Temporal and spatial variation in predation on juvenile herring (*Clupea harengus* L.) by Northeast Arctic cod (*Gadus morhua* L.) in the Barents Sea in 1984–1997

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Previous studies indicate that predation by Northeast Arctic cod is an important cause of natural mortality of juvenile Norwegian spring-spawning herring in the Barents Sea. In this paper broad scale temporal and spatial variation in the predator–prey interaction between these two species in the Barents Sea was analysed. The analysis was based on cod stomach data from this area in 1984–1997. The predator–prey interaction between cod and juvenile herring in the Barents Sea was highly variable in time and space. On a yearly basis the most intense predation occurred in years with strong year classes of herring in the Barents Sea. Intensity of predation increased with decreasing abundance of capelin. Seasonal variation in intensity of predation on juvenile herring was low. Maps of the spatial distribution of cod feeding on herring illustrated a difference between the first and second halves of the year. In late winter and spring herring was consumed by cod in a restricted area in the southern part of the Barents Sea. In late summer, autumn and early winter herring was consumed by cod in a wide area south of the Polar Front. Climatic variation influenced the spatial distribution in the second half of the year. The results were discussed in the context of broad scale ecosystem dynamics in the Barents Sea.

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Introduction

The Norwegian spring-spawning herring (*Clupea harengus* L.) has its nursery areas in fjords along the Norwegian coast and in the Barents Sea. After a growth period of about one to two years in the fjords or three to four years in the Barents Sea the juveniles migrate westwards and join the spawning stock in the Norwegian Sea (Dragesund, 1970; Dragesund *et al.*, 1980; Hamre, 1990). High recruitment to the spawning stock and fishery depends on abundant year classes in the Barents Sea. In periods with high spawning stock abundance, the individuals descending from this area usually constitute about 80% of an individual year class when fully recruited to the spawning stock (Holst and Slotte, 1998).

The Norwegian spring-spawning herring exhibits very high variation in year-class strength. Strong year classes seem to be correlated with periods of high inflow of Atlantic water into the Norwegian and Barents Sea (Hamre, 1994). Some of this variation may be an effect of the ecological interactions between cod (*Gadus morhua* L.), capelin (*Mallotus villosus* Müller 1776) and juvenile herring in the Barents Sea (Hamre, 1994). Year classes of Norwegian spring-spawning herring that are abundant at the 0-group stage in the Barents Sea can be strongly reduced during the first years of life (Barros and Toresen, 1998). Barros *et al.* (1998) found that more than 90% of this inter-cohort variation in mortality can be explained by the ratio between the abundances of capelin and juvenile cod. They suggested that when the capelin–cod ratio is low, the cod consume more juvenile herring than if the ratio is high, to compensate for the shortage of capelin.

Earlier studies on the diet of cod in the Barents Sea (summarised by Bogstad and Mehl, 1997) emphasise capelin as the most important prey for cod in this area on a broad scale. However, studies by Mehl (1989) and

Orlova *et al.* (1995) demonstrate that cod also has the potential of generating high predation mortality on juvenile herring in the Barents Sea on a narrow temporal and spatial scale. For example, the 1984–1985 year classes were strong at the 0-group stage but suffered heavy predation from young cod and did not contribute to the adult stock as expected (Mehl, 1989).

The main purpose of this work is to identify important periods and geographical areas for predation on juvenile herring by cod in the Barents Sea based on stomach content data from cod covering the period 1984–1997. This is considered as vital information for future studies on cod as a cause of natural mortality of juvenile herring in the Barents Sea. The study will focus on broad scale temporal and spatial trends. The trends will be related to population dynamics and distribution of juvenile herring, and climatic variation in the Barents Sea. The analyses will cover the following aspects:

(i) Year-to-year and seasonal variation in the occurrence of herring in cod stomachs.
(ii) The relationship between occurrence of herring in cod stomachs and abundance of juvenile herring and capelin.
(iii) Identification of the main geographical areas for predation by cod on juvenile herring and its seasonal variation.
(iv) Climatic effects on the main geographical areas for predation by cod on juvenile herring.

The results will be discussed in the context of broad scale ecosystem dynamics in the Barents Sea, during the period of interest.

Materials and methods

This study is based on the analysis of stomach content from individual Northeast Arctic cod in the Barents Sea from the period 1984–1997.

The Barents Sea is defined as the area bordered by the continental slope towards the Norwegian Sea (west), a line between Spitsbergen and Franz Josef Land (north), Novaya Zemlya and a line from the northern tip of this island towards Franz Josef Land (east), and the coast of northern Norway and the Kola Peninsula (south) (Figure 1). It is a shallow continental shelf sea with an average depth of 230 m. The water masses are divided into a northern and a southern part by an east-west oceanic front at approximately 75–76°N (the Polar Front). Temperature variations depend mainly on the activity and properties of the inflow of Atlantic water. The temperature regime is characterised by alternating periods with high and low temperature of variable duration. In the southern part, which is dominated by Atlantic water masses, the temperature at 50–200-m depths fluctuates between 3–7°C throughout the year (Furevik, 2001). In the northern part, which is dominated by Arctic water masses, the temperature is mostly below 0°C. Details on the physical oceanography of the Barents Sea can be found in Loeng (1989, 1991), Tereshchenko (1996), and Loeng *et al.* (1997). The biological communities, with their function and productivity, are described by Hamre (1994), Loeng (1989), Sakshaug (1997), and Sakshaug *et al.* (1994).

Stomach content data from cod were extracted from the joint IMR-PINRO stomach database at the Institute of Marine Research (IMR). This database includes stomachs sampled during both Norwegian and Russian regular surveys. Note that most of these surveys are not targeted for stomach sampling. Most of the cod were caught by bottom trawl, mainly in the first quarter of the year and in August–October. A detailed description of the general survey methodology can be found in Jakobsen *et al.* (1997) and Lepesevich and Shevelev (1997). Note that some of the data are from surveys of pelagic fish and shrimp. The sampling design has undergone modifications during the study period. The maximum number of stomach samples per 5-cm group of cod has changed from five per haul in the period 1984–1991, two in 1992–1995 and one after 1995 (Bogstad *et al.*, 1995; Jakobsen *et al.*, 1997). Details about the sampling procedures are given in Mehl (1989) and Mehl and Yaragina (1992).

The data base contained a total of 99 705 stomach samples from the study area during the period 1984–1997. Of these, 143 were excluded because they had regurgitated their stomach content, leaving 99 562 stomach samples from 4095 trawl hauls.

The data were divided into five sample intervals of the year, motivated by the temporal distribution of hauls: 1 Jan–31 Mar, 1 Apr–31 May, 1 Jun–9 Jul, 10 Jul–15 Oct, and 16 Oct–31 Dec (Figure 2). In the following they are referred to as intervals 1–5, respectively. The time span of these intervals was kept as short as possible, at the same time trying to avoid that major surveys were spread over two intervals. Avoidance of major changes of the main physical and biological factors in the ecosystem within single intervals was also considered when choosing the time structure of the data. This was done to achieve as homogenous samples as possible within each interval. Note that the temporal and spatial distribution of hauls varied among years and intervals. The Appendix summarises the spatial distribution of the hauls representing the raw data.

The data were further refined in three steps to suit the analysis in this work. Stomachs sampled in intervals with fewer than eight hauls (Table 1), or where the hauls are aggregated around few (<3) positions (interval 3 in 1988, 1990, and 1992), were excluded from the analysis. Cod smaller than 20 cm constituted less than 1% of all cod that had eaten fish, and 0.5% of all cod that had eaten herring. As a consequence cod smaller than 20 cm were excluded from the data, because of their low
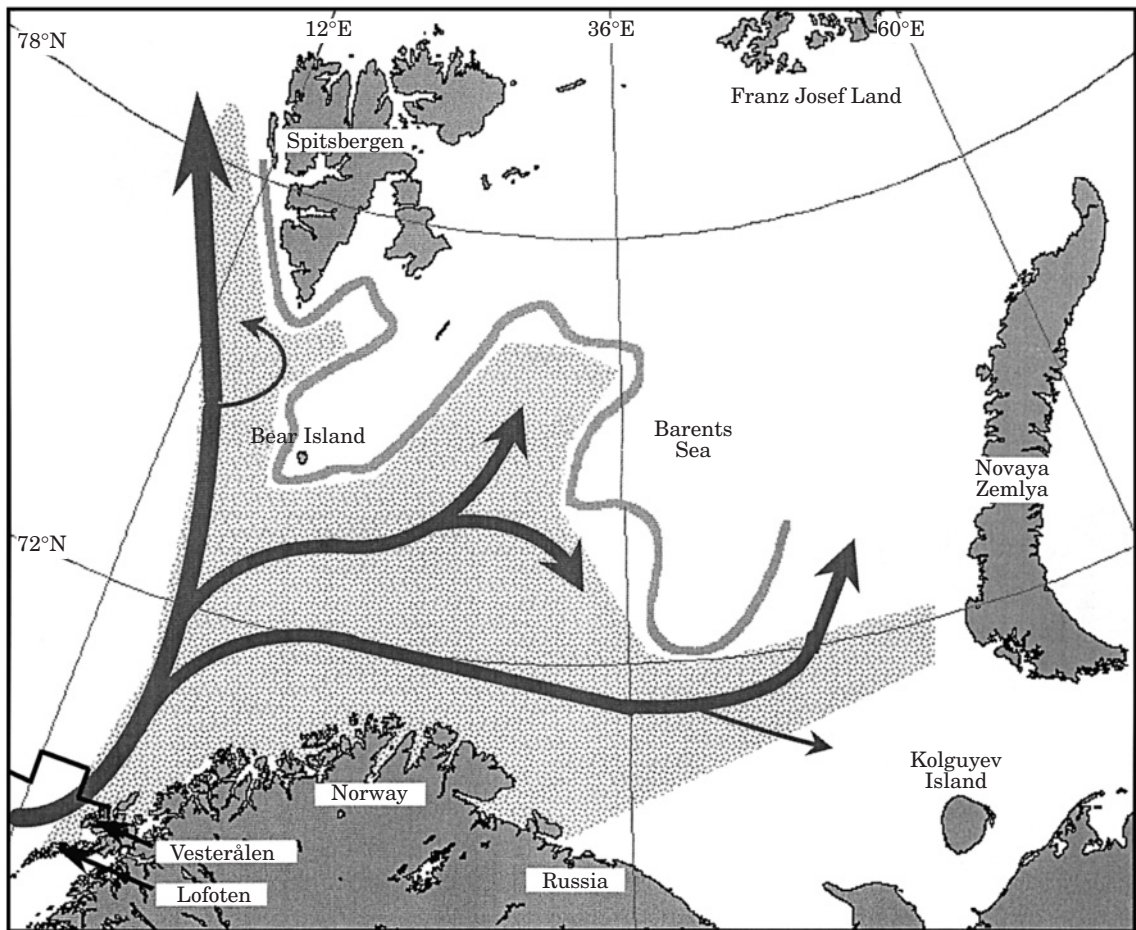
Figure 1. Map of the study area. Approximate location of the Polar Front indicated by light grey line. Note that the position varies considerably in the eastern part. Inflow of Atlantic water indicated by dark grey arrows. Grey shading indicates the potential distribution area of juvenile Norwegian spring-spawning herring. The black line in the southwestern corner indicates the southern limit of the study area along the Norwegian coast. Modified after Dragesund *et al.* (1980) and Loeng (1989).

propensity to eat fish. These actions resulted in a total of 91 586 stomach samples from 3954 trawl hauls in the Barents Sea in the period 1984–1997, 19 312 of these were empty.

Occurrence of herring in the cod stomachs was calculated for individual trawl hauls i as:

$$FO_i = \frac{m_i}{M_i}$$

where m_i denotes number of stomachs containing herring in haul i and M_i denotes number of non-empty stomachs from cod $\geqslant 20$ cm in haul i. This quantity is referred to as frequency of occurrence of herring by haul, and was calculated for hauls with more than four cod stomachs. Assuming that the cod stomachs in a trawl haul is a simple random sample from the area of the haul, and $M_i \ll$ total number of fish in the same area (i.e. infinite population), FO_i is an unbiased estimator of

the frequency of occurrence of herring in cod stomachs from this area (Cochran, 1977). The variance and standard deviation of FO_i were calculated as:

$$v(FO_i) = \frac{FO_i q_i}{M_i - 1}$$

and:

$$sd(FO_i) = \sqrt{\frac{FO_i q_i}{M_i - 1}}$$

respectively, where $q_i = 1 - FO_i$ (Cochran, 1977). FO_i was displayed on maps for each year and interval in order to analyse the spatial and temporal aspects of predation on herring by cod in the Barents Sea. The standard deviation was used to express the precision of each point estimate. Hauls with fewer than five
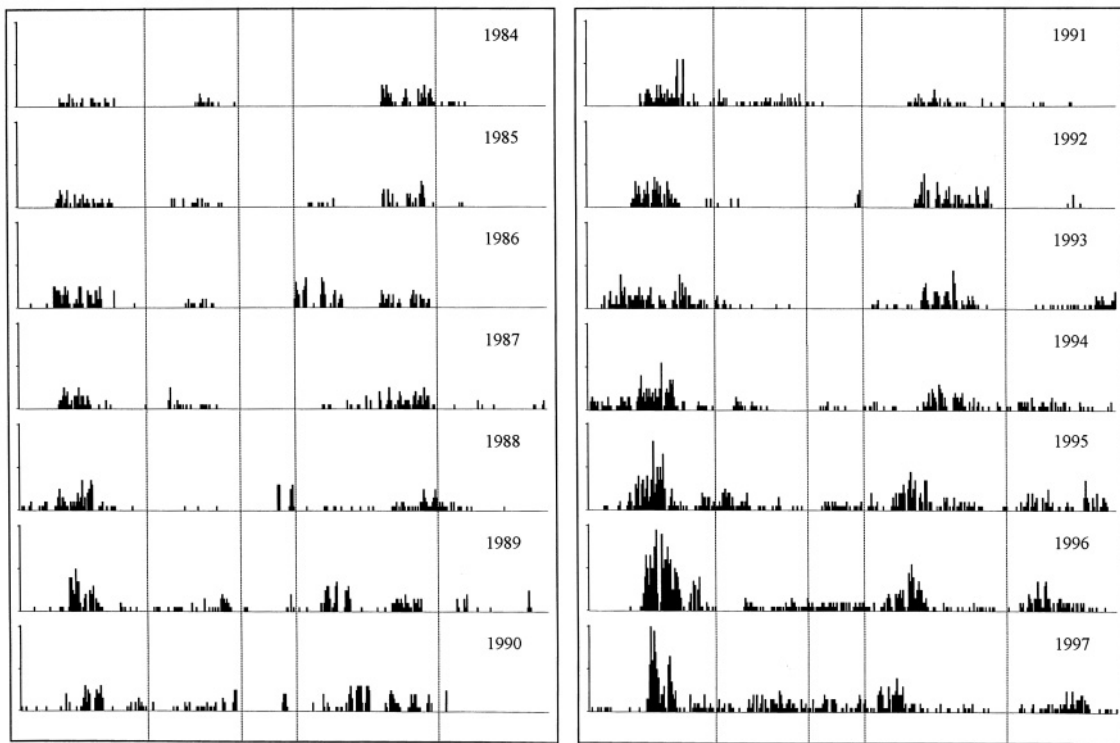
Figure 2. Temporal distribution of trawl hauls with stomach samples of cod from the Barents Sea in 1984–1997. Each column in the histograms represents one day and each x-axis starts with 1 January and ends with 31 December. The tick marks on each y-axis represents ten and 20 trawl hauls. The vertical broken lines represent the division of the year into the five sample intervals defined here.

stomachs, of which some contained herring, were indicated by a common symbol in the maps.

Note that the calculations were based on non-empty stomachs, limiting the analysis to feeding fish. This was chosen since the aim of this study is defining the relative importance of herring in the diet of cod in time and space, not absolute consumption. Preliminary analysis showed that the proportion of empty stomachs varied, particularly with respect to cod size (Figure 3). Including empty stomachs could have distorted the results, since the size distribution of cod varied between hauls. Since the proportion of empty stomachs vary with temperature (Waiwood *et al.*, 1991), local temperature conditions could also cause this. The effect of these problems is most important for the geographic analyses based on individual hauls. Excluding empty stomachs also relates to the problem of distinguishing between fish with empty stomachs and fish that have regurgitated their stomach content during the catch process (Treasurer, 1988).

Here, FO was preferred to mean number or mean weight of prey. This was done to include as much of the data as possible. In several of the stomach samples in the database number of prey was not counted. Weight of prey was measured in all samples, but is highly dependent on how digested the prey is. Possible limitations by using FO were tested with principal component analysis (PCA) in SAS/SIGHT® (SAS Inc., 2000). The analysis was carried out using FO, mean number and mean weight for herring as prey (log-transformed to homogenise the variance), calculated for individual trawl hauls with more than four stomach samples. The PCA showed that the variables were highly correlated, sharing 84% of the total variation among them. Information obtained when using FO was therefore found sufficient in this work. Macdonald and Green (1983) also found high correlation between these three variables in a similar analysis in the Northwest Atlantic.

I defined an area in the Barents Sea referred to as the herring region, based on visual inspection of the spatial distribution of hauls with occurrence of herring in cod stomachs for the whole time series. This procedure was chosen due to insufficient independent data on distribution of juvenile herring in the Barents Sea. A 5 nmi buffer zone was defined around its periphery and hauls within the region plus the buffer zone were recorded for each sample interval. The areas covered in km² by these hauls were calculated.

Mean frequency of occurrence per haul was calculated as the weighted average of all n hauls within each

Table 1. Summary of number of trawl hauls (n), with number of stomachs given as mean per haul, and minimum and maximum. Percent stomachs with food in each sampling interval and year is also presented.

| Year	Interval 1				Interval 2				Interval 3				Interval 4				Interval 5			
	n	Mean	Min–max	Stomachs with food (%)	n	Mean	Min–max	Stomachs with food (%)	n	Mean	Min–max	Stomachs with food (%)	n	Mean	Min–max	Stomachs with food (%)	n	Mean	Min–max	Stomachs with food (%)
1984	31	33.74	4–50	89.96	16	21.56	9–43	77.68	0	—	—	—	65	28.91	2–84	76.37	8	51.13	24–77	69.19
1985	49	35.67	1–98	74.43	18	28.44	2–61	40.63	0	—	—	—	53	31.26	2–131	75.80	2	50.50	33–68	57.43
1986	94	20.87	1–154	71.56	14	33.43	21–48	67.31	0	—	—	—	116	30.96	1–96	86.74	0	—	—	—
1987	58	27.47	5–90	57.44	22	41.50	20–103	83.46	0	—	—	—	83	36.48	1–68	84.05	10	32.30	24–50	78.02
1988	93	24.74	1–51	71.10	3	30.33	30–31	96.70	25	23.28	10–31	99.49	57	31.14	4–88	92.28	19	32.37	11–52	92.85
1989	95	29.07	1–83	82.04	40	34.90	6–85	72.71	10	41.50	11–98	83.61	109	28.94	7–72	91.53	21	12.43	1–25	95.40
1990	74	28.32	1–150	82.11	39	42.62	5–88	79.18	11	26.18	15–31	95.49	126	28.91	6–83	93.33	5	36.80	30–40	90.22
1991	105	36.83	3–135	86.16	46	29.74	9–72	73.68	5	50.80	19–69	77.56	44	31.84	7–68	76.30	5	3.40	2–5	100.00
1992	102	19.71	6–43	59.20	4	9.50	8–10	100.00	8	24.88	10–50	99.50	104	21.89	1–67	71.50	5	9.60	8–10	77.08
1993	150	16.65	1–53	73.38	10	31.80	2–100	61.95	0	—	—	—	100	37.01	1–76	77.76	41	16.76	3–30	47.16
1994	171	18.29	2–50	65.97	20	16.25	4–25	94.15	8	49.88	34–72	45.11	97	22.26	4–67	88.00	51	24.76	10–79	67.93
1995	199	19.69	1–78	67.59	62	26.52	9–55	82.00	28	27.25	12–52	84.67	143	20.69	1–50	86.58	81	12.46	1–50	84.24
1996	292	13.25	1–100	66.41	45	28.40	10–50	80.13	49	28.65	6–50	77.92	138	20.86	1–50	87.88	93	18.13	1–50	78.41
1997	201	16.97	2–53	70.21	87	27.80	1–92	69.24	52	28.21	2–56	70.82	108	25.09	1–50	82.21	75	18.53	1–40	58.63
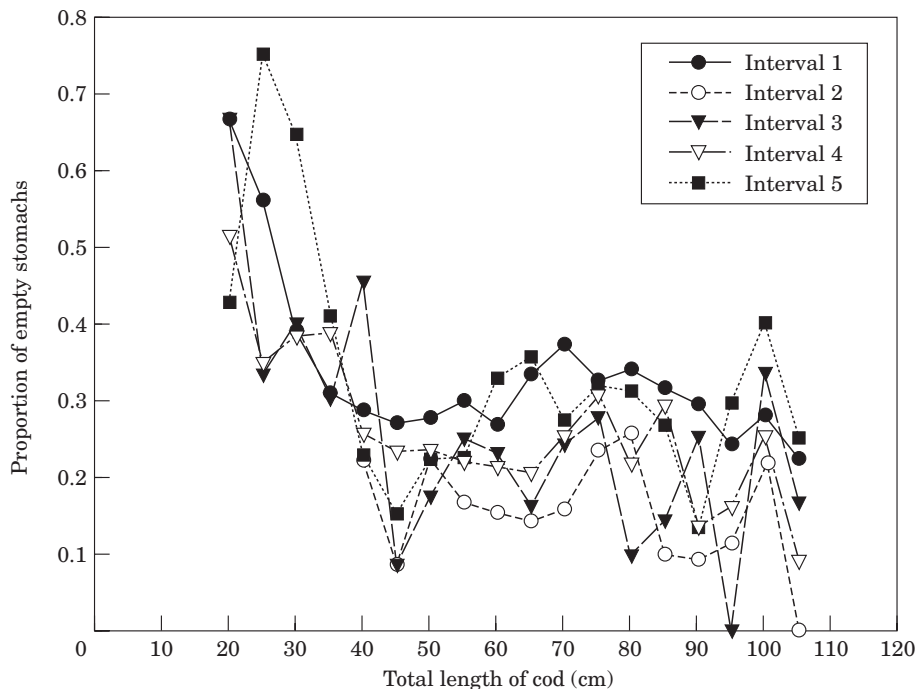
Figure 3. Plots of the relationship between length of cod and proportion of empty stomachs for intervals 1–5, covering the period 1984–1997.

year and interval with more than four stomachs, and occurrence of herring:

$$\hat{\mu}_{FO} = \frac{\sum\limits_{i=1}^{n} FO_i v(FO_i)^{-1}}{\sum\limits_{i=1}^{n} v(FO_i)^{-1}}$$

with standard deviation:

$$sd(\hat{\mu}_{FO}) = \sqrt{\sum\limits_{i=1}^{n} v(FO_i)^{-1}}$$

For each year and interval the number of hauls where herring occurred were calculated as a proportion of all the hauls taken within the herring region plus the buffer zone in the respective year and interval (P). This proportion was multiplied by the mean frequency of occurrence given above to take into account hauls with no occurrence of herring. This product is referred to as Index of Occurrence (IO):

$$IO = \hat{\mu}_{FO} \cdot P$$

This index was used to analyse temporal variation in occurrence of herring in cod stomachs. A sequence of Wilcoxon paired-sample tests (Zar, 1984) involving all combinations of intervals giving five or more pairs was

run to compare differences in IO between sampling intervals. A pair of observations is the IO values from the intervals compared within a year. Holm's sequentially rejective Bonferroni procedure was used to adjust the P-values for multiple tests (Wright, 1992).

The relationship between IO and abundances of juvenile herring and capelin was analysed by multiple regression. Estimates on acoustic abundance (billion individuals) of juvenile herring 0–3 group in 1984–1994 were taken from Toresen *et al.* (1998). For the years 1995–1997 acoustic estimates for 1–3 group were taken from ICES (2000b). For 0-group in this period, acoustic abundance are estimated with a simple linear regression between the 0-group index and acoustic abundance for 0-group in the period 1984–1994 (n=11, r^2=0.64, p=0.0033). Estimates from one year were applied from interval 4 this year and assumed to be representative for the intervals 1–3 next year. Estimates on acoustic abundance (billion individuals) of capelin 1–5 group in 1984–1997 were taken from ICES (2000b). Estimates from previous autumn were applied to each year. The model was formulated according to the notation in Kleinbaum *et al.* (1988):

$$Y = \beta_0 + \beta_1 X + \beta_2 Z + \beta_3 XZ + E$$

where Y=IO of herring in cod stomachs (arcsine-square root transformed), X=abundance of juvenile herring
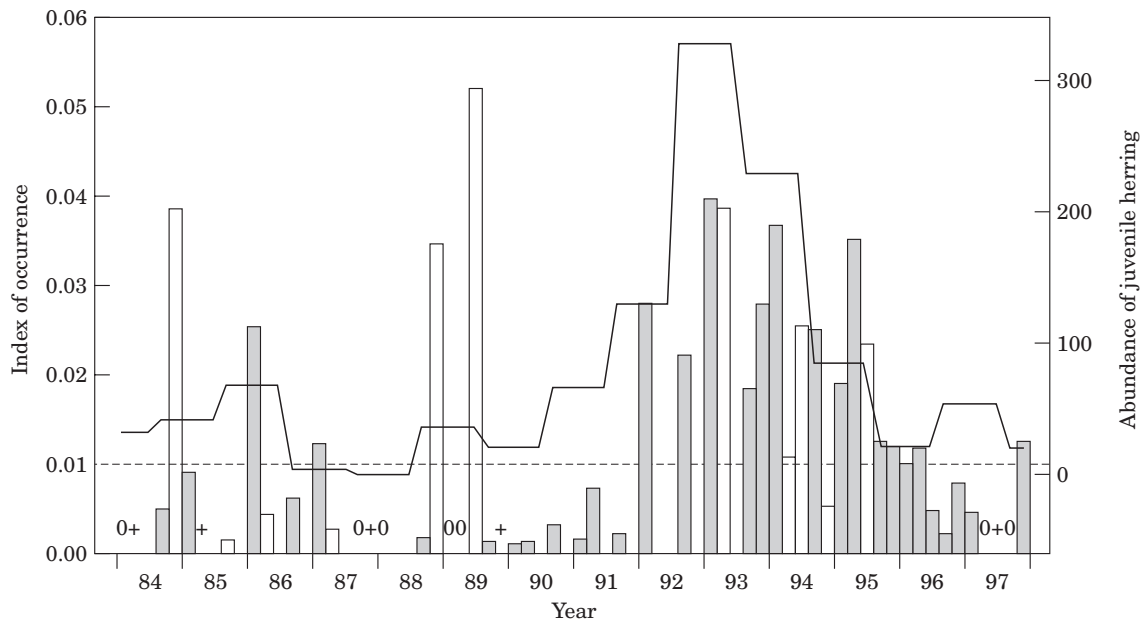
Figure 4. Index of occurrence (IO) of herring in cod stomachs in the Barents Sea during the period 1984–1997. Mean IO represented by broken line. Each bar represents one sampling interval. Bars without fill indicate estimates of low precision due to few trawl hauls or small area coverage (<23 hauls or <632 100 km^2). 0 and + indicates intervals with IO=0 for high and low precision as defined above, respectively. The continuous line indicates acoustic abundance (billion individuals) of juvenile herring 0–3 group (data from Toresen *et al*., 1998). For the years 1995–1997 acoustic estimates for 1–3 group are taken from ICES (2000b). For 0-group in this period, acoustic abundance was estimated with a simple linear regression between the 0-group index and acoustic abundance for 0-group in the period 1984–1994 (n=11, r^2=0.64, p=0.0033).

(square root transformed), Z=abundance of capelin (square root transformed), $\beta_0 - \beta_3$=parameters in the model, E=error term of the model. The assumptions of the model were assessed by diagnostic methods for linear models (Kleinbaum *et al*., 1988; SAS Institute Inc., 2000). The model was run with the GLM procedure in SAS$^{\circledR}$ (Littell *et al*., 1991).

The effects of climate on spatial variation in predation by cod on herring was analysed by mapping the three coldest (1986, 1987, and 1997) and the three warmest (1990, 1991, and 1992) years in the period 1984–1997. Cold and warm years were defined by yearly average sea temperature from the 0–200-m depth interval from the Russian oceanographic section off the Kola Peninsula, located along 33°30′E, between 70°30′N and 72°30′N (Tereshchenko, 1996). Due to seasonal variation in the spatial distribution of herring in cod stomachs, the analysis of climatic effects was done separately for the intervals 1–3 and 4–5.

The maps were displayed in polar stereographic projection with the GIS-software MapInfo 4.1 for Windows (MapInfo Corporation, New York, NY, USA). The area calculations were also done with this software. Database operations, calculations and statistical analysis were done with SAS$^{\circledR}$ 8.0 for Windows (SAS Institute Inc., Cary, NC, USA).

Results

Herring was found in the stomachs of cod in 417 out of the 2938 trawl hauls within the herring region. The number of hauls outside this region was 991. Of all hauls where herring was eaten and the number of stomachs exceeded four, the cumulative percent of FO of 0.10, 0.20, and 0.50 was 51.4%, 78.0%, and 95.2%, respectively. Highest observed FO was 0.80. Proportion of total hauls with herring (P) and weighted mean FO by interval within years were not correlated. Table 2 summarises the occurrence of herring in cod stomachs in the Barents Sea by year and interval. Note that this table also includes hauls with less than five stomachs.

Occurrence of herring in cod stomachs expressed as IO varied temporally during the 14 years covered by this study (Figure 4). Some of this variation was due to variation between sample intervals in number of hauls and the absolute size of the area covered by the hauls within the herring region. Quartiles in the distribution of these quantities were used to segregate the intervals in four groups of different number of hauls or different area coverage. The variance in IO was significantly different among these groups (Levene's test, F: 3.0473, p<0.05 for number of hauls and F: 2.7933, p<0.05 for area coverage). The first quartile (number of hauls <23;

Table 2. Summary of observations of herring in cod stomachs. H, h, and P denotes number of stomachs, number of hauls taken within the herring area, number of hauls where herring was found in one or several stomachs, and the ratio h/H, respectively. Frequency of occurrence (FO) per haul is given as mean, minimum and maximum within each sample interval and year.

Year	Interval 1					Interval 2					Interval 3					Interval 4					Interval 5				
				FO					FO					FO					FO					FO	
	H	h	P	Mean	Min–max	H	h	P	Mean	Min–max	H	h	P	Mean	Min–max	H	h	P	Mean	Min–max	H	h	P	Mean	Min–max
1984	29	0	0.00%	—	—	16	0	0.00%	—	—	—	—	—	—	—	40	6	15.00%	0.03	0.02–0.24	8	5	62.50%	0.06	0.03–0.17
1985	47	13	27.66%	0.03	0.02–0.60	15	0	0.00%	—	—	—	—	—	—	—	30	1	3.33%	0.04	—	—	—	—	—	—
1986	81	23	28.40%	0.09	0.03–0.47	11	1	9.09%	0.05	—	—	—	—	—	—	89	10	11.24%	0.05	0.04–0.09	—	—	—	—	—
1987	51	4	7.84%	0.15	0.10–0.57	15	1	6.67%	0.04	—	—	—	—	—	—	51	0	0.00%	—	—	10	0	0.00%	—	—
1988	87	0	0.00%	—	—	—	—	—	—	—	—	—	—	—	—	45	3	6.67%	0.02	0.02–0.05	16	3	18.75%	0.18	0.12–0.42
1989	83	0	0.00%	—	—	40	0	0.00%	—	—	9	3	33.33%	0.16	0.08–0.43	94	3	3.19%	0.04	0.04–0.08	13	0	0.00%	—	—
1990	63	5	7.94%	0.01	0.01–0.13	34	1	2.94%	0.04	—	—	—	—	—	—	98	5	5.10%	0.06	0.05–0.09	—	—	—	—	—
1991	95	3	3.16%	0.05	0.04–0.06	37	5	13.51%	0.05	0.03–0.25	—	—	—	—	—	23	1	4.35%	0.05	—	—	—	—	—	—
1992	90	23	25.56%	0.11	0.06–0.75	—	—	—	—	—	—	—	—	—	—	52	24	46.15%	0.05	0.02–1.00	—	—	—	—	—
1993	137	38	27.74%	0.14	0.06–0.75	10	1	10.00%	0.38	—	—	—	—	—	—	54	21	38.89%	0.05	0.02–0.35	38	6	15.79%	0.18	0.14–0.33
1994	138	39	28.26%	0.13	0.05–0.80	18	3	16.67%	0.06	0.04–0.23	8	2	25.00%	0.10	0.10–0.11	42	10	23.81%	0.10	0.03–0.67	41	4	9.76%	0.05	0.04–0.07
1995	154	34	22.08%	0.08	0.03–0.60	45	22	48.89%	0.07	0.02–0.57	20	7	35.00%	0.07	0.04–0.63	102	14	13.73%	0.09	0.04–0.45	58	14	24.14%	0.05	0.02–0.60
1996	211	21	9.95%	0.10	0.04–1.00	33	5	15.15%	0.08	0.05–0.14	39	4	10.26%	0.05	0.03–0.14	101	2	1.98%	0.11	0.08–0.14	71	7	9.86%	0.08	0.05–1.00
1997	175	12	6.86%	0.07	0.04–0.25	38	0	0.00%	—	—	42	0	0.00%	—	—	94	0	0.00%	—	—	64	8	12.50%	0.10	0.04–0.35

Table 3. Results of the multiple regression describing Index of Occurrence (IO) as a function of herring abundance and capelin abundance. IO was arcsine-square root transformed and abundance of herring and capelin were square root transformed. Note that the interaction term was not significant. Analysis is based on sum of squares of type III (Littell *et al.*, 1991).

Source of variation	d.f.	Sum of squares	Mean square	F-ratio	p
Abundance of herring (X)	1	0.0627	0.0627	30.06	<0.0001
Abundance of capelin (Z)	1	0.0096	0.0096	4.59	0.0392
Error	35	0.0730	0.0021		

area <632 100 km^2) had higher variance than the others, indicating lower precision of the estimates of IO in intervals with low number of hauls or restricted area coverage. Intervals corresponding to the first quartile as described above were not emphasised when discussing the year-to-year trends in IO.

A prolonged period of high occurrence occurred in the period from interval 1 1992 to interval 2 1996. Occurrence of herring in cod stomachs was also higher than average in interval 1 1986, interval 1 1987 and interval 5 1997 (Figure 4).

The results of the analysis of the multiple regression between IO as a function of herring abundance and capelin abundance are summarised in Table 3. In this analysis the intervals with low precision were not included. The interaction term was not significant, and

was deleted from the model. There were significant effects of abundance of herring and capelin abundance on IO (r^2=0.48; d.f.=37; F=15.98; p<0.0001). Estimates of the significant parameters in the model showed that IO was positively correlated to herring abundance (β_1=0.0117) and negatively correlated to capelin abundance (β_2= −0.0020). The effect of the interplay between herring and capelin abundance is illustrated in Figure 5, as a negative correlation between the ratio IO/herring abundance and abundance of capelin.

Index of occurrence did not differ between sample intervals 1, 2, 4, and 5, all years combined. There were only five observations from interval 3 in the data, excluding this interval from the comparisons.

The spatial distribution of occurrence of herring in cod stomachs in each of the 5 sample intervals is
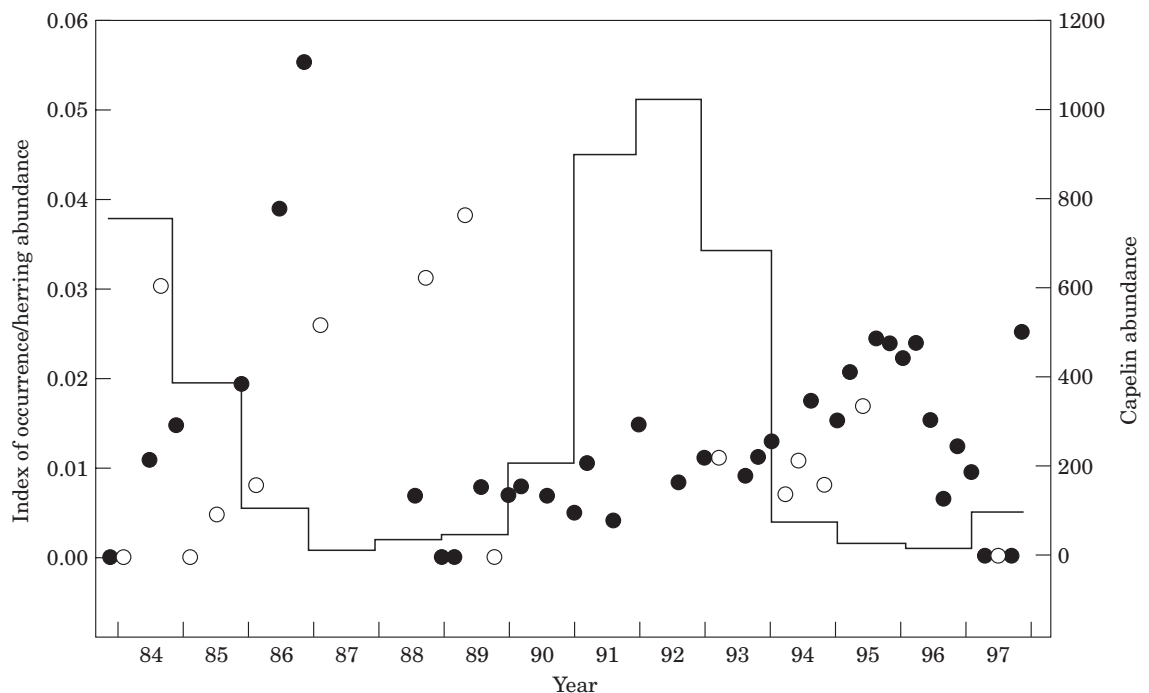
Figure 5. Ratio between Index of occurrence (IO) and acoustic abundance of juvenile herring 0–3 group (as defined in Figure 4) in the Barents Sea during the period 1984–1997. Black and white dots indicate estimates of high and low precision, respectively. Note that the ratios are arcsine-square root transformed. The continuous line indicates acoustic abundance (billion individuals) of capelin 1–5 group taken previous autumn (ICES, 2000b).

illustrated for 1984–1997 combined in Figure 6a–e. Herring were found in cod stomachs in an area south of the Polar Front in the Barents Sea, with minor exceptions. In general the most intense predation was observed in an area east of the 27°E longitude, reaching towards 44°E (approximately). In interval 1 the spatial pattern was similar to the general pattern, with south-eastern limit at 41°E. In this interval, herring also occurred in stomachs in more western areas, particularly in an area north-west of Vesterålen (the southwest tip of the herring region). The first quartile in the length distribution of this herring was 20.5 cm, and they had a mean size of 24.5 cm, indicating that they were adolescents or adults. They were significantly longer than herring in stomachs from the rest of the Barents Sea (t-test, $t=8.571$, $p=0.0001$), which had the first quartile at 12.5 cm and mean of 16.0 cm. Note that prey length are recorded as length intervals in the stomach database (5 cm groups in 1984–1992, and 1 cm groups in 1993–1997), so the length measures referred to here were based on the mid-point of these length intervals. The spatial pattern in interval 2 resembled that in interval 1, but was more restricted in the east-west direction. The same applies to interval 3, although it was difficult to judge this interval due to insufficient sampling. The spatial pattern in intervals 4 and 5 were similar to each other, but different from that in the three first intervals. Herring occurred in stomachs in almost the entire herring region in these intervals. Most of the predation was observed east of the 24°E longitude (approximately), and herring was found in stomachs at the eastern border of the herring area. In addition cod also fed on herring in an area around Bear Island (the northwest tip of the herring region). Most of the herring consumed in this latter area was 10.0–14.9 cm long.

The spatial distribution of herring in cod stomachs did not differ much between cold and warm years in intervals 1–3 (Figure 7a). One exception was two clusters of hauls with high occurrence of herring in an offshore area between 72–73.2°N and 29–34°E. This was from interval 1 in 1986 (cold year), and the size of most of the herring eaten here was 15–19.9 cm. In intervals 4–5, the distribution of herring in cod stomachs was more oceanic in warm years compared to cold years (Figure 7b).

Discussion

Broad scale temporal variation

Predation on juvenile herring by cod in the Barents Sea varied considerably on a yearly basis. Two periods of increased predation on herring by cod were found, characterised by IO above average. These periods were related to the high abundance of juvenile herring observed in this area in 1984–1985 and 1991–1994

(Dragesund *et al.*, 1997; Toresen *et al.*, 1998). The positive correlation between IO and abundance of juvenile herring can be interpreted as an increase in the proportion of the cod population eating herring when abundance of herring increased. Such an increase may be caused by increased encounter rates between cod and herring when herring is abundant.

The use of IO is motivated by the need to summarise the information in FO of herring in cod stomachs by haul and proportion (P) of hauls where herring was eaten. The lack of correlation between mean FO and P within sampling intervals indicates that these two indices contain different information, reflecting different characteristics of the predator prey interaction between cod and herring. Some characteristics of the two measures are therefore discussed below.

FO by haul as calculated here, contains information about the proportion of cod consuming herring given that herring are present. Since it is calculated on a restricted temporal and spatial scale, it is useful for studying variation in predation between different areas within the study area on smaller scales than is possible with IO.

Mean FO within intervals never exceeded 0.18. In interval 2 1993 herring was eaten by cod in only one haul, with FO=0.38. FO was 0.10 or less in approximately half of the hauls, and values higher than 0.50 were rare. This did not change if the analysis was restricted to 1992–1995. These levels of FO are in line with other studies on cod's predation on herring from the same area on a broader temporal and spatial scale (Ponomarenko and Yaragina, 1979; Orlova *et al.*, 1995). The low levels of FO by haul indicates that juvenile herring is of limited importance as prey for the cod population in the Barents Sea, as indicated by consumption estimates (Bogstad and Mehl, 1997). However, this does not rule out the possibility of cod as a significant cause of natural mortality of juvenile herring. Occurrence of hauls with high FO indicates that consumption of herring by cod can be high when considered on restricted temporal and spatial scale. In a study on spatial variability of the predator–prey interaction between cod and capelin in Newfoundland waters, Horne and Schneider (1997) suggest that population interactions among mobile organisms are highly localised in space. This may in turn lead to underestimation of predation rates when field observations made at the scale of predator–prey interactions are averaged over the spatial scale of a population. The local effect of predation on herring by cod is also observed and discussed by Mehl (1989) and Orlova *et al.* (1995). It may be a source of considerable natural mortality of juvenile Norwegian spring-spawning herring, as indicated for the 1984 year class (Mehl, 1989).

The proportion of hauls where herring were eaten by cod contains some information about the spatial
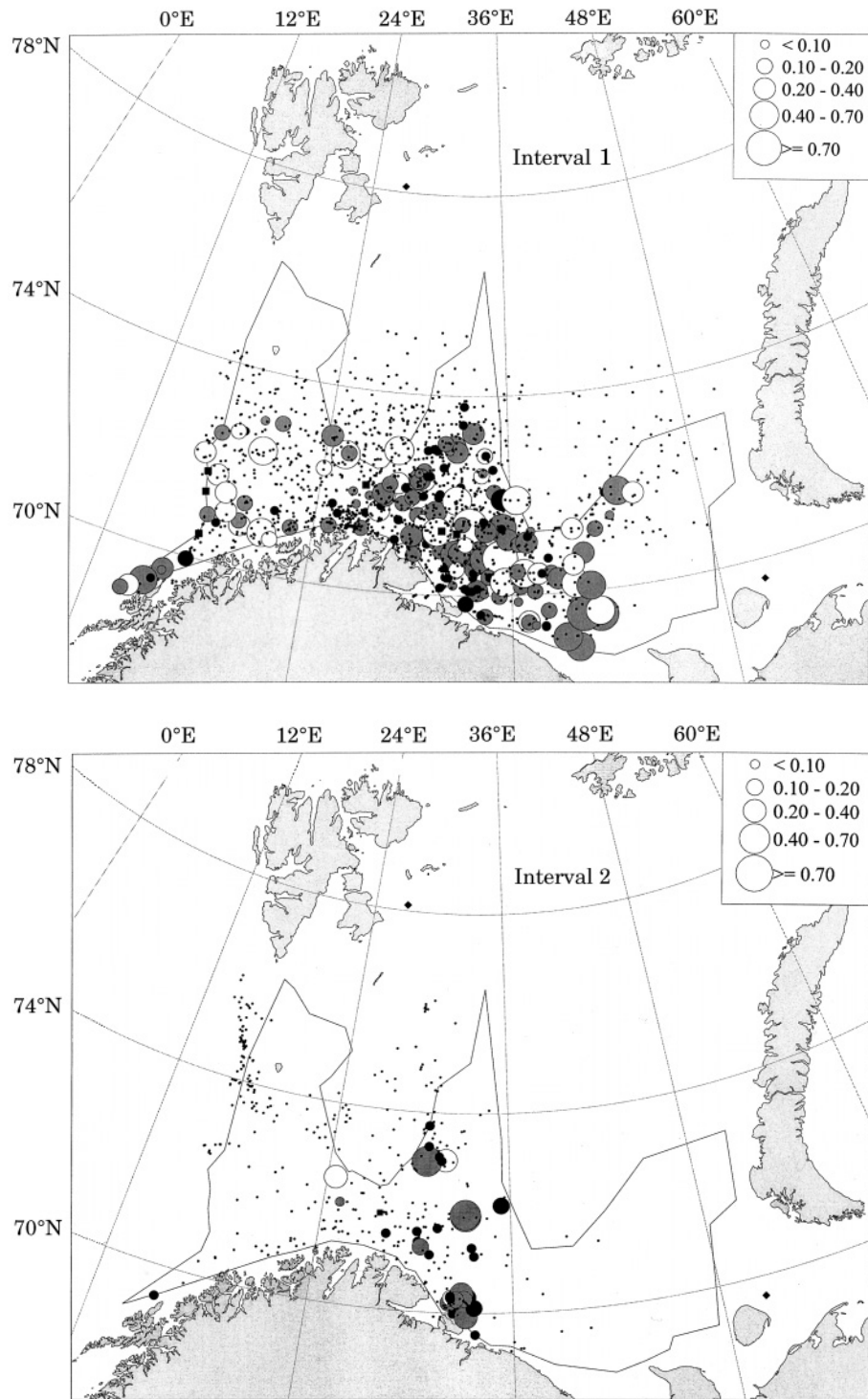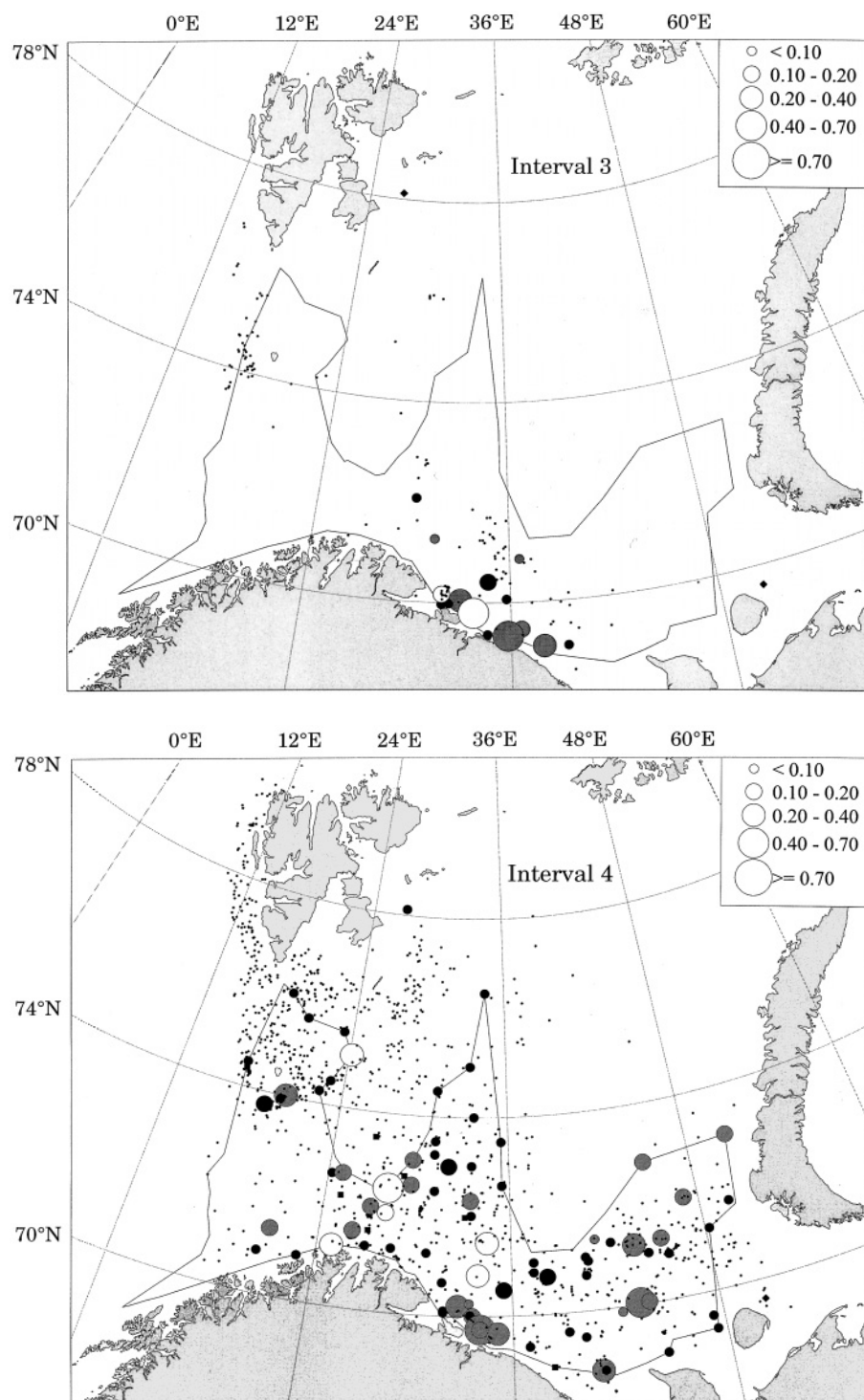
Figure 6. (a) and (b).
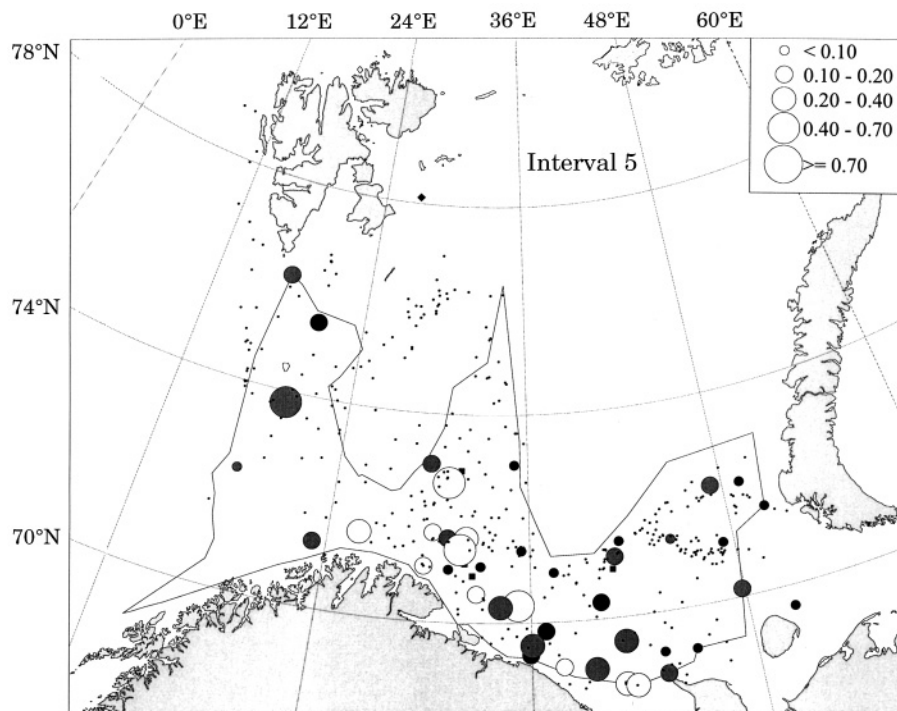
Figure 6. (c) and (d).

Figure 6 (e).

Figure 6. (a)–(e) Map of individual trawl hauls with samples of cod stomachs in the Barents Sea in the period 1984–1997. Dots indicate hauls where herring was not found in the stomachs. Circles indicate hauls where herring was found in the stomachs, with diameter indicating frequency of occurrence (FO) according to the legend in upper right corner of the map. Black circles indicate standard deviation <0.07, grey 0.07≤s.d.<0.14 and white s.d.≥0.14. Black squares indicate hauls with fewer than five stomach samples. The continuous line defines the herring region, with black diamonds indicating hauls with herring outside this region.

structure of the predator–prey interaction between these two species in the Barents Sea. The patchiness of herring and the area of distribution where cod and herring overlap will influence this measure.

Herring was found in cod stomachs in 14% of the hauls, when considering the entire stomach database. However, inspection of Table 2 reveals considerable temporal variation in this quantity, with high levels in some intervals in 1984–1986 and in most of the period 1992–1995. P rarely exceeded 30% indicating that herring rarely were found in stomachs from more than one-third of the hauls in spite of increased predation as indicated by the level of IO. This low proportion probably reflects the patchy and geographically restricted distribution characterising juvenile herring in the Barents Sea (Dragesund, 1970; Røttingen, 1990). This species has a distinct schooling behaviour (Pitcher et al., 1996; Fernö et al., 1998), developing at a length of 35–40 mm around onset of metamorphosis (Fuiman, 1993; Gallego and Heath, 1994). In samples of patchy distributed organisms the probability of zero counts is high (Horne and Schneider, 1997), and this effect should

be considered when analysing stomach samples containing herring. In addition to increased probability of zero counts, patchy distribution of prey also leads to increased positive spatial and temporal autocorrelation of stomach contents. This effect is an important source of variation when estimating predation from survey data (Bogstad et al., 1995; Tirasin and Jørgensen, 1999).

Predation of cod in relation to abundance of juvenile herring and capelin

The positive correlation between IO and the abundance of herring is discussed above as an effect of increased encounters between herring and cod as the abundance of juvenile herring in the Barents Sea increases. This relationship was however not directly proportional, as the ratio between IO and abundance estimates of juvenile herring varied with time. This ratio increased towards the end of the two herring periods, compared to early in these periods. The increased predation by cod on juvenile herring was probably an effect of decreased availability of capelin as prey for cod. Figure 5 show a
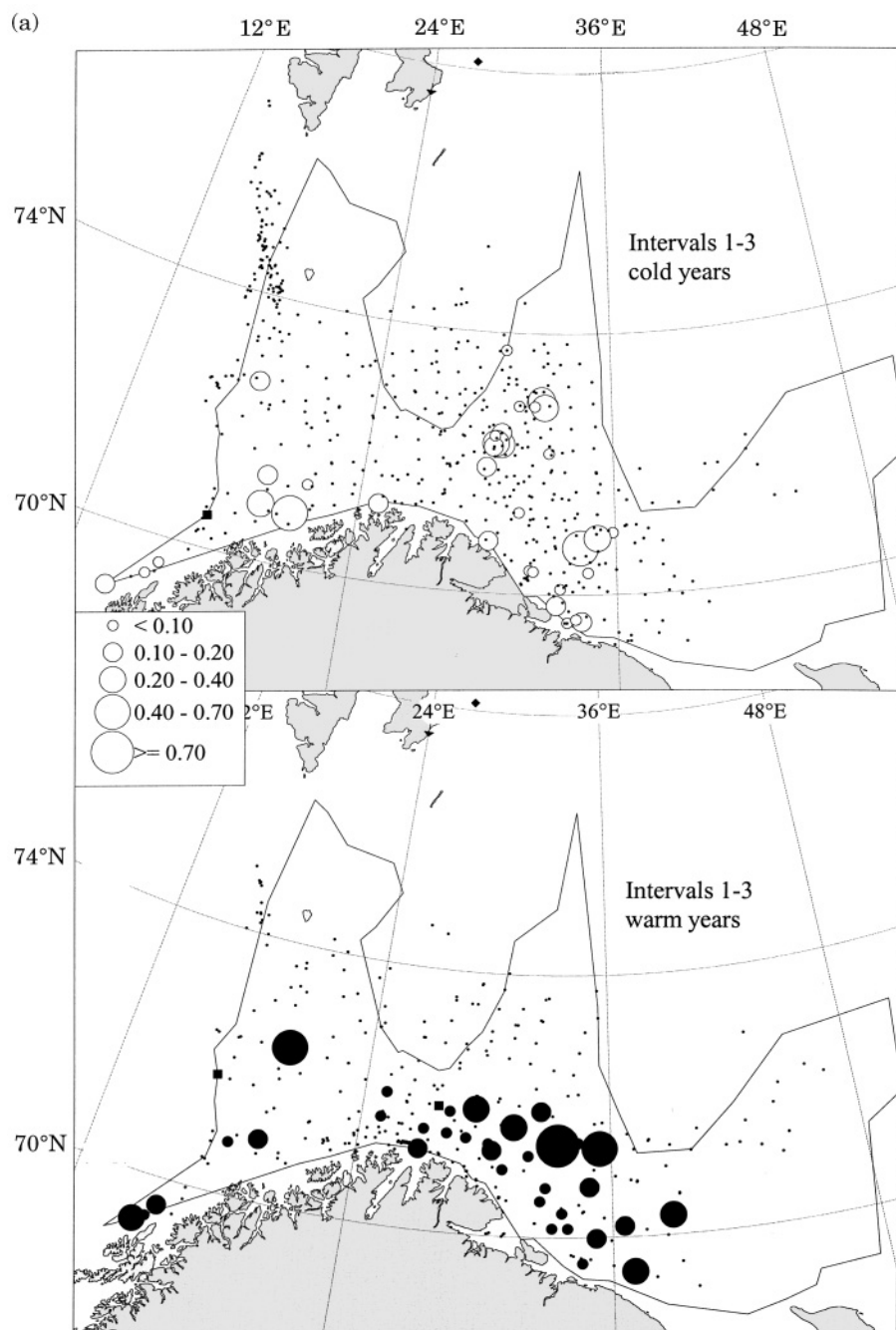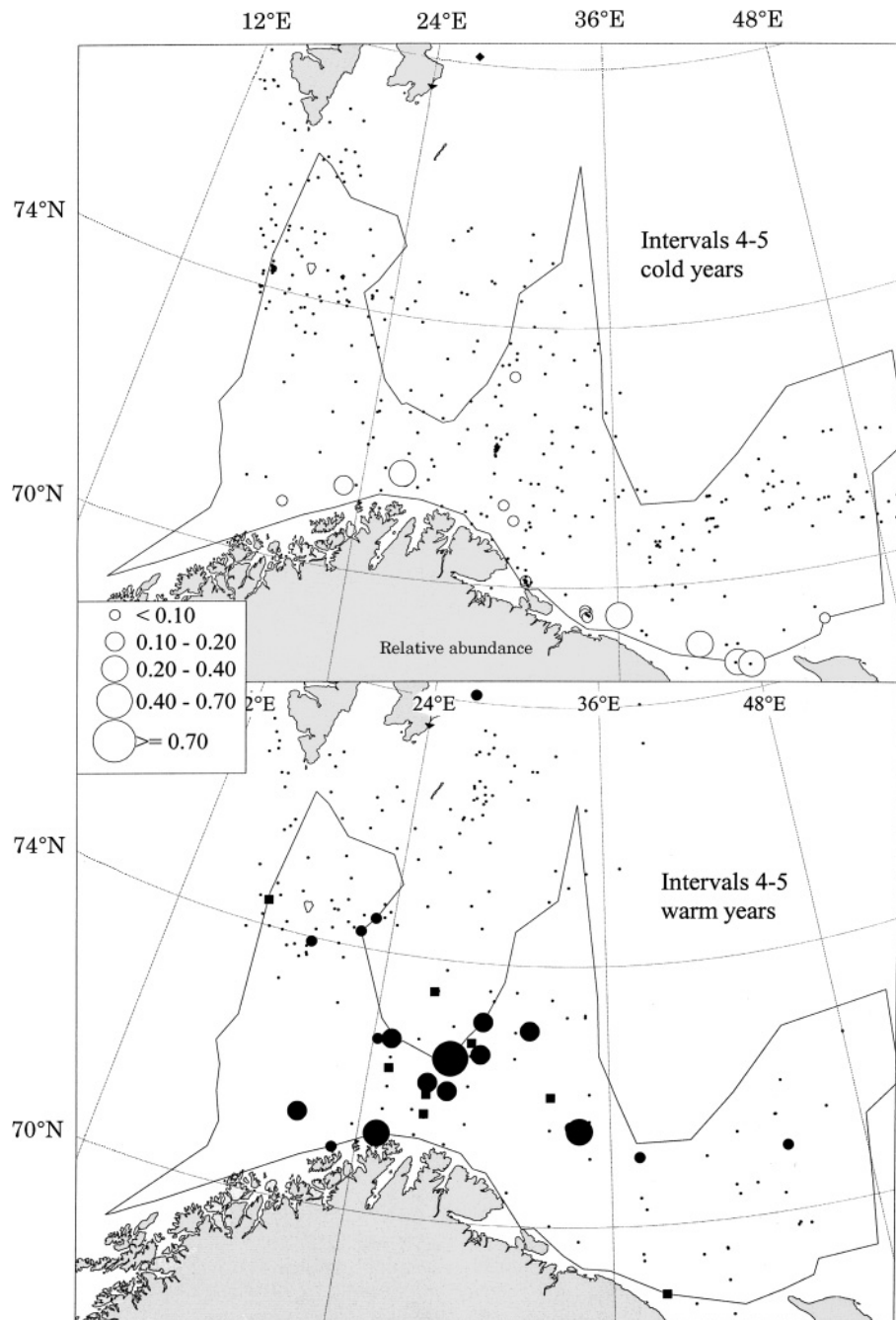
(a)

Figure 7. (a).

Figure 7. (b).

Figure 7. (a)–(b) Map of single trawl hauls with samples of cod stomachs where herring was found in the Barents Sea from the cold years 1986, 1987, and 1997 (white circles) and the warm years 1990–1992 (black circles). Dots indicate hauls where herring was not found in the stomachs. The diameter of the circles indicates frequency of occurrence (FO) according to the legend in the intersection between the maps. Black squares indicate hauls with fewer than five stomach samples. Maps (a) and (b) are from intervals 1–3 and 4–5, respectively.

negative correlation between this ratio and the abundance of capelin in the Barents Sea. The parameter estimates of the multiple regression of IO on herring and capelin abundance reflected this. The response of IO with herring abundance was stronger the lower the capelin abundance. This indicates that the proportion of the cod stock in the Barents Sea eating herring was higher when the capelin abundance was low. Increased predation on juvenile herring when the capelin stock is low is in agreement with the hypothesis on the relationship between herring, capelin and cod in the Barents Sea, as first put forward by Hamre (1994). According to this hypothesis some of the variation in natural mortality of juvenile herring in the Barents Sea is caused by predation by cod. The level of this predation mortality is thought to depend on the potential of the capelin stocks as food for cod (Hamre, 1994; Barros *et al.*, 1998).

In studies of consumption of various prey by cod in the Barents Sea, it has been found that the effect of cod predation on juvenile herring is small (Bogstad and Mehl, 1997). However, consumption estimates depend on the size of the cod stock, and in the two periods of increased predation found here, the cod stock was small compared to historic levels, particularly in the first period (ICES, 2000a). It is therefore likely that the consumption estimates do not reflect the potential for cod regulating the abundance of juvenile herring through predation. In periods of high abundance of cod and declining capelin stock, the effect of cod's predation on survival of juvenile herring in the Barents Sea may be more important than indicated by the consumption estimates based on the time series of stomach content available so far.

Figure 5 seems to indicate that the pattern in the relationship between the ratio between IO and herring abundance and capelin abundance was less clear in the 1980s compared to the 1990s. This may be an effect of the abundance of juvenile herring in the Barents Sea being underestimated in the 1980s due to bad weather conditions during surveys and mixing of herring and capelin schools (Røttingen, 1990). The estimates from the 1990s are probably more reliable due to a change in the acoustic equipment at the beginning of the 1990s (ICES, 1998). The abundance of juvenile herring in the Barents Sea in the 1980s was probably more than double that indicated by the estimates (Barros and Toresen, 1998; R. Toresen, IMR, pers. comm.).

Seasonal variation

IO did not differ between the sampling intervals 1, 2, 4, and 5, thereby indicating no clear seasonal trend in the proportion of the cod population in the Barents Sea feeding on juvenile herring. Note that the samples from 1 June–9 July (interval 3) were too sparse to draw any conclusions regarding this period of the year. According to earlier estimates of consumption of herring by cod in the Barents Sea, intensity of predation varies seasonally as an effect of seasonal variation in the vertical distribution of herring (Zatsepin and Petrova, 1939; Orlova *et al.*, 1995). This is explained as an effect of deeper vertical distribution of herring in winter compared to summer. In the summer juvenile herring is distributed in the upper part of the water column feeding on zooplankton, making it less available to the cod (Orlova *et al.*, 1995). This view is not supported by the results in this work, which suggests a more or less random seasonal variation in cod's predation on juvenile herring in the Barents Sea. There are several observations on distribution of juvenile herring in deeper water in summer (Røttingen, 1990), and the cod in the Barents Sea is not restricted to the demersal habitat (Yousif and Aglen, 1999; Aglen *et al.*, 1999). There are also observations of more intense predation by cod on pelagic schools of herring compared to demersal schools in the Barents Sea in winter (Ajiad, 1990). The discrepancy between the results in this work and the consumption estimates can however be explained by seasonal variation in the biomass of herring both available to and consumed by cod. Seasonal size specific migrations and stock fluctuations in the two stocks, such as the westwards emigration of 3–4 years old herring in spring, and spawning migration of mature cod may generate seasonal variation in the consumption estimates.

Important sources of error in IO

IO is influenced by errors related to both FO by haul and P. Availability of alternative prey and variation in vertical overlap between the predator and prey are important sources of bias in FO. High availability of alternative prey may increase the number of stomachs in a haul containing food, and thereby decreasing the FO of the prey of interest. With respect to vertical overlap between cod and its prey, Ajiad (1990) found higher FO of herring in cod stomachs from the Barents Sea in pelagic trawl hauls compared to demersal. Although the study was limited to cod with body length 30–40 cm, and the sample sizes were small, it indicates that geographical variation in vertical distribution of predator and prey or use of sampling gear could lead to bias in FO. The level of IO depends on the number of hauls taken, and their area coverage. Low number of hauls means that the probability of catching cod that has fed on herring may be low due to the patchy distribution of this prey. Low area coverage of the hauls increases the probability of missing the areas with herring concentrations. This is illustrated by the higher variability in IO in intervals with low number and area coverage of hauls. The intervals with low precision in IO due to these effects are therefore ignored in this discussion.

G. O. Johansen

Broad scale spatial variation

The total area where juvenile herring was eaten by cod (referred to as the herring area here) agreed well with the known distribution area of juvenile herring in the Barents Sea (Dragesund *et al.*, 1980; Røttingen, 1990). The most intense predation occurred in an area between 27–44°E, with northern and southern limits at the Polar Front and the coast of Finmark/Kola respectively. This is in agreement with the distribution of the 1983 year class of herring as 1–3 group (Røttingen, 1990), and probably represents the core area of the distribution of juvenile herring of these age groups in the Barents Sea.

In interval 1, 2, and 3 (1 January–9 July) the spatial distribution of herring in cod stomachs was similar. In this period herring was mostly found in cod stomachs within the core area. The eastern limit in this period was at 41°F, but it was difficult to assess due to insufficient sampling. When considering the intervals 4 and 5 it is reasonable to believe that it may have extended towards 44°E longitude (approximately). Note that in some years sufficient sampling in eastern areas of the Barents Sea in intervals 1 and 2 may have been prevented due to ice conditions in this period of the year (Loeng, 1989). The sparse coverage of hauls in intervals 2 and 3 made it difficult to assess the spatial distribution of the predation in these intervals. The distribution of juvenile herring in these intervals is not different from that in interval 1 (Røttingen, 1990; Gjøsæter and Bogstad, 1998), so the spatial distribution observed here most likely reflected the spatial coverage of the hauls. The hauls in interval 2 have a more westerly distribution, and those from interval 3 a more southern distribution (see Appendix). In addition most of the hauls from interval 3 is taken in 1995–1997, when the abundance of juvenile herring in the Barents Sea was declining (ICES, 2000b). The distribution may therefore represent the coastal distribution that is observed for weak year classes of juvenile herring in this area (Dragesund, 1970). It is therefore no reason to conclude that the differences between interval 1 and intervals 2 and 3 in the spatial distribution of herring in the cod stomachs reflect different geographic location of the predator–prey interaction.

It is interesting that most of the predation in interval 1 occurs in the same area and at the same time that capelin migrates towards the coast to spawn (Gjøsæter, 1998). This indicates that the 3–6 years old cod following the capelin migrations to feed (Mehl *et al.*, 1986) also feed on juvenile herring. The feeding migration directed towards capelin may therefore also increase the mortality of juvenile herring in the Barents Sea.

The high occurrence of herring in cod stomachs observed in western areas in interval 1, are probably adult and adolescent herring. This is confirmed by the fact that herring found in these stomachs are larger than the herring found further east. The adult and adolescent

part of the stocks spends the winter near this area (Dragesund *et al.*, 1997), and predation from cod on this herring can be considerable (Bogstad and Mehl, 1997).

In interval 4 and 5 the spatial distribution differed from that in intervals 1–3. Herring was found in cod stomachs throughout the whole herring region, and the intense predation observed in the core area in intervals 1–3, was more scattered towards more oceanic areas. The distributions in intervals 4 and 5 were similar, and minor differences may have been caused by more limited coverage of trawl hauls in interval 5 compared with interval 4.

The oceanic distribution of herring in cod stomachs observed in interval 4 and 5 may be an effect of the distribution of juvenile herring when it enters the Barents Sea, and seasonal variation in the distribution of cod. In this period (10 July–31 December) the 0-group herring enters the nursery area in the Barents Sea after drifting along the Norwegian coast from the spawning grounds. In years with strong year classes 0-group herring is widely distributed in the Barents Sea (Dragesund, 1970; Røttingen, 1990). Most of the herring consumed by cod around Bear Island in interval 4 and 5 was smaller than 15 cm. In this period of the year this corresponds to 0 or 1-group (Dragesund, 1970; Røttingen, 1990; Orlova *et al.*, 1995). Observations on the strong 1959 year class showed that it had an extensive oceanic distribution in the Barents Sea, both as 0, 1, and 2-group. Individuals from this year class were found in the stomachs of cod around Bear Island and in other oceanic areas (Dragesund, 1970). In this period mature cod migrates towards the northern and northeastern parts of the Barents Sea to feed along the Polar Front. Smaller cod also migrates in the same way, although their migration range is smaller (Mehl *et al.*, 1986). In years with a large cod stock, the younger cod are distributed further towards northeast (Ottersen *et al.*, 1998). The broadening of the distribution area of cod in this period may therefore also be a cause to the distribution of herring in cod stomachs observed in intervals 4–5. Most of the observations of cod feeding on herring in the eastern parts are from 1994–1996, which was years with a large cod stock in the Barents Sea (ICES, 2000a). However, the more eastern distribution of trawl hauls in intervals 4–5 in these years (see Appendix) makes it difficult to separate the effects of the spatial distribution of cod, and that of the stomach samples. The effect of seasonal variation in distribution of herring is difficult to deduce, as little is known about distribution of juvenile herring in the Barents Sea in this period of the year.

Note that the wide distribution towards the southeastern parts of the Barents Sea observed in intervals 4–5 may represent two different herring types not distinguished in the stomach data. In this area the juvenile Norwegian spring-spawning herring may mix with the Chosa herring, also called Arctic herring (*Clupea pallasii*

suworowi Rabinerson 1927). Knowledge about the biology and taxonomic status of this herring stock is limited. According to Orlova *et al*. (1995) it has its main distribution area east of 40°E, in the White Sea, and is found in stomachs of cod in this area.

As stated earlier there was no indication of seasonal differences in the intensity of predation on herring by cod in the Barents Sea. Instead there seems to be a broadening of the area where the predation takes place from the first to the second half of the year.

Climatic effects

Part of the geographic variability in occurrence of herring in cod stomachs was explained by climatic variation. The effect of climate differed seasonally, with no effect in the first half of the year and more oceanic distribution in warm years compared to cold years in the second half of the year. The differences in spatial distribution of cod's predation on herring in the two last intervals can be explained as a combination of the life history of Norwegian spring-spawning herring, climatic effects on the recruitment of this stock, and the seasonal migrations of cod. Production of strong year classes of juvenile herring with oceanic distribution in the Barents Sea is restricted to warm years (Hamre, 1994). This means that herring are more available to cod in these areas in warm years compared to cold. In addition the cod migrate towards north and east during summer and early autumn, and the range of the distribution towards these areas increases in warm years (Nakken, 1994). These factors combined will give the seasonal pattern observed here. The predation on herring in coastal areas in cold years, indicates that the distribution of herring may be the most important of these factors. Alternating periods of cold and warm years is a characteristic feature of the climate in the Barents Sea (Loeng, 1991). This has profound effects on the whole ecosystem (Sakshaug, 1997). The results in this work indicate that it also affects ecological interactions in the fish community in this area.

There was some oceanic distribution of herring in cod stomachs in a restricted area in the central Barents Sea from cold years in intervals 1–3. These observations were from interval 1 in 1986, and this incident of intense predation was also reflected in the high IO in this interval. Inspection of the spatial distribution of trawl hauls in the stomach database revealed a large cluster of hauls in the area of intense predation. Seventeen of 23 hauls where herring was eaten in this interval stem from this restricted area. This illustrates the significance of the spatial and temporal distribution of samples when analysing patchy distributed predator–prey interactions. According to the length distribution of this herring, it was dominated by 3-group belonging to the strong 1983 year class (Røttingen, 1990). In January 1986 this year

class had a more eastern distribution, and in May it was distributed more to the west compared to the area with intense predation found here (Røttingen, 1990). The findings here most likely reflect the westward migration of this year class in the period between January and May, and thereby add more information to the knowledge of the distribution of this year class in 1986.

Applicability of the results

The analyses presented here give a comprehensive picture of the broad scale temporal and spatial aspects of the predator–prey interaction between cod and juvenile herring in the Barents Sea during a period of 14 years. The most important periods and areas for this interaction are identified, and can be used when estimating consumption by cod and in constructing multispecies models for this area. The results can be combined with information on the population dynamics and distribution of other species in the area, to identify periods and areas for studies on the relative suitability of different prey species for cod.

The size dependent distribution patterns of juvenile herring and cod in the Barents Sea is likely to generate size dependent differences in availability of herring to cod. A detailed size structured analysis of the predator–prey interaction between these to species should therefore be conducted to gain more insight.

In the future, sampling of cod stomachs in the Barents Sea should be carried out in a way that gives more uniform distribution of samples throughout the year and sample area. With respect to the predator–prey interaction between cod and herring in the Barents Sea, two improvements would be particularly useful. More samples should be taken in April–July, when the mature cod returns from the spawning grounds, and meets the adolescent herring migrating westwards to join the adult stock. In August–December more samples should be allocated to the south-western part of the Barents Sea since the 0-group herring first arrives at this area when they drift along the western coast of Norway.

In order to fully understand ecological processes like predator–prey interactions, the temporal and spatial structuring of these interactions has to be considered. Temporal and spatial variation are themselves important features of the ecosystem, and ignoring them can lead to severe biases in estimates of parameters important for ecological interactions (Legendre, 1993).

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Appendix

Spatial distribution of hauls

The spatial distribution of hauls varies both between and within years. The maps in Figure A1a–d describes the spatial distribution of hauls each year and interval. The regions covered each interval were subjectively defined based on visual inspection of the spatial distribution of trawl hauls. Note that sporadic hauls are taken outside the main region covered in some intervals and years. Table A1 gives the area covered in each interval each year.

GIS (Geographical Information System) software was used to make the maps and do the area calculations.

Appendix A1. Approximately area coverage ($km^2 \times 10^3$) of trawl hauls with cod stomachs in the IMR-PINRO stomach database.

Year	Interval				
	1	2	3	4	5
1984	145	84	0	214	51
1985	158	78	0	101	0[a]
1986	198	40	0	257	0
1987	153	48	0	210	48
1988	185	0[a]	0[a]	252	56
1989	200	64	30	329	24
1990	172	103	0[a]	326	0[a]
1991	279	135	0[a]	324	0[a]
1992	273	0[a]	0[a]	432	0[a]
1993	350	45	0	530	123
1994	396	25	28	283	48
1995	481	100	85	531	411
1996	471	124	81	405	247
1997	285	92	37	184	217

[a]Missing due to insufficient sample size or spatial coverage.
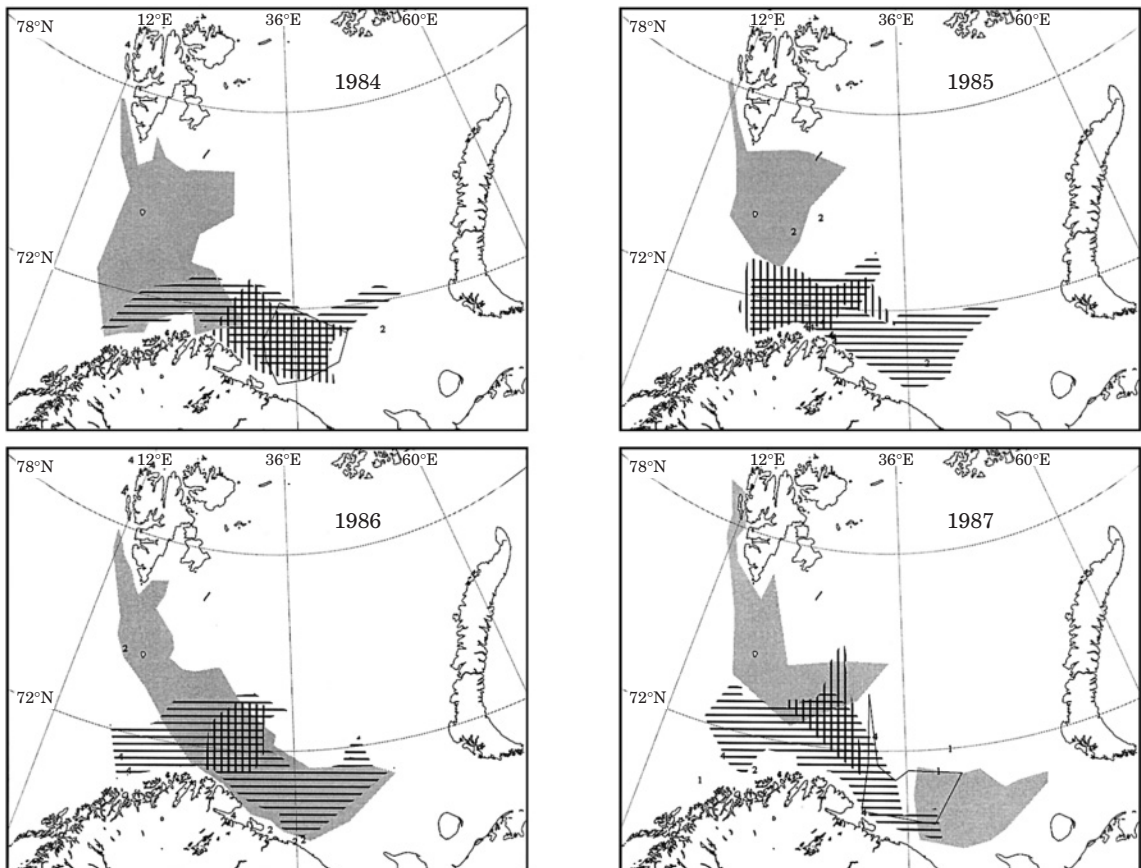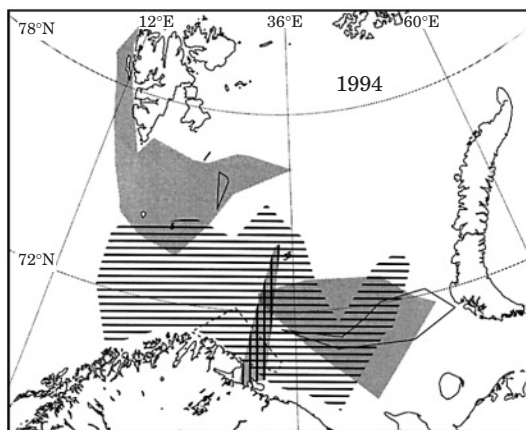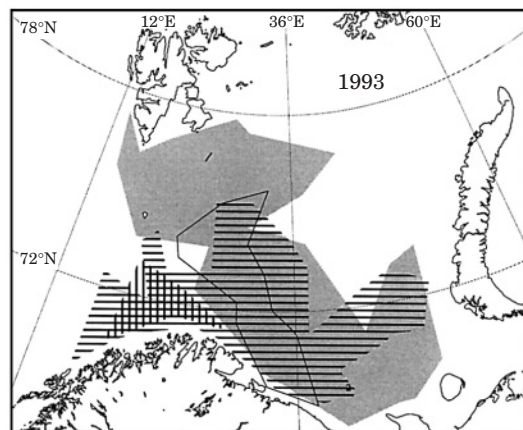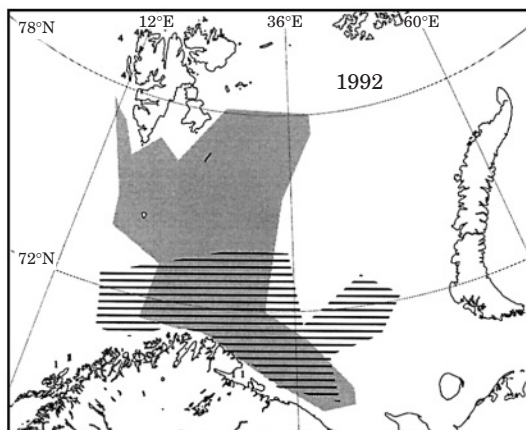

Figure A1. (a).
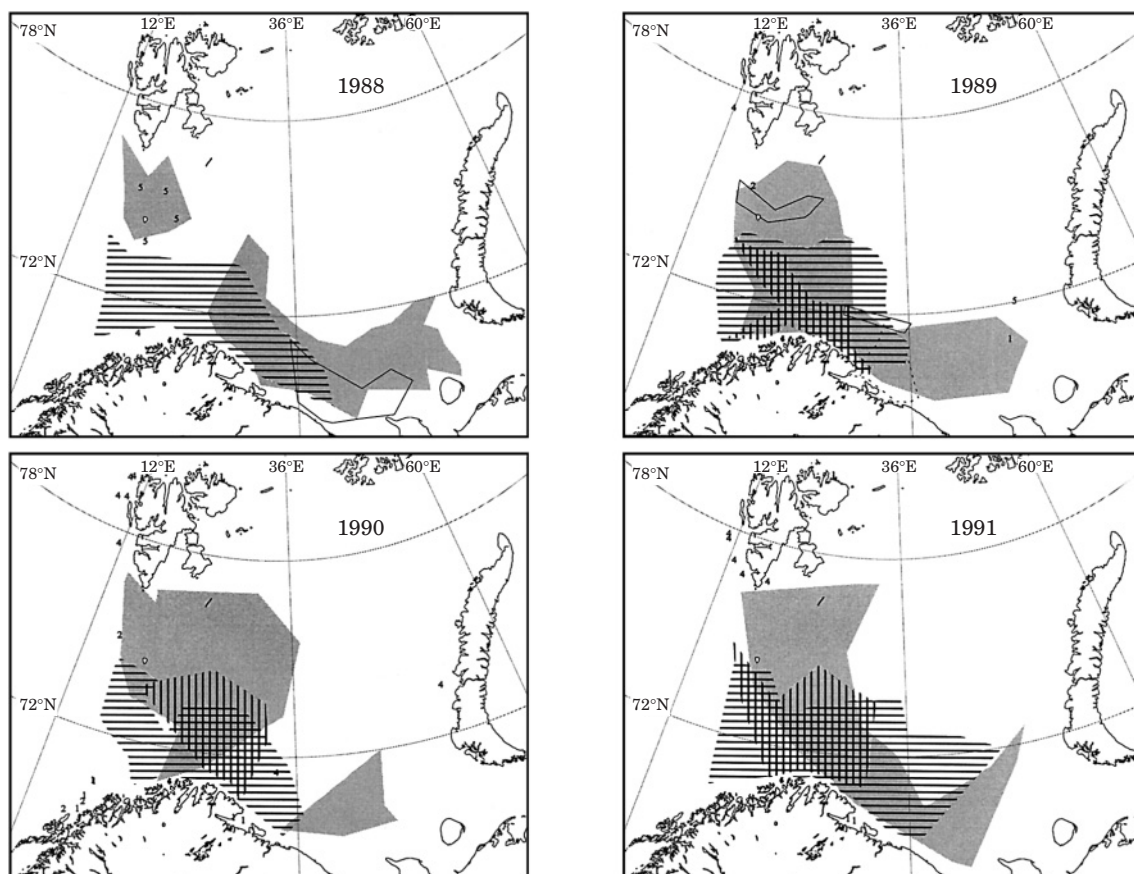
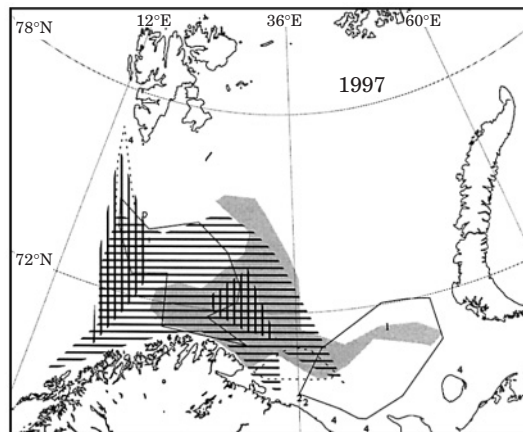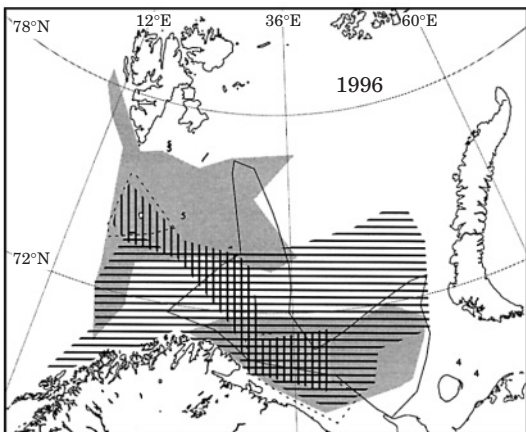Figure A1. (b).
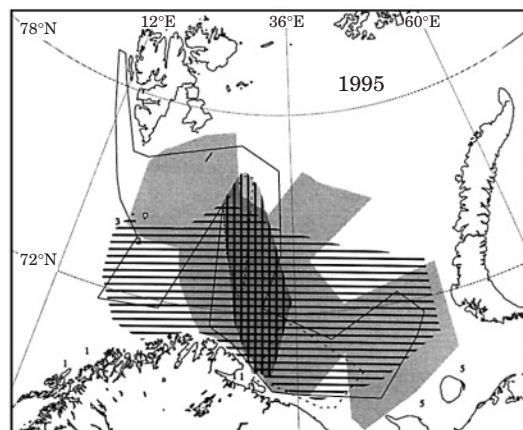
Figure A1. (c).

Figure A1. (d).

Figure A1. (a) Spatial distribution of trawl hauls by year in 1984–1987. Distributions in sample intervals 1–5 are denoted by horizontal hatching, vertical hatching, broken line, grey colour and continuous line, respectively. Sporadic hauls are denoted by numbers according to the sample interval they are taken in. Interval 3 is excluded from the analysis all four years, and interval 5 is excluded in 1985–1986. (b) Spatial distribution of trawl hauls by year in 1988–1991. Distributions in sample intervals 1–5 are denoted by horizontal hatching, vertical hatching, broken line, grey colour and continuous line, respectively. Sporadic hauls are denoted by numbers according to the sample interval they are taken in. Interval 3 is excluded from the analysis in 1988 and 1990–1991, and Interval 5 in 1990–1991. (c) Spatial distribution of trawl hauls by year in 1992–1995. Distributions in sample intervals 1–5 are denoted by horizontal hatching, vertical hatching, broken line, grey colour and solid line, respectively. Sporadic hauls are denoted by numbers according to the sample interval they are taken in. Interval 2 is excluded from the analysis in 1992, interval 3 in 1992–1993, and interval 5 in 1992. (d) Spatial distribution of trawl hauls by year in 1996–1997. Distributions in sample intervals 1–5 are denoted by horizontal hatching, vertical hatching, broken line, grey colour and continuous line, respectively. Sporadic hauls are denoted by numbers according to the sample interval they are taken in.