The influence of spatio-temporal egg production variability on the modelled survival of the early life history stages of mackerel (*Scomber scombrus*) in the eastern North Atlantic

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An individual-based model (IBM) that simulates the transport, growth, and mortality of mackerel (*Scomber scombrus*) eggs and larvae, is used to determine the modelled survival of mackerel post-larvae in the eastern North Atlantic. Larval and post-larval growth is modelled as a function of length, temperature, and food distribution; mortality is modelled as a function of length and absolute growth rate. Simulations have previously been carried out for the years 1998, 1999, and 2000, in all cases using the same 1998 initial egg distribution as the input field. In the present contribution, the effects of varying the input field are examined by comparing simulations for 1998 and 2001 using initial egg distributions for 1998 and 2001, respectively, and also for a 2001 simulation using the 1998 egg data as input. Results showed that, for the first two cases, the estimated number of survivors for the years 1998 and 2001 was similar, although total egg production (i.e. the magnitude of the input field) in 2001 was only ~65% of that during 1998. The higher relative survival rate in 2001 results from differences in the timing of peak production, which was 5 weeks later in 2001 than in 1998, and also from greater overall food availability in 2001. Modelling survival for 2001 using 1998 egg data as the initial input field “wrongly” increases survival by 60% compared with using actual 2001 egg data for initialization. This is mainly a function of the increased egg production in 1998 compared with 2001.

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Keywords: growth, individual-based model, mackerel larvae, mortality, survival indices.

Received 7 October 2004; accepted 3 April 2005.

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Introduction

Natural environmental variability strongly influences fish recruitment (e.g. Cowan and Shaw, 2002), with evidence that its influence is most pronounced during early life history (e.g. Pepin, 1991). It is during this early period that there can be marked changes in mortality, for example, as a consequence of variations in available food, predation pressure, or transport to unfavourable areas (Cushing, 1974; Parrish et al., 1981; Bailey and Houde, 1989). Understanding these processes by “traditional” observational field ecology and correlation techniques is problematic, first because of the range of spatial scales to be included, and second because they do not directly address the underlying mechanisms. More recently, individual-based modelling techniques have allowed examination of complex relationships for a large range of scenarios.

Various modelling studies have shown the important role of water mass circulation for survival of fish larvae, but in most studies, only the physical environment was considered, the influence of biotic factors such as growth not being incorporated (Bartsch and Coombs, 1997; Hannah et al., 2000). There have been a number of approaches relating the dynamics of growth and mortality in marine fish to environmental variables (for example, in terms of food availability, Bailey et al., 1995, or temperature, Pepin, 1991), but only a few have incorporated biological attributes such as prey distributions in individual-based models (IBMs; e.g. Werner et al., 1996; Hermann et al., 2001). The development of sophisticated circulation models has allowed spatially explicit IBMs to become a useful tool in the study of dispersal, growth, and mortality of marine
populations (Werner et al., 2001b). Consequently, IBMs have been successfully used in modelling studies of the early life history of various marine fish species in recent years (Rice et al., 1993; Werner et al., 1996, 2001a), and they have an acknowledged potential for advancing our understanding of the recruitment process (Crowder et al., 1992; DeAngelis and Gross, 1992; Werner et al., 2001b).

Mackerel (Scober scombrus) spawn along the European shelf-edge from the Iberian Peninsula to the west of Scotland. Spawning starts in January/February in the south, and moves progressively north following the seasonal warming, ending around July to the west of Scotland (Lockwood et al., 1981). Eggs take about 1 week to hatch into larvae about 3 mm long. The duration of the larval and early post-larval stages extends to 50–100 d, at which time the post-larvae may be up to 80 mm. Eggs, larvae, and early post-larvae essentially drift passively, but they become increasingly mobile as they increase in size.

During the EU-funded SEAMAR (Shelf-Edge Advection, Mortality And Recruitment) programme, an IBM was developed for the simulation of year-to-year survival of the early life history stages of mackerel in the eastern North Atlantic. The ultimate aim was to estimate in a hindcast scheme was formulated on the basis that larval and post-larval growth is dependent on water temperature and food availability, and that mortality is inversely related to larval growth rate, i.e. faster growing individuals survive better (e.g. Anderson, 1988). Therefore, the two main determinants of survival are temperature and food availability. For modelling purposes, these two parameters are required over the entire model area at the model spatial and temporal grid resolution.

In a previous study, a comparison of model output with field data (model survivor index, MSI, versus field abundance index, FAI) showed that the MSI compared favourably with the FAI for 1998 and 1999, but not for 2000 (Bartsch et al., 2004). In 2000, juvenile catches dropped sharply compared with the previous years, but there was no equivalent drop in modelled survivors. One conclusion from this study was that the breakdown in correspondence between model output and field data for 2000 could have resulted from use of the same initial egg distribution for all years simulated, i.e. the observed egg distribution from 1998. This paper sets out to elucidate this issue, i.e. to determine the influence of spatio-temporal egg production variability on the modelled survival of mackerel larvae and post-larvae.

Material and methods
Modelling scheme
The model system used in this investigation consists of two components which are run separately. These are a physical circulation model and an individual-based bio-physical transport model (IBM).

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 area of investigation. The horizontal grid resolution is 10’ of latitude (18.5 km), and 15’ of longitude (15.9 km at 55°N). Physical input data for the IBM, such as three-dimensional (3D) current fields, 3D temperature fields, and 2D sea surface elevation (SSE) fields, are provided by the circulation model at a daily time-step.

The model area (Figure 1) and the horizontal and vertical (12-layer z-coordinate system) grid resolution of the IBM are the same as that of the circulation model. The IBM is run with a time-step of 1 h and simulates transport (advection and diffusion), growth, and mortality. Briefly, growth is temperature- and food-dependent, and both of these input fields (temperature and food concentration) to the IBM are spatially and temporally homogeneous on a daily and weekly basis, respectively. Mortality is dependent on absolute growth rates and length, so mortality is implicitly dependent on temperature and food concentration.

Individual-based model
The IBM is composed of a number of physical and biological modules to simulate transport, growth, and mortality. It is an i-space configuration model (DeAngelis and Rose, 1992), in which large numbers of individuals are described as discrete entities. Details of the model formulation, the various modules and their outputs are provided by Bartsch and Coombs (2004), with the derivation of the temperature mediation of the logistic growth curve described in Bartsch (2002). Here, only the more important modules for development, growth, and mortality are described briefly.

Egg development and mortality module
The egg development module calculates the time needed for eggs to develop from spawning to hatching. The equation used is

\[ E = \frac{H}{T} \]  

where \( E \) is the egg development time in days, \( H \) is 80 degree-days, and \( T \) is the temperature in °C. This is a close approximation to the formula given by Lockwood et al. (1981) based on incubation experiments, but it is more amenable to manipulation in conjunction with the temperature module than the original formulation. The temperatures used are the daily averages calculated in the temperature module for each individual particle.
Egg mortalities are set at 10% per day, based on the experimental results of Lockwood et al. (1977) and Danielssen and Iversen (1977), as well on field observations in the eastern North Atlantic (Thompson, 1989; SEFOS, 1997). As the duration of egg development is related to the ambient temperatures encountered, this results in slight seasonal and regional differences in cumulative egg mortality.

Egg vertical distribution module
The number of particles per model grid box is derived from the initial temporal and weekly spatial egg distributions. These particles are then distributed vertically, based on field sampling results given in Coombs et al. (2001). Essentially, the eggs are fairly evenly distributed through the top 200 m of the water column early in the season when there is no thermal stratification, then progressively restricted to the upper 25 m with development of the seasonal thermocline. An exponentially declining function is fitted to the observed egg distributions, the rate of decline in egg abundance with depth being related to surface temperature (Coombs et al., 2001).

Larval vertical distribution and migration module
There is generally less information available on the vertical distribution of larvae than on eggs, especially on post-larvae, which are difficult to sample by any reliable quantitative method, as a result of their greater sensory awareness and locomotory ability. Investigations have concluded that with increasing size, Atlantic mackerel larvae appear to have a more distinct vertical distribution, and suggest that, in common with other fish larvae, they carry out diel vertical migration (Neilson and Perry, 1990; Hillgruber et al., 1997). This has been evident in studies in the North Sea (Grave, 1981), Northwest Atlantic (Ware and Lambert, 1985), and over the Porcupine Seabight area and the Celtic Sea (Coombs et al., 1981; Hillgruber et al., 1997).

Hillgruber et al. (1997), during a 5-d drift study in the Celtic Sea, found larvae throughout the sampled depth (100 m), the smallest ones (<3.5 mm) in the 20—40-m depth stratum. Variability in both depth distribution and aggregation decreased with development; larvae >6 mm were found above and below the thermocline. Coombs et al. (2001), in a summary of mackerel egg and larval...
sampling studies between 1974 and 1995, found no significant changes in the larval distribution between months or size classes; larvae (>11.9 mm) were fairly evenly distributed in the mixed layer above the seasonal thermocline, and predominantly in the upper 50 m.

As part of the SEAMAR programme, sampling at various depth layers was carried out on five cruises, directed particularly at the post-larval stages (SEAMAR, 2002). Most of the data used in the larval vertical distribution module are based on the Celtic Sea drift study of Hillgruber et al. (1997). For lengths >15 mm, the data are based on the results of the SEAMAR cruises of RV “Challenger” in 1999, RV “Heincke” in 1999, and RV “Cornide” 2000a (SEAMAR, 2002).

Based on these observations, the vertical distribution of larvae and post-larvae for each length class, and day and night separately, was derived (Figure 2). This simplified scheme was adopted and applied universally. The switch from day to night-time distributions was based on sunrise and sunset times calculated daily for the centre of the model area.

Food distribution module

The food concentrations used in the IBM were modelled from egg production rates of representative large (Calanus) and small (Acartia) copepods. These constitute 39–58% of the diet of larval and post-larval mackerel (Hillgruber et al., 1997; Conway et al., 1999; Hillgruber and Kloppmann, 2001; SEAMAR, 2002). Based on the formulations given in Prestidge et al. (1995), the egg production rates were calculated from the input variables of satellite-derived sea surface temperature and chlorophyll a concentration, providing monthly fields interpolated to weekly averages for each year.

Egg production per female was converted to total egg production for the entire population, by multiplying the egg production with the number of females present (numbers per l) in each model grid box. The number of females was derived from Continuous Plankton Recorder (CPR) long-term (1948–1999) monthly mean abundance data for Calanus (e.g. see Figure 7 of Colebrook, 1982) by interpolating standard CPR rectangles of 1° latitude × 2° longitude onto the SEAMAR model grid (Figure 1). Allowances were incorporated to account for the CPR sample size of 3 m³, and for the proportion of the CPR category “Calanus stages V and VI”, which are mature females (25%). These allowances were based on more detailed analysis of net-plankton samples taken throughout the model area. Missing data were interpolated from adjacent sampled rectangles, and by reference to results from routine plankton sampling stations along the north coast of Spain and off Plymouth.

The conversion of production to biomass uses an empirical relationship given in Table 2 of Lynch et al. (2001), in which the total standing stock biomass of all Calanus eggs, nauplii, and copepodite stages at quasi-steady-state is used, together with an egg production rate of 52.08 eggs female⁻¹ d⁻¹ at 5°C. For the SEAMAR model area at a mean temperature of 15°C, the standing stock biomass in carbon units is 8.05-μg carbon per unit egg production, using a Q₁₀ of 3 (Huntley and Lopez, 1992; Kiørboe and Sabatini, 1995) for temperature-adjusted development time, and a carbon content of 40% (Lindley et al., 1997).

Total available food biomass for mackerel larvae was estimated by raising the biomass estimates of Calanus, using the observed proportion (12.5%) represented by Calanus in the gut contents of mackerel larvae and post-larvae (Conway et al., 1999).

In the absence of sufficient detailed information on the spatial and seasonal changes in the vertical distribution of food particles, the food concentration data are specified as being vertically homogeneous within the entire depth range of the larvae and post-larvae (the upper 60 m of the water column). The data were computed as weekly fields for the modelled area for weeks 3–37 (mid-January–mid-September) for each of 1998 and 2001.
Growth module

The growth rates of larvae and post-larvae are calculated daily as a function of temperature, length, and ambient food concentration. A first analysis of growth from field data sampled on cruises during 1999 showed that a logistic curve was an appropriate approximation of mackerel larval and early post-larval growth (SEAMAR, 2002), using a variable exponential parameter $r$ (Bartsch and Coombs, 2004):

$$L = L_\infty (1 + \exp(-rt + c))^{-1}$$  \hspace{1cm} (2)

where $L$ is the length (mm) at time $t$, $L_\infty$ a constant representing the maximum length attainable in the initial larval and early post-larval growth stanza (set at 80 mm), $r$ the function of temperature and food concentration (see below), $c$ the constant of integration, and $L$ is 3 mm at time $t = 0$, i.e. at hatching.

The absolute growth rate is a function of length and the exponential parameter $r$:

$$\frac{dL}{dt} = G = rL(1 - (L/L_\infty))$$  \hspace{1cm} (3)

Temperature and food mediation of parameter $r$ is carried out as follows:

$$r = (r_{opt} - d(T_{opt} - T)^2)F_i$$  \hspace{1cm} (4)

where $r_{opt}$ is the maximum specific growth rate ($r_{opt} = 0.125$), $d$ is a constant (0.00085), $T_{opt}$ is the optimum temperature for growth ($19^\circ C$), $T$ is the ambient temperature, and $F_i$ is a model food index (Bartsch and Coombs, 2004).

Mortality module

A major problem in individual-based models is that large numbers of individuals are needed at the start of the simulation. The standard solution can lead to loss of variation, irregular dynamics, and large sensitivity to the seed value of the random number generator (Scheffer et al., 1995). The concept developed within SEAMAR to solve this problem is similar to the super-individual concept introduced by Scheffer et al. (1995).

In the IBM, each particle represents a super-individual, comprising $10^6$ “virtual” individuals at the outset of the simulation. The daily mortality rates of the super-individuals are calculated as a function of length and absolute growth rates. This determines the daily decrease in the numbers represented by each super-individual. Mortality was based on the empirical relationship given by Pepin (1991):

$$M = 5.17G^{0.74}L^{-1.17}$$  \hspace{1cm} (5)

where $G$ is the absolute growth rate (mm d$^{-1}$) and $L$ is length (mm).

This equation was modified slightly after a range of sensitivity tests (Bartsch and Coombs, 2004), and the formulation for the daily mortality rate in the IBM was set to

$$M = 5.0G^{0.7}L^{-1.3}$$  \hspace{1cm} (6)

IBM simulations

The initial fields for the spawning distributions for the model simulations were based on egg distribution data from the 1998 and 2001 ICES mackerel triennial egg surveys. For 2001, only data for the western component of the stock were available, so all simulations carried out in this modelling study used data for that stock component only. Because of the wide spawning area and the extended spawning season, the spatial and temporal coverage of the surveys was inevitably incomplete. Generalized Additive Models were used to interpolate for missing data from week 5 (29 January–4 February) to week 34 (20–26 August), to provide weekly input data for the IBM (Beare and Reid, 2002). In the present contribution, the effects of varying the input field are examined by comparing the output of simulations for 1998 (R1998) and 2001 (R2001), using initial egg distributions for 1998 and 2001, respectively, and also for a 2001 simulation using the 1998 egg data as input (I2001). An overview of these scenarios is given in Table 1.

The IBM was used to carry out 16 simulations (with starting dates staggered from week 10 to week 25; 5 March–24 June) for each of the three scenarios. Each of the 16 simulations is carried out separately using the appropriate egg field for the specific starting week provided by the GAM. All particles are released at the relevant midweek date of the starting week (e.g. 5 March for week 10). The overall physical forcing (currents and temperature) and the food distributions are different for each simulation owing to the different starting dates. The 16 starting (spawning) weeks covered by the simulations correspond to the main part of the mackerel spawning season, i.e. >95% of the egg production of the Western stock component (Figure 3).

For each simulation, data were stored daily for the egg phase (6—9 d, depending on temperature), then for a subsequent period of 60 d for the larval and early post-larval phases. The IBM simulations were restricted to 60 d because mackerel post-larvae cannot be considered as horizontally passive thereafter owing to their increased

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<th>Scenario</th>
<th>Initial egg field</th>
<th>Physical forcing</th>
<th>Food concentration</th>
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locomotive ability; additionally, the parameterization of growth, and hence mortality, cannot be supported thereafter owing to the mathematical properties of the logistic growth curve.

Model output

For simulations R1998 and I2001, some 128 000 super-individuals were introduced into the model domain. For simulation R2001, some 83 000 particles were released. Owing to the spatially and temporally heterogeneous physical (temperature and currents) and biological (food distribution) environment, all i-state histories of the super-individuals are potentially different. These i-states are, for example, position, length, and mortality. In order to summarize the regional distributions of i-states at a particular time, a weighted average is calculated for each model grid box where the weights are the current number of virtual individuals of each super-individual.

A model survivor index (MSI) is calculated for each grid box and for four recruitment areas (Bartsch et al., 2004), by summing the numbers of all virtual individuals reaching a length of at least 50 mm within the 60-d larval and post-larval simulation time. The recruitment areas considered are the Hebrides, the Porcupine Bank/NW Ireland, the Celtic Sea, and the Bay of Biscay.

Model outputs are presented primarily as composite charts, i.e. the output data for all 16 simulations are superimposed. It must be emphasized that the resultant distributions do not represent the situation for a specific calendar date, but rather relate to an elapsed time of 60 d after introduction into the model domain (excluding the egg stage) for the particle and length distributions. The MSI represents the situation for a specific minimum length reached (50 mm) by the super-individuals after their introduction into the model domain.

Results

Transport of eggs, larvae and post-larvae

The initial egg distributions (i.e. the composite egg distributions for the 16 weeks 5 March–24 June) for 1998 and 2001 are shown in Figure 4a and b, respectively. These represent the composite starting positions of the particles for scenarios R1998 and I2001 (Figure 4a), and for R2001 (Figure 4b). It should be noted, though, that the input fields for each simulation were different in both spatial distribution of particles, as well as in terms of absolute numbers of particles released. There were three main differences in mackerel egg production between 1998 and 2001. First, total egg production in 2001 only reached ~65% of the egg production in 1998 (Figure 3). Second, the timing of peak production in 2001 was 5 weeks later than in 1998 (Figure 3). Third, Figure 4a and b show that the highest egg concentrations were distributed farther north in 1998 (peaks over Porcupine Bank and along the shelf-edge of the eastern Porcupine Seabight) than in 2001 (peaks in the Goban Spur area and in the northwestern Bay of Biscay). It is also evident that egg concentrations were much higher in 1998 than in 2001 in most areas.

The resultant particle distributions at 60-d post-hatch from spawning for scenarios R1998, R2001, and I2001, are
shown in Figure 5. Common to all is a separation into two large areas of higher concentration of post-larvae north and south of 50°N. The main part of the northern high concentration area is located over the Porcupine Bank. In Figure 5a (scenario R1998), the southern area of high concentration of post-larvae stretches along the Celtic Sea shelf-edge from Goban Spur southeastwards to about 47°N. In Figure 5b (scenario R2001), the southern area of high post-larval concentration is in the central Bay of Biscay, with a branch protruding away from the shelf-edge over deeper water between 46°N and 47°N. In scenario I2001 (Figure 5c), there are more post-larvae over the Porcupine Bank than in scenario R1998 (Figure 5a). It is also evident that overall post-larval concentrations and peak concentrations are much lower for scenario R2001 than for the other two scenarios.

Regional distributions of larval and post-larval lengths

Regional differences in growth rate are evident for all three scenarios from the differences in average length (mm) achieved by super-individuals after 60 d (Figure 6). Similar patterns are seen for all three scenarios. Two main regions of faster growth (post-larvae reaching lengths of 50–70 mm) are evident. One is a northern area, including the area over the Porcupine Bank extending onto the Irish Shelf and northwesternly into the eastern part of the Rockall Trough. In 1998 this region extends up to the Hebrides (Figure 6a; R1998), but in 2001 this region extends as far as the Orkney and Shetland Isles (Figure 6b, c; R2001 and I2001). The other region of fast growth lies in the south, essentially over the Armorican Plateau. Outside these two main areas, the lengths achieved are markedly smaller, e.g. 20–35 mm in the Celtic Sea and adjacent shelf-edge area (Figure 6a–c).

To exemplify interannual variations in growth, average lengths attained during 1998 (Figure 6a; R1998) were subtracted from those attained in 2001 (Figure 6b; R2001). Most areas show positive values, implying that growth was faster during 2001 (Figure 7). Although some areas, notably the Celtic Sea, the central Bay of Biscay beyond the shelf-edge, and an area west of the Hebrides show negative values, these are usually only in the range 0–5 mm. It is also evident that interannual variations can be as large as 20–30 mm, for instance over the southwestern part of the Porcupine Bank, in the Goban Spur area, and in the entrance to the English Channel. In some inner shelf areas of the Armorican Plateau, length differences of 15–20 mm are evident.

Survival indices

The normalized Model Survivor Indices (MSI), i.e. MSI/10^5 (termed MSI subsequently) for each recruitment area for all scenarios are shown in Figure 8a. For R1998 and R2001, most survivors are consistently found in the Porcupine Bank/NW Ireland area (74% and 67% of the total for all areas in 1998 and 2001, respectively). The second largest contribution comes from the Hebrides area in 1998 (23%), and from the Celtic Sea in 2001 (20%). Input from the Bay of Biscay varies between 2% and 3% for these scenarios.

Scenario I2001 also identifies the Porcupine Bank/NW Ireland area as the main contributor to the overall MSI (75%). In this simulation, the contribution from the Hebrides is 18%, while the contributions from the Celtic Sea and from the Bay of Biscay are small and range between 2% and 4%. Combining the MSI for all areas allows a comparison of annually simulated model survival for the three scenarios (Figure 8b). It is evident that the total MSI for R1998 (1.1) is slightly higher than that for R2001 (0.96), by about 14%. In contrast, the total MSI for I2001 (1.56) is about 42% higher than that for R1998, and approximately 60% higher than that for R2001.

Discussion

Larval transport

Results from the particle drift simulations show that the area of continuous egg concentration from the northwest of

![Figure 5. Distribution of all particles after 60 d of drift for (a) 1998 (scenario R1998), (b) 2001 (scenario R2001), and (c) 2001, using the initial egg distribution from 1998 (scenario I2001).](https://academic.oup.com/icesjms/article-abstract/62/6/1049/616028)
Ireland, through the Porcupine area, and along the shelf-edge of the Celtic Sea, separates into two nearly distinct areas of larval distribution. This separation is in the vicinity of 50°–51°N, and is a consequence of the divergent current field just south of the Porcupine Bank in the upper mixed layer of the water column, as observed previously in field investigations (Pingree, 1993; Mohn, 1999).

North of 51°N, eggs and larvae are retained over the Porcupine Bank as a consequence of the an anticyclonic gyre trapped over the bank. This circulation pattern is a consistent phenomenon, and is usually only destroyed by strong winds (Mohn et al., 2002). The existence of an anticyclonic gyre over the Porcupine Bank has been shown by previous modelling studies (Bartsch and Coombs, 1997) and by field investigations (Mohn et al., 2002). North of the Porcupine Bank, the shelf-edge current transports the particles polewards, to the west and north of Scotland, as evidenced by the northeastward trail of particles.

South of 51°N, transport of eggs and larvae is generally southeastwards along the shelf-edge. This is consistent with drift-buoy tracks (Pingree, 1993), and with the results of a SEAMAR drifter study in 1999 on the outer Celtic Shelf (SEAMAR, 2002). At about 48°N, a strong off-shelf component of the surface current reduces the southward flow along the shelf-edge. This is especially evident in the particle plot for R2001 (Figure 5b) as the west/south-westerly extension of the Celtic Sea shelf-edge concentra-
Growth and mortality parameterization

The common logistic curve, which specifies a constant value for the parameter \( r \), hatching length and \( L_{\infty} \) being fixed (Equation 2), yields one growth curve for some “mean” individual (or population), and does not take into account any environmental variation (Jorgensen, 1986). The parameterization of larval and post-larval growth as a function of temperature and food concentration in the IBM (Equations 2 and 4) results in different growth histories for each super-individual, even if released into the model domain in the same region and at the same time. In principle, this parameterization yields a large set of individual growth curves, in which every growth curve is a specific realization of a multitude of temperature conditions and food concentrations encountered by each super-individual. This set of individual growth curves is enveloped by two extreme growth curves (see also Figure 3 of Bartsch, 2002). First there is the growth curve exhibited by super-individuals encountering the lowest temperatures and food concentrations within the model area, which results in the lowest individual growth rate possible in the IBM. Second, there is the growth curve realized by super-individuals encountering only the optimum temperature as specified in the IBM, as well as the highest food concentrations, which results in the highest growth rate possible in the IBM.

A comparison of length-at-age data from otolith readings from the SEAMAR cruises with data output from the IBM showed that the field data exhibited a high variability, in terms of different lengths measured for a specific age, but that the data cloud lay within the two enveloping growth curves described above (J. Bartsch, unpublished data; SEAMAR, 2002). A detailed description of this validation exercise is beyond the scope of the current work, but the conclusion from this exercise is that the growth parameterization used in the IBM for mackerel in the northeastern Atlantic is a valid approximation of larval and post-larval growth up to an age of 60 d.

Comparing mortality rates from field to mortality data from the IBM is difficult, but such a validation study was carried out within SEAMAR. In essence, model data corresponded very well with field data where such a comparison was possible, this being the case for two cruises in May and June/July 1999 (J. Bartsch, unpublished data; SEAMAR, 2002). Also in this case, the conclusion is that the mortality parameterization in the IBM is a suitable approximation of larval and post-larval mortality in the northeastern Atlantic.

Inevitably, in putting together an IBM which ranges from ocean-basin-scale circulation to the energetics of larval feeding, there are weaknesses, and although the validation exercises showed the appropriateness of the growth and mortality parameterizations, these could be improved (Bartsch and Coombs, 2004). However, the results from these parameterizations, as given by the IBM output in terms of regional distributions of post-larval lengths, regional distributions of survivors (Bartsch et al., 2004), and survivor indices, are nonetheless considered valid, at least to the extent that the IBM was not producing unrealistic results.

Larval and post-larval lengths

The length distributions after 60 d of larval and post-larval growth are influenced by temperature and the food concentration distribution. The regional north–south temperature gradient, which is reflected in the distributions of length when only temperature mediation is employed in the growth parameterization (Bartsch and Coombs, 2001), is not discernible in Figure 6a–c, because it is masked by the effect of food distribution. This is especially clear for the area along the shelf-edge of the Celtic Sea, where temperatures are generally higher than at the Porcupine Bank, but owing to lower food levels, growth is consistently lower.

The highest variability in growth rates, both spatial and temporal, and thus in lengths attained, is generally found over the Porcupine Bank and in the area between the Hebrides and the Orkney and Shetland Isles. In contrast, the area between the Porcupine Seabight/Goban Spur and the northwestern Bay of Biscay, as well as the Celtic Sea, shows a much reduced variability in space and time, as well as consistently slow growth rates and hence low lengths attained.

The interannual variability in the food environment that the larvae and post-larvae experience is exemplified by Figure 9. The distributions show the difference in food availability (\( \mu g C l^{-1} \)) for week 21 (21–27 May) and week 28 (9–15 July) between 2001 and 1998, i.e. the food concentrations in 1998 were subtracted from those in 2001. Therefore, positive values denote higher food concentrations in 2001.

It is evident from Figure 9a (week 21) that food concentrations were higher in 2001 by about 1–10 \( \mu g C l^{-1} \) in the Hebrides area, large parts of the Porcupine Bank, and along the shelf-edge towards the southeastern Bay of Biscay and on the Armorican Plateau. Higher food concentrations in 1998 (negative values) are restricted to a few small, interspersed areas on the shelf and along the shelf-edge.

From Figure 9b (week 28) it is evident that food concentrations were higher in 2001 by about 0.1–1 \( \mu g C l^{-1} \) from the Porcupine Bank south to the southeastern Bay of Biscay. From the Porcupine Bank north to the Orkney and Shetland Isles, food concentrations were higher in 2001 by about 1–10 \( \mu g C l^{-1} \), in the Hebrides area even by 10–100 \( \mu g C l^{-1} \). It is also evident that all shelf areas, except small parts of the Celtic Sea and small areas off
western Ireland, show higher food concentrations in week 28 in 2001.

Generally, at the beginning of the spawning season (from week 10; 5–11 March), food concentrations were higher in 2001 than in 1998 in the south only (i.e. Bay of Biscay). As the season progressed, this positive difference in food concentrations progressively moved north, until all areas where mackerel post-larvae were found in the model encountered a better food environment in 2001 than in 1998.

Mackerel spawning peaked during week 15 (9–15 April) during 1998, in contrast to the situation in 2001 when spawning peaked during week 20 (14–20 May). Owing to the later timing of spawning in 2001, super-individuals released from about week 18 onwards during scenario R2001, generally encountered more favourable food conditions than their counterparts released during 1998. Super-individuals released during the I2001 scenario (1998 initial egg distribution) also benefited from this enhanced food environment, although peak spawning was 5 weeks earlier.

Moreover, analysis of model temperature data between March and August in 1998 and 2001 did not find major differences in the data. This is due to the fact that the temperature in the circulation model, which feeds into the IBM, is drawn towards the (daily) mean by a Newtonian damping term. Hence, the differences in the lengths attained in the three scenarios are mainly due to the different food environment as well as the timing of spawning. It should be noted, though, that the temperature difference at peak spawning between 1998 and 2001, generally about 1–1.5°C in the model area, plays a secondary role.

Survival indices

Areas of low growth are intrinsically linked to areas of high mortality and hence low numbers of model survivors (Bartsch and Coombs, 2004). Conversely, areas of fast growth are linked to areas of low mortality and hence high numbers of model survivors. To a large extent, the model survivor indices reflect the distribution of lengths, but the MSI is also a function of the numbers of particles or super-individuals, each representing a certain number of virtual individuals (model survivors) found within model grid boxes, and hence larger aggregated areas.

In the Porcupine Bank area, a combination of high particle numbers and good food conditions result in large lengths attained, and hence a high MSI in all scenarios. The Porcupine Bank is by far the largest contributor to the total MSI for all modelled years and scenarios (67–75%). In contrast, relatively few particles are usually found in the Hebrides area, and although large lengths are generally reached in this area owing to good food conditions late in the season, this results in a relatively low MSI in all scenarios (11–23%). The contributions to the MSI from the other two areas are very small. This is due to a combination of low particle numbers with good food conditions (Bay of Biscay), or low to medium numbers of particles and poor food conditions (Celtic Sea). One exception is scenario R2001, where relatively high numbers of particles are found off the shelf-edge, resulting in a contribution of 20% for the Celtic Sea in 2001.

The total MSI for 1998 is slightly higher (by 14%) than for 2001. Although egg production in 2001 was less than in 1998, i.e. only about 65% of the 1998 production, the better food environment and the later timing of spawning produced an MSI for 2001 that is similar to that for 1998. The MSI for I2001 (1.56), the scenario that used the 1998 egg distribution, is 60% higher than the MSI for scenario R2001, which used the appropriate egg field from 2001. This is due to the great increase in particle numbers, even though the timing of spawning in 1998 (5 weeks earlier) with respect to temperature and food was not as good as in 2001. Hence, the effect of using the correct egg distribution in 2001 results in a modelled survival index that is markedly different from the MSI which is calculated using the “wrong” initial egg distribution data.

Potential for use of the model for management purposes

The IBM used in this study is crucially dependent on a number of input data sets. One prerequisite is the...
availability of a circulation model to provide the physical input data needed to simulate transport (currents) and growth (temperature). Other important and essential input data are the initial egg distributions from field surveys, as well as the modelled food concentrations. Meteorological forcing data for the circulation model, as well as the modelled food concentration data for the IBM, were readily available from the PML (Plymouth Marine Laboratory), with only a short time-lag, usually about 2–4 weeks. However, egg distribution data for mackerel are only available every 3 years, with a time-lag of about 1 year, for example during the SEAMAR Programme.

Egg distributions, key elements for the prediction of model survivors in the IBM, because they represent a model estimate of recruitment, are highly variable in both time and space. It is evident from this study that using the “wrong” initial egg distribution data (scenario I2001) severely limits the predictive capability of the IBM, because the predicted MSI can potentially be too low or much too high (this study). Therefore, data from the triennial surveys can essentially only be used to make predictions for the specific year of the survey.

In order to make full use of this IBM in terms of aiding management of fish stocks in the EU (this statement is not restricted to mackerel), annual egg surveys are needed. All other input data needed for the circulation model and the IBM are or could be readily available. If appropriate egg data were available, IBM simulations could be completed well in advance of the appearance of the respective year class in the fishery, at an age of 3 or 4 years. Hence, these hindcast predictions of model survivors can be used to apply appropriate management measures in due time.

Acknowledgements

I acknowledge the collaborative input of the other scientists who participated in the SEAMAR programme at the following laboratories: MBA, Plymouth, UK; PML, Plymouth UK; IEO, Santander, Gijon, Malaga, and Madrid, Spain; IHF, Hamburg, Germany; AZTI, San Sebastian, Spain; MLA, Aberdeen, UK; NUI, Galway, Ireland; IPIMAR, Lisbon, Portugal; BAH/AWI, Bremerhaven, Germany; CEFAS, Lowestoft, UK; HYDROMOD, Wedel, Germany.

References


Egg production variability and modelled survival of early stage mackerel


