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A method for estimating the consumption of capelin by cod in the Barents Sea

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A method for estimating how much capelin (*Mallotus villosus* Müller) is consumed by cod (*Gadus morhua* L.) during the winter capelin spawning migration has been developed. The method is based on an analysis of cod stomach content data and a model for stomach evacuation rate, and rests on various assumptions about temperature, stock size, and age distribution of cod, an initial stock size estimate of maturing capelin, and overlap between cod and capelin in space and time.

The method is now in use by the ICES Atlanto-Scandian Herring and Capelin Working Group for stock assessment purposes. The maximum amount of Barents Sea capelin consumed by north-east Arctic cod in winter of the years 1991–1993 has been estimated in the range 500 000–800 000 tonnes. This is a substantial part of the total amount of capelin at the start of the spawning migration, which in these years ranged from 2.1 to 2.6 million tonnes.

Key words: cod, capelin, consumption, stock assessment, multispecies interactions, Barents Sea.

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Introduction

The fishery on the Barents Sea capelin stock consists of a winter fishery on pre-spawning concentrations approaching the northern Norwegian and Russian coast in January to March, and an autumn fishery taking place in the capelin feeding areas in the central and northern Barents Sea (Hamre, 1991; Gjøsæter, in press). The winter fishery is one of the major fisheries for pelagic fish in the northern Atlantic, with historical catches of up to 1.5 million metric tonnes.

During the spawning migration, the capelin is subject to heavy predation by young cod in the southern Barents Sea. During winter, only the maturing part of the capelin stock is found together with the cod stock in the southern Barents Sea. Figure 1 shows the typical capelin migration routes and the spawning areas, and the distribution area of the young cod.

The Barents Sea capelin stock has been managed by a target spawning stock strategy. It has been impossible to obtain reliable estimates of the spawning stock during winter/spring. The assessment procedure is, therefore, based on an acoustic stock estimate in the autumn, a maturation model (at present all capelin above 14.0 cm are assumed to spawn next spring), natural mortality on maturing capelin in the autumn after the survey, consumption by cod from January till spawning, and individual growth of the maturing capelin from autumn till spawning (Anon., 1993b). Based on these input data, the assessment model "Captool", used by the ICES Atlanto-Scandian Herring and Capelin Working Group, presents TAC options for the capelin winter fishery.

The natural mortality of mature capelin in the period October to April was previously estimated based on the reduction in the number of immature individuals during the whole year. Prior to 1984, when the stock sizes of both cod and capelin were rather stable, and the cod stock size was small, this method of estimating natural mortality seemed to be satisfactory. During the early 1980s, the recruitment to the cod stock improved considerably following an increased inflow of Atlantic water rich in nutrients and plankton (Skjoldal *et al.*, 1992). Consequently, a more turbulent situation emerged, where the mortality on capelin sharply increased, and became more variable (Gjøsæter, in press). The capelin stock collapsed in 1984–1986. The fishery probably played a minor role in the dramatic changes in the stock size that took place (Hamre, 1991; Gjøsæter, in press). Nevertheless, the methods used to manage the capelin fishery proved to be inadequate (Tjelmeland and Bogstad, 1993).

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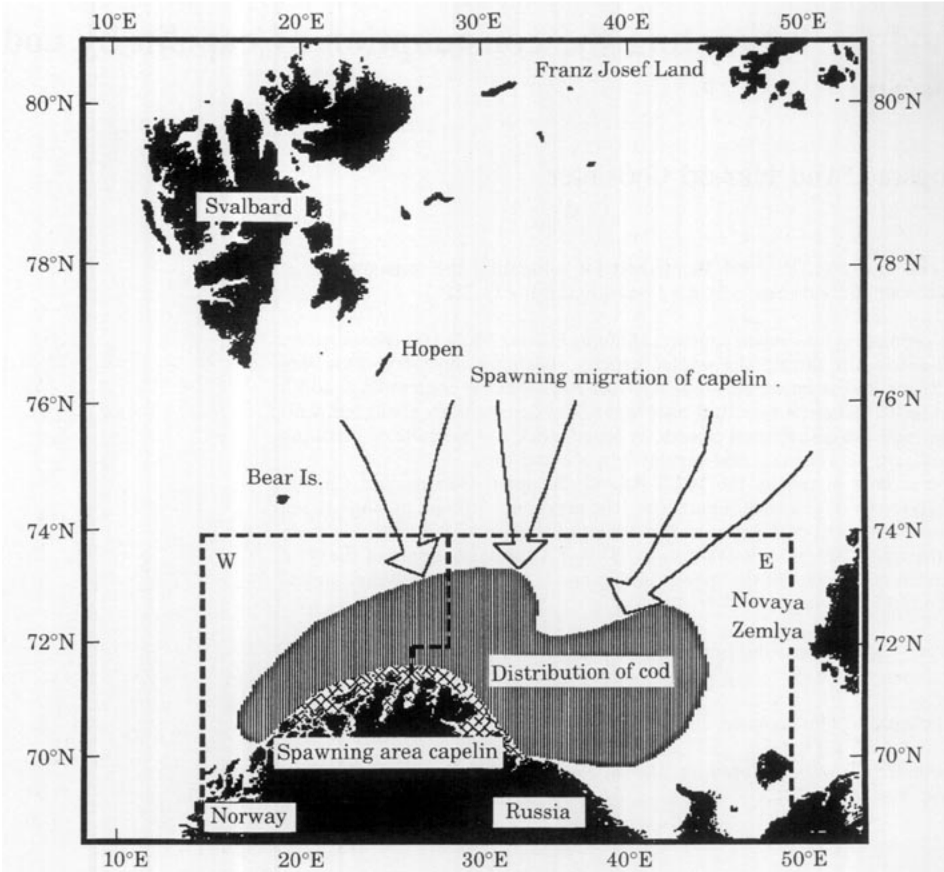

Figure 1. Map showing typical distribution areas of cod and capelin in the Barents Sea during winter.

Since the rebuilding of the capelin stock in 1990, an alternative way of estimating a large and variable part of the capelin natural mortality during the winter season has been developed. A calculated consumption of capelin by immature cod has been used in the assessment of the stock in 1990–1992 (Anon., 1991, 1993b). In this paper this method is presented, together with a discussion of the assumptions underlying it. Due to the problems with measuring the spawning stock size directly, it is impossible to assess the accuracy of the prediction of capelin consumption.

Materials and methods

Data sources

1. The main data source is stomach content data for cod from the relevant geographical area and season. Such data have been gathered by the Institute of Marine Research, Bergen, and PINRO, Murmansk, since 1984, and stored in a joint database (Mehl, 1989). The data needed in these computations are the mean stomach content/cod body weight ratio and the proportion of capelin in the stomach content. The most relevant data for these computations are those sampled during an annual Norwegian survey to assess the biomass and distribution of young cod and haddock in February–March.
2. Temperatures representative for the area during the period January to April are measured during the annual survey mentioned above.
3. An exponential model for stomach evacuation rates for relevant sizes of cod and for relevant temperatures is taken from dos Santos and Jobling (1992).
4. The number, mean weight, and the proportion of immatures by age of the north-east Arctic cod stock by 1 January. This information is taken from the 1992 report of the ICES Arctic Fisheries Working Group (Anon., 1993a).

Assumptions made

1. Only immature cod of age 3 and older prey on mature capelin in the period January to March (Mehl, 1989).
2. When there is geographical overlap between cod and capelin, the cod will eat capelin at a rate where the stomach content/predator weight ratio reaches a

given level, balanced by intake and stomach evacuation. This stomach content/predator weight ratio is found from stomach content data.

3. Overlap in time and space between immature cod and mature capelin can be described by a number of days, with complete overlap between the two stocks.
4. The initial meal size S_0 (see below) is not known in field studies. This entity has to be related in some way to the observed stomach content. According to the results from sequential meal experiments (dos Santos and Jobling, 1992), the evacuation rate will be affected by additional food intake in the evacuation period. In the field, the cod were probably eating more or less continuously, and, therefore, the total stomach content was used as an approximation to the initial meal size.

Computations

According to dos Santos and Jobling (1992), the evacuation of a single capelin meal for cod can be described in the following way (assuming exponential evacuation):

$$S(t)=S_0 e^{\frac{-t \times e^{cT} \times \ln 2}{H\left(\frac{S_0}{W}\right)^b}}, \quad (1)$$

where t=time (hours), S_0=initial meal size, W=cod body weight, T=temperature (°C), c=0.11, b=0.54, S(t)=stomach content at time t, H=283 (specific for capelin). H is a theoretical value expressing (for a given prey species) the half-life (in hours) of a meal of the same size as the fish body weight (S_0=W) at 0°C.

When we assume a balance between food intake and stomach evacuation (assumption 2 above), and the initial meal size is set equal to the average stomach content (assumption 4), the consumption, C, becomes:

$$C = -\frac{dS}{dt} = \frac{e^{0.11T} \times \bar{S} \times \ln 2}{283 \times \left(\frac{\bar{S}}{W}\right)^{0.54}}, \quad (2)$$

where $\bar{S}$ is the average stomach content.

Assuming that $\bar{S}$=rW, where r is the stomach content/body weight ratio, the consumption by the immature cod stock becomes:

$$C = \sum_a \frac{N_a \times W_a \times (1-M_a) \times \ln 2 \times e^{0.11 \times T} \times r \times 24 \times D_a}{283 \times r^{0.54}} \quad (3)$$

where a=age group, N_a=number of cod, W_a=mean weight of cod, M_a=proportion of mature individuals, D_a=overlap period (days).

Table 1. Estimated consumption (C) of mature capelin by immature cod in 1991–1993. All biomasses are given in thousand tonnes. The estimates for 1991 and 1992 are hindcasts, that for 1993 is a forecast.

Year	1991	1992	1993
Biomass immature cod	739	740	857
Temperature (°C)	3	3	3
Overlap (days)	60	45	45
C (r=0.02)	600	450	522
C (r=0.03)	723	543	628
C (r=0.04)	825	619	717
Maturing capelin stock 1 Oct prev. year	2620	2117	2201
Capelin catch in weight 1 Oct–1 May	681	1087	717

Results

Calculations for the period 1991–1993

Stomach content data from periods and areas where "excess" feeding by cod on capelin (i.e. situations where the amount of capelin available is not a limiting factor for the consumption) have taken place (winter 1985 and winter 1991) show that the average stomach content then is about 3–4% of cod body weight (r=0.03–0.04). In Table 1 we have made a hindcast of the consumption in winter 1991–1992, and a forecast for the winter 1993, for r=0.02, 0.03, and 0.04. In these calculations we have used the best estimate available of overlap period and temperature in the overlap area.

Sensitivity analysis

In Figures 2 and 3 we have indicated how the calculated consumption for 1991 varies with temperature, overlap period, and r. In Figure 2 we have kept r equal to 0.03, and shown how the consumption varies with temperature for different length of the overlap period. In Figure 3 the temperature is set equal to 3°C, and the figure shows how the consumption varies with r for different overlap periods.

Discussion

The method presented can be used both to estimate the actual amount of capelin consumed by cod in previous years, and to forecast the consumption, for fisheries management purposes. The use of the data sources, and the assumptions that have to be made, will be discussed first. Then, the two ways of using the method will be briefly discussed before going into detail on the method itself, and on the results of the calculations carried out.

Data sources

The stomach content data should give reasonably good information on the total amount of food, and the

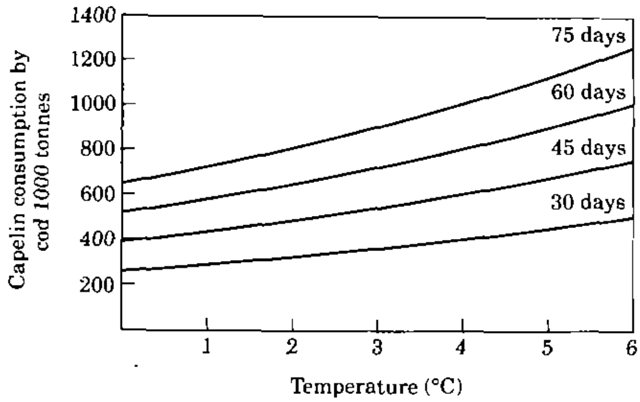

Figure 2. Estimated capelin consumption by cod in 1991, for variable temperature and number of overlap days. r (stomach content/body weight ratio)=0.03.

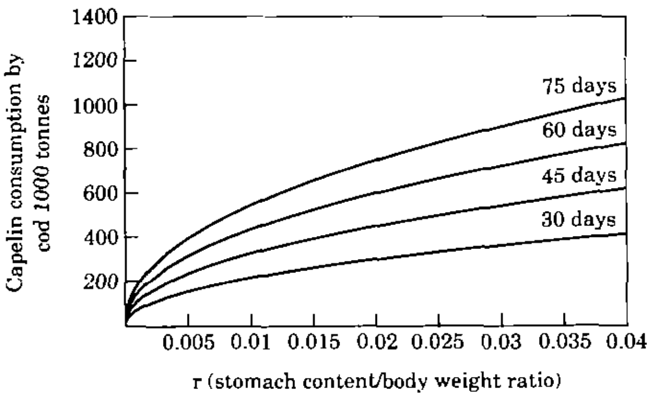

Figure 3. Estimated capelin consumption by cod in 1991, for variable r and number of overlap days. T=3°C.

proportion of capelin in this food, for cod of different sizes in the sampling area at the time of the survey. The main problem is that the sampling does not adequately represent the variation in feeding on capelin in time and space. The lack of capelin in a cod stomach may either be interpreted as if capelin is of no importance in the feeding of cod or, that this particular sample of cod was taken outside the area and/or period of overlap between cod and capelin. Obviously, there is need for independent information about overlap. In hindcasting such information can partly be extracted from the observed geographical distribution of the two stocks during relevant surveys, and partly from other sources such as capelin and cod fishing activity, spawning places, and spawning time for the capelin. In forecasting, overlap has to be predicted based on general knowledge about the stock distribution under certain hydrographic situations, the size of the two stocks, etc.

The approach used so far, to use a stomach content/predator body weight ratio observed in a situation where the cod has excess of capelin available, should result in a maximum daily consumption of capelin. If the assumption of excess of capelin available seems unlikely, this method would not give reliable estimates of the amount of capelin consumed by cod.

An analysis of the cod stomach content database (Table 2) shows that in years with high abundance of food in the cod stomachs (e.g. 1985, 1991), capelin makes up between 90 and 100% of the stomach content. Consequently, the approximation made in the computation is valid, assuming that capelin is the only food item.

The second data source, the amount of cod in the relevant age groups at the start of the season, may be an important source of error. These figures have so far been extracted from the reports of Arctic Fisheries Working Group, and are forecasts based on virtual population analysis (VPA). Such forecasts rest on assumptions about natural mortality, maturity ogives, predicted growth, etc., and may be quite uncertain. The cod weight at age at 1 January used by the Arctic Fisheries Working Group is an arithmetic average of the observed weights at the autumn Russian survey and the winter Norwegian survey. Since the Norwegian survey takes place in the relevant period, these weights may be more appropriate to use.

The temperature (which affects the stomach evacuation rate) is entered as one single figure, representing a large area, a large depth interval, and a long time period. Although the temperatures do change from year to year, distributions of cod and capelin in relation to water temperatures indicate that the temperatures in the overlap area changes little. The sensitivity analysis of temperature (Fig. 2) shows that within the relevant temperature range of 2–4°C, the consumption changes by almost 20%. So far, the temperature used has been found from comparing the distribution maps of cod, capelin, and temperature in different depth layers in the relevant period. However, a less subjective method would be preferable.

The model for stomach evacuation rates is developed based on a large number of measurements in several feeding experiments (dos Santos and Jobling, 1992). The experimental design was set up to be as representative for the Barents Sea environment as possible. Therefore, it is reasonable to conclude that this is not a major source of error in the consumption model.

Assumptions made

The first assumption of restricting the consumption of capelin to immature cod individuals of age 3 and older seems to be quite reasonable. During this period, the mature part of the cod stock has moved to the spawning areas further south and west and cod younger than 3 years, with lengths less than 30 cm, do not eat significant amounts of mature capelin (Table 2).

The calculated consumption (Table 2) is dependent on which assumption is made on the initial meal size in the underlying gastric evacuation model. Setting the initial meal size equal to the average stomach content implies continuous feeding, increasing the value implies a more pulse-like feeding. The distribution and variance of the stomach content gives information about the feeding behaviour, and this information can be utilized in the consumption calculations.

Preferably, the method should allow for estimates of overlap in space and time separately. However, as long as there is not enough information to give reasonable estimates, it is more practical to pool these variables.

When forecasting a consumption, few of the quantities needed for doing the computations are known and therefore have to be estimated. This applies for the amount of cod present, the overlap in time and space, the actual stomach content of cod, and the water temperature. The overlap between cod and capelin and the actual amount of capelin consumed by each individual of cod need some more discussion.

The consumption of capelin may take place over a period of about 3 months. Even if the cod is known to follow the capelin towards the spawning area, it is not possible to assume that all of the cod will have access to capelin even in parts of the overlap time. A portion of the cod stock is known to be distributed in the Svalbard area in the autumn. Some of these fish also stay in this area during the winter–spring season. The most valid description of the situation is probably that some portion of the cod stock will have access to some portion of the capelin stock in some time during the period January to April. Moreover, the amount of capelin available to each cod will vary considerably over this period, and so will the actual amount of capelin consumed.

Various methods are possible to approach this problem. The most straightforward method is to find (from historical stomach content data) a typical capelin stomach content/predator weight ratio for periods and areas when the capelin is available in excess. This ratio can then be applied to estimate overlap period and overlap area when this assumption (capelin available in excess) is valid. Instead of estimating overlap area and overlap time separately, which would be quite difficult, both variables are estimated together as a period with complete overlap between the stocks. The estimation involves studying cod, capelin, and temperature distribution maps, cod stomach content data, and time and area of capelin fishery. Relevant data are obtained from annual surveys to assess the stock size and distribution of young cod in the period January to March. These surveys cover the distribution area of young cod, as well as that of mature capelin approaching the coast for spawning. It has not been possible, however, to obtain acoustic estimates of the entire capelin spawning stock in this period.

At least two different approaches can be used when calculating consumption for previous years. One possibility is to use all relevant cod stomach data and to let the observed capelin stomach content/predator weight ratio represent the actual rate of overlap in time and space. This method demands that stomach data from the whole period and the whole geographical area sampled in a representative way is available. This demand is not fulfilled for any year. The alternative approach is to use the method outlined for forecasting: to estimate a maximum stomach content/body weight ratio and to estimate the relevant overlap. In contrast to the forecast situation, more data are available to do this estimate: the geographical distribution of both stocks are monitored during most of the relevant period, and so are the temperatures.

Discussion of calculation of consumption in 1991–1993

The calculation of consumption was undertaken for a stomach content/body weight ratio (r) of 0.02, 0.03, and 0.04. This range of r-values was found to be appropriate

Table 2. Number of cod stomachs sampled, and stomach content (capelin only and total food items) in per cent of cod body weight, 1 quarter 1984–1992, by length group and area. The areas west (W) and east (E) are shown in Figure 1. A '+' indicates less than 0.1% of cod body weight.

	West			East		
Length group	n	Total	Capelin	n	Total	Capelin
1984						
20–29	12	1.3	0.1	326	1.6	0.7
30–39	60	2.7	2.1	346	1.5	0.3
40–49	42	2.9	2.1	393	1.2	0.2
50–59	74	2.0	1.4	253	1.1	0.2
60–69	62	1.5	1.2	148	0.9	+
70–79	32	1.3	0.9	115	1.1	0.1
80–89	2	9.5	9.5	37	0.4	+
1985						
20–29	21	0.5	0.2	407	1.9	1.1
30–39	41	2.4	2.1	295	2.3	1.7
40–49	136	3.5	3.5	370	3.1	2.6
50–59	115	3.7	3.7	260	2.0	1.6
60–69	75	3.8	3.6	133	1.5	0.8
70–79	33	3.7	2.6	37	1.5	0.9
80–89	20	2.6	2.6	28	3.2	2.0
1986						
20–29	11	0.7	0.0	306	1.7	1.0
30–39	34	1.8	1.0	549	1.7	0.8
40–49	49	1.5	1.0	552	1.6	0.7
50–59	87	0.8	0.4	563	1.5	0.5
60–69	71	1.2	0.6	319	2.1	0.6
70–79	38	1.5	1.0	74	3.3	1.3
80–89	7	2.4	0.1	15	3.6	0.0
1987						
20–29	68	1.5	0.8	290	0.7	0.3
30–39	151	0.6	0.3	403	1.2	0.6
40–49	185	0.6	0.1	595	1.4	0.4
50–59	145	0.5	+	455	1.3	0.1
60–69	158	0.8	+	207	1.9	0.3
70–79	37	1.4	0.0	84	1.9	0.5
80–89	8	1.1	0.0	16	3.5	0.3
1988						
20–29	39	2.3	0.0	232	0.7	0.3
30–39	106	1.6	0.7	236	1.2	0.8
40–49	214	0.5	0.1	587	0.7	0.3
50–59	229	0.6	0.1	294	0.5	0.1
60–69	108	0.6	+	45	0.5	0.2
70–79	38	1.1	+	18	1.9	+
80–89	9	0.8	0.0	7	1.2	0.0
1989						
20–29	62	1.1	0.0	124	1.6	0.5
30–39	184	0.8	0.5	334	2.9	1.3
40–49	282	0.8	0.4	372	3.0	1.6
50–59	350	0.8	0.3	311	2.5	1.7
60–69	237	0.7	0.1	149	1.4	0.8
70–79	61	0.9	0.1	35	2.5	1.6
80–89	24	0.8	0.0	15	2.4	1.4
1990						
20–29	12	1.1	0.9	155	1.5	1.0
30–39	68	1.1	0.7	181	2.0	1.7
40–49	137	1.3	1.0	221	2.1	1.9
50–59	191	1.1	0.7	250	2.5	1.8
60–69	218	1.0	0.8	156	2.8	2.3
70–79	157	1.1	0.7	59	2.6	2.5
80–89	26	0.4	0.2	2	3.7	0.0

Table 2. *Continued*

Length group	West			East		
	n	Total	Capelin	n	Total	Capelin
1991						
20–29	50	0.6	0.4	201	1.8	1.7
30–39	55	2.6	2.5	249	2.9	2.8
40–49	104	3.1	2.8	217	4.4	4.2
50–59	151	3.9	3.6	200	4.8	4.7
60–69	144	2.9	2.8	194	4.7	4.5
70–79	153	3.2	2.9	171	5.0	4.8
80–89	47	2.3	2.1	57	5.9	5.3
1992						
20–29	20	0.7	0.0	198	2.3	2.1
30–39	25	1.5	0.9	175	2.4	2.2
40–49	90	1.3	0.9	199	3.0	2.5
50–59	100	1.4	0.8	165	2.7	2.4
60–69	91	1.1	0.7	102	2.0	0.9
70–79	78	0.4	0.1	79	1.1	0.7
80–89	57	0.4	0.2	47	1.1	0.8

when capelin comprised nearly all the stomach content and capelin were present in excess. These figures probably represent the maximum ratio for cod feeding on capelin. In 1991–1992 capelin was the main food item for cod in the relevant area and period. Consequently, this method of calculating the consumption of capelin should be applicable for these years.

If other types of prey (e.g. herring) are present in large quantities, care must be taken when calculating consumption using this method. One of the reasons for this is that herring is evacuated at a slower rate than capelin (the half-life parameter H in the stomach evacuation rate formula [Equation (1)] is 452 for herring vs. 283 for capelin). Equation (1) does not take into consideration cases where the stomach content consists of several types of prey; the evacuation rate for a given prey type will be affected by both the total stomach content and the prey composition. A situation with mixed consumption of capelin and herring may occur in the winter of 1993. Therefore, the forecast made for this period may be somewhat uncertain.

Discussion of the sensitivity analysis

Four options for the overlap period are given in Figures 2 and 3. The shortest, 30 days, would represent a late spawning migration, or a migration along a route mainly outside the cod distribution area. The longest, 75 days, would, on the other hand, represent an early migration through the cod distribution area. The time and route of the capelin spawning migration have varied considerably in the last years, and so has the cod distribution area (Bogstad and Tjelmeland, 1992; unpublished IMR survey data).

From Figures 2 and 3 it can be seen that for a given overlap period, the rate of change in the consumption slows down for increasing values of r. This implies that there are only slight differences between the consumption calculated on the basis of r-values of 0.03 and 0.04. Even though the rate of change in consumption increases with increasing temperature, in the most relevant interval (2–4°C) the rate of change is moderate. It can thus be concluded that the overlap in space and time (here approximated by a number of days of complete overlap) is the dominant factor.

Capelin stock management

The Barents Sea capelin stock has been managed by a target spawning stock strategy. The target spawning stock has varied from 400 000 to 500 000 tonnes, based on single species yield and stock–recruitment considerations. Tjelmeland and Bogstad (1993) outlined how a new management procedure for capelin taking multispecies considerations into account can be developed. There is reason to believe that the new target spawning stock size will be lower than the previous targets.

In some years, a considerable overlap between cod and capelin has been found during autumn. No attempts have so far been done to estimate the consumption during this period. This consumption has been accounted for by a natural mortality coefficient for the autumn period, assumed equal to that of the immature part of the stock, and derived from the reduction of one year class between the two most recent autumn surveys.

The consumption by cod in spring may, in years with a large stock of young cod relative to the capelin, constitute a large portion of the total natural mortality of the capelin. Since 1990, attempts have been made to use the present method of calculating the consumption of capelin by cod (Anon., 1993b).

One of the main problems with the use of this method is the combination of acoustic capelin stock measurements and VPA estimates of cod stock size, which are relative quantities, with a calculated consumption, which in theory is an absolute quantity (Bogstad and Tjelmeland, 1992).

Another problem is the spatial overlap between the stocks. This problem is considered by Bogstad and Tjelmeland (1992), where predation mortalities on capelin are calculated using an area-structured cod–capelin model.

Conclusions

The method presented is a first attempt to bring multispecies considerations into practical capelin assessment work. More sophisticated methods for calculating the magnitude of stock interactions are being developed (Bogstad and Tjelmeland, 1992; Tjelmeland and Bogstad, 1993). Heretofore, stock interactions have been taken into account in management only on a few occasions despite the fact that a lot of effort has been put into multispecies research in the last decade.

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