International Council for the
Exploration of the Sea

C.M. 1990/ G: 22
Sess. O

THE CONSUMPTION RATE OF NORTHEAST ARCTIC COD - A COMPARISON OF GASTRIC EVACUATION MODELS

by

Bjarte Bogstad and Sigbjørn Mehl

Institute of Marine Research
P.O. Box 1870 - Nordnes
N-5024 Bergen, Norway

ABSTRACT

The consumption rates in fish are important but also often weak points in multispecies models. In the Barents Sea multispecies model (MULTSPEC), as in many other models, quantitative stomach content data are combined with gastric evacuation data or models to produce consumption rates of important prey species. To evaluate the evacuation model presently used for cod in the Barents Sea and the derived consumption rates, we have combined stomach data from 1984 with five other evacuation models for cod. The results are compared and judged against data on prey stock sizes, individual cod growth, daily rations and food conversion efficiency. The rations derived from the different models ranged from 0.5 to 1.2% of the BW daily on average for all agegroups of cod or from 2.1 to 4.4 times the biomass of the total cod stock annually. Food conversion efficiency varied between 6 and 59% for the different models and agegroups.

INTRODUCTION

One essential requirement for multispecies models are estimates of the food consumption by the main predator stocks over the area of distribution. In addition to data on the number and distribution of the different predator agegroups, good estimates of the annual food requirements are needed. The latter can be estimated in two ways:

- from quantitative stomach content data and data on gastric evacuation rates (models)
- from consideration of energy requirements

The first method has been chosen in several investigations, may be because it consists of more or less straight forward measurements. But these measurements which results in the consumption rates by/of the actual predator/prey stocks are important and perhaps sometimes weak points in the models they are used in.

This is the situation for the MSVPA models both in the North Sea and the Baltic, and it has the same importance for the multispecies research in the Barents Sea (see Bogstad and Tjelmeland, 1990, where the first results of the multispecies modeling work in this area is presented.) In the latter area stomach data were previously combined with temperature-correlated evacuation rates from the North Sea to calculate the cod's consumption rates (Mehl, 1989). But the estimated consumption per cod was much lower than that found in other investigations and too low to explain the individual growth. Later evacuation rates based on feeding experiments in Northern Norway have been taken into use (Mehl, 1989; Mehl and Sunnanå, 1990).

To evaluate the goodness of the new evacuation rates and their effect on the consumption rates, we have chosen to test them against five other evacuation models (data) on a set of stomach data for one year. The resulting consumption rates and total consumption are compared with prey stock sizes, individual growth data for the cod stock, daily ration data from other investigations and food conversion efficiency.

MATERIALS AND METHODS

Stomach data from 1984 have been used in the calculations, because each quarter was covered fairly well with samples and the main prey stocks were still at an almost normal level. Details about stomach sampling, analysis and aggregation of data are given in Mehl (1986, 1989).

VPA-data from the Northeast Arctic Working Group (Anon., 1990) are used when the total cod stock's consumption is estimated. For details, see Mehl (1989).

The geographical and seasonal distribution of the different cod agegroups are based on survey data, both acoustic and bottom trawl data (Hylen _et al_., 1989; Jakobsen _et al_., 1989 and unpubl. data).

The table below presents the mean length (cm) and weight (grams) at January 1 and annual weight increment (grams) of cod in 1984 by agegroup (Anon., 1990 and unpubl. data):

	Cod agegroup						
	1	2	3	4	5	6	7
Length at January 1	12.7	22.5	34.4	50.4	60.0	70.2	85.0
Weight at January 1	25	211	530	1200	1900	2910	3970
Weight increment	98	250	380	510	1040	1260	1070

We denote the daily ration for each cod age group by R, the average stomach content by S, the average predator weight by W (all in grams), and the average length by L (cm). T is the temperature in ^{0} C.

The six gastric evacuation models, data and ways to calculate the consumption rates were:

1. SANMOD. Exponential model based on experiments with different prey species and temperatures done in Northern Norway (dos Santos, pers. comm.; Mehl, 1989; Bogstad and Tjelmeland, 1990). The actual evacuation rates used were:

$$\text{amphipods and capelin} \quad E = 0.0077 + 0.0072T$$
$$\text{all other prey species} \quad E = -0.0011 + 0.0066T$$

where E is rate of evacuation per hour. The consumption per day is then given by :

$$R = E \cdot S \cdot 24$$

2. NORMOD. Linear model from the North Sea with constant digestion time for the different predator length groups (Daan, 1973). 2S is taken to be the initial meal size, and the daily ration is calculated as:

$$R = 2S/D$$

where D is the digestion time in days. The digestion times for the different cod agegroups are found by $D = \delta \cdot L$, where the digestion coefficient δ is estimated to 0.06 (Daan, 1973).

3. NORTEMP. The North Sea model, applying the same temperatur correlation for the digestion coefficient as used by the Multispecies Assessment Working Group in the North Sea (Anon., 1987; Mehl, 1989):

$$\delta = \delta_o \cdot e^{0.096(T_o - T)}$$

where δ_o is the experimentally obtained digestion coefficient at temperature T_o. The digestion experiments of Daan (1973) were carried out at 12^{0} C.

4. ICEMOD. Icelandic model for daily consumption (Magnusson and Palsson, 1989, 1990), based on data obtained by Jones (1974):

$$R = 2.6 \cdot (L/40)^{1.15} \cdot 1.09^{T-6} \cdot S^{0.5} \text{ g/day}$$

5. BODMOD. Food consumption dependent on body size (weight) and proportional to the stomach weight (from Ursin *et al.*, 1984):

$$R = 7.2 \cdot W^{-0.38} \cdot S \text{ g/day}$$

6. BROMOD. Linear model with constant amount of food digested per hour, derived from Bromley (1989).

$$R = 2 \cdot S \cdot (1.76/100) \cdot 24 \text{ g/day}$$

where $2 \cdot S$ is taken to be the initial meal size. Bromley found an average evacuation rate of 1.59% of the initial meal size per hour for *Nephrops* and 1.76% for sprat. We have chosen to use 1.76% for all prey species, because we believe most species eaten by Northeast Arctic cod, included crustaceans as *Pandalus borealis*, are more digestible than *Nephrops*.

We see that in SANMOD, NORTEMP and ICEMOD the evacuation rate, and thus the consumption rate, increases with temperature, while it is independent of temperature in the other models. We also see that in NORMOD and BODMOD the consumption, given an average stomach content, decreases with fish size, while it in ICEMOD increases slightly with fish size. ICEMOD also differs from the other models because the consumption in ICEMOD is proportional with the square root of the stomach content, while it in all the other models is proportional to the stomach content itself. It should also be noted that SANMOD is the only model with a prey-dependent evacuation rate.

The temperatures used in SANMOD, NORTEMP and ICEMOD are calculated by a temperature model which is also used by the multispecies model for the Barents Sea. Data from standard hydrographic sections (Fugløya-Bjørnøya, Vardø N, Kola section) are used. At different depths and over different parts of the sections Fourier analysis is used on the temperature data. The temperature is then integrated over time and area to give one temperature for each year, area and month.The procedure is documented in Alvarez and Tjelmeland (1989). We have used a depth of 100m in our calculations.

RESULTS

The cod stock's total consumption

Table 1 presents the consumption of the main prey species for the different evacuation models.

Table 1. The Northeast Arctic cod stock's consumption in 1000 tonnes of the main prey species in 1984, by gastric evacuation model (1-6)

	Gastric evacuation model					
Prey-species	SAN MOD	NOR MOD	NOR TEMP	ICE MOD	BOD MOD	BRO MOD
Amphipods	23	26	13	17	19	19
Shrimp	801	1215	585	814	847	1025
Capelin	1450	1319	608	948	927	1430
Herring	127	194	97	108	131	146
Cod	48	37	18	51	27	60
Haddock	70	109	53	74	81	90
Redfish	539	681	321	546	477	726
Others	546	826	411	531	605	633
Total	3604	4407	2106	3089	3114	4129
Tot/TSB	3.6	4.4	2.1	3.1	3.1	4.1

The total consumptions range from 2.1 million tonnes (NORTEMP) to 4.4 million tonnes (NORMOD). Because the biomass of the cod stock was almost 1 million tonnes (997.000) January 1 1984, the ratios total consumption/total stock biomass (TSB) also range from 2.1 to 4.4 and the total consumption per day from 0.6% of the stock biomass to 1.2%.

In all six models capelin contributed most, SANMOD the highest with 1.45 mill. tonnes. NORMOD gave the highest consumption of deep sea shrimp (1.2 mill. tonnes) , herring and haddock, while BROMOD resulted in the highest consumption of redfish and cod. ICEMOD and BODMOD came out with the most similar results.

Consumption per cod

The next table summarizes annual consumption per cod for the different models.

Table 2. Annual consumption per cod (grams) in the Northeast Arctic cod stock in 1984 by agegroup and gastric evacuation model (1-6).

	Gastric evacuation model					
Age-group	SAN MOD	NOR MOD	NOR TEMP	ICE MOD	BOD MOD	BRO MOD
1	165	615	298	171	496	198
2	1202	2386	1156	883	1518	1361
3	2651	3551	1691	2163	2433	3096
4	4029	3660	1732	4050	2695	4678
5	7369	5605	2699	6859	4120	8517
6	11639	7363	3519	10601	5388	13096
7+	17032	8700	4189	14580	6855	18749

The differences between the six models are more pronounced here than for the total stock's consumption. The largest differences are observed in the youngest and oldest agegroups. For age 1 SANMOD gave the lowest annual consumption (165 g) and NORMOD the highest (615 g). In agegroup 2 and 3 NORMOD again came out highest and ICEMOD and NORTEMP lowest. For all older agegroups (4-7) NORTEMP gave the lowest consumption per cod, while BROMOD resulted in the highest consumption.

Table 3 gives the daily consumption per cod in percent of the body-weight (daily coefficient).

Table 3. Daily coefficient by agegroup and gastric evacuation model for Northeast Arctic cod in 1984.

	Gastric evacuation model					
Age-group	SAN MOD	NOR MOD	NOR TEMP	ICE MOD	BOD MOD	BRO MOD
1	1.8	6.7	3.3	1.9	5.4	2.2
2	1.6	3.1	1.5	1.1	2.0	1.8
3	1.4	1.8	1.1	1.1	1.3	1.6
4	0.9	0.8	0.4	0.9	0.6	1.1
5	1.1	0.8	0.4	1.0	0.6	1.2
6	1.1	0.7	0.3	1.0	0.5	1.2
7+	1.2	0.6	0.3	1.0	0.5	1.3

All models gave highest coefficients for the youngest agegroups and lowest for the older. In NORMOD the coefficient ranged from 6.7 to 0.6 (variation with a factor 11), while in SANMOD, ICEMOD and BROMOD the coefficients only ranged from about 2 to 1. Otherwise the differences between the models show the same trend as for the annual consumption per cod. In most models agegroup 4 came out with a low coefficient compared to the older agegroups.

Food conversion efficiency

Table 4 presents the annual weight increment in percent of the annual consumption (food conversion efficiency - FCE).

Table 4. Food conversion efficiency (%) by agegroup and gastric evacuation model in the Northeast Arctic cod stock in 1984.

	Gastric evacuation model					
Age-group	SAN MOD	NOR MOD	NOR TEMP	ICE MOD	BOD MOD	BRO MOD
1	59	16	33	57	20	49
2	21	10	22	28	16	18
3	14	11	22	18	16	12
4	13	14	29	13	19	11
5	14	19	39	15	25	12
6	11	17	36	12	23	10
7+	6	12	26	7	16	6

Here the picture is a little bit more complex. SANMOD, ICEMOD and BROMOD had the highest efficiency for the youngest agegroups and the lowest for the oldest fish. The FCE ranged from above 50% to below 10%. NORMOD, NORTEMP and BODMOD had less variance (from 9 to 14%) between the different agegroups, and age 5 and 6 came out with the highest FCEs. In all models age 5 had a higher FCE than age 4. All over NORMOD had the lowest FCE and NORTEMP the highest (opposite of consumption per cod).

DISCUSSION

The total consumption of capelin calculated by the different models seem to be reasonable compared to the stock estimate of 2.8 million tonnes autumn 1984 (Anon. 1985). The biomass of shrimp in the Barents Sea and Spitsbergen area in 1984 was estimated to about 475.000 tonnes (Hylen et al., 1984), and all the models have higher consumption estimates of shrimp. But it must be taken into account that also the production of the shrimp stock is available for predation, and that the biomass estimate only is an index for what is caught by bottom-trawl in a limited area and not represents the biomass of the total shrimp stock. But still the consumptions estimated by NORMOD and BROMOD seems a little too high. SANMOD seems to give the most correct relationship between consumption of capelin and of shrimp.

For the other prey species it is difficult to compare the consumption and stock estimates, because it is mainly young agegroups (0-3) that are preyed upon and the stock estimates of these agegroups are either not available or they are very uncertain. But in the work of Mehl (1989) where NORTEMP was used, several agegroups of herring, cod and haddock were found to be "overconsumed", either because the consumption was overestimated or the stock bimasses underestimated. For the other models this "overconsumption" will be even larger.

If the stomach content is very large, which may occur when the cod is feeding heavily on mature capelin, all models except ICEMOD may give an overestimate of the consumption. The reason for this is that the consumption in all models except ICEMOD is proportional to the average stomach content. There obviously is an upper limit on how much can be evacuated in grams per hour, and the calculated consumption rate may exceed this limit if the stomach content is very large. This may, at least in part, explain why the consumption of capelin gets too big in relation to the stock size, when one uses SANMOD on capelin in 1985 (see Mehl, 1989).

The consumption per cod calculated by SANMOD, ICEMOD and BROMOD seems to be too low for young cod(the FCE gets too high), while the result for the other three models seems reasonable. For older cod (4+), the consumption is similar for SANMOD, ICEMOD and BROMOD, while NORMOD and BODMOD give a somewhat lower consumption. NORTEMP undoubtedly gives too low consumption for older fish. In the Barents Sea, the diet of old cod differs less in prey species and size from the diet of young cod than in the North Sea, and the evacuation rate probably decreases less with increasing age.

The daily coefficients range from 1.8% (SANMOD) to 6.7% (NORMOD) for age 1 cod (12.7 cm) and from 0.3% (NORTEMP) to 1.3% (BRODMOD) for age 7 cod (85 cm). Daan (1973), using NORMOD, found a daily coefficient of 5.3% for 10 cm cod and 0.6% for 80 cm cod in the North Sea. Magnusson and Palsson (1989) estimated the daily coefficient to 0.6-1.5% for cod in Icelandic waters, using ICEMOD. For costal Norwegian cod, Kristiansen (1987) found values of 0.5 to 1.7% for 15-35 cm fish, and 0.6 to 1.9% for 35-50 cm fish, using the evacuation model of Jones (1974). In the Northwest Atlantic Durbin et al. (1980) estimated daily coefficients of 0.9 to 1.5% for cod > 30cm. In all these as well as in other investigations the lower and upper values for small and large cod seem to be reasonably well within the same range. But if one is interested in consumption rates to be used in multispecies models for management, this is not precise enough. The evacuation models and stomach data bases must be improved, and the resulting evacuation rates evaluated against other observations.

Bromley (1986) calculated the FCEs for the MSVPA predator species. He found efficiencies of 20-30% for young fish and of 7-9% for old mature fish. Except for agegroup 1, this is almost similar to the results of SANMOD, ICEMOD and BROMOD.

Jobling (1988) gives the food conversion efficiency expressed as kJ required per g gain. If the food is assumed to be capelin with a caloric content of 7.7 kJ/g, this gives FCEs ranging from 23.7% for 250g (age 2) cod to 14.2% for 2000g (age 5) cod at 4^0 C. Because the average caloric content of the food of cod in the Barents Sea is less, and wild fish has a lower FCE than fish in capture, this can be regarded as an upper limit for the FCE.

When comparing this to the results in Table 4, we see that NORTEMP gives a too high FCE. The other FCEs seem reasonable, except for age 1 for SANMOD, ICEMOD and BROMOD. For the oldest age groups, NORMOD and BODMOD seem to give a somewhat high FCE. The increase in FCE from age 4 to age 5 reflects the stomach data. This can be improved if we use age-length keys to age-distribute the fish sampled, instead of using the age reading only of the fish used for stomach sampling. We would then be able to use a larger material of age-readings, and thus get a more representative age distribution.

The consumption calculated by NORMOD, NORTEMP and BODMOD would be somewhat lower, especially for the younger age groups, if the mean length/weight during the year had been used instead of the length/weight at January 1. The reason for this is that the evacuation rate for these models for a given stomach content decreases with increasing fish size. The opposite is true for ICEMOD, but the effect here is smaller.

In ICEMOD, the consumption is proportional to the square root of the average stomach content. Magnusson and Palsson (1989) have found that $av(\sqrt{s}) = 0.84 \sqrt{(av(s))}$, where s is the stomach content. They have based this conversion factor on a few samples, as they usually do not record the stomach content of individual fish. We have calculated this conversion factor for each area/time/age group combination used in our consumption calculations. The result is shown in table 5.

Table 5. Conversion factor between the average of the square root of the stomach content and the square root of the average of the stomach content, by area, halfyear and age group, calculated from stomach samples of cod from the Barents Sea in 1984.

Age-group	1.halfyear Area		2.halfyear Area		
	II+IV	III+V	II+IV	III+V	VI+VII
1	.80	.63	.57	.62	.68
2	.85	.78	.70	.76	.81
3	.86	.77	.73	.75	.83
4	.92	.82	.75	.75	.83
5	.89	.86	.80	.65	.81
6	.84	.85	.74	.75	.85

We see that this conversion factor is very variable, and in most cases lower than 0.84. Thus, we would get a somewhat lower consumption if we had computed the average of the square root of the stomach content directly instead of using the square root of the average stomach content and the 0.84 conversion factor.

In dos Santos (1990) a more sophisticated model for stomach evacuation, which includes both temperature effects, prey species effects and meal size effects is presented. This work was finished so late that it was impossible for us to make use of it in this paper. A quick calculation shows, however, that the consumption calculated by this new model seems to be lower than the consumption calculated by SANMOD.

In both Magnusson and Palsson (1989) and Bogstad and Tjelmeland (1990), it was found that the acoustic abundance estimate of capelin, the consumption rate and the VPA estimate of cod did not match. In both cases, the capelin abundance estimate was scaled up in order to make the data source fit together. We have shown that the models for consumption used in these two papers give a similar result (somewhat higher consumption with SANMOD than with ICEMOD), which is reasonable. Using a model which gives a lower consumption, e.g. Santos' new model, would reduce or eliminate the need for scaling. However, SANMOD and ICEMOD gives reasonable FCEs for older fish.

When evaluating these calculations, one should always keep in mind that the representativity of the samples may be seriously questioned. This applies both to geographical distribution, pelagic/demersal samples and distribution in time. Aijad (1990) has demonstrated that for data sampled in the Barents Sea in February 1986 the average stomach content is significantly higher in pelagic samples than in demersal samples. Due to the difficulties of sampling cod with a pelagic trawl, the cod residing in the pelagic layer is usually underrepresented in the stomach samples. This will lead to an underestimate of the average stomach content, and hence the consumption, for all models.

CONCLUSIONS

NORTEMP gives too low consumption and too high FCE, and this shows that it is not valid to transport a temperature relationship between very different areas or areas with a large difference in temperature.

The consumption for the youngest age-groups is too low in some models because these age-groups have not been included in the feeding experiments. In other models, there may be too high consumption for the older age groups, because these models are based on stomach data from areas with other prey composition than in the Barents Sea.

It is very important with evacuation models as accurate as possible. A variation in FCE between 10% and 20% means a variation in consumption of 100%, and this is too much when the consumption of some important prey species are of the same order of magnitude as the catch. The evacuation rates must be based on experiments with fish of different sizes from the actual predator stocks, fed natural prey at the actual temperatures. Different meal sizes and combined meals (more than one prey species at the same time) should be included. The results should be measured against upper limit FCEs from other experiments.

None of the six models are totaly satisfactory in this respect, but SANMOD, with the above mentioned exeptions, seems to meet these requirements best for cod in the Barents Sea.

REFERENCES

Aijad, A.M. 1990. Variabilities in stomach contents of cod, collected by demersal and pelagic trawl in the southern part of the Barents Sea. ICES CM 1990/G:3.

Alvarez, J., and Tjelmeland, S. 1989. Multspec og oseanografi. IMR internal documentation.

Anon., 1985. Report of the Atlanto-Scandian Herring and Capelin Working Group. ICES Headquarters, 29 October to 1 November 1984. ICES CM 1985/Assess: 4.

Anon., 1987. Report of the ad hoc Multispecies Assessment Working Group. Copenhagen, 12-18 November 1986. ICES CM 1987/Assess: 9.

Anon., 1990. Report of the Arctic Fisheries Working Group. Copenhagen, 19-28 September 1989. ICES CM 1990/Assess: 4.

Bogstad, B., and Tjelmeland, S. 1990. Estimation of predation mortalities on capelin using a cod-capelin model for the Barents Sea. ICES CM 1990/H: 16.

Bromley, P.J. 1986. An appraisal of the MSVPA feeding data. Discussion document for 1986, North Sea MSVPA Working Group. Unpubl., 11pp.

Bromley, P. J. 1989. Gastric evacuation, feeding and growth in cod (Gadus morhua L.). ICES 1989 MSM Symp., Paper No. 9.

Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, Gadus morhua. Neth. J. Sea. Res., 6(4): 479-517.

dos Santos, J. 1990. Aspects of the eco-physiology of predation in Atlantic cod (Gadus morhua L.) Dr. scient thesis, University of Tromsø, 1990. 116pp.

Durbin, E., Durbin, A., Langton, R. Bowman, R., and Grosslein, M. 1980. Analysis of stomach contents of Atlantic cod (Gadus morhua) and silver hake (Merluccius bilinearis) for the estimation of daily rations. ICES CM 1980/L: 60.

Hylen, A., Loeng, H., Mehl, S., and Nedreaas, K. 1989. Estimates of stock size of cod, haddock, redfish and Greenland halibut in the Barents Sea and the Svalbard area autumn 1988. ICES CM 1989/G: 39.

Hylen, A., Tveranger, B., and Øynes, P. 1984. Norwegian investigations on the deep sea shrimp (Pandalus borealis) in the Barents Sea in April - May 1984 and in the Spitsbergen area in July - August 1984. ICES CM 1984/K: 21.

Jakobsen, T., Mehl, S., Nakken, O., Nedreaas, K., and Sunnanå, K. 1989. Estimates of stock size of Northeast Arctic cod and haddock, Sebastes mentella and Sebastes marinus from survey data, winter 1989. ICES CM 1989/G: 42.

Jobling, M. 1988. A Review of the Physiological and Nutritional Energetics of Cod, Gadus morhua L., with Particular Reference to Growth under Farmed Conditions. Aquaculture 70, 1-19.

Jones, R. 1974. The rate of elimination of food from the stomach of haddock (Melanogrammus aeglefinnus), cod (Gadus morhua) and whiting (Merlangius merlangus). J. Cons. int. Explor. Mer, 35(3): 225-243.

Kristiansen, T. S. 1987. Vekst og ernæring til utsatt oppdrettet torskeyngel og vill torsk (Gadus morhua L.) i Heimarkspollen, Austevoll. Thesis, University of Bergen, 1987. 134p.

Magnusson, K. G., and Palsson, O. K. 1989. Trophic ecological relationships of Icelandic cod. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 188: 206-224.

Magnusson, K. G., and Palsson, O. K. 1990. Predator-prey interactions of cod and capelin in Icelandic waters. Rapp. P.-v. Reun. Cons. int. Explor. Mer, xxx: 000-000.

Mehl, S. 1986. Stomach contents of Northast Arctic cod and possible changes in the diet the last years. ICES CM 1986/G: 29.

Mehl, S. 1989. The Northeast Arctic cod stock's consumption of commercially exploited prey species in 1984-1986. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 188:185-205.

Mehl, S., and Sunnanå, K. 1990. Changes in growth of Northeast Arctic cod in relation to food consumption in 1984-1988. Rapp. P.-v. Reun. Cons. int. Explor. Mer, xx: 000-000.

Ursin, E., Pennington, M., Cohen, E. B., and Grosslein, M. D. 1984. Stomach evacuation rates of Atlantic cod (Gadus morhua) estimated from stomach contents and growth rates. ICES CM 1984/G: 43.