Variability in transport of fish eggs and larvae. II. Effects of hydrodynamics on the transport of Downs herring larvae

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ABSTRACT: A 10-layered, finite-volume advection-dispersion model with real-time meteorological and freshwater runoff drivers investigated the interannual differences in the transport of Downs herring *Clupea harengus* L. larvae in the southern North Sea. Simulations were carried out for the winters of 1989 and 1996 to 2003. As they grew, the concentrations of herring larvae developed vertical behaviour. Meteorological forcing transported Downs herring larvae to the nursery grounds in the eastern North Sea with large interannual differences. Diel vertical movement was relatively unimportant in the transport of larvae in the hydrographically mixed southern North Sea. Year classes with less transport of larvae from the hatching area (which was generally warmer) were associated with greater abundances of young Downs herring in the ICES International Bottom Trawl Survey. This implies that retention, rather than dispersal or delivery of larvae to nursery grounds, is associated with the determination of year class strength in Downs herring.

KEY WORDS: *Clupea harengus* · Biophysical models · Downs · Recruitment · Nursery · Drift

INTRODUCTION

It has been suggested that the interannual variability in transport of herring *Clupea harengus* L. larvae in the North Sea plays a role in the determination of year class strength (e.g. Bartsch et al. 1989, Nichols & Brander 1989) and that variability in meteorology results in interannual differences in the successful delivery of juveniles to nursery grounds. These studies, centred on herring in the northern North Sea, found that whilst the broad characteristics in the transport of larvae could be reproduced, the interannual variability was difficult to model. It was, however, possible to replicate the interannual variability of the growth of larvae and juveniles in response to hydrography (Heath et al. 1997).

The spawning component of Downs herring in the southern North Sea (Heincke 1898, Cushing & Burd 1957) has recently increased in abundance. It has different meristic characteristics and life history strategies (Cushing & Bridger 1966, Geffen 2009) but is almost genetically indistinguishable (Mariani et al.

2005) from the other components of North Sea herring. With the recent recovery in abundance of Downs herring, studies were required to determine if interannual variability in larval transport was also large, as suggested for the northern components. For the North Sea herring stock, the strength of each year class is usually determined in the first 5 mo of life (Nash & Dickey-Collas 2005). Thus recruitment strength is determined prior to the delivery of herring to the nursery grounds. In the late 1970s, increased larval survival resulted in recruitment compensation associated with stock recovery (Nash et al. 2009), and decreased larval survival resulted in the recent series of poor recruitment (Payne et al. 2009). Thus an investigation of the interannual variability in transport should not only look at delivery of herring but also the period during which recruitment strength is determined (i.e. the first few months, see Oeberst et al. 2009).

The interaction of spawning site and hydrographic conditions plays an important role in the determination of larval drift or transport (Heath 1989, Laprise & Pepin

1995). Most of the dispersive drift from the spawning grounds of herring stocks in western European waters is in an easterly direction (Heath & Richardson 1989), although other studies have suggested that retention of larvae is important for recruitment success (Iles & Sinclair 1982, Sinclair & Tremblay 1984). On the continental shelf, the local hydrography is highly influenced by meteorological forcing through wind, pressure and runoff, with additional far-field effects (Otto et al. 1990), whilst near the shelf, edge hydrography is also influenced by large-scale basin effects and oceanographic currents (Fernand et al. 2006). Most of the previous studies (e.g. Bartsch et al. 1989, Nichols & Brander 1989) of North Sea herring larval drift were carried out prior to the use of geostrophic (density-driven) real-time models and thus failed to replicate most of the interannual variability. In addition, they did not account for the influence of freshwater runoff, which is important in the southern North Sea.

In the present study we modelled the transport of substances (larvae) as a function of advective and dispersive transport in order to investigate the interannual variability in transport. The larvae were assigned behaviour in the vertical plane, which is different from individual-based modelling approaches or particle tracking of ichthyoplankton (Heath et al. 1997, Hinrichsen et al. 2003). We did not model behaviour in the horizontal plane, as this is less important for herring prior to the onset of metamorphosis (Henderson 1987, Gallego & Heath 1994). The sensitivity of the modelled transport to many of the assumptions about diel vertical behaviour was tested, and the final results were compared to empirical data and indices of recruitment in Downs herring.

DATA AND METHODS

Hydrodynamic model. The hydrodynamic model used in the present study was Delft3D (Roelvink & Van Banning 1994), and has been tested and verified (Lesser et al. 2004). The model incorporates a large number of processes, such as wind shear, wave forces, tidal forces, density-driven flows, stratification, atmospheric pressure changes and the exposure and inundation of intertidal flats input in 6 hourly bins. The model was forced by data from the HIRLAM meteorological model obtained from the Royal Dutch Meteorological Service and open boundary forcing based on tidal constituents. The present study used a grid based on Erftemeijer et al. (2009) but reduced its resolution in the coastal areas to reduce computation time. The grid had 8710 computational elements and was designed to cover the southern North Sea (Roelvink et al. 2001). The flow of 18 rivers (or discard points) was included in

the model (Erftemeijer et al. 2009, this volume). The vertical resolution of the model was 10 layers, subdivided by a sigma-coordinated approach (Stelling & Van Kester 1994). The model was run for 9 yr from December of one year until June of the following year (1988–1989 and 1995–1996 to 2002–2003).

Hatching sites and times. Herring lay eggs on the sea bed (Geffen 2009), which incubate for 10 to 15 d depending on temperature, thus the modelling of transport began from the spawning locations. To replicate the benthic hatching, concentrations of newly hatched larvae were released from specific points that corresponded with hatching sites from empirical observations over the last 30 yr (Fig. 1). An equal amount of larvae were released each year, as during the years of simulation the stock size had no influence on recruitment strength (Nash et al. 2009). Mortality of the larvae was not modelled. In the Downs area, spawning starts in the western area in December and spreads to the entire area by early January. In response to the hydrodynamics over the hatching period, the transport of larvae in certain years was sensitive to time of release (e.g. 1995–1996), whereas in others it was not (e.g. 2001–2002). Therefore, surveys of herring larvae were used to determine the peak hatching time for each year (ICES unpubl. data; Table 1) and thus the release times of the larvae. The models were run from the date of start of hatching until 1 June.
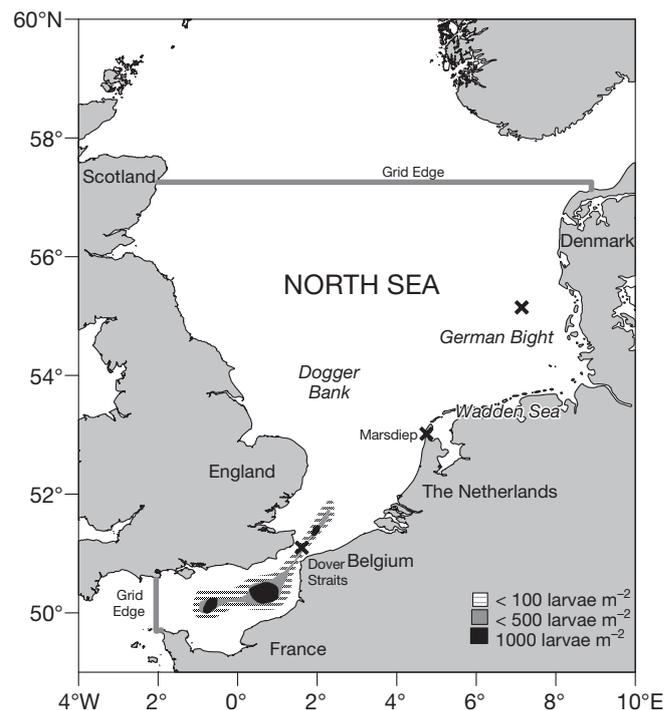

Fig. 1. Modelled area showing grid edges, locations of sampling sites (✕: Dover Strait, Marsdiep and German Bight) and release site of hatching herring larvae on the seabed

Table 1. Hatch dates (d/mo/yr) of Downs herring larvae used for each of the annual simulations

Simulation period	Hatch date
1988–1989	16/12/1988
1995–1996	03/01/1996
1996–1997	02/01/1997
1997–1998	29/12/1997
1998–1999	18/12/1998
1999–2000	05/01/2000
2000–2001	20/12/2000
2001–2002	05/01/2002
2002–2003	26/12/2002

Growth of larvae. Herring larvae change their growth rate with size, temperature and feeding, the latter of which is in turn influenced through prey density, turbulence and light (Gallego 1994, Gallego & Heath 1997). Many studies have tried to measure growth rates empirically, but it is often difficult to resolve the variability in the field due to the interaction of sampling effects and the influencing variables themselves (Gallego et al. 1996, Folkvord et al. 2004). This is confounded by the inability to accurately read the otoliths of slow-growing larvae (Fox et al. 2003). Energetic models can provide information on maximum possible growth rates (Fiksen & Folkvord 1999) and, assuming that the survivors of a population of larvae tend to be the fastest growing (Houde 2008), these maximum growth rates can be used as long as the assumptions are acknowledged. The growth of larvae in the present study was modelled based on the energetics model of Fiksen & Folkvord (1999), assuming food was not limiting; thus specific growth was only dependent on temperature.

In the model, 3 stages of larvae were assumed and distinguished as follows:

Stage 1: Downs larvae hatch at 9 mm. The Fiksen & Folkvord (1999) model is weight-based so the length was converted to dry weight using the relationship $W = 6.1807e^{0.263L}$, where W is weight in μg and L is length in mm (C. Clemmesen unpubl. data). The concentrations of yolk-sac larvae then developed and respired dependent on the ambient sea temperature, until they reached 80% of their initial hatch weight. This 80% threshold was the trigger to start feeding and begin Stage 2.

Stage 2: The concentrations of larvae developed, assuming an unlimited food supply, through Stage 2 according to the growth model of Fiksen & Folkvord (1999) until they were 16.5 mg in dry weight. This is the weight of a 30 mm larvae following the length–weight relationship described above. This threshold triggered Stage 3.

Stage 3: The 30 mm length represents the beginning of metamorphosis (Heath et al. 1997), which can last until 50 to 55 mm in length (Gallego & Heath 1994).

Throughout Stage 3, the concentrations of larvae still followed the optimum growth trajectory as described by Fiksen & Folkvord (1999).

Behaviour of larvae. The present study tried to simulate the vertical behaviour of the herring larvae, as the assumption that larvae are passive drifters results in unrealistic simulation results (Blaxter 1973, Werner et al. 1993). The stage-dependent behaviours were applied to the concentrations of larvae, which grow as described above. The 10 layers of the hydrodynamic model were used to model behaviour of the herring larvae.

Stage 1: The concentrations of yolk-sac larvae hatched into the bottom layer and increased their buoyancy, thus they rose into the upper water column (Blaxter & Ehrlich 1974, Ying & Craik 1993). However, the buoyancy increase was reparameterised to fit the present model. Other than increasing buoyancy, the concentrations of larvae were passive.

Mechanism for diel migration: Field studies suggest that as larvae grow, they begin to search for food and this search becomes more extensive the larger they are (Gallego 1994, Fox et al. 1999). With plenty of food and light and a well-mixed water column, the main driver of their transport will be the hydrodynamics. However, if food is limited, the larvae will take on water as they starve (and thus become more buoyant) and they will also increase their search area. For smaller larvae, this change in behaviour is insignificant to the effect of hydrodynamics, but for larger larvae the individual movement can be significant in relation to the hydrodynamics. The search for food results in diel vertical migrations with larvae accumulating nearer the surface during day (Stephenson & Power 1988, Munk et al. 1989, Heath et al. 1991).

This development to diel migration was replicated in behavioural Stages 2 and 3 of the model (Table 2, Fig. 2). Vertical migration of herring larvae was achieved by a settling and/or buoyancy velocity. This acted as a proxy for the influence of zooplankton on feeding behaviour, and larvae were made to aggregate nearer to the surface during the day and influenced by dispersion due to turbulence alone during the night. The larvae were concentrated in a specific part (larval layer shown as z_{bot} and z_{ampl} in Fig. 2) of the water column. Concentrations of larvae which resided above this layer were given a settling velocity: larvae within the layer had a neutral settling velocity and larvae that resided below this layer were given a negative settling velocity (i.e. buoyant). During a 24 h day:night cycle, the larval layer increased and decreased according to a sine curve on the bottom of the layer (z_{ampl}, Fig. 2).

Stage 2: The amplitude of the z_{ampl} sine curve was increased during this stage. Thus the new Stage 2 larvae began with small vertical movements. As the lar-

Table 2. Growth and behavioural stages used in the simulation of herring transport

Stage	Period	Behaviour	Source
1	From hatching to 80% of initial hatch weight	From hatching, increases buoyancy until in top 10 m of the water column	Blaxter & Ehrlich (1974), Ying & Craik (1993)
2	From end Stage 1 to 30 mm (16.5 mg dry weight)	Begins to develop feeding behaviour resulting in diel migrations which increase in magnitude with time	Munk et al. (1989), Heath et al. (1991), Fiksen & Folkvord (1999)
3	From 30 mm onwards	Full dynamics of diel migrations caused by feeding; movement not restricted	Heath et al. (1997)
Not modelled	From 60 mm onwards	Metamorphosis begins and individuals begin to aggregate	Gallego & Heath (1994), Fiksen & Folkvord (1999)

vae grew, the amplitude of the aggregations would increase to the maximum amplitude at the beginning of Stage 3.

Stage 3: The Stage 3 larvae were assumed to show the full potential for diel migration (Table 2). Thus once the concentrations of larvae were >30 mm in length, they moved onto the third behaviour of unrestricted diel migration.

Larval fish are known to show oriented swimming at a small size (Leis et al. 2006), but the present model could not account for this. Swimming and shoaling (aggregation) of herring larvae is also known to become more active after metamorphosis (Heath & Richardson 1989), but this was not included in the model. Initial runs of the model suggested that the lar-

vae never reached full metamorphosis during the simulated time period. The influence of salinity was not modelled.

Analysis of model output. The outputs of the model were quantified in 4 ways. First, contour plots were generated of the depth-integrated concentrations (no. m^{-2}) on a chosen day of the model run. Second, the term 'transport success' was used to describe the number of larvae in a pre-determined nursery area (described in Fig. 4 of Erftemeijer et al. 2009). Third, time of arrival at a given point was used as an indicator of the concentrations of larvae. This was mapped as a time series at 3 chosen points: Dover Strait (51° 05' N, 1° 30' E), Marsdiep at the southern end of the Wadden Sea (52° 58' N, 4° 40' E, chosen to compare with empir-

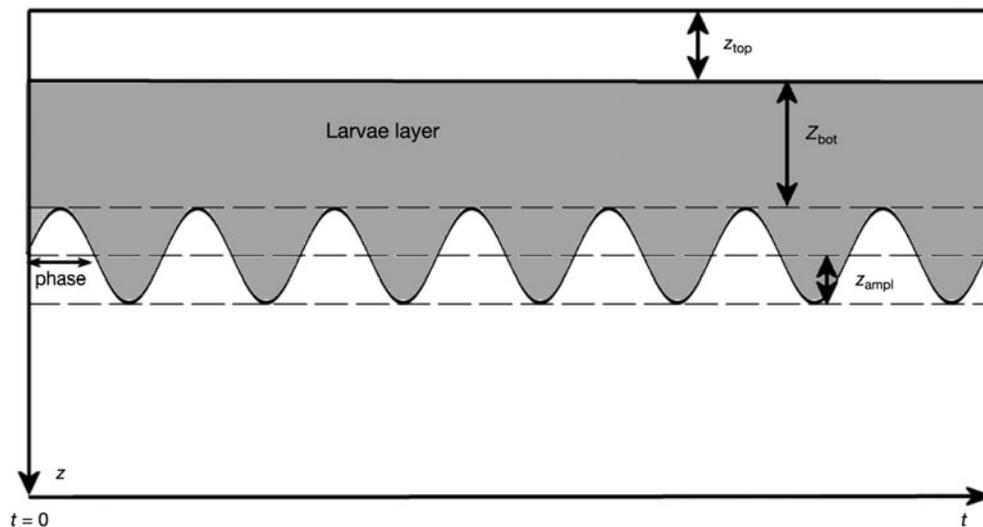Fig. 2. Schematisation of the vertical migration of herring larvae. Larvae were not present in surface layer (z_{top}), but were present in $z_{bot} + 2z_{ampl}$ (z_{bot} = depth of main larval layer; z_{ampl} = depth of amplitude of diel migration). The diel vertical distribution was driven by the amplitude and phase of the sine wave. This schematisation represents the behaviour of Stage 3 larvae. Stage 2 larvae began at $z_{ampl} = 0$ and finished the stage with the same z_{ampl} as Stage 3. Top and bottom of diagram represent sea surface and bottom, respectively

ical data) and a point in the middle of the German Bight (55° 00′ N, 7° 00′ E). Lastly, an index of the mean distance travelled was estimated by determining the weighted position of the centre of the concentration of larvae for each day of the model run (depth-integrated) and summing the distance the centre moved each day.

Various aspects of the assumed diel behaviour and growth were tested to ensure that the model was not overly sensitive to its assumptions.

Comparisons with empirical data. In addition to the ICES herring larvae survey, which was used to create the hatching grid and the average hatch dates, there are 3 survey time series that can provide information to compare to the model simulations and validate the results: (1) ICES coordinated Methot Isaacs-Kidd net surveys (MIK), (2) Wageningen IMARES Wadden Sea stow net larvae surveys (Stow) and (3) ICES coordinated International Bottom Trawl Surveys (IBTS). Importantly, no information from these 3 surveys was used to initially calibrate the model. The behaviour rules and growth parameters were taken from published information and models.

Recruitment time series. There are no stock assessment-based estimates of the recruitment of Downs herring, only estimates for the whole North Sea herring stock. The MIK net surveys provide an index of year class strength, but this series has historically had poor spatial resolution in the southern North Sea in the 1990s. The IBTS has been used as an indicator of Downs herring abundance by using the length of herring (Wood 1959, ICES 2009); there are many untested assumptions in this procedure, but it has been generally accepted as suitable.

RESULTS

Transport of larvae to destinations

The simulations suggest that interannual variability in hydrodynamics and hatching date results in different transport of herring larvae between years. However, some characteristics of transport were common (Fig. 3). Almost no larvae moved westward out of the
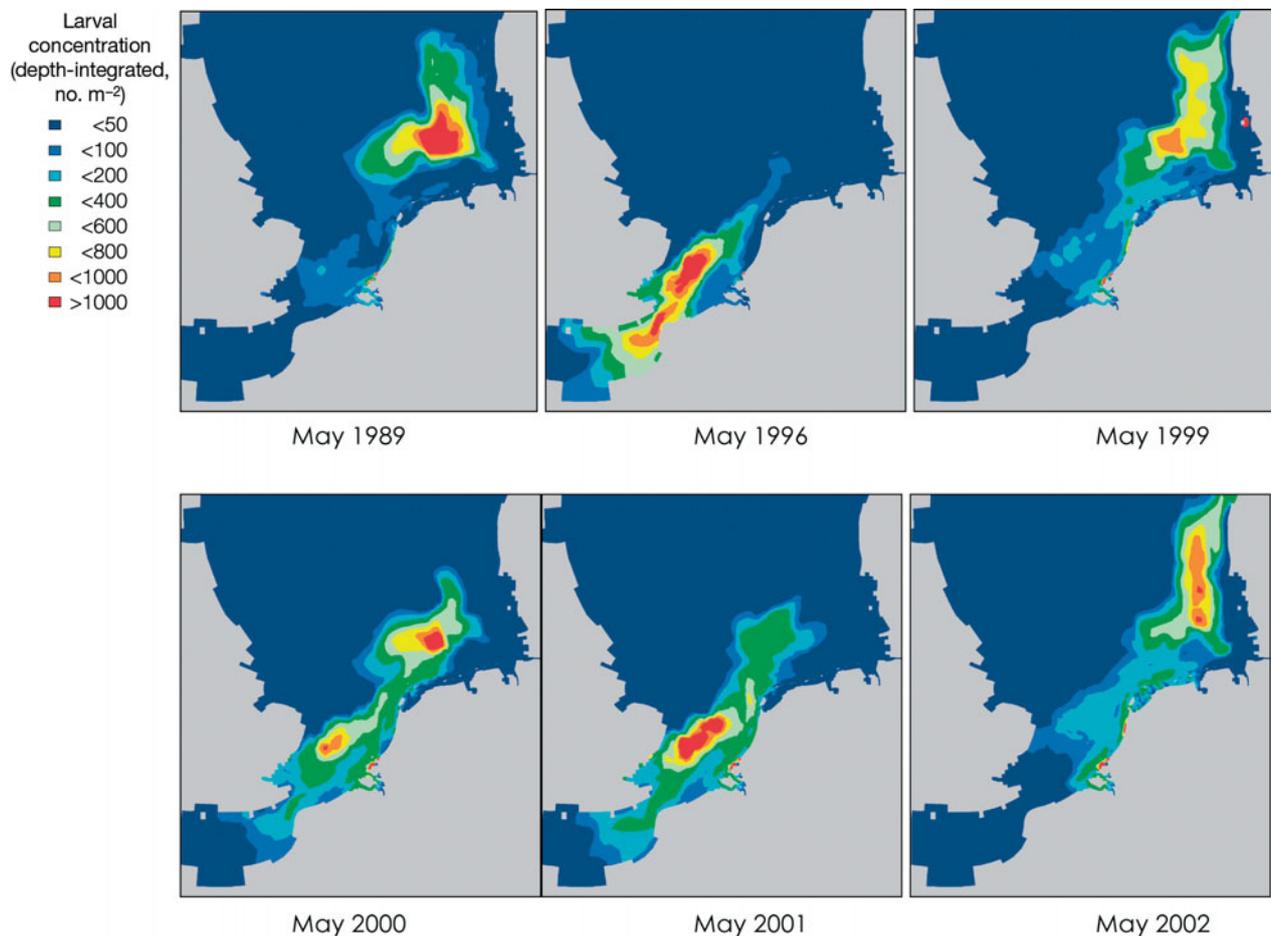

Fig. 3. Predicted concentrations of late-stage herring post-larvae on 31 May by year

model grid. Loss from the total grid was low (Table 3). In most years the concentrations of larvae were in the German Bight by late May. There were 3 outliers: (1) 1995–1996 larvae remained in the south and with little transport; (2) 1998–1999 larvae reached the northeast of the grid; and (3) 2001–2002 larvae reached the northeast of the grid.

In 1988–1989 and 1998–1999 the larvae moved through the mouth of the English Channel in one pulse in early January (Fig. 4), a pulse also occurred in 1996–1997 but this was later in early February. The winters of 1995–1996 and 2002–2003 were noticeable as the concentrations remained high in the eastern mouth of the Channel from January to March. The lar-

Table 3. Location of concentrations of larvae by the end of the model run (31 May). Values are the proportion (%) of the total larvae hatched at the beginning of the run. Locations described in Fig. 1 of Erftemeijer et al. (2009, this volume). Year describes winter–spring seasons

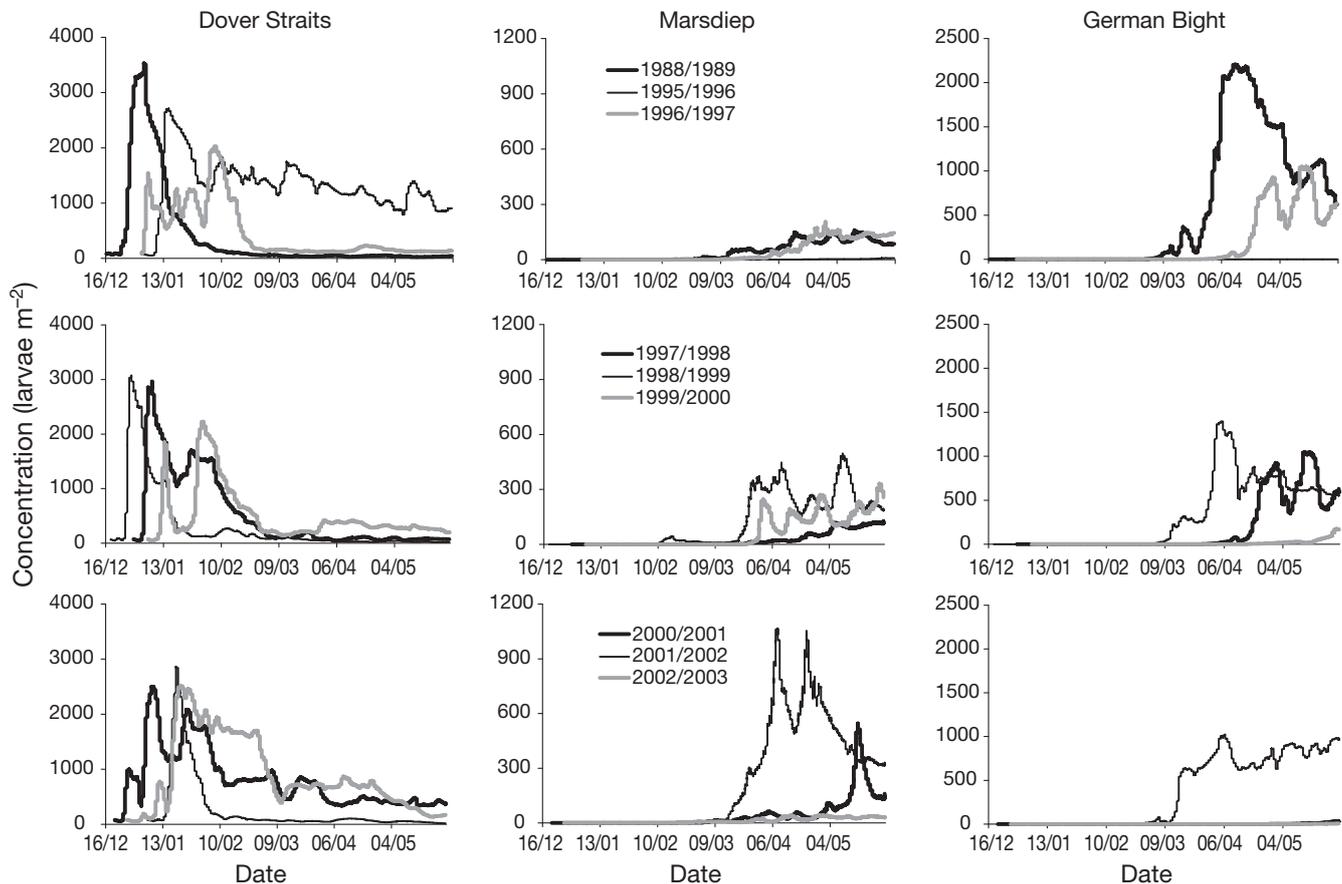| Year	Lost from grid	Coastal	English Channel	Southern North Sea	German Bight	Central North Sea
1988–1989	5.5	3.5	0.8	5.8	60.8	23.6
1995–1996	13.3	8.3	29.8	45.6	0.6	2.4
1996–1997	8	6.3	4.9	24.1	26.8	29.9
1997–1998	3.1	3.7	1.6	15.5	60.1	16.0
1998–1999	8.3	5.4	0.5	8.2	66.5	11.1
1999–2000	4.6	7.5	5.1	33.4	29.7	19.7
2000–2001	9.6	9.2	34.7	51.6	0.0	0.0
2001–2002	7.8	8.2	0.5	10.6	67.0	5.9
2002–2003	6.8	5.9	4.4	53.1	13.0	16.8
Mean	6.9	6.4	9.1	27.5	36.1	13.9
CV (%)	44	31	145	69	78	71

Fig. 4. Concentrations of larvae (depth-integrated, no. m^{-2}) by date at 3 points in the model grid: Dover Strait, Marsdiep and German Bight (see Fig. 1). Dates are dd/mm

vae entered the Wadden Sea from late March onwards, probably peaking in late April–early May. The interannual variability in the delivery of larvae to the Wadden Sea was large (Fig. 4). By late May, the open sea had higher concentrations of herring, with over 90 % found in areas >20 m depth (Table 3). Of the coastal areas, both the English coast and the Scheldt estuary had higher numbers of larvae than the Wadden Sea.

Modelled growth

There was little difference between the years in the duration of the yolk-sac phase (mean = 6 d, coefficient of variation [CV] = 5 %, Fig. 5). The variability in the duration to 30 mm in length (the end of Stage 2 in this simulation) increased slightly to CV = 8 % (mean = 71 d, Fig. 5). Unsurprisingly, the variability in duration is caused by the average temperatures of the larvae (7.9 to 9.2°C, Fig. 5). The mean temperature of the larvae up to 30 mm in length for all 9 annual simulations was 8.5°C, CV = 5 %.
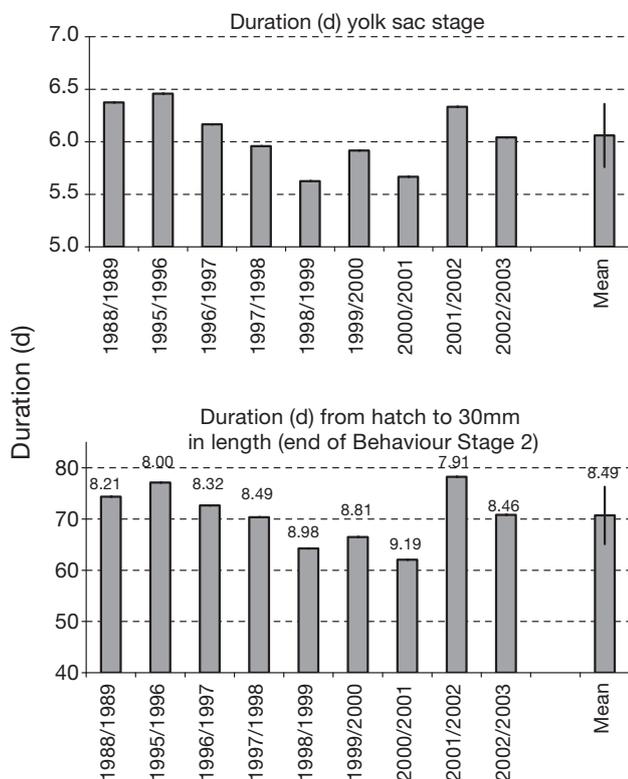

Fig. 5. Interannual variability in stage duration of herring larvae. (a) Simulated duration of yolk-sac stage in days. (b) Simulated duration from hatch to 30 mm in length in days; values above bars indicate mean temperature (°C) of the larvae for that year. Error bars denote SD of the mean duration

The model suggests that the larvae should be between 37 to 40 mm in length by the time they enter the Wadden Sea. The only exception was simulated year 2001–2002 (the coldest year), when larvae began to enter the Wadden Sea at just 30 mm in length.

Impact of interannual variability

In mid-February, by when year class strength is determined (Nash & Dickey-Collas 2005), there appears to be little difference between the years in the distribution of larvae (Fig. 6). Closer inspection does show differences, e.g. in spring 2002 the centre of the concentration of larvae was 340 km further away from the hatch site compared to the centre in spring 1996. The index of mean distance travelled varied between years with a range of approximately 200 km at 30 mm in length (Fig. 7).

In general, the years with greater horizontal movement (distance travelled) were associated with lower temperatures, although this was not the case for spring 1996. Apart from spring 1996, the shorter stage durations were associated with years where the larvae moved less distance (Figs. 5 & 7).

No relationship was found between most of the recruitment and transport indices (total North Sea herring recruitment from the stock assessment, total North Sea MIK net index and southern North Sea MIK index). However, the Downs IBTS index (which uses size to distinguish Downs spawned herring from other North Sea herring in the IBTS) showed a strong relationship to the distance travelled (Fig. 7). It was judged to better fit an exponential relationship rather than a linear relationship (although both were significant), as a linear model would lead to the assumption that there was a maximum distance travelled or displacement which would result in a Downs IBTS index of zero.

Sensitivity of model to assumptions about behaviour

The effect of a day–night compared to a night–day diel migration was found to be <0.2 % on the final location of the larvae or the timing of delivery. A larger maximum amplitude for the diel migration (from 5 to 10 m) resulted in slightly more shoreward movement of concentrations of larvae. This reflected the shoreward movement of water closer to the seabed in the coastal areas. The differences in transport caused by these assumptions were small when considering transport to the main nursery area (central and eastern North Sea, 2 % change), but were more substantial when considering transport to the coastal areas (5 to 20 % change).

The removal of individual stages of behaviour affected the results. If Stage 1 was removed and the larvae hatched immediately into Stage 2, then the larvae moved further. However, this did not result in major differences in the delivery of larvae to the German Bight. In contrast, the removal of Stage 2 or 3 had little effect on the transport of larvae, suggesting that the transport of the herring larvae in the southern North Sea is not sensitive to the development of diel migration.
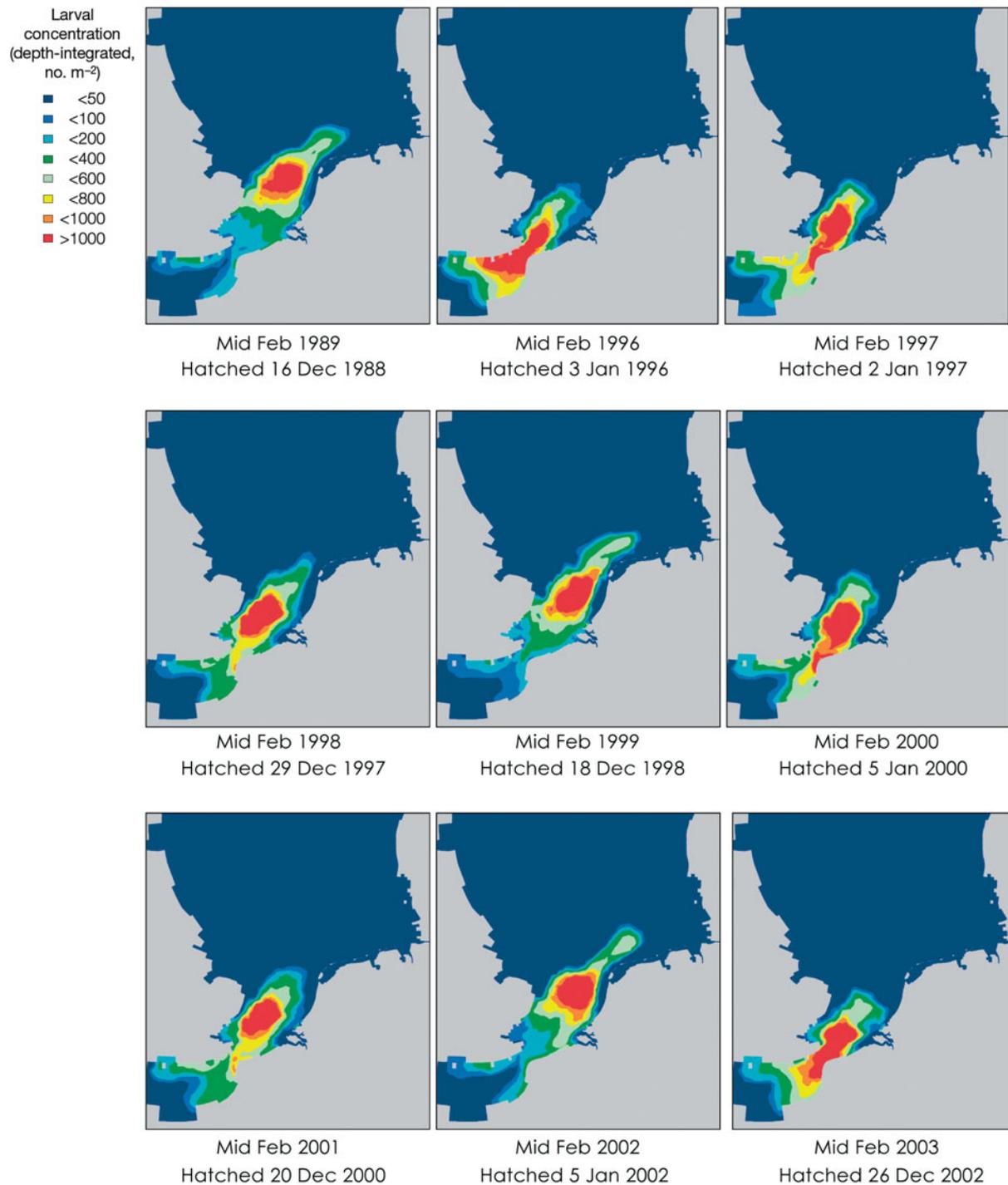

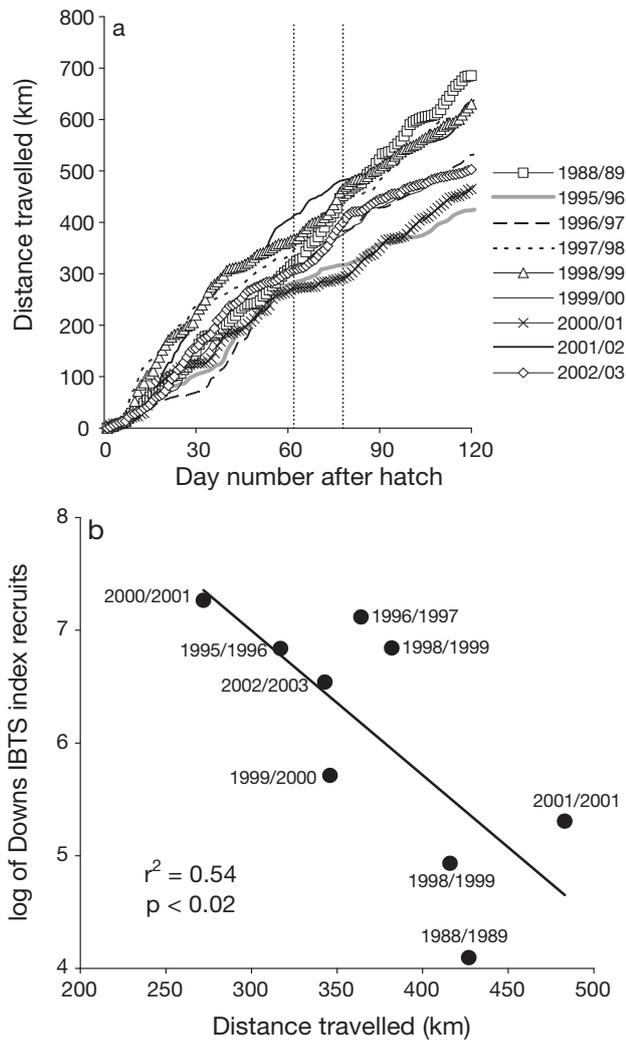Fig. 6. Predicted concentrations of late stage herring post-larvae in mid-February by year

Fig. 7. Mean distance travelled by larvae by year. (a) Sum of the total daily horizontal distance travelled from hatch by year. Dotted vertical lines denote the approximate time when the larvae reach 30 mm in length. (b) Downs herring International Bottom Trawl Surveys (IBTS) index (logged)—as a proxy for recruitment of Downs herring—over mean total distance travelled by larvae from hatching to 30 mm in length by year

Simulations were carried out with constant temperature (8, 9 and 10°C). There was no discernable effect of temperature on the transport of the larvae. Fixing temperature affected the estimated development times and the time to 30 mm in length (onset of metamorphosis) varied by 24 d between 8 and 10°C, but this had little influence on larval transport.

Comparisons with empirical data

The ICES MIK net survey targets late and/or post-larvae of herring and shows broad agreement with the simulated results of the present study. Larvae by mid-February are generally in the Southern Bight and off the Belgian and the southern Dutch coasts (ICES 2009, their Fig. 2.3.3.1). Due to the poor sampling resolution of the MIK net survey, direct year-to-year comparisons of spatial variability were not possible. Also, the present study did not model mortality or variable hatching, thus direct comparisons of abundance were not possible. The mean length of larvae caught in the MIK net is 18 mm, which is in agreement with the simulated results of the transport model in the present study (Fig. 8).

The stow net survey from the Wadden Sea (1967–1989) is the most relevant of the surveys to the present study, as it sampled at a high temporal resolution the abundance of herring larvae at the mouth of the Wadden Sea (the Marsdiep). The estimated arrival of the Downs component of herring larvae from the modelled simulations is April (Fig. 4), which is similar to that from the stow survey. Unfortunately, only one year of simulations and surveys overlap, 1988–1989, and here both the simulations and survey show larvae appearing after mid-April. However, in all years and particularly in 1989, the model predicts that larvae continuously arrive in the Wadden Sea, whereas the surveys show clear peaks with no more larvae entering after May. An explanation for this is that the simulations do not account for selective mortality and the avoidance of the stow net by growing and aggregating young herring. The simulations overestimate growth, as by the middle of April the larvae were 37 to 40 mm in length, whereas those caught in the stow net were between 30 and 34 mm in length.

The IBTS describes the juvenile nursery grounds of herring in the southern North Sea from all spawning components (ICES 2009, their Fig. 2.3.3.3). The desti-
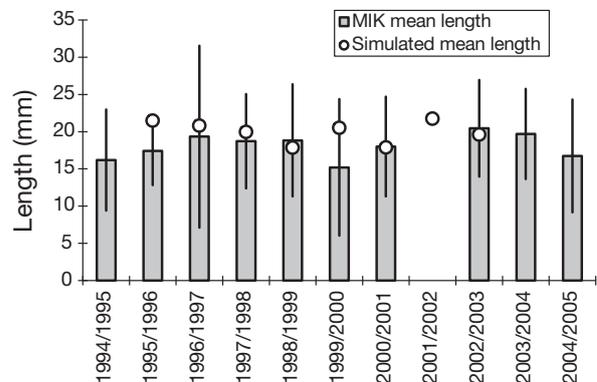

Fig. 8. Mean lengths of herring larvae (mm) in mid-February by year as estimated from empirical catches in the Methot Isaacs-Kidd (MIK) net surveys and by the temperature-dependent growth model used in the simulation of larval transport. Error bars are 95% confidence intervals of empirical estimates

nation for the herring larvae can be inferred from location of juveniles in the IBTS (autumn surveys). The IBTS shows that the German Bight and the Dutch coast are the most important nursery areas for herring, in agreement with the simulations.

DISCUSSION

The present study shows that almost all Downs herring larvae move east after hatching (Figs. 3 & 6). There was no incident of westerly movement of larvae in any of the 9 yr studied (Table 3). Meteorological differences, which force the hydrography, resulted in interannual differences in transport of Downs larvae but generally the larvae were delivered to the nursery grounds in the southeastern North Sea. It appears that the diel vertical migration is not a crucial part of the transport mechanism in Downs herring (see Stephenson & Power 1988). This may be due to the mixed and highly variable hydrodynamics of the southern North Sea in winter and spring. The situation for the other components of North Sea herring may be different (Heath et al. 1997), as they spawn in autumn where the water column is more structured (stratified). These simulations appear to support some of the findings of previous North Sea studies (Bartsch et al. 1989, Nichols & Brander 1989) in that interannual variability in transport does appear linked to recruitment variability (Fig. 8). It is not the delivery of the larvae that is related to year class strength but other mechanisms associated with transport as shown by the relationship with larval retention (distance travelled, Fig. 7). Holding larvae in areas of higher productivity has been suggested as a mechanism for larval survival (Dickey-Collas et al. 1997). Iles & Sinclair (1982) viewed retention as an important mechanism for the success of herring spawning. Their argument related to areas of thermal stratification; however, as many herring spawn in autumn and winter when the water column is mixed, this argument was dismissed by some. We suggest that retention (less distance travelled) may well be associated with year class strength in Downs herring, which is determined by mid-February, but not as a result of retentive areas associated with gyres and fronts, but as a result of differences in meteorological forcing of the hydrography. The retention of larvae is also associated with higher year class strength in North Sea plaice larvae (see Bolle et al. 2009, this volume). Other than 1995–1996, the years with less larval transport were associated with warmer temperatures, and hence faster development. Although development time was not significantly related to year class, there was a trend in that years with shorter stage durations were associated with stronger year classes (linear correlation, p < 0.1).

The use of a finite-volume advection-diffusion model for investigating the transport of fish larvae rather than a particle tracking model could be viewed as unusual. However, as long as the limitations of this approach are acknowledged, the approach can still investigate the transport of substances (larvae), especially when they are given behaviour (Werner et al. 1993) and coastal dynamics are taken into account. The hydrodynamic model closely replicated the salinity and transport fields in along the Dutch and German coasts (Erftemeijer et al. 2009). The tidal flat component ensured that the model had 'soft edges' and described the coastal dynamics well. The model did not account for far-field drivers such as oceanic input from beyond the grid, but the validation studies suggest that these influences are less in the southern North Sea than the northern North Sea (Erftemeijer et al. 2009, Hjøllo et al. 2009, Petitgas et al. 2009).

The choice of hatching sites was based on the survey time series from ICES (ICES 2009) and also corresponded to those described by Burd & Howlett (1974). The energetic approach used by Fiksen & Folkvord (1999) proved useful and was in agreement with the larval lengths in the MIK net surveys (Fig. 8), but overestimated larval length by mid-April (as estimated from the stow net survey). The assumption that all larvae fed well in the present study may not be correct, although larvae were caught in the stow net as large as the simulated larvae, suggesting that the potential maximum growth was correctly estimated. Heath et al. (1997) used a similar approach and also overestimated the growth of Downs larvae by 9%. The small interannual variability in growth in Downs herring (stage duration, Fig. 5) was also found by Heath et al. (1997), who suggested that variability in growth was larger in the northern component of the stock compared to the southern.

Vertical behaviour was not important in determining transport in Downs herring larvae. Removing Stage 2, lengthening a stage duration (by lowering the temperature) or changing the phase of the diel cycle or the amplitude of the migration had little impact on the delivery of larvae to the German Bight. Transport to the coastal regions was slightly more affected. However, this diel migration must be incorporated into the model as it is an important larval behaviour and could impact larval transport if not accounted for (see Fox et al. 2006, Bolle et al. 2009).

The model used in the present study did not account for active horizontal movement. Temperate larvae may show less directional swimming at slower speeds than those in the tropics (Leis et al. 2006) and also require a point of reference, whether sound, light or the seabed. When considering the older larvae modelled in the present study did not reach full metamorphosis, the

impact of lack of directional swimming on larval transport is thought to be small.

Downs herring was the first North Sea component to collapse due to overexploitation in the 1960s, and took the longest to recover once fishing was reduced (ICES 2009). North Sea herring is currently experiencing a series of poor recruitments despite a relatively high biomass of mature fish (Payne et al. 2009). It should not be assumed that the processes that determine year class strength are the same for all spawning components of North Sea herring, or the same over the entire time series (Nash et al. 2009). Reduced transport from the hatching site may be implicated as a proxy for the processes that determine recruitment strength in Downs herring, but it may not be generalisable to the other spawning components of North Sea herring. In conclusion, meteorological forcing transports Downs herring larvae east from the spawning sites to the nursery grounds. The hydrodynamic model appeared to simulate transport and growth well. The interannual variability in transport (distance travelled) of larvae by the time of year class determination (February) is associated with relative year class strength over the period studied, and not delivery success to the nursery grounds.

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