REGULAR ARTICLE

Recruitment of European sea bass (*Dicentrarchus labrax*) in northerly UK estuaries indicates a mismatch between spawning and fisheries closure periods

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Abstract

European sea bass (*Dicentrarchus labrax*) is a species of high commercial and recreational value, but it exhibits highly variable recruitment rates and has been subject to recent declines. Emergency management measures put in place to protect spawning stocks include the annual closure of commercial and recreational fisheries over a 2-month, February–March, window. Whether this protection measure is having the desired outcome for this data-poor species remains unclear. Otolith microstructural analyses (counts and widths of daily growth rings and check marks indicative of settlement) were used to estimate (1) spawn timing, (2) pelagic larval duration and settlement timing, (3) growth rate and condition, and (4) the otolith-fish size relationship for juvenile European sea bass caught from two estuaries in Wales (Dwyryd, Y Foryd), located at the northern edge of the species range. We observed a significant mismatch between the timing of fisheries closures and the spawning, with 99.2% of recruits having been spawned after the fishery had reopened (back-calculated median spawn date = May 5 ± 17 days SD), suggesting that the closure may be too early to adequately protect this population. Further, we present the first empirically derived estimates of pelagic larval duration for sea bass recruits settling in UK habitats, which showed a strong negative relationship with spawn date. Finally, we found significant differences in fish condition between the two estuaries, suggesting local variation in habitat quality. The results suggest that the timing of current fisheries closures may not be adequately protecting the spawners supplying these northernmost estuaries, which are likely to become increasingly important as sea bass distributions shift northward in our climate future.

KEYWORDS
European sea bass, fisheries, larval migration, otolith microstructure, phenology, spawning

1 | INTRODUCTION

Larval recruitment of marine fish species into estuarine nursery grounds is a key process shaping population persistence and is considered one of the most important issues in fisheries biology given climate-related changes in marine ecosystems (Rijnsdorp et al., 2009). Following offshore spawning events, which involve large numbers of fishes aggregating for the sole purpose of reproduction (Domeier, 2011), propagules of neritic shelf-spawning species disperse in a largely passive process, drifting inshore on ocean currents (Martinho, 2009). Dispersal distances are largely defined by the pelagic larval duration (PLD), and the resulting biphasic life cycle between inshore juvenile life stages and offshore adult life stages has been identified as a critical ecological and evolutionary process driving genetic structure (Doherty et al., 1995), population connectivity (Carr et al., 2017), and intraspecific competition (Ward et al., 2006). When ready to settle, larvae respond to environmental cues, triggering movements into nearshore nursery habitats (Jennings & Pawson, 1992), after which commences a phase of nursery habitat occupation and increased growth (Thresher et al., 1989). Despite the evolutionary advantages that have manifested this life-history strategy, there are numerous risks faced by settling offspring. Primary causes of mortality include a failure to identify suitable nursery ground (Bailey et al., 2008), and high levels of predation at both egg (Fuiman et al., 2015) and post-settlement stages (Almany & Webster, 2006). Furthering our understanding of the factors underpinning juvenile fish recruitment has the potential to greatly improve fisheries and habitat management. For example, more accurate predictors of spatial and temporal dispersal patterns and juvenile mortality rates could help to tailor spatial management plans and stock assessments (Fogarty & Botsford, 2007; Le Pape et al., 2020).

Fish spawning aggregations (FSAs) support highly productive commercial, recreational, and subsistence fisheries globally (Erisman et al., 2017). The targeting of FSAs has been heavily implicated in population declines for many marine species (Sadovy de Mitcheson, 2016). Mature fish typically gather and release multiple batches of eggs, creating within-season pulses of reproduction that have been observed in both freshwater (Garvey et al., 2002; Kwarfo-Apegyah & Ofori-Danson, 2010) and marine (Ings et al., 2008; Smith & Sinerchia, 2004; Williams, 1983) species. This strategy spreads risk across cohorts, producing temporally varied settlement pulses. Focused protection of spawning aggregations offers an efficient, measurable method to promote sustainable fisheries management, particularly, because FSAs are often spatially and temporally predictable (Grüss et al., 2014). This predictability, however, can be complicated by individual plasticity and environmental stochasticity, with spawning times known to vary in response to biotic and abiotic cues (Kaemingk et al., 2014). Given rapid environmental change and mounting stressors facing today's marine ecosystems (Gissi et al., 2021; Przeslawski et al., 2015), spawning phenology is likely to shift in the future and become more unpredictable in the future. For this reason, regular monitoring of spawn timing is essential to confirm whether management measures aimed to protect FSAs are correctly timed or broad enough to account for this interannual variability.

Despite both the theoretical and observed importance of fish recruitment, there is often a serious lack of quantitative data on the abundance, growth, and survival of early life stages (Cowen & Sponaugle, 2009). This is particularly apparent for pelagic larval phases, due to high mortality and the inherent challenges associated with sampling small organisms across large distances and habitat types. In response to a data-poor field, novel methods of gathering data on early life history of fish have emerged. One such method involves the analysis of growth rings in fish otoliths, small, calcified structures used by the fish for balance and hearing (Schulz-Mirbach et al., 2019). Otoliths have formed a key component of fisheries biology for more than a century, primarily used for age determination via their daily and annual growth rings, which provide a biochronology similar to that of tree rings (Albrechtsen, 1968; Campana, 2005; Pannella, 1971). They are metabolically inert and deposit new material continuously with circadian periodicity throughout the fish's life. Crucial to their role as a biochronometer, otoliths are not resorbed, even during periods of negative somatic growth (Campana, 1984; Campana, 1999; Reis-Santos et al., 2013). Because otoliths are formed at the start of ontogenesis, it is possible to reconstruct previously elusive information on larval and juvenile life-history patterns at increasingly fine temporal resolutions (Reis-Santos et al., 2022). For example, as somatic and otolith growth tends to be positively correlated, the spacing of growth increments can be used to infer fish size and growth (Campana, 1990). Also, optical discontinuities, herein referred to as check marks, can be used to reconstruct the timing of major life-history transitions, such as nursery ground settlement and metamorphosis (Pinto et al., 2021; Regner & Dulčić, 1994).

The European sea bass (*Dicentrarchus labrax*, Linnaeus, 1758) is a euryhaline and eurythermal species widely distributed from the eastern North Atlantic to Morocco, with a genetic break point between northern populations and those in the Mediterranean (Pérez-Ruzafa & Marcos, 2014; Vázquez & Muñoz-Cueto, 2015). Temperature exerts a major influence on sea bass ecology and physiology (Person-Le Ruyet et al., 2004), with the northerly extent of spawning bound by a 9°C thermocline (Pickett & Pawson, 1994). Rising sea temperatures have been associated with a northward range expansion (Cardoso et al., 2015), which would suggest increasing importance of northern UK nursery grounds for the productivity and resilience of the fishery in the future (Hyder et al., 2018). This study focuses on juvenile sea bass sampled from estuaries in North Wales, one of the most northerly regions of documented sea bass nursery habitat in the UK (Hyder et al., 2018). Individuals from the northern stock, as defined by ICES (2022), are characterized by slow growth and late maturity. Mature sea bass have been seen to migrate to spawning areas in the Celtic Sea and southern North Sea from mid-October onward (Graham et al., 2023; Pawson et al., 1987). Recent modeling work has posited additional possible spawning ground locations, suggesting juveniles recruiting into North Wales estuaries have primarily come from spawning grounds in the Irish and Celtic seas (Lincoln et al., 2024).

FIGURE 1 Geographic locations of Dwyryd and Y Foryd estuaries where juvenile sea bass were collected in summer 2021. Inset map shows the area relative to the rest of the UK.

Sea bass are a species of economic importance, supporting a commercial fleet, a highly prized recreational fishery, and a large aquaculture industry (Tidbury et al., 2021; Vandeputte et al., 2019). Commercial catches dropped from their peak in 1983–1984 (~1000 t) to a low in 1985–1986 (~600 t) (Pickett, 1990), likely as a result of overfishing. Technical measures were first introduced in 1990; however, further emergency measures were implemented by the European Commission in 2015 as a result of rapid population declines from 2014 (ICES, 2022; Pickett et al., 2004). Strict measures continue to be implemented, which include a closed season around the UK and France for commercial and recreational fishing between February 1 and March 31 aimed at protecting spawning aggregations (Marine Management Organisation, 2023). With the ongoing formation of new UK legislation post-Brexit, there is a growing interest in assessing the effectiveness of this closure period (Department for Environment, Food and Rural Affairs, 2023).

Limited research has been conducted on the juvenile life stages of European sea bass (Stamp et al., 2021); however, previous studies have suggested peak spawning in mid-March (Jennings et al., 1991) and a typical PLD of 70–90 days (Pickett & Pawson, 1994). The present study uses otolith microstructural analyses to estimate the age, growth rate, spawn timing, and PLD of 0-group sea bass sampled from two estuaries in North Wales during summer 2021. We structure the

results and discussion around the following research questions. First, we explore variation in spawn timing among the recruits and whether (1) there is multimodality in spawn dates, suggesting multiple recruitment pulses, and (2) the distribution of spawn dates falls inside or outside the fishery closure period. Second, we compare PLD among the two estuaries and assess whether it is influenced by spawn date. Third, we quantify geographic differences in fish growth and condition that could be indicative of local variation in habitat quality. Finally, we describe the relationship between otolith size and fish size for sea bass to aid future size and growth reconstructions using otolith biochronologies.

2 | MATERIALS AND METHODS

2.1 | Study area

This study focuses on juvenile sea bass that settled in two estuaries in North Wales, UK: Dwyryd and Y Foryd in summer 2021 (Figure 1). The Dwyryd is a large estuarine system located in the northeast of Cardigan Bay, Wales, UK. It measures approximately 10 km² and has several tributaries extending from it (Mahamod, 1989). Y Foryd is a partially enclosed bay situated at the southwest entrance of the

Menai Strait, 3 km west of Caernarfon, which is comparatively smaller in size than the Dwyryd estuary, at around 2.5 km^2 (McGaw, 1991). Sampling of juvenile sea bass was conducted along mudflat channels within tidal and subtidal saltmarsh for Y Foryd (co-ordinates of sampling site: 53.105187, −4.310772), and sand flats for Dwyryd estuary (52.920315, −4.084060), which constitutes roughly 70% of the habitat (Mahamod, 1989). The Dwyryd is a designated sea bass nursery area (BNA), which means fishing from a vessel has been prohibited there since 1999 (Bass [Specified Areas] [Prohibition of Fishing] [Variation] Order 1999), whereas Y Foryd is a designated Site of Specific Scientific Interest (SSSI) due to importance for native and migratory birds but has not been designated as an official BNA.

2.2 | Fish sampling

Sampling was conducted under dispensation from the Welsh Government Marine and Fisheries Division (DISP120) and following ethical approval from Bangor University Animal Welfare and Ethical Review Process. Sampling began on 10/06/2021 and was conducted weekly in alternating estuaries until 08/09/2021, discontinued after no sea bass were caught after 45 min of hauls. To collect samples, a seine net measuring 6 × 1 m with 4-mm mesh-size was drawn alongshore of sheltered creeks leading from the main channels by two people on foot, commencing 2 h before high tide. The net was dragged at a steady pace maintaining an arc while ensuring the weighted footrope remained in contact with the benthos and was pulled onto the bank at the conclusion of tows for sample collection. Tows were continued until the permitted sample size was met or until 45 min had passed. Upon capture, sea bass were transferred to a holding bucket until the permitted sample size was collected. Sea bass were then transferred to a 1-L pot and euthanized according to UK ASPA (Animals [Scientific procedures] Act 1986) guidelines using a Schedule 1 method by overdosing in a phenoxyethanol solution (25:1), and they were then transported to the laboratory for further processing.

Individual fish were measured (total length [TL] in millimeters; TL ±0.1 mm) and weighed (wet weight [WW] in grams) before being frozen in individual centrifuge tubes. Fulton's *K* condition index was calculated as:

$$K = 10^5 * \frac{WW}{TL^3}$$

where WW is the wet weight in grams and TL is the total length of individual fish in millimeters. The scaling factor (10^5) was used to ensure that the final *K* values were roughly centered around 1.

2.3 | Otolith microstructure analysis

A total of 152 individuals were selected for otolith microstructural analysis. When a single sampling event yielded >20 fish, 20 were selected for otolith analysis, and if <20 fish were collected for a

sampling event, all fish were selected. Selected fish were left to defrost for 30 min. Left sagittal otoliths were extracted, cleaned of organic material with Milli-Q water, air-dried for 30 min, and mounted on microscope slides using Crystalbond adhesive with the sulcal groove facing down and rostral tip pointing right. Otoliths were ground in the sagittal plane to the central primordia using a range of silicon-carbide abrasive papers and were then polished using a combination of MetPrep Alphacloth synthetic cloth and Metprep Dry Power Alpha 0.3 μm as per methods described by Morales-Nin et al. (2010).

To image the juvenile sea bass daily growth increments (Aguilera et al., 2009), prepared otoliths were digitally imaged at 400× magnification using a Meiji MT8000 compound microscope equipped with a Lumenera Infinity 3 camera and Image Pro Premier 9.1 software. Otoliths were imaged segmentally with the aim of having all daily growth rings in focus and subsequently stitched into a composite image using the MosaicJ plugin for ImageJ software. Composite images were aligned in GIMP GNU Image Manipulation Program, which allows counting of rings across multiple focuses. Otolith daily increments were counted and their width measured using the TreeRings package created for ObjectJ plugin, ImageJ software (Vischer & Nastase, 2009).

Daily rings were counted and measured twice per otolith. Both reads were performed by the same reader (J.D.), first from primordia to the edge and second from edge to primordia, along the dorsal growth axis, as per methods described by Denechaud et al. (2018). The CV was calculated for paired readings, and precision was assessed using the Chang index (Chang, 1982). If the index was above 10% for a given otolith, a third reading was undertaken, and if the result remained >10%, the otolith was rejected (after Lincoln et al., 2024; Morales-Nin & Panfili, 2002). Among-reader precision was assessed by comparing final counts with those estimated by two experienced otolith readers for a subset of the otoliths (10% read by H.L., 5% read by F.M.).

Fish age was determined as the mean daily ring count plus 2, accounting for a 2-day delayed onset of ring formation after hatching (Regner & Dulčić, 1994). Hatch date was calculated by subtracting a fish's age from the individual's catch date. Spawn date was estimated by adding 6 days to the hatch date to account for the typical embryonic period prior to hatching (Ré et al., 1986).

Check marks were used as a proxy for estuarine settlement (Figure 2b) following Pinto et al. (2021). PLD was estimated as the number of daily rings counted between the primordium and the start of the check mark plus 2 to account for the delay in ring formation mentioned above (Regner & Dulčić, 1994). PLD was not estimated for individuals without a clear check mark (e.g., Figure 2a).

2.4 | Data analysis

All analyses were performed in R software (R Core Team, 2021). Fish length, weight, *K*, and age were compared among sites using a *t*-test or a Wilcoxon rank-sum test if data were not normally distributed.
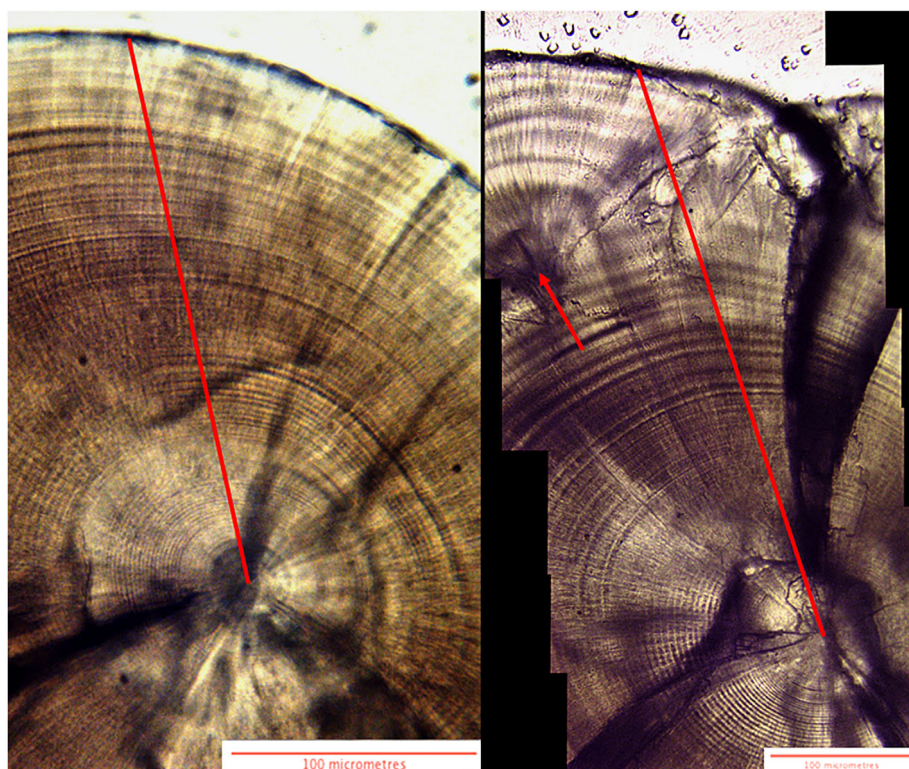
FIGURE 2 Polished sagittal otoliths of 0-group sea bass imaged at 400×. Daily increments counted and measured along the dorsal axis (long arrow) were used to estimate age and growth rate from core to edge. (a) shows a bass otolith with no clear check mark, whereas (b) shows an otolith with a check mark used to estimate settlement timing, indicated by a red arrow.

Generalized linear models (GLM) were used to test for relationships between age and K, and age and TL, including an interaction with capture site in case of site-specific slopes or intercepts. Given linear relationships between length and age, daily somatic growth rates were estimated using the slope of the regression line, a common approach used to estimate larval and juvenile fish growth rate (e.g., Fey & Greszkiewicz, 2021; Rheinberger et al., 1987).

To assess whether otolith size correlates with body length or fish age (and thus whether daily increment widths can be used to infer somatic growth rates and otolith radius to reconstruct fish size and age), the otolith radius from core to the dorsal edge was regressed against TL and age. We also tested for an interaction with capture site, but as it was non-significant, it was dropped from both models.

Recruitment pulses were inferred by fitting multimodal models to spawn date distributions using the "normalmixEM" function from the *mixtools* package (Benaglia et al., 2009).

Finally, a GLM was used to test if an individual's PLD was related to its spawn date, including an interaction with the site, which was later dropped as non-significant.

3 | RESULTS

A total of 332 wild juvenile *D. labrax* were caught during July–September 2021 (Table 1). It took roughly 1 month from the commencement of sampling in June to when the first juvenile bass were caught. All individuals were 0-group sea bass (size range = 17–51 mm), with the largest individual (51.3 mm) caught on 25/08/2021 found to be 120 days old, and all individuals within the 0-group size range reported by previous studies (Jennings et al., 1991). Growth increments ($n = 22,789$) were measured on a subset of individuals ($n = 152$), with 132 fish remaining in the final dataset after quality control assessments had been performed (see methods).

3.1 | Sea bass spawning phenology

The juveniles analysed for this study had been spawned over a 92-day period, from March 28 to June 28, 2021 (Table 1; Figure 3a). The spawning period was around 2 weeks earlier for juvenile sea bass that recruited into Y Foryd (March 28 to June 2) than Dwyryd (April 10 to June 28), with peak spawning (median date) occurring on May 6 (Y Foryd) and May 1 (Dwyryd). Only one individual (0.8% of all recruits) had been spawned during the February–March fishery closure period (Figure 3a).

There was some suggestion of bimodal distributions in spawn dates within each estuary that could represent separate recruitment pulses, although the model fits were not significant ($p = 0.3$, Figure 3b,c). Both pulses were observed at similar times (late April and mid to late May), although the strength of pulses appeared to differ between the two estuaries. The first pulse to the Dwyryd was larger and had a mean spawning date of April 27 (lambda = 0.61, sigma = 7.21), with a second, smaller pulse peaking on May 21 (lambda = 0.39, sigma = 17.34) (Figure 3b). On the contrary, the first pulse to Y Foryd was smaller, with a mean spawn date of April 20 (lambda = 0.36, sigma = 11.32), followed by a larger pulse on May 12 (lambda = 0.64, sigma = 10.11) (Figure 3c).

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TABLE 1   Data for every survey conducted in two estuaries (Y Foryd and Dwyryd) in North Wales in 2021.

Sample date	Estuary	N Caught	N aged	Min.	Mean	Max.	Mean spawn date	Spawn date range
08/07/2021	Y Foryd	17	14	64	84	102	14/04/2021	28/03/2021–05/05/2021
14/07/2021	Dwyryd	78	18	66	77	89	28/04/2021	16/04/2021–09/05/2021
23/07/2021	Y Foryd	47	20	72	85	104	28/04/2021	10/04/2021–12/05/2021
27/07/2021	Dwyryd	87	19	65	88	108	29/04/2021	10/04/2021–23/05/2021
04/08/2021	Y Foryd	39	20	70	91	112	05/05/2021	14/04/2021–26/05/2021
10/08/2021	Y Foryd	8	6	86	91	98	10/05/2021	04/05/2021–16/05/2021
18/08/2021	Dwyryd	12	10	51	77	89	01/06/2021	21/05/2021–28/06/2021
23/08/2021	Y Foryd	12	7	86	97	104	18/05/2021	11/05/2021–29/05/2021
25/08/2021	Y Foryd	29	15	84	100	128	16/05/2021	19/04/2021–02/06/2021
02/09/2021	Dwyryd	2	2	100	112	123	13/05/2021	02/05/2021–25/05/2021
08/09/2021	Y Foryd	1	1	120	120	120	11/05/2021	11/05/2021

Abbreviations: max., oldest fish aged from survey; mean, mean age of aged fish; min., youngest individual aged from survey; N, number of individuals caught per sample; N aged, number of individuals successfully aged from survey.
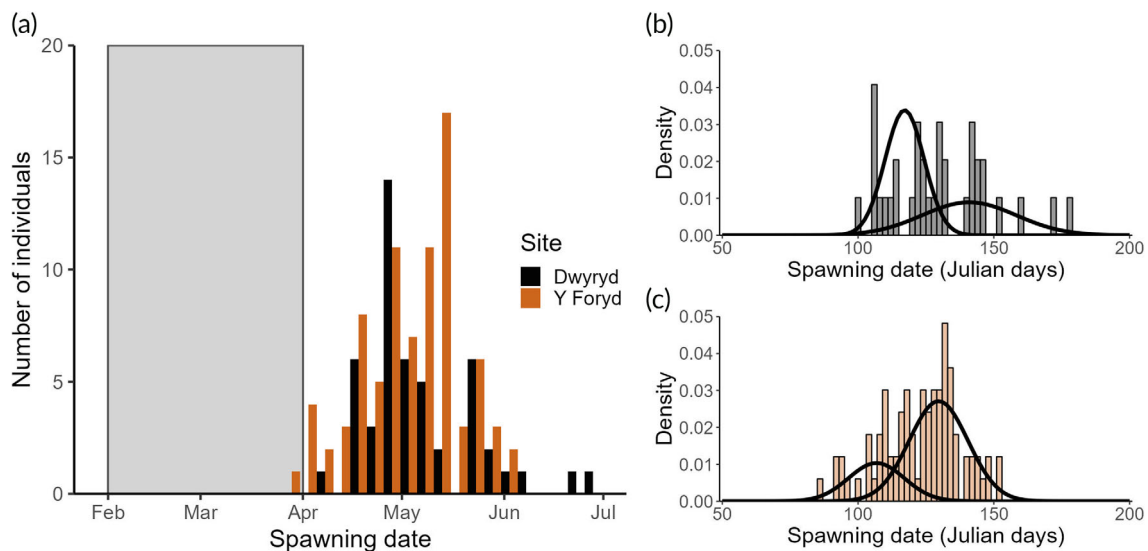

FIGURE 3   Spawn dates for 0-group sea bass sampled from two estuaries in North Wales, estimated from otolith daily increment counts. (a) Frequency histogram of spawn dates for juveniles sampled from the Dwyryd (black bars; $n = 49$) and Y Foryd (orange bars; $n = 83$) estuaries. Gray area represents the current annual fisheries closure period. (b, c) Finite mixture models demonstrating pulses of recruitment in Julian days for juveniles sampled in Dwyryd (b) and Y Foryd (c) estuaries.

3.2 | Pelagic larval duration

Of the 132 otoliths used for age analysis, 71 exhibited clear check marks (Figure 2b) that were used to estimate settlement date and PLD (20 from Dwyryd and 51 from Y Foryd). PLD ranged from 49 to 96 days, with a mean settlement age of 78 days (Figure 4a). There was no influence of estuary on PLD ($F_{1,69} = 0.08$, $p = 0.78$), but PLD was strongly negatively correlated with spawn date (Figure 4b, $F_{1,69} = 104.9$, $p < 0.001$).

3.3 | Sea bass size, age, and condition

Overall, the fish caught from Y Foryd were longer, heavier, older, and had a higher K condition factor compared to those from the

Dwyryd (Table 2). However, as sampling effort was not completely balanced through the season among the sites (Table 1), condition and size were also compared using an ANCOVA that accounted for age.

After accounting for a significant positive effect of age on K ($F_{1,130} = 18.08$, $p < 0.001$), fish from the Dwyryd had significantly higher K than those caught from Y Foryd ($F_{1,130} = 2.263$, $p < 0.001$) (Figure 5a). There was no significant interaction between age and site ($F_{3,128} = 9.594$, $p = 0.7$).

Length was positively and linearly related to age ($F_{1,130} = 113.2$, $p < 0.001$; Figure 5b), and there was no difference in length-at-age between the two sites ($F_{3,128} = 39.11$, $p = 0.1$), with similar daily growth rates obtained from the slope of the two lines (Dwyryd: 0.38 mm d^{-1}, $n = 49$; Y Foryd: 0.46 mm d^{-1}; $n = 83$).

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10958649, 2024, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/jfb.15843 by Test, Wiley Online Library on [06/01/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License
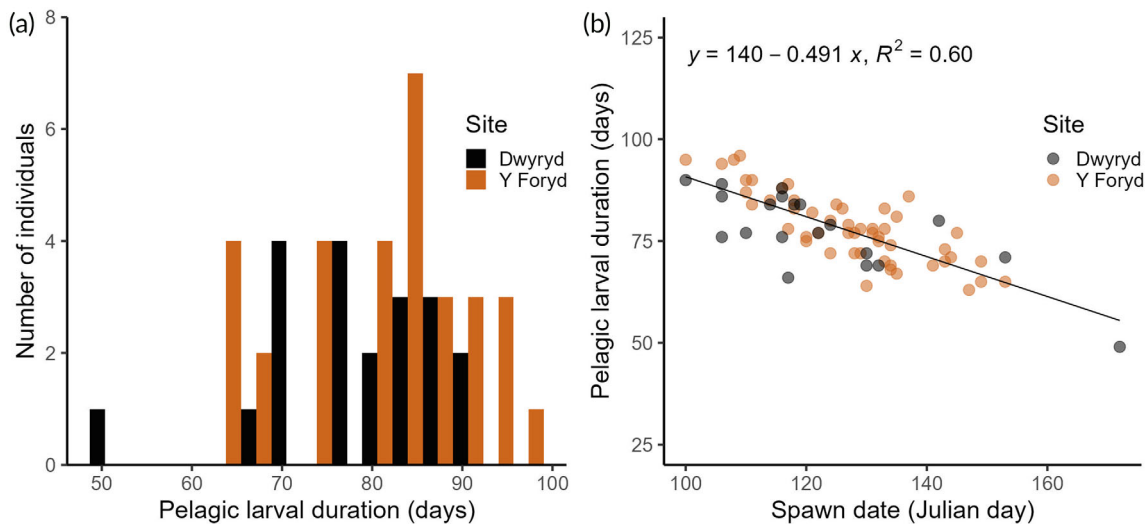
FIGURE 4   (a) Distribution of pelagic larval duration (PLD) estimates, equivalent to settlement age for 0-group sea bass collected from Dwyryd (black; $n = 20$) and Y Foryd (orange; $n = 51$) estuaries in North Wales in 2021. (b) The relationship between spawn date and PLD for both estuaries combined (regression equation and R^2 value displayed on the plot).

TABLE 2   Outputs of parametric and non-parametric tests analysing inter-site variation across several parameters for 0-group sea bass caught in North Wales, 2021.

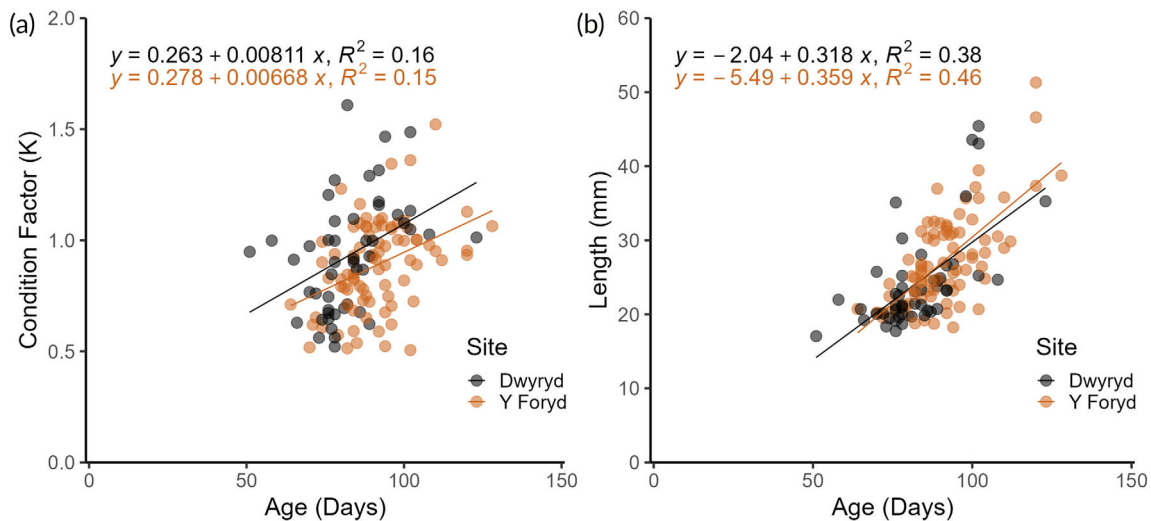| Parameter	Dwyryd Mean ± SD	Y Foryd Mean ± SD	Test	Test statistic	p-Value
Total length (mm)	22.74 ± 4.03	27.23 ± 6.99	Wilcoxon rank-sum test	$W = 8530$	<0.001
Weight (g)	0.12 ± 0.14	0.25 ± 0.23	Wilcoxon rank-sum test	$W = 8201$	<0.001
Age (days)	83 ± 13	91 ± 12	Welch's two sample t-test	$t_{94} = -3.62$	<0.001
Condition	0.84 ± 0.22	0.96 ± 0.21	Wilcoxon rank-sum test	$W = 9554$	<0.001

FIGURE 5   Ontogenetic changes in condition (a) and length (b) of group-0 sea bass sampled from Dwyryd (black; $n = 49$) and Y Foryd (orange; $n = 83$) estuaries in North Wales in 2021. Differences among estuaries were only detected for condition (a). Regression equations and R^2 values are displayed on each plot.
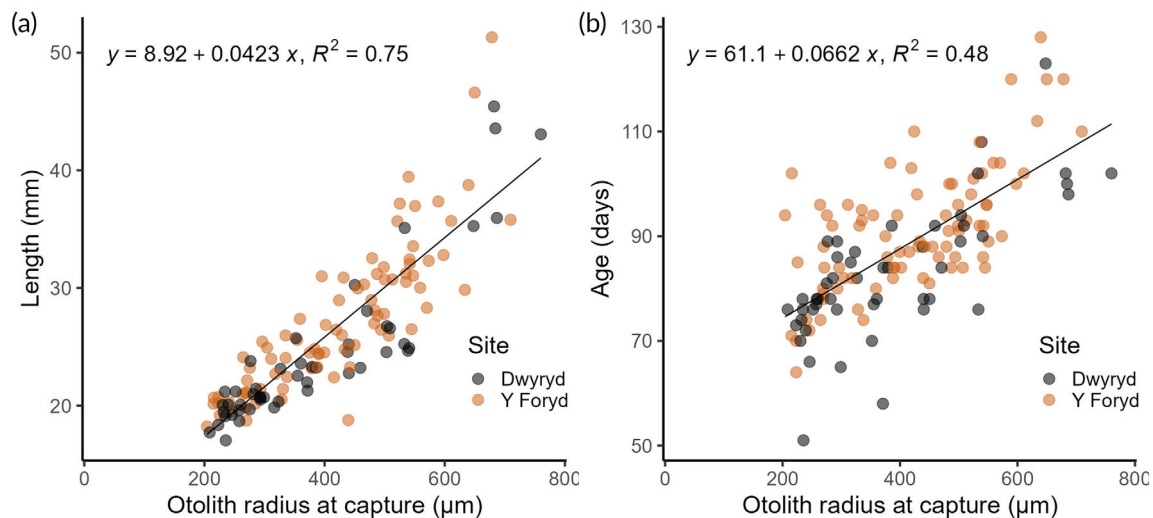
FIGURE 6   Otolith radius relationships between length (a) and age (b) of 0-group sea bass from Dwyryd (black; $n = 49$) and Y Foryd (orange; $n = 83$) estuaries in North Wales in 2021. No differences were found between sites. Regression equation and R^2 value are displayed on each plot.

3.4 | Otolith size, fish size, and age relationships

Sea bass otolith radius exhibited strong positive relationships with fish length ($F_{1,130} = 416.3$, $p < 0.001$) and age ($F_{1,131} = 110.8$, $p < 0.001$) (Figure 6), explaining 48% and 75% of the variation in each metric, respectively. There was no difference in the relationships among sites ($p = 0.3$ and $p = 0.2$, respectively). Settlement size was backcalculated for individuals with a visible check mark, producing reconstructed settlement lengths of 17.1–28.6 mm (mean = 23.5 mm).

4 | DISCUSSION

The results presented herein indicate that UK sea bass are spawning outside of the current fisheries closure period, which is in place to conserve spawning stock biomass. This is of particular importance given the recent population declines and recruitment variability (ICES, 2022). Recruitment phenology suggested that spawning occurred over a 3-month period from April to June; however, there was some suggestion of recruitment pulses within this period. PLD was defined for the first time for UK sea bass using otolith microstructural analysis, providing valuable data to parameterize connectivity forecasting models (Cowen et al., 2007). We also observed significant differences in body condition between juveniles inhabiting two closely located estuaries, suggesting that drivers of juvenile sea bass health can vary over relatively fine geographic scales. This is likely the result of local habitat quality and prey abundance and forms the basis for the nursery role hypothesis (Beck et al., 2001) and habitat mosaic concept (Fulford et al., 2011).

4.1 | Spawning and recruitment phenology

This study provides a detailed account of spawning and recruitment of sea bass *D. labrax* into estuaries at the northern edge of UK nursery

areas (Jennings et al., 1991; reviewed in Hyder et al., 2018; Lincoln et al., 2024). Recent evidence has suggested rapid northerly shifts in sea bass distributions, with individuals caught in the Dutch Wadden Sea (Cardoso et al., 2015) and southeastern Baltic Sea (Bagdonas et al., 2011). In the UK, juvenile sea bass have been observed as far north as the Ribble Estuary (Moore et al., 2020); however, this is not currently considered an established nursery (Hyder et al., 2018). Ongoing monitoring of these higher latitude estuaries will be key to predicting how UK sea bass will respond to future climate change, given that early life stages at range margins are particularly sensitive to environmental perturbations (Pörtner & Peck, 2010).

To examine the implications of a mismatched closure period, sea bass catches during the peak spawning period observed in this study (April–May) were extracted from the Marine Management Organisation (2024). Using monthly catch data from 2014 to 2023, the average weight and value of sea bass landed by UK vessels into UK ports in April and May combined was 98.7 t and £576,000 per year, respectively. This represents 17% of both the total annual catch and value (Marine Management Organisation, 2024). It is also worth noting that the majority of sea bass catches in the UK are from under-10-m fishing vessels that have been going through changes in catch reporting (Ares et al., 2022). Therefore, it may be that the true catch numbers are higher. Targeting of a species during the peak spawning period may result in increased removal of larger and older individuals as they aggregate on spawning grounds (van Overzee & Rijnsdorp, 2015). As larger females tend to have higher fecundity and produce higher-quality gametes (Hixon et al., 2014), fishing these spawning aggregations may have serious implications for population dynamics and recruitment.

Such a prevalence of sea bass recruiting into North Wales nursery habitats from spawning periods outside of the closed season is concerning and is also supported by other studies. Lincoln et al. (2024) also found that the majority of spawning fell outside the current seasonal closure period based on otolith microstructure analysis of juveniles collected from estuaries in the Irish and Celtic seas, whereas

Bradley et al. (2022) showed similar results using gonadosomatic indices of market-sampled adults across years and regions. Preservation of spawners at range margins should be of high priority in the face of climate change, as species encounter different selection pressures at the leading edge of range expansions to those experienced by the core population (Angert et al., 2020; Burton et al., 2010). Pawson et al. (1987) first hypothesized warmer winters would lead to shorter spawning migration distances for the more northerly populations, paired with higher 0-group survival rates. Furthermore, sea bass have displayed philopatry to spawning locations (de Pontual et al., 2019), and future studies should examine whether the spawning population providing the recruits documented in this study is exploiting novel spawning grounds and driving a northward range shift.

Sea bass exhibit a latitudinal gradient in the onset of spawning, with spawning occurring earliest in lower latitudes (Vinagre et al., 2009). This is likely driven by differences in temperature, resulting in delayed gonad maturation in higher latitudes (Lam, 1983; Pickett & Pawson, 1994). As marine environments warm with climate change, this would suggest earlier spawning periods for UK sea bass in the future. If so, for the populations included in this study, the mismatch between the closure period and peak spawning should lessen in the future. However, climate change is also likely to result in increased variability in temperature and weather patterns, which could result in increased volatility in match–mismatch dynamics and recruitment. Future studies should explore the level of mismatch between peak spawning and the closure period across multiple regions and years to better predict the effects of future climate scenarios.

The timing of spawning and recruitment can have large impacts on survival of juvenile fishes (match–mismatch dynamics, sensu Cushing, 1990) and subsequent contribution rates of different nursery grounds to the adult stock. Here, group-0 sea bass were caught over a narrower time window than suggested by previous studies from similar geographic locations. For example, Jennings et al. (1991) sampling the Bristol Channel in 1988 and 1989 caught 0-group sea bass from July 20 to October 3 (cf. from July 8 to September 8 in our study). One explanation for this could be increased net avoidance due to differences in water clarity and the smaller net used in this study. Later settlement timing into northern estuaries may also be driven by longer travel distances from the central spawning aggregations. This could be problematic for pioneering northern populations as density-dependent size-specific winter mortality tends to select most heavily against the smallest individuals (Hurst, 2007), favoring earlier arrivals that have had a longer growing period prior to the onset of winter (Shuter et al., 1980). Multiple recruitment pulses were not observed in this study, but this may have been due to the relatively low sample sizes. Indeed, Dufour et al. (2009) identified several recruitment pulses to nursery habitats along the French Mediterranean coast, whereas other studies suggested a late-autumn secondary settlement pulse in the Portuguese Atlantic coast (Bento et al., 2016; Martinho et al., 2008). Should such pulses also be present in UK waters, this may indicate multiple spawning ground locations (e.g., Lincoln et al., 2024), contradicting more traditionally held assumptions of

limited sea bass spawning areas around the UK (Pawson et al., 1987). Future studies should increase sample sizes and geographic spread to better assess recruitment pulses into UK estuaries, and to use tools such as otolith chemistry to estimate nursery ground contribution rates to the adult stock to better understand spatiotemporal patterns in selection.

4.2 | Pelagic larval duration

This study represents the first use of otolith check marks to calculate the PLD of sea bass into UK nurseries. Such estimates are useful both for predicting recruitment success and population connectivity (Abesamis et al., 2016; Treml et al., 2012). Current predictions of sea bass PLD have been largely informed from Portuguese samples, which were, on average, 14 days shorter than the average found in this study (Pinto et al., 2021). This would be expected given faster development times at higher temperatures, resulting in larvae entering nurseries earlier (Beraud et al., 2018). This hypothesis was supported by the individuals included in the present study, with those born later in the year, when waters were warmer, exhibiting a significantly shorter PLD (Figure 6b). Subsequent studies should explore further methods to validate the use of otolith visual check marks to signify estuarine settlement, such as element signatures signaling a physiological and/or habitat transition (Hussy et al., 2021).

4.3 | Juvenile size, condition, and growth

Length–weight relationships, and variations thereof, have long been effective proxies of juvenile condition (Htun-Han, 1978; Le Cren, 1951) and used to infer habitat quality and potential young fish survival (Amara et al., 2007; Karakiri et al., 1989; Vasconcelos et al., 2009). Here, we found significant differences in juvenile condition between two closely located estuaries, suggesting habitat quality may vary at scales smaller than might be expected or typically managed for. The expectation is that habitats containing optimal temperatures and water quality, limited predators, and high prey availability will support high growth, condition, and survival of juvenile fish, whereas fish growing in areas impacted by stressors and disturbances (e.g., marine heatwaves, pollution) will exhibit low condition and fitness (Besson et al., 2020; Toft et al., 2018). Intertidal saltmarsh habitat has traditionally been hypothesized as ideal sea bass nursery habitat due to high levels of primary and secondary production (Laffaille et al., 2001). Interestingly, however, in this study, juvenile recruits were in better condition in the sandy Dwyryd estuary, despite it being subjected to increased anthropogenic pressures and lacking comparable saltmarshes in the areas sampled.

As expected, there was a strong relationship between otolith size and fish size, which forms the basis of all otolith-based growth reconstructions (Campana & Jones, 1992; Morrongiello & Thresher, 2015). This tightly coupled relationship means that otoliths can be used as a proxy to quantify direct and indirect effects of environmental

TABLE 3 Average somatic growth rates and size ranges of 0-group *Dicentrarchus labrax* by geographic area.

Geographical area	Average growth rate (mm d^{-1})	Size range (mm)	Study
UK, North Wales coast	0.33	17–51	Present study
UK, Bristol Channel	0.2	5–11	Jennings and Pawson (1992)
France, Marseille	0.25	15–120	Guérin-Ancey (1973)
Portugal, West coast	0.54	48–90	Vinagre et al. (2009)
Controlled conditions (10.5°C)	0.24	Unknown	Ré et al. (1986)

conditions at both the individual and species levels (Smoliński et al., 2020). Given that each relationship is species specific, this paper provides first equation for juvenile sea bass, allowing future studies to reconstruct growth and size using increment widths and otolith radius. As expected, the relationship between otolith size and fish age was less strong, resulting from noise introduced by variation in individual growth rates. Using the otolith size–fish size relationship provided in the results, settlement size of all recruits was reconstructed, producing sizes overlapping the smallest fish observed in this study; however, there may be a short lag between settlement and the production of the check mark (most fish <20 mm did not have a visible mark), so future validation work will be carried out to assess this.

Juvenile bass growth rates were remarkably similar in the two estuaries in this study, exhibiting an overall mean rate of 0.33 mm day^{-1}. Bento et al. (2016) found a negative relationship between latitude and growth rates for juvenile sea bass inhabiting Portuguese estuaries and an overall mean growth rate of 0.45 mm d^{-1}. Given that our growth rates were 1.4 times lower than those of the Portuguese populations, the results presented here support the importance of temperature on sea bass growth. However, a wide range of growth rates have been observed, including slower growth rates of 0-group sea bass at similar latitudes (Table 3), suggesting the importance of local factors and interannual variation in temperature. Studies examining growth rates of juvenile sea bass around the UK are scarce, likely owing to the lack of sea bass aquaculture in UK waters and limited juvenile sampling. Maximum observed growth rates were from a hatchery-reared Mediterranean population, which found optimum growth occurred at temperatures of 26°C (Person-Le Ruyet et al., 2004). It could be posited that individuals from Atlantic populations may achieve optimal growth at lower temperatures, and future studies should examine the possibility of regional temperature adaptations.

4.4 | Conclusion

Importantly, this study suggests that current fisheries closures aiming to protect sea bass spawning aggregations may not be effective and may require reassessment. It also suggests that nursery habitat quality can vary across fine spatial scales, and that traditionally held beliefs of drivers of nursery area quality may be incorrect or oversimplified for this species. Overall, given the sensitivity of early life stages to environmental change and their naturally high mortality rates, it is paramount that we better understand the factors driving recruitment and

the subsequent impacts on fisheries productivity. There is growing recognition that sustainable marine fisheries rely on a mosaic of nursery habitats that are often closer to shore and thus more vulnerable to human activities and climate extremes. It is thus critical that we better monitor and predict recruitment dynamics and consider multiple life stages in fisheries management (Le Pape et al., 2020; Sun et al., 2009). In a rapidly changing climate, it would be prudent for fisheries to consider increasingly dynamic management plans that incorporate a suite of parameters relating to habitat quality and environmental conditions to better predict recruitment success and stock size.

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