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## ORIGINAL ARTICLE

## Variability in cannibalism in Northeast Arctic cod (*Gadus morhua*) during the period 1947–2006

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### Abstract

Cannibalism is probably the most important and also the most variable cause of natural mortality for age 1–4 Northeast Arctic cod. Also, the proportion of cod in the diet of Northeast Arctic cod increases with increasing size of the predatory cod. For this stock, long time series describing diet composition are available (qualitative stomach content data for 1947–2005 and quantitative data for 1984–2006). These data were analysed together with survey indices for young cod and abundance of capelin, the most important prey item for cod. The abundance of age 1–3 cod indicated by the survey indices and the abundance of young cod in cod stomachs are well correlated. An inverse relationship between mortality induced by cannibalism and capelin abundance was found. Cannibalism was at a high level from 1947 to 1965 and then again in the mid-1990s. The high level of cannibalism in the mid-1990s was comparable to that observed in the 1950s. It is outlined how the qualitative and quantitative stomach content data could be combined to include cannibalism in the estimates of cod abundance back to 1947.

**Key words:** *Cod, cannibalism, Barents Sea, capelin*

### Introduction

Cod (*Gadus morhua*) cannibalism is known to be a widespread natural phenomenon. Cod predation on their own recruits has been described for various marine and meromictic areas, including the Barents Sea (Zatsepin & Petrova 1939; Brown & Cheng 1946; Ponomarenko et al. 1978; Korzhev & Tretyak 1992; Bogstad et al. 1994; Dolgov et al. 1995; Neuenfeldt & Köster 2000; Hardie et al. 2008). A detailed study of cod cannibalism in the Barents Sea, Icelandic waters and the Newfoundland area was carried out by Bogstad et al. (1994). That analysis focused on the period 1984–1992, when cannibalism in Northeast Arctic (NEA) cod in the Barents Sea was low or moderate. In the present analysis of cannibalism in NEA cod, we examine long time series of cod stomach content data available, covering periods with both high and low cannibalism.

Cannibalism is probably the most important and also the most variable cause of natural mortality for

age 1–4 NEA cod (Bogstad et al. 1994, 2000; Dolgov 1999; ICES 2007). Incorporation of the data on NEA cod cannibalism into the VPA model has been shown to improve the overall quality of the assessment and the accuracy of recruitment estimation (Kovalev & Korzhev 2004). Therefore, since 1995 the ICES Arctic Fisheries Working Group (AFWG) has used annual cod stomach content data to estimate cannibalism in the NEA cod assessment (ICES 2007). Cod up to age 6 may be eaten by older conspecifics, but cannibalism on age 5 and 6 is estimated to be so low (ICES 2007) that we in the present analysis only consider cannibalism on age 1–4 cod, although cannibalism on age 5–6 cod is also included in the NEA cod assessment.

There is an inconsistency in the time series of (VPA) number at age from 1946 to present, as cannibalism is only taken into account in 1984 and later years, when quantitative stomach content data are available. To improve the understanding of the population dynamics of NEA cod (especially stock–

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Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

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recruit relationships), it would be of great value to have estimates of the stock abundance including cannibalism through the entire time series. Thus, a VPA-based estimate of abundance of age 1–4 cod with natural mortality due to cannibalism taken into account should give a better picture of recruitment variability than the existing VPA, if cannibalism can be hindcasted in a reasonable way by combining the available data.

Long time series describing diet composition are available for the NEA cod stock, including qualitative stomach content data for 1947–2005 and quantitative data for 1984–2006. Our goal was to hindcast back to 1947 natural mortality of NEA cod at age 1–4 due to cannibalism based on combined qualitative and quantitative stomach content data for 1984–2006, using a similar approach to that undertaken by Marshall et al. (2000) regarding the Barents Sea capelin (*Mallotus villosus*) abundance. The capelin abundance was in that paper calculated back to 1947 based on the frequency of occurrence of capelin in cod stomachs and acoustic abundance estimates of capelin going back to 1973. The correlation between these indices of capelin abundance was found to be positive and fairly strong.

The data on stomach content were analysed together with survey indices, VPA estimates of abundance and natural mortality for young cod, and abundance of capelin, the most important prey item for cod (Bogstad & Mehl 1997; Dolgov 2002). We investigated the consistency between the VPA estimates of abundance and the survey data for young cod as well as the reasons for the NEA cod cannibalism rate variability during this long time period.

## Materials and methods

### *Qualitative stomach content data*

The frequency of occurrence of cod and capelin in cod stomachs ( $FO_{\text{cod}}$  and  $FO_{\text{cap}}$ ) was estimated using cod feeding observations which have been collected year-round on commercial and research vessels as part of a sampling programme initiated by Russia in 1947 (Ponomarenko & Yaragina 1978; Ponomarenko et al. 1978). For cod selected at random, it was recorded which of the following categories of prey items were observed in their stomachs: capelin, juvenile cod, redfish (*Sebastes* spp.), herring (*Clupea harengus*), shrimp (*Pandalus borealis*), euphausiids, and other.  $FO_{\text{cod}}$  and  $FO_{\text{cap}}$  are simply the percentage of non-empty cod stomachs, which contain cod and capelin (Ponomarenko & Yaragina 1984).  $FO$  values are disaggregated by geographic region (Southern Barents Sea (SBS)

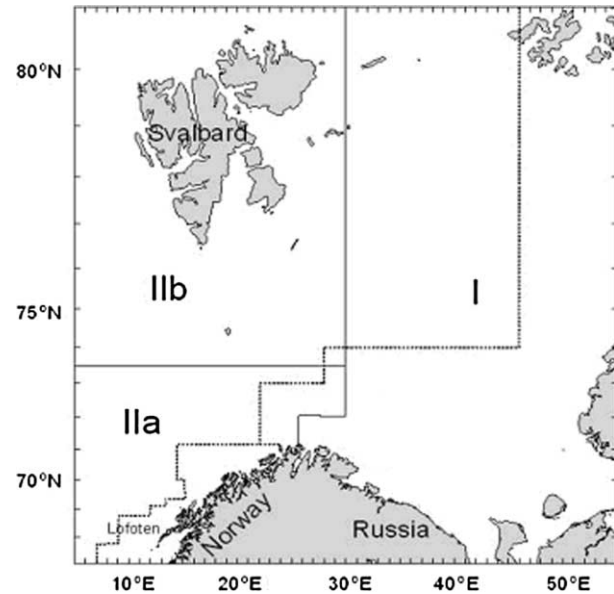


Figure 1. The area of distribution for Northeast Arctic cod. Boundaries of Russian subareas for the southern Barents Sea (SBS), Svalbard area and Norwegian coast are indicated by dashed lines. The ICES statistical Area I and Sub-areas IIa and IIb are indicated by solid lines.

and Svalbard area, see Figure 1). The total number of cod stomachs examined for the SBS region ranges from a minimum of 5129 in 1948 to a maximum of 75,739 in 2000, while for the Svalbard area, the range is 2870 in 1948 and 109,443 in 2002. The length range of cod sampled for the qualitative stomach database was rather wide (15–125 cm); however, generally fish that dominated in commercial trawl catches prevailed. Predator length was recorded for each cod sampled, but information on prey length was not recorded.

### *Quantitative stomach content data*

Since 1984, Norway and Russia have annually collected quantitative stomach content data for cod. These data are sampled from scientific surveys mainly, including also some data from commercial fishing vessels. For each fish analysed, the predator length, weight and usually also age is recorded, together with prey weight, species and size composition. The methodology is described by Mehl & Yaragina (1992). On average about 10,000 stomachs have been analysed annually. The annual number of stomachs sampled and the geographical distribution of the sampling is shown in Dolgov et al. (2007). Cod stomachs sampled south of 69°N and west of 18°E were excluded from our analysis because at the main spawning grounds in the Lofoten area small Northeast Arctic cod is hardly found, and including data from that area could bias calculations of the effect of cannibalism. The diet of cod at the

92 spawning grounds is dominated by herring (Michal-  
93 sen et al. 2008).

94 The average Partial Fullness Index (PFI; Lilly &  
95 Fleming 1981) of prey species  $i$  was used as a  
96 measure of stomach fullness. PFI is given by

$$97 \quad \text{PFI}_i = \frac{S_i}{L^3} \times 10^4 \quad (1)$$

98 where  $S_i$  is the weight (g) of prey species  $i$  found in  
99 the stomach of the predator  $k$ , and  $L$  is the length  
100 (cm) of the predator.

101 Similarly, the total fullness index, TFI, is defined  
102 by

$$103 \quad \text{TFI} = \frac{S}{L^3} \times 10^4 \quad (2)$$

104 where  $S$  is the total stomach content weight (g) of  
105 the stomach of the predator.

106 These indices are based on the assumption that  
107 stomach capacity is a power function of length.  
108 Length is used in preference to weight as a measure  
109 of predator size because length is not influenced by  
110 changes in the weight of liver, gonads and stomach  
111 contents. These indices permit comparisons of  
112 quantities of prey in stomachs of cod of various sizes.

113 The proportion of the TFI which is  
114 cod ( $P_{\text{cod}} = \text{PFI}_{\text{cod}}/\text{TFI}$ ) was calculated for all cod  
115  $> = 40$  cm. The 40 cm limit is set because few cod are  
116 found in stomachs of cod less than 40 cm. Also the  
117  $\text{FO}_{\text{cod}}$  is calculated based mostly on fish  $> = 40$ cm,  
118 thus a cut-off at 40 cm for the  $P_{\text{cod}}$  calculation gives  
119 approximately the same length range of predators in  
120 both data sets.

### 121 *Survey data*

122 The bottom trawl indices from the Norwegian  
123 (2000–2005 Joint Norwegian–Russian) demersal  
124 fish survey in the Barents Sea in January–March  
125 (Jakobsen et al. 1997; updated time series is given in  
126 ICES 2007) was used as indices of abundance of age  
127 1–3 cod. Only the period 1994–2006 was included in  
128 the analysis, because a change in spatial coverage as  
129 well as in survey gear took place in 1994, and these  
130 changes significantly affected the indices for the  
131 younger age groups.

132 Joint Norwegian–Russian acoustic surveys of capelin  
133 stock abundance and biomass have been  
134 conducted annually in September–October since  
135 1973 (Gjøsæter et al. 1998). Updated data series  
136 (on fish at age 1 and older) are given in the AFWG  
137 report (ICES 2007).

### *Cod stock assessment data*

The ICES AFWG performs annual assessments of  
cod, and the time series (age 3–13+) go back to  
1946. The notation 13+ indicates that all age classes  
age 13 and older have been combined into a single  
age class. Values of stock number at age are deter-  
mined using a version of cohort analysis known as  
extended survivor analysis (XSA) (Shepherd 1999).

The AFWG has for many years calculated the  
consumption by cod of various prey species, using  
data from the joint Norwegian–Russian stomach  
content data base (Mehl & Yaragina 1992) and the  
method described by Bogstad & Mehl (1997). For  
cod and haddock as prey, the number eaten by prey  
age group and year has also been calculated, and  
these numbers are used to extend the VPA for those  
species down to age 1 for the period 1984–present,  
assuming  $M = 0.2 +$  mortality induced by predation  
from cod ( $M_2$  in multispecies VPA (MSVPA)  
terminology: see Sparre 1991).

The following calculation scheme is used when  
including cod cannibalism in the cod assessment  
(ICES 2007). As a starting point the number of cod  
consumed by cod is estimated from the stock  
estimates in the last assessment. Then the number  
of cod consumed at age is included as additional  
catches, and a VPA (XSA) is run. The resulting stock  
estimate then leads to new estimates of the number of  
cod consumed by cod. This procedure is repeated  
until the consumed numbers at age for the latest year  
differ less than 1% from the previous iteration. In  
order to calculate a matrix of natural mortality which  
includes predation, the fishing mortality estimated in  
the final XSA analysis is split into mortality caused by  
the fishing fleet (true  $F$ ) and the mortality caused by  
cod cannibalism ( $M_2$ ) by using the number caught  
by fishing and by cannibalism. In 2007, AFWG  
presented two sets of VPA runs. The numbers used in  
this paper are taken from the ‘NOR-IUU’ run, on  
which the management advice was based.

Index of young cod abundance in year  $y$  (fish at  
age 1 and 2), which are the age groups which  
primarily are subject to cannibalism, is represented  
here by the sum of the VPA numbers of these  
cohorts at age 3, i.e. the sum of the number of age  
3 cod in years  $y + 1$  and  $y + 2$ .

### *Statistical analysis*

STATISTICA software and Microsoft Excel were  
used for the analysis of results. Regression analysis  
was used to quantify relationships between natural  
mortality induced by cannibalism ( $M_2$ ) and differ-  
ent population variables (frequency of occurrence of  
cod and capelin in cod stomachs; total cod and  
capelin stock biomass).

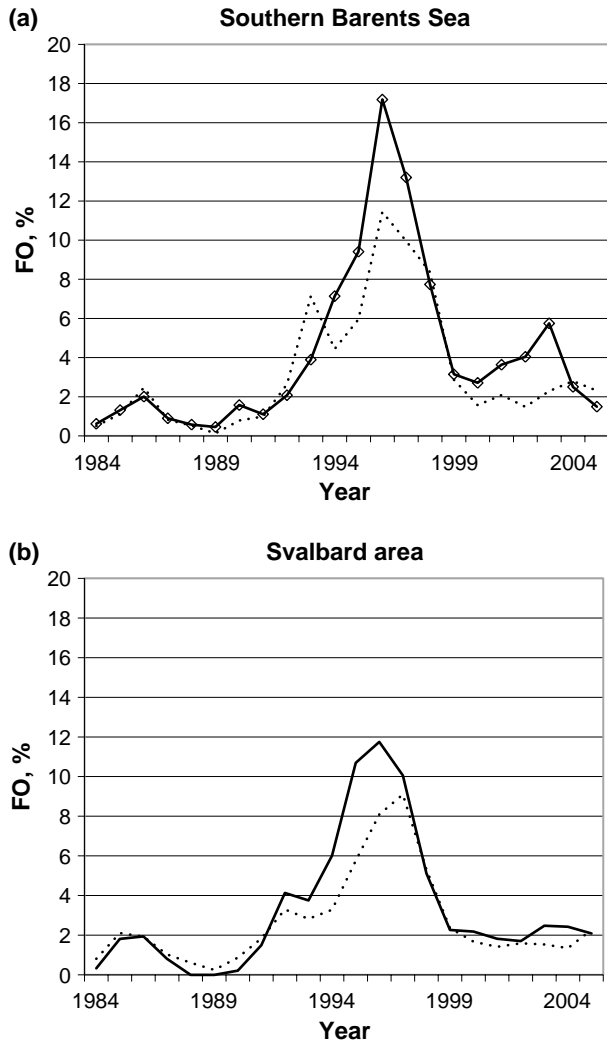


Figure 2. Comparison between FO<sub>cod</sub> from qualitative (dotted line) and quantitative (solid line) stomach content data registered for the Southern Barents Sea (a) and the Svalbard area (b) in 1984–2005.

## Results

### Comparison of qualitative and quantitative data sets

The mean FO<sub>cod</sub> from the qualitative and quantitative data from 1984 to 2005 is shown in Figure 2a,b. Pattern of FO<sub>cod</sub> variation in 1984–2005 was similar in both data sets. The correlation between the FO<sub>cod</sub> from the qualitative and quantitative data is strong ( $R^2 = 0.83$  for SBS and 0.89 for the Svalbard area), as could be expected. FO<sub>cod</sub> peaks seem to be slightly higher in the SBS than in the Svalbard area in 1996–1998 for both data sets.

### Temporal variations in FO<sub>cod</sub>

There was no clear pattern in the quarterly variation of FO<sub>cod</sub> for the total area for the years 1984–2005,

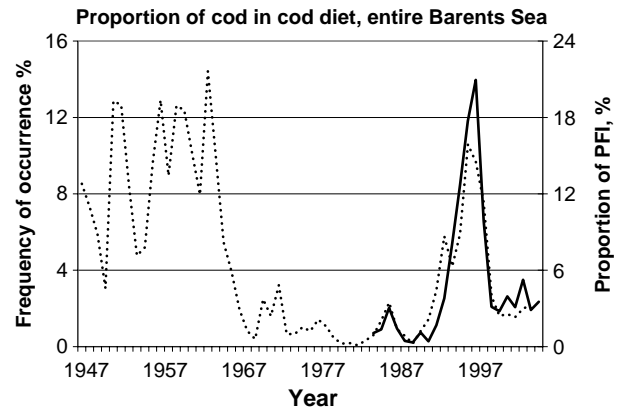


Figure 3. FO<sub>cod</sub> by years (the Southern Barents Sea and the Svalbard area combined) obtained from the qualitative database (dotted line) versus proportion of cod in cod diet obtained from the quantitative database (solid line).

although on average the values in the fourth quarter were highest.

FO<sub>cod</sub> for the two areas combined for the period 1947–2005 is shown in Figure 3, together with the proportion of the TFI which is cod ( $P_{cod}$ ) for the period 1984–2005. The FO<sub>cod</sub> and the  $P_{cod}$  are strongly correlated ( $R^2 = 0.86$ ). The highest level of FO<sub>cod</sub> observed is about 15%, while the highest level of  $P_{cod}$  is about 20%. It is reasonable that  $P_{cod}$  is higher than FO<sub>cod</sub> because cod is a large prey, so that stomachs where cod are found on average have larger stomach content than other stomachs with food.

We see that cannibalism was at a high level from 1947 to 1965 and then again in the mid-1990s.

Figure 4 compares the time series of FO<sub>cod</sub> to the variation in number of age 1 and 2 cod. This figure indicates that the low FO<sub>cod</sub> from the late 1960s to the end of the 1980s cannot be explained by low cod recruitment during this period. For example, the strong year classes 1969, 1970, 1975 and 1983 had rather small effect on the FO<sub>cod</sub> values in the years

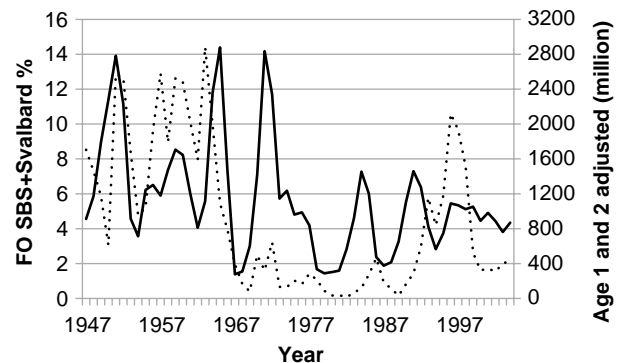


Figure 4. FO<sub>cod</sub> (dotted line) vs. abundance of cod at age 1 and 2, calculated as the sum of the VPA abundance at age 3 of the relevant cohorts (solid line), for the period 1947–2005.

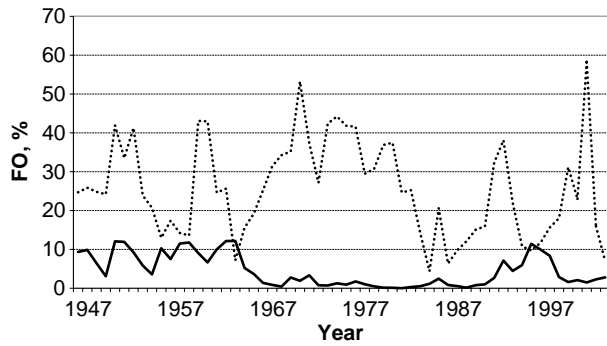


Figure 5.  $FO_{cod}$  (solid line) vs.  $FO_{cap}$  (dotted line) for the Southern Barents Sea in 1947–2005.

when they were at age 1 and 2, while the strong year classes 1963–1964 resulted in increase of  $FO_{cod}$  values already from the year, when these cohorts were at age 0 (Figure 4). The low  $FO_{cod}$  from the late 1960s to the end of the 1980s could be connected with cod mainly feeding on capelin due to high capelin stock biomass in most of this period (Figure 5).

Figure 5 compares the  $FO_{cod}$  and  $FO_{cap}$  in the southern Barents Sea for the period 1947–2005. Although some years with low  $FO_{cap}$  coincide with years with high  $FO_{cod}$ , a significant relationship for the whole period was not found ( $R^2=0.02$ ,  $p=0.31$ ,  $N=59$  years). For the period 1947–1983, however, there is a significant inverse relationship between  $FO_{cod}$  and  $FO_{cap}$  ( $R^2=0.14$ ,  $p=0.02$ ,  $N=37$  years). Comparison of the  $FO_{cod}$  and  $FO_{cap}$  for the southern Barents Sea and Svalbard area com-

pared revealed a weak, but significant, inverse relationship for the whole period ( $R^2=0.07$ ,  $p=0.04$ ,  $N=59$  years). For the period 1947–1983, the inverse relationship between  $FO_{cod}$  and  $FO_{cap}$  for two areas combined was stronger ( $R^2=0.25$ ,  $p=0.002$ ,  $N=37$  years). Three different periods might be identified in the data sets: (1) 1947 to the end of the 1960s; (2) the end of the 1960s to the end of the 1980s; (3) the end of the 1980s to 2005. There is large variability of both quantities in the first and the last period and these periods could be perceived as similar to each other. The intermediate period differs from the two other periods as variation was only observed in  $FO_{cap}$  values, whereas  $FO_{cod}$  values were at a very low level and almost constant (Figure 5).

#### Spatial variations in $FO_{cod}$

The spatial distribution of cod cannibalism from the quantitative stomach data is shown in Figure 6. For each square ( $1^\circ N \times 2^\circ E$ ), the average  $PFI_{cod}$  for cod (predators)  $\geq 40$ cm for the entire period 1984–2006 is shown. Squares with less than 50 stomachs are omitted. The highest values are found in the south-eastern Barents Sea and in the areas located along the Polar Front.

The data showed that cod might feed on their own conspecifics all the year round over the entire Barents Sea, although a certain spatial pattern in cod cannibalism is observed, connected probably with the areas of settlement of cod prey.

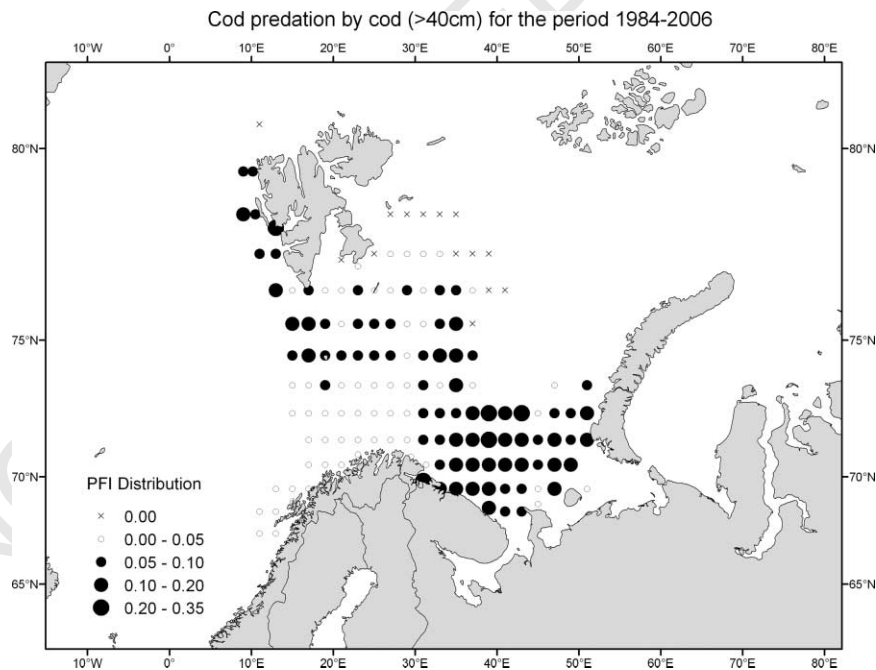


Figure 6. Geographical distribution of partial fullness index (PFI) for cod in cod stomachs. Data for 1984–2006, including only predators  $\geq 40$ cm and squares with more than 50 stomachs sampled.

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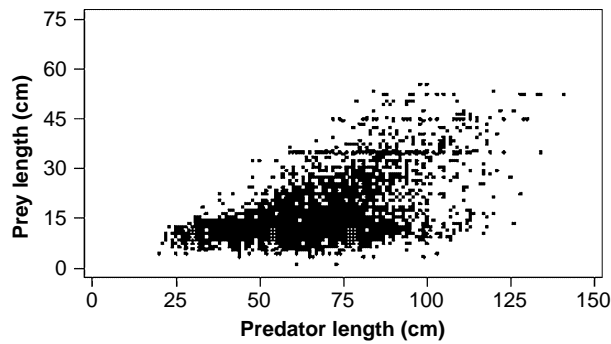


Figure 7. Prey size vs. predator size for cod preying on cod, data for the period 1984–2006. Note that prior to 1993 the prey length was recorded in length groups which were wider than 1 cm. In such cases, the midpoints of the length group are shown in the plot. Thus, e.g. prey length 35 cm (midpoint in 30–39 cm group) is quite common in the plot.

#### Predator length–prey length relationships

The relationship between predator size and prey (cod) size is shown in Figure 7 based on the quantitative data. Note that before 1993, the resolution of the length measurement varied by the size of the prey and length groups wider than 1 cm were used (Mehl & Yaragina 1992; Dolgov et al. 2007), but from 1993 onwards, all prey items were measured to the nearest cm. The length of predators ranged from 15 to 150 cm, while the length of cod as prey ranged from 1 to 55 cm. Very few cod < 5 cm were found in cod stomachs, and some of these could represent errors in the data base. Cod of 10–14 cm is the most abundant prey length group, and the abundance of this length group in cod stomachs is much higher than the abundance of 5–9 cm cod. This indicates that there is relatively little predation by cod on cod before the 0-group cod settle to the bottom, as the mean length of cod during the 0-group survey in August–September, just before bottom settling, is in the range 5.5–9.0 cm (Ottersen & Loeng 2000). The predator length is in general at least twice the prey length, and the length range of the prey increases with increasing predator length. Figure 8 shows how the proportion of cod in the cod diet increases with increasing cod length. The proportion of cod in the cod diet is negligible for cod (predator) length < 25 cm, and then increases to about 30% for cod > 100 cm.

#### Variations in cannibalism level (M2)

The correlation between the cannibalism mortality values (M2) in same year for different age groups is shown in Table I. The correlations between M2 for adjacent age groups (1–2, 2–3, 3–4) are positive and generally high, although the correlation between ages 1 and 2 is less strong ( $R^2 = 0.45$ ). Figure 9

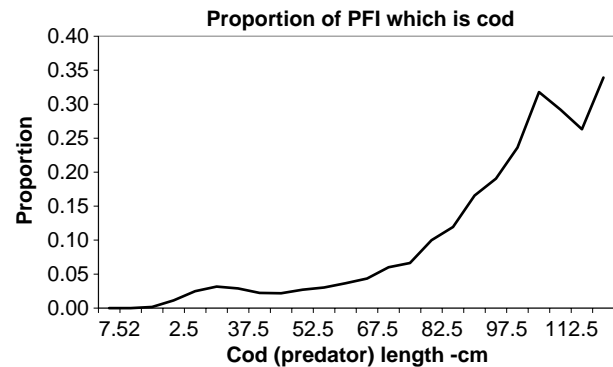


Figure 8. Proportion of total partial fullness index (PFI), which is cod, by predator 5 cm length groups. Midpoints of length groups (cm) are shown on the x-axis.

indicates an inverse relationship between M2 values and capelin stock size. The relationship is clearest for age 1 M2 vs. capelin biomass ( $R^2 = 0.25$ ,  $p = 0.017$ ,  $N = 22$  years) and age 2 M2 vs. capelin biomass ( $R^2 = 0.24$ ,  $p = 0.021$ ,  $N = 22$  years). An insignificant relationship is found for age 3 M2 vs. capelin biomass ( $R^2 = 0.15$ ,  $p = 0.07$ ,  $N = 22$  years).

For the period 1984–2005,  $FO_{\text{cod}}$  from the qualitative stomach content data both from SBS and the Svalbard area was related to the natural mortality induced by cannibalism for cod age groups 1–4. The correlations were positive and significant in all cases, with  $R^2$  values for single age groups and combinations of age groups ranging from 0.49 to 0.78 (Table II). The strongest correlations were observed for the mean M2 values of cod at age 1–4 and 1–2. The M2 for ages 1–2 for the time period 1947–1983 can be estimated using the following regression model (based on the 1984–2005 data):

$$M2_{\text{age}1-2} = 0.317 + 0.136 FO_{\text{cod}} \text{ SBS}, \quad (3)$$

where  $FO_{\text{cod}} \text{ SBS}$  is the frequency (%) of cod occurrence in cod stomachs in the Southern Barents Sea,  $R^2 = 0.75$ ,  $p < 0.0001$ ,  $N = 22$  years.

#### Comparison of bottom trawl indices with cod XSA estimates and frequency of occurrence of cod

Figure 10a–c shows the relationships between the number of cod of ages 1–3 from the VPA with cannibalism, and bottom trawl abundance indices

Table I. Coefficients of determination ( $R^2$ ) between M2 of cod at different ages for 1984–2006. All values are significant at the  $p = 0.01$  level.

Age, years	1	2	3
1			
2	0.45		
3	0.44	0.66	
4	0.34	0.52	0.85



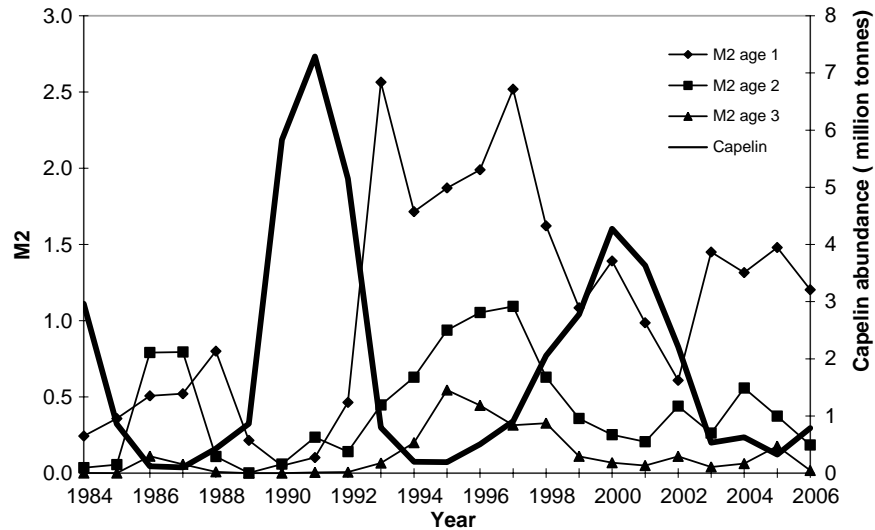


Figure 9. Cannibalism mortality (M2) values for cod at age 1 (line with diamonds), 2 (line with squares) and 3 (line with triangles) vs. capelin stock size in million tons (solid line).

for age 1–3 cod observed in the demersal fish survey in February (Jakobsen et al. 1997). The figures show direct proportionality between survey indices and XSA estimates of age 1 and 2 cod ( $R^2 = 0.86$  and  $0.83$ , respectively, intercept not significantly different from zero), indicating that the trends in abundance at age registered by the survey indices and estimated by including cannibalism in the XSA are quite consistent. For age 3, the relationship is also strong, but the intercept is significantly different from zero. Note that the indices for age 1–3 shown here are not included in the XSA tuning, thus these data series are independent. (The ‘age 3’ data from this survey included in the XSA tuning is really age 4 data shifted to the end of the previous year.)

Figure 11 shows that there is a good correlation ( $R^2 = 0.79$ ,  $p < 0.01$ ) between the survey biomass (bottom trawl) of age 1–2 cod from the demersal fish survey in February and  $FO_{\text{cod}}$  for the period 1994–2005.

Table II. Coefficients of determination ( $R^2$ ) between frequency of cod occurrence (%) in cod stomachs in the Southern Barents Sea (SBS) and Svalbard area (Sval) for 1984–2005 and the natural mortality of cod at age 1–4 induced by cannibalism from the analytical assessment (ICES 2007). All values are significant at the  $p = 0.01$  level.

Age, years	Frequency of occurrence in SBS	Frequency of occurrence in Sval
1	0.68	0.49
2	0.58	0.59
3	0.64	0.70
4	0.58	0.63
1–2	0.75	0.60
3–4	0.64	0.70
1–4	0.78	0.67

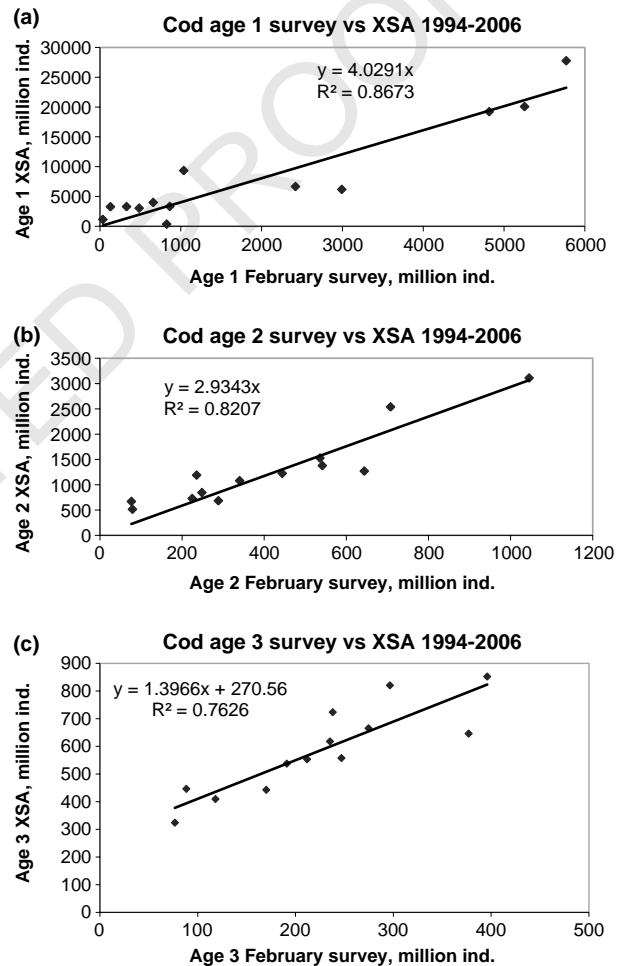


Figure 10. Bottom trawl survey estimates of age 1–3 cod (in February) vs. XSA estimates with cannibalism included (1 January) of the corresponding age group. Data for 1994–2006, million individuals. (a) Age 1, (b) age 2, (c) age 3.

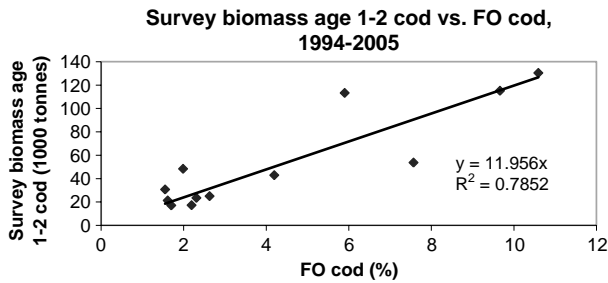


Figure 11. Survey biomass of age 1–2 cod (in February) vs.  $FO_{cod}$ , 1994–2005.

### Spawning stock–recruitment relationships

Figure 12a–c shows that for the year classes 1984–2003, there is significant correlation between the recruitment at age 1 (calculated by VPA with cannibalism included) and the SSB (spawning stock biomass) ( $R^2=0.44$ ,  $p<0.001$ ). The correlation between the recruitment at age 3 with cannibalism included and the SSB is not significant ( $R^2=0.13$ ,  $p=0.10$ ). When cannibalism is not included, there is no correlation at all between the recruitment at age 3 and the SSB ( $R^2<0.01$ ). This indicates that cod cannibalism, particularly on age 1 and 2 cod has considerable influence on the year-class strength. It would be useful to carry out an analysis of the factors (cannibalism, temperature, food abundance, size-at-age, etc.) affecting the survival from one life stage to the next one, starting from spawning stock/egg production until age 3.

## Discussion

### General comments

We have shown that the qualitative and quantitative data on cod cannibalism are strongly correlated. The data also suggested that NEA cod, as a generalist and omnivorous species, tends to concentrate on the most abundant/profitable preys. The NEA cod diet data could reflect long-term alterations in the Barents Sea prey communities.

Cannibalism appears to be an important source of natural mortality of young cod (age 1–3); hence year class strength at the 0-group stage can be modified severely before cod is recruited to the fishery. Number of cod eaten at age 1, 2 and 3 average about 4500, 400 and 60 million specimens, respectively, for the period 1984–2006 (ICES 2007), compared to an average year-class strength at age 3 of about 600 million individuals. The NEA cod cannibalism mortality values for different age groups in the same year appeared to be strongly correlated.

The proportion of cod in the cod diet is well correlated with the abundance of young cod esti-

mated from the surveys, while the cannibalism mortality is inversely related to capelin abundance.

### Variation in time

Cannibalism was at a high level from 1947 to 1965 and then again in the mid-1990s. The high levels of cod cannibalism observed in the mid-1990s are comparable to those observed in the 1950s and early 1960s, which allows to hindcast cod mortalities induced by cannibalism in the historical period. The reasons for cannibalism variability are not entirely clear; they are most likely multiple and interacting ones. One plausible reason could be the variability in cod year class strength. For example, the strong 1950 and 1963–1964 year classes resulted in increases of frequency of cod occurrence in cod stomachs. However, the strong 1969–1970 and 1983 year classes were only to a small extent reflected in

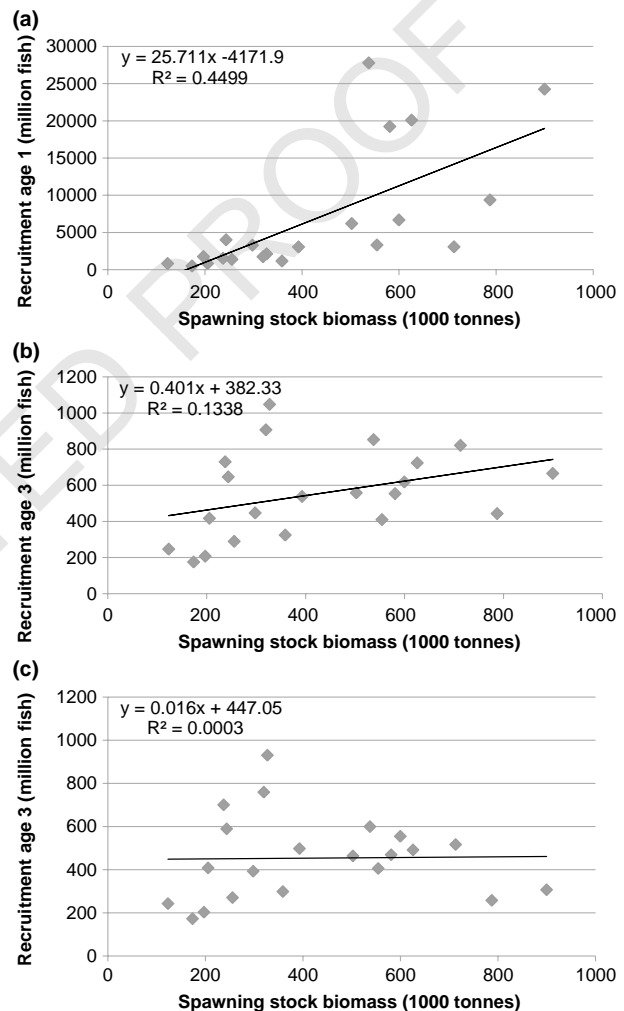


Figure 12. Spawning stock biomass–recruitment plots for the NEA cod cohorts 1984–2003. (a) Recruitment at age 1 from VPA with cannibalism included. (b) Recruitment at age 3 from VPA with cannibalism included. (c) Recruitment at age 3 from VPA not including cannibalism.

cod diet; the frequency of cod occurrence was low from the late 1960s to the end of the 1980s. This low  $FO_{\text{cod}}$  is possibly connected with increased predation by cod on capelin predominantly due to long-term increase in capelin stock biomass.

The high capelin abundance from the late 1960s to the mid-1980s was likely caused by the Norwegian spring-spawning herring collapse followed by absence of herring predation on capelin larvae (Gjøsæter & Bogstad 1998). This assumption coincides with a tendency for cannibalism levels to be inversely related to the capelin abundance. The high capelin biomass observed from the beginning of the 1970s to the mid-1980s resulted in high and more stable  $FO_{\text{cap}}$  in these years, destroying the inverse relationship between the  $FO_{\text{cod}}$  and  $FO_{\text{cap}}$  in that period. Nevertheless, in the recent period, after the first capelin stock collapse in the end of the 1980s, that relationship was restored.

Another possible reason for such fluctuations in cannibalism level is the influence of predators themselves, i.e. the cod stock abundance and length/age structure. Cannibalism is highly variable depending on the cannibals' size. Almost all cannibals were at least twice as long as their prey, and the contribution of cannibalism to the diet of cod increases with increasing cod length. This is consistent with results reported earlier (Bogstad et al. 1994). Cannibalism could thus be expected to be low when proportion of large cod in the stock is low, and this was also the case: the proportion of large, mature fish, which are main consumers of young cod, in the NEA cod population, was rather low in the 1970s–1980s; the SSB in those years totalled 18.9% of the total (3+) stock biomass, compared to 34.5% in the 1990s and 27.5% in the second half of the 1940s.

A third reason for fluctuations in cannibalism is variation in geographical overlap between older (predator) and younger (prey) cod. The geographical distribution of cod in the Barents Sea is related to temperature conditions (e.g. Maslov 1944; Milinsky 1967; Nakken & Raknes 1987; Ottersen et al. 1998). An analysis of the effect of geographical distribution on cod cannibalism is outside the scope of the present paper; it is, however, possible to do so for the period 1984–present, when both survey and quantitative stomach content data are available.

#### *Use of results in cod assessment and management*

Our future goal is to calculate the consumption of age 1–4 cod by older cod for the period 1947–1983, so that we can make the VPA time series of cod consistent (i.e. cod cannibalism included for all years). We will then be able to study stock-recruit-

ment relationships for this long times series using both age 1 and age 3 as the recruitment age, and see whether the SSB-age 1 recruitment correlation is also stronger than the SSB-age 3 correlation (Figure 12) when the entire time series is taken into account. This should also be linked to the recent work on replacing SSB with a more appropriate measure of reproductive potential such as total egg production (Marshall et al. 2006).

Since cannibalism is highly length-selective and size-at-age has varied strongly (e.g. mean length of age 3 cod in the Norwegian survey has ranged from 28 to 42 cm), variations in size-at-age (particularly for cod as prey) are relevant to consider when modelling cannibalism. However, very little information on mean size-at-age is available for young cod prior to 1984 – variability of young cod length is likely to be less than variability in abundance of cod (predators as well as prey) so the hindcast has to be based on an age-based analysis.

The first estimates of young cod natural mortality due to cannibalism were made by PINRO in the 1980s and early 1990s (Tretyak 1984; Korzhev et al. 1989; Korzhev & Tretyak 1992) based on cod stomach data and the MSVPA model. Skagen et al. (1990) outlined an approach for fitting a single-species VPA with cannibalism to stomach data, using the same techniques for calculating suitability (i.e. prey preferences) and M2s as in the MSVPA (Sparre 1991). This approach was implemented for North-East Arctic cod, while capelin and other food were included as additional prey items that were not assessed within the model; it could be developed further to calculate age-dependent prey preferences for cod eating cod based on the stomach data for the period 1984–2006. A (MS)VPA approach is not applicable to capelin, however, as this species has almost total spawning mortality (Gjøsæter et al. 2002).

The question is then how to combine these age-dependent prey preferences with the other information for the period 1947–1983: The existing VPA input data (cod catch-at-age for each year), annual values of  $FO_{\text{cod}}$  (and  $FO_{\text{cap}}$ ) and the regression between M2 and  $FO_{\text{cod}}$  given in Equation 3 in order to calculate VPA numbers-at-age, which includes cannibalism down to age 1 also for this period. The necessary information is available, but the algorithm needs to be worked out in detail. An iterative procedure needs to be applied. This approach will give point estimates of number at age 1 and older back to 1947. However, given the lack of prey age distribution for the period 1947–1983, for stock-recruitment studies, it would be useful to calculate a large number of VPAs spanning the uncertainty due to this lack of information, and base the stock-

recruitment studies on resampling from the stock-recruitment relationships derived from these VPAs.

Updating the NEA cod catch-at-age time series with the aid of inclusion of discards and by-catches (ICES 2007), combined with the inclusion of cannibalism back to 1947, as outlined above, would improve considerably the understanding of cod stock dynamics. It can also be used to improve existing analyses of long-term yield of both cod and capelin (Kovalev & Bogstad 2005; Tjelmeland 2005).

### Acknowledgements

We warmly thank two anonymous referees for their comments and suggestions, which greatly helped improve the manuscript. We also thank Padmini Dalpadado, Institute of Marine Research, Bergen, for making Figure 6.

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