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The role of predation on early life stages of cod in the Baltic

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Abstract

Only scarce information is available that can be used to assess the importance of predation on the developmental success of early life stages of cod in the Baltic Sea. Among all possible predators, the two commercially utilized pelagic species, herring and sprat, appear to have the highest potential as predators of the early pelagic stages of cod in the central Baltic, and their effect on the cod stock may be important with regard to the fishery management in this area. In recent years, successful reproduction of cod in the Baltic proper has been restricted by the hydrographic conditions to the Bornholm Basin. Concentrating on this area, the present report summarizes new results from stomach content analysis for herring and sprat during the cod spawning seasons 1987-1991. The results are used to obtain preliminary estimates on the consumption of early life stages of cod in this area. Larvae and 0-group cod appear not to be substantially affected by predation, whereas the eggs were found to be more heavily preyed upon, especially by sprat in spring. The daily egg consumption, calculated for the entire sprat population in the central Bornholm Basin, ranged from 90% to well above 100% of the standing stock of cod eggs during spring dates. In summer, consumption estimates remained well below corresponding standing stock or production values. Herring appeared to be generally less important as a predator due to a smaller population size in this area. The importance of predation on eggs for the recruitment success of cod in the central Baltic is discussed in relation to the hydrographic conditions. Implications for future research activities are highlighted in connection to process orientated recruitment studies and multispecies modelling.

Keywords: cod, recruitment, predation, early life stages.

Introduction

During the last decade predation has been discussed as a major factor controlling recruitment of marine fish species (e.g. Hunter 1984, Sissenwine 1984). However, field studies that have been designed adequately for estimating predation mortalities of early life history stages are scarce. Bailey & Houde (1987) suggested that methodological problems are responsible for the limited success in this area, and these are mainly related to:

1. identifying eggs and larvae in predator guts;
2. quantifying prey consumed by each predator;
3. estimating abundances of predators;
4. estimating the number of eggs and larvae available as prey.

In general a wide spectrum of organisms may be considered as potential predators for the early life stages of marine fish species. However, in the central Baltic the predator field appears to be restricted, and for the purpose of an integrated fisheries management, the most important processes are considered to be interactions among commercially important species. The reproductive success of cod in the central Baltic has decreased continuously during the last decade. The decreasing stock size of the predatory cod is related to increased stocks of herring and sprat since 1987 (Anon. 1993a). Thus, predation by herring and sprat on the early life stages of cod may be especially important at present in this area.

Predation on early life stages of cod by herring and sprat has been reported frequently for the North Sea area (Daan 1976, Garrod & Harding 1981, Pommeranz 1981, Hopkins 1988). A first attempt to quantify this effect was made by Daan *et al.* (1985). They estimated that herring consumed 0.04-0.19% of the total egg production of cod in the North Sea. Also, a considerable number of herring and sprat stomachs have been analysed from the Baltic Sea, but no field study has concentrated on spawning areas of cod during spawning time and, consequently, no relevant information is available for comparison.

In cod spawning areas, the salinity is usually sufficient to keep the eggs floating in the surface layers. However, in the central Baltic cod eggs occur exclusively in the intermediate and bottom water, concentrating in a narrow depth range within and below the halocline (Müller & Pommeranz 1984, Wieland 1988). Therefore they are available as prey in relatively dense aggregations. When herring and sprat stay close to the bottom or above the oxygen-depleted bottom water during daytime, they might consume a substantially greater number of cod eggs in this area than estimated for the North Sea by Daan *et al.* (1985). Furthermore, there are differences in the timing and the extension of the spawning, i.e. mainly February in the North Sea (Daan 1979) and March to August in the Baltic Sea (Müller & Bagge 1984). Thus, considerable deviations in the feeding intensity and prey selection by herring and sprat can be expected from differences in the available food concentrations during the cod spawning season.

In the Baltic Sea, the predation by herring and sprat on fish eggs has frequently been observed (Hinrichs 1985, 1986). These observations refer to the Arkona and Bornholm Basin as well as to the southern Gotland Sea and cover the period May/June 1980-83. Also Popiel (1951) and Lohmeyer & Hempel (1977) found considerable amounts of fish eggs ingested by herring from the Slupsk Furrow in May 1949 and the Kiel Bight in January/February 1976. Fish larvae were found only occasionally and in small numbers in stomachs of herring. They were identified as sprat and rockling. Small fish, mostly gobiids, were much more abundant, but no 0-group cod has been reported from the conducted stomach content analysis (Popiel 1951, Lohmeyer & Hempel 1976). In sprat stomachs both fish larvae and small fish were virtually absent. Analysis of stomach contents by Shvetsov & Starodub (1986), Starodub *et al.* (1992) and Załachowski *et al.* (1975) confirmed the low importance of fish and macrozooplankton as prey of sprat, probably due to the size range of these organisms being above the optimum for prey of sprat.

In summary, the available literature suggests that predation by both herring and sprat might have a substantial effect on cod egg survival, whereas the effects on larvae and 0-group fish appear more restricted. New information is presented here from a case study on the reproductive ecology of cod, allowing a first attempt to test this hypothesis and to quantify the consumption of early life stages of cod by herring and sprat in the Bornholm Basin. Considering the methodological problems stated by Bailey & Houde (1987), sampling of herring and sprat stomachs was conducted together with an ichthyoplankton survey designed to describe the horizontal and vertical distribution of early life stages of cod and to estimate mortality rates of cod eggs in relation to the hydrographic regime (Wieland 1988, Wieland & Zuzarte 1991). Quantifying the number of early life stages of cod consumed by each individual predator, requires the estimation of gastric evacuation and daily consumption rates (Bailey & Houde 1987). Two different approaches have been applied for comparison and methodological aspects related to their sensitivity are discussed below.

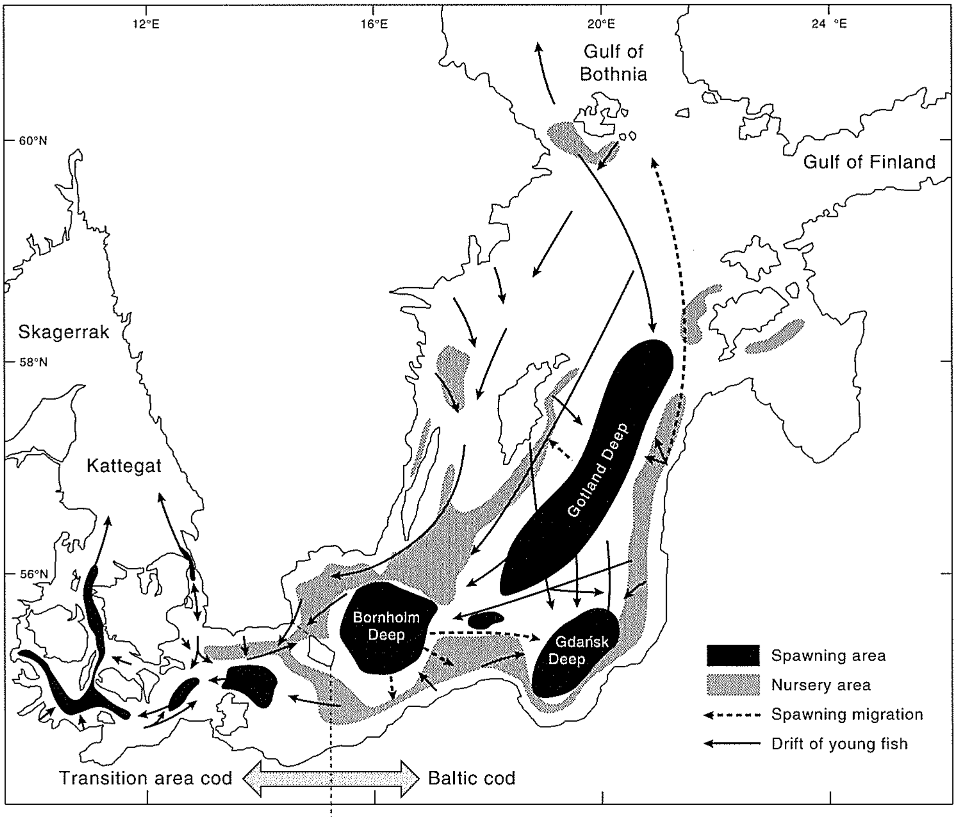


Figure 1. Spawning and nursery areas of cod in the Baltic (from Bagge *et al.* 1993).

The analysis of stomach contents here concentrates mainly on the years 1988 and 1991. Due to the hydrographic situation in the central Baltic, the Bornholm Basin (Figure 1) appears to be the only important spawning ground of cod in the central Baltic since 1986 (Plikshs *et al.* 1993). However, in 1988 and 1991 the hydrographic conditions in the Bornholm Basin were obviously different. While 1988 was included in the stagnation period of the last decade (Nehring & Matthäus 1991), a small inflow in 1991 resulted in conditions more favourable for the cod egg development (Bagge 1993)

Material and methods

Stomach sampling

Sampling of stomachs of herring and sprat in the Bornholm Basin was carried out on several cruises from March 1987 to August 1991. The fish were caught either by bottom trawl in water depths of 60-85 m or by pelagic trawl at different depths over 70-100 m. The daily vertical migration of herring and sprat dictated that the bottom trawl was used during daytime only. Pelagic trawling was carried out close to the bottom or above the oxygen-depleted bottom water during day and in the upper part of the water column in 5-30 m depth during night. At dawn intermediate depths of 20-60 m were chosen. On some cruises, especially in 1988, hauls were made at a fixed position at different times of the day to determine the diurnal feeding cycle of herring and sprat in relation to their vertical migration. On other cruises, especially in 1991, a greater part of the cod spawning area was covered in order to describe the spatial variability of predation. In view of an expected fast digestion of ichthyoplankton, especially if small larvae had been ingested (Hunter & Kimbrell 1980), the duration of trawling and the handling time on deck was reduced as far as possible, i.e. to 45-75 min. from catching to conservation. Stomachs of both predators were collected according to a length stratified sampling scheme. The samples were fixed and preserved using a 8% formaldehyde/seawater solution buffered with borax.

Stomach content analysis

The amount of food in the stomachs was determined by weighing the stomachs before and after emptying. The number of eggs and larvae as well as fish in the stomachs were determined from 10 stomachs per 2 and 1 cm length class for herring and sprat, respectively. The eggs, larvae and fish were identified to species as far as possible. Fish eggs were classified into six different developmental stages according to Thompson & Riley (1981). The remaining stomach content was differentiated into major taxonomic groups. These prey groups were quantified as wet weight by estimating the proportion they contributed to the total volume of the stomach content. Arithmetic mean numbers of eggs, larvae and fish as well as weights of all major prey groups were derived for each cruise by computing total averages over all length classes, weighted by the proportion of each length class in the overall length distribution of herring and sprat during the cruise. The mean number of unidentified eggs was allocated to species according to the species composition of identified eggs. Only stomachs sampled between sunrise and sunset, i.e. the daily feeding period, were taken into consideration. However, for larvae and fish in the stomachs of both predators average numbers were also calculated from night- time samples for comparison. This is of special interest because larvae and 0-group fish are mainly distributed in the upper 50 m water column (Wieland & Zuzarte 1991), where herring and sprat stay only during night-time.

Daily consumption of cod eggs

On the basis of repeated 24-h sampling, the diurnal feeding cycle was described and the main feeding period was determined. From the reduction in the average stomach contents during night and within special deck-tank experiments (Köster *et al.* 1990), evacuation rates of fish eggs were estimated by two different approaches:

The first method assumes that the instantaneous evacuation rate of eggs in numbers (dS/dt) is a power function of the instantaneous stomach content of eggs (S)

$$dS/dt = -R \cdot S^B$$

This general model with R and B as constants has been suggested by Tyler (1970) and Jones (1974) for total stomach contents in terms of weight. By applying it to the fraction of eggs it is assumed that the evacuation rate of fish eggs is not influenced by the amount and composition of other food in the stomach and that the evacuation of cod eggs is not significantly different from other fish eggs. Instantaneous evacuation rates were estimated as the difference in gut content (median number of eggs) between successive samples. Estimates of the constants B and R were then obtained by linear regression of ln-transformed evacuation rates on the ln-transformed mean stomach contents of the corresponding intervals (Temming & Köster 1990) The data sets employed for both predators were taken from all 24-h sampling and tank experiments conducted (Table 1). To avoid a bias introduced by an increasing number of zero observations (Olsen & Mullen 1986), only medians greater than zero have been included in the estimation procedure. From the 24-h

Table 1. Number of 24-h surveys and deck-tank experiments utilized for the estimation of evacuation rates of fish eggs by herring and sprat on basis of Method 1 (number of eggs) and Method 2 (total stomach content in weight).

	Method 1		Method 2	
Species	24-h surveys	Tank experiments	24-h surveys	Tank experiments
Herring	1	3	4	6
Sprat	5	5	5	5

sampling, only periods with decreasing stomach contents were taken into consideration. Due to a retarded digestion in the beginning of the deck-tank experiments, data from the first interval have been excluded (Köster *et al.* 1990). According to the low water temperature of 3.5-7.0°C in the intermediate and bottom water, where herring and sprat are feeding during daytime, tank experiments were performed from April to the beginning of June only. Nevertheless, similar to the 24-h sampling, they refer to a wider temperature range of 4.4-14.0°C.

According to Pennington (1985) the feeding rate per hour (F_h) can be estimated as:

$$F_h = R \cdot \overline{S}^B + (S_t - S_0) / T$$

with

S_t: average stomach content at the end of the feeding period
S_0: average stomach content at the beginning of the feeding period
T: duration of the feeding period

$\overline{S^B}$ was calculated by raising individual stomach contents from each sample to the power of B, and averaging these values over the feeding period. As the samples were more or less evenly distributed over time, no further weighting or subdividing into smaller time sections was required. Setting S_0 to zero at the start of feeding period and calculating the total amount eaten per feeding period, the daily ration (F_T), was estimated by:

$$F_T = R \cdot \overline{S^B} \cdot T + S_t$$

The stomach content at the end of the feeding period (S_t) was set to be equal to the average stomach content over the feeding period, assuming no significant general trend after a first short period of increase.

The second method applied is based on the the same general model of gastric evacuation and all subsequent computation steps are similar, with the exception that the total stomach content in terms of weight has been used. Based on daily rations of total food intake (F_a), daily rations of fish eggs (F_e) were derived by assuming the same ratio between food intake and average stomach content for eggs in numbers as for total food in weight:

$$F_e = S_e \cdot F_a / S_a$$

with

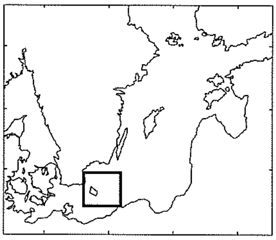
S_e: average number of fish eggs per stomach
F_a: daily ration of total food in g
S_a: average stomach content in g

The estimates derived by this procedure are based on the results from the same 24-h sampling period and deck-tank experiments as mentioned above. For herring, additional 24-h sampling and tank experiments were included, which were carried out mainly in times without any fish eggs in the plankton (Table 1). As a final step, the daily ration of cod eggs ingested was calculated on the basis of daily rations of fish eggs in total and the proportion of cod eggs within the total number of fish eggs.

Herring and sprat population sizes in the cod spawning area

The sizes of the herring and sprat populations in subdivision 25 were determined by VPA on the basis of catch at age in numbers reported by the different countries participating in the fishery. Values for natural mortality were taken from Anon. (1993a). Tuning of the VPA was performed according to Laurec-Shepherd using stock estimates derived by the annual hydroacoustic surveys in subdivision 25. Monthly population sizes (ages 1+) were calculated, by assuming an equal distribution of fishing and natural mortality over the year.

Hydroacoustic surveys were conducted in subdivision 25 in May/June 1979-86 (5 cruises by GDR, USSR and Poland) and July/August 1981-88 (4 cruises by Poland and Sweden). The results were broken down to ICES statistical rectangles. These results were used to estimate the proportion of the total stocks concentrated in the central Bornholm Basin, i.e. the area within the 80-m depth contour (Figure 2). Due to a lack of hydroacoustic data in March and April, the spawning period



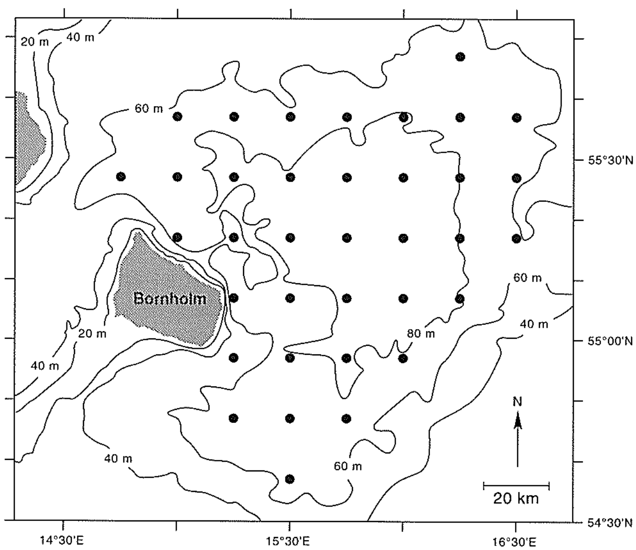


Figure 2. Study area: ichthyoplankton station grid in the Bornholm Basin, southern central Baltic.

of the spring spawning herring, the population sizes in numbers were determined by using the May/June values. They were corrected according to the difference in the average CPUE values from pelagic trawl hauls performed for stomach sampling in April compared to May/June 1990-93. Sprat is concentrated in the Bornholm Basin during its spawning season from March to July (Anon. 1992). Therefore the mean percentage for May/June was also applied for March/April. This is consistent with highest CPUE-values found on the southern slope of the Bornholm Basin during the Polish young fish surveys in March (Grygiel 1990) and with the CPUE-values from the pelagic trawl surveys conducted. A detailed description of the performed VPA and the splitting according to hydroacoustic and CPUE data is given in Anon. (1994).

Daily consumption compared to daily production of cod eggs

The total daily consumption of cod eggs in the central Bornholm Basin was calculated from individual consumption rates determined for herring and sprat by the second method, and from the size of the predator populations in the area derived by VPA. Only those cruises covering the central Bornholm Basin adequately were considered, i.e. July 1988 for herring, June 1990 and April, May, July and August 1991 for both predators.

The daily consumption is compared to the available standing stock of cod eggs and to preliminary estimates of the daily egg production derived from the ichthyoplankton surveys in the same period. The plankton was sampled in a standard station grid (Figure 2) using bongo nets of 0.3 and 0.5 mm mesh size in double oblique tows covering the entire water column. The daily production was calculated by dividing the abundance of the youngest egg stage IA (including non fertilized eggs) by the corresponding stage duration derived from incubation experiments at

Table 2. Cod eggs standing stock (all stages and stage IA) in the central Bornholm Basin, mean temperature in water layers with maximum numbers of cod eggs and corresponding duration of egg stage IA according to Wieland *et al.* (1994), daily production of egg stage IA assuming a mortality of 0.09 per day within the egg stage IA (Wieland 1987)

Month/year	Standing stock Total (10^9)	IA (10^9)	Temperature, °C	Stage duration, days	Daily production, (10^9)
July 1988	132.4	73.5	5.7	2.57	32.5
June 1990	95.8	55.8	6.3	2.27	27.7
April 1991	97.7	60.9	4.5	3.30	22.6
May 1991	129.3	86.7	4.5	3.30	31.7
July 1991*	292.8	142.6	5.9	2.47	65.4
August 1991**	156.3	72.3	5.9	2.47	32.4

* average values from two ichthyoplankton surveys.
** mean temperature from the following and preceding month.

different temperatures (Wieland *et al.* 1994). Mean *in situ* temperatures (Table 2) were taken from water layers, where maximum numbers of cod eggs occurred during the cruise (Wieland, unpubl.). As a correction for mortality within the egg stage IA, a preliminary estimate of the mortality between stage IA and IB derived by the constant birth method (Wieland 1987) was applied to the corresponding half stage duration.

Larvae and fish in the stomachs of herring and sprat in other areas of the central Baltic

As larvae and 0-group cod are expected to drift out of the study area thus the role of predation on these stages may be underestimated when restricted to the Bornholm Basin only. Therefore stomach contents of herring and sprat from other areas of the central Baltic have also been checked using information from the Latvian and the Estonian Fisheries Research Institute to the international database on herring and sprat stomach contents. On most of a total of 362 and 718 stations covered by the two countries in subdivisions 26, 28 and 29, stomach sampling was conducted by mid-water trawls covering a depths range of 0-230 m. As abundances of prey items are not given in the data sets, the analysis was carried out using only the percentages of occurrence of larvae and small fish per stomach and quarter, averaged over the time period 1977-1991.

Results

Diurnal feeding cycle

Results from several 24-h sampling periods combined are summarized in Figures 3 & 4. The average stomach content in weight and the corresponding mean number of fish eggs found in the stomachs at different times of the day are expressed as percentage deviation from the average stomach content over the whole 24-h period. The percentages increase after sunrise and decrease after sunset. Thus the feeding activity of herring and sprat is clearly related to the daylight and the feeding period

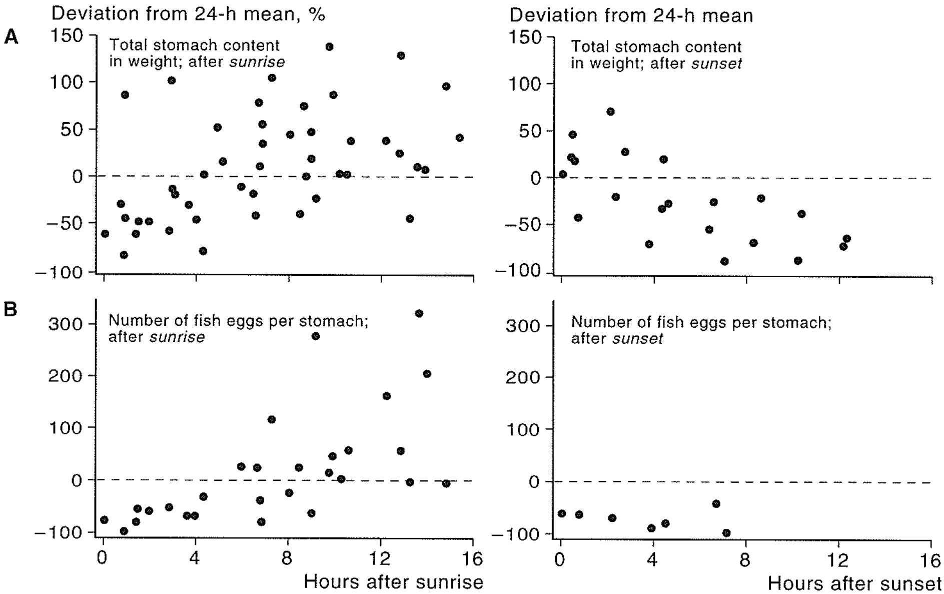


Figure 3. Herring stomach content: Diurnal variation in average total weight of stomach content (A) and number of fish eggs per stomach (B). Values are given from samples obtained during four (A) and one (B) 24-h survey, expressed as percentage deviation from corresponding 24-h mean.

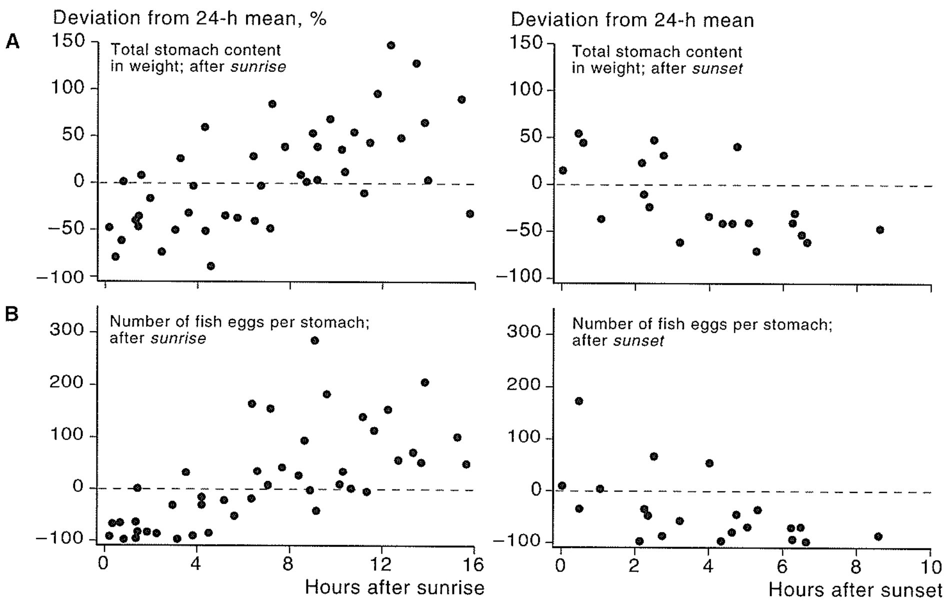


Figure 4. Sprat stomach content: Diurnal variation in average total weight of stomach content (A) and number of fish eggs per stomach (B). Values are given from samples obtained during five 24-h surveys, expressed as percentage deviation from corresponding 24-h mean.

may be defined as hours with daylight. This is confirmed by an increase in the average degree of digestion from early morning until late night. However, at the beginning of the feeding period some food was also observed in an advanced stage of digestion, which was probably left from the day before. This happened especially during summer with only few hours of darkness and intensive feeding during the day, but it was observed rarely for fish eggs.

General food composition and fish eggs in the stomachs

In order to assess the relative importance of fish in the diet of herring and sprat and to identify possible relationships to the availability of other food sources, a summary on the results of the general food composition resolved into major taxonomic groups is first presented (Figures 5 & 6). Additional information on the number of stations covered, stomachs analysed and the mean length of predators is given in Tables 3 & 4. In terms of weight, copepods were generally the dominating prey items, but from April to August also cladocera were regularly present. Cladocera formed one major food component in the time period from May onwards. In August 1988 and 1991 they were the most important prey group for sprat. Larger prey organisms, like mysiids, amphipods, cumacea, polychaetes and small fishes were found in herring, but rarely in sprat stomachs. In total, the combined group

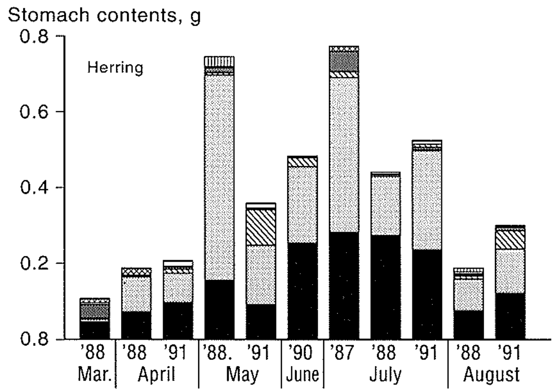


Figure 6. Sprat: Average food composition by wet weight, split up into major taxonomic groups and months for the period 1987-1991.

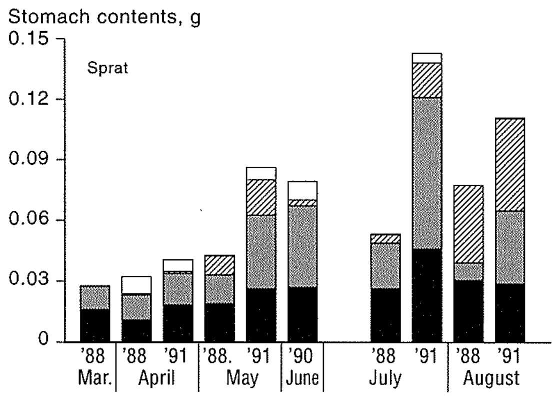


Figure 6. Sprat: Average food composition by wet weight, split up into major taxonomic groups and months for the period 1987-1991.

Table 3. Herring stomach content: Average numbers of fish eggs per stomach at different sampling dates and fish egg species composition according to their proportion among identifiable eggs; length = mean length of herring in the population, s.e. = standard error of the average number of total fish eggs per stomach.

Month/year	No. of stations	No. of stomachs	Length, cm	Fish eggs per stomach Total	s.e.	Cod	Sprat	Flounder	Rockling
March 1988	12	598	20.8	9.43	0.76	2.87	2.01	3.85	0.7
April 1988	1	193	22.9	3.22	0.36	0.07	1.17	1.27	0.71
April 1991	7	283	19.6	11.69	1.22	2.95	7.46	1.08	0.2
May 1988	1	261	22.4	3.61	0.29	0.2	2.72	0.33	0.36
May 1991	12	474	21.8	31.54	2.7	9.04	22.22	0.18	0.1
June 1990	12	562	23.4	11.86	1.34	5.31	6.03	0.51	0.01
July 1987	3	148	24.5	3.39	0.31	1.88	0.56	0	0.95
July 1988	8	233	23.6	4.45	0.51	2.66	1.29	0	0.5
July 1991	15	473	21.4	13.53	1.8	11.14	2.26	0	0.13
August 1988	4	165	22.7	3.35	0.74	0.8	<0.01	0	2.54
August 1991	11	461	21.3	1.71	0.21	1.68	0.01	0	0.02
September 1988	1	306	23.5	<0.01	<0.01	no eggs identified to species			

Table 4. Sprat stomach content: Average numbers of fish eggs per stomach at different sampling dates and fish egg species composition according to their proportion among identifiable eggs; length = mean length of sprat in the population, s.e. = standard error of the average number of total fish eggs per stomach.

Month/year	No. of stations	No. of stomachs	Length, cm	Fish eggs per stomach Total	s.e.	Cod	Sprat	Flounder	Rockling
March 1988	11	539	13.5	6.17	0.91	0.99	0.26	4.68	0.24
April 1988	5	200	13.7	27.7	3.65	25.75	0	0	1.95
April 1991	9	355	13.7	28.67	3.52	3.37	17.24	6.71	1.35
May 1988	2	97	12.7	6.42	2.51	0.41	2.67	1.67	1.67
May 1991	14	526	13.9	31.43	3.11	7.55	20.8	1.8	1.28
June 1990	12	506	13.7	54.84	4.39	3.98	49.17	1.68	0
July 1988	2	87	13.7	3.26	0.83	0	3.26	0	0
July 1991	14	535	13.8	13.36	1.14	4.7	7.62	0	1.04
August 1988	3	86	14.1	0.09	0.05	no eggs identified to species			
August 1991	11	326	14.1	0.06	0.02	0	0.01	0	0.05

of macrozooplankton and fish added up to 10% of the average stomach content by weight. Only in March 1988 a significantly higher proportion of mysiids occurred.

Fish eggs and larvae were of minor importance for herring, where they contributed at maximum only 2-5% of the total weight (March 1988, April and May 1991). For sprat corresponding maximum values were found to be higher, i.e. 7-25% in April 1988 and 1991, May 1991 and June 1990. Thus, in these months fish eggs and larvae were the second important prey group for sprat.

Fish eggs, by numbers, amounted up to 510 and 840 for individual herring and sprat, respectively. Highest numbers were generally found in the period March to June, except for herring sampled in April and May 1988 (Tables 3 & 4). The two low values in spring 1988, however, are both based on one station only, placed in an area of low egg abundance. In comparison to herring, sprat stomachs contained generally higher numbers of eggs during the first months of the spawning period. In July, the numbers of eggs were similar for both species, and in August the numbers were substantially lower in sprat.

The amount of cod eggs per stomach was similar on average for both predators. Substantial differences were observed only in July 1991, where a maximum of cod eggs was found in herring, and in April 1988 with a maximum of cod eggs in sprat stomachs. In the latter month, the corresponding value for herring is uncertain and not well comparable for the reasons mentioned above.

Average daily consumption of fish eggs by individual predators

Logarithmic regressions of the evacuation rates on mean stomach contents are presented in Figures 7 & 8 for fish eggs in numbers and for total food in weight. The slopes of the regression lines, corresponding to the exponents B of the power function, showed values of 0.85 and 1.09 for fish eggs and 1.17 and 1.19 for the food in total for herring and sprat, respectively. These values of B close to 1 indicate eva-

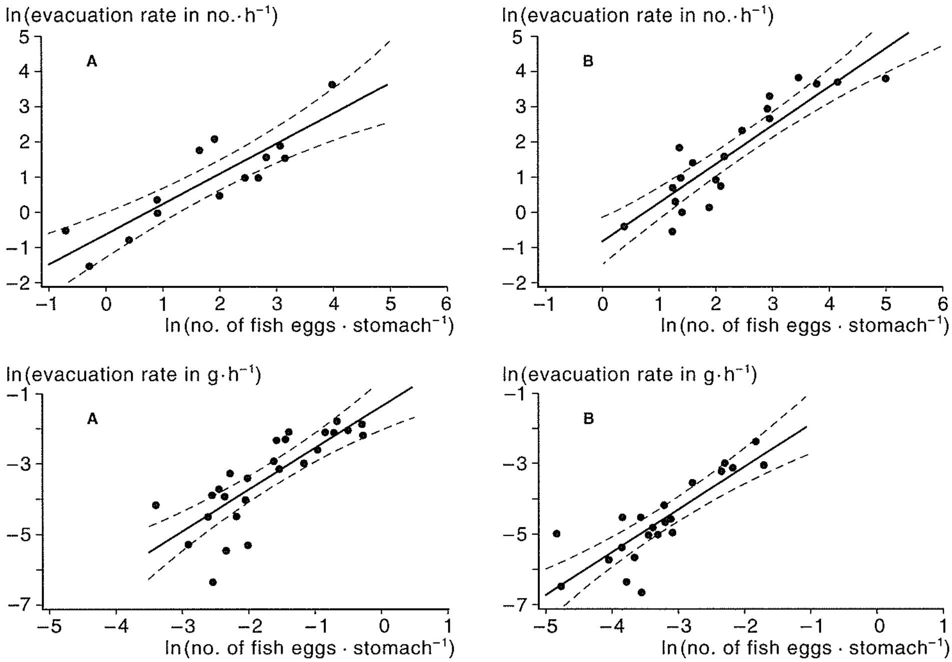


Figure 7 (upper panel). Evacuation rate of fish eggs in numbers (ds/dt). Logarithmic regression of evacuation rate on average number of fish eggs per stomach with 95% confidence limits from combined 24-h surveys and deck-tank experiments. A: herring: slope b = 0.85, intercept a = −0.64, r^2: 0.77, power function ds/dt = $0.53 \cdot S^{0.85}$; B: sprat: slope b = 1.09, intercept a = − 0.87, r^2: 0.80, power function ds/dt = $0.42 \cdot S^{1.09}$.

Figure 8 (lower panel). Evacuation rate of stomach content in weight (ds/dt). Logarithmic regression of evacuation rate on average total stomach content with 95% confidence limits from combined 24-h fisheries and deck-tank experiments. A: herring: slope b = 1.17, intercept a = −0.42, r^2: 0.63, power function ds/dt = $0.24 \cdot S^{1.17}$; B: sprat: slope b = 1.19, intercept a = − 0.77 r^2: 0.69, power function ds/dt = $0.46 \cdot S^{1.19}$.

Table 5. Daily rations of fish eggs in numbers consumed by individual herring and sprat, based on the evacuation rate as a function of 1) the total number of fish eggs per stomach (Method 1) and 2) the total stomach content in weight (Method 2). Values are given for each cruise on which at least three different stations were covered.

		Herring				Sprat			
		Method 1		Method 2		Method 1		Method 2	
Month/year	Feeding period, hours	Fish eggs	Cod eggs	Fish eggs	Cod eggs	Fish eggs	Cod eggs	Fish eggs	Cod eggs
March 1988	11.54	45.7	13.9	31.9	9.7	47.9	7.7	27.12	4.4
April 1988	14.25	not calculated				268.8	249.9	142.9	132.8
April 1991	14.25	65.0	16.4	45.3	11.4	281.7	33.1	146.9	17.3
May 1991	16.1	170.6	48.9	140.8	40.4	349.4	84.0	192.1	46.2
June 1990	17.19	75.7	33.9	57.6	25.8	663.6	48.2	356.4	25.9
July 1987	16.52	26.5	14.7	17.3	9.6	not analysed			
July 1988	16.52	32.4	19.3	21.0	12.5	not calculated			
July 1991	16.52	78.7	64.8	65.0	53.5	140.3	49.4	91.7	32.3
August 1988	15.06	20.6	4.9	13.5	3.2	0.7	–	0.5	–
August 1991	15.06	11.6	11.4	7.1	7.0	0.4	0.0	0.3	0.0

cuation curves similar to negative exponential curves. Table 5 presents the estimated daily rations in numbers of fish eggs and in numbers of cod eggs, for herring and sprat. Values are given for each cruise on which at least three different stations were sampled. In general the first method revealed the highest daily rations, whereas the estimates derived by the second method were 17-48% lower.

Total daily consumption of cod eggs in relation to the standing stock and daily production of eggs

The size of the population of herring and sprat in subdivision 25 is presented in Figure 9 for the period 1980-92. From these data, which refer to the beginning of the year, corresponding values have been derived for the sampling dates. This information is summarized in Tables 6 & 7 (next page) together with the values obtained for total daily consumption and the ratios of the consumption to the standing stock and to the daily production of cod eggs.

The total consumption by the sprat population appeared to be high in June 1990 and in April and May 1991, when 90% to well above 100% of the standing stock

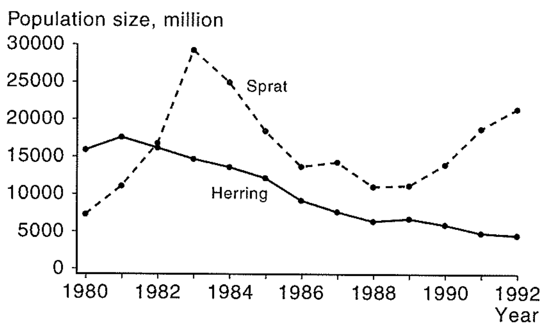


Figure 9. Herring and sprat population size (age 1+) in subdivision 25 estimated by VPA.

Table 6. Herring population size in the central Bornholm Basin and daily consumption of cod eggs by herring related to standing stock and daily production of cod eggs in the area.

Month/year	Stock size (numbers) (10^6)	Daily consumption (10^9)	Ratio of daily consumption to abundance	Ratio of daily consumption to production
April 1991	44	0.5	0.01	0.02
May 1991	379	15.3	0.12	0.48
June 1990	437	11.3	0.12	0.41
July 1988	996	12.5	0.09	0.38
July 1991	784	42.0	0.14	0.64
August 1991	754	5.3	0.03	0.16

Table 7. Sprat population size in the central Bornholm Basin and daily consumption of cod eggs by sprat related to standing stock and daily production of cod eggs in the area.

Month/year	Stock size (numbers) (10^6)	Daily consumption (10^9)	Ratio of daily consumption to abundance	Ratio of daily consumption to production
April 1991	5160	89.1	0.91	3.94
May 1991	4993	230.6	1.78	7.28
June 1990	3566	92.3	0.96	3.33
July 1991	555	17.9	0.06	0.27
August 1991	537	0.0	0.00	0.00

of cod eggs was estimated to be consumed per day (Table 7). In July and August 1991 the predation pressure by sprat appeared to be significantly lower than in the earlier months, with only 0-6% of the standing stock consumed per day. The total consumption by the herring population was calculated to be much lower than for sprat, reaching in general only 9-14% of the standing stock. Minimum values occurred in April and August 1991, when 1 and 4%, respectively, were consumed (Table 6).

The estimates for the daily production of cod eggs were on some dates significantly lower than those obtained for the daily consumption by sprat (June 1990, April and May 1991). However, in July and especially August 1991 the production was well above the consumption by sprat (Table 7). For herring, the effect of predation was highest in July 1991 with the daily consumption being 64% of the egg production (Table 6).

From the average frequency distribution of cod egg stages in the stomachs and in the sea, a positive selection of older egg stages is indicated for both herring and sprat (Table 8). Cod eggs belonging to the oldest stage V were neither found in the stomachs nor in the plankton samples (for discussion see Wieland *et al.* 1994).

Table 8. Average frequency distribution (%) of cod egg stages in stomachs of herring and sprat compared to the corresponding distribution *in situ* as derived from parallel ichthyoplankton surveys in July 1988, June 1990 and April to August 1991

Egg stage	Herring stomachs	Sprat stomachs	*In situ*
IA	22.6	26.8	58.3
IB	26.7	36.7	16.7
II	21.3	7.9	15.4
III	26.5	19.2	8.3
IV	2.8	9.6	1.3

Occurrence and abundance of larvae and small fish found in the stomachs of herring and sprat

In general, few larvae, small juvenile and adult fish were observed in the stomachs of herring and sprat. This was independent of the subdivision and season of sampling (Tables 9 & 10). Cod larvae were detected in only 10 out of 15 972 herring stomachs. 0-group cod were found in 9 herring stomachs. In sprat only 4 out of 17547 stomachs contained cod larvae and small fish were almost absent.

Table 9. Percentage occurrence of fish larvae and small fish in herring stomachs from subdivision 25, 26, 28 and 29; * not identified to species.

Sub-div.	Quarter	No. of stations	No. of stomachs	Percentage occurrence of larvae				Percentage occurrence of fish				
				Cod	Sprat	Herring	Other	Cod	Sprat	Herring	Other	Gobiids
25	1	12	598	0.17	0.67	0	0	0	0	0	0	0.84
	2	33	1773	0	1.18	0	0.06	0	0	0	0	0.85
	3	42	1786	0.22	2.07	0	0	0.5	0.39	0	0.06	2.8
	4	4	1863					0	0	0	0.16*	0
26	1	33	964	0	0	0	0	0	0	0	0	0.1
	2	46	1171	0	0.09	0	0	0	0	0.34	0	0
	3	81	2279	0.22	0	0.04	0	0	0	0	0	0
	4	20	543	0	0	0	0	0	0	0	0	0
28	1	34	1112	0	0	0	0	0	0.45	0	0	0
	2	43	1182	0	0	0	0	0	0.34	0	0	0
	3	50	1329	0	0.08	0	0	0	0.98	0	0.15	0
	4	30	817	0	0	0	0	0	0	0	0	1.84
29	1	–	–									
	2	4	80	0	0	0	0	0	0.25	0	0	0
	3	4	80	0	0	0	0	0	0	0	0	0
	4	17	395	0	0	0	0	0	0	0	0	0

Table 10. Percentage occurrence of fish larvae and fish in sprat stomachs from subdivisions 25, 26, 28 and 29; * not identified to species.

Sub-div.	Quarter	No. of stations	No. of stomachs	Percentage occurrence of larvae				Percentage occurrence of fish				
				Cod	Sprat	Herring	Other	Cod	Sprat	Herring	Other	Gobiids
25	1	11	528	0	0	0	2.84	0	0	0	0	0
	2	41	1684	0.12	2.85	0	0.06	0	0	0	0	0
	3	30	1034	0.19	0.1	0	0	0	0	0	0.10*	0
	4	–	–									
26	1	106	2267	0	0	0	0	0	0	0	0	0
	2	100	2256	0	0	0	0	0	0	0	0	0
	3	148	2748	0	0	0	0	0	0	0	0	0
	4	28	546	0	0	0	0	0	0	0	0	0
28	1	73	1435	0	0	0	0	0	0	0	0	0
	2	101	2141	0	0	0	0	0	0	0	0	0
	3	114	2157	0	0	0	0	0	0	0	0	0
	4	31	479	0	0	0	0	0	0	0	0	0
29	1	–	–									
	2	3	59	0	0	0	0	0	0	0	0	0
	3	3	94	0	0	0	0	0	0	0	0	0
	4	11	119	0	0	0	0	0	0	0	0	0

Table 11. Average number of fish larvae, 0-group fish and gobiids per 100 stomachs of herring and sprat at different sampling dates during day and night; * not identified to species. –: not analysed.

		Herring					Sprat				
Month/ year	Time	No. of stations	No. of stomachs	Larvae	0-group	Gobiids	No. of stations	No. of stomachs	Larvae	0-group	Gobiids
Mar. '88	day	12	598	1.04	0	0.87	11	528	6.06	0	0
Apr. '88	day	1	193	1.57	0	0	5	200	1.1	0	0
	night	–	–	–	–	–	–	1	29	6.9*	0
Apr. '91	day	7	283	0.2	0	4.17	9	355	0	0	0
May '88	day	1	261	6.05	0	0	2	97	0	0	0
	night	–	–	–	–	–	1	110	0	0	0
May '91	day	12	474	1.04	0	0	14	526	0.07	0	0
	night	2	89	0	0	0	–	–	–	–	–
June '90	day	12	562	5.35	0	0	12	506	74.56	0	0
July '87	day	3	148	3.48	0	0	–	–	–	–	–
	night	1	37	5.41	0	0	–	–	–	–	–
July '88	day	8	233	0.07	0	0	2	87	0	0	0
	night	–	–	–	–	–	18	0	0	0	
July '91	day	15	473	0.23	0.07	0	14	535	2.29	0.76*	0
	night	1	125	1.6	0	0	4	146	3.19	0.68*	0
Aug. '88	day	4	165	0.57	0.65*	0	3	86	0	0	0
	night	4	344	8.43	7.56	0	4	138	0.22	0	0
Aug. '91	day	11	461	29.45	5.9	1.3	11	326	0	0	0
	night	5	223	13.9	18.39	0	6	119	0.36	0	0
Sep. '88	day	1	306	0	0	36.28	–	–	–	–	–
Oct. '88	day	4	1202	–	0.16*	0	–	–	–	–	–
	night	2	661	–	0.15*	0	–	–	–	–	–

Corresponding to the low frequency of occurrence, the average number per stomach, available only for the Bornholm Basin, was also rather low for the prey categories fish larvae, 0-group fish and gobiids. This result is independent of the time of sampling during the day (Table 11). In herring a total of 254 fish larvae were identified in 4975 stomachs. 82 larvae were identified to species, of which 4 were cod larvae. Also small fish appeared to be scarce in herring stomachs and most of them were gobiids. From a total of 233 small fish found in 6838 herring stomachs, only 2 were identified as cod. In sprat somewhat higher numbers of fish larvae were encountered. From 340 larvae found in 3817 sprat stomachs, 153 were identified to species, including 5 cod larvae.

Discussion

Diurnal feeding cycle and feeding period

The results of the diurnal feeding cycle of herring and sprat in the Bornholm Basin indicate a high feeding intensity during daytime and a very limited consumption during the night. Comparable results from 24-h sampling periods are scarce in the literature; however, several authors observed an increase in the average stomach content from dawn to dusk (Popiel 1951, Lohmeyer & Hempel 1977, Daan *et al.* 1985, Hopkins 1988). This supports the described feeding cycle. For sprat, Hinrichs (1986), Shvetsov & Starodub (1986) and Starodub *et al.* (1992) presented data from 24-h sampling performed in the central Baltic and showed similar increases in the stomach content during the day and decreases during the night. Therefore the assumption seems to be well supported, that the feeding activity is restricted to daylight hours.

A zero stomach content at the start of the feeding period may be assumed only for fish eggs although it does not introduce any major bias. The average stomach content at the end of the feeding period includes a high variability in the given data. Using the average over the feeding period probably underestimates this final value.

Early life stages of fish in the diet

For sprat there was a distinct seasonal change in the diet: the large amount of fish eggs ingested in March/April was substituted by cladocera in later months. This shift in the diet can be explained by an increase in the abundance of all cladoceraspecies in the plankton during the summer months (Müller 1982). The absence of a comparable shift in the diet of herring may be explained by a difference in the vertical distribution of the two predator species. After spawning activity ceases in July (Müller *et al.* 1990), sprat concentrate at intermediate depths and in more shallow areas (Starodub & Kondratjeva 1988). In those areas cladocera occur in higher abundances (Müller & Zuzarte 1989) and fish eggs are low in numbers (Wieland & Zuzarte 1991).

The generally low occurrence of fish larvae in the diets may be due to a limited overlap in the vertical distribution of predator and prey. Apart from the more shallow vertical distribution of sprat in summer, feeding herring and sprat concentrate at depths deeper than 50 m during daytime. The vertical distribution of fish larvae show highest concentrations above 50 m (Wieland & Zuzarte 1991). Occasionally, substantial numbers of larvae were also encountered below 50 m, as for example in June 1990. This may explain the relatively high numbers of larvae ingested by sprat in this month. Herring was not feeding on these larvae at the same time, which might be explained by the small average size of the newly hatched larvae of less than 6 mm. The larvae ingested by herring in August 1991 were mostly 15 mm and larger, and thus probably more suitable as prey for herring than for sprat.

Larger prey organisms, i.e. macrozooplankton and small fish were found in herring but rarely in sprat stomach. This corresponds to results of Hinrichs (1985, 1986), Starodub *et al.* (1992) and Załachowski *et al.* (1975). The numbers of juvenile fish ingested by herring were low. This may be explained by a limited vertical overlap as described above for larvae. However, it might also be due to drift of older larvae and 0-group fish out of the Bornholm Basin (Grauman 1976, Aro *et al.* 1991). The database on herring and sprat stomach contents did not indicate a substantial predation in other areas of the central Baltic.

The amount of food in the stomachs may have been generally underestimated if digestion and evacuation continues during the time from catching to preservation. This time lag was long (45-75 min.) compared to digestion times of less than 60 min. reported for small larvae as prey of planktivore fish (Hunter & Kimbrell 1980). This possible bias may be of minor importance for two reasons: the digestion time for larvae is reported to be prolonged significantly if less quickly digestible prey organisms (e.g. copepods) were also ingested (Christensen 1983, Balfoort 1984). Secondly, stomach evacuation seems to be retarded as a reaction to stress during the catching and handling process (Lockwood 1980, Köster *et al.* 1990).

Average daily consumption of fish eggs by individual predators

In both approaches for calculating daily consumption, as a working hypothesis, it is considered that the evacuation rate and digestion time of cod eggs is not significantly different from other fish eggs. Method 1 includes the assumption of an exponential evacuation curve for numbers of fish eggs. The results of 24-h sampling and deck-tank experiments support this assumption although they may be a consequence of an exponentially decreasing feeding rate on fish eggs before the start of the experiments. Due to its second assumption, that the evacuation rate for fish eggs is not influenced by the amount and composition of other food, Method 1 appears to be applicable only for experiments where fish eggs were the major food ingested. This was the case in some experiments conducted with sprat only. A larger amount of other type of food will certainly reduce the dependence of the evacuation rate on the number of eggs in the stomach. Method 2 does not include this second assumption, but assumes a similar evacuation rate for fish eggs and other prey organisms in terms of weight instead of numbers. This appears to be the more valid approach.

The observed curvilinearity of the stomach evacuation in terms of weight is in agreement with the findings of Jobling (1986), who suggests exponential evacuation for fish feeding on small particles (e.g. zooplankton).

Total daily consumption of cod egg
in relation to the standing stock and daily production of eggs

The population sizes of herring and sprat estimated for subdivision 25 by VPA have been compared to results from an MSVPA for the central Baltic (Anon. 1994). Stock sizes for subdivision 25 were derived by allocating the proportions of the stocks in subdivisions 25-27 and 25-28 to individual subdivisions using informations from the annual international hydroacoustic surveys in October. For herring, the population sizes revealed by the two methods agree for recent years. For sprat, the estimates are also in good agreement, apart from the most recent years. From 1989 onward, the stock sizes from the VPA are significantly lower (41-48%) than those derived from the MSVPA (Anon. 1994). Thus, the values for the size of the sprat populations used to calculate the daily consumptions of cod eggs appear to be conservative estimates. The use of the lower values for daily rations by using Method 2 may prevent a substantial overestimation of the total daily consumption of cod eggs by sprat.

The estimates of the daily egg production, on the other hand, should be regarded as first estimates. No direct observations are available for April and August 1991 on the vertical distribution of cod eggs in the area and the applied mortality within the egg stage IA is also only approximate. At present a model is being developed on the vertical distribution of cod eggs in relation to the current hydrographic conditions. This model together with revised egg mortalities within the youngest egg stage, taking into account fertilization failure (Markle & Waiwood 1985), may enable a more precise determination of the daily egg production.

The indicated positive selection of older egg stages by herring and sprat may be due to a better visibility of the more developed stages. It may be essential to determine the daily consumption separately for individual egg stages and to compare these with the corresponding daily production of each egg stage. This would require reliable estimates of the egg mortality within each developmental stage, presently not available.

Despite the above reservations, together with the order of magnitude estimated for the cod egg abundance and the daily egg production in the area compared to the daily consumption the findings indicate that predation on cod eggs may be substantial at times by sprat and to a lesser extent also by the herring population. Only in August 1991, the daily consumption of eggs by both predators was calculated to be well below the production.

Conclusions

Predation on larvae and 0-group stages does not appear to be important in controlling the recruitment of cod in the central Baltic. Predation on cod eggs is more substantial, especially by sprat. The consumption of cod eggs by the entire population of sprat in the central Bornholm Basin is estimated to be very substantial compared to the production of eggs in the period April-June, but seems to be low in summer. Compared to sprat, predation by herring seems to be generally less important, mainly due to a smaller population size of this species in the area. Herring, however, does not show a similarly pronounced shift from copepods and fish eggs to copepods and cladocera as described for sprat. They remain in the central Bornholm Basin during the feeding period in summer. For July and August, this resulted in daily consumptions of cod eggs higher than those estimated for sprat.

Despite the uncertainties in the available results, it may be concluded that in 1991, when the peak-spawning of cod was rather late in the season, predation should not have affected a significant part of the total egg production, as it mainly takes place during the first months of the spawning season. In preceding years, peak-spawning activity usually occurred earlier in the season, as in 1988, when the peak was in May. For such years, a rather high predation can be assumed from the given information.

The importance of predation in the recruitment process of cod also depends, however, on other causes of mortality. Even a high predation on eggs may have no effect on the recruitment of cod, if eggs not eaten die, for instance, due to low oxygen concentrations within and below the halocline (e.g. Ohldag *et al.* 1991, Wieland *et al.* 1994). In contrast to 1988, the hydrographic situation in 1991 allowed a successful egg development in major parts of the bottom water throughout the spawning period (Bagge 1993). Thus, predation probably created a high cod egg mortality from April to June 1991. This is in agreement with the observation, that most of the surviving 0-group cod in 1991 originated from cohorts which hatched late in the spawning season (Anon. 1993b).

Future perspectives

In most recent years, the Bornholm Basin appeared to be the only spawning area of cod in the central Baltic, where the environmental conditions have allowed some successful egg development (Plikshs *et al.* 1993). Cod recruitment above average probably requires favourable conditions in more than one of the traditional spawning areas. For those other areas, in which the vertical distributions of cod eggs differ from that in the Bornholm Basin, no adequate data on stomach content are available at present. Therefore, investigations on the predation of cod eggs by herring and sprat should be extended to the other major spawning areas of cod in central Baltic.

Furthermore, herring and sprat may not be the only important predators on early life stages of cod. Among the variety of potential predators especially predation of 1-group and older cod on 0-group specimens (Jensen & Sparholt 1992, Sparholt 1994) and cannibalism by larvae and 0-group cod may be possible. Cannibalism by larvae and 0-group cod has been reported by Oiestad (1985) from experiments in large enclosures and by Bogstad *et al.* (1993) from field sampling in Icelandic waters. Also other fish, for example sticklebacks, may contribute to the predation mortality of early life stages. Invertebrates identified as predators of fish larvae, like cyclopoid copepods and chaetognaths (Brewer *et al.* 1984) concentrate in the high-salinity bottom water of the central basins (Müller 1982, Müller & Pommeranz 1984), where the abundance of cod larvae is usually low. Other potential predators, like mysiids, avoid areas with low oxygen concentrations in the bottom water (Välipakka 1991) typical for the spawning areas of cod. Therefore these invertebrates are thought to be of minor importance as predators on early life stages of cod. Exceptions may be the scyphomedusae of *Aurelia aurita* and *Cyanea capillata*, which have been identified as predators of fish larvae (e.g. Fraser 1969, Möller 1980) and which occur in high densities in the central basins in late summer and autumn. Thus, available data on feeding habits of other potential predators (e.g. juvenile cod, medusae) should be evaluated and gaps in the knowledge of their feeding strategies should be filled by a stomach-sampling and analysis program. Furthermore, field and laboratory experiments designed to determine evacuation rates of identified predators have to be conducted.

The impact of predation on the mortality of early life stages and on the process of predation itself depends on the hydrographic situation in the central Baltic. A better understanding is required of the abiotic factors influencing the distribution and mortality of eggs, larvae, and 0-group cod and the distribution of predators. Consequently, process orientated research on cod recruitment is needed as well as stock assessment related activities like hydroacoustic surveys and multispecies modelling.

It has been suggested (Anon. 1994) to incorporate predation on early life stages into an extended MSVPA and MS-forecast model. However, this would require major changes in both programmes and in the data-base. Following the methodology outlined by Daan (1986), the predation on early life stages should be modelled on a number basis with appropriate time scales introduced into submodels. Furthermore, the predation on early life stages of sprat has to be taken into consideration, because the recruitment of sprat itself depends on cannibalism and predation by herring. Although this integration is in principal possible, it appears to be essential first to describe and quantify sufficiently the impact of predation and other factors as well as possible interactions on the recruitment of cod, sprat and herring.

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References

Anon., 1992: Report of the Working Group on Multispecies Assessments of Baltic Fish. – ICES, C.M. 1992/Assess: 7.

Anon. 1993a: Working Group on Assessment of Pelagic Stocks in the Baltic.– ICES, C.M. 1993/Assess: 17.

Anon., 1993b: Report of the Study Group on the Evaluation of Baltic Fish Data. – ICES, C.M. 1993/J:5.

Anon., 1994: Report of the Working Group on Multispecies Assessment of Baltic Fish. – ICES, C.M. 1994/Assess: 1.

Aro, E., K. Myrberg, A. Salli, & T. Sønnichsen, 1991: Estimation of Baltic cod eggs and larvae drift by two-layer flow model with variable winds. – ICES, C.M. 1991/J: 15.

Bagge, O., 1993: Possible effects on fish reproduction due to the changed oceanographic conditions in the Baltic proper. – ICES, C.M. 1993/J: 31.

Bagge, O., J. Bay & E. Steffensen, 1993: Fluctuations in abundance of the Baltic cod (*Gadus morhua*) stock in relation to changes in environment and the fishery. – NAFO Sci. Counc. Stud. 18: 35-42.

Bailey, K.M. & E.D. Houde, 1987: Predators and predation as a regulatory force during the early life of fishes. – ICES, C.M. 1987/Mini No. 2.

Balfoort, H., 1984: Experiments on digestion rate of herring larvae in fish stomachs. – ICES, C.M. 1984/H: 32.

Bogstad, B., G. Lilly, S. Mehl, Ó.K. Pálsson & G. Stefánsson, 1993: Cannibalism and year-class strength in Atlantic cod (*Gadus morhua*) in the arcto-boreal ecosystems Barents Sea, Iceland and eastern Newfoundland. – ICES 1993/Cod and Climate Change Symp. No. *43*: 1-29

Brewer, G.D., G. Kleppel & M. Dempsey, 1984: Apparent predation on ichthyoplankton by zooplankton and fishes in nearshore waters of southern California. – Mar. Biol. *80*: 17-28.

Christensen, V., 1983: Predation by sand eel on herring larvae. – ICES, C.M. 1983/L: 27.

Daan, N., 1976: Some preliminary investigations into predation on fish eggs and larvae in the southern North Sea. – ICES, C.M. 1976/L:15.

Daan, N., 1979: Comparison of estimates of egg production of the Southern Bight cod stock from plankton surveys and market statistics. – ICES, C.M. 1979/DS: 1.

Daan, N., 1986: Trial runs with a multispecies virtual population analysis based entirely on numbers of prey organisms observed in stomachs. – ICES, C.M. 1986/G: 53.

Daan, N., A.D. Rijnsdorp & G.R. Overbeeke, 1985: Predation by North Sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*. – Trans. Am. Fish. Soc. *114*: 499-506.

Fraser, J.H., 1969: Experimental feeding of some Medusae and Chaetognatha. – J. Fish. Res. Bd Can. 26: 1743-1762.

Garrod, D. & D. Harding, 1981: Predation by fish on the pelagic eggs and larvae of fishes spawning in the west-central North Sea in 1976. – ICES, C.M. 1981/L :11.

Grauman, G.B., 1976: On the distribution and passive migrations of Baltic sprat eggs and larvae in Bornholm-Slupsk spawning ground. – ICES, C.M. 1976/P: 8.

Grygiel, W., 1990: Fluctuations in Polish sprat catches in 1981-1986 and sprat biological characteristics vs the stocks of this species. – Bull. Sea. Fish. Inst. *1-2*: 117-118.

Hinrichs, R., 1985: Menge und Zusammensetzung der Nahrung bei Hering und Sprott der Ostsee in den Jahren 1980-1982. – Fisch. Forsch. *24*(2): 70-81.

Hinrichs, R., 1986: Nahrungsuntersuchungen und diurnaler Rhythmus der Nahrungsaufnahme von Hering und Sprott der Ostsee. – Fisch. Forsch. *24*(2): 31-37.

Hopkins, P.J., 1988: Predation by herring on fish eggs and larvae in the northern North Sea. – ICES, Early Life History Symp. 1988: 1-17.

Hunter, J.R., 1984: Inferences regarding predation on the early life stages of cod and other fishes. In E. Dahl, D. Danielssen, E. Moksness & P. Solemdal (eds): The propagation of cod, pp. 533-562. Flødevigen Rapp. 1.

Hunter, J.R. & C.A. Kimbrell, 1980: Egg cannibalism in the northern anchovy, *Engraulis mordax*. – Fish. Bull. 78(3): 811-816.

Jensen, H. & H. Sparholt, 1992: Estimation of predation mortality of cod in the central Baltic using the MSVPA. – ICES, C.M. 1992/J: 23.

Jobling, M., 1986: Mytical models of gastric emptying and implications for food consumption studies. – Envir. Biol. Fish. *16*(1-3): 35-50.

Jones, R., 1974: The rate of elimination of food from the stomachs of haddock (*Melanogrammus aeglefinus*), cod (*Gadus morhua*) and whiting (*Merlangius merlangus*). – J. Cons. int. Explor. Mer *35*: 225-243.

Köster, F.W., W. Schober, A. Korves & R. Schneider, 1990: Tank experiments on board: a useful tool for the estimation of stomach evacuation rates?. – ICES, C.M. 1990/G: 34.

Lockwood, S.J., 1980: The daily food intake of 0-group plaice (*Pleuronectes platessa* L.) populations. – J. Cons. int. Mer *39*: 154-159.

Lohmeyer, U. & G. Hempel, 1977: Winter food of the Baltic herring (*Clupea harengus*). – ICES, C.M. 1977/P: 7.

Möller, H., 1980: Scyphomedusae as predators and food competitors of larval fish. – Meeresforsch. *28*: 90-100.

Müller, A., 1982: Das Räuber-/Beute-Verhältnis im Zooplankton des Bornholm Beckens im April des Jahres 1975. – Inst. Meereskunde Kiel, Abschlußbericht zum Forschungsprogramm Mu 479/1. pp. 1-19.

Müller, A. & O. Bagge, 1984: The occurrence of cod eggs and the size of fish eggs in Bornholm Basin. – ICES, C.M. 1984/J: 17.

Müller, A. & T. Pommeranz, 1984: Vertical distribution of fish eggs in the Bornholm Basin, Baltic. – Int. Symp. on Early Life History of Fishes and 8th Annual Larval Fish Conf., Vancouver 1984.

Müller, A. & F. Zuzarte, 1989: Vertical distribution, seasonal composition and abundance of zooplankton in the Bornholm Basin, Baltic 1987. – 11th Baltic mar. Biol. Symp., Szczecin 1989, Poster 27.

Müller, A., K. Muhsin & F.W. Köster, 1990: Ovarian maturation and batch fecundity in Baltic sprat from the Bornholm Basin, 1988. – ICES, C.M. 1990/J: 30.

Nehring, D. & W. Matthäus, 1991: Current trends in hydrographic and chemical parameters and eutrophication in the Baltic Sea. – Int. Rev. ges. Hydrobiol. *76*: 297-316.

Ohldag, S., D. Schnack & U. Waller, 1991: Development of Baltic cod eggs at reduced oxygen concentration levels. – ICES, C.M. 1991/J: 39.
Oiestad, V., 1985: Predation on fish larvae as a regulatory force, illustrated in mesocosm studies with large groups of larvae. – NAFO Sci. Counc. Stud. *8*: 25-32.
Olsen, R.J. & A.J. Mullen, 1986: Recent developments for making gastric evacuation and daily ration determinations. – Envir. Biol. Fish. *16*(1-3): 183-191.
Pennington, M., 1985: Estimating the average food consumption by fish in the field from stomach contents data. – Dana *5*: 81-86.
Plikshs, M., M. Kalejs & G. Grauman, 1993: The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. – ICES, C.M. 1993/J: 22.
Popiel, J., 1951: Feeding and food of the herring (*Clupea harengus* L.) in the Gulf of Gdansk and in the adjoining waters. – Pr. morsk. Inst. Ryb. Gdynia *6*: 29-56.
Pommeranz, T., 1981: Observations on the predation of herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* L.) on fish eggs and larvae in the southern North Sea. – Rapp. P.-v. Réun. Cons. int. Explor. Mer *178*: 402-404.
Shvetsov, F.G. & M.L. Starodub, 1986: K metodike raschjota sutochnogo ratsiona baltijskogo shprota. – Fisch. Forsch. *24*(2): 50-51.
Sissenwine, M.P., 1984: Why do fish populations vary? – *In* R. May (ed.): Exploitation of marine communities, pp. 59-94. Springer-Verlag, Berlin.
Sparholt, H., 1994: Fish species interaction in the Baltic. – Dana *10*: 131-162.
Starodub, M.L. & N.M. Kondratjeva, 1988: Feeding and fatness dynamics of Baltic sprat in 1982-1987. – ICES, C.M. 1988/J:6.
Starodub, M.L., F. Shvetsov & S. Hoziosky, 1992: The feeding of sprat in the eastern Baltic. – ICES, C.M. 1992/J:26.
Temming, A. & F.W. Köster, 1990: Stomach evacuation rates of cod and herring from ship-board tank experiments and field data. – ICES, C.M. 1990/G:31.
Thompson, B.M. & J.D. Riley, 1981: Egg and larval development studies in the North Sea cod (*Gadus morhua* L.). – Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 553-559.
Tyler, A.V., 1970: Rates of gastric emptying in young cod. – J. Fish. Res. Bd Can. *27*(7): 1177-1189.
Välipakka, P., 1990: Zur Verbreitung, Biologie und Ökologie von Mysidacea (Crustacea, Malacostraca) in der Mecklenburger Bucht und in den küstenfernen Gebieten der eigentlichen Ostsee (1985-1988). – Diss. thesis, Wilhelm-Pieck-Univ. Rostock. 156 pp.
Wieland, K., 1987: Untersuchungen zur Sterblichkeit von Dorscheiern im Bornholm Beken. – Dipl. thesis Inst. Meereskunde Kiel. 97 pp.
Wieland, K., 1988: Distribution and mortality of cod eggs in the Bornholm Basin (Baltic Sea) in May and June 1986. – Kieler Meeresforsch. *6*: 331-340.
Wieland, K. & F. Zuzarte, 1991: Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987-1990. – ICES, C.M. 1991/J: 37.
Wieland, K., U. Waller & D. Schnack, 1994: Development of Baltic cod at different levels of temperature and oxygen content. – Dana *10*: 163-177.
Załachowski, W., J. Szypula, S. Krzykawski & I. Krzykawska, 1975: Feeding of some commercial fishes in the southern region of the Baltic Sea in 1971 and 1972. – Pol. Arch. Hydrobiol. *22*(3): 429-448.