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Modelling the growth of herring from four different stocks in the North Sea

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Abstract

Variations in growth of the 1961–1983 year classes of North Sea herring larvae and juveniles from four different stocks in the North Sea have been modelled in a two-stage process. First, the ERSEM transport model and a database of temperature conditions in the North Sea have been used to simulate the year-specific dispersal and timing of recruitment of larvae to a model of juvenile growth. The juvenile model was forced by temperature and continuous plankton recorder (CPR) data, and migration was modelled from survey data on the relative distribution of stock components in the North Sea. The model explains the observed differences in mean growth from hatching to 1.5 years old of herring of different stock origins over the period 1970–1981, and therefore it has been concluded that the growth differences are generated mainly by the hydrographic conditions and plankton abundance along the drift trajectory of the larvae and migration route of the early juveniles. Comparison of the time series of modelled size-at-age for juveniles from the Shetland stock with observations for the same period shows that the model explains short-term year-to-year variability in growth, correctly identifying extreme years, but fails to explain the longer-term underlying trends. The model performed best over the period 1970–1981 when population biomass was uniformly low, and deviated during 1961–1969 when biomass was declining from high levels. The inclusion of population biomass as an independent explanatory variable in the comparison of model results with the longer-term data accounts for up to 58% of the total variance in the observations. Thus, it is concluded that hydrographic and planktonic conditions in the North Sea account for the short-term year-to-year variability in growth, but the major underlying trends over the last 40 years are due primarily to density dependence. Crown Copyright © 1997 Published by Elsevier Science B.V.

Keywords: herring (*Clupea harengus*, L); growth model; larval dispersal; annual variation; stock characteristics

1. Introduction

Traditional approaches to fisheries management have rarely taken into account the influences of environmental effects on fish stocks, other than to ac-

knowledge that there are effects on recruitment (Saville and Bailey, 1980; Burd, 1991; Corten, 1991). In the majority of cases however, the relationship between recruitment and environmental factors is obscure, and it has only rarely been possible to incorporate this into fisheries management strategies (Megrey et al., 1996). In reality, treating the environmental influence in this way masks effects on a range

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of time scales from interannual to decadal. More significantly, the signatures of environmental influences on fish stocks are not only reflected in recruitment, but also in physiological and behavioural characteristics of the fish and these may be of equal importance for stock management (Burd, 1978, 1991; Walsh and Martin, 1986; Stephenson and Kornfield, 1990).

Differences in meristic and morphometric characteristics and growth rate between fish of the same species but different geographical origins have been recognised for many years (Hodgson, 1936; Wood, 1936; Einarsson, 1951; Postuma and Zijlstra, 1958). The environmental plasticity of these characteristics has long been recognised (Blaxter, 1958), but they have still been used extensively for stock discrimination (Meng and Stocker, 1984; Misra and Carscadden, 1987; Johannessen and Jørgensen, 1991). The arguments relating to stock structure hinges on whether the maintenance of such characteristics in fish visiting the same spawning grounds in subsequent years is evidence of fish returning to their parental spawning area and hence of discrete stock structure (Stephenson and Gordon, 1991). Long-term trends in growth rate and meristic characteristics within stocks have also been documented, and recently Brander (1995) has summarised the changes in size at age of juvenile and adult cod caught from different stocks around the North Atlantic. Analysis of these data shows that a very high proportion of the variance in size at age, both between stocks and through time within certain stocks, can be explained by regional temperature indices. Similar though less successful attempts at relating cod growth to temperature have previously been described by Hermann and Hansen (1965), May et al. (1965) and Taylor (1958). Once established, such relationships have major consequences for the development of medium-term harvesting strategies which are invariably orientated towards regulating the biomass removed from the ocean.

Progress from an empirical knowledge of a relationship between regional indices of sea temperature and a predictive capability of fish growth and production under different climatic scenarios is far from straightforward. Brander (1995) alluded to one of the key factors as being that the size at age of a fish represents the cumulative effect of its environmental experience from hatching. This will be extremely

complicated for migratory species, and certainly not well represented by an index based on observations at a fixed, albeit regionally representative, site. In addition, the cumulative food consumption over the life time must also influence size at age. There is some debate as to whether prey abundance is normally limiting for growth in fish, but it is certainly a factor which must be taken into account.

Usually, the variations in growth between related stocks in the same regional sea area, and within single stocks over time, are rather small so that the opportunity for obtaining data for model development is somewhat restricted. Exceptions are the Færoese and West Greenland cod as documented by Brander (1995), and North Sea herring. The case of North Sea herring is interesting because of the very long history of meristic and morphometric data purporting to show distinct stock structure within the North Sea (Parrish and Saville, 1965; Harden Jones, 1970). However, the basis for environmental control of for example, the growth characteristics of herring of different hatching origins, and the sensitivity to spawning time and environmental change has never been quantitatively examined. Decadal time scale changes in size-at-age of herring have been documented in the North Sea (Cushing and Burd, 1957; Parrish, 1962; Parrish and Saville, 1965; Bailey, 1991). Initially, these were attributed to large scale changes in plankton abundance (Glover, 1957) but later investigators have explained them in terms of density dependence since they were correlated with the collapse and recovery of the population in the 1960s–1980s (Burd, 1978, 1984; Bailey, 1991).

In this paper we investigate, firstly the basis for the observed differences in growth rate between herring stocks in the North Sea. Secondly, we investigate the scope for the time series of observed changes in size-at-age of fish from the different stocks over the period 1961–1983 to have been generated at least in part by environmental changes.

2. North Sea herring demography and biology

There is an extremely extensive literature extending over several decades detailing the demography and biological changes which have occurred in the herring population of the North Sea. A brief sum-

mary of the aspects pertinent to this study is given below.

2.1. *Demography and abundance*

Parrish and Saville (1965) considered the herring of the northeast Atlantic to be composed of “Oceanic” and “Shelf” populations. These were further subdivided into stocks on the basis of spawning times, meristic and morphometric characteristics. The Oceanic group included the Icelandic and Norwegian winter–spring and summer spawners, and west of Scotland/Ireland winter–spring spawners. The Shelf group was made up of summer–autumn spawning stocks in the Irish Sea, west of Scotland, Belt Sea and southern Baltic, Kattegat, and North Sea. Within the North Sea, four main spawning stocks were identified — Shetland, Buchan, Banks and Downs. A number of minor spawning stocks are recognised, for example in the Thames estuary, Milford Haven, and along the Dutch and German coasts.

The commercial fisheries represent the major source of biological and demographic information on the herring in the North Sea. Exploitation has occurred over many centuries and extensive records are available (Saville and Bailey, 1980). Decadal scale fluctuations in abundance are well documented from the early 1900s onwards but the North Sea as a whole suffered a major collapse during the 1970s resulting in a ban on herring fishing from 1977 to 1983. Since 1983 exploitation of the stocks has been subject to a total allowable catch (TAC) system for the international fleet, and the North Sea herring biomass rose to an estimated 1.5 Mt in the early 1990s, although this was less than half the estimated biomass during the pre-collapse era in the 1950s.

The overall collapse of herring abundance during the 1970s did not happen uniformly over the North Sea. At the same time as the whole North Sea population abundance declined, so the proportional contribution of the Shetland stock increased and the distribution of spawning activity moved northwards until, during the minimum abundance period in 1976–1977, the population was concentrated at Shetland. As the population recovered in size during the 1980s, so the contribution from the more southerly stocks increased again.

2.2. *Biological characteristics of stocks*

The discriminating characteristics of the main stocks in the North Sea are at the population level, spawning area and time and juvenile distribution, and at the individual level, fecundity, growth, morphometric and meristic properties. The main details are summarised in Table 1.

Within each stock, there have been changes over time in the size at age and meristic characteristics. Early investigators often interpreted these in terms of changes in the degree of mixing between stocks (Cushing, 1958). However, Hulme (1995) has cast doubt on such interpretations showing conclusively that changes in meristic characteristics are closely related to sea temperatures at certain stages in early development.

The evidence for stock separation from genetic studies of North Sea herring is heavily weighted against the existence of reproductively separate groupings. The gene flow between morphologically and meristically distinct ‘stocks’ is apparently sufficient to eliminate any genetic distinction (Smith and Jamieson, 1986; Smith et al., 1990; Jennings and Beverton, 1991).

2.3. *Scientific survey data*

The nomenclature in the scientific literature for assigning herring to age classes is sometimes confusing. The term 2-ring or 2-group, for example, is often used. This refers to the number of winter growth rings in the scales or otolith used to determine fish age, and relates to calendar years rather than actual birth dates of fish. For example, fish hatched between autumn 1990 and spring 1991 would metamorphose in spring–summer 1991 and throughout that year would be referred to as an 0-group fish. They would all become 1-group on 1 January 1992, and 2-group on 1 January 1993.

Scientific surveys of the distribution, abundance and biological characteristics of herring are carried out for stock assessment purposes at various stages in the life cycle (Table 2).

In addition to the above annual surveys, a coordinated series of quarterly bottom trawl surveys of the North Sea was carried out in 1991, specifically to document the seasonal changes in the distributions

Table 1
Summary of the characteristic features of the main North Sea herring stocks

Characteristic	Shetland	Buchan	Banks	Downs	References
Spawning area	Shetland-Fair Isle	Aberdeen Bank	Yorkshire coast/Dogger Bank	English Channel	Burd, 1985; Cushing, 1967; Corten, 1986; Rankine, 1986
Juvenile area	Moray Firth, Skagerrak, eastern North Sea	Eastern North Sea, Skagerrak	German Bight, eastern North Sea	Southern North Sea, German Bight	Munk and Christensen, 1990; Postuma et al., 1960; Corten, 1986
Spawning time	August	August–September	September–October	December	Burd, 1985; Heath, 1993
Fecundity		2×10^5 eggs kg^{-1} incl. males	1.7×10^5 eggs kg^{-1} incl. males	1×10^5 eggs kg^{-1} incl. males	Baxter, 1959; Cushing, 1967; Almatar, 1987
Egg size		$160 \mu\text{g}$ dry weight	$200 \mu\text{g}$ dry weight	$350 \mu\text{g}$ dry weight	Baxter, 1959; Blaxter and Hempel, 1963; Zijlstra, 1969
Larvae hatch length		7.0 mm	7.2 mm	7.5 mm	Blaxter and Hempel, 1963
Larvae stage duration	7 months	7 months	7 months	6 months	Sinclair and Tremblay, 1984
Length at metamorphosis	40–50 mm	40–50 mm	40–50 mm	40–50 mm	Sinclair and Tremblay, 1984
Age at maturation	3–4 years	3–4 years	3–4 years	3–4 years	Cushing, 1967
l_1 (length of 1-group at 1 January)	> 19 cm	16–19 cm	13–16 cm	< 13 cm	Burd and Hulme, 1984
Vertebral count		56.3–56.6	56.3–56.4	56.4–56.6	Zijlstra, 1969; Rosenberg and Palmén, 1982; Hulme, 1995
Keel scale count		14.1–14.4	14.3–14.5	14.2–14.4	Zijlstra, 1969; Rosenberg and Palmén, 1982

Table 2
Summary of scientific surveys routinely carried out on herring stocks

Life stage	Survey type	Duration	Reference
Early larvae 0–1 month	Plankton sampling in all spawning regions during September–January.	1946–present day	Heath, 1993
Late larvae in February (2–6 months old)	Isaacs–Kidd plankton trawl sampling over the whole North Sea	International Young Fish Surveys, 1970–present day	Munk and Christensen, 1990; Anon., 1981; Anon., 1995
0-Group in August (8–12 months old)	Small mesh bottom trawl surveys over whole North Sea	English and Scottish Ground Fish Surveys, 1970–present day	Knijn et al., 1993
1-Group in February (14–18 months old), and annually thereafter	Small mesh bottom trawl surveys over the whole North Sea	International Young Fish Surveys, 1970–present day	Anon., 1981; Anon., 1995
2-Group in July (31–35 months old), and annually thereafter	Acoustic and pelagic trawling surveys in	International Herring Acoustic Surveys, 1980–present day.	Simmonds et al., 1994

of all fish species. The annual February and August surveys provided the first and third quarter distributions, and additional surveys were carried out in spring and winter.

In reality, as will be described below, the quarterly trawl surveys provide a rather poor record of the spatial distribution of herring in the North Sea, and bear little relation to the distribution of catches by the commercial fleets. This is not surprising since the bottom trawl used for the surveys is a poor sampler of schooling pelagic species.

3. Model description

The model we describe is an age-structured cohort system in which the size of fish varies with age according to a dynamic model of individual growth (Broekhuizen et al., 1994) set in the context of the European Regional Sea Ecosystem Model (ERSEM) of the North Sea. The basic system was described by Bryant et al. (1995) and we have elaborated upon this to model the growth of herring from different stocks within the North Sea, and to carry out long-term simulations of the growth history of North Sea herring.

The individual growth model described by Broekhuizen et al. (1994) represents the time dynamics of weight and length of fish under varying prey and temperature conditions. An individual is assumed to be composed of two fundamental tis-

sue types: structure and reserve. Structural tissue is an analogue for length and represents skeletal and nervous tissue which cannot be remobilised under starvation conditions. Reserve tissues can be sacrificed to meet metabolic demands under starvation conditions. The physiology of uptake and assimilation is modelled as a function of the ratio of reserve to structure tissue, and death through starvation corresponds to a minimum value of this ratio. The age-structured cohort model described by Bryant et al. (1995) simulated the population numbers, individual length and weight, and population uptake rate of prey by the entire North Sea herring population. The model was dynamically linked to ERSEM such that the uptake of prey groups by the fish was reflected in the biomass of these groups in ERSEM, and the mass balances of carbon and nutrient elements were conserved by returning defecation and excretion products, and mortalities in the fish model to ERSEM as dissolved and particulate organic matter. The fish model itself was not explicitly represented at every spatial node in ERSEM. Rather, the fish model was configured as a global object and the proportion of uptake from, and return to specific ERSEM spatial compartments was prescribed as a forcing time series to represent the seasonal migrations of herring around the North Sea.

The individual model of Broekhuizen et al. (1994) did not represent larval stages, which appear to have markedly different relationships between physiology

and the reserve to structural tissue ratio. Therefore, Bryant et al. (1995) made no attempt to model the larval stage in the population model and initiated each age class in the cohort model at 1 January with a weight of 36 mg C and a length of 30 mm corresponding crudely to the timing of recruitment of post larvae. Spawning was simulated as an instantaneous shedding of reserve biomass at day 270 each year by mature age classes. The shed biomass was passed directly to the detritus component of ERSEM in the interest of mass conservation.

The above system has been modified in a number of respects to address the hypotheses set out in the introduction, i.e. that differences in growth between herring stocks are a consequence of environmental experience, and that long-term trends in size at age mainly reflect changes in the North Sea environment:

(a) The individual stocks of herring in the North Sea have been modelled explicitly, rather than treat the whole North Sea population as a single unit.

(b) The population abundance aspects of the system have been dispensed with and the model now produces the growth through time of an average individual in the population.

(c) The fish population model has been decoupled from ERSEM and forced by spatially and temporally resolved data on mesozooplankton biomass and temperature for the years 1961–1985.

(d) The larval stage has been modelled explicitly. The dispersal of larvae is modelled as a passive tracer in the ERSEM transport model, whilst larval growth is modelled as a function of temperature alone.

(e) In this paper growth has been modelled only up to 1.5 years of age, the precise age depending on stock affiliation.

3.1. Specification of separate herring stocks

Bryant et al. (1995) did not discriminate between the various stocks of herring in the North Sea and modelled the whole North Sea population as a single unit. This was mainly dictated by the lack of data with which to define the time dependent changes in the spatial distribution of fish from the various stocks. Now, we specify four different herring stock in terms of the following. (a) The spatial and temporal distribution of spawning which determines the location and date of injection of passive tracers into

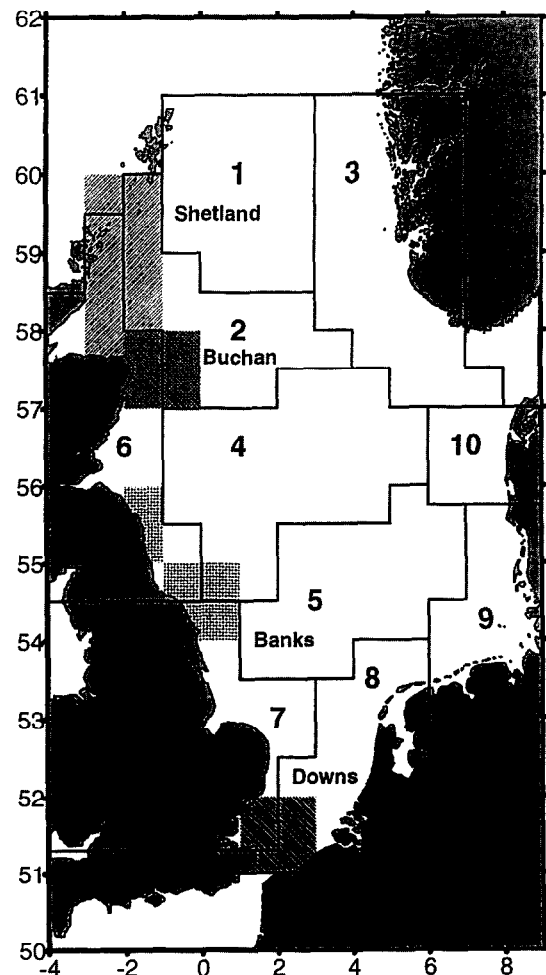


Fig. 1. Configuration of the upper 10 compartments of the 15-box implementation of ERSEM, and the locations of the designated spawning areas of the four herring stocks.

the ERSEM transport model to simulate the dispersal of larvae. (b) The spatial and temporal distribution of juveniles which can now be at least crudely assigned to stocks on the basis of much improved data compared to those available to Bryant et al. (1995).

The four stocks modelled were Shetland, Buchan, Banks and Downs. The time base for each year class in the model was days from the beginning of the year in which hatching occurred. The prescribed hatch locations of each stock are given in Fig. 1 and times in Table 3.

Table 3
Prescribed hatching times of each herring stock in the model

Stock	Modelled hatching period	Mean hatch day
Shetland	1–30 August	225
Buchan	1–30 September	255
Banks	1–30 October	285
Downs	1–30 January	375

3.2. Modelling the larval phase

3.2.1. Background

Herring eggs are laid and adhere strongly to stones and gravel on the seabed, but the larvae which emerge quickly migrate to the upper layers of the water column (Ewart, 1884; Bowers, 1969). During the period from hatching at 7–9 mm length (Blaxter and Hempel, 1963) to metamorphosis at around 40–50 mm (Blaxter et al., 1983; Langsdale, 1993) herring larvae may be regarded as passive tracers with regard to horizontal dispersal. Beyond this stage schooling behaviour is well developed (Gallego and Heath, 1994) and the fish are capable of undertaking active horizontal migrations.

The size of larvae at hatching is related to egg diameter (Blaxter and Hempel, 1963), which in turn varies systematically between stocks. In general the northern stocks have high fecundity and small diameter eggs and vice versa for the southern stocks (Baxter, 1959; Cushing, 1967; Almatar, 1987). Larvae hatching in the southern North Sea in December and January have a mean length of around 9 mm compared to 7 mm in the northern North Sea. Temperature is probably one of the main factors influencing egg size and fecundity (Tanasichuk and Ware, 1987).

Newly hatched herring larvae carry a substantial yolk reserve and do not have to feed for up to one week after hatching (Blaxter and Hempel, 1966). First feeding larvae primarily consume the eggs and early naupliar stages of copepods. As the larvae grow, so the size range of prey increases in line with the changing mouth size, and the diet progresses through copepodites and ultimately adult stages of copepods (Blaxter, 1963; Cohen and Lough, 1983). Larvae show distinct prey species preferences, taking *Pseudocalanus* sp. and *Temora* sp., and rejecting *Acartia* sp. and *Calanus* sp. (Checkley, 1982). Ju-

venile and adult herring consume a wide range of planktonic organisms including copepods, euphausiids, and larvae of other fish species (Last, 1982, 1989).

3.2.2. Formulation of size at hatching and growth

The relationship between size of larvae at hatch and temperature was derived from data presented by Blaxter and Hempel (1963):

$$W_0 = 0.125 - 0.005T,$$

where W_0 = dry weight (mg) at hatch and T = temperature. Carbon weight was estimated by assuming that carbon constituted 40% of dry weight.

In this study we take a simple approach to modelling the growth rate of herring larvae, using an empirical relationship between weight specific growth rate and temperature. This in no sense implies that we do not believe food and many other factors are involved, but reflects the fact that temperature has been shown to be the major factor accounting for large spatial scale, seasonal and interannual variations in growth rate of many species of fish larvae. For example, cod and haddock larvae in the northwest Atlantic (Campana and Hurley, 1989), striped bass in Chesapeake Bay (Rutherford and Houde, 1995), pollock in Alaska (Halderson et al., 1989), plaice in the North Sea (Hovenkamp and Witte, 1991). Nutritional factors are certainly involved but at these scales temperature explains most of the variability. On shorter time scales and smaller space scales where temperature variations are small, a range of other factors including prey density (Govoni et al., 1985) and turbulence (Gallego et al., 1996) assume increased importance. In any case, there are no North Sea wide seasonal data on the abundance of food items for herring larvae. The only comprehensive spatially and temporally resolved data on zooplankton in the North Sea are from the continuous plankton recorder surveys (CPR), but the mesh size of the sampler used is too large to retain the relevant species and size classes.

Following from examples given by Houde (1989, 1996), a simple linear relationship between weight specific growth rate and temperature was assumed:

$$G = -0.030 + 0.008T,$$

where G = fractional weight gain per day and T = temperature.

The coefficients a and b were estimated from a field study of the overwinter growth of herring larvae in the North Sea (Munk et al., 1991) and from a compilation of laboratory investigations on the effects of temperature on larval fish growth rates (Houde, 1989). For comparison, the equivalent relationship for striped bass in Chesapeake Bay tributaries (temperature range 14–24°C) was $G = 0.04 + 0.007T$ (Rutherford and Houde, 1995).

3.2.3. Dispersal of larvae and construction of temperature histories for year classes of fish in each stock

Our objective was to calculate the temperature history of larvae from each stock based on modelled dispersal patterns and spatially and temporally resolved temperature data. To achieve this we used the 130 box (1° latitude × 1° longitude) North Sea implementation of the ERSEM transport model (Lenhart et al., 1995, 1997), treating the larvae as inert passive tracers. Hatching was simulated by setting a forcing value of the tracer concentration at the appropriate times of year in the upper compartments coinciding with each of the designated spawning sites. The hydrodynamic scenario used to drive the transport model was a 25-year (1961–1985) time series of daily exchange coefficients between ERSEM compartments derived from hindcast simulations of North Sea circulation with a 3-dimensional flowfield model (Pohlmann, 1996) and provided by J. Pätsch of the Institut für Meereskunde, Hamburg, Germany. The results of this exercise (time series of proportion of original tracer abundance in each of the 130 ERSEM compartments) were condensed to monthly time resolution and the coarser spatial resolution of the 15-box North Sea implementation of ERSEM (Baretta et al., 1995) for further modelling. This was necessary to match the temporal and spatial resolution of the temperature data, and because the next stage of the model (growth of juveniles) was constrained to the 15-box resolution by the data used to specify the relative distribution of juveniles across the North Sea.

The temperature histories of the populations of larvae from each spawning area were determined by projecting the monthly proportional distributions across ERSEM compartments onto a database of monthly mean temperatures from 1961–1985 at the

same spatial resolution. This was prepared as described later from the international database of North Sea hydrographic records held at the International Council for the Exploration of the Sea (ICES).

3.3. Modelling juveniles

3.3.1. Recruitment timing and growth rate of juveniles

The modelling of both dispersal and growth of herring changed when the larvae from a particular spawning area reached a carbon weight of 148 mg, equivalent to a length of 50 mm (Coull et al., 1989) and assuming carbon represents 17% of wet weight). From this point onwards, growth in length and weight were simulated from temperature and zooplankton food concentrations by the Broekhuizen et al. (1994) growth model parameterised for herring as in Bryant et al. (1995). The time varying distribution across ERSEM compartments was deterministic and is described later. The timing (day of year) at which recruitment to the juvenile model occurred was not prescribed, but was determined each year by the outcome of the larval growth model for each stock.

3.3.2. Migration patterns of juveniles

Bryant et al. (1995) argued that there was insufficient understanding of the processes governing fish migrations on an annual basis to merit any attempt at dynamically linking fish distribution to prey or environmental data. The relative distribution of the whole population across the spatial compartments of the model was therefore specified from data on a quarterly basis to represent the annual migrations of fish in the North Sea. We have continued with this approach in this paper. However, the only data available to Bryant et al. (1995) were commercial catch statistics in the form of quarterly stock biomass landed from ICES statistical rectangles. These data have been criticised on the grounds that commercial data may not be a true reflection of fish concentration, and because they were not resolved by age class. Significantly more detailed data were available to us in this study.

Data from the 1991 quarterly bottom trawl surveys of the North Sea were obtained from ICES. Catch per unit effort data were provided as mean number and biomass, and mean length resolved by

age class and ICES statistical rectangle. The first appearance of herring in the catches was as 0-group in the third quarter of the year when the fish were 6–10 months old. Data on 1-group in the first three quarters of the year showed a consistent distribution and relatively stable abundance. Thereafter, the abundance of older age classes showed strong seasonality in catch rate with few fish being caught in the fourth quarter (Fig. 2). Analysis of the data on other species caught in the surveys, especially the gadoid fish, showed that this was a feature exclusively of the herring catch, and not a reflection of the overall catching efficiency of the surveys. In conclusion, the survey data probably give a good account of the distribution of 1-group herring, but not of the older age classes.

Discrimination between 1-group fish of different hatching origin on the basis of length composition in the quarter 1 trawl surveys has been described by Rosenberg and Palmen (1982) and Burd and Hulme (1984). In each year the cumulative abundance by length class for the North Sea as a whole shows sharp discontinuities corresponding to the size limits of fish from different origins. With increasing age the geographical segregation of length groups within each age class becomes less distinct as the stocks appear to intermingle extensively, possibly only separating at spawning time. Thus, although mean lengths of 2- and 3-group fish from the commercial catches have been resolved by spawning group in published literature, the actual hatching origin of these fish is uncertain. There was certainly no basis for assigning the catches of fish older than 1-group in the 1991 quarterly trawl survey data to hatching origin. Hence, in this paper where we are primarily concerned with stock comparisons, we are restricted to modelling the growth of fish up to day 756, corresponding to the mid-point of quarter 1 (15 February) in the 1-group year or 1.25–1.5 years of life depending on stock origin.

We assigned the catch rate of 1-group fish in each ICES rectangle during the 1991 quarter 1 survey to one of the four stocks on the basis of mean length. The distinguishing length ranges for the stock were: Downs <130 mm; Banks 130–160 mm, Buchan 160–190 mm, Shetland >190 mm. We then aggregated the results to estimate the proportional distribution of each stock across the ten ERSEM areas

(Fig. 3), and used the results to prescribe the distribution of juvenile herring on day 765 of each modelled year class. Hence, we assume the relative distribution in 1991 of juveniles from the 1989 year class is representative of that for other year classes between 1961 and 1983. We have little alternative to making this assumption since comparable data are not available for the earlier years. In defence, the coarse spatial resolution of the ten ERSEM areas mitigates against major long-term changes in the pattern of distribution. Qualitative comparisons of earlier maps of juvenile herring abundance certainly suggest that the pattern is not markedly different.

At each time step in the juvenile phase of the model the proportion of fish in each ERSEM area was determined by linear interpolation between that on the day when larvae attained 148 mg C and that prescribed for juveniles on day 765. Thus, the distribution of fish was smoothly changed from the terminal distribution of larvae to the prescribed distribution on day 765, simulating an active migration.

3.4. *Compilation of forcing data*

The forcing data required to support the larval and juvenile growth models were year-class specific time series of temperature and prey concentration along the drift and migration trajectories of each stock. In this study, these requirements were met by projecting the trajectories derived as described above onto spatially and temporally resolved hydrographic and CPR data.

Monthly mean surface (0–30 m) and bottom (30 m–seabed) temperature and salinity for the years 1961–1985 were compiled on an ICES statistical rectangle spatial resolution by the ICES Hydrographic Office from all records submitted to their database. These data were then restructured to the compartmental resolution of the 15-box North Sea implementation of ERSEM. Missing values were filled by one of two methods. First, isolated single missing values were replaced by the average of valid data from adjacent months. Where more than one consecutive missing value was encountered a time series decomposition method similar in principle to that described by Broekhuizen and McKenzie (1995) was used to interpolate the missing segment of data. Essentially, a climatological seasonal cycle of tem-

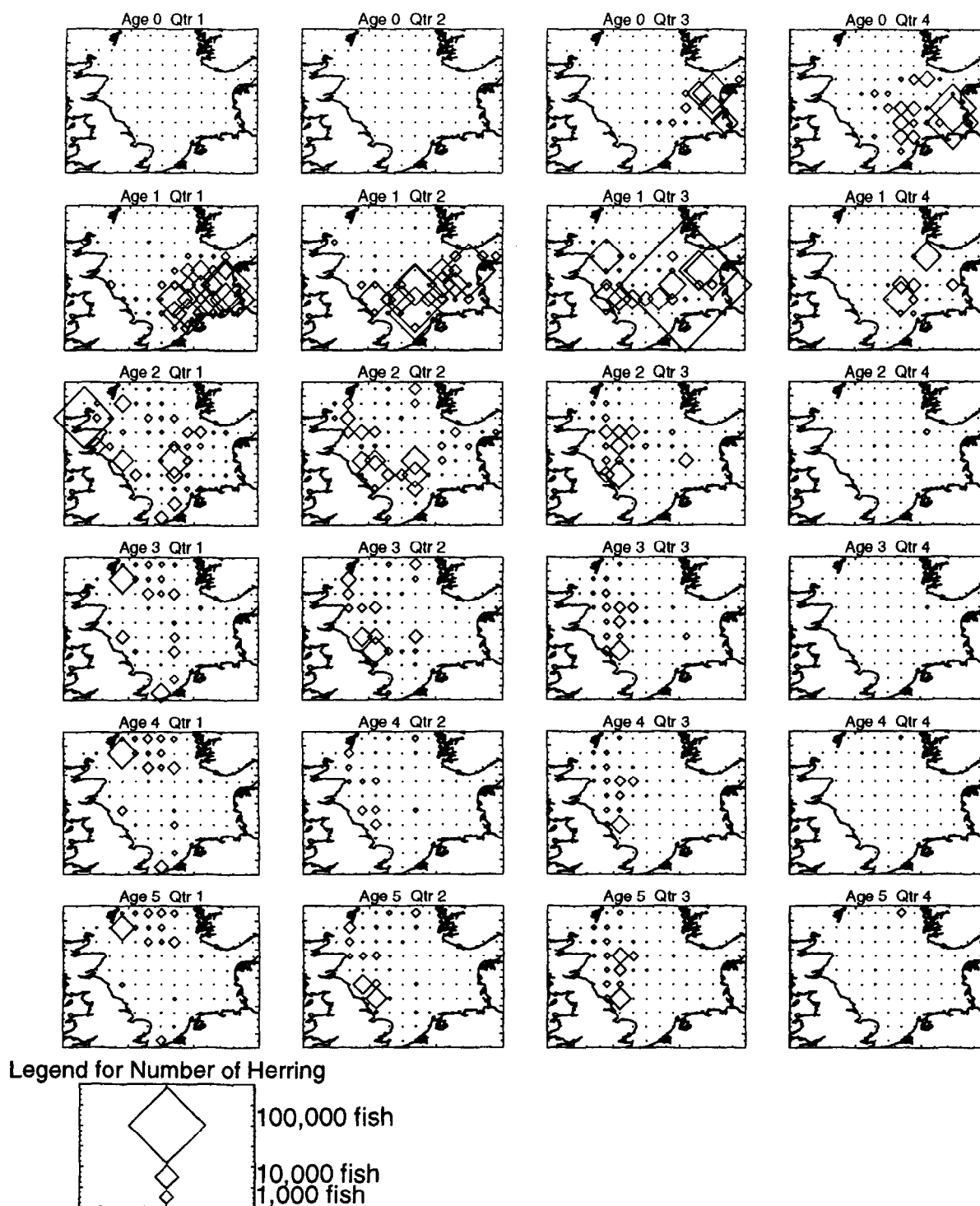


Fig. 2. Quarterly distribution of herring by age class across ICES statistical rectangles from the International Bottom Trawl Survey (IBTS) database for 1991.

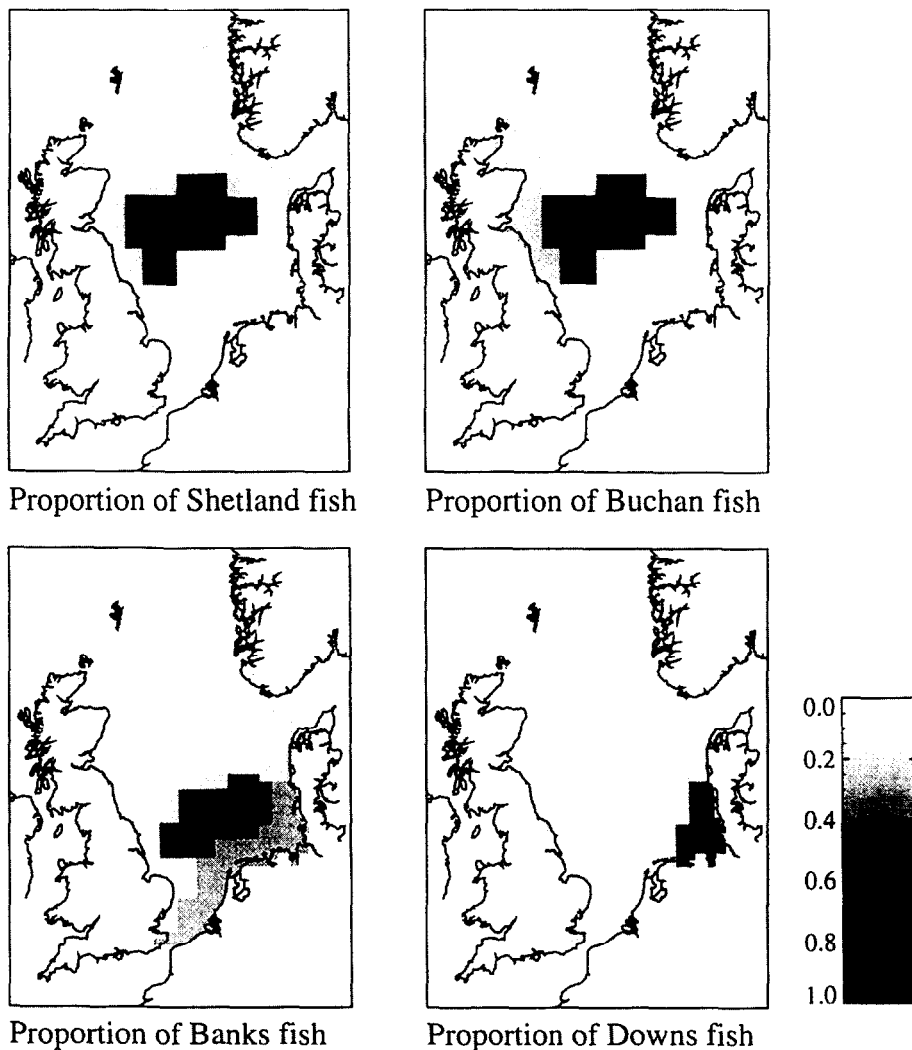


Fig. 3. Maps of the proportional distribution of 1-group (14–18 months old) herring from the four stocks across the upper 10 compartments of the 15-box implementation of ERSEM at 15 February, based on data from the IBTS database.

perature or salinity was calculated from the existing data for each spatial compartment (Fig. 4). The valid data were then deseasonalised by a 12-month running average to produce a continuous time series of the deviation from the long-term mean. This deviation was then applied to the climatological mean for each compartment to reconstruct the missing segment of the time series.

Monthly mean zooplankton biomass values (mg C m^{-3}) for the years 1961–1985 at the spatial resolution of the 15-box North Sea ERSEM implementation were obtained by time series deconvolution

of CPR survey data as described by Broekhuizen and McKenzie (1995). All copepod species recorded by the surveys were included in the analysis. The biomass of each constituent species was estimated as the product of numbers per unit volume and an average carbon weight per individual for each species, and the bulk population biomass estimated by summation. Since the CPR surveys only sample the upper 10 m of the water column, a raising factor was applied to convert these data to depth average values as derived by Broekhuizen et al. (1995). Climatological mean seasonal cycles of zooplankton biomass,

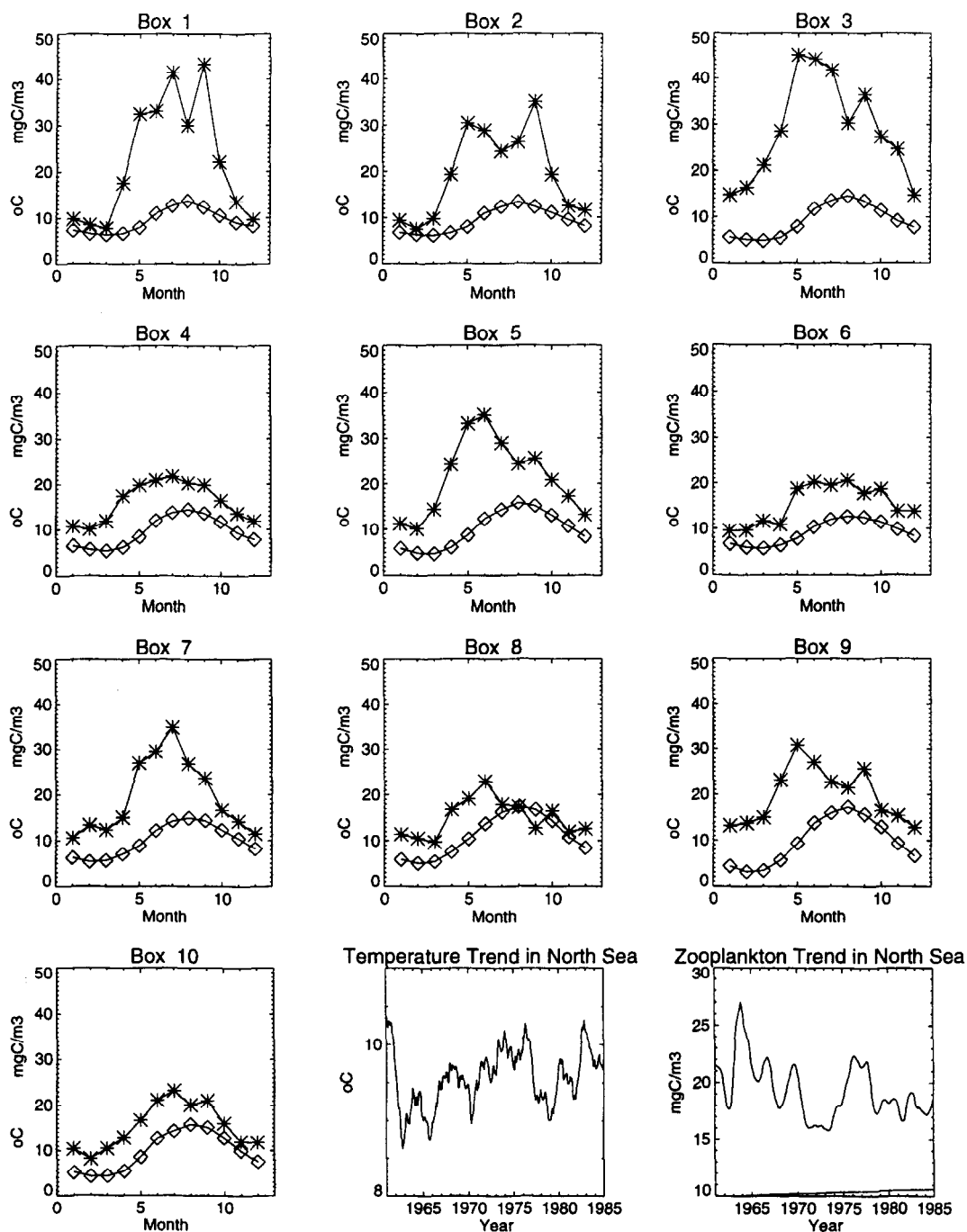


Fig. 4. Mean (1960–1984) annual cycle of temperature and zooplankton biomass in the upper compartments of the ERSEM boxes, together with the North Sea average deseasonalised long-term trends. Box numbers as in Fig. 1.

and the North Sea wide long-term time series are shown in Fig. 4.

4. Results

4.1. Dispersal of larvae

The long-term average (1961–1983 year class) distribution of larvae from each stock at the end of the passive transport modelling phase is shown in Fig. 5. Note that the average age, and average day of

the year corresponding to the end of the larval phase, differs between stocks due to the different hatching times and growth rates. Larvae from each stock were widely distributed across the North Sea but retained separate centres of distribution. In general, the modelled long-term average distribution of each stock at 50 mm length was similar to the distribution at 15 February the following year prescribed from the trawl survey data in that the majority of fish from all stocks were found in the southern and eastern North Sea (Fig. 3). Thus, the active juvenile migration

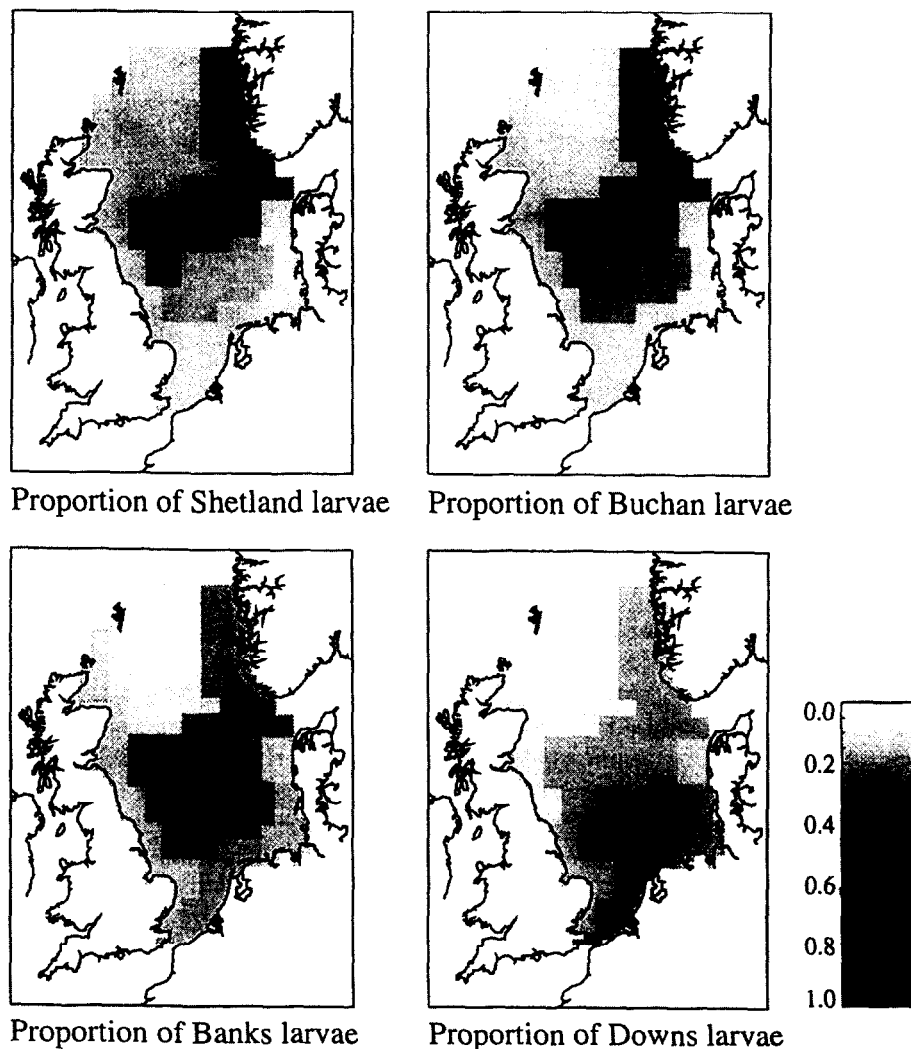


Fig. 5. Maps of the modelled average (1961–1983 year classes) proportional distribution of herring larvae across the ERSEM boxes at 148 mg C body weight.

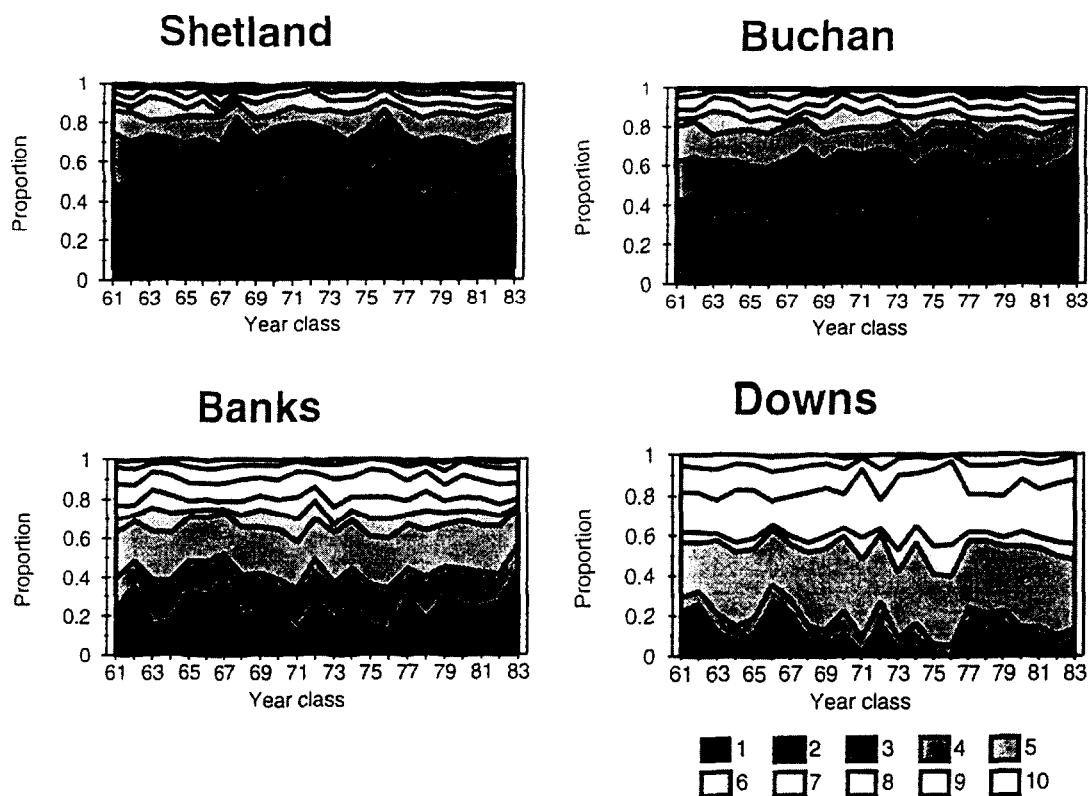


Fig. 6. Modelled long-term (1961–1983) data on the percentage distribution of herring larvae across ERSEM boxes 1 to 10 at 148 mg C body weight.

model involved, on average, only small redistribution of each stock across the spatial compartments compared to the passive drift period.

The year-to-year variability in dispersal of larvae from each stock predicted by the model is shown in Fig. 6. The results show that the variability in dispersal increased from north to south. At the coarse spatial resolution of the ERSEM compartments the dispersal pattern of Shetland larvae showed only two years (1968 and 1976) with significant variations in patterns when >60% of the larvae were retained in the northern areas 1, 2 and 3. In contrast, the variation in dispersal of Downs larvae was high. Less than 1% of Downs larvae reached the Norwegian coastal compartment (area 3) in 1971 and 1976, whilst in 1961, 1962, and 1966 >20% arrived off the Norwegian coast.

4.2. Growth of larvae and juveniles.

The age of larvae from each stock at the end of the passive tracking phase (148 mg C) is shown in Fig. 7a. The results show that on average the larvae from the Shetland and Downs stocks achieved the highest growth rates, reaching 148 mg C within 250 days. Larvae from the Buchan and Banks stocks took on average >260 days to attain the same size. However, the year-to-year variability was considerably higher for the Shetland stock than for the others which contrasts with the variability in the dispersal pattern. The reason for the differing growth rates of larvae from the various stocks in the model was related solely to the timing of hatching in relation to the seasonal cycle of temperature along the drift trajectory (Fig. 8).

The modelled differences between stocks in the weight and length at age 12 months (Fig. 9) mirror

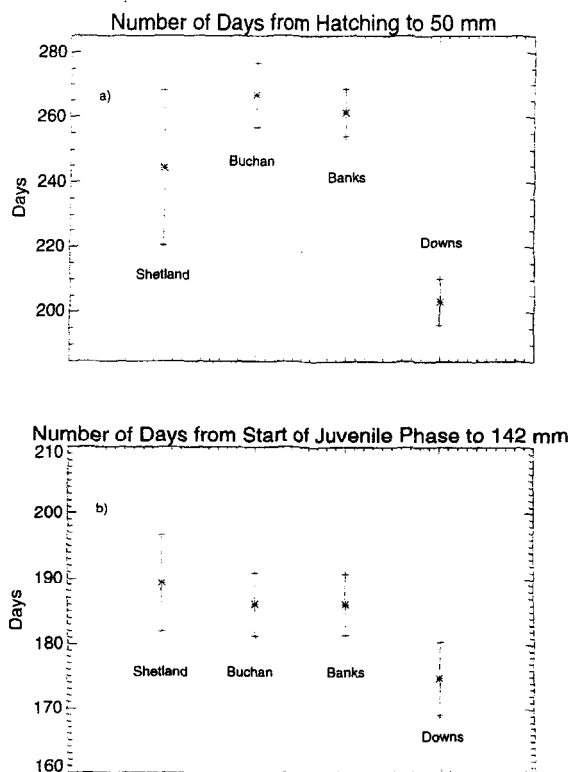


Fig. 7. Modelled average ± 1 standard deviation of the 1961–1983 year-class larval and juvenile stage durations for each stock. (a) Age (days) of larvae from each stock at 148 mg C body weight. (b) Time (days) for juveniles from each stock to grow from their recruitment weight of 148 mg C body weight to a weight of 3300 mg C (19.4 g wet weight).

almost exactly the growth rates during the larval phase. Note that fish achieve 12 months age on different dates depending on hatching origin. Fish of Shetland and Downs origin were on average >11 g and >115 mm, whilst Buchan and Banks fish were <9 g and <100 mm at the same age. The time taken to increase in weight from 148 mg C to 3300 mg C (50 mm to 142 mm) varied between stocks, but the magnitude of variation was less than that in the larval phase duration (Fig. 7b). The differences between stocks in juvenile growth were related to the timing of recruitment to the juvenile model in relation to the seasonal cycles of temperature and zooplankton abundance (Fig. 10). Nevertheless, the model suggests that the larval phase accounts for a greater proportion of the variation between stocks in size-at-age than the juvenile phase.

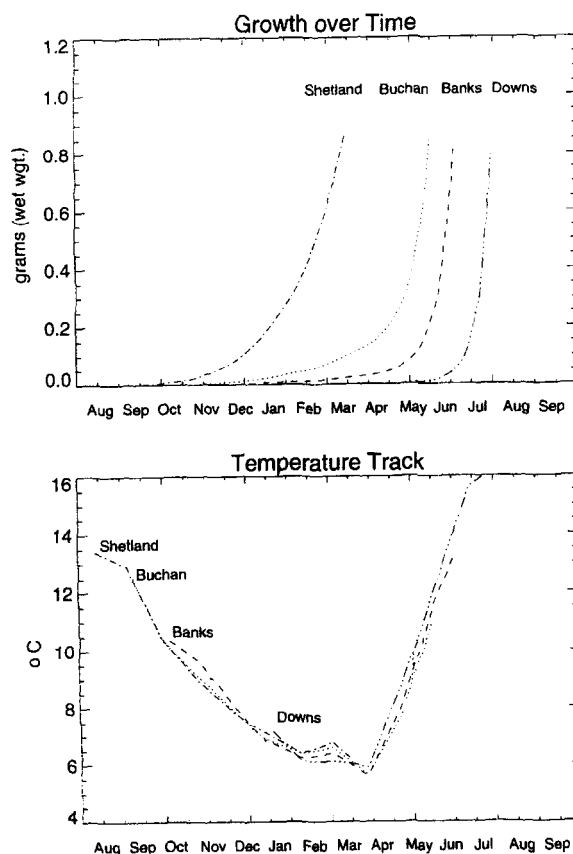


Fig. 8. Modelled growth trajectories and temperature histories of the 1974 year class of larvae from different stocks.

To investigate the relative importance of spatial and temporal patterns of hatching time in determining the differences in growth rate between stocks, we simulated hypothetical hatching in September at Downs, using the 1974 year class as an example. The results (Fig. 7a and b) show that spatial factors have a relatively small influence on the outcome of the larval phase. Simulated hatched at Downs in September resulted in growth at approximately the same rate as those of Buchan larvae released at the same time.

Data on the mean lengths (l_1) of 1970–1981 year class fish sampled as 1-group in the 1972–1983 February trawl surveys have been documented by Burd and Hulme (1984). These authors discriminated between fish of Northern North Sea (Shetland), Central North Sea (Banks) and southern North Sea (Downs) origin on the basis of length compositions.

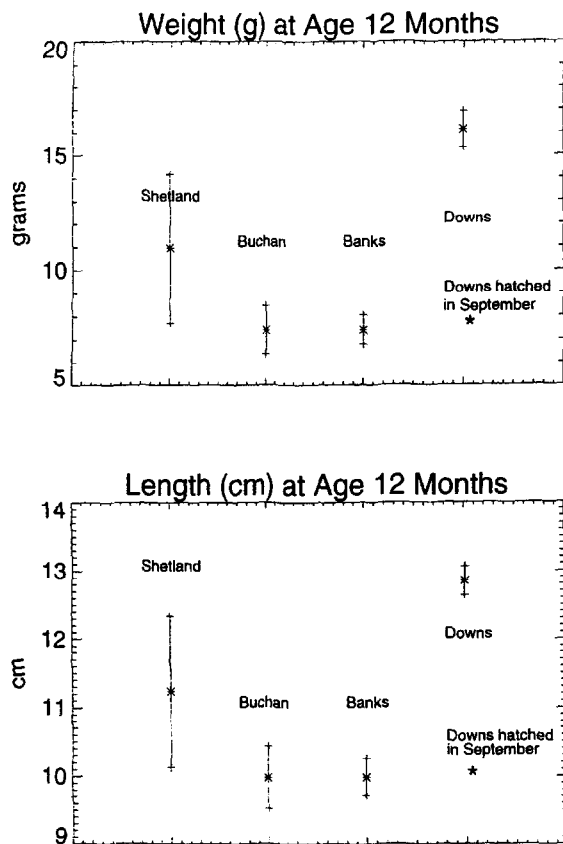


Fig. 9. Modelled average ± 1 standard deviation of the weight and length of fish from each stock at 12 months age for year classes 1961–1983. Additional symbol indicates the consequences of simulating hatching in September at Downs for the 1974 year class only.

Their data should be directly comparable to the model results on day 765 of each year-class simulation. The mean and standard deviations of length and weight for the 1970–1981 year classes of each stock predicted by the model correspond well with the observations (Fig. 11). The length and weight of fish from the Northern and Central areas were very close to the observed values (1% for Shetlands and 0.3% for Banks) but were slightly over predicted for the Southern fish (9% for Downs). Shetland fish were clearly the largest in both the model and observations, and Downs fish the smallest.

The variations in modelled values of l_1 for the 1961–1983 year class and corresponding observed data for the 1970–1981 year classes (Burd and

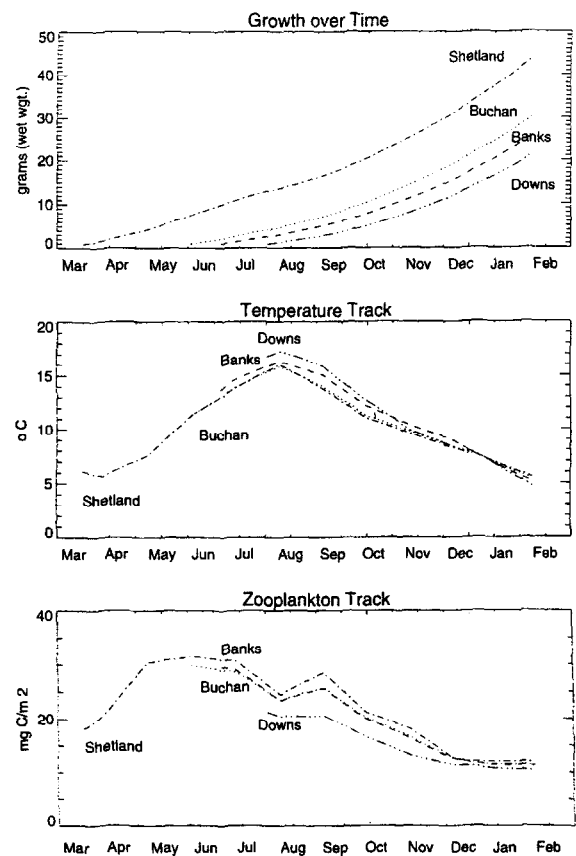


Fig. 10. Modelled growth trajectories and temperature and food histories of the 1974 year class of juvenile herring from different stocks.

Hulme, 1984) are shown in Fig. 12. The model results correspond well to the data for the Shetland stock, but less well for the Banks and Downs stocks. However, in all cases the extreme small size of fish from the 1978 year class is predicted by the model, as are the large sizes of fish from the 1972–1973 year classes. Examination of the forcing data for the model shows that the 1978 year class experienced an exceptionally cold period in the North Sea, whilst the 1972–1973 classes were subjected to high temperatures.

The time series of observations of l_1 can be extended for the Shetland stock by incorporating back-calculated values derived from annual increment measurements on scales and otolith of spawning 3-group and older fish caught by the Shetland commercial fisheries between 1928 and 1973. These

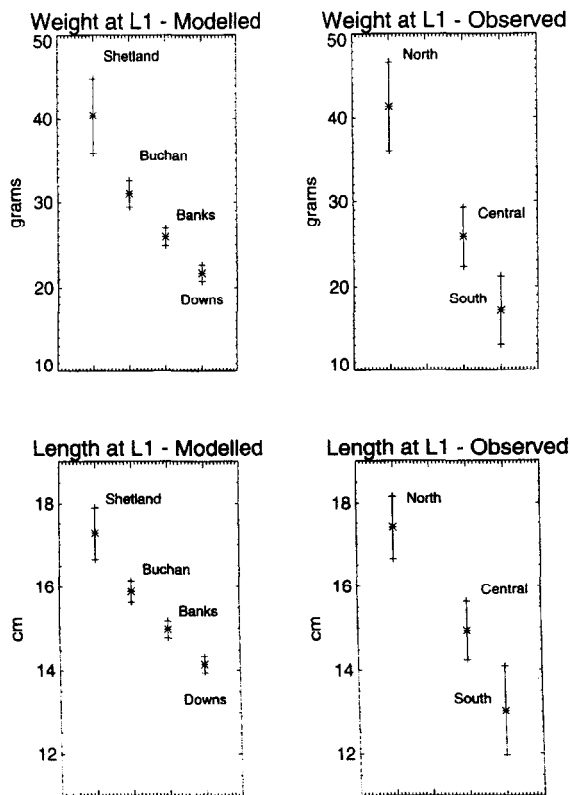


Fig. 11. Modelled average ± 1 standard deviation of the weight and length of 1-group fish from each stock at 15 February (14–18 months age) for the 1961–1983 year classes, and corresponding data from the annual trawl survey for 1970–1981 year classes compiled by Burd and Hulme (1984).

data have been compiled from sampling records at the Marine Laboratory Aberdeen by Heath and Baird (1983). Although these data are not strictly comparable to those of Burd and Hulme (1984), the correspondence for the 1968–1972 year classes is good, suggesting that combining the two sources is a reasonable approach. The combined data for the Shetland stock, together with the model results for the 1961–1983 year classes are shown in Fig. 13a. It is clear that although the model agrees with the data in terms of both mean level and time dependence for the 1970–1981 year classes, the mean levels diverge markedly between 1961 and 1968. However, the model still reproduced exceptional years in the pre-1970 observations, for example the 1961 year-class fish were exceptionally large (relative to the 5-year mean) in 1961, and the 1962 fish were exception-

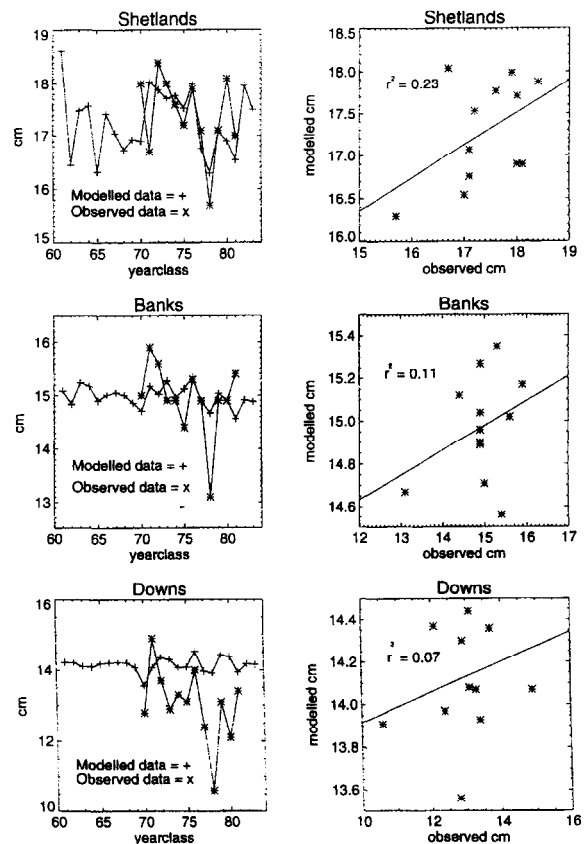


Fig. 12. Modelled 1961–1983 time series of l_1 for each stock (+), and (*) corresponding available data from the annual trawl surveys (1970–1981 year classes) compiled by Burd and Hulme (1984).

ally small in both the model and observations. These years were unusually warm and cold, respectively, in the North Sea, whilst zooplankton concentration was average in both years.

Between the late 1940s and 1968, the spawning population biomass of herring in the northern North Sea declined from 4.4×10^9 kg wet weight to $< 0.5 \times 10^9$ kg. Between 1968 and 1983 the biomass remained below 0.5×10^9 kg, reaching a minimum of 58×10^6 kg in 1977 (Anon., 1989) (Fig. 13b). A multiple regression including both the growth model results and the spawning biomass as independent variables accounted for 58% of the variance in the observed l_1 data for the 1961–1981 year classes (Fig. 13a), although a simple regression including only biomass performed almost as well (54% of

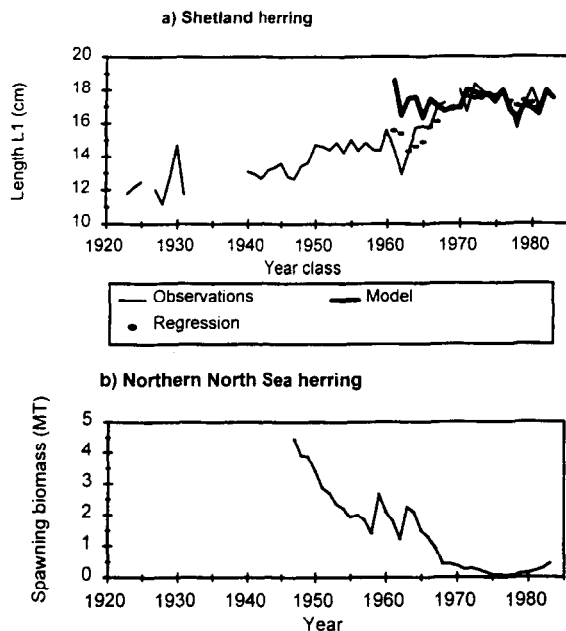


Fig. 13. Long-term (1924–1981) changes in northern North Sea herring stock characteristics. (a) Composite data on l_1 for 1924–1981 year classes of the Shetland stock (solid line), together with modelled 1960–1983 time series for the same stock (heavy solid line), and a regression model including the growth model results and population biomass as independent variables (dotted line). (b) Time series of herring spawning population biomass (Mt wet weight) in the northern North Sea (1947–1981).

observed variance). Hence the conclusion is that the growth model driven by North Sea hydrodynamics, temperature and zooplankton abundance accounts for short-term variability in the growth of herring, and variability during the low stock abundance period in the 1970s. However, long-term trends are correlated with the spawning biomass implying that density dependent processes are involved.

5. Discussion

5.1. Dispersal of larvae

The dispersal of herring larvae from the various North Sea spawning groups has been extensively investigated in the field, and modelled using particle tracking techniques (Bartsch, 1988, 1993; Bartsch et al., 1989). These studies suggest that there is considerable interannual variability in the dispersal patterns of larvae, and that this may be a contributory

factor to recruitment success. Transport of larvae to a favourable area for juvenile growth and survival is seen as a “necessary but not solely sufficient” requirement for good recruitment. Particle tracking studies suggest that dispersal is particularly variable for the northern stocks which is completely contrary to the ERSEM transport model results reported here. However, this is not terribly surprising as the two studies are performed at very different spatial scales.

The main element of variability in particle tracking studies is the success or otherwise of transport from the Shetland and Buchan spawning areas to the Skagerrak. The area north of Jutland is thought to be a particularly important nursery area of northern stock herring and there are some indications that failure to reach this area is related to poor recruitment. However, aggregation of the ERSEM transport model results to 10 coarse areas completely masks this aspect of variability. The Norwegian coastal box (3) in the coarse scheme will contain concentrations accumulated from the entrance to the Skagerrak. As described, the aggregation to coarse areas was necessary to match the spatial distributions to the resolution of the forcing data on zooplankton and the final distribution of juveniles. In fact, the modelled growth rates should be relatively unaffected by the aggregation to coarse boxes since the temperature throughout each of the compartments is reasonably uniform compared to the seasonal range of variability. The coarse ERSEM boxes were originally chosen on the basis of hydrographic subdivisions of the North Sea.

Particle tracking models have also shown that the dispersal of herring larvae and plankton organisms in general is sensitive to vertical migration parameters, especially in tidal waters (Hill, 1991). Diurnal vertical migration behaviour is the predominant pattern for herring larvae in the North Sea, although other patterns have been observed under some circumstances (Heath et al., 1988, 1991; Munk et al., 1989). We made no attempt to simulate vertical migration in the ERSEM transport model, treating larvae as inert neutrally buoyant tracers, and vertically integrated modelled concentrations after the simulation was complete. At the coarse scale of aggregation used to model the growth of individuals from each stock this is almost certainly a reasonable approximation.

Accepting the limitations of the larval transport modelling outlined above, the latitudinal variability in dispersal is interesting. Even though year-to-year variations in the pattern of dispersal is markedly less for the Shetland stock than for Downs, this is not reflected in the variability in larval stage duration. In fact, Shetland larvae show larger variability in stage duration than Downs. The explanation for this is that at the level of spatial aggregation used here, year-to-year hydrographic variability is greater in the northern North Sea than in the south, and this dominates any year-to-year variation in the transport model results.

In summary, the coarse aggregation of the transport model results probably masks much of the year-to-year variability which is portrayed in particle tracking analyses of larval herring dispersal. However, for the purposes of growth modelling described here the box modelling approach was probably adequate since most of the variability in temperature experience was generated by between-year hydrographic variations and the timing of simulated hatching in relation to the seasonal cycle of temperature.

5.2. *Growth of larvae and juveniles*

Sinclair and Tremblay (1984) and Sinclair (1988) noted that taking all the herring stocks in the north Atlantic together, spawning takes place throughout the year although individual stocks have rather well-defined spawning periods. Despite this, metamorphosis of larvae is restricted to a 5-month period from April to August. These authors hypothesised that for each stock the timing of spawning is adapted to the growth conditions along the average drift trajectory of the larvae to ensure arrival at the correct size for metamorphosis at the most appropriate time of year. Our model reproduces the restriction of metamorphosis timing relative to spawning time. The mid-points of the spawning time was prescribed for each stock ranged from 15 August to 15 January (150 d), whilst the long-term average dates of recruitment to the juvenile model ranged from 19 April to 15 August (116 d). Although the constriction of timing is less extreme than implied by the compilation of observations (Sinclair and Tremblay, 1984) the principle of feature is correctly simulated.

The model shows a 62% variation in weight of 12-month old herring depending on stock origin generated entirely by environmental conditions. The simulated 1961–1983 year-class average weight and length at 12 months age was highest for Downs fish (16.1 g, 12.8 cm) and lowest for Buchan (7.4 g, 9.5 cm). Note that these results refer to fish of a given age, not on a given date, so they genuinely reflect differences in modelled growth rate and not simply that the hatching dates of the fish are different. Comparison with observations is only possible for particular survey dates when the fish are different ages by virtue of their different hatching times. Presentation of the model results in this format shows that size-at-date is overpredicted by the model for Downs fish by factors of 1.27 on weight and 1.09 on length, but approximately correct for Shetland fish compared to February trawl survey data. Returning to the estimated variation in size-at-age, this implies that the true variation in weight-at-age is approximately 30%.

The differences in size-at-age between juveniles from different hatching areas are generated mainly during the larval phase and in the model they are a consequence of the relationship between hatching date and the seasonal cycle of temperature in the North Sea. The amplitude of the seasonal temperature signal is larger in the southern North Sea than the north, southern areas being warmest in the summer and coldest in the winter. This, combined with the timing of hatching from the four stocks relative to the seasonal cycle results in the highest average temperature over the larval phase for Downs fish, and lowest for Buchan and Banks.

There are a number of possible reasons why the growth rate of Downs fish may be overpredicted. Most likely is that temperature alone is not sufficient to describe the growth rate of larvae, and that the low zooplankton concentrations in the southern North Sea in winter lead to the greatest error in modelled growth rate for Downs larvae. Unfortunately there is no convincing way of including prey concentration in the model for the larval phase since the required data do not exist. Simply scaling the CPR data for larger zooplankton categories is unlikely to provide adequate insight.

The juvenile phase adds relatively little to the average variability in growth between stocks. This is

primarily because the spatial distribution of juveniles is similar for all stocks, being concentrated in four of the ten compartments by the end of the modelled period. However, the between-year variability in growth of juveniles from a given stock is as high as that of larvae. This is partly because modelled growth of juveniles is also dependent on temperature, but also because of year-to-year variations in food concentration.

Large changes in the length-at-date of herring in the regional fisheries of the North Sea were noted in the early 1950s, and these continued to the mid-1970s. For example, the mean length of 3-group herring in the northern North Sea increased from 25.5 cm to 28.5 cm over the period 1950–1975, corresponding to a weight increase from 134 g to 189 g wet weight. Various hypotheses were proposed to explain the phenomenon when the increase was first detected including changes in the pattern of recruitment to the stocks, and an increase in zooplankton abundance which occurred around the same period. However, zooplankton abundance subsequently declined to minimum levels for the century in the early 1970s whilst length-at-age of herring carried on increasing. Maximum length at age and minimum age at maturity occurred around 1975 and thereafter has returned to pre-1960 values. Bailey (1991) assembled size-at-age data on 2- and 3-group fish from 1947–1989 and noted a general inverse correlation with population biomass, concluding that the trends reflected density dependence of growth.

The variations in size at age of herring predicted for the 1970–1981 year classes by our model give a good account of the observed changes in the Shetland stock in particular (23% of observed variance), although less satisfactory for the Banks and Downs fish. During this period the outstanding year class in both the modelled and observed time series for all stocks is 1978, and this coincides with both low temperatures and low zooplankton abundance. Exceptionally warm years (1972, 1973, 1976) also coincide with fast growing year classes in the model and observed time series. The extended time series of l_1 observations from 1924 puts the 1970–1981 series of year classes into a wider context. The data show steadily increasing growth rates between the late 1940s and 1970. Throughout the 1970s, l_1 was variable from year-to-year, but with no underlying

trend. Population biomass declined steadily through the period 1947 to 1970, and was stable at a low level thereafter. The environmentally driven growth model explained short-term variations in l_1 between 1961 and 1970, for example the unusually high and low l_1 of the 1961 and 1962 year classes, respectively, but completely failed to explain the underlying increases in growth rates over the same period. Since the growth model did not include any representation of population biomass, we conclude that at pre-1968 population biomass levels ($> 0.5 \times 10^9$ kg), density dependence does play a role in the growth of herring. Anthony and Fogarty (1985) arrived at a broadly similar conclusion for Gulf of Maine herring, showing that the beneficial effects of high temperatures on the growth were overridden by high population biomass. Our results are slightly different in that the environmental signal is always reflected in short-term year-to-year variations in growth, and the underlying trend is explained by population biomass.

Clearly, the use of spawning population biomass in the context of this study is merely as a surrogate for year-class abundance at some influential early stage in the life history. It is not at all clear how or when in the life cycle density dependence of growth might operate. Our model suggests that most of the variability in growth rate is generated in the larval phase, but field studies of herring larvae suggest that density dependence is only likely to operate, if at all, in the centres of very high abundance close to the spawning areas (Kjørboe et al., 1988). These concentrations are rapidly dispersed to levels where competition between larvae for food seems highly unlikely (Heath and MacLachlan, 1987). Inclusion of density dependence in a model of the larval stage would be an extremely difficult task, requiring the model to be coupled to a validated dynamic model of the categories of zooplankton consumed by the larvae, and also taking into account the population numbers of larvae. Even then, it is not certain that such a model would be capable of operating at spatial resolutions corresponding to the scales at which the density dependent interactions are actually occurring.

Bryant et al. (1995) coupled the juvenile model used in this study to ERSEM such that a model herring population interacted dynamically with the omnivorous and carnivorous zooplankton groups in

the ecosystem model. In an experiment where the herring population biomass was reduced by 30% by imposing a mortality term, the individual weight-specific growth rate increased by approximately 8%. This was taken to be evidence of scope for density dependent growth. However, two factors suggest that this apparently correct result may have been arrived at for the wrong reasons. First, the model was configured to represent the situation in the North Sea during the mid-1980s with a population biomass (including juveniles) of approximately 10^9 kg. This is only marginally higher than the 0.5×10^9 kg spawning biomass indicated by our study as being a 'threshold' below which density dependence is of minor importance. Second, as noted by Broekhuizen et al. (1995) the underlying ecosystem model systematically underpredicted the zooplankton biomass during the winter and spring months of the year so the modelled herring may have been unrealistically food limited during these periods. The results underline the importance of ensuring that the basic ecosystem function is adequately modelled before attempting to address issues of density dependence in higher trophic levels.

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