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

Lincoln, Harriet; Robins, Peter; Wilmes, Sophie-Berenice; Pérez-Mayol, S.; Moore, Alec; Simpson, Sam; Goward Brown, Alice; Heney, Charlie; Malham, Shelagh; Morales-Nin, B.; Hold, Natalie; McCarthy, Ian

Fisheries Research

DOI:

10.1016/j.fishres.2023.106884

Published: 01/02/2024

Peer reviewed version

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA): Lincoln, H., Robins, P., Wilmes, S.-B., Pérez-Mayol, S., Moore, A., Simpson, S., Goward Brown, A., Heney, C., Malham, S., Morales-Nin, B., Hold, N., & McCarthy, I. (2024). Predicting potential spawning areas of European bass, Dicentrarchus labrax, in the Irish and Celtic Seas. Fisheries Research, 270, Article 106884. https://doi.org/10.1016/j.fishres.2023.106884

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

• Users may download and print one copy of any publication from the public portal for the purpose of private study or research.

- You may not further distribute the material or use it for any profit-making activity or commercial gain
 You may freque distribute the LIPL identifying the publication in the public portal?
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1	Predicting potential spawning areas of European bass, <i>Dicentrarchus labrax</i> , in the Irish
2	and Celtic Seas
3	H. Lincoln ^{1*} , P.E. Robins ¹ , SB. Wilmes ¹ , S. Pérez-Mayol ² , A.B.M. Moore ¹ , S. Simpson ¹ ,
4	A. Goward-Brown ¹ , C. Heney ¹ , S. Malham ¹ , B. Morales-Nin ² , N. Hold ¹ , I.D. McCarthy ¹
5	¹ School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, Wales,
6	UK
7	² IMEDEA (CSIC/UIB), C/ Miquel Marquès, 21, 07190 Esporles, Balearic Islands, Spain
8	*Corresponding author: e-mail: <u>harriet.m.lincoln@cyfoethnaturiolcymru.gov.uk</u>
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
1.5	

estuaries in the Irish and Celtic seas, to estimate the timing of spawning. These timings 15 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 northwest England. Surface temperatures and wind- and tide-driven surface currents 23 24 determined the connectivity between spawning and settlement sites. Atmospheric drivers are expected to change in the future and management needs to account for potential regional shiftsin spawning times and locations.

27

28 Keywords

bio-physical model, particle back-tracking, larval dispersal, natal origins, otolith daily growth
 increments, fisheries management

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

The European bass, *Dicentrarchus labrax* (hereafter bass), is a valuable commercial and recreational species, with landings into the European Union (EU) and UK in 2017 conservatively valued at £54 million and £166 million, respectively (EUMOFA, 2021). Four stock units are recognised by the International Council for the Exploration of the Sea (ICES), with the major fisheries focused on the northern stock (Irish and Celtic seas, English Channel and southern North Sea) and the Bay of Biscay stock (De Pontual *et al.*, 2019). Population 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 Pawson, 1991; Vinagre et al., 2009). 63

64

65 Spawning locations for bass are not well resolved and shift as the season progresses with changes in sea temperature. Offshore areas (ca. 50-90 m depth) are considered optimal for 66 spawning with the western English Channel and the Celtic Sea both key areas for the northern 67 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 et al., 2007; De Pontual et al., 2019; Stamp et al., 2021). Increasing water temperatures are 73 74 thought to have extended the inshore summer feeding season, thus delaying migration and thereby reducing migration distances and allowing bass to spawn further north and east,
allowing a northern range expansion (Pawson *et al.*, 2007; Bagdonas *et al.*, 2011; Cardoso *et 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 development positively correlated with photoperiod and sea temperature, with temperatures 86 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

To aid our understanding of recruitment drivers and dispersal pathways, bio-physical models (i.e. hydrodynamic ocean models coupled with Lagrangian particle tracking algorithms) are commonly used to simulate the potential dispersal of marine larvae from spawning areas based 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 (in days) and spawning dates. The study aims to advance knowledge on bass spawning both 117 118 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 whether localised spawning events from as-yet unknown spawning locations may also provide 123 124 recruits to bass nurseries in the Irish Sea. This will contribute information needed for bass stock management in the Northeast Atlantic. More broadly this study aims to demonstrate how integrating individual-based traits with bio-physical models can reduce model uncertainties, and improve understanding of connectivity in marine species, particularly those that form 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 \times 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 dispensation) to select those fish that had most recently settled and to facilitate otolith age 142 143 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

Sagittal otoliths were removed, cleaned and dried. The right sagitta was weighed (µg) and
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 μ m and 3 μ m lapping film consecutively, polished using cloths and a 152 solution of 0.3 μ m aluminium oxide. Once otolith primordium and daily growth increments 153 (DGIs) were visible, otoliths were rinsed with distilled water.

154

Prepared otoliths were viewed using an optical microscope (Zeiss Axio Imager A1) and images 155 156 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, the nearest possible axis to the dorsal axis was chosen. Readings were conducted twice by the 161 162 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 and Dulčić, 1994; Aguilera et al., 2009), two days were added to averaged age estimates to 167 168 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 were used as particle release dates for the larval dispersal model (see model description below). 173 174 To account for variability in PLD and fish age the dates were also calculated using either a minimum (51 days) or maximum (63 days) PLD and using either the minimum, mean, or
maximum age of fish at each nursery site in each year (see Figure A2 in Supplementary
Material).

178

179 2.3. Larval dispersal model

To estimate the potential spawning locations of the 0-group bass recruits collected from the nursery sites (i.e., the estuaries) sampled in 2014 and 2019, a larval dispersal model was developed for the Irish Sea. Virtual particles representing bass larvae were 'released' from the seven sampled nursery sites and transported, backwards in time, by simulated ocean currents for the duration of their assigned PLD. The particle trajectories were tracked to enable estimation of the likely larval dispersal patterns from sink to source and therefore, isolate likely 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 $1/400^{\circ}$ longitude per $1/240^{\circ}$ 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 01 January to 31 December 2014. The model was forced at the open boundaries with 10 tidal 196 197 constituents, including the dominant semi-diurnal M₂ (lunar) and S₂ (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

For 2019, the North West-European Shelf analysis and forecast system (Atlantic - European
North West Shelf - Ocean Physics Analysis and Forecast,
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 $\times 1.5$ 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 observations. In this setup, in-situ and satellite-derived sea surface temperatures together with 223 224 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 drive the hindcast larval dispersal simulations. Caution should be applied when backtracking 234 235 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

For the larval dispersal model, for each simulation, a cohort of 2500 particles was released from the estuary mouth of each nursery site, randomly distributed within an area of approximately 100 m^2 (see Tables 1 and 2). For each nursery site, three different release dates were chosen (meaning three different larval dispersal periods were simulated), based on the capture date of the juveniles and considering a 'residency period' representing the time the bass had spent within the nursery estuary (post settlement) before the capture date – the residency 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 were released from the nursery sites on a date determined by the capture date minus the 252 253 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

To describe environmental factors that could affect larval dispersal between years, sea surface 291 292 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 details on the reanalysis and its validation) were used. The data have a horizontal resolution of 295 296 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

Table 1. Bass larval behaviour strategies for each model run (described in Beraud *et al.* 2018), where "Age" is the minimum, average or maximum age of 0-group bass sampled at each nursery site. The pelagic larval duration (PLD) is composed of 4 stages (i.e. 1 egg, 2 hatchling, 3 larva and 4 fry). In control runs 1a-1c, floating behaviour was assigned to stage 1-4, associated with passive drifting of particles. In runs 2a-2c and 3a-3c stage 4 was assigned as tidal, a behaviour associated with directional movement (see Figure A2 in Supplementary Material for a schematic of these model runs and Beraud *et al.* 2018, for a detailed 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 $(23 \pm 3 \text{ mm})$ than in 2019 $(30 \pm 7 \text{mm})$ 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 in 2019. Low numbers were collected at the Dee in 2019, however, due to the successful sampling in 2014 and its importance as a recognised bass nursery area this site remained in the study to provide a comparison. The number of individuals in table 4 reflects final numbers 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

Table 2: The key dates, number of individuals and age summaries (in days) for 0-group bass
at each sample site in 2014 and 2019. Residency period is the number of days 0-group bass
were estimated to have been resident in the nursery area post-settlement and prior to capture.
The spawning date, settlement date and residency period are the average calculated for each
site.

339

Year	Site	Capture date	Sample size		Age (day	s)	Spawnin g date	Settlemen t date	Residenc y 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
2010	Y Foryd	17 Jul	21	74	118	92	10 Apr	06 Jun	41 days
2019	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

340

341

342 3.3. Larval dispersal model outputs

343 Larval dispersal predictions are presented in Figure 3 as density distribution maps from each 344 of the sample sites and for both years. The density distribution maps represent averages of the 345 nine behaviour scenarios (three migration strategies \times three dispersal periods determined by 346 bass age), thus capturing the uncertainty associated with PLD and larval behaviour. Therefore, 347 Figure 3 displays a degree of variability in the predictions of precise spawning locations during 348 2014 and during 2019 (this variability is described below). However, our results indicate that 349 the 0-group bass sampled were most likely derived from spawning regions close (i.e., <200 km) 350 to their nursery of origin. The predicted spawning areas from several of the sample sites had a 351 degree of overlap with those predicted for other nursery areas in the proximity (i.e., where there 352 is overlap, larvae from those spawning locations have the potential to reach multiple nursery 353 sites).

354

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 being the Dee (N. Wales), which is more sheltered and hence there was markedly less 362 363 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 the predicted variability between each of the nursery sites, giving us confidence that the 365 366 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 the Irish Sea and also further south (Figures 3 & 4). Although overall, potential spawning 375 376 grounds appeared to be widespread through the Irish Sea, a clear regional separation was apparent: little to no overlap was simulated between potential spawning sites that seeded the 377 378 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 & 2019), the potential spawning areas extended offshore across the mouth of the Bristol 386 387 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.

Furthermore, in 2014, temperatures at all potential spawning locations at the calculated spawning times were between 10-11°C; well within upper and lower spawning limits of sea bass (8.5-15°C) (Figure 5). In 2019, sites in south (Loughor and Milford) and mid Wales (Dwyryd) showed temperatures between 9.5-11°C at the estimated spawning time, again within spawning temperature limits. However, the northern sites had much lower temperatures in 2019 at their estimated spawning dates, only reaching 9°C and less at the estimated spawning times.
Offshore, in the northern Irish Sea, temperatures remained below 8.5°C. At the northern sites
in 2019, spawning was limited to inshore and restricted offshore locations (Figures 4 and 5) at
which temperatures were around the spawning limit of 8.5°C.

In summary, in 2014, the Irish and Celtic Sea waters had warmed above the spawning temperature threshold by the estimated spawning dates. In 2019, offshore waters exceeded the spawning threshold temperature at estimated spawning date only for the southern and mid-Wales sites, whereas at the northern sites, the spawning threshold was exceeded only in coastal 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 into the nursery areas. Winds were generally more westerly in 2014 and more south-westerly 426 427 in 2019.

428

For 2014, larvae arriving at the three southern sites (Milford, Loughor and Swansea) experienced a number of strong westerly and SSW wind events (wind speeds greater than 10 m/s). This corresponds with spawning locations which are generally to the west of the estuaries (see Figure 3). In contrast, in 2019, larvae transported to Milford were subjected to 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 in 2019. In 2014, larvae arriving at the Dee, Y Foryd and the Dwyryd encountered moderate 436 437 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

The results of our study suggest that: (1) it is unlikely that one offshore spawning area seeded all the sampled nursery grounds within the Irish and Celtic Seas, with spawning possible from a range of locations but probably within 200 km of each nursery ground; and (2) that there is separation between spawning locations supplying bass to nursery grounds in north and south Wales. We have based this finding on age estimates from juvenile bass and then simulated their early life stages backwards using a backtracking larval dispersal model that accounted for a range of plausible larval behaviour traits.

451

452 4.1. Timing of spawning

Here, we estimate bass spawning in the Irish and Celtic Seas between April and May for 2014 and 2019, which lies within the spawning times reported for the UK, i.e. January-May (Jennings and Pawson, 1991; Pawson *et al.*, 2007), and is consistent with timings reported for this region based on egg and larval aging studies (Kennedy and Fitzmaurice, 1972; Jennings and Pawson, 1992; Lancaster *et al.*, 1998), with visual gonad maturity assessments carried out 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 0-group bass entering in high numbers between 17 June and 8 July (Jacobs Engineering 461 462 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

473

472 4.2. Location of spawning

Whilst the modelling in the current study predicts all potential spawning locations from a 474 475 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., 2020; Hold et al., 2021), suggesting the front may also be influencing larval connectivity in 496 497 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 been caught further north in the Wyre and the Lune estuaries (Lancashire) (this study and 521 522 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

530

529 4.3. Larval dispersal model

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 causing Celtic Sea larvae to potentially disperse hundreds of kilometres towards South Wales 547 548 (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, allowing spawning to take place when favourable conditions occur (Hočevar et al., 2021). 553 554 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 \leq 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 the difference is relatively small. The precision of the larval dispersal can be improved through 563 564 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

578

577 5. Conclusions

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 spawning in the Irish Sea. Further study is needed of the importance of these potential northern 585 586 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

601 ACKNOWLEDGEMENTS

602 This research was funded by the Bluefish Project (Grant Agreement No. 80991, part-funded 603 by the European Regional Development Fund (ERDF) through the Ireland Wales Co-operation 604 Programme), the European Fisheries Fund, and the European Maritime Fisheries Fund (Fisher-605 Scientist Project, 81920). We thank all those involved with field and laboratory work collecting 606 juvenile sea bass and preparing otoliths for the age readings (R. Bater, J. Brewin, T. Chapman, 607 L. Southworth, R. Turner), with particular thanks to John Lancaster for his seine netting 608 training and site identification. Many thanks to all the bass fishers who gave knowledge and 609 insight of spawning areas. J. Tinker and E. O'Dea at the UK Met Office provided ocean model 610 data and additional support. In-house modelling was supported by Supercomputing-Wales 611 (http://www.supercomputing.wales; a collaboration between Welsh universities and Welsh Government supported by A. Fewings and A. Owen). We thank Jacobs Engineering for providing data on larval bass recruitment into Milford Haven. Dispensations for the sampling of 0-group bass were obtained from the Welsh Government Marine and Fisheries Division (ref: DISP128) and the North Western Inshore Fisheries and Conservation Authority (no.20264 SCI19). The authors thank the two anonymous reviewers whose insights greatly improved this manuscript. In memory of Giulia Cambiè who started this research study.

618

619 AUTHORS CONTRIBUTIONS

Conceptualization and design (NH, HL, IM, SM); methodology (AG-B, HL, BM-N, PR, SPM, SW); data collection (CH, HL, AM, IM, SS); data analysis (HL, BM-N, SP-M, PR, SS,
SW); drafting manuscript (HL, IM, PR, SW); revising (NH, HL, AM, IM, BM-N, SP-M, PR,
SW) manuscript.

624

625 **REFERENCES**

- 626 Aguilera, B., Catalán, I. A., Palomera, I., and Olivar, M. P. 2009. Crecimiento del otolito en
- 627 larvas de lubina europea (Dicentrarchus labrax, L.) bajo régimen de alimentación
- 628 constante o variable. Scientia Marina, 73: 173–182.
- Bagdonas, K., Nika, N., Bristow, G., Jankauskiene, R., Salyte, A., and Kontautas, A. 2011.
- 630 First record of Dicentrarchus labrax (Linnaeus, 1758) from the southeastern Baltic Sea

631 (Lithuania). Journal of Applied Ichthyology, 27: 1390–1391.

- 632 Bento, E. G., Grilo, T. F., Nyitrai, D., Dolbeth, M., Pardal, M. Â., and Martinho, F. 2016.
- 633 Climate influence on juvenile European sea bass (Dicentrarchus labrax, L.) populations
- 634 in an estuarine nursery: A decadal overview. Marine Environmental Research, 122: 93–
- 635 104.
- 636 Beraud, C., Van Der Molen, J., Armstrong, M., Hunter, E., Fonseca, L., and Hyder, K. 2018.

- 637 The influence of oceanographic conditions and larval behaviour on settlement success -
- 638 The European sea bass Dicentrarchus labrax (L.). ICES Journal of Marine Science, 75:
 639 455–470.
- 640 Cabral, H., Drouineau, H., Teles-Machado, A., Pierre, M., Lepage, M., Lobry, J., Reis-
- Santos, P., *et al.* 2021. Contrasting impacts of climate change on connectivity and larval
 recruitment to estuarine nursery areas. Progress in Oceanography, 196.
- 643 Cambiè, G., Kaiser, M. J., Hiddink, J. G., Salomonsen, H., Pantin, J. R., and McCarthy, I.
- 644 2015. Population dynamics of the European sea bass (Dicentrarchus labrax) in Welsh
- 645 waters and management implications. Fisheries & Conservation report No. 56: 1–76.
- 646 http://fisheries-conservation.bangor.ac.uk/wales/documents/56.pdf (Accessed 25 July
- 647 2022).
- Cambiè, G., Kaiser, M. J., Marriott, A. L., Fox, J., Lambert, G., Hiddink, J. G., Overy, T., *et al.* 2016. Stable isotope signatures reveal small-scale spatial separation in populations of
 European sea bass. Marine Ecology Progress Series, 546: 213–223.
- 651 Cardoso, J. F. M. F., Freitas, V., Ouilez, I., Jouta, J., Witte, J. I., and Van Der Veer, H. W.
- 652 2015. The European sea bass Dicentrarchus labrax in the Dutch Wadden Sea: From
- visitor to resident species. Journal of the Marine Biological Association of the UnitedKingdom, 95: 839–850.
- 655 Carrère, L., Lyard, F., Cancet, M., Guillot, A. and Picot, N., 2016, May. FES 2014, a new
- tidal model—Validation results and perspectives for improvements. In Proceedings of
- the ESA living planet symposium (pp. 9-13).
- 658 Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age
- determination. Canadian Journal of Fisheries and Aquatic Sciences, 39: 1208–1210.
- 660 Christensen, A., Daewel, U., Jensen, H., Mosegaard, H., St. John, M., and Schrum, C. 2007.
- 661 Hydrodynamic backtracking of fish larvae by individual-based modelling. Marine

- 662 Ecology Progress Series, 347: 221–232.
- 663 Coscia, I., Wilmes, S. B., Ironside, J. E., Goward-Brown, A., O'Dea, E., Malham, S. K.,
- 664 McDevitt, A. D., *et al.* 2020. Fine-scale seascape genomics of an exploited marine
- species, the common cockle Cerastoderma edule, using a multimodelling approach.
- 666 Evolutionary Applications, 13: 1854–1867.
- 667 Cucchi, P., Sucré, E., Santos, R., Leclère, J., Charmantier, G., and Castille, R. 2012.
- Embryonic development of the sea bass Dicentrarchus labrax. Helgoland Marine
 Research, 66: 199–209.
- 670 Dambrine, C., Woillez, M., Huret, M., and de Pontual, H. 2021. Characterising Essential Fish
- 671 Habitat using spatio-temporal analysis of fishery data: A case study of the European
- 672 seabass spawning areas. Fisheries Oceanography, 30: 413–428.
- 673 Dando, P. R., and Demir, N. 1985. On the spawning and nursery grounds of bass,
- dicentrarchus labrax, in the plymouth area. Journal of the Marine Biological Association
- 675 of the United Kingdom, 65: 159–168.
- 676 Davies, A.M., Hall, P., Howarth, M.J., Knight, P. and Player, R., 2001. A detailed
- 677 comparison of measured and modelled wind-driven currents in the North Channel of the
- 678 Irish Sea. Journal of Geophysical Research: Oceans, 106 (C9): 19683-19713.
- 679 De Mitcheson, Y. S. 2016. Mainstreaming Fish Spawning Aggregations into Fishery
- 680 Management Calls for a Precautionary Approach.
- 681 De Pontual, H., Lalire, M., Fablet, R., Laspougeas, C., Garren, F., Martin, S., Drogou, M., et
- *al.* 2019. New insights into behavioural ecology of European seabass off the West Coast
- 683 of France: Implications at local and population scales. ICES Journal of Marine Science,
- 684 76: 501–515.
- 685 Dee, D. P., Uppala, S. M., Simmons, A. J., Berrisford, P., Poli, P., Kobayashi, S., Andrae, U.,
- 686 *et al.* 2011. The ERA-Interim reanalysis: Configuration and performance of the data

687	assimilation system. Quarterly Journal of the Royal Meteorological Society, 137: 553-
688	597.

689	De Mitcheson, Y.S., 2016. Mainstreaming Fish Spawning Aggregations into Fishery
690	Management Calls for a Precautionary Approach, BioScience, 66: 295–306
691	Denechaud, C., Thorsen, A., and Vischer, N. 2018. ObjectJ: Measuring Growth Rings in Fish
692	Otoliths. 5 pp.
693	https://sils.fnwi.uva.nl/bcb/objectj/examples/otoliths/MD/Tutorial_Otoliths_ObjectJ.pdf
694	(Accessed 3 June 2020).
695	Domeier, M.L. 2012. Revisiting Spawning Aggregations: Definitions and Challenges. In:
696	Sadovy de Mitcheson, Y., Colin, P. (eds) Reef Fish Spawning Aggregations: Biology,
697	Research and Management. Fish & Fisheries Series, vol 35. Springer, Dordrecht.
698	Doyle, T. K., Haberlin, D., Clohessy, J., Bennison, A., and Jessopp, M. 2017. Localised
699	residency and inter-Annual fidelity to coastal foraging areas may place sea bass at risk
700	to local depletion. Scientific Reports, 7. 10.1038/srep45841.
701	Earl, N., Dorling, S., Hewston, R. and Von Glasow, R., 2013. 1980–2010 variability in UK
702	surface wind climate. Journal of Climate, 26(4), 1172-1191
703	Egbert, G. D., and Erofeeva, S. Y. 2002. Efficient inverse modeling of barotropic ocean tides.
704	Journal of Atmospheric and Oceanic Technology, 19: 183–204.
705	EUMOFA. 2020. COMMERCIAL AND RECREATIONAL FISHERIES FOR WILD
706	SEABASS IN THE ATLANTIC. Luxembourg. EUMOFA Publications office of the
707	European Union, Luxembourg (Accessed 7 March 2022).
708	Green, J. M., and Wroblewski, J. S. 2000. Movement patterns of Atlantic cod in Gilbert Bay,
709	Labrador: Evidence for bay residency and spawning site fidelity. Journal of the Marine

- 710 Biological Association of the United Kingdom, 80: 1077–1085.
- 711 Gutiérrez, E., and Morales-Nin, B. 1986. Time series analysis of daily growth in

712 Dicentrarchus labrax L. otoliths. Journal of Experimental Marine Biology and Ecology,
713 103: 163–179.

714 Hočevar, S., Hutchings, J. A., and Kuparinen, A. 2021. Multiple-batch spawning as a bet-

715 hedging strategy in highly stochastic environments: An exploratory analysis of Atlantic

- cod. Evolutionary Applications, 14: 1980–1992.
- 717 Hold, N., Robins, P., Szostek, C. L., Lambert, G., Lincoln, H., Le Vay, L., Bell, E., et al.
- 718 2021. Using biophysical modelling and population genetics for conservation and

719 management of an exploited species, Pecten maximus L. Fisheries Oceanography, 30:

- 720 740–756.
- 721 ICES. 2018. Seabass (Dicentrarchus labrax) in Divisions 4.b-c, 7.a, and 7.d-h (central and
- southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea). Report

of the ICES Advisory Committee, 2018: 7. https://doi.org/10.17895/ices.pub.4472.

724 ICES. 2023. Seabass (Dicentrarchus labrax) in Divisions 4.b-c, 7.a, and 7.d-h (central and

southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea). In

Report of the ICES Advisory Committee, 2023. ICES Advice 2023, bss.27.4bc7ad-h.

727 https://doi.org/10.17895/ices.advice.21840747.

Jennings, S., and Pawson, M. G. 1991. The development of bass, Dicentrax labrax, eggs in
relation to temperature. J. mar. biol. Ass. U.K., 71: 107–116.

730 Jennings, S., and Pawson, M. G. 1992. The origin and recruitment of bass, dicentrarchus

- 731labrax, larvae to nursery areas. Journal of the Marine Biological Association of the
- 732 United Kingdom, 72: 199–212.
- Jones, B. 1999. The use of numerical weather prediction model output in spill modelling.
 Spill Science and Technology Bulletin, 5: 153–159.
- 735 Kelley, D. 1979. Bass Populations and Movements on the West Coast of the U.K. Journal of
- the Marine Biological Association of the United Kingdom, 59: 889–936.

Kelley, D. F. 1988. The importance of estuaries for sea-bass, Dicentrarchus labrax (L.).
Journal of Fish Biology, 33: 25–33.

Kennedy, M., and Fitzmaurice, P. 1972. the Biology of the Bass, Dicentrarchus. Journal of the Marine Biological Association of the United Kingdom, 52: 557–597.

- 741 King, N. G., Wilmes, S. B., Smyth, D., Tinker, J., Robins, P. E., Thorpe, J., Jones, L., et al.
- 742 2021. Climate change accelerates range expansion of the invasive non-native species,
- the Pacific oyster, Crassostrea gigas. ICES Journal of Marine Science, 78: 70–81.
- Lancaster, J. E., Pawson, M. G., Pickett, G. D., and Jennings, S. 1998. The impact of the 'Sea
 Empress' oil spill on seabass recruitment. Marine Pollution Bulletin, 36: 677–688.
- 746 Lewis, H. W., Manuel Castillo Sanchez, J., Siddorn, J., King, R. R., Tonani, M., Saulter, A.,
- 747 Sykes, P., et al. 2019. Can wave coupling improve operational regional ocean forecasts

for the north-west European Shelf? Ocean Science, 15: 669–690.

- 749 López, R., De Pontual, H., Bertignac, M., and Mahévas, S. 2015. What can exploratory
- 750 modelling tell us about the ecobiology of European sea bass (Dicentrarchus labrax): A

751 comprehensive overview. Aquatic Living Resources, 28: 61–79.

- 752 Mayorga-Adame, C., Polton, J. A., Fox, A. D., and Henry, L. A. 2022. Spatiotemporal scales
- of larval dispersal and connectivity among oil and gas structures in the North Sea.
- 754 Marine Ecology Progress Series, 685: 49–67.
- 755 Moore, A. B. M., Bater, R., Lincoln, H., Simpson, S. J., Brewin, J., Chapman, T., Delargy,
- A., et al. 2020. Bass and ray ecology in Liverpool Bay. http://sustainable-fisheries-
- 757 wales.bangor.ac.uk/documents/Bass-and-ray-ecology-in-Liverpool-Bay_FINAL.pdf
 758 (Accessed 25 July 2022).
- 759 Morales-Nin, B., Grau, A., Pérez-Mayol, S., and Gil, M. del M. 2010. Marking of otoliths,
- 760 age validation and growth of Argyrosomus regius juveniles (Sciaenidae). Fisheries
- 761 Research, 106: 76–80.

- 762 O'Neill, R., Ó Maoiléidigh, N., McGinnity, P., Bond, N., and Culloty, S. 2018. The novel use
- of pop-off satellite tags (PSATs) to investigate the migratory behaviour of European sea
 bass Dicentrarchus labrax. Journal of Fish Biology, 92: 1404–1421.
- 765 Osuna, P. & Wolf, J. 2005. A numerical study on the effect of wave-current interaction
- 766 processes in the hydrodynamics of the Irish Sea, Ocean Waves Measurement and
- Analysis, Fifth International Symposium WAVES 2005, 3rd-7th, July, 2005, Madrid,
- 768 Spain, Paper number: 93
- 769 Panfili, J., De Pontual, H., Troadec, H., and Wright, P. J. 2004. Manual of Fish
- 770 Sclerochronology. Ifremer: 464 p.
- 771 Pantin, J. R., Murray, L. G., Hinz, H., Le Vay, L., and Kaiser, M. J. 2015. The Inshore
- Fisheries of Wales : a study based on fishers' ecological knowledge. Fisheries &

773 Conservation report: 1–60. http://fisheries-

- conservation.bangor.ac.uk/wales/documents/42_003.pdf (Accessed 26 July 2022).
- Pawson, M. G., Kelley, D. F., and Pickett, G. D. 1987. The distribution and migrations of
- bass, dicentrarchus labrax l., in waters around england and wales as shown by tagging.
- Journal of the Marine Biological Association of the United Kingdom, 67: 183–217.
- Pawson, M. G., and Pickett, G. D. 1996. The annual pattern of condition and maturity in bass,
- 779 Dicentrarchus labrax, in waters around England and Wales. Journal of the Marine
- 780 Biological Association of the United Kingdom, 76: 107–125.
- 781 Pawson, M. G., Pickett, G. D., Leballeur, J., Brown, M., and Fritsch, M. 2007. Migrations,
- fishery interactions, and management units of sea bass (Dicentrarchus labrax) in
- 783 Northwest Europe. ICES Journal of Marine Science, 64: 332–345.
- Pickett, G. D., Kelley, D. F., and Pawson, M. G. 2004. The patterns of recruitment of sea
- bass, Dicentrarchus labrax L. from nursery areas in England and Wales and implications
- for fisheries management. Fisheries Research, 68: 329–342.

- Regner, S., and Dulčić, J. 1994. Growth of sea bass, Dicentrarchus labrax, larval and juvenile
 stages and their otoliths under quasi-steady temperature conditions. Marine Biology,
 119: 169–177.
- 790 Robins, P. E., Neill, S. P., Giménez, L., Jenkins, S. R., and Malham, S. K. 2013. Physical and
- biological controls on larval dispersal and connectivity in a highly energetic shelf sea.
- Limnology and Oceanography, 58: 505–524.
- Sabatés, A. 2004. Diel vertical distribution of fish larvae during the winter-mixing period in
 the Northwestern Mediterranean. ICES Journal of Marine Science, 61: 1243–1252.
- Sala, E., Mayorga, J., Bradley, D., Cabral, R. B., Atwood, T. B., Auber, A., Cheung, W., et
- *al.* 2021. Protecting the global ocean for biodiversity, food and climate. Nature, 592:
 397–402.
- Shchepetkin, A. F., and McWilliams, J. C. 2005. The regional oceanic modeling system

(ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model.
Ocean Modelling, 9: 347–404.

- 801 Souche, E. L., Hellemans, B., Babbucci, M., Macaoidh, E., Guinand, B., Bargelloni, L.,
- 802 Chistiakov, D. A., et al. 2015. Range-wide population structure of European sea bass
- 803 Dicentrarchus labrax. Biological Journal of the Linnean Society, 116: 86–105.
- Stamp, T., Clarke, D., Plenty, S., Robbins, T., Stewart, J. E., West, E., and Sheehan, E. 2021.
- 805 Identifying juvenile and sub-adult movements to inform recovery strategies for a high
- 806 value fishery—European bass (Dicentrarchus labrax). ICES Journal of Marine Science,
- 807 78: 3121–3134.
- 808 Surette, T., LeBlanc, C. H., Claytor, R. R., and Loots, C. 2015. Using inshore fishery acoustic
- 809 data on Atlantic herring (Clupea harengus) spawning aggregations to derive annual
- 810 stock abundance indices. Fisheries Research, 164: 266–277.
- 811 Thompson, B. M., and Harrop, R. T. 1987. The distribution and abundance of bass

 Journal of the Marine Biological Association of the United Kingdom, 67: 263 Thursson JJ H 2011, How to reverse time in stochastic particle tracking and data 	-274.
914 Thursdon II H 2011 How to reverse time in stachastic norticle tracting models	
or 1 mygesen, υ. π. 2011. now to reverse time in stochastic particle tracking models.	Journal of
815 Marine Systems, 88(2), 159–168.	
816 Tonani, M., Sykes, P., King, R. R., McConnell, N., Péquignet, A. C., O'Dea, E., Gr	raham, J.
A., <i>et al.</i> 2019. The impact of a new high-resolution ocean model on the Met O	Office
818 North-West European Shelf forecasting system. Ocean Science, 15: 1133–115	8.
819 Torrado, H., Mourre, B., Raventos, N., Carreras, C., Tintoré, J., Pascual, M., and	
820 Macpherson, E. 2021. Impact of individual early life traits in larval dispersal:	A
821 multispecies approach using backtracking models. Progress in Oceanography,	192:
822 102518.	
823 Vera, M., Maroso, F., Wilmes, S.B., Hermida, M., Blanco, A., Fernández, C., Grov	es, E.,
824 Malham, S.K., Bouza, C., Cockle's Consortium and Robins, P.E., 2022. Geno	mic
825 survey of edible cockle (Cerastoderma edule) in the Northeast Atlantic: A base	eline for
826 sustainable management of its wild resources. Evolutionary applications, 15(2): 262-
827 285.	
828 Vinagre, C., Ferreira, T., Matos, L., Costa, M. J., and Cabral, H. N. 2009. Latitudin	al
829 gradients in growth and spawning of sea bass, Dicentrarchus labrax, and their	
830 relationship with temperature and photoperiod. Estuarine, Coastal and Shelf S	cience, 81:
831 375–380.	
832 Ward, D. 2008. The biology and ecology of bass (Dicentrarchus labrax) in the Men	ai Strait,
and an assessment of the applicability of otolith microchemistry and body-sha	pe
834 morphometric analyses as methods of discriminating between juvenile bass fro	om
disparate nursery are. MSc Thesis, Bangor University, 94pp.	
836 Ward, S.L., Robins, P.E., Owen, A., Demmer, J. and Jenkins, S.R., 2023. The impo	ortance of

837	resolving nearshore currents in coastal dispersal models. Ocean Modelling, 183,
838	p.102181.
839	
840	
841	
842	
843	
844	
845	
846	
847	