

Species interaction in assessment of fish stocks with special application to the North Sea

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Abstract

A multispecies Virtual Population Analysis model is presented in which natural mortality is split into a variable mortality due to predation and a constant mortality due to other causes. Predation is calculated within the model from the food selection of the predators, their yearly food intake and the average stock sizes. The model is tested on a set of data from the North Sea. The results indicate that predation is very important. On average the total biomass of fish dead due to predation amounts to 1.6 times that removed by the fishery. Furthermore the introduction of predation mortality changes the exploitation pattern calculated by traditional VPA.

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1. Introduction

Fish stock assessment within ICES (The International Council for the Exploration of the Sea) is mostly based on the models of Beverton & Holt (1957), in particular through one of its derivatives, virtual population analysis (VPA).

These models (including VPA) are single-species models, i.e. each fish species is treated independently of the others and there is indeed nothing in the calculations which allows for species interaction. The models are not only used for assessment of past history of the fish stocks and their fishing but also for predictions and recommendations. Often these recommendations call for measures which would lead to a change in the stock size of a major species by an order of magnitude. Of course nobody expects such a drastic change not to influence other species. Nevertheless conclusions are drawn from such calculations.

Common sense tells us that interaction between fish species can mainly be ascribed to two factors: predation and food-competition. Indeed these two effects not only relate one species to another, but also one fish to another within the same species.

Models of species interactions are numerous. We refer to a survey paper by Ursin (1982a) for a general discussion of such models. We are mainly interested in models which resemble as closely as possible the commonly used VPA, for only such models are likely to be taken up in routine assessment work. At least two papers have appeared on models of this kind: one by Pope (1979) and the other by the present authors (1979). The latter model has been modified by Sparre (1980). These models start with the standard formulas of VPA but replace the assumed values of natural mortality by expressions whereby this mortality is described as being partly caused by predation. The other factor mentioned above as being an evident cause of species interaction, namely food-competition, is not treated directly in either of these two models. In particular the growth rate of each individual is assumed to be a function of its age only, e.g. not dependent upon the quantity of available food.

Our model and that of Pope differ mainly in three ways. Firstly with respect to food selection (which of course influences the predation mortalities) Pope makes the simple assumption that all food items below a certain size (which for fish-prey is translated into the nearest corresponding age-class) are equally suitable for a specific individual. We on the other hand borrow from Andersen & Ursin (1977) a more detailed description of the size-preference of food items. Secondly the models differ with respect to availability of 'other' food, i.e. food which is not fish-prey, covered by the model. Pope assumes this food to amount to a fixed proportion of the diet of each individual. We make the assumption that a fixed quantity of other food is available and that each predator makes its choice by comparing the quantities of currently available fish-prey with that of other food. Thus the fish-consumption of each individual is positively correlated with the abundance of fish at any time.

The third main difference between Pope's model and ours concerns the treatment of 0-group fish. VPA-calculations go backwards in time and age and are usually terminated at the age of first capture. For North Sea species this usually amounts to 1-year old fish. However the 0-groups are usually an important source of food for fish. Therefore both models incorporate the 0-groups but in different ways with regard to time dynamics. In both models all calculations concerning the exploited year-classes are done by yearly averages and for example assume each

age-class to have a constant (average) weight during a whole year. Pope treats the young fish in the same way. Since fish grow very fast in the first year, we feel that the 0-groups have to be treated differently. Their growth and abundance are therefore described by differential equations rather than the difference equations with 1-year time steps used for the exploited age-groups. This may be more relevant in our model than in Pope's due to the dynamic relationship between other food and fish-prey (i.e. mainly the 0-groups) in our model.

As stated above, our multispecies VPA (MSVPA) is intended as a practical tool for fish-stock assessment. We have incorporated some but not all of the basic ideas of Andersen & Ursin (1977) into traditional VPA. Yet our model may be unnecessarily complicated as a first step from single- to multi-species assessment. There are lots of parameters to be estimated or guessed. A simpler model, however, does not necessarily free the model maker from assigning values to parameters. It may rather be that simplifications (conscious or not) basically amount to fixing parameters at trivial values (like 0 or 1).

Our MSVPA shares its main weakness with traditional VPA, namely that it is not based on statistical foundations. All the information contained in the catch at age numbers is used in computing the fishing-mortality rates. A statistically founded version of VPA, like that of G. Gudmundsson (1982) and G. Gudmundsson *et al.* (1982), might help in assigning values to some of the (unknown) parameters needed to describe the predation interaction. In such a version of MSVPA the fishing-mortality rates would be tied together functionally, thus retaining some information content which could be used for estimation of the predation parameters.

2. Mathematical description of the model

The model incorporates several species of fish which are split into age-groups. The age-groups are treated differently according to whether they are recruited to the fisheries or not. We will first describe the model equations for the exploited groups (called 'old' fish) and then briefly the calculations concerning the unexploited groups ('young' fish) and the interactions between these two classes.

Consider an area in which s different fish species coexist and are subjected to fishing. Let us first develop the theory regarding the fish caught in the fishery. Assuming time-independent mortality rates (i.e. constant within the year) the number of individuals of (recruited) age-group a of species i is given by:

$$N_{ia}(t) = N_{ia}(1) \exp(-(F_{ia} + M_{ia})(1 - t)) \quad (2.1)$$

where

- t : Time within the year; $0 \leq t \leq 1$.
- $N_{ia}(t)$: Number of fish of species i and age a at time t .
- $N_{ia}(1)$: Number of fish of species i and age a at the end of the year.
- F_{ia} : Fishing mortality rate (per year) for age-group a of species i .
- M_{ia} : Natural mortality rate (per year) for age-group a of species i .

Furthermore the catch in numbers equals:

$$C_{ia} = N_{ia}(1) \frac{F_{ia}}{F_{ia} + M_{ia}} (\exp(F_{ia} + M_{ia}) - 1) \quad (2.2)$$

Standard VPA is based on inserting a known catch-number and a given value for natural mortality into equation (2.2) to obtain the fishing mortality. Stock size in the beginning of the year is calculated by formula (2.1) and then the argument can be repeated for the preceding year.

Our extension of the method consists of dividing the natural mortality into two components:

P_{ia} : Mortality rate (per year) for age-group a of species i due to predation by fishes within the model

and

D_{ia} : Mortality rate due to all other natural causes.

Thus

$$M_{ia} = P_{ia} + D_{ia} \quad (2.3)$$

To describe the predation mortality we have adopted a simplified version of the approach developed by Andersen & Ursin (1977). In order to obtain computationally convenient formulas and to adhere to conventions in VPA-calculations we use a discrete version of their expressions with a time unit of one year.

As a starting point we assume the food-consumption rate, R_{ia} , to be related to the average weight of the fish in the following way:

$$R_{ia} = v_i w_{ia}^m \quad (2.4)$$

where

v_i : Species specific constant ($\text{kg}^{1-m}/\text{year}$)

w_{ia} : Average weight of a fish belonging to class ia (kg).

m : General exponent relating food consumption to fish size.

In order to calculate the composition of the food consumed the biomass of available food for class ia , Φ^{ia} , is divided into three parts: 'old' fish included in the model, Φ_o^{ia} ; 'young' fish, Φ_y^{ia} ; and all other food, Φ_x^{ia} , found in the area, i.e.:

$$\Phi^{ia} = \Phi_o^{ia} + \Phi_y^{ia} + \Phi_x^{ia} \quad (2.5)$$

where

$$\Phi_o^{ia} = \sum_{j=1}^s \sum_{b=t_j^c}^{t_j^M} \Phi_{jb}^{ia} \quad (2.6)$$

and:

Φ_{jb}^{ia} : Total biomass (average over the year) of 'old' fish class jb as available food for class ia (kg).

t_j^C : Age (in years) at first capture of species j by the fisheries. (If not an integer, corresponding adjustments are made).

t_j^M : Maximum age (in years) of species j .

We intend the definition of 'available food' to take account of the suitability of the food items, and will later return to the question of how suitability is computed. At this point it is sufficient to say that suitability is defined in such a way that it can be assumed that the relative composition of the ingested food is roughly proportional to the biomasses of available food items. Hence the (average) rate of total predation of class jb by class ia equals:

$$\frac{\Phi_{jb}^{ia}}{\Phi^{ia}} R_{ia} \bar{N}_{ia} \quad (2.7)$$

where

\bar{N}_{ia} : Average number of fish of species i and age a .

Inserting (2.4) into (2.7) and summing over all predators ia we obtain the following expression for the total biomass of fish of class jb predated in the year:

$$\sum_{i=1}^s \sum_{a=t_i^c}^{t_i^m} \frac{\Phi_{jb}^{ia}}{\Phi^{ia}} v_i w_{ia}^m \bar{N}_{ia} \quad (2.8)$$

Here we assume that young fish do not predate upon old fish.

The total predation on class jb may also be formulated as:

$$\int_0^1 P_{jb} w_{jb} N_{jb}(t) \cdot dt \quad (2.9)$$

which because P and w are constant equals:

$$P_{jb} w_{jb} \bar{N}_{jb} \quad (2.10)$$

since:

$$\bar{N}_{jb} = \int_0^1 N_{jb}(t) \cdot dt \quad (2.11)$$

Now equating (2.8) and (2.10) we get:

$$P_{jb} = \frac{1}{w_{jb} \bar{N}_{jb}} \sum_{i=1}^s \sum_{a=t_i^c}^{t_i^m} \frac{\Phi_{jb}^{ia}}{\Phi^{ia}} v_i w_{ia}^m \bar{N}_{ia} \quad (2.12)$$

On the other hand

$$\begin{aligned} \bar{N}_{ia} &= \int_0^1 N_{ia}(t) dt \quad (2.13) \\ &= N_{ia}(1) \int_0^1 \exp((F_{ia} + M_{ia})t)(1-t) dt \\ &= N_{ia}(1) \frac{1}{F_{ia} + M_{ia}} (\exp(F_{ia} + M_{ia}) - 1) \\ &= \frac{C_{ia}}{F_{ia}} \end{aligned}$$

So now:

$$P_{jb} = \frac{F_{jb}}{w_{jb} \cdot C_{jb}} \sum_{i=1}^s \sum_{a=t_i^c}^{t_i^M} \frac{\Phi_{jb}^{ia}}{\Phi^{ia}} v_i w_{ia}^m \frac{C_{ia}}{F_{ia}} \quad (2.14)$$

Next let us return to the problem of finding an expression for the total biomass of available food for class ia . Obviously the available food is only a fraction of the total biomass of potential food. Some of it consists of food items too large to be swallowed or too small to be noticed; some food items are scarcely ever met, while others are too difficult to catch. The potential food biomasses must therefore be weighted. Hence we introduce a coefficient, G_{jb}^{ia} , ranging between 0 and 1 and expressing the suitability of class jb as food for ia . Thus we write:

$$\Phi_{jb}^{ia} = G_{jb}^{ia} w_{jb} \bar{N}_{jb} \quad (2.15)$$

or due to (2.13):

$$\Phi_{jb}^{ia} = G_{jb}^{ia} \cdot w_{jb} \frac{C_{jb}}{F_{jb}} \quad (2.16)$$

Now the expression for the predation mortalities becomes a bit simpler:

$$P_{jb} = \sum_{i=1}^s \sum_{a=t_i^c}^{t_i^M} \frac{G_{jb}^{ia}}{\Phi^{ia}} v_i w_{ia}^m \frac{C_{ia}}{F_{ia}} \quad (2.17)$$

Following the ideas of Ursin (1982) and Andersen & Ursin (1977) G_{jb}^{ia} is expressed as the product of three factors all ranging between 0 and 1:

$$G_{jb}^{ia} = o_j^i \cdot \rho_j^i \cdot g_{jb}^{ia} \quad (2.18)$$

where the first factor, o_j^i , expresses the degree of the overlap of the habitats of species i and j , the second factor, ρ_j^i , reflects the general vulnerability of species j to predation by species i (due to different behaviour etc.) and the third factor deals with size-preference:

$$g_{jb}^{ia} = \exp \left(\frac{\left(\ln \left(\frac{w_{ia}}{w_{jb}} \right) - \eta_i \right)^2}{2\sigma_i^2} \right) \quad (2.19)$$

In this expression η_i is the natural logarithm of the optimal weight-ratio of predator to prey for species i and σ_i a constant indicating how particular the predator is about the size of its prey items. A more detailed description of the general vulnerability and this expression of size-preference can be found in Andersen & Ursin (1977).

The degree of overlap of the habitats of species i and species j can be computed if we assume that we know the relative distribution of both species within the sea area. In more precise terms this implies that we are able to describe their distributions by the density functions $E_i(x, y)$ and $E_j(x, y)$, which for each point (x, y) within the area expresses the relative concentration of i and j respectively.

Let us next define a distance function $\text{dist}((x_i, y_i), (x_j, y_j))$ which for every pair of coordinates, (x_i, y_i) and (x_j, y_j) , expresses the degree of contact between a fish at (x_i, y_i) and one at (x_j, y_j) .

In the North Sea we know the distribution of some of the species in winter from the International Young Fish Survey. During this survey the North Sea is divided into a number of squares, each of an area of approx. 30×30 nautical miles. In each square one or more hauls are made with standard gear and the average catch in numbers per hour and age-group computed. If we assume that only fish who occupy the same square are available as food for each other we can as an approximation define the function dist by:

$$\text{dist}(x_i, y_i), (x_j, y_j) = \begin{cases} 1.0 & \text{if } (x_i, y_i) \text{ and } (x_j, y_j) \in q \\ 0.0 & \end{cases}$$

where q is an arbitrarily chosen square. If furthermore (a_q, c_q) , (a_q, d_q) , (b_q, c_q) and (b_q, d_q) mark the corners of square q we have:

$$o_j^i = \sum_q \int_{a_q}^{b_q} \int_{c_q}^{d_q} \int_{a_q}^{b_q} \int_{c_q}^{d_q} E_i(x_i, y_i) \cdot E_j(x_j, y_j) \cdot \text{dist}((x_i, y_i), (x_j, y_j)) \cdot dx_i \cdot dy_i \cdot dx_j \cdot dy_j \quad (2.20)$$

As we assume the concentration of fish not to change within q we can put $E_i(x_i, y_i)$ equal to E_i^q and $E_j(x_j, y_j)$ equal to E_j^q , where E_i^q and E_j^q are the fractions of the i and j stock which are found within q . In this way o_j^i becomes:

$$o_j^i = \sum_q E_i^q \cdot E_j^q \quad (2.21)$$

As regards the description of the young fish, i.e. fish before the time of first capture, the basic formulas are the same with the exception that they show an instantaneous instead of an average state of affairs. This is mainly done in order to account for the very high growth rate of 0-group fish.

The weight of young fish is assumed to have a linearly decreasing specific growth rate, i.e.:

$$\frac{1}{w_i(t)} \frac{dw_i(t)}{dt} = h_i \cdot (t_i^C - t) + g_i \quad (2.22)$$

for $t_i^R \leq t \leq t_i^C$ where

t_i^R : Time of recruitment to the model (years)

t_i^C : Time of first capture by the fisheries (years)

The parameters h_i and g_i in equation (2.22) are determined from given weights at the time of recruitment and of first capture and from the rate of growth immediately after the time of first capture. The stock size of the young is described by the differential equation:

$$\frac{dN_{ia}(t)}{dt} = -(P_{ia}(t) + D_{ia}) \cdot N_{ia}(t) \quad (2.23)$$

with boundary value $N_{ia}(t_i^C)$, which is supplied by the calculation phase for old fish.

Analogous to (2.17) the expression for the instantaneous rate of predation mortality becomes:

$$P_{jb}(t) = \sum_{i=1}^s \left\{ \sum_{a=t_i^c}^{t_i^c} \frac{G_{jb}^{ia}(t)}{\Phi^{ia}(t)} v_i \cdot w_{ia}(t)^m \cdot N_{ia}(t) + \sum_{a=t_i^c}^{t_i^m} \frac{G_{jb}^{ia}(t)}{\Phi^{ia}} v_i \cdot w_{ia}^m \cdot \frac{C_{ia}}{F_{ia}} \right\} \quad (2.24)$$

Here the first part of the sum accounts for predation by young fish upon young fish, whereas the second one takes care of predation by old fish upon young fish.

Food supply for young age-classes differs somewhat from that for old fish (cf. (2.5)):

$$\Phi^{ia}(t) = \Phi_y^{ia}(t) + \Phi_x^{ia}(t) \quad (2.25)$$

since young fish are not supposed to predate upon old fish.

Other expressions like those for $G_{jb}^{ia}(t)$ and $\Phi_y^{ia}(t)$ when a and b correspond to young age-groups are entirely analogous to those for the old ones and will not be repeated here. Also the supply of young fish as food for the old needed in formula (2.5) is computed by averaging the instantaneous values (from a formula similar to (2.15)) over the whole year:

$$\Phi_y^{ia} = \sum_{jb} \int_0^1 G_{jb}^{ia}(t) \cdot w_{jb}(t) \cdot N_{jb}(t) \cdot dt \quad (2.26)$$

Here the summation ranges over all groups of young fish.

As to the expression for the supply of other food, first of all the biomass of other food is supposed to be constant in time, and secondly it is assumed to consist of food items of different weight.

We assume the weight distribution of other food to be log-normal, i.e. having the density function:

$$DB(w) = \frac{1}{w\beta\sqrt{2\pi}} \exp\left(-\frac{1}{2} \left(\frac{\log w - \alpha}{\beta}\right)^2\right), \quad w > 0 \quad (2.27)$$

The parameters α and β can be expressed in terms of the mean weight w of other food items and its variance d by:

$$\begin{aligned} \beta^2 &= \log((d/\bar{w})^2 + 1) \\ \alpha &= \log \bar{w} - \frac{1}{2} \cdot \beta^2 \end{aligned} \quad (2.28)$$

Analogous to equations (2.15) and (2.6) the other available food for fish ia can be expressed as:

$$\Phi_x^{ia} = o_x^i \cdot \rho_x^i \cdot B_x \cdot \int_0^\infty g_x^{ia}(w) \cdot DB(w) \cdot dw \quad (2.29)$$

where o , ρ and g have the same meaning as in equation (2.18) but B_x is the total weight of the biomass of other food.

Using a size-preference function like (2.19) the right hand side of (2.29) can be evaluated:

$$\Phi_x^{ia} = o_x^i \cdot \rho_x^i \cdot B_x \cdot \frac{\sigma_i}{\sqrt{\sigma_i^2 + \beta^2}} \cdot \exp\left(-\frac{1}{2} \cdot \frac{(\ln w_{ia} - \eta_i - \alpha)^2}{\sigma_i^2 + \beta^2}\right) \quad (2.30)$$

Here w_{ia} refers to the weight of fish of group ia , η_i and σ_i describe its size-preference for food, and α and β refer to equation (2.28).

In the algorithm actually used other food is divided into pelagic and demersal food.

The equations developed in this chapter are transformed into a computational algorithm which is described in Appendix 1.

3. Application to the North Sea

3.1 Estimation of parameters

Members of ICES have until now collected catch-at-age data and run single species VPA's on eleven North Sea stocks, i.e. saithe, cod, haddock, whiting, Norway pout, sandeel, herring, sprat, mackerel, plaice and sole. In the present exercise they have all been included except sole, whose predatory interactions with other species is believed to be small. Furthermore we have followed traditional ICES working group procedures by splitting plaice into males and females and by treating sandeels from the northern and southern part of the North Sea separately.

One of the interesting aspects of this exercise is to compare the situation in the second part of the sixties, before the decline of the pelagic stocks, with the situation in the seventies. Unfortunately, for some of the species catch-at-age data do not exist prior to the early seventies. In order to run the model back into the sixties a set of likely catch-at-age data was therefore constructed where real information was missing. This was done either by using the average age-composition in the earliest years from which catch-at-age data existed or by using some reported measure of total mortality to calculate the age composition of the catch. This way of constructing catch-at-age data has several drawbacks. It seems to give reasonable biomass figures, but has of course the undesirable effect of obliterating any difference between good and bad year classes.

The terminal fishing mortalities used were as far as possible taken directly from ICES working group reports. Where they were lacking they were guessed from the scanty information on fishing effort available.

Before the calculations can start quite a lot of parameters not used in single species VPA have to be estimated or chosen. We thus need information on:

1. Mean weights at age for old age-groups.
2. Rate of mortality not due to fishing or predation.
3. Time of year of recruitment to the model and time of first capture together with corresponding weights.
4. Rate of food intake as a function of body size.
5. Biomass and size distribution of other food, both pelagic and benthic.
6. Parameters of food selection.

The mean weights at age for the old age-groups were taken from the working group reports. In this application we have used the mean weight in the catch, but separate weight-at-age data can easily be introduced when calculating stock biomass and total catch in weight.

It is difficult or impossible to estimate the rate of mortality not due to fishing or predation by species included in the model, i.e. mortality caused by disease, preda-

Table 1. Time of year of recruitment to the model and first capture (months) and respective weights (g).

Species	Time of recruitment (months)	Weight at recruitment (g)	Time of first capture (months)	Weight at first capture (g)
Saithe	6	0.1	18	80.0
Cod	5	0.1	12	20.0
Haddock	5	0.1	8	5.0
Whiting	5	0.1	8	5.0
Norway pout	6	0.1	8	3.0
Sandeel, south NS	5	0.1	6	1.3
Sandeel, north NS	5	0.1	6	1.4
Sprat	8	0.1	10	2.5
Herring	2	0.1	8	10.0
Mackerel	7	0.1	18	200.0
Plaice ♂♂	5	0.1	13	60.0
Plaice ♀♀	5	0.1	13	60.0

tion by seals and sharks, spawning stress, etc. In order to end up with total natural mortalities for the oldest age-groups close to the ones used by the working groups we chose to use a value of 0.2 for saithe, cod, haddock and whiting and 0.1 for the rest.

Very little is known about the interactions in the larval stages. The weight at recruitment to the model was therefore set to 0.1 g for all species and the time of recruitment chosen accordingly. The time of first capture and the corresponding weight was determined for most of the species from data collected from the Danish industrial fishery (Popp Madsen, pers. comm.), Table 1.

3.1.1 Rate of food intake as a function of size

For some of the species estimates of the rate of food intake exist based either on data on mean stomach content in the North Sea and the rate of stomach evacuation or deduced from data on total metabolism and growth. Daan (1973) used data on the average stomach contents of North Sea cod and found that the yearly food intake could be described by:

$$\begin{aligned} \text{yearly food intake (kg)} &= 1.95 \cdot 10^{-3} \cdot \text{length}^2 \text{ (cm)} \\ \text{or since } w \text{ (kg)} &= 10.4 \cdot 10^{-6} \cdot \text{length}^3 \text{ (cm)} \\ \text{yearly food intake (kg)} &= 4.09 \cdot w^{2/3} \end{aligned}$$

Jones (1978) used both stomach contents and total energy metabolism to calculate the yearly food uptake of cod and haddock. The results obtained with both methods were in good agreement and converting his rates from kcal · year⁻¹ to kg wet weight · year⁻¹ the food intake can be expressed as:

$$\text{yearly food intake (kg)} = v \cdot w^{0.92} \quad (4 \leq v \leq 7) \text{ cod}$$

and

$$\text{yearly food intake (kg)} = v \cdot w^{0.80} \quad (v \sim 5) \text{ haddock}$$

It has not been possible to find reliable information for the rest of the species and their food intakes were therefore estimated on the assumption that relative rate of food intake in some way must be related to the rate of growth.

In the growth equation:

$$\frac{dw}{dt} = H \cdot w^m - k \cdot w^n$$

the first part, $H \cdot w^m$, is usually thought to represent the build-up of new tissue, the second part, $k \cdot w^n$, the breakdown. Ursin (1967, 1979) subdivided the build-up into several components, one being the rate of food intake, i.e.:

$$H \cdot w^m = \beta \cdot (1 - \alpha) \cdot \frac{dR}{dt}$$

where

β : assimilation efficiency

α : fraction of assimilated food used in all energy consuming processes associated with feeding, i.e. chewing, active transport, deamination, etc.

dR/dt : rate of food intake

Thus the rate of food intake can be expressed by:

$$\frac{dR}{dt} = \frac{H}{\beta \cdot (1 - \alpha)} \cdot w^m = v \cdot w^m$$

Majkowski & Wainwood (1981) used this equation to estimate the yearly food intake of the cod population in the southern gulf of St. Lawrence by assuming $m = 0.56$, $n = 0.83$, $\beta = 0.8$ and $\alpha = 0.4$ and by adding the food intake used for reproductive purposes.

Let us here assume that α , β and m are constant and non species-specific and that m equals 0.67 as found by Daan (1973). If H_i and v_i are known for one species i , but not for another species j for which we only have an estimate of H_j , we estimate v_j from:

$$v_j = v_i \cdot \frac{H_j}{H_i}$$

This equation and Daan's (1973) estimate of the rate of food intake for North Sea cod, i.e. $v = 4.09$, which seems to be low compared to the values given by Jones (1978), were used to estimate the rates of food intake for the other species (Table 2). The values of H were taken from the literature except for plaice males and females for which H values were calculated using the working group estimates of stock weight at age. All have been estimated under the assumption of $m = 0.67$ and $n = 1.0$. The last assumption, $n = 1.0$, seems rather unrealistic in view of the present knowledge of metabolic processes in fish. However, for the present purpose it was assumed to be sufficient (see also discussion in Majkowski & Wainwood 1981).

Compared to the value of v for cod the values for the rest of the species seem rather low (Table 2). If, however, we look at the average food intake as a propor-

Table 2. Coefficients of food intake and average annual food intake of ages 1 to 5 expressed as a proportion of body weight.

Species	H $g^{(1-0.67)} \cdot \text{year}^{-1}$	Source	Coefficient of feeding, ν $kg^{(1-0.67)} \cdot \text{year}^{-1}$	Average annual food-intake in g per g body weight of ages 1 to 5
Saithe	9.11	Ursin (1967)	2.29	2.27
Cod	16.29	Pauly (1978)	4.09	2.76
Haddock	7.87	Ursin (1967)	1.97	2.59
Whiting	5.71	—	1.43	2.72
Norway pout	6.97	Anon. (1978)	1.75	4.89
Sandeel, south NS	4.79	—	1.20	4.98
Sandeel, north NS	9.05	—	2.27	6.68
Sprat	5.47	Ursin (1967)	1.37	5.37
Herring	6.67	Pauly (1978)	1.67	2.98
Mackerel	9.60	Ursin (1967)	2.41	3.38
Plaice ♂♂	5.12	Estimated from	1.29	2.08
Plaice ♀♀	4.16	weight at age	1.04	1.56

tion of body weight for ages 1 to 5 this difference disappears. As we would expect, small species like sandeel and active ones like mackerel eat relatively more than large species like saithe and cod and sluggish ones like plaice.

3.1.2 Total biomass and size distribution of other food

In this application of the MSVPA the term other food by definition represents all food items available to the 12 fish stocks other than the fish stocks themselves. Other food includes many species which show a pronounced seasonal fluctuation in biomass. Especially for the pelagic food this fluctuation makes it difficult to find an average biomass and size distribution valid for the whole North Sea. Most of the pelagic feeders i.e. herring, sprat, mackerel and sandeel obtain the bulk of their food in the period from April to October and we therefore decided to use only biomass estimated from this period when calculating the biomass of other pelagic food.

Based on material collected with the continuous plankton recorder E. Kirkegaard (pers. comm.) estimated the average biomass of copepods in the period from April to October in the northwestern, northeastern and southern parts of the North Sea (Fig. 1). Using a factor of 5 to convert from dry to wet weight his figures give an average total biomass of zooplankton of approx. $1.3 \cdot 10^6$ tonnes wet weight in the North Sea. However, Steele (1974) gives an estimate of 6 g dry weight per m^2 for the total zooplankton in the same period in the northern North Sea. The estimates based on the continuous plankton recorder for this area, 0.48 and 1.04 g dry weight $\cdot m^{-2}$, or on average 0.62 thus seem rather low. For lack of better information we have used a number close to Steele's, i.e. a total biomass of $10 \cdot 10^6$ tonnes for other pelagic food. This biomass was then divided between the areas in agreement with the relative values found with the continuous plankton recorder (Fig. 1). The total biomass is thought to include euphausiids and small mesopelagic fish and

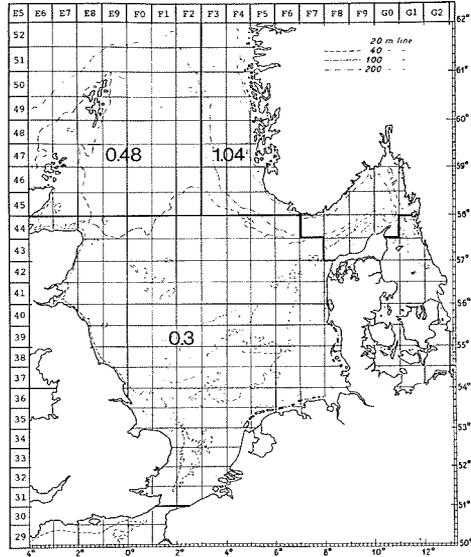


Fig. 1. Average biomass of copepods from April to October in g dry weight per m². Values from E. Kirkegaard (pers. comm.).

the average weight of an individual was hence set to 0.05 g corresponding to the weight of an adult *Calanus finmarchicus*. The standard deviation of the size distribution was chosen to be 0.1. The resulting biomass distribution can be seen in Fig. 3.

According to McIntyre (1978) the subtidal part of the macrobenthos in the North Sea can be divided into three strata or étages. The open sea étage comprises the Fladen Ground and the deeper parts of the northern North Sea, the coastal and infralittoral étages the central and southern part, respectively. The biomass of the

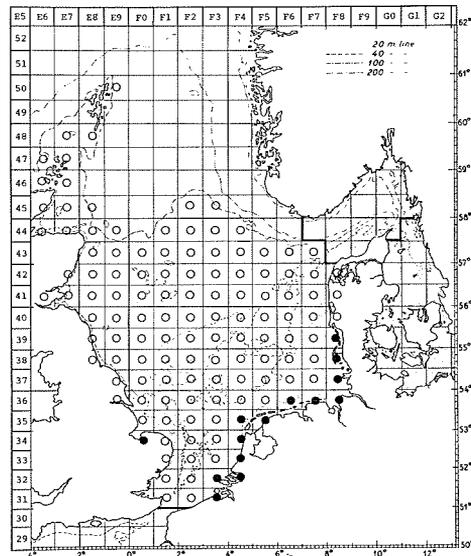


Fig. 2. Biomass distribution of macrobenthos. Open sea (6.42 g dry weight/m²): blank. Coastal and infralittoral (4.79 and 5.47 g dry weight/m²): ○. Intertidal zone (19.7 g dry weight/m²): ◉. From McIntyre (1961, 1978).

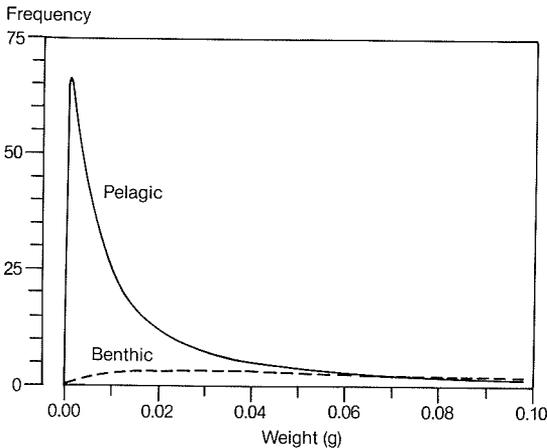


Fig. 3. Weight distribution of other food.

macrobenthos on Fladen Ground was estimated by McIntyre (1961) to be 6.42 g dry weight per m^2 . Observations cited in McIntyre (1978) from the coastal and infralittoral étages indicate biomasses of 4.79 and 5.47 g dry weight $\cdot \text{m}^{-2}$ respectively. Finally, in the shallow tidal zone McIntyre (1978) cites a biomass figure of 19.7 g dry weight $\cdot \text{m}^{-2}$.

Because of the small difference in biomass between the coastal and the infralittoral étages they were combined into one zone. The biomass values were converted to wet weight by multiplying by 5 and the resultant biomass distribution is shown in Fig. 2. The total biomass of macrobenthos in the North Sea can be estimated to approx. $15 \cdot 10^6$ tonnes wet weight. The average weight of one individual was more or less arbitrarily set to 1 g and the standard deviation of the size distribution to 2.0 (Fig. 3).

3.1.3 Parameters of food selection

If sufficient data on the food composition of the species existed the parameters of food selection could be estimated within the model by a method suggested by Sparre (1980). At present, however, such data covering the whole of the North Sea do not exist for any of the species involved.

In order to use the model we have thus been forced to make some 'guesstimates' based on the general knowledge of the feeding ecology of the species. The next section gives a short review of the available information and the following sections describe how the values of the different parameters were chosen.

3.1.3.1 Food composition

Saithe

Information on the food of saithe in the North Sea is very sparse.

Scott (1901) found a total of 10 whiting, 1 haddock, 1 long rough dab and 1 common dab in the stomachs of 4 saithe. Todd (1905, 1907) found several haddock, two other gadoids, 3 flatfish, 143 sandeel, 3 *Loligo forbesi* and one *Crangon* sp. in 8 saithe stomachs from the northern North Sea. Nordgaard (1901) mentions

capelin, herring, sprat, sandeel, haddock and whiting from the stomachs of saithe, but in addition stresses the importance of euphausiids as food. Ehrenbaum (1936) describes the food of saithe as consisting of sandeel, capelin, various gadoids and herring.

Wagner (1959) examined the stomach contents of 894 saithe from the northern North Sea. Approximately 75% of the examined stomachs contained only fish, 5% only crustaceans and 5% a mixture of crustaceans and fish. The rest were empty. The stomachs were sampled during February and March and the most important food item was Norway pout. Meis (1978) examined 25 saithe stomachs of which 4 were empty. The rest contained remains of fish, some also of crustaceans. A total of 59 Norway pout and 119 sandeels were found besides various other small species such as poor cod, *Gadiculus thori*, *Maurolicus muelleri* and *Argentina* sp.

In the Barents Sea Mironova (1961) reported that the diet of saithe consisted of crustaceans such as euphausiids and a variety of fish species including capelin, herring, whiting, blue whiting, Norway pout, cod and saithe. Out of the 780 stomachs containing food, fish occurred in 58.9% and crustaceans in 32.6%. The most important fish in the stomachs was capelin followed by herring and young gadoids.

The food of the pelagic 0-group in the northern North Sea has been described by Robb & Hislop (1980). They found that young saithe of a length between 50 and 139 mm mainly ate young Norway pout and sandeels.

Bertelsen (1942) examined the food of young saithe at the Faroes. In the beginning of May the pelagic 0-group were eating mainly copepods. Later on when the 0-group could be found in the littoral zone of the fjords their main food item was amphipods. The I and II groups were living on the same diet, but in addition ate a lot of the smaller saithe.

Cod

With respect to food composition cod is the best investigated species in the North Sea, and in this context it would be too extensive to review the entire literature. The following review therefore only deals with the more comprehensive investigations.

Todd (1905, 1907) reported from his investigations in the southern part of the North Sea that cod of a length less than 15 cm fed exclusively on crustaceans. In the next length group (15-30 cm) 11% of the stomachs contained fish. In the length group 30-60 cm the percentage was 52 and for cod larger than 60 cm the percentage increased to 67. The most important fish species found were sandeel, whiting, dab and *Clupea* sp.

Graham (1923) examined the food of large cod (>75 cm) caught by commercial vessels in the central North Sea. The dominant fish species occurring in the stomachs were herring and haddock followed by whiting, mackerel, sandeel and various flatfishes.

Hertling (1940) found herring, sprat, whiting and plaice in stomachs from the southwestern North Sea.

Rae (1967) analysed samples from most of the North Sea. In the southern part

Table 3. Average percentage by weight of fish in the stomach contents of North Sea cod, 1966-1972. Data from Daan (1973).

Age group	Length group (cm)		Average percentage food composition*										
	Central and northern NS	Southern NS	Cod	Haddock	Whiting	Other gad-oids	Sandeel	Sprat	Her-ring	Mack-erel	Plaice	Total	Fish total**
I	10-29	10-39	9.8	0	0.3	2.7	5.0	3.5	0.1	1.1		22.5	33.4
II	30-49	40-59	8.0	9.5	1.6	11.0	11.9	9.6	2.7	4.4		58.7	65.8
III	50-69	60-69	6.4	21.8	6.9	15.5	2.7	5.9	5.8	7.7	0.2	72.9	80.0
IV	70-79	70-79	7.2	31.5	6.6	5.5	2.6	3.0	13.7	3.9	1.1	75.1	84.8
V	80-89	80-89	12.6	18.2	2.2	8.9	1.9	1.2	8.2	9.1	1.5	63.8	82.5
VI+	≥90	≥90	8.2	29.1	5.7	3.5	0.6	3.2	5.4	7.8	4.6	68.1	92.1

* Assuming that 25 % of the total cod stock can be found in what Daan (1973) defines as the southern North Sea.

** Including species such as dab and sole.

he found sandeels and flatfishes to be important while in the northern part herring, mackerel, haddock, Norway pout and whiting were also common.

The most detailed information on cod feeding in the North Sea was collected by Daan (1973). From 1966 to 1972 a total of 7430 cod stomachs were examined, of which 5705 were sampled in the southern part of the North Sea and 1725 in the central. All of the samples were grouped according to predator length and worked up on a weight basis. It was thus possible to assess the percentage food composition of each length group in the two areas.

For the present purpose these length-groups were converted to age-groups by use of the age-length key given by Daan (1974), and the average food composition of each age-group and area calculated. Assuming that 25 % of the cod stock can be found in the area defined by Daan (1973) as the southern North Sea and furthermore that the food composition in the northern part is the same as in the central, the average total North Sea food-composition of each age-group was calculated (Table 3).

Robb & Hislop (1980) investigated the food composition of juvenile cod in the pelagic phase. They found Norway pout to be the most dominant food item. In July it constituted 94 % of the total weight of the stomach content of 20 to 119 mm long cod. In the area west of Scotland Nagabushanam (1965) however found calanoid copepods to be the main food item.

The prey size preference of cod was investigated by Daan (1973) and Ursin (1973). Daan found that a cod on average preferred prey which weighed one percent of its own weight, a result which agrees nicely with Ursin (1973) who found cod preferring prey weighing 0.6 percent of their own weight.

Haddock

A considerable amount of work has been done to determine the food composition of haddock, most of it unfortunately only on a qualitative basis.

Brook (1885), Smith (1888, 1890) and Scott (1901) examined the food of haddock in Scottish waters and found the haddock eating mainly bottom invertebrates.

Todd (1907) describes the chief food of haddock in the central and southern North Sea as consisting of Mollusca, Polychaeta, Echinodermata and Crustacea. Fish were found only occasionally in the stomachs and the two species recorded were sandeel and *Gobius* sp. occurring in only 3 and 2 percent of the stomachs, respectively.

Ritchie (1937) provided a detailed report on the stomach content of haddock in Scottish waters. According to his results haddock only devour fish in certain areas such as the Moray Firth and the Great Fisher Bank. Sandeel and mackerel were the only fish species found in the samples from the North Sea, although stomachs obtained from the area west of Scotland also contained Norway pout.

Hertling (1940) found no sandeel in haddock stomachs from the southern North Sea. Instead he recorded juvenile cod, gobies, *Myxine* and *Branchiostoma* sp.

Jones (1954) examined about 900 stomachs from the northern North Sea. His findings are quite in agreement with those of Ritchie (1937) with respect to the frequency of fish in the samples. The most important fish prey was sandeel, but in addition he noted Norway pout, gurnard, redfish, gobies, long rough dab and

Table 4. Weight percentage of fish in the stomach contents of haddock as a function of length. Data from Hertling (1940).

Length group (cm)	15-21	20-33	26-45	33-63
Per cent fish	0.01	0.40	13.77	7.31

Table 5. Tentative food composition of North Sea haddock. Average weight percentage of different fish in the food.

Prey	Age		
	0-1	2-3	4-10
Saithe	0	0	0
Cod	0	0.1	0.2
Haddock	0	0	0
Whiting	0	0.1	0.2
Norway pout	0	0.2	2.0
Sandeel	0.1	5.0	6.0
Sprat	0	1.0	2.0
Herring	0	0.1	2.0
Mackerel	0	0	0.1
Plaice	0	0	0
Total	0.1	6.5	12.5

herring. Furthermore his results indicate an increase in the proportion of fish in the stomachs with age, an observation also made by Todd (1907) and Hertling (1940) (Table 4).

Meis (1978) examined 528 haddock stomachs sampled throughout most of the North Sea. In the central North Sea fish were only found in 4% of the stomachs and the main species were sprat, sandeel, Norway pout, whiting, sole, *Callionymus lyra* and *Lumpenus lampetiformis*. Near the northern English and Scottish

coasts fish occurred in 12 % of the stomachs, the species being sandeel, whiting, herring and other clupeoids. In the northeastern North Sea 54 % of the stomachs contained fish. Sandeels were of very great importance as food, but Norway pout were also abundant.

Table 5 shows a tentative average food composition for haddock. Due to the apparently large geographical differences in food composition the figures are subject to a large uncertainty.

Whiting

According to the literature whiting seems to be at least as great a fish predator as cod and saithe.

Mathews (1886) examined 400 whiting stomachs from the northwestern North Sea and found that the food consisted almost entirely of small fish and Crustacea. Among the prey species found he noted sprat, herring, sandeel, young cod and haddock. Fish occurred in 57 % of the stomachs, Crustacea in 53 % and only 17 % contained food of other kinds.

Smith (1888, 1890) reports from the same area that fish such as herring, sprat, sandeel, whiting, haddock and flatfish together with Crustacea dominate the food of whiting.

Todd (1905, 1907) studied the food of whiting in the southern North Sea and found Crustacea in 67 %, fish in 40 % and other food in 11 % of the stomachs.

Hertling (1940) went into more detail. First of all he recorded the weight of the different food items found in the stomachs, secondly he grouped the samples according to the length of the whiting. He thus found (Table 6) that the percentage of fish increased as a function of the size of the whiting.

Table 6. Weight percentage of fish in the stomach contents of whiting as a function of length. Data from Hertling (1940).

Length group (cm)	12-21	14-32	25-43
Per cent fish	21.5	57.5	77.3

The species found were herring, sprat, *Callionymus lyra*, *Agonus cataphractus*, whiting, four-bearded rockling, gobies, dab and plaice. The mean predator to prey weight ratio was on the order of 1:200.

The most comprehensive investigation up to now was made by Jones (1954). He examined a total of 4300 stomachs obtained from the northwestern part of the North Sea. The stomachs mostly contained fish and Crustacea such as *Crangon allmanni*. Besides recording the percentages weight of the different food items he also calculated the geometric mean of the total stomach contents at different times of the year, thus making it possible to calculate an average yearly food composition by weighting the food composition from the mean weight of the stomach contents in the various months (Table 7a).

Meis (1978) recently examined the food in different parts of the North Sea. A total of 1215 stomachs sampled during the winter 1977 were analysed. In the southern North Sea 38 % of the stomachs contained fish, mainly sprat. In the central

Table 7. Average percentage by weight of fish in the stomach contents of whiting.

a: Northern North Sea, data from Jones (1954)						
Length (cm)	<21	21-25	26-30	31-35	36-40	41-45
Age (approx.)	0	1	2	3-4	5-6	6-8
Prey						
Whiting	3.0	6.2	2.2	6.0	13.6	6.4
Norway pout	2.3	47.0	60.2	51.7	63.4	83.8
Sandeel	45.4	15.0	11.2	0.1	0.5	
Herring		6.0	0.8		0.1	7.1
Other fish	9.6	9.8	9.7	28.4	7.5	1.1
Total	60.3	84.0	84.1	86.2	85.1	98.4
b: Total North Sea, estimated values						
Length (cm)	<21	21-25	26-30	31-35	36-40	41-45
Age (approx.)	0	1	2	3-4	5-6	6-8
Prey						
Whiting	3.3	6.0	2.9	4.9	13.6	8.6
Norway pout	1.2	23.5	30.1	25.8	31.7	41.9
Sandeel	34.0	23.3	21.4	16.3	16.0	18.5
Herring		5.8	1.0		0.1	9.5
Sprat	11.3	15.8	15.8	16.2	16.2	18.5
Other fish	10.5	9.6	12.9	23.0	7.5	1.4
Total	60.3	84.0	84.1	86.2	85.1	98.4

54% contained fish also mostly sprat. In the northwestern part 68% contained fish. Here the clupeoids were the dominant food item as well, but in addition Norway pout was abundant. Finally in the northeastern part, where 73% had fish remains in their stomachs, Norway pout were dominant succeeded by sandeels.

In order to arrive at an approximate average food composition for the whole North sea it was assumed that the same percentage of the stomach contents consisted of fish in the southern part as in the northern. Furthermore it was assumed that 75% of the fish food in the southern part in summer consisted of sandeels; in winter it was assumed that 75% consisted of sprat. The remaining fourth was divided between herring, whiting and others in the same proportion as in the northern part. Finally the food composition for the whole North Sea given in Table 7b was estimated under the assumption that half of the population can be found in the southern North Sea, the other half in the northern.

Norway pout

The food of Norway pout has been examined by Raitt & Adams (1964). Although their main conclusion was that Norway pout eat copepods and other pelagic Crustacea, a conclusion confirmed by investigations in other areas (Nagabushanam 1965, Gordon 1977), they also found that the juveniles especially consumed

fish larvae at certain times. In April, for instance, 17% of the volume of the stomach contents of the juveniles consisted of fish larvae. For the adults the maximum monthly average was found in March when 6% of the stomach contents of the adults consisted of fish larvae.

The observations of Robb & Hislop (1980) confirm these findings with respect to the juveniles. They found that up to 25% of the stomach contents of juvenile Norway pout in July consisted of fish larvae.

Sprat

Surprisingly little information is available on the food composition of sprat in the North Sea and most of the existing information is based on very restricted sampling.

Scott (1901) examined the stomach contents of 30 sprat and found only crustaceans. Lebour (1921) investigated the food of young sprat and recorded no fish larvae. Robertson (1938) examined the food of sprat caught in the English winter fishery. Most of the stomachs were empty and those which contained some food did not contain any fish or fish-larvae. Anon. (1970) does not mention any feeding on fish in the North Sea.

De Silva (1973) made a comparison between the food of herring and sprat in the area west of Scotland. In contrast to those of herring, sprat stomachs never contained fish larvae. Moore & Moore (1976) described the food of sprat in the Severn Estuary as consisting almost exclusively of *Gammarus salinus*.

Though it thus seems that sprat do not eat fish larvae in the North Sea it has been reported to do so in other areas (Anon. 1970).

Sandeel

Ammodytes marinus is by far the most abundant species in the landings from the industrial fishery for sandeels in the North Sea.

According to Macer (1966) the food of *A. marinus* consists of copepods and other pelagic invertebrates.

Herring

The results of investigations of the importance of fish in the diet of herring are rather dissimilar and indicate great areal and seasonal differences.

Brook & Calderwood (1885) examined the food of herring from Scottish waters. On the east coast *Hyperia* and euphausiids formed the main winter diet supplemented in certain estuaries with young sprat, in the Moray Firth with sandeels and on the spawning ground with their own eggs. During the summer months the food consisted of copepods.

Scott (1901) recorded no fish-larva in stomach samples from Scottish waters.

Hardy (1924) examined the stomach contents of a large number of herring from the Shields area, the area between the English coast and the Dogger Bank, and concluded that sandeels accounted for 41% of the total annual food, copepods, euphausiids and *Hyperia* being second in importance. He also examined the food of larval and young herring and found that fish started to appear in the stomachs when the herring had reached a length of approx. 8 cm.

Lissner (1925) reported copepods, euphausiids, and in small amounts sandeels in herring stomachs from the western North Sea.

Ogilvie (1934), working in Scottish waters, found sandeels to be important only in areas near the coast. Other fish species, which were seldom found, included clupeoids and various gadoids, such as saithe and haddock.

Savage (1937) compared samples from the northern North Sea with samples from the Shields area. In the northern North Sea sandeels and fish larvae only made up 1% of the total volume of the food, whereas in the Shields area fish constituted 9% of the diet, sandeel being the principal species. The last figure is low compared to the one given by Hardy (1924). However this may not reflect any significant difference, as Savage mentions that the factors used by him and Hardy for converting number of sandeels and other fish into volume differ by a factor of ten.

No detailed investigation of the food of herring in the North Sea has been published since that time. Hansen (1955) examined the food in the Bløden area, but unfortunately took no samples in the main feeding season.

Mackerel

Ehrenbaum (1923, p. 27) describes the feeding habits of mackerel in the following words: 'The mackerel is undoubtedly one of the greediest of fishes, devouring almost everything that comes in its way. Its principal food organisms, however, are probably certain fishes, as well as a number of Crustacea found in shoals, belonging to the families of Schizopods, Amphipods and Copepods.' As the most important fish species in the diet he mentions young herring, sprat and sandeels supplemented in late summer and autumn with young pelagic gadoids. Furthermore he mentions cannibalism to be important both in the adult stage and among the juveniles.

Recently Walsh & Rankine (1979) published a paper in which they review data collected in the North Sea between 1970 and 1979. Their data show that fish is an important part of the food in the western North Sea, but not in the eastern. Among the species found were sprat, herring, hake, whiting, *Maurolicus muelleri*, sandeel and gobies, of which sandeels were the most important. It is very difficult to base any firm conclusions on their data because of the great difference between areas, but they indicate that at least for the older stock components, carnivores are probably as important in the diet as herbivores.

Grave (1981) published information on the juveniles which points at the importance of cannibalism. Within the size-group from 13 to 19 mm 83% of the food consisted of mackerel larvae, a rather astonishing result in so far as mackerel larvae only accounted for less than 0.1% of the total number of organisms found in the plankton samples.

Plaice

The food of plaice seems mostly to consist of various bottom invertebrates, fish occur only seldom. Todd (1915) investigated the stomach content of 4689 plaice from the North Sea and found only a very few fish, the only species recorded was sandeel. Ritchie (1938), however, found sandeels to be important on some locations

in the Moray Firth, St. Andrews Bay and Firth of Forth. Jones (1952) found only a very few fish remains in stomachs from plaice caught off the Cumberland coast.

3.1.3.2 Geographical overlap

By use of eq. (2.21) the geographical overlap, o_i^j , between two stocks, i and j , can be calculated as the sum over all international squares of the product of the fraction of the two stocks which occur within each particular square. However, to do this we need to know the relative distribution of the various stocks on a per square basis.

For most of the roundfish species in the North Sea the average relative distribution has been derived from the International Youngfish Surveys. For the other species we have been forced to use less detailed information. Fig. 4 to 20 show the resulting density distributions and indicate the sources from which they were obtained. The results from the Youngfish Surveys have generally been split into three types in order to simplify the picture a bit. The first type encompasses squares where more than 0.5 % of the population on average was found (indicated by black dots in the figures), the second where a few but less than 0.5 % were found (indicated by circles) and the third squares where no or only very few individuals occurred. For species not represented properly in these surveys we have either used the catch distribution (e.g. sandeel) or tried to find information on where they occurred during their main feeding season (e.g. mackerel and herring). The distribution of other food has already been shown in Figs 1 & 2.

The resulting matrices of coefficients of overlap are given in Table 8.

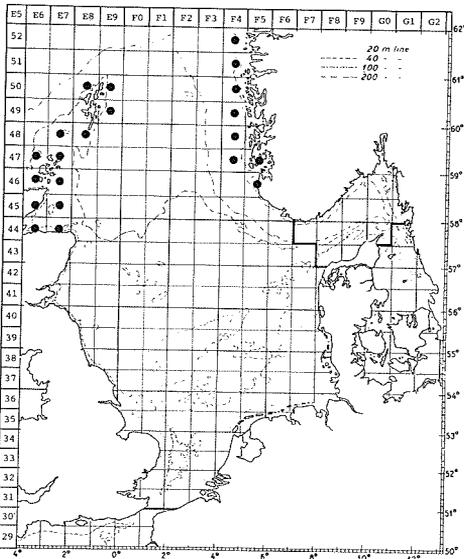


Fig. 4. Saithe. Distribution of young fish. 100 % of population assumed to occur within area marked: ●. From Reinsch (1976).

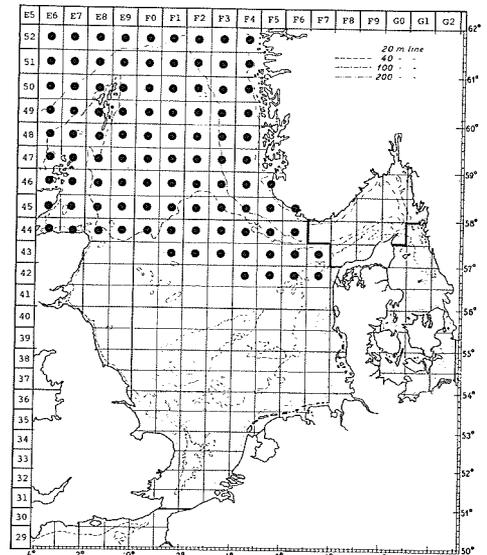


Fig. 5. Saithe. Distribution of old fish. 100 % of population assumed to occur within area marked: ●. From Reinsch (1976).

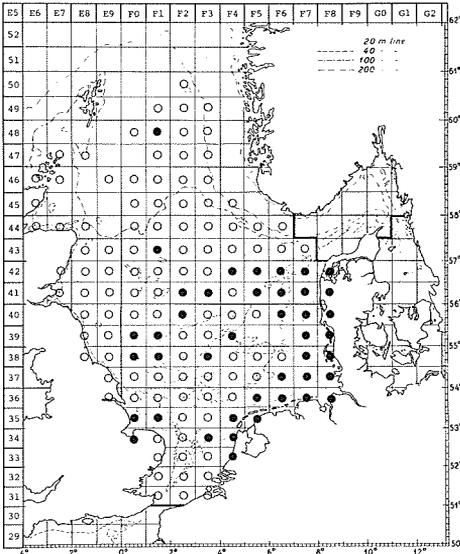


Fig. 6. Cod. Distribution of young fish. 85% of population assumed to occur within area marked: ○. 15% within area marked: ●. From Anon. (1977a).

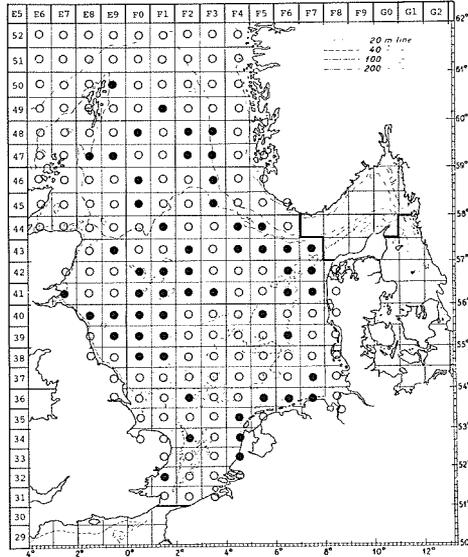


Fig. 7. Cod. Distribution of old fish. 84% of population assumed to occur within area marked: ●, 16% within area marked: ○. From Anon. (1977a).

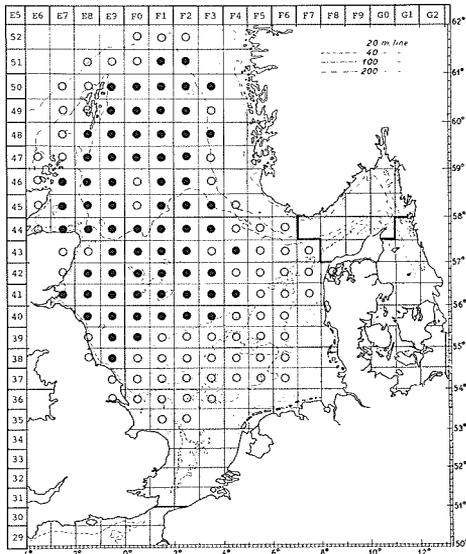


Fig. 8. Haddock. Distribution of young fish. 92% of population assumed to occur within area marked: ●, 8% within area marked: ○. From Anon. (1977a).

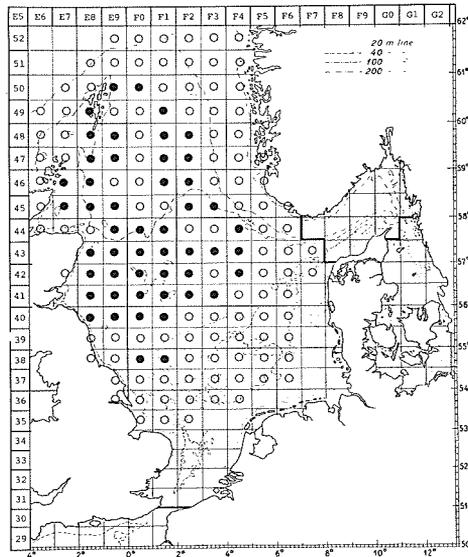


Fig. 9. Haddock. Distribution of old fish. 81% of population assumed to occur within area marked: ●, 19% within area marked: ○. From Anon. (1977a).

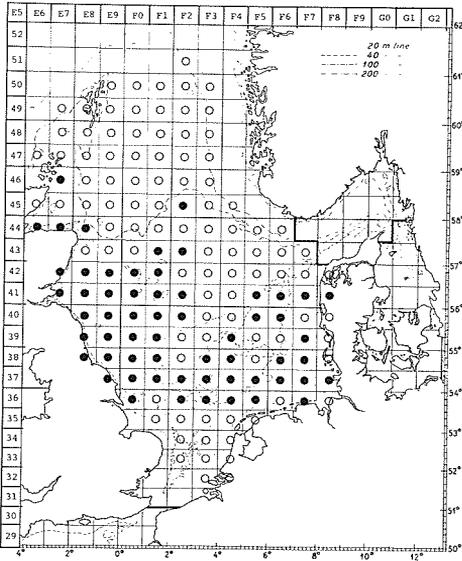


Fig. 10. Whiting. Distribution of young fish. 86% of population assumed to occur within area marked: ●, 14% within area marked: ○. From Anon. (1977a).

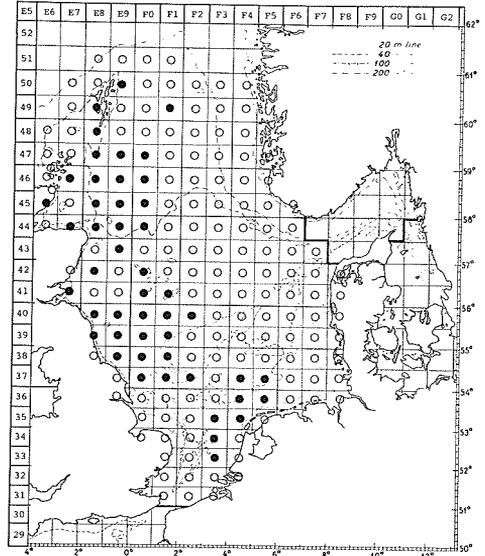


Fig. 11. Whiting. Distribution of old fish. 85% of population assumed to occur within area marked: ●, 15% within area marked: ○. From Anon. (1977a).

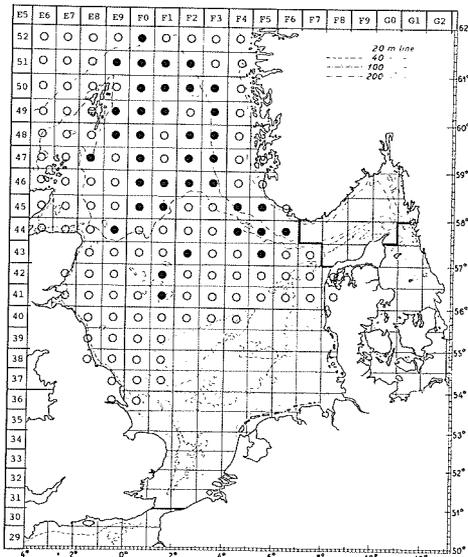


Fig. 12. Norway pout. Distribution of population. 92% assumed to occur within area marked: ●, 8% within area marked: ○. From Anon. (1977a).

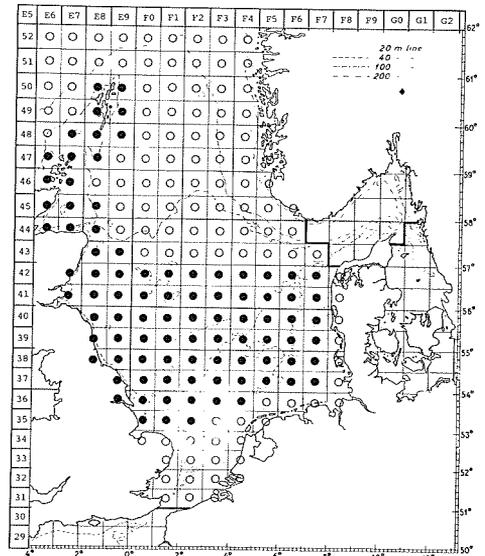


Fig. 13. Sprat. Distribution of population. 95% assumed to occur within area marked: ●, 5% within area marked: ○. From Anon. (1978b, 1970).

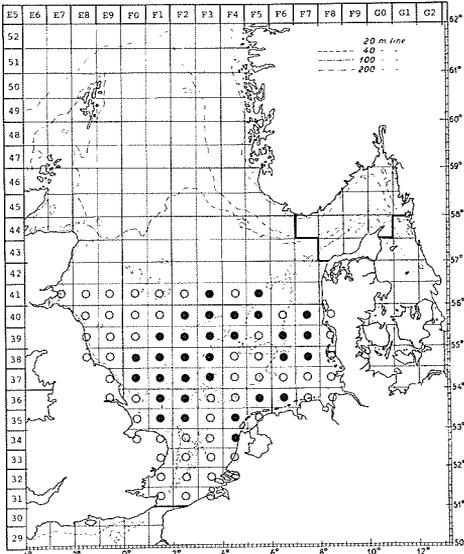


Fig. 14. Sandeel, southern North Sea. Distribution of population. 95% assumed to occur within area marked: ●, 5% within area marked: ○. From Anon. (1977b, 1978a).

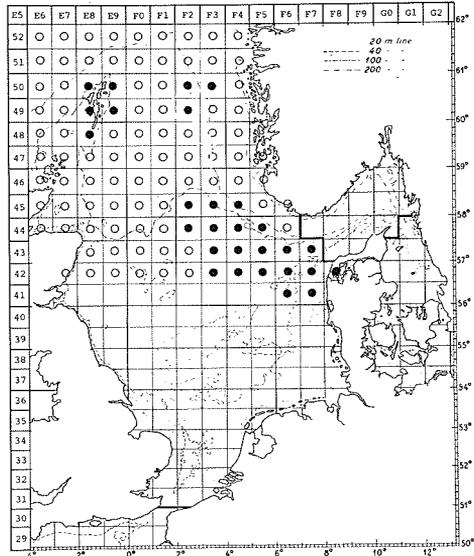


Fig. 15. Sandeel, northern North Sea. Distribution of population. 96% assumed to occur within area marked: ●, 4% within area marked: ○. From Anon. (1977b, 1978a).

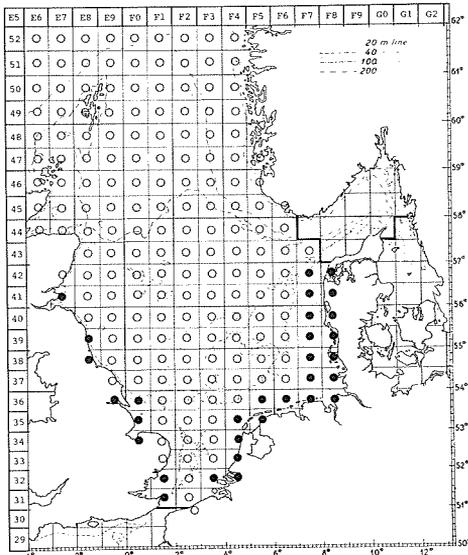


Fig. 16. Herring. Distribution of young fish. 90% of population assumed to occur within area marked: ●, 10% within area marked: ○. From Anon. (1978b).

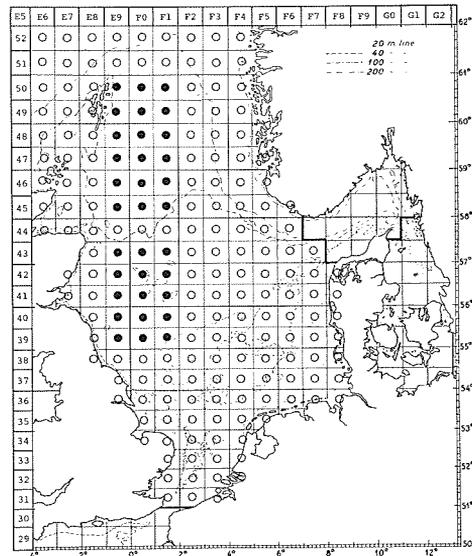


Fig. 17. Herring. Distribution of old fish. 75% of population assumed to occur within area marked: ●, 25% within area marked: ○. From Anon. (1979).

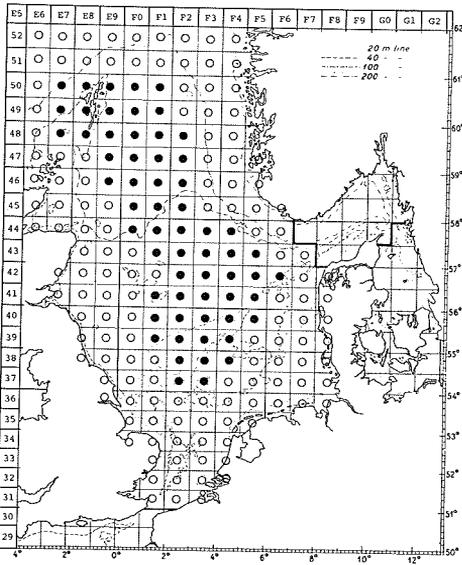


Fig. 18. Mackerel. Distribution of population. 60% assumed to occur within area marked: ●, 40% within area marked: ○. From Anon. (1979).

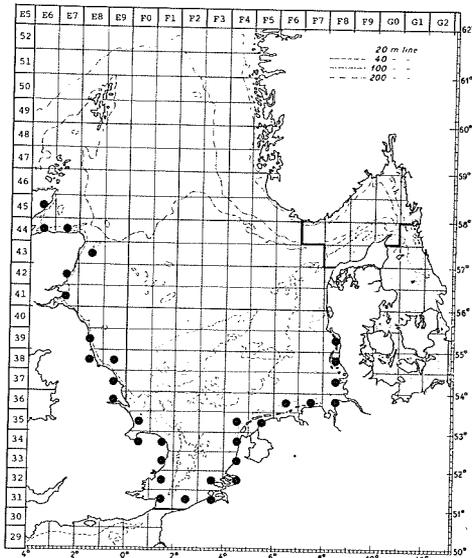


Fig. 19. Plaice. Distribution of young fish. 100% of population assumed to occur within area marked: ●.

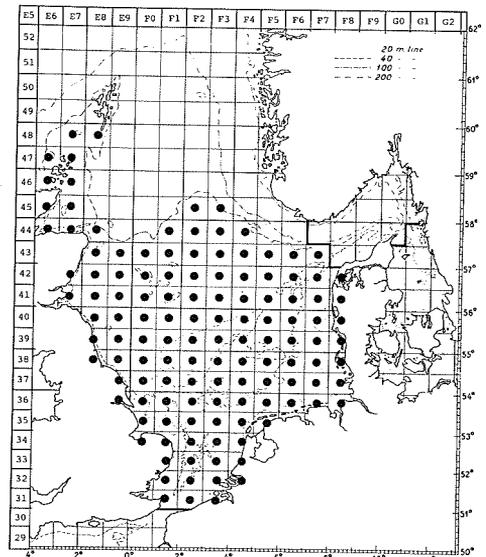


Fig. 20. Plaice. Distribution of old fish. 100% of population assumed to occur within area marked: ●.

Table 8. Geographical overlap, $o_j^i \times 10^2$. See text for explanation.

A. Overlap of old fish														
Species	Saithe	Cod	Had-dock	Whit-ing	N. pout	Sandeel s.NS	Sandeel n.NS	Sprat	Her-ring	Mack-erel	Plaice ♂♂	Plaice ♀♀	Other food pelag.benth.	
Saithe	1.02	0.44	0.60	0.41	0.94	0.00	0.88	0.26	0.56	0.57	0.24	0.24	0.66	0.27
Cod	0.44	1.30	0.75	0.73	0.70	0.61	0.71	0.54	0.74	0.54	0.57	0.57	0.47	0.56
Haddock	0.60	0.75	1.33	0.79	0.67	0.28	0.62	0.59	0.91	0.63	0.51	0.51	0.48	0.41
Whiting	0.41	0.73	0.79	1.48	0.43	0.59	0.35	0.70	0.85	0.51	0.57	0.57	0.43	0.49
Norway pout	0.94	0.70	0.67	0.43	2.31	0.03	0.69	0.19	0.92	0.64	0.13	0.13	0.64	0.22
Sandeel, s.NS	0.00	0.61	0.28	0.59	0.03	2.93	0.00	0.90	0.23	0.59	0.77	0.77	0.36	0.68
Sandeel, n.NS	0.88	0.71	0.62	0.35	0.69	0.00	3.30	0.47	0.32	0.68	0.54	0.54	0.52	0.42
Sprat	0.26	0.54	0.59	0.70	0.19	0.90	0.47	0.99	0.50	0.52	0.71	0.71	0.40	0.51
Herring	0.56	0.74	0.91	0.85	0.92	0.23	0.32	0.50	1.74	0.66	0.40	0.40	0.48	0.38
Mackerel	0.57	0.54	0.63	0.51	0.64	0.59	0.68	0.52	0.66	0.71	0.49	0.49	0.48	0.45
Plaice ♂♂	0.24	0.57	0.51	0.57	0.13	0.77	0.54	0.71	0.40	0.49	0.77	0.77	0.38	0.69
Plaice ♀♀	0.24	0.57	0.51	0.57	0.13	0.77	0.54	0.71	0.40	0.49	0.77	0.77	0.38	0.69

B. Overlap of old and young fish														
Young Old	Saithe	Cod	Had-dock	Whit-ing	N. pout	Sandeel s.NS	Sandeel n.NS	Sprat	Her-ring	Mack-erel	Plaice ♂♂	Plaice ♀♀	Other food pelag.benth.	
Saithe	1.02	0.18	0.63	0.19	0.94	0.00	0.88	0.26	0.09	0.57	0.09	0.09	0.66	0.27
Cod	0.18	0.67	0.66	0.65	0.70	0.61	0.71	0.54	0.59	0.54	0.41	0.41	0.47	0.56
Haddock	0.50	0.36	1.03	0.63	0.67	0.28	0.62	0.59	0.14	0.63	0.16	0.16	0.48	0.41
Whiting	0.54	0.48	0.77	0.82	0.43	0.59	0.35	0.70	0.34	0.51	0.41	0.41	0.43	0.49
Norway pout	0.18	0.11	0.86	0.25	2.31	0.03	0.69	0.19	0.08	0.64	0.03	0.03	0.64	0.22
Sandeel, s.NS	0.00	1.10	0.21	0.86	0.03	2.93	0.00	0.90	0.70	0.59	0.34	0.34	0.36	0.68
Sandeel, n.NS	0.82	0.57	0.64	0.28	0.69	0.00	3.30	0.47	0.35	0.68	0.01	0.01	0.52	0.42
Sprat	0.68	0.61	0.55	0.86	0.19	0.90	0.47	0.99	0.46	0.52	0.47	0.47	0.40	0.51
Herring	0.34	0.38	1.02	0.61	0.92	0.23	0.32	0.50	0.19	0.66	0.15	0.15	0.48	0.38
Mackerel	0.48	0.49	0.65	0.49	0.64	0.59	0.68	0.52	0.32	0.71	0.29	0.29	0.48	0.45
Plaice ♂♂	0.38	0.73	0.45	0.73	0.13	0.77	0.54	0.71	0.74	0.49	0.77	0.77	0.38	0.69
Plaice ♀♀	0.38	0.73	0.45	0.73	0.13	0.77	0.54	0.71	0.74	0.49	0.77	0.77	0.38	0.69

C. Overlap of young fish														
Species	Saithe	Cod	Had-dock	Whit-ing	N. pout	Sandeel s.NS	Sandeel n.NS	Sprat	Her-ring	Mack-erel	Plaice ♂♂	Plaice ♀♀	Other food pelag.benth.	
Saithe	4.55	0.04	0.41	0.26	0.18	0.00	0.82	0.68	0.06	0.48	0.41	0.41	0.79	0.35
Cod	0.04	1.75	0.29	0.77	0.11	1.10	0.57	0.61	1.28	0.49	0.83	0.83	0.37	0.85
Haddock	0.41	0.29	1.25	0.60	0.86	0.21	0.64	0.55	0.12	0.65	0.16	0.16	0.49	0.38
Whiting	0.26	0.77	0.60	1.28	0.25	0.86	0.28	0.86	0.60	0.49	0.50	0.50	0.38	0.57
Norway pout	0.18	0.11	0.86	0.25	2.31	0.03	0.69	0.19	0.08	0.64	0.03	0.03	0.64	0.22
Sandeel, s.NS	0.00	1.10	0.21	0.86	0.03	2.93	0.00	0.90	0.70	0.59	0.34	0.34	0.36	0.68
Sandeel, n.NS	0.82	0.57	0.64	0.28	0.69	0.00	3.30	0.47	0.35	0.68	0.01	0.01	0.52	0.42
Sprat	0.68	0.61	0.55	0.86	0.19	0.90	0.47	0.99	0.46	0.52	0.47	0.47	0.40	0.51
Herring	0.06	1.28	0.12	0.60	0.08	0.70	0.35	0.46	2.54	0.32	1.81	1.81	0.37	1.06
Mackerel	0.48	0.49	0.65	0.49	0.64	0.59	0.68	0.52	0.32	0.71	0.29	0.29	0.48	0.45
Plaice ♂♂	0.41	0.83	0.16	0.50	0.03	0.34	0.01	0.47	1.81	0.29	3.03	3.03	0.36	1.16
Plaice ♀♀	0.41	0.83	0.16	0.50	0.03	0.34	0.01	0.47	1.81	0.29	3.03	3.03	0.36	1.16

Table 9. Vulnerability, ρ_j^i . See text for explanation.

A. Old fish preying on old fish and other food														
Predator	Prey													
	Saithe	Cod	Had-dock	Whit-ing	N. pout	Sandeel s.NS	Sandeel n.NS	Sprat	Her-ring	Mack-erel	Plaice ♂♂	Plaice ♀♀	Other food pelag. benth.	
Saithe	1.00	1.00	1.00	1.00	1.00	0.40	0.40	0.80	0.80	0.80	0.50	0.50	1.00	0.00
Cod	1.00	1.00	1.00	1.00	1.00	0.40	0.40	0.40	0.40	0.40	0.50	0.50	0.00	1.00
Haddock	0.25	0.25	0.25	0.25	0.25	0.50	0.50	0.00	0.00	0.00	0.50	0.50	0.00	1.00
Whiting	1.00	1.00	1.00	1.00	1.00	0.40	0.40	0.40	0.40	0.40	0.50	0.50	0.50	0.50
Norway pout	1.00	1.00	1.00	1.00	1.00	0.40	0.40	0.80	0.80	0.80	0.00	0.00	1.00	0.00
Sandeel, s.NS	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.80	0.80	0.80	0.00	0.00	1.00	0.00
Sandeel, n.NS	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.80	0.80	0.80	0.00	0.00	1.00	0.00
Sprat	0.50	0.50	0.00	0.50	0.50	0.40	0.40	0.80	0.80	0.80	0.00	0.00	1.00	0.00
Herring	0.50	0.50	0.00	0.50	0.50	0.40	0.40	0.80	0.80	0.80	0.00	0.00	1.00	0.00
Mackerel	0.50	0.50	0.00	0.50	0.50	0.40	0.40	0.80	0.80	0.80	0.00	0.00	1.00	0.00
Plaice ♂♂	0.25	0.25	0.25	0.25	0.25	0.50	0.50	0.00	0.00	0.00	0.50	0.50	0.00	1.00
Plaice ♀♀	0.25	0.25	0.25	0.25	0.25	0.50	0.50	0.00	0.00	0.00	0.50	0.50	0.00	1.00

B. Old fish preying on young fish and other food														
Predator	Prey													
	Saithe	Cod	Had-dock	Whit-ing	N. pout	Sandeel s.NS	Sandeel n.NS	Sprat	Her-ring	Mack-erel	Plaice ♂♂	Plaice ♀♀	Other food pelag. benth.	
Saithe	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.50	0.50	1.00	0.00
Cod	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.00	1.00
Haddock	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00	1.00
Whiting	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50	0.50
Norway pout	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Sandeel, s.NS	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Sandeel, n.NS	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Sprat	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Herring	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Mackerel	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Plaice ♂♂	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00	1.00
Plaice ♀♀	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00	1.00

C. Young fish preying on young fish and other food														
Predator	Prey													
	Saithe	Cod	Had-dock	Whit-ing	N. pout	Sandeel s.NS	Sandeel n.NS	Sprat	Her-ring	Mack-erel	Plaice ♂♂	Plaice ♀♀	Other food pelag. benth.	
Saithe	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Cod	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Haddock	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Whiting	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Norway pout	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Sandeel, s.NS	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Sandeel, n.NS	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Sprat	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Herring	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Mackerel	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00	0.00
Plaice ♂♂	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00	1.00
Plaice ♀♀	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.50	0.00	1.00

3.1.3.3 *General vulnerability*

The general vulnerability, ρ_j^i , is intended to describe all differences in food selection which cannot be ascribed to differences in horizontal distribution and relative size of prey and predators. As such it must take account of a mixture of factors such as the vertical distribution and behaviour of the different species. For this reason it is almost impossible to make any rule of thumb which could substitute data on the average yearly food composition when estimating vulnerability. What we have done here is for each predator to start with a vector of vulnerabilities all equal to one and then on the basis of what is known about the vertical distribution and stomach contents gradually to reduce some of the ρ_j^i 's.

As reflected by the stomach contents saithe and Norway pout feed in the water column whereas cod and whiting include benthos in their food. The vulnerability of pelagic species as food for cod and whiting was therefore reduced to 0.5. As a prey item sandeel represents a special problem as it can be found both half buried in the sediment and schooling in the water column. If we assume that it spends half of the time buried and the other half swimming and furthermore is accessible only when swimming, its vulnerability to predation by the four species could as first approximation be set to 0.5. Schooling in itself is another problem. As shown by Brock & Riffenburgh (1960) schooling is advantageous for prey species at least in theory because it reduces predation. The vulnerability of schooling species such as sandeel, sprat, herring and mackerel was therefore reduced by 20 per cent. The vulnerability of plaice was set to 0.5 in order to take account of their strictly demersal life and for predators their somewhat unsuitable body shape.

Haddock seem to prefer food items situated at or just below the bottom surface. The vulnerability of saithe, cod, whiting, Norway pout and haddock itself was therefore reduced to 0.25 and the vulnerability of the pelagic species set to 0.0. Presumably haddock only feed on sandeels when they are buried, and using the same argument as above their vulnerability was reduced to 0.5. The vulnerability of plaice was set to 0.5.

All species seem on the basis of their vertical distribution to be equally suitable for sandeel, except the schooling ones and plaice, for which the vulnerability was reduced to 0.8 and 0.0, respectively.

The pelagic species, i.e. sprat, herring and mackerel, due to their vertical distribution and feeding habits and in order to take account of schooling, were thought to meet only half of the populations of saithe, cod, whiting and Norway pout, no haddock and plaice, and half of the sandeel population and to have a reduced vulnerability as food for each other.

Plaice was assumed to meet only a quarter of the populations of saithe, cod, haddock, whiting and Norway pout whose vulnerability thus was reduced to 0.25. As shown by the stomach contents plaice is able to feed on the buried sandeels and their vulnerability was therefore set to 0.5, as was the vulnerability of plaice itself.

The vulnerabilities of other pelagic and benthic food were assessed, using the available stomach content data.

The resulting matrix of vulnerability which expresses the vulnerability of old fish and other food to predation by old fish is given in Table 9A.

All of the young fish except for plaice and to some extent saithe are pelagic in the period prior to the time of first capture. The simplest way of estimating their vulnerability to predation by old fish is thus once more to look at the vertical distribution of their potential predators. The vulnerability matrix is given in Table 9B.

The vulnerability of young fish as food for other young fish was in general kept at 1.0, except for young plaice which were only allowed to predate upon one another, Table 9C.

3.1.3.4 Size preference

Except perhaps for cod only very sparse data exist from which the size preference parameters η_i and σ_i can be estimated. Most of the values were thus chosen after trial runs with the model in which it was attempted to obtain a size distribution of stomach contents in accordance with the available stomach data (Table 10). The value of σ_i , which indicates how particular the predator is about the size of its prey, was set to 2.0 for all species.

Table 10. Size preference, η_i and σ_i .

Species	Saithe	Cod	Had-dock	Whit-ing	N. pout	Sand-eel	Sprat	Her-ring	Mack-erel	Plaice
η_i	6.21	5.01	7.60	1.61	6.91	8.01	8.01	8.01	8.01	7.60
$\exp(\eta_i)$	500	150	2000	50	1000	3000	3000	3000	3000	2000
σ_i	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0

4. Results

4.1 Trial runs and subsequent changes of parameters

In the first runs the size-preference parameters were adjusted as described in the preceding section. No attempt was made to change the general suitability as it was felt that the stomach content data reviewed in section 3.1.3.1 were too few to allow any firm conclusions on the actual food composition in the period 1965 to 1978.

In order to check how well the food intake of the various stocks compared to their biomass production the ratio of biomass production to food intake was calculated. The biomass production within a year should by definition equal:

$$\int \frac{dw(t)}{dt} \cdot N(t) dt$$

However, as the weights at age is assumed to be constant within the year for the old age-groups, and $dw(t)/dt$ thus equals zero, the biomass production was approximated by adding together the catch, the production of egg and sperm (~15 % of the spawning stock biomass), other mortality, predation and the increase in biomass all expressed in tonnes. On average this sum should be comparable to biomass production.

Table 11. Average ratio of production to food intake 1965-78 for two sets of ν .

	ν $\text{kg}^{(1-0.67)} \cdot \text{y}^{-1}$	$\frac{\text{production}}{\text{food intake}}$	ν $\text{kg}^{(1-0.67)} \cdot \text{y}^{-1}$	$\frac{\text{production}}{\text{food intake}}$
Saithe	2.29	0.29	2.29	0.29
Cod	4.09	0.27	4.09	0.27
Haddock	1.97	0.35	2.41	0.29
Whiting	1.43	0.45	2.32	0.29
Norway pout	1.75	0.45	2.90	0.28
Sandeel, s.NS	1.2	0.22	1.2	0.23
Sandeel, n.NS	2.27	0.18	2.27	0.19
Sprat	1.37	0.25	1.37	0.25
Herring	1.67	0.24	1.67	0.24
Mackerel	2.41	0.11	2.41	0.11
Plaice ♂♂	1.29	0.08	1.29	0.08
Plaice ♀♀	1.04	0.11	1.04	0.11
All species		0.26		0.24

Though the results (Table 11) to some extent depend on the actual life history of the species some of the ratios seem very high, especially for haddock, whiting and Norway pout. Most likely this is due to the very conservative estimates of the rates of food intake.

A second run in which the rates of food intake were slightly increased for the three above mentioned species resulted only in a minor increase in the overall predation and was therefore adopted. Before additional information becomes available any further changes seemed to be unjustified.

4.2 Food composition

For each stock the computer programme generates a table with the yearly food composition and tables with the average food composition of each age-group over selected ranges of years. To review these tables for all stocks would be too extensive and Table 12, which shows the average food composition in the period 1965 to 1978, thus only represents a very small part of the available output. Due to the lack of data on stomach contents it is very difficult to draw any firm conclusions on how good the description of food selection in fact is. However, the calculated food compositions do not seem to be in conflict with the available information.

The only species for which more detailed data exist is cod. Table 13 shows the yearly average food composition of the cod stock in the years from 1965 to 1978. Note the decline of the percentages of herring and mackerel and the increased importance of Norway pout. It is also interesting to see how the large 1967 year-class of haddock shows up in the food in 1968 and 1969. In order to compare the food composition of cod with stomach content data we can look at the period from 1966 to 1972 in more detail. In the previous chapter the average food composition of the cod stock in this period was estimated on the basis of the investigation made by Daan (1973). Table 14 shows the average food composition of each age-group of cod from 1966-72 as calculated by MSVPA and should be comparable to Table 3.

Table 12. Average percentage food composition 1965-78 estimated by MSVPA.

Predator	Prey													
	Saithe	Cod	Had- dock	Whit- ing	N. pout	Sandeel s.NS	n.NS	Sprat	Her- ring	Mack- erel	Plaice ♂♂	♀♀	Other food pelag. benth.	
Saithe	0.6	0.1	3.2	2.7	44.5	0.0	8.1	13.5	4.5	0.7	0.1	0.1	22.1	0.0
Cod	0.8	1.5	7.4	7.9	19.5	10.1	3.8	8.2	5.6	2.8	0.6	0.8	1.0	30.0
Haddock	0.0	0.0	0.0	0.0	0.2	0.7	0.3	0.0	0.0	0.0	0.0	0.0	0.8	97.9
Whiting	0.2	0.1	3.4	7.9	15.4	13.3	2.4	17.0	4.1	0.2	0.1	0.1	4.3	31.6
Norway pout	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	99.7	0.0
Sandeel, s.NS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
Sandeel, n.NS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
Sprat	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	0.0
Herring	0.0	0.0	0.2	0.1	1.1	0.4	0.1	1.2	0.0	0.1	0.0	0.0	96.8	0.0
Mackerel	0.1	0.0	0.5	0.3	4.0	6.6	1.4	6.9	0.3	0.1	0.0	0.0	79.9	0.0
Plaice ♂♂	0.0	0.0	0.0	0.0	0.0	0.5	0.1	0.0	0.0	0.0	0.0	0.0	99.4	0.0
Plaice ♀♀	0.0	0.0	0.0	0.0	0.0	1.2	0.2	0.0	0.0	0.0	0.0	0.0	98.6	0.0

Although the general picture looks all right the two tables show some discrepancies.

First of all the computed percentage of fish in the food seems somewhat high. In particular the one-year old cod eat far more fish in the model than in Daan's investigation. Most likely this is due to the high average weight at age used for this age-group. Converted into length the weight, 267 g, corresponds approximately to an average length of 29.9 cm, while the average length of the one-year olds examined by Daan was 20.9 cm corresponding to a weight of only 91.3 g. If we use 91.3 g as the weight of one-year old cod in the calculations we obtain a decrease in the percentage of fish in the food of this age from 49 to 26 per cent.

A second difference between the two tables is the high percentage of Norway pout and whiting and low percentage of cod in Table 14. For Norway pout, which is included in the group 'other gadoids' in Table 3, this may be due to the fact that Daan's investigation mainly dealt with the southern North Sea.

Table 13. Percentage food composition of cod in the years 1965 to 1978.

Prey	'65	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75	'76	'77	'78
Saithe	0.4	0.5	0.7	0.9	1.6	1.4	0.8	0.8	0.8	1.2	1.1	0.9	0.3	0.4
Cod	1.2	1.6	1.6	0.9	1.1	2.3	2.0	1.3	1.3	1.2	1.3	1.1	1.7	2.0
Haddock	3.8	3.5	9.7	23.5	17.9	6.8	5.0	6.8	6.3	8.6	7.1	4.2	1.9	2.9
Whiting	9.3	7.7	9.0	13.2	11.5	5.5	5.4	10.8	12.4	8.4	7.6	7.5	3.7	4.8
Norway pout	5.7	10.5	15.6	14.6	18.5	22.1	24.4	23.1	21.8	22.0	21.4	28.2	26.9	16.6
Sandeel, s.N.S.	13.5	11.0	8.0	4.5	3.1	8.2	10.5	9.4	7.3	7.9	9.9	10.6	14.2	18.3
Sandeel, n.NS	0.6	0.9	1.2	1.5	2.4	3.8	4.5	4.9	5.8	6.2	4.7	5.4	5.6	5.8
Sprat	9.3	10.5	10.5	7.6	6.4	5.3	5.5	6.4	9.7	12.4	10.6	10.4	7.2	7.7
Herring	13.7	11.2	8.2	7.1	8.3	5.7	4.9	5.7	4.3	3.0	2.6	2.0	1.2	2.1
Mackerel	5.4	5.4	4.8	3.1	3.1	3.2	2.1	2.7	2.8	2.6	1.8	1.7	0.7	0.9
Plaice, ♂♂	0.9	0.9	0.8	0.6	0.8	0.5	0.4	0.5	0.8	0.8	0.6	0.6	0.3	0.5
— ♀♀	1.0	1.1	1.2	1.0	1.3	0.8	0.5	0.6	0.8	0.8	0.6	0.6	0.3	0.4
Other food	35.3	35.1	28.8	21.6	24.1	34.4	34.0	27.0	25.8	25.0	30.7	26.8	36.0	37.7

Table 14. Percentage food composition of different age-groups of cod. Average 1966-72. y: young fish, o: old fish.

Prey		Total	Age													
			0	1	2	3	4	5	6	7	8	9	10	11	12	
Saithe	y	0.0	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	o	1.0	0.00	0.0	0.1	0.7	2.0	3.1	3.9	4.4	4.9	5.1	5.3	5.5	5.5	
Cod	y	0.0	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	o	1.6	0.00	0.0	0.0	1.7	3.4	4.8	5.8	6.3	6.9	7.3	7.6	7.2	7.7	
Haddock	y	0.2	0.00	0.3	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	o	10.7	0.00	2.1	6.3	16.7	19.4	20.9	20.2	20.7	21.5	20.1	21.5	20.9	21.6	
Whiting	y	0.2	0.00	0.2	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	o	8.7	0.00	1.9	5.9	13.6	14.8	15.4	15.9	16.3	16.0	16.2	16.5	17.3	15.8	
Norway pout	y	1.0	0.00	1.6	1.3	0.7	0.5	0.3	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	o	19.0	0.00	19.8	22.8	19.8	16.5	15.0	13.6	12.5	11.8	11.5	11.2	11.7	11.1	
Sandeel s. NS	y	0.2	0.00	0.3	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	o	7.4	0.00	9.6	9.9	6.3	4.6	3.9	3.5	3.1	2.8	2.8	2.7	2.8	2.6	
Sandeel n. NS	y	0.1	0.00	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	o	3.0	0.00	3.4	3.8	2.9	2.3	2.2	2.1	2.0	1.8	1.9	1.9	2.1	1.8	
Sprat	y	0.5	3.09	0.7	0.7	0.4	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	o	6.4	0.00	6.6	8.1	6.9	5.5	4.3	3.7	3.3	3.1	3.0	2.8	2.7	2.8	
Herring	y	0.5	0.00	0.6	0.6	0.4	0.3	0.3	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	o	6.0	0.00	1.9	4.0	9.0	10.5	10.3	10.7	10.6	10.6	10.8	10.1	9.9	10.5	
Mackerel	y	0.4	0.04	0.1	0.2	0.6	1.0	0.9	0.9	0.9	0.9	0.9	0.8	0.7	1.0	
	o	2.7	0.00	0.0	0.0	3.5	6.2	7.5	8.8	9.4	9.7	10.4	10.1	9.8	10.0	
Plaice, ♂♂	y	0.0	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	o	0.5	0.00	0.0	0.1	0.8	1.2	1.4	1.5	1.6	1.6	1.7	1.6	1.6	1.7	
Plaice, ♀♀	y	0.0	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	o	0.9	0.00	0.0	0.1	1.1	2.0	2.4	2.7	2.8	3.0	3.1	3.0	2.9	3.1	
Other food, benthic		28.0	0.00	50.6	35.2	14.4	9.3	6.9	5.8	5.1	4.6	4.5	4.2	4.3	4.2	
Other food, pelagic		0.9	96.87	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

In case of cod several possible explanations exist. The cannibalism found by Daan (1973) was only important in 1970 and 1971 and most of the cod eaten were below 15 cm and thus belonged to the 0-group. Daan suggests that a combination of an increased competition for food due to the large 1969 year-class and the increased abundance of small cod in 1970 and 1971 due to the large 1970 year-class might provide the explanation. The results from the MSVPA in Table 13 also show an increase in the percentage of cod in the food of cod in 1970 and 1971, but not to the same extent as the results in Table 3.

Some of this discrepancy might be due to the various biases introduced in the calculations behind Table 3. Most of the cannibalism took place in the central North Sea. In 1970 it amounted to 20% of the food of cod in this area, while the corresponding figure for the southern part was only 3%. The figures from the central part were not corrected for seasonal and annual differences in sampling intensity. More than 80% of the samples from this area were collected during autumn and winter where cannibalism could be expected to be high, and more than half of them were taken in 1970 and 1971. Hence the overall estimate of the food-composition in this area is possibly biased towards cannibalism. Furthermore the food-composition presented in Table 3 is very dependent on the weighting factors

used for combining the areas. With respect to cannibalism it might not be appropriate to apply the stomach content data from the central North Sea to the northern part. According to Anon. (1977a) and Fig. 6 only very few young cod are caught in the northern North Sea during the International Young Fish survey in February.

Before more detailed data become available it is thus difficult to find out whether cannibalism is as important as Table 3 suggests. If not this will of course change the other figures as well.

Several years of stomach content data would be needed to validate the model of food selection. It would then be possible to compare the food-compositions calculated by the model with measured values and to find out whether observed changes from one year to another are reflected by the model or not.

4.3 Mortality

Table 15 shows the average total natural mortality in the years 1965-67 and 1973-75. Except for the small species, sprat, sandeel and Norway pout, the predation mortality is only important for the younger age-groups. The same result was found by Pope & Knights (1982). Furthermore the table shows a general decrease in the predation mortality for the young fish from a high level in the sixties to a lower one in the seventies. This decrease is a result of the decline of the herring and mackerel stocks. The same can be seen for haddock in more detail in Fig. 21. The predation mortality of the pelagic young fish decreases from 1965 to 1970 while it remains fairly stable for the demersal 0 and I-group.

The relatively higher natural mortality of the younger age-groups of course affects the estimates of the fishing mortality. As an example Fig. 22 shows the average 1965-75 fishing and total natural mortality for haddock calculated by

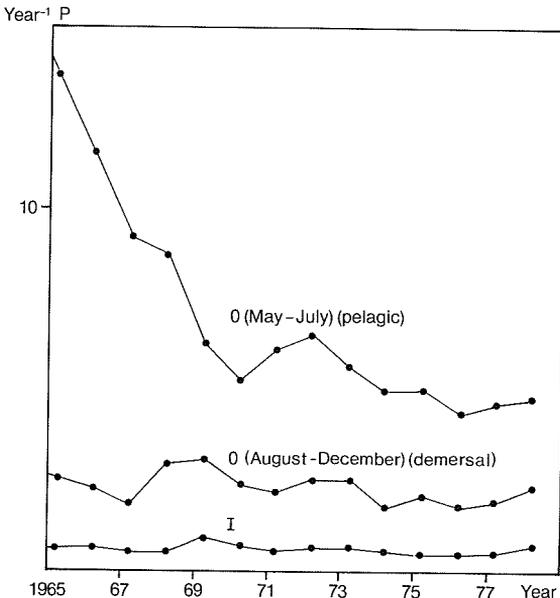


Fig. 21. Haddock. Predation mortality, P , of 0 and I group 1965-1978.

Table 15. Average total natural mortality (= $P + D$) as calculated by MSVPA. $D = 0.2$ for saithe, cod, haddock and whiting, $D = 0.1$ for the rest. t_r = time of recruitment to the model, t_c = time of first capture. A = 1965-67, B = 1973-75.

Age	Saithe		Cod		Haddock		Whiting		Norway pout		Sandeel			
	A	B	A	B	A	B	A	B	A	B	south NS		north NS	
0														
t_r	8.8	4.7	5.2	2.5	11.7	5.4	8.3	3.8	13.3	6.5	10.6	4.5	12.8	6.4
t_c					2.5	2.4	2.8	2.6	3.0	2.7	2.5	1.4	3.0	1.8
1	0.84	1.0	0.41	0.40	0.82	0.77	0.98	0.84	1.8	1.9	1.6	1.0	0.95	0.90
t_c	0.50	0.59												
2	0.24	0.25	0.30	0.30	0.41	0.40	0.49	0.43	1.2	1.2	0.83	0.68	0.60	0.61
3	0.22	0.22	0.21	0.21	0.29	0.30	0.36	0.34	1.0	1.0	0.67	0.58	0.47	0.49
4	0.21	0.21	0.20	0.20	0.25	0.25	0.31	0.30	0.85	0.88	0.62	0.54	0.42	0.43
5	0.20	0.20	0.20	0.20	0.24	0.24	0.28	0.29	0.79	0.82	0.60	0.53	0.38	0.39
6	0.20	0.20	0.20	0.20	0.23	0.23	0.27	0.27			0.59	0.52	0.38	0.39

Age	Sprat		Herring		Mackerel		Plaice			
	A	B	A	B	A	B	males		females	
0										
t_r	10.6	4.7	3.9	1.9	10.1	4.6	0.66	0.58	0.66	0.59
t_c	4.0	2.1	1.1	1.1						
1	1.4	1.1	0.57	0.57	0.36	0.39	0.32	0.29	0.32	0.29
t_c					0.14	0.15	0.27	0.24	0.29	0.26
2	1.1	0.96	0.26	0.27	0.13	0.14	0.20	0.19	0.17	0.16
3	0.76	0.73	0.20	0.21	0.13	0.13	0.16	0.15	0.15	0.14
4	0.72	0.70	0.17	0.18	0.12	0.13	0.14	0.14	0.13	0.13
5	0.71	0.68	0.16	0.17	0.12	0.12	0.13	0.14	0.13	0.13
6			0.16	0.17	0.12	0.12	0.13	0.13	0.12	0.12

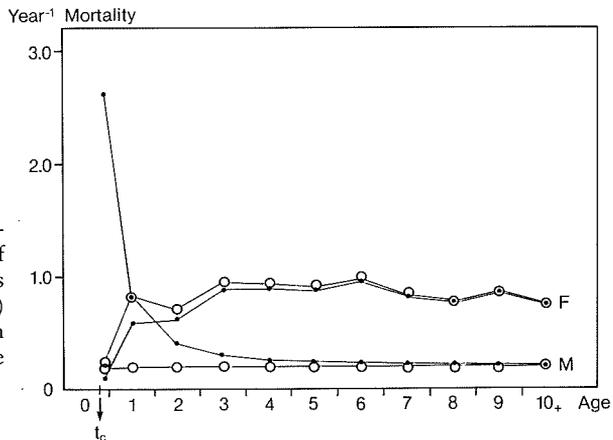


Fig. 22. Haddock. Total natural mortality, M , and fishing mortality, F , of ages 0 to 10 averaged over the years 1965-1975, estimated by MSVPA (●) and VPA (○). M in VPA and D in MSVPA both set equal to 0.2. t_c = age at first capture.

MSVPA and traditional VPA. As the figure shows, the increased natural mortality of the younger age-groups results in a changed exploitation pattern. The younger age-groups are relatively less exploited in the MSVPA-run than in the VPA.

4.4 Stock biomass

The estimated stock biomasses and spawning stock biomasses are given in Tables 16 & 17. In most cases the stock biomasses exceed the stock biomasses estimated by ICES working groups as a result of the increased natural mortality of the juveniles. The estimated spawning stock biomasses are more in accordance (Fig. 23). Differences are due to small differences in natural mortality and to the use of a constant weight at age throughout the whole period, whereas the working groups in many cases have used a separate set of weight-at-age data for each year. Most of our catch-at-age data were taken from the 1981 working group reports and even though we hoped that they would remain more or less unchanged some major revisions have already been made. The 1981 Roundfish working group report thus estimated the total biomass of haddock at the beginning of 1968 to be 3.1×10^6 tonnes. A revision of the numbers at age discarded changed this estimate to 1.7×10^6 tonnes in the 1982 report (Anon. 1982).

For Norway pout, sandeel and sprat for which no catch-at-age data are available from the sixties and whose short lifespan makes VPA a less reliable method for stock assessment, the results should only be regarded as tentative. However, for Norway pout the increase in stock biomass from a low level in 1965-66 to a higher level from 1967 onwards is reflected in catch per unit of effort data (Lahn-Johannesen *et al.* 1978). For sandeel and sprat such data can not be used. It is thus not certain at all whether the biomass of sprat was as high as 1.4×10^6 tonnes in the late sixties or whether it was at a low level until the decline of herring in the seventies.

These uncertainties make it very difficult to conclude whether the total biomass of exploited fish species in the North Sea has remained at a more or less constant level around 9×10^6 tonnes as found by Ursin (1982) or whether there has been a

Table 16. Stock biomasses at 1 Jan. from MSVPA (tonnes $\times 10^{-3}$).

Year	Saithe	Cod	Haddock	Whiting	N. pout	Sandeel s. NS	Sandeel n. NS	Sprat	Herring	Mackerel	Plaice ♂♂	Plaice ♀♀	Total
1965	283	402	790	1033	238	1154	44	1227	3435	3385	278	449	12716
66	355	492	632	848	391	915	60	1287	2540	3127	279	452	11377
67	398	549	587	650	649	772	98	1425	1892	2681	267	465	10433
68	554	549	2216	1314	1133	701	150	1452	1673	2303	225	485	12753
69	743	495	1962	1113	844	362	207	1012	1398	1363	202	478	10177
70	950	573	1282	689	1084	298	313	693	1104	894	180	389	8449
71	972	633	824	516	1225	1138	477	757	1115	1382	152	356	9547
72	950	568	800	813	1445	878	478	782	1045	1398	146	335	9638
73	877	494	566	1055	938	836	497	1295	881	1324	156	290	9208
74	826	382	814	782	1467	618	756	1859	510	1110	168	268	9559
75	884	385	934	796	1148	1066	639	1668	590	991	179	256	9534
76	821	352	610	778	1300	960	469	1755	424	933	182	230	8815
77	598	542	452	676	1873	1246	806	1096	350	837	170	214	8859
78	538	590	411	555	1084	1503	516	1050	445	648	163	207	7710

Table 17. Spawning stock biomasses at 1 Jan. from MSVPA (tonnes $\times 10^{-3}$).

Year	Saithe	Cod	Had-dock	Whiting	N. pout	Sandeel s. NS	Sandeel n. NS	Sprat	Her-ring	Mack-erel	Plaice ♂♂	Plaice ♀♀	Total
1965	84	250	739	560	166	351	16	271	2607	3249	161	305	8759
66	93	315	519	554	306	321	22	307	2105	2799	239	400	7980
67	157	361	258	354	550	300	34	348	1564	2164	231	397	6718
68	201	414	293	357	1048	297	57	561	1115	1676	193	382	6594
69	259	414	1848	926	771	188	83	415	814	1166	168	435	7487
70	290	359	1229	484	1010	115	139	309	812	543	139	338	5767
71	406	302	519	227	1139	102	160	270	562	518	111	305	4621
72	510	350	429	316	1387	593	204	294	587	1227	110	296	6303
73	567	388	479	431	864	371	266	237	590	1200	108	246	5747
74	519	275	354	523	1425	351	270	368	385	1055	89	194	5808
75	409	241	437	325	1089	330	383	742	261	840	122	198	5377
76	297	217	561	476	1239	583	193	442	346	768	144	189	5455
77	253	240	351	393	1846	421	257	495	280	712	125	168	5541
78	260	233	251	317	1077	549	253	374	325	596	107	161	4503

decline as Table 16 and Fig. 23 would suggest. Yang (1982) estimated the total biomass of fish in the North Sea including non-commercial species to be 10×10^6 tonnes in 1977-78.

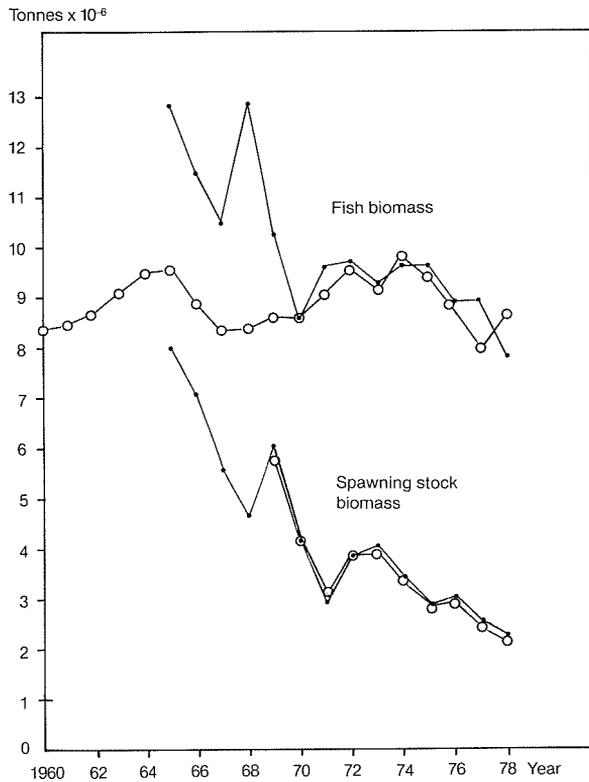


Fig. 23. Total fish biomass and spawning biomass. Fish biomass from MSVPA (●) compared to Ursin (1982) (○). Total spawning stock biomass excluding Norway pout, sandeel and sprat, from MSVPA (●) and ICES Working Group reports (○)

4.5 Recruitment

One of the major differences between VPA and MSVPA is the estimate of recruitment. Due to the high predation mortality on the younger age-groups the number of recruits are substantially higher when estimated by MSVPA, and it was hoped that these estimates would show a better correspondence with the indices of recruitment obtained from young fish surveys.

Table 18 shows the index of abundance at age 1 for haddock, whiting and cod obtained during the International Young Fish Survey (IYFS) and the corresponding estimates from VPA and MSVPA. The estimates of year-class strength from MSVPA do not seem to be better correlated to the IYFS index than the results from VPA. A geometric mean regression furthermore reveals not only an increased slope for the MSVPA/IYFS regression, but also an increased intercept. Thus the calculated predation mortalities do not improve the correspondence between the IYFS-index and recruitment estimated from catch-at-age data.

Table 18. Indices of abundance of the number of 1 year old haddock, whiting and cod derived from IYFS, VPA and MSVPA.

Year class	Haddock			Whiting			Cod		
	IYFS	VPA $n \times 10^{-6}$	MSVPA $n \times 10^{-6}$	IYFS	VPA $n \times 10^{-6}$	MSVPA $n \times 10^{-6}$	IYFS	VPA $n \times 10^{-6}$	MSVPA $n \times 10^{-6}$
1964				418	1895	5302	16.0	212	265
1965	12	801	1143	600	1365	3305	20.2	257	346
1966	62	2153	3435	501	1645	3264	28.5	240	316
1967	5855	12517	23698	2019	4558	10960	5.4	97	127
1968	81	453	1394	19	730	2112	6.5	104	146
1969	27	333	606	69	1146	2330	73.8	469	626
1970	873	2211	3707	274	1710	3278	99.7	493	634
1971	740	2278	4569	332	2811	5647	4.1	84	111
1972	187	517	998	1156	3409	7149	37.7	205	262
1973	1072	3689	5618	322	1611	2945	14.6	135	176
1974	1168	3791	6130	893	3049	5388	95.7	267	332
1975	177	370	604	679	1934	3456	8.8	117	151
r*		0.983	0.991		0.897	0.908		0.851	0.832
GM-regression									
slope		2.08	3.91		1.98	4.58		3.87	5.05
intercept		707.6	1078.0		953.8	1815.6		90.8	118.1

*Correlated with IYFS Index.

4.6 Food requirements and energy flow

The overall results of this preliminary North Sea exercise in terms of food intake and fish production are presented in Table 19. Note how the predation of fish exceeds the catch in all of the years from 1965 to 1978.

Our main purpose has been to illustrate the amount of data needed in a multi-species assessment and to present some preliminary estimates of the importance of

Table 19. Fish biomass, consumption and production calculated by MSVPA (tonnes $\times 10^{-3}$).

Year	Bio- mass	Food consumption				Biomass production					
		Fish	Other food benth.	pelag.	Total	Catch	Preda- tion	Other mort.	Spawn- ing	Biomass change	Total
1965	12716	6311	5693	29130	41133	2792	6311	1165	1226	-1339	10154
1966	11377	5502	5127	27051	37680	3008	5502	1034	1074	-944	9674
1967	10433	5432	6716	28009	40158	2965	5432	1016	937	2320	12670
1968	12753	5830	11612	25134	42577	3683	5830	1167	938	-2576	9043
1969	10177	4558	8561	21192	34311	3122	4558	987	1045	-1728	7984
1970	8449	4388	5900	24548	34836	2888	4388	893	795	1098	10062
1971	9547	4679	5589	28591	38859	2446	4679	909	652	91	8777
1972	9638	4905	5603	26417	36924	2644	4905	895	889	-430	8903
1973	9208	5098	5058	27303	37459	2600	5098	862	816	351	9727
1974	9559	4287	5426	30955	40667	3066	4287	870	845	25	9092
1975	9534	4516	5711	28172	38398	3068	4516	852	791	-719	8507
1976	8815	4142	4410	31409	39962	2997	4142	795	778	44	8756
1977	8859	4031	4366	30861	39257	2668	4031	760	817	-1149	7126
1978	7710	3256	4144	22760	30160	2452	3256	656	665	-114	6914
Average	9913	4781	5994	27252	38027	2886	4781	919	876	-362	9099

predation and for this purpose we have been forced to make a lot of assumptions. However, the results obtained are not very different from the results obtained from energy budget calculations. Thus Jones (1982) quotes estimates of the total annual production of benthos and pelagic herbivores of 30 and 175 kcal/m²/year, respectively. Assuming 1 kcal to equal 1 g wet weight and the area of the North Sea to be 0.57×10^{12} m² the total annual production of benthos becomes 17×10^6 tonnes and the total annual production of pelagic herbivores 100×10^6 tonnes. On average the annual consumption by the fish stocks in the MSVPA equals 6×10^6 tonnes of

Table 20. Average annual consumption of other pelagic food (tonnes $\times 10^{-6}$).

	1965-67	1973-75
Saithe	0.2	0.3
Cod	—	—
Haddock	—	—
Whiting	0.1	0.1
Norway pout	3.5	8.1
Sandeel, s.NS	5.1	4.6
Sandeel, n.NS	0.7	4.4
Sprat	5.1	6.7
Herring	5.9	1.5
Mackerel	7.4	3.2
Plaice ♂♂	0.0	0.0
Plaice ♀♀	0.0	0.0
Total	28.1	28.8

benthic and 27×10^6 tonnes of pelagic food and their food requirements can thus easily be satisfied by the production. In the same paper Jones estimates the total annual food requirements of the commercial fish species to be between 23×10^6 tonnes and 46×10^6 tonnes in the years 1968-70. The estimate from the MSVPA is approximately 37×10^6 tonnes.

It is furthermore interesting to note that the annual consumption of other pelagic food remains more or less constant throughout the period despite the decline of the herring and mackerel stocks. As Table 20 shows, the increased stocks of Norway pout and sandeel in the northern North Sea and to some extent also sprat took over their role as the most important pelagic feeders.

5. Conclusion

The most salient effect of introducing predatory interactions in the VPA for the North Sea is the increased natural mortalities for the younger age-groups and hence the increased estimates of the number of recruits. This effect was also conspicuous in the output presented from the multispecies cohort analysis of Pope (1979) and Pope & Knight (1982). Besides acting on recruitment the increased natural mortality also affects the exploitation patterns, resulting in relative lower fishing mortality for the younger age-groups.

A changed exploitation pattern and a higher natural mortality for the younger age-groups will change both the yield per recruit and the mesh-size assessments. It thus seems likely that much of the current advice, which is based on calculations where the same natural mortality has been applied to all ages, is wrong.

However, before a new set of natural mortalities can be estimated, far better estimates of food composition and food intake must be available. Furthermore some of the mechanisms described in the MSVPA still need to be checked. The selection of food is at present assumed to be directly proportional to the relative biomasses of the various suitable food items and possible mechanisms such as predator prey switching have not been taken into account. The interactions among the young fish themselves should also be investigated in more detail in order to quantify the importance of interspecies predation and cannibalism. Finally although it may be appropriate to assume that the amount of other food remains constant from year to year it seems unrealistic to neglect the variation within the year.

A satisfactory description of the interactions might thus first be obtained when the calculations are made with a smaller time step (e.g. one month) and the variation in the amount of other food and in the geographical distribution of the stocks described in more detail.

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Appendix 1

Algorithm for the MSVPA

The equations outlined in section 2 can be used to design an iterative algorithm. The total biomass is divided into four classes: recruited fish (called old fish), pre-recruited fish (young fish), other pelagic food and other demersal food. In the following description we shall not distinguish between these two classes of other food. The old fish prey on old fish, young fish and other food whereas young fish only prey on young fish and other food. As in VPA the algorithm works backwards in time. Also like in traditional VPA boundary values have to be given i.e. stock sizes for the oldest age-classes in all years and for all age-classes in the last year. Within each year the fishing and predation rates for the old fish are computed as yearly averages assuming a specified amount of young fish as food supply. Then the predation rates for young fish are calculated instantaneously (i.e. by solving differential equations) knowing the (average) predation caused by the old fish. Simultaneously the amount of (average) supply of young fish as food for the old is recalculated and the step dealing with the old fish is repeated, etc. After this

iterative process has converged, the stock sizes at the beginning of the year are computed and the whole process repeated for the previous year and so on.

The calculations within each year are in detail as follows:

STEP 0: Guess initial values for the supply of young fish as food for the old:
 Φ_y^{ia} .

STEP 1: Use equations (2.2), (2.3), (2.5), (2.6), (2.17) to compute the mortality rates P_{ia} and F_{ia} for all the old fish ia simultaneously.

STEP 2: The set of differential equations (2.23) together with equations (2.24) and (2.25) are solved backwards in time from the end of the year to the beginning. At the same time formula (2.26) is used to recompute Φ_y^{ia} .

STEP 3: If the new values of Φ_y^{ia} differ from the old ones by more than a prescribed tolerance then go to STEP 1. Otherwise stop.

It has been shown (Magnus & Magnusson 1983) that a solution to the general system of equations always exists. The question of uniqueness of the solution is not fully settled, but Magnus & Magnusson give inequalities which if satisfied guarantee uniqueness. The inequalities are not easy to verify for real examples if the number of age-classes is large. Basically the solution is unique if external food is sufficiently large and/or predation is not too large compared to the catch.

Dekker (1982) has also analysed this problem and is sceptical about the general existence and uniqueness of solutions to our model. He even gives a counter-example which on the other hand is incorrect.

In runs with this algorithm convergence has never been a problem.