

Bio-physical models reveal the role of tides, wind and larval behaviour in early transport and retention of Atlantic herring (*Clupea harengus* L.) in the Celtic Sea.

Inge Deschepper^{1,3}, Kieran Lyons², Olga Lyashevskaya¹, Deirdre Brophy^{1*}

¹. Marine and Freshwater Research Centre, Galway Mayo Institute of Technology, Dublin rd Galway H91 T8NW, Ireland.

². Marine Institute, Renville, Oranmore, Co. Galway, H91 R673, Ireland

³. *Current affiliation*: Department of Biology, Laval University , 2325, rue de l'Université, Québec, G1V 0A6, Canada

*Corresponding author: tel: +353 91 742484, email: deirdre.brophy@gmit.ie

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16 **Abstract**

17 Fish are adapted to spawn where their larvae will be retained in, or transported to suitable
18 juvenile habitat. Variability in circulation and behaviour produces variation in larval transport
19 with consequences for recruitment. A bio-physical model was used to simulate early larval
20 dispersal of Celtic Sea herring during wintertime in six years (2002, 2003, 2004, 2005, 2008,
21 2010). After 30 days, particles occurred in three areas: inshore Celtic Sea, offshore Celtic Sea
22 and south Irish Sea, with the majority (70-78% on average) of particles retained in the Celtic
23 Sea. Inclusion of tidal forcing increased transport to the Irish Sea and decreased transport
24 offshore, as did release during a spring tide. Retention in the Celtic Sea was increased by diel
25 vertical migration and decreased by horizontal diffusion. Strong and frequent west/south-
26 westerly winds increased transport offshore while strong and frequent east/south-southeast
27 winds increased inshore retention in the Celtic Sea and transport into the Irish Sea. The study
28 shows how tides, winds and behaviour influence larval transport and retention and highlights
29 potential impacts of climate change on population persistence.

30

31 **Introduction**

32 Larval transport processes exert a critical influence on the dynamics of fish populations.
33 Physical oceanographic mechanisms interact with the behaviour of spawning adults and their
34 developing eggs and larvae to regulate delivery to suitable nursery habitats via dispersal or
35 retention (Pineda et al. 2007; Stephenson et al. 2015; Zölck et al. 2015). The distribution of
36 eggs and larvae in relation to ocean currents determines spatial overlap between different
37 spawning events and drives population connectivity (Cowen and Sponaugle 2009; Cowen et
38 al. 2007). Inter- and intra-annual variability in hydrodynamic and meteorological conditions
39 can contribute to temporal variation in larval distribution (Pacariz et al. 2014), survival
40 (Hinrichsen et al. 2012), growth (Vikebø et al. 2005) and abundance (Nielsen et al. 1998), with
41 consequences for subsequent recruitment success (Baumann et al. 2006) and population
42 exchange (Huwer et al. 2016; Nielsen et al. 1998).

43 Atlantic herring is a species that is characterised by highly variable recruitment and complex
44 population structure (Geffen 2009; Parrish and Saville 1965). For over a century,
45 investigations of how larval transport processes influence recruitment and population
46 structure in herring have informed the pivotal theories that continue to direct fisheries
47 science research (Sinclair 2009; Stephenson et al. 2009). The interaction between larval
48 biology and physical oceanographic features is central to Hjort's aberrant drift hypothesis
49 (Hjort 1914) and Iles's and Sinclair's member/vagrant hypothesis (Iles and Sinclair 1982).
50 Advances in oceanographic modelling of the larval environment have provided insight into
51 the mechanisms underlying variability in transport and retention of herring larvae and have
52 helped to identify hydrographic and meteorological drivers of year-class strength (Bartsch et
53 al. 1989; Corten 2013; Dickey-Collas et al. 2009; Skagseth et al. 2015).

Coupled biophysical models provide a means to reconstruct larval transport processes that are difficult to observe directly (Hinrichsen et al. 2011). The development and refinement of this approach has enabled the examination of larval dispersal at high spatial and temporal resolution and at an individual level (Miller 2007). Coupled biophysical models can be used to validate the biological assumptions on which fisheries models are based and to evaluate management measures (Hinrichsen et al. 2011). By reconstructing larval transport under different conditions, dispersal simulations can help to forecast the likely impacts of changing circulation patterns on the connectivity of life history stages within the context of climate change (Llopiz et al. 2014; Rijnsdorp et al. 2009).

In the Celtic and Irish Seas mixing of herring spawning components creates difficulties for the management and assessment of the fisheries. The Celtic Sea herring stock is comprised of an autumn and winter spawning component which are managed as a single unit (ICES, 2016) although reproductive exchange between the components appears to be limited by spawning season fidelity (Brophy et al 2006). Celtic Sea herring spawn at discrete locations along the south coast of Ireland (O’Sullivan et al 2013) (Figure 1). The distribution of the two spawning components overlaps, but autumn spawning is more common in the western Celtic Sea and winter spawning is more common in the eastern Celtic Sea (O’Sullivan et al 2013). In the Irish Sea, herring spawning activity is concentrated along the coast of the Isle of Man in September and October; some spawning also occurs on the north east coast of Ireland in autumn (ICES, 2016). This stock is managed as discrete unit, but due to juvenile mixing recruitment is difficult to forecast. Therefore, a priority for the management of the Irish and Celtic Sea herring fisheries is to determine the degree of mixing that occurs during the juvenile phase (ICES, 2016).

Larval transport and retention processes are likely to play a particularly important role in population connectivity and recruitment dynamics of Celtic and Irish Sea herring. Evidence from otolith microstructure indicates that during the larval phase the Celtic Sea winter spawning population splits into two components: one that disperses to Irish Sea and a second that is retained within the Celtic Sea (Brophy and Danilowicz 2002). Differences in larval otolith growth patterns between the dispersed and the retained components suggest that transport happens early in the larval phase within a month of hatching. During the juvenile phase, the dispersed winter spawned herring from the Celtic Sea occur in the Irish Sea together with juveniles from the resident autumn spawned population (Brophy and Danilowicz 2002; Burke et al. 2009). The dispersed and retained components of the Celtic Sea winter spawned stock show marked differences in juvenile growth rates and maturation patterns (Brophy and Danilowicz 2003). The dispersed component appear to return to the Celtic Sea as adults to spawn but are on average a year older at the time of first spawning than the retained component (Brophy and Danilowicz 2003; Brophy et al. 2006). The relative abundance of winter spawned Celtic Sea herring in the Irish Sea shows considerable inter-annual variability (Burke et al. 2009). Variability in larval dispersal is therefore likely to contribute to variation in growth, recruitment and lifetime fecundity of Celtic Sea herring.

The Celtic and Irish Seas are highly dynamic environments, influenced by winds, tides and salinity gradients (Horsburgh et al. 1998; Pingree 1980) and subject to high tidal mixing. The formation of a tidal mixing front and stratification creates a cyclonic circulation pattern in the Celtic Sea that flows along the contours of bottom density (Brown et al. 2003; Young et al. 2004). From November to March the influence of winds on circulation forms a fully mixed water column (Horsburgh et al. 1998; Pingree 1980; Young et al. 2004). Based on prevailing currents, the predominant direction of transport is expected to be in a westward direction,

along the south coast of Ireland (Brown et al. 2003; Pingree 1980). This general pattern of movement is consistent with evidence from field studies and particle tracking which shows that larval herring are distributed along the south coast of Ireland. However, larval distributions also show that some larvae from Celtic Sea spawning grounds disperse in a north-eastward direction into the Irish Sea (Grainger 1978; Özcan 1974) and low levels of transport to the Irish Sea from a spawning ground to the east of the Celtic Sea during winter has been demonstrated by particle tracking (O’Sullivan et al. 2013).

This study uses an Individual Based Model (IBM) coupled offline to a hydrodynamic model to reconstruct the dispersal of larval herring from a known spawning ground in the Celtic Sea and to investigate the influence of currents, winds and tides as well as larval behaviour and diffusion processes on the direction of movement. The study investigates dispersal from a Celtic Sea spawning ground and connectivity with the Irish Sea during early larval life. By comparing model outputs between and within years, intra and inter-annual variability in dispersal is quantified. The consequences of environmentally driven variation in dispersal and retention for recruitment of Celtic Sea herring are evaluated.

Methods

The Celtic Sea herring stock comprises autumn and winter spawning components with spawning occurring from September through to February. In more recent years the fishery has been dominated by the winter component (Harma et al. 2012; O’Donnell et al. 2015), which spawns from November to February, with larvae hatching from December to March. In the subsequent text the term “year-class” rather than “year” is used to describe the larval period. For example, the 2002 year-class hatch from December 2002 until March 2003.

124 *Study design*

125 The study aimed to quantify inter-annual and intra-annual variability in the dispersal and
126 retention of larvae that hatch on different dates using a coupled biophysical model.
127 Simulations were run on multiple years and on multiple release dates within each year in
128 order to partition inter- and intra-annual variability in the fate of the particles. Simulation
129 settings were varied to examine the influence of tides, vertical migration behaviour and
130 diffusion on transport and retention. The influence of observed wind and tidal conditions on
131 model outputs were also examined.

132 *Background information on recruitment and juvenile abundance*

133 Annual estimates of the biomass of spawning adult herring (spawning stock biomass, SSB) and
134 the number of recruits to the Celtic Sea fishery were obtained from the ICES annual stock
135 assessment report (ICES 2016). For each year-class a measure of pre-recruitment survival was
136 derived by dividing the recruitment estimate for that year-class (calculated two years after
137 hatching) by the estimated SSB in the year-class's birth year (recruits per tonne of SSB). An
138 index of juvenile (0-group) herring biomass in the Irish Sea was provided by the Agri-food and
139 Biosciences Institute annual herring acoustic survey (ICES 2016).

140 *Selection of years for simulation*

141 Hydrodynamic data were available for the period 2002-2012. From this time period, six year-
142 classes were selected for inclusion in the simulation: 2002, 2003, 2004, 2005, 2008, 2010.
143 Time series of 0-group juvenile herring abundance, spawning stock biomass and recruitment
144 (ICES 2016) were examined to evaluate if the selected years were representative in terms of
145 conditions for larval transport/retention and pre-recruitment survival. The recruitment index
146 from the stock assessment provided an index of survival to age two for Celtic Sea herring. The

2003 and 2005 year-classes showed relatively high rates of survival to age 2 (>15 recruits per tonne SSB) while pre-recruitment survival was relatively low for the 2002 and 2010 year classes (<10 recruits per tonne SSB) and close to average for the 2004 and 2008 year-classes (10-14 per tonne SSB) (Table 1). The index of 0-group herring biomass in the Irish Sea reflects the abundance of both the resident Irish Sea population and herring that disperse from the Celtic Sea and appear to return as adults to spawn with their parent stock (Brophy et al 2006). It was hypothesised that when transport from the Celtic Sea to the Irish Sea was relatively high, 0-group herring biomass in the Irish Sea would be high relative to the SSB of both the Irish and Celtic Sea stocks. Accordingly, the 2002 and 2008 year-classes were predicted to show relatively high rates of transport to the Irish Sea while transport was predicted to have been relatively low in 2004 (Table 1). Without direct observations of larval and juvenile distributions from the time period of interest it is not possible to determine actual rates of transport. The study was designed to quantify variation in transport and retention across years rather than to compare specific years; the available data describing recruitment strength and estimated transport rates (Table 1) provided a basis for subsequently evaluating any annual trends in modelled larval dispersal trajectories.

Selection of particle release dates

Four release dates were randomly selected in each year to coincide with the hatching period of winter-spawning herring (December-February). Atlantic herring are benthic spawners, releasing their eggs onto gravel substrates in near-shore areas at depths of 15 to 36m. As eggs remain adhered to the sediment during incubation and are not subject to ocean transport, the simulations commenced on hatching.

Simulation of larval transport

Simulations were carried out using the open source, Java-based Ichthyop modelling tool (Lett et al. 2008). Ichthyop is an IBM designed to simulate the effects of physical transport and biological drivers on the dynamics of fish larvae and eggs using archived hydrodynamic model velocity, temperature and salinity fields (Lett et al. 2008). For this study, the original Ichthyop code was modified to incorporate the behavioural parameters of herring.

After hatching, larval herring feed endogenously on yolk sac reserves. At a temperature of 8-10°C the estimated duration of the yolk-sac period is approximately 10 days, during which time the larvae have weak swimming abilities and their movement is largely passive (Pepin 1991; Russell 1976). Therefore, at the initiation of the run there was a 10-day period of passive transport. After the initial passive transport phase, and at the point of yolk-sac absorption, herring begin to vertically migrate. Larval herring display diel vertical migration (DVM) in response to light and feeding conditions (Ferreira et al. 2012). Reported patterns of DVM differ between populations and include type I (deep during the daytime and shallow at night; (Ferreira et al. 2012; Seliverstov 1974), type II (surface during the daytime and deep at night (Haslob et al. 2009; Heath et al. 1988; Munk et al. 1989) and semi-diel migration (Stephenson and Power 1988). As herring larvae are visual feeders, light intensity is the most influential determinant of vertical distribution and concentration in surface waters during the day is common (Bartsch 1993; Dickey-Collas et al. 2009). For herring on the west coast of Ireland, Grainger (1980) showed that early larvae (7-12mm) were concentrated between 5m and 15m depth during the daytime. It was therefore assumed that Celtic Sea herring larvae display type II diel vertical migration. In the Ichthyop simulation, after the initial 10 day period of passive transport, particle depths were set at 10m during the day. At night, each particle occupied a randomly generated depth between 10m and 30m at night (10-30m DVM). Five release dates

which showed contrasting patterns of dispersion and retention in the main simulation, were selected to investigate the influence of diel vertical migration behaviour on particle transport: 7th February 2003; 28th February 2003; 24th January 2005; 7th February 2009; 26th December 2010. The additional simulations were run without diel vertical migration (no DVM) and with randomly generated night time depths of between 10m and 100m (10-100m DVM) and the outputs were compared.

Celtic Sea herring spawn in specific areas of gravel and rocky substrates (O’Sullivan et al. 2013). The release area for the simulations was the spawning ground offshore of Dunmore East on the south east coast of Ireland (Breslin 1998), (Figure 2, area A) which is thought to be the main source of the winter spawned Celtic Sea herring that move into the Irish Sea during the first year of life (O’Sullivan et al. 2013). On each date 3,000 particles were released, in three replicate batches of 1,000 particles. On each run, particles were released at the bottom and at randomly selected positions within the release area. Larval transport was simulated for 30 days with DVM behaviours included for 20 days after day 10. During the first 30 days movements of herring larvae would be largely controlled by passive transport and DVM (~10 days after hatching) and larvae would be too small to be capable of directional swimming (Graham and Townsend 1985; Pepin 1991; Townsend and Graham 1981).

Mechanism for ocean circulation

The three dimensional velocity fields used to drive advection and dispersion in Ichthyop were taken from the Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis (2002-2014) (Sotillo et al. 2015). This is an ocean physics reanalysis based on version 2.3 of the NEMO model (Madec 2008). The horizontal resolution of the model is 1/12° and there are 75 vertical levels with a resolution of 1 metre near the surface, coarsening to 200 metres in the deep ocean.

Atmospheric forcing is provided by ECMWF (European Centre for Medium-Range Weather Forecasts) ERA-Interim dataset and tidal forcing is also included. The data assimilation component constrains the model solution using sea level anomaly, sea surface temperature and in situ profiles of temperature and salinity. The data from this reanalysis is available from the Copernicus website under the product name, IBI_REANALYSIS_PHYS_005_002. Monthly mean, daily mean, and hourly mean fields of temperature, salinity, velocity and sea surface height are provided.

Simulations were run using two different velocity fields setups:

Daily Mean Currents

For these simulations, the daily mean velocity fields from IBI_REANALYSIS_PHYS_005_002 were used. In effect, the daily averaging process removes most of the tidal signal from the velocity fields so these fields represent the residual velocity due to wind forcing and baroclinicity. These simulations were run in Ichthyop with a time step of 7,200 seconds. The working hypothesis is that the residual currents alone would not result in the transport of particles in the Irish Sea. This model is henceforth referred to as the “non-tidal simulation”

Derived Hourly Currents

To simulate the effect of the tides on the velocity fields, a higher temporal resolution is required. The IBI_REANALYSIS_PHYS_005_002 provides hourly barotropic velocity fields, but full three dimensional velocity fields are required for the Ichthyop simulations. Ideally, the hourly three dimensional velocity fields simulated by the NEMO model itself would have been used in the simulations, but, in the absence of this data being available, the solution was to derive the three dimensional fields from the hourly barotropic velocities using the empirical formula presented in Soulsby (1990) (henceforth referred to as the Soulsby method).

This model is henceforth referred to as the “tidal simulation”

$$U(z) = \left(\frac{z}{0.32h}\right)^{1/7} \bar{U} \quad \text{for } 0 < z < 0.5h$$

$$U(z) = 1.07\bar{U} \quad \text{for } 0.5h < z < h$$

where h is the water depth, z is the vertical depth, $U = \sqrt{u^2 + v^2}$ is the current speed and \bar{U} is the depth averaged current speed obtained by,

$$\bar{U} = \frac{1}{h} \int_0^h U(z)$$

These simulations were run in Ichthyop with a time step of 1,200 seconds. The size of the study area was reduced to the area from 50° to 53° North and 4° to 10° West for computational efficiency (Figure 2).

Validation of the velocity fields for the tidal model

The Soulsby method was validated using a three-dimensional ocean model for the region, which utilizes the Regional Ocean Modelling System (ROMS) code and has been operational since 2012. The operational model has a horizontal resolution of 1.2 to 2 km with 40 vertical levels (variable thickness depending on water depth). Model fields are archived at hourly intervals and the parameters archived include 3-dimensional velocity fields as well as depth averaged velocities. One month (i.e. one full spring-neap tidal cycle) of archived data from an area covering the eastern Celtic Sea and southern part of the Irish Sea was used for this validation exercise. This area equated to 3,420 grid points so the validation was based on 3,240 velocity time series, each one month in length. For each time series the full 3-dimensional velocity fields were calculated from the depth averaged velocity fields using the Soulsby method and these velocities were compared to the ROMS 3D velocity profiles. The mean correlation coefficient for the full profile was 0.92 and 0.99 for the u and v velocity components, respectively, while the normalised root mean squared error (RMSE) estimates

were 4.8% and 2.1%, respectively (Table 2). The correspondence between the Soulsby estimates and the ROMS velocity fields was lowest for the near surface u component, but the match was still reasonable (correlation coefficient 0.89; RMSE 9.3%; Table 2). The validation indicated that the 3D velocity profiles could be estimated from depth averaged velocities with an acceptable level of accuracy using the Soulsby method.

Impact of horizontal diffusion on particle distributions

Small-scale horizontal diffusion can have a significant impact on the transport of larvae (Andutta et al. 2012; Werner et al. 2007). Measured diffusion coefficients for the study area were not available. It was therefore not possible to include realistic simulation of local diffusion processes within Icthyop and diffusion settings were not activated within the main simulations. In order to evaluate the sensitivity of the model outputs to diffusion, a series of simulations were run on five release dates which showed contrasting patterns of dispersion and retention in the main simulation (7th February 2003; 28th February 2003; 24th January 2005; 7th February 2009; 26th December 2010). On each date, three replicate releases of 1,000 particles were simulated with the diffusion coefficient set to $0 \text{ m}^2.\text{s}^{-3}$, $10^{-9} \text{ m}^2.\text{s}^{-3}$, $10^{-8} \text{ m}^2.\text{s}^{-3}$, $10^{-7} \text{ m}^2.\text{s}^{-3}$ and $10^{-6} \text{ m}^2.\text{s}^{-3}$ and the outputs were compared.

Wind and tidal data

Hourly records of wind speed and direction for the period 1962-2016 were acquired from the Met Éireann synoptic weather station at Cork airport (52° 51'N; -8° 28.8'E, Figure 2). Hourly records were placed into six categories based on the direction of the wind: 150-210 degrees (SSE-SSW); 210-270 degrees (SSW-W); 270-330 degrees (W-NNW); 330-30 degrees (NNW-NNE), 30-90 degrees (NNE-E) and 90-150 degrees (E-SSE). For each of the 30 day release periods the number of hours in each category was summed (count) and the mean speed of

the winds in each category was calculated (speed). For each category a wind index (ind) was derived from the product of count and speed ($\text{ind} = \text{count} \times \text{speed}$), producing six wind indices: ind150-210, ind210-270, ind90-150, ind270-330, ind330-30 and ind30-90. Mean monthly count, speed and wind index for each category was also calculated for the entire time series and long term trends were plotted (Figure 2).

The timing of the new moon was used to derive an index of tidal state on each release date. In each lunar cycle, the new moon was defined as day 0. Release dates that fell between days 1 and 3 or between days 15 and 17 were classed as spring tides, those that fell between days 7 and 9 or days 23 and 25 were classed as neap tides while those that fell on any other day were classed as moderate tides.

Statistical analysis

The distribution of the particles at the end of each simulation run (endpoints) was mapped using MATLAB_R2015b. Particles were categorised according to their position at the end of the 30 day simulation period: transported to the Irish Sea (area B, Figure 2), transported offshore in the Celtic Sea (area C, Figure 2) or retained inshore in the Celtic Sea (areas A and area D, Figure 2). The Celtic Sea retention area was defined with reference to available data describing the distribution of juvenile herring in the Celtic Sea (Clarke et al 2010; O'Donnell et al 2015). The area outside of this and within the Celtic Sea was classed as offshore. Three replicate batches of 1,000 particles were released in each simulation. The inclusion of replicates allowed for statistical partitioning of intra- and inter-annual variation. For subsequent analysis the proportion of particles in each area was estimated from the combined totals of the three replicate releases (3,000 particles). To determine if the number of particles used in the simulations was sufficient to reliably determine the relative numbers

dispersed to each area, simulations using 1,000, 3,000, 5,000 and 10,000 particles were run on two release dates (February 28th 2003 and February 7th 2005) and the outputs were compared. The number of particles in the simulation did not have a marked influence on the estimated percentage in each area; the difference between estimates was never more than 2% (Table 3).

The percentage coefficient of variation (%CV) in the number of particles in each area at the end of the 30-day simulation period was calculated across replicate runs on each release date (replicate CV), across release dates within each year-class (release date CV) and across all runs (total CV). Variation due to differences between replicates, differences between release dates within each year-class (intra-annual variation) and variation between year-classes (inter-annual variation) was expressed as a proportion of the total variation as follows:

$$\text{Variation between replicates} = \frac{\text{replicate CV}}{\text{total CV}}$$

$$\text{Intra – annual variation} = \frac{\text{release date CV} - \text{replicate CV}}{\text{total CV}}$$

$$\text{Inter– annual variation} = \frac{\text{total CV} - \text{release date CV}}{\text{total CV}}$$

A multinomial logit model with mixed effects was fitted in a Bayesian framework using Markov chain Monte Carlo (MCMC) methods (Hadfield 2010), in order to analyse variation in the endpoint distributions between the non-tidal and tidal hydrodynamic simulations, between year-classes, between release dates and between replicate runs. Model was included as a fixed effect with two levels (non-tidal/tidal). Year-class, release date and replicate were included as random effects with release date nested within year-class and

replicate nested within release date. The analysis was conducted using the MCMCglmm package (Hadfield 2010) in R version 3.3.2. Model selection was based on deviance information criterion (DIC) values.

Multinomial linear models were used to determine the influence of DVM behaviour, diffusion setting, wind conditions and tidal conditions on the probability of arriving in each of the three areas using the nnet package (Venables and Ripley 2002) in R version 3.3.2. This analysis was conducted using the outputs from the tidal simulation only. Model selection was based on AIC values and Log likelihood ratio tests. The effect of the six wind indices was tested using a series of models, each containing one wind index as an explanatory variable. In addition to selection based on AIC values, the fit of these models was assessed using the R squared values from the regression of predicted versus observed probability of arriving in each of the three areas at the end of the 30 day simulation (Table 4).

Correlations between each of the wind variables for the period December-March and recruitment strength (recruitment/SSB: Figure 4) were investigated using Pearson and Spearman correlation tests.

Results

Distribution of larval endpoints at end of simulation

At the end of the 30 day simulation period three general distribution patterns were observed:

1. Particles remained in the release area or moved west/southwest and were retained close to shore within the Celtic Sea (areas A and D)
2. Particles had moved north/northeast of the release area across George's Channel were transported to the Irish Sea (area B)

3. Particles had moved south of the release area and were dispersed offshore in the Celtic Sea (area C)

Across all the release dates, the most common outcome of the simulation was retention within the Celtic Sea (70% and 78% of particles on average for the non-tidal and tidal simulations respectively), followed by dispersal offshore in the Celtic Sea (27.6% and 17.9% on average for the non-tidal and tidal simulations respectively). Dispersal to the Irish Sea was the rarest outcome (2.8% and 4.1% on average for the non-tidal and tidal simulations respectively). There was also considerable variability between release dates in the proportions of particles ending up in each area; the percentage of particles retained in the Celtic Sea or dispersed offshore ranged from 0-100%, while the proportion transported to the Irish Sea ranged from 0-34% (Table 6, Figure 5). For most of the releases, when tidal forcing was included in the simulation (tidal simulation) more particles were retained in the Celtic Sea and transported to the Irish Sea, while fewer were dispersed offshore in the Celtic Sea compared to the non-tidal simulation. When particles were transported into the Irish Sea their distributions at the end of the simulations tended to extend further into the Irish Sea when tidal forcing was included in the model (Figures 6 and 7). Particle trajectories were plotted for two release dates on which more particles were transported to the Irish Sea in the tidal simulations compared to the non-tidal simulations (31 January 2003 and 2 January 2009) to demonstrate how tides influenced particle transport (Figure 8); tidal movements appeared to push the particles across St. George's Channel and further into the Irish Sea relative to particles released from similar locations in the non-tidal simulations. While particles moved backwards and forwards across the Channel with the ebb and flow of the tide, overall transport was predominantly in a North-eastward direction, possibly due to asymmetry in the tidal flow.

Model sensitivity to diel vertical migration

The relative probabilities of particles occurring in each of the three areas at the end of the simulations was significantly influenced by the diel vertical migration (DVM) settings (Chi-square = 4,791; $p < 0.0001$). The interaction between release date and DVM setting was also significant (Chi-square = 1,024; $p < 0.0001$), indicating that the effect of DVM on larval transport varied between release dates. There was no significant difference between replicates nested within release dates (Chi-square = 5.1; $p = 0.9$) and so this term was excluded from the model. On two of the five dates tested, all particles were retained in the Celtic Sea in the simulations without DVM behaviour. On two out of the remaining three dates tested, the probability of particles being transported offshore or into the Irish Sea decreased and the probability of retention in the Celtic Sea increased when DVM behaviour was included in the simulation (Figure 9). The increased retention in the Celtic Sea was most pronounced when particles were allowed to migrate to deeper depths at night-time (10-100m DVM). On one of the dates tested (7th February 2005) the probability of retention in the Celtic Sea remained above 0.99, regardless of the DVM setting while on another (7th February 2003) transport of particles to the Irish Sea occurred only when the 0-30m DVM setting was employed.

Model sensitivity to diffusion settings

The relative probabilities of particles occurring in each of the three areas at the end of the simulations was significantly influenced by the diffusion setting (Chi-square = 5,153; $p < 0.0001$). The interaction between release date and diffusion setting was also significant (Chi-square = 2960; $p < 0.0001$), indicating the effect of diffusion varied between release dates. In all cases probability of retention in the Celtic Sea was lowest and probability of dispersal offshore was highest at the maximum diffusion setting tested ($10^{-6} \text{ m}^2.\text{s}^{-3}$) (Figure 9). There was no significant difference between replicates nested within release dates (Chi-square =

14.4; $p=0.2$). With one exception (26th December 2010), probability of retention in the Celtic Sea was highest in the absence of diffusion. On three of the five dates, retention in the Celtic Sea relative to dispersal offshore or to the Irish Sea declined steadily as the diffusion setting was increased.

Main analysis: sources of variation in larval endpoint distributions

For the main analysis, the observed variability in the number of particles in each area at the end of the 30 day simulation period (endpoints) is summarised in Table 7. With regards to endpoints in the inshore or offshore areas of the Celtic Sea, intra-annual variation accounted for the largest proportion of the total %CV (0.68-0.89) while inter-annual variation was relatively minor (0.07-0.16). In contrast, the inter-annual variation in transport to the Irish Sea was more substantial (0.36-0.50) and of similar magnitude to the observed intra-annual variation (0.48-0.49). In all cases, variation between replicates (due to randomised differences in particle starting points and night-time depth) accounted for a relatively minor proportion of the total %CV (0.02-0.16).

DIC values indicated that the multinomial mixed effects model that included all of the terms (model, year-class, release date nested within year-class and replicate nested within release date) provided the best fit to the data (DIC= 132,866.3). The probability of particles occurring in the Irish Sea at the end of the simulations was significantly higher for the tidal simulation compared to the non-tidal simulation ($p<0.001$), indicating that the inclusion of tidal forcing influenced transport to the Irish Sea. Transport offshore was significantly less likely for the tidal simulation compared to the non-tidal simulation ($p=0.01$). Partition of variance between the random effects showed that most of the variance in endpoint distributions was due to the effect of release date nested within year-class (proportion of explained variance calculated

from modes of the posterior distribution = 0.65), while the effects of replicate nested within release date and of year-class were relatively minor (proportion of explained variance calculated from modes of the posterior distribution = 0.0024 and 0.025 respectively). The 95% credibility intervals of the posterior probability distributions did not overlap zero for any of the random effects, indicating that all were significant.

Comparison with a priori estimates of transport rates

Prior to the analysis, it was predicted, based on abundance of juveniles in the Irish Sea, that transport of herring larvae from the Celtic Sea to the Irish Sea would be relatively high for the 2002 and 2008 year classes and low for the 2004 year class (Table 1). Most of the variability in relative rates of transport and retention was between release dates within year classes. There was therefore no basis for defining year classes as “high transport” or “high retention years” and a detailed comparison between years was not made. It was noted that the highest rate of transport to the Irish Sea (29.7%; tidal simulation) was observed on January 31st 2003 (2002 year class) while transport occurred on just one of the tested dates in 2004/05 and was less than 1% (tidal simulation, 19th December 2004). However, similarly low rates of transport to the Irish Sea were observed in 2004/05 when moderate rates of transport were expected.

Influence of winds and tides on larval endpoint distributions

The multinomial logistic regression analysis modelled endpoint probabilities (the probability of particles being transported to the Irish Sea and offshore areas relative to the probability of being retained in the Celtic Sea) as a function of each of the six wind indices and the tidal state index. In all cases, the inclusion of tidal state improved the fit of the model compared to the wind index alone. The model with the lowest AIC value included ind210-270 and tidal state as the explanatory variables (Table 4). This model provided the most accurate predictions of the

probabilities of retention in the Celtic Sea ($R^2=0.55$) and transport offshore ($R^2 = 0.61$), but was a relatively poor predictor of the probability of transport to the Irish Sea ($R^2 = 0.18$). The model which provided the most accurate prediction of transport to the Irish Sea ($R^2=0.38$) included ind90-150 and tidal state. The two wind indices were significantly, but weakly correlated ($r=-0.12$, $p<0.0001$) so both were included together with tidal state in a combined model. The combined model had a significantly lower AIC value (Log Likelihood test, $p<0.001$) than either of the single wind index models. Its predictive power was high for the Celtic Sea and offshore areas (least squares mean $R^2 = 0.76$ and 0.77 respectively, $p<0.0001$). Predictions of the rarer outcome of transport to the Irish Sea was more prone to error ($R^2 = 0.42$, $p<0.0001$) (Figure 10).

The multinomial model outputs showed that strong and frequent E-SSE winds (ind90-150) were associated with a higher probability of transport to the Irish Sea and retention in the Celtic Sea and a lower probability of transport offshore. Winds from the SSW-W (ind210-270) were associated with higher rates of transport to offshore areas and lower rates of retention in the Celtic Sea (Figure 11, Table 5).

The model predicted probability of retention in the Celtic Sea was highest and the probability of transport offshore was lowest when the release date coincided with a spring tide. The probability of transport into the Irish Sea was highest on release dates that coincided with a moderate tide (Figure 12., Table 6).

Long-term variation in wind patterns

The prevailing winds in the Celtic Sea during winter time are from a westerly-south-westerly direction (Cooper 1961). This was reflected in the wind data obtained from the Met Éireann synoptic station at Cork airport; SSW-W winds were the most dominant winds during the

December – March (ind210-270: mean monthly hours 175), followed by W-NNW winds (ind270-330: mean monthly hours 127) and SSE-SSW winds (ind150-210: mean monthly hours 118). Winds from the north, northeast, east and south east (ind330-30; ind30-90 and ind90-150) were much less frequent (mean monthly hours 64, 54 and 10 respectively).

Examination of temporal trends in wind speed and direction revealed marked changes in the prevailing wind patterns in the Celtic Sea in recent decades (Figure 3); after increasing steadily during the 1970's and 1980's, the mean monthly speeds of winds from the SSE-SSW (ind150-210), SSW-W (ind210-270) and W-NNW (ind270-330) decreased and remained below the long-term mean for much of the remaining time series. Winds from the SSW-W were more frequent after the 1990's compared to the 1960's-1980's. The 30 day wind index which reflected the combined effects of speed and frequency (mean speed*count) showed marked declines in winds from the SSE-SSW and SSW-W after 1990. None of the wind variables were significantly correlated with the recruitment strength of Celtic Sea herring ($r < 0.3$; $p > 0.05$).

Discussion

The results of the biophysical model simulations indicate that circulation patterns in the Celtic Sea during winter generally favour the retention of herring larvae in inshore areas along the south of Ireland although transport offshore in the Celtic Sea and to the Irish Sea also occurs. Comparison of the outputs from the tidal and non-tidal simulations showed that tides were instrumental in delivering larvae across St. George's Channel to the Irish Sea and reduced dispersal offshore. Vertical migration behaviour, which was previously proposed as a mechanism to enhance larval retention (Stephenson and Power 1988), was shown here to increase the probability of retention inshore in the Celtic Sea while horizontal diffusion increased transport offshore and into the Irish Sea. The depth of night-time migrations and

the size of the diffusion coefficient both influenced particle distributions. The proportion of particles delivered to each of the three areas varied substantially between release dates within each year while inter-annual variability was relatively minor. Intra-annual variability was linked with variation in wind-driven circulation, reflecting the highly dynamic nature of the system. Additional field data describing herring DVM behaviours and diffusion processes in the Celtic Sea are needed to accurately predict exact rates of retention and dispersal of larvae from spawning grounds in the Celtic Sea. However, the bio-physical modelling results presented here demonstrate the extent to which relative rates can vary due to wind patterns and tidal conditions during the early larval period.

The model predicted distribution of particles retained in the Celtic Sea or transported to the Irish Sea is broadly consistent with field evidence, which shows that the distribution of herring larvae in February and March extends along the south coast of Ireland and into the south Irish Sea (O'Sullivan et al. 2013). The retention of larvae close to the south coast of Ireland is also in agreement with reported distributions of juvenile herring in the Celtic Sea (Brophy and Danilowicz 2002; Clarke et al. 2010). Six to nine months after hatching, the distribution of 0-group winter spawned juvenile herring in the Irish Sea extends to the North Irish Sea (Brophy and Danilowicz 2002; Burke et al. 2009). This is up to 240km away from where the particles that were transported to the Irish Sea were located after 30 days of simulation. However, it is conceivable that ocean currents, together with developing swimming abilities of the larvae and early juveniles could facilitate further transport of herring to nursery grounds in the north Irish Sea. Although a southward flow along the Irish coast occurs during certain meteorological conditions, the annually averaged current flows in the Irish Sea are in a south to north direction (Dabrowski et al. 2010; Heaps and Jones 1977; Horsburgh et al. 1998). Transport of larvae from the east coast of Ireland in a westward direction towards the Isle of

Man during April-July has also been demonstrated (van der Molen et al. 2007). Thirty days after hatching herring have reached a length of between 11 and 14 mm (Graham and Townsend 1985; Pepin 1991; Townsend and Graham 1981) and are entering the post-flexion period of development after which routine swimming at $1\text{-}2\text{cm.s}^{-1}$ can be expected, increasing to 4cm.s^{-1} at juvenile metamorphosis (35-40mm) (Moyano et al. 2016). As their swimming speeds develop, larvae can use directional swimming to move towards areas of higher food density (Munk and Kiorboe 1985; Voosenek et al. 2018) and to position themselves in inshore areas (Drake et al. 2018). Therefore, herring larvae that cross St. George's channel during the 30 day early larval period and continue to travel with the currents in a general northward direction as late larvae, could be delivered to nursery grounds on the east coast of Ireland and the west coast of the Isle of Man with the aid of directional horizontal swimming. Other possible sources of winter spawned juveniles in the Irish Sea must also be considered, including small contributions from local spawning events around the Isle of Man and off the north coast of Ireland (Dickey-Collas et al. 2001; ICES 2016) as well as potential transport of larvae southwards through the North Channel of the Irish Sea (Davies et al. 2002; Young et al. 2000). This could be addressed through further hydrodynamic modelling studies and larval surveys within the Irish Sea.

The transport of larval herring from the Celtic Sea creates the potential for connectivity with the Irish Sea stock. Although the proportion of larvae that are transported is low relative to the rate of retention in the Celtic Sea (0-31%, average 4.1%), given the relative sizes of the two stocks, this could make a comparatively substantial contribution to assemblages of juvenile herring in the Irish Sea. For the 2004-2008 cohorts, the mean estimated number of recruits produced by the Celtic Sea stock was $871,181 \times 10^3$, over four times that of the Irish Sea stock at $195,838 \times 10^3$ (ICES, 2016). Winter-spawned 0-group juvenile herring are widely

dispersed across the Irish Sea outnumbering the autumn spawned juveniles from the resident population at many locations (Brophy and Danilowicz 2002; Brophy and Danilowicz 2003, Burke et al 2009). The results of this study together with previous evidence from larval surveys (O’Sullivan et al 2013) indicate that at least some of these fish are advected into the Irish Sea during the early larval phase. This movement is facilitated by tidal features, which act to push larvae across St George’s Channel and reduce the likelihood of offshore dispersal. It has been proposed that despite extensive juvenile mixing, the Celtic and Irish Sea stocks remain discrete due to spawning season fidelity, with winter spawned herring returning to their spawning grounds of origin as adults. Evidence from otolith microstructure shows that adult spawning assemblages in the Irish Sea in autumn are almost entirely of autumn spawned origin (Brophy et al 2006). There is no winter-herring fishery in the Irish Sea and only low and infrequent levels of winter spawning have been recorded (Dickey-Collas et al. 2001). In this context, larvae that are transported to the Irish Sea may not be the “vagrants” of Sinclair’s member/vagrant hypothesis and the Irish Sea could be considered as part of the geographic area of retention for Celtic Sea herring. Although the Irish Sea has been shown to be less favourable for growth and maturation (Brophy and Danilowicz 2003) the persistence of winter-spawned juveniles in the Irish Sea through to the 1-group stage (up to 80,000 tonnes biomass, ICES 2016) suggests that conditions there promote survival.

Variation in the fate of simulated larvae between release dates was linked to variability in wind patterns across the 30 days of the simulation and tidal conditions at the time of release. When the prevailing west/south-westerly winds (210-270°) were stronger and more frequent than average, the probability of retention in the Celtic Sea or transport to the Irish Sea decreased and transport offshore increased. Strong and frequent east/south easterly winds (90-150°) increased the probability of transport to the Irish Sea and retention in the Celtic Sea

and reduced the probability of transport offshore. On some of the release dates examined the majority of particles were dispersed offshore in the Celtic Sea, away from known juvenile herring habitat. In reality, relationships between wind patterns and transport/retention will be overlaid by the effects of diffusion, which are likely to increase rates of transport offshore. Nonetheless, the results indicate that the delivery of herring larvae to nursery grounds in the Celtic and Irish Seas will be influenced by variation in meteorological conditions which could operate over both short (within year) and long (yearly, decadal) temporal scales. Future changes in wind patterns as a consequence of climate change are predicted (La Sorte and Fink 2017; Reyers et al. 2016) and stronger, more persistent westerly winds are forecast under future climate scenarios (Li et al. 2018). For herring in the Celtic Sea increasing prevailing winds could result in greater transport of larvae offshore which would threaten life-cycle closure and population persistence. Further investigation is needed to fully understand the potential impacts of climate change on larval dispersal (Petitgas et al. 2013). Coupling forecasted climate scenarios with biophysical hydrodynamic models could help to predict the consequences of future change for larval dispersal and nursery ground connectivity in the Celtic Sea (Hollowed et al. 2009).

Temporal trends in wind patterns from 1962-2016 show strong prevailing winds prior to 1990 followed by a period of relative calm. Multi-decadal local wind measurements are affected by changes in instrumentation and station exposure (from buildings, trees etc.) making it difficult to discern long term trends (Dwyer 2013). However, the broad changes noted here are also reflected in the meteorological and climatic trends evident from pan-European analyses (Donat et al. 2011; Krueger et al. 2012; Matulla et al. 2008). Strong prevailing wind conditions prior to 1990 may have favoured transport offshore and reduced retention in the Celtic Sea and transport to the Irish Sea. If such changes occurred this is not manifested in

corresponding changes in year-class strength as no correlations were detected between estimated recruitment at age 2 and wind patterns during December-March. This may indicate that larval survival is not influenced by rate of transport to each of the three areas or that year class strength is determined after the early larval phase. Alternatively, temporal fluctuations in the timing of spawning due to changes in the relative strength of the autumn and winter spawning components (Harma et al. 2012) may override any effects of changing wind patterns on larval dispersal.

Iles and Sinclair (1982) first proposed that stock discreteness in Atlantic herring was maintained by geographically stable retention areas as evidenced by the location of spawning grounds in the vicinity of thermal stratification features and the temporally stable distribution of young fish close to the spawning grounds. Since then, studies have demonstrated that meteorological forcing may ensure retention under typical conditions (Bauer et al. 2013; Dickey-Collas et al. 2009; Skagseth et al. 2015) but that in some years, unusual or variable wind conditions may alter larval transport trajectories leading to variability in year class strength (Dickey-Collas et al. 2009) or greatly elevated recruitment (Skagseth et al. 2015). In the present study, there was a notable degree of intra-annual variability in the larval dispersal patterns such that retention close to the coast in the Celtic Sea was a common but not a stable property of the system. Diel vertical migration behaviours appeared to enhance retention, while diffusion increased offshore dispersal. For Celtic Sea herring, the degree of retention will be determined by the timing of hatching in relation to meteorological and tidal conditions and by the behaviour of developing larvae. In the face of such dynamic hydrodynamic conditions at the spawning grounds in the Celtic Sea, the extended herring spawning season may have adaptive significance. Life history theory predicts that in a constant environment the forces of stabilizing selection will favour short and synchronized spawning periods while

in variable and unpredictable environments protracted spawning can confer an advantage by dampening variability in larval survival and maximising the overall reproductive output of the population (Wright and Trippel 2009). A protracted spawning season comprising of multiple spawning waves, often differing in their age structure or genetic composition is typical of Atlantic herring (Lambert 1987; McPherson et al. 2003; Oskarsson and Taggart 2009). The phenomenon appears particularly pronounced in the Celtic Sea where spawning may continue for up to 20 weeks. This diversity in reproductive strategies may increase the resilience of the population to both short-term fluctuations and long-term trends in meteorological conditions which influence larval retention. Preservation of stock complexity may help to reduce variability in recruitment and protect the sustainability of the fishery (Melvin et al. 2009).

When interpreting the output from any biophysical model, the potential restrictions imposed by the resolution of the forcing data and by the model itself must be considered (Miller 2007). The hydrodynamic model used here had a horizontal resolution of 5-6 km which is typical of regional scale models. However, larvae encounter and interact with circulation at spatial scales that are several orders of magnitude smaller (Miller 2007; Wood et al. 2014). At a spatial resolution of several kilometres, a hydrodynamic model will fail to capture smaller-scale turbulent motion (e.g. local eddies) that can influence transport by entraining larvae and increasing local retention rates or moving particles into unfavourable areas (Cowen 2002; Cowen and Castro 1994; Cowen and Sponaugle 2009). Comparisons of model predictions with observed planktonic distributions show that deviations can occur even at resolutions of 3km (Helbig and Pepin 2002). To fully and accurately capture the finer scale movements of the dispersing larvae, particularly in near-shore areas, very fine resolution models, or models which incorporate local diffusion processes are required (Andutta et al. 2012; Werner et al.

2007). In addition, the realism of model outputs can be increased by including individual temperature dependant growth rates and complex behaviours (Leis 2007; Staaterman and Paris 2014). In the present study, rates of retention and dispersal were sensitive to the diffusion settings used and the nature of DVM behaviour. The simulation model presented here does not fully capture sub-mesoscale hydrodynamic processes, includes only rudimentary vertical migration behaviours and does not include individual temperature dependant growth rates. However, validation assessments indicate that the hydrodynamic model will accurately predict broad scale flows and its temporal variation (Sotillo et al. 2015). Furthermore, the predicted distributions of particles at the end of the simulations correspond well with previous reports of larval and juvenile herring in the Celtic Sea (Brophy and Danilowicz 2002; Clarke et al. 2010; O’Sullivan et al. 2013) suggesting that the model outputs are realistic.

In conclusion, the results show that currents acting under atmospheric and tidal forcing in the Celtic Sea split the larval herring population along three trajectories. While retention in the Celtic Sea is the most common outcome, strong and frequent prevailing winds from a west/south-westerly direction result in substantial transport away from the Celtic Sea retention area, into deeper offshore waters while strong and frequent east to south-southeast winds increase transport across St. George’s Channel into the Irish Sea. Hatching during a spring tide appears to reduce the probability of offshore transport and increase the likelihood of retention in the Celtic Sea while larvae that hatch during a neap tide are less likely to be transported into the Irish Sea. Due to the high degree of variability between release dates, the fate of larvae will be determined by the timing of hatching in relation to meteorological and tidal conditions. The protracted spawning period of Celtic Sea herring may reflect adaptation to dynamic hydrodynamic conditions and maintaining life history diversity

may be key to preserving the stock's resilience. Further investigation of larval transport under future climate scenarios is warranted given the potential impact of changing meteorological and hydrographic conditions on transport, connectivity and the structure and persistence of herring populations.

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References

- Andutta, F.P., Kingsford, M.J., and Wolanski, E. 2012. 'Sticky water' enables the retention of larvae in a reef mosaic. *Estuarine Coastal and Shelf Science* **101**: 54-63. doi:10.1016/j.ecss.2012.02.013.
- Bartsch, J., Brander, K., Heath, M., Munk, P., Richardson, K., and Svendsen, E. 1989. Modeling the advection of herring larvae in the North Sea. *Nature* **340**(6235): 632-636. doi:10.1038/340632a0.
- Bartsch, J. 1993. Application of a circulation and transport model system to the dispersal of herring larvae in the North Sea. *Continental Shelf Research* **13**(12): 1335-1361. doi:10.1016/0278-4343(93)90087-e.
- Bauer, R.K., Stepputtis, D., Grawe, U., Zimmermann, C., and Hammer, C. 2013. Wind-induced variability in coastal larval retention areas: a case study on Western Baltic spring-spawning herring. *Fisheries Oceanography* **22**(5): 388-399. doi:10.1111/fog.12029.

- 683 Baumann, H., Hinrichsen, H.H., Mollmann, C., Koster, F.W., Malzahn, A.M., and Temming, A.
684 2006. Recruitment variability in Baltic Sea sprat (*Sprattus sprattus*) is tightly coupled
685 to temperature and transport patterns affecting the larval and early juvenile stages.
686 Canadian Journal of Fisheries and Aquatic Sciences **63**(10): 2191-2201.
687 doi:10.1139/f06-112.
- 688 Breslin, J. 1998. The location and extent of the main herring (*Clupea harengus*) spawning
689 grounds around the Irish coast. University College Dublin.
- 690 Brophy, D., and Danilowicz, B.S. 2002. Tracing populations of Atlantic herring (*Clupea*
691 *harengus* L.) in the Irish and Celtic Seas using otolith microstructure. ICES Journal of
692 Marine Science **59**(6): 1305-1313.
- 693 Brophy, D., and Danilowicz, B.S. 2003. The influence of pre-recruitment growth on
694 subsequent growth and age at first spawning in Atlantic herring (*Clupea harengus* L.).
695 ICES Journal of Marine Science **60**(5): 1103-1113.
- 696 Brophy, D., Danilowicz, B.S., and King, P.A. 2006. Spawning season fidelity in sympatric
697 populations of Atlantic herring (*Clupea harengus*). Canadian Journal of Fisheries and
698 Aquatic Sciences **63**(3): 607-616. doi:10.1139/f05-235.
- 699 Brown, J., Carrillo, L., Fernand, L., Horsburgh, K.J., Hill, A.E., Young, E.F., and Medler, K.J. 2003.
700 Observations of the physical structure and seasonal jet-like circulation of the Celtic
701 Sea and St. George's Channel of the Irish Sea. Continental Shelf Research **23**(6): 533-
702 561. doi:http://doi.org/10.1016/S0278-4343(03)00008-6.
- 703 Burke, N., Brophy, D., Schon, P.J., and King, P.A. 2009. Temporal trends in stock origin and
704 abundance of juvenile herring (*Clupea harengus*) in the Irish Sea. ICES Journal of
705 Marine Science **66**(8): 1749-1753. doi:10.1093/icesjms/fsp140.

- 706 Clarke, M., Egan, A., and Molloy, J. 2010. A Survey of Nursery Grounds for Celtic Sea and VIIj
707 Herring. Irish Fisheries Investigations 22; Marine Institute 17pp.
- 708 Corten, A. 2013. Recruitment depressions in North Sea herring. ICES Journal of Marine Science
709 **70**(1): 1-15. doi:10.1093/icesjms/fss187.
- 710 Cowen, R.K. 2002. Chapter 7: Oceanographic influences on larval dispersal and retention and
711 their consequences for population connectivity. *In Coral Reef Fisheries: dynamic and*
712 *diversity in a complex ecosystem. Edited by P.F. Sale. pp. 149-170.*
- 713 Cowen, R.K., and Castro, L.R. 1994. Relation of coral-reef fish larval distributions to island scale
714 circulation around Barbados, West-Indies. Bulletin of Marine Science **54**(1): 228-244.
- 715 Cowen, R.K., and Sponaugle, S. 2009. Larval Dispersal and Marine Population Connectivity.
716 Annual Review of Marine Science **1**: 443-466.
717 doi:10.1146/annurev.marine.010908.163757.
- 718 Cowen, R.K., Gawarkiewicz, G., Pineda, J., Thorrold, S.R., and Werner, F.E. 2007. Population
719 connectivity in marine systems an overview. Oceanography **20**(3): 14-21.
- 720 Dabrowski, T., Hartnett, M., and Olbert, A.I. 2010. Influence of seasonal circulation on flushing
721 of the Irish Sea. Marine Pollution Bulletin **60**(5): 748-758.
722 doi:10.1016/j.marpolbul.2009.11.018.
- 723 Davies, A.M., Hall, P., Howarth, M.J., and Knight, P. 2002. Modelling and measuring the wind
724 forced inflow to the Irish Sea through the North Channel. Continental Shelf Research
725 **22**(5): 749-777. doi:10.1016/s0278-4343(01)00083-8.
- 726 Dickey-Collas, M., Nash, R.D.M., and Brown, J. 2001. The location of spawning of Irish Sea
727 herring (*Clupea harengus*). Journal of the Marine Biological Association of the United
728 Kingdom **81**(4): 713-714.

- 729 Dickey-Collas, M., Bolle, L.J., van Beek, J.K.L., and Erftemeijer, P.L.A. 2009. Variability in
730 transport of fish eggs and larvae. II. Effects of hydrodynamics on the transport of
731 Downs herring larvae. Marine Ecology Progress Series **390**: 183-194.
732 doi:10.3354/meps08172.
- 733 Donat, M.G., Renggli, D., Wild, S., Alexander, L.V., Leckebusch, G.C., and Ulbrich, U. 2011.
734 Reanalysis suggests long-term upward trends in European storminess since 1871.
735 Geophysical Research Letters **38**(14): n/a-n/a. doi:10.1029/2011GL047995.
- 736 Drake, P.T., Edwards, C.A., Morgan, S.G., and Satterthwaite, E.V. 2018. Shoreward swimming
737 boosts modeled nearshore larval supply and pelagic connectivity in a coastal upwelling
738 region. Journal of Marine Systems **187**: 96-110. doi:10.1016/j.jmarsys.2018.07.004.
- 739 Dwyer, N. 2013. The status of Ireland's climate. Environmental Protection Agency, Climate
740 Change Research Programme Report 26. 147pp.
- 741 Ferreira, A.S.d.A., Stenevik, E.K., Vollset, K.W., Korneliussen, R., and Folkvord, A. 2012. Vertical
742 migration of Norwegian spring-spawning herring larvae in relation to predator and
743 prey distribution. Marine Biology Research **8**(7): 605-614.
744 doi:10.1080/17451000.2011.653370.
- 745 Geffen, A.J. 2009. Advances in herring biology: from simple to complex, coping with plasticity
746 and adaptability. ICES Journal of Marine Science **66**(8): 1688-1695.
747 doi:10.1093/icesjms/fsp028.
- 748 Graham, J.J., and Townsend, D.W. 1985. Mortality, growth, and transport of larval Atlantic
749 herring *Clupea harengus* in Maine coastal waters. Transactions of the American
750 Fisheries Society **114**(4): 490-498. doi:10.1577/1548-
751 8659(1985)114<490:mgatol>2.0.co;2.

- 752 Grainger, R.J.R. 1978. Herring abundance off the west of Ireland in relation to oceanographic
753 variation. ICES Journal of Marine Science **38**(2): 180-188.
754 doi:10.1093/icesjms/38.2.180.
- 755 Grainger, R.J.R. 1980. The distribution and abundance of early herring (*Clupea harengus* L.)
756 larvae in Galway Bay in relation to oceanographic conditions. Proceedings of the Royal
757 Irish Academy. Section B: Biological, Geological, and Chemical Science **80B**: 47-60.
- 758 Hadfield, J.D. 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models:
759 The MCMCglmm R Package. Journal of Statistical Software; Vol 1, Issue 2 (2010).
760 doi:10.18637/jss.v033.i02.
- 761 Harma, C., Brophy, D., Minto, C., and Clarke, M. 2012. The rise and fall of autumn-spawning
762 herring (*Clupea harengus* L.) in the Celtic Sea between 1959 and 2009: Temporal
763 trends in spawning component diversity. Fisheries Research, **121–122**: 31-42.
- 764 Haslob, H., Rohlf, N., and Schnack, D. 2009. Small scale distribution patterns and vertical
765 migration of North Sea herring larvae (*Clupea harengus*, Teleostei: Clupeidea) in
766 relation to abiotic and biotic factors. Scientia Marina **73**.
- 767 Heaps, N.S., and Jones, J.E. 1977. Density currents in the Irish Sea. Geophysical Journal
768 International **51**(2): 393-429. doi:10.1111/j.1365-246X.1977.tb06926.x.
- 769 Heath, M.R., Henderson, E.W., and Baird, D.L. 1988. Vertical distribution of herring larvae in
770 relation to physical mixing and illumination. Marine Ecology Progress Series **47**.
- 771 Helbig, J.A., and Pepin, P. 2002. The effects of short space and time scale current variability
772 on the predictability of passive ichthyoplankton distributions: an analysis based on HF
773 radar observations. Fisheries Oceanography **11**(3): 175-188. doi:10.1046/j.1365-
774 2419.2002.00195.x.

- 775 Hinrichsen, H.-H., Dickey-Collas, M., Huret, M., Peck, M.A., and Vikebø, F.B. 2011. Evaluating
776 the suitability of coupled biophysical models for fishery management. *ICES Journal of*
777 *Marine Science* **68**(7): 1478-1487. doi:10.1093/icesjms/fsr056.
- 778 Hinrichsen, H.H., Hussy, K., and Huwer, B. 2012. Spatio-temporal variability in western Baltic
779 cod early life stage survival mediated by egg buoyancy, hydrography and
780 hydrodynamics. *ICES Journal of Marine Science* **69**(10): 1744-1752.
781 doi:10.1093/icesjms/fss137.
- 782 Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe, viewed in the light of
783 biological research. *Rapports et Procès-Verbaux des Réunions du Conseil Permanent*
784 *International pour l'Exploration de la Mer*, 1914, vol. 20 (pg. 1-228)
- 785 Hollowed, A.B., Bond, N.A., Wilderbuer, T.K., Stockhausen, W.T., A'Mar, Z.T., Beamish, R.J.,
786 Overland, J.E., and Schirripa, M.J. 2009. A framework for modelling fish and shellfish
787 responses to future climate change. *ICES Journal of Marine Science* **66**(7): 1584-1594.
788 doi:10.1093/icesjms/fsp057.
- 789 Horsburgh, K.J., Hill, A.E., and Brown, J. 1998. A summer jet in the St George's Channel of the
790 Irish Sea. *Estuarine Coastal and Shelf Science* **47**(3): 285-294.
- 791 Huwer, B., Hinrichsen, H.H., Hüsey, K., and Eero, M. 2016. Connectivity of larval cod in the
792 transition area between North Sea and Baltic Sea and potential implications for
793 fisheries management. *ICES Journal of Marine Science* **73**(7): 1815-1824.
794 doi:10.1093/icesjms/fsw043.
- 795 ICES. 2016. Report of the Herring Assessment Working Group for the Area South of 62°N
796 (HAWG), 29 March-7 April 2016, ICES HQ, Copenhagen, Denmark. ICES CM
797 2016/ACOM:07. 867 pp.

- 798 Iles, T.D., and Sinclair, M. 1982. Atlantic herring: Stock discreteness and abundance. *Science*
799 **215**(4533): 627-633.
- 800 Krueger, O., Schenk, F., Feser, F., and Weisse, R. 2012. Inconsistencies between long-term
801 trends in storminess derived from the 20cr reanalysis and observations. *Journal of*
802 *Climate* **26**(3): 868-874. doi:10.1175/JCLI-D-12-00309.1.
- 803 La Sorte, F.A., and Fink, D. 2017. Projected changes in prevailing winds for transatlantic
804 migratory birds under global warming. *Journal of Animal Ecology* **86**(2): 273-284.
805 doi:10.1111/1365-2656.12624.
- 806 Lambert, T.C. 1987. Duration and intensity of spawning in herring clupea-harengus as related
807 to the age structure of the mature population. *Marine Ecology Progress Series* **39**(3):
808 209-220. doi:10.3354/meps039209.
- 809 Leis, J.M. 2007. Behaviour as input for modelling dispersal of fish larvae behaviour,
810 biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet
811 hydrography. *Marine Ecology Progress Series* **347**: 185-194.
- 812 Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., and Blanke, B. 2008. A
813 Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling &*
814 *Software* **23**(9): 1210-1214. doi:10.1016/j.envsoft.2008.02.005.
- 815 Li, C., Michel, C., Graff, L.S., Bethke, I., Zappa, G., Bracegirdle, T.J., Fischer, E., Harvey, B.J.,
816 Iversen, T., King, M.P., Krishnan, H., Lierhammer, L., Mitchell, D., Scinocca, J.,
817 Shiogama, H., Stone, D.A., and Wettstein, J.J. 2018. Midlatitude atmospheric
818 circulation responses under 1.5 and 2.0 degrees C warming and implications for
819 regional impacts. *Earth System Dynamics* **9**(2): 359-382. doi:10.5194/esd-9-359-2018.
- 820 Llopiz, J.K., Cowen, R.K., Hauff, M.J., Ji, R.B., Munday, P.L., Muhling, B.A., Peck, M.A.,
821 Richardson, D.E., Sogard, S., and Sponaugle, S. 2014. Early life history and fisheries

- 822 oceanography new questions in a changing world. *Oceanography* **27**(4): 26-41.
 823 doi:10.5670/oceanog.2014.84.
- 824 Madec, G. 2008. NEMO Ocean General Circulation Model Reference Manuel. Internal Report.
 825 LODYC/IPSL, Paris.
- 826 Matulla, C., Schöner, W., Alexandersson, H., von Storch, H., and Wang, X.L. 2008. European
 827 storminess: late nineteenth century to present. *Climate Dynamics* **31**(2): 125-130.
 828 doi:10.1007/s00382-007-0333-y.
- 829 McPherson, A.A., Stephenson, R.L., and Taggart, C.T. 2003. Genetically different Atlantic
 830 herring *Clupea harengus* spawning waves. *Marine Ecology-Progress Series* **247**: 303-
 831 309.
- 832 Melvin, G.D., Stephenson, R.L., and Power, M.J. 2009. Oscillating reproductive strategies of
 833 herring in the western Atlantic in response to changing environmental conditions. *ICES*
 834 *Journal of Marine Science* **66**(8): 1784-1792. doi:10.1093/icesjms/fsp173.
- 835 Miller, T. J. 2007. Contribution of individual-based coupled physical biological models to
 836 understanding recruitment in marine fish populations. *Marine Ecology Progress*
 837 *Series*, 347: 127-138.
- 838 Moyano, M., Illing, B., Peschutter, P., Huebert, K.B., and Peck, M.A. 2016. Thermal impacts on
 839 the growth, development and ontogeny of critical swimming speed in Atlantic herring
 840 larvae. *Comparative Biochemistry and Physiology a-Molecular & Integrative*
 841 *Physiology* **197**: 23-34. doi:10.1016/j.cbpa.2016.02.020.
- 842 Munk, P., and Kiorboe, T. 1985. Feeding behavior and swimming activity of larval herring
 843 (*Clupea harengus*) in relation to density of copepod nauplii. *Marine Ecology Progress*
 844 *Series* **24**(1-2): 15-21. doi:10.3354/meps024015.

- 845 Munk, P., Kjørboe, T., and Christensen, V. 1989. Vertical migrations of herring, *Clupea*
 846 *harengus*, larvae in relation to light and prey distribution. Environmental Biology of
 847 Fishes **26**.
- 848 Nielsen, E., Bagge, O., and MacKenzie, B.R. 1998. Wind-induced transport of plaice
 849 (*Pleuronectes platessa*) early life-history stages in the Skagerrak-Kattegat. Journal of
 850 Sea Research **39**(1-2): 11-28. doi:10.1016/s1385-1101(97)00014-2.
- 851 Oskarsson, G.J., and Taggart, C.T. 2009. Spawning time variation in Icelandic summer-
 852 spawning herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic
 853 Sciences **66**(10): 1666-1681. doi:10.1139/f09-095.
- 854 O'Donnell, C., Lynch, D., Lyons, K., Keogh, N., and O'Donovan, M. 2015. Celtic Sea Herring
 855 Acoustic Survey Cruise Report 2015, 02-22 October 2015. FSS Survey Series: 2015/04.
 856 Marine Institute.
- 857 O'Sullivan, D., O'Keefe, E., Berry, A., Tully, O., and Clarke, M. (2013). An Inventory of Irish
 858 Herring Spawning Grounds. Irish Fisheries Bulletin No. 42: Marine Institute
 859 <http://hdl.handle.net/10793/874>
- 860 Özcan, A. 1974. A review of the herring stocks to the west of the British Isles. Phd thesis,
 861 School of biological sciences, University of east Anglia, Norwich.
- 862 Pacariz, S., Bjork, G., and Svedang, H. 2014. Interannual variability in the transport of fish eggs
 863 in the Kattegat and Oresund. ICES Journal of Marine Science **71**(7): 1706-1716.
 864 doi:10.1093/icesjms/fsu044.
- 865 Parrish, B.B., and Saville, A. 1965. The Biology of the North-East Atlantic herring populations.
 866 Oceanography and Marine Biology Annual Review **3**: 323-373.

- 867 Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates
868 of the pelagic early life-history stages of marine fish. *Canadian Journal of Fisheries and*
869 *Aquatic Sciences* **48**(3): 503-518.
- 870 Petitgas, P., Rijnsdorp, A.D., Dickey-Collas, M., Engelhard, G.H., Peck, M.A., Pinnegar, J.K.,
871 Drinkwater, K., Huret, M., and Nash, R.D.M. 2013. Impacts of climate change on the
872 complex life cycles of fish. *Fisheries Oceanography* **22**(2): 121-139.
873 doi:10.1111/fog.12010.
- 874 Pineda, J., Hare, J.A., and Sponaugle, S. 2007. Larval transport and dispersal in the coastal
875 ocean and consequences for population connectivity. *Oceanography* **20**(3): 22-39.
- 876 Pingree, R.D. 1980. Physical oceanography of the Celtic Sea and English Channel. *In* The north-
877 west European shelf seas: the sea bed and the sea in motion. 2. Physical and chemical
878 oceanography, and physical resources., Publ. by: *Edited by* F.T. Banner and M.B.
879 Collins and K.S. Massie. Elsevier; Amsterdam (Netherlands)., 1980., p. , English. pp.
880 415-466.
- 881 Reyers, M., Moemken, J., and Pinto, J.G. 2016. Future changes of wind energy potentials over
882 Europe in a large CMIP5 multi-model ensemble. *International Journal of Climatology*
883 **36**(2): 783-796. doi:10.1002/joc.4382.
- 884 Rijnsdorp, A.D., Peck, M.A., Engelhard, G.H., Möllmann, C., and Pinnegar, J.K. 2009. Resolving
885 the effect of climate change on fish populations. *ICES Journal of Marine Science:*
886 *Journal du Conseil* **66**(7): 1570-1583.
- 887 Russell, F.S. 1976. The eggs and planktonic stages of British marine fishes. Academic Press,
888 London (UK).

- 889 Seliverstov, A.S. 1974. Vertical migrations of larvae of the AtlantoScandian herring (*Clupea*
890 *harengus* L.). *In* The Early Life History of Fish. *Edited by* J.H.S. Blaxter. Springer, New
891 York, NY.
- 892 Sinclair, M. 2009. Herring and ICES: a historical sketch of a few ideas and their linkages. ICES
893 Journal of Marine Science **66**(8): 1652-1661. doi:10.1093/icesjms/fsp115.
- 894 Skagseth, O., Slotte, A., Stenevik, E.K., and Nash, R.D.M. 2015. Characteristics of the
895 Norwegian coastal current during years with high recruitment of Norwegian Spring
896 spawning herring (*Clupea harengus* L.). Plos One **10**(12).
897 doi:10.1371/journal.pone.0144117.
- 898 Sotillo, M.G., Cailleau, S., Lorente, P., Levier, B., Aznar, R., Reffray, G., Amo-Baladron, A.,
899 Chanut, J., Benkiran, M., and Alvarez-Fanjul, E. 2015. The MyOcean IBI Ocean Forecast
900 and Reanalysis Systems: operational products and roadmap to the future Copernicus
901 Service. Journal of Operational Oceanography **8**(1): 63-79.
902 doi:10.1080/1755876x.2015.1014663.
- 903 Soulsby, R.L. 1990. Tidal-current boundary layers. *In* The Sea, Ocean Engineering Science. John
904 Wiley & Sons,, New York.
- 905 Staatterman, E., and Paris, C.B. 2014. Modelling larval fish navigation: the way forward. ICES
906 Journal of Marine Science **71**(4): 918-924. doi:10.1093/icesjms/fst103.
- 907 Stephenson, R.L., and Power, M.J. 1988. Semidiel vertical movements in Atlantic herring
908 *Clupea harengus* larvae: a mechanism for larval retention? Marine Ecology Progress
909 Series **50**: 3-11.
- 910 Stephenson, R.L., Melvin, G.D., and Power, M.J. 2009. Population integrity and connectivity in
911 Northwest Atlantic herring: a review of assumptions and evidence. ICES Journal of
912 Marine Science **66**(8): 1733-1739. doi:10.1093/icesjms/fsp189.

- 913 Stephenson, R.L., Power, M.J., Laffan, S.W., and Suthers, I.M. 2015. Tests of larval retention
914 in a tidally energetic environment reveal the complexity of the spatial structure in
915 herring populations. *Fisheries Oceanography* **24**(6): 553-570. doi:10.1111/fog.12129.
- 916 Townsend, D.W., and Graham, J.J. 1981. Growth and age structure of larval Atlantic herring,
917 *Clupea harengus harengus*, in the Sheepscot river estuary, Maine, as determined by
918 daily growth increments in otoliths. *Fishery Bulletin* **79**(1): 123-130.
- 919 van der Molen, J., Rogers, S.I., Ellis, J.R., Fox, C.J., and McCloghrie, P. 2007. Dispersal patterns
920 of the eggs and larvae of spring-spawning fish in the Irish Sea, UK. *Journal of Sea*
921 *Research* **58**(4): 313-330. doi:10.1016/j.seares.2007.07.003.
- 922 Venables, W.N., and Ripley, B.D. 2002. *Modern Applied Statistics with S*. . Fourth ed. Springer
923 New York.
- 924 Vikebø, F., Sundby, S., Adlandsvik, B., and Fiksen, O. 2005. The combined effect of transport
925 and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-
926 Norwegian cod. *ICES Journal of Marine Science* **62**(7): 1375-1386.
927 doi:10.1016/j.icesjms.2005.05.017.
- 928 Voesenek, C.J., Muijres, F.T., and van Leeuwen, J.L. 2018. Biomechanics of swimming in
929 developing larval fish. *Journal of Experimental Biology* **221**(1).
930 doi:10.1242/jeb.149583.
- 931 Werner, F.E., Cowen, R.K., and Paris, C.B. 2007. Coupled biological and physical models
932 present capabilities and necessary developments for future studies of population
933 connectivity. *Oceanography* **20**(3): 54-69.
- 934 Wood, S., Paris, C.B., Ridgwell, A., and Hendy, E.J. 2014. Modelling dispersal and connectivity
935 of broadcast spawning corals at the global scale. *Global Ecology and Biogeography*
936 **23**(1): 1-11. doi:10.1111/geb.12101.

- 937 Wright, P.J., and Trippel, E.A. 2009. Fishery-induced demographic changes in the timing of
938 spawning: consequences for reproductive success. *Fish and Fisheries* **10**(3): 283-304.
939 doi:10.1111/j.1467-2979.2008.00322.x.
- 940 Young, E.F., Aldridge, J.N., and Brown, J. 2000. Development and validation of a three-
941 dimensional curvilinear model for the study of fluxes through the North Channel of
942 the Irish Sea. *Continental Shelf Research* **20**(9): 997-1035. doi:10.1016/s0278-
943 4343(00)00008-x.
- 944 Young, E.F., Brown, J., Aldridge, J.N., Horsburgh, K.J., and Fernand, L. 2004. Development and
945 application of a three-dimensional baroclinic model to the study of the seasonal
946 circulation in the Celtic Sea. *Continental Shelf Research* **24**(1): 13-36.
- 947 Zölck, M., Brophy, D., Mohn, C., Minto, C., and McGrath, D. 2015. Bio-physical model provides
948 insight into dispersal of plaice (*Pleuronectes platessa* L.) from putative spawning
949 grounds to nursery areas on the west coast of Ireland. *Journal of Sea Research* **99**: 61-
950 73. doi:10.1016/j.seares.2015.02.003.
- 951

Table 1. Estimates of biomass and abundance of juvenile and adult herring in the Irish and Celtic Seas taken from the ICES herring stock assessment report (ICES 2016) and used to assess possible relative rates of pre-recruitment survival and dispersal of Celtic Sea herring to the Irish Sea. The year-classes included in the simulations are shown in boldface type. Year-class indicates the year when the 0-group juveniles were spawned (i.e. 1 year prior to the estimation of their biomass as 0-group juveniles).

Year-class	Celtic Sea			Irish Sea		Juvenile /adult biomass		Celtic Sea recruitment success	Hypothesised transport from Celtic to Irish Sea
	Recruits (N)	Spawning stock Biomass (parent stock)	Recruits per tonne SSB	0-group juveniles (t)	Spawning stock Biomass (parent stock)	Irish Sea adults	Celtic Sea adults		
2002	383,169	49,749	7.7	13,295	5,754	2.31	0.27	Low	High
2003	1,169,010	38,746	30.2	11,240	5,438	2.07	0.29	High	Moderate
2004	408,108	36,467	11.2	5,676	7,689	0.74	0.16	Moderate	Low
2005	917,257	56,092	16.4	18,616	9,127	2.04	0.33	High	Moderate
2006	395,932	72,288	5.5	18,423	9,578	1.92	0.25	Low	Moderate
2007	1,465,500	79,355	18.5	42,891	13,377	3.21	0.54	High	High
2008	1,169,110	99,065	11.8	38,544	16,413	2.35	0.39	Moderate	High
2009	1,541,530	121,558	12.7	13,962	17,452	0.80	0.11	Moderate	Low
2010	1,104,530	142,470	7.8	42,000	19,438	2.16	0.29	Low	Moderate
2011	588,701	164,809	3.6	8,560	20,135	0.43	0.05	Low	Low
2012	539,982	163,226	3.3	58,719	19,602	3.00	0.36	Low	High
Mean	880,257	93,075	12	24,721	13,091	1.91	0.28		

Table 2: Summary statistics from a comparison of ROMS 3D velocity profiles with 3D velocity fields calculated from the depth averaged velocity fields using the formula of Soulsby (1990). The normalised root mean square error (RMSE) represents the RMSE of the difference between the velocities divided by the range of the ROMS velocity.

Level	U component velocity	V component velocity
<i>Correlation Coefficient (Mean of all time series)</i>		
Full Profile	0.92	0.99
Top 10 levels (near surface)	0.89	0.99
Middle 20 levels	0.98	0.99
Bottom 10 levels (near seabed)	0.94	0.99
<i>Normalised RMSE (%) (Mean of all time series)</i>		
Full Profile	4.8	2.1
Top 10 levels (near surface)	9.3	3.5
Middle 20 levels	3.6	1.4
Bottom 10 levels (near seabed)	5.8	2.2

Table 3: Results of comparative simulations run on two dates using different numbers of particles. Table shows the proportion of the particles in each area at the end of the 30 day simulation and the maximum difference between simulations.

Endpoint distribution	Date	Particle number				Max. difference
		1,000	3,000	5,000	10,000	
Retained in Celtic Sea (areas A and D)	Feb 28 th 2003	0.702	0.700	0.705	0.710	0.01
	Feb 7 th 2005	1	0.999	0.998	0.998	0.002
Dispersed offshore in Celtic Sea (area C)	Feb 28 th 2003	0.188	0.180	0.180	0.169	0.019
	Feb 7 th 2005	0	0	0	0	0
Transported to Irish Sea (area B)	Feb 28 th 2003	0.111	0.121	0.115	0.121	0.01
	Feb 7 th 2005	0	0.001	0.002	0.002	0.002

Table 4. Model fitting diagnostics for the multinomial models that were used to investigate the influence of wind and tidal state on larval endpoints (the area in which the particle is located at the end of the 30 simulation). The final selected model is highlighted in bold. The six wind indices reflect the strength and duration of the winds within six directional categories: 150°-210 ° (SSE-SSW); 210°-270° (SSW-W); 270°-330° (W-NNW); 330°-30° (NNW-NNE), 30°-90° (NNE-E) and 90°-150° (E-SSE). The tidal index relates to the state of the tide on the release date (spring, neap or moderate tides). Refer to the text for a full description of how the indices are calculated.

Model	AIC	R ² observed vs predicted		
		CS	OS	IS
endpoint~ind150-210	82,409	0.29	0.21	0.08
endpoint~ind210-270	73,654	0.54	0.62	0.03
endpoint~ind90-150	83,456	0.14	0.19	0.14
endpoint~ind270-330	90,805	0.001	0.003	0.03
endpoint~ind330-30	86,576	0.15	0.07	0.14
endpoint~ind30-90	89,094	0.06	0.07	0.002
endpoint~ind150-210+tidal state	78,565	0.29	0.24	0.25
endpoint~ind210-270+tidal state	72,409	0.55	0.61	0.18
endpoint~ind90-150+tidal state	80,635	0.27	0.30	0.38
endpoint~ind270-330+tidal state	87,423	0.0003	0.009	0.21
endpoint~ind330-30+tidal state	83,821	0.13	0.11	0.30
endpoint~ind30-90+tidal state	84,677	0.09	0.11	0.14
endpoint~ind90-150+ ind210-270+tidal state	68,132	0.76	0.77	0.42

Table 5. Summary statistics from the multinomial model relating larval endpoint to two wind indices and the tidal state index (endpoint~ind90-150+ ind210-270+tidal state)

Model term	Chi-square	P value	Area	Relative risk ratios (exp(coeff))
<i>Ind90-150</i>	4280.1	<0.0001	IS	1.0006
			OS	0.9988
<i>Ind210-270</i>	12506.7	<0.0001	IS	0.9997
			OS	1.0020
			IS Neap	0.2388
<i>Tidal state</i>	916.4	<0.0001	IS Spring	0.1810
			OS Neap	1.0162
			OS Spring	0.6258

Table 6. Summary of the outcomes from 144 releases of 3000 particles (3 replicate releases of 1,000 particles on 4 dates within each of 6 years using 2 model types) simulated over a 30 day simulation period. Table shows the mean percentage in each area \pm standard deviation, with the range in parenthesis. Particles were released from a known herring spawning area in the Celtic Sea.

Endpoint distribution	Percentage of particles	
	<i>Non-tidal simulation</i>	<i>Tidal simulation</i>
Retained in Celtic Sea (areas A and D)	70.1 \pm 25.1 (0-100)	78.0 \pm 25.9 (0-100)
Dispersed offshore in Celtic Sea (area C)	27.6 \pm 26.0 (0-100)	17.9 \pm 26.0 (0-99.9)
Transported to Irish Sea (area B)	2.8 \pm 7.1 (0-34.2)	4.1 \pm 7.2 (0-31.0)

1 Table 7. Sources of variation in the number of particles in each area at the end of the 30-day simulation period.

Area	Mean % coefficient of variation (CV)			Proportion of CV due to:		
	Replicate runs	Release dates	Overall	replicate variation	Intra-annual variation	Inter-annual variation
<i>Non-tidal simulation</i>						
Celtic Sea inshore	1.56	32.21	36.52	0.04	0.84	0.12
Irish Sea	6.39	156.13	311.08	0.02	0.48	0.50
Celtic Sea offshore	11.85	81.84	94.09	0.13	0.74	0.13
<i>Tidal simulation</i>						
Celtic Sea inshore	1.29	30.83	33.25	0.04	0.89	0.07
Irish Sea	25.91	111.20	174.50	0.15	0.49	0.36
Celtic Sea offshore	22.84	121.91	145.14	0.16	0.68	0.16

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7 **Figure legends:**

8 **Figure 1.** Map illustrating the distribution of herring in the Celtic and Irish Seas during
9 the first year of life. The dark grey shaded areas show the general location of herring
10 spawning grounds taken from O’Sullivan et al (2013) (Celtic Sea; autumn and winter
11 spawners) and Dickey-Collas et al (2001) (Irish Sea; autumn spawners). The light grey
12 shading indicates the general distributional extent of larval herring in the Celtic Sea
13 during the December-March period as evidenced by larval surveys from 1978-1985 and
14 1989-1990 (O’Sullivan et al, 2013). Locations in the Celtic Sea where juvenile 0-group
15 herring were recorded by Brophy et al (2002) and Clarke et al (2010) are marked with
16 black circles. Black triangles denote locations where winter-spawned 0-group juvenile
17 herring (of likely Celtic Sea origin) occurred together with autumn spawned 0-group
18 juveniles (of likely Irish Sea origin) as reported by Brophy et al 2002 and Burke et al
19 (2009)

20

21 **Figure 2.** Map of the Celtic and Irish Seas showing the particle release area on the
22 Dunmore East spawning grounds (A). At the end of each simulation, particle endpoints
23 were mapped and the numbers of endpoints in the Irish Sea (B), Celtic Sea offshore (C)
24 and Celtic Sea inshore (D) were counted and compared between runs. The dashed box
25 indicates the boundary of the study area used in the simulations. The position of the
26 Met Éireann synoptic station from which wind measurements were obtained is
27 indicated by a black square.

28 **Figure 3.** Long-term trends in mean monthly wind speed (left), hours (centre) and wind
29 index (speed*hours, standardized to 30 days, right) during December-March. Wind

variables are calculated across six categories based on the direction of the wind as indicated by the labels in the right hand bar. Wind data was obtained from the synoptic weather station at Cork airport maintained by Met Éireann.

Figure 4. Long-term trends in recruitment strength of Celtic Sea herring expressed as the number of two year olds (R) divided by the Spawning Stock Biomass of the parent stock. The horizontal line indicates the mean for the time series.

Figure 5. Proportion of particles in each area (offshore Celtic Sea: light grey, retention in Celtic Sea: black, transport to Irish Sea: dark grey) at the end of the 30 day simulation period using the non-tidal simulation (NT) and the tidal simulation (T). Panel borders separate the various year classes for which larval transport is simulated; e.g. the 2002 year class corresponds to the period December 2002-March 2003. The simulation start date is shown over each pair of simulations.

Figure 6. Particle distributions at the end of each 30 day simulation using the **non-tidal simulation**. Particles are colour coded according to their position in relation to the three predefined areas indicated by the boundary lines in the maps: Celtic Sea (green), Irish Sea (blue), offshore (purple). The first day of the simulation is indicated above each plot.

Figure 7. Particle distributions at the end of each 30 day simulation using the **tidal simulation**. Particles are colour coded according to their position in relation to the three predefined areas indicated by the boundary lines in the maps: Celtic Sea (green),

Irish Sea (blue), offshore (purple). The first day of the simulation is indicated above each plot.

Figure 8. Particle trajectories for particles released from similar locations within the Celtic Sea spawning area in the non-tidal (left hand panels) and tidal (right hand panels) simulations on two dates. Circles represent the release locations and triangles represent the positions at the end of the 30 day simulation period.

Figure 9. Predicted proportion of particles in each area (offshore Celtic Sea: light grey, retention in Celtic Sea: black, transport to Irish Sea: dark grey) at the end of the 30 day simulation period under three conditions of diel vertical migration (DVM: none, 0-30m at night, 0-100m at night; top panel) and with five diffusion parameter settings (diffusion coefficient set to 0, 10^{-9} , 10^{-8} , 10^{-7} and $10^{-6} \text{ m}^2.\text{s}^{-3}$; bottom panel). The simulation start date is shown over each set of simulations.

Figure 10. Predicted versus observed proportions of particles in each area at the end of the 30 day simulation period using the full oceanographic model (tidal simulation). Predicted values are based on the multinomial model of larval endpoint probabilities as a function of two wind indices (WI 210-270 WI 90-150) and the tidal range index.

Figure 11. Mean predicted probabilities (plotted line) with 95% confidence limits (grey shading) of a particle occupying each of the three areas (Celtic Sea, Irish Sea, offshore) at the end of the 30 day simulation period in relation to the strength and frequency of

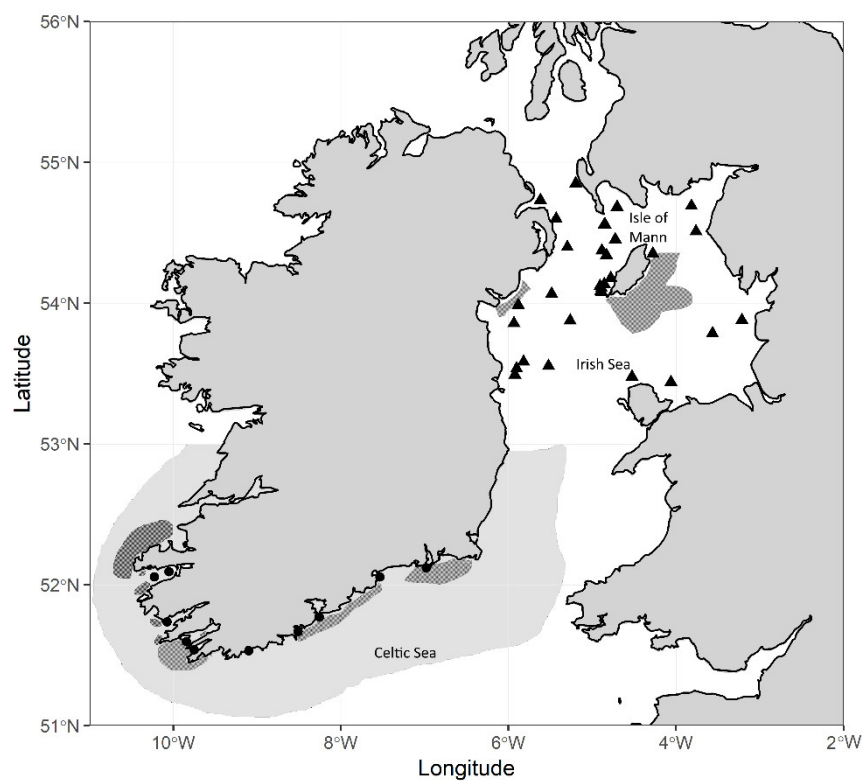
76 E-SSE winds (ind90-150) and SSW-W winds (ind210-270). The vertical line indicates the
77 mean wind index across all of the years.

78 Figure 12. Mean predicted probabilities (with 95% confidence limits) of a particle
79 occupying each of the three areas (Celtic Sea, Irish Sea, offshore) at the end of the 30
80 day simulation period for each tidal state category .

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83 Figure 1.



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Figure 2.

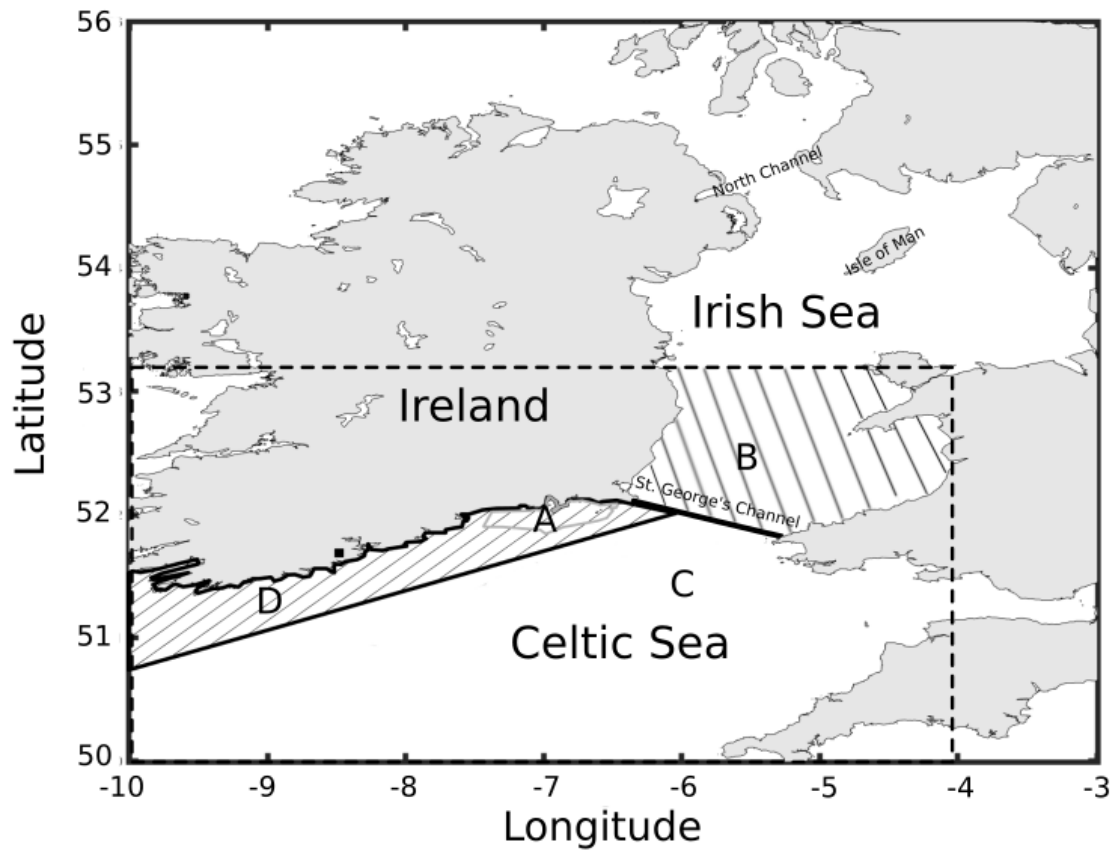
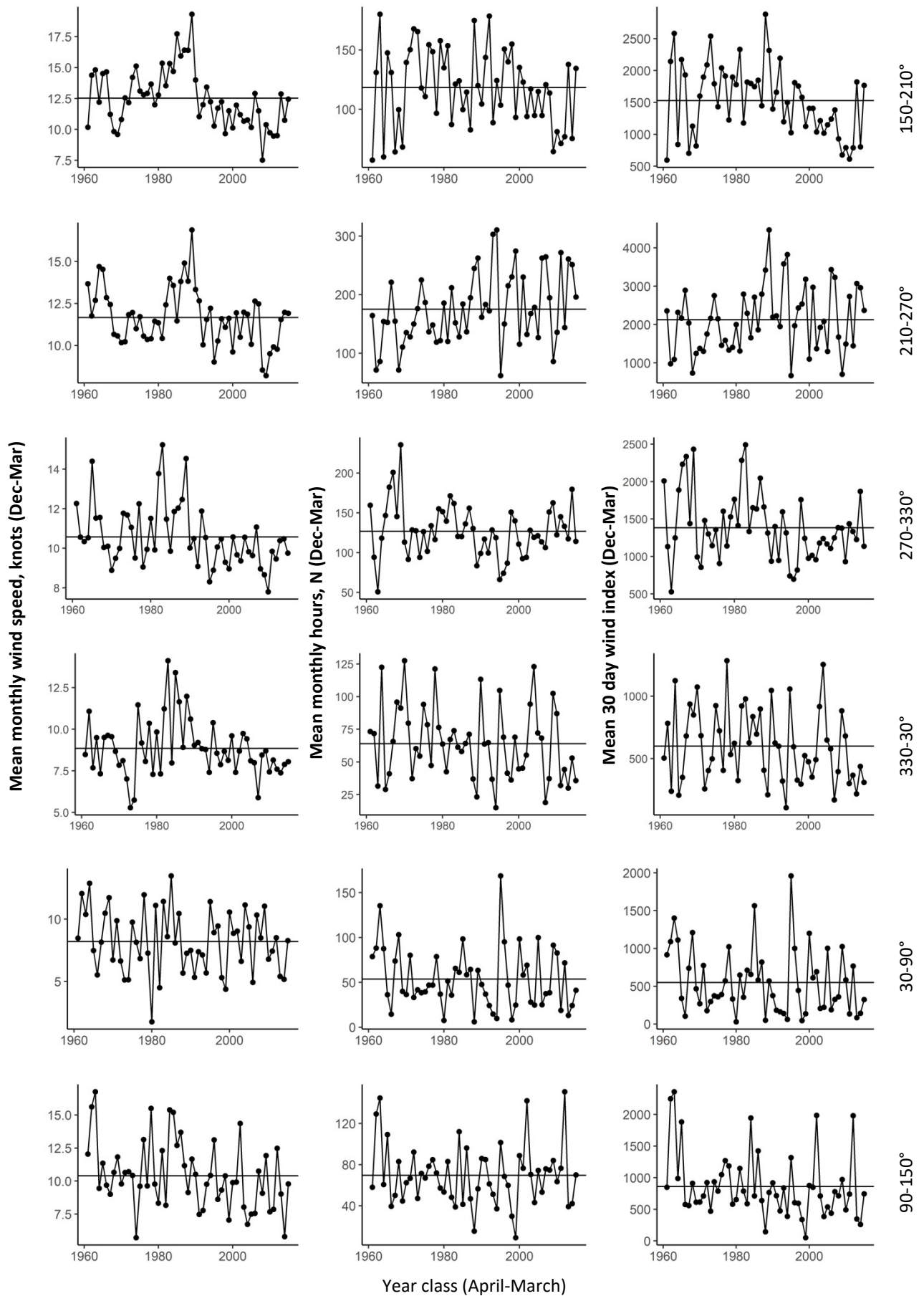
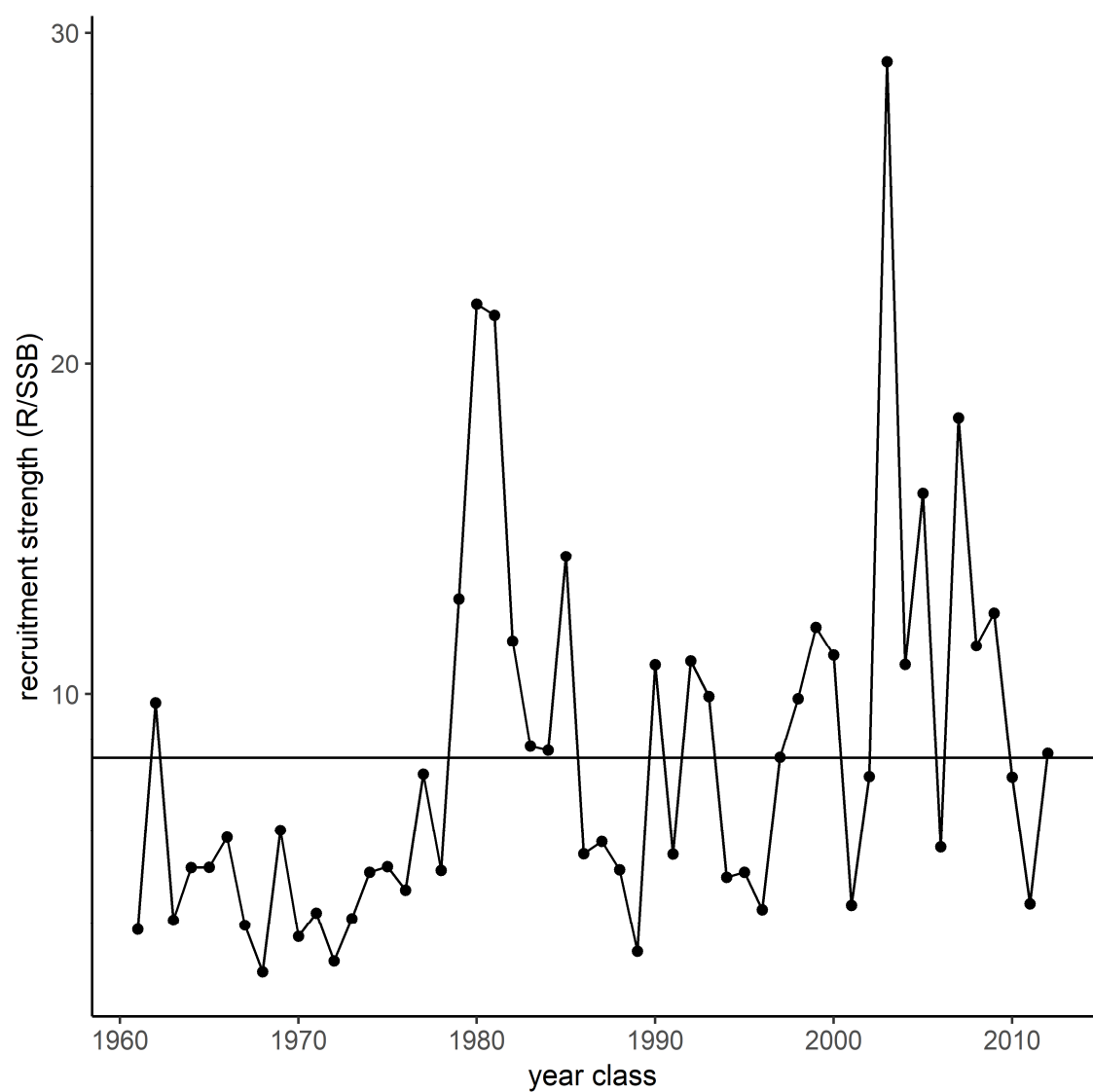


Figure 3.



117 Figure 4.



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Figure 5.

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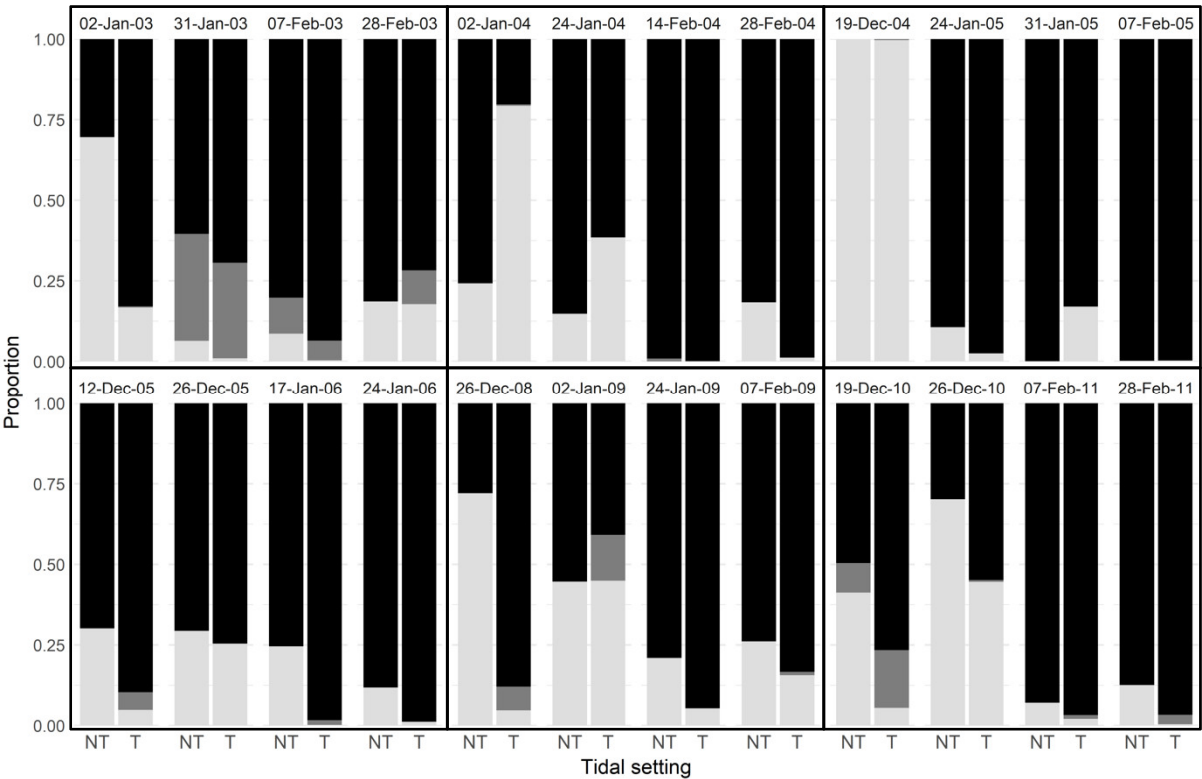


Figure 6.

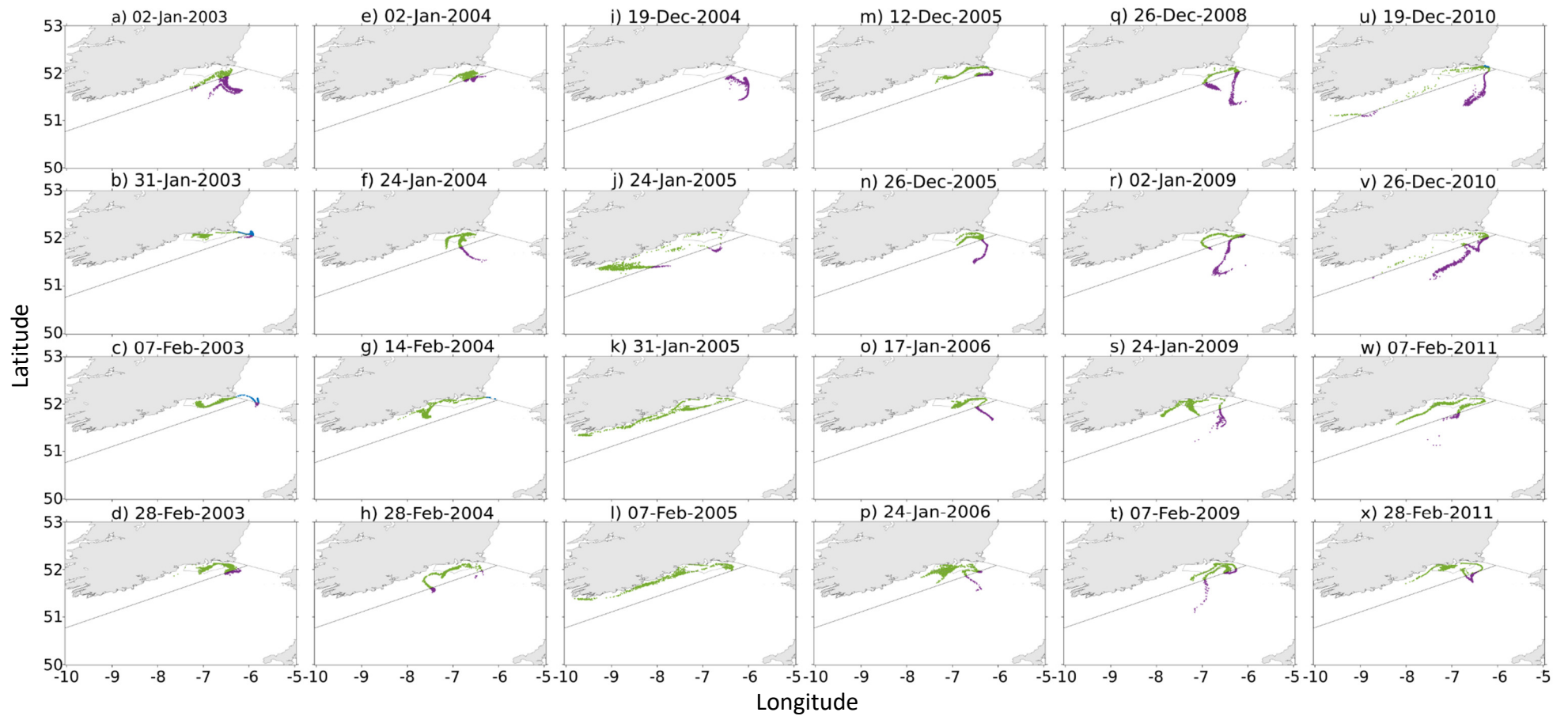
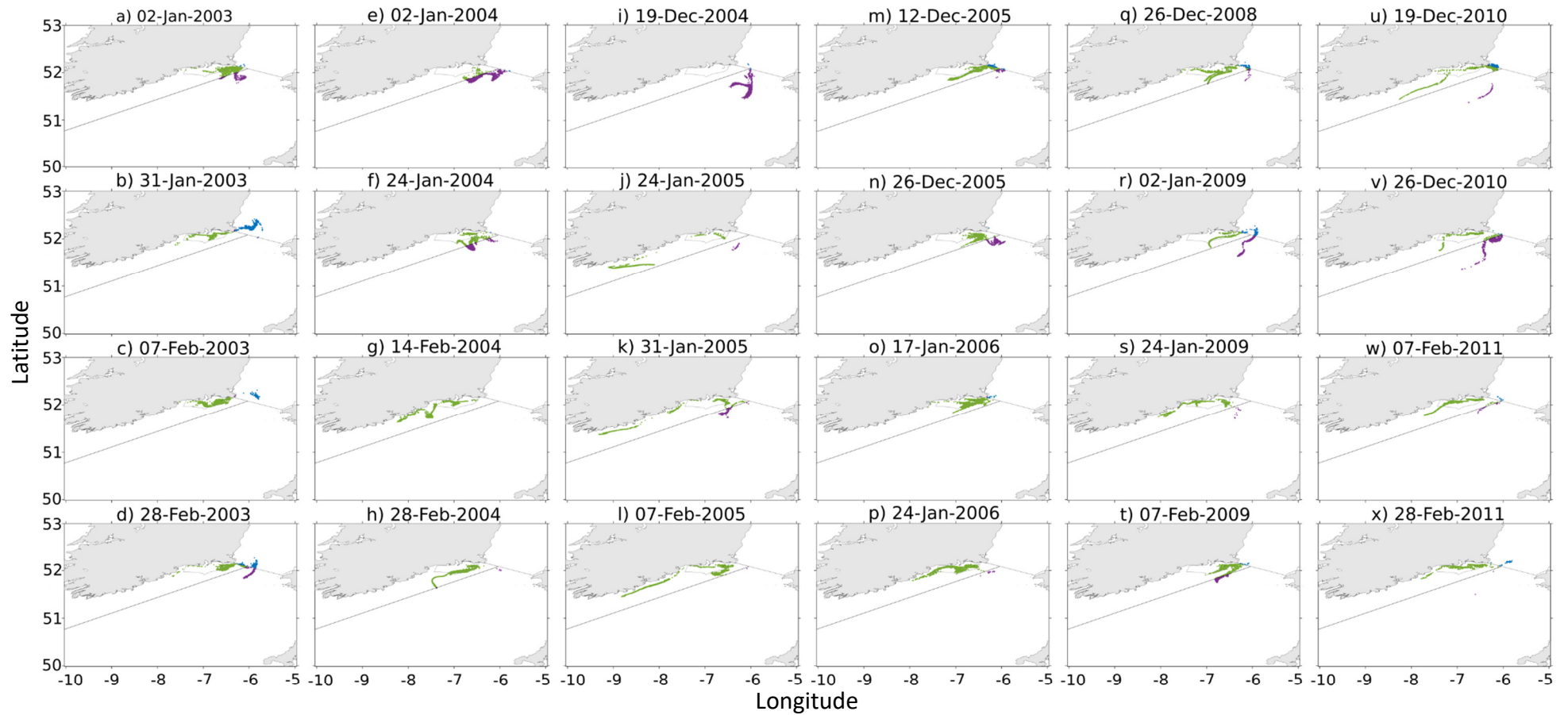


Figure 7.



148 Figure 8.

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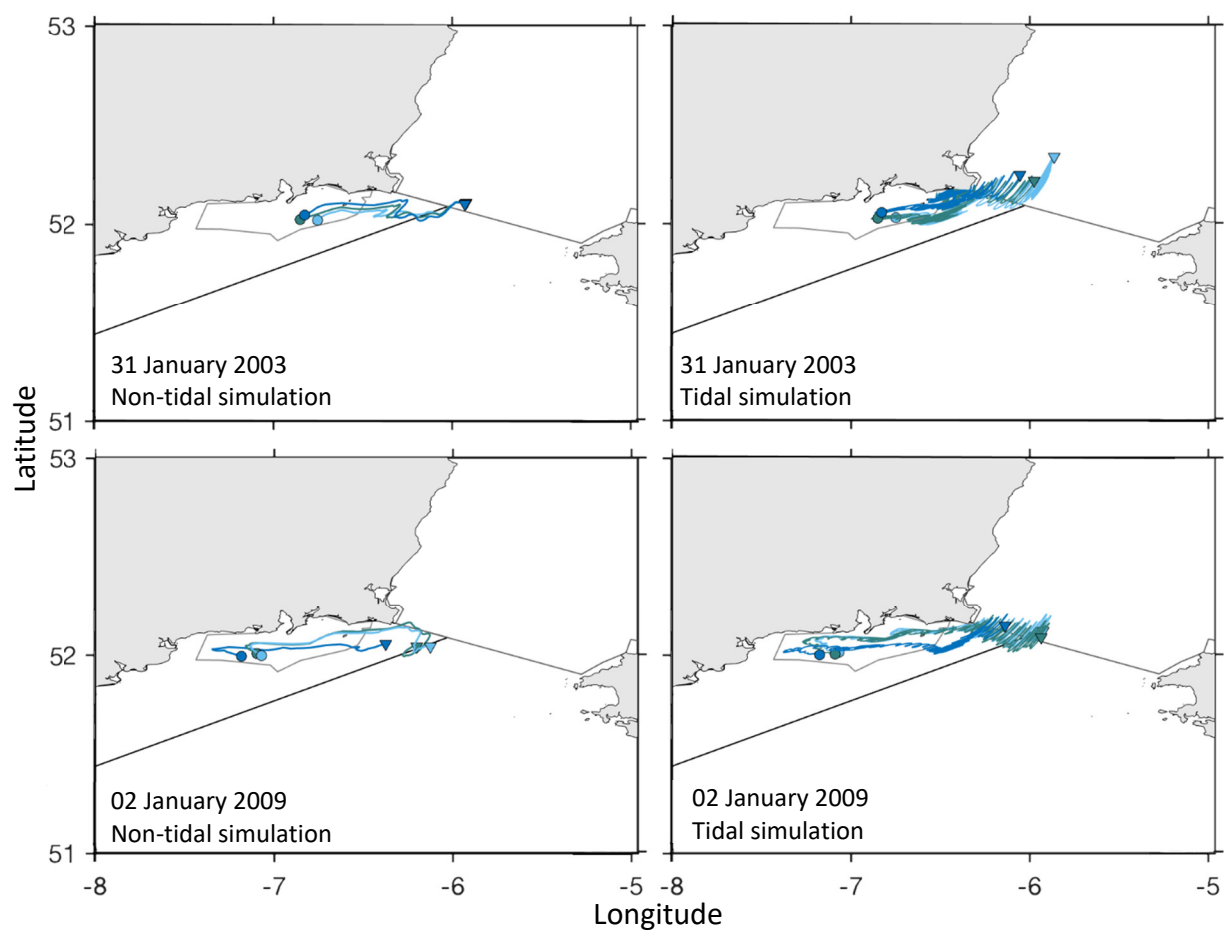


Figure 9.

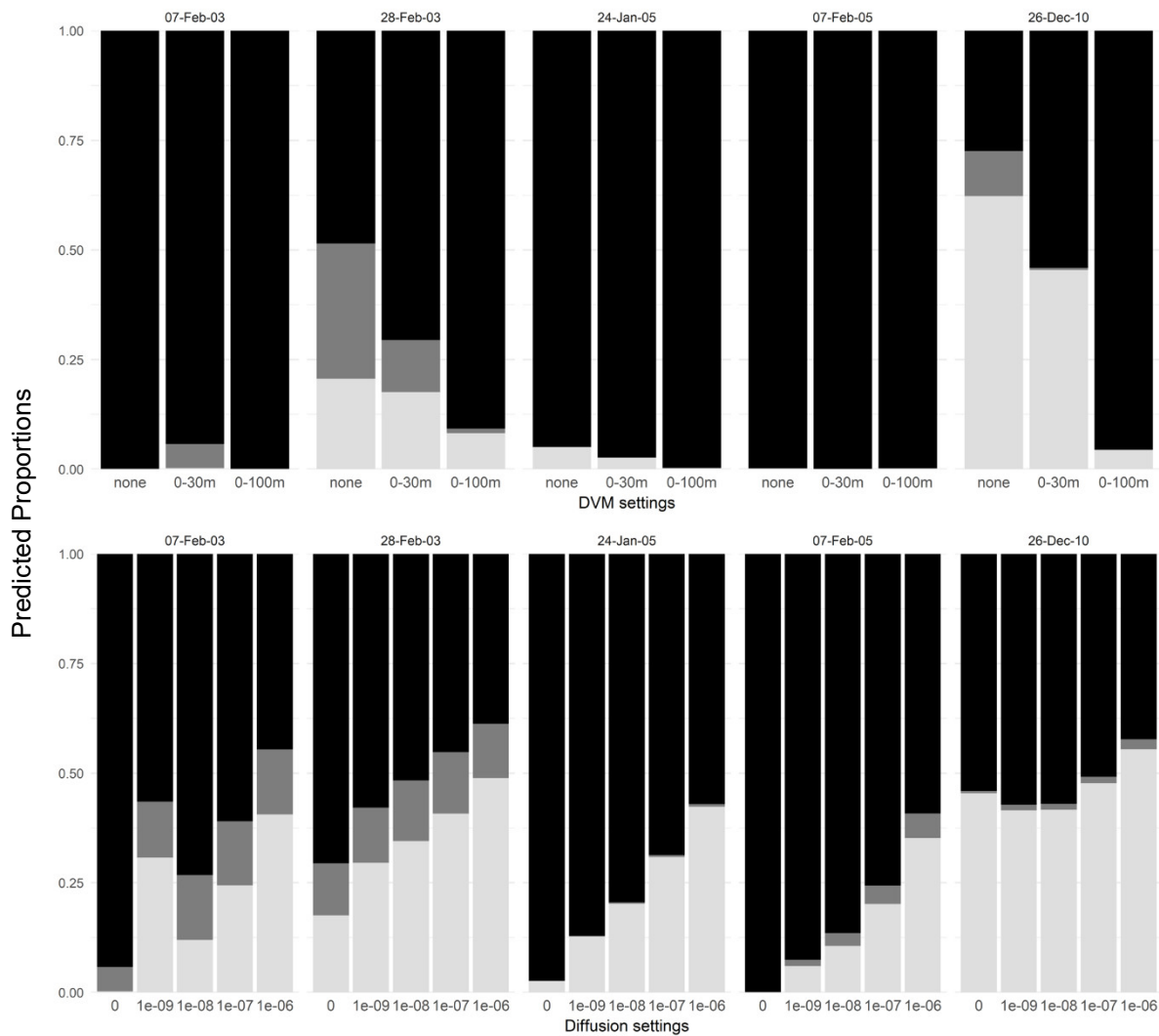


Figure 10.

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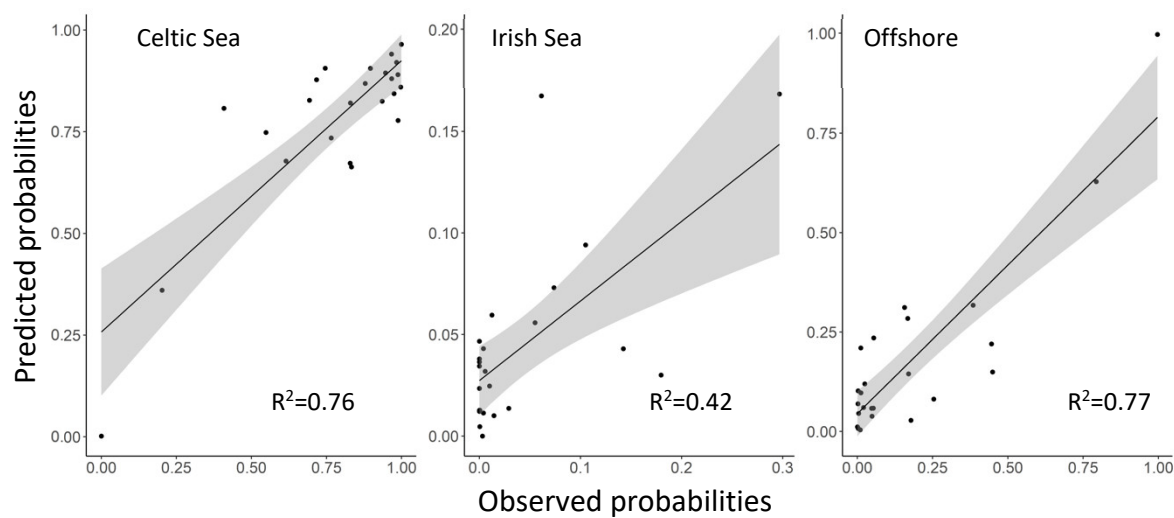


Figure 11.

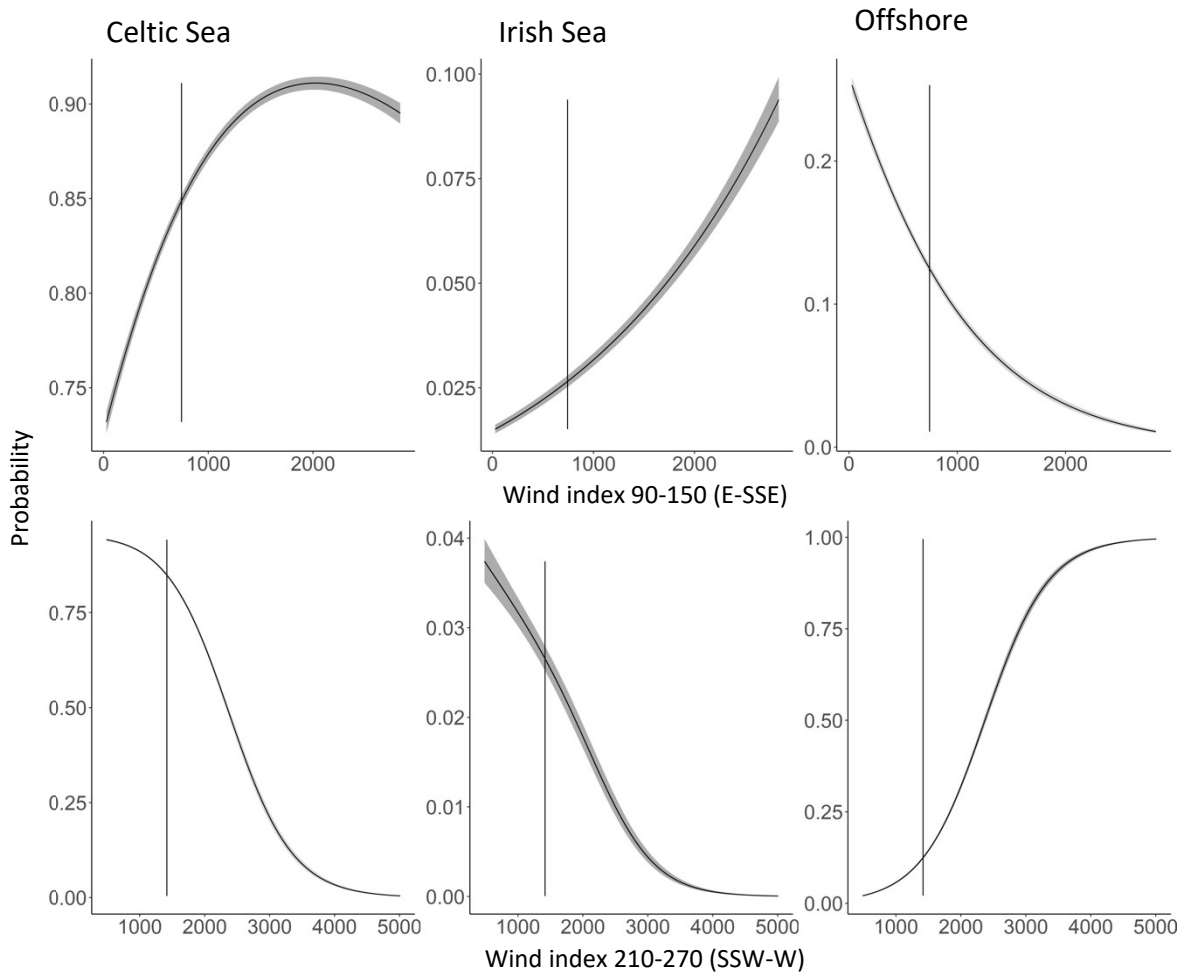


Figure 12.

