

Eco-physiological approach for estimating the food  
consumption of cod and the maximal possible contribution  
of various fish species in the diet of the cod population  
inhabiting the southern Gulf of St. Lawrence

by

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Abstract

This paper documents an attempt to evaluate the food biomass consumed by the cod population inhabiting the southern Gulf of St. Lawrence (NAFO Subarea 4T) during 1978. For this purpose, the relatively well verified Ursin fish growth theory relating food consumption to growth is employed. Using (i) the empirical cod growth data for area 4T in 1977-1978, (ii) the values of required physiological parameters for cod, evaluated on the basis of laboratory studies, and (iii) the numbers-at-age of cod for this area in 1978, the food biomass consumed by the cod population is estimated to be equal to 0.705 million tons. Sensitivity of this estimate to changes in the input parameters is examined. Values of some other physiological parameters for cod are presented. Utilizing (i) the calculated value of food biomass consumed by the cod population, (ii) the instantaneous rates of natural mortality, and the numbers-at-age for various potential fish prey species, the maximal possible contribution of each fish species in the cod diet is estimated to be equal to 14%, 2.8%, 0.2% and 4.3% for capelin, plaice, herring and young cod, respectively. These results are discussed in the light of knowledge concerning this ecosystem. Further application possibilities of the physiological approach for examining properties of marine ecosystems are discussed.

## Résumé

L'article qui suit décrit l'étude entreprise en vue d'évaluer la biomasse consommée par la population de morues franches du golfe Saint-Laurent méridional (division 4T de l'OPANO) en 1978. A cette fin, nous avons utilisé la théorie d'Ursin, assez bien vérifiée, de la croissance des poissons. Cette théorie établit la relation entre consommation de nourriture et croissance. A l'aide (i) des données empiriques recueillies en 1977-1978 dans la division 4T sur la croissance de la morue, (ii) des valeurs des paramètres physiologiques nécessaires à la morue, évalués à la suite d'études en laboratoire et (iii) des nombres à un âge donné de morues dans cette région en 1978, nous avons estimé à 0.705 millions de tonnes la biomasse consommée par la morue. Nous examinons la sensibilité de cette estimation aux changements dans les paramètres d'entrée. Les valeurs de certains autres paramètres sont données. A partir de (i) la valeur calculée de la biomasse alimentaire consommée par la population de morues et (ii) les taux instantanés de mortalité naturelle et les nombres à un âge donné de poissons proies possibles, nous estimons que la contribution maximale possible de ces poissons au régime alimentaire de la morue est de 14%, 2.8%, 0.2% et 4.3% pour le capelan, la plie canadienne, le hareng et les jeunes morues respectivement. Nous analysons ces résultats en regard de nos connaissances de cet écosystème. D'autres applications possibles de l'approche physiologique à l'examen des propriétés d'écosystèmes marins sont examinées.

## INTRODUCTION

In recent years, many scientists (e.g. Larkin 1963, 1978; Riffenburgh 1971; Agger and Nielson 1972; Andersen and Ursin 1975a, b, 1977; Parrish 1975; Horwood 1976; Lett and Kohler 1976; Majkowski 1975, 1977; Mandecki 1976; Lett 1978) have come to realize that the single-species approach can lead to an unrealistic description of the dynamics of fish populations. Interactions between species can influence the fish population dynamics to a large extent, and therefore, cannot be ignored.

One of the possibly important interactions among fish species is predation. Cod appears to be a key fish predator in southern Gulf of St. Lawrence, NAFO area 4T, (Powles 1958; Kohler and Fitzgerald 1969). This paper documents an attempt to evaluate the food biomass consumed by the cod population inhabiting area 4T during the year 1978. Then, the maximal possible contribution of each fish species appearing in the cod diet is estimated on the basis of the instantaneous rates of natural mortality and the numbers-at-age for potential fish prey species.

### Physiology of Cod Feeding

Empirical data concerning cod feeding are generally fragmentary. Recent studies indicate that the cod feeding rate and composition of its food is strongly conditioned by cod size, the relative abundance of cod and their food resources, distribution, season and temperature (Powles 1958; Kohler 1964; Ursin 1967, 1973, 1979; Kohler and Fitzgerald 1969; Daan 1973; Andersen and Ursin 1977; Minet and Perodou 1978; Waiwood 1978). Evaluation of the cod food ration in nature on the basis of turnover of gut contents (see review Conover 1978) is extremely difficult (see discussion in Beamish and Dickie 1967; Mann 1978). Since the natural conditions usually differ from those in the laboratory, the direct use of experimental results, even if they are complete, is questionable. Therefore, the relatively well verified Ursin (1967, 1979; Andersen et al. 1973; Andersen and Ursin 1977) fish growth theory relating food consumption to growth is employed.

### Outline of the Ursin Growth Theory

A full description of this theory and its empirical support has been presented elsewhere (Ursin 1967, 1979; Andersen et al. 1973, Andersen and Ursin 1977), hence only a brief description is included here. The fish growth equation derived from the theory has the following form:

$$(1) \quad \frac{dw_i}{dt} = \beta_i (1 - \alpha_i) \frac{dR_i}{dt} - k_i w_i^{n_i} - e_i(t, w_i)$$

where  $w_i$  is the body weight (g),  $t$  is time (years),  $\alpha_i$  is the fraction of assimilated food lost in feeding catabolism,  $\beta_i$  is the assimilated fraction of food eaten by a fish,  $\frac{dR_i}{dt}$  is the instantaneous rate of food consumption (g/years);  $k_i$  is the coefficient of the term for fasting catabolism ( $g^{1-n_i}$ /years),  $n_i$  is the power value of the term for fasting catabolism,  $e_i$  is the instantaneous rate of spawning (g/years), subscript  $i$  identifies parameters and variables with age and year. The above equation can be presented in the form:

$$(2) \quad \frac{dw_i}{dt} = \beta_i(1-\alpha_i)\frac{dR'_i}{dt} - k_i w_i^{n_i}$$

where

$$(3) \quad \frac{dR'_i}{dt} = \frac{dR_i}{dt} - \frac{e_i(t, w)}{\beta_i(1-\alpha_i)}$$

The rate  $\frac{dR'_i}{dt}$  can be interpreted as the consumption rate of food utilized

for somatic growth and maintenance expenses. It has been demonstrated for various animal species that the instantaneous rate of food consumption can be approximated by a power function of the animal's body weight (see review Majkowski and Uchmański 1980). This is particularly valid in the case of fish, for which Ursin (1967, 1979) proposed the following relationship:

$$(4) \quad \frac{dR_i}{dt} = \hat{H}_i w_i^{m_i}$$

where the parameter  $\hat{H}_i$  ( $g^{1-m_i}$ /years) is implicitly dependent on the level of available food and temperature, i.e.  $\hat{H}_i$  can change its value from one year to another (see Ursin 1967, 1979).

Since the rate  $\frac{e_i(t, w_i)}{\beta_i(1-\alpha_i)}$  is much smaller than  $\frac{dR_i}{dt}$  (see Feeding Rate section), it can be safely assumed that

$$(5) \quad \frac{dR'_i}{dt} = \hat{H}'_i w_i^{m_i}$$

where the parameter  $\hat{H}'_i$  ( $g^{1-m_i}$ /years) is implicitly dependent on the level of available food and temperature.

#### Application

Determination of parameter values. The simplest way to estimate the parameter values for the Ursin growth theory is to fit equations (2) and (5) to empirical growth data. However, the Ursin growth

equation contains a number of parameters, so this method of parameter evaluation can lead to the values which generate curves well approximating the empirical data, but do not correspond with their biological interpretation (see discussion in Majkowski 1978; Klekowski et al. 1980; Majkowski and Uchmański 1980). Therefore the parameters treated as independent of the actual feeding rate (i.e.  $\alpha_i$ ,  $\beta_i$ ,  $m_i$ ,  $n_i$ , and  $k_i$ ) are determined on the basis of laboratory studies whereas  $\hat{H}_i$  are found by fitting the solution of differential equations (2) and (5) to the empirical growth data for the southern Gulf of St. Lawrence in 1977-78 (Lett 1978; and data obtained by the Marine Fish Division, Bedford Institute of Oceanography).<sup>2</sup>

The assimilated fraction of food eaten by the cod,  $\beta_i$ , is treated as independent of cod size, and actual feeding rate and equal to 0.8 (Winberg 1956; Ursin 1967, 1978; Andersen and Ursin 1977; Grosslein et al. 1979). The fraction of assimilated food,  $\alpha_i$ , lost in feeding catabolism is assumed to be also independent of cod size and actual feeding rate and equal to 0.4 (cf. Ursin 1967, 1978; Andersen and Ursin 1977). The values of powers  $m_i$  and  $n_i$  are estimated (cf. Andersen and Ursin 1977) as equal to 0.56 and 0.83, respectively, on the basis of laboratory studies.

The coefficient of the term for fasting catabolism,  $k_i$ , is evaluated on the basis of laboratory experiments carried out by Kohler (1964) concerning the so-called maintenance food ration for a cod under similar physical environmental conditions (temperature) as those in the southern Gulf of St. Lawrence. According to equation (1) the

maintenance food ration,  $\frac{dR_i}{dt}_{\text{main}}$ , should satisfy the following condition:

$$(6) \quad \beta(1 - \alpha) \frac{dR_i}{dt}_{\text{main}} - k_i w_i^n = 0$$

The yearly maintenance food ration for 513 and 751 g cod is determined by Kohler (1964) as equal to 1176 and 1375 g/years, utilizing equation (8), Kohler's observations and the values of parameters evaluated above, it is possible to evaluate  $k_i$ . Two values are found to be equal to 3.18 and 2.70, for smaller and larger cod, respectively. Since  $k_i$  should be independent of cod age (Ursin 1967, 1979; Andersen and Ursin 1977), the mean value of  $k$  equal to 2.94 is used in further calculations.

The values of  $\hat{H}_i$  are estimated by fitting<sup>3</sup> the solution of differential equations (2) and (5) to the empirical growth data in 1977-1978 (Lett 1978; and data obtained by the Marine Fish Division, Bedford Institute of Oceanography). Table 1 displays the calculated values of  $\hat{H}_i$ . Since it was impossible to find the value of  $\hat{H}_i$  for the 12-th, 14-th and 15-th age-group (see Table 1), it is assumed that  $\hat{H}_{12}$  is equal to  $\hat{H}_{11}$ ; similarly,  $\hat{H}_{14}$  and  $\hat{H}_{15}$  are assumed to be equal to  $\hat{H}_{13}$ .

<sup>2</sup> All data (not included in the proper text) needed for implementation of calculations are presented in Appendix.

<sup>3</sup> Finite difference Levenberg-Marquardt algorithm (Marquardt 1963; Brown and Dennis 1972) is used to fit the solution of differential equations (2) and (5) to the growth data. Equations (2) and (5) are solved with the aid of Runge-Kutta-Verner method on the fifth order (Hull et al. 1976).

Feeding rate. The yearly average rate  $\frac{dR'_i}{dt}$  estimated on the basis of equation (5), using the values of  $H_i^1$  and  $m$  and the average body weights of cod within each age-group during 1978 (see Appendix), are presented in Table 2. Since  $\frac{dR'_i}{dt}$  is the yearly consumption of food utilized for somatic growth and maintenance expenses only, the total yearly food consumption,  $\frac{dR_i}{dt}$ , can be calculated by adding the yearly consumption of food utilized for reproduction i.e.

$$(7) \quad \frac{dR_{Ei}}{dt} = \frac{1}{\beta(1-\alpha)} \int_0^1 e_i(t, w_i(t)) dt$$

Bagenal (1973, 1978) has shown that the fecundity of a fish increases with its body size according to the allometric law. Thus, the biomass of reproductive products laid during the year by an average mature cod belonging to the  $i$ -th age-group,  $E_{mi}$ , can be treated as:

$$(8) \quad E_{mi} = aw_i^b$$

where  $a$  and  $b$  are positive constants. Ware (1980) evaluates the power value  $b$  for cod on the basis of Powles's (1958) data as equal to 1.38. Grosselein et al. (1979) and Parrish (1975) apply a simplified formula:

$$(9) \quad E_{mi} = 0.1w_i$$

Tentatively, it is assumed in the calculations carried out in this paper that the average yearly biomass of reproductive products for a large cod (i.e. 7000 g) is equal to about 15% of its weight. This condition leads to the values of  $a$  equal to 0.0052. Under the above assumptions, the yearly value of reproductive products for a small mature cod is less than 10% of its weight whereas for a large mature cod it is greater than 10%. This agrees well with formula (9). It will be shown later (see Sensitivity Analysis section) that accurate estimation of  $\alpha$  is not required for the present application.

The percent of mature cod increases with their body length (Powles 1958). Using (i) Powles's (1958) data for the southern Gulf of St. Lawrence, (ii) the relationship between the body weight,  $w$ , and the body length,  $l$ :

$$(10) \quad w = 0.004 \times l^{3.2} \quad (\text{Gray pers. comm.})$$

and (iii) the average cod weights-at-age for the southern Gulf of St. Lawrence in 1978, the percent of mature cod,  $p_i$ , is estimated as equal to 0.0% for the first four age-groups, 20% for the fifth age-group, 50% for the sixth age-group, 80% for the seventh age-group and 100% for the older age-groups. Consequently, the biomass of reproductive products laid during the year by an average cod belonging

to the  $i$ -th age-group of this species is calculated (Table 2) as equal to:

$$(11) \quad E_i = \frac{P_i}{100} E_{mi}$$

where  $p_i$  is determined above and  $E_{mi}$  is calculated on the basis of formula (9).

The yearly consumption of food utilized for reproduction  $\frac{dR_{Ei}}{dt}$ , calculated as equal to  $\frac{1}{\beta(1-\alpha)} E_i$ , is presented in Table 2. The values of  $\frac{dR_{Ei}}{dt}$  are much smaller than those of  $\frac{dR_i}{dt}$  and therefore, as it was mentioned before (Outline of the Ursin Growth Theory), their accurate estimation is not particularly important.

The sum of  $\frac{dR'_i}{dt}$  and  $\frac{dR_{Ei}}{dt}$  provides an estimate of the total yearly food consumption,  $\frac{dR_i}{dt}$ , of a cod belonging to the  $i$ -th age-group (see Table 2).

Other physiological parameters. The average yearly rate of food assimilation can be calculated within this model as a constant fraction ( $\beta = 0.8$ ) of  $\frac{dR_i}{dt}$ .

According to the Ursin model the average yearly catabolism rate,  $\frac{dC_i}{dt}$ , can be estimated as a sum of the average yearly rates of fasting

$$\text{catabolism, } \frac{dC_i}{dt} \text{ fast.} \quad \left( \frac{dC_i}{dt} \text{ fast.} = kw_i^n \right), \text{ and feeding}$$

$$\text{catabolism, } \frac{dC_i}{dt} \text{ feed.} \quad \left( \frac{dC_i}{dt} \text{ feed.} = \alpha\beta \frac{dR_i}{dt} \right), \text{ (see Table 2). The}$$

displayed results show that the rate of total catabolism is about 2 times higher than that of feeding catabolism. This agrees well with Winberg (1956; see also Kerr 1971a, b, c; Ware 1975; Mann 1978) bioenergetic generalizations regarding fish living in the natural environment.

The average rate of total production,  $\frac{dP_i}{dt}$ , can be evaluated on the basis of the following equation:

$$(12) \quad \frac{dP_i}{dt} = \beta(1-\alpha) \frac{dR_i}{dt} - kw_i^n$$

(see Table 2). Utilizing the values of  $\frac{dP_i}{dt}$  and  $\frac{dR_i}{dt}$ , the instantaneous

coefficient of utilization of consumed food for total production,  $K_{1i}$ , can be calculated as:

$$(13) \quad K_{1i} = \frac{dP_i}{dt} / \frac{dR_i}{dt}$$

(see Table 2). The coefficient displays a trend to be a decreasing function of cod age. This agrees well with the general knowledge of fish bioenergetics (Parker and Larkin 1959; Jones and Hislop 1978). The range of values for  $K_{1i}$  is consistent with that expected for fish living in natural conditions.

Cod feeding in the southern Gulf of St. Lawrence. Since the cod population leaves area 4T for about four months from January to May (McKenzie 1956; McCracken 1959; Martin and Jean 1964) during which the cod weight is approximately constant (Lett 1978), the food consumption during these four months,  $R_{Vni}$ , is estimated (see Table 2) to be equal to 1/3 of the yearly average fasting catabolism divided by  $\beta(1-\alpha)$  (for explanation see equation (6)). Finally, the food consumption in area 4T,  $R_{4Ti}$ , by a cod belonging to each age-group is calculated as a difference between  $\frac{dR_i}{dt}$  and  $R_{Vni}$  (see Table 2).

#### Food Biomass Consumed by the Cod Population in Area 4T

The average number of cod ( $\bar{N}_i$ ) within each age-group during 1978 is calculated as follows (see Ricker 1975):

$$(14) \quad \bar{N}_i = \frac{N_{oi}(1 - e^{-Z_i})}{Z_i}$$

where  $N_{oi}$  is the number of cod within the  $i$ -th age-group at the beginning of the year 1978 (Gray 1979) and  $Z_i$  is the instantaneous rate of total mortality for the  $i$ -th age-group (Gray 1979)<sup>4</sup>. The values of  $N_i$  are presented in Table 3.

The food biomass consumed in the southern Gulf of St. Lawrence during 1978 by cod belonging to each age-group is calculated (Table 3) as a product of  $R_{4Ti}$  and  $\bar{N}_i$ . The total food biomass consumed by the cod population in area 4T during 1978 is evaluated to be equal to 0.705 million tons. The last estimate does not include the food consumption of cod belonging to the 0-th age-group.

#### Predictions of Fish Species Contribution in the Cod Population Diet

Method. Cod diet is strongly diversified (Powles 1958; Kohler 1964; Kohler and Fitzgerald 1969; Daan 1973; Minet and Perodou 1978). The composition of its food ration is determined by the relative abundance and distribution of cod and their potential prey, the relative sizes of cod and their different available prey and the prey species preferences (see Ursin 1973; Andersen et al. 1973; Andersen and Ursin 1977; and the last quoted references). Since the above mentioned factors are very changeable, the cod diet varies from one year to another. Analysis of cod stomachs in the southern Gulf of St. Lawrence

<sup>4</sup>  $Z_i = F_i + M_i = 0.2$  (Gray 1979) and  $F_i$  are present in Appendix.



(Powles 1958; Kohler and Fitzgerald 1969) show that the following fish species can potentially be the most frequent prey for cod: capelin, flatfish, herring and young cod. Since the fraction of natural mortality of these species caused by cod predation is not known, and the recent data on cod stomach content are very fragmentary, the contribution of each fish species in the cod diet cannot be predicted precisely. However, the maximal possible contribution can be evaluated.

For each age-group ( $j$ ) of capelin, flatfish, herring, and young cod the biomass lost during the year 1978 due to natural mortality can be estimated as follows:

$$(15) \quad B_{nj} = \int_{m_{1j}}^{m_{2j}} M_j N(t)_j w_j dt$$

where  $[m_{1j}, m_{2j}]$  is the time interval during which cod prey on the  $j$ -th age-group in area 4T,  $M_j$  is the instantaneous rate of natural mortality,  $N_j$  is the number of fish belonging to the  $j$ -th age-group and  $w_j$  is the the average weight (during 1978) of a fish belonging to the  $j$ -th age-group. The time variability of  $N_j$  is determined by the following equation (see Ricker 1975):

$$(16) \quad N(t)_j = N_{oj} e^{-Z_j t}$$

where  $N_{oj}$  is the number of fish belonging to the  $j$ -th age-group at the beginning of the calendar year and  $Z_j$  is the instantaneous rate of total mortality for the  $j$ -th age-group.

After integration,  $B_j$  can be expressed as:

$$(17) \quad B_j = \frac{M_j}{Z_j} w_j N_{oj} (e^{-Z_j m_{1j}} - e^{-Z_j m_{2j}})$$

Summing  $B_j$  over the age-groups of a given fish species, the biomass of this species lost during 1978 due to natural mortality can be estimated. The calculated sum divided by the yearly food biomass consumed by the cod population in area 4T provides a maximal possible contribution of a given fish species in the food of the cod population in this area.

Capelin. Unfortunately, the data regarding the capelin population are extremely poor. The biomass of capelin in the Gulf of St. Lawrence is estimated (Carscadden 1979) to be equal to about 1 million tons. The biomass of this species in the area 4T is evaluated to be approximately one third of that (Dr. J. Carscadden, pers. comm.). The estimate of this last biomass obtained by O'Boyle and Lett (1977) is very similar. Since the age-structure of the capelin stocks in the southern Gulf of St. Lawrence is very poorly known, equation (15) is not directly applied for this particular species. The biomass of capelin lost during year 1978 due to natural mortality,  $B_n$  is estimated on the basis of the following equation (Ricker 1975):

$$(18) \quad B_n = M \bar{B}$$

where  $M$  is the instantaneous rate of natural mortality ( $M = 0.3$ , Carscadden 1979) and  $B$  is the average biomass of capelin ( $B = 0.33$  mln t, Dr. J. Carscadden pers. comm.). The biomass  $B_n$  is calculated to be equal to 0.099 million tons. Thus, the maximal possible contribution of capelin in the food of the cod population is about 14%.

Plaice. Plaice is the most numerous flatfish species in the southern Gulf of St. Lawrence (Ms. K. Metuzals, pers. comm.). Since the plaice population stays the whole year in area 4T, it is assumed that cod prey on plaice during its stay in this area ( $m_1 = \frac{4}{12}$ ,  $m_2 = 1.0$ ) The instantaneous rate of natural mortality for plaice is  $\frac{4}{12}$  quoted by Metuzals (1979) for this area to be equal to 0.15. The instantaneous rates of fishing mortality are assumed in calculations to be the same as those estimated by Metuzals (1979)<sup>5</sup>. The last source of information also provides estimates for  $N_{0j}$ . The weights of female and male plaice as well as the sex ratio (1:1) used in calculations are provided by Metuzals (pers. comm.). The results of calculations performed with the aid of formula (17) and under the above assumptions are presented in Table 4. The total biomass of plaice (excluding plaice belonging to the 0-th age-group) lost during the year 1978 due to natural mortality is estimated to be equal to about 0.020 million tons. According to this, the maximal possible contribution of plaice (older than that belonging to the 0-th age-group) in the food of the cod population is about 2.8%.

Herring. The herring population stays in area 4T from April 30,  $m_1 = \frac{4}{12}$  to November 15  $m_2 = \frac{10.5}{12.0}$  (Dr. M. Sinclair, pers. comm.). The

instantaneous rate of natural mortality for this species in this area is quoted by Winters and Moores (1979) as equal to 0.2. The instantaneous rate of fishing mortality are assumed in calculations to be the same as those estimated by Winters and Moores (1979)<sup>6</sup>. The last source of information also provides estimates for  $N_{0j}$  and  $w_j$ . Using the above values calculations were performed with the aid of formula (17) separately for spring and fall spawning herring populations. The results are presented in Table 5. The total biomass of herring (excluding the 0-th age-group) lost during the year 1978 due to natural mortality is estimated to be equal to about 0.001 million tons.

Thus, the maximal possible contribution of herring (older than that belonging to the 0-th age-group) in the food of cod population is about 0.2%.

Cod. Since cod prefers as potential prey fish which have about ten times smaller body weight than that of itself (Andersen et al. 1973; Ursin 1973; Majkowski 1975, 1977; Mandecki 1976; Andersen and Ursin 1977), the cod cannibalism can occur upon the first four age-groups (see Majkowski 1975, 1977; Mandecki 1976). For these

<sup>5</sup> See Appendix

<sup>6</sup> See Appendix

age-groups are performed calculations based on formula (17). According to those, the maximal possible biomass of cod (excluding cod belonging to the 0-th age-group) lost during 1978 due to the cod cannibalism is estimated to be equal to 0.030 million tons. Thus, the maximal possible contribution of cod (older than those belonging to the -0-th age-group) in the food of cod population is about 4.3%.

### Sensitivity Analysis

Method. Identification of parameters to which the model output is most sensitive leads not only to a better understanding of the system but also eliminates unnecessary empirical and theoretical investigations concerning non-critical parameters. An effective approach to this identification is sensitivity analysis of a mathematical model of the system being studied (e.g. Tomovic 1963; Kowal 1971; Miller 1974; Miller et al. 1976; Waide and Webster 1976; Klekowski and Majkowski 1980; Majkowski and Bramall 1980; Majkowski et al. 1980; Majkowski et al. submitted). The procedure provides information about the performance of the model when its parameters are slightly changed indicating parameters which, if changed, produce either strong or weak changes in the output from the model.

One after another, the value of each parameter (see Table 7) were increased and decreased by various fixed percentages,  $u$ . The effects of such perturbations on the model performance were determined by analysing the relative changes (expressed in percentages) in the total food biomass consumed by the cod population in area 4T during 1978. This last value will be traditionally called the D-measure (see Miller 1974; Miller et al. 1976; Majkowski and Bramall in print; Majkowski et al. submitted). In the case of  $w_i$ ,  $p_i$  and  $\bar{N}_i$  (see Table 7) each value within the appropriate vector ( $i = 1, 2, \dots, 15$ ) is increased and decreased by various percentages. We wish to emphasize that a change in  $\alpha$ ,  $\beta$ ,  $m$  or  $n$  causes some changes in the estimates of  $k$  and  $\hat{H}_i$  (see Determination of Parameter Values section). Similarly, a change in  $k$  or  $w_i$  effects the estimates of  $\hat{H}_i$ . The above mentioned facts are taken into account in the sensitivity analysis.

Results. Several facts are evident from the displayed results of sensitivity analysis (see Table 7):

- (i) For majority of input parameters (i.e. excluding  $b$ ,  $n$  and  $\beta$ ) the D-measure (see Method section) can be treated as a linear function of  $u$ , for values of  $u$  in the range up to tens percentages.
- (ii) The D-measure is very sensitive to changes in (listed in order of importance): in  $w_i$  (June 1978),  $\bar{N}_i$ ,  $k$ ,  $\beta$ ,  $\alpha$ ,  $w_i$  (Jan. 1977),  $b$  and  $m$ .
- (iii) The D-measure is insensitive to changes in  $a$ ,  $p_i$  and  $n$ .

## DISCUSSION

The results presented in this paper indicate that the fish contribution in the diet of cod population inhabiting the southern Gulf of St. Lawrence is small in 1978. As it was emphasized earlier, the composition of cod food can change from one year to another year and therefore, the conclusion concerning a small fish contribution cannot be automatically generalized for a longer period of time (for comparison see results of cod stomach content analysis reported by Powles (1958); Kohler and Fitzgerald (1969) for the same area). The decrease in the fish contribution in the cod population diet in respect to the previous mentioned years can be explained by the decrease in the vulnerability of fish prey species to cod predation, caused by a reduction in the abundance of these species, changes in their spatial distribution or in their resistance to cod predation.

Recently, capelin appears to be potentially a most frequent fish prey for cod. Its maximal possible contribution in the cod diet is similar to that reported by Powles (1958) on the basis of cod stomach content analysis. Kohler and Fitzgerald (1969) do not point out capelin presence in the cod diet - however, a significant fraction of fish in cod stomachs was not identified by them and therefore the usefulness of their data is limited. Unfortunately, there is lack of historical data concerning the capelin abundance and this makes it impossible to interpret the present result in a wider sense.

Young cod becomes recently to be potentially a second major fish item in the cod diet. However, its possible contribution is small. Its presence in cod stomachs is also reported by Powles (1958), Kohler and Fitzgerald (1969).

The maximal possible contribution of plaice in the cod diet calculated in this paper is smaller than that discovered by Powles (1958). This allows us to presume that the abundance of plaice decreased in respect to the fifties. Kohler and Fitzgerald (1969) do not indicate presence of plaice in cod stomachs.

According to the present calculations herring should not be found in cod stomachs in recent years. The high herring contribution in the cod food in the fifties (see Powles 1958) can be explained by a weak resistance of the herring population to cod predation at this time due to the epizootic disease. Kohler and Fitzgerald (1969) point out also that herring is the most frequent fish item in the cod diet. At these times, when their data were collected, herring was much more abundant (see Winters 1976) than in 1978 and this can explain the present result.

The conclusions presented in this paper can be verified by the results of cod stomach content analysis (see Waiwood et al. 1980).

The results of this paper indicate the usefulness of physiological approach applied for identification of interactions among fish species through predation. The results of this approach in conjunction with the results of fish stomach content analysis can provide us with a new method for estimating the instantaneous rates of predation mortality. Since the predation mortality is usually a major component of natural mortality, this method allows us to verify the instantaneous rates of natural mortality. The last rates are needed as input data for the cohort analysis (Pope 1972), the most frequently used procedure for assessing the population abundance and the age-structure of fish stocks. Since the results of cohort analysis are very sensitive to changes in these rates (see Ricker 1975; MacKay 1976), accurate estimation of these rates becomes very important. Unfortunately, accurate evaluation of these rates is extremely difficult. Thus, verification of estimates for these rates is an important task. Another potential application of the physiological approach is presented in Majkowski (submitted).

Since evaluation of the food biomass consumed by the fish population becomes an important task, it should be considered how the present procedure can be improved. The results of sensitivity analysis suggest that an increase in the accuracy of empirical growth data (see Table 7) can strongly decrease the uncertainty in the estimate of food consumption. Also, reliable estimates for the numbers-at-age of fish are needed. Unfortunately, it is usually difficult to satisfy this last condition. It is recommended to extend the research program for the purpose of more accurate evaluation of the following parameters:  $k$ ,  $\beta$ , and  $\alpha$ . The parameter  $k$  is dependent on temperature (see Ursin 1967, 1979), and therefore, can change its value from one year to another. This relationship should be experimentally investigated and possibly included to the present procedure. It can be expected that the parameters  $\beta$  and  $\alpha$  are dependent on the cod feeding rate, temperature and body size. However, it is generally claimed (see The Ursin Growth Theory (Outline) and Determination of Parameter Values sections) that the last three parameters insignificantly influence  $\beta$  and  $\alpha$ . Nevertheless, this should further be examined. It is also desired to verify the estimates for  $b$  and  $m$ . The results of sensitivity analysis clearly indicate that the accurate estimates for  $a$ ,  $p_1$  and  $n$  are not particularly important from the view point of objective for these studies.

There is also another possibility of slight improvement in the estimates for the food consumption. The present calculations are performed in wet mass units. Such units are also used by Ursin (1967, 1979; Andersen et al. 1973; Andersen and Ursin 1977). Energy units seem to be more appropriate for majority of implementation purposes of this growth theory. However, the studies proceeded by Daan (1975) for the cod population inhabiting the North Sea indicate that the energy equivalents for cod body weight, reproductive products and food are very similar (differences in the range of 10%) and therefore the use of energy units can improve the results of the procedure only slightly.

Since there is lack of estimates for these equivalents for the southern Gulf of St. Lawrence, the calculations are performed in mass units.

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15  
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- $\hat{H}_i$  - Coefficient of the formula relating the consumption rate of food utilized for somatic growth and maintenance expenses to body weight expenses for a cod belonging to the  $i$ -th age-group ( $g^{1-m_i}$ /years)
- $i$  - Index denoting age-groups of cod species (pure number)
- $j$  - Index denoting age-groups of fish (pure number)
- $k_i$  - Coefficient of the term for fasting catabolism for a cod belonging to the  $i$ -th age-group ( $g^{i-n_i}$ /years)
- $l$  - Body length (cm)
- $m_i$  - Power value of the formula relating the food consumption rate with the body weight for a cod belonging to the  $i$ -th age-group (pure number)
- $[m_{1j}, m_{2j}]$  - Time interval during which cod prey on the  $j$ -th age-group in area  $4T$  (years)
- $M_j$  - Instantaneous rate of total natural mortality for the  $j$ -th age-group ( $\text{years}^{-1}$ )
- $n$  - Exponent of the term for fasting catabolism (pure number)
- $\bar{N}_i$  - Average number of cod belonging to the  $i$ -th age-group during the year 1978 (pure number)
- $N_{oi}$  - Number of cod belonging to the  $i$ -th age-group at the beginning of 1978 (pure number)
- $N_j$  - Number of fish belonging to the  $j$ -th age-group (pure number)
- $N_{oj}$  - Number of fish belonging to the  $j$ -th age-group at the beginning of 1978 (pure number)
- $t$  - Time (years)
- $w_i$  - Weight (current or average) of a cod belonging to the  $i$ -th age-group (g)
- $w_j$  - Average weight of a fish belonging to the  $j$ -th age-group (g)
- $Z_j$  - Instantaneous rate of total mortality for the  $j$ -th age-group ( $\text{years}^{-1}$ )
- $\alpha_i$  - Fraction of assimilated food lost in feeding catabolism by a cod belonging to the  $i$ -th age-group (pure number)
- $\beta_i$  - Assimilated fraction of food consumed by a cod belonging to the  $i$ -th age-group (pure number)

Table 1. The values of parameter  $H_i'$  estimated on the basis of the empirical growth data for cod inhabiting the southern Gulf of St. Lawrence during 1977-78; are the data obtained by the Marine Fish Division, Bedford Institute of Oceanography.

Age-group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
$H_i' (g^{0.44}/years)$	40.72	40.72	49.26	52.72	55.92	58.72	59.49	57.55	64.30	59.23	73.45	*	70.36	*	*

\* No value is estimated because the empirical growth data are evidently inconsistent for this age-group.

Table 2. Evaluation of physiological parameters for a cod belonging to each age-group for 1978 (for explanation of symbols see Application section or Glossary).

Age-group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
$w_i (g)$	100.	200.	380.	680.	1040.	1670.	2260.	2780.	4050.	4320.	5850.	5540.	6260.	5040.	7000.
$\frac{dR_i'}{dt} (g/years)$	537.	791.	1371.	2033.	2736.	3746.	4495.	4883.	6736.	6432.	9454.	9170.	9406.	8331.	10014.
$E_i (g)$	0.	0.	0.	0.	15.	73.	177.	294.	495.	541.	822.	762.	902.	669.	1053.
$\frac{dR_{E_i}}{dt} (g/years)$	0.	0.	0.	0.	32.	152.	369.	613.	1031.	1126.	1712.	1588.	1879.	1394.	2193.
$\frac{dR_i}{dt} (g/years)$	537.	791.	1371.	2033.	2768.	3898.	4863.	5497.	7766.	7559.	11166.	10758.	11286.	9724.	12206.
$\frac{dC_i}{dt_{fast}} (g/years)$	135.	239.	407.	661.	940.	1392.	1790.	2125.	2905.	3064.	3941.	3767.	4169.	3483.	4574.
$\frac{dC_i}{dt} (g/years)$	306.	492.	846.	1311.	1825.	2640.	3346.	3884.	5390.	5483.	7514.	7210.	7781.	6595.	8480.
$\frac{dP_i}{dt} (g/years)$	123.	141.	251.	315.	389.	478.	545.	513.	823.	564.	1418.	1397.	1248.	1185.	1285.
$K_{ii}$	0.23	0.18	0.18	0.16	0.14	0.12	0.11	0.09	0.11	0.07	0.13	0.13	0.11	0.12	0.11
$R_{V_{mi}} (g/years)$	93.	166.	283.	458.	652.	966.	1242.	1475.	2015.	2126.	2734.	2613.	2892.	2416.	3173.
$R_{4T1} (g/years)$	443.	625.	1089.	1575.	2116.	2932.	3622.	4022.	5751.	5433.	8432.	8145.	8393.	7308.	9033.



Table 6. The biomass ((g/years) x 10<sup>6</sup>) of the youngest four age-groups of cod lost during 1978 due to natural mortality.

Age-group	1	2	3	4
Biomass	2847.2	4662.3	7217.7	15367.9



Table 7. Results of the sensitivity analysis measured by relative changes (expressed in percentages) in the food biomass consumed by the cod population inhabiting area 4T during 1978.

Perturbed value	-25%	-5%	-1%	+1%	+5%	+25%
$w_i$ (June 1978) <sup>a</sup>	30.35	6.15	1.23	-1.23	-6.18	-31.18
$\bar{N}_i$ <sup>a</sup>	25.00	5.00	1.00	-1.00	-5.00	-25.00
k	12.96	2.61	0.52	-0.52	-2.62	-13.15
$\beta$	-16.05	-2.52	-0.48	0.47	2.27	9.48
$\alpha$	6.79	1.54	0.32	-0.32	-1.65	-9.60
$w_i$ (Jan 1977) <sup>a</sup>	-8.35	-1.57	-0.31	0.31	1.53	7.28
b	2.17	0.97	0.24	-0.26	-1.65	-31.96
m	4.16	1.01	0.21	-0.21	-1.11	-6.72
n	-4.23	-0.50	-0.09	0.08	0.37	0.68
a	0.58	0.12	0.02	-0.02	-0.12	-0.58
$p_i$ <sup>a</sup>	0.58	0.12	0.02	-0.02	-0.12	-0.58

<sup>a</sup> All values (i.e. for  $i = 1, 2, 3 \dots, 15$ ) are perturbed simultaneously by the same percentage indicates in the first row.

## Appendix

Data Base (not included in the proper text) needed for implementation of calculations performed in this paper.

Table 8. Empirical weights-at-age (in grams) for 1977 (Lett 1978) and 1978 (data obtained by the Marine Fish Division, Bedford Institute of Oceanography), the numbers-at-age and the instantaneous rates of fishing mortality (Gray 1979) for cod in area 4T for 1978.

Age-group	Weight <sup>a</sup>		Number 1978 (Jan.)	Instantaneous rate of fishing mortality for 1978
	1977 (Jan.)	1978 (June)		
1	-	100 <sup>b</sup>	157075 <sup>d</sup>	0.00 <sup>e</sup>
2	60	200 <sup>b</sup>	128602 <sup>d</sup>	0.00 <sup>e</sup>
3	230	380	105291	0.01
4	480	680	130796	0.10
5	1030	1040	79142	0.19
6	1660	1670	28428	0.25
7	2410	2260	15483	0.25
8	3500	2780	5851	0.25
9	4280	4050	1157	0.25
10	4870	4320	1222	0.25
11	6240	5850	412	0.25
12	5680	5540	373	0.25
13	5970	6260	129	0.25
14	6000	5040	40	0.25
15	6000	11711 (7000 <sup>c</sup> )	30	0.25

<sup>a</sup> Data provided by Dr. D.F. Gray pers. comm.

<sup>b</sup> Due to lack of empirical data for this particular age the weight is approximately estimated with the aid of the graph displaying the relation between the body weight of cod and its age for June 1978.

<sup>c</sup> The value of 11711 is not reliable due to the extremely small number of samples (Dr. D.F. Gray, pers. comm.). Since this value is not consistent with growth data of the 1963 year-class of cod, the weight of 7000 g (approximately estimated with the aid of the graph displaying the relation between the body weight of cod and its age for the 1963 year-class) is used in the calculations performed in this paper.

<sup>d</sup> This number is estimated assuming that for this age-group  $M_i$  is equal to 0.2 (Gray 1979),  $F_i$  is equal to 0.0 (Dr. D.F. Gray, pers. comm.) and the recruitment to the first age-group was the same during the period 1977-1978.

<sup>e</sup> Dr. D.F. Gray pers. comm.

Table 9. Yearly average empirical weights-at-age (in grams) (data obtained by the Marine Fish Division, Bedford Institute of Oceanography), numbers-at-age (in thousands) at the beginning of the calendar year 1978 and the instantaneous rates of fishing mortality for plaice in area 4T for year 1978 (Metuzals 1979).

Age-group	Weight <sup>a</sup>	Number	Instantaneous rate of fishing mortality
1	15	365865 <sup>b</sup>	0.00 <sup>d</sup>
2	30	314903 <sup>b</sup>	0.00 <sup>d</sup>
3	60	271040 <sup>c</sup>	0.20 <sup>d</sup>
4	105	190998 <sup>c</sup>	0.20 <sup>d</sup>
5	170	134594 <sup>c</sup>	0.20 <sup>d</sup>
6	230	94847	0.10
7	255	60271	0.11
8	270	58629	0.11
9	355	26489	0.12
10	370	20913	0.12
11	425	16290	0.12
12	480	8052	0.15
13	535	9423	0.13
14	670	3604	0.12
15	805	3501	0.12
16	950	737	0.18
17	880	490	0.19
18	1250	515	0.19
19	1970	329	0.16
20	1450	191	0.17
21	1670	285	1.02

<sup>a</sup> Data provided by Ms. K. Metuzals, pers. comm.

<sup>b</sup> This values is estimated assuming that for this age-group  $M_i$  is equal to 0.15 (Ms. K. Metuzals, pers. comm.),  $F_i$  is equal to 0.0 (Ms. K. Metuzals, pers. comm.), and the recruitment to the first age-group was the same during the period 1973-78.

<sup>c</sup> This value is estimated assuming that for this age-group  $M_i$  is equal to 0.15 (Ms. K. Metuzals, pers. comm.),  $F_i$  is equal to 0.20, (Ms. K. Metuzals, pers. comm.), and the recruitment to the first age-group was the same during the period 1973-1978.

<sup>d</sup> The value approximately evaluated by Ms. K. Metuzals, (pers. comm.)

Table 10. Yearly average empirical weights-at-age (in grams), the numbers-at-age (in thousands) and the instantaneous rates of fishing mortality for the spring and fall spawning herring populations for area 4T and 1978 (Winters and Moores 1979).

Age-group	Weight		Number (Jan. 78)		Instantaneous rate of fishing mortality	
	Spring spawning	Fall spawning	Spring spawning	Fall spawning	Spring spawning	Fall spawning
1	35 <sup>a</sup>	15 <sup>a</sup>	2443 <sup>b</sup>	2443 <sup>b</sup>	0.00 <sup>c</sup>	0.00 <sup>c</sup>
2	95	70 <sup>a</sup>	2000	2000	0.09	0.01
3	150	130	1050	1227	0.18	0.18
4	200	190	7770	3466	0.11	0.09
5	245	230	710	1613	0.08	0.10
6	295	260	1016	422	0.08	0.11
7	305	290	170	319	0.09	0.12
8	325	315	148	1334	0.09	0.13
9	340	315	23	134	0.10	0.13
10	345	320	402	77	0.11	0.14
11+	375	365	190	1283	0.13	0.14

<sup>a</sup> Due to lack of empirical data for this particular age the weight is approximately estimated with the aid the graph displaying the relation between the body weight of herring and its age for 1978.

<sup>b</sup> This value is estimated assuming that for this age-group  $M_i$  is equal to 0.2 (G.H. Winters and J.A. Moores 1979),  $F_i$  is equal to 0.0 (Dr. M. Sinclair, pers. comm.) and the recruitment to the first age-group was the same during the period 1977-1978.

<sup>c</sup> Dr. M. Sinclair, pers. comm.