

Consumption of juvenile herring (*Clupea harengus*) by cod (*Gadus morhua*) in the Barents Sea: a new approach to estimating consumption in piscivorous fish

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Abstract: Consumption of different age groups of juvenile, Norwegian, spring-spawning herring (*Clupea harengus*) by northeast Arctic cod (*Gadus morhua*) in the Barents Sea in 1992–1997 is estimated using cod stomach content data. We present a new approach to the problem of estimating consumption by fish. The new method is based on the estimation of digestion time for single prey items based on the difference between fresh weight at ingestion and weight in the stomach at time of sampling. Estimation is based on a gastric evacuation model for cod and area-specific sea temperatures. This is used to estimate the time (t_{\max}) it takes for a prey to become digested to a stage where length is no longer measurable. Predation rate is then estimated for all prey with digestion time $\leq t_{\max}$ as number of prey eaten in the time range defined by t_{\max} . This rate is combined with estimates of the proportion of the cod stock consuming the prey and area-specific abundance of cod, giving consumption of herring on a seasonal and yearly basis. The consumption estimates differ from those obtained using current methods. Predation mortality of herring is estimated directly from the consumption estimates by combining them with acoustic herring abundance data.

Résumé : Une analyse des contenus stomacaux de morues nous a permis d'estimer la consommation des diverses classes d'âges des jeunes harengs de Norvège à reproduction printanière (*Clupea harengus*) par les morues arctiques (*Gadus morhua*) dans la mer de Barents en 1992–1997. La méthodologie nouvelle que nous proposons pour estimer la consommation par les poissons est basée sur l'évaluation du temps de digestion des différentes proies individuelles d'après la différence entre la masse humide à l'ingestion et la masse dans l'estomac au moment de l'échantillonnage. L'estimation se base sur un modèle d'évacuation gastrique chez la morue et sur les températures de la mer spécifiques à chaque région. Ces données permettent d'estimer le temps (t_{\max}) nécessaire pour qu'une proie soit digérée au point où la longueur devient impossible à mesurer. Le taux de prédation peut alors être calculé pour toutes les proies dont le temps de digestion est $\leq t_{\max}$ comme étant le nombre de proies mangées dans l'intervalle de temps défini par t_{\max} . Ce taux est ensuite combiné à des estimations de la proportion du stock de morues qui consomme la proie et aux abondances de morues en fonction de la région pour ainsi estimer la consommation de harengs sur une base saisonnière et annuelle. Ces estimations de consommation diffèrent de celles obtenues par les méthodes courantes. La mortalité des harengs due à la prédation est alors estimée directement à partir des estimations de consommation en les combinant à des données acoustiques d'abondance des harengs.

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Introduction

The Barents Sea is an important nursery area for juvenile, Norwegian, spring-spawning herring (*Clupea harengus*) during their first 3–4 years of life (Dragesund 1970; Dragesund et al. 1980). Hamre (1994), in his conceptual view on the relationship among herring, capelin (*Mallotus villosus*), and cod (*Gadus morhua*) in the Barents Sea, points to the importance of juvenile herring as a component of the fish

community in this area. He describes potential ecological interactions between juvenile herring and the other two species and stresses the role of herring both as food for cod and as a predator on capelin larvae.

The natural mortality of juvenile herring in the Barents Sea is highly variable between years. Year classes of Norwegian spring-spawning herring that are abundant at the 0-group stage can be strongly reduced during the first year of life (Barros and Toresen 1998). Barros et al. (1998) found

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that more than 90% of this intercohort 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. In a study on herring in cod stomachs from the Barents Sea, Johansen (2002) found that a higher proportion of the cod population consumed juvenile herring when the capelin stock was low. This is in accordance with Hamre's (1994) conceptual view, as well as with the results of Barros et al. (1998).

In this study, consumption of juvenile, Norwegian, spring-spawning herring by northeast Arctic cod in the Barents Sea is estimated from cod stomach data. A new approach to the estimation of consumption is presented and tested. In this approach, consumption is estimated for individual fish using stomach content data and the local environmental temperature as input to a stomach evacuation model describing the digestion of individual prey items. The estimation method uses only prey in the early stage of the digestion process. The main purpose of this is to circumvent the problem of estimating initial meal size, avoid the use of unidentified stomach content when estimating stomach evacuation, and increase the precision when estimating digestion time. Consumption rate is given in number of prey per time unit, which can be directly converted to predation mortality, and is useful for studying behavioural mechanisms governing the predation process. The consumption rate estimates are combined with area-specific estimates of cod abundance to calculate total consumption for the sampled area. The total consumption is then compared with estimates of natural mortality of juvenile herring.

Materials and methods

Stomach content data from cod were taken from the joint IMR (Institute of Marine Research, Bergen, Norway) – PINRO (Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, Russia) stomach content database. This database includes stomachs sampled during both Norwegian and Russian regular demersal fish surveys in 1984–1997. Most of the cod were caught by bottom trawl, mainly in the first quarter of the year and in September–October. A detailed description of the general survey methodology can be found in Jakobsen et al. (1997) and Lepesevich and Shevelev (1997). Some of the data are from surveys of pelagic fish and shrimp. The sampling design has undergone modifications during the period considered in this study. The maximum number of stomach samples per 5-centimetre group of cod per haul has changed from two in 1992–1995 to one after 1995 (Bogstad et al. 1995; Jakobsen et al. 1997).

Each stomach was frozen or preserved in 4% formalin separately as soon as possible after sampling. In the laboratory, the prey items were identified to the lowest taxonomic level possible and then split into size groups. In the period 1992–1993, there was a gradual change in the methods for recording the prey size of herring, from 5-cm to 1-cm groups. The material sampled before 1992 was therefore considered too imprecise for this study, and the analyses were restricted to the period 1992–1997. The prey items were damp-dried on bibulos paper and total wet weight, measured to the nearest milligram, was recorded for each

size group and prey category. Details about the sampling procedures are given in Mehl (1989) and Mehl and Yaragina (1992).

The data were divided into five sample intervals of the year, motivated by the temporal distribution of hauls. The sample intervals were defined as follows: 1 January – 31 March, 1 April – 31 May, 1 June – 9 July, 10 July – 15 October, and 16 October – 31 December, referred to as intervals 1–5, respectively. Most of the surveys providing the data were not targeted for stomach sampling, so the temporal and spatial distribution of hauls varied between years and intervals.

A detailed description of the temporal structuring and the temporal and spatial distribution of the hauls representing the raw data is given by Johansen (2002). Cod body length was measured to the nearest centimetre below and divided into 10-cm groups in the analyses. Cod ≥ 90 cm were aggregated in the largest group (Table 1). Cod smaller than 20 cm were excluded from the data because of their low propensity to eat fish (Johansen 2002).

Consumption of herring by individual cod was estimated as the number of herring consumed per time unit, referred to as predation rate. This limited the analysis to prey that was counted. The consumption estimates were based on estimating the digestion times for the consumed herring, i.e., the time that the prey has been digested in the stomach of the predator. Digestion times were estimated by using a gastric evacuation model (GEM), which describes the reduction in weight of a prey in a predator stomach because of digestion as a function of time (Bromley 1994). A similar approach is described in Mergardt and Temming (1997) for estimating the diel pattern of food intake in whiting (*Merlangius merlangus*). Digestion times for herring were estimated by relating the weight of the partly digested prey (W_p) in the cod stomach to the weight of that prey when it was ingested (W_i). The weight of ingested prey was estimated from a length–weight regression based on survey data from IMR. In these data, length is recorded to the nearest 0.5 cm and weight to the nearest gram. A log-linear length–weight regression was fitted ($df = 13\ 214$, $r^2 = 0.99$, $p < 0.0001$):

$$(1) \quad \log(W_p) = -5.755 + 3.225 \log(L)$$

where W_p is the weight of fresh prey (g) and L is the total body length of prey (cm). This limited the analysis to prey with measured lengths. This resulted in 648 herring observations with counted prey number and length measured from 427 cod stomachs. A herring observation is a record of herring of the same length group and same digestion stage within a cod stomach and may include several individual herring.

Gastric evacuation model (GEM)

The GEM used in this study is based on the general GEM (Jones 1974).

$$(2) \quad dS/dt = -R \cdot S^B$$

where S is the stomach content weight (g), R is the standard evacuation rate, and B is a constant defining degree of curvilinearity. Integrating (2) gives

$$(3) \quad S_t = [S_0^{(1-B)} - R(1-B)t]^{1/B}$$

Table 1. Number of trawl hauls with stomach samples from cod ≥ 20 cm for each year and interval and number of cod stomachs by 10-cm length groups in the data set.

Interval	Hauls	No. of stomachs by cod size (cm)								Total	N(h) ^a	N(m) ^b
		20–29	30–39	40–49	50–59	60–69	70–79	80–89	≥ 90			
1992												
1	102	261	244	349	316	238	187	129	62	1786	48	20
2	4	0	1	7	3	8	15	4	0	38	0	0
3	8	0	1	15	26	34	56	39	28	199	0	0
4	97	219	329	258	374	239	215	197	149	1980	43	13
5	5	0	0	0	3	10	12	13	10	48	8	7
1993												
1	150	236	357	433	474	410	221	142	91	2364	108	53
2	10	7	20	65	121	66	17	9	11	316	5	5
3	0	0	0	0	0	0	0	0	0	0	0	0
4	100	494	432	591	565	643	297	160	126	3308	43	14
5	41	21	33	39	90	260	114	52	75	684	7	2
1994												
1	166	325	376	457	529	587	347	125	79	2825	100	55
2	20	19	33	61	56	50	55	27	24	325	5	4
3	8	31	56	75	68	64	54	20	19	387	9	4
4	97	186	243	230	445	413	317	111	124	2069	39	31
5	51	3	22	121	433	387	236	45	16	1263	4	3
1995												
1	188	351	398	554	763	651	439	232	78	3466	70	47
2	62	1	27	210	575	472	238	89	32	1644	75	60
3	28	0	16	89	295	230	96	27	10	763	22	11
4	143	203	268	408	648	682	335	140	74	2758	39	15
5	81	25	27	85	231	335	139	78	82	1002	25	24
1996												
1	268	370	372	482	617	657	356	204	131	3189	49	20
2	45	6	48	199	395	315	183	100	32	1278	11	8
3	49	23	49	174	375	387	180	95	121	1404	4	3
4	138	292	282	335	482	567	393	159	74	2584	4	3
5	93	88	89	135	351	404	391	132	63	1653	9	4
1997												
1	201	223	288	411	778	631	480	186	109	3106	15	9
2	87	23	86	292	776	590	369	206	77	2419	0	0
3	52	1	66	184	427	322	233	144	90	1467	0	0
4	108	209	263	379	573	506	267	158	135	2490	0	0
5	75	31	120	190	350	399	164	91	28	1373	18	12

^aNumber of cod stomachs with herring observations.

^bNumber of cod stomachs with measurable herring.

for $B \neq 1$. In this model, S_t is the stomach content (g) at time t , t is the time after ingestion, and S_0 is initial stomach content (g). R incorporates the effects of temperature, food type, predator size, and other factors (Jones 1974). Following Temming and Andersen (1994), eq. 3 was expanded to a multivariable model describing the effects of temperature, predator size, and meal size.

$$(4) \quad S_t = [M^{1-B} - R'e^{AT}W^C M^D(1-B)t]^{1/B}$$

with additional variables M being the meal size (g) (substitute for S_0), T is temperature ($^{\circ}\text{C}$), W is predator weight (g), A is the temperature coefficient, C is the predator weight coefficient, D is the meal size coefficient, and R' is the food

type constant. According to Temming and Andersen (1994), the effect of including the meal size correction on R' is negligible when fitting the GEM to experimental data. They recommend the use of a simpler model without this term.

$$(5) \quad S_t = [M^{1-B} - R'e^{AT}W^C(1-B)t]^{1/B}$$

Back-calculation of digestion times for individual cod

To calculate digestion times of herring, we rearranged eq. 5 to

$$(6) \quad t = \frac{(S_t^{(1-B)} - M^{(1-B)})}{-R'e^{AT}W^C(1-B)}$$

Table 2. Length of herring in 2-cm groups (TL_{herring}) and median weight of the cod ($W_{\text{med cod}}$) used to find the expected breakpoint in the relationship between the cumulative frequency of measurable herring as a function of digestion time grouped within 1-h intervals.

TL_{herring} (cm)	n	$W_{\text{med cod}}$ (kg)	t_{max} (h)
<8	41	0.98	6.151
8–9	53	0.93	9.298
10–11	41	1.11	12.932
12–13	57	1.38	17.020
14–15	86	1.71	21.535
16–17	116	1.88	26.456
18–19	91	2.90	31.764
20–21	52	3.72	37.446
22–23	30	3.55	43.488
≥ 24	39	3.73	49.878

Note: Maximum time range (t_{max}) in hours within which all herring within the given 2-cm group were measurable at 4 °C is estimated by $\ln(t_{\text{max}}) = -1.3829 + 1.6442(TL_{\text{herring}})$.

where t is an estimate of digestion time. Substituting W_p for S_i and W_f (from eq. 1) for M enables the estimation of the digestion time of a herring of weight W_p and length L in the stomach by

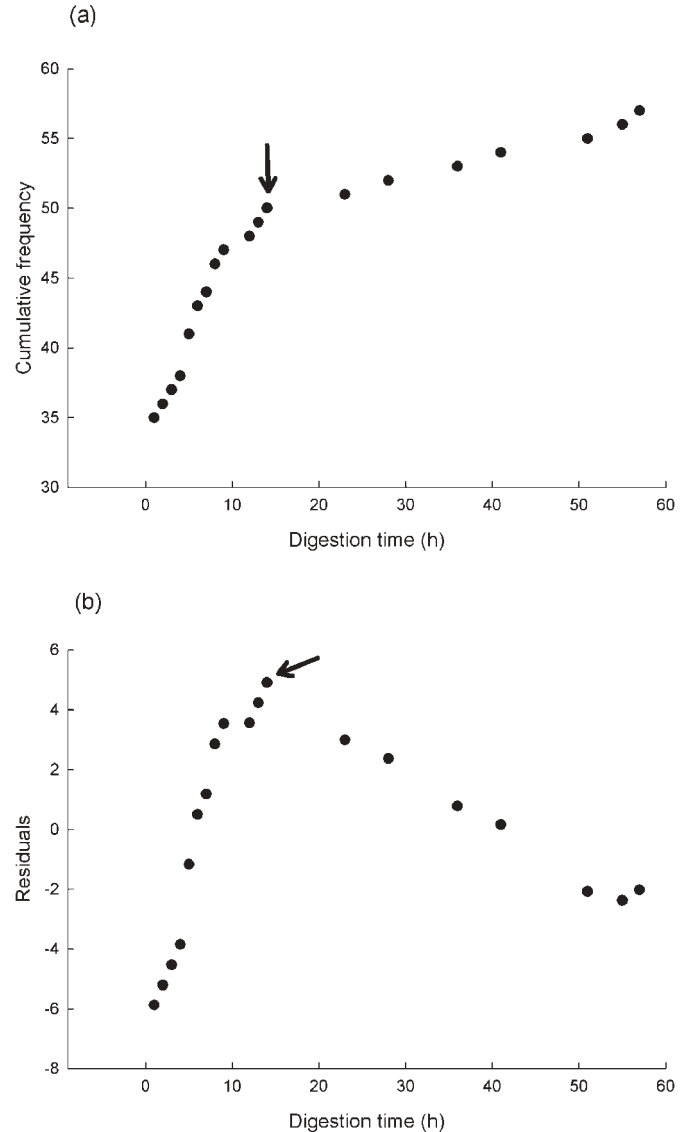
$$(7) \quad t = \frac{(W_p^{(1-B)} - W_f^{(1-B)})}{-R' e^{AT} W^C (1-B)}$$

The parameters $B = 0.43$, $R' = 0.02886$, $A = 0.137$, and $C = 0.047$ are estimates from experiments on gastric evacuation in cod with herring as prey, reported in Temming and Andersen (1994). Temperature was taken from a digital temperature atlas for the Barents Sea based on IMR's hydrographic measurements. The temperature was averaged for 50 m and below at each station and then averaged horizontally within each area.

Consumption estimates

The herring was divided into 2-cm size groups, and predation rate for cod containing measurable herring of the given size group was estimated as the number of prey in the stomach with an estimated digestion time $\leq t_{\text{max}}$ divided by t_{max} . t_{max} was defined as the upper limit of the time range within which total body length of all herring were measurable and was estimated as follows: for each size group of herring, digestion time was obtained from eq. 7 using the environmental temperature and setting cod weight equal to the median weight of cod that had measurable herring of the given size group in the stomach (Table 2). t_{max} was found by plotting the cumulative frequency of measurable herring as a function of digestion time grouped within 1-h intervals. Assuming a uniform distribution of cod stomachs at different levels of digestion for all data, there is an expected linear relationship between these variables, until the digestion time reaches a level where the total body length of herring starts to become immeasurable because of digestion. This breakpoint in the relationship defines t_{max} . The breakpoint was found by visual inspection of the plot and the residuals of a linear regression of the relationship (Fig. 1). Assuming that

Fig. 1. Example of the relationship between (a) digestion time and cumulative frequency of observations within 1-h groups and (b) the residuals from a simple linear regression of this relationship. The temperature was set to 4 °C and the size group of herring (*Clupea harengus*) was 12–14 cm. The arrow indicates how the breakpoint was found by visual inspection of the plots.



the total body length of herring becomes immeasurable when a certain proportion of its weight is digested and setting predator weight constant, rearranging eq. 7 gives a log-linear relationship between herring body length (TL_{herring}) and t_{max} . A linear regression of this relationship at the reference temperature 4 °C (T_4) ($\log(t_{\text{max}}) = -1.3829 + 1.6442\log(TL_{\text{herring}})$, $df = 8$, $r^2 = 0.96$, $p < 0.0001$) was used to estimate t_{max} for different 2-cm size groups of herring (Table 2). t_{max} at other temperatures for the same size groups were estimated by the relationship $t_{\text{max},T} = \frac{\exp(A \times T_4)}{\exp(A \times T)} t_{\text{max},T_4}$

The mean predation rate for cod containing measurable herring was estimated for each age group of herring, a , and for each 10-cm length group of cod, L , as

Fig. 2. Stratification and extrapolation scheme for estimating consumption of herring (*Clupea harengus*) in the Barents Sea in 1992–1997. Grey shading, crosshatching, and left slanting indicates extrapolation to 100%, 50%, or 25% of the cod (*Gadus morhua*) population in that stratum, respectively (see Appendix A). In cases where only a part of a stratum is marked, the marking indicates the spatial distribution of herring in cod stomachs in that stratum. Panels (a), (b), and (c) indicate sampling intervals 1–2, 3, and 4–5, respectively.

$$(8) \quad \mu_{a,L} = \frac{1}{n_L} \sum_{j=1}^{n_L} \sum_{i=1}^{m_{a,j}} (Y_{a,j,i} / t_{\max,T,i})$$

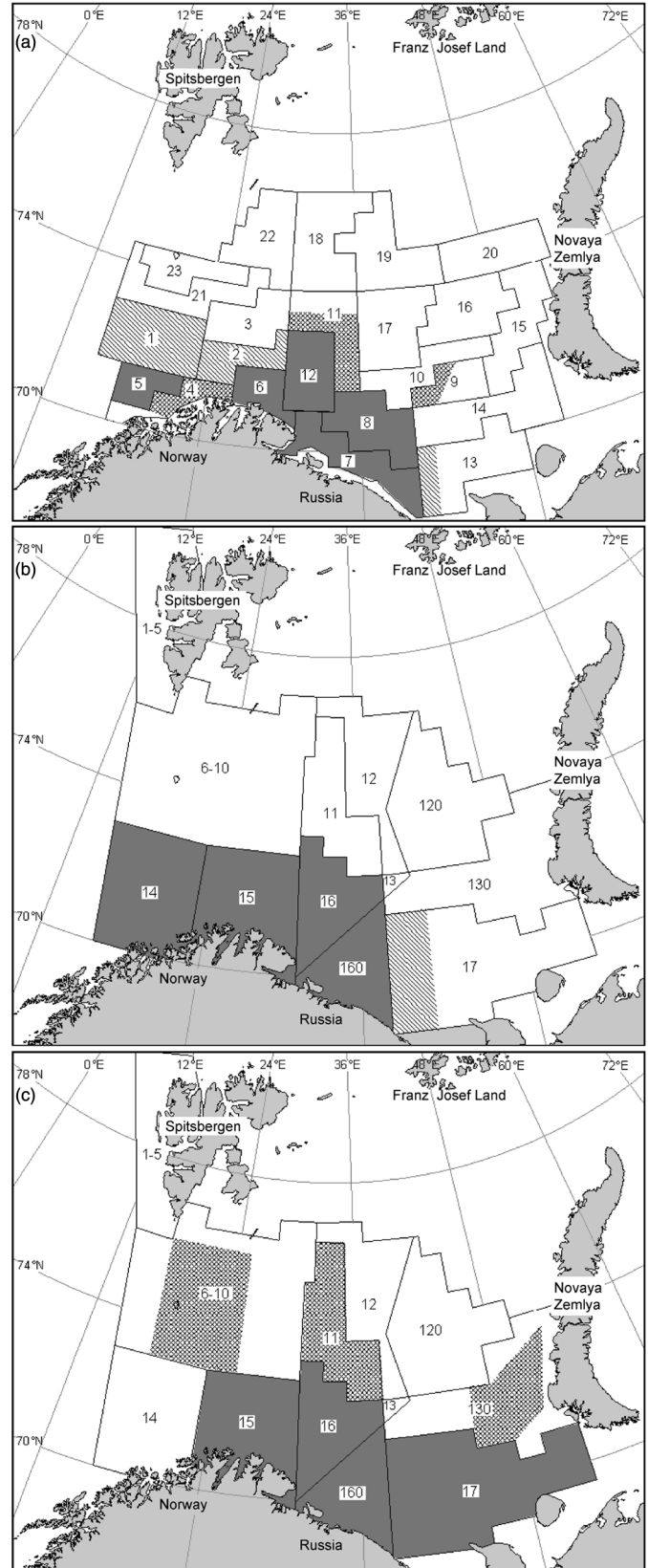
where $y_{a,j,i}$ is the number of herring of age a in herring observation i in cod stomach j with digestion time $\leq t_{\max}$, $m_{a,j}$ is the number of length-measurable herring observations of age a in cod stomach j , and n_L is the number of cod stomachs in length group L containing length-measurable herring. The mean predation rate is expressed as number of herring consumed per cod per hour. Consumption was then calculated for each year, time interval, area, age group of herring, and length group of cod as

$$(9) \quad C_{y,q,s,a,L} = N_{y,q,s,L} \times P_{y,q,s,L} \times \mu_{y,q,s,a,L} \times h_q$$

where $N_{y,q,s,L}$ is the number of cod of length group L in year y , interval q , and area s ; $P_{y,q,s,L}$ is the proportion of all cod stomachs from length group L sampled in year y , interval q , and area s containing measurable herring; $\mu_{y,q,s,a,L}$ is the year, interval, and area-specific mean predation rate as defined in eq. 8; and h_q is the duration in hours of interval q . The areas used correspond to the strata systems used by IMR during standard bottom trawl surveys on demersal fish in the Barents Sea in winter and autumn (Fig. 2). The winter system was used in intervals 1–2 and the autumn system in intervals 3–5. In the following, the areas will be denoted as strata.

Age of herring in the cod stomachs was estimated using length-at-age relationships for juvenile spring-spawning herring in the Barents Sea based on survey data on length at age from IMR. Individual juvenile herring (13 235) from the area north of 68°N and east of 19°E in the period 1992–1997 were included. Age was determined with scales or otoliths. The age-length keys and details about how they are derived can be found in Johansen (2003).

Abundance of cod ($N_{y,q,s,L}$) was calculated by scaling the bottom trawl survey index to the virtual population analysis (VPA) estimate of total abundance in the following way: the number at age A in the beginning of year y ($NV_{y,A}$) is available from the VPA (ICES 2001). The stock abundance in time period q can then be calculated as $NV_{y,q,A} = NV_{y,A} e^{-(F_{y,A} + M_{y,A})t_q/12}$, where t_q is the number of months from the start of the year to the midpoint of time period q . F and M are the fishing mortality and natural mortality, respectively. Adjustments also need to be made for the proportion of the total stock that is outside the survey area: one should adjust for the proportion by age found in the Lofoten (ICES 2001) and Svalbard areas for the winter survey (intervals 1 and 2). For the summer survey, one may assume that the entire stock is covered.



Assume that a survey estimate of abundance by stratum s and length L is available at time q in year y is $n_{y,q,s,L}$. The total survey estimate (entire area) of age A fish is given by $n_{y,q,A}$. These abundance indices are calculated in the same

way as described in Jakobsen et al. (1997). Age-length keys are calculated on main areas o , consisting of several strata. Let $R_{y,q,o,A,L}$ be the proportion of fish in year y , interval q , and main area o , which is of age A and length L . The survey-to-VPA scaling factor by age is given by $\alpha_{y,q,A} = NV_{y,q,A}/n_{y,q,A}$. One can then calculate abundance by length in each main area using the age-length key and use this to calculate the abundance by length in each stratum. The abundance by length in each main area is given by

$$(10) \quad N_{y,q,o,L} = \sum_A n_{y,q,o,A} \alpha_{y,q,A} R_{y,q,o,A,L}$$

and the abundance by length in each strata by

$$(11) \quad N_{y,q,s,L} = \frac{n_{y,q,s,L}}{n_{y,q,o,L}} N_{y,q,o,L}$$

Note that swept-area estimates from autumn 1995 were used in autumn 1994 because of missing data in 1994.

The consumption estimates were summed over length groups of cod and strata to get total consumption of different age groups of herring in each interval. Owing to variable temporal and spatial coverage in the temperature and stomach data, some extrapolation was needed to estimate the yearly consumption (Appendix A).

A brief sensitivity analysis was undertaken to study the effect of randomly encountering one stomach containing the prey of interest compared with the situation where the prey are not found. This was done by artificially adding a single stomach observation in a "no-herring observation" situation to evaluate the effect of this with respect to the estimates of total consumption. This was done in a stratum to which data were not extrapolated, as extrapolation would cancel out the effect of adding the stomach. The stomach was assigned predation rates corresponding to the minimum, maximum, and mean for the whole period for the herring age used. The stomach was added to a stratum in the centre of the area of the interaction between cod and herring, in an interval from which data were extrapolated to other intervals, to maximize the effect.

The biomass of herring consumed was calculated for each year y , time interval q , and age group of herring a as

$$(12) \quad B_{y,q,a} = C_{y,q,a} \text{GMW}_{y,q,a}$$

where $C_{y,q,a}$ is consumption in number of individuals and $\text{GMW}_{y,q,a}$ is the geometric mean of the weight of juvenile herring in the Barents Sea. $\text{GMW}_{y,q,a}$ was estimated from survey data on weight at age for juvenile spring-spawning herring in the Barents Sea from IMR. In cases with fewer than 20 weight measurements, the weight was estimated by the log-linear length-weight regression given in eq. 1. In these cases, length was approximated by the midpoint in the length range of the age group, taken from the length-at-age relationships used to age determine the herring.

Predation mortality

The consumption estimates were compared with estimates of herring stock sizes and mortalities derived from acoustic surveys of immature herring carried out in the Barents Sea in May-June each year (Toresen et al. 1998). The analysis was limited to the 1991-1992 year classes of herring be-

cause the relative precision of the acoustic estimates of the following weak year classes was considered too low for such calculations. Cod's accumulated consumption of 1-group herring in intervals 3-5 in year y and of 2-group herring in intervals 1-2 in year $y + 1$ (C_{1-2}) was compared with $N_{1,y} - N_{2,y+1}$, where $N_{1,y}$ and $N_{2,y+1}$ are the estimated herring stock sizes of 1- and 2-group herring during the acoustic surveys. The total instantaneous mortality coefficients generated by cod on herring (M_{pred}) were estimated by $\log(N_{1,y}/N_{2,y+1})C_{1-2}/(N_{1,y} - N_{2,y+1})$. In these calculations, the acoustic estimates of immature herring in the Barents Sea were considered absolute estimates of stock abundance. The catchability (i.e., survey index/true stock size) of the acoustic surveys of immature herring, however, may not equal 1. The survey-based total mortality estimates calculated using the formula $\log(N_{1,y}/N_{2,y+1})$ are still valid provided that the catchabilities of age 1 and 2 herring in the Barents Sea survey are equal. Note that fishing mortality of juvenile herring in the 1990s was negligible, as exploitation of this herring has been prohibited since 1977 (Toresen and Jakobsson 2002). Assuming that the acoustic estimates for each age group a in May-June approximately corresponds to the mean stock size $N_{a,y}$ during the year, predation mortality can also be calculated for each age group and year by

$$(13) \quad M_{\text{pred},a,y} = C_{a,y}/N_{a,y}$$

where $C_{a,y}$ is the consumption of age a herring during the year y . These calculations were limited to age group 1 in 1992-1993 and age group 2 in 1992-1994. Database operations, calculations, and statistical analysis were done with SAS[®] 8.1 for Windows (SAS Institute Inc., Cary, N.C.).

Results

Mean predation rate of different age groups of herring for the whole Barents Sea is calculated for the five sample intervals in 1992-1997 (Table 3). Mean predation rate tended to be highest for 0-group herring and lowest for 3+-group herring. In most of the intervals, the coefficient of variation was high. Inspection of the relationship between mean predation rate and cod size revealed that the number of herring eaten per cod tended to increase with cod size for the two oldest age groups of herring (Fig. 3). For 0- and 1-group herring, there was no such systematic trend.

The distribution of the strata-specific, per capita daily consumption of herring (consumption rate) for different size groups of cod is calculated as the product of the mean predation rate and the proportion of cod that had measurable herring in the stomach (Fig. 4). There was a tendency for cod smaller than 50 cm and larger than 70 cm to eat more herring than cod between these sizes. It can be seen that the pattern in Fig. 4 is a reflection of a similar pattern in the mean predation rate (Fig. 3), with exception of the smallest and largest cod size groups. For cod smaller than 40 cm and larger than 80 cm, multiplying with the proportion of cod eating herring increased the daily consumption relative to the estimate for the intermediate length groups in most cases. The proportions were dependent on the sample size of stomachs (Fig. 5). The size groups of cod with the highest per capita consumption of herring were also the size groups with the lowest stomach sample sizes (Fig. 6).

Table 3. Mean predation rate (number of herring eaten per cod per hour) for cod ≥ 20 cm eating juvenile herring in the Barents Sea for each year and interval in the period 1992–1997.

Interval	N(m)	N(t_{max})	0 group			1 group			2 group			3+ group		
			N	Mean	CV	N	Mean	CV	N	Mean	CV	N	Mean	CV
1992														
1	20	18	—			4	0.131	66.6	11	0.104	148.5	6	0.059	74.9
2	0	0	—			—			—			—		
3	0	0	—			—			—			—		
4	13	13	9	0.293	109.8	3	0.053	44.5	3	0.052	82.3	1	0.026	
5	7	4	0			2	0.042	12.9	3	0.102	86.3	0		
1993														
1	53	47	—			17	0.111	90.6	10	0.068	93.6	23	0.042	125.9
2	5	3	—			0			2	0.079	55.9	1	0.032	
3	0	0	—			—			—			—		
4	14	13	7	0.118	55.8	7	0.081	104.9	0			0		
5	2	1	1	0.879		0			0			0		
1994														
1	55	48	—			27	0.291	96.8	18	0.059	63.0	17	0.033	66.5
2	4	3	—			3	0.165	90.2	2	0.127	99.2	1	0.263	
3	4	1	—			0			1	0.033		0		
4	31	19	15	0.263	77.5	11	0.059	59.6	5	0.054	45.2	0		
5	3	1	1	0.117		0			0			0		
1995														
1	47	33	—			3	0.063	43.7	20	0.089	93.4	15	0.041	107.2
2	60	46	—			5	0.129	101.9	27	0.102	123.3	21	0.042	85.0
3	11	9	—			1	0.056		7	0.056	75.9	4	0.037	40.2
4	15	11	1	0.053		4	0.062	76.2	6	0.061	67.7	1	0.023	
5	24	22	1	0.076		8	0.070	67.1	15	0.061	92.6	2	0.040	47.1
1996														
1	20	15	—			1	0.053		6	0.191	186.6	11	0.032	52.7
2	8	6	—			0			3	0.044	50.3	3	0.031	38.3
3	3	2	—			0			1	0.188		1	0.020	
4	3	2	0			0			2	0.044	71.7	0		
5	4	4	4	0.202	48.5	0			0			0		
1997														
1	9	6	—			2	0.084	16.1	1	0.042		3	0.041	71.2
2	0	0	—			—			—			—		
3	0	0	—			—			—			—		
4	0	0	—			—			—			—		
5	12	11	8	0.251	81.6	3	0.045	18.3	0			0		

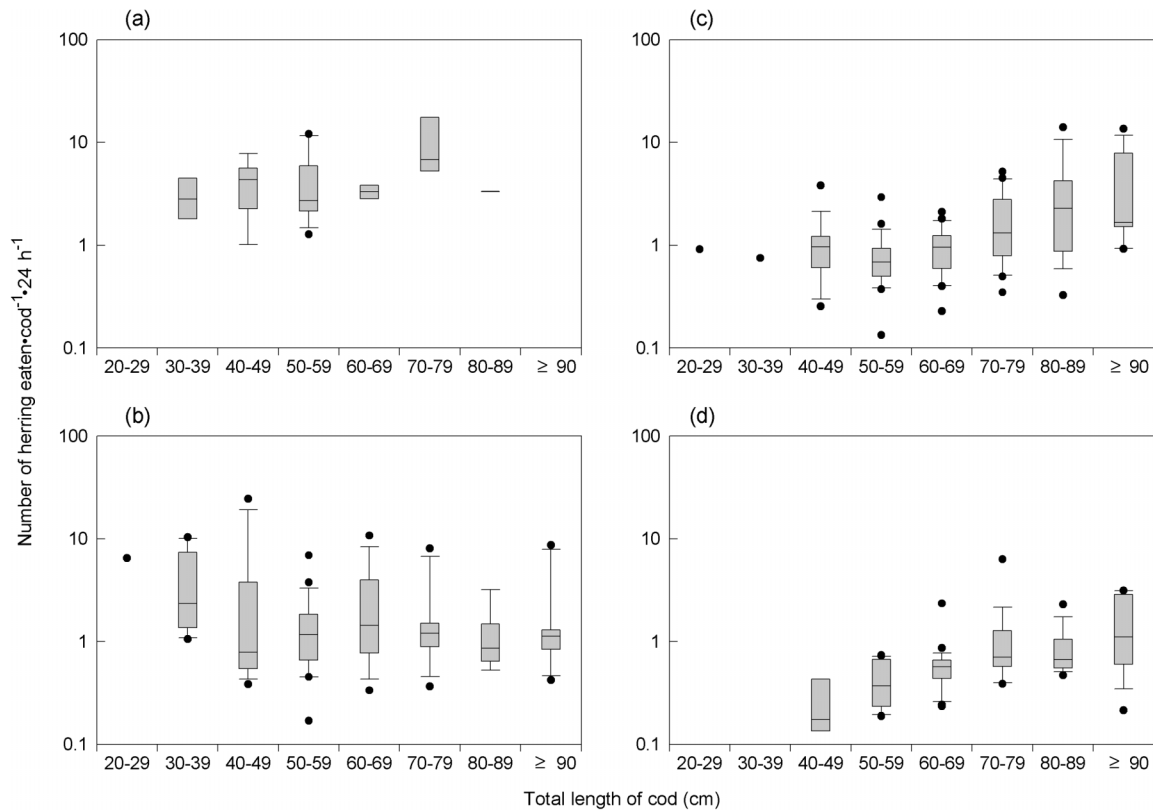
Note: N(m) is the number of cod stomachs with measurable herring. N(t_{max}) is the number of cod stomachs with herring observations with digestion time $\leq t_{max}$ on which the analyses are based. N is number of cod stomachs on which the mean predation rate calculation is based. CV is the coefficient of variation in %.

Cod's consumption of individual herring ($\times 10^9$) and biomass of different age groups of herring in the Barents Sea is calculated for the five sample intervals in 1992–1997 (Table 4). Consumption of herring was highest in the period 1992–1994. 1994 was the year of highest consumption, with total consumption being about 3.5 and 4 times higher in numbers and about 2 and 3 times higher in biomass compared with 1992 and 1993, respectively. The high consumption in 1994 can be seen in all age groups of herring.

Mortality is estimated for 1- to 2-year-old herring of the 1991–1992 year classes (total mortality and mortality generated by cod) using acoustic stock size estimates from May–June and estimated consumption of herring (taken from

Table 4) in the year between the estimates (Table 5). For both year classes, cod generated an instantaneous mortality coefficient of about 0.1. This is about 1/3 of the total mortality for the 1991 year class and about 1/5 of the total mortality for the stronger 1992 year class. Predation mortalities generated by cod on 1-group herring in 1992–1993 and on 2-group herring in 1992–1994 are also estimated, assuming that the acoustic estimates for each age group in May–June approximately correspond to the mean stock size during the year (Table 6). The mean predation mortality on 1- and 2-group herring, found by averaging the estimated predation mortality for these age groups within the year class, was 0.05 for the 1991 year class and 0.08 for the 1992 year class.

Fig. 3. Distribution of mean daily predation rate (number of herring (*Clupea harengus*) eaten per cod (*Gadus morhua*) per 24 h) for cod that has measurable herring in the stomach in the Barents Sea in 1992–1997. Predation rates are averaged by stratum. Panels (a), (b), (c), and (d) show herring age groups 0, 1, 2, and 3+, respectively. The x axis shows 10-cm groups of cod. Note that the y axis is \log_{10} . The lines within the boxes denotes the median, the vertical boundaries of the boxes denote the 25th and 75th percentiles, the whiskers denote the 10th and 90th percentiles, and the points show extreme values or single observations.



However, 2-group herring in 1992 (1990 year class) seems to have suffered higher predation mortality (0.18).

The sensitivity analysis was done by adding one stomach to the data set from a cod of size group 40–49 cm, stratum 8, interval 1 in 1994. The total number of stomach samples from this size group of cod within this stratum and interval was 38. The herring was assumed to be of age 2 to enable calculation of new predation mortalities. Predation rates were set to 0.033, 0.082, and 0.191, corresponding to the minimum, mean, and maximum predation rates, respectively, for this age group of herring for the whole data set. Total number of consumed herring of age group 2 in 1994 increased by 5%–34% with increasing predation rate (Table 7). This resulted in mortality estimates of 0.14, 0.15, and 0.17, compared with the original estimate of 0.13. Addition of a single stomach with the same characteristics and predation rate of 0.082 was also done in interval 4 in 1997 to test the effect of single stomach observations in an interval with consumption originally estimated to zero. In this case, the new consumption estimate was 0.106×10^9 individuals.

Discussion

In this study, we quantified the consumption of juvenile herring by northeast Arctic cod directly through data on cod stomach content by combining a model of gastric evacuation in cod with measures of environmental temperature. The re-

sulting estimates of per capita consumption of herring by cod were then scaled up with spatially distributed abundance estimates of cod to get total consumption. As consumption rate estimated by the new method is given as number of prey per time unit, independent estimates of natural mortality can be calculated directly to assess the effect of cod predation on the variable mortality of juvenile herring observed in this area. These mortalities are compared with predation mortalities on herring by cod in other areas. In addition, the consumption estimates by the new method are compared with consumption estimates by other methods, as well as with estimates of the consumption of herring by other predators.

Methodological considerations

The estimation of consumption directly from stomach data requires a model for the digestion of food as a function of time, here referred to as GEM. Several models have been proposed for describing this process (Elliott and Persson 1978; Jobling 1981; Bromley 1994). In most models, the evacuation rate is dependent on the size of the initial meal. In field studies, this parameter is difficult to estimate because of the large individual, regional, and seasonal flexibility characterizing feeding in fish (Wootton 1990). This high variability is also typical for cod (Daan 1973). The method of modelling gastric evacuation without meal size as a variable proposed by Temming and Andersen (1994) offers a way around the problem of estimating the initial meal size.

Fig. 4. Distribution of daily consumption rate (number of herring (*Clupea harengus*) eaten per cod (*Gadus morhua*) per 24 h) for each stratum in the Barents Sea in 1992–1997. Consumption rate is calculated as the product of the mean predation rate and the proportion of cod that has measurable herring in the stomach. Panels (a), (b), (c), and (d) denotes herring age groups 0, 1, 2, and 3+, respectively. The x axis shows 10-cm groups of cod. Note that the y axis is \log_{10} . The lines within the boxes denotes the median, the vertical boundaries of the boxes denote the 25th and 75th percentiles, the whiskers denote the 10th and 90th percentiles, and the points show extreme values or single observations.

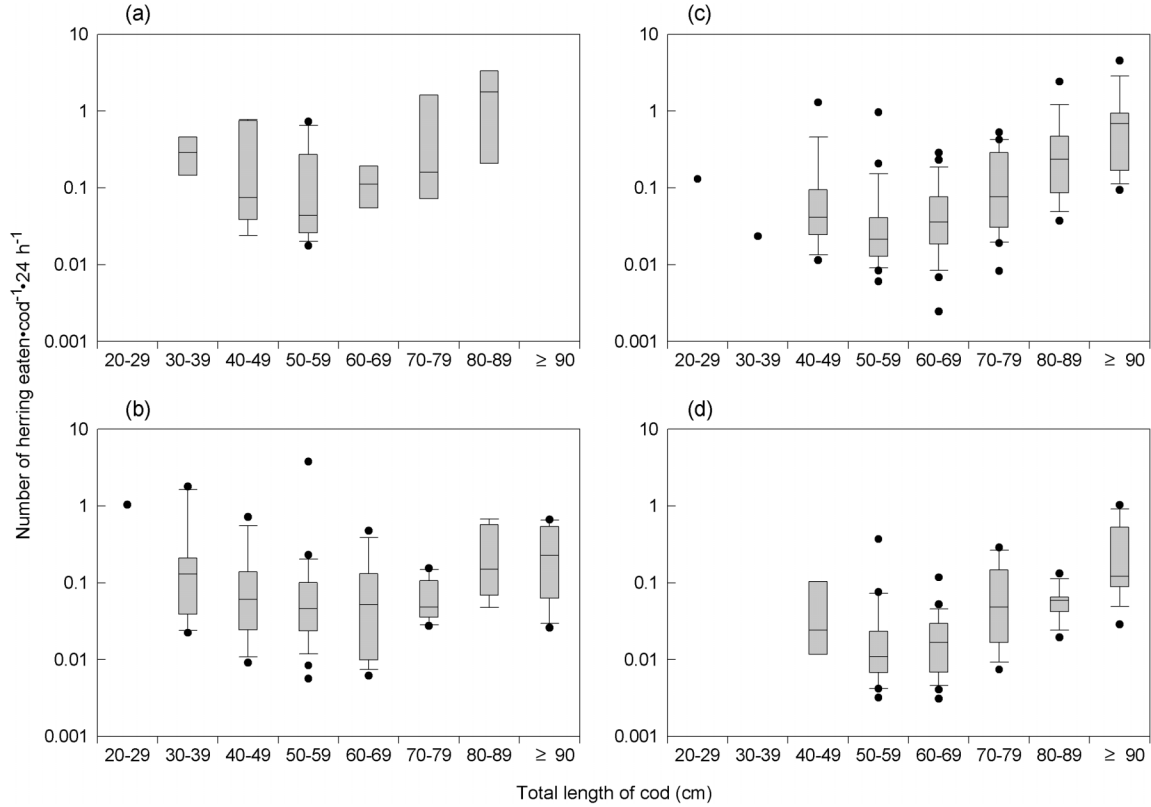
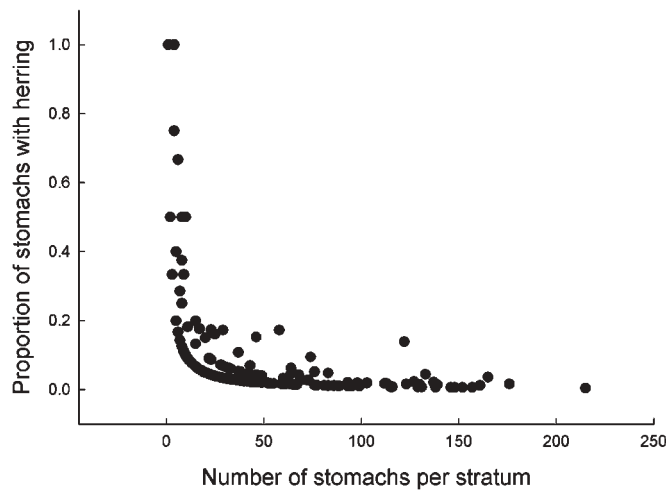


Fig. 5. Relationship between stomach sample size and proportion of cod (*Gadus morhua*) in the samples that has measurable herring (*Clupea harengus*) in the stomachs.

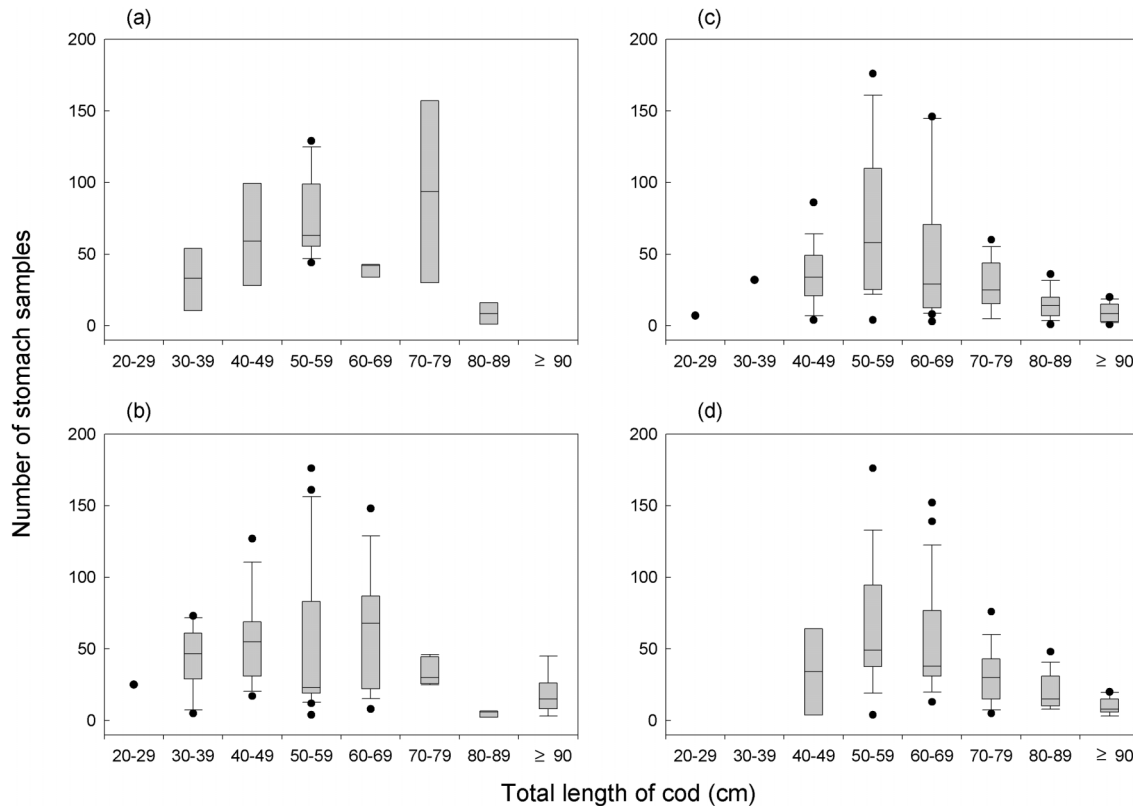


Mergardt and Temming (1997) presented a method for estimating the digestion time of single prey items in whiting (*Merlangius merlangus*), where they used the model of Temming and Andersen. The concept of estimating t_{\max} presented here is based on ideas presented in their paper. t_{\max} is

defined as the upper limit of the time range within which all prey items of a given size are measurable, given cod size and environmental temperature. This means that only length-measured prey can be included, excluding highly digested stomach content from the analysis. Prey items with digestion times above t_{\max} are assumed to be in a state of digestion where prey lengths are starting to be immeasurable because of fragmentation of the prey. A central assumption of the method presented here is that all prey items with digestion time below t_{\max} are eaten within the time range defined by this variable.

The advantages of the method presented here are several. When using this method, the data set is truncated and only relatively newly ingested prey are used in the calculations. The digestion rate is more variable towards the end of the digestion process (Bromley 1994), and by concentrating on the early stages of digestion, the method offers higher precision in the estimation of the digestion rate compared with a method where the whole digestion process from ingestion of the prey to total evacuation is estimated. Identifying stomach content is often made difficult by digestion (Bowen 1983). One advantage of concentrating on prey in the early stages of digestion is that all prey items are readily identified to the prey categories relevant for the study. When all stomach content is included when using the GEM to estimate consumption, unidentified prey items are redistributed into

Fig. 6. Distribution of stomach sample sizes within interval and stratum by size group of cod (*Gadus morhua*). Panels (a), (b), (c), and (d) show sample size for cases with consumption of herring (*Clupea harengus*) age groups 0, 1, 2, and 3+, respectively. The x axis shows 10-cm groups of cod. The line within the boxes denotes the median, the vertical boundaries of the boxes denote the 25th and 75th percentiles, the whiskers denote the 10th and 90th percentiles, and the points show the extreme values.



groups of identified prey. This relies on the assumption that earlier meals have the same relative occurrence of different prey categories as the latest meal. This assumption is doubtful considering the high variability characterizing feeding in fish discussed above. The approach presented in this study avoids the redistribution of undetermined prey into groups of determined prey. Other advantages relate to increasing the efficiency of stomach processing and survey time. Since the method relies on modelling the digestion of measurable prey only, processing of stomach samples can be more efficient by limiting the processing to measurable prey only. This means that the number of stomachs examined per time unit increases, allowing larger sample sizes per unit survey time. Another advantage related to increasing time efficiency arises when data for t_{\max} are already estimated for the relevant prey categories. In these cases, measuring the weight of prey is redundant, and the processing of stomachs is limited to determination of prey category, length measurement, and counting. The advantages related to increasing time efficiency depends on specific targeting of the study and pre-planning the use of the method and do not apply to retrospective analyses. However, the method could make possible retrospective analyses of data that are insufficient for other methods, provided they contain the relevant prey measures.

A potential problem of using the new method is the reduction of the amount of useable stomach data when excluding immeasurable stomach content. Because of intracluster cor-

relation, the number of stations, more so than the number of stomachs collected, determines the precision of estimated average stomach contents (Bogstad et al. 1995). Using only stomachs with measurable herring will not reduce the number of stations from which consumption rates can be calculated, and thus it should have a minor impact on the precision of the estimates.

The stomach content excluded is the content associated with the most imprecise estimation with reference to both the digestion process and the identification of prey. This will counteract the potential higher uncertainty in the consumption estimates arising from reducing the sample size. The proportion of total number of stomachs with herring containing measurable herring varied between 0.29 and 1.00, with a mean of 0.61. There was little systematic variation in this proportion except for a tendency for lower proportions in the second half of the year. The reduction of sample size as an effect of digestion time of herring being above t_{\max} is negligible.

The back calculation of fresh weight of prey based on a length-weight relationship used here may influence the precision of the consumption estimates. In natural populations, there is always some variation in weight at a given length, and this variation will increase with length. For prey with larger than average fresh weight, digestion time will be underestimated and vice versa. Simulations done by Mergardt and Temming (1997) show that this problem has small effects on the estimation of digestion time. In our method, this

Table 4. Consumption of juvenile herring in the Barents Sea by northeast Arctic cod in the period 1992–1997.

Interval	0-group		1-group		2-group		3+-group		Total number	Total biomass
	Number	Biomass	Number	Biomass	Number	Biomass	Number	Biomass		
1992										
1	—	—	0.539	3.304	1.087	41.816	0.245	26.609	1.871	71.729
2	—	—	0.332	3.177	0.680	42.699	0.149	15.458	1.161	61.334
3	—	—	0.113	1.130	0.433	20.316	0.077	8.164	0.623	29.610
4	2.449	16.045	0.561	11.349	0.139	10.888	0.013	1.735	3.162	40.017
5	5.876	40.432	0.426	14.919	0.159	12.387	0.003	0.593	6.464	68.331
Total	8.325	56.477	1.971	33.879	2.498	128.106	0.487	52.559	13.281	271.021
1993										
1	—	—	1.756	11.159	0.434	9.727	0.320	28.449	2.510	49.335
2	—	—	1.119	8.683	0.432	11.532	0.202	24.127	1.753	44.342
3	—	—	0.632	5.491	0.132	3.255	0.117	7.599	0.881	16.345
4	1.003	4.878	0.733	15.188	0.000	0.000	0.000	0.000	1.736	20.066
5	3.568	16.870	0.209	5.152	0.000	0.000	0.000	0.000	3.777	22.022
Total	4.571	21.748	4.449	45.673	0.998	24.514	0.639	60.175	10.657	152.110
1994										
1	—	—	12.379	66.694	4.734	87.963	0.863	40.783	17.976	195.440
2	—	—	2.031	16.917	2.630	66.801	0.557	51.456	5.218	135.174
3	—	—	1.743	14.517	0.135	3.642	0.005	0.289	1.883	18.448
4	17.594	93.398	2.073	40.686	0.225	10.150	0.000	0.000	19.892	144.234
5	0.027	0.212	0.000	0.000	0.013	0.665	0.000	0.000	0.040	0.877
Total	17.621	93.610	18.226	138.814	7.737	169.221	1.425	92.528	45.009	494.173
1995										
1	—	—	0.067	0.558	0.377	5.717	0.148	7.598	0.592	13.873
2	—	—	0.184	1.760	1.162	25.955	0.526	28.387	1.872	56.102
3	—	—	0.012	0.117	0.142	3.607	0.046	2.376	0.200	6.100
4	0.086	0.457	0.131	2.575	0.226	9.524	0.008	0.937	0.451	13.493
5	3.149	16.716	0.388	7.768	0.440	21.835	0.023	2.499	4.000	48.818
Total	3.235	17.173	0.782	12.778	2.347	66.638	0.751	41.797	7.115	138.386
1996										
1	—	—	0.002	0.017	0.107	2.843	0.086	4.242	0.195	7.102
2	—	—	0.000	0.000	0.083	2.317	0.064	5.003	0.147	7.320
3	—	—	0.000	0.000	0.031	0.987	0.010	0.716	0.041	1.703
4	0.000	0.000	0.000	0.000	0.061	3.025	0.000	0.000	0.061	3.025
5	1.425	5.391	0.000	0.000	0.000	0.000	0.000	0.000	1.425	5.391
Total	1.425	5.391	0.002	0.017	0.282	9.172	0.160	9.961	1.869	24.541
1997										
1	—	—	0.047	0.392	0.007	0.181	0.052	3.873	0.106	4.446
2	—	—	0.011	0.091	0.000	0.000	0.004	0.285	0.015	0.376
3	—	—	0.007	0.064	0.000	0.000	0.004	0.322	0.011	0.386
4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5	0.631	3.083	0.180	4.470	0.000	0.000	0.000	0.000	0.811	7.553
Total	0.631	3.083	0.245	5.017	0.007	0.181	0.060	4.480	0.943	12.761

Note: The estimates for numbers and biomass are $\times 10^9$ individuals and $\times 10^3$ tonnes, respectively.

is only a problem for prey items with digestion times around t_{\max} , and is assumed to have minor influence on the consumption estimates, especially since inspection of the length–weight data shows that weight at 1-cm length groups is approximately symmetrically distributed around the mean. However, it is important to ensure that the estimation of t_{\max} is based on a sufficient number of observations. Another factor that may influence the estimation of fresh weight of

prey is that the prey tends to curl up during the digestion process within the stomach of the predator. The lengths of prey in the stomach database may therefore be slightly underestimated, leading to an underestimation of the fresh weight, and thereby the digestion times.

Another source of error when estimating consumption by a GEM is the differences between digestion rates of single item meals, several prey of same type, and mixed prey meals.

Table 5. Acoustic estimates of stock sizes in numbers of 1- and 2-year-old herring (N_1 and N_2 , respectively) in May–June, estimated consumption of 1- and 2-year-old herring by cod (C_{1-2}) in the period between (1-group in intervals 3–5 in year one and 2-group in intervals 1–2 in year two), and resulting total (Z) and predation (M_{pred}) instantaneous mortality coefficients.

Year class	N_1	N_2	C_{1-2}	Z	M_{pred}
1991	32.6	25.8	2.0	0.23	0.07
1992	102.7	59.2	8.9	0.55	0.11

Note: Stock sizes and consumption are $\times 10^9$ individuals.

A large meal consisting of several prey may contain prey of different levels of digestion, as the prey tend to form a food bolus with a common surface accessible to digestion enzymes (Knutsen and Salvanes 1999). Inspection of the data used in this study showed that 85% of the cod that had eaten herring had less than or equal to three herring in the stomach, indicating that this effect is small. The digestion of single prey is a function of its energy content relative to other prey in the stomach (Andersen 2001). Capelin is the most common prey found in cod stomachs in the Barents Sea (Bogstad and Mehl 1997; Bogstad and Gjøsaeter 2001), making it the most likely prey species to mix with herring in the cod stomachs. Inspection of the data used here showed that 10% of the cod stomachs that contained herring also contained capelin. The energy content of juvenile herring and capelin is similar, with some seasonal variation in capelin (Mårtensson et al. 1996; Lawson et al. 1998). Assuming that herring is digested as a single prey should therefore be a reasonable approximation even if it occurs together with capelin in the stomach. Crustaceans are another important prey type of cod in the Barents Sea (Bogstad and Mehl 1997) and may be important in mixed meals with herring. The digestion of mixed meals of fish and crustaceans is probably more complicated than mixtures of fish alone and could bias the consumption estimates (Andersen 2001). Singh-Renton and Bromley (1996) found no difference in the digestion rate of herring in whiting when mixed with crustaceans in the diet. In the data used here, 20% of the cod stomachs that contained herring also contained crustaceans. In 76% of these mixed meals, the weight of crustaceans was less than half the weight of herring.

When estimating total consumption, we multiply the mean predation rate for cod that have eaten herring with the proportion of cod with measurable herring in their stomachs. The proportion is based on the stomach samples, and it is obvious from our results that it depends on the stomach sample size. The effect of this is that per capita consumption of herring may be overestimated for certain combinations of strata and cod size group where the number of stomachs sampled is low. In this study, small sample sizes mainly occur in size groups at both extremes of the size distribution of cod. The abundance of the largest cod is low, making the potential bias in the estimate of total consumption due to imprecise estimates of the proportion less pronounced compared with the smallest cod. The relationship between sample size and the proportion of cod with measurable herring in their stomachs given here indicates that a sample size of at least 20 is required to minimize this problem. Aggrega-

tion of size groups to attain the required sample size should be considered when the sample sizes are low.

A sensitivity analysis was done by adding one stomach with herring belonging to the cod size group 40–49 cm, which is among the most abundant size groups of cod in the area. This maximizes the effect of the addition, as the consumption estimates are calculated by multiplying consumption rate by cod abundance. Adding the observation to a stratum to which data are not extrapolated will also maximize the effect. Extrapolation involves the averaging of data from several strata and dilutes the effect of a single stomach. As such, the simulation presented here represents a maximum impact situation. The effects shown in the sensitivity analysis are moderate, but must be taken into consideration when inspecting the data set before estimating consumption by the method presented here. These results emphasise the importance of keeping the sample size above a certain limit, as discussed above. The effect of single stomachs will be highly exaggerated in situations with few stomach samples.

Estimation of error in the calculations is complicated because the calculation routine involves several parameters with associated uncertainty. The spatial and temporal extrapolation also makes error estimation difficult. Here we study the robustness of the method through a sensitivity analysis. Comprehensive error estimation is beyond the scope of this work, but we view this as an important objective for further refinement of the method.

Consumption of herring by cod in the Barents Sea

Year and interval-specific mean predation rate (number of herring eaten per cod per hour) of different age groups of juvenile herring by cod in the Barents Sea varied from 0.879 for 0-group herring in interval 5 in 1993 to 0.020 for 3+-group herring in interval 3 in 1996. Both of these extremes are estimates from one cod stomach. The estimates were also often characterized by a high coefficient of variation. It is reasonable to find such high variation in a measure based on individual fish, both as a reflection of individual variation in feeding of fish (Ehlinger 1989; Salvanes and Hart 1998) and as an effect of temporal and spatial variation in prey abundance, abundance of alternative prey, and abiotic factors (Daan 1973; Rose and Leggett 1989; Greenstreet et al. 1998). The cases with high coefficient of variation were not confined to the cases with low sample size, and there was no obvious trend in the relationship between these statistics.

Mean predation rate tended to decrease with the age of herring. It also increased with cod size for the two oldest age groups of herring. This is most likely a reflection of the stomach capacity of cod. There is room for more small herring than large herring in a cod stomach, and the stomach capacity of cod increases with its size. Note that size variation of the predator is incorporated in the GEM, adjusting for possible effects of predator size on digestion rate. However, there is no clear consensus concerning the influence of predator size on gastric evacuation rate (Andersen 1999). Earlier work on the size-specific predation on herring by cod in the Barents Sea also shows an increasing importance of older age groups of herring in cod diet as the size of cod increases. However, small size groups are still included in the diet as cod grows, leading to increased size spectre of con-

Table 6. Predation mortalities (M_{pred}) on 1- and 2-year-old herring given as the relationship between consumption estimate of age a herring (C_a) and acoustic estimate of age a herring (N_a), assuming acoustic abundance estimates give mean annual stock size.

Age	1992			1993			1994		
	C_a	N_a	M_{pred}	C_a	N_a	M_{pred}	C_a	N_a	M_{pred}
1	2.0	32.6	0.06	4.4	102.7	0.04	—	—	—
2	2.5	14.0	0.18	1.0	25.8	0.04	7.7	59.2	0.13

Note: For a given herring age a , $M_{pred} = C_a/N_a$.

Table 7. Results of the sensitivity analyses where one stomach observation was added to the data set in stratum 8 in interval 1 in 1994.

Interval	Original estimates	Min. predation rate (0.030)	Mean predation rate (0.082)	Max. predation rate (0.191)
1	4.734	5.004	5.406	6.299
2	2.630	2.797	3.049	3.599
3	0.135	0.117	0.145	0.208
4	0.225	0.225	0.225	0.225
5	0.013	0.013	0.013	0.013
Total	7.737	8.156	8.838	10.344

Note: Cod (*Gadus morhua*) size was 40–49 cm and herring (*Clupea harengus*) were of 2-group age. Calculations were done for minimum (Min.), mean, and maximum (Max.) predation rate for 2-group herring for the whole data set. Results are individual herring consumed $\times 10^9$.

Table 8. Comparison of the yearly consumption (tonnes $\times 10^3$) of herring by cod in the Barents Sea in 1992–1997, calculated by (i) the method presented in this study, (ii) the International Council for the Exploration of the Sea Arctic Fisheries Working Group (ICES 2002a), and (iii) the method given by Temming and Andersen (1994).

Year	Yearly consumption		
	This study	ICES 2002a	Temming and Andersen 1994
1992	271	332	259
1993	152	164	143
1994	494	147	129
1995	138	115	93
1996	24	47	36
1997	13	5	4

Note: All estimates are based on the same stomach content data, whereas there are differences in the gastric evacuation rate model and the spatial and temporal resolution used in the calculations.

sumed herring with cod size (Johansen 2003). An increased size spectrum of prey with increasing predator size is common in marine fish (Scharf et al. 2000).

Total consumption of juvenile herring by cod in the Barents Sea in the period 1992–1997 shows high consumption in the period 1992–1994, with a peak in 1994. In the period 1995–1997, consumption gradually decreased. The herring year classes 1991–1993 were strong (Toresen et al. 1998), and this explains the high consumption in this period. The peak observed in 1994 can be explained by an accumulation of juvenile herring from the year classes 1991–1993 in the Barents Sea. The increase in consumption was observed for all herring age groups.

Another factor influencing consumption of herring may be the dynamics of the capelin stock in this period. In 1994, the abundance of capelin in the Barents Sea was very low (Gjøsæter et al. 1998), and the predation on herring may have increased. The work of Barros et al. (1998) indicates that the mortality of juvenile herring in the Barents Sea increases as the ratio capelin/cod abundance decreases. Johansen (2002) also found that a higher proportion of the cod population consumed juvenile herring when the capelin stock was low.

The estimates of total consumption throughout the whole year are vulnerable to variation in sampling effort between the different times of the year. The sampling effort is particularly low in intervals 2 and 3, making it difficult to evaluate the estimates in these intervals. The temporal extrapolation of data is done to counteract the effect of insufficient sampling in certain periods. The predator–prey interaction between cod and herring in the Barents Sea shows little variation in intensity with season (Johansen 2002), justifying the temporal extrapolation done here. Interval 3 is most uncertain with respect to this, but the fact that this is the interval covering the shortest time span minimizes the problem.

Other estimates of consumption of herring by cod in the Barents Sea

The consumption of herring by cod in the Barents Sea has been calculated for the period 1984–2001 by the International Council for the Exploration of the Sea (ICES) Arctic Fisheries Working Group (ICES 2002a), using the method described by Bogstad and Mehl (1997), based on a GEM by Dos Santos and Jobling (1995). These estimates are based on the same stomach content data as used in this study, while there are differences in the gastric evacuation rate model and the spatial and temporal resolution used in the

calculations. For comparative purposes, we want to use the pooled data used by Bogstad and Mehl (1997) and the same spatial and temporal resolution also when using the GEM by Temming and Andersen (1994). The Temming and Andersen method does not require an approximation for the initial meal size. However, the method by Temming and Andersen is based on using data from individual stomachs. Thus, a correction factor is needed to account for the difference between individual and pooled stomachs. This factor will depend on the feeding pattern; we use the factor (1.2/1.35), which can be deduced from the experiments made by Dos Santos and Jobling (1995). We compared the two consumption estimates based on different GEM with the estimates from this study to see how much of the difference is due to the choice of evacuation rate model vs. other differences in methodology (Table 8). The estimates from the new method seem to correspond relatively well to the estimates from the other two in 1992, 1993, and 1995, whereas there are large relative differences for 1994, 1996, and 1997. The differences in 1996 and 1997 are not so large in absolute terms, but the difference in 1994 is more worrying. The estimates from the two other methods were quite similar, indicating that the GEM used is not responsible for the difference between the new method and the two others. The estimates from the method by Temming and Andersen (1994) were a bit lower compared with those from the method by Dos Santos and Jobling.

If stomach content is set to 20 g, cod weight to 1000 g, and temperature to 5 °C, the Dos Santos and Jobling (1995) approach gives an hourly consumption rate of 0.32 g, whereas the Temming and Andersen (1994) approach gives 0.26 g. The difference between the two models is strongly dependent on the cod body weight; for this example, a cod weight of about 350 g gives the same consumption. The Temming and Andersen approach gives the highest consumption for cod <350 g, whereas the Dos Santos and Jobling approach gives the highest consumption for cod >350 g. As most of the herring is eaten by larger cod (Johansen 2003), it is reasonable that the Dos Santos and Jobling model gives the highest consumption. The body weight dependency for herring as prey in the Temming and Andersen (1994) model is very low, because of a limited range of predator size in the experiment. Temming and Herrmann (2003) estimated this parameter to 0.305, which is close to the Dos Santos and Jobling value of 0.26. The choice of parameters for the GEM depends on the availability of proper laboratory results, and care should be taken when evaluating and selecting these. However, the principles of the estimation method presented here are not influenced by the specific parameter estimates, which may be adjusted when new and better parameter estimates becomes available.

The calculations based on the methods used by Bogstad and Mehl (1997) and Temming and Andersen (1994) divide the Barents Sea into three areas and calculate the consumption for each half-year, cod age group, and herring length group (5-cm groups for herring <20 cm and 10-cm groups for larger herring). Those two methods thus differ from the method presented in this paper both in spatial and temporal resolution and in choice of GEM. In those two methods, the estimates were calculated by cod age, and cod that were not

age determined were omitted from the analysis. Excluding these cod stomachs from the present analyses decreased the consumption by about 70 000 tonnes in 1994, mostly influencing consumption of 1-group in the first quarter. Another factor that may affect the consumption estimates for the second half-year of 1994 is the area distribution of cod. Owing to missing survey data on area distribution of cod in this period, the area distribution from 1995 was used in the present paper, while in the other two methods, the diet in the western and eastern area in the second half-year of 1994 was assumed to be the same. Together, these factors may explain some of the large discrepancy between the estimates from the new method and those from the other two approaches.

The new method for estimating consumption presented here is developed for predatory fish that swallow the prey whole. In cases where the predators masticate the prey, measuring the length of individual prey becomes difficult or impossible, and the method as presented here is less useful. The method is best suited to situations with a high level of sampling effort. At least 20 stomachs within each study unit are recommended. The method is best suited to relatively simple ecosystems with predator-prey interactions involving few species. In such situations, the uncertainty connected to the digestion of mixed meals is smaller. The method was applied to a boreal ecosystem with relatively low water temperature. If the water temperature is high, the digestion process may be too quick to get reliable estimates of t_{\max} , especially for small prey. We do not recommend the direct application of the method in areas of high water temperature without carefully testing if the assumptions and principles of the method hold. The method is appealing in that it provides consumption estimates in the number of prey, which is easily converted to predation mortality. Number of prey is also useful in studies of the behavioural basis for predator-prey interactions related to prey selection mechanisms and size dependency.

Predation mortality of juvenile herring in the Barents Sea

The highly variable natural mortality of different year classes of juvenile herring in the Barents Sea is an example of how the abundance of a fish stock is determined at the juvenile stage. It has been suggested that predation by north-east Arctic cod is the main factor determining this variation (Mehl 1989; Barros et al. 1998). Toresen et al. (1998) argued that the acoustic estimates of immature herring in the Barents Sea are internally consistent and are also consistent with the relative abundance estimates of the year classes as measured as adults. However, data on the abundance of the 1991 and 1992 year classes at the 0-group stage (trawl surveys) and at age 3 (VPA estimates) suggest that the difference in abundance and mortality between these year classes at age 0 to age-3 is much smaller than indicated by the acoustic abundance estimates of these year classes at age 1 and age 2. The 0-group indices of these two year classes are 1.19 and 1.05, respectively, whereas the VPA estimates at age 3 are 23.5 and 26.4 × 10⁹ individuals, respectively (ICES 2002b). The mortality estimates presented here should therefore be treated with caution. For calculating predation mortalities, we considered the acoustic estimates to be absolute estimates of stock abundance. This is a strong assumption.

In ICES stock assessments, acoustic abundance estimates are usually treated as indices with associated catchabilities that may be different from 1 and may vary between age groups. In this study, we made the even stronger assumption that the acoustic estimates for each age group in May–June approximately correspond to the mean stock size during the year. If total mortality Z is constant during the year, the time within the year when stock size is reduced to its mean value for the year is a function of Z and can easily be calculated (Salvanes and Ulltang 1992). It will be sometime in June, i.e., approximately at the time of the surveys, with the level of Z estimated for herring.

Juvenile herring in the Barents Sea seem to be vulnerable to significant natural mortality because of predation from the cod stock in the area. The level of this mortality varies from year to year, and this may explain some of the variation in recruitment to the adult stock. It is worth noting that the cod stock in this area was low in the period studied here compared with the period 1950–1970 (Nakken 1994). If the abundance of the cod stock in the Barents Sea should increase in the future, it is likely that the natural mortality of juvenile herring also increases. This may be important to consider when dealing with the stock of Norwegian spring-spawning herring in a management context. The relationship between natural mortality of herring at the 0-group stage and the ratio between abundance of cod and capelin in the Barents Sea found by Barros et al. (1998) could not be tested with the mortality estimates found in this study. The high and variable consumption of 0-group herring by cod warrants a rigorous testing of such an ecosystem effect, applying longer time series of suitable stomach data from cod and estimates of predation mortality for 0-group herring.

To predict the mortality of young herring in the Barents Sea, predation by sea mammals should be taken into consideration in addition to predation by cod. Minke whales (*Balaenoptera acutorostrata*) and harp seals (*Phoca groenlandica*) consume considerable amounts of juvenile herring in certain years (Nilssen et al. 2000; Lindstrøm et al. 2002), and their consumption in such years may be of the same order of magnitude as that of cod. Predation by other predators on juvenile herring seems to be of minor importance in this system (Bogstad et al. 2000).

In conclusion, the results from applying the new method for estimating consumption in fish presented here are promising. The new method has proven to be an interesting alternative to other methods and is worthy of further development. Future refinement of the method involves inclusion of error estimates, detailed studies of the different stages in the estimation procedure, and testing the method on other species and in other ecosystems.

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Appendix A

Extrapolation of temperature data

The temperature data were given on a quarterly basis, and data from quarters 1, 2, 3, and 4 were used to estimate temperature in intervals 1, 2, 4, and 5, respectively. For interval 3, temperature data for quarters 2 and 3 were combined. In quarter 4 in 1994–1997, some stratum means were missing and were estimated as follows: the difference between average temperature in stratum s in year y and quarter Q ($T_{y,Q,s}$) and the year and quarter-specific mean temperature for the 0- to 200-m depth range from the Russian hydrographic section off the Kola peninsula ($\bar{K}_{y,Q}$) (Tereshchenko 1996 and data provided by Polar Research Institute of Marine Fisheries and Oceanography, Murmansk) were calculated for the period 1992–1997 as $\text{dif}_{y,Q,s} = T_{y,Q,s} - \bar{K}_{y,Q}$. A linear regression of these differences in quarters 3 and 4 ($\text{dif}_{y,4,s} = -0.0092 + 0.8566(\text{dif}_{y,3,s})$, $df = 37$, $r^2 = 0.81$, $p < 0.0001$), combined with the mean Kola section temperature in quarter 4, was used to estimate the missing stratum means.

Spatial extrapolation of stomach data

The stomach data were segregated on size groups of cod and age groups of herring. Results from earlier studies (Johansen 2002, 2003) were used to set the rules used when extrapolating. If a stratum contained less than five trawl hauls with stomach samples, predation rates (averaged over the neighboring strata with at least five hauls with stomach

Table A1. Scheme for temporal extrapolation of stomach data.

Interval	Strata	Interval extrapolated from	Strata extrapolated from	Herring age
2	All	1	The same	All
3	14 (summer strata)	1	Average of 1, 4, 5 (winter strata)	All
3	15 (summer strata)	1	Average of 2, 4, 6 (winter strata)	All
3	16 (summer strata)	1	Average of 7, 8, 11, 12 (winter strata)	All
3	160 (summer strata)	1	Average of 7, 8 (winter strata)	All
3	17 (summer strata)	1	Average of 7, 8, 13 (winter strata)	All
5	All, except 11	4	The same	1+
5	17, 130	4	Average of all strata	0

samples in the same interval) was extrapolated in space. The proportion of cod with measurable herring in their stomachs was calculated for the neighboring strata combined. If neighboring strata also lacked sufficient data, temporal extrapolation from other intervals was carried out, preferably from the same stratum. In intervals 1–2, this was done if the target stratum had less than two neighboring strata with at least five hauls with stomach samples, whereas in intervals 3–5, only one neighboring stratum with sufficient data was required. In interval 1 in 1995–1997, missing data in stratum 9 were completed with data from stratum 8, as this is the only neighboring stratum with data in this period. If the stratum contained some hauls with stomach samples, these data were included. In some strata, the predation on herring by cod only occurs in parts of the stratum, or the part of the cod population involved is lower compared with the main areas (Johansen 2002). When extrapolating to such strata, the proportion of cod with measurable herring in their stomachs was corrected according to the approximate proportion of the cod population assumed to consume herring in that stratum (Fig. 2).

Temporal extrapolation of stomach data

An overview of the scheme for temporal extrapolation of the predation rate is given in Table A1. In intervals 1, 2, and 3, similar spatial distribution of herring in cod stomachs was assumed (Johansen 2002). Note that the strata system used in interval 3 was different from intervals 1 and 2, because the distribution of cod in interval 3 is assumed to be more similar to the distribution found during the autumn survey. In intervals 4 and 5, similar spatial distribution of 1 year and older herring in cod stomachs was assumed (Johansen 2002, 2003), except for stratum 11 (Fig. 2). Herring is not found in cod stomachs in this stratum in interval 5 (Johansen 2002). In interval 5, 0-group herring has a more southeastern distribution compared with interval 4 (Reidar Toresen, Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway, personal communication) and is not found in stomachs west of 36°E (Johansen 2003). For this age group, the total average for all strata in interval 4 was applied to strata 17 and 130 in interval 5.