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Simulation of mackerel (*Scomber scombrus*) recruitment with an Individual-Based Model and comparison with field data

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ABSTRACT

An Individual-Based Model (IBM) for the simulation of year-to-year survival during the early life-history stages of the north east Atlantic stock of mackerel (*Scomber scombrus*) was developed within the EU funded SEAMAR (Shelf-Edge Advection, Mortality and Recruitment) programme. The IBM included transport, growth and survival and was used to track the passive movement of mackerel eggs, larvae and post-larvae and determine their distribution and abundance after approximately two months of drift. One of the main outputs from the IBM, namely distributions and numbers of surviving post-larvae, are compared to field data as recruit (age-0 / age-1 juveniles) distribution and abundance for the years 1998, 1999 and 2000. The juvenile distributions show more inter-annual and spatial variability than the modelled distributions of survivors; this may be due to the restriction of using the same

initial egg distribution for all three years of simulation. The IBM simulations indicate two main recruitment areas for the north east Atlantic stock of mackerel, these being Porcupine Bank and the south eastern Bay of Biscay. These areas correspond to areas of high juvenile catches, although the juveniles generally have a more widespread distribution than the model simulations. The best agreement between modelled data and field data for distribution (juveniles and model survivors) is for the year 1998. The juvenile catches in different representative nursery areas are totalled to give a field abundance index. This index is compared to a model survivor index which is calculated from the total of survivors for the whole spawning season. The model survivor index compares favourably to the field abundance index for 1998 and 1999 but not for 2000; in this year, juvenile catches dropped sharply compared to the previous years but there was no equivalent drop in modelled survivors.

Keywords: Individual-based model; mackerel larvae; mortality; super-individual; juvenile distributions; model survival index; field abundance index

INTRODUCTION

Understanding variability in recruitment of commercially exploited fish populations is an important element in their management (Needle, 2002). Indices of potential recruitment can be used for both short-term and medium-term predictions of changes in stock size. For short-term projections, models such as ICA (Integrated Catch-at-age Analysis; Patterson and Melvin, 1996) can use an in-year survey index to provide a one year forecast. Problems may arise, however, when the time series of historical recruitment shows a long-term trend. In such cases it may be possible to use a surrogate, or environmental correlate in lieu of a measured recruitment index; for example the use of an upwelling index to predict anchovy

(*Engraulis encrasicolus*) recruitment in the Bay of Biscay (Borja *et al.*, 1998). For medium term projections, it is common practice to use some form of stock/recruit relationship such as those described by Beverton and Holt (1957), Ricker (1954) and others (see reviews in Hillborn and Walters (1992) and Quinn II and Deriso (1999)). However, the choice between different stock/recruitment models and parameterisation of these models is often difficult, particularly in cases where the supporting data are weak (Needle, 2002).

The western spawning component of the north east Atlantic (NEA) mackerel (*Scomber scombrus*) is an interesting example of the problems which can be encountered in quantifying recruitment in both short- and medium-term projections. Historically, an index of recruitment was obtained from bottom trawl surveys carried out across the western European shelf from Scotland to Spain. This index was discontinued for short-term predictions in 1995 (Anon., 1995), due to perceived trends in the recruitment index, which were not reflected in the assessment time series. As any short or medium term prediction needs to have some estimate of recruitment, the survey index was replaced by a long term mean value (from 1972) based on recruitment as calculated by the ICA stock model. Obviously, this approach is fairly insensitive to change. It is based on over 20 years of data, and the addition of a new value would not be expected to alter the mean to any great extent.

To make the picture even more complicated, the mackerel fishery is targeted mainly on adult fish (3 years and older). Therefore, it takes at least three years before a year class appears in the commercial fishery, and thus, any estimate of recruitment from the ICA for the most recent years is highly unreliable. For short-term prediction purposes, the management then uses the stock/recruit relationship to provide values in the most recent years. Unfortunately, the stock/recruit relationship in mackerel is not well established. A simple Occam or knife-edge recruitment model is used. Therefore, for all stock levels above the historic lowest value, recruitment is assumed to be constant (the long-term geometric mean). Below that value, it is assumed to follow a straight line to the origin.

As a result, the short-term predictions, and hence the management (TAC, quotas etc.) are substantially independent of the recent pattern of recruitment. Potentially, there could be very weak recruitment for two years, at least, before this showed up in the commercial fishery, and hence had an impact on the stock assessment. Therefore, for management purposes, it would be very useful to have an index of recruitment, either from surveys or the type of model described here, which could be used immediately.

Various modelling studies have shown the important role of circulation for dispersal and potential survival of fish larvae (e.g. Berntsen *et al.*, 1994; Bartsch and Coombs, 1997); but in most studies, only the physical environment was considered, the influence of biotic factors not being incorporated. In the past decade, the development of individual-based models (IBMs), which couple biological and ecological formulations to circulation models, has made it possible to investigate the effects of variability in the physical environment on the dispersal, growth and mortality of marine populations (see Werner *et al.*, 2001). In this respect, IBMs have been successfully used in modelling studies of the early life-history dynamics of various marine fish (e.g. Rice *et al.*, 1993; Hermann *et al.*,1996; Werner *et al.*, 1996).

The present paper sets out to use a dynamic individual-based transport, growth and survival model to track the passive movement of mackerel eggs, and then the larval and early post-larval stages, to determine their distribution and abundance at a length of 50 mm, i.e. after, at most, 60 days. This model output is then compared to the distributions of juvenile mackerel from bottom trawl surveys in the fourth quarter and the following first quarter of each study year.

Details of the model formulation and outputs are provided by Bartsch and Coombs (in press), with derivation of the temperature mediation of the logistic growth curve described in Bartsch (2002). This work has been part of the EU supported SEAMAR (Shelf-Edge Advection, Mortality and Recruitment) programme, with a full description being available in

the final project report (SEAMAR, 2002) and available on the SEAMAR website (www.ieo.es/seamar/seamar.htm).

MATERIALS AND METHODS

Modelling scheme

The SEAMAR model system consists of two components which are run separately, these are the physical circulation and the individual-based bio-physical transport model.

The three dimensional non-linear baroclinic numerical circulation model is based on HAMSOM (HAMBurg Shelf Ocean Model), which was developed at the Institut für Meereskunde, Hamburg (Backhaus, 1985) and transferred to the SEAMAR area. Physical input data for the IBM, such as three-dimensional (3D) current fields, 3D temperature, as well as 2D sea surface elevation (SSE) fields, are provided from the circulation model at a daily rate.

Simulated current, temperature and salinity data from HAMSOM have been validated for the North Sea (Bartsch, 1990; Bartsch, 1993), the Porcupine Bank area (see details in Bartsch and Coombs, in press) and Bay of Biscay (J.B., unpublished data). Discrepancies between simulated and observed currents (from moorings) are usually due to local effects not resolved by the horizontal numerical grid (Bartsch, 1993) but the large scale flow and density field is reproduced well by the model. Hence, the output from HAMSOM can be used with confidence to simulate the transport of the early life-stages of mackerel in the eastern North Atlantic and adjacent shelf for a duration of approximately two months.

The IBM is composed of a number of physical and biological modules, each performing a specific task. The IBM is an i-space configuration model (DeAngelis and Rose, 1992) in which large numbers of individuals are followed as discrete entities. The model area

(Fig. 1) and the horizontal (18 km at the centre of the model area) and vertical (12 layer z-coordinate system) grid resolution of the IBM are the same as the circulation model, which is run with a time-step of one hour. The IBM simulates transport, growth and mortality, details of which are given in Bartsch and Coombs (in press). Briefly, growth is temperature and food dependent and both of these input fields (temperature and food concentration) to the IBM are spatially and temporally inhomogeneous on a daily and weekly basis, respectively. Mortality is dependent on absolute growth rates and length; thus mortality is also dependent on temperature and food concentration.

In the IBM, each particle represents a super-individual comprising 10^6 “virtual” individuals at the outset of the simulation. For each particle/super-individual followed in the model, the number of virtual individuals is decreased daily according to the formulations for growth and mortality (Bartsch and Coombs, in press).

IBM simulations

The initial fields for the spawning distributions for all model simulations were based on egg distribution data from the 1998 ICES mackerel triennial egg survey, which took place from mid-January to the beginning of July (Anon., 1999). Because of the wide spawning area and the extended spawning season, the spatial and temporal coverage of the surveys was inevitably incomplete, to some extent. It was therefore useful to interpolate for missing data using a Generalized Additive Model. A GAM is a statistical method, analogous to regression, but without the assumptions of normality or linearity that relate a response variable, in this case egg abundance, to time and location (see Swartzman *et al.*, 1992 and Borchers *et al.*, 1997 for an outline of the GAM methodology). These data, from week 5 (29 January – 4 February) to week 34 (20 – 26 August), were interpolated spatially and temporally with the GAM to provide weekly input data for the IBM (Beare and Reid, 2002). The same 1998 egg distribution data were used for initialization of all simulations examined (i.e. for 1998, 1999

and 2000), since the 1998 survey is the most comprehensive survey carried out to date and no subsequent extensive egg surveys were conducted until 2001.

The IBM was used to simulate 12 weekly runs for each of the years 1998 – 2000. These 12 weeks (week 11 to week 22; 12 March – 3 June) cover the main part of the mackerel spawning season, in which more than 85% of the eggs are spawned (Anon., 1999). Within each of these simulations, data for all i-states were stored daily for the time of the egg phase (6-9 days, depending on temperature) and then for a subsequent period of 60 days for the larval and early post-larval phases. All particles were released at the relevant mid-week date for each week concerned. The IBM simulations were restricted to 60 days because mackerel post-larvae cannot be considered as being horizontally passive after this time due to their increased locomotory ability; additionally the parameterization of growth, and hence mortality, cannot be supported after this time due to the mathematical properties of the logistic growth curve.

Model output

Model output is primarily as charts of distribution and abundance of survivors at a length of 50 mm. The number of survivors in a particular geographical area is a function of both the number of accumulated particles (super-individuals) and the cumulative mortality experienced by each super-individual i.e. number of surviving virtual individuals for each super-individual, which are summed for comparisons between areas (see Fig. 2).

In order to determine the effect of mortality on the number of virtual individuals and their spatial distribution, the number of virtual individuals represented by each super-individual, at a length of 50 mm, was totalled for all super-individuals within each model grid box (approximately 18 x 18 km at the centre of the model area). In the case of mortality, a cut-off length needs to be specified, since mortality is formulated as being length-specific and not age-specific. Using an age cut-off would give an incorrect indication of survivors, because

longer super-individuals have suffered higher mortality (fewer remaining virtual individuals) over a particular time span, compared to shorter ones which have grown poorly (more remaining virtual individuals). Although using a longer cut-off length would emphasise differences in mortality, a length of 50 mm was chosen as a compromise, so that most super-individuals would reach this length within the 60 day simulation time of larval and post-larval growth. It should be emphasised that the resultant distributions do not represent the situation for a specific calendar date, but relate to a specific length reached (50 mm) after their introduction into the model domain.

Recruit surveys

There are no data on mackerel juveniles in the 50 – 80 mm length range (corresponding to the largest post-larvae in the model simulations) as they are not targeted at this size by any fishery. Hence, the earliest information on the distribution and abundance of recruits is based on results from the ICES autumn bottom trawl surveys (for the most recent report, see Anon., 2003) when the juveniles are around 170 mm in length. However, there is good evidence that in many species year-class size is determined at a pre-recruit stage (e.g. Bannister *et al.*, 1974) and thus the relative abundance of mackerel pre-recruits at 50 – 80 mm length range might be assumed to be similar to the relative abundance of the juveniles at around 170 mm in length. The best representation of recruit distribution and abundance, for comparison with the model output, was considered to be the average catch rate per ICES statistical rectangle from the juvenile trawl survey data for the fourth quarter (September – December) of the year of spawning and the first quarter (January – March) of the following year. Examination of the 4th and 1st quarter data for a number of years showed that the overall catch rates and the general distribution was fairly stable between quarters. Additionally, the findings of Uriarte *et al.*, (2001), from tagging studies of juvenile mackerel, indicated that these fish did not tend to travel away from the nursery areas prior to recruitment to the adult stock after approximately

two years. The most complete coverage of the model area is in the fourth quarter surveys; the main weakness is in relatively patchy sampling in the areas of the Celtic Sea, Western Approaches to the English Channel and west of Ireland. Addition of data from the first quarter surveys in the following year extended coverage into the northern North Sea, which sometimes contains large numbers of young mackerel.

Sub-areas for comparison of model output and field data

The geographical sub-areas (Fig. 2) selected to analyse the relationship between model simulations and observed recruit distributions were based on the location of historical “nursery grounds”, where consistently high concentrations of first winter mackerel have been found:

Iberia – this includes both a western area (off Portugal and north west Spain), where juveniles are relatively abundant, and a northern region (along the north coast of Spain), where catch rates are lower. These regions have been combined because relatively little spawning occurs along the Portuguese coast, and it is assumed that juveniles occurring in this area are spawned further north, most probably from along the north coast of Spain.

Biscay – this refers to the main central deep water area of the Bay of Biscay as well as the adjacent French continental shelf where juveniles are usually more abundant than along the north coast of Spain.

Celtic Sea - including the main continental plateau, shelf-edge and adjacent deep water, which comprise a fairly important nursery area.

Porcupine Bank – including the neighbouring western Irish shelf, which are considered as one unit; in the recruit surveys, juveniles are abundant in shelf areas, particularly off north west Ireland, although recruit survey coverage is rather poor on Porcupine Bank itself.

Hebrides + northern North Sea - during the early and mid 1990s the area west of the Hebrides represented a major nursery area for mackerel recruits, although the occupation was intermittent. During this period, first winter mackerel were also observed intermittently as large catch rates along the shelf break in the northern part of the North Sea. Subsequent examination of the population structure of both the western and North Sea spawning components, indicated that these fish were from the western spawning component (Anon., 1999). For the purposes of the present paper, the two areas were combined.

The central and southern North Sea were not included as significant potential nursery areas for NEA mackerel. Juveniles in those areas are considered to be derived mostly from the less abundant North Sea mackerel spawning component (Anon., 2000).

Survival indices

To take the comparison between survey and model data one step beyond the comparison of distributions, the juvenile catches in the different representative nursery areas (Fig. 2) are summed to give a field abundance index (FAI). This FAI is compared to the model survivor index (MSI) calculated for the same nursery areas by summing the numbers of surviving virtual individuals within these areas. For the MSI, these data are derived from model data for a time period covering approximately 85% of the spawning season. As the numbers obtained for the FAI and the MSI are not directly comparable, the comparison is based on the relative

contribution of the different areas to the FAI or MSI, respectively, i.e. for each year as a percentage contribution of each area to the total FAI or MSI.

RESULTS

Comparison of model distributions with juvenile recruit surveys

From the same initial egg distribution (Fig. 3a), the combined effects of growth and mortality on survival are shown in the plots of remaining numbers of virtual individuals for the model simulations for the years 1998 – 2000 (Fig. 3b,c,d). In all three years, there are two main regions showing high numbers of survivors: a northern area centred over the north eastern Porcupine Bank and extending along the adjacent shelf, and a southern area of more sporadic occurrences around the shelf margin of the Bay of Biscay. Between these two areas, there is a region of low abundance.

The juvenile distributions (Fig. 4a-c) vary more from year to year, with much more local variation, which is due, at least partly, to sampling variability. In the winter of 1998/99, highest juvenile catch rates were off north west Ireland (Fig. 4a). Further substantial catches were made in the northern North Sea, in the south eastern Celtic Sea, off the French coast of the Bay of Biscay and off the central Portuguese coast. The best correspondence with the model results for 1998 (Fig. 3b) was between the high catch rates of juveniles to the north west of Ireland and the high numbers of surviving virtual individuals over Porcupine Bank and northwards. In the south, the model simulations showed highest numbers of survivors along the north coast of Spain compared with field observations of juveniles further north, off the coast of France. Within the duration of the simulations, there were no modelled survivors penetrating as far as the northern North Sea, but an extension of only a few weeks would be required for the strong shelf-edge current in this area to transport elements of the population

from north and west of Scotland into the northern North Sea. Although the locus of high juvenile catch rates off the Portuguese coast was outside the southern model grid boundary, there was no evidence in the model runs of particles being transported to this area.

During the winter of 1999/2000, the areas of high juvenile catch rates (Fig. 4b) were generally similar to those in 1998/1999, but with a noticeable increase in juveniles off the south coast of Ireland and in the Goban Spur area. The modelled results for 1999 again showed comparable concentrations of survivors both on Porcupine Bank and northwards (Fig. 3c), but elsewhere there was a generally poor correspondence with the juvenile distributions. Improvements in fit of the modelled results to the juvenile field observations were noted in the Goban Spur area, where there was a small increase in numbers of modelled survivors, and off the French coast of the Bay of Biscay, where modelled survivors extended further northwards from the north coast of Spain, compared with the simulations for the previous year

In the winter of 2000/2001, juvenile catch rates were lower in nearly all areas (Fig. 4c) compared with the two previous years; this is particularly apparent off north west Ireland, in the Celtic Sea and off Portugal. Relatively high juvenile catch rates were recorded in the south eastern Bay of Biscay, slightly up on the previous year, and there were also high catch rates in the northern North Sea. Because of the marked reduction in numbers of juveniles in most of the western areas, where the bulk of the modelled survivors were distributed (Fig. 3d), the correspondence between the juvenile field observations and simulation output was the poorest for the three years studied. It was only in the more southern areas, including the Bay of Biscay and the Iberian regions, that there was a reasonable agreement between the juvenile distribution and model results.

Survival indices

The comparisons between the MSI and FAI abundance indices (Model Survival Index and Field Abundance Index, respectively) for the five areas (Iberia, Biscay, Celtic Sea, Porcupine Bank/NW Ireland and Hebrides/northern North Sea) for 1998, 1999 and 2000 are shown in Fig. 5a-c. For the model output, the majority of survivors are consistently in the Porcupine Bank/NW Ireland area (around 60% of the total). Over all the years, the Hebrides area provides around 12%, Iberia 12% and Biscay 9% of all survivors. The smallest contribution is from the Celtic Sea which, averaged for the three years, totals < 6%, but with most contribution in the year 2000. For the juvenile survey results, over all years, the main contributions are from the Porcupine Bank (around 45% of the total) and the Hebrides and northern North Sea (35%) areas. Input from the Iberian, Biscay and Celtic Sea areas varies between 5% and 8%, on average, over the three years.

For 1998/1999 (Fig. 5a), the majority of survivors, both in the model (64%) and in the juvenile surveys (82%), were in the Porcupine Bank area. There were also similar proportions for the model output and field surveys, respectively, in the Hebrides (14% and 11%) and Celtic Sea (3% and 2%) areas. Greater differences are seen for the Biscay and Iberian regions, although in both areas the relative contribution to overall survival was low.

For 1999/2000 (Fig. 5b), although the proportion of juveniles in the Porcupine Bank area was lower (44%) than in 1998, this was still comparable to the modelled proportion (58%) for that area. Conversely, relatively more juveniles were recorded in the Hebrides/NNS area (41%) than in 1998, but this was not reflected in the proportion of modelled survivors (11%). For the three areas of lower abundance (Biscay, Iberia and the Celtic Sea), the most noticeable change, compared with 1998, was the increased proportion of juveniles in the Celtic Sea area, whereas for these areas in the model, there was relatively little difference from the preceding year.

The pattern of juvenile survival in 2000/2001 (Fig. 5c) was significantly different from the previous two years because of the substantial drop in juvenile catch rates in the Porcupine

Bank/NW Ireland area (8%). This resulted in relatively higher proportions being recorded for the Hebrides/northern North Sea area (52%), as well as in the Iberian and Biscay areas. The relative distribution of the modelled output was similar to the previous years, hence resulting in a marked dissimilarity in the Porcupine Bank/NW Ireland and Hebrides/northern North Sea areas, in particular.

Combining the MSI and FAI indices for all areas, allows a comparison of annually simulated model survival and observed juvenile abundance (Fig. 6). The model results show a progressive increase in survival, with 1999 showing a 28% increase over 1998 and a further 5% increase in 2000. While the juvenile field data also show an increase in numbers of 6% between 1998/99 and 1999/00, this is followed by a large decrease of 92% in 2000/01. Thus, in terms of overall relative recruitment between years, the major difference between modelled simulations and juvenile survey results was for 2000, with the other two years being more closely comparable.

DISCUSSION

Regional distribution of model survivors

In the model, the effects of particle drift, growth and mortality resulted in the fairly continuous initial egg distribution developing into just two main areas of survivors. These were a northern region in the Porcupine Bank, Hebrides and adjacent shelf and shelf-edge areas, and southern region around the Biscay margin. The low number of survivors in the intervening area, across the Celtic shelf and shelf-edge, is due to relatively low growth rates, and hence high mortalities (Bartsch and Coombs, in press), in this area.

The calculation of model survivor indices (MSI) by area (Fig. 5a-c) demonstrated the dominant contribution of the Porcupine Bank area (around 60% of all survivors). The other

four areas (Hebrides/northern North Sea, Celtic Sea, Biscay and Iberia) all had similar contributions of <15% but with the Celtic Sea area providing the smallest input (~ 2% in two of the three modelled years, 1998 and 1999).

Comparison of model output against recruit data

Strictly speaking, there is no corresponding model output dataset to compare with the juvenile distributions derived from the autumn/winter surveys. Model runs are only carried out for a period of 60 days of simulated larval and post-larval transport. This is because, after this time, the hypothesis of particle passivity becomes increasingly less justifiable and the parameterisation of growth cannot be considered as remaining valid. Given a peak spawning in mid May, the model would then be expected to provide distributions at the end of the passive transport phase in mid July. The first of the bottom trawl surveys takes place in October, representing a lag of three months from the end of the model runs when most of the post-larvae have reached a size of between 50 and 80 mm, whereas at the time of the autumn juvenile surveys they are around 170 mm in length. Furthermore, the model was designed to deal with passive transport only, while juvenile mackerel between 50 and 170 mm in length may be expected to be capable of some directed movements. Nevertheless, model distributions and abundance of post-larvae having reached a size of 50 mm, are considered to be the closest representation possible, using the existing model, of age-0 mackerel distribution and abundance.

In general terms, there were some similarities between the model output and the juvenile survey data. High catches of juveniles were made mostly off north west Ireland, where the model consistently indicates high numbers, although centred rather more to the south, over Porcupine Bank. Both model and juvenile data indicated low numbers in the Celtic Sea, except for juveniles in the winter of 1999/2000, despite locally high levels of

spawning. In Biscay, most juvenile catches were made on the French shelf, which agrees, to some extent, with model simulations for 1999 and 2000.

The juvenile nursery areas tend to be more inshore than the modelled distributions and without any striking similarity between the two sets of distributions. This implies that, following the end of the passive transport phase, the young fish actively migrate to the nursery areas. For example, in the area to the north west of Ireland, at the end of the passive transport phase, these individuals might migrate the short distance to this area from Porcupine Bank and its surrounding region. In other areas, there were significant numbers of survivors close to identified nursery grounds, for example, in the inner corner of the Bay of Biscay. Conversely, there are some juvenile nursery areas, such as off the Portuguese coast and in the northern North Sea, where there are few modelled survivors, mostly due to reduced transport to these regions within the 60 day (post-hatch) simulations. At least for the northern North Sea, subsequent potential migration of juveniles from west of the Hebrides would be assisted by the Northeast Atlantic slope current (Huthnance, 1986). There is little spawning off Portugal, hence the concentration of juveniles in that area is assumed to be derived from migration of survivors originating along the north coast of Spain. It is also possible that survivors from the north coast of Spain area may migrate to the south eastern Biscay area. Similarly, some of the survivors extending southwards from Porcupine Bank might migrate to areas of the Celtic Sea where they were recorded in the juvenile surveys, particularly in the 1999/2000 season.

Year to year differences

In general, there was more year to year variability in the juvenile survey results than in the model output. The most noticeable differences in the juvenile plots are the reduced numbers to the north west of Ireland and off Portugal in 2000, neither of which is reflected in

corresponding changes in the model output. Similarly, although a concentration of juveniles was recorded in 1999 to the south of Ireland and in the Goban Spur area, there was no increased survivorship noted in the model output in that area for the same year. The relatively small year to year changes in the model output is, at least, partly due to using the same 1998 egg distribution for the start of the simulations in all three years (1998 – 2000). This was necessary because extensive egg surveys are only carried out every three years. If any differences in the timing and distribution of spawning were used in the IBM, these would lead to more variability in model output.

It should also be recognised that the juvenile survey data have much weaker coverage in both time and space than available from the egg surveys. Furthermore, they are derived from bottom trawl surveys, which are not particularly appropriate for schooling pelagic species, with a few very large catches and many small or zero catches. These limitations will tend to over-emphasise the variability of the juvenile distributions.

Comparison of modelled and fisheries-predicted stock recruitment

Over the three years studied, the model results indicated that survival increased by 28% from 1998 to 1999 and by a further 5% from 1999 to 2000. The juvenile survey catches also increased by 56% from 1998 to 1999, but then fell by 92% in 2000. Thus, the model indicates a slightly improved recruitment in 2000, while the juvenile surveys show the worst fall in recent years. One possibility, is that the 2000/2001 juvenile surveys were un-representative. However, the observed decline is general throughout all areas, although more marked off north west Ireland and off Portugal; additionally, the survey was carried out by several vessels and extended over several months, making it unlikely that the drop in catches is the result of procedural failures. Furthermore, the most recent assessment by the ICES assessment working group (Dave Reid, pers. comm.), based on tentative analysis as this year-class starts to show

up in the fishery, is that 2000 did produce weak recruitment, although the scale of the reduction is not yet clear.

There is also a qualification of the model survival estimates due to using the same 1998 initial egg distribution data for all three years of simulation. Over the more recent series of triennial mackerel egg surveys, there has been a declining trend in annual egg production (1.94, 1.49, 1.37 and 1.21×10^{15} eggs in 1992, 1995, 1998 and 2001, respectively). Assuming that egg production in 1999 and 2000 conformed to this trend, and discounting the effects of other variables, this would tend to lower the model survival estimates for 1999, and more so for 2000.

The timing and distribution of spawning will also affect model output. The 1998 egg initialisation data used for the model runs, while being the most complete set of egg survey results, also indicated spawning unusually early in the season for that year. Historically, peak egg production is from mid-April to the end of May. In this respect, 1995 was fairly typical with peak production in the middle of May. However, in 1998, peak egg production was much earlier, at the beginning of April. The time of peak spawning in 2001 was again similar to that found in 1995. Thus, due to the early peak of egg production, 1998 was an unusual year. In terms of distribution, in 1998 spawning was more concentrated in the Porcupine Bank area than in 1995. The 2001 spawning distribution was broadly similar to 1998; the main difference was a southward shift of peak production away from the Porcupine area towards Goban Spur. Any possible changes in spawning distribution in the modelled years of 1999 and 2000 are unknown, but preliminary findings on varying the input egg distribution (J. B., unpublished data) show that modelled survival can be greatly overestimated if the initial egg distribution does not correspond to the year of simulation.

The timing of peak spawning is also crucial for the simulation, as the wind field (and thus currents), as well as temperature and food distribution, are markedly different 4 – 6 weeks later. In respect to the above mentioned egg distribution and production data used for

the simulations, it is worth noting that the best agreement between modelled data and field data for both distribution (juveniles and virtual individuals) and indices (FAI and MSI) is for the year 1998.

There are also a number of other factors which may affect recruitment, which were not included in the simulations. Most importantly, is a consideration of survival from the end of the model scope (60 days) to the time of the juvenile surveys (120 – 240 days from spawning). Other potentially important factors are, for example, predation, including cannibalism, and the effect of turbulence (Borja *et al.*, 2002) on feeding.

Potential for use of the model for stock assessment

An understanding of the pattern of recruitment is important for both short and medium term predictions for management purposes. If it was possible to use the model described here to simulate recruitment success based on external factors, this would be a useful tool for management. However, there are several known limitations, such as the difficulty in incorporating the year-to-year variability of the initial egg distributions, as well as the acknowledged simplicity of the model parameterisations and extent of controlling processes and life-stages considered. At its present level of implementation, the IBM developed here, is more realistically a heuristic tool for research purposes. In order to use the model as a management tool, an essential requirement is the provision of the actual initial egg distribution for each year to be modelled.

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REFERENCES

- Anon. (1995) Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy. *ICES CM 1995/Assess:2*.
- Anon. (1999) Report of the working group on mackerel and horse mackerel egg surveys. *ICES CM 1999/G:5*.
- Anon. (2000) Report of the working group on the assessment of mackerel, horse mackerel, sardine and anchovy. *ICES CM 2000/ACFM:5*.
- Anon. (2003) Report of the international bottom trawl survey working group. *ICES CM 2003/D:5*.

Backhaus, J.O. (1985) A three-dimensional model for the simulation of shelf sea dynamics.

Dt. hydrogr. Z. **38**:165-187.

Bannister, R.C.A., Harding, D. and Lockwood, S.J. (1974) Larval mortality and subsequent year-class strength of the plaice (*Pleuronectes platessa* L.). In: *The early life history of fish. Proceedings of an international symposium at Dunstaffnage, May 17-23, 1973*. J.H.S.

Blaxter (ed). Berlin: Springer Verlag, pp. 21-37.

Bartsch, J. (1990) Zur Simulation der Verdriftung von Heringslarven in der Nordsee. (On the simulation of herring larvae drift in the North Sea). *PhD thesis, Universität Hamburg,*

Mitteilungen des Zentrums für Meeres- und Klimaforschung **1**:150 pp.

Bartsch, J. (1993) Simulating the transport of herring larvae in the North Sea. *Cont. Shelf Res.*

11:1335-1361.

Bartsch, J. and Coombs, S.H. (1997) A numerical model of the dispersion of blue whiting larvae, *Micromesistius poutassou* (Risso), in the eastern North Atlantic. *Fish. Oceanogr.*

6(3):141–154.

Bartsch, J. (2002) Modelling the temperature mediation of growth in larval fish. *Fish.*

Oceanogr. **11**:310-314.

Bartsch, J. and Coombs, S.H. (In press) An individual-based model of the early life-history of mackerel (*Scomber scombrus*) in the eastern North Atlantic, simulating transport, growth

and mortality. *Fish. Oceanogr.*

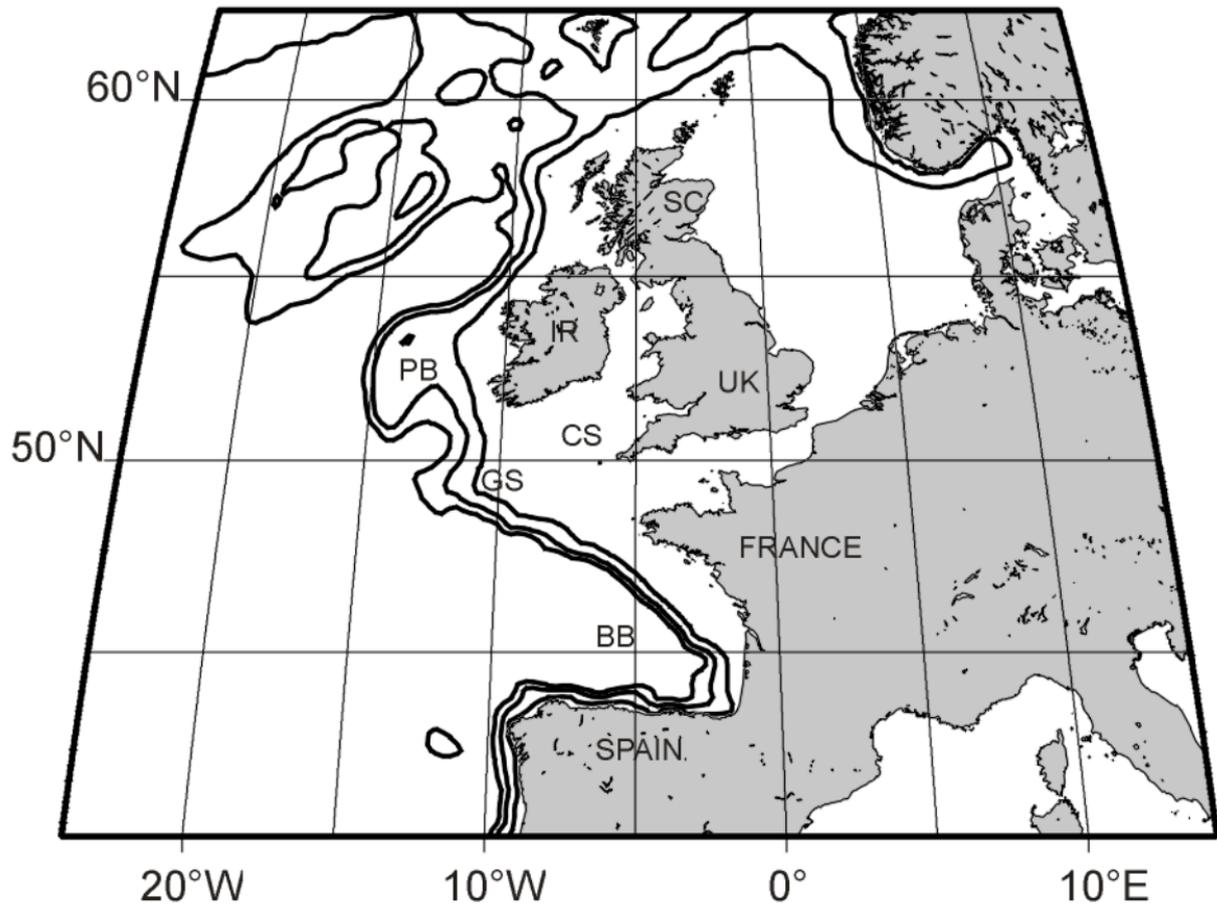
- Beare, D.J. and Reid, D.G. (2002) Investigating spatio-temporal change in spawning activity by Atlantic mackerel between 1977 and 1998 using Generalized Additive Models. *ICES J. mar. Sci.* **59**:711-724.
- Berntsen, J., Skagen, D.W. and Svendsen, E. (1994) Modelling the transport of particles in the North Sea with reference to sandeel larvae. *Fish. Oceanogr.* **3(2)**:81-91.
- Beverton, R.J.A. and Holt, S.J. (1957) On the dynamics of exploited fish populations. *MAFF. Fish. Invest., Ser:II* **19**:533 pp.
- Borchers, D.L., Buckland, S.T., Priede, I.G. and Ahmadi, S. (1997). Improving the precision of the daily egg production method using generalized additive models. *Can. J. Fish. Aquat. Sci.* **54**:2727–2742.
- Borja, A., Uriarte, A., Egaña, J., Motos, L. and Valencia, V. (1998) Relationship between anchovy (*Engraulis encrasicolus*) recruitment and environment in the Bay of Biscay. *Fish. Oceanogr.* **7**:373-380.
- Borja, A., Uriarte, A. and Egaña, J. (2002) Environmental factors and recruitment of mackerel, *Scomber scombrus* L. 1758, along the north east Atlantic coasts of Europe. *Fish. Oceanogr.* **11**:116-127.
- De Angelis, D.L. and Rose, K.A. (1992) Which individual-based approach is most appropriate for a given problem? In: *Individual-based models and approaches in ecology*:

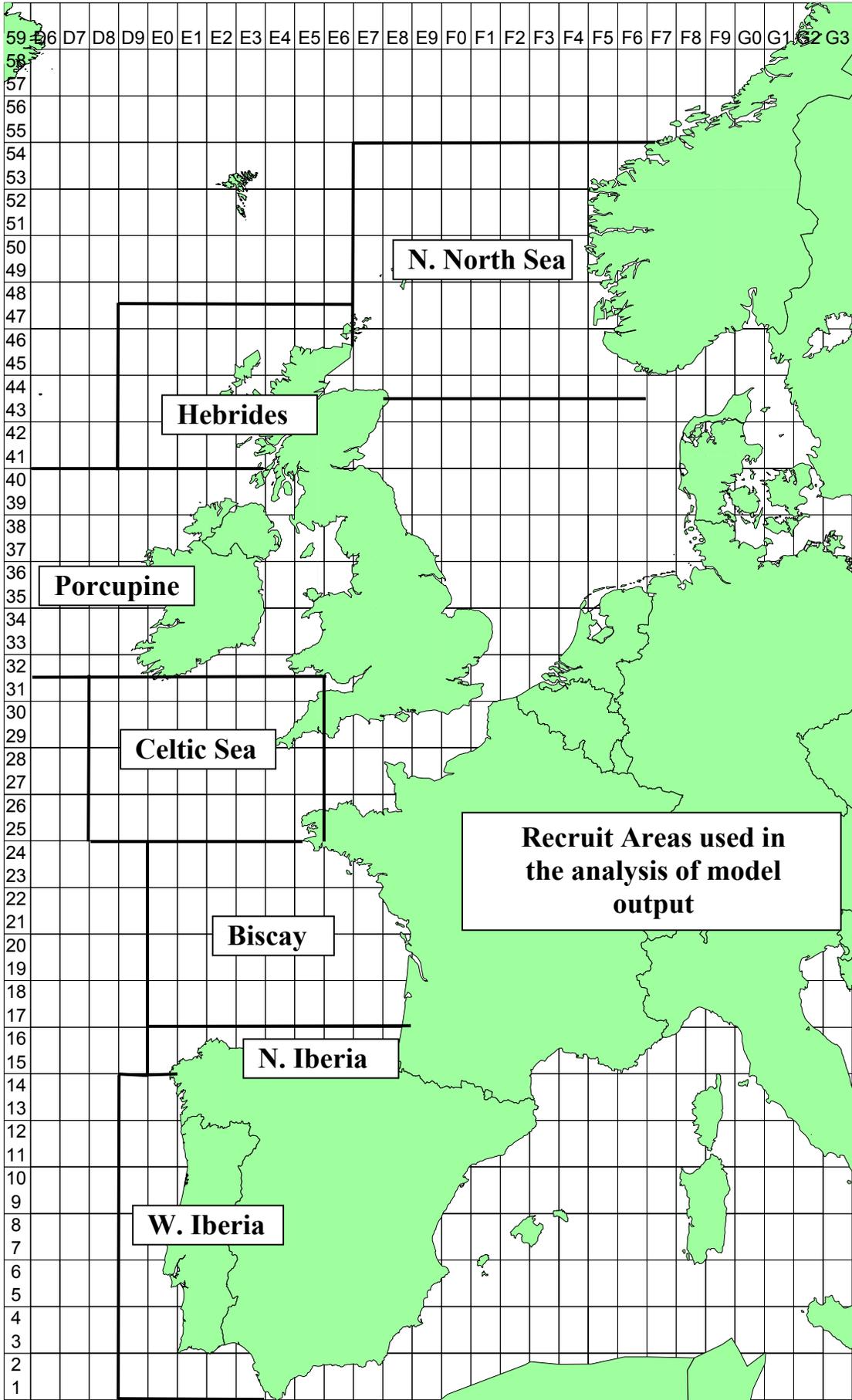
- populations, communities and ecosystems*. D.L. DeAngelis and L.J. Gross (eds). New York: Chapman and Hall, pp. 66-87.
- Hermann, A.J., Hinckley, S., Megrey, B.A. and Stabeno, P.J. (1996) Interannual variability of the early life history of walleye pollock near Shelikof Strait as inferred from a spatially explicit, individual-based model. *Fish. Oceanogr.* **5 (1)**:39-57.
- Hillborn, R. and Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment: Choice, dynamics and uncertainty*. New York: Chapman and Hall, 570 pp.
- Huthnance, J. M. (1986) The Rockall slope current and shelf-edge processes. *Proc. of the Royal Soc. of Edinburgh* **88B**:83-101.
- Needle, C.L. (2002) Recruitment models: diagnosis and prognosis. *Rev. Fish Biol. Fisher.* **11(2)**:95-111.
- Patterson K.R. and Melvin, G.D. (1996) Integrated Catch-at-age Analysis Version 1.2. *Scot. Fish. Res. Rep.* **58**:60 pp.
- Quinn, T.J. II and Deriso, R.B. (1999) *Quantitative Fish Dynamics*. Oxford: Oxford University Press, 542 pp.
- Rice, J.A., Miller, T.J., Rose, K.A., Crowder, L.B., Marschall, E.A., Trebitz, A.S. and DeAngelis, D.L. (1993) Growth rate variation and larval survival: Inferences from an individual-based size-dependent predation model. *Can. J. Fish. Aquat. Sci.* **50**:133–142.

- Ricker, W.E. (1954) Stock and recruitment. *J. Fish. Res. Bd. Can.* **11**:559-623.
- SEAMAR (2002) Shelf-Edge Advection, Mortality And Recruitment. Contract No. CT98-3695, Final Report, May 2002. EU, Brussels.
- Swartzman, G., Huang, C. and Kaluzny, S. (1992). Spatial analysis of Bering Sea groundfish survey data using generalized additive models. *Can. J. Fish. Aquat. Sci.* **49**:1366–1378.
- Uriarte, A., Alvarez, P. Iversen, S., Molloy, J., Villamor, B., Manuel, M. and Myklevoll, S. (2001) Spatial pattern of migration and recruitment of North East Atlantic mackerel. *ICES CM 2001/O:17*.
- Werner, F.E., Perry, R.I., Lough, R.G. and Naimie, C.E. (1996) Trophodynamic and advective influences on Georges Bank larval cod and haddock. *Deep Sea Res. II* **43**:1793–1822.
- Werner, F.E., Quinlan, J.A., Lough, G. and Lynch, D.R. (2001) Spatially-explicit individual based modeling of marine populations: a review of the advances in the 1990s. *Sarsia* **86**:411-421.

FIGURE LEGENDS

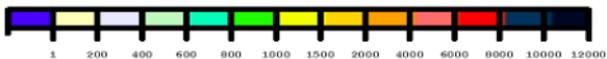
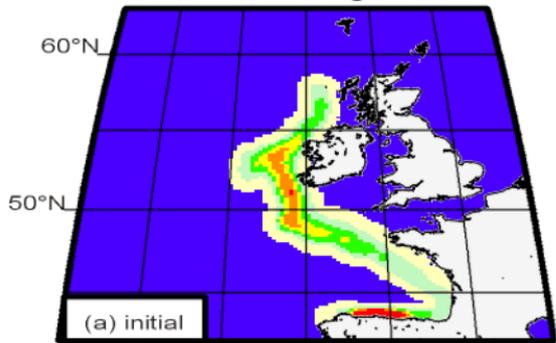
- Figure 1.** Model area and bathymetry. The 200 m, 1000 m and 2000 m depth contours are shown. SC – Scotland, IR – Ireland, UK – United Kingdom mainland, PB – Porcupine Bank, GS – Goban Spur, CS – Celtic Sea and BB – Bay of Biscay.
- Figure 2.** Areas used for comparison of observed recruit abundance and model simulated survival.
- Figure 3.** (a) Initial particle (egg) distribution for 12 March – 3 June, as used in all model runs; (b) regional distribution of the total remaining virtual individuals within each model grid box at a length of 50 mm for 1998, (c) for 1999 and (d) for 2000.
- Figure 4.** (a) Combined quarter 4 and quarter 1 ICES survey data (as mean catch rate per hour) for age-0 mackerel during 1998/1999, (b) 1999/2000 and (c) 2000/2001.
- Figure 5.** (a) Comparison of observed recruit abundance (FAI index, see text) and model simulated survival (MSI index, see text) for the modelled years of 1998, (b) 1999 and (c) 2000. Values are plotted as the percentage contribution by area (see Fig. 2) to each index for each year.
- Figure 6.** Model simulated survival (MSI index, see text) and observed recruit abundance (FAI index, see text) for the modelled years of 1998, 1999 and 2000.



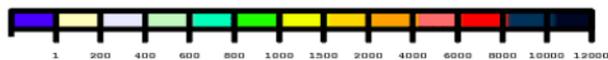
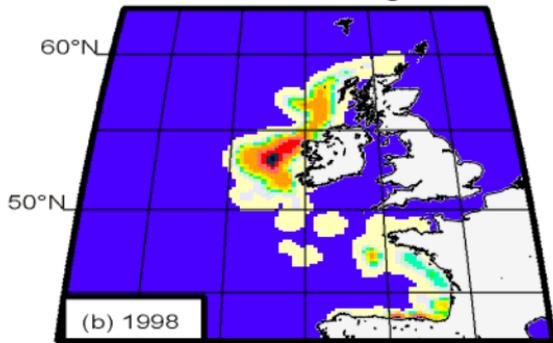




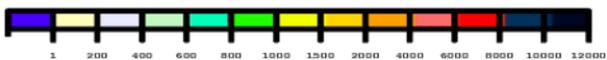
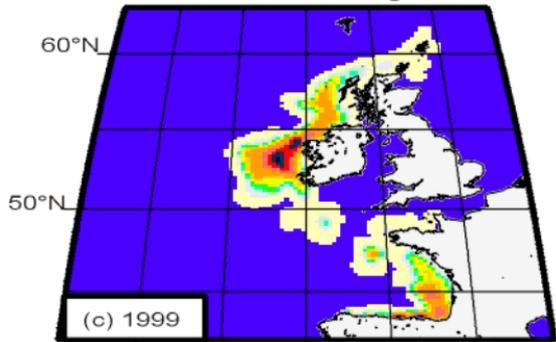
Particle nos. / grid box



Virtual individuals / grid box



Virtual individuals / grid box



Virtual individuals / grid box

