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RECENT CHANGES IN THE GROWTH AND FEEDING OF BALTIC HERRING AND SPRAT IN THE NORTHEASTERN BALTIC SEA

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Abstract. The mean weight at age of Baltic herring remained rather stable from the 1940s to the 1960s. Since the second half of the 1970s, the mean weight of herring began to increase in most regions of the Baltic Sea. High values of the mean weight and length in all age groups were observed until the mid-1980s; then a sudden drop in all growth parameters followed.

Since the 1990s a decrease can be observed in the growth of Baltic sprat. The results of feeding investigations conducted in 1982—92 show changes in the prey composition and an increase in the proportion of fish with empty stomachs. These changes, probably induced by hydrological conditions prevailing since the mid-eighties, may at least partly be responsible for drastic alterations in fish growth.

Preliminary calculations show that the Gulf of Finland herring and sprat stocks without the 0-group consume 15.2×10^5 t of zooplankton and 3.9×10^5 t of nektobenthic organisms.

Key words: Baltic herring, Baltic sprat, growth, feeding.

INTRODUCTION

Baltic herring (*Clupea harengus membras* L.) and sprat (*Sprattus sprattus balticus* Schn.) are the most abundant commercial fishes in the Baltic Sea. During the last 25 years, the biomass of herring has decreased from 3.5 million tonnes in 1974 to 1.7 million tonnes in 1993 in the main basin of the Baltic Sea, i. e. without the Bothnian Sea and the Gulf of Bothnia (Anon., 1994). Still, in some parts of the sea, e. g. in the Gulf of Riga, the herring biomass follows an increasing trend.

The most important fishing area for Estonian herring fishery is the Gulf of Finland, where over 50% of the catches are taken presently. The herring stock in the Gulf of Finland was assessed separately by the ICES working group until 1990. Later, herring has been assessed as a part of the main basin herring stock. Therefore, there are no estimations available for the biomass of the herring stock in the Gulf of Finland since 1989. Comparative estimations available for both stocks show that the biomass of the Gulf of Finland stock constituted about 5—13% of the biomass of the total stock in 1970—89. The biomass of the Baltic sprat fluctuated between 0.6 and 2.2 million tonnes in 1974—93, not showing any distinct trend (Fig. 1; Anon., 1990, 1994).

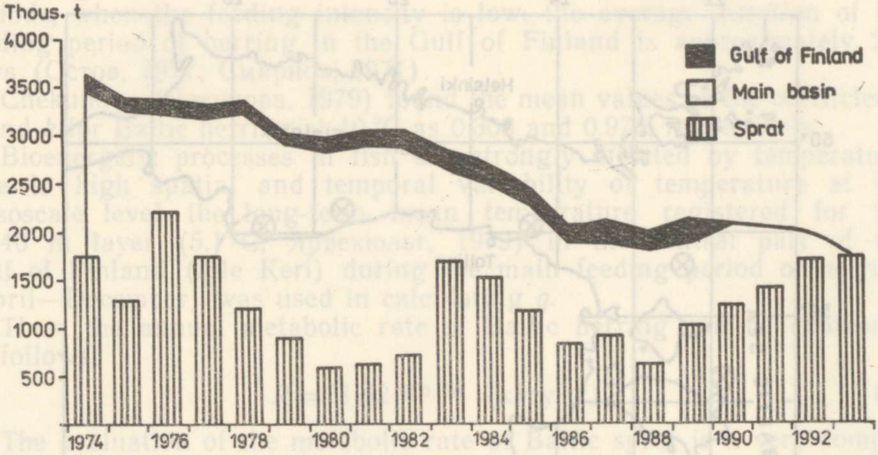

Fig. 1. Total biomass of herring in the main basin of the Baltic Sea and in the Gulf of Finland and the biomass of sprat in the Baltic Sea in 1974—93 (Anon., 1990, 1994).

It is obvious that all major changes in main biological parameters of those large fish stocks have serious implications on the ecosystem of the Baltic Sea.

Since the second half of the 1980s, particularly in the 1990s, the mean weight at age of Baltic herring has decreased remarkably in all regions. This serious trend affects fishery, fish marketing, as well as stock assessment.

Despite the relative stability of the mean weight at age in the 1970s—80s, a slight decrease in the mean weight of Baltic sprat can be observed from the beginning of the 1990s.

Since the growth processes are closely related to feeding, the hydrological situation, stock abundance, etc., it is not surprising that the problems connected with the growth and feeding of herring and sprat and with the energetic role of pelagic fish in the ecosystem have become topical among the fisheries biologists around the Baltic Sea (e. g. Aro & Kotilainen, 1989; Flinkman et al., 1992; Parmanne, 1990, 1992; Raid & Lankov, 1989, 1991, 1993; Davidyuk et al., 1992; Arrhenius & Hansson, 1993; Fetter & Davidyuk, 1993; Naglis & Sidrevics, 1993; and others).

MATERIAL AND METHODS

The basic material on herring and sprat feeding used in the present work was collected in 1982 and 1985—92 during the trawl surveys performed in April and November—December. The sampling sites were located westwards of Saaremaa Island (ICES Subdivision 29) and in the southern part of the Gulf of Finland (Subdivision 32; Fig. 2). All trawl hauls were carried out in daytime, exploiting the densest fish concentrations at the given site to get a representative sample.

Stomach contents of fish were examined using standard hydrobiological methods (Инструкция . . ., 1971). A total of 4207 herring and 1014 sprat were analysed.

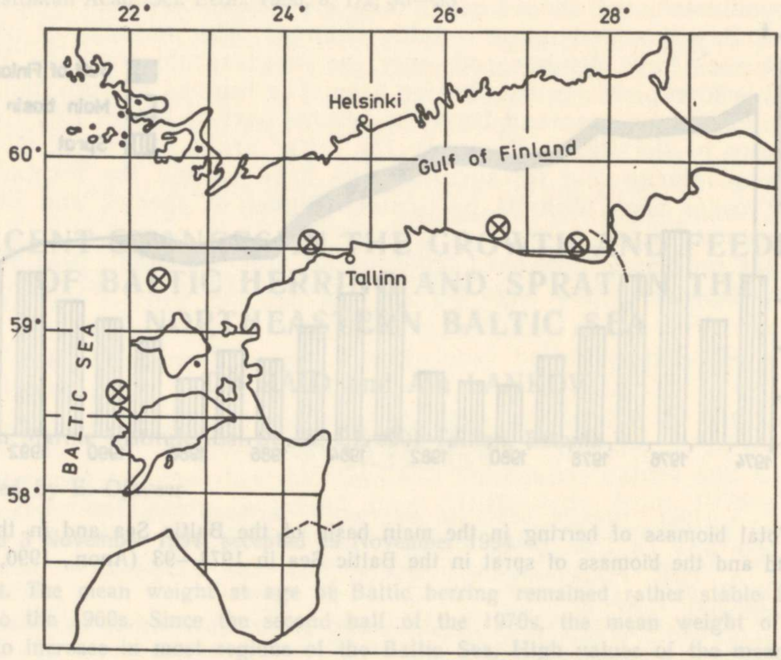

Fig. 2. Location of the sampling sites in the northeastern Baltic.

To characterize the consumption rate of zooplankton and nektobenthos by Baltic herring and sprat, the advanced Winberg's energy budget method complemented by available data on marine fish energetics from the literature (e.g. Winberg, 1956; Green, 1978; Aneer, 1979; Мельничук, 1980; Rudstam, 1988) was used.

The energy budget method in combination with data on fish growth and population size was used to calculate the consumption by the herring and sprat stocks.

The annual ration (C) for both Baltic herring and sprat can be expressed by the equation:

$$C = R + P + Pq + F \quad \text{(kJ)}, \tag{1}$$

where P is the energy used annually for growth, Pq is the energy released for spawning, and F stands for fecundity. The energy used daily in metabolism (R) can be expressed as:

$$R = \frac{a \times 20.33 \times 24 \times W^k \times 1.5}{q} \quad (\text{J} \cdot \text{day}^{-1}) \tag{2}$$

or

$$R = \frac{a \times 20.33 \times 24 \times W^k \times 1.5}{q \times Cc} 10^{-3} \quad (\text{g} \cdot \text{day}^{-1}), \tag{3}$$

where the coefficients a and k describe the relationship between metabolism R and body weight W as:

$$R = a W^k, \tag{4}$$

and q is Krogh's temperature correction coefficient and Cc is the energetic value (varying for herring seasonally from 5.12 to 5.94 $\text{J} \cdot \text{g}^{-1}$; see Aneer, 1975).

Taking into account the mean duration of spawning and wintering periods, when the feeding intensity is low, the average duration of the feeding period of herring in the Gulf of Finland is approximately 270 days (Остов, 1971; Смирнов, 1971).

Chekunova (Чекунова, 1979) found the mean values of the coefficients a and k for Baltic herring at 10 °C as 0.306 and 0.978, respectively.

Bioenergetic processes in fish are strongly affected by temperature. Due to high spatial and temporal variability of temperature at the mesoscale level, the long-term mean temperature registered for the 0—40 m layer (5.1 °C, Ярвекюльг, 1979) in the central part of the Gulf of Finland (Isle Keri) during the main feeding period of herring (April—December) was used in calculating q.

Thus, the annual metabolic rate of Baltic herring can be expressed as follows:

$$R = 31.62\, W^{0.978} \quad (\text{kJ·yr}^{-1}). \tag{5}$$

The evaluation of the metabolic rate of Baltic sprat is a very complicated task, as in this case no data are available on coefficients a and k. Therefore, in the present work the coefficients $a = 0.35$ and $k = 1.01$ estimated for Falkland sprat, *Sprattus fuegensis*, at 10 °C (Чекунова & Наумов, 1977) were applied. Moreover, unlike Baltic herring, sprat can feed also at relatively low temperatures. So, despite of the fact that the feeding sprat is mainly concentrated in the temperature range of 2.4—3.9 °C in winter, it can feed even at 0.2—0.3 °C (Mankowski, 1947). Sprat does not interrupt feeding during the spawning period either, because it is a batch spawner and its gonads remain relatively small throughout its long spawning period.

Substituting the above parameters into Eq. (2) yields the annual metabolic rate for Baltic sprat:

$$R = 45.4\, W^{1.01} \quad (\text{kJ} \cdot \text{yr}^{-1}). \tag{6}$$

Energy used annually for growth equals for both species:

$$P = 5.53 \Delta W \quad (\text{kJ} \cdot \text{yr}^{-1}), \tag{7}$$

where 5.53 is the mean value of Cc from Eq. (3) and ΔW is annual growth increment.

Energy released at the spawning of herring was calculated applying the fecundity data and the mean weight of gonads. Fecundity was calculated using the relationship between fecundity (F) in thousand eggs and body weight (W) in grams (Раннак, 1970):

$$F = 225\, W + 4390. \tag{8}$$

Assuming that the mean diameter of the egg is 1.0 mm, the specific gravity is 1000 g·m^{-3}, and dry/wet weight ratio is 0.24 (Green, 1978), the weight of gonads (GW) will equal:

$$GW = \pi/6 \times 1^3 \times 0.24 \times F \times 10^{-3} \quad (\text{g}) \tag{9}$$

or

$$GW = 0.126\, F \quad (\text{g}). \tag{10}$$

Lasker (1973) estimated the energy content (Cc) of the gonads of the planktivorous Pacific sardine *Sardinops caerulia* to be 22.73 kJ·g^{-1} for ovaries and 20.31 kJ·g^{-1} for testes. Since no respective data for the species investigated here were available to the present authors, the mean energetic value of clupeid gonads (ovaries and testes) presented in Green, 1978 ($Cc = 21.94$ kJ·g^{-1}), was used both for herring and sprat.

Then the equation of energy released at the spawning of herring (Pq) reduces to:

$$Pq = 2.76(225\,W + 4390) \times 10^{-3}\ (\mathrm{kJ \cdot yr^{-1}}). \quad (11)$$

The gonads of sprat make up about 1/8 of its body weight (Veldre, 1986). Thus, the energy released at the spawning of sprat can be expressed as:

$$Pq = 1/8\,W \times 0.24 \times 21.9\ (\mathrm{kJ \cdot yr^{-1}}) \quad (12)$$

or

$$Pq = 0.66\,W\ (\mathrm{kJ \cdot yr^{-1}}). \quad (13)$$

In Eq. (1) F expresses energy losses through faecal material and excretion. For the fish feeding on animal prey, it forms about 20% (Мельничук, 1980).

The energy content of prey organisms was taken at the level of 2850 $J \cdot g^{-1}$ wet weight (Laurence, 1976) in case of zooplankton, 2976 $J \cdot g^{-1}$ for juvenile and 3720 $J \cdot g^{-1}$ for adult mysids (Wiktor & Szaniawska, 1988). For amphipods, the energy content 3980 $J \cdot g^{-1}$ (Hill et al., 1992) was used.

Since the evacuation rate of stomach contents is often highly variable and depends on hydrological conditions, particularly on temperature, the estimation of food consumption by fish in natural conditions is a rather complicated task (Szpula & Zalachowski, 1984).

GROWTH AND FEEDING OF BALTIC HERRING AND SPRAT IN RECENT DECADES

Growth

Herring. The growth rate of herring and sprat diminishes in the Baltic Sea towards its northern and northeastern parts. So the mean weight of herring in the Gulf of Finland in most age groups makes up only 20—50% of the respective values of southern or even central regions (Anon., 1990). The relatively severe environmental conditions, like low temperature and salinity, combined with a short vegetation period are most likely the main reason for a low growth rate of herring in the northern and northeastern Baltic (Ojaveer, 1981).

The growth rate of herring and sprat was rather stable during a long period. Observations of the mean weight at age of herring on spawning grounds have been carried out in Estonian coastal areas since the 1940s. No long-term trend was observed in the 1950s and 1960s (Ojaveer & Rannak, 1980). Later, in the 1970s, the mean weight started to increase gradually. In the Gulf of Finland, the mean weight of herring of younger age groups reached its highest values in the late 1970s and that of the older age groups in the mid-1980s (Table 1, Fig. 3.)

Later, in 1986—90, the mean weight of herring decreased in the most abundant age groups (1—6) to the level of 1976—80. The decline of the mean weight was particularly remarkable in 1991—93. So, in 1993 the mean weight of herring in older age groups made up approximately 50% of the level of the mid-1980s or even less (Fig. 3). The mean weight of herring has been decreasing not only in the Gulf of Finland, but almost in all regions of the Baltic Sea (Anon., 1994).

The decline of the mean weight was followed by an aggravation of the condition of fish (Aro et al., 1992; Parmanne, 1992), and an increase in the share of dystrophic herring, often invaded by various parasites. So, in different samples taken in the Gulf of Finland in 1991—92 the share of meagre herring was found to be 3—16% (Turovsky et al., 1992).

Table 1

Mean weight at age of Baltic herring in Estonian trawl catches in the Gulf of Finland, g (1970—1993)

Years	Age 1	2	3	4	5	6	7	8	9	10+
1970	16.3	19.2	21.5	29.3	30.3	31.5	28.9	36.3	41.3	75.7
1971	14.7	20.7	24.6	26.1	33.2	34.1	36.8	41.0	40.8	43.6
1972	14.8	18.4	24.7	28.4	27.1	32.0	36.4	37.0	35.2	51.3
1973	15.0	18.1	21.7	31.4	28.4	31.7	38.7	38.1	43.3	38.4
1974	15.0	19.2	24.9	25.7	35.4	32.2	36.5	44.7	39.6	46.1
1975	17.0	19.5	24.6	27.6	27.6	33.6	33.7	36.0	34.9	40.3
1976	16.3	22.7	27.5	32.7	34.2	36.3	43.8	45.8	45.3	52.8
1977	18.9	21.8	26.7	34.2	36.5	42.4	40.8	57.0	46.6	97.6
1978	13.9	27.4	33.5	38.3	40.6	42.2	48.6	45.6	62.4	59.7
1979	16.0	24.4	31.2	36.7	40.4	42.6	45.6	47.8	49.2	53.8
1980	14.7	26.7	31.1	36.2	47.1	43.4	49.8	47.7	74.3	59.6
1981	16.2	19.9	30.5	36.9	49.5	52.8	65.6	67.6	76.4	79.9
1982	17.3	20.8	30.2	39.0	45.3	72.0	52.7	60.0	115.7	81.7
1983	15.3	20.7	30.2	39.5	46.6	50.2	48.1	58.8	43.7	128.1
1984	14.7	18.9	29.1	37.7	41.4	44.6	54.9	62.6	78.9	72.5
1985	15.0	16.3	22.5	33.8	45.1	60.9	58.2	72.4	63.7	97.4
1986	14.3	17.4	21.6	27.7	32.5	48.1	55.4	82.8	80.4	87.4
1987	14.87	17.5	24.4	33.0	39.7	51.2	56.2	72.6	74.3	85.8
1988	10.6	15.9	24.4	29.7	34.6	45.8	59.6	63.3	57.6	91.8
1989	13.6	17.4	23.6	30.1	35.5	44.5	51.9	63.0	64.7	88.5
1990	13.0	18.0	22.2	25.2	29.4	37.7	42.7	44.3	51.5	76.9
1991	11.3	17.7	20.7	22.8	24.5	26.4	33.1	42.1	48.8	57.6
1992	8.8	16.2	19.6	21.9	22.0	24.7	24.2	35.7	41.5	40.2
1993	9.9	13.6	18.1	21.1	22.2	24.2	25.6	29.5	32.0	41.9
1971—75	15.3	19.2	24.1	27.8	30.3	32.7	36.4	39.4	38.8	43.9
1976—80	16.0	24.6	30.0	35.6	39.8	41.4	45.7	48.8	55.6	64.7
1981—85	15.7	19.3	28.5	37.3	45.6	56.1	55.9	64.3	75.7	91.9
1986—90	13.2	17.2	23.2	29.1	34.3	45.5	53.2	65.2	65.7	86.1
1991—93	9.8	15.8	19.5	21.9	22.9	25.1	27.6	35.8	40.77	46.57
1979—90	14.63	19.5	26.8	33.8	40.6	49.5	53.4	61.9	69.2	83.62
1970—90	15.12	20.0	26.2	32.3	37.2	43.3	46.9	53.5	58.09	71.85
1970—93	14.45	19.5	25.4	31.0	35.4	41.0	44.5	51.3	55.92	68.69

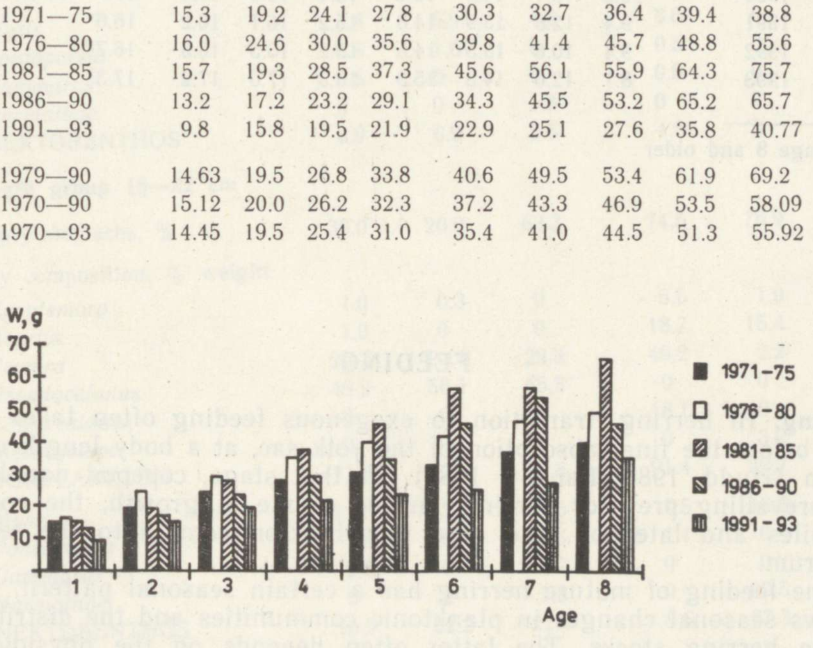

Fig. 3. Mean weight at age of herring in the Gulf of Finland in 1971—93.

Sprat. Against the background of the prevailing situation of herring growth, it is quite surprising that the mean weight at age of another planktivorous clupeid—the Baltic sprat—remained almost stable during the recent decades till 1992, when a slight decrease in its mean weight was observed in the northeastern Baltic (Aps, 1992; see Table 2).

Table 2

Baltic sprat in subdivisions 27 and 29 to 32. Mean weight at age in catches, g (Anon., 1993, 1994)

Years	Age									
	1	2	3	4	5	6	7	8	9	10+
1975	9.4	11.3	12.0	12.2	12.4	12.9	13.5	13.2	14.2	12.3
1976	8.7	10.8	12.2	12.8	13.7	13.9	14.0	13.2	13.8	14.2
1977	7.8	10.5	13.1	13.5	13.9	14.8	14.2	14.5	15.6	14.4
1978	9.8	10.9	12.4	13.0	13.6	14.1	14.4	14.9	14.1	14.5
1979	11.4	12.9	13.7	14.0	14.3	14.4	14.9	15.0	15.1	15.0
1980	11.0	12.6	14.6	14.3	14.2	15.3	14.3	14.9	13.8	15.0
1981	9.5	12.6	14.6	14.8	15.8	15.8	16.2	15.6	15.6	14.0
1982	9.8	12.5	14.6	15.2	16.1	15.9	16.1	16.7	16.5	16.2
1983	7.6	12.6	14.9	16.2	16.0	16.4	16.5	16.7	17.7	17.1
1984	8.2	12.1	13.8	15.2	16.1	16.3	16.4	16.9	16.9	16.7
1985	7.4	11.2	13.0	15.2	15.3	15.8	15.7	16.5	15.4	15.6
1986	10.1	12.4	13.9	14.9	15.6	15.6	16.2	16.7	16.2	16.3
1987	9.9	12.2	14.0	14.6	15.4	16.3	16.6	17.4	15.5	16.5
1988	10.0	13.2	13.8	15.7	16.1	16.6	17.2	17.3	16.4	16.8
1989	11.8	12.4	14.9	15.4	16.7	17.2	17.3	16.8	17.4	16.9
1990	10.8	13.1	14.0	15.6	16.4	16.6	16.4	17.0	17.0	16.4
1991	9.4	12.8	13.9	14.8	15.2	16.1	16.2	16.6*		
1992	9.4	10.6	13.5	14.5	15.2	15.5	16.3	16.7*		
1993	8.1	12.0	14.3	15.3	16.3	17.0	17.2	17.3*		

* age 8 and older

FEEDING

Herring. In herring, transition to exogenous feeding often takes place even before the final absorbtion of the yolk sac, at a body length of 8—9 mm (Hudd, 1980; Lankov, 1986). At that stage, copepod nauplii are the prevailing prey for herring. In the course of growth, the copepod juveniles and later on also other zooplankton come into the feeding spectrum.

The feeding of mature herring has a certain seasonal pattern, which follows seasonal changes in planktonic communities and the distribution of the herring stocks. The latter often depends on the physiological status of the fish.

Table 3

Baltic herring in subdivisions 29 and 32. Feeding data for April

Stomach contents	1986	1987	1988	1989	1990	1991
Length group <14 cm						
Empty stomachs, %	18.8	19.4	13.6	29.4	39.4	98
Prey composition, % weight						
Eurytemora	9.5	24.8	2.8	18.4	6.2	0
Acartia	6.8	0	0	6.9	81.9	0
Temora	35.6	42.7	34.8	58.8	6.9	0
Pseudocalanus	40.6	32.0	61.1	15.9	0.4	0
Limnocalanus	0	0	0	0	3.1	0
Mesocyclops	0	0	0	0	1.5	0
ZOOPLANKTON	92.5	99.5	98.7	100	100	0
Mysis	7.5	0.5	1.3	0	0	0
Pontoporeia	0	0	0	0	0	0
Gammarus	0	0	0	0	0	100
NEKTOBENTHOS	7.5	0.5	1.3	0	0	100
Length group 14—18 cm						
Empty stomachs, %	30.5	15.3	42.9	51.5	69.1	86.5
Prey composition, % weight						
Eurytemora	1.0	6.7	4.9	5.7	7.0	0
Acartia	0.5	0	0	29.5	50.6	0
Temora	31.8	33.3	35.3	44.3	34.1	31.3
Pseudocalanus	58.7	53.1	54.0	13.4	0.3	0
Limnocalanus	1.1	0	0.3	2.3	4.7	0
Mesocyclops	0	0	0	0	3.3	0
ZOOPLANKTON	93.1	93.1	94.2	95.2	100	31.3
Mysis	5.8	5.9	4.2	3.8	0	64.4
Pontoporeia	0.6	1.0	0	0.5	0	4.3
Gammarus	0.5	0	0	0.5	0	0
Harmothoe	0	0	1.3	0	0	0
NEKTOBENTHOS	6.9	6.9	5.5	4.8	0	68.7
Length group 18—22 cm						
Empty stomachs, %	38.0	26.0	63.3	74.5	76.9	76.0
Prey composition, % weight						
Eurytemora	1.0	0.3	0	5.5	1.9	0
Acartia	1.0	0	0	18.7	15.4	0
Temora	20.7	21.4	22.3	49.2	2.2	12.3
Pseudocalanus	49.2	56.1	55.3	0	0	2.6
Limnocalanus	0	0	0	18.1	0	0
Mesocyclops	0	0	0	0	3.2	0
ZOOPLANKTON	71.9	77.8	77.6	91.4	22.7	14.9
Mysis	11.6	13.6	9.5	7.5	16.8	7.5
Pontoporeia	1.8	8.6	9.4	1.1	0	19.5
Gammarus	2.5	0	1.7	0	0	0
Harmothoe	0	0	1.8	0	60.5	58.1
NEKTOBENTHOS	15.9	22.2	22.4	8.6	77.3	85.1
FISH	12.2	0	0	0	0	0

Table 3 continued

Stomach contents	1986	1987	1988	1989	1990	1991
Length group >22 cm						
Empty stomachs, %	47.9	26.9	72.7	77.8	78.6	91.7
Prey composition, % weight						
Eurytemora	1.4	0	3.9	2.1	0	0
Acartia	1.1	0	0	29.2	13.6	0
Temora	9.4	8.8	11.9	35.6	0	0
Pseudocalanus	44.7	46.7	38.6	0	0	0
Limnocalanus	0	0	0	33.1	0	0
Mesocyclops	0	0	0	0	5.5	0
ZOOPLANKTON	56.6	55.5	54.4	100	19.1	0
Mysis	22.7	11.3	14.9	0	0	55.3
Pontoporeia	19.5	8.6	6.9	0	0	0
Gammarus	1.2	10.8	0	0	4.2	37.7
Harmothoe	0	0	0	0	76.7	7
Leander	0	0	23.8	0	0	0
NEKTOBENTHOS	43.4	30.7	45.6	0	80.9	100
FISH	0	13.8	0	0	0	0

Zooplankton, mainly copepods, dominates in the herring diet after wintering. Mysids and other nektobenthic organisms prevail in autumn. However, the observations conducted in the Gulf of Finland revealed certain changes in the herring food composition in the 1980s compared with the "traditional" food spectrum. As our results show, the importance of zooplankton, particularly that of *Temora longirostris,* has increased, while the share of mysids has diminished, even in autumn (Tables 3 and 4).

The share of herring with no food in the stomach has increased rapidly since the second half of the 1980s reaching 80—90% in 1991—92. This occurred both in April and November—December (Fig. 4).

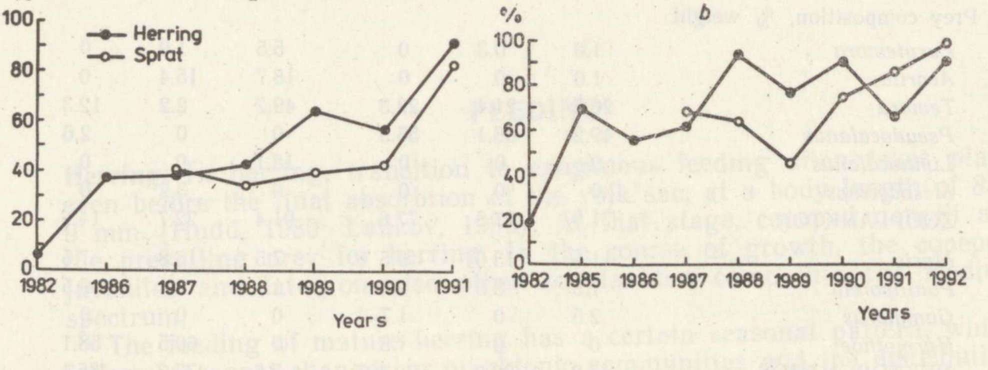

Fig. 4. Proportion of herring and sprat with empty stomachs in the northeastern Baltic in April 1982—91 (*a*) and in November—December 1982—91 (*b*).

Table 4

Baltic herring in subdivisions 29 and 32. Feeding data for November—December

Stomach contents	1985	1987	1988	1989	1990	1991	1992
Length group <14 cm							
Empty stomachs, %	81.3	57.6	83.3	70.3	80.5	90.9	91.0
Prey composition, % weight							
Eurytemora	7.2	18.9	100	30.9	8.9	0	38.8
Acartia	11.7	39.3	0	21.8	26.6	0	0.9
Temora	9.7	13.4	0	14.2	46.8	100	51.7
Pseudocalanus	0	0.6	0	0	0	0	6.2
Limnocalanus	0	0	0	3.0	0	0	0
Mesocyclops	0	0	0	8.5	0	0	2.4
Bosmina	0	3.1	0	0	0	0	0
Podon	0	10.9	0	0	0	0	0
Ceriodaphnia	0	0.8	0	0	0	0	0
ZOOPLANKTON	28.6	87.0	100	78.5	83.2	100	100
Mysis	69.1	13.0	0	21.6	4.8	0	0
Pontoporeia	2.3	0	0	0	0	0	0
Gammarus	0	0	0	0	12.9	0	0
NEKTOBENTHOS	71.4	13.0	0	21.6	17.7	0	0
Length group 14—18 cm							
Empty stomachs, %	81.1	79.3	66.7	79.2	92.0	60.6	94.8
Prey composition, % weight							
Eurytemora	0.8	12.5	4.5	18.4	0.3	0	0
Acartia	0.8	9.2	0	0	0.5	0	0
Temora	3.2	19.9	10.1	67.6	2.4	8.0	0
Pseudocalanus	2.0	3.0	14.5	0	0	0	0
Limnocalanus	0	0	0	3.2	0	0	0
Mesocyclops	0	0	0	10.8	0	0	0
Bosmina	0	6.8	0	0	0	0	0
Podon	0	7.1	0	0	0	0	0
Ceriodaphnia	0	0.5	0	0	0	0	0
ZOOPLANKTON	6.8	59.0	29.1	100	3.2	8.0	0
Mysis	42.8	36.9	69.6	0	96.8	71.8	83.0
Pontoporeia	20.4	0.8	1.3	0	0	17.4	7.4
Gammarus	0	0	0	0	0	2.8	0
Idothea	0	0.6	0	0	0	0	9.6
NEKTOBENTHOS	93.2	38.3	70.9	0	96.8	92.0	100
FISH	0	2.7	0	0	0	0	0
Length group 18—22 cm							
Empty stomachs, %	62.1	58.3	18.8	88.2	100	50.0	87.5
Prey composition, % weight							
Eurytemora	0	1.5	0	0	0	50.0	0
Acartia	0	1.5	0	0	0	0	0
Temora	0	34.8	0	69.0	0	0	0
Pseudocalanus	0.1	0	1.9	0	0	0	0
Limnocalanus	0	0.9	0	0	0	0	0
ZOOPLANKTON	0.1	38.7	1.9	69.0	0	50.0	0

Stomach contents	1985	1987	1988	1989	1990	1991	1992
Mysis	95.9	60.9	94.6	31.0	0	20.1	100
Pontoporeia	4.0	0.4	1.1	0	0	10.2	0
Mesidothea	0	0	0	0	0	3.7	0
Harmothoe	0	0	0	0	0	66.0	0
NEKTOBENTHOS	99.9	61.3	95.7	31.0	0	100	100
FISH	0	0	2.4	0	0	0	0
Length group >22 cm							
Empty stomachs, %	47.1	57.1	26.7	50.0	100	100	0
Prey composition, % weight							
Eurytemora	0	6.6	0	0	0	0	0
Acartia	0	0	0	0	0	0	0
Temora	0	46.7	0	1.6	0	0	0
Pseudocalanus	0	37.5	0.3	0	0	0	0
ZOOPLANKTON	0	90.8	0.3	1.6	0	0	0
Mysis	96.5	9.0	94.0	10.8	0	0	100
Pontoporeia	3.0	0	1.9	0	0	0	0
NEKTOBENTHOS	99.5	9.0	95.9	10.8	0	0	100
FISH	0.5	0	3.8	87.6	0	0	0

The proportion of fish with empty stomachs in April has increased in all length groups since 1987. Still, the increase has been particularly obvious in older fish (with total length over 18 cm, Table 3). In November—December the trend was the most obvious among the bigger herring, reaching 100% in herring bigger than 22 cm (Table 4). This probably indicates to serious problems in the feeding of bigger herring, usually known as grazing mostly on big, energy-rich nektobenthic prey in autumn.

Sprat. Baltic sprat passes to exogenous feeding at a size of 6—7 mm. Larval food is dominated by phytoplankton, which accounts for over 80% of the food for smaller larvae, being supplemented by copepod nauplii and juvenile stages of different copepods (*Temora*, *Acartia*, *Eurytemora*). Later, the share of phytoplankton decreases gradually, and after sprat reaches 10 mm in length, zooplankton remains its only prey (Raid & Simm, 1986). Sprat over 30 mm in size has already the food spectrum of the adult fish, which consists of copepods and cladocerans (*Evadne*, *Podon*, *Bosmina*).

An analysis of data on sprat feeding revealed trends very similar to those of herring: the abundance of starving fish has been increasing and the prey spectrum has been shrinking during the recent few years.

So, while the mean share of sprat in the northeastern Baltic with no food in the stomachs was found to be around 50—60% in the 1980s, the respective value was 80—90% in the 1990s having reached almost the same level as herring (Fig. 4). *Temora*, *Acartia*, and *Pseudocalanus* were dominating in the sprat diet in the 1980s. Since 1990, *Temora* has gained a position of the main prey (Tables 5 and 6).

Table 5

Baltic sprat in subdivisions 29 and 32. Feeding data for April

Stomach contents	1987	1988	1989	1990	1991
Length group <8 cm					
Empty stomachs, %	31.0	100	67.3	100	0
Prey composition, % weight					
Eurytemora	3.3	0	4.6	20.0	0
Acartia	0	0	0	80.0	0
Temora	28.9	0	65.6	0	0
Pseudocalanus	67.8	0	27.7	0	0
Limnocalanus	0	0	2.1	0	3.1
ZOOPLANKTON	100	0	100	100	0
Length group 8—12 cm					
Empty stomachs, %	53.8	0	34.8	41.4	88.2
Prey composition, % weight					
Eurytemora	0	0	2.5	15.4	0
Acartia	0	0	35.4	69.0	4.0
Temora	13.0	54.5	42.0	10.8	72.0
Pseudocalanus	87.0	45.5	14.2	1.4	24.0
Limnocalanus	1.1	0	5.9	2.6	0
Mesocyclops	0	0	0	0.2	0
Evadne	0	0	0	0.6	0
ZOOPLANKTON	100	100	100	100	100
Length group >12 cm					
Empty stomachs, %	87.5	40.9	20.0	49.2	78.3
Prey composition, % weight					
Eurytemora	0	0.4	0.5	5.8	0
Acartia	0	0	2.8	72.1	7.9
Temora	16.7	65.3	79.1	17.1	42.1
Pseudocalanus	83.3	34.3	9.0	0	50.0
Limnocalanus	0	0	8.6	4.8	0
Evadne	0	0	0	0.2	0
ZOOPLANKTON	100	100	100	100	100

Feeding conditions and growth. Growth processes depend largely on feeding. The share of starving fish and the prey composition reflect the feeding conditions for herring. Lumberg & Ojaveer (1991), analysing the dynamics of zooplankton abundance and biomass in the Gulf of Finland during the recent 30 years, revealed the occurrence of a zooplankton-rich period (1974—82) followed by a sudden decrease in zooplankton abundance in 1982—84. The difference in zooplankton abundance between these two periods was estimated to be two- to three-fold.

The high abundance of zooplankton in the late seventies and early eighties coincided with a period of increased salinity (Kalejs & Ojaveer, 1989). The period since the mid-1980s up to the present can be characterized as a period of low salinity and active vertical mixing. The decreased salinity has caused both changes in the species composition of zoo-

Baltic sprat in subdivisions 29 and 32. Feeding data for November—December

Stomach contents	1985	1987	1988	1989	1990	1991	1992
Length group <8 cm							
Empty stomachs, %	100	0	100	0	66.7	100	100
Prey composition, % weight							
Acartia	0	0	0	0	33.3	0	0
Temora	0	0	0	92.3	66.7	0	100
Pseudocalanus	0	0	0	7.7	0	0	0
ZOOPLANKTON	0	0	0	100	100	0	100
Length group 8—12 cm							
Empty stomachs, %	98.6	64.3	91.7	42.9	80.0	76.0	100
Prey composition, % weight							
Eurytemora	0	10.8	100	0	0	0	0
Acartia	0	7.0	0	0	10.2	0	0
Temora	0	16.1	0	100	89.8	100	0
Pseudocalanus	0	0.8	0	0	0	0	0
Mesocyclops	0	4.5	0	0	0	0	0
Bosmina	0	14.0	0	0	0	0	0
Podon	0	34.9	0	0	0	0	0
Ceriodaphnia	0	1.9	0	0	0	0	0
Bivalvia larvae	0	0.3	0	0	0	0	0
ZOOPLANKTON	0	100	100	100	100	100	0
Mysis	100	0	0	0		0	0
Length group >12 cm							
Empty stomachs, %	97.0	70.8	48.9	60.0	79.2	95.8	100
Prey composition, % weight							
Eurytemora	0	2.2	44.2	4.2	0	0	0
Acartia	0	3.7	0.4	0	5.3	0	0
Temora	100	49.3	42.3	95.8	94.7	100	0
Limnocalanus	0	0	13.1	0	0	0	0
Bosmina	0	2.9	0	0	0	0	0
Podon		39.0	0	0	0	0	0
Bivalvia larvae		2.9	0	0	0	0	0
ZOOPLANKTON	100	100	100	100	100	100	0

plankton and a decrease in its abundance (Lumberg & Ojaveer, 1991; Sidrevics et al., 1993).

As a consequence of increased vertical mixing the vertical stratification of the water column has weakened, providing the planktonic and nektobenthic animals with a much wider zone of optimum living conditions, compared to a period of strong stratification, like in the early 1980s.

Therefore, herring as a plankton- and nektobenthos-feeding fish has faced very unfavourable changes in its feeding conditions during almost a decade (scattering of food concentrations, forced transition to the use of energetically less valuable prey, etc.).

The feeding conditions of sprat as a plankton-feeding fish remained relatively stable for a longer period in the 1980s, since the changed distribution pattern of nektobenthic organisms does not affect its feeding.

The above allows us to conclude that an increase in the mean weight at age of herring and sprat will be very unlikely unless the salinity conditions change in the Baltic Sea.

ANNUAL FOOD RATION DYNAMICS OF HERRING AND SPRAT IN THE GULF OF FINLAND AND NORTHEASTERN BALTIC

The data on mean weight, abundance, and biomass of herring and sprat, provided by the ICES Working Group on the Assessment of Pelagic Stocks in the Baltic, served as a basis for the calculations (Anon., 1990, 1994). In addition, the mean weight and abundance of sprat in the northeastern Baltic (Aps, 1989, 1992) were used. The annual food consumption of herring and sprat stocks was calculated for age groups 1 and older, because the data on mean weight and abundance of larvae and 0-group are not representative due to sampling problems.

Herring. During the period of separate assessment of the Baltic herring stock in the Gulf of Finland and the whole Baltic Sea (1970—89), its abundance in the Gulf of Finland varied from 4646 to 10 547 million (Anon., 1990). If we assume the area of the Gulf of Finland to be 29 498 km^2 (Elmgren, 1984), the mean abundance of herring will be 0.2—0.4 individuals per m^2. Herring biomass varied between 133 and 244 thousand tonnes or 4.5 and 8.7 $g \cdot m^{-2}$ during the same period (Anon., 1990, Fig. 1). The dynamics of both herring biomass and, particularly, of its abundance show increasing trends since the second half of the 1980s.

Sprat. The abundance and biomass of Baltic sprat decreased in the northern Baltic (subdivisions 29 and 32) from its long-term maximum values in 1961 (110 739 million and 827 000 t, or 1.5 $ind \cdot m^{-2}$ and 11.4 $g \cdot m^{-2}$) to 7738 million and 86 000 t, or 0.1 $ind \cdot m^{-2}$ and 1.1 $g \cdot m^{-2}$ in 1987 (Aps et al., 1988). Since 1988 both the abundance and biomass of sprat in the Baltic Sea have increased continuously amounting to 156 108 million and 1 722 000 t, respectively, in 1993 (Anon., 1994). From the estimations of Elmgren (1984) it follows that the biomass of sprat in the Gulf of Finland was at a level of 37×10^{-3} t or 1.25 $g \cdot m^{-2}$ in the beginning of the 1980s.

Both Baltic herring and sprat, being pelagic species, invest a considerable part of the food energy in metabolism and only an insignificant part in production. Using the technique described above, the annual consumption of plankton and nektobenthos by the adult herring stock in the Gulf of Finland was estimated to have been in the range of 33—65 $g \cdot m^{-2}$ in the 1970s—80s. For sprat, the mean consumption rate of 11.4 $g \cdot m^{-2}$ was found in 1987 (Lankov, 1988).

From the results of Aneer (1979) it appears that herring in age groups 1—9 consume annually approximately 20 $g \cdot m^{-2}$ in the Gulf of Finland. The respective value retrieved from the data of Elmgren (1984), 56 $g \cdot m^{-2}$, falls into the same range. The consumption rate 10 $g \cdot m^{-2}$ for the sprat stock in the Gulf of Finland follows also from Elmgren's estimations.

Arrhenius & Hansson (1993), having included into calculations also the larvae and 0-group, estimated the mean annual consumption rate at

124 g·m^{-2} for herring and 60 g·m^{-2} for sprat in the whole Baltic Sea. At the same time, for the Gulf of Bothnia, the northernmost part of the sea with a low productivity, they assume the annual zooplankton consumption rate by herring and sprat at a level of 35 g·m^{-2}. Zooplankton production shows spatial differences in the Baltic Sea, which depend on climatic conditions. Henroth & Ackefors (1979) estimated the zooplankton production, converted into organic carbon production, to be 20 gC·m^{-2}·yr^{-1} in the southern and about 10 gC·m^{-2}·yr^{-1} in the northern Baltic Proper. Aneer (1979) suggested the mean production of zooplankton to be 15 gC·m^{-2}·yr^{-1} for the Baltic Sea. Kankaala (1987) estimated the zooplankton production in the Gulf of Bothnia at a level of 2.5—3.7 gC·m^{-2}·yr^{-1}.

Studies performed at Askö Laboratory in Sweden (Hansson et al., 1990) revealed that the production of net zooplankton (>90 μm) can vary from 8.6 to 12.3 gC·m^{-2}·yr^{-1}. Assuming that the mean value of zooplankton production in the Baltic Sea is 10—15 gC·m^{-2}·yr^{-1}, and the carbon content of zooplankton is 5% in wet weight (Aneer, 1979; Mullin, 1969), the zooplankton production expressed in wet weight will be 200—300 gwwt·m^{-2}·yr^{-1}.

ANNUAL CONSUMPTION OF HERRING AND SPRAT STOCKS

The feeding analyses revealed that in 1986—90 the mean annual food composition of the Baltic herring stock in wet weight consisted of 74.1% zooplankton, 18.2% mysids, 5.5% amphipods, 1.8% young fish, and 0.4% other taxa both in the northeastern Baltic Proper and the Gulf of Finland (Table 7).

Table 7

Food consumption by Baltic herring in the Gulf of Finland in 1986—90

Food	% of wet weight	% of consumed energy	Consumption (×10^5 t)
Zooplankton	74.1	67.8	11.8
Mysids	18.2	21.9	2.9
Amphipods	5.5	7.1	0.9
Young fish	1.8	2.9	0.3
Other	0.4	0.3	0.1
TOTAL	100.0	100.0	16.0

Taking into account the estimated stock composition and abundance, and the calculated individual consumption rates given above, the calculated mean consumption of herring in the Gulf of Finland in the same five-year period can be estimated at a level of 16×10^5 t or 54.1 g·m^{-2} (zooplankton + nektobenthos + young fish). For sprat the level is 3.4×10^5 t or 11.4 g·m^{-2} (zooplankton). Accordingly, the total zooplankton consumption by herring and sprat together is 15.2×10^5 t or 51.5 g·m^{-2}. The larval and 0-group fish consumption, which are estimated to be 45% and 50% of the total consumption by the herring and sprat stocks, respectively (Arrhenius & Hansson, 1993; Rudstam, 1988), should be added to the consumption values of both stocks.

If the mean zooplankton production in the Gulf of Finland can be assumed at a level of the whole Baltic Sea (200—300 gwwt·m^{-2}·yr^{-1}), the probable grazing rate of zooplankton by the adult stocks of pelagic fish will make up 58 g·m^{-2}+17 g·m^{-2}=75 g·m^{-2}, or 26—38% of the zooplankton production.

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