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### 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.

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*Herring transport, retention and connectivity*

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

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15

*Herring transport, retention and connectivity***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

*Herring transport, retention and connectivity***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 (Huyer 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).

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

63 In the Celtic and Irish Seas mixing of herring spawning components creates difficulties for the  
64 management and assessment of the fisheries. The Celtic Sea herring stock is comprised of an  
65 autumn and winter spawning component which are managed as a single unit (ICES, 2016)  
66 although reproductive exchange between the components appears to be limited by spawning  
67 season fidelity (Brophy et al 2006). Celtic Sea herring spawn at discrete locations along the  
68 south coast of Ireland (O'Sullivan et al 2013) (Figure 1). The distribution of the two spawning  
69 components overlaps, but autumn spawning is more common in the western Celtic Sea and  
70 winter spawning is more common in the eastern Celtic Sea (O'Sullivan et al 2013). In the Irish  
71 Sea, herring spawning activity is concentrated along the coast of the Isle of Man in September  
72 and October; some spawning also occurs on the north east coast of Ireland in autumn (ICES,  
73 2016). This stock is managed as discrete unit, but due to juvenile mixing recruitment is difficult  
74 to forecast. Therefore, a priority for the management of the Irish and Celtic Sea herring  
75 fisheries is to determine the degree of mixing that occurs during the juvenile phase (ICES,  
76 2016).

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

94 The Celtic and Irish Seas are highly dynamic environments, influenced by winds, tides and  
95 salinity gradients (Horsburgh et al. 1998; Pingree 1980) and subject to high tidal mixing. The  
96 formation of a tidal mixing front and stratification creates a cyclonic circulation pattern in the  
97 Celtic Sea that flows along the contours of bottom density (Brown et al. 2003; Young et al.  
98 2004). From November to March the influence of winds on circulation forms a fully mixed  
99 water column (Horsburgh et al. 1998; Pingree 1980; Young et al. 2004). Based on prevailing  
100 currents, the predominant direction of transport is expected to be in a westward direction,

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

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

**116 Methods**

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

123

*Herring transport, retention and connectivity*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

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147 2003 and 2005 year-classes showed relatively high rates of survival to age 2 (>15 recruits per  
148 tonne SSB) while pre-recruitment survival was relatively low for the 2002 and 2010 year  
149 classes (<10 recruits per tonne SSB) and close to average for the 2004 and 2008 year-classes  
150 (10-14 per tonne SSB) (Table 1). The index of 0-group herring biomass in the Irish Sea reflects  
151 the abundance of both the resident Irish Sea population and herring that disperse from the  
152 Celtic Sea and appear to return as adults to spawn with their parent stock (Brophy et al 2006).  
153 It was hypothesised that when transport from the Celtic Sea to the Irish Sea was relatively  
154 high, 0-group herring biomass in the Irish Sea would be high relative to the SSB of both the  
155 Irish and Celtic Sea stocks. Accordingly, the 2002 and 2008 year-classes were predicted to  
156 show relatively high rates of transport to the Irish Sea while transport was predicted to have  
157 been relatively low in 2004 (Table 1). Without direct observations of larval and juvenile  
158 distributions from the time period of interest it is not possible to determine actual rates of  
159 transport. The study was designed to quantify variation in transport and retention across  
160 years rather than to compare specific years; the available data describing recruitment  
161 strength and estimated transport rates (Table 1) provided a basis for subsequently evaluating  
162 any annual trends in modelled larval dispersal trajectories.

*163 Selection of particle release dates*

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

169

*Herring transport, retention and connectivity*170 *Simulation of larval transport*

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

176 After hatching, larval herring feed endogenously on yolk sac reserves. At a temperature of 8-  
177 10°C the estimated duration of the yolk-sac period is approximately 10 days, during which  
178 time the larvae have weak swimming abilities and their movement is largely passive (Pepin  
179 1991; Russell 1976). Therefore, at the initiation of the run there was a 10-day period of passive  
180 transport. After the initial passive transport phase, and at the point of yolk-sac absorption,  
181 herring begin to vertically migrate. Larval herring display diel vertical migration (DVM) in  
182 response to light and feeding conditions (Ferreira et al. 2012). Reported patterns of DVM  
183 differ between populations and include type I (deep during the daytime and shallow at night;  
184 (Ferreira et al. 2012; Seliverstov 1974), type II (surface during the daytime and deep at night  
185 (Haslob et al. 2009; Heath et al. 1988; Munk et al. 1989) and semi-diel migration (Stephenson  
186 and Power 1988). As herring larvae are visual feeders, light intensity is the most influential  
187 determinant of vertical distribution and concentration in surface waters during the day is  
188 common (Bartsch 1993; Dickey-Collas et al. 2009). For herring on the west coast of Ireland,  
189 Grainger (1980) showed that early larvae (7-12mm) were concentrated between 5m and 15m  
190 depth during the daytime. It was therefore assumed that Celtic Sea herring larvae display type  
191 II diel vertical migration. In the Ichthyop simulation, after the initial 10 day period of passive  
192 transport, particle depths were set at 10m during the day. At night, each particle occupied a  
193 randomly generated depth between 10m and 30m at night (10-30m DVM). Five release dates

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194 which showed contrasting patterns of dispersion and retention in the main simulation, were  
195 selected to investigate the influence of diel vertical migration behaviour on particle transport:  
196 7<sup>th</sup> February 2003; 28<sup>th</sup> February 2003; 24<sup>th</sup> January 2005; 7<sup>th</sup> February 2009; 26<sup>th</sup> December  
197 2010. The additional simulations were run without diel vertical migration (no DVM) and with  
198 randomly generated night time depths of between 10m and 100m (10-100m DVM) and the  
199 outputs were compared.

200 Celtic Sea herring spawn in specific areas of gravel and rocky substrates (O'Sullivan et al.  
201 2013). The release area for the simulations was the spawning ground offshore of Dunmore  
202 East on the south east coast of Ireland (Breslin 1998), (Figure 2, area A) which is thought to  
203 be the main source of the winter spawned Celtic Sea herring that move into the Irish Sea  
204 during the first year of life (O'Sullivan et al. 2013). On each date 3,000 particles were released,  
205 in three replicate batches of 1,000 particles. On each run, particles were released at the  
206 bottom and at randomly selected positions within the release area. Larval transport was  
207 simulated for 30 days with DVM behaviours included for 20 days after day 10. During the first  
208 30 days movements of herring larvae would be largely controlled by passive transport and  
209 DVM (~10 days after hatching) and larvae would be too small to be capable of directional  
210 swimming (Graham and Townsend 1985; Pepin 1991; Townsend and Graham 1981).

*211 Mechanism for ocean circulation*

212 The three dimensional velocity fields used to drive advection and dispersion in Ichthyop were  
213 taken from the Atlantic-Iberian Biscay Irish Ocean Physics Reanalysis (2002-2014) (Sotillo et  
214 al. 2015). This is an ocean physics reanalysis based on version 2.3 of the NEMO model (Madec  
215 2008). The horizontal resolution of the model is 1/12° and there are 75 vertical levels with a  
216 resolution of 1 metre near the surface, coarsening to 200 metres in the deep ocean.

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217 Atmospheric forcing is provided by ECMWF (European Centre for Medium-Range Weather  
218 Forecasts) ERA-Interim dataset and tidal forcing is also included. The data assimilation  
219 component constrains the model solution using sea level anomaly, sea surface temperature  
220 and in situ profiles of temperature and salinity. The data from this reanalysis is available from  
221 the Copernicus website under the product name, IBI\_REANALYSIS\_PHYS\_005\_002. Monthly  
222 mean, daily mean, and hourly mean fields of temperature, salinity, velocity and sea surface  
223 height are provided.

224 Simulations were run using two different velocity fields setups:

*225 Daily Mean Currents*

226 For these simulations, the daily mean velocity fields from IBI\_REANALYSIS\_PHYS\_005\_002  
227 were used. In effect, the daily averaging process removes most of the tidal signal from the  
228 velocity fields so these fields represent the residual velocity due to wind forcing and  
229 baroclinicity. These simulations were run in Ichthyop with a time step of 7,200 seconds. The  
230 working hypothesis is that the residual currents alone would not result in the transport of  
231 particles in the Irish Sea. This model is henceforth referred to as the “non-tidal simulation”

*232 Derived Hourly Currents*

233 To simulate the effect of the tides on the velocity fields, a higher temporal resolution is  
234 required. The IBI\_REANALYSIS\_PHYS\_005\_002 provides hourly barotropic velocity fields, but  
235 full three dimensional velocity fields are required for the Ichthyop simulations. Ideally, the  
236 hourly three dimensional velocity fields simulated by the NEMO model itself would have been  
237 used in the simulations, but, in the absence of this data being available, the solution was to  
238 derive the three dimensional fields from the hourly barotropic velocities using the empirical  
239 formula presented in Soulsby (1990) (henceforth referred to as the Soulsby method).

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

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241 
$$U(z) = \left( \frac{z}{0.32h} \right)^{1/7} \bar{U} \quad \text{for } 0 < z < 0.5h$$

242 
$$U(z) = 1.07\bar{U} \quad \text{for } 0.5h < z < h$$

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

245 
$$\bar{U} = \frac{1}{h} \int_0^h U(z)$$

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

249 *Validation of the velocity fields for the tidal model*

250 The Soulsby method was validated using a three-dimensional ocean model for the region,  
 251 which utilizes the Regional Ocean Modelling System (ROMS) code and has been operational  
 252 since 2012. The operational model has a horizontal resolution of 1.2 to 2 km with 40 vertical  
 253 levels (variable thickness depending on water depth). Model fields are archived at hourly  
 254 intervals and the parameters archived include 3-dimensional velocity fields as well as depth  
 255 averaged velocities. One month (i.e. one full spring-neap tidal cycle) of archived data from an  
 256 area covering the eastern Celtic Sea and southern part of the Irish Sea was used for this  
 257 validation exercise. This area equated to 3,420 grid points so the validation was based on  
 258 3,240 velocity time series, each one month in length. For each time series the full 3-  
 259 dimensional velocity fields were calculated from the depth averaged velocity fields using the  
 260 Soulsby method and these velocities were compared to the ROMS 3D velocity profiles. The  
 261 mean correlation coefficient for the full profile was 0.92 and 0.99 for the  $u$  and  $v$  velocity  
 262 components, respectively, while the normalised root mean squared error (RMSE) estimates

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

*Impact of horizontal diffusion on particle distributions*

269 Small-scale horizontal diffusion can have a significant impact on the transport of larvae  
270 (Andutta et al. 2012; Werner et al. 2007). Measured diffusion coefficients for the study area  
271 were not available. It was therefore not possible to include realistic simulation of local  
272 diffusion processes within Icthyop and diffusion settings were not activated within the main  
273 simulations. In order to evaluate the sensitivity of the model outputs to diffusion, a series of  
274 simulations were run on five release dates which showed contrasting patterns of dispersion  
275 and retention in the main simulation (7<sup>th</sup> February 2003; 28<sup>th</sup> February 2003; 24<sup>th</sup> January  
276 2005; 7<sup>th</sup> February 2009; 26<sup>th</sup> December 2010). On each date, three replicate releases of 1,000  
277 particles were simulated with the diffusion coefficient set to  $0 \text{ m}^2 \cdot \text{s}^{-3}$ ,  $10^{-9} \text{ m}^2 \cdot \text{s}^{-3}$ ,  $10^{-8} \text{ m}^2 \cdot \text{s}^{-3}$ ,  
278  $10^{-7} \text{ m}^2 \cdot \text{s}^{-3}$  and  $10^{-6} \text{ m}^2 \cdot \text{s}^{-3}$  and the outputs were compared.

*Wind and tidal data*

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

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

291 The timing of the new moon was used to derive an index of tidal state on each release date.  
292 In each lunar cycle, the new moon was defined as day 0. Release dates that fell between days  
293 1 and 3 or between days 15 and 17 were classed as spring tides, those that fell between days  
294 7 and 9 or days 23 and 25 were classed as neap tides while those that fell on any other day  
295 were classed as moderate tides.

*Statistical analysis*

297 The distribution of the particles at the end of each simulation run (endpoints) was mapped  
298 using MATLAB\_R2015b. Particles were categorised according to their position at the end of  
299 the 30 day simulation period: transported to the Irish Sea (area B, Figure 2), transported  
300 offshore in the Celtic Sea (area C, Figure 2) or retained inshore in the Celtic Sea (areas A and  
301 area D, Figure 2). The Celtic Sea retention area was defined with reference to available data  
302 describing the distribution of juvenile herring in the Celtic Sea (Clarke et al 2010; O'Donnell  
303 et al 2015). The area outside of this and within the Celtic Sea was classed as offshore. Three  
304 replicate batches of 1,000 particles were released in each simulation. The inclusion of  
305 replicates allowed for statistical partitioning of intra- and inter-annual variation. For  
306 subsequent analysis the proportion of particles in each area was estimated from the  
307 combined totals of the three replicate releases (3,000 particles). To determine if the number  
308 of particles used in the simulations was sufficient to reliably determine the relative numbers

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309 dispersed to each area, simulations using 1,000, 3,000, 5,000 and 10,000 particles were run  
 310 on two release dates (February 28<sup>th</sup> 2003 and February 7<sup>th</sup> 2005) and the outputs were  
 311 compared. The number of particles in the simulation did not have a marked influence on the  
 312 estimated percentage in each area; the difference between estimates was never more than  
 313 2% (Table 3).

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

$$321 \quad \text{Variation between replicates} = \frac{\text{replicate CV}}{\text{total CV}}$$

$$322 \quad \text{Intra – annual variation} = \frac{\text{release date CV} - \text{replicate CV}}{\text{total CV}}$$

$$323 \quad \text{Inter-annual variation} = \frac{\text{total CV} - \text{release date CV}}{\text{total CV}}$$

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

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

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

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

**345 Results***346 Distribution of larval endpoints at end of simulation*

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

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

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

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

*Herring transport, retention and connectivity*376 *Model sensitivity to diel vertical migration*

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

392 *Model sensitivity to diffusion settings*

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

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400 14.4;  $p=0.2$ ). With one exception (26<sup>th</sup> December 2010), probability of retention in the Celtic  
401 Sea was highest in the absence of diffusion. On three of the five dates, retention in the Celtic  
402 Sea relative to dispersal offshore or to the Irish Sea declined steadily as the diffusion setting  
403 was increased.

*404 Main analysis: sources of variation in larval endpoint distributions*

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

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

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

*Comparison with a priori estimates of transport rates*

429 Prior to the analysis, it was predicted, based on abundance of juveniles in the Irish Sea, that  
430 transport of herring larvae from the Celtic Sea to the Irish Sea would be relatively high for the  
431 2002 and 2008 year classes and low for the 2004 year class (Table 1). Most of the variability  
432 in relative rates of transport and retention was between release dates within year classes.  
433 There was therefore no basis for defining year classes as “high transport” or “high retention  
434 years” and a detailed comparison between years was not made. It was noted that the highest  
435 rate of transport to the Irish Sea (29.7%; tidal simulation) was observed on January 31<sup>st</sup> 2003  
436 (2002 year class) while transport occurred on just one of the tested dates in 2004/05 and was  
437 less than 1% (tidal simulation, 19<sup>th</sup> December 2004). However, similarly low rates of transport  
438 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*

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

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

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

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

*Long-term variation in wind patterns*

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

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

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

**482 Discussion**

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

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

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

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516 Man during April-July has also been demonstrated (van der Molen et al. 2007). Thirty days  
517 after hatching herring have reached a length of between 11 and 14 mm (Graham and  
518 Townsend 1985; Pepin 1991; Townsend and Graham 1981) and are entering the post-flexion  
519 period of development after which routine swimming at  $1\text{-}2\text{cm}\cdot\text{s}^{-1}$  can be expected, increasing  
520 to  $4\text{cm}\cdot\text{s}^{-1}$  at juvenile metamorphosis (35-40mm) (Moyano et al. 2016). As their swimming  
521 speeds develop, larvae can use directional swimming to move towards areas of higher food  
522 density (Munk and Kiorboe 1985; Voesenek et al. 2018) and to position themselves in inshore  
523 areas (Drake et al. 2018). Therefore, herring larvae that cross St. George's channel during the  
524 30 day early larval period and continue to travel with the currents in a general northward  
525 direction as late larvae, could be delivered to nursery grounds on the east coast of Ireland and  
526 the west coast of the Isle of Man with the aid of directional horizontal swimming. Other  
527 possible sources of winter spawned juveniles in the Irish Sea must also be considered,  
528 including small contributions from local spawning events around the Isle of Man and off the  
529 north coast of Ireland (Dickey-Collas et al. 2001; ICES 2016) as well as potential transport of  
530 larvae southwards through the North Channel of the Irish Sea (Davies et al. 2002; Young et al.  
531 2000). This could be addressed through further hydrodynamic modelling studies and larval  
532 surveys within the Irish Sea.

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

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

558 Variation in the fate of simulated larvae between release dates was linked to variability in  
559 wind patterns across the 30 days of the simulation and tidal conditions at the time of release.  
560 When the prevailing west/south-westerly winds (210-270°) were stronger and more frequent  
561 than average, the probability of retention in the Celtic Sea or transport to the Irish Sea  
562 decreased and transport offshore increased. Strong and frequent east/south easterly winds  
563 (90-150°) increased the probability of transport to the Irish Sea and retention in the Celtic Sea

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564 and reduced the probability of transport offshore. On some of the release dates examined  
565 the majority of particles were dispersed offshore in the Celtic Sea, away from known juvenile  
566 herring habitat. In reality, relationships between wind patterns and transport/retention will  
567 be overlaid by the effects of diffusion, which are likely to increase rates of transport offshore.  
568 Nonetheless, the results indicate that the delivery of herring larvae to nursery grounds in the  
569 Celtic and Irish Seas will be influenced by variation in meteorological conditions which could  
570 operate over both short (within year) and long (yearly, decadal) temporal scales. Future  
571 changes in wind patterns as a consequence of climate change are predicted (La Sorte and Fink  
572 2017; Reyers et al. 2016) and stronger, more persistent westerly winds are forecast under  
573 future climate scenarios (Li et al. 2018). For herring in the Celtic Sea increasing prevailing  
574 winds could result in greater transport of larvae offshore which would threaten life-cycle  
575 closure and population persistence. Further investigation is needed to fully understand the  
576 potential impacts of climate change on larval dispersal (Petitgas et al. 2013). Coupling  
577 forecasted climate scenarios with biophysical hydrodynamic models could help to predict the  
578 consequences of future change for larval dispersal and nursery ground connectivity in the  
579 Celtic Sea (Hollowed et al. 2009).

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

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

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

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

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

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636 2007). In addition, the realism of model outputs can be increased by including individual  
637 temperature dependant growth rates and complex behaviours (Leis 2007; Staaterman and  
638 Paris 2014). In the present study, rates of retention and dispersal were sensitive to the  
639 diffusion settings used and the nature of DVM behaviour. The simulation model presented  
640 here does not fully capture sub-mesoscale hydrodynamic processes, includes only  
641 rudimentary vertical migration behaviours and does not include individual temperature  
642 dependant growth rates. However, validation assessments indicate that the hydrodynamic  
643 model will accurately predict broad scale flows and its temporal variation (Sotillo et al. 2015).  
644 Furthermore, the predicted distributions of particles at the end of the simulations correspond  
645 well with previous reports of larval and juvenile herring in the Celtic Sea (Brophy and  
646 Danilowicz 2002; Clarke et al. 2010; O'Sullivan et al. 2013) suggesting that the model outputs  
647 are realistic.

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

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

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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		
<b>2002</b>	<b>383,169</b>	<b>49,749</b>	<b>7.7</b>	<b>13,295</b>	<b>5,754</b>	<b>2.31</b>	<b>0.27</b>	<b>Low</b>	<b>High</b>
<b>2003</b>	<b>1,169,010</b>	<b>38,746</b>	<b>30.2</b>	<b>11,240</b>	<b>5,438</b>	<b>2.07</b>	<b>0.29</b>	<b>High</b>	<b>Moderate</b>
<b>2004</b>	<b>408,108</b>	<b>36,467</b>	<b>11.2</b>	<b>5,676</b>	<b>7,689</b>	<b>0.74</b>	<b>0.16</b>	<b>Moderate</b>	<b>Low</b>
<b>2005</b>	<b>917,257</b>	<b>56,092</b>	<b>16.4</b>	<b>18,616</b>	<b>9,127</b>	<b>2.04</b>	<b>0.33</b>	<b>High</b>	<b>Moderate</b>
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
<b>2008</b>	<b>1,169,110</b>	<b>99,065</b>	<b>11.8</b>	<b>38,544</b>	<b>16,413</b>	<b>2.35</b>	<b>0.39</b>	<b>Moderate</b>	<b>High</b>
2009	1,541,530	121,558	12.7	13,962	17,452	0.80	0.11	Moderate	Low
<b>2010</b>	<b>1,104,530</b>	<b>142,470</b>	<b>7.8</b>	<b>42,000</b>	<b>19,438</b>	<b>2.16</b>	<b>0.29</b>	<b>Low</b>	<b>Moderate</b>
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		

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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.

<b>Level</b>	<b>U component velocity</b>	<b>V component velocity</b>
<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

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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 <sup>th</sup> 2003	0.702	0.700	0.705	0.710	0.01
	Feb 7 <sup>th</sup> 2005	1	0.999	0.998	0.998	0.002
Dispersed offshore in Celtic Sea (area C)	Feb 28 <sup>th</sup> 2003	0.188	0.180	0.180	0.169	0.019
	Feb 7 <sup>th</sup> 2005	0	0	0	0	0
Transported to Irish Sea (area B)	Feb 28 <sup>th</sup> 2003	0.111	0.121	0.115	0.121	0.01
	Feb 7 <sup>th</sup> 2005	0	0.001	0.002	0.002	0.002

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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 <sup>2</sup> 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
<b>endpoint~ind90-150+ ind210-270+tidal state</b>	<b>68,132</b>	<b>0.76</b>	<b>0.77</b>	<b>0.42</b>

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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)

<b>Model term</b>	<b>Chi-square</b>	<b>P value</b>	<b>Area</b>	<b>Relative risk ratios (exp(coeff))</b>
<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

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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.

<b>Endpoint distribution</b>	<b>Percentage of particles</b>	
	<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)

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952 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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*Herring transport, retention and connectivity*958 **Figure legends:**

959 **Figure 1.** Map illustrating the distribution of herring in the Celtic and Irish Seas during  
960 the first year of life. The dark grey shaded areas show the general location of herring  
961 spawning grounds taken from O’Sullivan et al (2013) (Celtic Sea; autumn and winter  
962 spawners) and Dickey-Collas et al (2001) (Irish Sea; autumn spawners). The light grey  
963 shading indicates the general distributional extent of larval herring in the Celtic Sea  
964 during the December-March period as evidenced by larval surveys from 1978-1985 and  
965 1989-1990 (O’Sullivan et al, 2013). Locations in the Celtic Sea where juvenile 0-group  
966 herring were recorded by Brophy et al (2002) and Clarke et al (2010) are marked with  
967 black circles. Black triangles denote locations where winter-spawned 0-group juvenile  
968 herring (of likely Celtic Sea origin) occurred together with autumn spawned 0-group  
969 juveniles (of likely Irish Sea origin) as reported by Brophy et al 2002 and Burke et al  
970 (2009)

971

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

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

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

984

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

988

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

995

996 Figure 6. Particle distributions at the end of each 30 day simulation using the **non-tidal**  
997 **simulation**. Particles are colour coded according to their position in relation to the  
998 three predefined areas indicated by the boundary lines in the maps: Celtic Sea (green),  
999 Irish Sea (blue), offshore (purple). The first day of the simulation is indicated above  
1000 each plot.

1001

1002 Figure 7. Particle distributions at the end of each 30 day simulation using the **tidal**  
1003 **simulation**. Particles are colour coded according to their position in relation to the  
1004 three predefined areas indicated by the boundary lines in the maps: Celtic Sea (green),

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1005 Irish Sea (blue), offshore (purple). The first day of the simulation is indicated above  
1006 each plot.

1007 Figure 8. Particle trajectories for particles released from similar locations within the  
1008 Celtic Sea spawning area in the non-tidal (left hand panels) and tidal (right hand panels)  
1009 simulations on two dates. Circles represent the release locations and triangles represent  
1010 the positions at the end of the 30 day simulation period.

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1012 Figure 9. Predicted proportion of particles in each area (offshore Celtic Sea: light grey,  
1013 retention in Celtic Sea: black, transport to Irish Sea: dark grey) at the end of the 30 day  
1014 simulation period under three conditions of diel vertical migration (DVM: none, 0-30m  
1015 at night, 0-100m at night; top panel) and with five diffusion parameter settings (diffusion  
1016 coefficient set to 0,  $10^{-9}$ ,  $10^{-8}$ ,  $10^{-7}$  and  $10^{-6}$   $\text{m}^2.\text{s}^{-3}$ ; bottom panel). The simulation start  
1017 date is shown over each set of simulations.

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1019 Figure 10. Predicted versus observed proportions of particles in each area at the end of  
1020 the 30 day simulation period using the full oceanographic model (tidal simulation).

1021 Predicted values are based on the multinomial model of larval endpoint probabilities  
1022 as a function of two wind indices (WI 210-270 WI 90-150) and the tidal range index.

1023

1024 Figure 11. Mean predicted probabilities (plotted line) with 95% confidence limits (grey  
1025 shading) of a particle occupying each of the three areas (Celtic Sea, Irish Sea, offshore)  
1026 at the end of the 30 day simulation period in relation to the strength and frequency of

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1027 E-SSE winds (ind90-150) and SSW-W winds (ind210-270). The vertical line indicates the  
1028 mean wind index across all of the years.

1029 Figure 12. Mean predicted probabilities (with 95% confidence limits) of a particle  
1030 occupying each of the three areas (Celtic Sea, Irish Sea, offshore) at the end of the 30  
1031 day simulation period for each tidal state category .

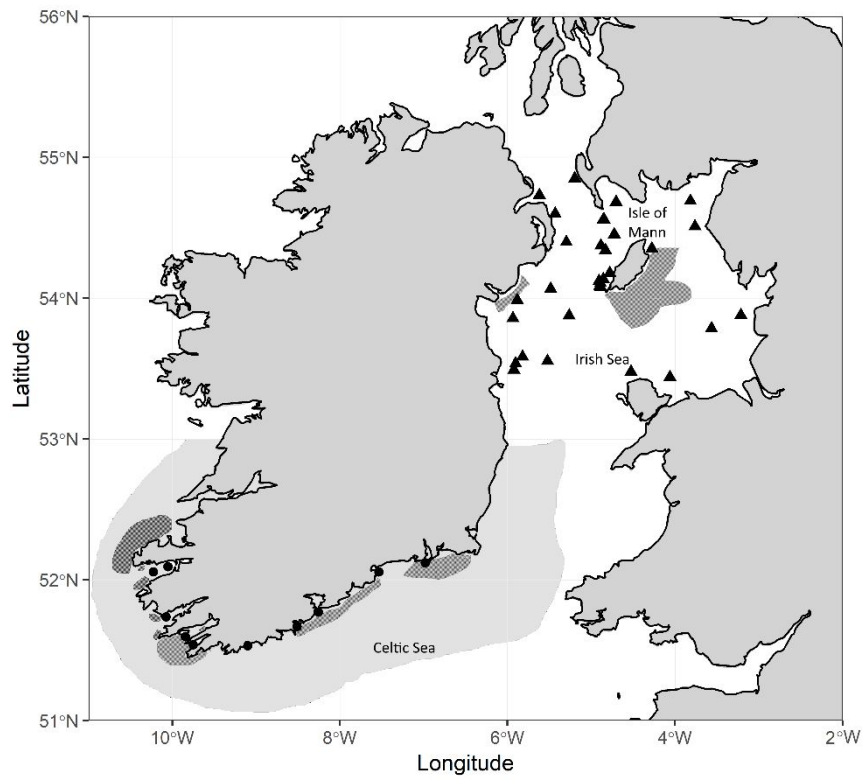
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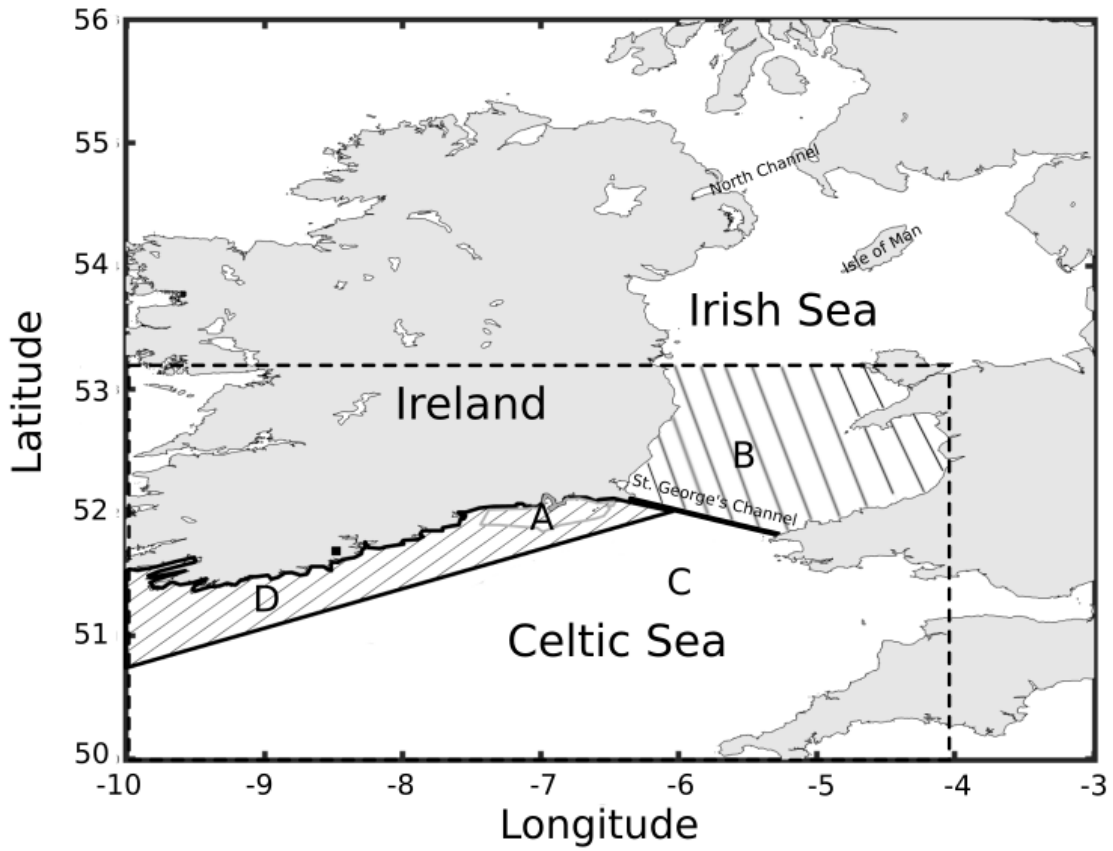
1034 Figure 1.



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1045 Figure 3.

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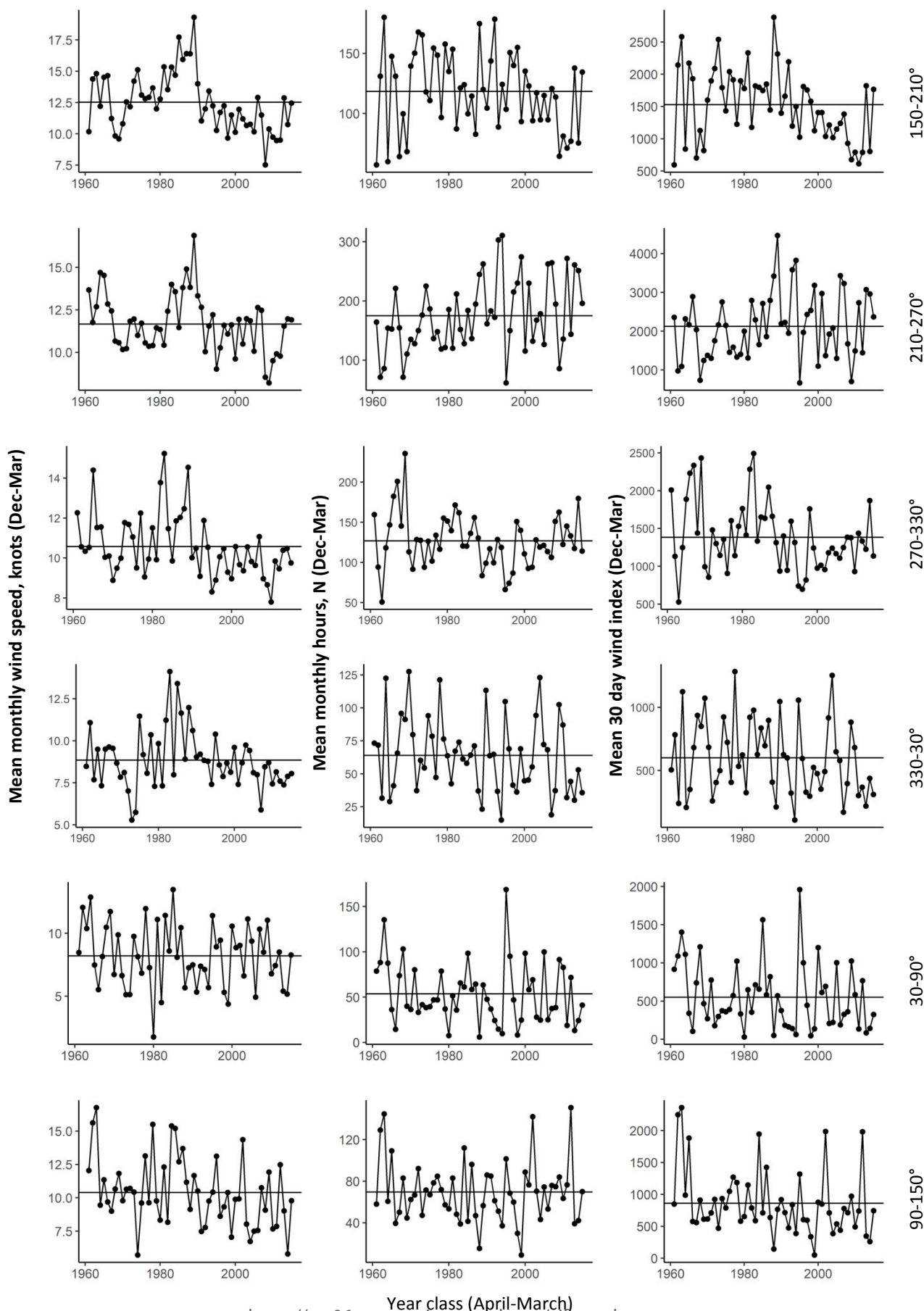
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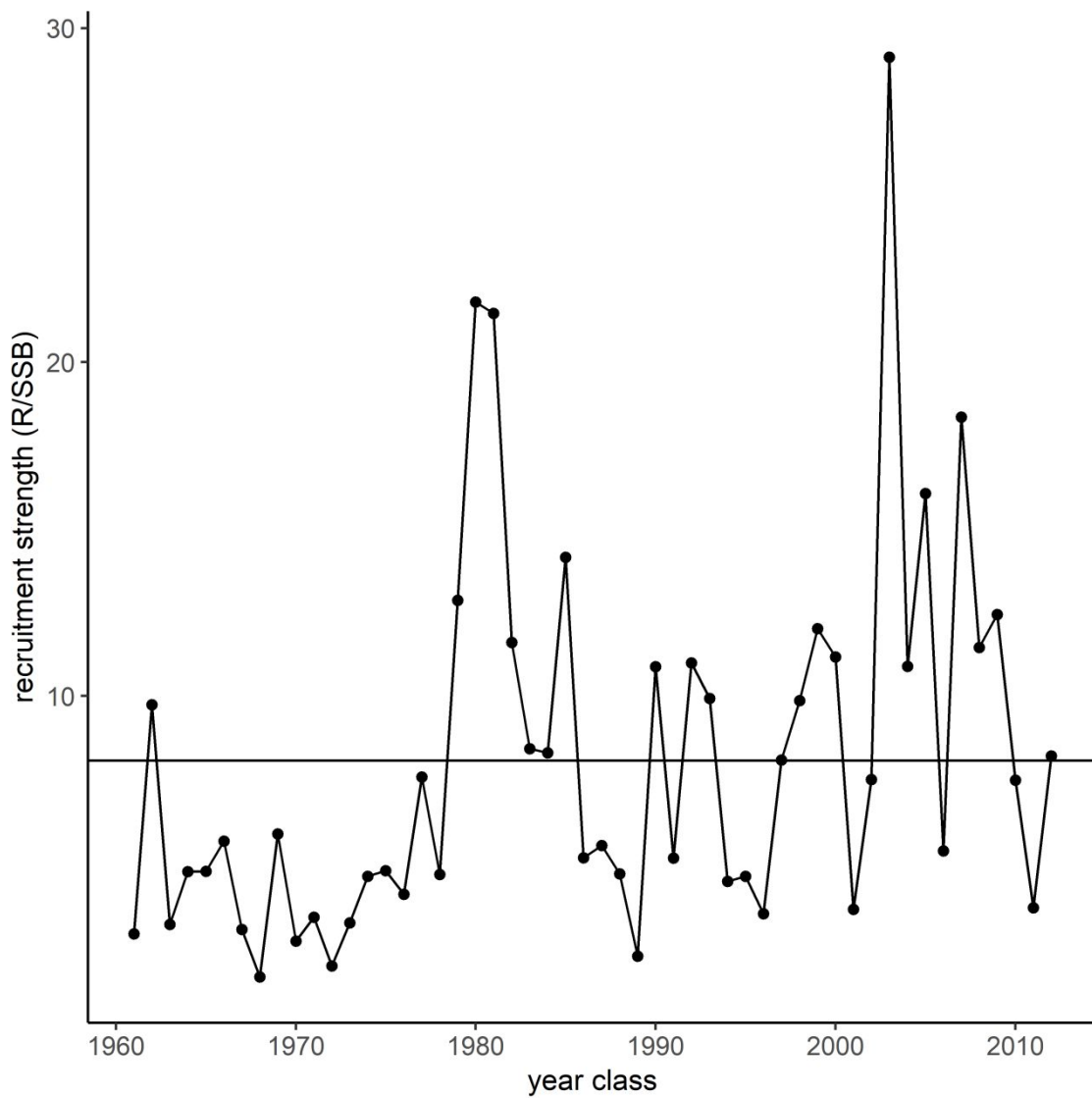
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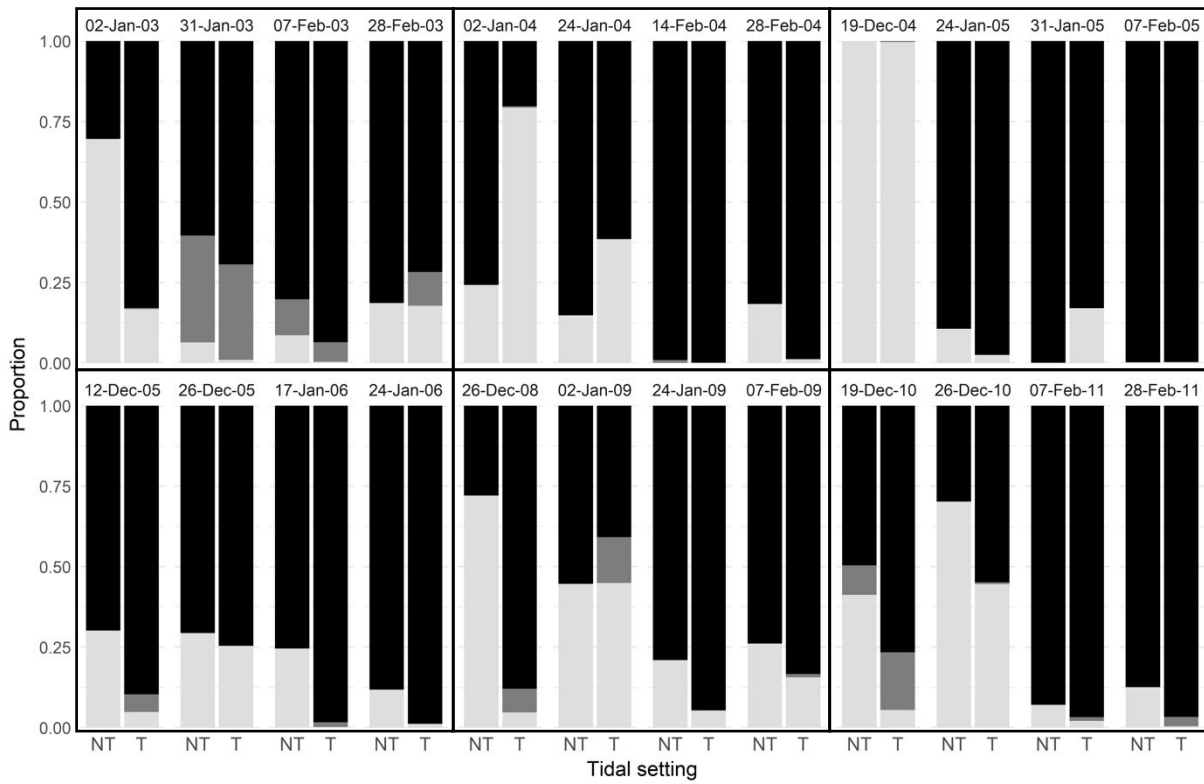
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1073 Figure 6.

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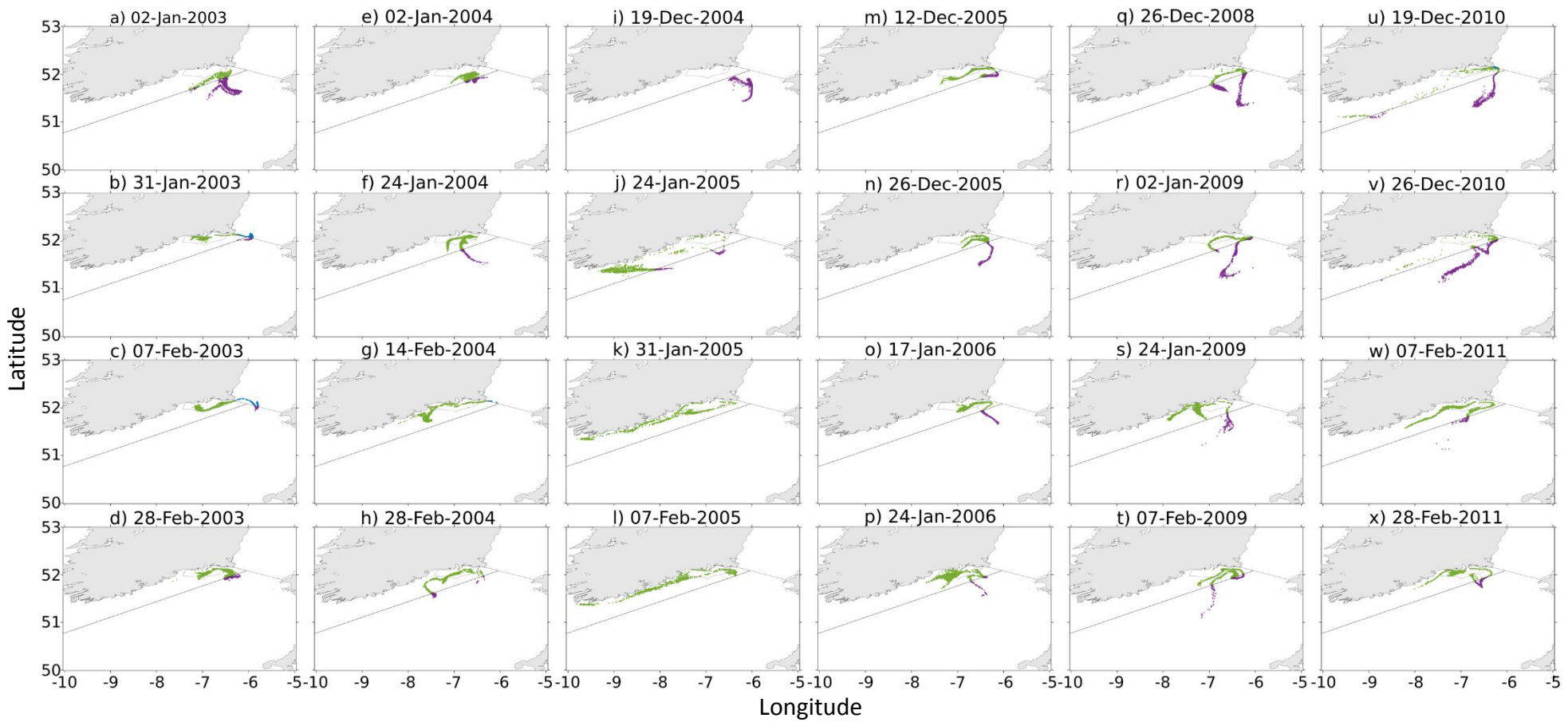
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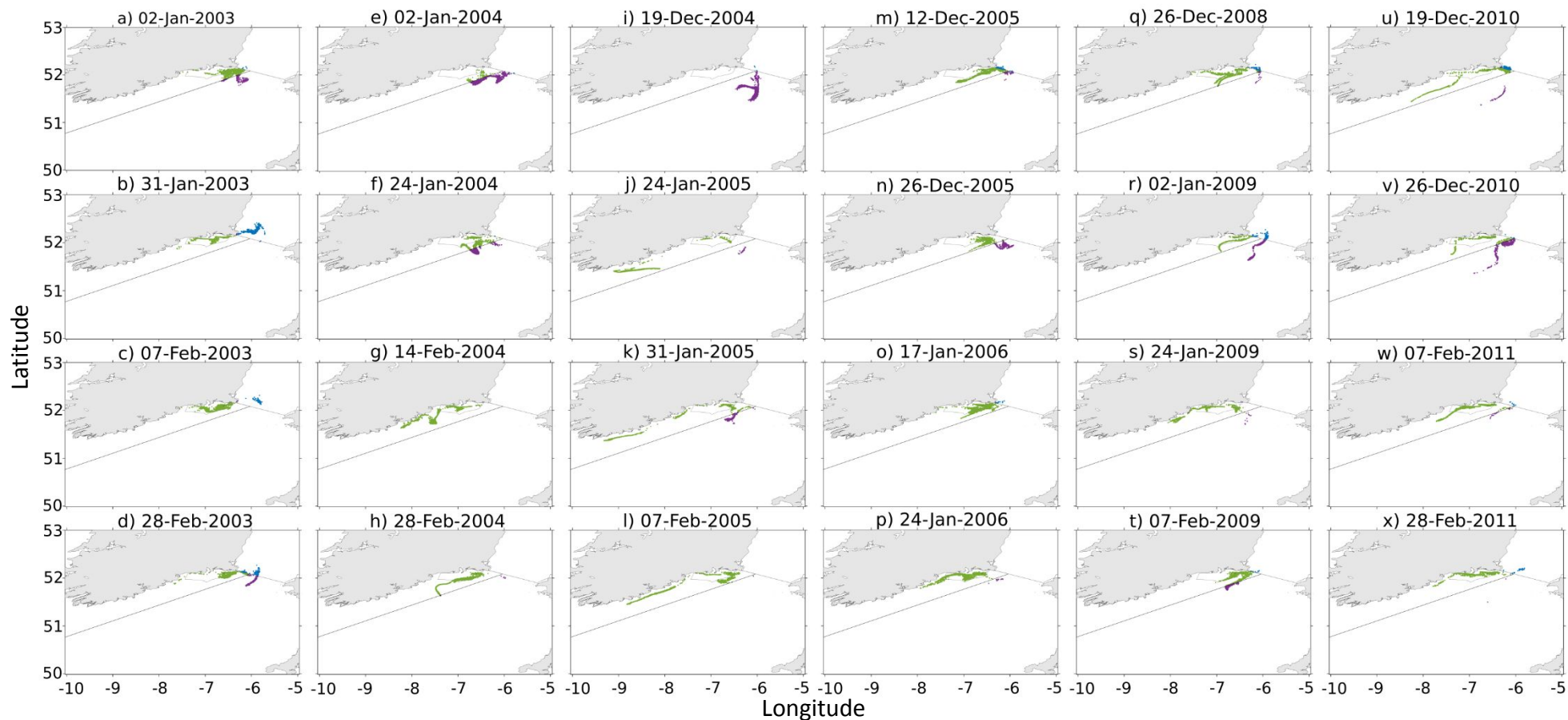
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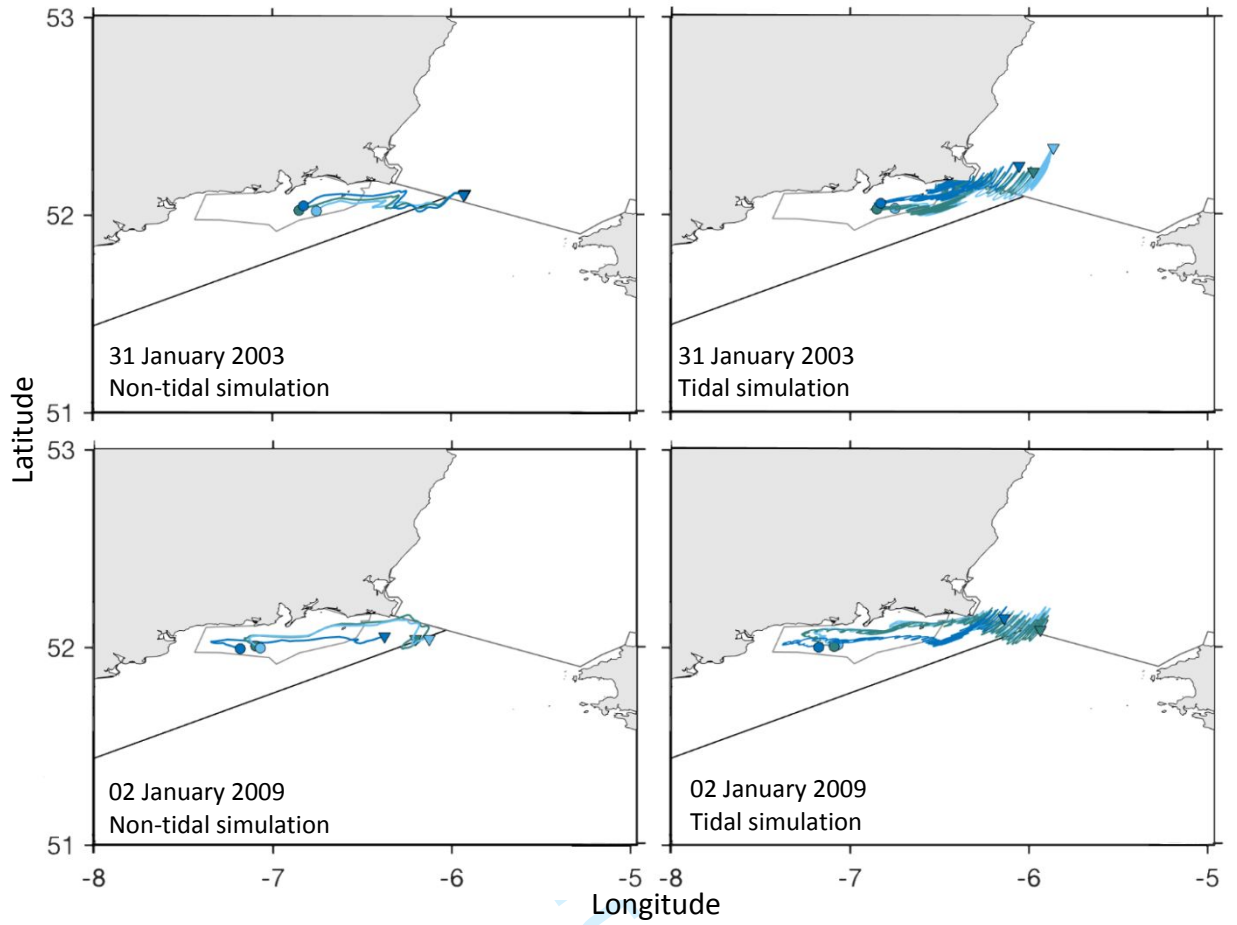
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1099 Figure 8.



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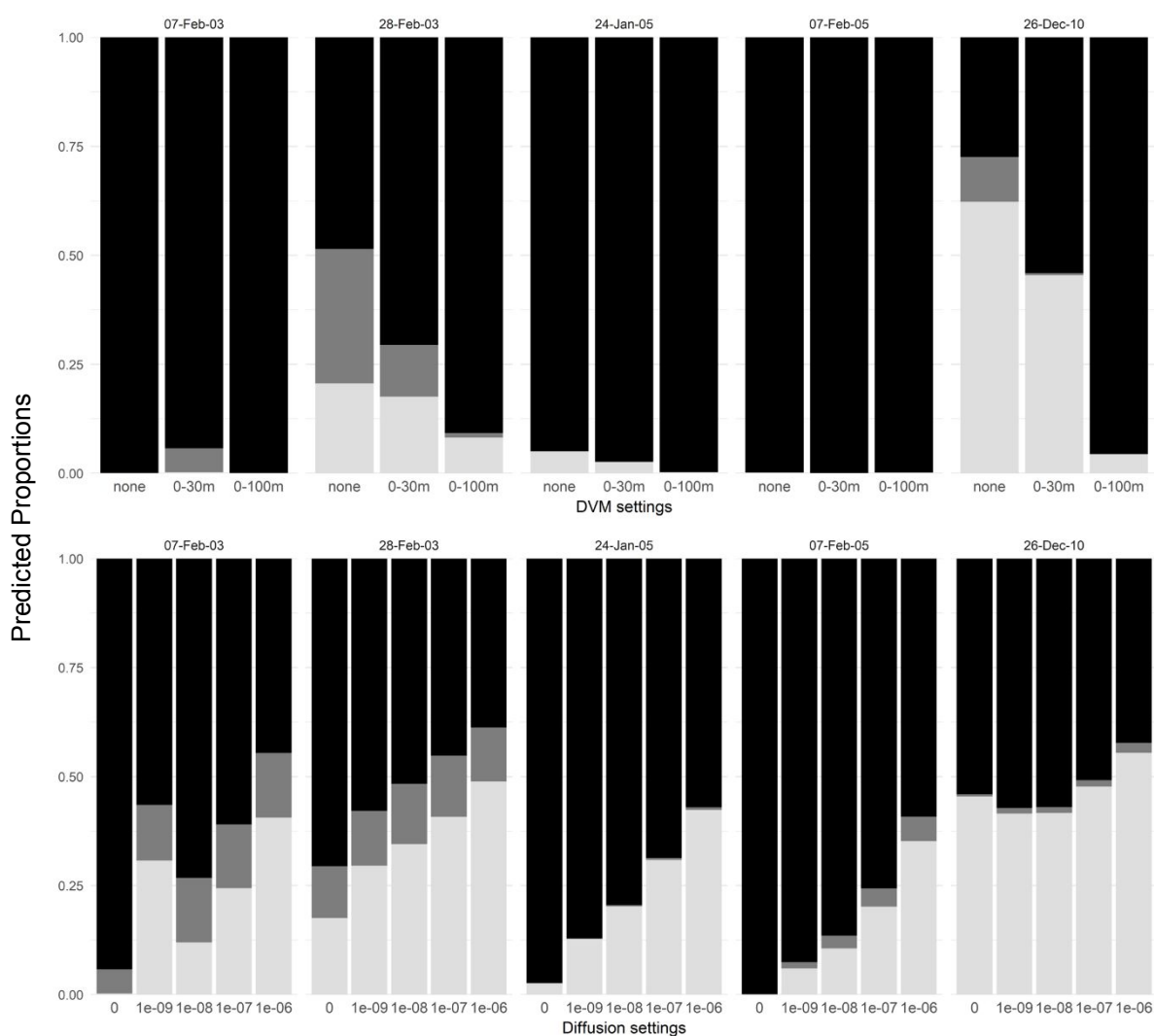
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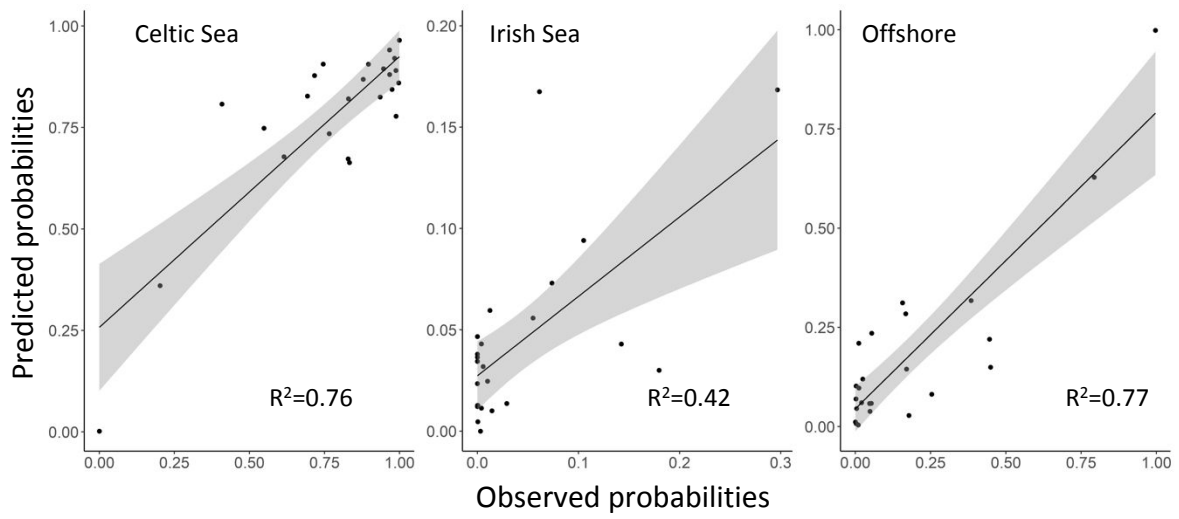
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1129 Figure 11.

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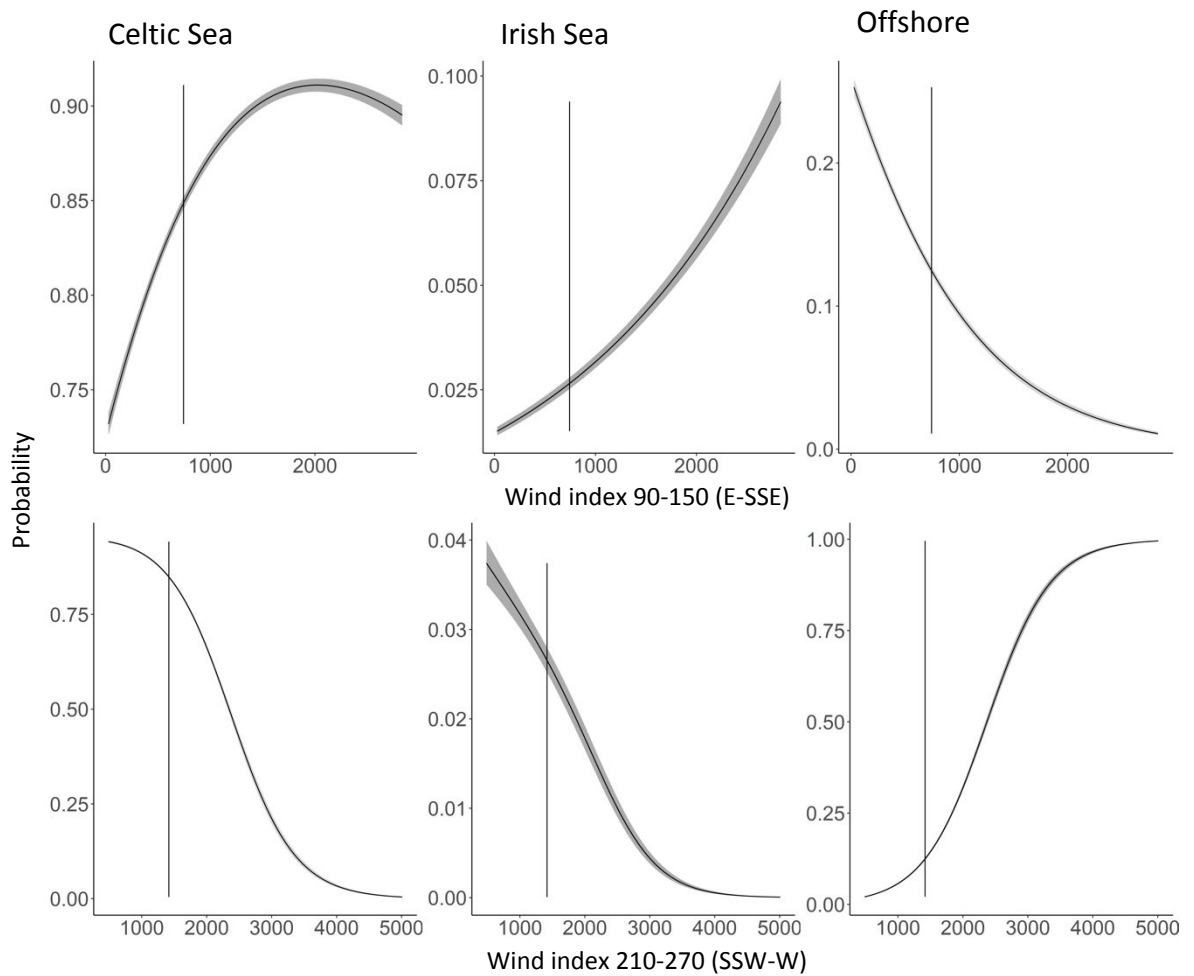
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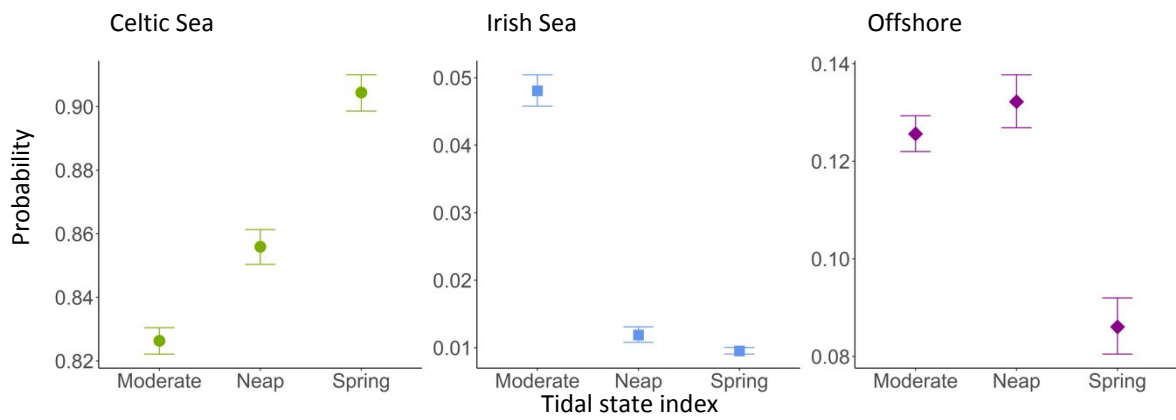
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