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Herring as a major consumer in the Norwegian Sea

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Using available information, the authors attempt to calculate the food consumption of the Norwegian Spring Spawning Herring in the Norwegian Sea in the years 1994–1996, and to calculate how much is taken of different prey organisms. Consumption/biomass ratios extracted from literature vary within the range 3.0–7.0. Based on the likely size of the herring stock in the Norwegian Sea and an annual consumption/biomass ratio of 4.5, the consumption in 1994, 1995, and 1996 was calculated to be 31, 40, and 47 million tonnes, respectively. Quantitative data are presented on the presence of different prey categories in herring stomachs in different water masses (Coastal, Coastal/Atlantic, Atlantic, and Atlantic/Arctic, respectively), and the results are used to estimate total consumption of the different prey categories by herring. Based on a consumption/biomass ratio of 4.5, the consumption of copepods in 1994, 1995, and 1996 was calculated to be 19, 24, and 29 million tonnes, respectively, making up 62% of the food consumed as a mean over the 3 years. Corresponding numbers for krill were 1.2, 3.3, and 1.8 million tonnes and 5%, and for amphipods 3.3, 5.2, and 6.6 million tonnes and 13%. The results are compared with the assumed production by the different prey organisms in the areas where the herring feed. For copepods it seems that the consumption by herring is at the same level as the production, but for other prey organisms the production seems to exceed consumption by herring.

Keywords: copepods, food consumption, krill, Norwegian spring-spawning herring, production.

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Introduction

The Norwegian Spring Spawning Herring is potentially the largest of the herring stocks in the northeast Atlantic. The stock collapsed by the end of the 1960s (Dragesund *et al.*, 1980; Jakobsson, 1980), and the traditional feeding and wintering areas in the Norwegian Sea were left unused. During the 1970s and early 1980s the stock was gradually rebuilt, and the first strong year class after the collapse came in 1983. Røttingen (1992) and Dragesund *et al.* (1997) have described the migratory pattern of the 1983 year class. By the early 1990s the stock had regained much of its previous distribution area and was again feeding in the Norwegian Sea. Since 1995 the migrations in the feeding area have been described each year in reports from the international cruises in the Norwegian Sea (see for example Anon., 1995, 1996; Vilhjalmsson *et al.*, 1997; Holst *et al.*, 1998, 1999, 2000).

The herring spawn along the Norwegian coast, from 59°N to 69°N. Larvae and 0-group herring drift northward with the coastal current and into the fjords and the Barents Sea (Devold, 1963; Dragesund *et al.*, 1980; Holst and Slotte, 1998). Strong year classes stay in the Barents Sea during the first years, and then migrate into the Norwegian Sea during the summer when they are approximately 3 years old. After the recovery of the stock, the larger and older herring have been feeding in the Norwegian Sea from April to September, moving in a clockwise fashion from the coast westwards and northwards and then back to the coast at about 69°N, while the smaller and immature herring have been found mostly in the eastern part on or near the shelf (Anon., 1995, 1996; Vilhjalmsson *et al.*, 1997; Holst *et al.*, 1998). In the 1990s most of the stock has migrated into the Vestfjord fjord system (about 68°20′N) in September–October, although some of the younger herring seem to winter on the outer part of the shelf outside Lofoten–Vesterålen. From October until the spawning migration starts in January the herring stay in deep water without feeding. Most of the herring mature as 5 years old, and spawn in February–April on the shelf (see for example Slotte and Dommasnes, 1998). The distribution and migration routes in 1994–1996 are shown in Figure 1.

In this paper we combine information about stock size, distribution, stomach contents and food requirements for

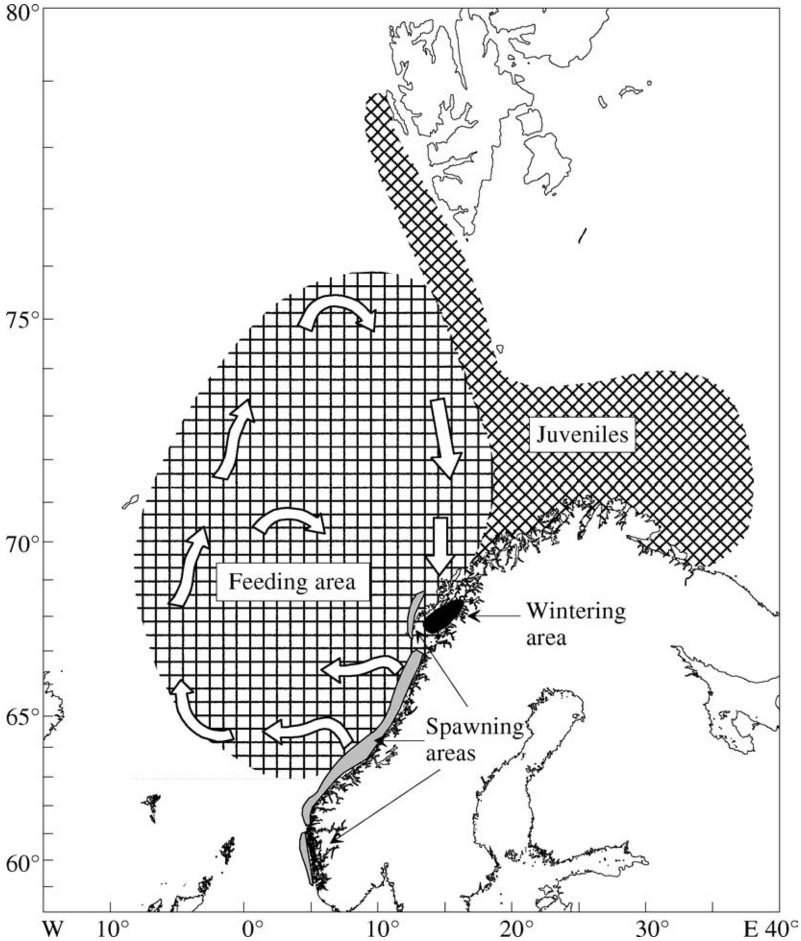

Figure 1. Distribution and migration routes of Norwegian Spring Spawning Herring in 1994−1996.

the Norwegian Spring Spawning Herring in order to quantify the consumption by the stock, and compare the consumption with information available on the production of the prey species. This approach may contribute to an understanding of the harvesting potential for the stock and of whether there may be "surplus" production on the trophic level below which can also be harvested.

Material and methods

The data sources we have used are:

- Acoustic estimates of Norwegian Spring Spawning Herring, stomach contents of herring, and hydrographic data from research cruises in the Norwegian Sea in 1994, 1995, and 1996.
- Data from Virtual Population Analysis (VPA) run by the ICES Northern Pelagic and Blue Whiting Working Group (WGNPBW) (ICES, 2002) giving stock numbers by age by 1 January for the years 1950−1998.
- Published data on consumption/biomass ratios and about the diet of herring.

The use of the basic data and how they have been combined is illustrated by the flowchart in Figure 2.

Acoustic estimates

The distribution of herring in the Norwegian Sea is based on acoustic estimates from Norwegian research cruises during the second and third quarters of the years 1994−1996, with one cruise in the second quarter and one cruise in the third quarter of each year (Table 1). Data available from the cruises include hydrographic data (temperature and salinity), acoustic data for herring (integrated backscattered energy, "s_A-values"), and biological data for herring (length, weight, age, and stomach contents).

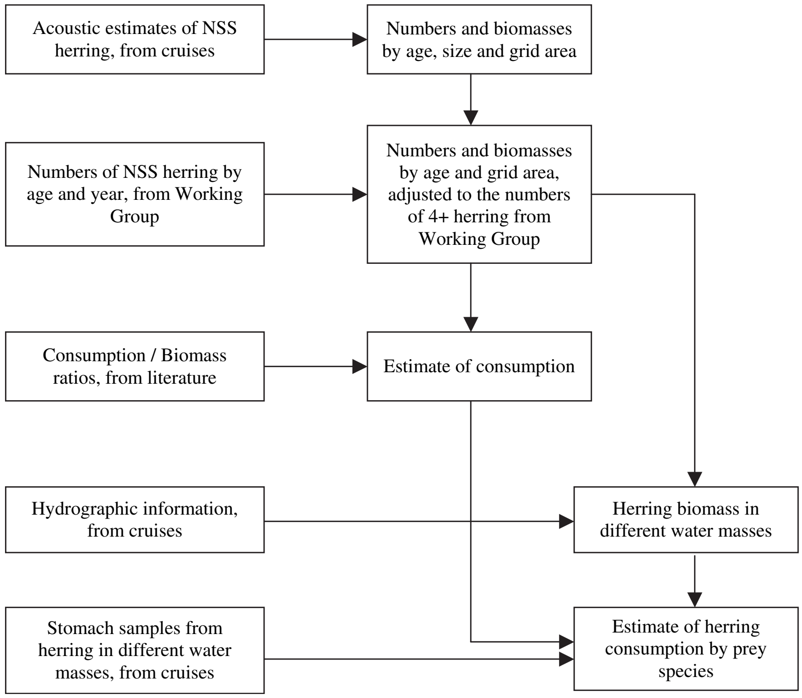

Figure 2. Illustration of data sources and the use of the data for the estimation of the consumption of different prey species by Norwegian Spring Spawning Herring.

Although acoustic estimates of herring from these cruises have been calculated previously and the cruises in 1995 and 1996 formed part of the international cruises in the Norwegian Sea (Anon., 1995, 1996), we have calculated new acoustic estimates in order to have uniform treatment of the data and to have access to age- and length-distributions as well as mean weights within each of the grid areas described below. As a basis for the calculations we have used a geographic grid of 1° latitude by 2° longitude. For each of the grid areas we have calculated a mean integrated backscattered energy ("s_A-value") for herring, and allocated biological samples to represent the biological parameters of herring in that grid area. Using standard methods (Dommasnes and Røttingen, 1984; Gjøsæter *et al.*, 1998; Toresen *et al.*, 1998), we have calculated "acoustic estimates" for numbers and biomass for ages 1–16 for 1-cm-length groups within each grid area and for the total area. The biomass was split between "small herring" (<30 cm) and "large herring" (≥30 cm). The cruise tracks and the grid used for calculating the acoustic estimates are shown in Figure 3.

Table 1. Cruises used to calculate the distribution of herring.

Year	Quarter	Cruise	
1994	2nd	RV "G.O. Sars"	30.05–27.06
	3rd	RV "Johan Hjort"	05.07–22.07
1995	2nd	RV "G.O. Sars"	26.05–22.06
	3rd	RV "Johan Hjort"	07.07–02.08
1996	2nd	RV "G.O. Sars"	29.04–28.05
	3rd	RV "G.O. Sars"	19.07–15.08

Estimates of stock numbers by VPA

Stock numbers for the years 1994, 1995, and 1996 have been based on the numbers by age from WGNPBW. The number by 1 July for each year class has been calculated as the average of the number by 1 January of the year in question and the number for the same year class by 1 January the following year. The numbers for 4 years and older herring have then been added to give numbers of 4+ herring by 1 July in each of the years (third column in Table 3).

Published data on consumption/biomass ratios

In order to find information about the consumption/biomass ratio (Q/B) for herring we have evaluated data from several studies. Christensen (1995), Dommasnes *et al.* (2001), and Pavshtiks and Timokhina (1972) gave Q/B data directly, while Ma *et al.* (1997), Blaxter and Holliday (1958, 1963), and Arrhenius and Hansson (1993) gave data that could be used to calculate Q/B ratios for herring. The results are summarized in Table 2, and the Q/B ratios obtained range from 3.0 year^{-1} to 7.0 year^{-1}.

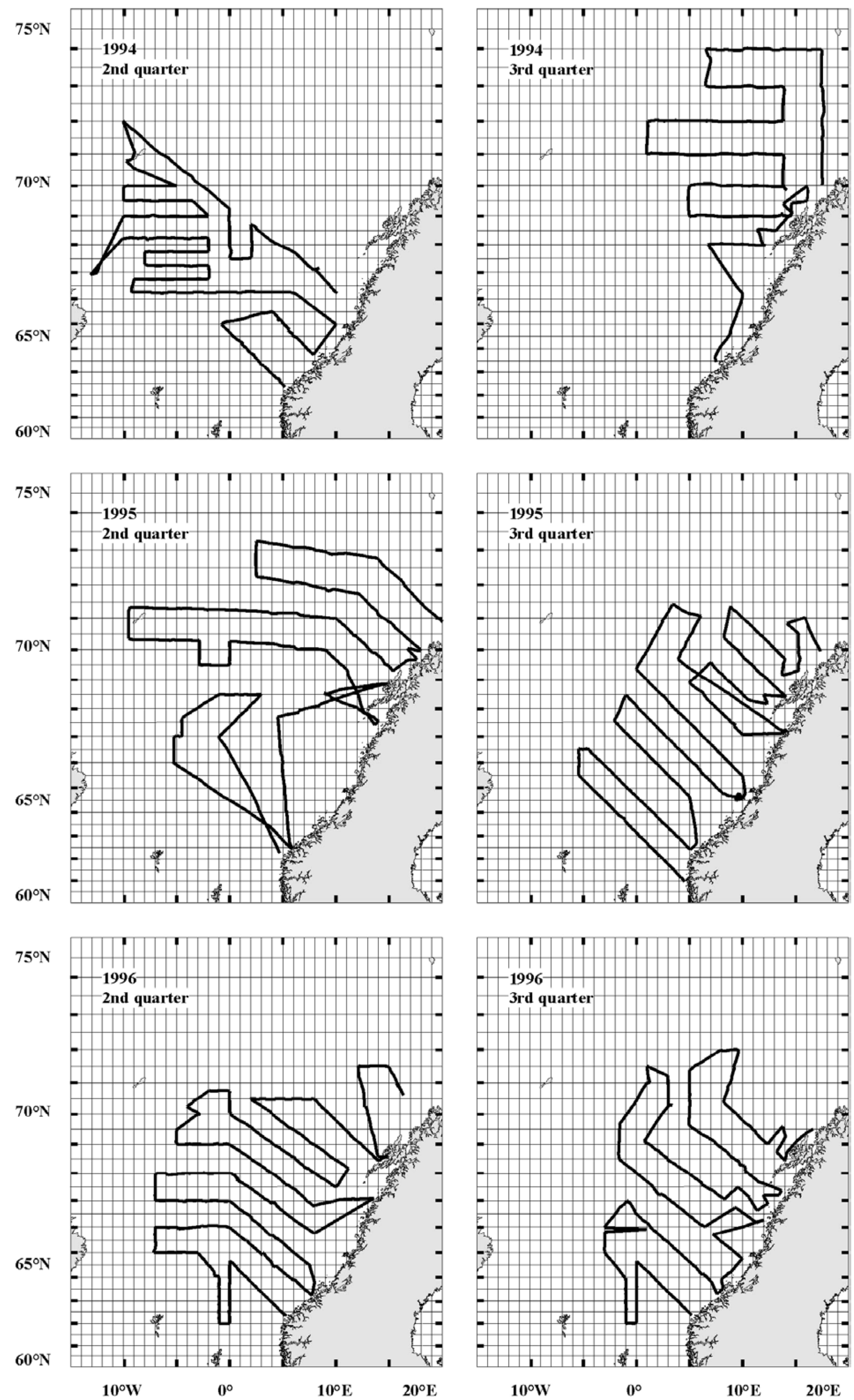

Figure 3. The grid system used and the cruise tracks for the cruises in the second and third quarters of the years 1994–1996 from which the oceanographic data, stomach samples, acoustic estimates and distribution of herring by grid areas have been obtained.

Table 2. Consumption data for herring from various authors and consumption/biomass ratios (Q/B) extracted by the present authors.

Author(s)	Estimate of consumption	Environment	Q/B ratios extracted by the present authors ($year^{-1}$)
Ma *et al.* (1997)	2.1 g $fish^{-1}$ day^{-1} for herring with mean weight 253 g	Aquarium	3.0
Blaxter and Holliday (1963)	64 mg (g $fish)^{-1}$ $week^{-1}$	Aquarium	3.4
Christensen (1995)	Q/B = 4.6 $year^{-1}$	The North Sea	4.6
Dommasnes *et al.* (2001)	Q/B = 4.47 $year^{-1}$	The Norwegian Sea	4.47
Arrhenius and Hansson (1993)	Bioenergetics model gave food consumption during one year for Baltic herring. Based on data from the paper, the mean Q/B ratio for ages 4−10 (mean weight 55.1 g) was 5.78 $year^{-1}$	The Baltic Sea	5.78
Pavshtiks and Timokhina (1972)	One tonne of herring consumes 6−8 tonnes of plankton $year^{-1}$	The Norwegian Sea	7

Characterization of water masses

Temperature and salinity data were obtained for each station using a CTD sonde. On the basis of the hydrographic data obtained at different depths (10, 50, 100, 200, 500 m) and using the description of water masses given by Johannessen (1986) the grid areas were classified for each cruise as belonging to five hydrographic regions: (1) Norwegian Coastal, (2) Mixed Coastal/Atlantic, (3) Atlantic, (4) Mixed Atlantic/Arctic, and (5) Arctic. A schematic presentation of the distribution of water masses in the Norwegian Sea has been given by Dalpadado *et al.* (1998). For a few grid areas where the water column was strongly stratified with different water masses at different depths we also checked the echo sounder data showing herring depth distribution before deciding to which water mass we would allocate these grid areas. As only few hydrographic stations were taken in Arctic water, and we had no stomach samples from Arctic water, these stations were pooled with the Atlantic/Arctic group.

Results

The numbers of 4+ herring calculated from the acoustic surveys are much lower than those calculated from the numbers by age and year given by WGNPBW (ICES, 2002) (Table 3, columns 3 and 4). We assumed that there is a variable bias in the acoustic estimates, and because the Norwegian Spring Spawning Herring migrate into the Norwegian Sea at an approximate age of 3 years we also assumed, for the purpose of this study, that all 4 years and older herring of the stock are present in the Norwegian Sea.

In order to get the best possible representation of the part of the stock in the Norwegian Sea we wanted to: (1) use the

Table 3. Adjustment of acoustic estimates. The table shows numbers of 4+ herring by 1 July 1994−1996 calculated from VPA stock numbers from WGNPBW (ICES, 2002), numbers of 4+ herring from the acoustic estimates, the "raising factors", and the application of the raising factors to the acoustic estimates of biomass.

		Numbers of 4+ herring (millions)			Biomasses of herring from acoustic estimates (million tonnes)		
Year	Quarter	Numbers by 1 July calculated from WGNPBW data	Acoustic estimates	Raising factor	"Original"	Raised	Mean raised
1994	2nd	18 728	6 194	3.02	2.233	6.752	6.781
	3rd		13 064	1.43	4.751	6.811	
1995	2nd	32 893	8 600	3.82	2.082	7.962	8.883
	3rd		20 387	1.61	6.076	9.803	
1996	2nd	45 859	43 418	1.06	8.311	8.778	10.349
	3rd		12 005	3.82	3.120	11.919	

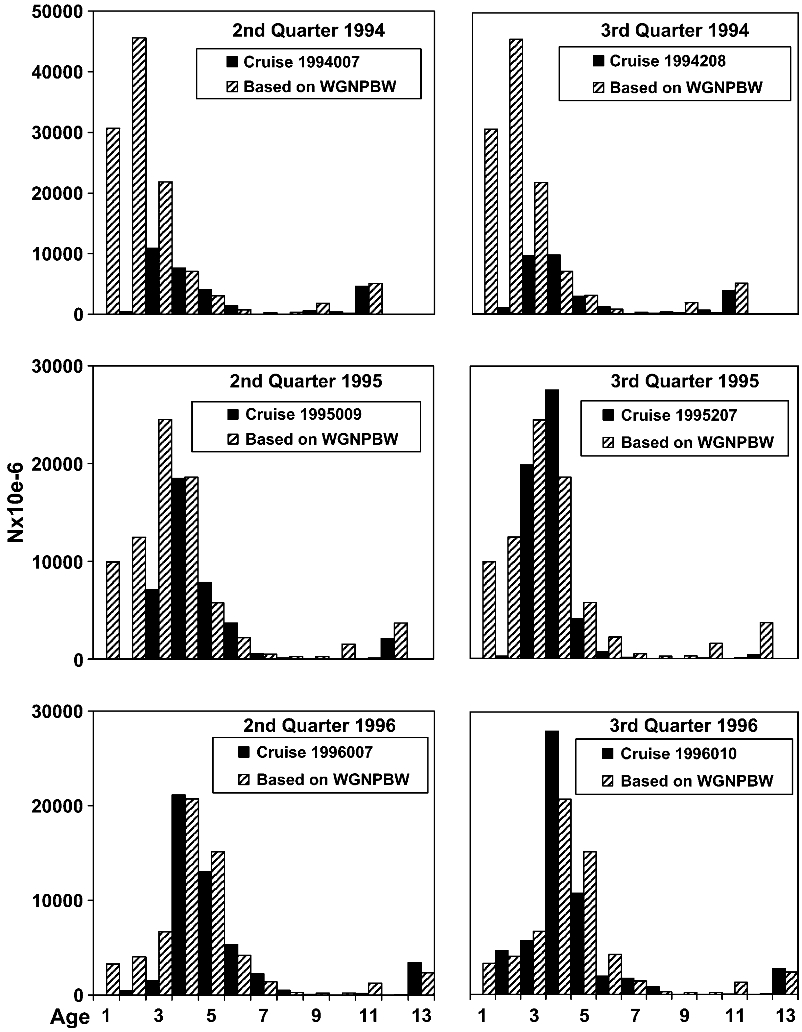

Figure 4. Age distributions (million individuals) from the recalculated acoustic estimates corrected by "raising factors" (see text) from each cruise, compared with the age distributions by 1 July based on VPA calculations by WGNPBW (see text).

numbers based on WGNPBW data for the size of the stock, (2) use the mean weights from the acoustic estimates to calculate the biomass, (3) use the relative distribution of biomass between grid areas to distribute the biomass of herring <30 cm and ≥ 30 cm between the water masses in the second and third quarters. The steps in this procedure are shown in Table 3. In order to compensate for the bias in the acoustic estimates we first calculated a "raising factor"

Table 4. Mean biomass of herring in the Norwegian Sea during the feeding season and consumption for the years 1994, 1995, and 1996, using different consumption/biomass (Q/B) ratios from literature.

Year	Biomass (million tonnes)	Consumption (million tonnes)		
		Ma *et al.* (1997) (Q/B = 3.0)	Dommasnes *et al.* (2001) (Q/B = 4.5)	Pavshtiks and Timokhina (1972) (Q/B = 7.0)
1994	6.781	20.343	30.514	47.467
1995	8.883	26.649	39.973	62.181
1996	10.349	31.047	46.570	72.443

Table 5. Biomass (thousand tonnes) of "small" (<30 cm) and "large" (⩾ 30 cm) herring feeding in different water masses in the second and third quarters of the years 1994−1996.

		Coastal		Coastal/Atlantic		Atlantic		Atlantic/Arctic		Sum	
Year	Quarter	<30 cm	≥30 cm	<30 cm	≥30 cm	<30 cm	≥30 cm	<30 cm	≥30 cm	<30 cm	≥30 cm
1994	2nd	4		609	24	1 982	1 849	163	2 113	2 758	3 985
	3rd	927	345	433	128	1 145	3 816			2 506	4 288
1995	2nd	1 048	585	892	325	1 685	2 063	18	1 334	3 643	4 307
	3rd	338	141	1 198	130	5 341	2 499		138	6 876	2 907
1996	2nd	61	7	121	33	3 293	2 629	167	2 498	3 643	5 167
	3rd	510	243	366	215	5 716	4 855	8	5	6 600	5 317

(Table 3, column 5) for each acoustic survey, which is the ratio between the number of 4+ herring by 1 July based on WGNPBW data and the number of 4+ herring calculated from that survey. The original biomasses calculated from the acoustic estimates (Table 3, column 6) were then multiplied with the raising factors to produce "raised biomasses" (Table 3, column 7) which are consistent with the numbers by 1 July calculated from the WGNPBW data. The raising factors have been applied to the biomasses of herring younger than 3 years as well, assuming that the acoustic estimates have the same bias for those as for the older herring. However, because most of the younger

Table 6. Stomach contents of herring in the second quarter of the years 1994−1996, as percentage occurrence by weight of prey categories in stomachs of "small" and "large" herring. "+" signifies that a prey category is present, but makes up less than 0.5% of the stomach contents.

			Atlantic		Atlantic/Arctic	
Prey category	Coastal	Coastal/Atlantic	<30 cm	≥30 cm	<30 cm	≥30 cm
Crustacea	1	11	6	3		+
Copepods	48	21	1	9	+	
Calanoidae	18	12	46	8	3	9
Calanus spp.	+	6	6	5	76	68
C. finmarchicus			20	68	18	20
C. hyperboreus					+	1
Krill	29	6	2	1		+
M. norvegica	1	3			2	
Thysanoessa spp.			+	2	+	+
T. inermis						
T. longicaudata					+	+
Amphipoda	+		2	1	1	+
Themisto spp.		3	3	+		+
T. abyssorum		6	1	+		+
T. compressa		1				+
Appendicularia		30				
Limacina						
Cladocera						
Chaetognatha			+			+
Fish	+					
Other*	2	1	12	3		
Number of stomachs	*35*	*101*	*122*	*119*	*51*	*87*

*Includes prey organisms not mentioned above as well as unidentified stomach content.

Table 7. Stomach contents of herring in the third quarter of the years 1994–1996, as percentage occurrence by weight of prey categories in stomachs of "small" and "large" herring. "+" signifies that a prey category is present, but makes up less than 0.5% of the stomach contents.

		Coastal/Atlantic		Atlantic		Atlantic/Arctic	
Prey category	Coastal	<30 cm	≥30 cm	<30 cm	≥30 cm	<30 cm	≥30 cm
Crustacea	9	15	13	34	14		
Copepods							
Calanoidae	3	9	3	13	9		
Calanus spp.		23	18	13	10		
C. finmarchicus	2	5	1	4	8		
C. hyperboreus							
Krill		2	4	3	2		
M. norvegica			+				
Thysanoessa spp.		15	20		2		
T. inermis		1	1				
T. longicaudata					+		
Amphipoda		1					
Themisto spp.	+	1	2	10	5		
T. abyssorum		+	1	9	15		
T. compressa					1		
Appendicularia		+	2	+	9		
Limacina	62	20	3		20		
Cladocera		1	2	7	+		
Chaetognatha		1	+	2	2		
Fish		2	24		+		
Other*	24	5	7	6	3		
Number of stomachs	*38*	*171*	*83*	*69*	*320*		

*Includes prey organisms not mentioned above as well as unidentified stomach content.

herring are found outside the Norwegian Sea the numbers for 1–3-year-old herring calculated from the acoustic estimates are still lower than those calculated from the WGNPBW data, even after multiplication with the raising factors (Figure 4).

Based on Table 2 a Q/B ratio of 4.5 year^{-1} (similar to the $Q/B = 4.47$ which was used by Dommasnes *et al.*, 2001) may be considered as a "middle" value, and the Q/B ratios of 3.0 year^{-1} (Ma *et al.*, 1997) and 7.0 year^{-1} (Pavshtiks and Timokhina, 1972) may be considered as "low" and "high" values, respectively. Multiplying the mean raised biomasses from Table 3 by those three Q/B ratios gives a range of values for the food consumption by herring in the Norwegian Sea for each of the years 1994–1996 (Table 4). For the "middle" value $Q/B = 4.5$ the consumption for the years 1994, 1995, and 1996 is 31, 40, and 47 million tonnes, respectively.

The raising procedure outlined in Table 3 was also applied to the herring biomasses obtained from the acoustic surveys within each of the grid areas. In addition, we used the length information from the surveys to separate the biomasses for "small" and "large" herring (<30 cm and ≥30 cm, respectively) because previous investigations showed that small and large herring to some extent select different prey (Dalpadado *et al.*, 2000). It was assumed that the herring in each grid area fed within the water mass that grid area had been assigned to. The resulting biomasses by year, quarter, length group, and water mass are shown in Table 5.

Based on the same material that was used by Dalpadado *et al.* (2000) to investigate the stomach contents of herring in different water masses in the Norwegian Sea, we have calculated the percentage occurrence by weight of different prey organisms in the stomachs of "small" and "large" herring for the second and third quarters, categorized by water masses (Tables 6 and 7). As the number of samples from each year was low for some of the water masses, data for the years 1994–1996 have been pooled, and for some of the water masses the herring size groups have been pooled as well.

If we assume that half the consumption occurs in the second quarter and half in the third quarter, it is possible to

Table 8. Annual consumption of different prey categories by Norwegian Spring Spawning Herring in the years 1994−1995, for a Q/B ratio of 4.5, in million tonnes and percentages (in italics).

	1994		1995		1996		Average	
Year	Million tonnes	%	Million tonnes	%	Million tonnes	%	Million tonnes	%
Copepods (pooled)	18.679	*61*	24.323	*61*	29.428	*63*	24.143	*62*
Copepods unspecified	2.836		6.721		5.929		5.162	
Calanoidae	4.432		6.053		7.342		5.942	
Calanus spp.	5.619		5.701		7.914		6.411	
C. finmarchicus	5.748		5.819		8.192		6.586	
C. hyperboreus	0.043		0.030		0.052		0.041	
Krill (pooled)	1.215	*4*	3.317	*8*	1.842	*4*	2.125	*5*
Krill unspecified	0.654		2.471		1.186		1.437	
M. norvegica	0.068		0.142		0.056		0.089	
Thysanoessa spp.	0.436		0.647		0.533		0.539	
T. inermis	0.016		0.026		0.019		0.021	
T. longicaudata	0.040		0.030		0.048		0.039	
Amphipods (pooled)	3.302	*11*	5.187	*13*	6.601	*14*	5.030	*13*
Amphipods unspecified	0.568		1.108		1.400		1.026	
Themisto spp.	0.935		1.777		2.160		1.624	
T. abyssorum	1.725		2.221		2.960		2.302	
T. compressa	0.074		0.080		0.080		0.078	
Appendicularia	1.188	*4*	1.372	*3*	1.090	*2*	1.216	*3*
Limacina	3.706	*12*	2.409	*6*	3.422	*7*	3.179	*9*
Cladocera	0.206	*1*	0.867	*2*	0.923	*2*	0.666	*2*
Chaetognatha	0.261	*1*	0.373	*1*	0.497	*1*	0.377	*1*
Fish	0.115	*0*	0.164	*0*	0.165	*0*	0.148	*0*
Other	1.843	*6*	1.961	*5*	2.603	*6*	2.135	*6*
	30.514	*100*	39.973	*100*	46.570	*100*	39.019	*100*

calculate the herring's consumption of each of the prey categories from the formula

$$C_j = (Q/B)\times 0.5\times \sum_q \sum_w \sum_s B_{qws}\times P_{qwsj} \qquad (1)$$

where

$C_j =$ consumption year^{-1} of prey organism j (million tonnes year^{-1}),
$(Q/B) =$ consumption/biomass ratio (year^{-1}),
$B_{qws} =$ biomass of herring of size s in water mass w and quarter q (million tonnes),
$P_{qwsj} =$ percentage by weight of prey j in the stomachs of herring of size s from water mass w and quarter q.

Table 8 shows the calculated annual and average consumption by prey categories for the years 1994−1996 based on the Q/B ratio of 4.5. The category "Crustacea" in Tables 6 and 7 has been distributed proportionally on copepods, krill, and amphipods, and percentages have been calculated for the main groups. There were no samples of stomach contents in Atlantic/Arctic water in the third quarter, and for this water mass we used information about stomach contents in the second quarter.

Copepods are the most important food item for the herring, making up 62% of the food intake by weight (Table 8). Other important groups are amphipods (13%), *Limacina* (9%), krill (5%), and "Other" (6%). Using the Q/B ratio of 4.5, the total prey consumption in 1996 was estimated to be 47 million tonnes for a herring population of 10 million tonnes (Tables 4 and 8). If Q/B ratio of 3.0 or 7.0 is used, the total consumption in 1996 was 31 or 72 million tonnes, respectively. Using the Q/B ratio of 4.5, we estimated that the herring consumed 29 million tonnes of copepods, 6.6 million tonnes of amphipods, 3.4 million tonnes of *Limacina*, 1.8 million tonnes of krill, and 2.6 million tonnes of "Other" prey in 1996 (Table 8). However, the consumption of krill was almost twice as high in 1995 (3.3 million tonnes) although the biomass of herring and the total consumption was lower compared to 1996. As we use the same set of stomach samples, such differences between the years must be due to different distribution of herring relative to the water masses.

Table 9. Consumption of major prey categories in tonnes per km^2 in the feeding areas, based on Table 8 and the sizes of the feeding areas as given in the text. The group "meso-zooplankton" includes the categories "Copepods (pooled)", "Appendicularia", "*Limacina*", "Cladocera", "Chaetognatha", and "Other" in Table 8, and therefore also includes the category "Copepods (pooled)" in this table.

Year	1994	1995	1996	Average
Feeding area utilized by herring (km^2)	421 952	355 437	370 491	382 627
Consumption (tonnes km^{-2})				
Krill (pooled)	2.9	9.3	5.0	5.6
Amphipods (pooled)	7.8	14.6	17.8	13.1
Copepods (pooled)	44.3	68.4	79.4	63.1
Meso-zooplankton (including copepods)	61.6	88.5	102.9	83.3

The feeding area of herring varies between years and does not include the whole Norwegian Sea in any given year. In order to get an estimate of the areas utilized by herring during the feeding season, and consumption per km^2 surface, we have added up the grid areas (Figure 3) where herring were found during either one or both of the cruises in the second and third quarter of each year (no grid area was counted twice). The areas added up to 421 952 km^2, 355 437 km^2, and 370 491 km^2 for the years 1994, 1995, and 1996, respectively, and can be considered as a minimum estimate of the feeding areas utilized in each of the years. Using these estimates, the annual consumption of the major prey categories given in Table 8 was standardised to tonnes per km^2 sea surface within the feeding areas (Table 9). All categories except krill, amphipods, and fish were combined in a new category "meso-zooplankton", which corresponds to the identically named group used by Holst *et al.* (2000), thus facilitating comparison with their production estimate for this group (Table 10).

Discussion

Data from this study show that herring consumed 19, 24, and 29 million tonnes of copepods in 1994, 1995, and 1996, respectively, and that copepods make up 62% of the food consumed as a mean over the 3 years (Table 8). Corresponding numbers for krill were 1.2, 3.3, and 1.8 million tonnes and 5%, and for amphipods 3.3, 5.2, and 6.6 million tonnes and 13%. Results from this study fall well within those reported by Gislason and Astthorsson (2002) for the Norwegian Spring Spawning Herring in the western Norwegian Sea, close to Icelandic waters. Their study showed that copepods were the most important prey in biomass, constituting 50−90%, while krill constituted up to 10% and amphipods up to 30%.

Our calculated consumption per km^2 by herring within the areas utilized for feeding (Table 9) can be compared with the estimates of biomass and annual production of zooplankton per km^2 sea surface in the Norwegian Sea and eastern parts of the Greenland and Icelandic Seas given by different authors (Table 10). The calculated consumption by herring is at the same level as the estimated production for the prey categories "copepods" and "meso-zooplankton", but it should be kept in mind that the estimates for production per km^2 in Table 10 are averages for large areas which do not take into account local variations in productivity, and we do not know to what extent herring adjust their feeding area in response to variations in stock size or zooplankton productivity. For the larger zooplankton in the categories "krill" and "amphipods", the calculated consumption is much lower than the production shown in Table 10. The high production of amphipods is mainly restricted to Arctic water (Dalpadado *et al.*, 1998), and therefore largely inaccessible to herring. There are also large stocks of blue whiting and mackerel feeding in the

Table 10. Biomass and production (wet weight) of zooplankton per km^2, based on data obtained from the Norwegian Sea and eastern parts of the Greenland and Icelandic Seas. Note that the group "meso-zooplankton" includes copepods, e.g. *Calanus finmarchicus* and *Calanus* spp. and other copepods.

Species/group	Biomass (tonnes km^{-2})	Production (tonnes km^{-2})	Original area (million km^2)	Source
Krill	29	44*	1.7	Dalpadado *et al.*, 1998
Amphipods	65	97*	1.7	Dalpadado *et al.*, 1998
C. finmarchicus	7†	28	2.9	Aksnes and Blindheim, 1996
Calanus spp.	10−40	39−161†	3.1	Hassel and Melle, 1999
Meso-zooplankton	24	96†	3.1	Holst *et al.*, 2000

*Based on production/biomass = 1.5 (Sakshaug *et al.*, 1994).
†Based on production/biomass = 4 (Sakshaug *et al.*, 1994).

Norwegian Sea, although the extent of their presence varies from year to year. The feeding areas of the three species overlap to a large extent and herring may experience competition for food from blue whiting and mackerel. The blue whiting mainly feeds on krill, amphipods, and mesopelagic fish and to a lesser extent on copepods (Timokhina, 1974; Bjelland and Monstad, 1997). Unpublished diet studies at IMR show that herring and mackerel have similar prey preferences, feeding mainly on *Calanus* during their main feeding season (Bjelland, personal communication). However, herring and mackerel have varying distribution, with herring occupying northern and eastern parts and mackerel mostly restricted to the southern part of the Norwegian Sea. Capelin, the fourth large stock of pelagic fish in the Norwegian Sea, has not overlapped with herring in the Norwegian Sea after the recovery of the herring stock. In the 1950s and early 1960s when herring were feeding north of Iceland there may have been considerable overlap during the feeding season, and Astthorsson and Gislason (1997) showed that capelin in subarctic waters north of Iceland consumed mostly *Calanus* copepods, with *Calanus finmarchicus* and *Calanus hyperboreus* dominating their diet.

The VPA runs produced by WGNPBW (ICES, 2002), which we have used to establish the biomass of the stock in the Norwegian Sea, use input from a ‘‘tuning’’ process based on several series of acoustic estimates, tagging data and catch by number and age, and establish the stock size that best fits all the data. The process is standardized and described in the WGNPBW reports (see for example ICES, 2002). Although the actual level of the calculated number for each year class changes somewhat from year to year, the data from WGNPBW are the most authoritative representation of numbers in the stock of Norwegian Spring Spawning Herring currently available.

Like in our acoustic estimates, the numbers at age in the acoustic estimates for herring used as input to the tuning process by WGNPBW tend to be lower than the stock numbers calculated through that process (see for example ICES, 2002). The low acoustic estimates may be due to several factors: (1) the target strength for herring is depth dependent so that deep recordings of herring will give a lower echo than the same herring situated near the surface (Huse and Ona, 1996; Vabø, 1999), (2) herring close to the surface may swim away from the track of the vessel (Olsen, 1979; Vabø, 1999), and (3) parts of the stock may have been distributed outside the area covered. The relative importance of the above factors may have been different from cruise to cruise and within different areas during the same cruise, and at present there is not enough information available to decide which has been most important in each case or to compensate for their effects. We believe that most of the 4+ herring were within the areas covered by the cruises in 1994−1996 and that (1) and (2) are the most important causes for the underestimates. In particular, herring feeding close to the surface may have made factor (2) an important reason for the large variation in bias for the acoustic estimates which is evidenced by the raising factors (Table 3).

We have assumed that the herring feed only in the second and third quarters, and that feeding is equally distributed between these two quarters. Unpublished data in IMR data files show that for maturing herring the weight increases from May to August−September and then gradually decreases from September to April. Assuming that feeding occurs only when the weight increases, it seems that the feeding period is fairly equally divided between the second and third quarter. Based on the same data it seems that immature herring grow slightly also in the period January−April, meaning that they also feed to some extent. But during this period the immature herring are usually found either close to the coast or in the fjords, and would not be feeding in the Norwegian Sea proper. We tried to modify Equation (1) so that 60% of the consumption occurred in the second quarter and 40% in the third quarter. This led to an increase in the proportion of copepods in the annual consumption from 62% to 66%, and a corresponding decrease in the proportion of the other prey items. Allocating 40% of the feeding to occur in the second quarter and 60% in the third quarter, led to a reduction of the proportion of copepods in the annual diet to 57%. These results indicate that changes in assumptions about when feeding occurs do not dramatically alter our calculations of prey consumption.

The consumption/biomass ratio (Q/B) is a key factor in the calculation of the herring's consumption (Equation (1)). The data in Ma *et al.* (1997) which we have used to calculate the ‘‘low’’ Q/B ratio of 3.0 originate from herring in a tank with limited space where, presumably, the activity to catch food was limited to feeding events of short duration. It is to be expected that Q/B values in this environment are lower than for a population which ranges through a large part of the Norwegian Sea during the feeding season. Dommasnes *et al.* (2001) used formulas described by Palomares and Pauly (1989) and Pauly *et al.* (1990) to calculate the Q/B ratio of 4.47, which is similar to 4.5 which we have used. The fact that Christensen (1995) used a Q/B ratio of 4.6 for herring in the North Sea gives additional credibility to the ‘‘middle’’ level for the Q/B ratio. Pavshtiks and Timokhina (1972), who have calculated the ‘‘high’’ Q/B ratio of 7.0 give no details about their calculations except a reference to Winberg (1956), and it is therefore difficult to evaluate the merits of this value compared to the values we have termed ‘‘middle’’ and ‘‘low’’. However, the Q/B ratio should not be seen as an unchangeable constant. Energy costs for feeding, migration, and other activity vary depending on how much energy the fish must expend in order to find and catch its food. For the Norwegian Spring Spawning Herring there is considerable difference in growth from year to year (ICES, 2002). The energy used for growth as well as for activity (effort needed to catch food) will therefore vary between years, leading to variations in the annual Q/B ratio.

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