Predicting potential spawning areas of European bass, Dicentrarchus labrax, in the Irish and Celtic Seas

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1   **Predicting potential spawning areas of European bass, *Dicentrarchus labrax*, in the Irish**

2   **and Celtic Seas**

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9

10   Abstract

11   Marine fish species that form spawning aggregations are often vulnerable to exploitation, such

12   as the European bass (*Dicentrarchus labrax*). Information on bass spawning aggregations is

13   not well resolved temporally and spatially. Otolith daily growth increment (DGI) counts were

14   conducted on 0-group bass collected in July-August 2014 & 2019 from seven settlement

15   estuaries in the Irish and Celtic seas, to estimate the timing of spawning. These timings

16   parameterised three-dimensional hydrodynamic and Lagrangian particle tracking models, run

17   in reverse, to identify probable spawning locations. Estimated spawning occurred between

18   April-May (inshore and offshore) <200 km from each settlement area. At least two broad

19   spawning areas were predicted: the central Irish Sea that led to post-larval recruitment in north

20   Wales and northwest England, and the southern Irish Sea/Celtic Sea that led to post-larval

21   recruitment in south Wales. Results indicate the current seasonal closure for northern stock

22   bass may not protect spawning events that drive recruitment into settlement sites in Wales and

23   northwest England. Surface temperatures and wind- and tide-driven surface currents

24   determined the connectivity between spawning and settlement sites. Atmospheric drivers are

25   expected to change in the future and management needs to account for potential regional shifts

26   in spawning times and locations.

27

28   Keywords

31

32   1.   Introduction

33   Many marine fish species form dense spawning aggregations in reoccurring locations each

34   year, resulting in spatially and temporally restricted mass point sources of offspring (Domeier,

35   2012). This spawning behaviour is typical in many marine exploited species (e.g., Green and

36   Wroblewski, 2000; Surette *et al.*, 2015). Species that form annual spawning aggregations are

37   particularly susceptible to exploitation as they are often targeted for fishing, reducing the

38   population densities resulting in lower reproductive success (De Mitcheson, 2016). Therefore,

39   identifying the location and timing of these events is critical for understanding population

40   dynamics, connectivity and establishing effective management strategies, such as the seasonal

41   closure of fisheries (De Mitcheson, 2016; Sala *et al.*, 2021).

42

43   The European bass, *Dicentrarchus labrax* (hereafter bass), is a valuable commercial and

44   recreational species, with landings into the European Union (EU) and UK in 2017

45   conservatively valued at £54 million and £166 million, respectively (EUMOFA, 2021). Four

46   stock units are recognised by the International Council for the Exploration of the Sea (ICES),

47   with the major fisheries focused on the northern stock (Irish and Celtic seas, English Channel

48   and southern North Sea) and the Bay of Biscay stock (De Pontual *et al.*, 2019). Population

49   decline in the northern stock, due to overfishing and poor recruitment of 0-group bass to coastal

50   nursery areas, led to the introduction of conservation measures in 2015 to promote stock

51   recovery. Although fishing mortality is now thought to be at sustainable levels, the estimated

52   spawning stock biomass is still below sustainable levels and recruitment remains low (ICES,

53   2023). Clearly, protecting the spawning stock and a better understanding of post-larval

54   recruitment drivers are critical to the future sustainability of bass fisheries.

55

56   Bass form spatially- and temporally-restricted annual spawning aggregations (Pickett *et al.*,

57   2004; De Pontual *et al.*, 2019) with regional differences in the timing of spawning in the

58   northern stock ranging from January to late May depending on location (Kennedy and

59   Fitzmaurice, 1972; Thompson and Harrop, 1987; Jennings and Pawson, 1992; Cambiè *et al.*,

60   2015). Photoperiod and sea temperature are considered the key drivers of spawning, with

61   temperatures of 8.5-9°C triggering the start and 15°C the end, which may account for the

62   regional differences in the timing of spawning (Thompson and Harrop, 1987; Jennings and

63   Pawson, 1991; Vinagre *et al.*, 2009).

64

65   Spawning locations for bass are not well resolved and shift as the season progresses with

66   changes in sea temperature. Offshore areas (*ca.* 50-90 m depth) are considered optimal for

67   spawning with the western English Channel and the Celtic Sea both key areas for the northern

68   stock (Thompson and Harrop, 1987; Jennings and Pawson, 1992; López *et al.*, 2015; Dambrine

69   *et al.*, 2021). Adult bass (>42 cm) migrate from inshore shallow summer feeding grounds

70   during autumn (October-November) to seek relatively warmer deeper offshore waters during

71   winter, though recent evidence suggests not all mature bass undertake winter migrations, either

72   skipping a spawning season or perhaps spawning inshore (Pawson and Pickett, 1996; Pawson

73   *et al.*, 2007; De Pontual *et al.*, 2019; Stamp *et al.*, 2021). Increasing water temperatures are

74   thought to have extended the inshore summer feeding season, thus delaying migration and

75   thereby reducing migration distances and allowing bass to spawn further north and east,

76   allowing a northern range expansion (Pawson *et al.*, 2007; Bagdonas *et al.*, 2011; Cardoso *et*

77   *al.*, 2015).

78

79   Research is ongoing to understand the drivers behind the poor recruitment seen over the last

80   two decades and the connectivity between spawning, nursery and adult feeding grounds (ICES,

81   2018). After spawning, bass eggs and larvae disperse towards coastal nursery settlement areas

82   such as estuaries and saltmarshes (Jennings and Pawson, 1992). Larval dispersal pathways are

83   determined by meteorological, oceanographic and biological drivers, with annual variations in

84   these factors thought to result in post-larval recruitment failure or success (Beraud *et al.*, 2018).

85   Bass pelagic larval duration (PLD) is estimated at between 2 to 3 months with larval

86   development positively correlated with photoperiod and sea temperature, with temperatures

87   remaining below 8.5°C resulting in failure of the eggs to hatch (Dando and Demir, 1985;

88   Thompson and Harrop, 1987; Jennings and Pawson, 1992; Cucchi *et al.*, 2012). Knowledge of

89   bass larval behaviour is limited, although a recent study by Beraud *et al.* (2018) described larval

90   behaviour patterns and modelled the settlement of 0-group bass. They considered four

91   behavioural scenarios to identify which was the most appropriate. The behaviour that produced

92   the highest settlement success, and best reproduced inter-annual variation and the observed

93   spatial distribution of settlers was positively buoyant eggs, hatchlings and larvae with tidal

94   migration at the final fry stage (see Beraud *et al.*, 2018, for more details).

95

96   To aid our understanding of recruitment drivers and dispersal pathways, bio-physical models

97   (i.e. hydrodynamic ocean models coupled with Lagrangian particle tracking algorithms) are

98   commonly used to simulate the potential dispersal of marine larvae from spawning areas based

99   on predictions of the oceanography and the larval migration behaviour (Beraud *et al.*, 2018;

100   Cabral *et al.*, 2021). Whilst such model predictions may have a high degree of uncertainty,

101   mainly due to a lack of knowledge of larval behaviour and uncertainty in model

102   parameterisations, they can cover spatio-temporal scales not achievable empirically and hold

103   great potential for exploring ecological questions relating to natal origins and population

104   connectivity. Hindcast backtracking modelling, where bio-physical models are run backwards

105   in time, has been effectively used to identify natal origins given information on the timing and

106   location of settlement and PLD (e.g. Christensen *et al.*, 2007; Torrado *et al.*, 2021). Thus, these

107   modelling methods can be a powerful way of investigating the potential location of spawning

108   aggregations and their connections to known recruitment areas. Moreover, the daily periodicity

109   of growth increments laid down in the bass otoliths offer a valuable tool to infer their early life

110   history traits, which in combination with backtracking bio-physical models would disentangle

111   recruitment patterns (Gutiérrez and Morales-Nin, 1986; Aguilera *et al.*, 2009).

112

113   In this study, we applied backtracking bio-physical modelling to identify potential bass

114   spawning locations in the Irish and Celtic Seas. The model was integrated with individual-

115   based early life history traits for 0-group bass collected from seven settlement estuaries for two

116   separate years using otolith daily growth increment (DGI) counts to provide estimates of age

117   (in days) and spawning dates. The study aims to advance knowledge on bass spawning both

118   spatially and temporally by: (1) identifying where the 0-group bass in the Celtic and Irish seas

119   could have originated (i.e. putative spawning areas) by applying a backward particle tracking

120   model; (2) identifying the timing of spawning events in this region; and (3) determining

121   whether the north-eastern Celtic Sea (a known bass spawning area; Jennings and Pawson,

122   1992) could be the supply source for 0-group bass to nursery areas throughout the Irish Sea, or

123   whether localised spawning events from as-yet unknown spawning locations may also provide

124   recruits to bass nurseries in the Irish Sea. This will contribute information needed for bass stock

125   management in the Northeast Atlantic. More broadly this study aims to demonstrate how

126   integrating individual-based traits with bio-physical models can reduce model uncertainties,

127   and improve understanding of connectivity in marine species, particularly those that form

128   spawning aggregations.

129

130   2.   Methods

131   2.1. Sample collection

132   The 0-group bass recruits used in this study were sampled from seven nursery areas (estuaries)

133   around the coast of Wales and north-west England in the eastern Irish Sea, Celtic Sea and

134   Bristol Channel (Figure 1). A total of twelve sites were originally sampled, seven identified in

135   Kelley (1988) and Lancaster *et al.* (1998) and five exploratory sites in areas of suitable habitat

136   (see Cambiè *et al.*, 2015; Moore *et al.*, 2020 for more detail on sampling sites). Fish were

137   captured towards the mouth of the estuaries, using a micromesh beach seine net (6 m × 1.5 m

138   with ~4 mm mesh size), in July-August 2014 and 2019 under dispensation from the regional

139   authorities. The sampling was timed to capture post-larval bass at the point of settlement to

140   coastal / estuarine nursery areas (Pickett *et al.*, 2004). Only the smallest individuals (<30mm)

141   were selected (where sample size allowed, ca. 50 individuals were retained as allowed by

142   dispensation) to select those fish that had most recently settled and to facilitate otolith age

143   reading. Fish were euthanized according to UK ASPA Schedule 1. The total length (to nearest

144   mm) of each individual was recorded prior to freezing to avoid measurement error due to

145   shrinkage.

146

147   2.2.Otolith interpretation

148   Sagittal otoliths were removed, cleaned and dried. The right sagitta was weighed (µg) and

149   mounted sulcus side down on a microscope slide using thermoplastic glue (Crystalbond®).

150   Otoliths were prepared using standard methods (see Morales-Nin *et al.*, 2010). Briefly, they

151   were ground using 5 µm and 3 µm lapping film consecutively, polished using cloths and a

152   solution of 0.3 µm aluminium oxide. Once otolith primordium and daily growth increments

153   (DGIs) were visible, otoliths were rinsed with distilled water.

154

155   Prepared otoliths were viewed using an optical microscope (Zeiss Axio Imager A1) and images

156   were taken using AmScope MU900 USB2.0 eyepiece digital camera and software at x100

157   magnification for the whole otolith and x400 for age readings. DGI counts were conducted

158   using the FIJI version of Image J free software with the Object J plug-in (Denechaud *et al.*,

159   2018). After a general overview of otolith growth structures, readings were performed along

160   the dorsal axis as this was the areas with clearest DGIs. When increments were poorly defined,

161   the nearest possible axis to the dorsal axis was chosen. Readings were conducted twice by the

162   same reader (HL), first from core to edge and then from edge to core. The coefficient of

163   variation (CV) of the two readings was calculated using the Chang Index (Chang, 1982), and

164   a third reading was conducted if values were above the 10% limit of acceptability. Otoliths

165   were rejected if they still crossed this threshold after a third reading (Panfili *et al.*, 2004). Since

166   increments begin to form 2 days after hatch in bass (Gutiérrez and Morales-Nin, 1986; Regner

167   and Dulčić, 1994; Aguilera *et al.*, 2009), two days were added to averaged age estimates to

168   calculate the age of fish from hatching. In addition, a further 5.25 days were added to account

169   for the average egg stage duration (Beraud *et al.*, 2018) to provide the estimated age of each

170   fish. The birth date was then back-calculated from capture date using the estimated age. To

171   calculate the average date of settlement into each nursery area the average assumed PLD

172   (Beraud *et al.*, 2018) of 56.75 days, was added to birth dates. These calculated settlement dates

173   were used as particle release dates for the larval dispersal model (see model description below).

174   To account for variability in PLD and fish age the dates were also calculated using either a

175 minimum (51 days) or maximum (63 days) PLD and using either the minimum, mean, or

176 maximum age of fish at each nursery site in each year (see Figure A2 in Supplementary

177 Material).

178

179   2.3. Larval dispersal model

180 To estimate the potential spawning locations of the 0-group bass recruits collected from the

181 nursery sites (i.e., the estuaries) sampled in 2014 and 2019, a larval dispersal model was

182 developed for the Irish Sea. Virtual particles representing bass larvae were 'released' from the

183 seven sampled nursery sites and transported, backwards in time, by simulated ocean currents

184 for the duration of their assigned PLD. The particle trajectories were tracked to enable

185 estimation of the likely larval dispersal patterns from sink to source and therefore, isolate likely

186 spawning areas.

187

188 Model-simulated ocean currents were used to force the larval dispersal model using the highest

189 resolution data available for 2014 and 2019 from validated ocean models. For 2014, a regional

190 ocean model (ROMS; Shchepetkin and McWilliams, 2005) was used that simulated 3D

191 velocities on an orthogonal horizontal grid with a resolution of 1/400° longitude per 1/240°

192 latitude, giving a mean cell size of approximately 270×460 m. The vertical plane was divided

193 into 20 equally-segmented terrain-following layers giving a mean resolution of 4.3 m at mean

194 sea level. The model was parameterised using EmodNET bathymetry data

195 (https://www.emodnet-bathymetry.eu/). A 12-month simulation was computed for the period

196 01 January to 31 December 2014. The model was forced at the open boundaries with 10 tidal

197 constituents, including the dominant semi-diurnal M_2 (lunar) and S_2 (solar) constituents, but

198 also N2, K1, O1, and P1 interpolated from the FES 2014 dataset (Carrere *et al.* 2016). Surface

199 forcing (including wind forcing) using synoptic meteorological fields was obtained from the

200 European Centre for Medium-Range Weather Forecasts-Interim reanalysis (Dee *et al.*, 2011),

201 available at 3-h intervals at a spatial resolution of 1.0°. A spin-up period of two months was

202 computed to enable the tides and density-driven currents to fully develop from a state of rest

203 and a spatially-constant temperature of 6°C. Whilst this model does not include Stokes drift

204 from wave-current interactions, these effects have generally been assessed to be small (a few

205 cm/s) in the Irish Sea in comparison with wind-driven shear and tidal residuals (e.g., Osuna

206 and Wolf, 2005; Lewis et al., 2019). The model was validated for the region against elevation

207 and flow data, together with a temperature record, producing errors in elevations of <12%,

208 velocities of <16% and temperature of <7% (see section A1 in the Supplementary Material for

209 further details of the model validation).

210

211 For 2019, the North West-European Shelf analysis and forecast system (Atlantic - European

212 North   West   Shelf   -   Ocean   Physics   Analysis   and   Forecast,

213 NORTHWESTSHELF_ANALYSIS_FORECAST_PHY_004_013,   see

214 https://doi.org/10.48670/moi-00054 for details) was used (see Lewis *et al.*, 2019; Tonani *et al.*,

215 2019) using the Atlantic Margin Model (AMM15) setup of the NEMO ocean model (v.3.6)

216 coupled with the wave model WAVEWATCH IIIv4.18. The horizontal resolution of the setup

217 is 1.9±0.4 km in longitude × 1.5 km in latitude with higher resolution in the northern part of

218 the domain. The native model has Hybrid S-σ-z-coordinates which have been interpolated to

219 33 regular depth levels. Tidal forcing from 11 constituents was included by both open boundary

220 forcing and as an equilibrium tide from the TPXO7.2 database (Egbert and Erofeeva, 2002). 3-

221 hourly atmospheric forcing including wind fields was provided by the operational ECMWF

222 Integrated Forecasting System. The 3DVar NEMOVAR system was used to assimilate

223 observations. In this setup, in-situ and satellite-derived sea surface temperatures together with

224 satellite-derived sea level anomalies and in-situ temperature and salinity profiles were

225　assimilated. Hourly, lateral boundary conditions came from the UK Met Office North Atlantic

226　Ocean forecast model and by the CMEMS Baltic forecast product

227　BALTICSEA_ANALYSIS_FORECAST_PHY_003_006. River discharge data was included

228　as a daily climatology. The underlying bathymetry was provided by EMODnet 2015. For a

229　detailed model evaluation see https://tinyurl.com/3eejb9bc.

230

231　For the larval dispersal model described below, 3D hourly-averaged velocity fields, derived

232　from the above hydrodynamic models for 2014 and 2019, were bi-linearly interpolated to a

233　uniformly-spaced latitude/longitude grid (0.02 degrees horizontal resolution) that were used to

234　drive the hindcast larval dispersal simulations. Caution should be applied when backtracking

235　and considering sub-grid-scale turbulence in 3D, since uncertainties can arise in the reversed

236　trajectory compared with the forwards trajectory; for example, the backtracked particle may

237　reach lower (weaker) flows and hence travel a shorter distance than the forwards tracked

238　particle. In our approach, outlined in our methods, vertical transport is driven solely by

239　behavioural traits (Beraud *et al.*, 2018) so that the backtracked particles occupy the same

240　vertical field that they would during their forwards trajectory. Other more computationally

241　expensive approaches to tackle this problem are outlined by Thygesen (2011).

242

243　For the larval dispersal model, for each simulation, a cohort of 2500 particles was released

244　from the estuary mouth of each nursery site, randomly distributed within an area of

245　approximately 100 m^2 (see Tables 1 and 2). For each nursery site, three different release dates

246　were chosen (meaning three different larval dispersal periods were simulated), based on the

247　capture date of the juveniles and considering a 'residency period' representing the time the bass

248　had spent within the nursery estuary (post settlement) before the capture date – the residency

249　period being determined by the observed variability in bass age: (a) minimum group age, (b)

250   mean group age, and (c) maximum group age. Therefore, for (a-c), the three different residency

251   periods were calculated (see methods in above *Otolith interpretation* section), then the particles

252   were released from the nursery sites on a date determined by the capture date minus the

253   residency period, as shown in Table 2 (for further detail see Figure A2 in Supplementary

254   Material). For each nursery site and for each release date (a-c), two larval behaviour strategies

255   were simulated. Firstly, a control strategy was performed (Runs 1a-c) where only surface-

256   drifting dispersal was considered (i.e., non-swimming particles). Secondly, for runs 2a-c and

257   3a-c, the larval behaviour described by Beraud *et al*. (2018) was applied. This behaviour had

258   produced the highest settlement success, and best reproduced inter-annual variation and spatial

259   distribution of settlers in their modelling (see Beraud *et al.*, 2018 for more details). Here, eggs

260   and larvae were positively buoyant for the larval stages 1-3 and at stage 4, when they became

261   fry, developed tidal migration behaviour to achieve directional movement. To account for

262   variations in development rate, these were run with the minimum PLD of 51 d (runs 2a-c) and

263   the maximum PLD of 63 d (run 3a-c). Within these latter two strategies (runs 2 and 3), the

264   virtual larvae either remained in the near-surface currents, or were synchronised with the tide,

265   migrating towards the surface during the flood tide and towards the bed during the ebb tide, a

266   strategy that is likely to promote transport towards the coast or estuary (Robins *et al.*, 2013).

267   During tidal migration, vertical swimming speeds were set to 0.002 m/s, following Beraud *et*

268   *al*. (2018). In total, therefore, nine simulations were performed per nursery site per year as

269   summarised in Table 1, with each run releasing 2500 particles, but varying in age of 0-group

270   bass modelled (i.e., minimum, average and maximum age of 0-group bass), the behaviour

271   exhibited in the pelagic phase (i.e., surface only for all stages, or tidal behaviour observed on

272   stage 4) and the duration of the pelagic phase (i.e. 51 or 63 days).

273

274 For each simulation, the particles were then transported, backwards in time, by the simulated

275 (reversed) ocean currents using hourly averaged current fields with an assigned PLD and larval

276 behavioural strategy, providing a range of potential larval dispersal patterns. Particles that

277 interacted with the coastline were reflected offshore to their position in the previous time-step.

278 Since the model spatial resolutions were relatively fine (<1.5 km) and we focus on large scale

279 larval transport, no additional stochasticity was added to represent unresolved turbulence,

280 following other similar studies (e.g. Mayorga-Adame *et al.*, 2022). The positions of the virtual

281 larvae during the final day of simulation (i.e., each larva at 24 different positions throughout

282 the final day) were considered as those that most likely represented the spawning location of

283 the bass larvae. These virtual larval positions were recorded to produce a series of density

284 distribution maps, providing the average of all simulations per nursery site per year. Density

285 distributions were created by discretising the domain into 2×2 km cells and calculating the

286 proportion of particles (from all nine behaviour/date simulations) within each cell. This was

287 done for each hour of the final day of the simulation (i.e., the initial day of spawning) and then

288 averaged into one density distribution map. This procedure was repeated for all nursery sites

289 and for both years.

290

291 To describe environmental factors that could affect larval dispersal between years, sea surface

292 temperature data from the CMEMS North-West European Shelf Ocean Reanalysis data product

293 (Atlantic- European North West Shelf- Ocean Physics Reanalysis,

294 NWSHELF_MULTIYEAR_PHY_004_009 ; see https://doi.org/10.48670/moi-00059 for

295 details on the reanalysis and its validation) were used. The data have a horizontal resolution of

296 7 km. The underlying ocean assimilation model is the 3D NEMOVAR which assimilates ocean

297 observations (sea surface temperatures and profiles of temperature and salinity). At the lateral

298 ocean boundaries, the global reanalysis model provides ocean forcing data, and atmospheric

299 forcing comes from the ECMWF ERA-5 atmospheric reanalysis. For wind data, 10 m u and v

300 wind strengths were obtained from the ERA-5 global reanalysis database from which wind

301 speeds and directions were calculated. The data have a horizontal resolution of 30 km.

302

303 **Table 1. Bass larval behaviour strategies for each model run (described in Beraud *et al.* 2018), where "Age"**

304 **is the minimum, average or maximum age of 0-group bass sampled at each nursery site. The pelagic larval**

305 **duration (PLD) is composed of 4 stages (i.e. 1 egg, 2 hatchling, 3 larva and 4 fry). In control runs 1a-1c,**

306 **floating behaviour was assigned to stage 1-4, associated with passive drifting of particles. In runs 2a-2c and**

307 **3a-3c stage 4 was assigned as tidal, a behaviour associated with directional movement (see Figure A2 in**

308 **Supplementary Material for a schematic of these model runs and Beraud *et al.* 2018, for a detailed**

309 **description of larval behaviour).**

Run	Age	Larval behaviour	Time at stage (days)				Total PLD (days)
			stage 1	stage 2	stage 3	stage 4	
1a	min		8	7	25	23	63
1b	avg	surface only	8	7	25	23	63
1c	max		8	7	25	23	63
2a	min		3	1	25	22	51
2b	avg	surface (stgs 1-3), tidal (stg 4)	3	1	25	22	51
2c	max		3	1	25	22	51
3a	min		8	7	25	23	63
3b	avg	surface (stgs 1-3), tidal (stg 4)	8	7	25	23	63
3c	max		8	7	25	23	63

310

311   3. Results

312   3.1. Length frequency of sampled bass

313 0-group bass ranged in length from 17-52 mm TL with the average length of fish sampled in

314 2014 smaller (23 ± 3 mm) than in 2019 (30 ± 7mm) due to greater lengths recorded in some

315 estuaries (Dwyryd, Milford and Loughor), (See Figure A3 in Supplementary Material for size

316 structure). No 0-group bass were caught at Swansea in 2019, and the Wyre was only sampled

317 in 2019. Low numbers were collected at the Dee in 2019, however, due to the successful

318 sampling in 2014 and its importance as a recognised bass nursery area this site remained in

319 the study to provide a comparison. The number of individuals in table 4 reflects final numbers

320 post otolith interpretation (see below).

321

322   3.2. Otolith interpretation

323 The success rate at ageing otoliths with a <10% CV between readings was 92%, with 18

324 rejected, resulting in a sample size of 208 0-group bass for which age and spawning date were

325 determined. The average age of bass across both sampling years was 84 days, ranging from 47-

326 102 days in 2014 and 62-126 days in 2019 (Table 2). Overall, 0-group bass collected between

327 July to mid-August from settlement areas in Wales and northwest England originated from

328 spawning events occurring between 10 April and 16 May. On average the 0-group bass used

329 in the study had earlier spawning dates in 2019 (10-27 April) than in 2014 (23 April - 16 May)

330 (Figure 2 & Table 2). This difference was particularly pronounced for spawning that fed into

331 the northern settlement sites (Dee, Y Foryd and Dwyryd). The dates of spawning that fed into

332 Milford and Loughor nursery sites in the south showed less difference between the two years.

333

334 *Table 2: The key dates, number of individuals and age summaries (in days) for 0-group bass*

335 *at each sample site in 2014 and 2019. Residency period is the number of days 0-group bass*

336 *were estimated to have been resident in the nursery area post-settlement and prior to capture.*

337 *The spawning date, settlement date and residency period are the average calculated for each*

338 *site.*

339

Year	Site	Capture date	Sample size	Age (days)			Spawning date	Settlement date	Residency period
				Min	Max	Avg			
2014	Dee	17 Jul	19	50	70	62	10 May	06 Jul	11 days

	Y Foryd	14 Aug	18	62	102	84	16 May	12 Jul	32 days
	Dwyryd	06 Aug	20	60	92	79	14 May	09 Jul	27 days
	Milford	23 Jul	19	64	94	79	30 Apr	25 Jun	27 days
	Loughor	22 Jul	19	56	85	68	09 May	05 Jul	17 days
	Swansea	09 Jul	13	47	84	71	23 Apr	19 Jun	20 days
	Wyre	09 Aug	19	78	126	107	18 Apr	14 Jun	56 days
	Dee	24 Jul	4	88	106	94	16 Apr	11 Jun	42 days
2019	Y Foryd	17 Jul	21	74	118	92	10 Apr	06 Jun	41 days
	Dwyryd	25 Jul	27	62	108	90	21 Apr	16 Jun	38 days
	Milford	31 Jul	13	80	112	96	20 Apr	16 Jun	44 days
	Loughor	30 Jul	16	66	115	88	27 Apr	23 Jun	36 days

3.3. Larval dispersal model outputs

Larval dispersal predictions are presented in Figure 3 as density distribution maps from each of the sample sites and for both years. The density distribution maps represent averages of the nine behaviour scenarios (three migration strategies × three dispersal periods determined by bass age), thus capturing the uncertainty associated with PLD and larval behaviour. Therefore, Figure 3 displays a degree of variability in the predictions of precise spawning locations during 2014 and during 2019 (this variability is described below). However, our results indicate that the 0-group bass sampled were most likely derived from spawning regions close (i.e., <200 km) to their nursery of origin. The predicted spawning areas from several of the sample sites had a degree of overlap with those predicted for other nursery areas in the proximity (i.e., where there is overlap, larvae from those spawning locations have the potential to reach multiple nursery sites).

The nine individual density distribution maps per nursery site and per year (Figures A4.1-A4.6 and A5.1-A5.6 in Supplementary Material) showed that potential spawning locations varied based on larval behaviour scenario and on spawning/larval transport period. Spawning timing seemed to be the larger of the two controls because the particles were mainly distributed in the surface layer in all behaviour strategies and therefore subjected to variable wind-driven

360   currents. Further, most nursery sites are exposed to prevailing south-westerly winds and so the

361   simulated variability in accordance with the wind climate was to be expected – the exception

362   being the Dee (N. Wales), which is more sheltered and hence there was markedly less

363   variability between the different scenarios than the other nursery sites. Importantly, the

364   predicted variability in spawning location between the nine scenarios was generally less than

365   the predicted variability between each of the nursery sites, giving us confidence that the

366   sensitivity tests do indeed capture much of the uncertainty in spawning location per nursery

367   site, and that the spatial patterns in potential spawning between nursery sites (shown in

368   Figure 3) are indeed meaningful.

369

370   When taking together all simulations, the predicted potential spawning sites spread from the

371   Celtic Sea up to the northern Irish Sea, across to the Irish coast to the west and the Welsh and

372   English coasts to the east (Figure 4). In 2014, the dispersal of virtual larvae and potential

373   spawning areas were more widespread (e.g., potential spawning grounds off the east coast of

374   Ireland) than in 2019 where potential spawning areas were mostly along the eastern coasts of

375   the Irish Sea and also further south (Figures 3 & 4). Although overall, potential spawning

376   grounds appeared to be widespread through the Irish Sea, a clear regional separation was

377   apparent: little to no overlap was simulated between potential spawning sites that seeded the

378   northern (Wyre, Dee, Y Foryd and Dwyryd estuaries) and southern (Milford, Loughor and

379   Swansea) nursery areas. The potential spawning sites predicted for the southern nursery areas

380   were in general to the south of the Celtic Sea Front (CSF) (Figure 1 & 4, and those for the

381   northern sites were to the north of the CSF. The model predicted inshore spawning close to all

382   the nursery areas.

383

384   The potential spawning areas for each year separately and combined (Figure 4) had the greatest

385   overlap in areas off the south and north Wales coasts. For the southern nursery grounds (2014

386   & 2019), the potential spawning areas extended offshore across the mouth of the Bristol

387   Channel and towards the Celtic Deep in the Celtic Sea, but also inshore along the south Wales

388   coast (e.g. Carmarthen and Swansea Bay). For the northern spawning areas (2014 & 2019), the

389   greatest overlap was observed inshore along the northern coasts of Wales (e.g., from north-east

390   Anglesey to the mouth of the Dee and the Ribble estuaries, Tremadog Bay and off the northern

391   tip of the Llŷn Peninsula).

392

393   3.4. Physical and environmental characteristics

394   We present no formal analysis of the environmental variables, however, here we provide a

395   description of the physical conditions for comparison to the modelled dispersion patterns

396   presented in section 3.3. Late winter to early spring sea temperatures were colder in 2014 than

397   in 2019 in the Celtic Sea. In 2019, sea surface temperatures in most of the Celtic Sea (with

398   exception of the Bristol Channel) had already exceeded 8.5°C by late winter (Figure 1). In

399   2014, this was only true for the southern part of the Celtic Sea. North of ~51.5°N, the 8.5°C

400   threshold was not exceeded until the beginning to the middle of March. In contrast, most of the

401   northern Irish Sea warmed about 20 days earlier in 2014 than 2019. However, the inner Bristol

402   Channel and north Wales coast inshore warmed approximately 5 days and 10 days later,

403   respectively, in 2014.

404   Furthermore, in 2014, temperatures at all potential spawning locations at the calculated

405   spawning times were between 10-11°C; well within upper and lower spawning limits of sea

406   bass (8.5-15°C) (Figure 5). In 2019, sites in south (Loughor and Milford) and mid Wales

407   (Dwyryd) showed temperatures between 9.5-11°C at the estimated spawning time, again within

408   spawning temperature limits. However, the northern sites had much lower temperatures in 2019

409   at their estimated spawning dates, only reaching 9°C and less at the estimated spawning times.

410   Offshore, in the northern Irish Sea, temperatures remained below 8.5°C. At the northern sites

411   in 2019, spawning was limited to inshore and restricted offshore locations (Figures 4 and 5) at

412   which temperatures were around the spawning limit of 8.5°C.

413   In summary, in 2014, the Irish and Celtic Sea waters had warmed above the spawning

414   temperature threshold by the estimated spawning dates. In 2019, offshore waters exceeded the

415   spawning threshold temperature at estimated spawning date only for the southern and mid-

416   Wales sites, whereas at the northern sites, the spawning threshold was exceeded only in coastal

417   waters but not offshore.

418

419   Because winds can influence surface ocean currents significantly (see e.g., Jones, 1999) and

420   are an important source of interannual variability, differences in wind climate between 2014

421   and 2019 for the PLD phase were reviewed. The wind roses show the direction the wind is

422   blowing from and the wind speed during the estimated PLD phase for the approximate

423   predicted spawning locations for each nursery population for 2014 and 2019 (Figure 3). In

424   general, the northern sites experienced prevailing north and north-westerly winds, and the

425   southern sites experienced prevailing west and south-westerly winds, dispersing the particles

426   into the nursery areas. Winds were generally more westerly in 2014 and more south-westerly

427   in 2019.

428

429   For 2014, larvae arriving at the three southern sites (Milford, Loughor and Swansea)

430   experienced a number of strong westerly and SSW wind events (wind speeds greater than

431   10 m/s). This corresponds with spawning locations which are generally to the west of the

432   estuaries (see Figure 3). In contrast, in 2019, larvae transported to Milford were subjected to

433   winds with a stronger southerly component which corresponds to a potential spawning area to

434   the southwest of the estuary. Similarly, larvae transported to Y Foryd experienced a relatively

435   large proportion of strong SSW winds which links with potential spawning areas to the SSW

436   in 2019. In 2014, larvae arriving at the Dee, Y Foryd and the Dwyryd encountered moderate

437   wind speeds with variable directions, and all three sites have potential spawning areas mainly

438   to the west (WNW and SWW) suggesting that for weaker winds, other factors such as tides,

439   may have a stronger influence on dispersal patterns. In contrast, during 2019, larvae transported

440   to the Wyre and the Dee were subjected to strong NW winds and correspondingly, part of

441   potential spawning areas are located to the north of the estuaries.

442

443   4.   Discussion

444   The results of our study suggest that: (1) it is unlikely that one offshore spawning area seeded

445   all the sampled nursery grounds within the Irish and Celtic Seas, with spawning possible from

446   a range of locations but probably within 200 km of each nursery ground; and (2) that there is

447   separation between spawning locations supplying bass to nursery grounds in north and south

448   Wales. We have based this finding on age estimates from juvenile bass and then simulated their

449   early life stages backwards using a backtracking larval dispersal model that accounted for a

450   range of plausible larval behaviour traits.

451

452   4.1. Timing of spawning

453   Here, we estimate bass spawning in the Irish and Celtic Seas between April and May for 2014

454   and 2019, which lies within the spawning times reported for the UK, i.e. January-May

455   (Jennings and Pawson, 1991; Pawson *et al.*, 2007), and is consistent with timings reported for

456   this region based on egg and larval aging studies (Kennedy and Fitzmaurice, 1972; Jennings

457   and Pawson, 1992; Lancaster *et al.*, 1998), with visual gonad maturity assessments carried out

458   around Wales (2004-2008 & 2013-2015) (Ward, 2008; Cambiè *et al.*, 2015) and with fisher

459 knowledge (Pantin *et al.*, 2015). Juvenile bass recruit into estuaries from late June (Jennings

460 and Pawson, 1992), and data from a bi-monthly survey in Milford Haven during 2014 showed

461 0-group bass entering in high numbers between 17 June and 8 July (Jacobs Engineering

462 unpublished data), overlapping our estimated entry date of 25 June supporting our age

463 estimations. Bass spawning was predicted to have occurred approximately one month earlier

464 during 2019 than during 2014, possibly due to warmer winter sea surface temperatures in the

465 Celtic Sea in 2019 (reaching 8.5°C by late winter) than 2014 (reaching 8.5°C by mid March)

466 or the earlier warming of close inshore waters in the Irish Sea and Bristol Channel (5-10 days

467 earlier in 2019 than 2014), since sea surface temperature is thought to be the primary trigger

468 for spawning (Pawson *et al.*, 1987). However, the difference in spawning times calculated

469 between the two years may also have been due to the variability in the location of 0-group bass

470 within estuaries, and sampling limitation.

471

472   4.2. Location of spawning
473
474 Whilst the modelling in the current study predicts all potential spawning locations from a

475 physical perspective, it does not tell us which are more plausible taking into account other

476 environmental factors. Our results agree with previous putative spawning areas highlighted in

477 the mouth of the Bristol Channel and the Celtic Sea (Jennings and Pawson, 1992; Lancaster *et*

478 *al.*, 1998) (Figure 6). However, our modelling suggests these areas largely supply recruits to

479 southern nursery areas, with juvenile bass found in estuaries along the north coast of Wales

480 and the northwest coast of England likely originating from separate northern spawning areas.

481 Records of ripe and running adult bass around the North Wales coast support this prediction

482 (Kelley, 1979; Cambiè *et al.*, 2015; Welsh commercial bass fishers, *Pers. comm.*). Regional

483 separation of Welsh bass in terms of feeding areas with two sub-populations separating to feed

484 in north/mid and south Wales has been suggested (Cambiè *et al.*, 2016; Doyle *et al.*, 2017).

485   The current study similarly suggests a potential regional separation for spawning. Further

486   research is required to determine whether these bass have migrated northwards from

487   overwintering and earlier spawning aggregations in the south or whether they are resident

488   overwinter in these northern areas. For example, bass potentially spawning in the

489   northern/central Irish Sea may have overwintered in the Western English Channel, perhaps

490   spawning early in the season before heading northwards to summer feeding areas around North

491   Wales (Pawson *et al.*, 1987). Alternatively, bass that spawn in the northern/central Irish Sea

492   may be resident (perhaps adolescent bass) and could indicate a separate stock group. Our

493   results highlight that a more regional management approach may be appropriate. A distinction

494   between populations north and south of the Celtic Sea Front, which separates the Irish Sea from

495   the Celtic Sea and Deep, has been reported for other species with a PLD phase (Coscia *et al.*,

496   2020; Hold *et al.*, 2021), suggesting the front may also be influencing larval connectivity in

497   bass.

498

499   Our modelling identifies that inshore spawning may be occurring around the Welsh and Irish

500   coasts and this has been reported for bass, often late in the spawning season (e.g. Kennedy and

501   Fitzmaurice, 1972; Kelley, 1979; Thompson and Harrop, 1987; Ward, 2008). In addition, bass

502   fishers around the Welsh coast report catching ripe and running bass inshore at the mouths of

503   the estuaries in Carmarthen Bay in the south (May-July), within the Aberdyfi estuary in mid

504   Wales (December-March) and around Puffin Island (east Anglesey) in the north (June) (*Pers.*

505   *comm.*) (Figure 6). These observations support the modelling simulations, suggesting some

506   spawning could occur inshore after bass return from winter migrations but also that some bass

507   could be resident inshore all year and spawn within estuaries (e.g., Aberdyfi). Recent electronic

508   tagging studies have confirmed differing migration patterns including inshore residency

509   (O'Neill et al., 2018; De Pontual et al., 2019; Stamp et al., 2021). We chose not to impose a

510   lethal temperature limit in the backtracking simulations due to some uncertainties in the exact

511   temperature limits [for example, Thompson and Harrop (1987) found eggs and larvae present

512   in waters around 8°C (see their Figure 2b)] but based the estimates of spawning locations

513   purely on hydrodynamic currents. For 2019, at the northern sites, our simulations suggest that

514   spawning was likely restricted to inshore waters, and here temperatures exceeded or were close

515   to 8.5°C (Figure 5).. Our results highlight how critical temperature may be for both the timing

516   and location of spawning events at the northern limit for bass populations.

517

518   In warmer than average years, bass return inshore earlier and remain there for longer, compared

519   with colder years (Pawson *et al.*, 2007). Kelley (1988), identified the Ribble estuary in

520   northwest England as the northern extent of bass nursery areas, though more recently bass have

521   been caught further north in the Wyre and the Lune estuaries (Lancashire) (this study and

522   Environment Agency unpublished data). Records of juvenile bass (15-18 cm) in March in the

523   Wyre (Wyre Rivers Trust unpublished data, *Pers. comm.*) as well as adolescents (34-38 cm)

524   show the recruits do survive the winters at these northern sites. With climate-induced ocean

525   warming, the northern limits of species are shifting (Pawson *et al.*, 2007; Bagdonas *et al.*, 2011;

526   Bento *et al.*, 2016; King *et al.*, 2021) and northern regions will likely become more important

527   spawning and nursery areas.

528

529   4.3. Larval dispersal model
530
531   Our simulations suggest that wind influenced bass larval dispersal between the two studied

532   years. Because bass larvae were assumed buoyant and spend much of their planktonic phase in

533   surface waters (Jennings and Pawson, 1992; Sabatés, 2004; Beraud *et al.*, 2018), they are

534   subjected to wind-driven surface circulation. In response to the UK wind climate (e.g., Earl et

535   al. 2013), the wind-driven component to the Irish Sea currents tends to produce notable surface

536 residuals over synoptic timescales (of the order of cm/s over several days; Davies et al. 2001)

537 that can direct larvae tens of kilometres, in contrast to tidal currents which, although stronger,

538 tend to be oscillatory and hence contribute less to net larval dispersal. Wind variability between

539 the years was evident in the north; for example, simulated residuals from prevailing NW winds

540 in 2014 transported larvae eastwards into the Dee (hence produced a widespread area of

541 potential dispersal across to the coast of Ireland), whereas in 2019 simulated residuals from SE

542 winds transported larvae westwards into the Dee (hence a smaller potential spawning area due

543 to the proximity of the English coast). Therefore, we can infer that larva from spawning

544 locations in the northern Irish Sea could be transported eastwards towards north Wales or

545 westwards towards Ireland depending on prevailing wind patterns. Wind variability between

546 the years was also seen in the south, with strong SW winds (> 14 m/s) in mid-April 2019

547 causing Celtic Sea larvae to potentially disperse hundreds of kilometres towards South Wales

548 (Milford). This pathway may not have been possible a few weeks later, when quiescent

549 conditions prevailed (generally westerly winds and strengths <10 m/s) – as seen in the

550 simulations from the Loughor estuary. The model results suggest that meteorological drivers

551 may determine larval pathways, spawning sites, and dictate successful recruitment of larvae to

552 nursery sites. The extended bass spawning season is a useful strategy in a variable environment,

553 allowing spawning to take place when favourable conditions occur (Hočevar *et al.*, 2021).

554 Future work could estimate the degree of interannual variability by sampling estuaries

555 repeatedly over a longer timescale and then repeating the backtracking modelling work to

556 estimate the interannual spatial stability of the potential spawning sites.

557

558 Simulated larval transport may differ from real dispersal patterns due to the model resolution,

559 i.e., kilometres and minutes, which does not resolve small-scale coastal features and near-shore

560 transport patterns such as riverine and estuarine processes that require spatial resolutions of

561   ≤100 m (Ward et al., 2023). However, given the correspondence between suggested (Jennings

562   and Pawson, 1992; Lancaster *et al.*, 1998) and our simulated spawning areas, it is likely that

563   the difference is relatively small. The precision of the larval dispersal can be improved through

564   further research into PLD and processes which determine vertical distribution of larvae within

565   the water column, e.g., larval behaviour and physical forcing processes such as turbulence.

566   Further work (beyond the scope of this study) could run a forward PTM (potentially

567   incorporating a temperature dependent PLD) with particle releases from estimated spawning

568   areas to cross-check virtual larvae are able to reach their capture estuaries. This could confirm

569   the separation of the spawning areas and further investigate uncertainties associated with e.g.,

570   turbulence or vertical location of larvae in the water column. However, our results tie in with

571   those from other studies (e.g., Coscia et al., 2020; Vera et al., 2021) running forward PTMs to

572   estimate bivalve larval dispersal. Their works suggest that coastal sites to the south of the Celtic

573   Sea front are largely separate entities from sites to the north of the front confirming findings in

574   this study which suggests limited exchange between areas to the south and the north of the

575   front.

576

577   5. Conclusions
578
579   DGI counts of 0-group bass otoliths provided hatch date estimations to inform a backtracking

580   larval dispersal model, and hence give a novel method to predict possible bass spawning

581   grounds. The timing and location of potential bass spawning estimated in this study represents

582   a snapshot based on 0-group bass collected in 2014 and 2019 in Irish Sea waters, and the

583   method could be more widely applied. The current study confirms the importance of the Celtic

584   Sea spawning region, but also indicates the potential for widespread northern and late season

585   spawning in the Irish Sea. Further study is needed of the importance of these potential northern

586   nursery and spawning areas, in light of future warming seas. The study revealed spawning in

587 the Celtic and Irish seas that currently falls outside the closed season (i.e., April onwards), and

588 in known bass fishing areas. The current seasonal closure (February and March) of the bass

589 fishery may not protect mature bass during the spawning events that feed recruits to nursery

590 areas in Wales and northwest England and more research is needed in this area. Although bass

591 in the northern stock are well mixed genetically (Souche *et al.*, 2015), increasing evidence for

592 site fidelity for feeding, and for broad spawning areas, highlights the potential for a regional

593 management approach, such as spatially appropriate seasonal closures, to be effective. Physical

594 drivers are likely to change in a future climate and management needs to be proactive to

595 respond to changes in bass spawning behaviour.

596

597

598 **DATA AVAILABILITY STATEMENT**

599 The data used for this study is available upon request to the corresponding author.

600

619 **AUTHORS CONTRIBUTIONS**

620 Conceptualization and design (NH, HL, IM, SM); methodology (AG-B, HL, BM-N, PR, SP-

621 M, SW); data collection (CH, HL, AM, IM, SS); data analysis (HL, BM-N, SP-M, PR, SS,

622 SW); drafting manuscript (HL, IM, PR, SW); revising (NH, HL, AM, IM, BM-N, SP-M, PR,

623 SW) manuscript.

624

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