MODELLING THE PREDATION, GROWTH AND POPULATION DYNAMICS OF FISH WITHIN A SPATIALLY-RESOLVED SHELF-SEA ECOSYSTEM MODEL

A.D. BRYANT[1], M.R. HEATH[2], N. BROEKHUIZEN[3], J.G. OLLASON[1],
W.S.C. GURNEY[3] and S.P.R. GREENSTREET[2]

[1] *Culterty Field Station, University of Aberdeen, Newburgh, Grampian AB41 OAA, UK*
[2] *Scottish Office Agriculture and Fisheries Department, Marine Laboratory, P.O. Box 101, Victoria Road, Aberdeen AB9 8DB, UK*
[3] *Department of Statistics and Modelling Science, University of Strathclyde, Livingstone Tower, 26 Richmond Street, Glasgow G1 1XH, UK*

ABSTRACT

The development and analysis of a fish population module within the European Regional Seas Ecosystem Model (ERSEM) is described. Fixed predation rates on ERSEM zooplankton and zoobenthos, which may be used in place of this dynamic module of fish, are described also. The dynamic module is age-structured, with state variables for the number of individuals and their weight, the latter partitioned into structural (skeletal, essentially) and remobilizable 'reserve' components. It is capable of prediction of observed patterns of both positive and negative changes in individual weight. The fish are modelled as one population for the whole North Sea, superimposed on the ERSEM box structure. Parameters have been derived from the literature where possible and, for herring, certain parameters have been adjusted to match independent estimates of growth in the field. Preliminary results show that herring growth rate depends inversely on biomass, when changes in the latter are caused by altered fishing mortality. The magnitude of these effects is in agreement with historical data for herring in the North Sea. The model is discussed in relation to previous attempts to model fish population dynamics, particularly in the North Sea.

1. INTRODUCTION

The maximum amount of fish which can be harvested from a marine ecosystem depends on the production of lower trophic levels in that system. On a global basis, the transfer efficiency from primary production to fish production appears to be approximately 0.1% (Parsons *et al.*, 1984), but this figure may show considerable regional variation depending on the trophic structure of particular ecosystems.

The link between primary production and fish production has been investigated in various ecosystems using static energy or mass balance budgets based either on trophic functional groups (Steele, 1965, 1974; Cohen *et al.*, 1982; Jones, 1982, 1984) or size hierarchies (Sheldon *et al.*, 1972, 1977, 1982). Such approaches are a useful way of comparing production in different ecosystems, but provide little or no insight into the scope for dynamic changes forced by the physical environment. Silvert & Platt (1978, 1980), however, have developed dynamic models of the size structure of the pelagic food chain from the steady-state theory of biomass spectra (Platt & Denman, 1977, 1978). These dynamic models are strategic and general, capable of predicting the impact of changes in the smaller sizes upon the larger sizes, and were presented as a framework for the analysis of new biomass spectrum data from specific ecosystems.

Traditional fisheries management has not been concerned with the potential impacts of the physical environment on fish populations, although evidence for such relationships is extremely widespread in the literature (*e.g.* Sutcliffe, 1972, 1973; Sutcliffe *et al.*, 1976, 1977, 1983; Leggett *et al.*, 1984; Shepherd *et al.*, 1984; Corten, 1990; Aebischer *et al.*, 1990). Single species fishery models have been in widespread use for many years (Schaefer, 1954; Beverton & Holt, 1957), but are forced solely by imposed fishing mortality rates. Growth is prescribed in such models rather than modelled as a physiological function. The underlying rates of natural mortality due to predation and other causes are usually treated as a constant, leaving no scope for assessing the possible conse-
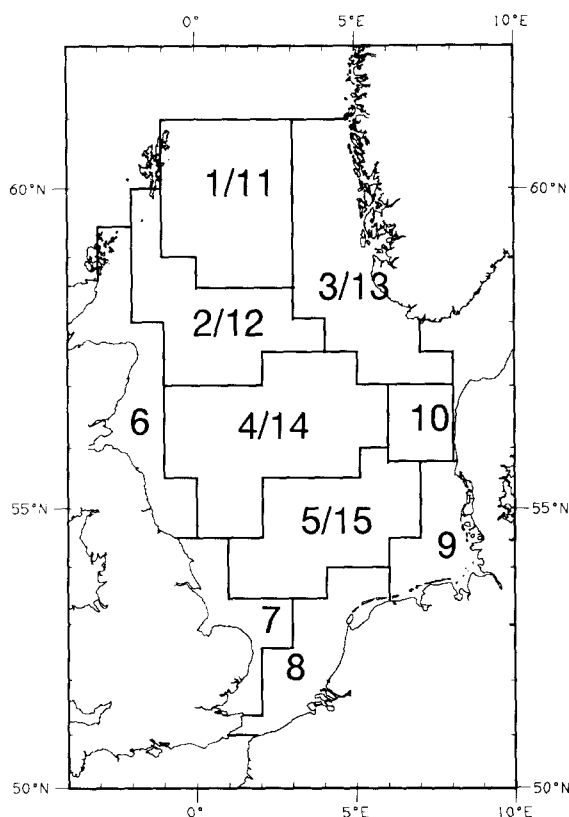
Fig. 1. The box structure used by ERSEM.

quences of exploitation for the population dynamics of potential prey or predator species.

The neglect of the potential impact of physical changes, and interactions between species, resulted from an absence of more sophisticated tools during the 1970s (Aron, 1981) and a general belief that the direct effects of fishing were more important (Sissenwine & Daan, 1991). Multi-species models were developed at this time, increasing in complexity through the decade (Riffenburgh, 1969; Agger & Nielsen, 1972; Parrish, 1975; Andersen & Ursin, 1977; Laevastu & Larkins, 1981). Multi-species fish population models have now come into tentative use for the management of fisheries (e.g. Laevastu et al., 1982; Sissenwine & Daan, 1991).

Andersen & Ursin's (1977) North Sea Model (NSM) represented an integrated ecosystem, in which a multi-species fish population model was built on top of a simple phosphate-based lower trophic level model. Phosphate was used as the currency for the model in recognition of the potential for air-sea exchange of other vital elements (carbon, nitrogen) and the consequent lack of a closed system. The whole North Sea was modelled as a single, horizontally homogeneous area, with vertical stratification.

Their model did not receive widespread acceptance because it was viewed at the time as being excessively complicated for the purpose of representing fish population dynamics, requiring too many untestable assumptions to allow reliable predictions for management purposes (Sissenwine & Daan, 1991). It did, however, establish the need for multi-species models and initiated the development of multi-species virtual population analysis (MSVPA) within the ICES community (Sissenwine & Daan, 1991).

The dynamic numerical marine ecosystem model, DYNUMES (Laevastu & Larkins, 1981; Laevastu & Favorite, 1980, 1981; Laevastu et al., 1982) represents rather a different approach. This is a gridded, biomass-based, difference equation model of the marine ecosystem, applied to northeastern Pacific fisheries management. Migration of species-aggregate and some single-species fish groups is forced between nodes using predetermined migration speed components (Laevastu & Favorite, 1981), with some random, temperature-related and food concentration-related diffusion. Zooplankton and phytoplankton concentrations are forced using a harmonic formula parameterized according to field data.

Twenty years after Andersen & Ursin's (1977) first attempt, the need for an ecological modelling approach to fisheries management in the North Sea is still unfulfilled. The requirements for construction of such a model are principally: 1. a spatially resolved model of the dynamics of prey resources for fish; 2. a mathematical technique for representing the migration of fish in such a model; 3. a model of prey selection by fish; and 4. a dynamic model of body growth for fish. The spatially resolved ERSEM model provides a basis for constructing such a system which was not available to Andersen & Ursin (1977). This paper describes the development and analysis of a model of migrating fish populations to overlay and interact with ERSEM. The development of a set of fixed fish predation rates on zooplankton and zoobenthos which may be used in place of, or in parallel with, the dynamic fish models is described also. Results representing the North Sea herring population are presented and compared with field data.

2. METHODS

ERSEM (version 5.2) simulates the seasonal cycling of carbon, nitrogen, phosphorus and silicon in the North Sea. It comprises modules which are coupled together, to describe chemical and biological processes in the pelagic and benthic systems. It has a spatial resolution of ten boxes, five of which are divided into a surface and a depth component (Fig. 1). Transport of planktonic elements of the system between boxes is effected by aggregated results of a general circulation model of the North Sea (Lenhart et al., 1995).
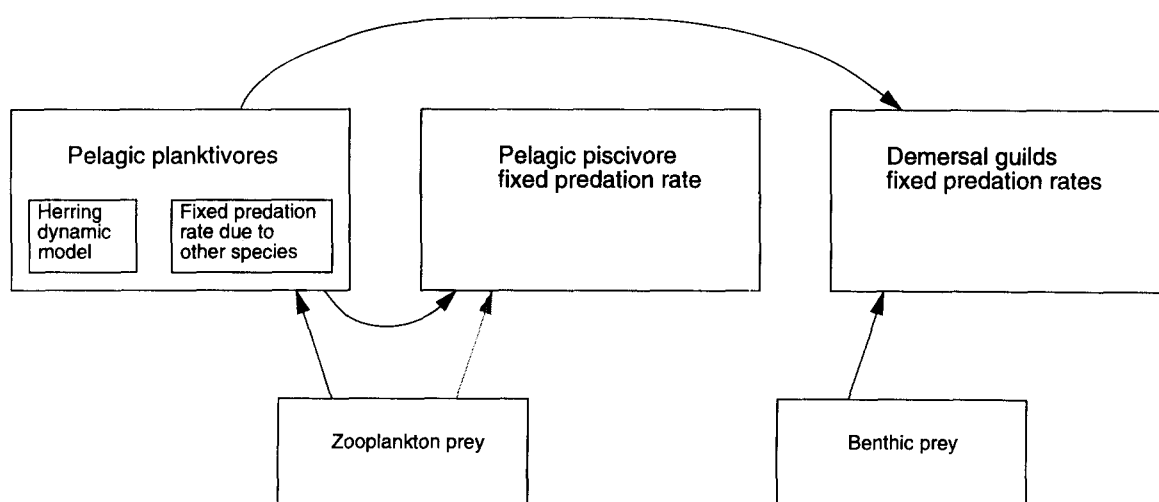
Two alternative modules to describe fish are

Fig. 2. Fish model schematic diagram. The guild structure is shown, indicating the split between dynamically modelled species and species represented by a fixed mortality rate. It is possible to model species dynamically within all guilds, although the model for herring is the only one which is described here.

included in version 5.2 of ERSEM. One module represents fish as a fixed predation rate on the zooplankton and zoobenthos, resulting in a flux of material from the relevant prey groups which is returned to dissolved nutrients and particulate detritus. This is referred to here as the static fish module. The alternative is a dynamic model of one or more fish populations, in parallel with fixed predation rates to represent fish species, aggregated into broad functional groups, which are not modelled dynamically (Fig. 2). A dynamic model for the population of herring, a species that accounts for 29% of the pelagic planktivorous fish biomass (Sparholt, 1990), is described here as an example of this approach.

2.1. FIXED PREDATION RATES: ESTIMATION AND IMPLEMENTATION

Fixed predation rates on the lower trophic levels were estimated from the consumption rates of fish and the biomasses of their prey. Consumption rates were estimated for the ten ERSEM North Sea areas (Fig. 1) for four guilds of fish: pelagic planktivores, pelagic piscivores, demersal piscivores and demersal benthivores. Prey were categorized according to ERSEM functional groups, and carbon consumption rates were estimated for each of the feeding links assuming the diet and food consumption rates of one archetypal species for each guild. The archetypes used were herring, mackerel, cod and plaice. The steps involved in calculating these consumption rates are described in full in Greenstreet (1992b) although some of the values used in this paper have been revised since that earlier report (Greenstreet, 1995).

The biomass of mesozooplankton in the ERSEM boxes for each month was estimated from various sources by Broekhuizen et al. (1995). The biomasses of benthic carnivores, suspension and deposit feeders (Ebenhöh et al., 1995) were estimated from the ICES North Sea Benthic Survey database (Heip et al., 1992; Basford et al., 1993). These data provided total infaunal biomass values in spring for 231 stations spaced approximately 30 miles apart throughout the North Sea. All stations were assigned to ERSEM boxes and the mean biomass values for those occurring in each box was calculated. The total infaunal biomass was apportioned between functional groups using the values in Table 1 (D. Basford & S.J. Hall, pers. comm., and with reference to Basford et al., 1993). Values for megabenthic fauna (Ebenhöh et al., 1995) were simply guessed on the basis of experience from epibenthic sledge data. For the conversion from ash-free dry weight to mg carbon we used a factor of 0.6. In the absence of detailed seasonal data, it was assumed that the spring biomass represented a seasonal minimum. The predation rate calculation used this minimum biomass for 1 April, a maximum density of double the minimum for 1 October, and a linear transition between extremes. Some of these assumptions are currently being tested, using unpublished data that have become available since this work was done.

The daily mortality rates which are imposed upon the prey groups in the model are given by the ratio of daily population consumption rate to prey biomass. The flux of material removed from the prey groups is returned to dissolved carbon dioxide, phosphate and ammonium (58 to 59% depending on fish guild) and to detritus (38 to 39%). The figure of 2 to 4% which is

TABLE 1

Assumed proportions of infaunal benthic functional groups in ERSEM boxes and total infaunal biomass for each box (biomass estimation is described in the text).

box number	% carnivores	% deposit feeders	% filter feeders	total biomass $(gAFDW \cdot m^{-2})$
6	2	59	39	5.9
7	2	59	39	3.93
8	2	59	39	13.22
9	2	59	39	10.21
10	2	59	39	5.14
11	5	80	15	3.89
12	5	80	15	2.26
13	5	85	10	4.97
14	2	59	39	6.98
15	2	49	49	10.02

not returned was estimated from the ratio of the consumption rate *by* fish and that *of* fish by top predators (Bryant & Doyle, 1992) and commercial fishing (Greenstreet, 1992a). As there are considerable uncertainties in these calculations, a sensitivity analysis of the predation rates is presented in section 3.1.

2.2. HERRING POPULATION DYNAMIC MODEL

The population model is age-structured and based upon a model of individual fish growth (Broekhuizen et al., 1994). In the growth model, it is assumed that an individual is composed of two fundamental tissue types: structural and reserve. Structural tissues cannot be remobilized once laid down and correspond to skeletal and nervous tissues. In contrast, reserve tissue can be remobilized to meet metabolic demands

when the assimilation rate is insufficient. Reserve tissue corresponds primarily to musculature. It is postulated that an individual seeks to maintain an 'ideal' ratio between reserve and structural tissue weights by devoting an increasing proportion of any net assimilate to rebuilding reserves when they are depleted. Broekhuizen et al. (1994) also postulate that the fish is able to modify both its potential consumption and metabolic rates in response to the degree by which reserves are depleted. When they are only slightly depleted, the fish becomes 'hungry' and responds by increasing its potential consumption rate. If the reserves become still more depleted, the fish enters a torpid state in which both the potential consumption rate and the metabolic rates are suppressed below the 'well-fed' levels. When food becomes abundant again, and the fish starts to recover, the sequence of physiological and behavioural changes is reversed.

The assimilation rate, A (mg $C \cdot d^{-1}$), is a standard Type II function (Holling, 1959), parameterized by an assimilation efficiency ε (Table 2), a search volume V ($m^3 \cdot d^{-1}$) and a handling time T ($d \cdot mg$ C^{-1}). Both V and T are related to structural weight with coefficient and exponent parameters (Table 3). Handling time has an additional coefficient ξ (Table 2), which takes a value other than unity when 'hungry' and when 'torpid'. At a food concentration F (mg $C \cdot m^{-3}$) the assimilation rate is:

$$A = \frac{\varepsilon F}{V^{-1} + \xi TF}$$

The model herring are assumed to feed on omnivorous and carnivorous zooplankton (Broekhuizen et al., 1995), exhibiting no preference for one over the other.

TABLE 2

Parameters of the individual model for herring (dimensionless unless stated).

parameter	value	source
ideal ratio of reserves to structure	1.5	Kleiber (1961)
reserve control sensitivity	2.3	Broekhuizen et al. (1994)
assimilation efficiency	0.65	
thresholds:		
'well-fed'/'hungry'	0.99	Broekhuizen et al. (1994)
'hungry'/'torpid'	0.92	Broekhuizen et al. (1994)
handling time coefficient, ξ:		
when 'hungry'	0.5	Broekhuizen et al. (1994)
when 'torpid'	1.5	Broekhuizen et al. (1994)
maintenance costs exponent	0.8	From & Rasmussen (1984)
maintenance costs coefficient when 'torpid'	0.3	Priede (1985)
linear function of potential weight spawned to 'ideal' weight:		
coefficient	0.246	Almatar (1987), Baxter (1959)
constant	-1820 mg C	Almatar (1987), Baxter (1959)

TABLE 3
Fitted parameters of the individual model for herring.

parameter		value	units
maintenance costs coefficient		0.018	d^{-1}
search volume	- coefficient	4.5	d^{-1}
	- exponent	0.44	-
handling time	- coefficient	0.35	$d·mg·mg^{-1}$
	- exponent	-0.52	-

2.2.1. AGE STRUCTURE AND SEASONAL EVENTS

The population model is structured as a chain of cohorts or year classes, within each of which we model the structural weight, reserve weight and the number of individuals. The individual model and its parameters, most of which specify allometric relationships, are common to all year classes of a given species. At specified times in the annual cycle the discrete events of spawning and recruitment occur (days 270 and 360 respectively; Daan et al., 1990). The former is also, for convenience, the point in the year that the contents of year class i are moved to i+1. At the spawning point the weight to be spawned is removed from an individual's reserve weight. The parameters relating weight spawned to mature fish weight are given in Table 2; to account for immaturity none of the individuals in years 1 and 2 spawn, 50% spawn in year 3 and 90% spawn in year 4 (Knijn et al., 1993). After spawning, the remaining reserve weight, structural weight and numbers, are passed to the next year class; year class 1 assumes a zero value for each variable. The number of individuals at the end of the chain is incremented by the number in the penultimate year class. The individual weight of the last year class (both reserve and structural weight) becomes the mean of the penultimate and last year class' individual weight, weighted by the number of individuals in the two year classes prior to the event, to maintain mass balance. At recruitment, year class 1 assumes predetermined, fixed starting values for structural and reserve weight and number of individuals (Greenstreet, 1992b). To allow investigation of the effects of recruitment variability the latter is implemented as a 30-year time series, at present filled with the same number of recruits for each year.

2.2.2. MOVEMENT

Migration of fish in the North Sea has been studied for many years by tagging and other methods. Despite this, the physiological motivation for migration is not understood in sufficient detail to be able to contemplate a dynamic representation in ERSEM. Migration was therefore treated as a forcing function.

Unfortunately, there are no scientific survey data which allow an internally consistent picture of the seasonal distribution of fish biomass in the North Sea. However, such data will be available within the next 3 to 4 years (Anonymous, 1990). As an alternative, we have analysed commercial catch statistics to generate a time series of proportional distributions of fish across ERSEM spatial compartments on a quarterly basis. The limitations of using catch data in this way are acknowledged, but there seems to be no alternative until the ongoing survey programme is completed. Daily proportions in each box were estimated by linear interpolation between quarterly values. We assume that herring can be represented as a single well-mixed population potentially feeding over the entire North Sea. Thus, the proportional distribution represents the proportion of time that the population spends in each box in each day. The product of the total fish numbers over the entire North Sea and the proportion in a box is considered to be a measure of fish-days or fish-equivalents in each box.

Notionally, every fish feeds from every box for which the corresponding value of fish-days is greater than zero. The net assimilation rate of an individual is calculated as the sum of the assimilation rates from each box, weighted for time spent in the box. The appropriate fluxes from prey in each box, and returns to detritus and dissolved nutrients, are calculated from the local individual feeding and egestion rates together with the local value of fish-days. There is the potential problem here that for each year class we model a single average individual, whereas in reality there will be some variation in growth rate over the North Sea. This may lead to boxes with low prey density suffering an artificially high predation rate, and vice versa.

TABLE 4
Predation rates on herring (proportion·d^{-1}, all year classes). The rates are implemented as linear interpolations of these quarterly estimates. An additional rate of 10^{-5} d^{-1} is imposed, to account for mortality arising from unspecified causes (e.g. disease, senility).

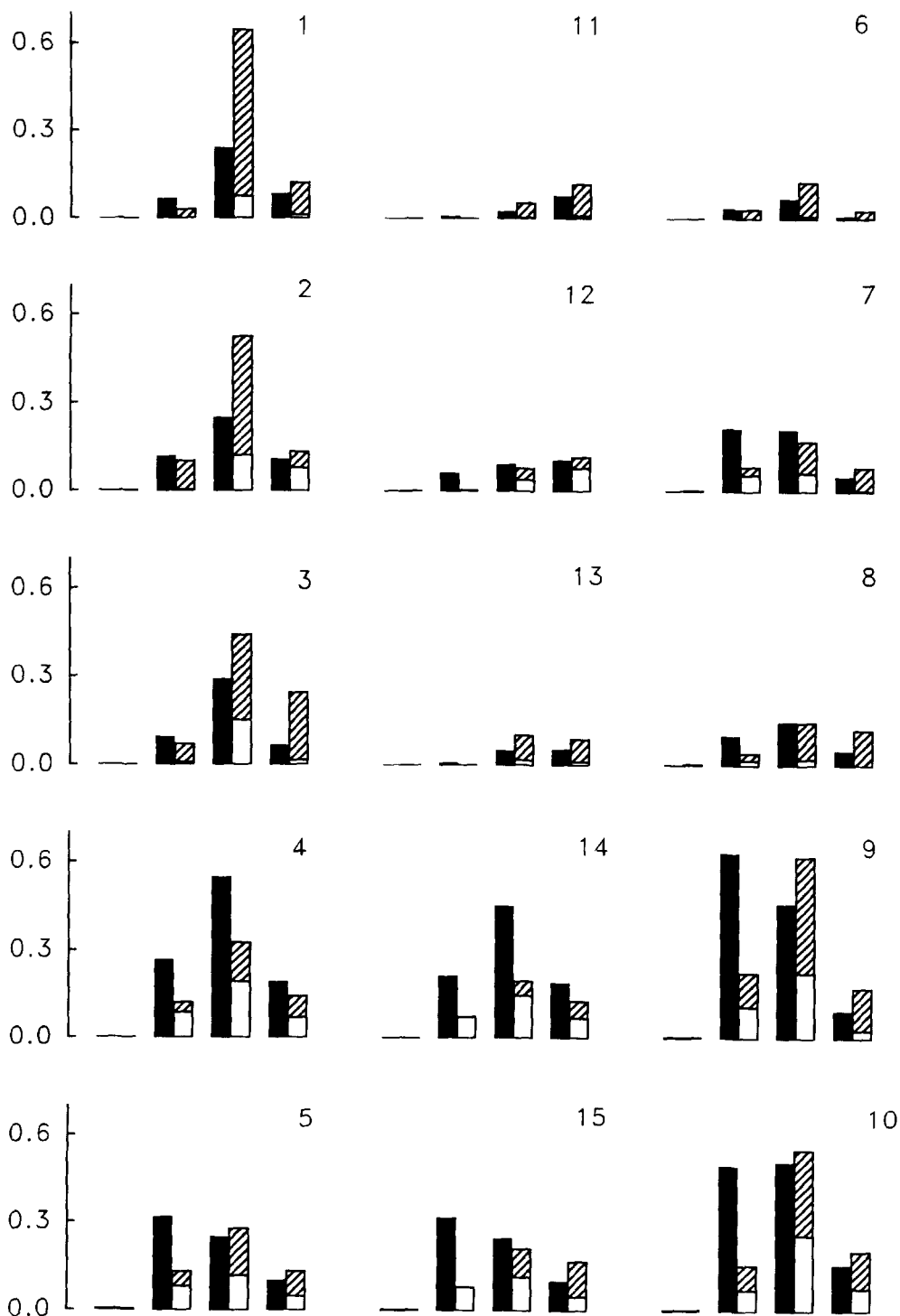| predator	quarter of the year			
	1	2	3	4
(static) demersal piscivores	$5.8·10^{-4}$	$4.7·10^{-4}$	$4.9·10^{-4}$	$5.5·10^{-4}$
birds / mammals	$7.3·10^{-5}$	$1.5·10^{-4}$	$1.3·10^{-4}$	$4.5·10^{-5}$
commercial fishing	$6.3·10^{-4}$	$2.4·10^{-3}$	$1.0·10^{-3}$	$4.5·10^{-4}$

Fig. 3. Planktivorous fish uptake fluxes for ERSEM boxes 1 to 15 (mg $C \cdot m^{-3} \cdot d^{-1}$). Each barchart shows data for the four quarters of the year, from left to right, for the static module (solid bar), for the static fish of the dynamic module (open bar) and for the dynamic fish (hatched bar).

2.2.3. MORTALITY

Estimates were made of the rate of removal of fish biomass by commercial fishing (Greenstreet, 1992a) and by seabirds and seals (Bryant & Doyle, 1992). These were divided by estimated fish biomass (Daan et al., 1990) to give instantaneous mortality rates according to spatial box and quarter of the year (Table 4). Linear interpolation between quarterly values was used to produce smoothly-varying time-dependent mortality rates. Mortality arising from piscivory was also implemented as a time-dependent mortality rate, to represent predation by fish species which are not modelled dynamically (Table 4). Of the material removed by fishing, 5% was returned to detritus, although little is known about the discarding practices for herring (Greenstreet, 1992a). The return of material from bird and seal predation to detritus was set at 20%, in the absence of information in the literature.

2.2.4. FIXED PREDATION RATES FOR FISH SPECIES NOT MODELLED DYNAMICALLY

The fixed predation rates which were described earlier for pelagic planktivores were adjusted downwards to account for the presence of the dynamic herring model. The adjustment was box-specific, that is, for each box the rate was multiplied by the non-dynamically represented species' abundance as a proportion of the total abundance within the functional group (Greenstreet, 1992a).

2.2.5. PARAMETER FITTING AND INITIAL VALUES

Certain parameters, such as those given in Table 2, can be derived accurately from the literature. Some parameters are known only approximately or are largely unknown, notably the search volume (Greenstreet, 1991), and some of the other uptake parameters. Values for the unknown parameters have been adjusted to give individual growth which corresponds to independent predictions for North Sea fish. Some parameter values are based on those given in Broekhuizen et al. (1994a). These are the 'well-fed' ratio of reserves to structure, the relative reserve thresholds and the factors by which handling time changes at those thresholds (Table 2).

The initial weights and numbers of individuals in each year class were taken from data compiled for a run of the MSVPA model (Greenstreet, 1992b). The 0-group data were used for the herring initial conditions on January 1st. Weights were converted to carbon units (Bryant & Doyle, 1992; Greenstreet, 1992a) and were split equally into reserve and structural weight, implying that the fish start the year in an underfed state.

These initial values were used as a starting point in the development of the parameter set for the herring model. Early work on the fitting of parameters for individual growth was done using a version of the model which was isolated from the rest of ERSEM. This used forced substrate, that is, time series of zooplankton concentration (Broekhuizen et al., 1995). The uptake and maintenance cost parameters were varied to fit the individual growth of herring over one year. Later work considered the herring model coupled to the full versions of ERSEM, using 1988 transport data and starting values for variables other than herring taken from the end of a 20-year run which used the static fish module. The general approach was to perform one-year, or latterly ten-year, runs of the model, altering one parameter or pairs of parameters at a time; for example, the shape of the uptake function against weight was changed by simultaneously altering both the coefficient and exponent of search volume, or handling time (Table 3). The end-of-run values of each variable, for each year class, were compared against the beginning-of-run values. Since each class undergoes a shift of weights and numbers to the next class in the chain once during each year, this beginning-end comparison indicates whether the predicted growth and survival for each year class matches that given by the data used to set the initial conditions. Thus, the growth and survival curves implied by the initial conditions were compared against those given by the herring state variables at the end of the run. The final run of this parameter fitting exercise was of a 20-year duration; results are presented from the final year of this run, and from one-year runs which used the end-values from the 20-year run as initial conditions.

3. RESULTS

3.1. STATIC FISH MODULE

Results from model runs incorporating static fish module are given by Broekhuizen et al. (1995) for mesozooplankton, and by Ebenhöh et al. (1995) for zoobenthos. There is variation in the flux of carbon to planktivorous fish, with season with ERSEM box (Fig. 3). The fluxes to planktivorous fish are virtually zero in the first quarter of the year and peak in either the second or third quarter. They are particularly low in the lower boxes 11 to 13 and the coastal box 6, and are relatively high in the coastal boxes 9 and 10. These differences are due to variation in both the standing stock of zooplankton and the predation rate. If the model predicted zooplankton densities which agreed closely with the data (those which were used in the calculation of the predation rates) then the model fluxes would match the estimated fish consumption rates. In boxes one to ten and the shallow lower boxes 14 and 15 there is broad agreement between model and estimated fluxes in quarters two and three. In quarters one and four, and in the deep lower boxes 11 to 13 in all seasons, the model fluxes are much
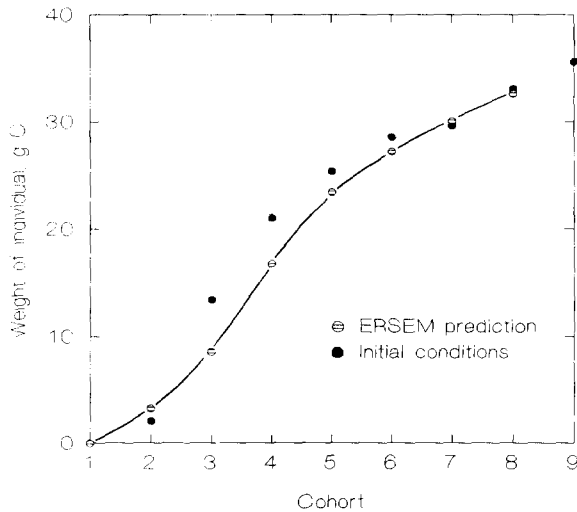
Fig. 4. Herring growth curve implied by the initial conditions (see text) and by the end conditions of a 20-year run of ERSEM. The line was drawn by hand and represents net growth over increments of one year.
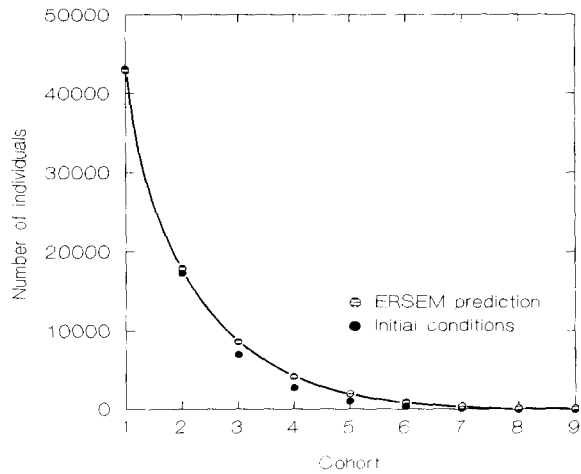
Fig. 5. Herring survival curve implied by the initial conditions (see text) and by the end conditions of a 20-year run of ERSEM. The line was drawn by hand and represents survival over increments of one year.

lower than the estimated fluxes, due largely to low zooplankton concentrations in those boxes and seasons.

The fish predation rates were simplified for a test of the sensitivity of the relevant prey groups. The time-dependent box-specific predation rate on mesozoo-plankton was replaced by an overall mean rate, which was then varied by +/- 20%. A five-year model run with the overall mean rate resulted in carnivorous mesozooplankton concentrations which differed by +20% to -30% (annual mean comparisons of individual boxes in the fifth year) from those given by the standard model. Increasing the rate by 20% had the effect of decreasing carnivorous zooplankton concentration by a similar percentage, and vice versa. The effect of changing the predation rates on omnivorous mesozooplankton was smaller: annual means differed from those in the standard model by no more than 5%. Thus, varying the fish predation rates has substantial effects on zooplankton dynamics, although these effects are small in the context of the fit of the zooplankton module to broadly scattered data (Broekhuizen et al., 1995).

The predation rates on the benthic system were subjected to various alterations to determine sensitivity generally and in particular the problem of extinction of deposit feeders and infaunal predators in boxes 14 and 15 (Ebenhöh et al., 1995). Recalculation of the predation rates assuming a single benthic functional group, and then applying this rate to all benthic groups in the model, resulted in adequate survival of deposit feeders and infaunal predators in

box 14, due to the removal of some of the extremes of the standard set of predation rates. Recalculation of the predation rates assuming recently-derived fish consumption rates (which are considerably lower than those used in the standard calculation) resulted in survival of deposit feeders and infaunal predators in both boxes 14 and 15. Using the recently-derived consumption rates and assuming a single benthic functional group, then averaging over seasons, then averaging over seasons and boxes, resulted in predicted benthic biomasses which were in similar agreement with the data to those of the standard model. The final overall-mean predation rate was varied by +/-20%, and this resulted in up to 5% variation in stable-cycle biomass of all benthic groups that are preyed upon by fish.

3.2. DYNAMIC FISH MODEL

A comparison of fluxes to static planktivorous fish alone against static planktivores in parallel with the dynamic herring model is given in Fig. 3. One should expect to see reasonable agreement between the fluxes to the static fish module and the sum of the fluxes to the dynamically and non-dynamically modelled components of the dynamic module, in all seasons and boxes. There is moderate agreement, except in quarter 2, in which the flux to static fish is the greater of the two in most boxes, and in quarter 3 in boxes 1 to 4 and 14.

With the parameters given in Tables 2 and 3, the model produces lifetime growth of individual herring

which matches closely that given by the original initial conditions (Fig. 4). The annual cycle of herring growth stabilized (to within 1% at January 1st) after five to ten years depending on year class. With the standard mortality parameters, calculated purely from consumption rate and prey biomass estimates (Table 4) the model produces herring survival which is very similar to that given by the initial conditions (Fig. 5). This curve stabilized (to within 1% at 1 January) after three to thirteen years, depending on year class, of the 20-year model run.

A limited sensitivity analysis of the fitted parameters (Fig. 6) revealed that growth is most sensitive to the handling time parameters, in particular the exponent parameter. Growth was affected also by changes in the handling time coefficient and maintenance costs. Altering the search volume parameters by +/-10% had little effect; perturbations of up to +/-50% were required to give changes in growth comparable to those in Fig. 6.

The growth of herring in the final year of the 20-year run is given in Fig. 7. Structural weight increases during July to October and remains static during the rest of the year. Reserve weight and total individual weight decrease substantially during November to May, then increase during June through to spawning at the end of September and during October. The period of weight gain occurs perhaps one to two months later in the year than one would expect (Coull et al., 1989; Iles, 1984), but is an inevitable consequence of the low biomass and production of zooplankton in the first three to four months of the year in ERSEM, relative to field data (Broekhuizen et al., 1995).

Variation of fishing mortality resulted in altered survival, which caused changes in the total herring biomass (Fig. 8). In this experiment with the model the mortality due to commercial fishing was set at double and then half the standard rate. This resulted in substantial changes in the total mortality on herring, which varied with season (Table 5). In addition to the obvious effect on survival, clear effects on the growth of herring were noted (Fig. 9). There was in general increased growth due to the lower densities which resulted from increased mortality, and vice versa, indicating that herring growth is to some extent resource-limited.

4. DISCUSSION

There is a fundamental difference, in modelling terms, between unicellular binary-fission organisms and metazoans. Unicellular phytoplankton, and to some extent the zooplankton, are amenable to biomass-only representation, since the biomass per individual of a species varies only marginally. For higher organisms such as fish the biomass per individual varies considerably over the life-cycle. Thus, for these long-lived organisms, it is necessary to model
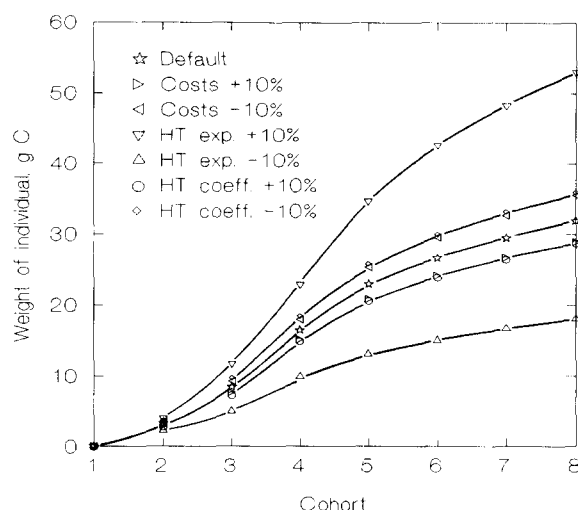

Fig. 6. Herring growth curves implied by the end conditions of 10-year sensitivity analysis runs. The lines were drawn by hand and represent net growth over increments of one year, for model runs in which maintenance costs and handling time exponent and coefficient were varied (all +/-10% of absolute value).

simultaneously the number of individuals in age or size groups, and their body weight.

Parrish (1975) constructed simple trophic webs from a generic numbers-and-biomass model of interacting animal species. The generic physiological model was considered to be applicable to marine fish species. The most complex web used a forced input of food at an undifferentiated base, two identical-competitor fish species and a predator of both those species; as such, these models were highly abstract and useful in asking general questions about the possible effect of, for example, web structure, age-structure and reproductive time-lags. The simulation approach was to calculate equilibrium states and then to displace just one state to examine the effect of that perturbation. This approach precluded the possibility of any representation of an annual cycle in the system.

Andersen & Ursin (1977) took a very different approach in their extension of the Beverton & Holt (1957) model of fish population dynamics. Their North Sea Model (NSM) comprised eleven abundant fish species, three zooplankton groups, three groups of benthic invertebrates, three algal groups and an account of nutrient (phosphorus) circulation. Each animal species had a number of age groups and was represented in terms of numbers and body weight. Everything was treated in terms of particle size and the food web was dynamic, that is, prey selection was based on a continuous (log-normal) function of predator body weight. The scope of the model could be varied to suit the questions being asked of it; for example, for fisheries studies the plankton section
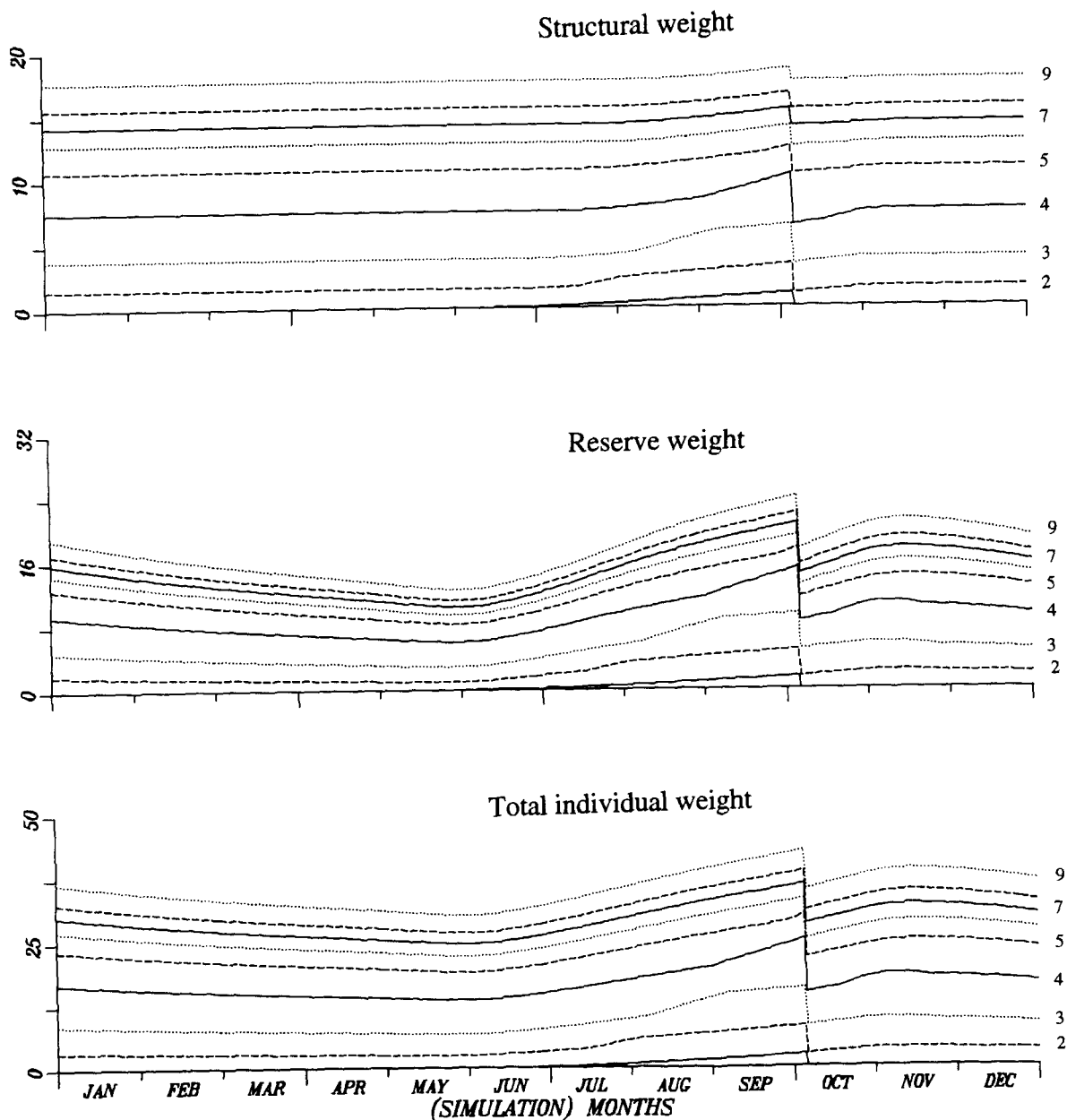
Fig. 7. Structural, reserve and total individual carbon weight (g C) for all year classes (1 to 9) of herring. The results of a one-year model run using initial conditions taken from the end of a 20-year run are shown.

was replaced with seasonal forcing and attention focused on the interaction between age groups of the species of fish.

Although the NSM incorporated vertical stratification, it considered the sea area to be horizontally homogeneous. We argue that it is important to consider the spatial distribution of prey in modelling the

dynamics of a fish population such as herring. ERSEM version 5.2 represents the North Sea area in a highly aggregated way, as ten boxes, five of which are split into surface and depth layers. We chose not to represent fish as local densities in ERSEM boxes for various reasons. Firstly, fish distribution is primarily determined by active migration, which is breeding-
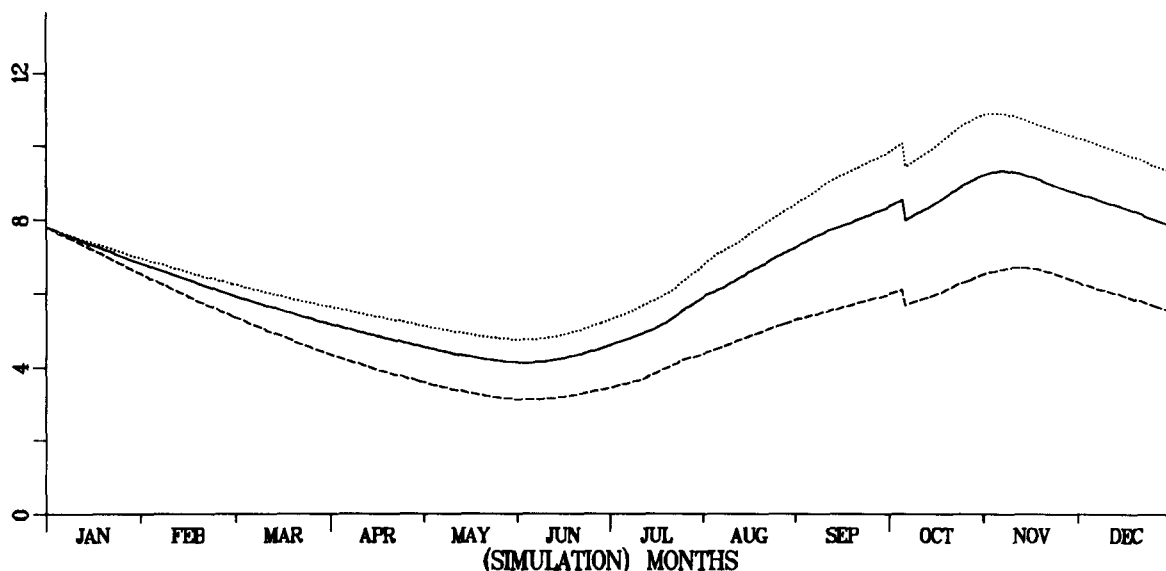
Fig. 8. Total North Sea biomass of herring (solid line, mg $C \cdot m^{-3}$) from a one-year model run using initial conditions taken from the end of a 20-year run. For comparison, the results of the same run but with fishing mortality doubled (dashed line) and halved (dotted line) are shown.

TABLE 5

Variation in total fixed mortality rate (proportion·d^{-1}) on herring with a halving and doubling of fishing mortality rate.

quarter of the year	1	2	3	4
standard fishing mortality	0.0013	0.0030	0.0016	0.0011
halved fishing mortality	0.0010	0.0018	0.0011	0.0008
doubled fishing mortality	0.0019	0.0054	0.0026	0.0015

related in the case of herring, rather than by passive transport. However, the dynamic rules which govern migration are not well known. Given detailed data on distribution, such as those being collected in the current ICES trawl surveys (Anonymous, 1990), it would be possible to contemplate moving fish around ERSEM boxes, or preferably between more closely-spaced nodes, according to those distribution patterns (cf. Laevastu & Larkins, 1981). A far more speculative approach would be to hypothesize rules for fish migration based on food density, temperature and

water current, to model fish behaviour on a fine-scale finite difference grid (cf. Reed & Balchen, 1982; Reed, 1983).

A second reason for our spatial representation of fish is that the changes in local density represent not minor interchange between populations, but large-scale migrations of whole groups of individuals. In the context of the nominal daily time-steps and the relatively coarse ERSEM box structure it would be inappropriate to model fish migration dynamically according to food concentration and temperature; these factors are likely to operate on much smaller spatial scales than those which we currently represent. As a comparison, one implementation of DYNUMES (Laevastu & Favorite, 1981) used a 15x15 grid with 95 km spacing between nodes, with fish moved on the basis of prescribed migration speeds, diffusion, food availability and environmental factors. On that scale such a representation of fish migration seems reasonable in principle, although one would have extreme difficulty in parameterizing it

TABLE 6

Estimates of total North Sea herring biomass in 10^3 kt live weight. ERSEM North Sea volume = $4.0477 \cdot 10^{13}$ m^3, 18% of herring live weight assumed to be carbon. Greenstreet's (1992b) numbers-at-age are based on means of those used for MSVPA for 1983 to 1988, weights-at-age are based on means for 1974 to 1989.

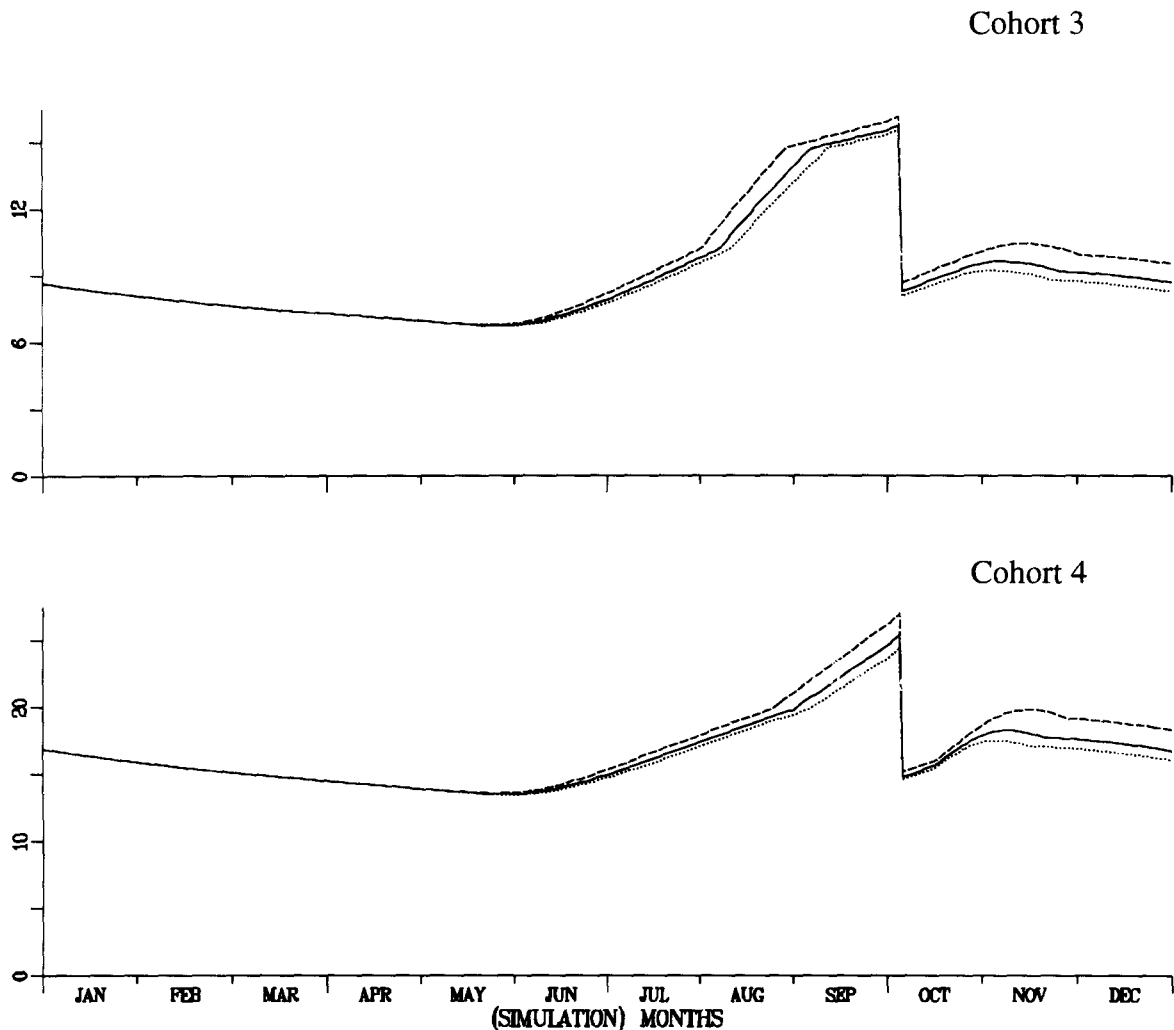| estimate	1 Jan.	1 June	1 Oct.	1 Nov.
ERSEM (Fig. 8)	1750	945 (min.)	1890	2090 (max.)
Greenstreet (1992b)	1350	-	1850	-
Sparholt (1990), 1983 to '85 MSVPA	993	-	1660	-
Yang (1982), 1978 VPA	286	-	-	-
1977 VPA	215	-	-	-

Cohort 3

Cohort 4

Fig. 9. Total carbon weight (g C) of individuals in herring year classes 3 and 4, from the same model runs (with the same lines) as shown in Fig. 8.

even for a relatively well-known fish ecosystem such as the North Sea.

The strategy adopted in the present study was to regard the North Sea population of herring as a global object, characterized by a central position and extent which changes systematically with time. The extent of the population is determined from commercial catch records and, within its current extent, the population is regarded as being uniformly distributed. Thus, the fish populations are superimposed on the main eco-system model, in a way which allows investigation of the effects of prey spatial distribution. The availability of more detailed and reliable trawl survey data, which is now imminent, will greatly improve our parameteri-zation of fish spatial distribution.

The assumption of uniform distribution is probably reasonable for truly pelagic species: herring are

regarded as being spatially mixed at times of the year other than the spawning season (Daan et al., 1990), although there is some variation in growth rates (Knijn et al., 1993; Jennings & Beverton, 1991). If a species shows substantial local differences in growth rate, greater than those in herring, the global object repre-sentation may be inappropriate and cause distortion of the pattern of uptake fluxes, with overgrazing of boxes with a low prey biomass and vice versa. The forced movement of all herring year classes together is another simplification, one which is potentially mis-leading, as their migration patterns are age- and breeding-related. With the data on fish distribution that are currently being collected (Anonymous, 1990) it will be possible to include the differential movement of herring year classes into the model.

Our model represents herring dynamically, with a

fixed predation rate imposed in parallel to represent fish species other than this archetype. A problem inherent in this approach is that the archetype may account for only a limited proportion of the biomass of the guild and the model may therefore be dominated by the fixed predation rate. This may artificially limit the potential for dynamic interaction between a fish guild and its prey. Herring account for 27 to 30% of the pelagic planktivore guild biomass (Daan et al., 1990); thus the flux to herring will be substantial but smaller than that to the static counterpart (Fig. 3). This problem will be more apparent for a demersal fish guild, for example, in which individual species account for a much smaller proportion of the biomass (Daan et al., 1990). An additional problem concerns distortion of the food web by a large flux to the static, relative to dynamic, fish; a piscivorous dynamic fish cannot feed from the static fish, whereas in reality this may be an important component of its diet.

With the fitting of parameters at the individual level, the model produces growth comparable to that implied by our initial conditions (Fig. 4). The survival curve, a function of the fixed mortality rates, closely resembles that given by the initial conditions (Fig. 5). The most important fixed mortality rates on herring are those due to fishing and demersal piscivorous fish (Table 4), the calculation of which was independent of the initial condition data.

We regard this calibration of the model as sufficient to perform preliminary experiments but essentially incomplete. The herring initial values are based on an aggregate over several years of those used for input to MSVPA (Greenstreet, 1992b; Table 6). Future work will consider individual years' results and also field observations of weight-at-age for northern North Sea herring. Parametric analysis of this model requires runs which are approximately equal in the number of simulation years to the number of age classes; these take several hours of computer time, so the scope for any such analysis is seriously limited. It will be necessary, therefore, to reconsider the fish model in isolation in future, using forced benthic and zooplankton substrate resolved by ERSEM box. Only then will a more thorough analysis of the herring parameters be possible. In addition, the spatial extent of the herring population will be varied, to determine the importance of distribution in relation to the spatially resolved resource base.

The one preliminary experiment which is presented in this paper concerns the growth of herring in response to density (Figs 7 and 8). The doubling of fishing mortality caused a 29% decrease in total herring biomass over the one-year period that was simulated. Over the same period there was a 10% increase in growth of total body weight in the third and fourth year classes, and an 8.5% increase in growth of structural weight. The decreased total biomass is equivalent to the levels that were estimated for 1972 and 1982 (Daan et al., 1990), whilst our standard

model run is representative for the situation in the late 1980s. Bailey (1991) reports that body length of three- and four-ring herring was inversely related to stock biomass over the period 1947 to 1989. Taking approximate medians from Bailey's graphs, length-at-age decreased over the period 1982 to 1986 by 2.8 to 3.0%, which represents a weight decrease of 8.4 to 9.1% (Coull et al., 1989). Hence, our prediction of an increased growth rate with increased mortality appears to be corroborated by the data. With the fish model in isolation and with a more fully developed parameter set, it will be possible to simulate specific years and to make more detailed comparisons with field data.

The total herring biomass predicted by the present model with standard mortality parameters (Fig. 8) is similar to that given by Greenstreet (1992b) (Table 6). This is to be expected as the latter data were used as the original initial conditions at the individual level, and the results from the end of the model run are similar to those initial conditions (by parameter fitting, in the case of weight-at-age). The biomasses given by Greenstreet (1992b) represent aggregate values for the years 1983 to 1988. There are various problems in comparing these biomasses with other published values (Table 6). Yang's (1982) estimates, based on single species VPA, were for two years in which the herring stocks were at a minimum following three decades of decline (to approximately 5% of the level in the early 1950s; Daan et al., 1990). The fishery for herring was closed in 1977. Sparholt (1990) aggregated results from MSVPA for the years 1983 to 1985, a period in which the biomass of herring increased by approximately 50% (Daan et al., 1990, fig. 13). The biomass of herring continued to increase beyond 1985 (Daan et al., 1990) and this is reflected in Greenstreet's (1992b) estimates, which exceed those given by Sparholt (1990). The experiments with the model that are planned will use biomass comparisons for specific years, to gain insights at both individual and population levels.

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