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A numerical model of the dispersion of blue whiting larvae (*Micromesistius poutassou*) in the eastern North Atlantic

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ABSTRACT

Within the EU funded SEFOS project (Shelf-edge Fisheries and Oceanography Studies) a numerical circulation and transport model system has been used to simulate the dispersion of larvae of blue whiting (*Micromesistius poutassou*) in the eastern North Atlantic. The area of the model extends from the northern Bay of Biscay to the Norwegian Sea and covers the shelf-edge and adjacent waters with a resolution of around 20 km. Larval input data were based on the long-term mean distribution, abundance and seasonal occurrence of larvae derived from historical data. The circulation model was run using tidal forcing and climatological density fields as well as both climatological meteorological forcing and realistic six-hourly wind stress fields for 1994 and 1995. Transport from the main spawning areas situated to the west of the British Isles and north of Porcupine Bank was associated with currents along the shelf-edge and in the Rockall Trough. Tracers were dispersed either to the north and north-east along the shelf-edge, extending into the northern North Sea and Norwegian Sea, or were retained in the Rockall Gyre. A less intense southerly flow from Porcupine Bank was observed both under climatological conditions and in the 1995 simulation, when winds were more variable than in the 1994 simulation. The results based on the 1995 meteorological conditions showed the most extreme retention of tracers in the Rockall/shelf-edge area west of Scotland and a low penetration of tracers onto the shelf. These results are discussed in relation to the observed distribution of 0-group juveniles and to indices of year-class strength, in particular in relation to the 1995 year-class which is the highest year-class estimate of blue whiting on record.

INTRODUCTION

The SEFOS project (Shelf-edge Fisheries and Oceanography Studies) was funded, in part, for a hydrographic study of the Shelf-Edge Current (SEC) extending from Portugal via Biscay and the west of the British Isles to the Norwegian Sea, and also to allow the formulation of a numerical hydrodynamic model of the same area. Biological studies of the fish stocks associated with the shelf-edge were also included in the study, with particular emphasis on their interaction with the SEC and on how changes in the current might affect different aspects of their life-history. The egg and larval stages of fish species which spawn at the shelf-edge were of particular interest since these planktonic stages are especially vulnerable to advection to areas of unsuitable larval food supply or to subsequent inappropriate nursery grounds; numerous studies

having indicated that much of the mortality regulating future year-class strength takes place during these early developmental stages (Beyer, 1989; Houde, 1987).

Blue whiting (*Micromesistius poutassou*) is one of the major fish stocks which spawn along the edge of the European continental shelf. The size of the stock, at around 4.5 million tonnes (Monstad *et al.*, 1996a), and both the extended spawning season and spatial distribution, from at least February/March in Biscay to June at the Faeroes (Bailey, 1982), creates excessive demands in ship-time and manpower to follow the spawning distribution at successive time intervals, even in a single year. It is in this context that a numerical transport model can be employed to investigate the effects of actual or long-term climatological wind patterns on the dispersion of the planktonic stages, either for a particular year or using long-term mean indices of distribution.

Similar modelling exercises have been carried out on other fish species. Examples of such studies are those carried out on walleye pollock in the Gulf of Alaska (Stabeno *et al.*, 1995), on cod and haddock on Georges Bank (Werner *et al.*, 1993) and on herring in the North Sea (Bartsch, 1993). A review of transport of fish eggs and larvae was compiled by Norcross and Shaw (1984).

THE CIRCULATION AND TRANSPORT MODEL SYSTEM

A three dimensional non-linear baroclinic numerical model is used to simulate the circulation of the North Sea, the shelf-edge area and adjacent oceanic regions of the eastern North Atlantic. The circulation model is based on HAMSOM (HAMBURG Shelf Ocean Model) which was developed at the Institut für Meereskunde, Hamburg and transferred to the northern SEFOS area. Details of the model have been published by Backhaus (1985).

The model area extends from 46°N to 63°N and from 25°W to 14°E (Fig. 1). The horizontal grid size is around 20km, with a vertical resolution of 16 layers, the layer depths ranging from 10m to 40m in the upper 100m and increasing progressively in the deeper layers up to a maximum depth of 5000m. The model is forced by the M_2 tide and either six hourly and air pressure fields from ECMWF (European Centre for Medium-Range Weather Forecasting) or mean monthly climate fields (Backhaus *et al.*, 1985), as well as monthly climatological density fields which are treated prognostically but relaxed towards the climatological monthly mean.

The time step of the circulation model is 20 minutes. Due to the high data storage requirements, the current data, as well as the variance of the current, were output only on a daily basis, i.e. the currents were integrated over two M_2 tidal cycles. The daily three-dimensional current and variance fields serve as input to the transport model. A schematic diagram of the model system is given in Fig. 2.

The simulations of the drift routes are performed by means of tracers, in essence "marked" water particles representing the fish larvae, which are introduced into the model area and are pursued in time and space domains. A simple method which was used for simulation of the transport of substances (particles) was the Monte-Carlo method (Bork and Maier-Reimer, 1978). It is assumed that the current field can be split into a large scale mean current (u) and a small scale random fluctuation (u'), i.e. $U = u + u'$. The small scale fluctuations are parameterised using the current variance (Backhaus, 1989; Bartsch and Knust, 1994). Thus, during each time-step the

tracers experience a directional transport by the mean current (advection) as well as a random transport, in both magnitude and direction, by the small-scale fluctuations (diffusion).

The boundary conditions in the transport model prescribe a no-flux condition at closed boundaries, whereas the tracers may leave the model area at open boundaries. The model area, grid size and the vertical resolution are in accordance with that of the circulation model, while the time step of the transport model is three hours.

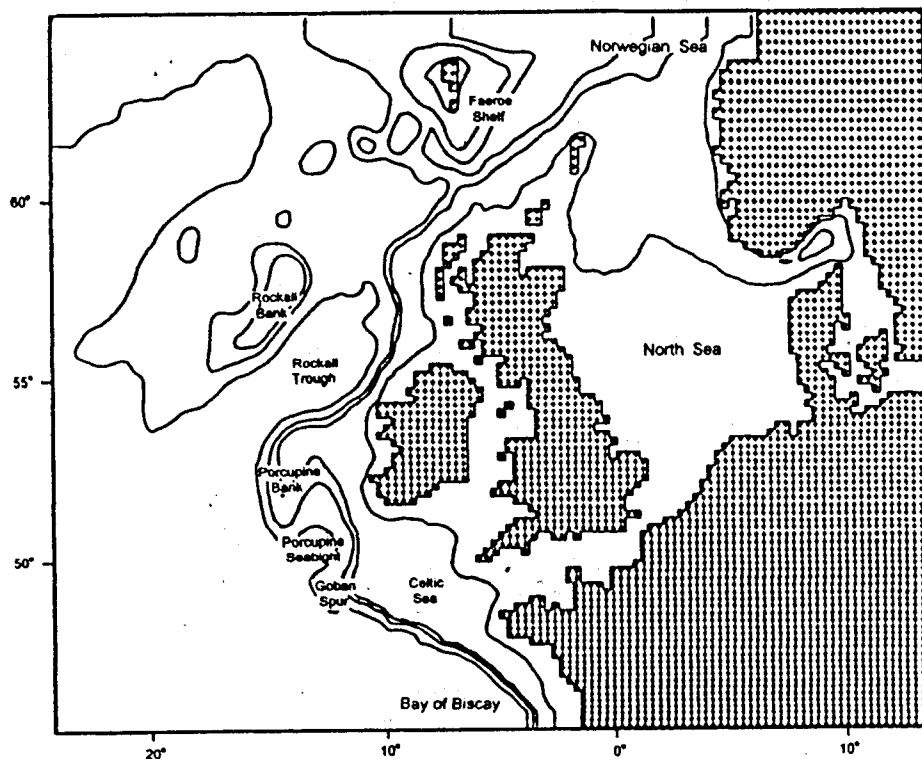


Fig. 1. Model area and bathymetry showing the 100m, 500m, 1000m and 2000m depth contours.

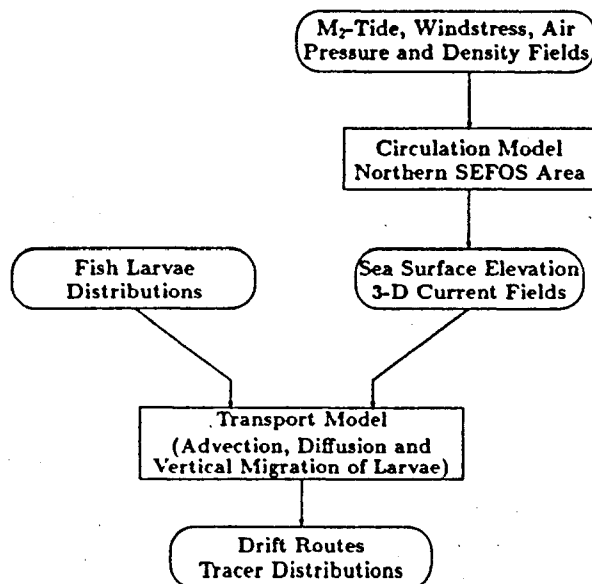


Fig. 2.. Schematic diagram of model system.

BIOLOGICAL PARAMETERS

(a) Spawning area and time of spawning

There have been no wide scale synoptic surveys of blue whiting egg or larval distributions, thus it was necessary to collate all published sources to generate the required information on time of spawning and larval distribution and abundance. Bailey (1982) produced a summary of spawning distribution and seasonal occurrence but without the detail required for the present purpose; much of the same sources as used in his synopsis have been used here, together with more recent additions.

Since the duration of development for blue whiting eggs is only in the region of 4 to 5 days (Coombs and Hiby, 1979), whereas the transport model was run for up to 120 days, the distribution of eggs (for which negligible data only are available) has not been included in the preparation of the chart of initial (spawning) distribution.

One of the main sources of information on larval distribution is the Continuous Plankton Recorder (CPR) Survey, results from which have been presented by Bainbridge and Cooper (1973), Coombs (1979 and 1980) and Coombs and Pipe (1978 and 1981). CPR sampling is at a single depth only (a nominal 10m); use of these data thus required conversion to the more usual numbers/m² by reference to their vertical distribution (Coombs *et al.*, 1981 and more recent unpublished data).

Other significant sources of distribution and seasonal information were Bailey (1974) for eggs and larvae in the area of Rockall and west of Scotland and Arbault and Boutin (1968 and 1969) for Biscay. A number of Russian contributions with a rather sparse station coverage, but having good annual continuity from 1983-1993, were used to add information on larval occurrence west of the British Isles, particularly over the deeper and more distant areas from the shelf-edge (Belikov *et al.*, 1993 and earlier papers cited therein). More recent contributions, as part of the SEFOS programme, have included detailed sampling around Porcupine Bank and surrounding areas (Kloppmann *et al.*, 1996; Monstad *et al.*, 1994 and 1995; McFadzen and Cook, 1996).

The overall chart of spawning distribution, i.e. the model input on day zero (Fig. 3), was based primarily on data from the above sources, using contour package interpolation and averaging routines where appropriate. The more limited information contained in a number of subsidiary publications was used to make small local adjustments. The final data were represented as numbers/m² allocated to logarithmic categories of 1-10, 10-100 and 100-1000/m² by grid rectangle of the model resolution (approximately 20 km square).

Again based primarily on the sources quoted above, the average seasonal time of spawning in each model rectangle was calculated in a similar way as for the spatial distribution of spawning, a ten-day discrimination in timing being employed. The average time of peak spawning was progressively later from south to north, this being from the beginning of March in north Biscay, late March/early April at Porcupine, mid-April west of Scotland and mid-May at the Faeroes.

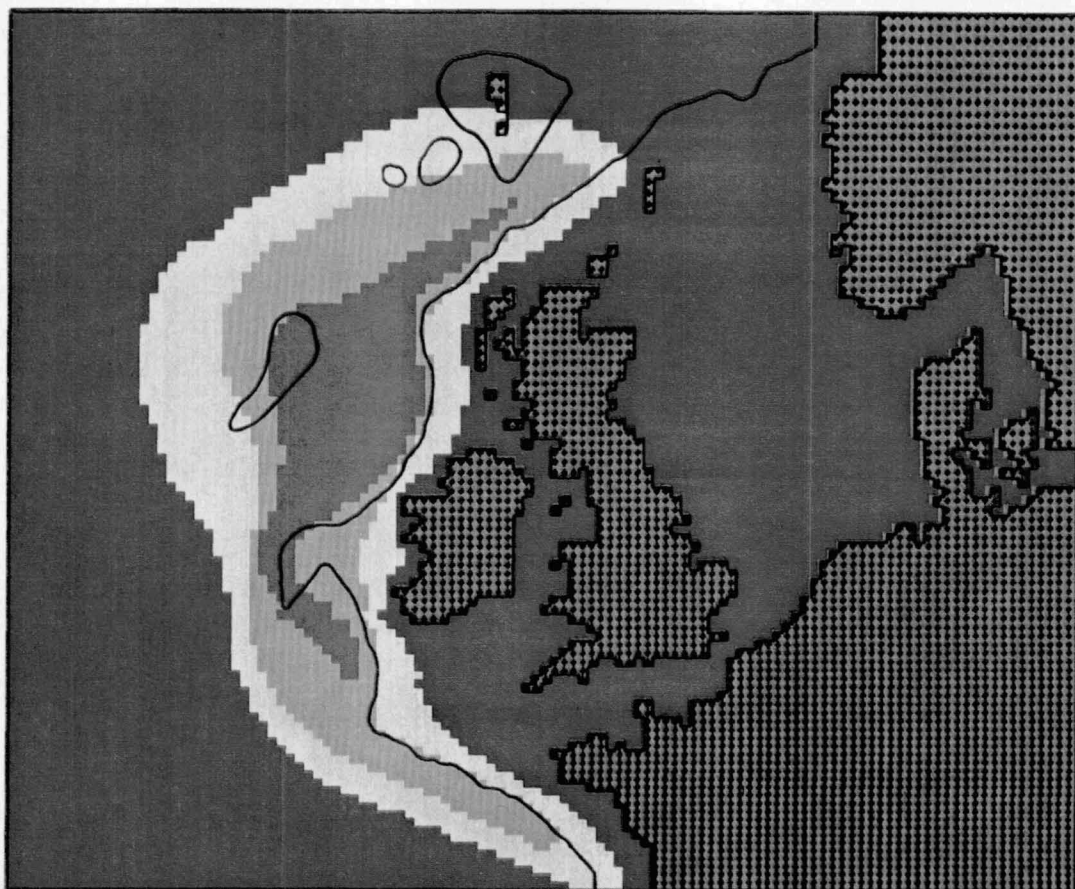


Fig. 3 Initial larval (tracer) distribution; abundance is represented at three category levels of 1-10, 10-100 and 100-1000/m². The 500m depth contour is also shown.

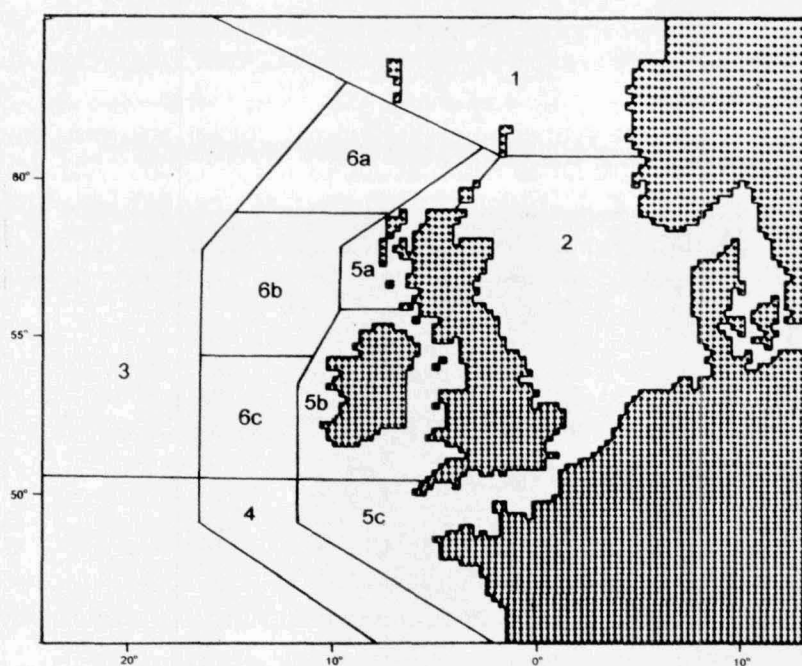


Fig. 4 Areas used for monitoring the flux of tracers - see Table 2.

(b) Vertical distribution

A simplified scheme based on historical and recent field data on the vertical distributions of blue whiting larvae along the shelf-edge was used in the transport model. Blue whiting spawn at depths of around 200-400m and, after hatching, there is an ontogenetic movement of the larvae towards the surface such that by a length of >5mm (approximately one week after hatching) they are concentrated in the upper 60m of the water column (Coombs *et al.*, 1981 and more recent un-published data). Since there is no clear evidence of diel vertical migration of the larvae (Hillgruber *et al.*, 1995; Coombs un-published data), the tracers representative of blue whiting larvae were thus given a random migration within the upper 60m of the water column i.e. spending an equal amount of time in the top four model layers between 0 and 60m and being subjected to the combined effects of the currents in these model layers.

TRACER SIMULATIONS

The spawning area and larval distribution as given in Fig. 3 provides the initial distribution for the three tracer dispersion scenarios examined. Larval abundance ranges over three orders of magnitude with the number of tracers per model grid box being taken as proportional to these values. In the absence of any information on differential larval mortality between areas, which would consequently affect the tracer distributions, no mortality was considered in the transport model; the abundance of tracers thus remained constant. As spawning progresses in time from south to north, the tracers are released into the model domain at the appropriate spawning time.

Three simulation scenarios were carried out over 120 days:

Scenario 1: Climatological, using mean monthly meteorological fields (1955-1982)

Scenario 2: 1994, using realistic meteorological fields from ECMWF for that year

Scenario 3: 1995, using realistic meteorological fields from ECMWF for that year

It should be noted, that the resultant tracer distributions are not for a specific calendar date but relate to the time elapsed after introduction into the model domain, which varies throughout the model area, i.e. each tracer was followed for the relevant simulation period (60 or 120 days) from its start time (time of spawning in the appropriate model grid box); the final tracer distributions are then the sum of all the individual tracer trajectories irrespective of their particular finish times.

To elucidate the results of the simulation scenarios, the model area was divided into ten areas in which tracers were counted at specific times (Fig. 4). This gives information on the flux of tracers between areas.

The transport model in the climatological scenario relies on currents simulated using the average wind stress for input to the circulation model, which thus lacks the effect of meteorological variability, but does provide a useful reference point for comparing the other model runs.

A comparison of the wind data for 1994 and 1995, as used for the other model runs, was based on averaged monthly winds by 45° compass quadrants at three selected station positions,

Porcupine Bank (52° 30' N 13° 30' W), Rockall Trough (56° 30' N 11° 50' W) and west of the Hebrides (57° 54' N 08° 30' W.). Since these sets of data were not significantly different from each other (Wilcoxon signed-rank tests $p > 0.01$) they were combined to give an average wind direction by month for the three positions (Table 1). An additional parameter, the index of stability (S), was also calculated as $S = (W/w) * 100$, where W is the averaged vectorial magnitude and w is the averaged arithmetic magnitude of wind stress respectively, i.e. the averaged magnitude irrespective of direction; thus a unidirectional wind will yield a stability of 100% and a highly variable wind equally from all compass quadrants will give an S of 0%. This is presented for the Rockall Trough position only, since averaging of vector values is not appropriate, although essentially the same pattern is seen at all three positions.

The differences between the wind data (this being essentially the only forcing function for the circulation model which varies between the different scenarios) for 1994 and 1995 shows that in 1995 winds were much more variable in all months, except in May, than in 1994 (Fig. 5). This variability is also seen in the persistence in wind direction; for example, in 1994 there were somewhat more persistent westerlies in March, April and June, easterlies in May and southerly winds in July compared with 1995 (Table 1). 1995 still had a relatively high proportion of westerly and southerly winds, as expected in these latitudes, but also had rather more northerly winds in April and May than did 1995 (Table 1).

Table 1. Wind direction by month for 1994 and 1995 as the percentage of observations by compass quadrant.

	N	NE	E	SE	S	SW	W	NW
March '94	2.4	0.3	2.1	1.1	13.1	12.0	62.7	6.4
March '95	10.4	1.1	3.5	1.9	13.3	12.3	43.5	14.1
April '94	13.5	9.9	4.4	2.2	12.7	9.9	37.2	10.2
April '95	20.9	5.0	16.3	1.9	12.4	13.2	24.2	6.1
May '94	6.1	16.5	37.6	6.7	9.9	7.7	13.9	1.6
May '95	18.1	8.5	6.7	6.7	28.8	4.8	17.3	9.1
June '94	3.9	0.6	1.1	2.5	20.7	19.8	47.9	3.6
June '95	25.6	9.1	12.1	2.8	10.5	7.4	24.2	8.2
July '94	4.5	0.5	7.5	6.9	47.2	15.7	14.9	2.7
July '95	13.1	2.4	11.7	9.1	22.4	9.9	24.3	7.2

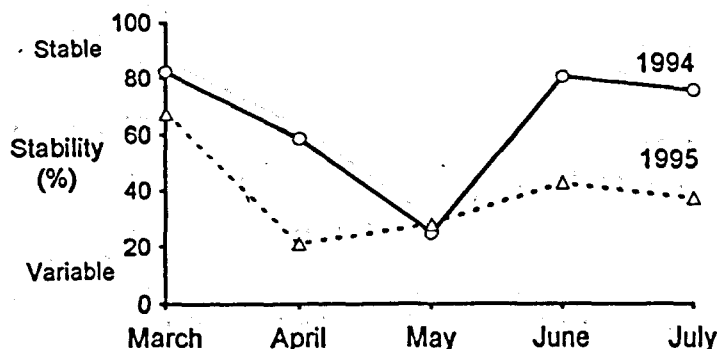


Fig. 5 Wind stability at the Rockall Trough position by months for 1994 and 1995.

RESULTS

Initial distribution

In the initial larval distribution the majority of blue whiting larvae (90.4%) are in area 6 which includes Porcupine Bank, Rockall Bank and the Rockall Trough as far as the southern area of the Faeroe Shelf (Fig. 3 and 4; Table 2). In this area about two-thirds of these larvae are found at Rockall Bank, Rockall Trough and the shelf-edge west of Scotland. Only about 2% of all larvae are found in area 3 (deep-water west of Porcupine and Rockall) while ~7% are in area 4 (shelf-edge south of Porcupine). Area 5 (all shelf areas <200m in depth) is practically devoid of larvae in the initial distribution (<1%).

Table 2. Percentage of tracers in different areas for different model runs.

Area	1	2	3	4	5	6	Total 1-6
Scenario	Norwegian Sea	North Sea	Deep water west of Rockall/Porcupine	Shelf-edge of Biscay	Western shelf	Porcupine/Rockall Faeroes	
Climate 0 days	0.0	0.0	2.1	6.6	0.9	90.4	100.0
Climate 60 days	4.0	4.7	1.1	8.0	13.1	68.9	99.8
1994 60 days	3.6	5.3	2.9	9.1	11.0	67.1	99.0
1995 60 days	5.3	1.6	1.4	7.4	5.0	78.9	99.6
Climate 120 days	1.0	13.9	1.6	8.7	28.5	44.2	98.0
1994 120 days	1.9	13.9	2.0	8.2	36.0	33.9	96.0
1995 120 days	2.8	9.6	0.9	8.3	17.4	56.5	95.4

Area	5a	5b	5c	6a	6b	6c	Total 5+6
Scenario	Shelf west of Scotland	Shelf west of Ireland	Shelf Celtic Sea	North Rockall Trough and Faeroes	Rockall Bank and Trough	Porcupine Bank	
Climate 0 days	0.3	0.2	0.4	9.6	61.0	19.8	91.3
Climate 60 days	6.9	3.8	2.5	4.2	47.7	17.0	82.1
1994 60 days	6.3	2.2	2.5	4.0	50.0	13.1	78.1
1995 60 days	1.6	1.6	1.8	7.7	54.1	17.1	83.9
Climate 120 days	13.6	10.3	4.6	2.8	27.7	13.7	72.7
1994 120 days	18.9	11.0	6.1	3.3	22.4	8.2	69.9
1995 120 days	7.4	6.0	4.0	4.3	38.5	13.7	73.9

Scenario 1 - mean climatological regime

After 60 days (Fig. 6a) the tracers have become dispersed, although the original areas of high concentration can still be discerned. A patch of tracers has moved along the shelf-edge and into the Norwegian Sea and also into the northern North Sea around the Shetland Islands; the complementary decrease in abundance of tracers south and south-east of the Faeroes is particularly marked. There is relatively less change in the distribution from Porcupine Bank to the south. In all areas, but particularly west of Rockall, the western fringes of the distribution have diminished in abundance.

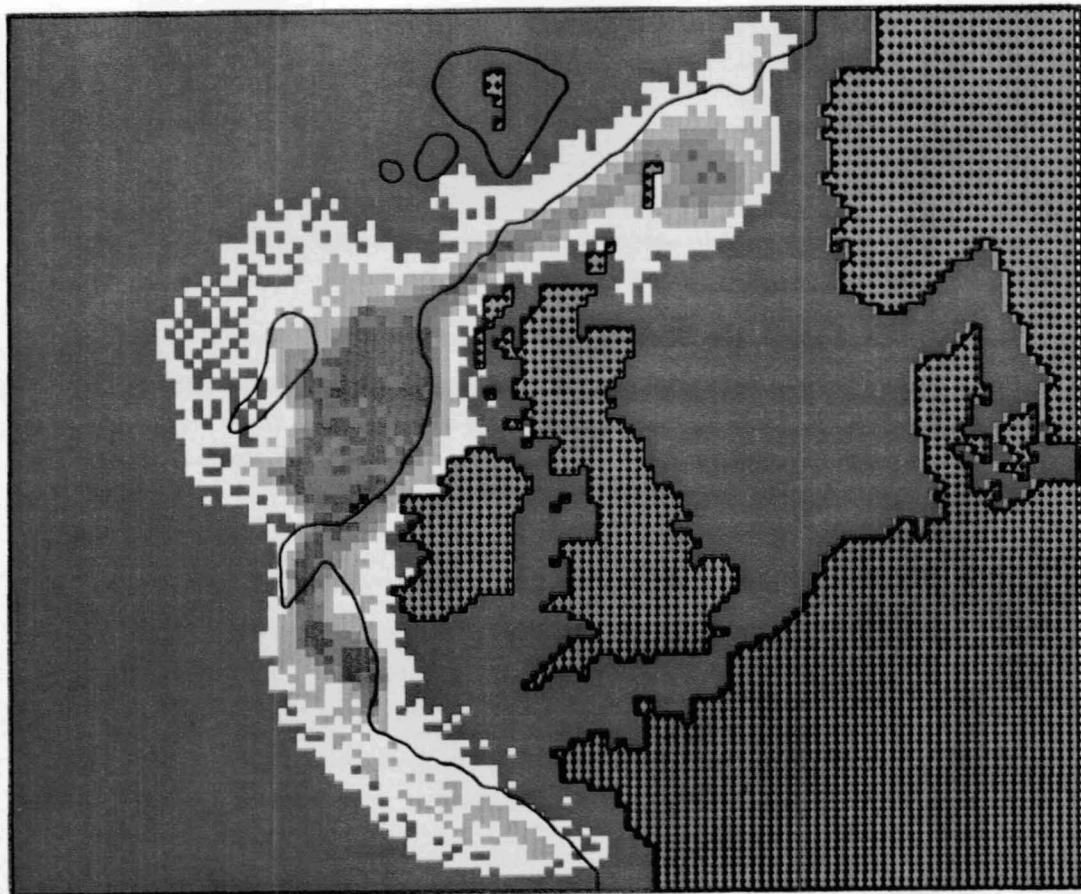


Fig. 6a. Tracer distribution after 60 days dispersion - climatological winds.

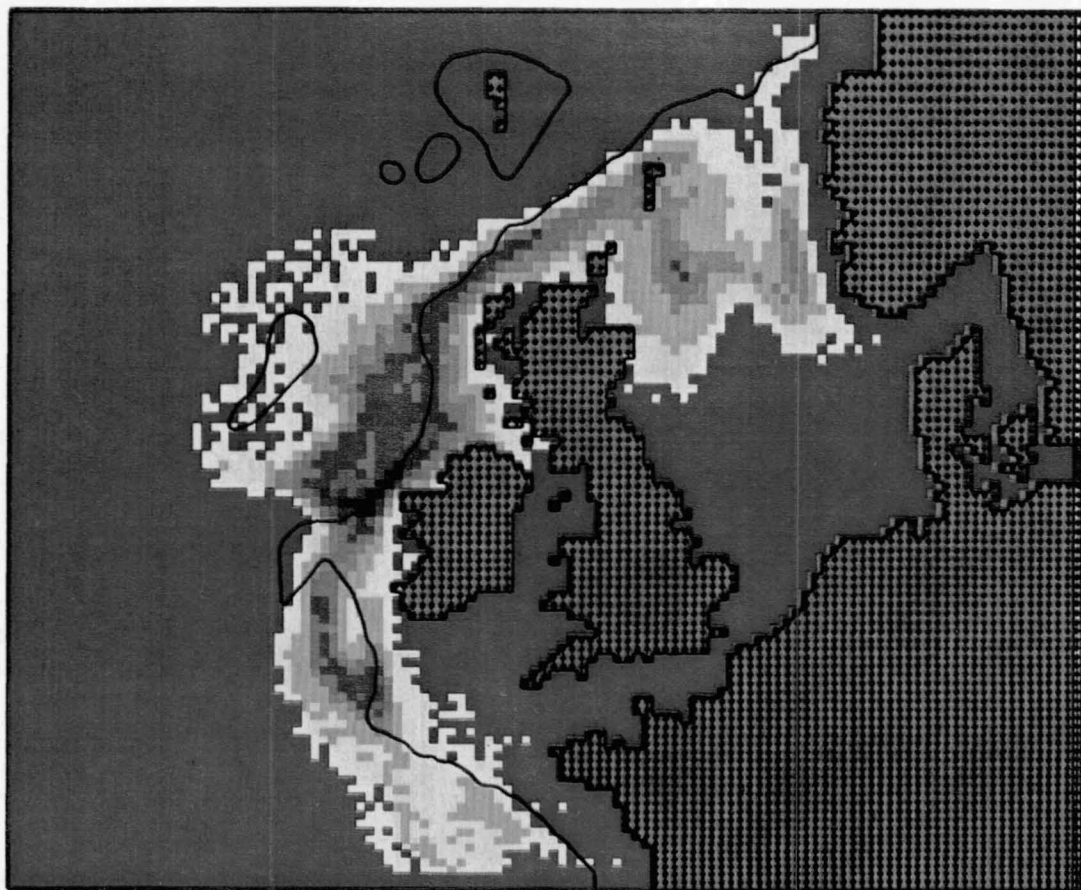


Fig. 6b. Tracer distribution after 120 days dispersion - climatological winds.

The distribution after 120 days (Fig. 6b) shows a continuation of the trends outlined above. High concentrations of tracers remain in the eastern Rockall Trough (around half the original numbers) due to retention in the currents of the Rockall Gyre. More tracers have ventured along the shelf-edge and into the northern North Sea (area 2) which now contains ~14% of all tracers released. The easterly drift and increase of tracers along the shelf-edge and onto the shelf (area 5) is also considerable (a net increase of ~28% of tracers - Table. 2). From Porcupine Bank tracers have moved south-eastwards towards Goban Spur into areas 4 and 5c (13.3% as opposed to 7% at the start). Only in the most southern area, the northern Bay of Biscay, have tracers shown any significant dispersion away from the shelf-edge. Finally, 2% of the tracers have been lost to the system (model area), in essence through the northern model boundary.

Scenario 2 - 1994 meteorological regime

After 60 days of forcing by the 1994 meteorological data transport into the Norwegian Sea and the North Sea (areas 1 and 2) is superficially similar to that of the climatological scenario (Fig. 7a cf. Fig. 6a), as is the retention in the main Rockall/west of Scotland area (area 6) and drift onto the shelf (area 5; see Table 2). Particular features are the patch of low abundance of tracers in the centre of the Rockall Channel, suggestive of a circulatory gyre, and the more complete separation of tracers north and south of Porcupine Bank.

After 120 days under the 1994 wind regime (Fig 7b), compared with the climatological scenario, more tracers have drifted onto the shelf (7.5% more in area 5) particularly west of Scotland (area 5a), while less have been retained in the main initial area of Porcupine and Rockall (~10% less in area 6; Table 2). The concentrations of tracers in the Porcupine Seabight and Goban Spur southwards into Biscay remain distinct from the concentrations to the north of Porcupine Bank. Tracer numbers in the Norwegian Sea and the North Sea are similar to the climatological scenario although slightly more tracers have been lost to the system (4%) than under mean climatological conditions (Table 2).

Scenario 3 - 1995 meteorological regime

After 60 days of the 1995 meteorological regime, the tracer distribution (Fig. 8a) is similar to the other 60 day distributions but with noticeably less drift into the North Sea (area 2) and somewhat more tracers reaching the Norwegian Sea (area 1; Table 2). Again, in contrast to both scenarios 1 and 2, less tracers have moved onto the shelf (area 5) while ~10% more have remained in the main initial area of Porcupine/Rockall/Faeroes (area 6; Table 2). The tracer concentrations are fairly continuous around Porcupine and into Biscay, with little evidence of drift away from the shelf-edge (Fig. 8a cf. Fig 7a).

After 120 days the above differences become more marked. The retention of tracers in the initial area of Porcupine/Rockall/Faeroes (area 6) is much higher with 56.5% remaining as opposed to 33.9% for 1994 and 44.2% for the climatological scenario (Table 2). The drift onto the shelf (area 5) is much reduced with only 17.4% of tracers in that area compared with 36.0% for 1994 and 28.5% under mean climate conditions. Drift into the North Sea is also reduced (about two-thirds of the numbers as in the other scenarios; Table 2) while more tracers reach both the Norwegian Sea and are lost to the system (~5%) compared with the other scenarios. The concentrations of tracers to the north of Porcupine maintain a continuity with those further south, extending into Biscay where there are fewer tracers dispersed over deeper water than in the other two scenarios.

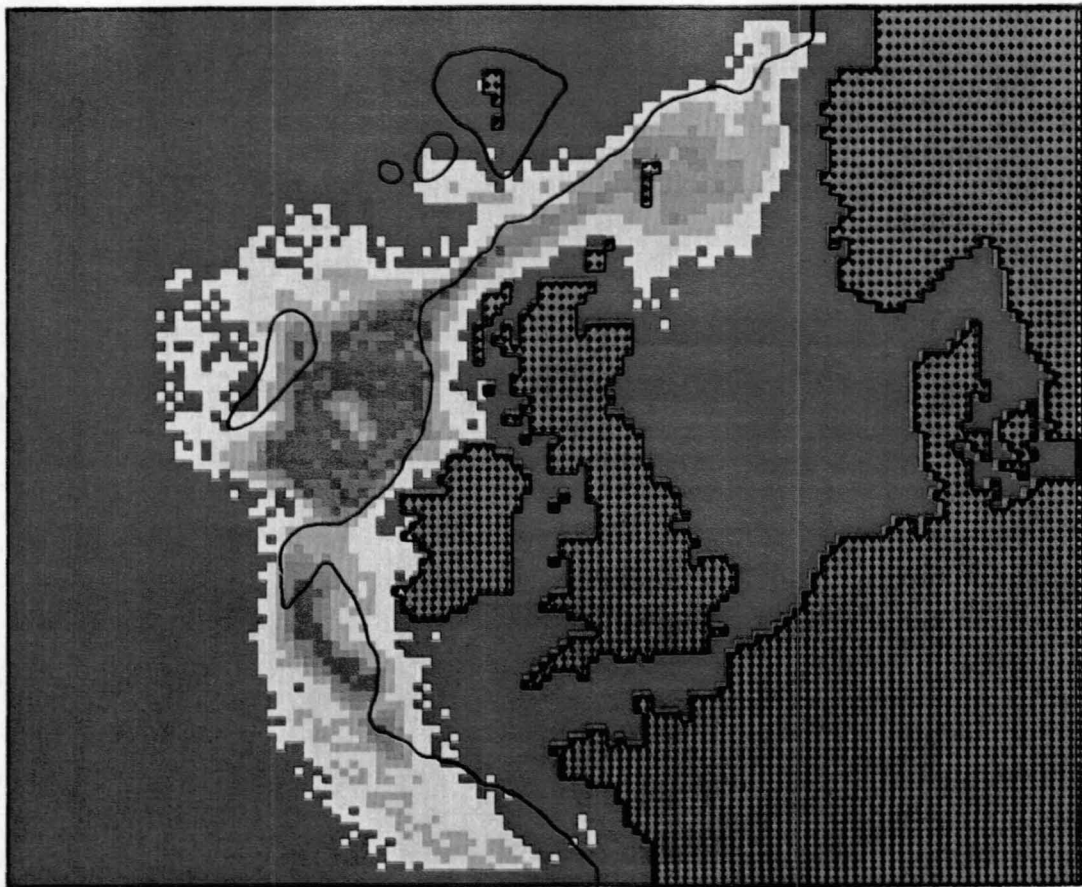


Fig. 7a. Tracer distribution after 60 days dispersion - 1994 winds.

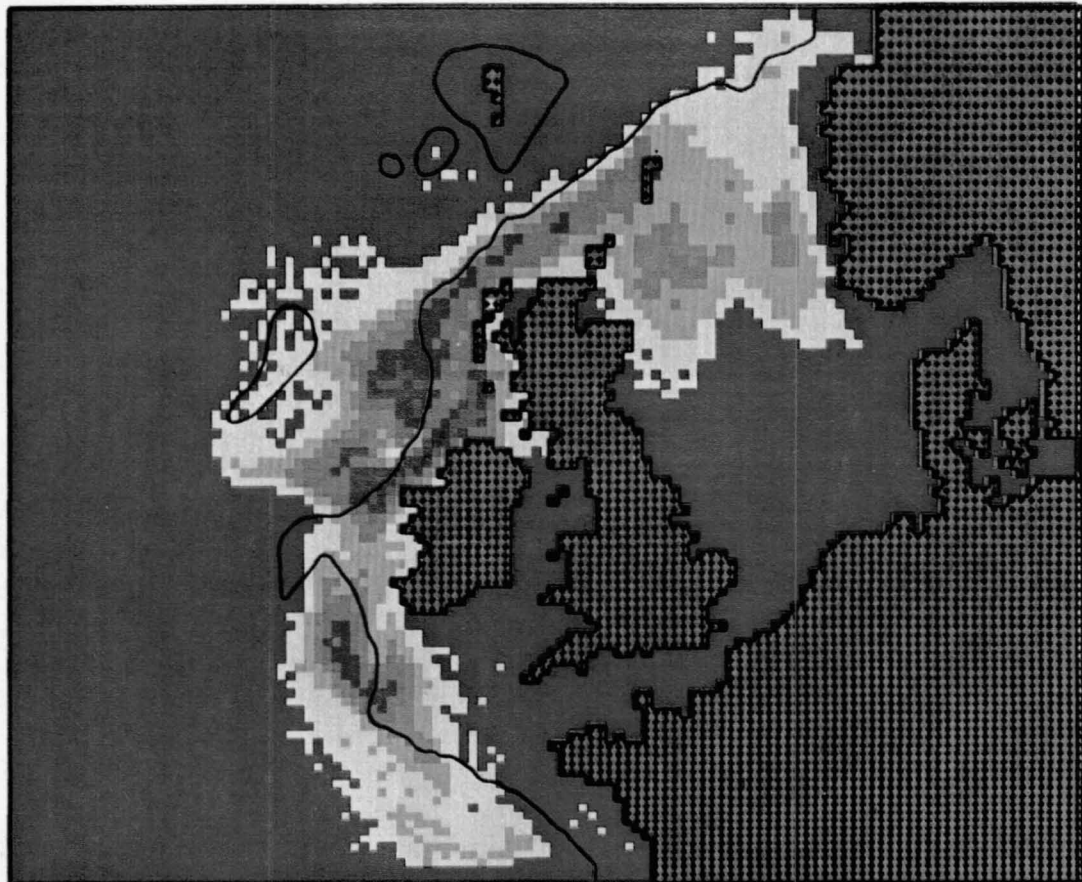


Fig. 7b. Tracer distribution after 120 days dispersion - 1994 winds.

DISCUSSION

Results from all three model simulations showed the same overall patterns. Most significantly these were the marked elongation of the distribution along the shelf-edge and into the northern North Sea and Norwegian Sea and the less pronounced generally easterly on-shelf drift of the tracers. Dispersion was evidently not a simple diffusive process but was strongly aligned to the bathymetry and driven by the shelf-edge current. This is seen most strikingly in the region south of the Faeroes Shelf where the widely-dispersed initial distribution is concentrated along the shelf-edge and flushed into the Norwegian Sea (Fig. 3 cf. Figs 6a, 7a and 8a). The general pattern of dispersion of the tracers being essentially similar to that first outlined for the drift of the larval stages by Fraser (1958) and as suggested by Bailey (1982); although somewhat more tracers are retained in the main spawning areas west of the British Isles (between one-third and two-thirds of tracers remaining in area 6 after 120 days - Table 2) than implied in Bailey (1982).

The predicted distribution of tracers after both 60 and 120 days shows some similarities with the distribution of O-group blue whiting as summarised by Bailey (1982), but which he acknowledged as not being well-defined; for example, the drift of tracers into the northern North Sea is supported by observations of O-group in that area and similarly for areas to the west of Scotland. However, the regular occurrence of young blue whiting in the international mid-water trawling surveys at the Faeroes is not supported by the results of the simulation studies which show few tracers ending in that area.

More recently, Monstad *et al.* (1996b) summarised the distribution of blue whiting, including O-group, in research trawl catches for the period 1979-1995. Although sampling was much less intensive than further south, there was still a remarkably low occurrence of the O-group in areas west of Scotland where the model results predict significant accumulation of tracers. Resolution of this apparent disparity requires a directed survey in that area for post-larvae and O-group.

In areas further afield, O-group blue whiting are regularly reported off Iceland and Greenland but it is likely that these are derived substantially from intermittent local spawning (Bailey, 1982; Sveinbjörnsson, 1975; Magnússon *et al.*, 1965). Equally, the occurrences of larvae, post-larvae and O-group off northern Norway (Zilanov, 1968) and in the Barents Sea (Boldovsky, 1939; Lahn-Johannesen, 1968) would appear to be attributable to local spawning, at least on the basis of the model results which do not indicate any significant drift north-westwards to that extent. In support of this are the observations of limited local spawning further south along the Norwegian coast (Bjørke, 1983 and 1984; Lopes, 1979).

Surveys of the O-group tend to reveal a more patchy distribution than shown in the model simulations. This may be attributed, in part, to the coherent long-term distribution used for the initial tracer distribution, when in reality in any particular year, more local variation is seen. Behavioural characteristics of the post-larvae, such as shoaling and vertical migration, may also influence subsequent dispersion as their increased motility makes them less dependent on passive planktonic drift. Growth rates of blue whiting post-larvae are not well established, but estimates of length after periods of 60 and 120 days are in the region of 10cm and 15cm respectively (Bailey, 1982). Juveniles at these lengths would typically have at least some degree of diel vertical migratory behaviour, as indicated by the observations of (Fraser, 1961), a shoaling instinct and significant swimming capability. Simulations of dispersion beyond about 60 days, and certainly beyond 120 days will be increasingly unrealistic without some input of these behavioural characteristics.

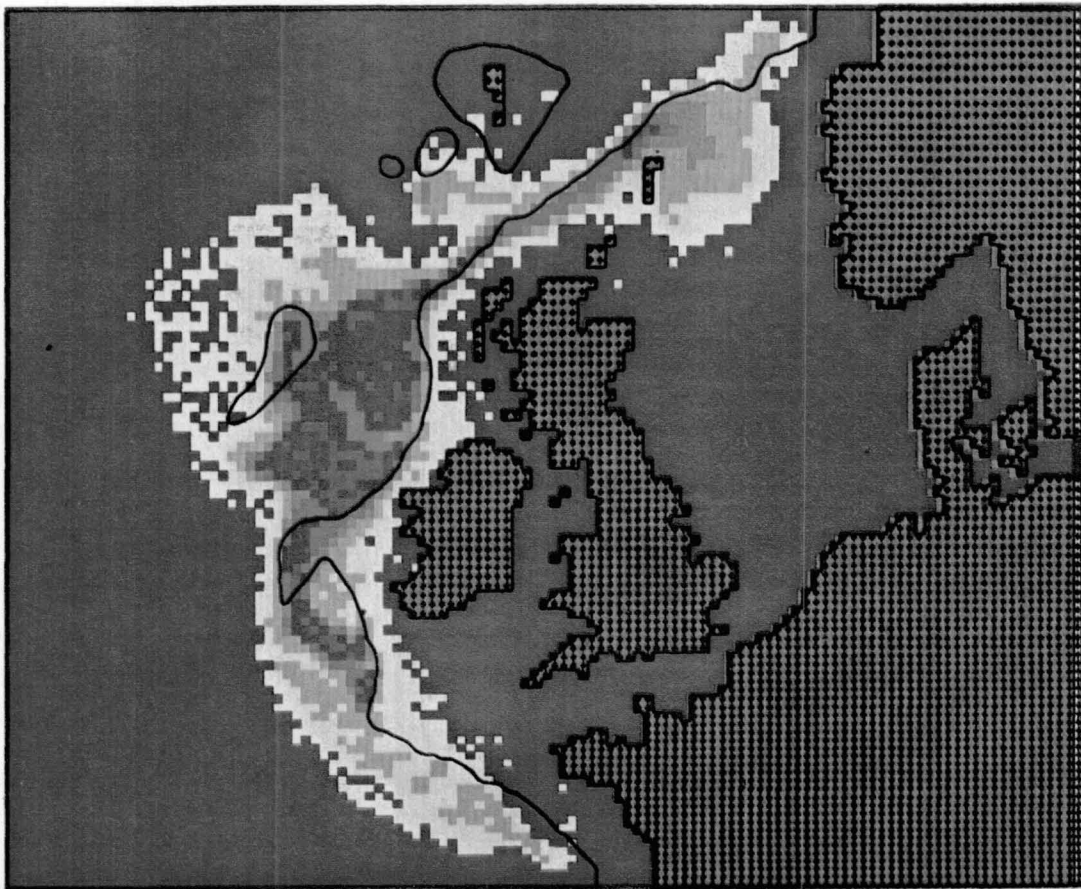


Fig. 8a. Tracer distribution after 60 days dispersion - 1995 winds.

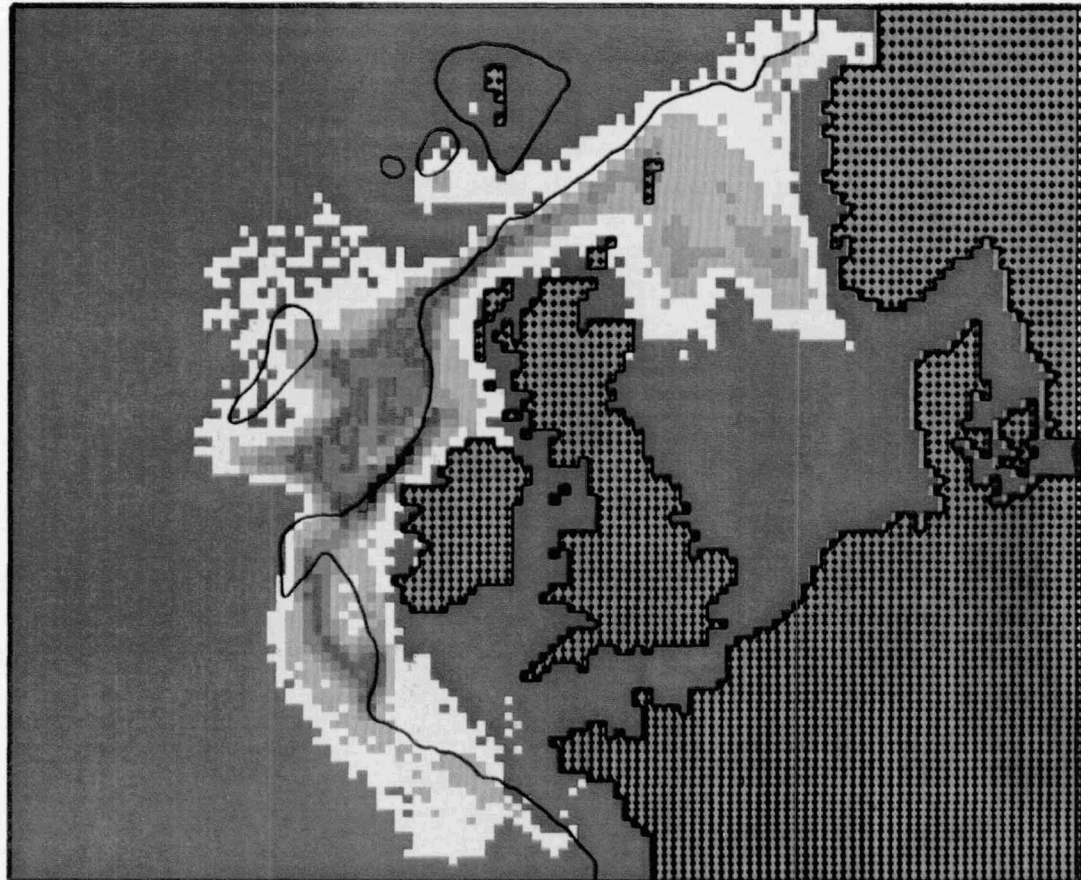


Fig. 8b. Tracer distribution after 120 days dispersion - 1995 winds.

In a discussion of the population age structure of blue whiting, Isaev and Seliverstov (1991) suggested the existence of separate Hebridean (i.e. west of Scotland) and Porcupine populations with a division at 56°N. Furthermore these authors suggested that a knowledge of the dispersion pattern of the eggs and larvae might assist in giving a clearer differentiation of these populations. The initial distribution shows a continuity from west of Scotland to south of Porcupine (Fig. 3); in contrast, the tracer distributions, in particular for the 1994 scenario (Fig. 7), show a degree of separation over Porcupine Bank at around 53°/54°N. This gives some justification for the proposals of some stock separation, but possibly with a more southerly division than indicated by Isaev and Seliverstov (1991).

While the most persistent winds were in 1994 (Table 1, Fig. 5), the resultant tracer distributions were not particularly different from the long-term climatological simulation (Fig. 7 cf. Fig. 6). The year-class strength for 1994, as recruits at age 0 (Anon, 1996), was somewhat lower than the 1981-1993 long-term mean (79% of the mean) but, allowing for the occasional previous years of much better recruitment (e.g. 1982, 1983 and 1989), the 1994 recruitment was about 10% higher than the mean of the other values. Thus, it might be concluded that recruitment for 1994 was not exceptional in any sense.

The situation for 1995 was very different, with this being the strongest year-class on record at nearly 4x the 1981-1994 long-term mean (including data for all years). The wind data for 1995 showed a low directional stability (Table 1, Fig 5) and, as a consequence, more retention of tracers in the Rockall/shelf-edge area west of Scotland and a low penetration of tracers onto the shelf. At a less marked level there was also a lower transfer of tracers to the North Sea and a slight increase in those entering the Norwegian Sea (Fig. 8).

Superficially this would indicate the survival benefits of retention in the spawning area, although as also observed in the 1995 simulation, the reduction in transport onto the shelf, irrespective of latitude, might be of more significance. A number of explanations can be postulated for enhanced survival along the shelf-edge, e.g. the elevated productivity in that region, and the benefits of avoidance of drift into relatively un-productive deep water. Inclusion of such differential mortality by areas will necessarily influence the resultant distributions.

It should be recognised that these results are derived from computer simulations and are dependent on how realistically the model reflects the actual situation. In this respect two factors should be considered relating to the horizontal resolution of the forcing functions (wind stress and density fields) and the circulation model itself. Firstly, the wind stress fields used in the simulations have a resolution of 1° which is interpolated onto the model grid. Small-scale fronts which are linked to strongly fluctuating momentum fluxes at the sea surface (von Storch, 1984) or mesoscale vortices which give rise to exceptional strong winds (Paulus, 1983) can cause strong local currents, but these phenomena are not resolved by the wind stress field used for the forcing of the circulation model. Secondly, as no quasi-synoptic density fields for the model area and the time under consideration are existent, monthly climatological density fields were used (Levitus, 1982). These data have a resolution of 1° which is interpolated onto the model grid. Although these data give a good approximation of the monthly density field for the area under consideration, they will nevertheless be different to the real density field for the time period concerned. These differences will influence the currents in specific regions and will not be reflected by the simulated currents.

Thus, the relatively coarse resolution of the input data and of the circulation model may not be ideal for studies of mesoscale phenomena. However, the large-scale circulation, which is of particular relevance to the regional drift of blue whiting larvae, is reproduced effectively. Equally there is some compensation in the capability of the circulation model to simulate the circulation over long time periods and by inclusion of the important forcing functions of the density field and real-time wind-stress.

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