

Prey selection by North Sea herring (*Clupea harengus*), with special reference to fish eggs

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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: 000–000.

The herring stock in the North Sea in recent years has recovered to a relatively high biomass, and here we investigate prey selection of individual North Sea herring when population numbers are high. The diet composition, and specifically pelagic fish eggs, was investigated in February 2004. Samples of herring from the International Bottom Trawl Survey were used for stomach analysis, and ichthyoplankton samples from the southern North Sea were used to investigate selection. Crustaceans were the main diet component. The average diameter of the fish eggs recovered from the stomachs was significantly larger than that of the eggs collected in the field. In addition, the frequency at which the latest developmental stages occurred in the herring stomachs was significantly different from the frequency at which these stages were found in the field. This shows selective foraging. There was a relationship between the amount of food and the number of eggs in a herring stomach: the fullest stomachs tended to contain fewer fish eggs. This suggests that herring forage on eggs when other prey are not available. Hence, it is likely that the dynamics of multiple trophic levels influence the ecological impact of a large herring stock on the North Sea ecosystem.

Keywords: egg predation, feeding, herring, ichthyoplankton, North Sea, size selection, visibility.

Received 7 March 2006; accepted 6 August 2006.

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Introduction

From a spawning biomass of 50 000 t in the 1970s, the herring (*Clupea harengus*) stock in the North Sea had recovered to almost 2 million tonnes by the early 2000s (ICES, 2004a). Changes in biomass of such magnitude will impact an ecosystem (Greenstreet *et al.*, 1997; Jennings *et al.*, 2002) and have led to interest in quantifying the impact of herring on the rest of the North Sea ecosystem and other fish stocks (ICES, 2004b). Quantifying the impact of herring is difficult, because the feeding behaviour and selection of prey by herring in the North Sea is not well described, and most of the recent studies took place against the backdrop of a much smaller population size (Daan *et al.*, 1985; Last, 1989). Raising these estimates from the 1980s is naïve, because an assumed linearity is probably inappropriate given the complexities of ecosystem dynamics, and ecosystem states may have changed (MacKenzie and Köster, 2004). Non-linearity in interactions may result in non-linear ecosystem dynamics and even in regime shifts between multiple equilibria (De Roos and Persson, 2002; Scheffer and Carpenter, 2003). This work on prey selection is a first step in considering the impact of the recent, larger herring stock on cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*) egg production in the southern North Sea.

The diet of Atlantic herring is widely accepted as being dominated by planktonic crustaceans (Hardy, 1924; Arrhenius and Hansson, 1992; Dalpadado *et al.*, 2000; Darbyson *et al.*, 2003; Möllmann *et al.*, 2003). In the North Sea, the diet varies by season, but is dominated by copepods (*Calanus* spp., *Temora* spp., and *Pseudocalanus* spp.) and juvenile sandeels (*Ammodytes* spp.), with fish eggs, amphipods, *Sagitta* spp., and *Oikopleura* spp. also

being major constituents (Hardy 1924; Bainbridge and Forsyth, 1972; Daan *et al.*, 1985; Last 1989). There are spatial differences in the prey (Savage, 1937). The interactions of predator and prey ensure that during summer feeding, the distribution of herring is coincident with that of zooplankton (Maravelias and Reid, 1997).

Recently, more information has become available about the feeding behaviour of herring. Adult herring are visual feeders (Batty *et al.*, 1990). They select for larger items (Dalpadado *et al.*, 2000) that tend to have greater energy content (Leggett and DeBlois, 1994), although prey type also plays a role (Casini *et al.*, 2004). The selection by type of prey item may reflect “learned” behaviour (Checkley, 1982, in larvae) or a response to other stimuli such as movement. Size selection was found in the Irish Sea (Ellis and Nash, 1997), where herring selected larger eggs, such as plaice, rather than the more available and numerous smaller eggs. This selection for larger eggs was suggested by both Daan *et al.* (1985) and Last (1989). Here we try to confirm these suggestions for North Sea herring.

Herring start foraging above a certain light threshold. Pigmentation and transparency of an item affects vulnerability to visual predators (Leggett and DeBlois, 1994). Fish eggs at later stages of development show increased light attenuation, up to 42% (Wieland and Köster, 1996), probably due to larger embryos and greater pigmentation. Ellis and Nash (1997) found that sprat (*Sprattus sprattus*) and herring in the Irish Sea consumed more plaice eggs in the later stages of development than expected. Also, Wieland and Köster (1996) noted that the frequency of cod eggs in the Baltic in an advanced stage of development was considerably greater in herring stomachs than in corresponding plankton

samples. Hence, in those two regions, herring apparently select later stage fish eggs.

Predation on fish eggs may also be affected by the availability of other prey. Hardy (1924) commented that he and previous authors found that when herring contained fish eggs, there were few other prey items in the stomachs. Daan *et al.* (1985) noticed that although fish eggs were available to herring, the relatively larger herring had mostly crustaceans in their stomachs. This current work also tests the hypothesis with field and stomach data that, when copepods are lacking, herring start eating fish eggs.

In an attempt to describe the feeding behaviour of herring in the southern North Sea better, particularly in terms of size selectivity and prey choice, a programme of sampling took place in February 2004. This programme coincided with the annual spawning of plaice and cod (Brander, 1994; Rijnsdorp and Witthames, 2005) and with an international ichthyoplankton survey designed to map the distribution of cod and plaice spawning in the North Sea (ICES, 2004c; Fox *et al.*, 2005).

Material and methods

Field sampling

Samples of herring were collected during the Dutch contribution to the International Bottom Trawl Survey (IBTS) of the North Sea in February 2004 (ICES, 2004d). Where possible, some 25 herring across the length distribution were taken from each haul (Figure 1). The size range of the sampled fish was 82–288 mm total length.

As ichthyoplankton is digested quickly (Hunter and Kimbrell, 1980), the samples were processed on deck as fast as possible. The fish were immediately cut open to expose the abdominal cavity, then fixed whole in 4% buffered formaldehyde. As the IBTS only takes samples during daylight, no samples were collected in

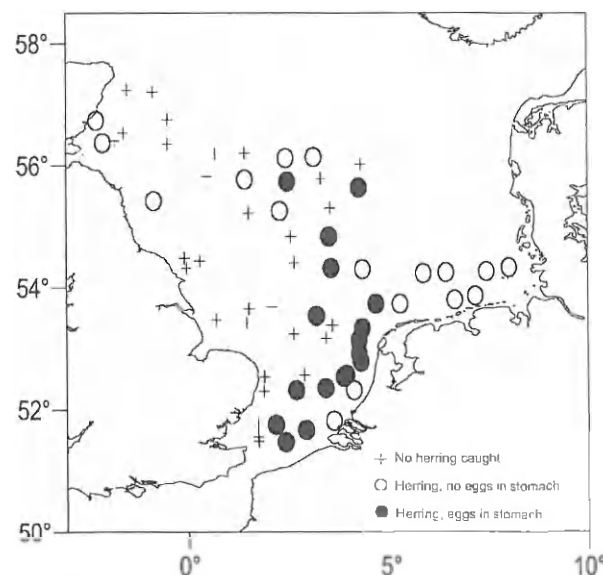


Figure 1. The locations of the hauls of the IBTS in February 2004. Crosses indicate that no herring were captured at that site, circles indicate that a sample of approximately 25 herring was collected, and filled circles show hauls that contained herring with fish eggs in their stomachs.

Table 1. Definition of stomach fullness categories.

Category	Description
0	Completely empty
1	Nearly empty
2	Several food items
3	Filled
4	Stuffed

darkness, thus preventing any study of potential night-time filter-feeding by herring, as shown by Batty *et al.* (1986).

Analysis of stomach contents and the diet composition

In the laboratory, each fish was weighed to the nearest 0.01 g and its total length was measured to the nearest 1 mm. After this, the stomach was removed and its contents analysed under a binocular microscope. No analysis of the contents of the intestine was undertaken.

A visual estimation of stomach fullness was made and the results allocated to one of five categories (Table 1). The eggs present were counted and diameters measured, if possible, to the nearest 0.01 mm. The developmental stages of the eggs were assessed using simplified categories (Table 2), because partially digested eggs are hard to stage. After removal of the eggs, the remaining stomach contents were identified to the lowest possible taxonomic level and counted.

Estimates of the importance of certain taxonomic food categories to southern North Sea herring were made. Preferred prey size can differ with fish length (Rijnsdorp and Jaworski, 1990), so we used methods that estimate the importance of food groups relative to the total of all groups. This was expressed in two ways, which allowed comparison of results. We calculated the numerical percentages (N) of the different food categories (Berg, 1979; Hyslop, 1980; Tičina *et al.*, 2000, and references therein). This method estimates the amount in numbers a food group contributed to the herring diet relative to the total amount in numbers of all groups:

$$N(\%) = \frac{n_i}{N_1} \times 100, \quad (1)$$

where n_i is the number of individuals of a particular taxonomic group and N_1 the total number of individuals of all taxonomic groups.

We also estimated the food importance index (F) (Tičina *et al.*, 2000, and references therein), which estimates the number of stomachs that contained the food group relative to the total number of stomachs that contained food. In this way, the importance of small prey items taken in large numbers by small herring is not overestimated:

$$F(\%) = \frac{n_s}{N_s} \times 100, \quad (2)$$

where n_s is the number of stomachs that contained the specific food item and N_s the total number of stomachs that contained food.

Egg consumption and selection

Developmental stages (Riley, 1973; Thompson and Riley, 1981) and diameters of field-sampled fish eggs were recorded as a byproduct of the ICES coordinated ichthyoplankton surveys (ICES,

Table 2. Description of stages to which the fish eggs in the herring stomachs were allocated in this study, and the corresponding stages of Thompson and Riley (1981) and Riley (1973).

Stage	Description	Stage following Thompson and Riley (1981) and Riley (1973)
1	No embryo visible. Yolk or blastodisc visible	1a and b
2	Short-tailed embryo visible	2 and 3
3	Embryo fills whole egg and has a long tail	4 and 5

2004c; Fox *et al.*, 2005). Only the data from the Dutch portion of the survey were used in this analysis. Sampling was carried out with a Gulf VII high-speed plankton sampler (Nash *et al.*, 1998) fitted with a 270 μm mesh net, deployed in a double-oblique manner to 2 m above the seabed. Samples were preserved in 4% formaldehyde or the eggs were picked out and identified at sea.

When considering size selectivity for fish eggs, the occurrence of temporal variation in the size composition of fish eggs in the southern North Sea has to be accounted for, as well as the frequencies at which the different developmental stages were present in the water column. Therefore, it was necessary to select egg survey data that had the closest overlap in space and time with the available stomach data. The data corresponding best with these requirements were sampled, from 15 to 19 February 2004. The distribution of the different diameters of eggs over the developmental stages for both field and stomach samples was tested using one-way ANOVA.

A χ^2 contingency table test was undertaken to test if the three egg stages occurred at the same frequencies in the field as in the herring stomachs. One-way ANOVA was used to compare the average diameters of the field and stomach eggs. To locate significant difference within the size spectrum of fish eggs, a Kolmogorov–Smirnov two-sample test was applied (Sokal and Rohlf, 1981).

Food type preference

If herring start eating eggs when crustaceans are lacking, it would be expected that a relationship exists between the level of fullness and the egg content of the stomachs. To explore this, a linear regression model was fitted on the log-transformed number of eggs. Fish weight and stomach fullness category were chosen as variables. Only fullness categories 2, 3, and 4 (Table 1) were taken into account, because by definition, empty or virtually empty stomachs will not contain eggs. Thus,

$$\text{Eggs eaten} = e^{(\alpha + \text{category} + \beta \times \text{weight})} + \varepsilon, \quad (3)$$

where α is the intercept, β the slope, and ε the normally distributed error term. The parameter category is a fullness classification variable.

Statistical analysis

All statistical tests, except the Kolmogorov–Smirnov two-sample test, were undertaken in SPSS, 12.0.1. The linear regression was done with SAS software (SAS Version 8.1, SAS Institute, Cary, NC, USA). We used the GENMOD procedure with log-transformed dependent variable to normalize the error term.

Results

Diet

Of the 855 analysed herring stomachs, 578 had food and 111 contained fish eggs, varying from 1 to 63 items per stomach. The

numerical percentage and food importance index for the most part gave the same result (Figure 2). A variety of taxonomic groups was found, with large variance in significance. As expected, copepods dominated the diet numerically (59%) and were also found in the most stomachs (40%). According to both indices, copepods, amphipods, and euphausiids appear to be taken most by southern North Sea herring in February. Fish eggs seem to be the preferred food type after crustaceans (Figure 2). Although numerically less important than crustaceans, fish eggs were present in a considerable proportion of the stomachs (19%).

Occasionally, many individuals from a particular haul contained large amounts of a certain taxonomic group, e.g. almost all the herring that contained crab larvae (Figure 2, Table 3) originated from one haul.

Selective consumption of fish eggs

Most fish eggs from the stomachs could not be measured because of their advanced state of digestion (Table 3). However, the distribution of egg diameters from the field is broader than the distribution of egg diameters found in herring stomachs in the same areas (Figure 3). The average diameter of the eggs in the stomachs was significantly larger than that of the eggs collected in the field (ANOVA, $F_{1,1313} = 58.4$, $p < 0.001$).

The relative frequency distributions of the field and stomach eggs differ (Figure 4). The egg diameters were rounded to one decimal. The frequency at which eggs with a diameter of 0.9–1.3 mm were found in the field was significantly higher than the frequency at which those sizes were encountered in the stomachs, because the Kolmogorov–Smirnov statistic (D) was significant ($D_{0.01} = 1.67$) over this size range. The highest value ($D_{\max} = 0.348$) was at 1.2 mm.

The 95% confidence interval in egg diameter for cod eggs was 1.28–1.67 mm and for plaice eggs 1.66–2.22 mm (ICES

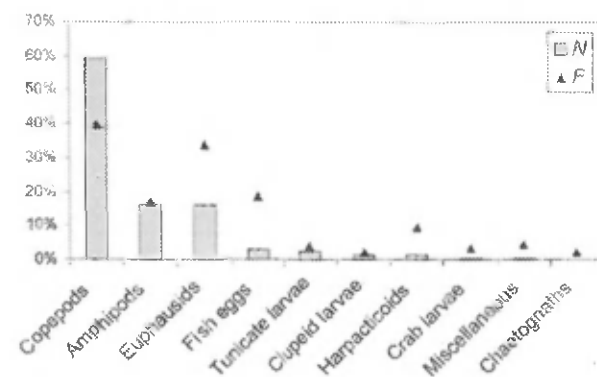


Figure 2. Numerical percentage (N) and food importance index (F) grouped by taxonomic group encountered in herring stomachs. Of the 855 herring stomachs analysed, 578 had food and 111 contained fish eggs, varying from 1 to 63 prey items per stomach.

Table 3. Description of the stomach contents of herring originating from hauls in which fish had foraged on eggs.

Sample location	52°78'N 4°28'E	53°73'N 4°67'E	54°32'N 3°55'E	53°33'N 4°32'E	52°57'N 3°92'E	54°83'N 3°50'E	55°63'N 4°25'E	55°73'N 2°48'E	53°53'N 3°18'E
Number of herring in sample (number of herring with food in their stomachs)	28 (28)	22 (10)	24 (13)	25 (14)	25 (25)	25 (14)	26 (22)	25 (10)	25 (21)
Remaining stomach contents when eggs removed	Mostly copepods, some euphausiids	Euphausiids	Mostly copepods	Few crustaceans	Mostly crustaceans and tunicate larvae	Nearly empty, few crustaceans	Crustaceans	Few crustaceans	Mostly copepods
Number of herring with eggs in their stomachs	12	1	4	3	10	6	2	2	1
Total number of eggs from all stomachs	22	1	4	4	19	118	3	5	1
Identifiable eggs	8	1	0	1	3	11	0	1	0
Number of herring in sample (number of herring with food in their stomachs)	52°35'N 3°40'E	51°67'N 2°92'E	51°74'N 2°42'E	52°32'N 2°68'E	53°13'N 4°23'E	52°92'N 4°23'E	52°53'N 3°85'E	51°75'N 2°18'E	
Remaining stomach contents when eggs removed	Crustaceans	Mostly crustaceans	Mostly crustaceans and crab and fish larvae	Mostly copepods	Euphausiids	Copepods	Tunicate larvae	Only fish eggs	
Number of herring with eggs in their stomachs	14	6	25	1	2	13	6	3	
Total number of eggs from all stomachs	90	13	329	1	11	53	11	16	
Identifiable eggs	18	7	94	1	5	18	2	8	

"Identifiable eggs" means that the eggs could be measured and/or staged.

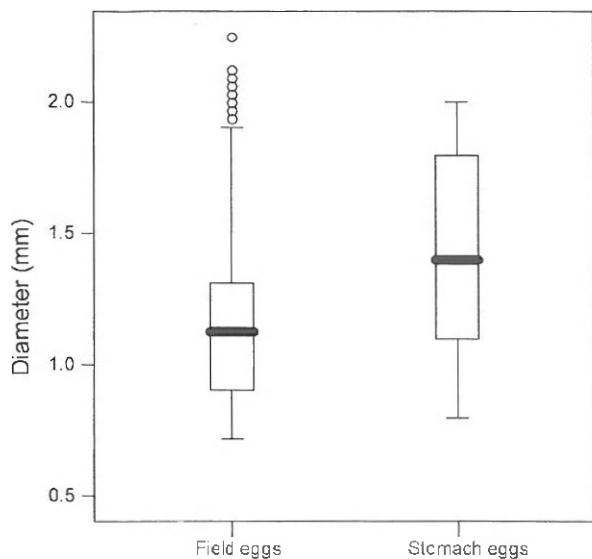


Figure 3. Box and whisker plots of fish egg diameters from field and stomach samples. The plots were constructed with the field and stomach data that had the greatest overlap in space and time. The boxes indicate the 25th, 50th, and 75th percentiles of the distributions, the whiskers show the 10th and 90th percentiles, and the open symbols represent outliers.

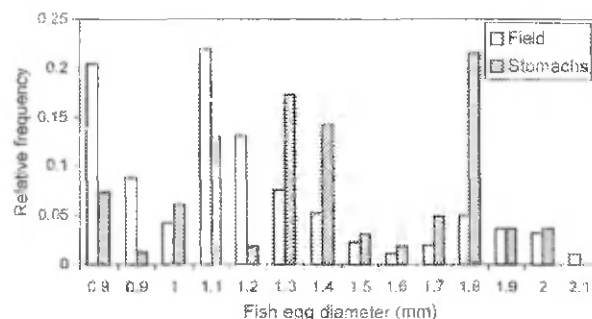


Figure 4. Bar chart of the relative frequencies of fish egg diameters from field and stomach samples. The plots were constructed with the field and stomach data that had the greatest overlap in space and time. The diameters are rounded to one decimal. For the size range 0.9–1.3 mm, the Kolmogorov–Smirnov statistic (D) was significant ($D_{0.01} = 1.666$), indicating that fish eggs in this size range were more frequent in the field than in herring stomachs. The highest value ($D_{\max} = 0.348$) was at 1.2 mm.

ichthyoplankton survey 2004, unpublished data). The frequencies of the stages in the stomachs differed significantly from those in the field (Table 4, χ^2 contingency test, $\chi^2_{2,123} = 24.9$, $p < 0.001$).

Difference in average diameter between stages

When the fish eggs collected from the stomachs are clustered by stage, there appear to be differences in average diameter between the three groups (Figure 5a). The effect of stage on diameter is significant (ANOVA, $F_{2,175} = 9.29$, $p < 0.001$). A Tukey's HSD *post hoc* test showed that the mean diameter of Stage 1 was significantly smaller than the mean diameter of Stages 2 and 3 eggs ($p = 0.002$

Table 4. Contingency table (Zar, 1999) of the frequencies at which the different developmental stages were found in herring stomachs and in the field.

Sample		Stage			Total
		1	2	3	
Field	Counted	565	425	158	1148
	Expected	545.8	422.6	179.6	
Stomachs	Counted	64	62	49	175
	Expected	83.2	64.4	27.4	

The "counted" values represent the frequencies observed, and the expected values are the frequencies at which the stages should occur if there was no selection. The predictions were calculated in SPSS 12.0.1.

and 0.001, respectively), but that Stages 2 and 3 eggs did not diverge in size ($p = 0.883$).

A similar result is found within the egg survey data (Figure 5b, ANOVA, $F_{2,5852} = 118.2$, $p < 0.001$). Egg size increases with stage. A Tukey's HSD test revealed that all the stages differ significantly in average diameter ($p < 0.001$ for all comparisons). Apparently, the difference in average diameter between the developmental stages of the eggs taken by herring is a reflection of the ichthyoplankton composition in the water column.

Food type preference

The number of eggs in the stomach was modelled as a function of body weight and fullness category. Both weight ($\chi^2_{1,368} = 243.2$, $p < 0.001$) and fullness category ($\chi^2_{2,368} = 495.8$, $p < 0.001$) have a significant effect, explaining 17 and 11% of the variation in the stomach data, respectively. The number of fish eggs eaten by herring increases with fish weight (Figure 6). Also, the model predicts more eggs in the stomachs of herring that contain less food and zero eggs when the stomach is full (Category 4).

Discussion

This study on prey selection of North Sea herring in the past 50 y was the first to take place when the stock biomass was high, with coincident ichthyoplankton sampling. It broadly supports the findings of previous studies, but it quantifies for the first time the effect of stomach fullness on selection of fish eggs and clearly demonstrates a preference for later stage eggs.

Diet composition

Numerically, crustaceans dominate the diet of herring in the southern North Sea in February. Also, they occurred in the greatest percentage of stomachs over all size classes of herring. This finding was expected, because it is in broad agreement with that of other studies (Hardy, 1924; Last 1989; Arrhenius and Hansson, 1992; Dalpadado *et al.*, 2000; Darbyson *et al.*, 2003). The occurrence of other food groups, such as fish larvae and tunicates, led Hardy (1924) to conclude that herring are opportunistic. Our findings support this conclusion, because occasionally many individual herring in a particular haul contained crab or fish larvae. This reflects the clustering described by Pennington *et al.* (2002), and perhaps also the spatial spread of Savage (1937), and for this reason only a maximum of 25 fish from every available haul were analysed in this study.

Interestingly, in contrast to the large quantities of juvenile sandeel in herring stomachs collected in the spring of 1922, 1923, 1984, and 1986 (Hardy, 1924; Last, 1989), no sandeels were found during the current study, similar to the situation in spring 1983

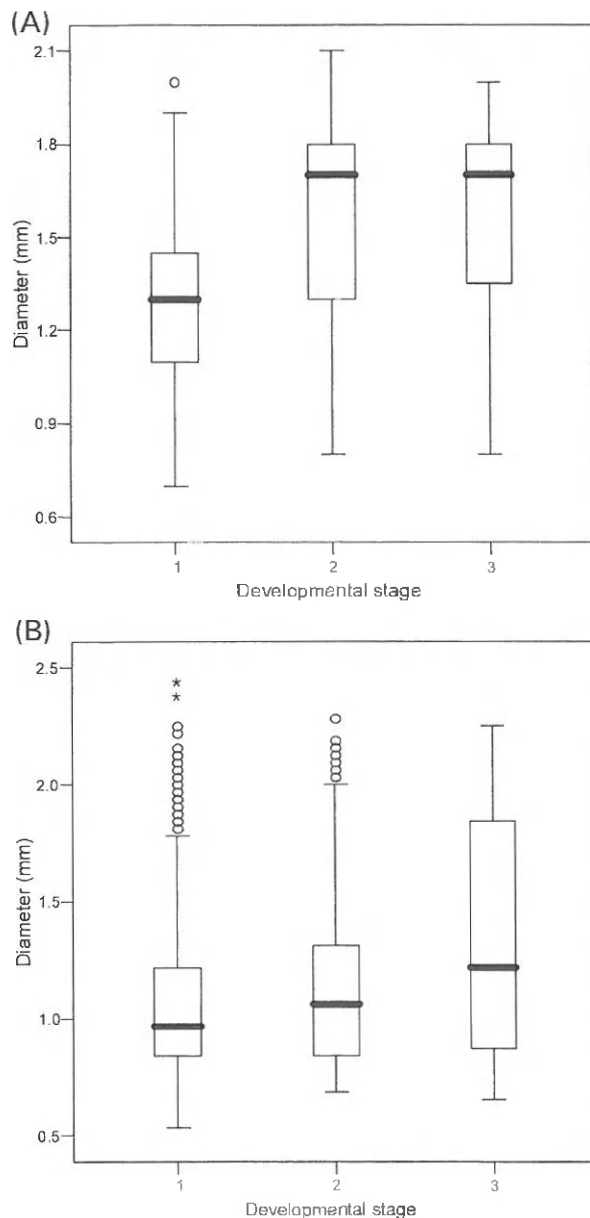


Figure 5. Box and whisker plots of the distribution of the diameters per stage for (a) eggs collected from stomachs and (b) for those found in the field during egg surveys. The plots were constructed with all field and stomach data available, so overlap in space and time was not considered. The boxes indicate the 25th, 50th, and 75th percentiles of the distributions, the whiskers show the 10th and 90th percentiles, and the open symbols and asterisks represent outliers.

(Last, 1989). Hardy (1924) found that herring preyed on juvenile sandeel in early spring and that crustaceans dominated the diet after April. He hypothesized that herring used sandeel for growth and copepods for gonad maturation. This may be an over-interpretation of the data, and this switch in prey type may purely be a reflection of prey availability then.

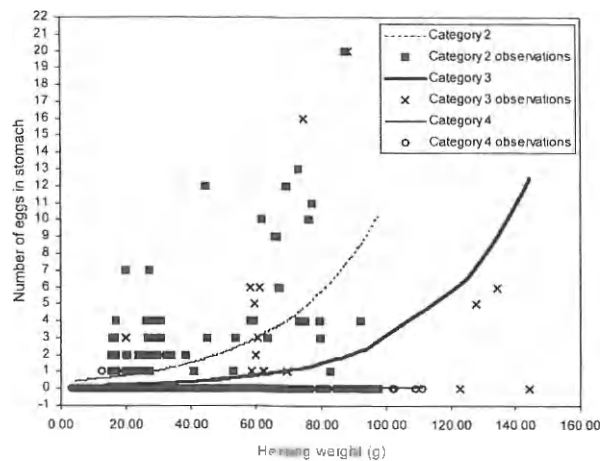


Figure 6. Predicted and observed quantities of eggs in stomachs plotted against fish weight for the different fullness categories. The graph is constructed with predictions the model made for the herring used in this study. For clarity, some outliers were removed when constructing this graph, all belonging to category 2 (the numbers were 28, 33, 39, 39, 57, and 63, and the weights were, respectively, 65.30, 67.92, 61.18, 87.43, 61.27, and 97.00 g).

Hyslop (1980) proposed that the best measure of dietary importance is one where both the number and the volume of a food category are recorded. The methods used in this study do not take the volumes of the food type into account. Therefore, they overestimate the importance of small prey items taken in large numbers (Hyslop, 1980). In contrast, numerical methods give an indication of the amount of effort exerted in selecting and capturing prey organisms (Ball, 1961). Additionally, numerical methods have an advantage in that they are fast and simple to execute, and when the prey items are in the same size range, as in planktivorous fish, they operate well (Hyslop, 1980). Therefore, the bias introduced into this study by the choice of this method is considered to be small, particularly because larger prey items were rare.

The numerical percentage and food importance index reflect the significance of certain taxonomic groups for southern North Sea herring in February. However, the results of the diet composition analysis do not provide a population average, because the length-stratified samples were not raised to the size composition of the population (Morgan and Hoenig, 1997; Gerritsen *et al.*, 2003). As every effort was made to ensure that all lengths in the catch were sampled, the results will be skewed towards larger fish. We do not consider the bias in these results to be of great importance, because the objective of this study was to describe the feeding selectivity of individual fish and not to make an estimation of the total quantities consumed.

Selective egg consumption

The results imply that daylight-feeding herring select for eggs that are larger and in later developmental stages. This is probably caused by the greater visibility of those eggs. The works of Wieland and Köster (1996) and Ellis and Nash (1997) support this hypothesis.

When foraging on fish eggs, North Sea herring consume mainly eggs of cod and plaice, because these species produce relatively large eggs (Russell, 1976; ICES, unpublished). Comparing

the relative frequency distributions of the stomach and field eggs reveals that herring select eggs >1.3 mm diameter. The eggs of cod and plaice are in the size category that herring prefer to eat (1.3–2.2 mm, respectively) (ICES, unpublished).

Further, herring select plaice and cod eggs that are in later developmental stages. Consequently, studies such as that of Daan *et al.* (1985), who estimated predation on initial egg production (i.e. all eggs were newly spawned), underestimated the impact of herring predation on mortality during the egg phase in plaice and cod, because there is an exponential decline in the number of eggs from spawning to hatching, through natural mortality. The estimates of predation pressure should be calculated as a percentage of the number of average-age eggs in the water column.

Inaccuracies in the staging of the eggs can be caused by damage to the eggs through the mechanical stress of being caught, preserved, or eaten (Pommeranz, 1974; Geldmacher and Wieland, 1999). Before hatching, the embryo becomes active and the chorion softens as a result of enzymes (Blaxter, 1988), so later developmental stages are more likely to be damaged and the estimates of the quantities of these eggs can be negatively biased. The effect of stage-dependent variability in the level of damage to eggs on the conclusions of this study is difficult to quantify, so we have assumed that damage will be random, i.e. independent of stage.

Difference in average diameter between stages

As shown in other studies, the most visible eggs for herring are those that are relatively big (Batty *et al.*, 1990; Ellis and Nash, 1997). We assumed that there would be no interaction between egg size and stage. However, Stage 1 eggs collected from our herring stomachs had a significantly smaller average diameter than Stages 2 and 3 eggs. Therefore, it would be expected that only larger Stage 1 eggs would be selected as food.

The distribution of the diameters of the staged stomach eggs resembles the diameter distribution of the stages of the eggs collected in the ichthyoplankton survey. The field-caught eggs also have an increasing average diameter with stage. If we presume that the field egg diameter distribution is a reliable reflection of the ichthyoplankton composition in the water column, then herring automatically eat more Stage 3 eggs when they are picking out the larger eggs, and vice versa. It would be difficult to test whether visibility through size or stage is the dominant process in herring egg selectivity. Nevertheless, it appears that herring mainly select on stage and not on size, or else Stage 1 stomach eggs would not have had a significantly smaller average diameter.

There is virtually no evidence to support the possibility that egg size varies with stage. Davenport *et al.* (1981) suggest that changes in the chorion may result in slight increases in cod egg size with stage, but such a change is likely to be too small to cause the differences observed here.

An explanation for the significantly larger average diameter of later stage field eggs can be the interaction of species and temporal spawning patterns (Fox *et al.*, 2000). If plaice spawning is declining during the survey period and cod spawning increasing, then the smaller eggs could be at an earlier stage and the larger eggs could be older. There is also a decline in egg size as the spawning of plaice progresses (Rijnsdorp and Jaworski, 1990). In addition, the finding that earlier stage eggs are smaller may be due to an additional consequence of greater predation. There is an exponential decline in the abundance of marine organisms with increasing size (Peters, 1983). As a result, the average number of potential predators will be greater for smaller eggs (Rijnsdorp and Jaworski,

1990). Bigger eggs have a greater chance of reaching the later developmental phases, and therefore this egg type might be at a greater frequency in the water column than relatively small eggs in near-to-hatch stages; however, this phenomenon has rarely been seen in field-based studies.

Food type preference

The results of our study reveal that herring with moderate stomach fullness (Category 2 or 3) consumed more eggs than a herring with a completely full stomach (Category 4). Also, the number of fish eggs found in a stomach increased with the weight of the animal, in accordance with the results of a study done by Pepin (2006) on capelin (*Mallotus villosus*). The greater egg consumption by larger herring is probably due to size-related food preferences, but as other prey types in the stomachs were not measured, we cannot state this with certainty.

It is uncertain as to which biological processes cause the near absence of eggs in full stomachs. It seems that herring only eat eggs when crustaceans are not available. A cod egg is high in energy and dry weight (80–90 µg) (Kjesbu *et al.*, 1996), compared with a single *Temora* or *Pseudocalanus* (dry weight 15–20 µg) (MD-C, unpublished), although similar to that of an adult *Calanus* (80 µg) (MD-C, unpublished). Therefore, there is reason for fish eggs to be preferred to copepods.

Perhaps, fish eggs are less visible to herring than crustaceans. When many optically denser organisms are present, herring may have difficulty in spotting fish eggs among the copepods. It may only eat fish eggs when encountered in dense patches with few copepods, because predatory fish switch prey type when encountered frequencies change (Murdoch *et al.*, 1975; Hughes and Croy, 1993). Pepin (2006) noticed that fish eggs were more likely to be eaten by Atlantic capelin at the onset of feeding activity after dusk, and he suggested that when the fish are hungry, they may be more likely to eat anything that passes by rather than the more abundant prey.

If the quantity of copepods available affects the quantity of eggs taken, any ecosystem shift or large interannual variation in copepod production (Edwards and Richardson, 2004) will affect the impact of herring as a predator on plaice and cod eggs. Similarly, the availability of sandeel larvae may affect the predation pressure on fish eggs. The number of herring with fish eggs in their stomachs in this study was higher than that reported by Hardy (1924), who found that sandeels were an important prey item for herring. Sandeels were absent from the stomachs of herring in the southern North Sea in February 2004, so eggs may have been taken in greater number in the absence of sandeels. Further investigation is required to quantify the effect of alternative prey types on the predatory impact of herring on fish eggs.

Conclusion

This study has contributed to a growing understanding of ecosystem dynamics in the North Sea. The effect of the present large herring biomass on the North Sea ecosystem is not easy to predict, because it seems that the dynamics of multiple trophic levels can influence the outcome of any such analysis. However, from the results of this work, herring seemingly have the potential to be a major predator of the eggs of cod and plaice. We believe, therefore, that a new estimate of the predation impact of herring should be made, one that considers the factors mentioned above and which estimates the consumption as a percentage of the number of eggs of an average age.

Acknowledgements

We thank Jan-Jaap Poos and Olvin van Keeken for help with the GENMOD procedure in SAS, Loes Bolle and Cindy van Damme for the use of the egg survey data, and the crew of the "Tridens" and Henk Heessen for helping us with sampling the herring. Richard Nash and Pierre Pepin made valuable comments on the manuscript. The work was partly funded by the EC project UNCOVER.

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doi:10.1093/icesjms/fsl002