

Trophodynamic control by clupeid predators on recruitment success in Baltic cod?

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Throughout the 1980s, reproductive success of the top-predator cod declined and stock sizes of the main prey species herring and especially sprat, important planktivorous predators in the system, increased substantially. Although the hydrographic conditions conducive for survival of early life stages improved during the 1990s, recruitment success of cod remained far below average. As clupeids have been identified as major predators on cod eggs and larvae in the Baltic, increased predation may be an important factor hampering stock recovery. Results from stomach content analysis of herring and sprat during the spawning season of 1988–1995 and ichthyoplankton surveys in the Bornholm Basin (the only important spawning area of cod in the Central Baltic in this period) allow a comparison of estimated consumption rates by the predator populations with standing stocks and production rates of cod eggs and larvae. Despite uncertainties in the estimation procedure, the findings confirm substantial predation on cod eggs by both clupeid species. Especially at the beginning of the cod-spawning season, characterized by low zooplankton availability, sprat consumed a considerable proportion of the eggs produced. In 1993, the relative importance of zooplankton as prey increased, while fish eggs were encountered more rarely. In contrast, predation by herring remained on the same level or even increased, especially late in the spawning season. The larval stage of cod is not substantially affected by predation owing to limited spatial overlap between prey and predator.

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Key words: Baltic cod, early life history stages, predation by herring and sprat.

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Introduction

Owing to a combination of reproduction failure and overfishing, the Central Baltic cod stock decreased to historical low levels in 1992 (Bagge *et al.*, 1994; ICES, 1997). The recruitment failure has been related to the hydrographic regime of the Baltic, and especially to the absence of inflow of oxygen-enriched water from the North Sea and the Western Baltic (MacKenzie *et al.*, 1996). Stagnation and increasing oxygen demand due to eutrophication limited the volume of water where successful egg development was possible (Plikshs *et al.*, 1993). Thus, hydrographic conditions in the eastern spawning grounds of the Gotland Basin and Gdańsk Deep (Fig. 1) have in general not allowed successful cod egg development since 1986. Consequently, recruitment has been almost entirely dependent on the survival of early life stages in the Bornholm Basin, the only remaining major spawning area. The hydrographic conditions for egg development have

improved in this area since 1991, and especially in 1993/1994, due to a major inflow situation at the beginning of 1993 (Matthäus and Lass, 1995). However, cod recruitment has remained fairly low, suggesting that other processes are limiting reproductive success (Bagge, 1996).

Several potential factors have been identified (Schnack and Köster, 1998). Predation effects, specifically cannibalism (Neuenfeldt and Köster, 1999; Uzars and Plikshs, 1999) and predation on early life stages by clupeids, were considered as potentially important causes of mortality. Egg predation by herring and sprat in particular may have become a bottleneck, as the decline in the abundance of cod is associated with increasing stocks of its major prey species, especially sprat (Sparholt, 1994).

In contrast to cod stocks in other areas, a pronounced temporal overlap exists in the Baltic between the extended spawning season of cod (from March to August; Bagge *et al.*, 1994) and the major feeding period

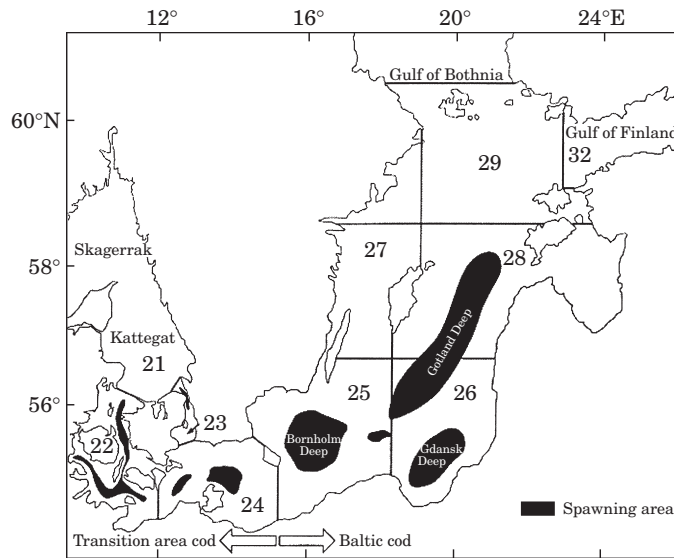


Figure 1. Main cod spawning areas in the Baltic and ICES Subdivisions (modified from [Bagge et al., 1994](#)).

of herring, which starts after the return of spring spawners from their coastal spawning grounds in May ([Aro, 1989](#)). Sprat concentrate in the same areas as cod for spawning ([Elwertowski, 1960](#)). In addition to the temporal and horizontal overlap of cod, early life stages and planktivorous clupeids, the vertical overlap between prey and predator is important, which depends on the specific hydrographic regime encountered in the Central Baltic basins. Owing to salinity stratification, cod eggs occur exclusively in a narrow depth range within or below the halocline in the Central Baltic basins ([Müller and Pommeranz, 1984](#); [Wieland, 1988](#)), where also the larvae hatch ([Wieland and Zuzarte, 1991](#); [Grønkvær and Wieland, 1997](#)). Therefore, eggs, and to a lesser extent early larvae, should be available in relatively dense aggregations for the clupeids, which stay close to the bottom or above the oxygen-depleted bottom water below and in the halocline during their main feeding period in daytime ([Köster and Schnack, 1994](#)).

The first attempts to quantify the consumption of cod eggs by herring and sprat in the Bornholm Basin revealed a significant predation pressure during the spawning seasons in 1988–1991, especially by sprat in spring ([Köster and Schnack, 1994](#)). In later years, predation by sprat declined, coinciding with major changes in the hydrographic environment in 1993, whereas the predation pressure by herring in the summer months increased ([Köster and Möllmann, 1997](#)). Fish larvae and also 0-group cod were relatively rarely observed in stomachs, which has been explained by a limited vertical overlap between the medium-sized to larger larvae and juveniles inhabiting the upper water layers above the halocline and the clupeids concentrating in deeper layers ([Köster and Schnack, 1994](#)).

We address the hypothesis that cod recruitment in the Baltic is presently controlled by clupeid fish through predation on early life stages by quantifying species interactions at this stage. To this end we present (a) results from stomach content analysis conducted between 1988 and 1995, (b) new estimates of daily rations based on evacuation experiments and diel sampling programmes, and (c) updated predator abundance. Finally, we compare the daily consumption rates by predator populations to updated standings stocks of eggs and larvae and revised production estimates derived from ichthyoplankton surveys carried out concurrently with the stomach sampling.

Material and methods

Stomach sampling

In total, 5888 herring and 7126 sprat stomachs were collected in the Bornholm Basin during 18 cruises between April 1988 and July 1995 ([Table 1](#)). During the day, 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 mainly covered areas with water depths greater than 70 m, with trawling depths varying between 60 m and 100 m, depending on the echo-traces encountered. In line with the daily vertical migration of herring and sprat, nocturnal pelagic trawling was carried out at depths between 5 m and 30 m, and trawling at dawn in intermediate depths of 20–60 m. On several occasions, notably in 1988 and 1991, hauls were made at a fixed position at different times of the day, to describe the diurnal feeding cycle of herring and sprat in relation to

Table 1. Ambient temperature (T), number of stations sampled (n), number of stomachs analysed (N) for herring and sprat, and the duration of the feeding period (D) by survey period and year (n.a.: not yet analysed).

Month/year	T °C	Herring		Sprat		D h:min
		n	N	n	N	
Spring						
Apr. 1988	5.7	1	193	5	200	14:09
Apr. 1991	4.9	7	283	9	355	14:51
Apr. 1992	6.1	12	159	11	441	13:52
Apr. 1993	4.5	10	138	10	412	14:51
Apr./May 1994	3.8	16	410	16	517	15:33
Apr. 1995	5.0	12	262	13	555	13:48
Early summer						
May/Jun. 1990	6.4	12	562	12	506	17:06
May/Jun. 1991	4.9	12	474	14	526	16:54
May 1992	6.1	n.a.	n.a.	13	446	16:38
May/Jun. 1993	4.5	10	281	9	292	16:41
May/Jun. 1994	3.8	13	311	14	328	17:06
May 1995	5.6	18	451	18	782	16:18
Summer						
Jun./Jul. 1988	5.6	8	233	2	87	17:20
Jul./Aug. 1988	5.6	4	165	3	86	15:45
Jul. 1991	5.6	15	473	14	535	16:56
Aug. 1991	5.6	11	461	11	326	14:56
Aug. 1994	4.3	14	391	9	169	15:26
Jul. 1995	6.8	19	641	17	563	16:23

their vertical migration and to estimate stomach evacuation rates (Temming and Köster, 1990; Köster and Schnack, 1994). Since 1990, cruises have regularly covered the greater part of the cod spawning area in order to describe the spatial variability in predation (Köster and Schnack, 1994).

In view of an expected rapid digestion of ichthyoplankton, especially if small larvae had been ingested (e.g. Hunter and Kimbrell, 1980), haul duration and handling time on deck were reduced as far as possible (range 45–75 min from capture to preservation). Stomachs were collected according to a length-stratified sampling scheme, with class widths of 2 cm and 1 cm for herring and sprat, respectively. Samples were preserved in a 4–8% formaldehyde/seawater solution buffered with borax.

The amount of food per stomach was determined as the difference in weight between the full and emptied stomach. Per length-class, 6–10 stomachs were analysed. Eggs, larvae, and fish were identified down to species and developmental stage as far as possible, and counted. The remaining stomach content was classified by major taxonomic group and their wet weight was quantified 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 per predator, were derived for each cruise by weighting the averages of all length-classes by the proportion each length

class contributed to the length distribution of herring and sprat caught. Owing to the low variability in length distributions on different stations covered within one survey, no calculation of a weighted average over all length classes by station has been performed, but the entire length distribution obtained during the cruise has been utilized. Unidentified eggs were allocated to species according to the species composition of identified eggs. Only stomachs sampled between sunrise and sunset, corresponding to the feeding period of herring and sprat in the Baltic basins, were taken into consideration.

Daily rations

In preceding studies (Köster and Schnack, 1994; Köster and Möllmann, 1997), a general model of gastric evacuation (e.g. Tyler, 1970; Jones, 1974) was used, which did not take temperature explicitly into account. The data sets employed were derived from 3210 herring and 3802 sprat stomachs sampled during several 24-h periods as well as several tank experiments (Köster *et al.*, 1990). For a summary of information on performed experiments, see Anon. (1998). Although these data had been collected only in April/May to avoid excessively high temperatures in surface layers and on board, the ambient temperature (4.4–14.0°C) was higher than observed in the halocline and the bottom water (3.5–7.0°C), where the fish feed during the day. This may

result in biased daily rations due to enhanced digestion (Köster and Möllmann, 1997), and therefore we applied an alternative approach by incorporating actual temperatures following Temming (1996). The median stomach contents as well as the corresponding 25th and 75th percentiles were fitted to a simplified exponential gastric evacuation model, which appeared to be reasonable since the exponent of the general evacuation model was close to 1 for both species:

$$S_t = S_o \cdot \exp(-R' \cdot t \cdot \exp(A \cdot C))$$

where S is stomach content (g), R' a food type constant, A temperature coefficient, C the ambient temperature ($^{\circ}\text{C}$), and t the time interval.

The data sets considered for fitting the function using a non-linear regression technique (Marquard algorithm) consist of those described above and results from additional deck tank experiments carried out at higher temperatures (11–18 $^{\circ}\text{C}$). To avoid bias introduced by an increasing number of zero observations (Olson and Mullen, 1986), only medians and percentiles greater than zero have been included in the estimation procedure. Based on an approach proposed by Pennington (1985), the average individual daily rations (FT) were then estimated by:

$$F_T = R' \cdot S \cdot T \cdot \exp(A \cdot C) + S_t - S_o$$

where T is duration of the feeding period, S_t the average stomach content at the end and S_o the average stomach content at the beginning of the feeding period.

Average temperatures in ICES Subdivision 25 per quarter and year in the 60–80 m depth layer were derived from the ICES hydrographic database and assumed to be representative of the ambient temperatures for both species. The daily feeding period of herring and sprat was taken as the hours of daylight (Köster and Schnack, 1994; Fetter and Davidjuka, 1996). Values for S_t and S_o were estimated by calculating mean relative deviations from the average stomach content during daytime, 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. Finally, the daily ration of cod eggs ingested was calculated by distributing the daily ration of all fish eggs according to the encountered species composition.

To estimate the daily rations of fish larvae ingested, an average digestion time of 2 h was applied in a simple Bajkov (1935) approach. This average digestion time was estimated from two digestion experiments conducted with herring that had ingested relatively large amounts of fish larvae (Köster, 1994).

Predator population sizes

Population sizes of herring and sprat in ICES Subdivision 25, the management area which encloses the Bornholm spawning ground (Fig. 1), were determined by scaling down results of Multispecies Virtual Population Analysis (MSVPA) for the entire Central Baltic (ICES, 1996a) according to hydroacoustic data. Stock sizes calculated for Subdivisions 25–27 (herring) or 25, 26, and 28 (sprat) were allocated to individual Subdivisions by using information on the relative horizontal distributions obtained during annual international hydroacoustic surveys in October (Köster, 1994; ICES, 1996b). Population sizes (ages 1+) referring to specific stomach sampling dates were derived by interpolation between quarters, assuming an equal distribution of fishing and natural mortality within each quarter.

Within Subdivision 25, hydroacoustic surveys have been conducted in May/June 1979–1986 (5 cruises by former GDR, USSR and Poland) and July/August 1981–1988 (4 cruises by Poland and Sweden). The results (Köster, 1994) were broken down to ICES statistical rectangles and utilized to estimate the average proportions of the total populations aggregating in the entire and inner part of the Bornholm Basin (areas enclosed by the 60 m and 75 m depth contours, respectively), by considering the different horizontal distributions of eggs and larvae. Because of a lack of hydroacoustic data in March/April, population sizes of herring at this time of year were derived using May/June values corrected for the difference in average c.p.u.e. from pelagic trawl hauls in April compared to May/June 1990–1993 (Köster, 1994). Sprat concentrate in the Bornholm Basin during the spawning season from March to July. Therefore, the mean percentage obtained for May/June was also applied to March/April.

Hydroacoustic surveys conducted in August 1994 and May 1995 (Anon., 1998) enabled a comparison between calculated and directly observed population sizes in the Bornholm Basin, as a check of the various assumptions made in the estimation procedure.

Prey abundance and production

Information on the standing stock of cod eggs in the central Bornholm Basin (area enclosed by the 75 m depth contours) was obtained by standard ichthyoplankton surveys (Wieland, 1988) conducted prior to the stomach sampling (Fig. 2). Since differentiation between dead and live eggs in the diet was impossible, the abundance values include dead eggs encountered in plankton samples.

Daily production values of cod egg developmental stage IA were estimated on the basis of stage-specific abundance values (Table 2) and corresponding stage duration times (Wieland *et al.*, 1994) determined on the

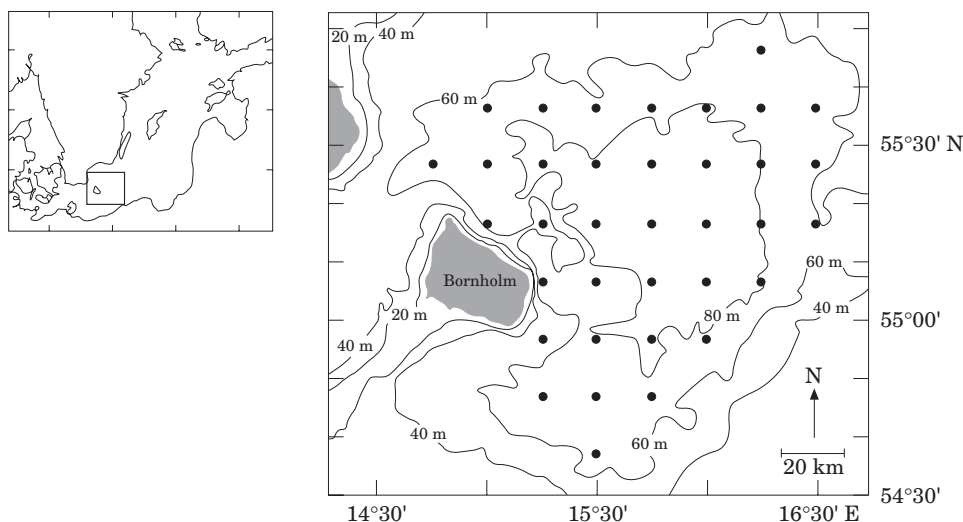


Figure 2. Study area in the Bornholm Basin and the ichthyoplankton survey grid.

Table 2. Ambient temperature (T) and abundance of cod eggs by developmental stage IA and IV as well as dead eggs in the area of the Bornholm Basin enclosed by the 75-m depth contour.

Month/year	T °C	Abundance of cod eggs (n*10 ⁻⁹) by stage		
		IA	IV	Dead
Spring				
Apr. 1988	5.7	9.11	0.30	1.11
Apr. 1991	4.5	7.98	0.32	3.33
Apr. 1992	6.4	2.74	0.04	0.43
Apr. 1993	4.6	10.42	0.32	6.89
Apr./May 1994	3.1	9.17	0.13	6.70
Apr. 1995	5.3	1.05	0.02	1.14
Early summer				
May/June 1990	6.3	5.46	0.21	3.16
May/June 1991	4.5	10.83	0.32	3.45
May 1992	6.2	3.10	0.07	0.20
May/June 1993	4.6	8.63	0.05	9.40
May/June 1994	3.2	43.85	0.05	26.64
May 1995	5.3	13.86	0.12	9.84
Summer				
Jun./Jul. 1988	5.5	8.27	0.33	5.45
Jul./Aug. 1988	5.5	6.72	0.29	4.68
Jul. 1991	5.9	14.92	0.99	12.72
Aug. 1991	5.9	6.19	0.49	7.83
Aug. 1994	4.2	52.35	1.67	32.91
Jul. 1995	5.0	98.99	0.72	62.26

basis of ambient temperatures encountered in the depths with maximum cod egg densities (Wieland and Jarre-Teichmann, 1997). The values were corrected for mortality within the egg stage by applying estimates of age-dependent egg mortality (Anon. 1998) to half the

stage duration time. To account for the different hydrographic situations (Hinrichsen and Wieland, 1996), average mortality rates derived for 1987/1988 and 1991–1996 (0.17 and 0.29 d⁻¹) were applied to the periods 1988–1990 and 1991–1995, respectively. Finally, abundance values of dead eggs were allocated to egg stages according to the stage composition of alive eggs and the respective values derived for stage IA were added to the determined production values.

Cod larvae production values were estimated for each sampling date based on abundance values of the oldest egg stage derived from the ichthyoplankton surveys (Table 2). Mortality rates determined for the latest egg to the earliest larval stage by period (Anon., 1998) were applied to account for late egg and hatching mortality (0.19 and 0.54 d⁻¹ for the periods 1988–1990 and 1991–1995, respectively). The calculated daily consumption rates by clupeid populations are also compared to the corresponding standing stocks in the Bornholm Basin (Grønkjær *et al.*, 1995; Voss, 1996). Because of the different vertical distribution of post yolk-sac larvae compared to eggs and a related drift out of the basin's centre (Hinrichsen *et al.*, 1997), the wider area of the entire Bornholm Basin (enclosed by the 60 m depth contour) was assumed to be the border line of the distribution.

Results

Diet composition

The stomach contents of both herring and sprat (Fig. 3) in different years were in general lowest in April and increased in May/June and July/August, although variations were considerable, particularly during summer.

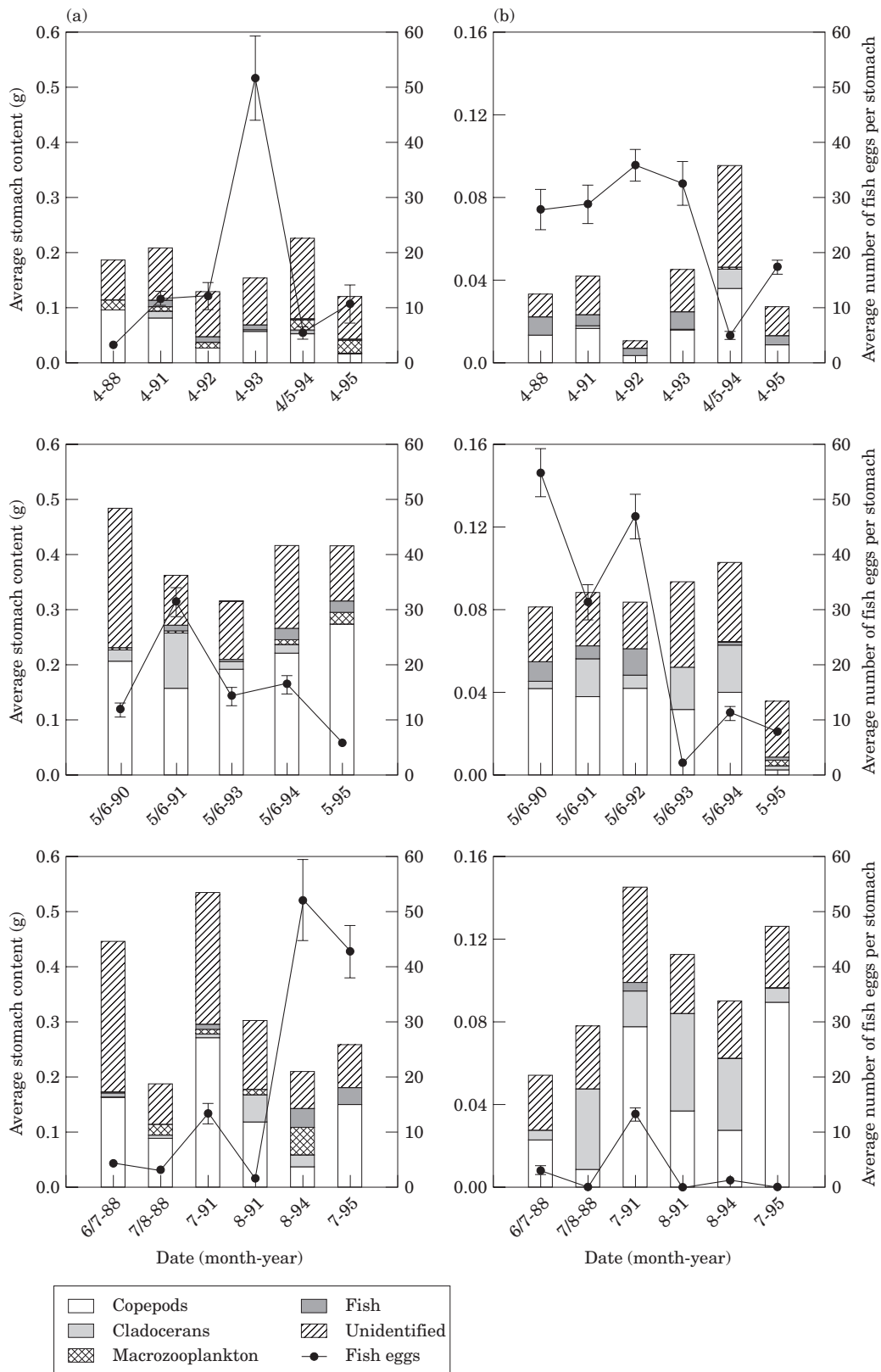


Figure 3. Average stomach content weight (in g wet weight) of the main taxonomic groups and average number of fish eggs (\pm s.e.) by survey, grouped by broad survey periods (spring, early summer, summer), 1988–1995. a. herring; b. sprat.

The diet composition of both species was dominated by mesozooplankton.

Copepods were the most important prey taxon for herring in nearly all months investigated. The combined group of macrozooplankton and small fish comprised in general up to 10% of the average stomach content in weight. Fish eggs contributed up to 16%, but in general the percentage was well below 5%. In terms of numbers, maximum values of around 50 eggs per stomach were observed in April 1993, July 1995, and August 1994. Intermediate numbers were observed for most May/June dates, while remaining values were mostly lower. Fish larvae were only occasionally identified in herring stomachs.

Copepods were also the main prey of sprat, with the exception of August dates when cladocerans were intensively fed upon regularly (Fig. 3). Ichthyoplankton was in general the second most important prey group in April, contributing 13–34% to the diet in terms of weight (with the exception of a low value in April/May 1994). The average number of fish eggs was in the order of 30 per stomach from 1988 to 1993, while in recent years much lower numbers were encountered. In late spring/early summer, cladocerans replaced fish as the second most important prey group, especially since 1993. The amount of fish eggs in stomachs has been considerably lower compared to preceding years. In summer, fish contributed only marginally to the diet (<3%). The number of fish larvae in the diet was, similar to herring, in general also fairly low.

In April, cod eggs contributed on average between 2% and 37% to the total number of fish eggs found in herring stomachs (Fig. 4). In general, sprat, rockling, or flounder eggs were more important at the beginning of the cod spawning season. In May/June the percentage of cod eggs increased to 29–58%. The proportion increased further during summer, when 60–98% of the eggs were identified as cod (with the exception of 1988 when an unusually high proportion of rockling eggs was observed). By far the highest numbers of cod eggs of up to 50 were encountered in July 1995 and August 1994.

Sprat feed mostly on their own eggs (Fig. 4). Flounder eggs were also important in April and rockling eggs in summer. Exceptionally high proportions of cod eggs were identified in April 1988, May/June 1993, and August 1994, although the latter two dates were associated with very low amounts of fish eggs ingested in total. Apart from April 1988 (26 cod eggs per stomach), the average number of cod eggs observed was less than 9 per stomach.

The average amount of fish larvae found in the diet of herring and sprat was low, independent of month and year of sampling. Maximum number of larvae per stomach was identified in August 1991 for herring (0.3) and April 1993 for sprat (2.0). The relatively high standard errors calculated indicate an occasionally high

consumption of larvae by single predators (up to 117 larvae have been found in one sprat stomach).

From the total of 368 and 796 fish larvae found in herring and sprat stomachs, 40% and 56%, respectively, were identified to species level. Most were identified as sprat larvae. Those found in sprat stomachs were in general <10 mm, while herring had ingested more specimens >10 mm. Only 7 and 12 larvae encountered, respectively, were identified as cod.

Small fish were found in limited numbers in herring stomachs only (on average about 0.01 fish per stomach). They were mostly identified as gobiids. Only two juvenile cod were encountered.

Daily rations

The daily rations for herring, estimated for the different sampling dates on the basis of the exponential evacuation model (Table 3; food type constant $R'=0.084$; temperature coefficient $A=0.129$), amounted to 0.5–3.1% body weight per day, with a clear seasonal pattern of increasing rations from April (average 0.6 g d^{-1}) to May/June (1.4 g d^{-1}), similar levels in July and a reduction in August (0.8 g d^{-1}). The individual rations of cod eggs (Table 3) were fairly constant in May/June (21–44 eggs per day), with the exception of 1995. At the beginning and end of the cod spawning season, daily rations were more variable, with particularly high values in July 1995 and August 1994. Daily rations of fish larvae were generally low, and in 12 out of 17 cases cod larvae in particular were below the detection limit.

For sprat, a less pronounced impact of temperature on the evacuation process ($R'=0.108$; $A=0.073$) was found compared to herring. The estimated individual daily food intake (Table 3) amounted to 0.5–3.4% body weight per day, showing a clear seasonal trend of increasing rations from April (on average 0.16 g d^{-1}) to May/June (0.34 g d^{-1}) and July/August (0.40 g d^{-1}). The corresponding daily consumption of cod eggs varied greatly in spring, with a particularly high value in 1988 ($83 \text{ cod eggs d}^{-1}$), intermediate rations in 1991–1993 and lower ingestion rates in later years. A similar trend of declining cod egg rations over the period is obvious for late spring/early summer. In summer, daily rations were even lower, with the exception of July 1991. The daily rations of fish larvae (Table 3) were, with two exceptions, well below 1 larva per day and for cod larvae even in 13 out of 18 cases below the detection limit.

Egg consumption and production

According to historic hydroacoustic surveys carried out in May/June and in August, on average 22% and 34%, respectively, of the herring population in Subdivision 25

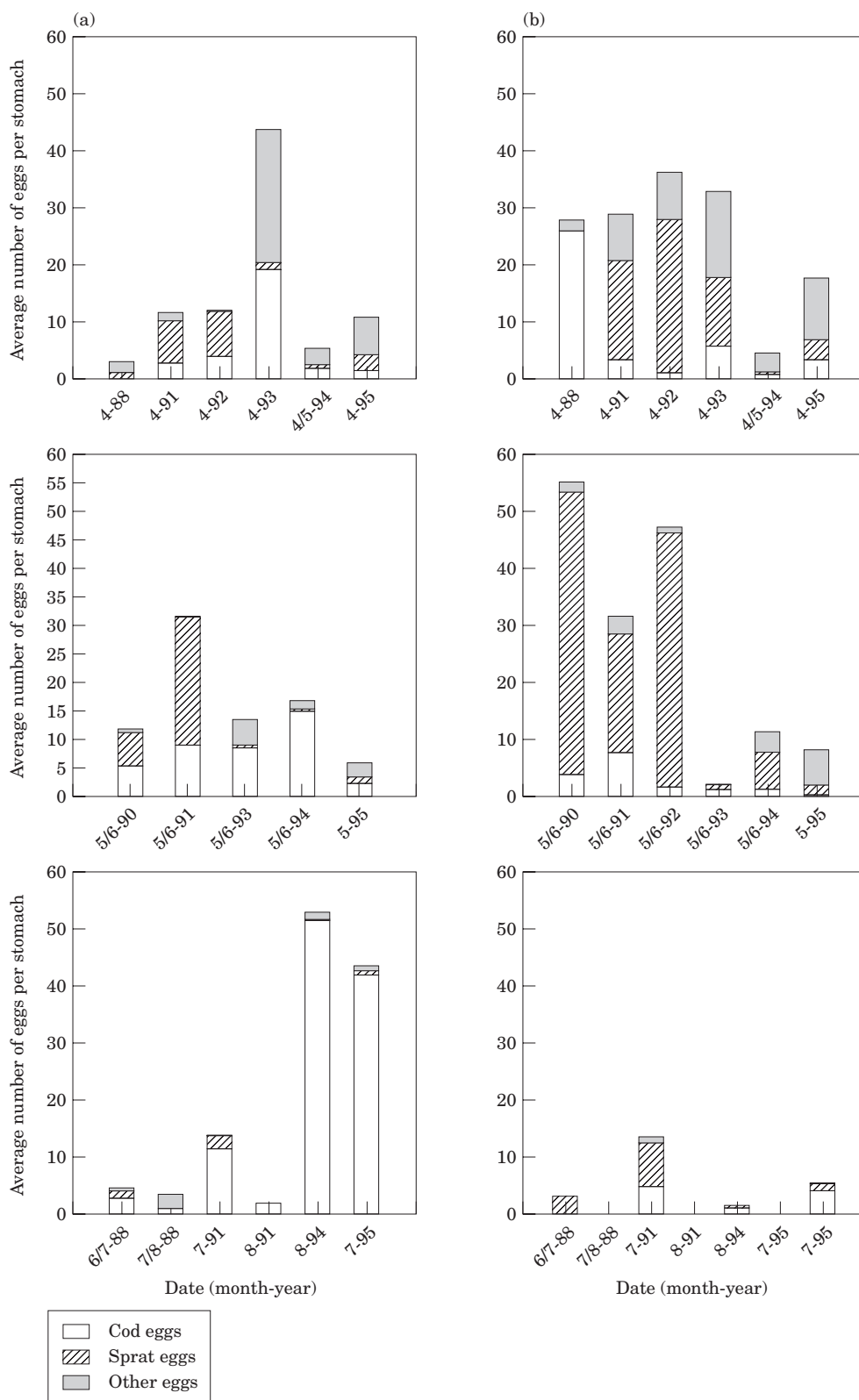


Figure 4. Average number of fish eggs per stomach and species composition by survey (see also Fig. 3). a. herring; b. sprat.

Table 3. Estimated daily food intake (R: wet weight in g) and numbers of eggs and larvae consumed per day for herring and sprat.

Month/ year	Herring					Sprat				
	R	Eggs		Larvae		R	Eggs		Larvae	
		Fish	Cod	Fish	Cod		Fish	Cod	Fish	Cod
Spring										
Apr. 1988	0.67	9.9	0.2	0.11	0	0.15	89.0	82.8	0.08	0.08
Apr. 1991	0.72	34.4	8.7	0.01	<0.01	0.18	91.5	10.7	0	0
Apr. 1992	0.52	38.1	12.8	1.59	0	0.08	116.0	3.5	0.03	0
Apr. 1993	0.54	146.0	53.9	0.98	0	0.19	101.6	17.5	14.86	0.23
Apr./May 1994	0.72	14.6	5.2	0.23	0	0.34	15.5	2.0	0	0
Apr. 1995	0.44	29.9	3.8	0.71	0	0.08	52.8	9.5	0	0
Early summer										
May/Jun. 1990	2.03	45.9	20.5	0.46	0	0.37	210.5	15.3	6.37	0.07
May/Jun. 1991	1.31	103.0	29.5	0.09	0	0.36	110.2	26.5	0.01	<0.01
May 1992			n.a.			0.36	173.6	6.1	0	0
May/Jun. 1993	1.10	44.7	26.0	0	0	0.37	7.2	4.2	0	0
May/Jun. 1994	1.34	48.8	43.7	0.02	0	0.39	37.5	4.3	0.11	0
May 1995	1.55	19.9	7.3	0	0	0.19	28.3	1.0	0	0
Summer										
Jun./Jul. 1988	1.73	16.0	9.5	0.01	<0.01	0.25	12.1	0	0	0
Jul./Aug. 1988	0.74	11.2	2.7	0.04	<0.01	0.32	0.3	0	0	0
Jul. 1991	2.02	47.9	39.5	0.02	0.02	0.58	48.9	17.2	0.19	0.05
Aug. 1991	1.08	5.5	5.4	2.20	0.25	0.42	0.2	0	0	0
Aug. 1994	0.70	148.1	144.2	0.19	0.07	0.33	4.7	3.1	0.44	0
Jul. 1995	1.00	145.5	140.2	0	0	0.49	0.2	0	0	0

is found in the entire Bornholm Basin, and 12% and 25%, respectively, in the centre of the basin. The tenfold increase in c.p.u.e. from March/April to May/June, as determined from trawl surveys 1988–1993, indicates that only about 1–2% of the herring population stayed in the area during March/April.

The hydroacoustic surveys indicate that approximately 58% and 36% of the sprat population aggregate in May/June in the entire and central Bornholm Basin, respectively. After the end of the spawning season sprat tend to leave the area, resulting in a reduction of the proportions to about 21% and 8%, respectively. The estimated population sizes of the two species in the central and the entire Bornholm Basin at the time of the stomach sampling cruises and based on the acoustic data are given in Table 4.

Comparing the daily consumption rates by the herring population with the standing stock and daily production of cod eggs in the central Bornholm Basin (Table 4) reveals a low predation pressure in April (<7% and <13% per day, respectively). In May/June the consumption increased to 9–22% of the standing stock, which corresponds to 16–59% of the daily egg production. An exception was May 1995, when a very low consumption value was computed. In the summer months, daily consumption rates of cod eggs by herring were more variable: 4–26% of the standing stock and 13–84% of the production, with highest predation rates in July 1991

and 1995 as well as in August 1994, the latter being actually higher than the estimated production value.

For sprat, ingestion rates determined for the spring dates were considerably higher, being in general well above the corresponding standing stock and daily production estimates. The only sampling date without high predation pressure was April/May 1994. In late spring/early summer, the calculated consumption rates were reduced considerably, although still being close to or above the standing stock and production until 1992. In May/June 1993, the consumption declined to 30% and 82% of the standing stock and production rate and in the following years the consumption rates dropped further to below 10% of the egg production. In summer, when sprat switch to cladocerans as most important prey organisms, the daily consumption of cod eggs was, independently of the sampling year, in general low.

Similar estimates for cod larvae in the entire Bornholm Basin (Table 5) indicate that the average daily consumption rate by herring is low in spring and early summer and only marginally higher in summer (<1% and <15% of the abundance and daily production, respectively). Sprat occasionally consumed considerable amounts of cod larvae in spring: on average 44% of the abundance was estimated to be consumed per day. During the main spawning period of cod in summer, however, the predation pressure by sprat appears to be low (3% of the production).

Table 4. Estimated population sizes of herring (H) and sprat (S) the central Bornholm Basin (area enclosed by the 75 m depth contour) and the estimated consumption of cod eggs by these stocks in comparison with the abundance of cod eggs (N) and daily production rates (P).

Month/year	Cod eggs					
	Population (n*10 ⁻⁶)		Consumption (n*10 ⁻⁹)		Abundance (n*10 ⁻⁹)	
	H	S	H	S	N	P
Spring						
Apr. 1988	92	4807	0	398	105	31
Apr. 1991	104	7389	1	79	76	37
Apr. 1992	126	9580	2	34	22	13
Apr. 1993	86	11 691	5	205	102	58
Apr./May 1994	296	6066	2	12	78	54
Apr. 1995	114	5978	0	57	12	7
Early summer						
May/Jun. 1990	819	3196	17	49	59	29
May/Jun. 1991	894	7058	26	187	113	45
May 1992	1087	9164	n.a.	56	28	12
May/Jun. 1993	660	11 108	17	47	98	58
May/Jun. 1994	965	5781	42	25	295	266
May 1995	989	5701	7	6	198	72
Summer						
Jun./Jul. 1988	1600	926	15	0	92	43
Jul./Aug. 1988	1553	894	4	0	87	33
Jul. 1991	1876	1534	74	26	204	88
Aug. 1991	1831	1503	10	0	77	46
Aug. 1994	1963	1193	283	4	948	220
Jul. 1995	2036	1183	285	0	1171	513

Table 5. Average estimated population sizes of herring (H) and sprat (S) in the entire Bornholm Basin (area enclosed by the 60 m depth contour) and the estimated consumption of cod larvae by these stocks in comparison with the abundance of cod larvae (N) and daily production rates (P) by season.

Month/year	Cod larvae					
	Population (n*10 ⁻⁶)		Consumption (n*10 ⁻⁹)		Abundance (n*10 ⁻⁹)	
	H	S	H	S	N	P
Spring 1988–1995	324	12 149	<0.01	0.82	1.86	0.28
Early summer 1990–1995	1723	11 215	0.00	0.06	1.05	0.20
Summer 1988–1995	2461	3058	0.14	0.03	14.30	0.96

Discussion

The estimated consumption rates of cod eggs by the predator populations exceeded egg production rates in all spring and early summer dates 1990–1992. The deviations between predation and production rates were quite considerable in some months, indicating either an overestimation of the consumption or an underestimated production. Different methodological problems were encountered in the present study.

To calculate the average species composition of fish eggs ingested by sprat, only a low fraction of eggs could be identified to species level (0.5–4.4%) and consequently

a large raising factor has been applied to calculate the overall egg composition in the diet. In contrast, herring had considerably higher proportions of identifiable eggs in their stomachs (on average 15%).

Introduction of a new gastric evacuation model, taking into account ambient temperatures (Temming, 1996), reduced the predation rates compared to former estimates (Köster and Möllmann, 1997) by 13–36% for herring and by 36–53% for sprat. However, this did not completely solve the inconsistency between predation and corresponding production rates. Implementing an exponential evacuation model is in agreement with findings of Jobling (1986), who suggests exponential

Table 6. Comparison of herring and sprat population sizes within the 60 m and 75 m depth contours derived from acoustic surveys and those obtained by downscaling MSVPA results according to the horizontal distribution observed in the past.

Month/year	Area	Method	Population size ($n \cdot 10^{-6}$)	
			Herring	Sprat
Aug. 1994	>60 m	Survey	3924	818
		MSVPA	2670	3025
	>75 m	Survey	2427	542
		MSVPA	1963	1193
May 1995	>60 m	Survey	1267	7053
		MSVPA	1888	9132
	>75 m	Survey	759	3746
		MSVPA	989	5701

evacuation for fish feeding on small particles, such as zooplankton. Applying similar evacuation rates and digestion times for cod eggs and other fish eggs may be responsible for an overestimation of consumption rates. Cod eggs are significantly larger than other fish eggs (Müller and Bagge, 1984), which might lead to a slower digestion and could thus bias the species composition in the diet. Furthermore, a similar evacuation rate for fish eggs and other prey organisms is assumed, which in fact might not be valid. However, modelling the evacuation of fish eggs independent of other, in most cases dominating, prey appears less appropriate (Köster and Schnack, 1994).

A further source of uncertainty is the estimation of predator population sizes. As indicated by hydroacoustic surveys conducted in August 1994 and May/June 1995, the sprat population in the Bornholm Basin might be 45% lower than estimated, while population sizes for herring were in considerably better agreement (Table 6). Any overestimate of the predator population results in a corresponding deviation in consumption rates. When sprat consumption is reduced by 45%, the estimates are in the order of magnitude of the daily egg production for spring and early summer 1990–1992, but excessive consumption rates would still be obtained for April 1988 and 1995. The first case can be explained by a spatially restricted stomach sampling in an area of high cod egg concentration. The survey in April 1995 was characterized by a just started spawning season and, as the trawl survey followed the ichthyoplankton survey, the egg production might have increased to a higher level when the stomach sampling was conducted. In conclusion, estimation of the sprat population size appears to be one of the main problems and further effort is required to enhance the reliability of the estimates.

The estimates of the daily egg production have been improved, compared to an earlier study (Köster and Möllmann, 1997), by revised applying egg stage specific mortality rates. However, as the mortality estimates are

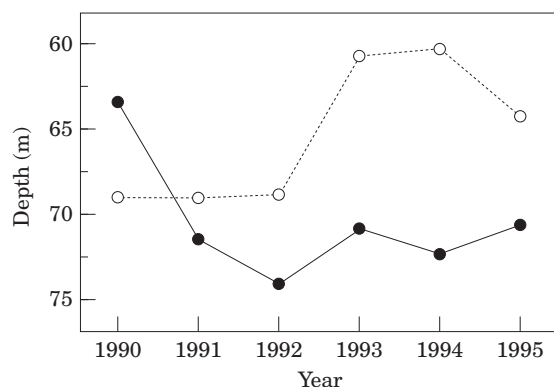


Figure 5. Average catching depth of clupeoids (closed symbols) and average depth of cod egg mass (open symbols) in May/June, 1990–1995.

variable within and between experiments (Anon., 1998), and the number of adequate experiments is limited, the daily production values are tentative only. A positive selection of older egg stages, because of better visibility of the more developed stages as suggested by Wieland and Köster (1996), indicates the necessity of estimating daily consumption rates for individual egg stages separately. These should be compared to the corresponding daily production of each egg stage.

The observed decline in cod egg predation by sprat during recent years is at present difficult to explain. Even when cod eggs were available in the plankton in high quantities, sprat did not prey intensively on them. Despite the differences in the amount of fish eggs in the stomachs, the broad diet composition, average stomach content, and total food intake were similar in both periods.

Comparing the vertical distribution of cod eggs in May/June 1990–1992 and 1993/1994 (Wieland and Jarre-Teichmann, 1997) revealed a significant difference between these periods. Increased salinity in and below the halocline, caused by the major Baltic inflow at the beginning of 1993 (Matthäus and Lass, 1995), resulted in maximum cod egg concentrations at depths of approximately 60 m, whereas egg densities in the years before were highest just below 70 m (Fig. 5). Changes in hydrographic conditions influence not only the vertical distribution of the prey but also that of the predators (e.g. Orłowski, 1989). After a small inflow at the beginning of 1991 (Matthäus and Lass, 1995) there was a clear increase in the average catching depth compared to the preceding year, as a result of enhanced oxygen conditions in the bottom water (Fig. 5). To account for this shift in the vertical distribution of prey and predator, adjusted average availability of cod eggs at the average catching depth was calculated for each May/June date sampled, using the relative vertical distributions and corresponding standing stocks of eggs.

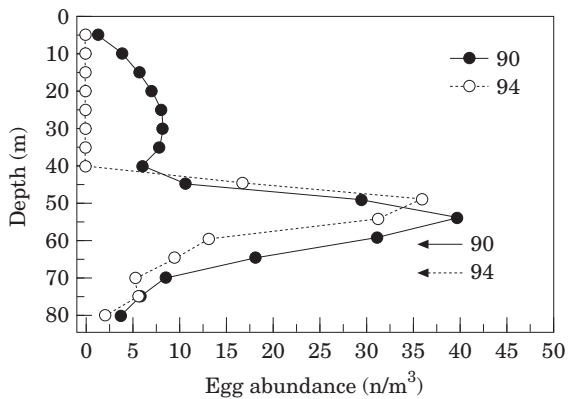


Figure 6. Vertical distribution of all fish eggs and average catching depth of clupeoids (arrows) in May/June 1990 and April/May 1994.

When these were related to daily rations by individual sprat, predation declined by factor 5 from May/June 1990–1992 to 1993/1994 and by almost a factor of 50 to May/June 1995. This clearly demonstrates that the changed vertical distribution of cod eggs alone does not explain the decline in cod egg consumption by sprat.

Variations in the abundance of other fish eggs could also contribute to the reduction in cod egg predation by sprat. Other fish eggs, known to occur in late spring/early summer in higher concentrations than cod eggs (e.g. Grauman, 1975), may act as a trigger for switching from zooplankton to fish eggs as prey. A limited data set on the abundance of fish eggs from different species is available for the study area, enabling a comparison of pre- (April and May 1988) and post-inflow situations (April/May 1994). The comparison revealed a higher abundance of sprat, rockling, and flounder eggs in 1988, indicating negative rather than positive switching. However, the vertical distribution of the different egg species might also be affected by the changed hydrographic conditions (Wieland and Zuzarte, 1991). A comparison of the vertical distribution of eggs of all species during stagnation (May/June 1990) with a post-inflow event (April/May 1994) revealed a significantly broader distribution in 1990 (Fig. 6). Comparing the availability of fish eggs at the average catching depths to corresponding daily rations revealed a consumption three times higher in 1990 than in 1994. Thus feeding on fish eggs is in better accordance with the abundance than described for cod eggs, although the deviation between the periods is still considerable.

Available data on the abundance and biomass of mesozooplankton showed a lower abundance of suitable food in May/June 1993 than in 1991 (Schöler, 1995). Assuming an inverse relationship between predation on eggs and the abundance of zooplankton suitable as food for sprat, as observed regularly during summer months

(Köster and Schnack, 1994), these data do not explain the reduction in predation on fish eggs by sprat in May/June 1993.

Apart from a seasonal trend of increasing cod egg consumption from spring to summer, caused by the return of spring-spawning herring from the spawning to the feeding grounds in the Bornholm Basin (Aro, 1989), the predation pressure by herring indicates no temporal trend. However, in comparison to egg production, fairly low daily rations were estimated for April/May 1988, May/June 1995, as well as August 1988 and 1991. Both estimates in 1988 suffer from a limited sampling area, but the other low estimates are more difficult to explain.

Despite reservations and uncertainties, the results suggest that predation on cod eggs by herring and sprat is at times a substantial source of egg mortality. Especially during the early months of the spawning season, when mesozooplankton is less available, sprat may exert a high predation pressure. The gradual shift in peak spawning time of Central Baltic cod from the end of May in 1989 to the end of July in 1996 (Wieland *et al.*, 1999) may increase cod egg survival rates, even when herring consume a considerable part of the egg production.

Other potential predators show only limited horizontal, vertical, or temporal overlap with cod eggs as prey. If spatially overlapping, they are either not able to detect or to capture the motionless and relatively large eggs (Köster, 1994). Only scyphomedusae of *Cyanea capillata* have been identified as predators on cod eggs of some importance (Margonski and Horbowa, 1996).

The importance of predation for the reproductive success of cod depends on other causes of mortality. Even a high predation on cod eggs will have no effect on recruitment if the eggs are subject to death due to other reasons (for overview, see Schnack and Köster, 1998). Especially the lack of oxygen in and below the halocline is supposed to be a major source of egg mortality (Plikshs *et al.*, 1993). Thus, the observed shift in peak spawning time to the summer months may have a negative effect on egg survival as a consequence of enhanced oxygen utilization at that time of year (MacKenzie *et al.*, 1996) in water masses advected into the spawning area in the preceding winters (Matthäus and Franck, 1992). In contrast to 1988, the hydrographic conditions in 1991, and especially after the 1993 inflow, allowed successful cod egg development in major parts of the bottom water throughout the spawning season (Hinrichsen and Wieland, 1996; MacKenzie *et al.*, in press). Thus, predation probably constituted a considerable source of cod egg mortality in these years, especially by sprat in April and, up to 1993, also in May/June, and by herring in summer 1994/1995. For the year class of 1991, most surviving 0-group cod indeed originated from cohorts which hatched late in the spawning season (ICES, 1993).

Cod larvae were in general not substantially affected by herring and sprat predation, and on many dates no larvae were observed at all. As a consequence, not much significance may be attached to the quantitative estimates, because obviously these prey were often below the detection limit with the given sample sizes. The absence of significant numbers in stomachs may be partly explained by a limited vertical overlap of prey and predator. Cod larvae show a bi-modal distribution with highest concentrations of medium-sized and larger larvae in intermediate and upper water layers (Wieland and Zuzarte, 1991; GrønkJær and Wieland, 1997). Only newly hatched larvae concentrate within or below the halocline, where they are available as prey to herring and sprat. Occasionally, a substantial predation was observed for sprat. A comparison of plankton data and diet composition during such events showed that sprat was in most cases obviously attracted to fish larvae as prey because of extraordinarily high abundance of sprat larvae (Köster and Möllmann, 1997). While foraging on these, they also consumed above average numbers of cod larvae.

Herring did not in general feed on cod larvae in spring and early summer, which may be related to their small size. With the increasing abundance of larger larvae, herring ingested cod larvae occasionally during the summer months, especially at dawn and dusk, while migrating into and down from the surface layers (Köster, 1994). The daily consumption was generally well below the determined daily production.

The number of fish larvae in stomachs may have been underestimated, because of continuing digestion during catching and handling of the fish until preservation. The unavoidable time-lag was long compared to digestion times of less than 60 min reported for small larvae as prey of planktivorous fish (Hunter and Kimbrell, 1980). However, this possible bias may be of minor importance for two reasons: (a) digestion time of larvae appears to be prolonged significantly if less quickly digestible prey organisms such as copepods are also ingested (Christensen, 1983; Balfoort, 1984); (b) stomach evacuation seems to be retarded as a reaction to stress during catching and handling (Lockwood, 1980; Köster *et al.*, 1990). These hypotheses should be tested by introducing new immunochemical techniques to assay predation on larvae (Brodeur and Bailey, 1996).

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