

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

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ABSTRACT

Marine fish species that form spawning aggregations are often vulnerable to exploitation, such as the European bass (*Dicentrarchus labrax*). Information on bass spawning aggregations is not well resolved temporally and spatially. Otolith daily growth increment (DGI) counts were conducted on 0-group bass collected in July-August 2014 & 2019 from seven settlement estuaries in the Irish and Celtic seas, to estimate the timing of spawning. These timings parameterised three-dimensional hydrodynamic and Lagrangian particle tracking models, run in reverse, to identify probable spawning locations. Estimated spawning occurred between April-May (inshore and offshore) < 200 km from each settlement area. At least two broad spawning areas were predicted: the central Irish Sea that led to post-larval recruitment in north Wales and northwest England, and the southern Irish Sea/Celtic Sea that led to post-larval recruitment in south Wales. Results indicate the current seasonal closure for northern stock 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 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 shifts in spawning times and locations.

1. Introduction

Many marine fish species form dense spawning aggregations in reoccurring locations each year, resulting in spatially and temporally restricted mass point sources of offspring (Domeier, 2012). This spawning behaviour is typical in many marine exploited species (e.g., Green and Wroblewski, 2000; Surette et al., 2015). Species that form annual spawning aggregations are particularly susceptible to exploitation as they are often targeted for fishing, reducing the population densities resulting in lower reproductive success (De Mitcheson, 2016). Therefore, identifying the location and timing of these events is critical for understanding population dynamics, connectivity and establishing effective management strategies, such as the seasonal closure of fisheries (De Mitcheson, 2016; Sala et al., 2021).

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 nursery areas, led to the introduction of conservation measures in 2015 to promote stock recovery. Although fishing mortality is now thought to be at sustainable levels, the estimated spawning stock biomass is still below sustainable levels and recruitment remains low (ICES, 2023). Clearly, protecting the spawning stock and a better understanding of post-larval recruitment drivers are critical to the future sustainability of bass fisheries.

Bass form spatially- and temporally-restricted annual spawning aggregations (Pickett et al., 2004; De Pontual et al., 2019) with regional differences in the timing of spawning in the northern stock ranging from January to late May depending on location (Kennedy and Fitzmaurice, 1972; Thompson and Harrop, 1987; Jennings and Pawson, 1992; Cambiè et al., 2015). Photoperiod and sea temperature are considered

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the key drivers of spawning, with temperatures of 8.5–9 °C triggering the start and 15 °C the end, which may account for the regional differences in the timing of spawning (Thompson and Harrop, 1987; Jennings and Pawson, 1991; Vinagre et al., 2009).

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 spawning with the western English Channel and the Celtic Sea both key areas for the northern stock (Thompson and Harrop, 1987; Jennings and Pawson, 1992; López et al., 2015; Dambrine et al., 2021). Adult bass (>42 cm) migrate from inshore shallow summer feeding grounds during autumn (October–November) to seek relatively warmer deeper offshore waters during winter, though recent evidence suggests not all mature bass undertake winter migrations, either 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 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).

Research is ongoing to understand the drivers behind the poor recruitment seen over the last two decades and the connectivity between spawning, nursery and adult feeding grounds (ICES, 2018). After spawning, bass eggs and larvae disperse towards coastal nursery settlement areas such as estuaries and saltmarshes (Jennings and Pawson, 1992). Larval dispersal pathways are determined by meteorological, oceanographic and biological drivers, with annual variations in these factors thought to result in post-larval recruitment failure or success (Beraud et al., 2018). Bass pelagic larval duration (PLD) is estimated at between 2 and 3 months with larval development positively correlated with photoperiod and sea temperature, with temperatures remaining below 8.5 °C resulting in failure of the eggs to hatch (Dando and Demir, 1985; Thompson and Harrop, 1987; Jennings and Pawson, 1992; Cucchi et al., 2012). Knowledge of bass larval behaviour is limited, although a recent study by Beraud et al. (2018) described larval behaviour patterns and modelled the settlement of 0-group bass. They considered four behavioural scenarios to identify which was the most appropriate. The behaviour that produced the highest settlement success, and best reproduced inter-annual variation and the observed spatial distribution of settlers was positively buoyant eggs, hatchlings and larvae with tidal migration at the final fry stage (see Beraud et al., 2018, for more details).

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; Cabral et al., 2021). Whilst such model predictions may have a high degree of uncertainty, mainly due to a lack of knowledge of larval behaviour and uncertainty in model parameterisations, they can cover spatio-temporal scales not achievable empirically and hold great potential for exploring ecological questions relating to natal origins and population connectivity. Hindcast backtracking modelling, where bio-physical models are run backwards in time, has been effectively used to identify natal origins given information on the timing and location of settlement and PLD (e.g., Christensen et al., 2007; Torrado et al., 2021). Thus, these modelling methods can be a powerful way of investigating the potential location of spawning aggregations and their connections to known recruitment areas. Moreover, the daily periodicity of growth increments laid down in the bass otoliths offer a valuable tool to infer their early life history traits, which in combination with backtracking bio-physical models would disentangle recruitment patterns (Gutiérrez and Morales-Nin, 1986; Aguilera et al., 2009).

In this study, we applied backtracking bio-physical modelling to identify potential bass spawning locations in the Irish and Celtic Seas. The model was integrated with individual-based early life history traits for 0-group bass collected from seven settlement estuaries for two

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 spatially and temporally by: (1) identifying where the 0-group bass in the Celtic and Irish seas could have originated (i.e. putative spawning areas) by applying a backward particle tracking model; (2) identifying the timing of spawning events in this region; and (3) determining whether the north-eastern Celtic Sea (a known bass spawning area; Jennings and Pawson, 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 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.

2. Methods

2.1. Sample collection

The 0-group bass recruits used in this study were sampled from seven nursery areas (estuaries) around the coast of Wales and north-west England in the eastern Irish Sea, Celtic Sea and Bristol Channel (Fig. 1). A total of twelve sites were originally sampled, seven identified in Kelley (1988) and Lancaster et al. (1998) and five exploratory sites in areas of suitable habitat (see Cambiè et al., 2015; Moore et al., 2020 for more detail on sampling sites). Fish were captured towards the mouth of the estuaries, using a micromesh beach seine net (6 m × 1.5 m with ~4 mm mesh size), in July–August 2014 and 2019 under dispensation from the regional authorities. The sampling was timed to capture post-larval bass at the point of settlement to coastal / estuarine nursery areas (Pickett et al., 2004). Only the smallest individuals (<30 mm) 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 reading. Fish were euthanized according to UK ASPA Schedule 1. The total length (to nearest mm) of each individual was recorded prior to freezing to avoid measurement error due to shrinkage.

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®). Otoliths were prepared using standard methods (see Morales-Nin et al., 2010). Briefly, they were ground using 5 μm and 3 μm lapping film consecutively, polished using cloths and a solution of 0.3 μm aluminium oxide. Once otolith primordium and daily growth increments (DGIs) were visible, otoliths were rinsed with distilled water.

Prepared otoliths were viewed using an optical microscope (Zeiss Axio Imager A1) and images were taken using AmScope MU900 USB2.0 eyepiece digital camera and software at x100 magnification for the whole otolith and x400 for age readings. DGI counts were conducted using the FLJI version of Image J free software with the Object J plug-in (Denechaud et al., 2018). After a general overview of otolith growth structures, readings were performed along 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 same reader (HL), first from core to edge and then from edge to core. The coefficient of variation (CV) of the two readings was calculated using the Chang Index (Chang, 1982), and a third reading was conducted if values were above the 10 % limit of acceptability. Otoliths were rejected if they still crossed this threshold after a third reading (Panfili et al., 2004). Since increments begin to form 2 days after hatch in bass (Gutiérrez and Morales-Nin, 1986; Regner and

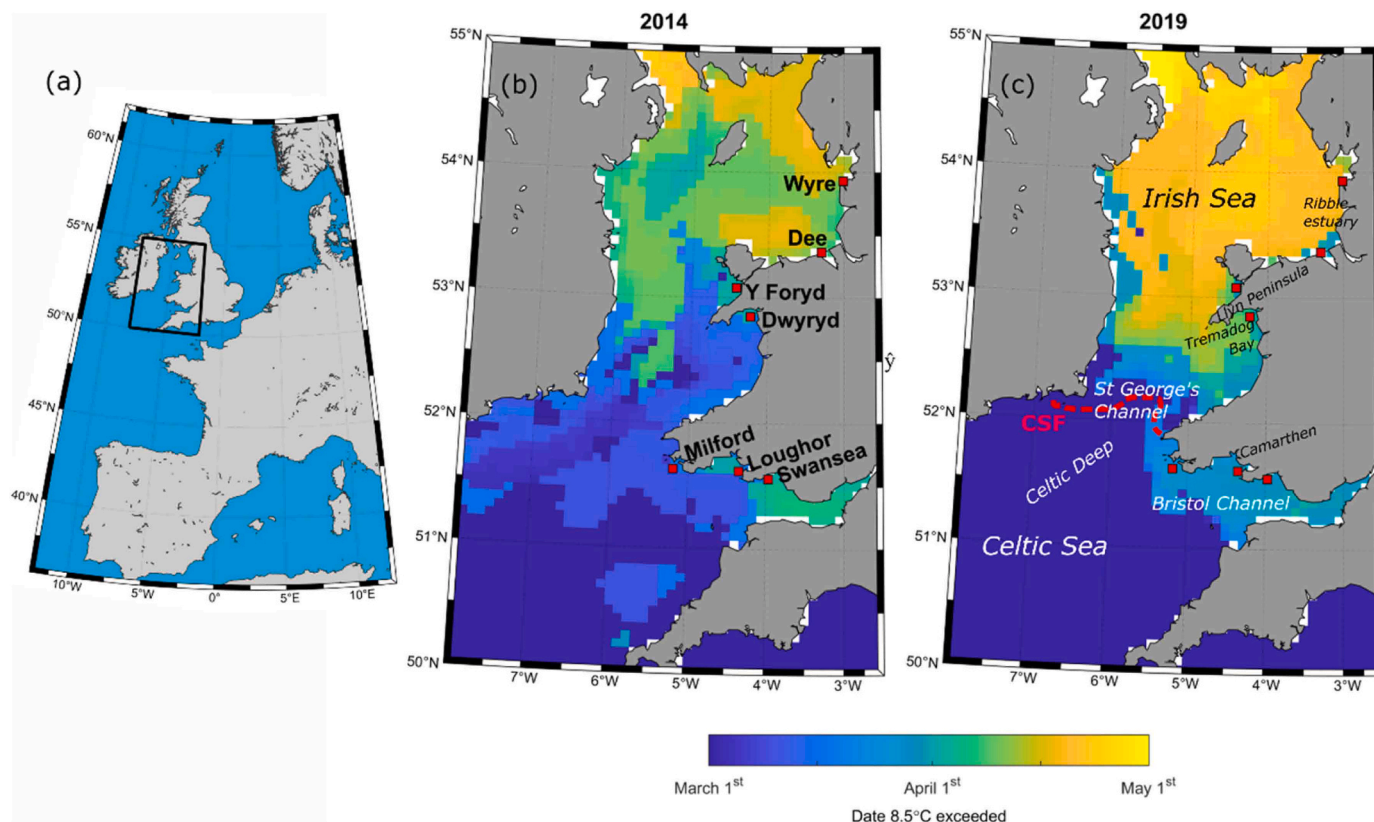


Fig. 1. (a) Map of sampling area within the European Shelf region. (b) and (c) Sampling sites of 0-group bass used in this study around the Welsh coast and up to northwest England in 2014 and 2019, indicated by red squares. These are also the release locations for the virtual larvae backtracking simulation. Shaded ocean areas show the date at which sea surface water temperature exceeded 8.5 °C. The Celtic Sea Front (CSF) is indicated by the red dotted line running through St George's Channel.

Dulčić, 1994; Aguilera et al., 2009), two days were added to averaged age estimates to calculate the age of fish from hatching. In addition, a further 5.25 days were added to account for the average egg stage duration (Beraud et al., 2018) to provide the estimated age of each fish. The birth date was then back-calculated from capture date using the estimated age. To calculate the average date of settlement into each nursery area the average assumed PLD (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). 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 Fig. A2 in Supplementary Material).

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.

Model-simulated ocean currents were used to force the larval dispersal model using the highest resolution data available for 2014 and 2019 from validated ocean models. For 2014, a regional ocean model (ROMS; Shchepetkin and McWilliams, 2005) was used that simulated 3D velocities on an orthogonal horizontal grid with a resolution of 1/400° longitude per 1/240° latitude, giving a mean cell size of approximately

270 × 460 m. The vertical plane was divided into 20 equally-segmented terrain-following layers giving a mean resolution of 4.3 m at mean sea level. The model was parameterised using EmodNET bathymetry data (<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 constituents, including the dominant semi-diurnal M_2 (lunar) and S_2 (solar) constituents, but also N_2 , K_1 , O_1 , and P_1 interpolated from the FES 2014 dataset (Carrère et al., 2016). Surface forcing (including wind forcing) using synoptic meteorological fields was obtained from the European Centre for Medium-Range Weather Forecasts-Interim reanalysis (Dee et al., 2011), available at 3-h intervals at a spatial resolution of 1.0°. A spin-up period of two months was computed to enable the tides and density-driven currents to fully develop from a state of rest and a spatially-constant temperature of 6 °C. Whilst this model does not include Stokes drift from wave-current interactions, these effects have generally been assessed to be small (a few cm/s) in the Irish Sea in comparison with wind-driven shear and tidal residuals (e.g., Osuna and Wolf, 2005; Lewis et al., 2019). The model was validated for the region against elevation and flow data, together with a temperature record, producing errors in elevations of < 12 %, velocities of < 16 % and temperature of < 7 % (see section A1 in the Supplementary Material for further details of the model validation).

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 <https://doi.org/10.48670/moi-00054> for details) was used (see Lewis et al., 2019; Tonani et al., 2019) using the Atlantic Margin Model (AMM15) setup of the NEMO ocean model (v.3.6) coupled with the wave model WAVEWATCH IIIv4.18. The horizontal resolution of the setup is 1.9 ± 0.4 km in longitude × 1.5 km in latitude with higher

resolution in the northern part of the domain. The native model has Hybrid S- σ -z-coordinates which have been interpolated to 33 regular depth levels. Tidal forcing from 11 constituents was included by both open boundary forcing and as an equilibrium tide from the TPX07.2 database (Egbert and Erofeeva, 2002). 3-hourly atmospheric forcing including wind fields was provided by the operational ECMWF 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 satellite-derived sea level anomalies and in-situ temperature and salinity profiles were assimilated. Hourly, lateral boundary conditions came from the UK Met Office North Atlantic Ocean forecast model and by the CMEMS Baltic forecast product BAL-TICSEA_ANALYSIS_FORECAST_PHY_003_006. River discharge data was included as a daily climatology. The underlying bathymetry was provided by EMODnet 2015. For a detailed model evaluation see <https://tinyurl.com/3eejb9bc>.

For the larval dispersal model described below, 3D hourly-averaged velocity fields, derived from the above hydrodynamic models for 2014 and 2019, were bi-linearly interpolated to a 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 and considering sub-grid-scale turbulence in 3D, since uncertainties can arise in the reversed trajectory compared with the forwards trajectory; for example, the backtracked particle may reach lower (weaker) flows and hence travel a shorter distance than the forwards tracked particle. In our approach, outlined in our methods, vertical transport is driven solely by behavioural traits (Beraud et al., 2018) so that the backtracked particles occupy the same vertical field that they would during their forwards trajectory. Other more computationally expensive approaches to tackle this problem are outlined by Thygesen (2011).

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 m² (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) mean group age, and (c) maximum group age. Therefore, for (a-c), the three different residency periods were

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 Fig. 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	stage	stage	stage	
			1	2	3	4	
1a	min	surface only	8	7	25	23	63
1b	avg		8	7	25	23	63
1c	max		8	7	25	23	63
2a	min	surface (stgs	3	1	25	22	51
2b	avg	1–3), tidal (stg	3	1	25	22	51
2c	max	4)	3	1	25	22	51
3a	min	surface (stgs	8	7	25	23	63
3b	avg	1–3), tidal (stg	8	7	25	23	63
3c	max	4)	8	7	25	23	63

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 residency period, as shown in Table 2 (for further detail see Fig. A2 in Supplementary Material). For each nursery site and for each release date (a-c), two larval behaviour strategies were simulated. Firstly, a control strategy was performed (Runs 1a-c) where only surface-drifting dispersal was considered (i.e., non-swimming particles). Secondly, for runs 2a-c and 3a-c, the larval behaviour described by Beraud et al. (2018) was applied. This behaviour had produced the highest settlement success, and best reproduced inter-annual variation and spatial distribution of settlers in their modelling (see Beraud et al., 2018 for more details). Here, eggs and larvae were positively buoyant for the larval stages 1–3 and at stage 4, when they became fry, developed tidal migration behaviour to achieve directional movement. To account for variations in development rate, these were run with the minimum PLD of 51 d (runs 2a-c) and the maximum PLD of 63 d (run 3a-c). Within these latter two strategies (runs 2 and 3), the virtual larvae either remained in the near-surface currents, or were synchronised with the tide, migrating towards the surface during the flood tide and towards the bed during the ebb tide, a strategy that is likely to promote transport towards the coast or estuary (Robins et al., 2013). During tidal migration, vertical swimming speeds were set to 0.002 m/s, following Beraud et al. (2018). In total, therefore, nine simulations were performed per nursery site per year as summarised in Table 1, with each run releasing 2500 particles, but varying in age of 0-group bass modelled (i.e., minimum, average and maximum age of 0-group bass), the behaviour exhibited in the pelagic phase (i.e., surface only for all stages, or tidal behaviour observed on stage 4) and the duration of the pelagic phase (i.e. 51 or 63 days).

For each simulation, the particles were then transported, backwards in time, by the simulated (reversed) ocean currents using hourly averaged current fields with an assigned PLD and larval behavioural strategy, providing a range of potential larval dispersal patterns. Particles that interacted with the coastline were reflected offshore to their position in the previous time-step. Since the model spatial resolutions were relatively fine (<1.5 km) and we focus on large scale larval transport, no additional stochasticity was added to represent unresolved turbulence, following other similar studies (e.g., Mayorga-Adame et al., 2022). The positions of the virtual larvae during the final day of simulation (i.e., each larva at 24 different positions throughout the final day) were considered as those that most likely represented the spawning location of the bass larvae. These virtual larval positions were recorded to produce a series of density distribution maps, providing the average of all simulations per nursery site per year. Density distributions were created by discretising the domain into 2 × 2 km cells and calculating the proportion of particles (from all nine behaviour/date simulations) within each cell. This was done for each hour of the final day of the simulation (i.e., the initial day of spawning) and then averaged into one density distribution map. This procedure was repeated for all nursery sites and for both years.

To describe environmental factors that could affect larval dispersal between years, sea surface temperature data from the CMEMS North-West European Shelf Ocean Reanalysis data product (Atlantic- European North West Shelf- Ocean Physics Reanalysis, NWSHELF_MUL-TIYEAR_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 7 km. The underlying ocean assimilation model is the 3D NEMOVAR which assimilates ocean observations (sea surface temperatures and profiles of temperature and salinity). At the lateral ocean boundaries, the global reanalysis model provides ocean forcing data, and atmospheric forcing comes from the ECMWF ERA-5 atmospheric reanalysis. For wind data, 10 m u and v wind strengths were obtained from the ERA-5 global reanalysis database from which wind speeds and directions were calculated. The data have a horizontal resolution of 30 km.

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.

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
	Dwryrd	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
2019	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
	Y Foryd	17 Jul	21	74	118	92	10 Apr	06 Jun	41 days
	Dwryrd	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. Results

3.1. Length frequency of sampled bass

0-group bass ranged in length from 17 to 52 mm TL with the average length of fish sampled in 2014 smaller (23 ± 3 mm) than in 2019 (30 ± 7 mm) due to greater lengths recorded in some estuaries (Dwryrd, Milford and Loughor), (See Fig. A3 in Supplementary Material for size 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).

3.2. Otolith interpretation

The success rate at ageing otoliths with a < 10% CV between readings was 92 %, with 18 rejected, resulting in a sample size of 208 0-group bass for which age and spawning date were determined. The average age of bass across both sampling years was 84 days, ranging from 47 to 102 days in 2014 and 62–126 days in 2019 (Table 2). Overall, 0-group bass collected between July to mid-August from settlement areas in Wales and northwest England originated from spawning events occurring between 10 April and 16 May. On average the 0-group bass used in the study had earlier spawning dates in 2019 (10–27 April) than in 2014 (23 April - 16 May) (Fig. 2 & Table 2). This difference was particularly pronounced for spawning that fed into the northern settlement sites (Dee, Y Foryd and Dwryrd). The dates of spawning that fed into Milford and Loughor nursery sites in the south showed less difference between the two years.

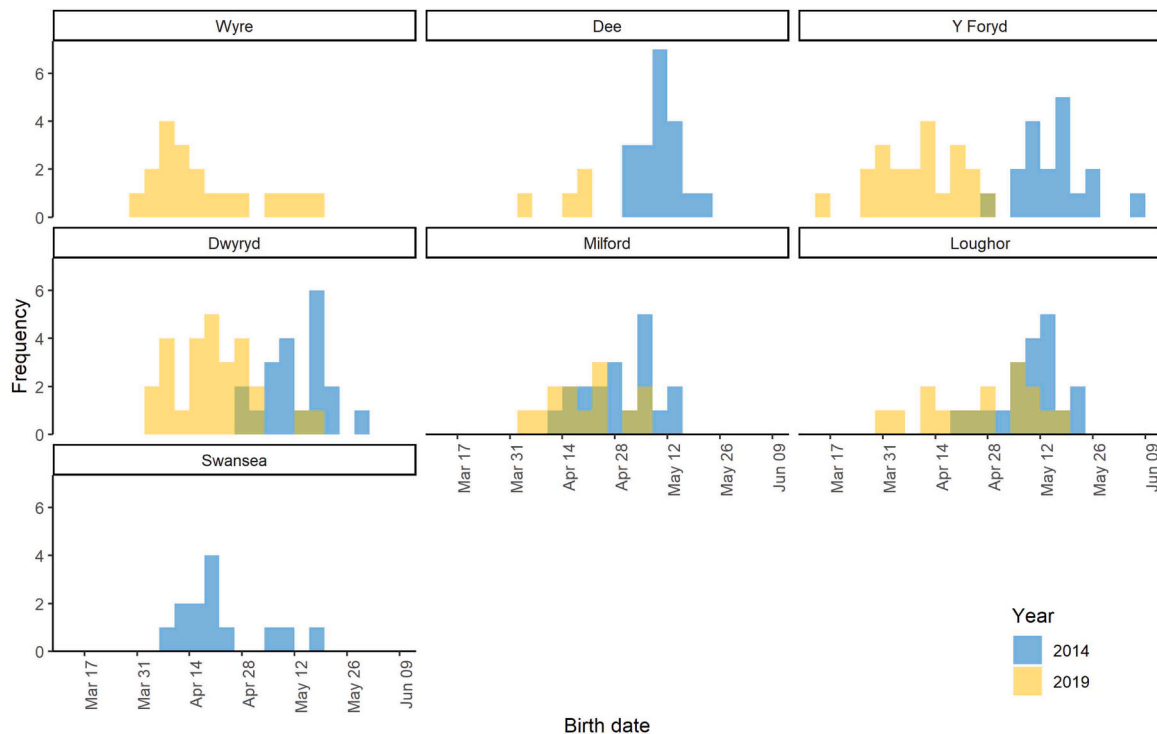


Fig. 2. The frequencies of calculated spawning dates for 0-group bass from each nursery area in 2014 (in blue) and 2019 (in yellow) ordered from north (Wyre) to south (Swansea) [see Fig. 1 for site locations].

3.3. Larval dispersal model outputs

Larval dispersal predictions are presented in Fig. 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, Fig. 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 (Figs. 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 currents. Further, most nursery sites are exposed to prevailing south-westerly winds and so the 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 variability between the different scenarios than the other nursery sites. Importantly, the

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 sensitivity tests do indeed capture much of the uncertainty in spawning location per nursery site, and that the spatial patterns in potential spawning between nursery sites (shown in Fig. 3) are indeed meaningful.

When taking together all simulations, the predicted potential spawning sites spread from the Celtic Sea up to the northern Irish Sea, across to the Irish coast to the west and the Welsh and English coasts to the east (Fig. 4). In 2014, the dispersal of virtual larvae and potential spawning areas were more widespread (e.g., potential spawning grounds off the east coast of Ireland) than in 2019 where potential spawning areas were mostly along the eastern coasts of the Irish Sea and also further south (Fig. 3 & 4). Although overall, potential spawning 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 northern (Wyre, Dee, Y Foryd and Dwyryd estuaries) and southern (Milford, Loughor and Swansea) nursery areas. The potential spawning sites predicted for the southern nursery areas were in general to the south of the Celtic Sea Front (CSF) (Fig. 1 & 4, and those for the northern sites were to the north of the CSF. The model predicted inshore spawning close to all the nursery areas.

The potential spawning areas for each year separately and combined (Fig. 4) had the greatest 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 Channel and towards the Celtic Deep in the Celtic Sea, but also inshore

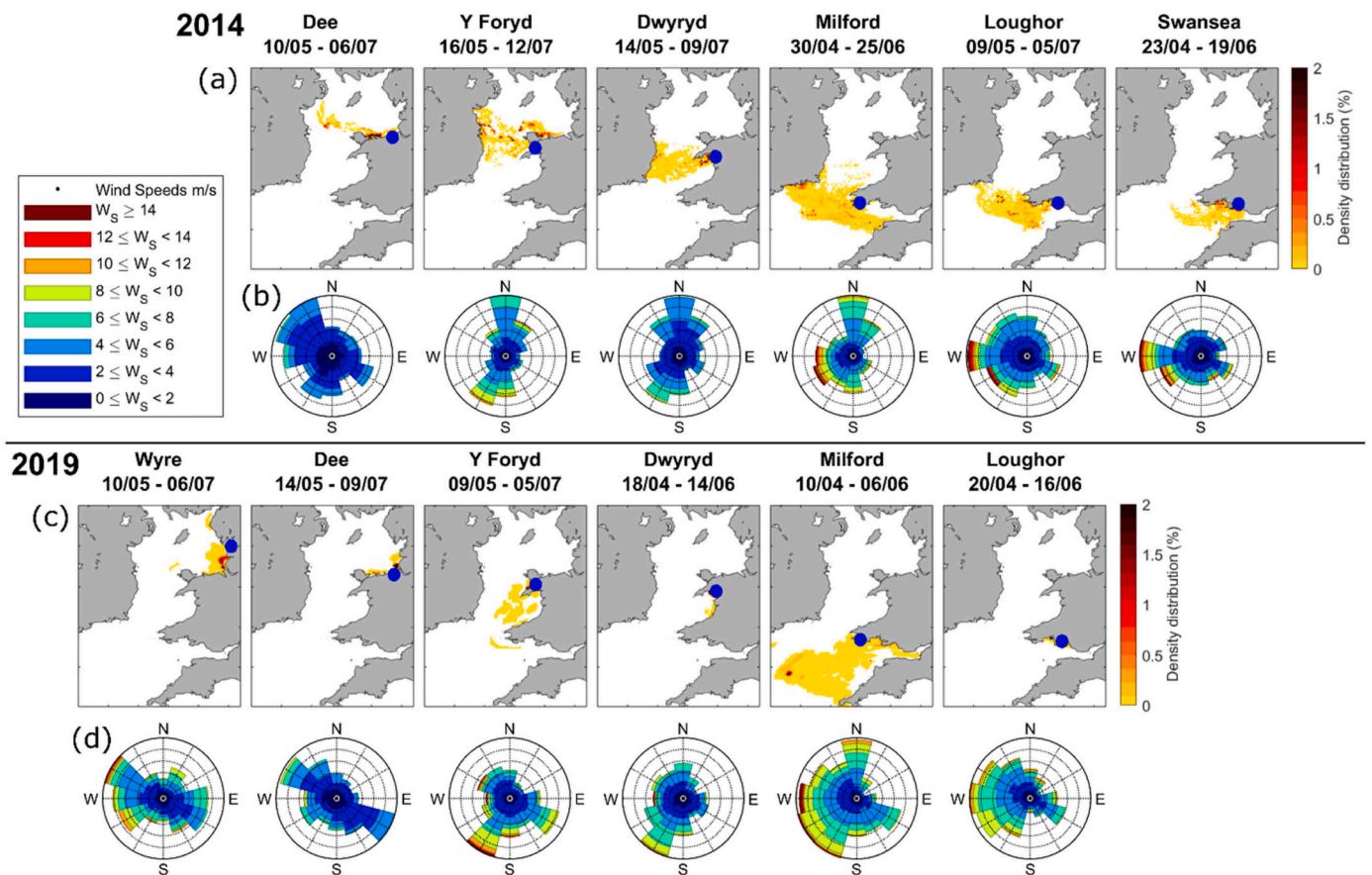


Fig. 3. Density distribution (%) heatmaps for (a) 2014 and (c) 2019 showing simulated potential spawning locations for bass for each sampled nursery area (indicated by blue dots), with site names and dates of the pelagic larval dispersal phase given in the title of each plot. The plots are aligned by nursery area, where two years of data were present. The wind roses below each heatmap show the direction the wind was blowing from at the potential spawning areas for each estuary during the associated larval phase for (b) 2014 and (d) 2019.

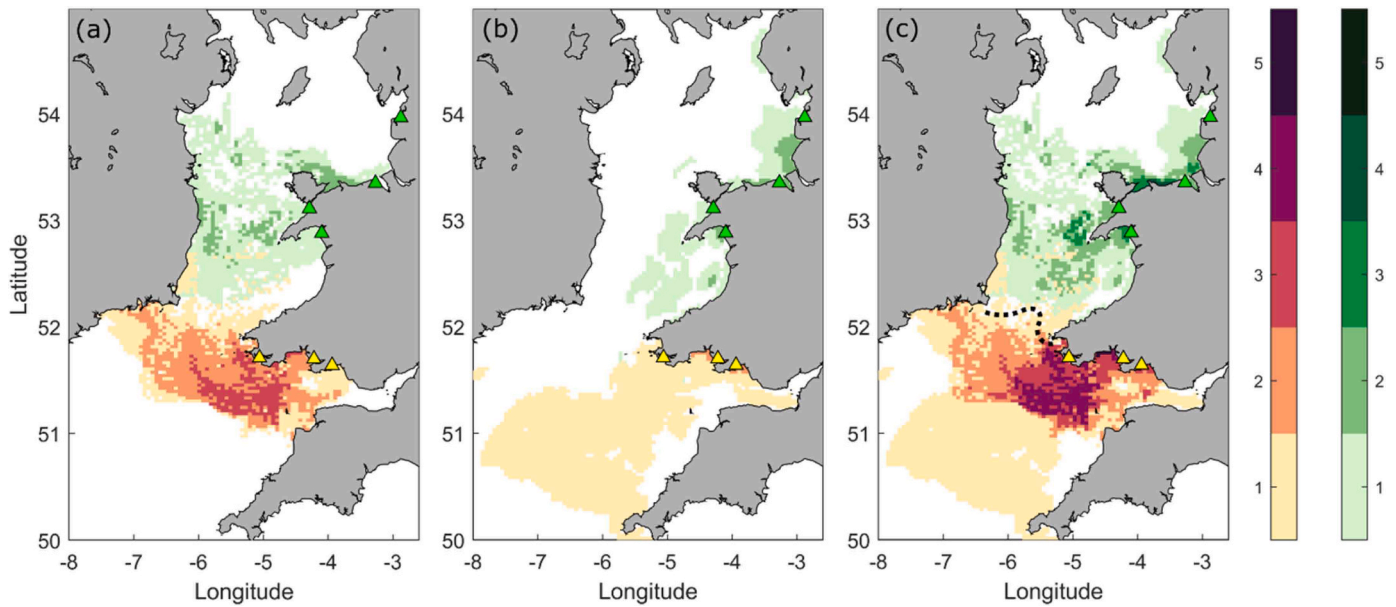


Fig. 4. Map of potential bass spawning areas with number of overlaps (indicated by scale bar) of potential locations shown for (a) 2014, (b) 2019, and (c) 2014 and 2019 combined. Estuaries are grouped into southern (Swansea, Milford and Loughor - yellow triangular markers) and northern (Dwryd, Y Foryd, Dee and Wyre - green triangular markers) sites. The Celtic Sea Front (CSF) is indicated with the black dotted line in plot (c). Spawning location overlaps for the southern sites are plotted in yellow to red colours and those from the northern sites in green shades. Darker colours indicate higher degree of overlap in the potential spawning sites. These areas of overlap are more widespread in 2014 reaching offshore and across to the Irish coast in the West. In 2019 the spatially coherent areas are much less extensive and remain restricted to inshore to the East along the Welsh coast.

along the south Wales coast (e.g. Carmarthen and Swansea Bay). For the northern spawning areas (2014 & 2019), the greatest overlap was observed inshore along the northern coasts of Wales (e.g., from north-east Anglesey to the mouth of the Dee and the Ribble estuaries, Tremadog Bay and off the northern tip of the Llŷn Peninsula).

3.4. Physical and environmental characteristics

We present no formal analysis of the environmental variables, however, here we provide a description of the physical conditions for

comparison to the modelled dispersion patterns presented in Section 3.3. Late winter to early spring sea temperatures were colder in 2014 than in 2019 in the Celtic Sea. In 2019, sea surface temperatures in most of the Celtic Sea (with exception of the Bristol Channel) had already exceeded 8.5 °C by late winter (Fig. 1). In 2014, this was only true for the southern part of the Celtic Sea. North of ~51.5°N, the 8.5 °C threshold was not exceeded until the beginning to the middle of March. In contrast, most of the northern Irish Sea warmed about 20 days earlier in 2014 than 2019. However, the inner Bristol Channel and north Wales coast inshore warmed approximately 5 days and 10 days later,

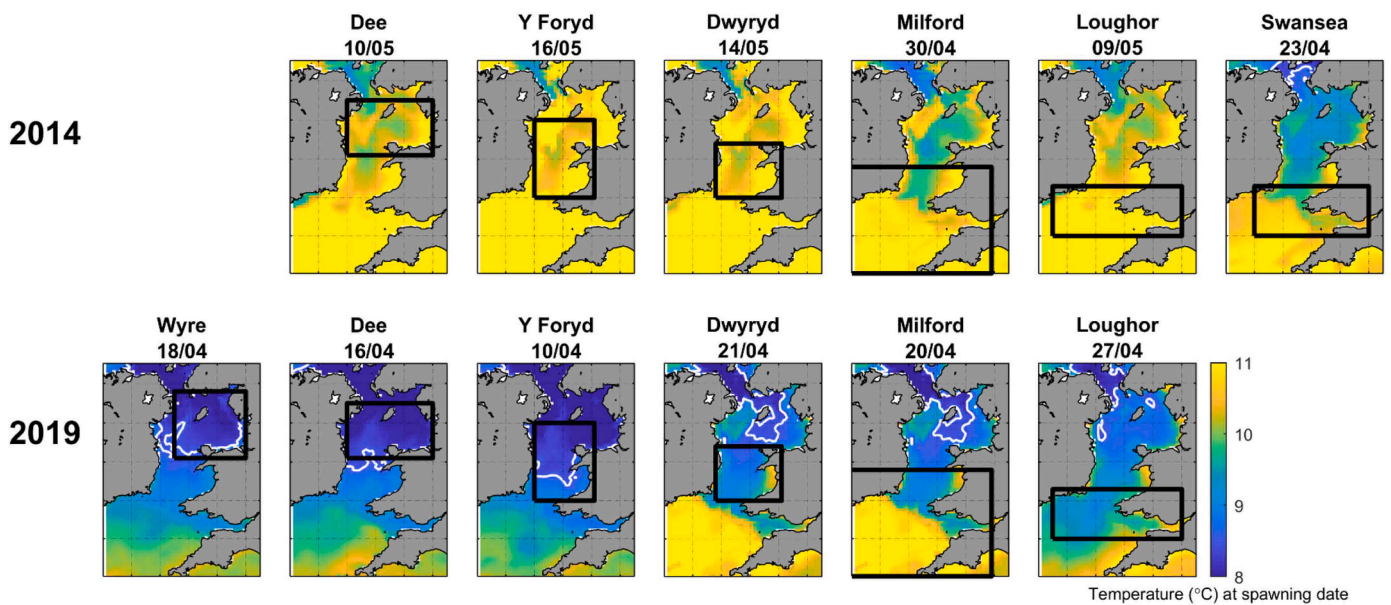


Fig. 5. Sea surface temperature at the estimated bass spawning locations during the calculated spawning periods. Potential spawning areas for each site are shown within the black boxes (joint estimates for 2014 and 2019). The figures show temperatures for 2014 and 2019. The white lines indicate the 8.5 °C contour (where applicable) at the time of spawning calculated for each estuary for 2014 and 2019.

respectively, in 2014.

Furthermore, in 2014, temperatures at all potential spawning locations at the calculated spawning times were between 10 and 11 °C; well within upper and lower spawning limits of sea bass (8.5–15 °C) (Fig. 5). In 2019, sites in south (Loughor and Milford) and mid Wales (Dwyrhyd) showed temperatures between 9.5 and 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 (Figs. 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.

Because winds can influence surface ocean currents significantly (see e.g., Jones, 1999) and are an important source of interannual variability, differences in wind climate between 2014 and 2019 for the PLD phase were reviewed. The wind roses show the direction the wind is blowing from and the wind speed during the estimated PLD phase for the approximate predicted spawning locations for each nursery population for 2014 and 2019 (Fig. 3). In general, the northern sites experienced prevailing north and north-westerly winds, and the 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 in 2019.

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 Fig. 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 the southwest of the estuary. Similarly, larvae transported to Y Foryd experienced a relatively 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 Dwyrhyd encountered moderate wind speeds with variable directions, and all three sites have potential spawning areas mainly to the west (WNW and SSW) suggesting that for weaker winds, other factors such as tides, may have a stronger influence on dispersal patterns. In contrast, during 2019, larvae transported to the Wyre and the Dee were subjected to strong NW winds and correspondingly, part of potential spawning areas are located to the north of the estuaries.

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.

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 knowledge (Pantin et al., 2015). Juvenile bass recruit into estuaries from late June (Jennings 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 unpublished data), overlapping our estimated entry date of 25 June supporting our age estimations. Bass spawning was predicted to have occurred approximately one month earlier during 2019 than during 2014, possibly due to warmer winter sea surface temperatures in the Celtic Sea in 2019 (reaching 8.5 °C by late winter) than 2014 (reaching 8.5 °C by mid March) or the earlier warming of close inshore waters in the Irish Sea and Bristol Channel (5–10 days earlier in 2019 than 2014), since sea surface temperature is thought to be the primary trigger for spawning (Pawson et al., 1987). However, the difference in spawning times calculated between the two years may also have been due to the variability in the location of 0-group bass within estuaries, and sampling limitation.

4.2. Location of spawning

Whilst the modelling in the current study predicts all potential spawning locations from a physical perspective, it does not tell us which are more plausible taking into account other environmental factors. Our results agree with previous putative spawning areas highlighted in the mouth of the Bristol Channel and the Celtic Sea (Jennings and Pawson, 1992; Lancaster et al., 1998) (Fig. 6). However, our modelling suggests these areas largely supply recruits to southern nursery areas, with juvenile bass found in estuaries along the north coast of Wales and the northwest coast of England likely originating from separate northern spawning areas. Records of ripe and running adult bass around the North Wales coast support this prediction (Kelley, 1979; Cambiè et al., 2015; Welsh commercial bass fishers, *Pers. comm.*). Regional separation of Welsh bass in terms of feeding areas with two sub-populations separating to feed in north/mid and south Wales has been suggested (Cambiè et al., 2016; Doyle et al., 2017). The current study similarly suggests a potential regional separation for spawning. Further research is required to determine whether these bass have migrated northwards from overwintering and earlier spawning aggregations in the south or whether they are resident overwinter in these northern areas. For example, bass potentially spawning in the northern/central Irish Sea may have overwintered in the Western English Channel, perhaps spawning early in the season before heading northwards to summer feeding areas around North Wales (Pawson et al., 1987). Alternatively, bass that spawn in the northern/central Irish Sea may be resident (perhaps adolescent bass) and could indicate a separate stock group. Our results highlight that a more regional management approach may be appropriate. A distinction between populations north and south of the Celtic Sea Front, which separates the Irish Sea from 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 bass.

Our modelling identifies that inshore spawning may be occurring around the Welsh and Irish coasts and this has been reported for bass, often late in the spawning season (e.g. Kennedy and Fitzmaurice, 1972; Kelley, 1979; Thompson and Harrop, 1987; Ward, 2008). In addition, bass fishers around the Welsh coast report catching ripe and running bass inshore at the mouths of the estuaries in Carmarthen Bay in the south (May–July), within the Aberdyfi estuary in mid Wales (December–March) and around Puffin Island (east Anglesey) in the north (June) (*Pers. comm.*) (Fig. 6). These observations support the modelling simulations, suggesting some spawning could occur inshore after bass return from winter migrations but also that some bass could be resident inshore all year and spawn within estuaries (e.g., Aberdyfi). Recent electronic

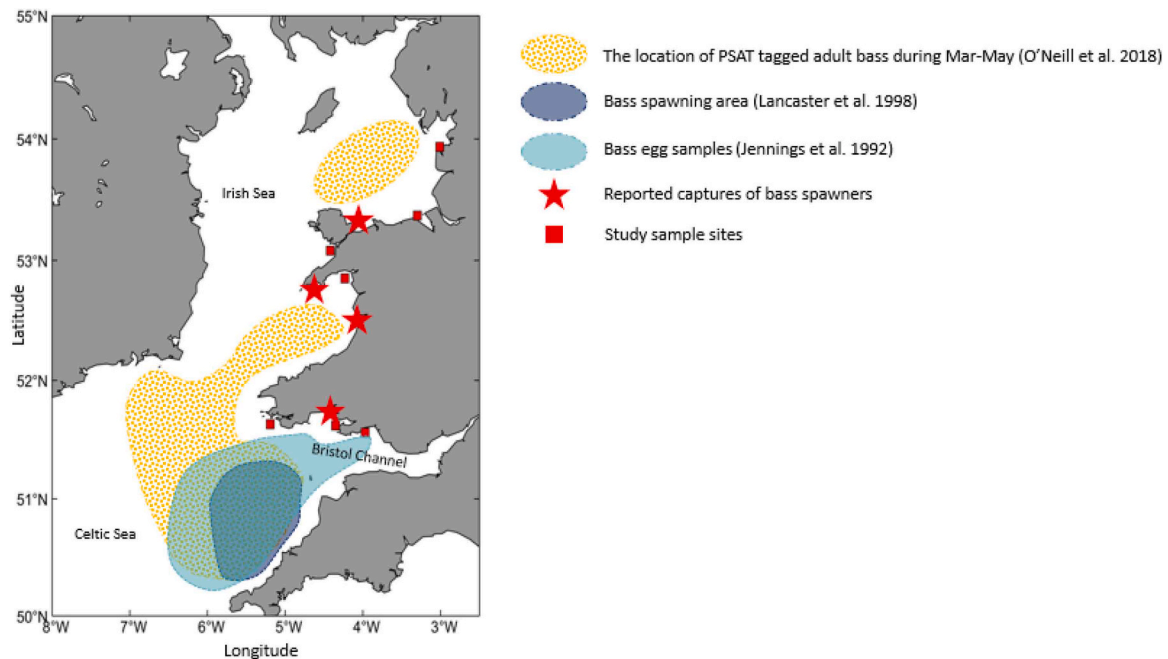


Fig. 6. Yellow areas indicate the location of PSAT tagged adult bass during Mar-May (O'Neill et al., 2018). This was identified as the spawning period that feeds 0-group bass into Welsh nursery areas. The dark blue area indicates the bass spawning area highlighted by Lancaster et al. (1998). The turquoise area indicates the location of successful samples of bass eggs (Jennings et al., 1992). Red stars indicate the areas where captures of bass spawners were reported by fishers, and the red squares show the sites sampled in the study, and where particles were released for the model.

tagging studies have confirmed differing migration patterns including inshore residency (O'Neill et al., 2018; De Pontual et al., 2019; Stamp et al., 2021). We chose not to impose a lethal temperature limit in the backtracking simulations due to some uncertainties in the exact temperature limits [for example, Thompson and Harrop (1987) found eggs and larvae present in waters around 8 °C (see their Fig. 2b)] but based the estimates of spawning locations purely on hydrodynamic currents. For 2019, at the northern sites, our simulations suggest that spawning was likely restricted to inshore waters, and here temperatures exceeded or were close to 8.5 °C (Fig. 5). Our results highlight how critical temperature may be for both the timing and location of spawning events at the northern limit for bass populations.

In warmer than average years, bass return inshore earlier and remain there for longer, compared with colder years (Pawson et al., 2007). Kelley (1988), identified the Ribble estuary in 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 Environment Agency unpublished data). Records of juvenile bass (15–18 cm) in March in the Wyre (Wyre Rivers Trust unpublished data, *Pers. comm.*) as well as adolescents (34–38 cm) show the recruits do survive the winters at these northern sites. With climate-induced ocean warming, the northern limits of species are shifting (Pawson et al., 2007; Bagdonas et al., 2011; Bento et al., 2016; King et al., 2021) and northern regions will likely become more important spawning and nursery areas.

4.3. Larval dispersal model

Our simulations suggest that wind influenced bass larval dispersal between the two studied years. Because bass larvae were assumed buoyant and spend much of their planktonic phase in surface waters (Jennings and Pawson, 1992; Sabatés, 2004; Beraud et al., 2018), they are subjected to wind-driven surface circulation. In response to the UK wind climate (e.g., Earl et al., 2013), the wind-driven component to the Irish Sea currents tends to produce notable surface residuals over synoptic timescales (of the order of cm/s over several days; Davies et al.,

2001) that can direct larvae tens of kilometres, in contrast to tidal currents which, although stronger, tend to be oscillatory and hence contribute less to net larval dispersal. Wind variability between the years was evident in the north; for example, simulated residuals from prevailing NW winds in 2014 transported larvae eastwards into the Dee (hence produced a widespread area of potential dispersal across to the coast of Ireland), whereas in 2019 simulated residuals from SE winds transported larvae westwards into the Dee (hence a smaller potential spawning area due to the proximity of the English coast). Therefore, we can infer that larva from spawning locations in the northern Irish Sea could be transported eastwards towards north Wales or westwards towards Ireland depending on prevailing wind patterns. Wind variability between 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 (Milford). This pathway may not have been possible a few weeks later, when quiescent conditions prevailed (generally westerly winds and strengths <10 m/s) – as seen in the simulations from the Loughor estuary. The model results suggest that meteorological drivers may determine larval pathways, spawning sites, and dictate successful recruitment of larvae to 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). Future work could estimate the degree of interannual variability by sampling estuaries repeatedly over a longer timescale and then repeating the backtracking modelling work to estimate the interannual spatial stability of the potential spawning sites.

Simulated larval transport may differ from real dispersal patterns due to the model resolution, i.e., kilometres and minutes, which does not resolve small-scale coastal features and near-shore transport patterns such as riverine and estuarine processes that require spatial resolutions of ≤ 100 m (Ward et al., 2023). However, given the correspondence between suggested (Jennings 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 further research into PLD and processes which determine vertical distribution of larvae within the water column, e.g., larval

behaviour and physical forcing processes such as turbulence. Further work (beyond the scope of this study) could run a forward PTM (potentially incorporating a temperature dependent PLD) with particle releases from estimated spawning areas to cross-check virtual larvae are able to reach their capture estuaries. This could confirm the separation of the spawning areas and further investigate uncertainties associated with e.g., turbulence or vertical location of larvae in the water column. However, our results tie in with those from other studies (e.g., [Coscia et al., 2020](#); [Vera et al., 2021](#)) running forward PTMs to estimate bivalve larval dispersal. Their works suggest that coastal sites to the south of the Celtic Sea front are largely separate entities from sites to the north of the front confirming findings in this study which suggests limited exchange between areas to the south and the north of the front.

5. Conclusions

DGI counts of 0-group bass otoliths provided hatch date estimations to inform a backtracking larval dispersal model, and hence give a novel method to predict possible bass spawning grounds. The timing and location of potential bass spawning estimated in this study represents a snapshot based on 0-group bass collected in 2014 and 2019 in Irish Sea waters, and the method could be more widely applied. The current study confirms the importance of the Celtic 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 nursery and spawning areas, in light of future warming seas. The study revealed spawning in the Celtic and Irish seas that currently falls outside the closed season (i.e., April onwards), and in known bass fishing areas. The current seasonal closure (February and March) of the bass fishery may not protect mature bass during the spawning events that feed recruits to nursery areas in Wales and northwest England and more research is needed in this area. Although bass in the northern stock are well mixed genetically ([Souche et al., 2015](#)), increasing evidence for site fidelity for feeding, and for broad spawning areas, highlights the potential for a regional management approach, such as spatially appropriate seasonal closures, to be effective. Physical drivers are likely to change in a future climate and management needs to be proactive to respond to changes in bass spawning behaviour.

CRediT authorship contribution statement

H. Lincoln: Conceptualization, Methodology, Investigation, Formal analysis, Writing – Original Draft, Writing Review & Editing. **P.E. Robins:** Methodology, Formal analysis, Writing – Original Draft, Writing Review & Editing. **S-B. Wilmes:** Methodology, Formal analysis, Writing – Original Draft, Writing Review & Editing. **S.P é rez-Mayol:** Methodology, Formal analysis, Writing Review & Editing. **A. Moore:** Investigation, Writing Review & Editing. **S. Simpson:** Investigation, Formal analysis. **A.Goward-Brown:** Methodology. **C.Heney:** Investigation. **S. Malham:** Conceptualization, Funding acquisition. **B.Morales-Nin:** Methodology, Formal analysis, Writing Review & Editing. **N.Hold:** Conceptualization, Writing Review & Editing, Supervision, Funding acquisition. **I.D.McCarthy:** Conceptualization, Investigation, Writing – Original Draft, Writing Review & Editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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Data availability

Data will be made available on request.

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Authors contributions

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

Appendix A. Supporting information

Supplemental data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2023.106884](https://doi.org/10.1016/j.fishres.2023.106884).

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