



## Contribution to the Symposium: ‘Gadoid Fisheries: The Ecology of Management and Rebuilding’ Original Article

### Recovery in eastern Baltic cod: is increased recruitment caused by decreased predation on early life stages?

Viola Neumann<sup>1\*</sup>, Friedrich W. Köster<sup>1</sup>, Matthias Schaber<sup>2</sup>, and Margit Eero<sup>1</sup>

<sup>1</sup>Technical University of Denmark, National Institute of Aquatic Resources, Charlottenlund Castle, Jægersborg Allé 1, DK-2920 Charlottenlund, Denmark

<sup>2</sup>Thünen-Institute of Sea Fisheries, Palmaille 9, 22767 Hamburg, Germany

\*Corresponding author: tel: +45 35 88 33 00; fax: +45 35 88 33 33; e-mail: [vneu@aqu.dtu.dk](mailto:vneu@aqu.dtu.dk)

Neumann, V., Köster, F. W., Schaber, M., and Eero, M. Recovery in eastern Baltic cod: is increased recruitment caused by decreased predation on early life stages? – ICES Journal of Marine Science, 71: 1382–1392.

Received 6 January 2014; revised 20 May 2014; accepted 30 May 2014; advance access publication 30 June 2014.

Cod (*Gadus morhua*) recruitment in the eastern Baltic Sea is influenced by predation on early life stages by sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), which is considered as one of the mechanisms preventing cod recovery in the 1990s. In the light of improved cod recruitment in the second half of the 2000s, new analyses of stomach content of sprat and herring were conducted, to elucidate the contribution of changes in predation pressure on cod recruitment. Comparison of stomach contents of sprat and herring in 2004–2008 with data from the 1990s showed a similar diet composition in the two periods; however, changes were found in the ichthyoplankton abundance and composition in the diet, indicating reduced predation pressure on cod eggs in the most recent period. The abundance of cod eggs in the field, availability of other prey, and horizontal and vertical overlap between predator and prey were investigated as potential factors influencing cod egg predation.

**Keywords:** Baltic Sea, clupeids, cod eggs, diet composition, predator–prey overlap.

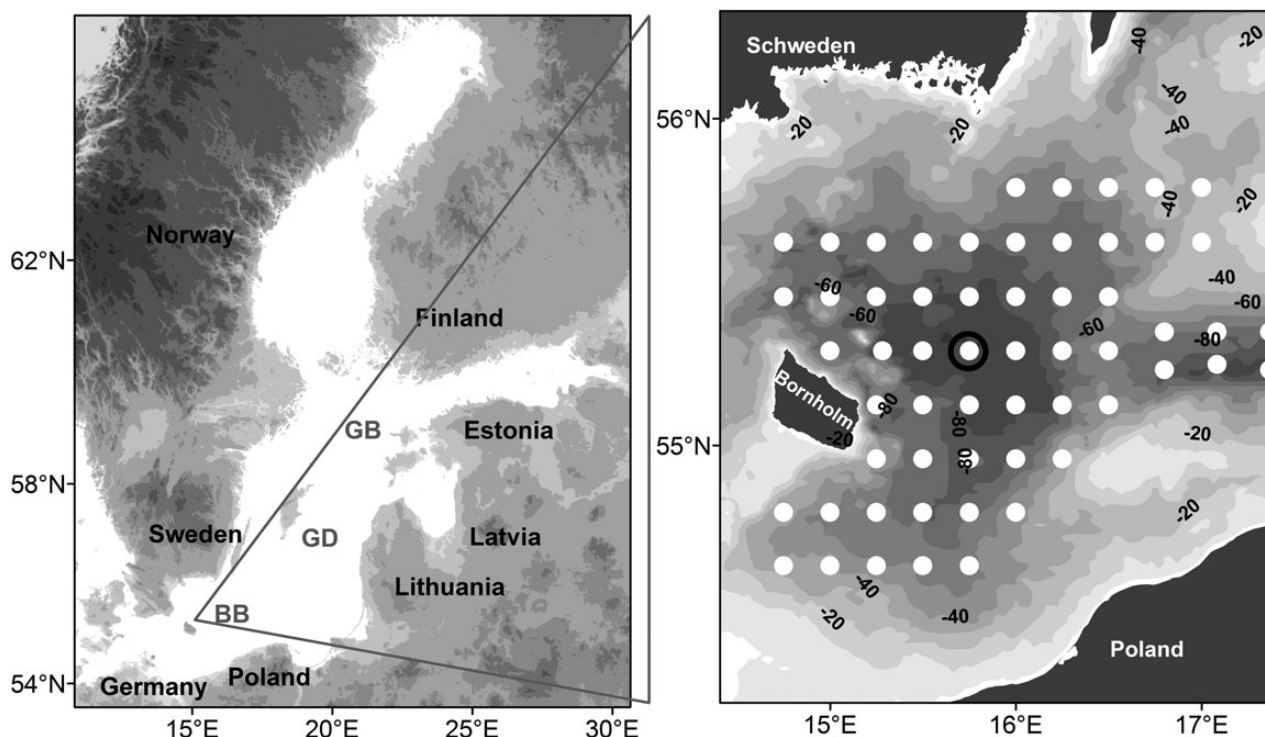
#### Introduction

Knowledge of species interactions as well as understanding the underlying processes is essential for developing an ecosystem-based approach to fisheries management (Pikitch *et al.*, 2004; Marasco *et al.*, 2007; Link *et al.*, 2009). Species interactions are generally best documented for predator species preying on forage fish (e.g. Kitchell *et al.*, 1994; Orlova *et al.*, 2013). However, predation by forage fish may also exert substantial mortality of early life stages of predator species with large impacts on population dynamics (Myers and Cadigan, 1993; Steele, 1997). Predation at prerecruit stages has been shown to be responsible for much of the variability in observed year-class strength on species like cod and haddock (Sissenwine, 1984; Bailey and Houde, 1989), and has been considered as one of the factors preventing the recovery of some gadoid stocks (e.g. Swain and Mohn, 2012).

The Baltic Sea is an example of an ecosystem that is characterized by strong predator–prey interactions and feedback loops. The central Baltic Sea fish community is dominated by only three species, i.e. the piscivore cod (*Gadus morhua* L.) and the planktivores clupeids sprat

(*Sprattus sprattus* L.) and herring (*Clupea harengus* L.). Adult cod preys on sprat and herring, which, in return, feed on early life stages of cod (Köster and Schnack, 1994; Köster and Möllmann, 1997). Predation on cod eggs by clupeids during a period of high sprat abundance in the 1990s is considered to have contributed to cod recruitment failure and prevented cod recovery in the Baltic Sea (Köster and Möllmann, 2000; Casini *et al.*, 2009). Several earlier studies have described diet composition, feeding preferences, and behaviour of Baltic clupeids (e.g. Arrhenius and Hansson, 1993; Köster and Schnack, 1994; Casini *et al.*, 2004; Möllmann *et al.*, 2004). However, only a few studies have explicitly addressed cod egg predation and the latest estimates originate from the period of a very low cod abundance in the 1990s (Köster *et al.*, 2005) and 2002–2003 (Voss *et al.*, 2011).

In recent years, cod recruitment in the eastern Baltic Sea increased substantially, contributing to a rapid recovery of the stock (Eero *et al.*, 2012a). To provide insights to the mechanisms behind the improved recruitment and the potential contribution of changes in predation pressure, the first aim of this paper is to



**Figure 1.** Baltic Sea map. Inlet indicates regular Bongo station grid within the Bornholm Basin. White dots, Bongo station; black circle, multinet station.

update the information on diet composition of clupeids for the years 2004–2008. This new information is then compared with the historical data from the 1990s, when substantial predation on cod eggs has been documented (Köster and Möllmann, 2000). Earlier studies suggested several factors influencing variability in cod egg predation, such as egg abundance, availability of alternative prey, and hydrographic conditions influencing predator–prey overlap (e.g. Köster and Möllmann, 1997; Uzars and Plikshs, 2000; Neuenfeldt and Beyer, 2003; Köster *et al.*, 2005). However, these hypotheses have not been validated, as data for such complex analyses are usually not available. In this paper, we use a unique dataset collected in 2004–2008 that allows investigating the potential effects of the abovementioned factors on cod egg predation, as a second aim of this paper. Our analyses provide new knowledge on clupeid foraging and predation on cod eggs in the Baltic Sea, contributing to identifying processes and mechanisms behind the biological interactions between cod and forage fish.

## Material and methods

Data on clupeid stomach content, horizontal and vertical distribution of clupeids, and cod egg abundance were collected during ten cruises conducted in 2004–2008 by the German RV “Alkor” in the Bornholm Basin, Baltic Sea (Figure 1; Table 1). This is the main reproduction area for the eastern Baltic cod since the 1990s (Köster *et al.*, 2009). Two cruises were conducted each year, in May/June and in July/August, from here on called spring and summer, respectively. Information on clupeid diet in earlier years (1990–1999) was available from EU projects CORE (1998) and STORE (2003), where a similar sampling procedure was applied.

**Table 1.** Sampling dates, number of stations covered, and number of stomachs analysed per cruise.

		Number of stomachs	
Cruise date	Number of stations	Herring	Sprat
Spring			
2–4 June 2004	21	193	274
29–31 May 2005	12	418	280
8–10 June 2006	9	323	258
28 May–2 June 2007	13	387	211
7–9 June 2008	16	262	265
Summer			
19–21 July 2004	19	299	51
22–25 July 2005	21	168	314
27–30 July 2006	13	542	350
2–5 August 2007	19	303	167
23–27 August 2008	13	317	65

## Sampling at sea

### Stomach samples

The samples of sprat and herring for stomach analyses were collected from pelagic fishery hauls, conducted with either an “Engel Kombitrawl” (KT) or an “Engel Young Fish Trawl” (YFT) with 10 or 11 mm mesh size in the codend (Table 1). Fishing was either conducted on a regular station grid employed for the collection of ichthyoplankton data (Figure 1) or along the longitudinal transects across the Bornholm Basin (Supplementary data SA). Fishing operations were conducted during daytime and targeted on fish

aggregations identified by a ship-mounted scientific Simrad EK60 echosounder. Trawling duration was on average 30 min, at a speed of ca. 3 knots. Stomach samples were taken by 2 and 1 cm length-classes for herring and sprat, respectively. Immediately after measuring and weighing the fish, the stomachs were dissected and preserved in borax-buffered 4% formaldehyde-seawater solution.

### Hydroacoustic measurements

Hydroacoustic data were recorded continuously during survey operations with a hull-mounted Simrad EK60 scientific echosounder operated at 38 kHz that had been calibrated before each survey using standard procedures (Foote *et al.*, 1986). Pulse frequency and duration were set to  $1 \text{ s}^{-1}/1.024 \text{ ms}$  in 2004 and  $0.5 \text{ s}^{-1}/0.256 \text{ ms}$  in 2006–2008. Post-processing and integration of hydroacoustic data were performed using Echoview 5 software (Myriax, 2013).

To obtain comparable data, only the datasets recorded at a ship speed of  $\sim 10$  knots were analysed. Post-processing of the data included correction for bottom echo and removal of noise, where necessary. To identify and quantify echoes originating from clupeid schools, an Echoview school-detection algorithm was applied. The settings according to Nilsson *et al.* (2003) were used: minimum total school length 2 m, minimum total school height 2 m, minimum candidate height 1.5 m, maximum vertical linking distance 3 m, and maximum horizontal linking distance 3 m. Distances were based on GPS data. Clupeid schools were integrated, and integration results including the mean position, depth, and NASC (nautical area scattering coefficient) were exported in 1 m depth bins with a horizontal dimension of 1 nautical mile. The NASC ( $\text{m}^2 \text{ nautical mile}^{-2}$ ) values then were utilized as a proxy for clupeid abundance.

To take into account diurnal vertical migration and feeding patterns of clupeids (e.g. Köster and Schnack, 1994; Nilsson *et al.*, 2003), only daytime (15 min after sunrise until 15 min before sunset) data were included. Further, only transect parts with water depths of or above 50 m were included in the analysis, as cod eggs are distributed within or below the permanent halocline in the Bornholm Basin ( $\sim 50$ – $80$  m depth; Müller and Pommeranz, 1984).

### Ichthyoplankton samples

Ichthyoplankton samples were collected over a grid of stations ( $\sim 36$ – $50$  stations per cruise) covering the survey area with  $\sim 9$  nautical miles distance between the stations (Figure 1). Double-oblique hauls were conducted using a Bongo net with mesh size ranging from 335 to 500  $\mu\text{m}$  from the surface to  $\sim 3$  m above the seabed. At preselected stations in the central Bornholm Basin (ca. 90 m water depths) that showing high egg abundance, the vertical distribution of fish eggs was investigated by deploying a Hydrobios multi-opening and -closing net consisting of 9 nets (50  $\mu\text{m}$  mesh size) at 5 m depths intervals. Towing speed was set to 3 knots. Three vertical profiles were performed per cruise, except in spring 2006 (two profiles). Both Bongo and multinet samples were preserved in 4% borax-buffered formaldehyde seawater solution. For the analyses of horizontal cod egg abundance, at least 100 eggs per sample were identified to species level and raised to the total sample. The total cod egg abundance ( $n \text{ m}^{-2}$ ) was calculated using the volume of filtered water and water depth at a given sampling station. Vertically resolved samples from the multinet were raised to total densities ( $n \text{ m}^{-3}$ ) using the volume of filtered water per depth stratum.

## Laboratory analyses and data processing

### Analyses of diet composition

The diet composition was analysed for five stomachs per length class, both for sprat and for herring. Altogether 3212 herring and 2231 sprat stomachs were analysed. The wet weight (g) of a full stomach was measured after removing adjacent connective and fatty tissue and drying the stomach with a paper tissue. Subsequently, the stomach was dissected and the content transferred into sorting solution (Steedman, 1976). The wet weight of the stomach content was measured by weighing the empty stomach. Fish eggs and larvae (ichthyoplankton) from the stomach content were counted and identified to the highest taxonomic level using identification keys published by Kazanova (1953). Only a few fish larvae were found in stomachs, thus the ichthyoplankton prey group primarily refers to fish eggs. Other prey items were classified into major taxonomic groups, including copepoda, cladocera, mysidacea, cumacea, and polychaeta. The remaining rare prey taxa were grouped into a category “others” consisting mainly of small crustaceans, mussel larvae, and fish scales.

The estimated volumetric percentages of all prey groups combined with the total weight of the stomach content were used to derive estimates of the weight of individual prey groups in stomachs. The prey groups containing  $<5\%$  of the volume of a particular stomach were disregarded. This implies that, for example, fish eggs in some cases do not appear as a prey group in the results of volumetric analyses. However, the numbers of ingested eggs were included always. Unidentified items were allocated to prey groups according to the volumetric proportion of the prey groups in the identified part of the stomach content. For stomachs containing exclusively unidentifiable prey items, the mean diet composition of a given length class and haul was applied. The average stomach content per survey was calculated by raising the length class-specific diet composition data with the length frequency in the population derived from trawl catches.

Earlier studies have suggested that sprat and herring prefer cladocerans and mysids to cod eggs, when both prey types are available (Hinrichs, 1985; Köster and Möllmann, 2000). These associations were tested using the new updated time-series of diet composition data, applying the Fisher's exact test.

### Calculation of predator–prey overlap

Coefficients ( $C$ ) of horizontal and vertical overlap between clupeids and cod eggs were calculated using the index described by Horn (1966):

$$C = \frac{2 \sum_{i=1}^n (A_i \times B_i)}{\sum_{i=1}^n A_i^2 + \sum_{i=1}^n B_i^2},$$

where  $n$  is the number of covered strata (depth for the vertical overlap and stations for the horizontal overlap).  $A$  and  $B$  are the relative abundance of predator (clupeids) and prey (cod eggs) in the respective strata. The coefficients of 0 and 1 correspond to no overlap and complete overlap, respectively.

To obtain the horizontal overlap coefficient (HOC), the distribution of clupeids from the hydroacoustic surveys was matched with corresponding Bongo stations. Hydroacoustic measurements (NASC, see above) from 1 nautical mile bins within a radius of 4 nautical miles around a given Bongo station were averaged and used as a proxy for clupeid abundance. The relative NASC and cod egg abundance per station were used to calculate HOC. To



determine the coefficient of vertical overlap (VOC), the relative abundances of predator and prey in 5 m depth strata were used. The vertical distribution of cod eggs was only available from one station per cruise that was assumed to represent the vertical distribution of cod eggs throughout the Bornholm Basin. The vertical distribution of clupeids from hydroacoustics was averaged per cruise. The coefficient of total overlap (TOC) was obtained as a product of HOC and VOC (Schaber *et al.*, 2011).

Out of the two clupeid species, sprat is relatively more abundant in Bornholm Basin in spring and herring in summer, which is related to spawning and feeding migrations of the species (Aro, 1989; Köster and Möllmann, 1997). Therefore, it is assumed that the VOC and HOC values derived from hydroacoustic measurements (for the two clupeid species combined) represent the overlap between cod eggs and the main predator in a given season, i.e. sprat in spring and herring in summer.

## Results

### Stomach contents of clupeids

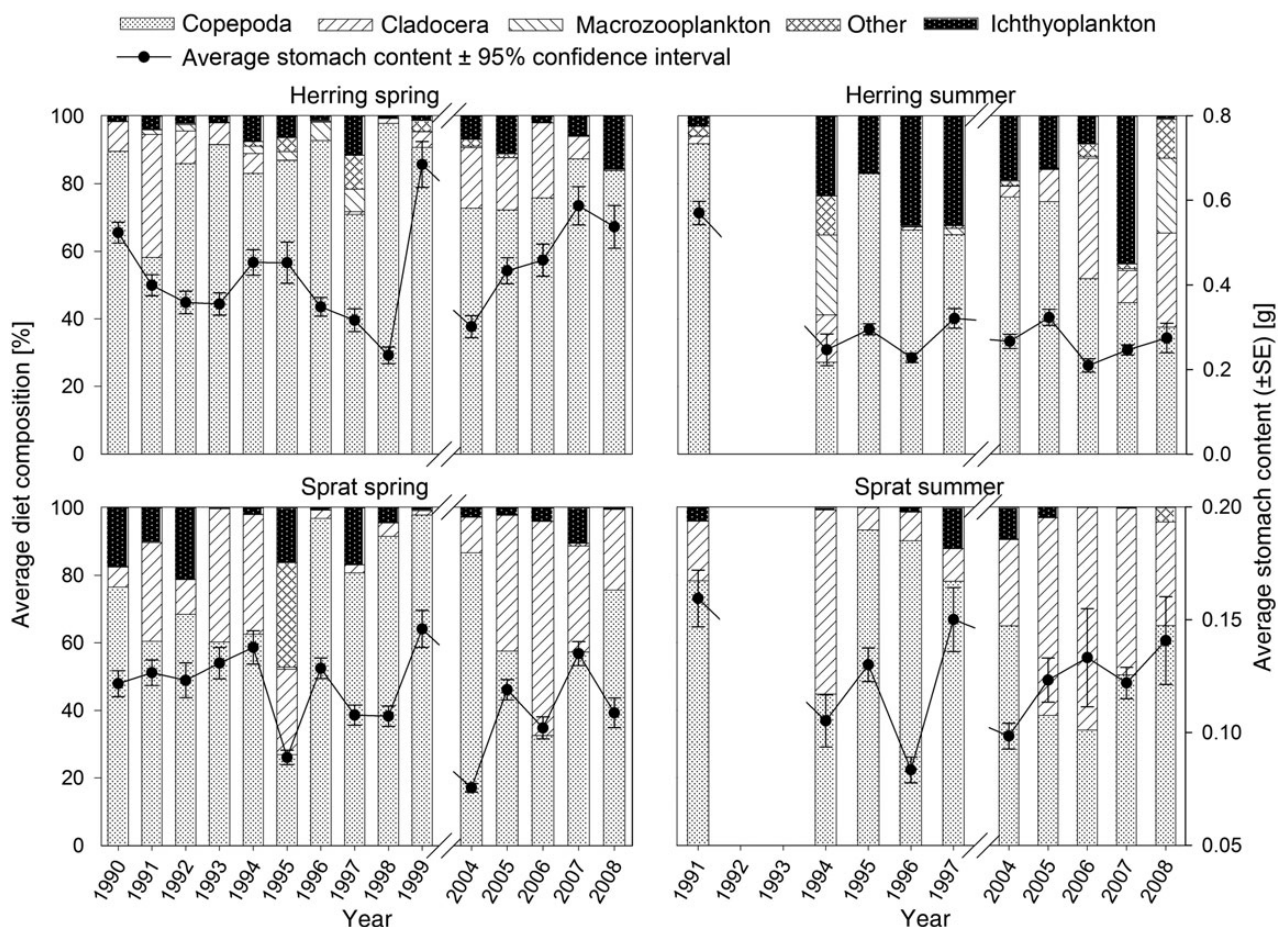
The stomach content (in g wet weight) of herring showed a higher interannual variability in spring than in summer (Figure 2). The range of interannual variability in the 2000s was similar to that in the 1990s, except for outstanding high values in spring 1999 and summer 1991. For sprat, the stomach content varied in a similar range in spring as in summer. In spring, the stomach content was

in several of the most recent years below the average of the 1990s, while there was no clear time-trend in summer (Figure 2).

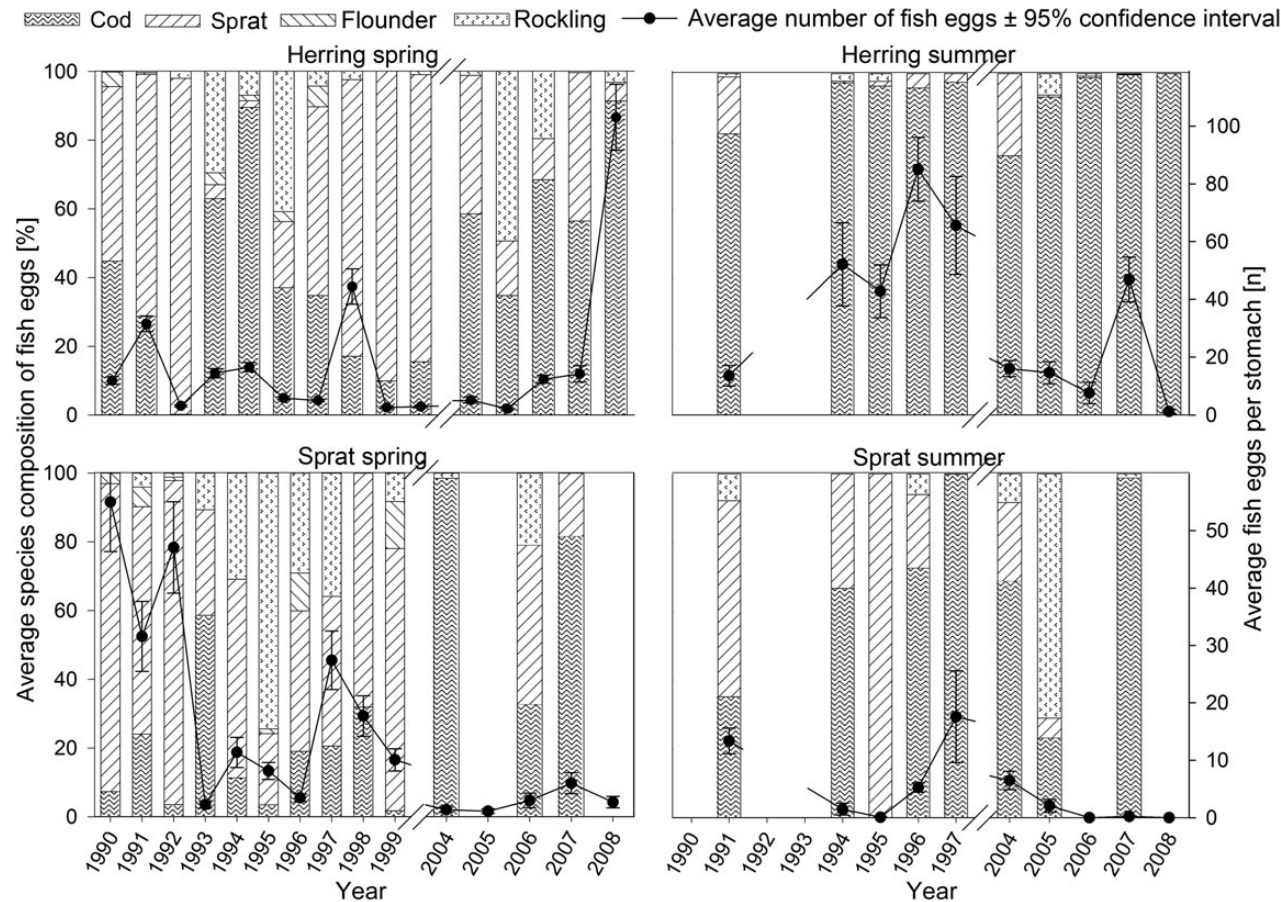
Seven major taxonomic groups were found in both herring and sprat stomachs. Copepods, cladocerans, and ichthyoplankton were regularly present in the diet of both species, both in the 1990s and in the 2000s. Macrozooplankton (mysidacea, amphipoda, cumacea, and polychaeta) contributed in general <7% of the herring diet, with outstanding values encountered only in summers of 1994 (24%) and 2008 (22%; Figure 2). In 2008, macrozooplankton consisted mainly of mysidacea (>60%). Macrozooplankton was hardly present in the diet of sprat. Other prey (e.g. small crustacean, bivalvia larvae) were in most years only in both species only present in minor fractions. The proportion of ichthyoplankton in the diet was variable, with the highest proportions found in herring stomachs in summer (max. 44% in 2007). In sprat, the highest proportions of ichthyoplankton in the diet were recorded in spring 1990–1992, 1995, and 1997 (max. 17%). In the 2000s, the proportion of ichthyoplankton in the diet was below 5% in most years (except for 10% in spring 2007).

### Ichthyoplankton in clupeid diet

The average number of fish eggs ( $n \pm 95\%$  CLM) encountered in herring diet in summer was lower in the 2000s compared with the 1990s (Figure 3), except for 2007, when the average number of eggs ( $46.8 \pm 7.8$ ) was not significantly different from that in



**Figure 2.** Relative mean diet composition (bars) of herring and sprat in spring (May/June) and summer (July/August). Average wet weight of individual stomach content (with 95% confidence limits) is displayed as black line. Data for 1990–1999 derived from STORE (2003).



**Figure 3.** Average species composition of fish eggs (bars) in the diet of herring and sprat in spring (May/June) and summer (July/August). The line shows the average number of fish eggs per stomach with 95% confidence limits. In spring 2005 and 2008, fish eggs in sprat diet were unidentified. Data for 1990–1999 derived from [STORE \(2003\)](#).

1994–1995 and 1997. Also, the average number of eggs encountered in 1991 ( $13.5 \pm 3.5$ ) was similar to that in 2004–2006. In all years, more than 70% of the fish eggs in herring diet were identified as cod, in later years close to a 100%. In spring, the species composition of ichthyoplankton in the herring diet was more variable, with the proportion of cod varying between <10% (in 1998) and close to 90% (in 1994, 2008). In spring, outstanding large numbers of fish eggs in herring stomachs were found in 2008 ( $103.0 \pm 22.4$ ), most of them being cod. High values of fish eggs were encountered also in spring 1991 ( $31.5 \pm 5.5$ ) and 1998 ( $44.4 \pm 12.0$ ), when most of the fish eggs in the diet were sprat. In all other years, the amount of eggs in stomachs was significantly lower. The proportion of stomachs that contained cod eggs was significantly higher for herring that had not eaten mysids ( $p < 0.001$ ). In the 2000s, the highest proportion of mysids in stomachs was found in summer 2008, corresponding to the sampling date with the lowest amount of fish eggs in herring stomachs in the entire time-series (Table 2).

The amount of fish eggs in sprat stomachs in spring fluctuated widely over time (Figure 3). In 1990–1992, significantly larger numbers were encountered than in any of the later years (max.  $54.8 \pm 8.6$  in 1990), with lowest values in 1993, 1995–1996, and 2004–2008 (max.  $5.8 \pm 1.8$  in 2007). In contrast to the 1990s, when most of the fish eggs in stomachs were sprat or rockling, the proportion of cod has increased in later years to above 80% (in

**Table 2.** Abundance of cod eggs in the prey field and in the diet of sprat; weight proportion of alternative prey (cladocerans) in sprat diet; and VOC, HOC, and TOC overlap between clupeids (mainly sprat) and cod eggs, in spring 2004–2008.

	Cod egg abundance				Alternative prey (cladocerans)	Mean (n)
Year	( $n\ m^{-2}$ )	VOC	HOC	TOC	in diet (%)	cod eggs/stomach
2004	12	0.75	0.18	0.18	10.5	1.2
2005	10	NA	NA	NA	40.3	0.0
2006	32	0.86	0.27	0.24	63.4	0.9
2007	48	0.59	0.37	0.22	31.5	4.8
2008	52	0.01	0.41	0.01	23.9	0.0

0, no overlap; 1, total overlap. NA, no data available.

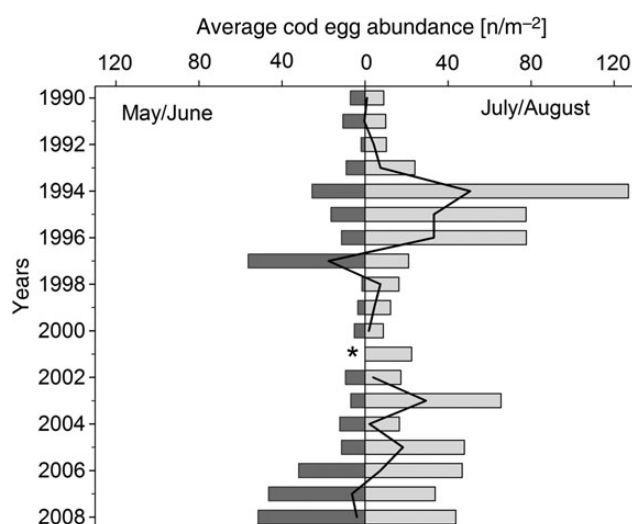
2004 and 2007). In summer, the numbers of fish eggs in sprat stomachs were lower than in spring with maxima in 1991 ( $13.3 \pm 2.2$ ) and 1997 ( $17.6 \pm 8.0$ ); significantly lower values in 2005 ( $2.0 \pm 1.1$ ) and 2007 ( $0.2 \pm 0.1$ ) and eggs were totally absent in the diet in 2006 and 2008 (Figure 3). The proportion of stomachs that contained cod eggs was significantly higher when sprat that had not eaten cladocerans ( $p < 0.001$ ). In the 2000s, the highest proportions of cladocerans in stomachs were found in spring 2005–2006, affiliated with small numbers of cod eggs in the diet (Table 3).



**Table 3.** Abundance of cod eggs in the prey field and in the diet of herring; weight proportion of alternative prey (macrozooplankton) in herring diet; and VOC, HOC, and TOC overlap between clupeids (mainly herring) and cod eggs, in summer 2004–2008.

Year	Cod egg abundance ( $n\ m^{-2}$ )	VOC	HOC	TOC	Alternative prey (macrozooplankton) in diet (%)	Mean ( $n$ ) cod eggs/stomach
2004	17	–	–	–	0.1	12.1
2005	48	–	0.35	–	0.2	13.6
2006	47	0.15	0.45	0.07	0.6	7.5
2007	35	0.24	0.50	0.12	0.5	46.7
2008	44	0.18	0.49	0.09	22.1	1.2

0, no overlap; 1, total overlap. –, no data available.

**Figure 4.** Average cod egg abundance ( $n\ m^{-2}$ ) in the Bornholm Basin in spring (left) and summer (right) from 1990 to 2008. Black line displays temporal trends in main spawning time of cod ( $n\ m^{-2}$ ) as calculated from average cod egg abundance in spring and summer. \*No data available.

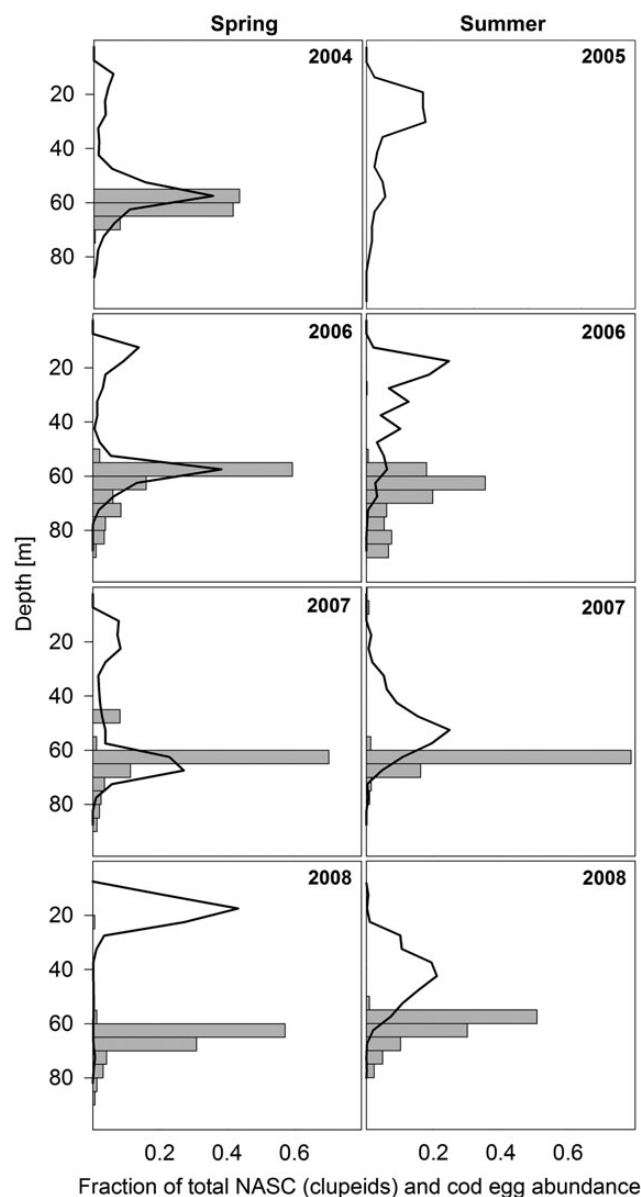
The number of fish larvae which could be identified to species level by both predators was low. In only 67 from a total of 3212 herring stomachs, 2 cod, 88 sprat, 3 flounder, and 201 unidentified larvae were found. Only one larvae (cod) was found in all analysed sprat stomachs.

### Abundance of cod eggs in the field

The abundance of cod eggs in the field (Figure 4) has varied substantially during the last two decades between years and seasons. At the beginning of the time-series in the early 1990s, the abundance of cod eggs was below  $12\ eggs\ m^{-2}$  both in spring and in summer. In the mid-1990s, the egg abundance increased to  $>120\ eggs\ m^{-2}$  in summer, during the main spawning season of cod in these years. This was followed by a period of low values again in the late 1990s and early 2000s ( $<22\ n\ m^{-2}$ ). Since 2005, the cod egg abundance has increased to around  $50\ eggs\ m^{-2}$ , both in spring and in summer, indicating an extension of the main spawning season, compared with the mid-1990s and early 2000s.

### Spatial overlap between clupeids and cod eggs

The largest proportion of cod eggs was distributed within and below the halocline in depth layers between 50 and 70 m (Figure 5). The vertical distribution of predators coincided to a large extent with that of cod eggs in spring 2004–2007 (VOC

**Figure 5.** Relative vertical distribution of cod eggs (bars) and clupeids (lines) in the Bornholm Basin in spring (May/June) and summer (July/August) in 2004–2008. No data available for spring 2005 and summer 2004 and no vertical cod egg distribution data available for summer 2005.

between 0.59 and 0.86; Table 2), although bimodal vertical distribution of clupeids was apparent (Figure 5). An exceptional situation was encountered in spring 2008, when the predators were mainly

distributed in shallow water layers (98% < 50 m), resulting in almost no vertical overlap between predator and prey (Figure 5; Table 2). In summer, the vertical overlap between clupeids and cod eggs was lower compared with spring (except in 2008), with overlap coefficients ranging between 0.15 and 0.24 (Table 3).

Horizontally, the highest abundances of cod eggs were found in the central part of the Bornholm Basin, at stations with water depths above 60 m (Figure 6; see Figure 1 for depth contours). Clupeid predators were mainly concentrated in peripheral regions of the Bornholm Basin in spring 2004–2007. In summer 2007 and spring 2008, high densities of clupeids were recorded in more central parts of the basin (Figure 6). Although the overlap was occasionally high on some stations (e.g. spring 2008), high predator abundances were also present in areas with low egg densities, resulting in overall moderate to low overlap in most years. The coefficient of horizontal overlap between predators and cod eggs in summer was 35–50% in 2004–2008 and lower in spring, i.e. 18–41% (Tables 2 and 3). The total overlap (TOC) between clupeids and cod eggs ranged from 0.01 to 0.24, being highest in spring 2004–2007 (0.18–0.24).

## Discussion

### Clupeid diet and predation on cod eggs

Our investigation revealed changes in the amount and composition of food in the stomachs of sprat and herring in the central Baltic Sea in 2004–2008 compared with earlier studies conducted in the 1990s. Taxonomically, the overall prey composition was similar in both periods. Also, the ichthyoplankton ingested by both sprat and herring in 2000s consisted mostly of eggs, with only a few fish larvae found in the stomachs, which is consistent with observations from earlier studies (e.g. Köster and Schnack, 1994; Köster and Möllmann, 1997). However, the composition and amount of fish eggs in clupeid diets was different compared with the 1990s, with larger proportions but overall reduced quantities of cod eggs. The larger proportion of cod eggs in the ichthyoplankton diet of clupeids recorded during the 2000s corresponds to increased cod egg abundance in the field. In the 1990s, the main species of fish eggs ingested was sprat, which can be related to a high sprat biomass in this period. Opposite, the low amount of sprat eggs in stomachs in recent years is probably related to a strong decline in sprat stock in the Bornholm Basin from the second half of the 1990s to the present (Eero et al., 2012b).

Clupeid predation on cod eggs, determined as daily individual consumption rates, is linearly related to cod egg abundance, when the vertical predator–prey overlap is considered (Köster and Möllmann, 2000; Köster et al., 2005). In our study, recent high cod egg abundances in the prey field were rarely reflected in the diet of herring. The availability of alternative prey might affect predation on fish eggs and larvae (Pepin and Shears, 1995; Segers et al., 2007). For example, larger individuals of North Sea herring forage on crustaceans, despite fish eggs being available, a process that was related to prey visibility (Daan et al., 1985; Segers et al., 2007). Visibility and size of prey have been identified as important factors determining prey selection by herring in the Baltic Sea, with largest and/or more visible prey types being preferred (Sandstroem, 1980; Flinkman et al., 1992; Wieland and Köster, 1996; Bernreuther et al., 2008). Bernreuther et al. (2013) confirmed that Baltic herring actively select certain copepod species. To determine whether the high amounts of cod eggs found in herring diet in summer 2007 and spring 2008 relate to a low availability of more

visibility alternative prey would require further investigations of the prey field.

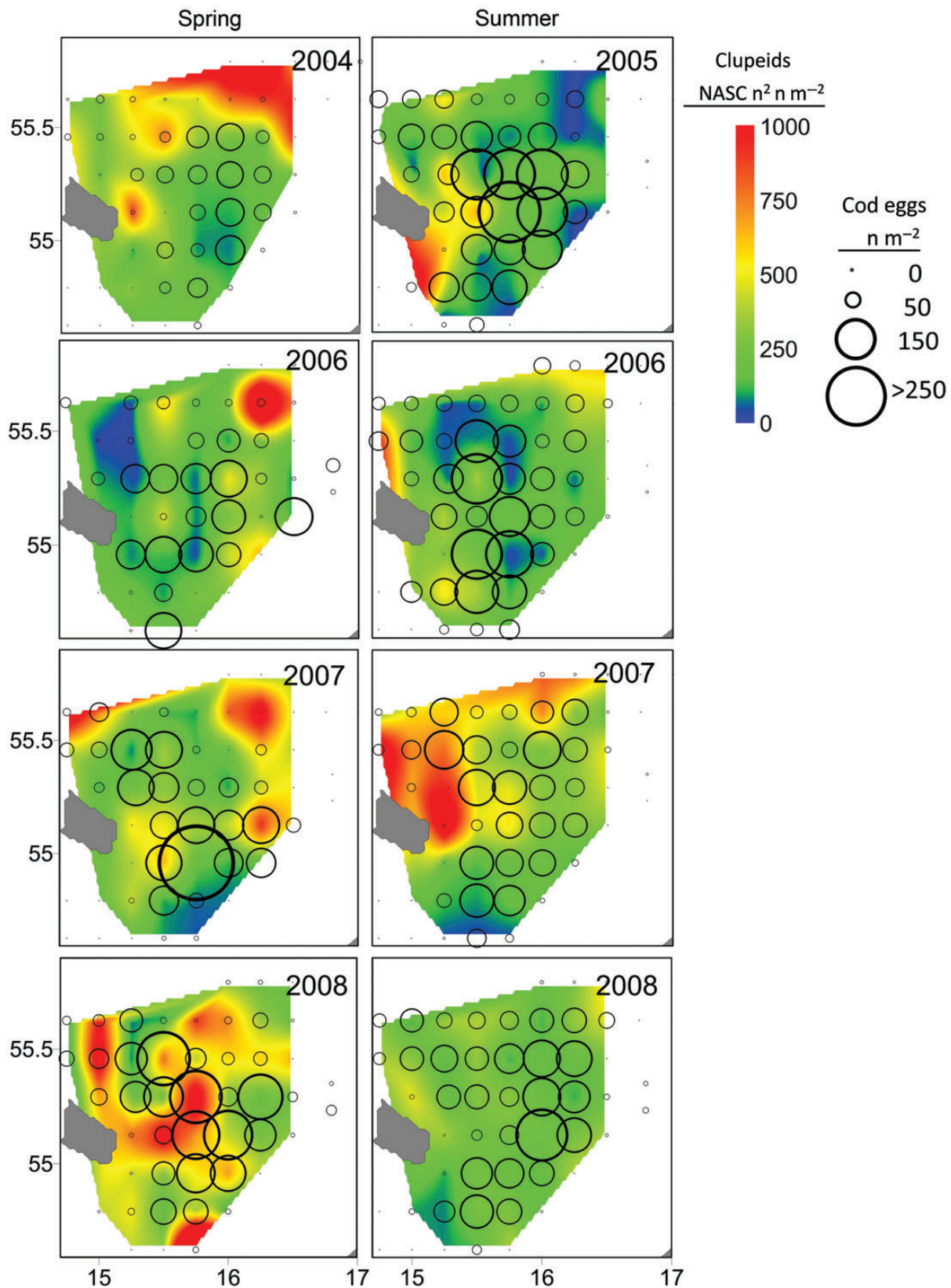
Baltic herring appear to favour macro-zooplankton (mainly mysids) over meso-zooplankton, if both are available (e.g. Aneer, 1980; Köster and Möllmann, 2000; Casini et al., 2004). The nocturnal and vertically migrating mysids are larger and more visible than eggs. However, they are more abundant in coastal areas and avoid deeper, oxygen-poor areas of the central Baltic Sea (Salemaa et al., 1990). Mysids may occasionally migrate into the basin (Salemaa et al., 1990), but they do not constitute a regular prey item for herring in the deeper parts of the Bornholm Basin. This results in large variations in the proportion of mysids in herring diet and could explain the low predation on cod eggs in periods when mysids are available, as in summer 2008.

Sprat predation on cod eggs was low throughout the 2000s, regardless of the more than threefold increase in egg abundance from 2004 to 2008. Similar to herring, prey selectivity has also been observed for sprat (e.g. Bernreuther et al., 2013). Cladocerans are abundant during the warm months of the year (Möllmann et al., 2002) and are a main prey type for clupeids (Bernreuther et al., 2013). Köster and Möllmann (2000) suggested an inverse relation of cladocerans and cod eggs in the diet, indicating that the higher the availability of cladocerans in the prey field, the lower the number of cod eggs ingested by sprat. This was confirmed in our study, as significantly lower amounts of cod eggs were eaten by individuals who had preyed on cladocerans. In terms of interannual variability, low amounts of cod eggs were eaten by sprat in years when the highest proportions of cladocerans were found in stomachs (e.g. in 2005, 2006). Cladocerans occur more regularly in sprat diet compared with mysids in herring; therefore, the interannual contrast in the availability of alternative prey is usually less for sprat compared with herring (Tables 2 and 3).

### Predator–prey overlap

Feeding interactions are influenced by overlap between predator and prey in space and time (Garrison et al., 2000; Hallfredsson and Pedersen, 2007). For example, a strong overlap between herring and capelin larvae in the Barents Sea has been found to be a key factor affecting early life stage mortality of capelin (Hallfredsson and Pedersen, 2009). In the Baltic Sea, sprat spawning overlaps temporally and spatially with cod spawning in spring (Bagge et al., 1994; Parmanne et al., 1994). In early summer, sprat disperses into more shallow coastal waters (Aro, 1989). Herring spawn in coastal areas during spring and migrate to its offshore feeding grounds, including the Bornholm Basin, around June/July (Popiel, 1984). Therefore, on a large scale, sprat mostly overlap with cod eggs in spring and herring in summer (Köster and Möllmann, 2000). In addition to these large-scale spawning and feeding migrations, smaller-scale changes in the overlap between clupeids and cod eggs are important to determine predation intensity on cod eggs.

In the Baltic Sea, ambient hydrography is a key factor affecting vertical distribution of both clupeids and cod eggs (Köster et al., 2005). Sprat generally prefer relatively warm and well-oxygenized water and avoid temperatures below 5°C and oxygen concentrations below 1 ml l<sup>-1</sup> (Stepputtis et al., 2011). Herring favour colder, high saline deeper layers during daytime, given that oxygen concentrations are sufficient (Orlowski, 1999). The lower vertical overlap between clupeids and cod eggs in summer compared with spring (except in 2008) is presumably related to a change in vertical migration behaviour of those sprat remaining in the basin during summer.



**Figure 6.** Horizontal distribution and abundance of cod eggs ( $n m^2$ , black circles) and clupeids (mean NASC  $m^2$  nautical mile $^{-2}$  per station, colour plot) in the Bornholm Basin in spring (May/June) and summer (July/August) 2004–2008. No data available for spring 2005 and summer 2004.



Concurrently with the warming of the intermediate water layer and high abundance of cladocerans in shallower water layers (between 0 and 10 m and 41 and 50 m, [Bernreuther et al., 2013](#)), sprat do not necessarily perform a daily migration into or below the halocline. In spring, the highest concentrations of clupeids were generally found in the layers with the highest cod egg densities. An exception is spring 2008, when the peak in clupeid abundance was in shallow water around 20 m depth. This unusual vertical distribution could be related to dense fog during daytime leading to distinctly reduced ambient light levels (M. Schaber, pers. comm.) potentially not exceeding the threshold required to exert diurnal vertical migration ([Nilsson et al., 2003](#)).

[Temming et al. \(2007\)](#) have demonstrated a horizontal aggregation effect of predators on high prey concentrations in the North Sea. No indication for such an effect could be shown in our study, as no high concentrations of clupeids were detected in areas of high cod egg abundance. Owing to the relatively large spatial scale of the station grid, fine-scale aggregation patterns may however not have been detected.

Potential sampling artefacts include catching fish during shooting and hauling of the trawl, i.e. in other (shallower) than the targeted layers. This could explain why some stomachs from the hauls conducted in the water layer with highest cod egg concentrations did not contain any cod eggs. In future, vertically stratified trawl tows with a closing mechanism in the codend could be applied to ensure targeted sampling in specific water layers. Both herring and sprat in the central Baltic Sea have been reported to remain within or below the permanent halocline during their feeding period at daytime ([Hinrichs, 1986](#); [Köster and Schnack, 1994](#)) when the stomach sampling was conducted. However, the encountered bimodal vertical hydroacoustic distributions indicate that not all clupeids concentrated during daytime within and below the halocline. Nevertheless, these methodological issues are not considered to invalidate the comparison of stomach content data from the 1990s and 2000s, as sampling procedures have been consistent in terms of area coverage, sampling time, and processing. The lower number of stations sampled in the 2000s compared with the 1990s could possibly lead to a higher random noise in the results in the later period, but should not jeopardize the conclusions on temporal developments in egg predation.

### Impact on cod recruitment

From the analyses conducted in this paper, it is apparent that inter-annual variability in cod egg predation cannot be explained by single factors, but is associated with a combination of certain environmental and ecological conditions. Sampling dates with largest portions of cod eggs in clupeid stomachs (e.g. in 2007) are characterized by a moderate to high degree of fulfilment of several conditions leading to high egg predation, i.e. relatively high cod egg abundance, at least an intermediate overlap between predators and prey, and a relatively small proportion of alternative prey in the stomachs (Tables 2 and 3). In a few obvious cases, e.g. in spring 2008, a complete lack of overlap between predators and prey can fully explain the absence of cod eggs in the diet. In other cases, when the conditions are met at some intermediate levels, the thresholds resulting in high or low egg predation are difficult to derive. Also, the relative importance of these conditions is unclear, as a combination of several pre-conditions seems to be necessary to result in high egg predation.

In terms of overall predation pressure, a high individual consumption rate and a high overlap between predator and prey does not necessarily imply overall high predation mortality on cod

eggs. One of the factors that additionally need to be considered for evaluating total consumption is predator abundance. Compared with the 1990s, the abundance of clupeids in Bornholm Basin in 2000s has been substantially lower. The bulk of the sprat stock is currently distributed in northeastern areas of the Baltic Sea ([Casini et al., 2011](#); [Eero et al., 2012b](#)), i.e. outside the cod main spawning area. The biomass of sprat in Bornholm Basin during most of the 2000s has been less than one-third of that observed during the peak sprat abundance in the second half of the 1990s ([Eero et al., 2012b](#)). The amount of cod eggs encountered in the diet of sprat were significantly lower in four out of five sampling dates in spring in the 2000s compared with the 1990s, which in combination with the changed large-scale distribution of sprat suggests that the predation pressure on cod eggs by sprat has reduced compared with the 1990s.

Herring has been identified as an important predator on cod eggs in summer, especially in the 1990s–early 2000s, when the main spawning period of cod was in summer ([Köster and Möllmann, 2000](#)). Similar to sprat, herring biomass in Bornholm Basin was lower in 2000s compared with the 1990s, although the reduction in herring was less pronounced ([Eero et al., 2012b](#)). Although the numbers of cod eggs ingested by herring were in some years (e.g. 2007) comparable with that in the 1990s, the reduced importance of summer as a spawning period for cod in combination with slightly lesser abundance of herring in Bornholm Basin can be expected to have contributed to an overall reduction in predation pressure on cod eggs, and subsequently increased the recruitment.

Our analyses do not provide quantitative estimates of cod egg mortality due to predation. Such analyses would require precise information on the abundance of predators in the area and at the time of cod spawning, as well as cod egg production compared with consumption rates. Thus, the analyses conducted in this paper provide a first step towards identifying the impact of predation on cod early life stages under present conditions. An important message demonstrated in our study is that predicting the effect of clupeid predation on cod recruitment is not straightforward, as it is influenced by several factors acting in combination. This is important to keep in mind in relation to the recent developments in fisheries management in the Baltic Sea that are aiming at taking into account species interactions ([STECF, 2012](#); [ICES, 2013](#)). Predation on cod eggs is not directly related to the overall stock size of clupeid predators, while the other important factors, such as horizontal and vertical overlap between predators and prey, are difficult to numerically take into account in management frameworks. However, egg predation may be important to consider for understanding the observed recruitment dynamics, e.g. to evaluate the effect of management measures on stock recovery, or in other cases to understand the lack of recovery in a gadoid stock despite the management efforts.

### Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

### Acknowledgements

We thank Thorsten Reusch and his team from the Helmholtz Centre for Ocean Research Kiel and Holger Haslob for support in conducting the sampling on board RV Alkor and the diet composition analysis at laboratory facilities of the institute. The research leading to presented results has received funding from the European Community's Seventh Framework Programme (FP7/2007-2013) under Grant Agreement No. 266445 for the project Vectors of

Change in Oceans and Seas Marine Life, Impact on Economic Sectors (VECTORS), as well as the International Femern Belt Fish and Fisheries Science Provision Contract. This paper does not necessarily reflect the views of the Commission.

## References

- Aneer, G. 1980. Estimates of feeding pressure on pelagic and benthic organisms by Baltic herring (*Clupea harengus membras* L.). *Ophelia*, Suppl. 1: 265–275.
- Aro, E. 1989. A review of fish migration patterns in the Baltic. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 190: 72–96.
- Arrhenius, F., and Hansson, S. 1993. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. *Marine Ecology Progress Series*, 96: 125–137.
- Bagge, O., Thurow, F., Steffensen, E., and Bay, J. 1994. The Baltic cod. *Dana*, 10: 1–28.
- Bailey, K. M., and Houde, E. D. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, 25: 1–83.
- Bernreuther, M., Herrmann, J. P., and Temming, A. 2008. Laboratory experiments on the gastric evacuation of juvenile herring (*Clupea harengus* L.). *Journal of Experimental Marine Biology and Ecology*, 363: 1–11.
- Bernreuther, M., Schmidt, J., Stepputtis, D., and Temming, A. 2013. Vertically resolved prey selectivity and competition of Baltic herring *Clupea harengus* and sprat *Sprattus sprattus*. *Marine Ecology Progress Series*, 489: 177–195.
- Casini, M., Cardinale, M., and Arrhenius, F. 2004. Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. *ICES Journal of Marine Science*, 61: 267–277.
- Casini, M., Hjelm, J., Molinero, J.-C., Loevgren, J., Cardinale, M., Bartolino, V., Belgrano, A., et al. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proceedings of the National Academy of Science of the United States of America*, 106: 197–202.
- Casini, M., Kornilovs, G., Cardinale, M., Möllmann, C., Grygiel, W., Jonsson, P., Raid, T., et al. 2011. Spatial and temporal density-dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. *Population Ecology*, 53: 511–523.
- CORE. 1998. Mechanisms influencing long term trend in reproductive success and recruitment of Baltic cod: implications for fisheries management. Final Report to the EU Commission, AIR-94-1226.
- Daan, N., Rijnsdorp, A. D., and Overbeek, G. R. 1985. Predation by North Sea herring *Clupea harengus* on eggs of plaice *Pleuronectes platessa* and cod *Gadus morhua*. *Transactions of the American Fisheries Society*, 114: 499–506.
- Eero, M., Köster, F. W., and Vinther, M. 2012a. Why is the Eastern Baltic cod recovering? *Marine Policy*, 36: 235–240.
- Eero, M., Vinther, M., Haslob, H., Huwer, B., Casini, M., Storr-Paulsen, M., and Köster, F. W. 2012b. Spatial management of marine resources can enhance the recovery of predators and avoid local depletion of forage fish. *Conservation Letters*, 5: 486–492.
- Flinkman, J., Vuorinen, I., and Aro, E. 1992. Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. *Canadian Journal of Fisheries and Aquatic Sciences*, 49: 73–77.
- Foot, K. G., Aglen, A., and Nakken, O. 1986. Measurement of fish target strength with a split-beam echosounder. *The Journal of the Acoustical Society of America*, 80: 612–621.
- Garrison, L. P., Michaels, W., Link, J. S., and Fogarty, M. J. 2000. Predation risk on larval gadids by pelagic fish in the Georges Bank ecosystem I. Spatial overlap associated with hydrographic features. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 2455–2469.
- Hallfredsson, E. H., and Pedersen, T. 2007. Effects of predation from 0-group cod (*Gadus morhua*) on mortality rates of capelin (*Mallotus villosus*) larvae in the Barents Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 64: 1710–1722.
- Hallfredsson, E. H., and Pedersen, T. 2009. Effects of predation from juvenile herring (*Clupea harengus*) on mortality rates of capelin (*Mallotus villosus*) larvae. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 1693–1706.
- Hinrichs, R. 1985. Menge und Zusammensetzung der Nahrung beim Hering und Sprotte der Ostsee in den Jahren 1980–1982. *Fischerei-Forschung*, 23: 70–81.
- Hinrichs, R. 1986. Nahrungsuntersuchungen und diurnaler Rhythmus der Nahrungsaufnahme von Hering und Sprott der Ostsee. *Fischerei-Forschung*, 24: 31–37.
- Horn, H. S. 1966. Measurement of overlap in comparative ecological studies. *The American Naturalist*, 100: 419–424.
- ICES. 2013. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). *ICES CM 2013/ACOM*: 10. 154 pp.
- Kazanova, I. I. 1953. Key for identification of the eggs and larvae of fishes of the Baltic Sea and its inlets. *Trudy VNIRO*, 26: 221–265 (in Russian).
- Kitchell, J. F., Eby, L. A., He, X., Schindler, D. E., and Wright, R. A. 1994. Predator–prey dynamics in an ecosystem context. *Journal of Fish Biology*, 45: 209–226.
- Köster, F. W., and Möllmann, C. 1997. Predation by sprat and herring on early life stages of cod and sprat in the central Baltic. *American Fisheries Society Lowell Wakefield Fisheries Symposium Series*, 14: 41–69.
- Köster, F. W., and Möllmann, C. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Science*, 57: 310–323.
- Köster, F. W., Möllmann, C., Hinrichsen, H.-H., Tomkiewicz, J., Wieland, K., Kraus, G., Voss, R., et al. 2005. Baltic cod recruitment—the impact of climate and species interaction. *ICES Journal of Marine Science*, 62: 1408–1425.
- Köster, F. W., and Schnack, D. 1994. The role of predation on early life stages of cod in the Baltic. *Dana*, 10: 179–201.
- Köster, F. W., Vinther, M., Mac Kenzie, B., Eero, M., and Plikshs, M. 2009. Environmental effects on recruitment and implications for biological reference points of eastern Baltic cod (*Gadus morhua*). *Journal of Northwest Atlantic Fishery Science*, 41: 205–220.
- Link, J. S., Bogstad, B., Sparholt, H., and Lilly, G. R. 2009. Trophic role of Atlantic cod in the ecosystem. *Fish and Fisheries*, 10: 58–87.
- Marasco, R. J., Goodman, D., Grimes, C. B., Lawson, P. W., Punt, A. E., and Quinn, T. J., II. 2007. Ecosystem-based fisheries management: some practical suggestions. *Canadian Journal of Fisheries and Aquatic Sciences*, 64: 928–939.
- Möllmann, C., Kornilovs, G., Fetter, M., and Köster, F. W. 2004. Feeding ecology of central Baltic Sea herring and sprat. *Journal of Fish Biology*, 65: 1563–1581.
- Möllmann, C., Köster, F. W., Kornilovs, G., and Sidrevics, L. 2002. Long-term trends in abundance of cladocerans in the Central Baltic Sea. *Marine Biology*, 141: 343–352.
- Müller, A., and Pommeranz, T. 1984. Vertical distribution of fish eggs in the Bornholm Basin, Baltic. *International Symposium on Early Life History of Fishes and 8th Annual Larval Fish Conference*, Vancouver, BC, Canada. 21 pp.
- Myers, R. A., and Cadigan, N. G. 1993. Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 50: 1576–1590.
- Myriax, 2013. Echoview 5. <http://www.echoview.com/> (last accessed 3 January 2014).
- Neuenfeldt, S., and Beyer, J. E. 2003. Oxygen and salinity characteristics of predator–prey distributional overlaps shown by predatory Baltic cod during spawning. *Journal of Fish Biology*, 62: 168–183.
- Nilsson, L. A. F., Thygesen, U. H., Lundgren, B., Nielsen, B. F., Nielsen, J. R., and Beyer, J. E. 2003. Vertical migration and dispersion of sprat

- (*Sprattus sprattus*) and herring (*Clupea harengus*) schools at dusk in the Baltic Sea. *Aquatic Living Resources*, 16: 317–324.
- Orlova, E. L., Dolgov, A. V., Renaud, P. E., Boitsov, V. D., Prokopchuk, I. P., and Zasshihina, M. V. 2013. Structure of the macroplankton–pelagic fish–cod trophic complex in a warmer Barents Sea. *Marine Biology Research*, 9: 851–866.
- Orlowski, A. 1999. Acoustic studies of spatial gradients in the Baltic: implications for fish distribution. *ICES Journal of Marine Science*, 56: 561–570.
- Parmanne, R., Rechlin, O., and Sjostrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. *Dana*, 10: 29–59.
- Pepin, P., and Shears, T. H. 1995. Influence of body size and alternate prey abundance on the risk of predation to fish larvae. *Marine Ecology Progress Series*, 128: 279–285.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, R., Bonfil, R., Conover, D. O., Dayton, P., *et al.* 2004. Ecosystem-based fishery management. *Science*, 305: 346–347.
- Popiel, J. 1984. On the biology of the Baltic herring. Reports of the Sea Fisheries Institute, 19: 7–16.
- Salemaa, H., Vuorinen, I., and Vaelipakka, P. 1990. The distribution and abundance of Mysis populations in the Baltic Sea. *Annales Zoologici Fennici*, 27: 7–253.
- Sandstroem, O. 1980. Selective feeding by Baltic herring. *Hydrobiologia*, 69: 199–207.
- Schaber, M., Haslob, H., Huwer, B., Harjes, A., Hinrichsen, H.-H., Storr-Paulsen, M., Schmidt, J. O., *et al.* 2011. Spatio-temporal overlap of the alien invasive ctenophore *Mnemiopsis leidyi* and ichthyoplankton in the Bornholm Basin (Baltic Sea). *Biological Invasions*, 13: 2647–2660.
- Scientific, Technical and Economic Committee for Fisheries (STECF) 2012. Expert Working Group on multispecies management plans for the Baltic (STECF-12-02). Rostock, Germany, 26–30 March 2012.
- Segers, F. H. I. D., Dickey-Collas, M., and Rijnsdorp, A. D. 2007. Prey selection by North Sea herring (*Clupea harengus*), with special reference to fish eggs. *ICES Journal of Marine Science*, 64: 60–68.
- Sissenwine, M. P. 1984. Why do fish populations vary? In *Exploitation of Marine Communities*, pp. 59–94. Ed. by R. M. May. Springer Verlag, Berlin. 366 pp.
- Steedman, H. F. 1976. Osmotic pressure in fixation and preservation. In *Monographs on Oceanographic Methodology*, 4. Zooplankton Fixation and Preservation. Ed. by H. F. Steedman. UNESCO Press, Paris. 186 pp.
- Steele, M. A. 1997. Population regulation by post-settlement mortality in two temperate reef fishes. *Oecologia*, 112: 64–74.
- Stepputtis, D., Hinrichsen, H.-H., Böttcher, U., Götze, E., and Morholz, V. 2011. An example of meso-scale hydrographic features in the central Baltic Sea and their influence on the distribution and vertical migration of sprat, *Sprattus sprattus balticus* (Schn.). *Fisheries Oceanography*, 20: 82–88.
- STORE (Stock Recruitment). 2003. Environmental and fisheries influences on fish stock recruitment in the Baltic. Final Report to the EU Commission, FAIR-98-3959.
- Swain, D. P., and Mohn, R. K. 2012. Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 997–1001.
- Temming, A., Flöter, J., and Ehrich, S. 2007. Predation hot spots: large scale impact of local aggregations. *Ecosystems*, 10: 865–876.
- Uzars, D., and Plikshs, M. 2000. Cod (*Gadus morhua* L.) cannibalism in the Central Baltic: interannual variability and influence of recruitment abundance and distribution. *ICES Journal of Marine Science*, 57: 324–329.
- Voss, R., Hinrichsen, H.-H., Stepputtis, D., Bernreuther, M., Huwer, B., Neumann, V., and Schmidt, J. O. 2011. Egg mortality: predation and hydrography in the central Baltic. *ICES Journal of Marine Science*, 68: 1379–1390.
- Wieland, K., and Köster, F. W. 1996. Size and visibility of Baltic cod eggs with reference to size-selective and stage-dependent predation mortality. *Journal of Applied Ichthyology*, 12: 83–89.

Handling editor: Francis Juanes