Egg cannibalism in Baltic sprat *Sprattus sprattus*

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ABSTRACT: Throughout the last 2 decades a shift from a cod- to a sprat-dominated system occurred in the upper trophic levels of the Central Baltic Sea. This was caused by a decline in the cod stock, due to recruitment failure and high fishing intensity, resulting in a decrease in predation pressure on sprat. Concurrently with the lowest cod stock size on record, sprat reached biomass values of above 2×10^6 t in 1992, being relatively stable afterwards. Besides predation mortality through cod and in recent years also an increasing fishing pressure, cannibalism on eggs may be a compensatory process limiting the reproductive success of sprat and hence contributing to the population regulation in the Central Baltic. Based on sprat stomach sampling on 21 cruises between March 1988 and July 1996 cannibalism on sprat eggs was investigated in the Bornholm Basin, one of the main spawning areas of Central Baltic sprat. Using a model of gastric evacuation to estimate daily food intake rates and a Virtual Population/Extended Survivor Analysis for computing predator population sizes, egg cannibalism rates were estimated. These were compared to egg abundance data from ichthyoplankton surveys and to preliminary estimates of seasonal egg productions. The study revealed significant interannual differences in the intensity of sprat egg cannibalism with considerable predation in 1990 to 1992 (>15% of the egg abundance during peak spawning and >60% of the seasonal production) and a reduction in most recent years (<16% of the corresponding abundance and production). As a possible reason for these differences a combination of changes in the vertical overlap of predator/prey and variability in the food environment were identified. Shortcomings of the applied methods and the possible impact of cannibalism on the reproductive success and population development of sprat in the Central Baltic Sea are discussed.

KEY WORDS: Baltic sprat · Egg cannibalism · Population development · Stomach content analysis · Daily food intake

INTRODUCTION

The upper trophic levels of the open-sea ecosystem of the Central Baltic are characterized by cod *Gadus morhua* L. as the major piscivore and the clupeids sprat *Sprattus sprattus* L. and herring *Clupea harengus* L. as abundant planktivores. Biological interactions within the system have been suggested to establish either a cod-dominated or a sprat-dominated system (Rudstam et al. 1994), whereas the population development of herring appears to be relatively independent. The first system state is maintained by intensive cod predation on sprat (e.g. Sparholt 1994), whereas high stock levels of sprat may be able to control the cod stock via predation on eggs (Köster & Möllmann 2000). Destabilization of the system is caused by either unfavourable hydro-

graphic conditions for reproduction and subsequent recruitment failure of one of the species or high mortalities caused by the fishery (Schnack 1997).

A corresponding shift in the state of the system was observed in the Central Baltic within the period of 1977 to 1996. Due to a combination of high fishing pressure and lack of inflows from the North Sea, the cod stock was reduced from high levels in 1979 to 1984 to its lowest stock size on record in 1992 (e.g. Bagge et al. 1994). The preferred prey species, sprat, showed a significant increase in population size from 1988 to highest levels on record in 1994 (Anonymous 1999), caused by a combination of high reproductive success, reduced predation pressure and relatively low fishing mortalities (Parmanne et al. 1994).

Beside the abovementioned interactions intensifying the dominance of one of the species, compensatory biological effects, e.g. cannibalism, are limiting the

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stock developments. This has been intensively studied for the Central Baltic cod stock (Sparholt 1995, Neuenfeldt & Köster 2000, Uzars & Plikshs 2000). For sprat only a preliminary study is available (Köster & Möllmann 1997), revealing some indications of a high predation pressure by sprat on their own eggs in the Bornholm Basin, a major spawning area of this species in the Central Baltic Sea (Fig. 1).

In the Baltic, sprat has a rather extended spawning season: from March to July with peak spawning time in May (e.g. Elwertowski 1960). Due to the salinity stratification, sprat eggs occur, contrary to other spawning areas, in deeper water layers. In spring, their upper vertical distribution is limited by the cold winter water (Wieland & Zuzarte 1991), i.e. the intermediate water between the developing thermocline and permanent halocline, whereas in summer sprat eggs may occur also in shallower water layers (e.g. Müller 1988). Especially in spring, there is a pronounced vertical overlap between sprat eggs and feeding sprat, concentrating above the oxygen-depleted bottom water during day-time, i.e. their daily feeding period (Köster & Schnack 1994).

The present study investigates whether there is significant predation by sprat on their own eggs and addresses the hypothesis that cannibalism is a controlling factor for sprat stock development. This continues a preliminary analysis conducted by Köster & Möllmann (1997) by presenting (1) new results from an extensive stomach content analysis, now covering the period 1988 to 1996, (2) new estimates of daily rations based on evacuation experiments and diurnal sampling programmes, and (3) updated predator abundances. Finally, we compare the daily consumption rates by predator populations to newly available standings stocks of sprat eggs derived from ichthyoplankton surveys carried out concurrently with stomach sampling and revised seasonal egg production estimates.
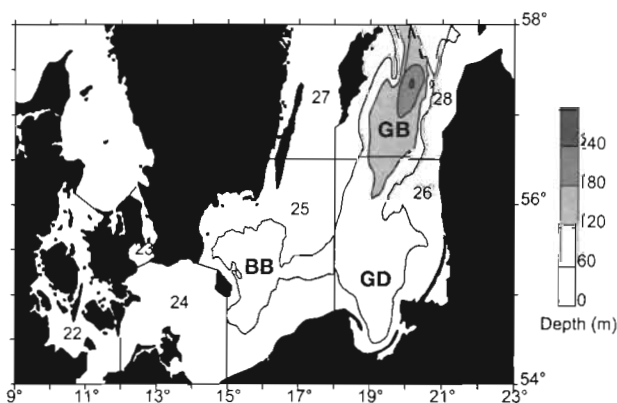
MATERIAL AND METHODS

Stomach sampling scheme. Sprat stomachs were sampled in the Bornholm Basin on 21 cruises from March 1988 to July 1996 (Table 1). During daytime, fish were caught either by bottom trawls or by pelagic trawls in different water layers, depending on the oxygen conditions in the bottom water. The sampling covered mainly areas with waters deeper than 60 m. Trawling depths varied between 50 and 100 m, depending on the echo-traces encountered. According to the daily vertical migration of sprat, nocturnal pelagic trawling was carried out in the upper water column at depths between 5 and 30 m, and trawling at dawn in intermediate depths of 20 to 60 m. On several surveys, notably in 1988, 1991 and 1992, hauls were made at a fixed position at different times of the day, to describe the diurnal feeding cycle of sprat in relation to their vertical migration and to estimate stomach evacuation rates (Köster & Schnack 1994). On cruises conducted since 1990, a larger part of the sprat spawning area was regularly covered in order to describe the spatial variability of predation. In view of an expected fast digestion of ichthyoplankton (Hunter & Kimbrell 1980), the duration of trawling and the handling time on deck was reduced as far as possible, to an average of 45 to 75 min from catching to conservation. Stomachs were collected according to a length-stratified sampling scheme. The conserve was a 4 to 8% formaldehyde/seawater solution buffered with borax.

Stomach content analysis. The amount of food per stomach was determined from 9154 sprat stomachs sampled at 245 different stations (Table 1) as the difference in weight between the full and emptied stomach. The number of eggs was determined from 6 to 10 stomachs per length-class, with class widths of 1 cm. Eggs were identified down to species and developmental stage as far as possible by visual inspection of morphological criteria and measurement of egg size (e.g. Heinen 1912, Mielck & Künne 1935). The remaining stomach content was classified in major taxonomic groups, which were quantified as wet weight by estimating the proportion they contributed to the total volume of the stomach content. Arithmetic mean numbers of eggs and wet weights of all major prey groups were derived for each cruise by computing total averages over all length-classes, weighted by the proportion each length class contributed to the overall length distribution 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, corresponding to the daily feeding period of sprat in the Baltic (Köster & Schnack 1994), were taken into consideration for the determination of diet composition.

Fig. 1. Major spawning areas of sprat in the Central Baltic (BB: Bornholm Basin; GD: Gdansk Deep; GB: Gotland Basin; numbers: ICES sub-divisions)

Table 1. Number of stations and stomachs, duration of the feeding period, ambient temperature, average stomach content of sprat eggs, estimated individual daily food intake and sprat population size (age 1+)

Sampling date (mo/yr)	No. of stations	No. of stomachs	Feeding period (h:min)	Ambient temperature (°C)	Stomach content (no. of sprat eggs)	Individual daily ration			Population size ($n \times 10^{-6}$)
						Wet weight (g)	No. of fish eggs	No. of sprat eggs	
Spring									
3/88	11	528	11:54	5.85	0.3	0.11	17.7	0.7	11969
4/88	5	200	14:09	5.68	0	0.15	89.0	0	11204
4/91	9	355	14:51	4.89	17.2	0.18	91.5	55.0	18420
4/92	11	441	13:52	6.10	26.6	0.08	116.0	81.8	19070
4/93	10	412	14:51	4.48	11.9	0.19	101.6	37.3	22296
4–5/94	16	517	15:33	3.82	0.4	0.34	15.5	1.4	19018
4/95	13	555	13:48	4.98	3.5	0.08	52.8	10.7	28433
Early summer									
5–6/90	12	506	17:06	6.37	49.2	0.37	210.5	188.8	7323
5–6/91	14	526	16:54	4.89	20.8	0.36	110.2	72.9	17269
5–6/92	13	446	16:38	6.10	44.2	0.36	173.6	163.7	18260
5–6/93	9	292	16:41	4.48	0.7	0.37	7.2	2.2	19993
5–6/94	14	328	17:06	3.82	6.5	0.39	37.5	21.7	18368
5/95	18	782	16:18	5.62	1.7	0.19	28.3	5.9	27579
5/96	18	883	16:35	3.51	2.3	0.33	10.5	7.5	20504
Summer									
6–7/88	2	87	17:20	5.63	3.3	0.25	12.1	12.1	3609
7–8/88	3	86	15:45	5.63	0	0.32	0.3	0	3458
7/91	14	535	16:56	5.63	7.6	0.58	48.9	27.9	5956
8/91	11	326	14:56	5.63	<0.1	0.42	0.2	<0.1	5805
8/94	9	169	15:26	4.25	0.5	0.33	4.7	1.5	6060
7/95	17	563	16:23	6.77	<0.1	0.49	0.2	0.2	9283
7/96	16	617	16:17	4.21	1.1	0.27	17.2	3.7	6942

Individual daily rations. To estimate the amount of the daily food intake by individual sprat an exponential form of the general model of gastric evacuation (Tyler 1970, Jones 1974) was applied, which incorporates the actual ambient temperature as a variable (Temming 1996):

$$S_t = S_0 \times \exp(-R' \times e^{A \times C} \times t)$$

where S: stomach content in terms of wet weight (g), S_0: average stomach content at the beginning of the feeding period (g), R': food type constant, A: temperature coefficient, C: ambient temperature (°C), t: time interval.

The function was fitted to median stomach contents as well as to corresponding 25th and 75th percentiles derived from 24 h fisheries and deck tank experiments (Köster 1994) performed in the Bornholm Basin. The determined values for the food type constant and the temperature coefficient were 0.108 and 0.073, respectively. A detailed description of the estimation procedure applied is given in Temming (1996).

Following a procedure suggested by Pennington (1985), the average individual daily ration was estimated by:

$$F_T = R' \times S \times e^{A \times C} \times T + S_t - S_0$$

where T: duration of the feeding period, S_t: average stomach content at the end of the feeding period (g).

Average temperatures per quarter and year in the 60 to 80 m depth-layer, the main water body where sprat concentrated during day-time in the Bornholm Basin, were derived from the ICES hydrographic database. On the basis of the conducted 24 h fishing periods, the daily feeding period of sprat was determined as the hours of daylight (Köster & Schnack 1994). Values for S_t and S_0 were also estimated from 24 h fishing periods by calculating mean relative deviations from the average stomach content within the daily feeding period 2 h before and after the food ingestion stopped and commenced, i.e. sunset and sunrise (Köster 1994).

The daily ration of fish eggs was derived by assuming the same ratio between daily food intake and average stomach content for eggs in numbers as for total food in weight. As a final step, the daily rations of sprat eggs ingested were calculated by distributing the daily rations of all fish eggs according to the encountered species composition of identifiable fish eggs.

Predator population sizes. Population sizes of sprat were calculated on basis of international catch-at-age in numbers (Anonymous 1997) using a Virtual Population Analysis (VPA) tuned with an Extended Survivor Analysis (XSA) (Darby & Flatman 1994) for combined

Sub-divisions 25, 26 and 28 (Fig. 1). XSA-tuning was performed using the international hydroacoustic surveys from 1985 to 1996 as a tuning fleet with the following settings: catchability dependent on stock size for ages <3 yr and catchability independent of age for ages ≥5 yr. Predation mortalities caused by cod, obtained by a recent Multispecies VPA (methodology: see Sparholt 1994) for the entire Central Baltic were incorporated.

The output of the VPA procedure was allocated to individual sub-divisions by using information on the relative horizontal distributions obtained during annual international hydroacoustic surveys in October 1978 to 1996 (Anonymous 1998). Assuming that the distribution of the stock in spawning time from March to July is represented by both the distribution in autumn of the preceding year and the year under consideration, average relative distribution patterns were calculated for 2 consecutive years. Population sizes (ages 1+) referring to specific stomach sampling dates were derived by interpolation between different years, assuming an equal distribution of fishing and natural mortality within each time period.

Within Sub-division 25, hydroacoustic surveys were conducted in May/June 1979 to 1986 (5 cruises in former GDR, former USSR and Poland) and July/August 1981 to 1988 (4 cruises in Poland and Sweden). The data available for ICES statistical rectangles (Köster 1994) were utilized to estimate the average proportions of the total populations aggregating in the Bornholm Basin (areas enclosed by the 60 m depth contours) as 58% in May/June and 21% in July/August. This procedure assumes a constant distribution pattern within Sub-division 25 between years, which is justified by the fact that the sub-division contains only 1 major spawning ground (e.g. Grauman 1980, Krenkel 1981), in which adults concentrate during the spawning season.

Sprat egg abundance and production. Information on the standing stock of sprat eggs in the Bornholm Basin was obtained by standard ichthyoplankton surveys conducted concurrently with the stomach sampling in March to August 1988 and May/June 1990 to 1996 (Wieland 1988). These data allowed identification of the main spawning period of sprat, assuming the year 1988 to be representative for the entire time period covered, and give an indication of the interannual variability in egg abundance. A comparison of egg abundance values and consumption rates, however, does not provide a reliable evaluation of the impact of cannibalism on sprat egg developmental success. Thus, seasonal egg productions to be compared to seasonal predation rates were estimated for each sampling year on the basis of the average batch fecundity of sprat sampled in the Bornholm Basin

(1986 eggs per batch; Müller et al. 1990) and the abundance of sprat age-group 2+ in Sub-division 25 in the second quarter (as determined above). An average sex ratio of 0.50 determined at 33 trawl stations covered in different years and months was utilized to calculate the female spawning stock, assuming all females to be mature. The average number of batches spawned per individual female was set to 10. This assumption is based on reported batch numbers of at least 10 in the western Baltic (Heidrich 1925) and the North Sea (Alheit 1988) as well as 8 to 10 in the southern Central Baltic (Petrowa 1960, Polivaiko 1980).

RESULTS

Diet composition

The diet composition of sprat was dominated by mesozooplankton (Fig. 2). Copepods were the main prey item, with the exception of August dates, when an intensive feeding on cladocerans regularly occurred. In spring, ichthyoplankton was in general the second most important prey group, contributing 13–34% to the diet in terms of weight, with the exception of 1994. The corresponding average numbers of fish eggs encountered in the stomachs ranged between 28 and 33 stomach^{-1} from 1988 to 1993, while in most recent years on average only 5 to 17 eggs were found in the diet (Table 1). From the fish eggs identified to species, a considerable fraction were sprat. An exception was April 1988, when almost all identifiable fish eggs were determined as cod, as sampling was performed in a restricted area of extremely high cod egg and unusually low sprat egg abundances (Köster 1994). In early summer, cladocerans replaced fish as the second most important prey group. This is especially apparent after 1993, when the amount of fish eggs in the stomachs was considerably lower (2 to 11 eggs per stomach) compared to preceding years (31 to 55 eggs per stomach). Again a high proportion of the eggs identified to species level were sprat. In summer, fish contributed only marginally to the diet.

Individual daily rations

The individual daily food intake (Table 1) amounted to 0.5–3.4% body weight per day, showing a clear seasonal trend of increasing rations from spring (on average 0.17 g d^{-1}) to early (0.34 g d^{-1}) and late summer (0.38 g d^{-1}). The daily consumption of fish eggs (Table 1) was at a relatively high level in April from 1988 to 1993

(89 to 102 eggs d^{-1}). In March 1988 — March is the month in which spawning of most fish species in the Bornholm Basin commences — the daily ration of fish eggs was significantly lower. In early summer 1990 to 1992, the individual egg consumption rates were even higher than in spring (110 to 211 eggs d^{-1}). However, a considerable reduction is obvious for later years (7 to 38 eggs d^{-1}), a tendency which is also apparent for spring dates in 1994 and 1995 (16 to 53 eggs d^{-1}). In summer, the daily rations were usually low, with the exception of July 1991, being on an intermediate level. The daily intake rates of sprat eggs closely followed the described seasonal and interannual trends, with highest consumption rates in spring and early summer 1990 to 1992 (55 to 189 eggs d^{-1}), while especially after early summer 1993 the corresponding values were considerably lower (2 to 22 eggs d^{-1}).

Egg consumption by the sprat population in relation to abundance and production

The estimated total daily consumption of sprat eggs by the sprat population in the Bornholm Basin is characterized by the decline in individual predation pressure and an increase in predator population size after 1993 (Table 1). The latter increase does not entirely compensate for the changes in individual daily rations. Consequently highest consumption values were determined for spring and early summer 1990 to 1993, with maximum values in 1992.

From a comparison of the daily consumption rates and abundance of sprat eggs, the intensity of cannibalism appears to be rather substantial in early summer 1990 and 1992, when up to 91 and 79% of the abundance were consumed per day respectively (Table 2). In early summer 1991, the daily consumption was only 15% of the abundance; however, abundance was by far the highest on record. A similar comparison for spring 1991 and 1992 is presently impossible, as abundance data from ichthyoplankton surveys are not available. In most recent years, the daily consumption by the sprat population in spring and early summer reached levels of 1 to 20% of the abundance values only. The impact of cannibalism in summer during the late phase of the spawning season is difficult to infer since ichthyoplankton samples from a considerable number of sampling dates are not available.
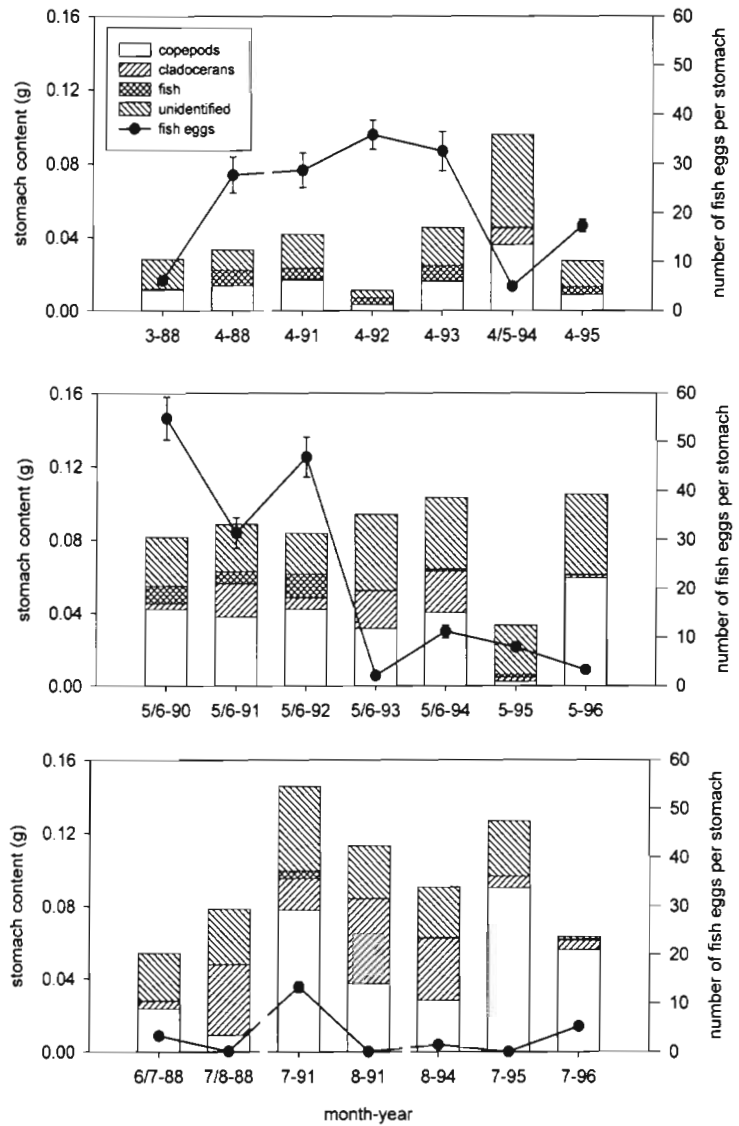

Fig. 2. Average stomach content (in g wet weight) of the main taxonomic prey groups and average number of fish eggs per stomach (with standard error) by survey and periods (spring, early summer, summer)

Comparing the total seasonal egg production of the sprat population in the period 1990 to 1996 with the total egg cannibalism rates in the period April to June, assuming the daily consumption rates to be representative for April and May/June, reveals a rather heavy predatory impact in 1990 to 1992 (Table 3). The calculated egg consumption rates were above the estimated seasonal egg production in 1990 and 1992. Also, in 1991 more than half of the seasonal egg production was estimated to be consumed by sprat in the 3 mo period. After 1993, however, cannibalism rates were well below the egg production (<15%).

Table 2. Estimated daily consumption rate of sprat eggs by the sprat population in comparison with the abundance of sprat eggs in the Bornholm Basin (–: lacking data)

Sampling date (mo/yr)	Consumption ($n \times 10^{-9}$)	Abundance ($n \times 10^{-9}$)
Spring		
3/88	8.7	125
4/88	0	360
4/91	1013.1	–
4/92	1560.2	–
4/93	832.4	3511
4–5/94	26.6	2993
4/95	303.6	–
Early summer		
5–6/90	1382.4	1522
5–6/91	1259.7	8703
5–6/92	2989.9	5373
5–6/93	44.4	5711
5–6/94	399.1	3927
5/95	161.9	1730
5/96	152.9	956
Summer		
6–7/88	43.5	15
7–8/88	0	<0.1
7/91	166.0	–
8/91	<0.1	<0.1
8/94	9.4	–
7/95	1.5	–
7/96	25.5	213

Table 3. Comparison of seasonal sprat egg production with consumption by the sprat population during the period April to June (*no data for April)

Year	Seasonal production ($n \times 10^{-9}$)	Consumption April–June ($n \times 10^{-9}$)	% consumption of production
1990	73163	84326*	115
1991	172518	107235	62
1992	182419	229190	126
1993	199735	27680	14
1994	183500	25143	14
1995	275518	18984	7
1996	204834	9327*	5

DISCUSSION

The diet composition analysis revealed a clear seasonal pattern in the abundance of fish eggs in the food of sprat. A replacement of fish eggs by cladocerans as the second most important prey taxon regularly takes place in summer, when cladocerans are abundant in open-sea areas of the Baltic (Dahmen 1997). This shift in the diet composition is coupled to a change in the vertical distribution of the predator to shallower water layers after spawning (e.g. Hoziosky et al. 1989), where high concentrations of cladocerans occur (Müller & Zuzarte 1996, Wolska-Pys & Ciszewska 1991), while fish eggs are less abundant (Wieland & Zuzarte 1991). Exceptions to this pattern were found in early summer 1991 (high quantities of cladocerans and fish eggs in the diet) as well as early summer 1995 and 1996 (neither cladocerans nor fish eggs in remarkable quantities in the diet). These situations can be explained by an extraordinarily high (first date) and low abundance (last dates) of sprat eggs in the plankton on early survey dates (mid-May) in most recent years, when cladoceran abundance is usually still low (Wolska-Pys & Ciszewska 1991, Dahmen 1997).

Clear interannual differences were encountered in the amount of sprat eggs in sprat stomachs, with a

reduction of 1 order of magnitude from 1990 to 1992 compared to subsequent years. In 1993 to 1996 sprat preyed less intensively upon their own eggs, although considerable quantities were available in the plankton. An explanation for the different feeding behaviour is a changed vertical overlap between predator and prey, due to significant alterations in the hydrographic regime of the Bornholm Basin after the major inflow in early 1993 (Matthäus & Lass 1995). For cod eggs a shift in the vertical distribution to shallower water layers as a consequence of the inflow has been previously described (Wieland & Jarre-Teichmann 1997), reducing the vertical overlap with clupeid predators during their daily feeding period (Köster & Möllmann 2000). A corresponding change in the vertical distribution of sprat eggs is indicated in Fig. 3, but appears to be less pronounced than for cod. However, changes in the vertical distribution of the combined group of fish eggs (Köster & Möllmann 2000) may have caused the reduction of sprat egg cannibalism in post inflow periods as the availability of fish eggs in general may act as a trigger to switch from zooplankton to eggs as prey (Köster 1994). Changes in hydrographic conditions do not only influence the vertical distribution of the prey, but also the dwelling depth of clupeids (e.g. Orlowski 1991). Favourable oxygen conditions during or after inflow periods allow the sprat to stay closer to the bottom (compare average catch depths in 1990 and later years in Fig. 3), resulting in a further reduction of the predator/prey overlap.

Apart from the temporal variability encountered, predation on fish eggs by sprat also varies spatially, with the amount of sprat eggs in the diet of sprat being lower in the Gdansk Deep and the Gotland Basin than in the Bornholm Basin. This difference in diet composition has been explained by a combination of deviating prey availability and light intensity in the dwelling depth of sprat (Geldmacher 1998).

A problem within the present study is the low fraction of eggs identifiable to species level (in general 0.5

to 4.4 %), which may introduce a significant systematic bias in the determined egg species composition if the digestion times are different for different egg species. However, from diurnal sampling and performed digestion experiments, no significant differences for the egg species which were dominant in the plankton and in the diet were detectable (Köster 1994). Thus, it appears to be unlikely that the described temporal trends are caused by major shortcomings in the diet composition analysis.

The comparison of estimated egg cannibalism rates by the sprat population with standing stocks and production rates of sprat eggs also revealed a decrease in predation pressure since 1993, although the sprat predator population increased substantially throughout the covered time period. However, consumption rates by the sprat population as well as egg abundance and production estimates are based on a variety of assumptions in the estimation procedures. Implementing an exponential evacuation model appears to be in good agreement with findings of Jobling (1986), who suggested exponential evacuation for fish feeding on small particles, e.g. zooplankton. Nevertheless, the assumed similar evacuation rate of fish eggs and other prey organisms, according to weight, might not be valid. The low proportion of fish eggs identifiable to species level indicates rapid digestion beyond identification, but the remains of eggs can be identified after several hours of digestion, thus being in the order of magnitude determined for mesozooplankton prey (Köster 1994). Therefore, the applied procedure appears to be more reasonable than a separate model for the evacuation of fish eggs on a number basis (for further discussion see Köster & Schnack 1994).
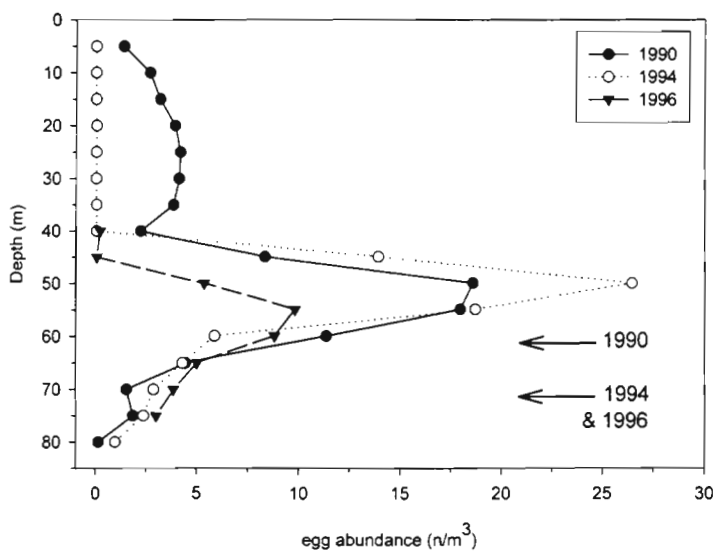
Table 4. Comparison of sprat population sizes in the Bornholm Basin derived by hydroacoustic surveys and by downscaling Virtual Population Analysis (VPA) results according to relative horizontal distributions obtained by hydroacoustic surveys

Sampling date (mo/yr)	Hydroacoustics $(n \times 10^{-6})$	VPA $(n \times 10^{-6})$
8/94	818	6060
5/95	7053	27579
7/96	6389	6942

As indicated by hydroacoustic surveys conducted in the Bornholm Basin in May 1995 (Table 4), the population size of sprat estimated in this study might by overestimated by a factor of 4, whereas in July 1996 both estimates were rather similar. In August 1994 an even higher deviation, by a factor of 7, was encountered, which can be partly explained by problems in splitting biomass values estimated by the hydroacoustic survey into those for sprat and herring (Anonymous 1998). Overestimating the population sizes has a direct effect on the population consumption estimates, but the comparison of sprat egg consumption and production rates is not affected by this, as both estimates are determined via population sizes derived by VPA.

The procedure for computing egg production values is based on various assumptions related to the spawning stock, i.e. constant sex ratio with age and knife edge maturity ogive, both invariate over time, as well as to the average batch fecundity and the number of batches spawned per female in a spawning season, i.e. ignoring interannual variability as well as size/age (see de Silva 1973, Alheit 1988, 1993). According to Alekseeva et al. (1997) the average batch fecundity of sprat in the southern Central Baltic in early summer 1992 to 1995 fluctuated between 1411 and 1851 eggs batch^{-1}, showing also significant differences between years. This indicates that the fecundity estimate in use may be overestimated by up to 30 % in specific years. However, an earlier study (Polivaiko 1980) gives a wider range of batch fecundities of Baltic sprat (1467 to 2576 eggs batch^{-1}), which agrees better with the average value assumed in the present study.

The estimated seasonal egg production by the sprat population increased from 1990 to 1995 by nearly a factor of 4, while the standing stock of eggs derived by ichthyoplankton surveys decreased from 1991 onwards, especially after 1994. This contradiction is mainly related to survey dates being 1 to 2 wk earlier

Fig. 3. Vertical distribution of sprat eggs and mean catching depths of clupeids (arrows) in spring 1994 and early summer 1990 and 1996

in May 1995 and 1996 compared to former years, probably not covering peak spawning time and consequently revealing below average egg abundances. Additionally, in 1996 the low ambient temperature resulted in a delay of spawning activity, as reported earlier by Grimm & Herra (1984), in combination with the early survey date explaining the extremely low egg abundance value derived for early summer 1996. As a further consequence of the early survey dates, the seasonal consumption by the sprat population determined for early summer 1995 and 1996 is expected to be slightly underestimated. This may explain the lower proportion of the seasonal production consumed by sprat in these years compared to 1993 and 1994.

Despite the described reservations and uncertainties, the results suggest cannibalism to be an important source of sprat egg mortality in the Bornholm Basin. This is especially the case during periods of low salinity and oxygen concentration in the bottom water, which resulted in a pronounced vertical overlap of predator and prey. The importance of cannibalism for the reproductive success of sprat, however, also depends on other causes of egg mortality. Especially the temperature in the intermediate water, but also temperatures within and below the halocline appear to be important factors determining the distribution of the spawning stock (Hoziosky et al. 1989), the timing of spawning activity (Grimm & Herra 1984) and egg mortality (Krenkel 1981). Also, low oxygen concentration in the bottom water affects the distribution of the spawning stock (Hoziosky et al. 1989) and its egg production as well as egg survival (Grauman & Yula 1989). This is especially of importance in spring and early summer, when sprat eggs concentrate mainly within and below the halocline (Wieland & Zuzarte 1991).

The intensive cannibalism on sprat eggs identified for the Bornholm Basin prior to the last major Baltic inflow in 1993 may explain the stable stock sizes in Sub-division 25, concurrent with a significant increase in other areas of the Baltic monitored by international hydroacoustic surveys (Anonymous 1998). In most recent years, when egg cannibalism was reduced, reproductive success in Sub-division 25 increased and resulted in the highest recruitment of 0-group sprat on record in 1994 and 1995 (Anonymous 1998). Whereas in 1994 the abiotic conditions were additionally favourable for sprat egg development, in 1995 only the low predation pressure explains a high reproductive success. Despite relatively low cannibalism intensity in 1996, temperature conditions did not allow above average survival of sprat early life history stages, as indicated by hydroacoustic survey results (Orlowski et al. 1997).

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