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Abstract

The stomach contents of 5408 herring, caught during the IYFS in February 1980, 1981 and 1983, were studied to estimate the quantitative consumption rate of plaice and cod eggs, taking into account the spatial distribution of different size categories of herring and the numbers at age from VPA. Mean weight of the stomach contents of feeding herring increased during the day and peaked around noon, suggesting a digestion time of 12 hours. Predation of plaice and cod eggs was generally confined to the southern North Sea, although plaice eggs were also found in herring of the Moray Firth. Only the youngest age groups of herring (age 2 and 3) contributed significantly to the predation on fish eggs. Occasionally larvae of herring and plaice were found. The fraction of eggs produced, which were consumed by herring, increased for plaice from 0.7% in 1980 to 1.9% in 1983 and for cod from 0.04% to 0.19%, probably reflecting the increasing size of the herring stock. These estimates only give a rough indication of the actual predation rate. However, predation appears to be so low that it is unlikely that the observed increase in recruitment of the demersal stocks in the seventies can be entirely accounted for by a reduced predation of herring on the egg stages.

Introduction

The simultaneous collapse of the North Sea herring stock (BURD,1978) and increase in various demersal fish stocks (BANNISTER,1978; DAAN,1978; SAHRHAGE and WAGNER,1978) have been causally linked by various authors (ANDERSEN and URSIN, 1978; DAAN,1980) in interpreting the apparent changes in the North Sea ecosystem in the late sixties. Since essentially the interspecific relations operating in nature have remained unresolved, the argument about the causal relationship between the two antagonistic developments in the pelagic and demersal subsystem has continued to be governed by personal belief and unbelief rather than by scientific evidence.

One obvious possibility would be that the herring stock by preying upon eggs and larvae of demersal fish affects the number of survivors and thus the average level of recruitment, even if it is not the main factor determining actual year class strength. Earlier investigations have indicated that indeed eggs of plaice and cod could be found in significant numbers in stomachs of herring when sampled at the right time and plaice (HARDY, 1924; DAAN, 1976; POMMERANZ, 1979; GARROD and HARDING, 1981). Although it is thus clear that the herring excersizes a mortality factor on the eggs, it has not yet been possible to estimate quantitatively the impact of the total herring stock, the main reason for this being that the information available so far has been collected rather haphazardly and that egg predation appears to be rather variable depending on the actual distribution of the herring in relation to the egg concentrations. Any reliable quantitative estimate of the predation mortality excersized by the herring would require sampling to be carried through systematically throughout the spawning season of the demersal fish and over a wide area covering the total prey and predator distributions.

A pilot study was initiated in 1980 in order to obtain such an estimate of egg predation mortality based on sampling during the International Young Fish Survey (IYFS). This survey appears to fullfill the basic requirements, since february represents the peak spawning time of both plaice (HARDING et al, 1978) and cod (DAAN, 1978). Furthermore, this survey is primarily directed towards the estimation of the year class strength of juvenile herring and data on the spatial distribution of the herring by age group are readily available.

In practice sampling of stomachs has largely been restricted to those statistical rectangles fished by R.V. TRIDENS. Although a few additional stomach samples have been provided by England, Federal Republic of Germany, Norway and Scotland, this has put severe limitations on the intensity of sampling achieved.

Stomach sampling yields information on the number of prey present in stomachs and in order to obtain estimates of consumption information on turnover time of the contents is required. Reliable data on digestion in herring are not available and some inference must be made from the distribution of stomach content weights over time of day. Lastly, in order to obtain predation rates estimates of consumption must be compared with estimates of numbers of eggs produced, which have been made on the basis of available literature.

Methods

Stomach samples

During the IYFS 1980, 1982 and 1983 herring were sampled from each positive haul. The herring were grouped in size classes (10-15, 15-20, 20-25, 25-30 and 30-40 cm) and up to 25 stomachs

per size class were collected. Fig 1 shows total North Sea area sampled over the three years. As prescribed by the timing of the surveys, with very few exceptions the stomachs were collected within the month of february. They were preserved in 4% formaline and processed in the laboratory. The analysis followed the general procedure established in the stomach sampling project (ANON., 1981) and the following information is available: standard haul information (date, time, position, depth, temperature and salinity), number of stomachs with food, number empty, species composition to the lowest possible taxonomic level by size class in number and weights.

Of eggs found in stomachs often only empty shells remain, which makes it hard to identify the various species. However, eggs of plaice and cod/haddock are readily identified by their size (1.7-2.2 and 1.4-1.6 mm respectively), even from empty shells. Since no eggs were found in the haddock spawning area in the northern North Sea all eggs of the second size class have been assumed to represent cod eggs. All other eggs were lumped and are not considered in this report.

Fish larvae found in the stomachs were few and belong to three species: plaice, herring and sprat. In the present report information on the composition of the stomach contents for other prey than fish eggs and larvae has been omitted.

In the analysis samples were combined by standard North Sea roundfish areas (cf fig 1) and table I summarizes information on sampling intensity by area and size class. Area 6, which corresponds to the main spawning area of plaice, has been most intensively sampled in all years, whereas in the other areas sampling has been rather variable. A total of 5408 herring stomachs has been analysed over the three year period.

Distribution of the herring population

Information on the spatial distribution of the herring by age classes is readily available from the standard survey output. Table II summarizes the estimated percentages of each age group in each area, based on extensive age length keys collected during the surveys. A problem in interpreting the relative catches by age group is that the catchability varies with age as is indicated in table III, where the percentage catches in the survey are compared with estimates provided by the North Sea Herring Working Group (ANON., 1984). For the purpose of estimating predation rates by area the stock sizes by age group provided by the Working Group (table IV) have been split according to the relative catches by area as obtained from the survey.

Estimates of egg production

The estimated egg production of the plaice and cod population in 1982 has been based on established fecundity/weight relationships:

Plaice: $F = -35.6 + .2815 \times W$ (RIJNSDORP et al, 1983)

Cod: $F = 569 (W - 1418)$ (OOSTHUIZEN and DAAN, 1974)

Table V provides the estimated production on the basis of VPA stock size estimates for the two species (ANON., 1983a, 1983b), assuming a sex ratio of 1.

RESULTS

Prey species composition

The statistical rectangles have served as the basic strata and the average abundance of a size class within a rectangle was used as a weighting factor to obtain the area average stomach contents by size class. In table VI the resulting information on stomach content composition by size class, area and year is summarized. The total average weights of the contents in february appear to be very low (generally less than 1 g per herring). Only in the northern North Sea (area 1) this value is exceeded in some cases. It must be concluded, also from the low fraction of herring with food in their stomachs, that feeding activity at this time of year is limited. Feeding on eggs and larvae is mainly restricted to areas 5, 6 and 7 and only in 1983 some eggs and larvae have been found in areas 2 and 3. Although the number of eggs is only a small fraction of the total number of food items, in the southern areas the other items are mainly represented by copepods, which have a lower average weight than eggs. and in terms of weight the eggs may amount up to 10% of the food in area 6. Altogether, however, from the herring point of view the contribution of eggs to the total food is very small.

Diel changes in stomach contents

In order to study possible effects of time of sampling on the stomach contents fig 2 shows the percentage of empty stomachs in samples collected during various times of the day in 1982. Clearly, the proportion empty decreases from high values in the morning to low values in the evening (since it is mandatory that hauls in the herring area are made during daylight hours no information is available for the rest of the 24 hour cycle). The suggestion that herring start feeding during daylight is further supported by fig 3, where mean weights of the stomach contents for selected size classes in the southern North Sea and for all size classes in the northern North Sea are plotted against time of day. Not only the proportion feeding thus increases during daylight, but also the mean weight of the stomach contents of feeding herring increase. It appears that in the southern area they start to feed earlier and reach a maximum around noon, whereas in the northern area feeding is delayed and the maximum is reached in late afternoon. Some of these differences may be related to differences in sunrise depending on latitude.

The important conclusion from these graphs is that digestion rates are less than 24 hours and more likely in the order of several hours, because even if the southern herring would stop

feeding completely at noon, 30% would have disappeared in 4 hours time. Particularly the data for the northern North Sea suggest that all herring start the day with empty stomachs.

Egg predation

The egg predation by size class was converted into the egg predation by age group for each area using area specific age size class keys and length frequency distributions of herring from the IYFS. Subsequently the average number of plaice eggs per herring for each age group was calculated by weighting over the number of rectangles in each area according to the percentage distribution given in table II. For areas which had not sufficiently been sampled in any particular year, the pooled samples of 1980, 1982 and 1983 have been used. Thus in 1980 this was done for area 5, in 1982 for area 4 and 7 and in 1983 for areas 4, 5 and 7. The results are given in table VII.

Apparently, only the youngest age groups of herring contribute significantly to the predation of plaice eggs. Yearly variation in the number of plaice eggs per herring appears to be small for the 2 and 3 year olds but increases with age. Undoubtedly, this will be caused to a large extent to differences in distributions of the older herring. Whereas the 2 and 3 year old herring were mainly distributed in the plaice egg area in all years, in 1983 the older herring were more widely spread over the central and southern North Sea than in the preceding years (cf table II).

To estimate the average number of cod eggs per herring by age group the same procedure was followed as for plaice eggs. The estimated number of cod eggs is generally lower than of plaice eggs, but in general the predation pattern is rather similar.

Larval predation.

Occasionally larvae of plaice were found in herring stomachs, although in very low numbers (table VI). It should be noted that in fact these values are based on only three larvae found.

Small numbers of herring larvae were found more consistently in the stomachs in area 6 in all years and also occasionally in areas 3 and 7.

DISCUSSION

The spatial distribution of predation of plaice eggs as observed in this study closely resembles the pattern in egg production as described by HARDING et al. (1978). In area 4 predation of plaice eggs could be expected but was not observed. However, in this area only in 1980 a small number of samples have been collected, the majority of which was empty.

Also for cod eggs the spatial distribution corresponded to the spatial pattern in egg production as observed by Daan (1978) in

the southern North Sea. In the northern North Sea extensive spawning of both cod and haddock is known to take place, but egg predation is apparently insignificant. In this area the larger size classes of herring are predominant and also within comparable size classes they had on average more food and larger food items (euphausiids versus copepods) in their stomach than in the southerly areas. This suggests that when food conditions are better eggs may be avoided.

The decrease in predation of plaice and cod eggs with increasing size of the herring probably is not only caused by differences in spatial distribution of the age groups but also by size specific preference. Comparing the average number of plaice eggs between size classes in area 6, the predation of plaice eggs strongly decreases in the herring greater than 20 or 25 cm. For cod eggs such a shift is less apparent. In an earlier paper, DAAN (1976) suggested on the basis of a comparison of stomach samples and plankton samples from a restricted area that in general herring appear to prefer the larger plaice eggs. Because the total egg production of plaice and cod in the North Sea is roughly similar (table V), and takes place in the same period, the observation that the predation of plaice eggs is greater than of cod eggs therefore also points to a preference of plaice eggs over cod eggs, especially by the smaller herring.

When number of eggs produced by year (table V), the herring stock sizes (table IV) and the average number of eggs per stomach (table VI) are known, some assumptions have to be made about the turnover time of eggs in the stomach and of the number of days over which predation takes place in order to be able to calculate the total consumption of plaice and cod eggs and thus the fraction of eggs being eaten.

With reference to the digestion rate, SAVAGE (1937) found that under experimental circumstances at 6.5 degrees C. food remained 30 hours in the guts. DA SILVA and BALBONTIN (1974) observed gut emptying times of 12 and 22 hours at 14.5 and 6.5 degrees C. respectively. These estimates however, cannot be readily used because they apply to the total gut rather than to stomach emptying time. The observation made here (fig 3) that the stomach weight peaks around noon and subsequently declines to about 30% of the peak value in 4 hours time indicates that stomach emptying time might be in the order of 12 hours and the stomach emptying time has been assumed accordingly. stomach emptying time of 12 hours has been assumed. In that case the daily consumption equals two times the average number of prey items per stomach, both in case feeding is constant over the 24 hour period and when feeding is restricted to 12 hours of the day only.

The time of year over which the egg predation takes place can only roughly be estimated from the published production curves of plaice eggs (HARDING et al. 1978) and cod eggs (DAAN 1979). The main spawning season of North Sea plaice covers the months

of January and February, whereas for southern North Sea cod it is virtually restricted to February. Therefore for plaice and cod egg predation periods of 8 weeks (56 days) and 4 weeks (28 days) have been assumed respectively.

In table VIII the thus calculated predation rates are given for the three years separately. For plaice the egg predation rates are in the order of 1%. For cod they are a factor 10 lower.

The estimated egg predation rates are very sensitive for the various assumptions made. The most important assumption appears to be the digestion rate. A reduction in the stomach emptying time from 12 to 6 hours for example would double the predation rate. On the other hand the number of days over which egg predation would operate is unlikely to be out by more than 50%.

An important reason why the predation is underestimated stems from the fact that the herring stock has been assessed under the assumption of a constant natural mortality of 0.1 (M) over all age groups. Recent observations indicate that particularly the younger age groups of herring are heavily preyed upon by cod and whiting. The value of natural mortality therefore, is almost certainly underestimated (DAAN 1983, ANON. 1984). The effect of increasing M in herring stock assessment could result in considerably larger stock sizes of the younger age groups, which represent the more important egg consumers. Although the effect of this has to await a reliable multispecies assessment, the effect could easily double predation rates.

The fair agreement between the average number of eggs per herring between the different years suggests that increased sampling effort is not likely to change markedly the estimated average level of predation. However, the possibility it can not be excluded that seasonal trends in the egg predation by herring exist, which might give rise to changes in the food intake and therefore in the egg predation in the course of the spawning season.

Taking all these proviso's into account it will be clear that the estimates can only give a rough indication of the actual predation rate. However, although the total biomass of herring in the years sampled was still well below the level observed before the sixties, it would not seem likely on the basis of the results presented here, that the observed increases in demersal recruitment can be accounted for entirely by a reduced predation of herring on the egg stages.

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Table I. Number of herring stomachs analysed and between parenthesis the number of statistical rectangles sampled.

Size group:	7-10	10-15	15-20	20-25	25-30	30-40	TOTAL
Year: 1980							
Round fish area							
1	0 (0)	0 (0)	25 (1)	39 (9)	101 (10)	80 (9)	245
2	0 (0)	20 (2)	42 (3)	8 (4)	1 (1)	0 (0)	71
3	1 (1)	49 (7)	73 (11)	114 (15)	38 (9)	4 (2)	279
4	0 (0)	76 (3)	54 (4)	13 (3)	2 (1)	0 (0)	145
5	0 (0)	0 (0)	25 (1)	0 (0)	0 (0)	0 (0)	25
6	95 (4)	423 (20)	390 (16)	83 (5)	25 (1)	0 (0)	1016
7	0 (0)	134 (6)	125 (5)	0 (0)	0 (0)	0 (0)	259
TOTAL	96 (5)	702 (38)	734 (41)	257 (36)	167 (22)	84 (11)	2040
Year: 1982							
Round fish area							
1	0 (0)	0 (0)	0 (0)	2 (1)	23 (3)	65 (4)	90
2	0 (0)	4 (1)	75 (3)	24 (1)	22 (1)	0 (0)	125
3	0 (0)	0 (0)	100 (4)	106 (5)	7 (3)	0 (0)	213
4	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
5	0 (0)	0 (0)	8 (2)	50 (2)	91 (4)	2 (1)	151
6	0 (0)	516 (22)	380 (17)	125 (10)	52 (1)	8 (2)	1081
7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
TOTAL	0 (0)	520 (23)	563 (26)	307 (19)	195 (12)	75 (7)	1660
Year: 1983							
Round fish area							
1	0 (0)	0 (0)	0 (0)	4 (2)	46 (5)	50 (5)	100
2	0 (0)	60 (8)	362 (30)	99 (11)	51 (8)	23 (4)	595
3	0 (0)	50 (7)	63 (7)	80 (9)	65 (10)	19 (4)	277
4	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
5	0 (0)	7 (1)	3 (1)	0 (0)	0 (0)	0 (0)	10
6	0 (0)	247 (22)	201 (24)	189 (19)	78 (12)	11 (3)	726
7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0
TOTAL	0 (0)	364 (38)	629 (62)	372 (41)	240 (35)	103 (16)	1708

Table II. Distribution (%) of herring by age group over the round fish areas in February in the International Young Fish Survey.

Age:	2	3	4	5	6+
Year: 1980					
Round fish area					
1	0.0	36.6	95.6	98.3	98.4
2	0.5	0.4	0.1	0.2	0.1
3	3.4	19.7	3.4	1.1	0.9
4	3.3	1.4	0.4	0.4	0.3
5	27.1	7.1	0.0	0.0	0.0
6	57.0	34.3	0.7	0.0	0.2
7	8.7	0.3	0.0	0.0	0.0
Year: 1982					
Round fish area					
1	0.0	5.2	49.5	75.6	88.6
2	7.5	12.2	12.8	4.7	9.1
3	21.2	22.2	10.1	1.5	2.1
4	15.4	5.6	3.0	0.6	0.2
5	26.7	3.6	13.9	0.0	0.0
6	16.1	48.0	9.1	17.7	0.0
7	13.1	3.2	1.6	0.0	0.0
Year: 1983					
Round fish area					
1	0.0	0.1	7.7	28.4	76.1
2	16.4	44.8	30.3	28.6	8.0
3	17.0	17.5	31.6	18.3	6.1
4	20.6	16.1	3.8	2.1	1.4
5	6.3	6.3	20.1	16.8	6.2
6	32.3	13.2	4.1	3.6	1.3
7	7.4	2.1	2.4	2.2	1.0

Table III. Age composition of the IYFS catch in comparison with that of the VPA (Anonymus 1984) for 1980, 1982 and 1983.

Age:		2	3	4	5	6+
1980	IYFS	84.3	5.1	4.5	2.1	4.1
	VPA	30.4	24.7	13.1	11.2	20.6
1982	IYFS	64.7	32.5	1.0	0.7	1.1
	VPA	53.6	24.8	6.3	5.2	10.1
1983	IYFS	79.8	13.0	3.6	1.4	2.3
	VPA	52.7	26.5	10.2	3.1	7.5

Table IV Herring stock size in 1980, 1982 and 1983 by age group in millions (from ANON. 1984).

Year:	1980	1982	1983
Age group:			
2	1420	3639	5742
3	418	1666	2495
4	339	773	1252
5	180	196	481
6+	437	476	502

Table V Estimated egg production (billions) of plaice and cod in 1980, 1982 and 1983.

Species:	PLAICE	COD
Year:		
1980	33	40
1982	36	39
1983	42	32

Table VI. Number of stomachs sampled (N), number of stomachs with food (S), mean stomach weight (SW), total number of prey items (I) and the number of cod and plaice eggs and herring larvae per herring stomach.

Year:	1980							1982							1983						
Size	N	S	SW	I	Cod	Plaice	Herr	N	S	SW	I	Cod	Plaice	Herr	N	S	SW	I	Cod	Plaice	Herr
Area 1																					
15-20	25	24	.41	11.8				0	0						0	0					
20-25	39	12	.26	6.2				2	0	.00	.0				4	4	1.98	35.5			
25-30	101	36	.22	6.6				23	16	.06	1.0				46	22	4.31	91.4			
30-40	80	17	.07	2.0				65	61	.51	55.2				50	24	3.03	65.9			
Area 2																					
10-15	20	3	.03	1.5				4	4	.07	4.5				60	22	.02	3.0			
15-20	42	9	.06	.5				75	74	.11	12.5				362	90	.01	1.2	.13	.01	
20-25	8	0	.00	.0				24	23	.79	7.0				99	45	.08	3.5			
25-30	1	0	.00	.0				22	19	.85	22.0				51	28	.41	10.0			
30-40	0	0						0	0						23	9	.14	4.6			
Area 3																					
7-10	1	1	.00	.0				0	0						0	0					
10-15	49	1	.04	2.5				0	0						50	25	.02	2.7		1.7	.01
15-20	73	2	.00	.2				100	69	.35	5.0				63	26	.02	2.2		1.9	
20-25	114	23	.07	1.4				106	54	.40	3.5				80	31	.06	2.4	.04		.04
25-30	38	7	.15	2.5				7	0	.00	.0				65	25	.32	7.5		.6	
30-40	4	0	.00	.0				0	0						19	4	1.02	33.6			
Area 4																					
10-15	76	12	.01	.4				0	0						0	0					
15-20	54	2	.00	.2				0	0						0	0					
20-25	13	1	.00	.4				0	0						0	0					
25-30	2	0	.00	.0				0	0						0	0					
Area 5																					
10-15	0	0						0	0						7	5	.02	2.6	.29	.71	
15-20	25	2	.00	.4	.44			8	0	.00	.0				3	2	.02	1.7		.33	
20-25	0	0						50	23	.02	.5	.32	.04		0	0					
25-30	0	0						91	15	.00	.5	.31	.08		0	0					
30-40	0	0						2	0	.00	.0				0	0					
Area 6																					
7-10	95	65	.05	52.1	.20	.10		0	0						0	0					
10-15	423	243	.09	48.0	.16	.32	.02	516	418	.08	132.8	.21	2.49	.05	247	107	.03	16.7	.16	1.01	
15-20	390	166	.09	9.4	.29	.40	.04	380	333	.09	86.6	1.11	6.01	.04	201	100	.03	12.6	.36	1.91	.02
20-25	83	24	.13	19.7		.05		125	81	.11	84.5	.17	.17		189	61	.02	10.0	.22	1.79	.03
25-30	25	24	.07	80.6			.01	52	41	.03	59.8	1.32	.27		78	34	.09	79.5	.19	.13	.02
30-40															11	10	.18	34.5	2.00	.56	
Area 7																					
10-15	134	72	.22	17.86		.96		0	0						0	0					
15-20	125	82	.55	25.38		1.65	.01	0	0						0	0					

Table VII. Average stomach content of herring in numbers of prey items per 1000 fish (corrected for missing samples).

Age:	2	3	4	5	6+
Year: 1980					
Cod eggs	167.1	56.8	.1	.3	.2
Plaice eggs	409.8	81.1	.1	.1	.0
Plaice larvae		9.7	.1		
Herring larvae	11.1	5.7	.6	.1	.1
Year: 1982					
Cod eggs	62.4	233.9	162.6		.1
Plaice eggs	657.7	579.8	36.6		.3
Herring larvae	8.2	3.5			
Year: 1983					
Cod eggs	97.7	56.4	73.9	56.5	25.9
Plaice eggs	808.1	452.6	168.2	134.9	24.7
Plaice larvae		1.2	.2	.2	
Herring larvae	3.2	7.1	5.5	1.0	.3
Year: Total (1980+1982+1983)					
Cod eggs	135.4	93.6	58.4	43.3	21.3
Plaice eggs	989.5	467.0	76.7	64.1	12.5
Plaice larvae		1.3	.0	.1	
Herring larvae	10.0	7.5	2.3	1.1	.1

Table VIII. Total consumption of fish eggs and larvae in numbers per day; total predation over the spawning season (P; millions) and the estimated fraction of the total number produced (F).

Year	Prey	N/Day	P	F
1980	Cod eggs	267.9	14980	.0004
	Plaice eggs	1643.2	237776	.0072
	Plaice larvae	0.6	?	?
	Herring larvae	18.3	?	?
1982	Cod eggs	711.5	39844	.0010
	Plaice eggs	4454.3	498904	.0139
	Plaice larvae	2.2	?	?
	Herring larvae	50.7	?	?
1983	Cod eggs	1114.2	62384	.0019
	Plaice eggs	6976.5	809274	.0193
	Plaice larvae	3.3	?	?
	Herring larvae	79.3	?	?

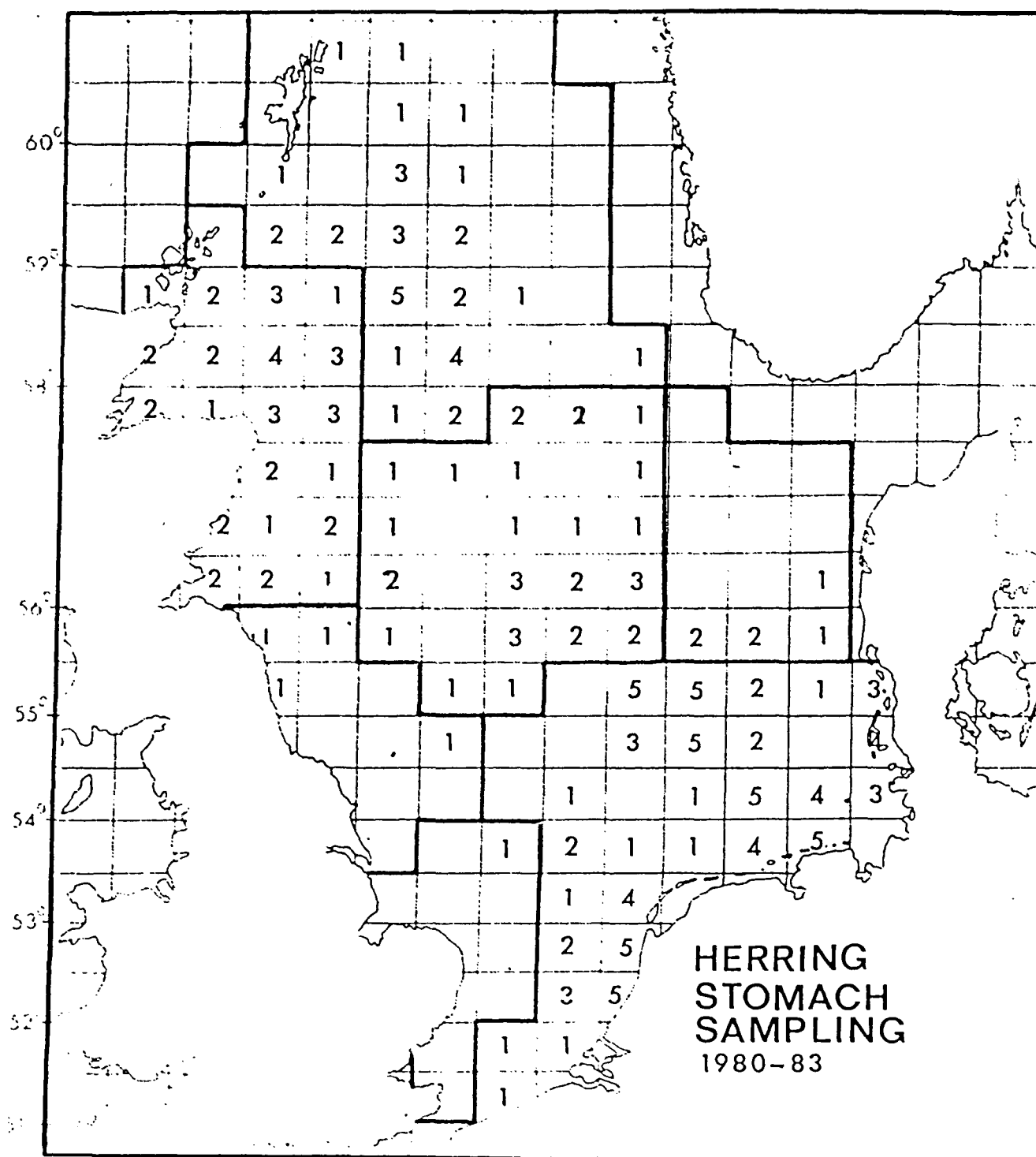


Figure 1 - Number of stomach samples of herring taken per statistical rectangle in 1980, 1982 and 1983.

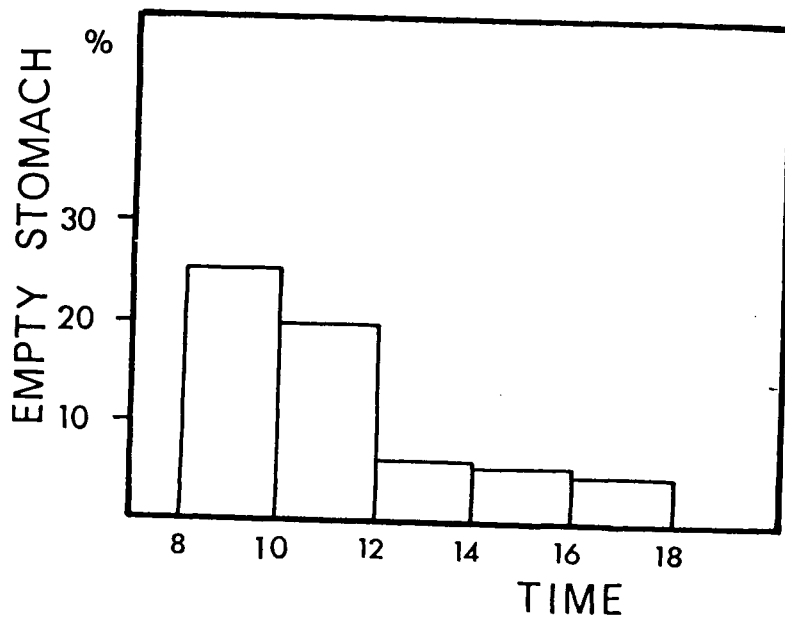


Figure 2 - Percentage of empty stomachs in the course of the day (February 1982).

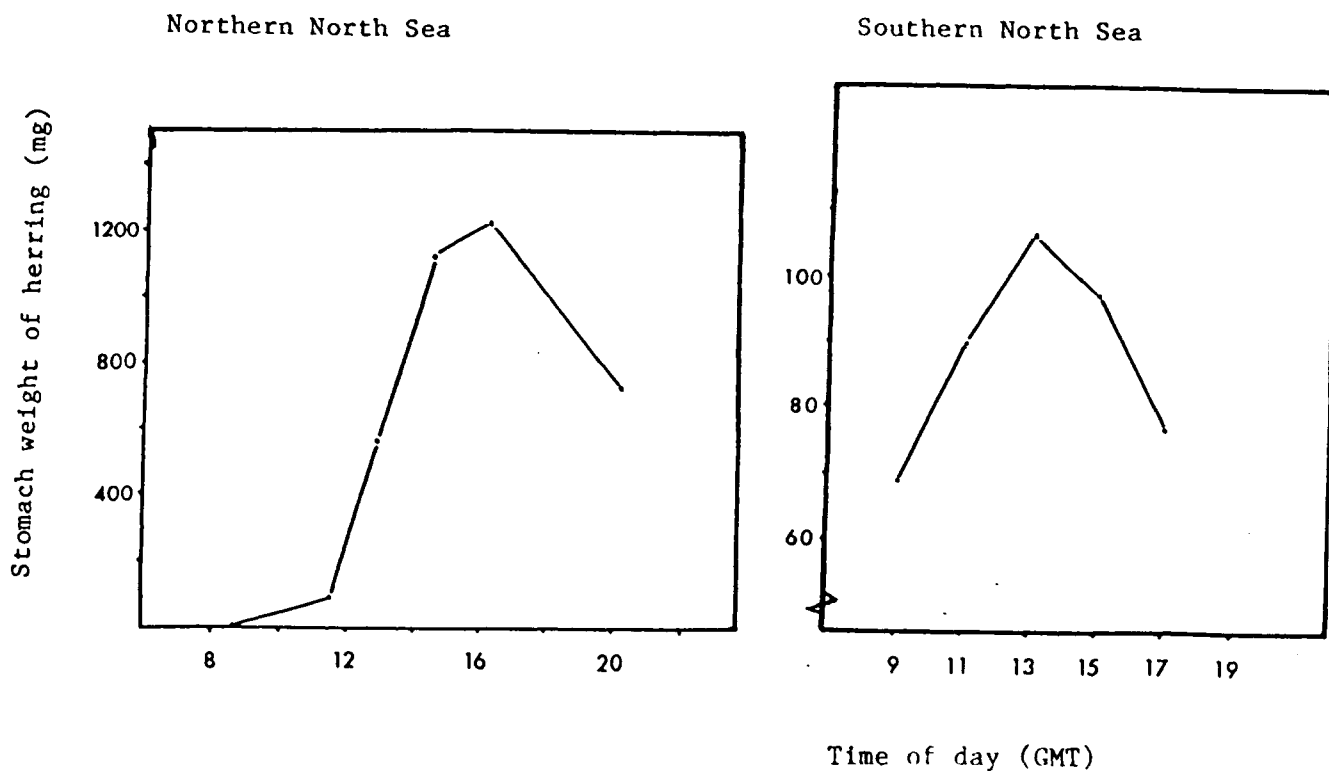


Figure 3 - Mean stomach weight (mg) in the course of the day in the in the northern and douthern North Sea