

# Feeding of mature cod (*Gadus morhua*) on the spawning grounds in Lofoten

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Many authors state that cod (*Gadus morhua*) do not feed during the spawning period. However, this more or less established fact has rarely been investigated in the field. Here, the content of stomachs from Northeast Arctic cod (NEAC) and Norwegian coastal cod (NCC) sampled from the spawning ground in Lofoten were examined over a 10-year period (1996–2006). The occurrence of food in the stomachs of spawning cod, stomach fullness, diet composition, and variation in these variables between NEAC and NCC, year, and sex were analysed and compared. The analysis shows that cod do feed, even when they are in a spawning state. NCC had a lower proportion of empty stomachs and the stomachs were fuller than those from NEAC. Females had a lower proportion of empty stomachs than males and their stomachs were in general fuller. Herring (*Clupea harengus*) dominated the diet of cod. However, cod consumption of herring on the spawning grounds seems to be a minor source of mortality on herring. Although spawning cod do feed, the proportion of empty stomachs was higher and stomach fullness was lower than in stomachs of NEAC from the Barents Sea.

**Keywords:** herring, mature cod, spawning, stomach contents.

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## Introduction

In some early studies of otolith structure and life-history characteristics, Rollefson (1933, 1934, 1935) points to a direct connection between the appearance of a particular zone in the otoliths and spawning of cod (*Gadus morhua*) based on the “fundamental change occurring with the ripening of the gonads, the spawning, the fast during spawning, the spawning migration and the stay in a new habitat” (cited from Rollefson, 1933). Since then, several authors have referred to these findings and it has more or less been taken as a fact that cod do not feed in their spawning period (Bergstad *et al.*, 1987; Jobling, 1994; Kjesbu *et al.*, 1998). However, to our knowledge, neither Rollefson (1933) nor any of the later studies have actually conducted detailed analysis of the stomachs from cod caught on their spawning grounds. The combination of lack of empirical support, knowledge of traditional fishing techniques with baited hooks in the spawning area, and personal field observations of the stomach contents of spawning cod, inspired us to take a closer look at this “common truth”.

The cod along the Norwegian coast and in the Barents Sea are subdivided into two types, Northeast Arctic cod (NEAC) and Norwegian coastal cod (NCC; Berg and Albert, 2003). NEAC is the main cod type in the Northeast Atlantic, and mature fish migrate long distances from the cold feeding grounds in the northern and eastern parts of the Barents Sea to the warmer spawning areas along the coast of Norway (see Ottersen *et al.*, 1998, for references). In contrast, NCC do not undertake large-scale seasonal migrations (Jakobsen, 1987), and may experience a cycle in temperature opposite to that of NEAC (Godø and Michalsen, 2000). Like most spring spawners, both NEAC and NCC build energy reserves during summer and

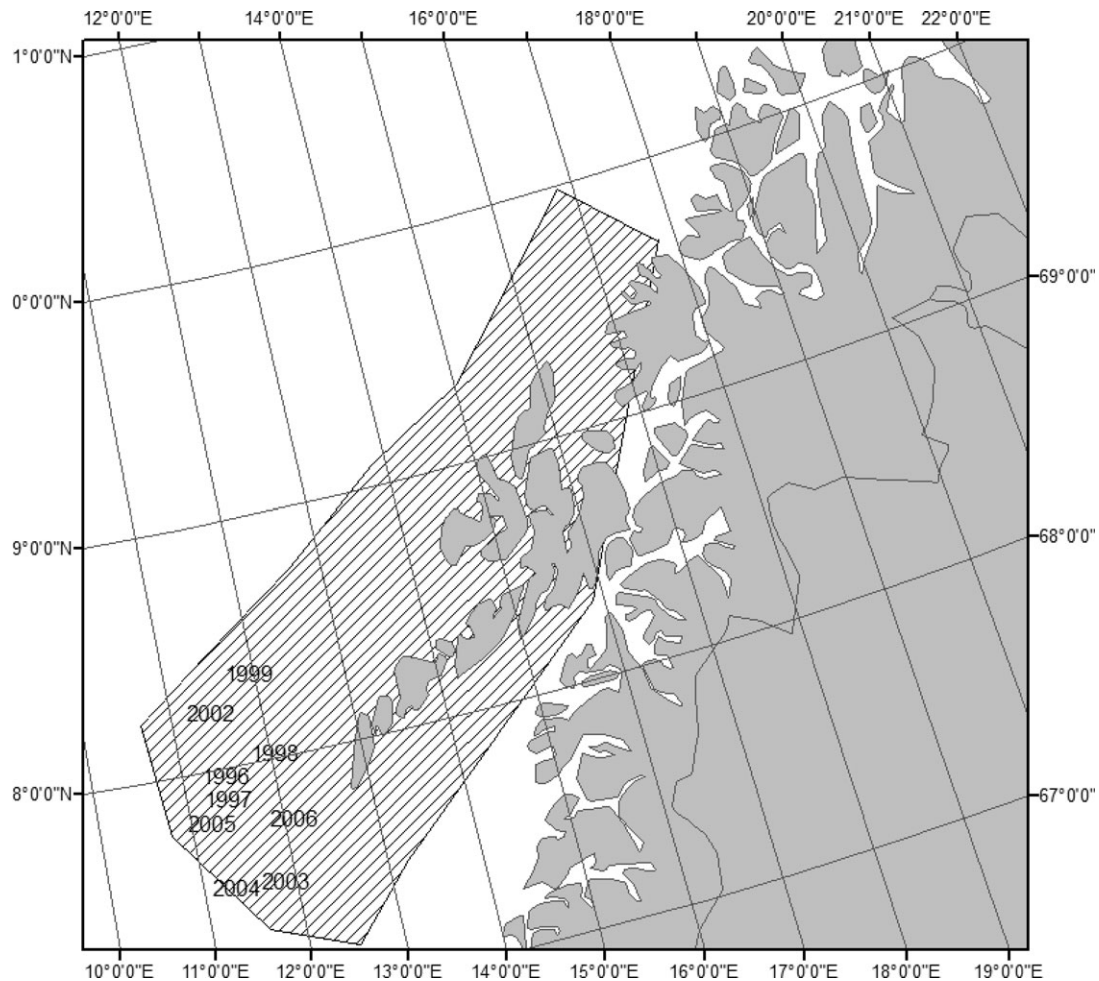
autumn, which they use later for maturation, migration, and spawning (Jobling, 1982; Lambert and Dutil, 2000). Differences in consumption rates and stomach content between females and males have been reported (Fordham and Trippel, 1999).

Spawning of NEAC and NCC takes place at several locations along the coast of northern Norway, but the most important spawning area is off the coast of the Lofoten peninsula (Sundby and Bratland, 1987; Figure 1). There, the spawning areas of the two cod types overlap (Jakobsen, 1987; Berg and Albert, 2003). Most cod eggs are spawned during March and April, with a peak in early April (Ellertsen *et al.*, 1981). Cod apparently spawn in the thermocline between 4°C and 6°C, but long-term hydrographic conditions along with short-term atmospheric forcing influence the depth of the thermocline and hence also the depth of spawning (Ellertsen *et al.*, 1989).

The objective of the current study was to determine whether cod feed during their spawning period and, if so, on which prey species. We also tested for differences in feeding between spawning NCC and NEAC, and between males and females. The research was accomplished primarily by analysing stomach data from 10 years of field observations in the main spawning area for NEAC. We also try to quantify consumption during the main spawning period, and investigate how important this consumption is as a source of mortality for herring (*Clupea harengus*). We also compared feeding of NEAC in the spawning period with feeding of NEAC during summer and winter in the Barents Sea.

## Material and methods

Annual abundance surveys on NEAC have been conducted at the main spawning ground in Lofoten in the period March/April



**Figure 1.** Surveyed area for spawning cod off the coast of the Lofoten peninsula (hatched area). The centres of mass of herring in the stomachs of cod by year are presented.

(Korsbrekke, 1997). These annual surveys have covered the same geographical area every year since 1982 (Figure 1). Although they are primarily acoustic surveys, bottom and pelagic trawls have been carried out for species and size verification and for biological sampling for population dynamics studies.

Stomachs of cod have been collected at trawl stations on a regular basis during these cruises since 1985. For the present study, however, only field observations from 1996 to 1999 and from 2001 to 2006 had sufficient stations ( $>10$ ) and stomach samples to be included in the analysis. Also, only mature cod are included (data from maturity stage 2, defined as large gonads, visible eggs, and male gonad products, and maturity stage 3, representing running gonads; see Kjesbu, 1990, for details). Most of the stomach data were from bottom trawls, but a few were from pelagic trawls (Table 1). Stomachs of fish that had regurgitated on capture were not included. Each stomach was frozen separately, and data on length, age, weight, sex, otolith type (see below), and maturity stage of each cod sampled was recorded. Fish prey was identified to species where possible, and the total length of the prey was measured, rounded downwards to the nearest centimetre. The methods used for stomach sampling, analysis, and data recording are described more fully in Mehl (1989) and Mehl and Yaragina (1992). Mature fish constituted 85% of the total number of fish from which stomach samples were taken. In

addition, a distinction between NEAC and NCC was made based on the structure of the otoliths (Mjanger *et al.*, 2005).

### Data analysis

We used the proportion of empty stomachs, total fullness index (TFI) and partial fullness index (PFI) to quantify cod feeding in the Lofoten area. The PFI (Lilly and Fleming, 1981) corrects for differences in stomach contents related to fish size, and is defined by  $PFI = 10^4 W_s / L^3$ , where  $W_s$  is the wet weight (g) of prey species  $s$  in the cod stomach and  $L$  is the length (cm) of the cod. Similarly,  $TFI = 10^4 W_t / L^3$ , where  $W_t$  is the total wet weight (g) of prey in the cod stomach.

The centres of mass of herring found in cod stomachs were calculated by year, based on the value of PFI of herring per station. The longitudinal and latitudinal coordinates of the centres of mass of distribution are averages of the coordinates of each trawl station weighted by the value of PFI of herring. We tested for differences between NEAC and NCC, year, and sex on cod feeding in Lofoten using three-way mixed effects ANOVA (Proc Mixed and the glimmix macro, SAS version 9.1, [www.sas.com](http://www.sas.com)). Cod length was entered as a covariate. Station was entered as a random variable in the statistical model, to account for statistical dependence between cod stomach samples taken from the same station (Bogstad *et al.*, 1995). When analysing the proportion of

**Table 1.** Sampling dates for stomachs, number of stations by gear, and the number of stomachs from spawning cod according to sex and stock affiliation (NEAC and NCC) sampled near Lofoten, 1996–1999 and 2001–2006.

Year	Date	Number of demersal trawl stations	Number of pelagic trawl stations	Number of NCC females	Number of NCC males	Number of NEAC females	Number of NEAC males
1996	19–28 March	16	3	39	79	132	305
1997	22–28 March	14	2	43	32	144	171
1998	21 March–1 April	13	0	45	68	106	149
1999	27 March–5 April	14	0	36	89	62	150
2001	25 March–7 April	17	1	39	133	93	153
2002	20–31 March	14	2	25	133	98	251
2003	26 March–2 April	18	1	69	210	127	267
2004	20 March–3 April	18	6	57	144	313	458
2005	21–26 March	19	4	43	43	200	276
2006	22 March–4 April	19	1	38	72	174	194

empty stomachs, we used a logistic link function and binomial error.

Sample sizes by year, sex, and cod type are listed in Table 1. Males constituted 65% of the cod sampled at Lofoten. The proportion of males in the bottom trawl was 0.67 [95% confidence interval (CI): 0.65–0.68], and in the pelagic trawl 0.54 (95% CI: 0.50–0.59). Because of the small sample sizes in pelagic hauls, data from both trawl types were pooled for the analysis.

We tested for seasonal variation in feeding of NEAC by performing a two-way mixed effects ANOVA using season and year as fixed factors, and station as a random variable. Feeding of cod was quantified using TFI and proportion of empty stomachs. When analysing the proportion of empty stomachs, we used a logistic link function and binomial error.

In addition to the data from the spawning season (Table 1), we included data from two surveys run in the Barents Sea: the combined acoustic and bottom trawl survey for demersal fish in the Barents Sea in winter (Jakobsen *et al.*, 1997), now run jointly with PINRO in February, and data from the demersal fish survey in the Barents Sea and Svalbard area in summer, now run as the joint IMR–PINRO ecosystem survey in August/September. We included only cod >50 cm in the analysis. We included the years 1996, 1999, and 2003–2005 because those years had good coverage in both summer and winter. The cod stomach samples were taken from cod caught by demersal trawl. On these surveys, a maximum of five stomachs per 5 cm length group of cod was sampled per station. The numbers of stomachs samples by year, sex, and season in summer and winter are listed in Table 2.

We also calculated the consumption by cod during the spawning migration, based on the stomach samples and a model for gastric evacuation rate. We used an approach similar to Bogstad and Mehl (1997), who calculated the consumption by cod in the Barents Sea. That method is described in the Appendix.

## Results

The size distribution of spawning females and males differed, males being smaller than females and NCC being smaller than NEAC (Figure 2).

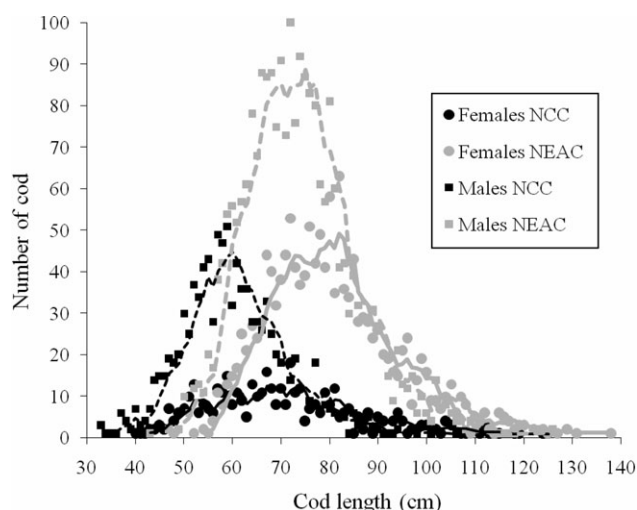
NCC had a lesser proportion of empty stomachs than NEAC (0.64 vs. 0.68). Females had a lesser proportion of empty stomachs than males, but there was a significant interaction between sex and year; the sex difference was pronounced in 1996 and 2001, but not in the other years (Table 3, Figure 3a). The data did not allow us to investigate possible reasons for this difference, such as differences in the geographic distribution of cod by sex and herring. No other interaction terms were significant.

The results for TFI were consistent with the pattern for the proportion of empty stomachs (Table 3, Figure 3b). Stomachs of NCC were fuller than stomachs of NEA (0.44 vs. 0.39, Figure 3b), there was no effect of cod length on TFI, and no interaction terms were significant (Table 3).

Herring was the most important prey species for both NEAC and NCC, followed by Norway pout (*Trisopterus esmarkii*) (Figure 4). The PFI of herring did vary significantly by year

**Table 2.** Number of stomachs sampled from large (>50 cm) NEAC on the winter survey in February and the summer survey in August/September.

Year	Number of females in winter	Number of males in winter	Number of females in summer	Number of males in summer
1996	763	624	431	412
1999	419	327	341	358
2003	648	499	307	302
2004	746	679	331	326
2005	625	512	265	266



**Figure 2.** Number of cod by 1 cm length group (points, with moving averages as lines) of spawning NCC and NEAC males and females with stomach samples off the Lofoten peninsula, 1996–1999 and 2001–2006.

(Table 3). No interactions were significant (Table 3). The annual variation in PFI of herring could partly be due to the variable degree of digestion found, leading to a varying level of species identification accuracy (Figure 5). However, when pooling data on herring and unclassified fish, assuming that most of the unclassified fish was indeed herring, year was still significant ( $p < 0.0001$ ). There has been a change in the spatial distribution of herring in cod stomachs over the years (Figure 1), which might be due to changes in the geographical distribution of herring, but we do not have data to investigate this relationship. The length distribution of herring in cod stomachs (Figure 6) shows a significant correlation between cod size and herring size ( $r = -0.27$ ,  $p = 0.02$ ,  $n = 77$ ).

There was no sex difference in TFI, or in the proportion of empty stomachs in winter and summer (one-way mixed model ANOVA sex effect; TFI winter,  $p = 0.63$ ; TFI summer,  $p = 0.34$ ; proportion of empty stomachs in winter,  $p = 0.11$ , and in summer,  $p = 0.09$ ). TFI values and the proportion of empty stomachs were compared between spawning NEAC at the spawning ground in Lofoten in April, cod  $> 50$  cm in the Barents Sea in February, and cod  $> 50$  cm in the Svalbard area and the Barents Sea in August/September of 1996, 1999, and 2003–2005. There

was a significant effect of season (winter, spawning season in spring and summer) and year, and a significant interaction between season and year on the proportion of empty stomachs (Table 4). There was also a significant effect of season and a significant interaction between season and year on TFI (Table 4). TFI was lower and the proportion of empty stomachs greater at the spawning ground in all years. Generally, the TFI was higher and the proportion of empty stomachs lower in summer than in winter (Figure 7). However, in 1999 and 2003, the difference between summer and winter was negligible.

The consumption of the various prey items by year and cod type is shown in Table 5. The biomass output through natural mortality (MOB) for herring is given in Table 6, together with the calculated consumption of herring. Also the proportion of the MOB corresponding to the calculated consumption of herring by cod is shown. The consumption of herring by cod during the spawning period of cod was  $< 100\,000$  t in all years. This is small compared with the MOB of herring (between 1% and 7% of the MOB).

## Discussion

In Canadian waters, cod generally move from offshore wintering areas, with a near absence of food intake, to inshore spawning areas where prey are abundant (Comeau *et al.*, 2002). Such variability in seasonal feeding indicates that stock-specific empirical data are needed to assess the seasonal growth patterns of cod. Here, we did not consider the effects of gonad development, migration, or environmental variation on the otoliths, but simply investigated whether cod in a spawning state do feed, how much, and on which species. After analysing 5258 stomachs of spawning cod, collected over a period of 10 years at the spawning grounds in Lofoten, it is clear that cod do feed, even when they are in a spawning state, but that NEAC feed less actively during spawning than at other times of the year.

## Differences between NEAC and NCC

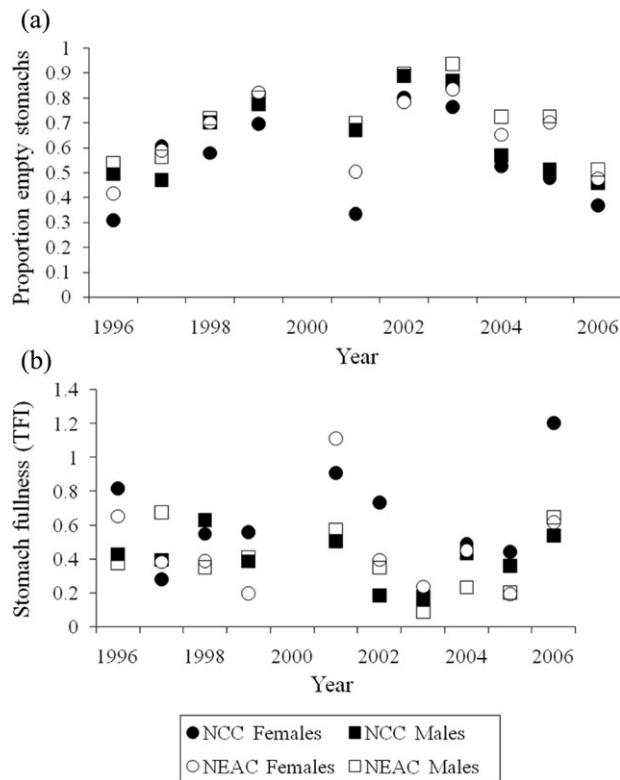
Although they were caught in the same area, our study has shown that NCC had a lesser proportion of empty stomachs and also fuller stomachs than NEAC. The diet of NCC was also slightly more diverse, close to half the stomach contents being herring. To understand why there is such a difference in feeding between the two cod types, more detailed studies on the distribution, life-history traits, and feeding ecology of the two types are needed. However, the greater proportion of invertebrates in the more stationary NCC diet could be a reflection of its smaller size

**Table 3.** Test statistics (three-way ANOVA) on the effect of year, sex, and stock on the proportion of empty stomachs, TFI, and PFI of herring.

Parameter	Proportion empty	TFI	PFI herring
Cod length	$F = 1.95$ , $p = 0.17$	$F = 0.00$ , $p = 0.95$	$F = 0.00$ , $p = 0.96$
Year	$F = 9.00$ , $p < 0.0001$	$F = 2.32$ , $p = 0.018$	$F = 2.95$ , $p = 0.027$
Sex	$F = 21.35$ , $p < 0.0001$	$F = 3.23$ , $p = 0.07$	$F = 0.64$ , $p = 0.43$
Stock	$F = 24.73$ , $p < 0.0001$	$F = 12.9$ , $p = 0.0003$	$F = 0.23$ , $p = 0.64$
Year $\times$ Sex	$F = 2.55$ , $p = 0.009$	$F = 1.7$ , $p = 0.09$	$F = 0.97$ , $p = 0.46$
Year $\times$ Stock	$F = 0.92$ , $p = 0.50$	$F = 0.87$ , $p = 0.54$	$F = 0.83$ , $p = 0.58$
Sex $\times$ Stock	$F = 0.56$ , $p = 0.46$	$F = 1.64$ , $p = 0.20$	$F = 2.27$ , $p = 0.13$
Sex $\times$ Year $\times$ Stock	$F = 0.87$ , $p = 0.54$	$F = 1.33$ , $p = 0.22$	$F = 0.97$ , $p = 0.46$

Cod length was included as a covariate.





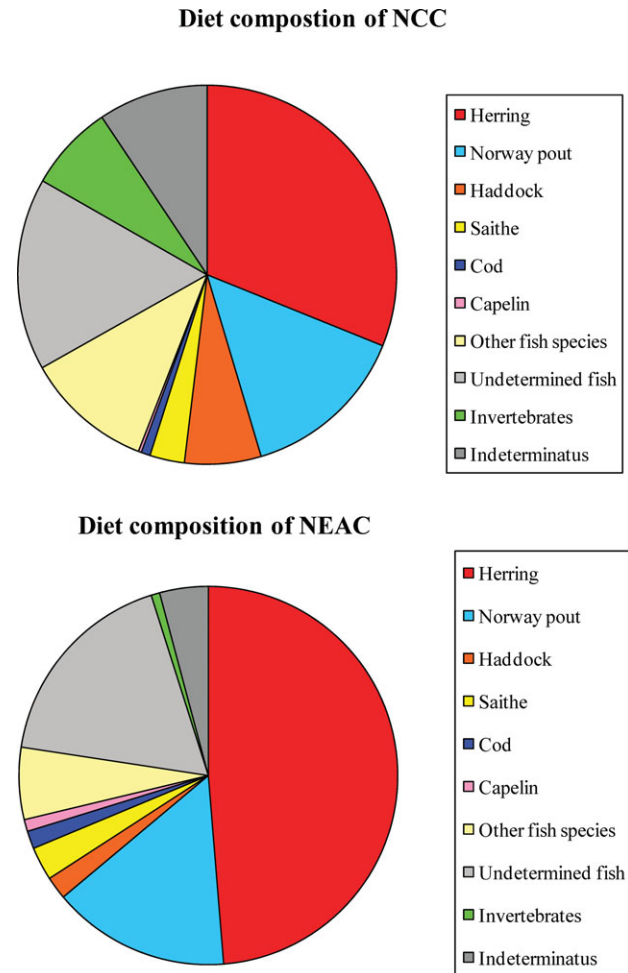
**Figure 3.** (a) Proportion of empty stomachs observed by sex, year, and cod type. (b) TFI by sex, year, and cod type.

(Link and Garrison, 2002) or a difference in habitat use, compared with NEAC.

Fish of the two cod types are distinguished through otolith morphology, and the cod type separation criteria developed by Rollesfsen (1933, 1934) are still used (Mjanger *et al.*, 2005). This is based on differences in shape between the two innermost translucent zones. Also, spawning zones in the otoliths are used to determine the age at sexual maturity based on identification of narrower opaque zones with conspicuous clear translucent bands. Rollesfsen (1933) suggested that these zones were the result of physiological changes in the fish during maturation, and both NEAC and NCC deposit these zones. However, identification of otolith spawning zones is, until now, only done by Norwegian and Russian scientists. Therefore, it is clear that the physiological basis for spawning zone formation is poorly understood and that this assumption should be validated or at least tested critically. Such a validation will also be of value to studying the process of skipped spawning in fish populations (Rideout *et al.*, 2000; Jørgensen and Fiksen, 2006), and it should include analyses to check for possible sex differences, such as in the timing of spawning migrations.

### Sex differences in feeding and spawning

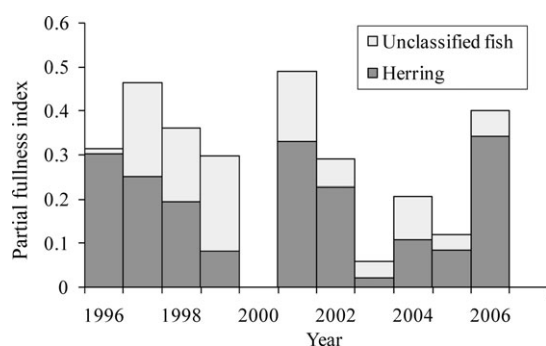
Males tended to be smaller than females, which is consistent with existing knowledge on sexual differences in growth and maturation (Ajiad *et al.*, 1999). Further, females fed more on the spawning grounds than males, but there was no sex difference in winter or summer feeding trends. The process of egg batch production in cod is a strenuous process, where after the release of a batch, protein and fat from the muscle and liver are mobilized



**Figure 4.** Diet composition (weight of prey, all stomachs combined) of spawning cod off Lofoten in March/April of 1996–1999 and 2001–2006. Upper panel, NCC; lower panel, NEAC.

to the ovary (Kjesbu *et al.*, 1998). In a study on non-migrating NCC (Eliassen and Vahl, 1982a, b), the effect of gonad production was investigated. They estimated that gonad growth could account for just 10% of the energy used and lost from a cod body and liver between January and April. They did discover a sex difference in liver weight, with smaller livers in male than in female cod. This was assumed to be a consequence of the observed earlier start of gonad growth in males than in females. However, their conclusion was reached under the assumption of a cessation of feeding in this prespawning period.

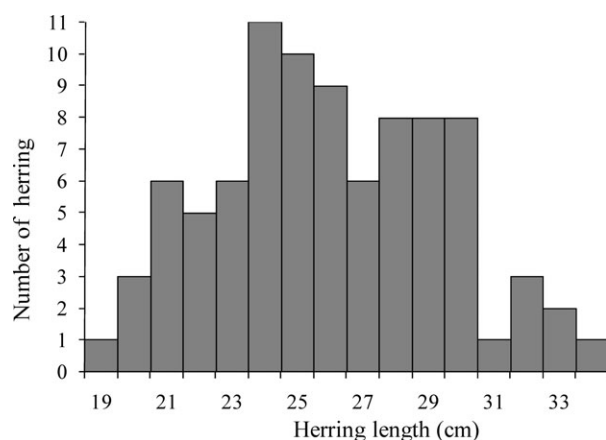
Another aspect of gonad growth and feeding was studied by Hroar *et al.* (1983). They suggested that feeding activity could be affected by less space being available in the body cavity for food, or possibly associated with a change in hormone levels during spawning, which might reduce an individual's appetite. As the feeding of males in our study was suppressed during spawning to an even greater degree than that of females, the thesis of lack of space does not seem convincing. Also Fordham and Trippel (1999) found that females consumed greater quantities of food than males during both winter and post-spawning periods. This suggestion is supported by the fact that in a large number of fish, females grow not only larger but also faster than males



**Figure 5.** PFI of herring and unclassified fish by year.

(Ajiad *et al.*, 1999) despite their production of a large quantity of gonad material (Lambert and Dutil, 2000). Clearly, female growth does not suffer from reproductive drain, space in the body cavity, or a lack of appetite.

We noticed that a greater proportion of males is caught by the bottom trawl than by the pelagic trawl. Rollefson (1954), working off the coast of the Lofoten islands, also found that the sex ratio varied, depending on the sampling gear used. Morgan and Trippel (1996) and Morgan *et al.* (1997) suggest that a skewed sex ratio is at least partly influenced by a sex-dependent vertical distribution, which will manifest as sex-selective gears. The vertical separation of sexes can probably be explained by sex-specific behaviour during spawning (Nordeide and Folstad, 2000), mature males being reported to aggregate on spawning grounds whereas females seem to be distributed peripherally or above the male aggregations (Morgan and Trippel, 1996; Nordeide, 1998). When ready to spawn, females enter male aggregations, then return after spawning (Brawn, 1961; Hutchings *et al.*, 1999). Laboratory studies have shown that, during the reproductive period, there is aggression between males defending “territories” (Brawn, 1961; Hutchings *et al.*, 1999). This sexual difference in spawning behaviour might also explain the difference in stomach contents, females being less aggressive and having more time available to find available food.



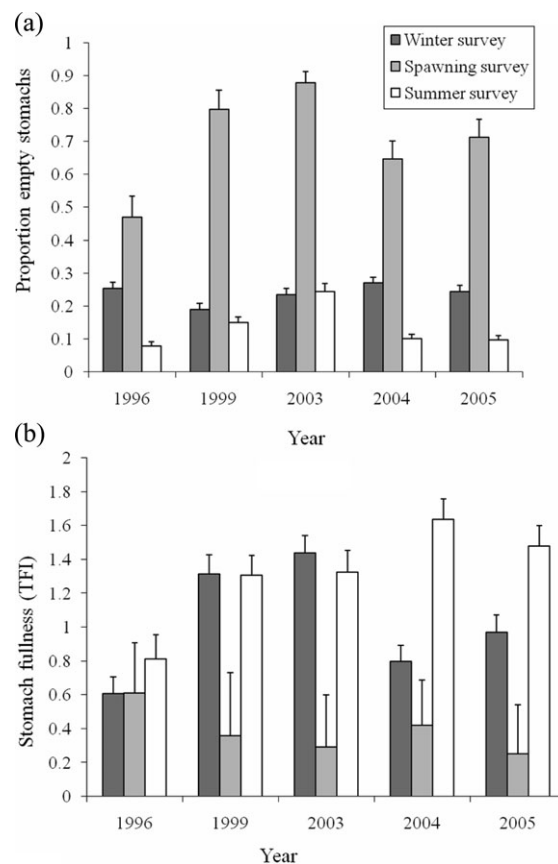
**Figure 6.** Length distribution of herring in cod stomachs off Lofoten (1 cm length intervals).

**Table 4.** Test statistics (two-way ANOVA) on the effect of season and year on the proportion of empty stomachs and TFI of NEAC > 50 cm.

Parameter	Proportion empty	TFI
Year	$F = 13.14, p < 0.0001$	$F = 1.40, p < 0.23$
Season	$F = 202.57, p < 0.0001$	$F = 21.86, p < 0.0001$
Year $\times$ Season	$F = 9.24, p < 0.0001$	$F = 3.93, p = 0.0001$

### NEAC feeding, in time and space

The overall proportion of NEAC empty stomachs was higher (71%) and the average TFI value lower (0.34) on the spawning grounds than in stomachs sampled from the same cod type in the Barents Sea in the same years (25% and 1.43, respectively). Seasonal variation in cod metabolism, with higher metabolic rates during spring attributable to migration, spawning, and higher temperatures in the spawning area than in the feeding area (Pedersen and Jobling, 1989) could lead to faster digestion and a greater proportion of empty stomachs. However, this



**Figure 7.** (a) Estimates of the proportion of empty stomachs with standard error bars in the winter survey of NEAC > 50 cm in February in the Barents Sea, in the spawning survey of NEAC in March/April in the Lofoten area, and in the summer survey of NEAC > 50 cm in the Svalbard area and the Barents Sea in August/September. (b) Estimates of TFI with standard error bars in the winter survey of NEAC > 50 cm in February in the Barents Sea, in the spawning survey of NEAC cod in March/April in the Lofoten area, and in the summer survey of NEAC > 50 cm in the Svalbard area and the Barents Sea in August/September.

**Table 5.** Consumption of prey items (in thousand tonnes) by mature NEAC (top panel) and NCC (lower panel) during the spawning period.

Year	Herring	Norway pout	Other fish	Invertebrates	Total
NEAC					
1996	80	32	11	2	125
1997 <sup>a</sup>	81	7	10	1	99
1998 <sup>a</sup>	32	5	23	8	68
1999 <sup>a</sup>	28	0	20	+	48
2001	68	11	16	+	96
2002	65	3	9	0	77
2003	18	25	48	8	99
2004	79	27	29	5	139
2005	36	34	16	7	92
2006	75	38	13	3	128
NCC					
1996	17	3	4	20	44
1997 <sup>a</sup>	0	0	18	1	19
1998 <sup>a</sup>	6	2	8	5	21
1999 <sup>a</sup>	4	0	9	0	13
2001	12	5	3	1	21
2002	5	+	5	+	11
2003	0	+	6	+	7
2004	2	2	3	1	9
2005	2	1	2	2	6
2006	1	3	1	1	6

<sup>a</sup>In the years 1997–1999, some stomachs were analysed in a simplified way on board ship. Then, only the most important prey species (including herring, but not Norway pout) were identified, and other fish were grouped into a single category. Therefore, some of the “other fish” in those years were probably Norway pout. +, consumption of between 0 and 500 t.

complex process has been poorly studied, so it is difficult to evaluate the potential importance of metabolism on the proportion of empty stomachs.

Geographical and temporal variation in prey availability, with less food available in the spawning areas at the time of spawning than in the Barents Sea in summer and winter, or a higher density of cod aggregating at the spawning areas, could both cause food competition and less feeding on the spawning

grounds. Coastal areas are assumed to be less productive than the Barents Sea (Sakshaug *et al.*, 1994). However, in some of the fjords along the coast, large schools of adult herring aggregate during winter, then migrate out into the open sea during spring, about the same time as cod spawn. The Norwegian spring-spawning herring (NSSH) is a large oceanic stock, with a spawning area all along the Norwegian coast (Misund *et al.*, 1998). Since 1987, a fjord system close to the main spawning areas of cod has been the overwintering ground for herring (Toresen and Østvedt, 2000). Herring enter the area at the beginning of October and start to migrate out of the fjord system and to the more southern spawning grounds in January (Røttingen, 1992). The presence of overwintering herring in this area may have had an influence on cod, not only through an increase in food availability, but also in influencing the timing and area chosen for spawning.

The dominant fish species in the Barents Sea ecosystem are cod, capelin (*Mallotus villosus*), haddock (*Melanogrammus aeglefinus*), and herring. Cod are believed to be the main fish predators on capelin and young herring (Bogstad and Mehl, 1997; Bogstad *et al.*, 2000). The geographic distribution of capelin during its spawning migration occasionally extends as far southwest as the Lofoten area (Ozhigin and Luka, 1985). The highest food ratios for cod in the Barents Sea are found in the area close to the polar front during summer, and close to the coast of northern Norway and Russia early in the year, when capelin migrate to the coastal areas to spawn (Orlova *et al.*, 1995).

NCC feed actively during winter (Hop *et al.*, 1992, 1993). In Balsfjorden, northern Norway, the food intake (indicated by stomach fullness) does not appear to decline during winter (Klemetsen, 1982), but the liver weight declines between January and March (Eliassen and Vahl, 1982a). On the other hand, studies from the North Sea have shown that stomach fullness is lowest during the period January–March (Daan, 1973; Hislop, 1997), which is more in accord with our results on seasonal variability in stomach contents of NEAC. Such variability in food intake indicates that stock-specific data are essential to understanding better the seasonal growth pattern seen in otolith structure.

### Concluding remarks

The feeding habits of cod during spawning could have implications for abundance surveys, aquaculture, bioenergetic models, multispecies approaches, and considerations in terms of gear efficiency, and could improve the scientific basis for management of

**Table 6.** Herring MOB (M-output biomass), and consumption of herring by cod (in thousand tonnes).

Year	MOB age 3+ herring	Consumption of herring by NEAC	Consumption of herring by NCC	Total consumption	Consumption by cod as % of MOB
1996	1 439	80	17	97	6.7
1997	1 330	81	0	81	6.1
1998	1 187	32	6	32	2.7
1999	1 108	28	4	32	2.9
2001	1 128	68	12	80	7.1
2002	1 317	65	5	70	5.3
2003	1 341	18	0	18	1.3
2004	1 323	79	2	81	6.1
2005	1 666	36	2	38	2.3
2006	1 725	75	1	76	4.4

the complex mixed fishery of Atlantic cod in the Lofoten area. Progress in understanding the causes of growth variability in cod has been hampered by incomplete knowledge of the growth implications of seasonal life-history events such as spawning and reproduction (Schwalme and Chouinard, 1999). By further assessing foraging habits of cod during spawning, we might be able to understand better their feeding habits and how these change under various conditions or states.

In defence of Rollefson's (1933) work, it needs to be noted that the spawning-stock biomass was estimated to be more than twice as large in the early 1930s than in the late 1990s, namely 1.2 million tonnes compared with around 0.5 million tonnes (Hysten, 2002; ICES, 2006a). With greater density at the spawning ground, the probability of finding food would be less, so it may have looked to researchers then as if cod voluntarily entered a period of little or no feeding. Based on the results from our study, however, it is quite clear that cod do feed, even when they are in a spawning state, if there is food available.

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## Appendix

### Method for calculating consumption by cod

The annual prey consumption by NEAC in the Barents Sea for the period 1984–2005 is calculated by ICES (2006a), using the method described by Bogstad and Mehl (1997). In the calculations, mature NEAC are assumed to be outside the Barents Sea during the spawning period (i.e. 3 months during the first half of the year), and the prey consumption of NEAC during that period is not included in the consumption estimates. Using the stomach content data from the Lofoten survey described above, we can calculate the annual prey consumption by cod during the spawning period by assuming that the stomach data from the Lofoten survey are representative of the diet of mature NEAC and NCC during a 3-month period. We used the abundance of mature NEAC and NCC from the 2006 stock assessments made by ICES (2006a), and estimated the consumption by cod using the methods described in Bogstad and Mehl (1997). The annual consumption of prey group  $p$  by mature cod of type  $s$  (NEAC or NCC) and age  $a$  during the spawning period in year  $y$  is then given by

$$C_{y,s,a,p} = N_{y,s,a} O_{y,s,a} R_{y,s,a,p} \times 24 \times 91.25, \quad (1)$$

where  $N_{y,s,a}$  is the number of cod of type  $s$  and age  $a$  at 1 April in year  $y$  (found by assuming a constant total mortality during the year and reducing the number of cod at the beginning of the year by one-quarter of the annual natural and fishing mortalities);  $O_{y,s,a}$  the maturity ogive for cod of type  $s$  and age  $a$  in year  $y$ ;  $R_{y,s,a,p}$  the consumption ( $\text{g h}^{-1}$ ) of prey  $p$  by each cod of type  $s$  and age  $a$  in year  $y$ .

$R_{y,s,a,p}$  is calculated using the formula

$$R_{y,s,a,p} = \frac{e^{0.13T_y} W_{y,s,a}^{0.26} S_{y,s,a,p} \ln 2}{\alpha_p (1.78 S_{y,s,a})^{0.52}}, \quad (2)$$

where  $T_y$  is the temperature ( $^{\circ}\text{C}$ ) 100 m deep at Eggum (68°22'N 13°38'E) at the end of March of year  $y$ ;  $W_{y,s,a}$  the mean weight (kg) of cod age  $a$  of type  $s$  on 1 April of year  $y$  (the weights at 1 April were calculated assuming a linear growth throughout the year, i.e. a given cohort has the same weight growth increment in all quarters in a given year);  $\alpha_p$  the prey-specific digestion (half-life) constant (in h);  $S_{y,s,a,p}$  the average stomach contents (g) of prey  $p$  of cod age  $a$  and type  $s$  in year  $y$ ;  $S_{y,s,a}$  the average total stomach contents (g) for cod of age  $a$  and type  $s$  in year  $y$ . For NCC, age groups 4–8+ (age 8 years and older) were used, and for NEAC, age groups 5–9+ (age 9 years and older) were used. Fish younger than the minimum age (4 or 5, respectively) were included together with the fish in the lowest age group. The prey groups used in the calculations were herring, Norway pout, other fish, and invertebrates. In a few instances, poor cod (*Trisopterus minutus*) were found in the stomachs, and these were grouped together with Norway pout. The digestion rate for Norway pout and for other fish was assumed to be the same as for cod, and the digestion rate for invertebrates was assumed to be the same as for amphipods and krill. The values used were herring 88, cod 84, krill and amphipods 41.

The weight of each prey species and size group was adjusted by distributing the unidentified component of the diet proportionally among the various identified components, taking into account the level of identification. To investigate how much of the natural mortality of herring was attributable to cod predation, we calculated the biomass output for herring through natural mortality (MOB), called the “ $M$ -output biomass” by Hamre and

Tjelmeland (1982), using the same approach as Bogstad *et al.* (2000). In general, the MOB is calculated using the catch equation, but with  $F$  and  $M$  interchanged, and the calculated number removed by natural mortality ( $M$ ) is multiplied by a relevant mean weight:

$$\text{MOB}_y = \sum_a W_{y,a} \frac{N_{y,a} M_{y,a} (1 - e^{-(F_{y,a} + M_{y,a})})}{F_{y,a} + M_{y,a}}, \quad (3)$$

where  $\text{MOB}_y$  is the  $M$ -output biomass in year  $y$ ,  $N_{y,a}$  the number of fish of age  $a$  at the beginning of year  $y$ ,  $F_{y,a}$  the fishing mortality of age  $a$  fish in year  $y$ ,  $M_{y,a}$  the natural mortality of age  $a$  fish in year  $y$ , and  $W_{y,a}$  the mean weight of age  $a$  fish during year  $y$ . These data are taken from the latest assessment of Norwegian spring-spawning herring (ICES, 2006b). The mean weight  $W_{y,a}$  is calculated as the average of the stock weights of this cohort at the beginning of years  $y$  and  $y+1$ ,  $w_{a,y}$  and  $w_{y+1,a+1}$ .

The herring found in the cod spawning area are almost exclusively aged 3 years and more, so age groups 3–16+ were used in the calculations of MOB:

$$\begin{aligned} \text{MOB}_y = & \sum_{a=3}^{15} \frac{(w_{y,a} + w_{y+1,a+1})}{2} \frac{N_{y,a} M_{y,a} (1 - e^{-(F_{y,a} + M_{y,a})})}{F_{y,a} + M_{y,a}} \\ & + \frac{w_{y,16} N_{y,16} M_{y,16} (1 - e^{-(F_{y,16} + M_{y,16})})}{F_{y,16} + M_{y,16}}. \end{aligned} \quad (4)$$

For age 3 and older herring,  $M$  is set to 0.15 for all ages and years.

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