A model of trophic interactions in the North Sea in 1981, the Year of the Stomach*

Villy Christensen
International Center for Living Aquatic Resources Management,
M.C. P.O. Box 2631, 0718 Makati, Metro Manila, Philippines

Abstract

This paper gives an overview of the trophic interactions in the North Sea in 1981 when 55 000 fish stomachs were sampled and analysed. The study is based on the data base of the ICES Multispecies Assessment Working Group (MS WG), and published information. A balanced, steady-state model of interactions and biomasses at all trophic levels is constructed using the ECOPATH II software. The results indicate that the food consumption rates used by the MS WG for three of the important gadoid species are unrealistically low, whereas other parameters appear very reasonable. Results from mixed trophic impact analysis, trophic aggregation, and other network analyses are presented, and the results are compared with earlier studies of the North Sea food web. Summaries are given to illustrate the distribution of flows between demersal and pelagic components, and between large ecological groupings.

Keywords: trophic model, food web, ecosystem dynamics, required primary production, ecological cost, ·mixed trophic impact, North Sea.

Introduction

Going back to Andersen & Ursin (1977) and Jones (1978), fisheries biologists have worked with multispecies modelling of the North Sea fish resources. In the last decade this has lead to the development of a multispecies virtual population analysis (MSVPA) by the Multispecies Working Group (MS WG) of the International Council for Exploration of the Sea (ICES), see Sparre (1991). This MSVPA is now being used increasingly for stock assessment in the North Sea area, and efforts are under way to repeat the success in the Baltic Sea (Sparholt 1991), and in the tropics (Christensen 1995a). The MS WG programs account for the trophic interactions in the exploited, upper part of the ecosystem based on extensive stomach data and digestion studies. As concluded by Hilborn & Walters (1992) 'the methods hold considerable promise, with a very expensive price tag'.

The MS WG analyses largely ignore the lower trophic levels, and therefore give a very incomplete picture of the overall flows in the North Sea. Control of mass balance on the lower trophic levels of the ecosystems is therefore not carried out, and the possibilities this offers for constraining parameter ranges are not considered. It is therefore of interest to produce a summary of the trophic interactions in the North Sea, to check the basic parameters and assumptions in the MS WG programs

---

*Dedicated to the memory of the late Rodney Jones, whose pioneering work on the energy flow structure in the North Sea was of major importance for our understanding of the North Sea as an ecosystem.

where possible, and to consider if the physiological rates are realistic. Noting the importance of the advice that are or may be based on the MS WG analyses a form for 'ecological auditing' is appropriate. To do so properly is a major exercise, here only a limited 'auditing' can be attempted due to the limited knowledge of flows at the lower trophic levels.

The present contribution is also of relevance in view of the increasing need for managing ecosystems. The ICES Working Group on Ecosystem Effects of Fishing Activities represents an important step in that direction, but so far only few and rather preliminary attempts to do ecosystem management have actually been conducted, (e.g. Nicol & de la Mare 1993). One reason for this is that both suitable models and especially data have been lacking. Analytic models as data-demanding as the MSVPA are not likely to be used widely in a foreseeable future. As a starting point it may, however, not be realistic nor necessary to describe the dynamics of a system (how it will evolve following perturbations), instead simpler, and less precise analysis of how the resources interact in a given ecosystem may be of interest. This will give the minimum of what is needed for managers to attempt to manage a full ecosystem rather than a few parts of it components.

One model of interest for such analysis is the ECOPATH II model, which was designed exactly for this purpose (Christensen & Pauly 1993b). The data requirements are much lower than for the analytical models, yet an overview of the trophic flows in a system is produced. The models are easy to construct and update, they can be used to assess the relative importance of different components of the ecosystem, and how these impact on each other trophically. Further, the data they require are part of what is needed for the more complex, analytical models; they can thus be seen as a stepping stone.

The major purpose of this contribution is to use ECOPATH II to give an overview of the trophic interactions at all trophic levels in the North Sea based on data from the ICES MS database supplemented by published information. A number of attempts to describe the North Sea trophic flows have been carried out earlier, e.g. by Jones (1978, 1984) and Bromley et al. (1993), these have, however, been of a very preliminary nature, and can with present knowledge and methodologies be taken some steps further.

Model methodology

The ECOPATH model was originally developed by Polovina (1984) to describe a coral reef ecosystem, and to obtain biomass estimates for the ecosystem components. It was in essence a simplification of the Bering Sea model developed by Laevastu and co-workers (Laevastu & Larkins 1981). Since then the model has been further developed into the ECOPATH II software system[1] described by Christensen & Pauly (1992a, b, 1995), extensive network analysis facilities have been added based notably on the work of Ulanowicz (1986), and the approach has up to now been used to describe more than 50 ecosystems worldwide, see e.g. the contributions in Christensen & Pauly (1993c).

1. Available with data files through the author.

Model parameterization

ECOPATH II models can be constructed using ranges for all input parameters. The estimation routine in a Monte-Carlo fashion balances the model, evaluates the run for mass balance and physiological considerations, and use this to come up with the most likely model giving constraints. In the present application a simpler approach is used, however, in which only average input parameters are used. The present ECOPATH II model therefore describes the North Sea ecosystem in a given, possible static situation only.

It is assumed that input equals output for the time period considered, allowing for accumulation and depletion of biomasses, and the model is constructed so that there is mass balance. For each of the groups i in the system it is assumed that

$$Q_i = P_i + R_i + U_i \tag{1}$$

where Q_i is consumption for group i, P_i the production of i, R_i respiration, and U_i is faeces and excreta from i; All rates are expressed per unit area and time, in the present model as g w.wt $\cdot$ m$^{-2} \cdot$ y^{-1}. From Eq. 1 the respiration is estimated once the other flows have been quantified.

Of the parameters in Eq. 1 the production is estimated from

$$P_i = M2_i + M0_i + EX_i + BA_i \tag{2}$$

where $M2_i$ is the predation mortality of group i, $M0_i$ is the non-predation mortality of i, EX_i is the export of i, and BA_i is the biomass accumulated (or depleted if negative) of i during the period considered.

Using the balance expressed in Equations (1) and (2), and noting that the predation term in Equation (2) can be estimated as the consumption of all predators on group i, and thus 'links' the predators and prey, it becomes possible for a given group to estimate any one of the basic parameters: biomass, production rate, consumption rate, and the non-predation mortality. The three remaining basic parameters and the diet composition must be given.

The term ecotrophic efficiency, EE, is used here to express the proportion of the production for any group that is utilized for either predation, catches or biomass accumulation in the system. EE scales from 0 to 1, and can for most groups be expected to be closer to 1 than to 0. The EE is linked to the non-predation mortality, $M0$,

$$EE_i = 1 - (M0_i/P_i).$$

As our knowledge of the non-predation mortality is very incomplete, this parameter, or rather EE, is estimated for most groups.

Network analysis

A major advantage of expressing the trophic interactions in a system in form of a quantified food web is that in addition to control of mass balance it opens up for the use of network analysis on the system (e.g. Wulff *et al.* 1989, and Christensen 1995b). For the present study several forms for network analyses are of interest, e.g.

trophic aggregation, required primary production, and mixed trophic impacts. These analyses are all implemented and described in the ECOPATH II system.

The trophic aggregation routine is based on an approach described by Ulanowicz (1995), which distributes the flows within groups onto discrete trophic levels. The first step is to assign a (fractional) trophic level to all groups in the system. To do this, primary producers and detritus are given a trophic level of one. For each of the n consumers the (mean weighted) trophic level is then calculated as 1 plus the sum of the trophic levels of its prey multiplied by the prey's proportion in the diet. In practice this in done by constructing a linear equation system with n equations and n unknowns, and solving for the unknown parameters using a standard inverse method. Once each group in the system has been assigned a trophic level, the flows can be aggregated on to discrete trophic levels reversing the routine used for calculation of the fractional trophic levels.

Based on the quantified food web all food chains in the system can be identified. Using an approach developed by Christensen & Pauly (1993a) an estimate of the amount of primary production (and detritus) required to sustain the consumption by each of the groups in the system can then be obtained. For each step in the food chains the flow is raised by the ratio between consumption and production. The summed requirements can then be seen as a measure of the ecological cost of maintaining a group in the system. Similarly the amount of primary production (and detritus) required to sustain the catches can be estimated from the catches and the food chains leading to the catches.

The mixed trophic impact routine is derived from economic input–output analysis as described by Ulanowicz & Puccia (1990). This analysis quantifies all the direct and indirect trophic impacts of all groups in the system based on the assumption that the direct impact between group a and group b can be estimated from the difference between the proportion that group a contributes to the diet of group b, and the proportion that group a takes from the production of group b.

Data sources

For the present model the North Sea was treated as one strata with a total area of 570 000 km^2 (Jones 1982b). The model includes 29 groups, 15 of which are fish groups, 7 invertebrates, 6 are groups of small plankton, and the remaining a detritus (DOM and POM) group. All rates and biomasses were expressed in wet weight and on an areal basis to facilitate comparisons with other systems.

The key data originate from the ICES Multispecies Assessment Working Group data base. The core of this data base describes the 1981 'Year of the Stomach' where more than 55 000 fish stomachs were sampled and analysed in detail through an ICES coordinated stomach sampling project. Where necessary, supplementary published information were also used. Not all the data pertain to 1981, notably the data for the groups not included in the ICES data base had to be taken from whatever published information could be found. Of course this to some degree invalidates the present description; still the main purpose is not to give a detailed picture but a broad overview.

A run of the ICES MSVPA program provided summary statistics on the consumption in 1981 for each of the MS predators, i.e. of cod, whiting, saithe, mackerel, and haddock. For the MS species (above mentioned predators plus herring, sprat, Norway pout, sandeel, plaice, and sole) information on average stock biomass was also available from the MSVPA. For these species the production could be estimated as stock size at the end of the year less stock size at the beginning of the year plus biomass predated plus biomass lost due to residual natural mortality and fishery.

As the MSVPA treats all other prey than the MS species as 'other food' more detailed diet compositions for cod, whiting, saithe, mackerel and haddock were obtained from Daan (1989) and Daan et al. (1990). The age-specific information was converted to stock estimates using information on size-specific stock composition from ICES (1991), and an assumed relative consumption rate proportional to the weight at age raised to the power $2/3$.

Information on consumption rates for other groups than the MS predators was obtained from the literature where available, supplemented in some cases by qualified guesses. This is described in more detail below in Appendix 1.

For all groups except the copepods it was assumed that 80% of the ingested food is assimilated. For copepods it was assumed that 60% is assimilated. These assumptions generally lead to realistic estimates for respiration/biomass ratios (Christensen & Pauly 1993a,c).

A summary of the input parameters is given in Table 1 along with parameters that are estimated using ECOPATH II. The diet compositions are presented in Table 2. An overview of how and from where the group-specific information was obtained is given in Appendix 1.

Representations of the North Sea food web

The description you give of an ecosystem is bound to be dependent on your interest in it. Fisheries biologists tend to look only at the fish groups while marine biologists often consider only interactions on the lowest trophic levels. In the present model an attempt is made to consider all levels at least to some degree. In addition to showing results for the model with all 29 groups, two separate representations of the model will be given below in order to focus the presentation of results, and to facilitate comparisons with other models and studies. All three representations are based on the same data, and differ only with respect to how the ecological groups are aggregated in the presentations; the calculations are made in disaggregated mode.

Focus on the plankton food web

The dominant flows in a marine ecosystem can be attributed to small plankton and decomposers as discussed by Fenchel (1988) in a review of the marine plankton food web. Fenchel also pointed out that two trophic levels should be added to the traditional description of the planktonic food web, namely nano- and picoplankton.

Table 1. Parameters used for describing the North Sea food web of 1981. *P/B* gives the production/biomass ratio, *Q/B* is consumption/biomass. Gross efficiency is the ratio between production and consumption. *EE*, the ecotrophic efficiency, expresses the proportion of the production that is used for predation, catches and biomass accumulation. For copepods only total production and consumption is known, not biomass (*B*), *P/B* and *Q/B*; similarly it is the total production and consumption that is estimated for the groups of small plankton, the split on *B* and *P/B* resp. *Q/B* is arbitrary. Legend: * indicates values estimated assuming mass balance, ^ indicates Q/B estimated from (*P/B*)/(*P/Q*), where *P/Q* estimates are qualified guesses. Such are also input estimates of *EE* = 0.95 for several groups. PS means photosynthetic, and PT phagotrophic.

Group name	Catches, $g \cdot m^{-2} \cdot y^{-1}$	Biomass, $g \cdot m^{-2}$	P/B, y^{-1}	Q/B, y^{-1}	Gross eff., (P/Q)	EE
1 Cod	0.57	0.57	1.11	3.2	0.35*	0.77*
2 Whiting	0.37	0.66	0.84	3.6	0.24*	0.60*
3 Saithe	0.21	0.65	0.58	3.3	0.18*	0.64*
4 Mackerel	0.11	0.46	0.29	5.8	0.05*	0.48*
5 Haddock	0.38	0.83	1.37	3.8	0.36*	0.64*
6 Herring	0.29	0.84	1.04	4.6	0.23*	0.75*
7 Sprat	0.34	0.55	1.21	8.6	0.14*	0.50*
8 Norway pout	0.81	1.94	2.48	16.5	0.15^	0.69*
9 Sandeel	1.16	2.58	2.02	13.5	0.15^	0.82*
10 Plaice	0.22	0.64	0.65	2.8	0.23*	0.86*
11 Sole	0.03	0.08	0.66	4.4	0.15^	0.85*
12 Ray	0.00	0.53	0.44	2.9	0.15	0.00*
13 Other predatory fish	0.00	1.5	0.87	5.8	0.15^	0.00*
14 Other prey fish	0.00	4.4	0.48	3.5	0.14*	0.95
15 Juvenile fish	0.00	2.0*	5	25	0.20^	0.95
16 Copepods	0.00	10	18	60	0.30*	0.93*
17 Euphausiids	0.00	9.1*	2.4	16	0.15^	0.95
18 Other crustaceans	0.00	16*	3	20	0.15^	0.95
19 Echinoderms	0.00	24	2	13	0.15^	0.78*
20 Polychaetes	0.00	32	2	13	0.15^	0.73*
21 Other macrobenthos	0.00	49	2	13	0.15^	0.70*
22 Other invertebrates	0.00	13	3	20	0.15^	0.95
23 Phytoplankton (PS micro)	0.00	43	54	0	–	0.23*
24 PT microplankton	0.00	11*	54	133	0.40^	0.95
25 PS nanoplankton	0.00	3.0	200	0	–	0.95
26 PT nanoplankton	0.00	4.4	200	500	0.40^	0.95
27 PS picoplankton	0.00	0.93	1000	0	–	0.95
28 PT picoplankton	0.00	1.4	1000	2500	0.40^	0.95
29 Detritus	0.00	50	–	–	–	1.00*

To focus attention on the dominant flows in the ecosystem a special version of the model was prepared in which:

- all fish groups were aggregated in one group;
- copepods and euphausiids were aggregated in one group called 'zooplankton';
- all other invertebrates were aggregated in one group called 'other invertebrates';
- it was assumed that groups feeding on phytoplankton actually feed 50% on photosynthetic microplankton and 50% on phagotrophic microplankton;
- the following seven groups were kept separate as in the original representation: phagotrophic microplankton, photosynthetic microplankton, phagotrophic nanoplankton, photosynthetic nanoplankton, phagotrophic picoplankton, photosynthetic picoplankton, and detritus.

The model thus includes 10 groups; it is parameterized top–down so that the flows at the lower levels are calculated to match the food demands of the upper levels.

Table 2. Diet composition matrix for the model of trophic flows in the North Sea in 1981. Groups 23 and 24 are photosynthetic and phagotrophic microplankton, respectively, and group 29 detritus. Groups 3, 4, and 10-13 have no predators in the model. Diets for the groups of small plankton is given in the text.

Predator										Prey									
	1	2	5	6	7	8	9	14	15	16	17	18	19	20	21	22	23	24	29
1 Cod	0.017	0.051	0.058	0.023	0.022	0.072	0.079	0.188	0	0	0.050	0.320	0.009	0.067	0.022	0.022	0	0	0
2 Whiting	0.001	0.018	0.031	0.028	0.077	0.118	0.253	0.187	0	0	0.099	0.099	0.003	0.025	0.031	0.031	0	0	0
3 Saithe	0.001	0.003	0.056	0.008	0.008	0.465	0.050	0.029	0	0	0.358	0	0	0	0	0.022	0	0	0
4 Mackerel	0	0	0	0.021	0.019	0.031	0.188	0.012	0	0.214	0.365	0.031	0	0.005	0	0.114	0	0	0
5 Haddock	0	0	0	0	0.001	0.029	0.078	0.286	0	0	0.099	0.099	0.139	0.126	0.072	0.072	0	0	0
6 Herring	0	0	0	0	0	0	0	0	0.111	0.201	0.575	0.113	0	0	0	0	0	0	0
7 Sprat	0	0	0	0	0	0	0	0	0	0.700	0	0.300	0	0	0	0	0	0	0
8 Norway pout	0	0	0	0	0	0	0	0	0.075	0.335	0.515	0.075	0	0	0	0	0	0	0
9 Sandeel	0	0	0	0	0	0	0	0	0.010	0.500	0	0.490	0	0	0	0	0	0	0
10 Plaice	0	0	0	0	0	0	0	0	0	0	0	0	0.300	0.500	0.100	0.100	0	0	0
11 Sole	0	0	0	0	0	0	0	0	0	0	0	0	0.200	0.800	0	0	0	0	0
12 Ray	0.003	0.011	0.038	0	0	0	0.189	0.125	0	0	0	0.542	0	0.092	0	0	0	0	0
13 Other pred. fish	0	0	0	0	0	0	0	0	0	0.044	0	0.244	0	0	0	0	0	0	0
14 Other prey fish	0	0	0	0	0	0	0	0	0.712	0	0	0	0.500	0.200	0	0.100	0	0	0.2
15 Juvenile fish	0	0	0	0	0	0	0	0	0	0.800	0	0.100	0	0	0	0.100	0	0	0
16 Copepods	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.475	0.475	0.050
17 Euphausiids	0	0	0	0	0	0	0	0	0	0.700	0	0.100	0	0	0	0.200	0	0	0
18 Oth. crustaceans	0	0	0	0	0	0	0	0	0	0	0	0	0.050	0.050	0.050	0	0.150	0.150	0.550
19 Echinoderms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.100	0.100	0.800
20 Polychaetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.000
21 Oth. macrobenth.	0	0	0	0	0	0	0	0	0	0	0	0	0.050	0.100	0	0	0.200	0.200	0.600
22 Oth. invertebr.	0	0	0	0	0	0	0	0	0	0	0	0	0.050	0.200	0	0	0.150	0.150	0.350

Demersal and pelagic groupings

In order to compare the relative roles of the demersal and pelagic sub-systems in the North Sea a representation was made in which the original groupings were aggregated in six ecological groups. As criteria were used ecological and trophic relationships, e.g. the fish groupings were based on whether the fish take most of their food from pelagic or benthic sources, not on what kind of fishery they are usually caught in.

The pelagic fish groups were defined as consisting of saithe, mackerel, herring, sprat, Norway pout, sandeel, other predatory fish, and the juvenile fish. The demersal fish group included cod, whiting, haddock, plaice, sole, ray, and other prey fish. The pelagic invertebrates included copepods, euphausiids, and the other crustaceans, while the demersal invertebrates were echinoderms, polychaetes, other macrobenthos and other invertebrates. The two remaining groups were (photosynthetic and phagotrophic) microplankton and detritus/decomposers including the small plankton. The nano- and picoplankton were ignored for this comparison as the corresponding benthic groups also were ignored.

Model sensitivity

By varying all input parameters between -50% and $+50\%$, and calculating the impacts this has on the estimated parameters of all other groups in the systems the results in Figure 1 are obtained. Trivial impacts are not shown, e.g. the actual calculations only deals with flows, therefore if for a given group the production (P) is fixed in order to balance the demands of consumers a reduction of the biomass (B) estimate of the group will result in a corresponding increase in the production/biomass ratio (P/B) of the group to keep production $(B \cdot P/B)$ constant.

Figure 1. Sensitivity of model output parameters to changes in input parameters. Shows all impacts for all fish groups where a 50% change results in at least a 10% change in an output parameter. Trivial within-group impacts are not shown. All impacts are found to be due to changes in consumption rates as follows: a is for Norway pout on the biomass (B) of euphausiids, b for N. pout on B of other invertebrates, c for N. pout on the ecotrophic efficiency (EE) of copepods and of other macrobenthos, d for N. pout on the EE of polychaetes, e for saithe on the EE of N. pout, f for N. pout on the EE of echinoderms and for sandeel on B of other crustaceans, g for N. pout on B of other crustaceans, h for whiting on the EE of sprat, i for N. pout on B of juvenile fish, and j for whiting on the EE of sandeel.
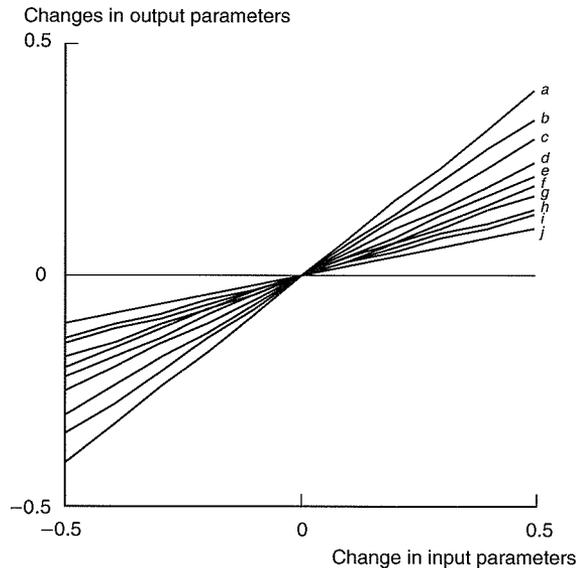
The main conclusion that can be drawn from Figure 1 is that the model is quite insensitive to changes in the basic input parameters (B, Q/B, P/B, and EE). The network has a dampening effect at least if the parameters vary randomly, and changes caused by parameter changes are mainly reflected within the group where they occur. This result is a function of the parameter combination. In this model the ecotrophic efficiency, EE, is calculated for nearly all groups. Because of this there is only limited 'cascading' in the food web, e.g. we do not have that an increased consumption for a top-predator must lead to increased production (and hence consumption) for a prey, whose prey in turn would produce (and consume) more, etc. Here the impacts are only passed one step down the food web.

Results and discussion

Parameter estimates

Some of the major results from this description of the 1981 North Sea food web structure are presented together with the input parameters in Table 1. A graphical representation of the quantified food web for the North Sea in 1981 is given in Figure 2. Here all groups are balanced so that input equals output. The flow chart is constructed following some rules of standardization aimed at enhancing visual interpretation (Pauly & Christensen 1993). The most important of the rules are given in the figure legend.

Some of the parameter estimates need commenting. Lindley (1980) gave estimates of production and biomass of two (out of three) dominant species of *Euphausiacea*, *Thysanoessa inermis* and *T. raschi*, in the NE North Sea and NW Skagerrak in 1966 and 1967. Assuming a carbon/wet weight conversion factor of 10, a mean depth of the northern North Sea of 100 m, that euphausiids occur in half of the North Sea, and that the third dominant species, *Meganyctiphanes norvegica*, adds 50% to the biomass, a biomass of 1.8 $g \cdot m^{-2}$ could be estimated. In the present model a much higher biomass of 9.1 $g \cdot m^{-2}$ is required to meet the consumption in the system, mainly of Norway pout (16.5 $g \cdot m^{-2} \cdot y^{-1}$). This discrepancy may be due to sampling problems for the euphausiids, and should certainly warrant increased attention to this trophically important, yet rather ignored group.

The 'gross food conversion efficiency', GE, given in Table 1 is for any group the ratio between its total production and total food consumption. This ratio is for most vertebrate groups constrained physiologically to the range from 0.05 to 0.25, whereas it can be higher for some groups of small invertebrates. It appears that GE's are unrealistically high for three of the four gadoid MS species (cod with 35%, whiting 24%, and haddock 36%). Efficiencies in the range of 5-15%, depending on species, size, food type etc., are much more realistic for fish groups (Paloheimo & Dickie 1966, Jones 1982a,b).

The conversion efficiencies for these MS predators are high because low consumption rates are used in the MS WG programs. These low consumption rates have however been adopted deliberately in order not to overestimate the effect of predation in the MS WG programs (H. Gislason, pers. comm.) Apart from these estimates the other estimates used here from the MS WG seem very reasonable, and the present model could easily be balanced with them.
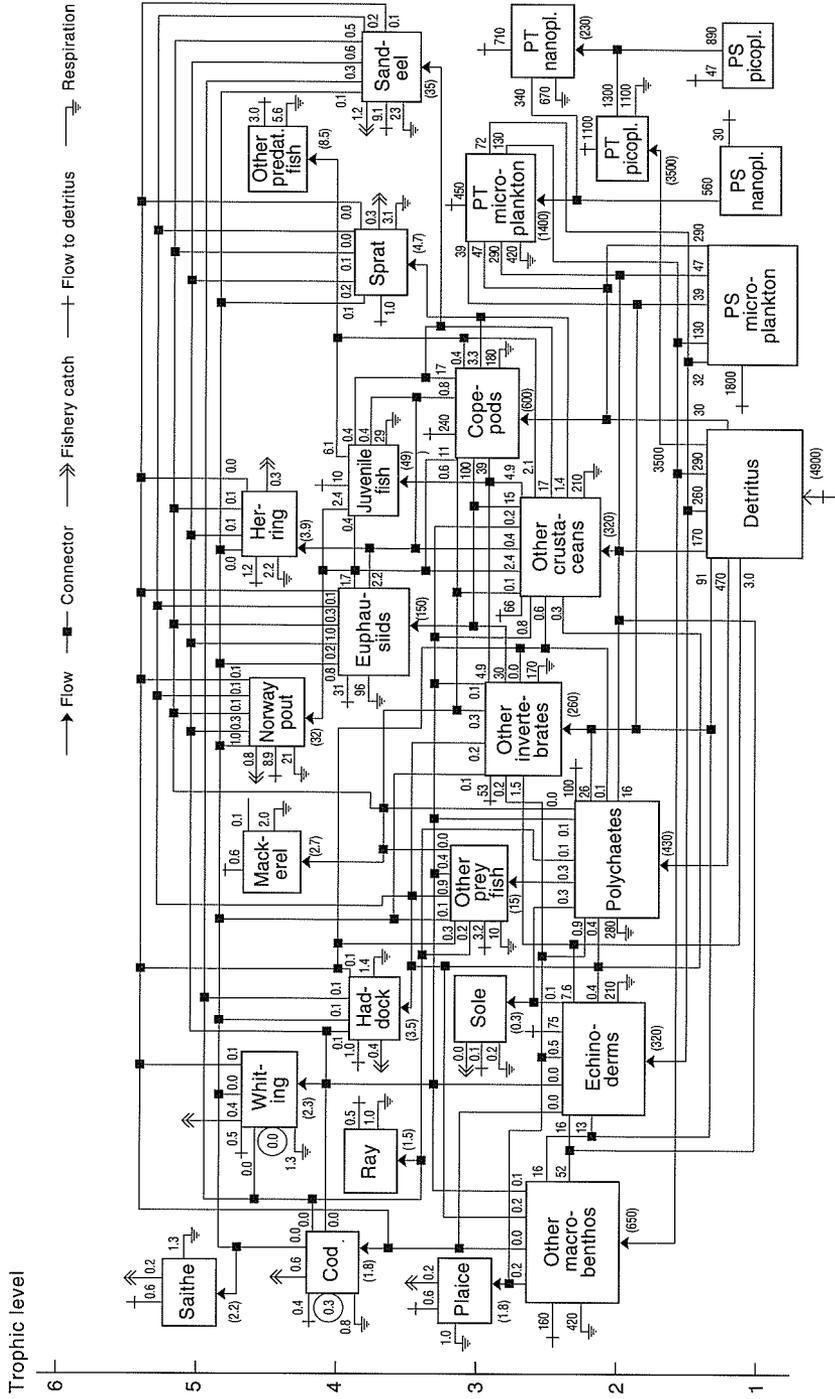
Figure 2. A quantified network of trophic interactions in the North Sea in 1981. The volume of the boxes (which are assumed cubed) are proportional to the biomasses of the groups. The boxes are arranged on the y-axis after trophic levels, and to some degree on a demersal to pelagic scale on the x-axis. All groups are balanced so that input equals output. Flow exiting a group do so from the top or sides of a box, while flow enter at the bottom. Flows are expressed in g w.wt·m^{-2}·y^{-1}.

Making ends meet – balancing supply and demands

Previous studies have discussed how food requirements of the North Sea fish can be met by the system. Steele's (1974) rather crude estimates of consumption by fish were based on known landings and assumed natural mortalities multiplied by 10 to account for food conversion efficiency. Steele found that as parameterized there would only be enough food if the fish were all herbivorous which of course is far from the case. The present study shows that the fishery is operating at a trophic level of around 5, i.e. the average catch is three trophic levels above the primary producers, and thus the demand for primary production is much higher than if all fish had been herbivorous. Incidentally the addition of the two extra trophic levels among the small plankton only adds little to the trophic level of the fishery, which when estimated without the extra small plankton groups would decrease by only half a trophic level.

The studies of the North Sea ecosystem by Jones (1978, 1982b, 1984) were more detailed, incorporating several invertebrate groups, yet the overall conclusion was the same as Steele's (1974): there was not enough primary production to sustain the catches. Jones concluded that either the primary production was underestimated or the transfer efficiencies between trophic levels was higher than 10% or both.

The present study comes to a different result than the previous studies: here less than half of the primary production is required to sustain the consumption in the system. This is well in line with the findings of large-scale autolysis of phytoplankton reported for the North Sea by, e.g. Fransz & Gieskes (1984), and Nielsen & Richardson (1989).

When comparing with the previous studies (Table 3) it seems that a major reason why it is now possible to balance the model is that the primary production estimate has been increased (from 1000 to 2300 g w.wt $\cdot$ m$^{-2} \cdot$ y^{-1} for microplankton), but also that feeding on detritus has been included. It is estimated here that around half of the flows in the system originates from the detritus, and this pool of organic material was overlooked in the previous studies. An additional reason why it is now possible to balance the model based on the available primary production is that the transfer efficiencies in the present study are estimated from production and consumption rates, and they are for many of the important groups higher than 10%.

Table 3. Estimates of production and consumption (g w.wt $\cdot$ m$^{-2} \cdot$ y^{-1}) from three studies of the trophic structure of the North Sea ecosystem.

	Steele (1974)		Jones (1982, 1984)		This study	
	Prod.	Cons.	Prod.	Cons.	Prod.	Cons.
Microplankton	900	–	1000	–	2300	560
Nano- and picoplankton	–	–	–	–	1500	2300
Detritus	–	–	–	–	4900	–
Zooplankton	175	600	175	–	200	750
Benthos		300	10	300	300	2000
Pelagic fish	8	96	–	17-46	13	69
Demersal fish	2.6	31	–	10-20	15	95

   To check the mass balance in the model we can see how respiration balances the primary production. We would expect the two rates to approximately balance as the system only to a limited extent is a net importer or exporter of organic material, and as respiration in ECOPATH II models is calculated as the difference between assimilated consumption and production, we can use this as a check of the model parameterization. For the present model we have that the total primary production by microplankton is some 2300 g w.wt$\cdot$m$^{-2}\cdot$y^{-1} while the photosynthetic nano- and picoplankton add another 1500 g$\cdot$m$^{-2}\cdot$y^{-1} bringing the total to around 3800 g$\cdot$m$^{-2}\cdot$y^{-1}, which corresponds closely to the total primary production.

   An additional requirement for a realistic flow pattern is that the respiration should be dominated by the lowest trophic levels. Here we find that the respiration of the phagotrophic micro-, nano- and phytoplankton amounts to 2200 g$\cdot$m$^{-2}\cdot$y^{-1}, or more than half of the total respiration. This seems to be a very reasonable estimate, especially as the respiration of the photosynthetic plankton is ignored since we only consider the net primary production.

The plankton food web

To focus on the plankton food web a special representation of the model was made where all fish groups were aggregated; so were all zooplankton, and all other large invertebrates, while the smaller plankton were described in six groups as discussed above. A summary of the flows is given in Figure 3. It illustrates the importance of

Figure 3. Flows in the aggregated version of the 1981 North Sea food web model focusing on the plankton compartments. All flows are expressed in g w.wt$\cdot$m$^{-2}\cdot$y^{-1}. The groups are arranged after approximate size on the x-axis and after estimated trophic level on the y-axis.

the lower trophic levels; around half of the total energy throughput for all of the living groups combined is estimated to be due to the nano- and picoplankton, two usually overlooked groups. Cautionary it may be added that the picture given of the plankton food web here is very uncertain. Different assumptions on ecotrophic efficiencies and diets of the consumers of these groups would lead to very different parameter estimates. The main purpose of including the groups here therefore really is to flag the importance they have for the overall flow patterns.

Primary production required to sustain consumption and catches
The primary production and detritus that is required to sustain the consumption of each of the groups in the systems and the catches can be quantified using the ECO-PATH II routine described above. Here all food chains in the food web are identified along with the amount of energy they transfer, and the transfer efficiencies with which this is done. Based on this the amount of primary production and detritus that is required for each of the food chains is calculated, and summed up for the terminal elements of the food chains.

Summing up the requirements we find that 29% of the primary production and detritus is required to sustain the catches in the system. Results for comparison from other aquatic systems are sparse, however Pauly & Christensen (1995) estimated for the global fisheries using a different approach than the present that 8% of the global aquatic primary production was necessary to support the worlds catches, while the requirements ranged from 24 to 35% of the system-specific primary production in freshwater-, upwelling- and shelf systems. Their results therefore seem very comparable with the present.

For the world's terrestrial systems Vitousek *et al.* (1986) estimated that close to 40% of the terrestrial primary production was used directly or indirectly by humans. As aquatic systems in general are less accessible to human utilization than terrestrial systems the 29% utilization in the present study is high.

Figure 4 gives the primary production and detritus required to sustain consumption and catches by ecological groups. Interestingly we know very little about the groups that require most, notably euphausiids, Norway pout, and copepods. As an ecological valuation measure the ratio between the required amount of primary production and detritus, and the consumption is also given on the Figure. As expected the fishes top the scale, and we find the piscivorous saithe and whiting at the very top. Comparing herring with the species that increased most in abundance after herring abundance declined in the late 1970s, sprat and sandeel, there is a marked cost difference; herring is 5-8 times as 'expensive' to have in the system.

The ecological cost factor presented here may be of interest as a measure of the 'food web price' for having a group in an ecosystem, and as such it is a measure related to the 'emergy' concept of Odum (1988). Emergy expresses how much solar energy equivalents a flow in a system represents. An advantage of the ecological cost factor as estimated here is that it is a quantifiable measure derived directly from the trophic dynamics of the ecosystem; there is no assumed conversion factor from material type to solar energy equivalents as for the emergy.

Required PP (g·m^{-2}·y^{-1})
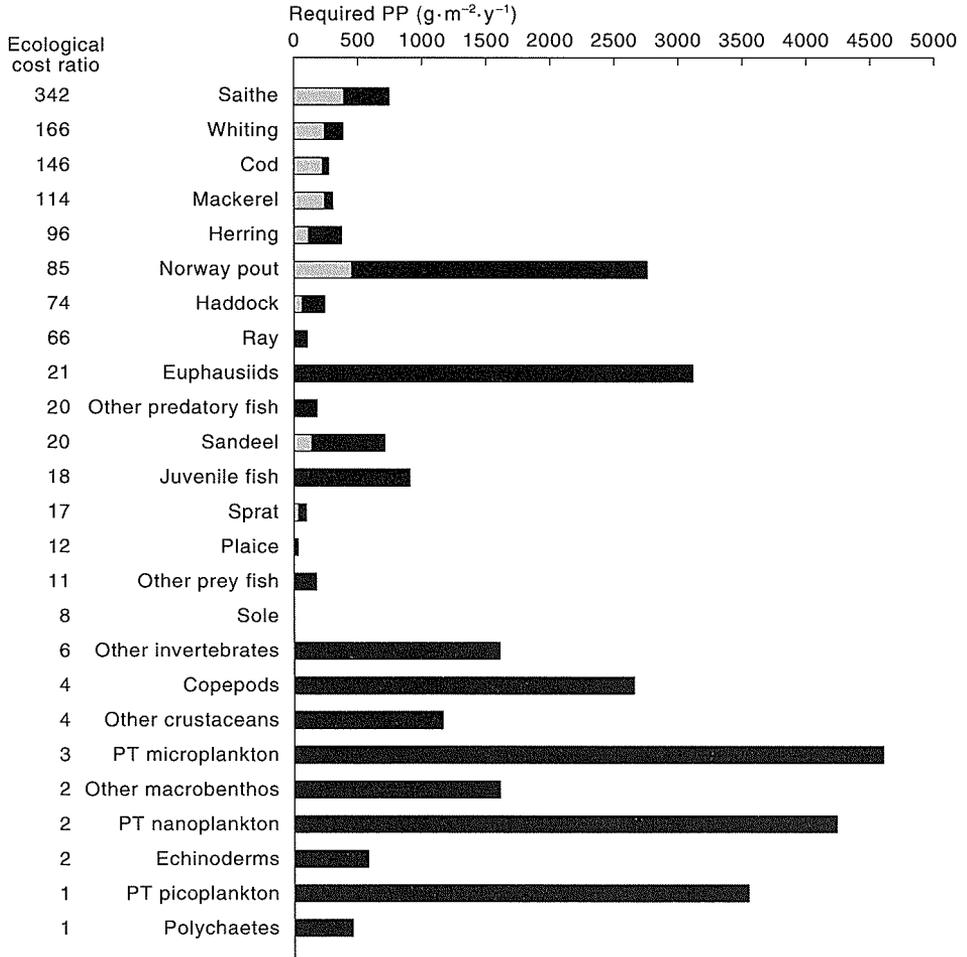
Figure 4. Estimates of primary production and detritus required (g·m^{-2}·y^{-1}) to sustain consumption (total bar area) and catches (grey bar area) in the North Sea ecosystem. The groups are arranged after ecological cost, i.e. after the ratio between the required primary production and detritus, and the consumption. The ecological cost ratio is given next to the group names.

Trophic aggregation

To clarify the trophic structure of the North Sea even further the flows in the system can be aggregated in discrete trophic levels using the method suggested by Ulanowicz (1995) and introduced above. The trophic aggregation routine of ECOPATH II produces the results in Table 4. The table shows that the important groups on trophic level II are the phagotrophic plankton along with larger invertebrates, on level III it is the phagotrophic plankton and zooplankton that dominate. On level IV the upper trophic levels are dominated by the Norway pout, and again the euphausiids and the juvenile fish.

Table 4. Absolute flows (g w.wt·m^{-2}·y^{-1}) by discrete trophic levels (I to VIII). The groups are sorted after their trophic levels (TL). Total flows (g w.wt·m^{-2}·y^{-1}) and total biomasses (g w.wt·m^{-2}) trophic level is also presented. The total biomasses excludes detritus, and are uncertain as some input biomasses are assumed.

TL	Group	I	II	III	IV	V	VI	VII	VIII
5.1	Saithe	–	–	0.0	0.8	0.7	0.3	0.2	0.1
4.5	Herring	–	–	0.7	1.7	0.7	0.4	0.4	0.0
4.5	Other predatory fish	–	–	1.7	3.8	1.4	0.8	0.9	0.0
4.5	Whiting	–	–	0.4	1.1	0.4	0.2	0.2	0.0
4.5	Mackerel	–	–	0.5	1.2	0.5	0.3	0.2	0.0
4.4	Norway pout	–	–	7.3	13	5.6	3.8	2.7	0.1
4.1	Cod	–	–	0.7	0.6	0.3	0.1	0.1	0.0
3.9	Juvenile fish	–	–	26	10	4.9	7.3	0.1	–
3.9	Euphausiids	–	–	80	33	14	21	0.6	–
3.8	Haddock	–	–	1.5	1.1	0.3	0.1	0.1	0.0
3.8	Ray	–	–	0.8	0.5	0.1	0.1	0.0	0.0
3.8	Sprat	–	–	2.7	0.9	0.4	0.6	0.0	–
3.7	Sandeel	–	–	21	6.8	2.8	4.0	0.1	0.0
3.2	Plaice	–	–	1.6	0.1	0.0	0.0	0.0	–
3.0	Sole	–	–	0.3	0.0	0.0	0.0	–	–
3.0	Other prey fish	–	3	11	0.9	0.3	0.4	0.0	–
3.0	PT microplankton	–	560	340	510	–	–	–	–
2.9	Copepods	–	310	110	68	103	–	–	–
2.7	Other invertebrates	–	130	95	14	17	4.2	–	–
2.6	PT nanoplankton	–	890	1300	–	–	–	–	–
2.5	Other crustaceans	–	220	62	13	18	1.7	–	–
2.4	Other macrobenthos	–	520	52	31	47	–	–	–
2.2	Echinoderms	–	290	13	7.7	12	–	–	–
2.0	Polychaetes	–	430	–	–	–	–	–	–
2.0	PT picoplankton	–	3500	–	–	–	–	–	–
1.0	PS microplankton	2300	–	–	–	–	–	–	–
1.0	PS nanoplankton	590	–	–	–	–	–	–	–
1.0	PS picoplankton	930	–	–	–	–	–	–	–
1.0	Detritus	4900	–	–	–	–	–	–	–
	Total flow by trophic level:	8700	6900	2200	720	230	45	5.7	0.3
	Total biomass by trophic level:	47	120	33	16	11	3.1	0.7	0.06

The groups are arranged after estimated fractional trophic levels in Table 4, and it is interesting to observe that herring has a higher trophic level than cod, and that the herring is way above the sprat and sandeel. The flatfishes are as expected placed on the lowest trophic levels among the fish groups.

Mortalities

For the fish species the ecotrophic efficiencies indicate that only 48 -86% of the production is actually used in the system, except for ray and 'other predatory fish' who do not seem to be used in the system, and therefore have an *EE* of 0 (Table 1). The efficiencies reflect that the residual mortalities in the MSVPA run have not been fully accounted for in the ECOPATH II model. The MSVPA only includes predation by the MS species. To compensate for this the MS WG assume an other pre-

Table 5. Mortality rates (all annual) based on ECOPATH and MSVPA analyses. Z is the total mortality rate, and is assumed to equal P/B, F is the fishing mortality, BA is the biomass accumulation rate, $M2$ is predation mortality, while $M0$ is non-predation mortality, and $M1$ is predation by other fish predators in the MSVPA. For ECOPATH II models $Z = F + BA + M0 + M2$; for the MSVPA run $Z = F + BA + M0 + M1 + M2$. The $M2$ of ECOPATH II corresponds to $M1+M2$ of MSVPA.

Group	Z	F	BA	ECOPATH $M0$	$M2$	MSVPA $M0$	$M1$	$M2$
1. Cod	1.11	1.01	− 0.23	0.27	0.07	0.20	0.07	0.06
2. Whiting	0.84	0.56	− 0.30	0.34	0.24	0.20	0.17	0.21
3. Saithe	0.58	0.31	0.06	0.21	0.00	0.20	0.00	0.00
4. Mackerel	0.29	0.24	− 0.10	0.15	0.00	0.15	0.00	0.00
5. Haddock	1.37	0.46	− 0.01	0.50	0.43	0.20	0.35	0.36
6. Herring	1.04	0.35	0.21	0.26	0.22	0.10	0.16	0.22
7. Sprat	1.21	0.63	− 0.55	0.60	0.53	0.20	0.39	0.54
8. Norway pout	2.48	0.41	0.48	0.77	0.81	0.20	0.57	0.81
9. Sandeel	2.02	0.45	0.47	0.37	0.73	0.20	0.28	0.62
10. Plaice	0.65	0.35	0.21	0.09	0.00	0.10	0.00	0.00
11. Sole	0.66	0.33	0.23	0.10	0.00	0.10	0.00	0.00
12. Ray	0.44	0.00	–	0.44	0.00	–	–	–
13. Other predatory fish	0.87	0.00	–	0.87	0.00	–	–	–
14. Other prey fish	0.48	0.00	–	0.02	0.45	–	–	–

dation mortality ($M1$) and a non-predation mortality ($M0$) for all groups. These mortalities are parameterized based on very limited information, especially $M0$ which is assumed to take values between 0.1 and $0.2 \cdot y^{-1}$ for the different groups. The $M1$ term is not included in ECOPATH models where all predation mortality is assumed accounted for.

The mortality rates from the MSVPA and the present ECOPATH II model are presented in Table 5 for comparison. For most groups the $M2$ values are slightly higher in the ECOPATH II model than in the MSVPA as more predators are included. Yet the ECOPATH II predation mortality, $M2$ is lower than the summed mortalities, $M1$ and $M2$ from the MSVPA indicating that not all of the (assumed) $M1$ mortality can be accounted for in the ECOPATH II model. This is reflected by the other mortality, $M0$ values of ECOPATH II being higher than the $M0$ of MSVPA. The $M0$ values of the ECOPATH II model also include discards, which are treated as contribution to detritus. This should have no serious consequences for the model.

Trophic impact
Based on economic input−output analyses the trophic impact any of the groups in a system has on other groups can be quantified. Result from the mixed trophic impact analysis are shown in Figure 5. The figure gives a very information-rich picture of how the different groups in the system impact each other trophically through direct as well as indirect interactions. These impacts may be cascading down the trophic web; whiting for example has a negative impact on Norway pout due to predation, but a positive impact on the euphausiids, the main prey of Norway pout. Generally the fish predators impact each other negatively and all fish but the 'other
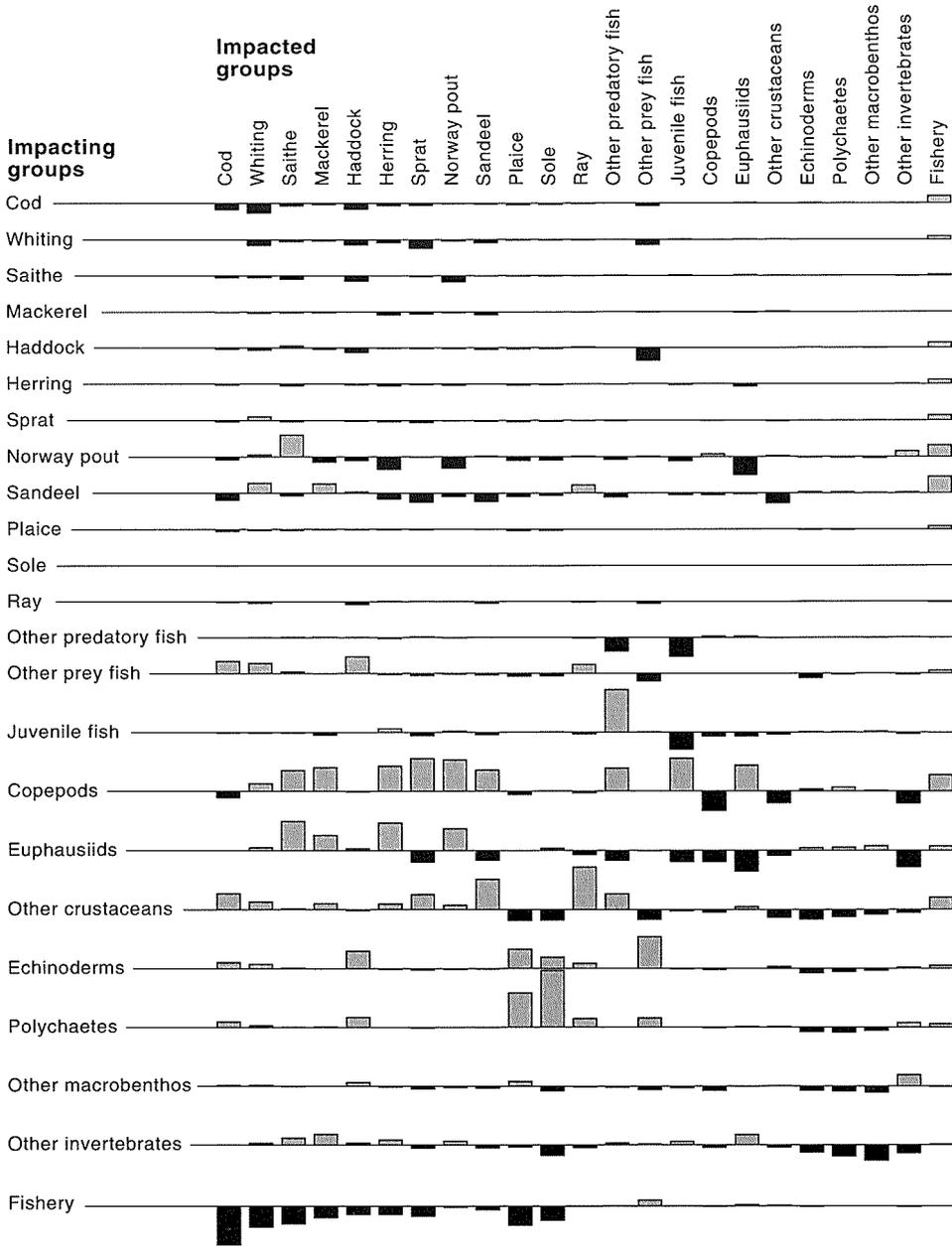
Figure 5. Mixed trophic impacts in the 1981 North Sea ecosystem. The bars quantify the direct and in-direct trophic impacts that the groups indicated on the left have on the groups mentioned at the top. The impacts are relative but comparable between groups. Positive impacts protrude above the baseline while negative are shown below it. Only impacts for fish groups and larger invertebrates are shown.

predatory fish' have a positive impact on the fishery. Whiting is found to have no impact on cod, the positive impact of whiting being a prey for cod is counteracted by the negative role whiting has as a competitor for food. Had the predation by whiting on juvenile cod been quantified in the model the impact would probably have changed to an overall negative.

Herring and sprat are assumed to compete for the same food resources. The impacts here are however negligble, indicating that the changes in abundance of herring and sprat over time are unlikely to be explained from food web dynamics as studied here. This may be in line with the findings of Corten (1986), who concluded that the changes in the sprat stock size should most likely be explained by environmental conditions.

Among the invertebrates the negative impact of euphausiids on sprat and sand eel is interesting. Tentatively one could speculate how changes in the fishing pattern could lead to changes in the abundance of various groups in the system. As an example, would increased catches of saithe lead to more Norway pout, less euphausiids, more copepods, sprat and sandeel? It is tempting to speculate over such cascading effects; the mixed trophic impact routine is however not designed for making predictions as it does not have a time dimension and cannot anticipate changes in the food web. Therefore it can mainly be used to increase our understanding of ecological linkages in systems, and certainly the brain exercises are good for creating hypotheses about trophic linkages.

In addition to allowing interpretations about such ecological impacts the mixed trophic impact routine can be seen as a simple sensitivity analysis. It gives an idea of how important the different groups in the system are for the systems trophic dynamics, and therefore of where gains from improved parameter estimation can be expected. Here for instance little can be gained from a better parameterization of sole or ray.

Demersal and pelagic subsystems

Aggregating 25 of the groups in the original model in six groups as described earlier a summary of the flows within and between the pelagic and demersal compartments can be made (Figure 6). For this comparison the flows involving the small, nano- and picoplankton groups, are ignored as the corresponding flows involving small benthic groups are also ignored.

The biomasses are found to be approximately evenly distributed between the pelagic and demersal fish, yet the turn-over rates are much more rapid for the pelagic groups, e.g. P/B is $2.2 \cdot y^{-1}$ for the pelagics and only $0.67 \cdot y^{-1}$ for the demersals.

The interaction between the demersal and pelagic subsystems is quite well defined, even with the rather coarse separation used here. This is illustrated by the demersal fish who only take some 18% of their diet from the pelagic groups and of this the 8% are pelagic fish (many of which spend part of the day schooling near the bottom). For the pelagic fish as little as 4% of the food is found to be taken from the demersal subsystem. A good part of the interaction is through the heterogeneous 'other crustaceans' group which includes both pelagic and benthic species, and which here have been assigned to the pelagic group where the majority of the flow takes place.
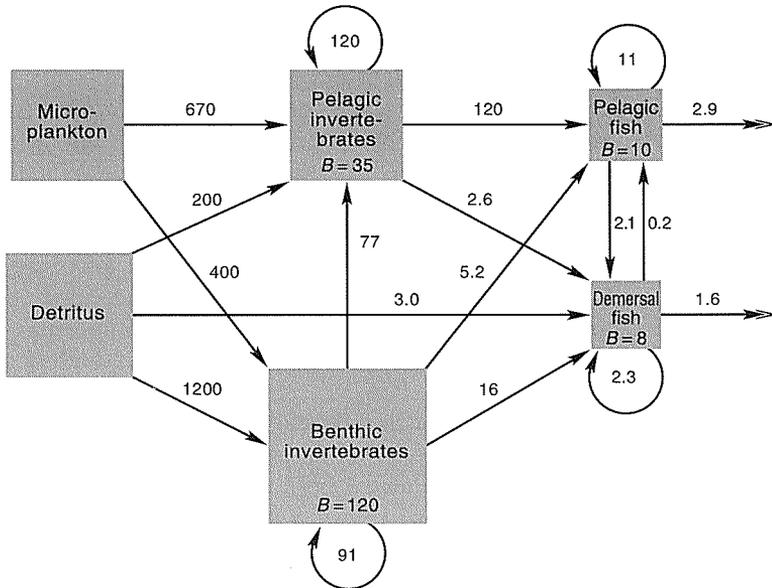
Figure 6. Flows in the demersal and pelagic subsystems in the 1981 North Sea food web. All flows are expressed in g w.wt·m^{-2}·y^{-1}, while biomasses are in g w.wt·m^{-2}. Double-headed arrows indicate fishery catches.

Estimation of the primary production and detritus required to sustain the consumption in the two subsystems leads to some interesting findings. The pelagic and benthic invertebrates require approximately the same amount while the pelagic fish because of their higher metabolic rates and slightly higher trophic levels require fourtimes as much as the demersal fish.

The flow chart derived here (Figure 6) resembles many previous attempts to illustrate the North Sea food web, see e.g. Steele (1974), Jones (1982b, 1984), and Bromley et al. (1993). A major difference is however that the previous representations operate at the coarse level of detail illustrated in Table 3 and Figure 6, whereas the present is based on aggregation from a much more detailed level. This can be expected to add robustness to the present representation.

Conclusions

The model presented here gives but one possible representation of the trophic interactions in the North Sea in a certain year and state. Other assumptions would lead to somewhat, but at least for the upper trophic levels not very, different representations. Especially would better parameter estimates for the non-MS groups help to restrain the range of possible descriptions of the system.

The problem with the low consumption rates for the gadoids is indicative of the problem of acquiring or maintaining an overview of large, complex models. As the costs for development and parameterization of such models are huge, effort should

not be spared when it comes to additional data analyses of the quality of the data set, especially when this can be done without additional data acquisition. Application of the present methodology is one example of this.

The limited availability of parameter estimates of the main invertebrate groups of the North Sea on an annual basis reflects a need for process-oriented studies aimed at producing such estimates. Valuable ecological work is conducted, but more studies focused on production aspects and on energy flows between the important invertebrate groups and to their predators are called for.

Fisheries biologists have over the last decade focused on energy flow studies in order to improve fisheries management, notably to parameterize the MS WG programs. A similar development in invertebrate biology could lead to both increased communication between the disciplines and better understanding of the ecology of the North Sea as a whole.

Of importance is also that such a development will address the increasing need for management of marine ecosystems so that the interests of not just the fishing industry are taken into account (Pauly 1994). As stressed by ICES also environmental concern should be taken (Anon. 1992). It is hoped that studies such as presented here may help to support this development.

Acknowledgements

References

Albert, O.T., 1994: Biology and ecology of Norway pout (*Trisopterus esmarki* Nilsson, 1855) in the Norwegian Deep. – ICES J. mar. Sci. *51*: 45-61.

Andersen, K.P. & E. Ursin, 1977: A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. – Meddr Danm. Fisk.- og Havunders. 7: 319-435.

Anon., 1992: ICES to strengthen its environmental side after wide discussion. – ICES/CIEM Information *19*: 1-2.

Baden, S.P., 1986: Recent changes in the Kattegat and Skagerrak ecosystem and their possible interdependence. – Nat. Swedish envir. Prot. Bd Rep. 3157. 91 p.

Bagge, O., 1978: Kattegatprojekt. – Delrapport. Intern. Rep. No. 96. – Danish Institute for Fisheries and Marine Research. 76 p.

Bromley, P.J., J.M. Last & J.G. Pope, 1993: Energy flow model of the North Sea ecosystem. – *In* V. Christensen & D. Pauly (eds.): Trophic Models of Aquatic Ecosystems, pp. 298-299. ICLARM Conf. Proc. 26. 390 pp.

Buchanan, J.B. & R.M. Warwick, 1974: An estimate of benthic macrofaunal production in the offshore mud of the Northumberland Coast. – J. mar. biol. Ass. U.K. *54*: 197-222.

Christensen, V., 1995a: A multispecies virtual population analysis incorporating information of size and age. – ICES C.M. 1995/D: 8. 14 pp.

Christensen, V., 1995b: Ecosystem maturity – towards quantification. – Ecol. Modelling 77: 3-32.

Christensen, V. & D. Pauly, 1992a: A guide to the ECOPATH II software system (version 2.1). – ICLARM Software *6,* 72 p. International Center for Living Aquatic Resources Management (ICLARM), Manila.

Christensen, V. & D. Pauly, 1992b: ECOPATH II – A software for balancing steady state models and calculating network characteristics. – Ecol. Modelling *61:* 169-185.

Christensen, V. & D. Pauly, 1993a: Flow characteristics of aquatic ecosystems. – *In* V. Christensen & D. Pauly (eds.): Trophic Models of Aquatic Ecosystems, pp. 338-352. ICLARM Conf. Proc. *26.* 390 pp.

Christensen, V. & D. Pauly, 1993b: On steady state modelling of ecosystems. – *In* V. Christensen & D. Pauly (eds.): Trophic Models of Aquatic Ecosystems, pp. 14-19. ICLARM Conf. Proc. *26.* 390 pp.

Christensen, V. & D. Pauly, (eds.) 1993c: Trophic Models of Aquatic Ecosystems. – ICLARM Conf. Proc. *26.* 390 pp.

Christensen, V. & D. Pauly, 1995: Fish production, catches, and the carrying capacity of the world oceans. – Naga, The ICLARM Quart. 18(3): 34-40.

Corten, A., 1986: On the causes of the recruitment failure of herring in the central and northern North Sea in the years 1972-1978. – J. Cons. int. Explor. Mer *42:* 281-294.

Creutzberg, F. & G.C.A. Duineveld, 1986: The role of the lesser weever *Trachinus vipera* and the dab *Limanda limanda* in the benthic system of the southern North Sea. – ICES. C.M. 1986/L: 4. 10 pp.

*Crisp, D.J. ,*1975: Secondary productivity in the sea. – Productivity of world ecosystems, pp. 71-89. National Academy of Sciences, Washington, DC.

Daan, N., (ed.), 1989. Data base report of the stomach sampling project 1981. – ICES Coop. Res. Rep. No. 164. 144 pp.

Daan, N., P.J. Bromley, J.R.G. Hislop & N.A. Nielsen, 1990: Ecology of North Sea fish. – Neth. J. Sea Res. *26:* 343-386.

Dahl, K. & E. Kirkegaard, 1987: The diet and consumption of horse mackerel (*Trachurus trachurus*) in the Eastern North Sea, August 1986. – ICES C.M. 1987/H: 43. 23 pp.

Fransz, H.G. & W.W.C. Gieskes, 1984: The unbalance of phytoplankton and copepods in the North Sea. – Rapp. P.-v. Réun. Cons. int. Explor. Mer *183:* 218-225.

Fenchel, T., 1988: Marine plankton food chains. – A. Rev. Ecol. Syst. *19:* 19-38.

Gordon, J.D.M., 1977: The fish populations in inshore waters of the west of Scotland. The biology of the Norway pout (*Trisopterus esmarkii*). – J. Fish Biol. *10:* 417-430.

Hannon, B. & C. Joiris, 1989: A seasonal analysis of the southern North Sea ecosystem. – Ecology 70(6): 1916-1934.

Heip, C., R. Huys, M. Vincx, A. Vanreusel, N. Smol, R. Herman & P.M.J. Herman, 1990: Composition, distribution, biomass and production of North Sea meiofauna. – Neth. J. Sea Res. *26:* 333-342.

Heip, C., D. Basford, J.A. Craeymeersch, J.-M. Dewarumez, J. Dörjes, P. de Wilde, G. Duineveld, A. Eleftheriou, P.M.J. Herman, U. Niermann, P. Kingston, A. Künitzer, E. Rachor, H. Rumohr, K. Soetaert & T. Saltwedel, 1992: Trends in biomass, density and diversity of North Sea macrofauna. – ICES J. mar. Sci. *49:* 13-22.

Hilborn, R. & C.J. Walters, 1992: Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. – Chapman and Hall, New York. 570 pp.

ICES, 1989: Report of the Multispecies Assessment Working Group, 7-16 June 1989, Copenhagen. – ICES Counc. Meet. 1989/Assess: 20. 125 pp.

ICES, 1991: Report of the Multispecies Assessment Working Group, 4-13 December 1990, Woods Hole. – ICES C.M. 1991/Assess: 7. 246 pp.

Jones, R., 1978: Further observations on the energy flow to the major fish species in the North Sea. – ICES C.M. 1978/Gen: 6, Symp. 10 pp.

Jones, R., 1982a: Ecosystems, food chains and fish yields. – *In* D. Pauly & G.I. Murphy (eds.): Theory and management of tropical fisheries, pp. 195-240. ICLARM Conf. Proc. *9.* 360 pp.

Jones, R., 1982b: Species interactions in the North Sea. – *In* M.C. Mercer (ed.): Multispecies approaches to fisheries management advice, pp. 48-63. Can. Spec. Publ. Fish. aquat. Sci. *59.* 169 pp.

Jones, R., 1984: Some observations on energy transfer through the North Sea and Georges Bank food webs. – Rapp. P.-v. Réun. Cons. int. Explor. Mer *183:* 204-217.

Knust, R., 1990: Food and condition of dab *Limanda limanda* (L.) from the Dogger Bank and the German Bight. – ICES C.M. 1990/G: 62. 7 pp.

Künitzer, A., 1990: A comparison of the *Amphiura filiformis*-associations north-east of the Dogger Bank and of the German Bight. – Neth. J. Sea Res. 25(1/2):199-208.

Laevastu, T. & H.A. Larkins, 1981: Marine fisheries ecosystem: its quantitative evaluation and management. – Fishing News Books, Farnham Surrey, England. 162 pp.

Lagardère, J.P., 1987: Feeding ecology and daily food consumption of common sole, *Solea vulgaris* Quensel, juveniles on the French Atlantic coast. – J. Fish Biol. 30: 91-104.

Last, J.M., 1982: The food of juvenile sprat *Sprattus sprattus* (Linnaeus 1758) and herring *Clupea harengus* (Linnaeus 1758), in inshore waters of the Southern North Sea. – ICES C.M. 1982/H: 12. 6 pp.

Last, J.M., 1985: Further observations on the food of 0-group sprat *Sprattus sprattus* (Linnaeus 1758) and herring *Clupea harengus* (Linnaeus 1758) from the North Sea. – ICES C.M. 1985/L: 35. 6 pp.

Last, J.M., 1989: The food of herring, *Clupea harengus*, in the North Sea, 1983-1986. – J. Fish Biol. 34: 489-501.

Lindley, J.A.: 1980. Population dynamics and production of Euphausiids. II. *Thysanoessa inermis* and *T. raschi* in the North Sea and American coastal waters. – Mar. Biol. 59: 225-233.

Meyer, T.L., R.A. Cooper & R.W. Langton, 1979: Relative abundance, behaviour, and food habits of the American sand lance, *Ammodytes americanus*, from the Gulf of Maine. – Fish. Bull. 77(1): 243-253.

Nicol, S. & W. de la Mare, 1993: Ecosystem management and the Antarctic krill. – Am. scient. 81: 36-47.

Nielsen, T.G. & K. Richardson, 1989: Food chain structure of the North Sea plankton communities: seasonal variations of the role of the microbial loop. – Mar. Ecol. Prog. Ser. 56: 75-87.

Odum, H.T., 1988: Self-organization, transformity, and information. – Science 242: 1132-1139.

Paloheimo, J.E. & L.M. Dickie, 1966: Food and growth of fishes. III. Relations among food, body size, and growth efficiency. – J. Fish. Res. Bd Can. 23(8): 1209-1248.

Palomares, M.L. & D. Pauly, 1989: A multiple regression model for predicting the food consumption of marine fish populations. – Aust. J. mar. Freshwater Res. 40: 259-273.

Pauly, D., 1989: Food consumption by tropical and temperate fish populations: some generalizations. – J. Fish. Biol. 35(Suppl. A): 11-20.

Pauly, D., 1994: Assessment methodologies and fisheries management: How to keep making sense. – *In* C.W. Voigtlander (ed.): The state of the world's fisheries resources, pp. 121-132. Proc. World Fisheries Congress, Plenary Sessions. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi..

Pauly, D. & V. Christensen, 1993: Graphical representation of steady state trophic ecosystem models. – *In* V. Christensen & D. Pauly (eds.): Trophic models of aquatic ecosystems, pp. 20-28. ICLARM Conf. Proc. 26. 390 pp.

Pauly, D. & V. Christensen, 1995: Primary production required to sustain global fisheries. – Nature 374: 255-257.

Peterson, W.T., 1988: Rates of egg production by the copepod *Calanus marshallae* in the laboratory and in the sea off Oregon, USA. – Mar. Ecol. Prog. Ser. 47: 229-237.

Polovina, J.J., 1984: Model of a coral reef ecosystem. Part I. The ECOPATH model and its application to French Frigate Shoals. – Coral Reefs 3: 1-11.

Rachor, E., 1982: Biomass distribution and production estimates of macro-endofauna in the North Sea. – ICES C.M. 1982/L: 2. 10 pp.

Raitt, D.F.S. & J.A. Adams, 1965: The food and feeding of *Trisopterus esmarkii* (Nilsson) in the northern North Sea. – Dept. Agriculture and Fish. Scotland, mar. Res. 3. 28 pp.

Reid, P.C., C. Lancelot, W.W.C. Gieskes, E. Hagmeier & G. Weichart, 1990: Phytoplankton of the North Sea and its dynamics: a review. – Neth. J. Sea Res. 26: 295-331.

Robb, A.P. & J.R.G. Hislop, 1980: The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. – J. Fish. Biol. 16: 199-217.

Salzwedel, H., 1980: Energy budgets for two populations of the bivalve *Tellina fabula* in the German Bight. – Veröff. Inst. Meeresforsch. Bremerh. 18: 257-287.

Salzwedel, H., E. Rachor & D. Gerdes, 1985: Benthic macrofauna communities in the German Bight. – Veröff. Inst. Meeresforsch. Bremerh. 20: 199-267.

Sparre, P., 1991: Introduction to multispecies virtual population analysis. – ICES mar. Sci. Symp. 193: 12-21.

Sparholt, H., 1990: An estimate of the total biomass of fish in the North Sea. – J. Cons. int. Explor. Mer 46: 200-210.

Sparholt, H., 1991: Multispecies assessment of Baltic fish stocks. – ICES mar. Sci. Symp. *193:* 64-79.

Steele, J.H., 1974: The structure of marine ecosystems. – Blackwell Scientific Publications, Oxford. 127 pp.

Stripp, K., 1969: Jahreszeitliche fluktuationen von makrofauna und meiofauna in der Helgoländer Bucht. – Veröff. Inst. Meeresforsch. Bremerh. *12:* 65-94.

Ulanowicz, R.E., 1986. Growth and development: ecosystem phenomenology. – Springer-Verlag, New York. 203 pp.

Ulanowicz, R.E., 1995. Ecosystem trophic foundations: Lindeman Exonerata. – *In* B.C. Patten & S.E. Jørgensen (eds): Complex ecology: The part-whole relation in ecosystems, pp 549-560. Prentice-Hall, Englewood Cliffs, New Jersey.

Ulanowicz, R.E. & C.J. Puccia, 1990: Mixed trophic impacts in ecosystems. – Coenoses *5:* 7-16.

Vitousek, P.M., P.R. Ehrlich, A.H. Ehrlich & P.A. Matson, 1986: Human appropriation of the products of photosynthesis. – BioScience *36*(6): 368-373.

Wulff, F., J.G. Field & K.H. Mann, (eds), 1989: Network analysis in marine ecology – Methods and applications. – Coastal and Estuarine Studies Vol. 32, Springer-Verlag, New York. 284 pp.

Appendix 1. Group-specific information

MS predators

Information on biomass, consumption and production for the MS predators, i.e. for cod (*Gadus morhua*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*), mackerel (*Scomber scombrus*), and haddock (*Melanogrammus aeglefinus*), is available from the MS WG database. For these species detailed diet compositions could be derived from information presented by Daan (1989) and Daan *et al.* (1990). The mackerel group is modelled to include both the North Sea mackerel, and the West mackerel occurring in the northern North Sea in the second and third quarters of the year.

Herring (Clupea harengus)

Information on biomass and production is available from the MS WG database. The consumption rate is from Pauly (1989). The weighted average diet composition is based on information from Last (1989) as follows: A mean of prey weights is taken over the three February surveys; the surveys in February, May and August are assumed to be representative for 5, 3, and 4 months, respectively, and it is assumed that the relative consumption rates in the survey periods are 1, 2, and 2, respectively, indicating a consumption rate in the summer half of the year twice as high as in the winter months.

Sprat (Sprattus sprattus)

Information on biomass and production is available from the MS WG database. The consumption rate is based on an estimate for *Sprattus fuegensis* given in Pauly (1989), which results in a reasonable gross food conversion efficiency of 14%. The actual diet composition is assumed but based on information in Last (1982, 1985).

Norway pout (Trisopterus esmarkii)

Information on biomass and production is available from the MS WG database. The consumption rate is estimated from an assumed gross food conversion efficiency of

15%. The diet composition for Norway pout is based on information presented by Raitt & Adams (1965, figure 1B & 2B). Raitt & Adams present average diets based on percent volume and on average volume per stomach. The percent volume under-estimates the importance of stomachs with large fullness of mainly fish prey, while at the same time over-representing large prey due to differential digestion time. Therefore the percent volume representation is accepted here as a compromise. The overall diet composition is assumed to be represented by the average diet composition of juveniles and adults. The diet information found by Raitt & Adams (1965) is supported by studies of Gordon (1977) and by a recent study in the Norwegian Deep (Albert 1994).

Sandeel (*Ammodytes* spp.)

Information on biomass and production is available from the MS WG database. The consumption rate is estimated from an assumed gross food conversion efficiency of 15%. Sandeels are predominantly zooplanktivorous, with small fish and benthos contributing to the diet (Baden 1986). Meyer *et al.* (1979) reports that copepods and *Sagitta elegans* contributes around 40% by weight each to the diet of American sand lance, the remaining being mainly animal remains. The actual diet composition is assumed based on these sources.

Plaice (*Pleuronectes platessa*)

Information on biomass and production is available from the MS WG database. Consumption rate is obtained as an average of the consumption rates given for female and male plaice by Palomares & Pauly (1989). The diet composition is based on mainly qualitative information of plaice feeding on invertebrates, mainly polychaetes, bivalves, and echinoderms (Bagge 1978).

Sole (*Solea solea*)

Information on biomass and production is available from the MS WG database. As no estimate for consumption rate was available a gross food conversion efficiency of 15% was assumed. The diet composition is based on qualitative information only, e.g. Lagardère (1987).

Ray (*Raja radiata*)

The biomass of ray is estimated from average trawl survey abundance as reported by Sparholt (1990), and re-evaluated by Daan *et al.* (1990). The food consumption/biomass ratio is estimated to $2.9 \cdot y^{-1}$ based on studies by M. Vinter, as reported in ICES (1989). Based on the same sources (Tables 8.4.1 and 8.4.2) the diet composition can be quantified. The mortality rate (production) of ray is not known. It is therefore estimated from the consumption/biomass ratio and an assumed gross food conversion efficiency of 15%.

Other predatory fish

The parameters for 'other predatory fish' were mainly based on horse mackerel, *Trachurus trachurus*. Biomasses for the 'other' fish species were based on average data (winter and summer trawl surveys) for 1983-1985 as estimated by Sparholt

(1990.) In these surveys horse mackerel constituted some 95% of the trawlable biomass of the 'other predatory fish'. Horse mackerel were only present in noticeable quantities on the autumn survey, and the biomass estimate used here is the average annual biomass. Only inconclusive estimates of food consumption by horse mackerel in the North Sea seem to be available (Dahl & Kirkegaard 1987). It was therefore assumed that the 'other predatory fish' have the same consumption/biomass ratio as mackerel. The diet is based on information for horse mackerel given by Dahl & Kirkegaard (1987) assuming the prey fish to be juveniles.

Other prey fish

The 'other prey fish' group is focused on dab, *Limanda limanda*. The biomass for this group was as for the 'other predatory fish' derived from Sparholt (1990.) Here the dab was estimated to contribute around 65% to the biomass of 'other prey fish'. Consumption rates were derived from information given by Creutzberg & Duineveld (1986) for dab in the southern North Sea. The production rate for 'other prey fish' is not known; therefore an ecotrophic efficiency of 0.95 is assumed, i.e. the 'other mortality' is assumed to be 5% of production, and production is estimated within ECOPATH to meet demands. Creutzberg & Duineveld (1986) also give average annual diet compositions for dab on mud and sand bottom. Baden (1986) reports various food studies of dab indicating that echinoderms and other benthos predominate in the diet, while Knust (1990) reports that the main part of the food of dab in the German Bight was brittle star, *Ophiura albida*, in spring, and crustaceans, chiefly amphipods, in summer. The actual diet composition is assumed based on these sources. No catches are reported for the other prey fish but it is known that there are considerable discards especially of dab in the southern North Sea. Discards are treated as contributions to detritus in the present model, i.e. they are included in the $(1-EE)$ part of the production and thus estimated indirectly.

Juvenile fish

This is a heterogeneous group intended to encompass all juvenile fish in the North Sea. Juvenile fishes are important prey for a large number of adult fishes, even though the predation to some extent is limited due to the juveniles generally occurring at shallower depths than adult fishes. The present implementation includes herring, Norway pout, sandeel, and 'other predatory fish' (*Trachurus*) as predators on the juvenile fishes, whereas the MS predators not are included even though they do feed on juveniles. Because of this the juvenile fish group should be considered poorly parameterized but it is considered important to 'flag' its existence nevertheless.

The data for juvenile fishes are mainly based on qualified guesses, i.e. a high natural mortality rate and a high gross food conversion efficiency is assumed. The diet composition is likewise based on general knowledge of most juvenile fishes being planktivorous, see e.g. Robb & Hislop (1980).

Copepods

For copepods in the North Sea, Crisp (1975) reports an annual consumption and production of 60 and 18 g $C \cdot m^{-2}$, respectively, and these estimates are used here.

This production is within the range of more recent estimates (Fransz & Gieskes 1984). Hannon & Joires (1989) reported a zooplankton production in the southern North Sea of 15-20 g C·m^{-2}·y^{-1}. This again brackets the estimate of Crisp but also shows that his value may be an underestimate as the copepod production may well be highest in the northern North Sea. In lieu of a biomass estimate for copepods it is assumed that the biomass is 10 g·m^{-2}. Therefore P/B is estimated to 18 g·y^{-1}, while Q/B is 60·y^{-1}, both based on Crisp (1975) and a conversion factor of 10 from carbon to wet weight. In the actual calculations only the total production and consumption rates are used, not the factors P/B, Q/B and B, therefore the use of an assumed biomass value does not influence the results.

The food conversion efficiency (production/consumption ratio) of 30% for copepods used here is well in line with the estimated gross efficiency of 33% found by Peterson (1988) to be nearly constant among different copepod species. Copepods are assumed to feed 95% on microplankton (evenly distributed between photosynthetic and phagotrophic forms) and 5% on detritus.

Euphausiids

Lindley (1980) gave estimates of production and biomass of two (out of three) dominant species, *Thysanoessa inermis* and *T. raschi*, of euphausiids in the northeastern North Sea and northwestern Skagerrak in 1966 and 1967. Based on this information a production/biomass ratio of 2.43·y^{-1} can be estimated. Lindley's estimate of biomass could not be used (see Parameter estimates in Results and discussion on page 9); instead it is assumed that the gross food conversion efficiency of euphausiids is 0.15, and that the ecotrophic efficiency of the group is 0.95. The diet is based on qualitative information only.

Macrobenthos (polychaetes, echinoderms, and other macrobenthos)

In a review of available information about the biomass of macrobenthos in the North Sea, Rachor (1982) estimated the average annual biomass to 28 g wet weight (w.wt)·m^{-2}. More recent studies have yielded higher biomasses at least partly due to changes in methodology, see e.g. the discussion by Künitzer (1990).

Heip *et al.* (1992) estimated the average total macrofauna biomass to 7 g ash-free dry weight (AFDW) based on 197 stations sampled during the ICES coordinated North Sea Benthos Survey in April-May 1986. Using a conversion factor of 15:1 for w.wt to AFDW (see Künitzer 1990 based on Salzwedel *et al.* 1985) this biomass estimate corresponds to approximately 105 g w.wt·m^{-2}. This can be distributed with $10^{0.20}$ = 1.6 g AFDW·m^{-2} (24 g w.wt·m^{-2}) to echinoderms, $10^{0.32}$ = 2.1 g AFDW·m^{-2} (32 g w.wt·m^{-2}) to polychaetes, and 49 g w.wt·m^{-2} to other macrobenthos. These biomass estimates are spring-time values which ought to be corrected for seasonal variation to obtain annual averages.

Stripp (1969) in a study of the seasonal variation of macrofauna in the Helgoland Bight found biomasses to be 1.4 times as high during May to November as compared to the period from December to April. However, Buchanan & Warwick (1974) found only slight annual biomass variation for macrobenthos in an offshore mudbottom study. Based on this an other information it is not clear how a seasonal

adjustment should be made, and for the present study seasonal variation is therefore ignored.

The average production/biomass ratio for macrobenthos in the North Sea was estimated by Rachor (1982) to be approximately $2 \cdot y^{-1}$, and this estimate is used here for the group.

Salzwedel (1980) estimated for a common bivalve, *Tellina fabula*, that 22% of the consumption was turned into flesh production; as detritivores may have a lower food conversion efficiency than herbivores the consumption/biomass ratio for macrobenthos was here estimated from a lower, assumed gross food conversion efficiency of 15%.

Other crustaceans and other invertebrates

Only very limited information was available for these groups. For both, a production/biomass ratio of $3 \cdot y^{-1}$, a gross food conversion efficiency of 15%, and an ecotrophic efficiency of 0.95 were assumed. The diet compositions are assumed based on qualitative information, e.g. various reports from the ICES Benthos WG.

The meiofauna is included in the 'other invertebrates' group. Estimates – claimed to be not much more than guesses – give a total meiofauna consumption of 10 g $C \cdot m^{-2} \cdot y^{-1}$, a biomass of 1-2 g d.wt $\cdot m^{-2}$, a production/biomass ratio of around $15 \cdot y^{-1}$, and a reasonable constant production/assimilation ratio of 0.4; nematodes are almost an order of magnitude more important than harpacticoids (Heip *et al.* 1990). These estimates are however not used directly here.

Microplankton

Phytoplankton is the major primary producer in the North Sea (Reid *et al.* 1990), and production by benthic producers is not included in this model.

The small plankton is here divided in three size groups, micro-, nano-, and picoplankton, all described largely based on Fenchel (1988). The microplankton encompasses the size group 20-200 µm. It is here separated in two groups, photosynthetic organisms, called phytoplankton, including mainly diatoms and dinoflagellates, and phagotrophic plankton, including ciliates, dinoflagellates, some small metazoan zooplankton, a.o.

It is assumed based on Fenchel's (1988) rule of thumb that phagotrophic micro-, nano-, and picoplankton incorporate about 40% of their uptake (be it in carbon, nitrogen or phosphorus), excrete about 30%, and mineralize or respire the remaining 30%. In addition it is assumed that the ecotrophic efficiency, *EE*, for the phagotrophic microplankton and for all nano- and picoplankton is 0.95, so that 95% of the production of these groups is consumed in the system. The *EE* for the photosynthetic microplankton is estimated.

The primary production for microplankton is estimated to some 200 g C $\cdot$ $m^{-2} \cdot y^{-1}$ based on Fransz & Gieskes (1984) and Reid *et al.* (1990). The estimate, which may be conservative, corresponds to approximately 2300 g w.wt $\cdot m^{-2} \cdot y^{-1}$, (conversion: 1 g C = 15 kcal; 1 g wet weight = 1.3 kcal; Jones 1984; ICES 1989, Figure 9.3.).

Based on information given by Hannon & Joires (1989) for the southern North Sea the phytoplankton (microplankton) biomass is estimated to 3.7 g C · m^{-2} (or 43 g w.wt · m^{-2}).

The phagotrophic microplankton is further assumed to take 60% of their uptake from phagotrophic nanoplankton and 40% from photosynthetic nanoplankton.

Nanoplankton

The nanoplankton includes the 2-20 μm size group. The photosynthetic group includes pigmented flagellates, chlorophytes, small diatoms and others while the phagotrophic mainly are non-pigmented flagellates. The phagotrophic nanoplankton was assumed to feed 60% on phagotrophic picoplankton and 40% on photosynthetic picoplankton.

Picoplankton

Picoplankton are as small as 0.2-2 μm, and includes both photosynthetic and phagotrophic organisms. The phagotrophic picoplankton is assumed to feed exclusively on detritus, primarily through uptake of DOM.

Detritus

ECOPATH II models always include a detritus box, and flow to the group consists of import, excreted and unassimilated food, dead organisms etc. Flow out of the detritus box is limited to detritus uptake by consumers and export.

For the detritus group an estimate of amount of dead organic material, i.e. detritus biomass, of 4.3 g C · m^{-2} (50 g w.wt · m^{-2}) was reported by Hannon & Joires (1989) for the southern North Sea.