then cease feeding completely before entering the river, although there are differences between stocks in the timing of ascent (Kadri *et al.*, 1995). Salmon from the northern rivers of the GoB fast for 3–4 months before spawning. In the course of prespawning fasting, salmon use up almost all their visceral fat reserves, along with a large proportion of their muscle fat (Kadri *et al.*, 1995). During exogenous vitellogenesis, stored energy is used in forming eggs, as well as for locomotion and basal metabolism (Mommensen and Walsh, 1988). Fasting was recorded in the present study as a ~10% loss of female body weight between arrival at the river and spawning.

To conclude, the results of our analysis point to a need for fishery decision-makers to be made aware that burgeoning sprat stocks at a time when the biomass of their main predator (cod) is depressed can have a negative impact on salmon stocks, by influencing the incidence of the M74 syndrome.

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