

Predation rates by North Sea cod (*Gadus morhua*) – predictions from models on gastric evacuation and bioenergetics

Sture Hansson, Lars G. Rudstam, James F. Kitchell,
Mikael Hildén, Barry L. Johnson, and Paul E. Peppard



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We compared four different methods for estimating predation rates by North Sea cod (*Gadus morhua*). Three estimates, based on gastric evacuation rates, came from an ICES multispecies working group and the fourth from a bioenergetics model. The bioenergetics model was developed from a review of literature on cod physiology. The three gastric evacuation rate models produced very different prey consumption estimates for small (<0.5 kg) and large (>2 kg) fish. For most size and age classes, the bioenergetics model predicted food consumption rates intermediate to those predicted by the gastric evacuation models.

Using the standard ICES model and the average population abundance and age structure for 1974–1989, annual prey consumption by the North Sea cod population (age ≥ 1) was 840 kilotons. The other two evacuation rate models produced estimates of 1020 and 1640 kilotons, respectively. The bioenergetics model estimate was 1420 kilotons. The major differences between models were due to consumption rate estimates for younger age groups of cod.

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S. Hansson: Department of Systems Ecology and Center for Marine Research, Stockholm University, S-106 91 Stockholm, Sweden. L. G. Rudstam: Cornell University Biological Field Station, Department of Natural Resources, 900 Shackleton Point Road, Bridgeport, NY 13030-9750, USA. J. F. Kitchell and P. E. Peppard: Center for Limnology, University of Wisconsin, Madison, WI 53706, USA. M. Hildén: National Board of Waters and the Environment, PO Box 250, SF-00101 Helsinki, Finland. B. L. Johnson: National Biological Service, Upper Mississippi Science Center, 2630 Fanta Reed Road, Post Office Box 818, LaCross, WI 54601-0818, USA.

Introduction

The potential for strong predator–prey interactions within commercially exploited fish populations precludes the management of these fisheries on a species-by-species basis (Daan, 1973). The International Council for the Exploration of the Sea (ICES) is therefore developing and using multi-species virtual population analysis (MSVPA, Daan, 1987; Hilborn and Walters, 1992) to account for both fishing mortality and mortality through predation.

Cod (*Gadus morhua* L.) is a major piscivore in the North Sea and has the potential for imposing significant mortality on commercial stocks of clupeid, gadoid, and flatfish species (Daan, 1973). Currently, MSVPA methods are used to estimate food consumption and predation by cod, combining diet analysis and gastric

evacuation rate models. The choice of evacuation model is crucial for predicting food consumption. An ICES working group (Anon., 1991) compared food consumption computed using their standard gastric evacuation rate model (based on Daan, 1973) and two alternative models (dos Santos, 1990; Bromley, 1991). The three models produced differences of up to 200% in estimates of total food consumption by the North Sea cod population. An alternative approach to the estimation of consumption is bioenergetics modelling based on the basic physiological principles of energy partitioning.

With bioenergetics models, food consumption is estimated from individual fish growth rates. Several models have been developed for marine species, including cod (Ursin, 1979; Kerr, 1982). However, such models have been used mainly in studies of freshwater fish (e.g. Kitchell *et al.*, 1977; Helminen *et al.*, 1990; Hansen *et al.*,

1993). In August 1991, a workshop on fish bioenergetics was held at Stockholm University, Sweden (Hildén, 1992). A major goal of this workshop was to develop parameters for a cod bioenergetics model and apply the model to cod populations in the North, Barents, and Baltic Seas. In this paper we present a refined version of the bioenergetics model developed during this workshop. We compare the bioenergetics model predictions of food consumption by individual cod with predictions based on the three gastric evacuation rate models discussed above. The analysis is extended to the North Sea cod population by including life table information, and the age-specific differences in estimated food consumption are elevated at the population level.

Methods

Consumption estimates based on gastric evacuation rates

Various methods have been developed to estimate *in situ* food consumption by fishes based upon the volume of the stomach contents and gastric evacuation rate (Elliott and Persson, 1978; Jobling, 1986; Persson, 1986). In the ICES studies cited in this paper, consumption was estimated from data on *in situ* gut fullness in North Sea cod combined with gastric evacuation rate models derived from laboratory studies. The consumption rates, referred to as the ICES standard estimates, were obtained by using the gastric evacuation rate model developed by Daan (1973). The two other estimates were derived using evacuation models described by dos Santos (1990) and Bromley (1991) and are referred to by the names of these authors.

The data we use on food consumption, estimated from gastric evacuation models, are taken from a publication by an ICES working group (Anon, 1991). These estimates are based on temperatures and growth data summarized in Table 1, where cod population abundances are also given.

Consumption estimates based on a bioenergetics model

The bioenergetics analyses were performed with a PC/DOS program developed by Hewett and Johnson (1992, available at cost from the Wisconsin Sea Grant Institute, University of Wisconsin, Madison, Wisconsin 53706, USA). In this bioenergetics model, consumption is calculated as:

$$\text{Consumption} = \text{Metabolic loss} + \text{Waste loss} + \text{Growth}$$

or

$$C = (R + \text{SDA}) + (F + E) + (S + G)$$

Table I. Input data used to estimate cod food consumption. Weights are from Daan (1974, 1975) and numbers are given as estimated average values for July 1, 1974–1989 (Anon., 1991). Temperatures are those used by ICES multispecies working groups and follow Daan (1989; N. Daan, pers. comm.).

Age (year)	Wet weight (gram)	Numbers (millions)	Quarter of the year	Temperature (°C)
1	32	273	1st	6
2	466	84.3	2nd	7
3	1856	24.8	3rd	9
4	3980	8.86	4th	8
5	5990	3.56		
6	8212	1.44		
7	9420	0.60		
8	10 622	0.27		
9	11 543	0.12		
10	12 235	0.079		

where: C=consumption, R=respiration, SDA=specific dynamic action, F=egestion, E=excretion, S=somatic growth and G=gonad production (Kitchell *et al.*, 1977).

The program uses equations for maximum consumption and respiration that are functions of fish weight and temperature. Consumption is estimated by calculating the proportion of maximum consumption that results in the observed growth rates. In addition to the physiological parameters and somatic growth, the model requires information about the caloric content of predator and prey, diet composition, temperature, and weight loss at spawning. An initial version of the model was developed during the fish bioenergetics workshop in 1991 (Hildén, 1992). We refined that model by reviewing more recent literature on cod energetics and by fitting equations to additional data for respiration and maximum consumption rates. Values for the model parameters, the assumptions involved, and the sources are summarized in Table 2.

To test the model, predicted growth from the bioenergetics model was compared with observed growth in experiments where cod were fed known quantities of either moist pellets or minced capelin (*Mallotus villosus*) (Braaten, 1984). Braaten's data are particularly suitable for this comparison because he measured the caloric content in both the fish and the prey. We used information from Braaten (1984) solely for development of the maximum consumption equation and this equation is not used when we compare growth of cod on known ratios with predictions made by the model. Thus, the growth observations of Braaten (1984) and the predictions from the model are independent.

Braaten's (1984) data and model predictions are presented in Figure 1. Regression analysis of predicted versus observed growth rates yielded an intercept not significantly different from zero and a slope not

Table 2. Definitions and parameters used in the bioenergetics models. The units are not consistently SI-units, but those used in Hewett and Johnson (1992). All weights, but for R, are wet weights. For details on how to run the model, see Hewett and Johnson (1992).

Symbol	Description	Value
C	Consumption ($\text{g g}^{-1} \text{d}^{-1}$)	—
E	Excretion ($\text{g g}^{-1} \text{d}^{-1}$)	—
F	Egestion ($\text{g g}^{-1} \text{d}^{-1}$)	—
F(T)	Temperature dependence function used in estimation of food consumption and metabolism	—
R	Respiration ($\text{g O}_2 \text{g}^{-1} \text{d}^{-1}$)	—
SDA	Specific dynamic action ($\text{g g}^{-1} \text{d}^{-1}$)	—
T	Temperature ($^{\circ}\text{C}$)	—
W	Fish weight (g)	—
Temperature dependence function: $F(T) = V^{X*} e^{(X*(1-V))}$		
V	$V = (T_{\text{max}} - T) * (T_{\text{max}} - T_{\text{opt}})^{-1}$	—
X	$X = (Z^{Z*} * (1 + (1 + 40/Y)^{0.5})^2) * 400^{-1}$	—
Y	$Y = \ln Q * (T_{\text{max}} - T_{\text{opt}} + 2)$	—
Z	$Z = \ln Q * (T_{\text{max}} - T_{\text{opt}})$	—
T_{max}	Different values for consumption and metabolism, given below	—
T_{opt}	Different values for consumption and metabolism, given below	—
Q	Different values for consumption and metabolism, given below	—
Consumption: $C = P * a * W^b * F(T)$		
P	Fitted coefficient	—
a	Intercept ($\text{g g}^{-1} \text{d}^{-1}$)	0.099 ^a
b	Weight exponent for consumption	-0.195 ^a
T_{opt}	Optimum temperature ($^{\circ}\text{C}$)	13.7 ^{a,b}
T_{max}	Maximum temperature ($^{\circ}\text{C}$)	21 ^c
Q	Slope for temperature dependence	2.41 ^a
Metabolism: $R = \alpha * W^{\beta} * F(T) * \text{ACT}$; $\text{SDA} = \text{sda} * (C - F)$		
α	Intercept ($\text{g O}_2 \text{g}^{-1} \text{d}^{-1}$)	0.0080 ^d
β	Weight exponent for respiration	-0.172 ^d
T_{opt}	Optimum temperature ($^{\circ}\text{C}$)	21 ^d
T_{max}	Maximum temperature ($^{\circ}\text{C}$)	24 ^d
Q	Slope for temperature dependence	1.88 ^d
ACT	Coefficient, activity multiplier	1.25 ^e
sda	Coefficient, specific dynamic action	0.17 ^f
Egestion and excretion: $F = f * C$; $E = \varepsilon * (C - F)$		
f	Proportion of consumed food egested	0.17 ^g
ε	Proportion of assimilated food excreted	0.09 ^h

^aJobling (1982, 1988) summarized experiments on cod fed at or near maximum rations (temperature range 3–16°C, size range 35–750 g) and we used these data to fit the equation $C_{\text{max}} = a W^b F(T)$ using non-linear least squares regression (Wilkinson, 1987; $n=48$, $r^2=0.94$). C_{max} is maximum consumption in $\text{g g}^{-1} \text{d}^{-1}$, W is wet weight in g, and F(T) is a dome shaped function of temperature that rises to a maximum of 1 at an optimum temperature. The equations are listed in the table. Values for a, b, T_{opt} and Q are from this fit to data.

^bThis value for T_{opt} is close to the final temperature preferendum of cod (13.5°C) computed by Jobling (1988).

^cTyler (1970) observed that cod ceased feeding at 21°C.

^dData on routine respiration (R_r , $\text{O}_2 \text{g}^{-1} \text{d}^{-1}$) from Saunders (1963) and Soofiani and Hawkins (1982) were used to fit the equation $R_r = \alpha * W^{\beta} * F(T)$ (W is weight in g, F(T) is a temperature function, α and β are constants). The “optimum” temperature was chosen to be 21°C (the temperature at which cod first ceases feeding; Tyler, 1970) and the maximum temperature was chosen to be 24°C (the highest temperature tolerated by cod; McKenzie, 1934). The resulting model showed an excellent fit to measured routine respiration ($n=78$, $r^2=0.99$). To convert respiration data to calories we assumed 1 g $\text{O}_2 = 3240$ cal.

^eFrom the effects of swimming on O_2 consumption (Soofiani and Priede, 1985), assuming an average swimming speed of 0.28 body length sec^{-1} (Jones, 1978), we estimated ACT to 1.25 (active respiration assumed to be 1.25 times higher than routine respiration, $R = R_r * 1.25$). This might be an overestimation since Smith (in Soofiani and Priede, 1985) gives cod a swimming speed of only 0.09 body lengths sec^{-1} . Soofiani and Hawkins (1985), however, caution that brief episodes in life, such as attack or escape manoeuvres, may make up a significant proportion of a fishes energy budget.

^fApparent specific dynamic action (SDA) is estimated to be 15% of ingested food for cod per Kerr (1982). This corresponds to 18% of assimilated (consumed–egested) rations. Ursin (1979) suggests an SDA of 32% of consumed food for fishes. Soofiani and Hawkins (1985), reporting on juvenile cod, give average values for SDA of 11.9% to 17.1% in different temperature (7–18°C). These average to 14.1% of ingested food or 17% of assimilated energy. Holdway and Beamish (1984) calculate SDA as 24.9% of assimilated energy for Atlantic cod. We will use a value of 17% of assimilated energy for SDA.

^gLiterature values for egestion by fish generally vary within the range of 2–31% of consumed energy (Elliott, 1979; Soofiani and Hawkins, 1985). Waiwood and Majikowski (1984) and Brett and Groves (1979) suggest fish fecal energy losses of 20%. Holdway and Beamish (1984) estimate egestion to be 16.6% of consumption at 5°C and 8°C for Atlantic cod. We assume egestion to be 17% of ingested energy.

^hHoldway and Beamish (1984) calculate excretion to be 6.6% of ingested energy at 5°C and 6.7% at 8°C for cod. We assume a constant rate of 7% of ingested energy which is equivalent to 9% of assimilated (consumed–egested) energy.

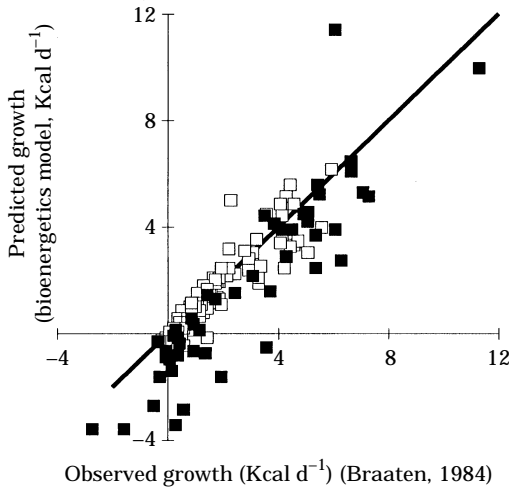


Figure 1. Observed growth of cod (Braaten, 1984), and growth of cod consuming equal rations as estimated from the bioenergetics model developed in this paper. Regression analysis revealed no significant differences from the 1:1 line. Food was (□) moist pellets, (■) capelin.

significantly different from 1.0. The slopes were also not significantly different from 1.0 when separate analyses were made for cod fed on moist pellets or minced capelin. However, for cod fed on capelin, the model predicted slightly lower growth rates than those observed. Nevertheless, this comparison indicates that the model gives reasonable predictions of cod growth rates when consumption is known, and should also serve for the estimation of food consumption if growth is known.

To apply the bioenergetics model on a fish population, data on abundance, age structure, growth, temperature, diet, and energy densities are needed. Growth rates, population abundances and temperatures are in Table 1. We further assumed that spawning losses were

12% of body weight for age 3 and older fish, that cod energy density is 1000 cal g^{-1} wet weight (Daan, 1975) and that prey can be divided into three categories (fat fish: 1400 cal g^{-1} , lean fish: 1000 cal g^{-1} , and others: 900 cal g^{-1}). Diets (Fig. 2) were taken from the compilation by Daan (1989).

Results

Comparisons between food consumption models

Individual food consumption

There are some very clear differences in consumption estimates for the three gastric evacuation rate methods (Fig. 3). Of all models, the ICES standard model generally predicts the lowest food consumption. For large cod, dos Santos' model predicts individual consumption rates that are 2–3 times higher than the ICES standard model. For age 1 cod, Bromley's model predicts a food consumption rate that is 3 times that predicted by the ICES standard model. The bioenergetics model consistently predicts consumptions higher than the standard ICES model. However, as discussed above, the bioenergetics model successfully predicts the growth of cod feeding on pellets, but over-estimates consumption when the cod are fed on capelin (Braaten, 1984). This indicates that the bioenergetics model may somewhat overestimate consumption.

To evaluate the predictions from the four models, growth efficiencies were estimated using:

$$\left(100 \times \frac{\text{growth in wet weight}}{\text{wet weight of consumed food}} \right)$$

For young, well fed piscivorous fish, this efficiency is generally between 20% and 30% (Braaten, 1984; Brett and Groves, 1979; Soofiani and Hawkins, 1985), decreasing with fish size (Ney, 1990). This general pattern is reflected in the growth efficiencies derived by the

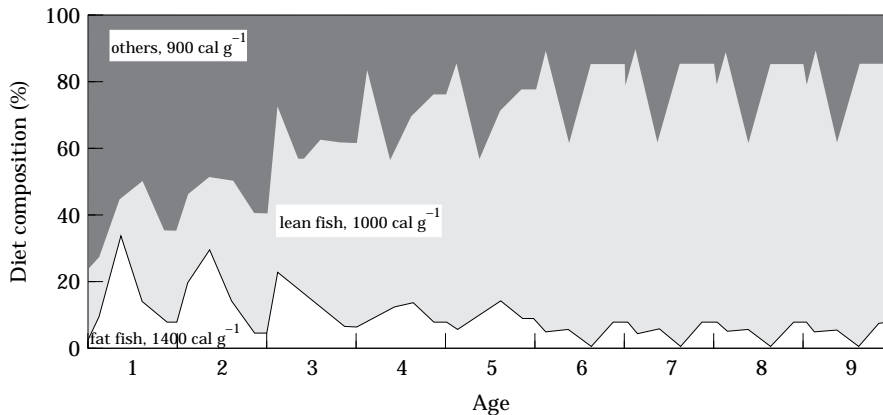


Figure 2. The diet of North Sea cod, as derived from Daan (1989). This diet composition was used in the bioenergetics model (energy densities are given on a wet weight basis). □=fat fish (1400 cal g^{-1}); □=lean fish (1000 cal g^{-1}); □=others (900 cal g^{-1}).

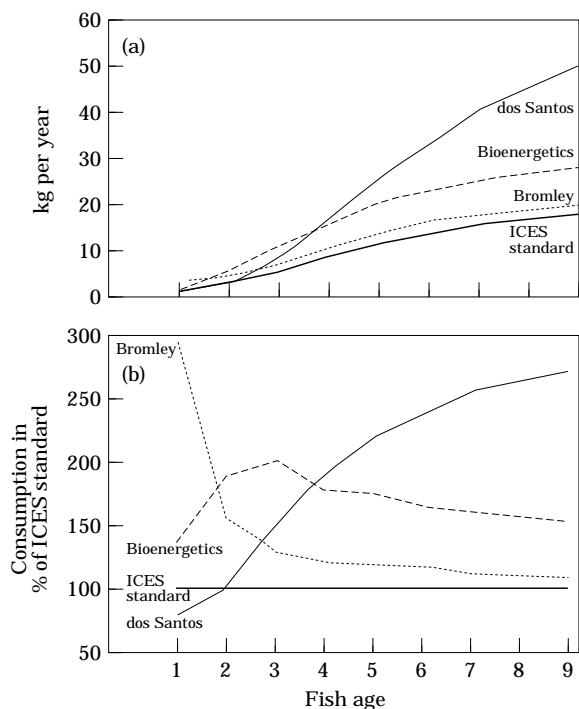


Figure 3. Comparisons of individual food consumption estimates for North Sea cod, derived from the four food consumption rate models. (a) Consumption in wet weight (kg) at different age, (b) annual consumptions relative to that estimated by the ICES standard method, which was set to 100%.

bioenergetics model (Fig. 4). The low food consumption rates estimated with the ICES standard and the dos Santos models for young fish (age 1–2) result in unlikely high growth efficiencies (>40%). Estimates from Bromley’s model are in the range of often reported growth efficiencies, but the low value estimated for age 1 (13%), with a drastic increase to 30% for cod age 2, could indicate model errors. Predictions from the bioenergetics model are all in the range of expected growth efficiencies, 30% for age 1 fish and then gradually decreasing. Our results are very similar to those presented by Daan (1975), based on his 1993 publication, which is actually one of the bases of the ICES standard model. This means that Daan’s original model will also produce predictions very similar to our bioenergetics model in other respects discussed in this paper. For comparison, data from Daan (1975) are included in Figure 4.

The cod used in the experiments on which the gastric evacuation rate models are based, were generally of intermediate size (0.5–2 kg). For that size of fish (age 2–3 yr), the three evacuation rate models gave relatively similar results. Major differences between models occurred mainly outside this size range and could consequently result from extrapolation errors. Experimental studies that focused on large and small fish could thus help resolve these conflicting results. For the present, however, we consider the bioenergetics model a good and flexible alternative for generation of food consumption estimates needed in MSVPA. The bioenergetics

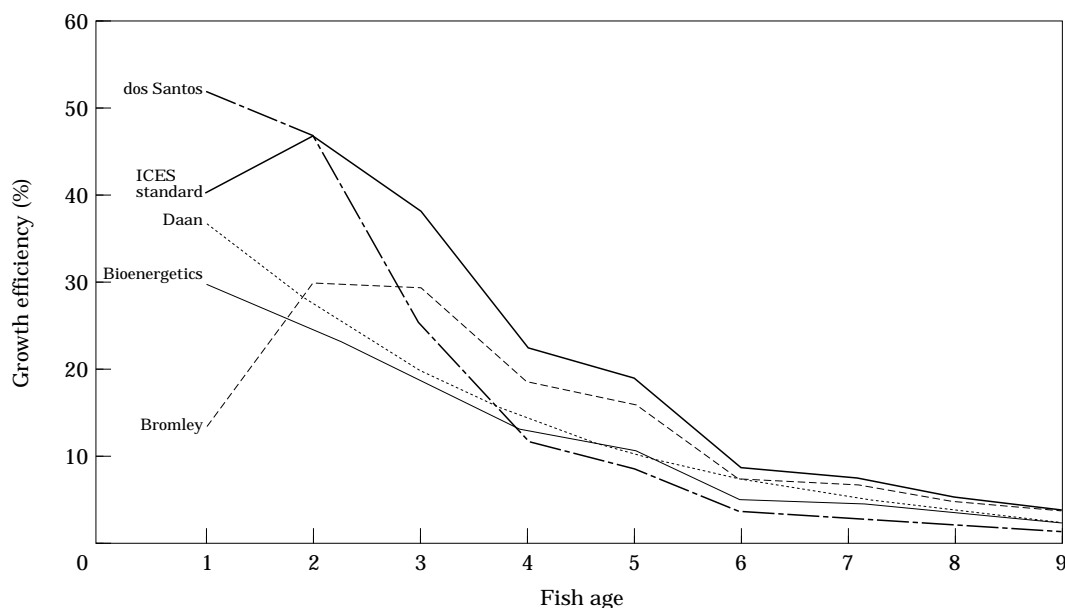


Figure 4. Growth efficiencies ($100 \times$ growth in wet weight/wet weight of consumed food) of North Sea cod, estimated from data generated by the four food consumption rate models and as given by Daan (1975).

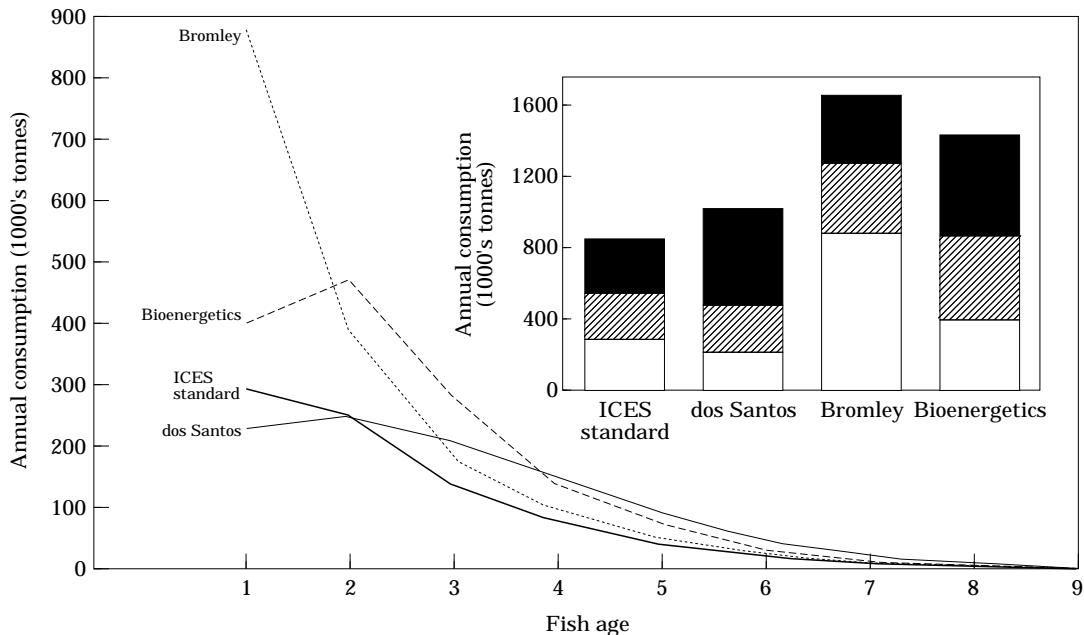


Figure 5. Estimates of annual population food consumption (in wet weights) by North Sea cod, derived from the four food consumption rate models. The main panel shows consumption by age class and the inserted panel, the total population consumption. Insert: □=age 1; ▨=age 2; ■=older.

model produces food consumption estimates that are within the range of those estimated by the three gastric evacuation rate models and is least likely to be biased due to extrapolation. Using the bioenergetics model, it is also easy to study possible effects of different changes in the environment or in growth or diet of cod (see section on analysing scenarios).

Population food consumption

The differences among the models with regard to consumption by young fish are particularly important, because those estimates are multiplied by fish abundance to estimate consumption by the entire population. Regardless of the food consumption model used, age groups 1 and 2 clearly consume more food than any other single age group (Fig. 5). The estimated annual food consumptions by age 1 fish varies by a factor of 3 between the lowest estimates (ICES standard model and dos Santos model) and the highest estimates (the Bromley model). The estimated proportion of food consumed by young fish, as compared with the consumption by older fish, varies considerably between the models. Based on the dos Santos model, age 1 cod accounts for 22% of the total population food consumption, while the corresponding value for Bromley's model is 54%. The comparatively high individual food consumption by old fish estimated from the dos Santos model (Fig. 3), does not substantially influence the total population consumption rates (Fig. 5).

The estimates of total population food consumption vary by a factor of 2 between the lowest estimate (840 kilotons, ICES standard model) and the highest (1640 kilotons, the Bromley model, Fig. 5). With the dos Santos model, the value is 1020 kilotons, whereas the bioenergetics model predicts a population food consumption (1420 kilotons) within the range predicted by the three gastric evacuation models. The significance of young fish for the predation pressure, as shown above, can be further stressed by recalling that food consumption by age 0 fish is not included in this analysis. From a management perspective, however, analysis based on total biomass consumed could be misleading. The size of prey eaten generally increases with predator size. Prey eaten by large cod are more likely to be the fishes that are of direct interest to commercial fisheries (Daan, 1987). Thus, when incorporating predation rate estimates into MSVPA models, consumption by large cod – and the differences between models in predicting consumption rates – will be more important than suggested by the result presented in Figure 5.

Analysing scenarios

Using the bioenergetics model, it is easy to test consequences of different assumptions, e.g. what effects on growth rate could be expected from changes in temperature or in prey species composition. Three examples of such analyses are given below. These kinds of

quantitative prediction are not more accurate than allowed by model assumptions, which of course can be improved by proper studies. However, already at this stage it is reasonable to assume that the model can be used to determine the relative significance of different changes in the cod's environment. Such analyses could be included in MSVPA, as food consumption is reflected in predation rates and, eventually, in the number of recruits. Errors in consumption rates could thus lead to flawed perceptions of the number of recruits, and major changes in food consumption rates can alter the perception of the dynamics of the ecosystem and may also affect management advice.

Importance of correct temperature data when estimating food consumption

Effects on food consumption by differences in ambient temperatures experienced by different age classes of cod have been discussed among North Sea fisheries managers (N. Daan, pers. comm.). To illustrate how this can be addressed by the bioenergetics model, we estimate an alternative food consumption for cod of age 1 and 2, assuming that they occur in 14°C water during the third quarter of the year, instead of 9°C as used in the standard run. For these age classes, the model predicts that the increased temperature increases annual food consumption by 5%. Thus, a substantial difference in the temperature assumption has a much smaller effect on total consumption than the choice between alternative models.

Significance of prey species composition on cod growth

The North Sea fish community structure has varied considerably over the last decades, with a nineteen-fold change in herring biomasses over the period 1974–89 (Anon., 1991). The diet of cod was probably influenced by this variation, resulting in changes in prey energy densities over time. If we assume that all fish eaten by cod age 5 were high energy density species (1400 cal g⁻¹), the observed growth suggests an annual fish consumption of 11.8 kg. If only low energy density species (1000 cal g⁻¹) were eaten, the corresponding figure would be 15.3 kg. Assuming a shift in diet from high to low energy density prey, but a fixed consumption of 11.8 kg yr⁻¹, growth would be reduced by ≈85% (from 2.2 to 0.4 kg yr⁻¹). This, and the example below, shows that changes in growth rate cannot be directly converted to changes in consumption.

Non-linear relationships between food consumption and growth

In assessing effects of predation, changes in the predators growth rate imply changes in its consumption rate. The relationship between growth rate and food consumption is, however, not constant. Fish have maintenance energy costs even when they do not grow. When

these maintenance costs are covered, a small increase in food consumption can result in a relatively substantial increase in growth. To illustrate this, assume that the annual growth of cod age 5 increases by 10% (from 2222 to 2444 g yr⁻¹). Intuitively, one could expect that this should reflect a 10% increase in food consumption, but as maintenance is covered already, the bioenergetics model predicts an increased food consumption of only 2.5% (from 20.7 to 21.2 kg).

Conclusion

The four methods compared predict considerably different food consumption rates. The standard model used by ICES consistently produces low rates, and for young cod (age 1), its prediction is unrealistically low. A second gastric evacuation-based model (based on Bromley, 1991) predicts annual consumption of age 1 cod that is 300% higher than that predicted by the ICES standard model. The third evacuation-based model (dos Santos, 1990) yields consumption rates of older fish (age 5) that are twice those of the other models. For all size and age groups, the bioenergetics model predicts rates intermediate to those of the three evacuation rate models. In other words, the bioenergetics model does not appear to suffer from the extrapolation errors found in other approaches.

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