REGULAR ARTICLE

What makes a habitat a home? Habitat associations of juvenile European sea bass, *Dicentrarchus labrax*, in estuarine nurseries

Howard A. Freeman[1] | Leanne J. Hepburn[1] | Martin I. Taylor[2] | Ewan Hunter[2,3] | Alex J. Dumbrell[1] | Benjamin H. Gregson[1,4] | Albert J. Smith[1] | Aaron Lamphierre[1] | Tom C. Cameron[1]

[1]School of Life Sciences, University of Essex, Colchester, UK

[2]School of Biological Sciences, University of East Anglia, Norwich, UK

[3]Lowestoft Laboratory, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, UK

[4]School of Life Sciences, Faculty of Science and Engineering, Anglia Ruskin University, Cambridge, UK

Correspondence
Howard A. Freeman and Tom C. Cameron, School of Life Sciences, University of Essex, Wivenhoe Park, Colchester, Essex CO4 3SQ, UK.
Email: hf18773@essex.ac.uk and tcameron@essex.ac.uk

Present addresses
Ewan Hunter, Agri-Food and Biosciences Institute, Belfast, Northern Ireland, UK; and Benjamin H. Gregson, School of Life Sciences, Faculty of Science and Engineering, Anglia Ruskin University, Cambridge, UK.

Funding information
Natural Environment Research Council, Grant/Award Number: NE/L002582/1; Cefas Seedcorn, Grant/Award Number: DP901P

Abstract

Selection of nursery habitats by marine fish, such as European sea bass (*Dicentrarchus labrax*), is poorly understood. Identifying and protecting the full range of juvenile nursery habitats is vital to supporting resilient fish populations and economically important fisheries. We examined how the condition, stomach fullness, and diet of juvenile European sea bass, along with their abundance, differ at high or low tide between the following estuarine habitats: saltmarsh, oyster reefs, shingle, sand, and mud edge habitats. Using a combination of fyke and seine netting we found no difference in sea bass abundance or condition across high-tide habitats, suggesting that rather than differentially selecting between them, juvenile sea bass use all available shallow habitats at high tide. Stomach fullness was significantly higher on saltmarsh and sand compared to mud, and thus these habitats may support better foraging. Dietary DNA metabarcoding revealed that sand and saltmarsh diets mostly comprised *Hediste* polychaetes, whereas zooplanktonic taxa dominated diets over mud. At low tide, sea bass abundance was highest in shingle and oyster reefs, where stomach fullness and condition were lowest. This may indicate a potential trade-off between using habitats for foraging and refuge. Although sea bass abundance alone does not capture productivity, the high abundance across all estuarine habitats at high tide suggests that it is important to consider the protection of a mosaic of interconnected habitats to support nursery functions rather than focus on individual habitat types.

KEYWORDS
diet, estuaries, metabarcoding, nursery, saltmarsh, sea bass

1 | INTRODUCTION

Many fish exhibit complex life histories involving a pelagic egg and larval stage, which settle in shallow coastal habitats, such as estuaries and wetlands, and remain as juveniles throughout their development (Cattrijsse et al., 1994; Couillard et al., 2022; Garcia et al., 2018; Green et al., 2009, 2012; Jennings & Pawson, 1992; Kelley, 1986; Kelley, 1988; Nash & Geffen, 2000; Pickett & Pawson, 1994; Pihl et al., 2005; Seitz et al., 2014; Vollrath et al., 2021; Wright et al., 2010). During this sedentary juvenile stage, food availability and

refuge from predation can influence the survival of juveniles in nursery habitats to adulthood and therefore influence recruitment dynamics of the population (Parsons et al., 2015; Tableau et al., 2016). Therefore, it is thought that increasing the area of nursery habitats available could increase, and influence interannual variation in recruitment in fish populations by providing habitat that supports growth and survival of juveniles (Beck et al., 2001; Schloesser & Fabrizio, 2019). However, we have a poor understanding of which habitats play key nursery roles (Litvin et al., 2018).

Historically, identification of nursery habitats was based on the abundance of juvenile fish present. However, Beck et al. (2001) suggested that those habitats that disproportionally contribute to the recruitment of juvenile fish per unit area, compared to other habitats where juveniles are found, provide a nursery function—the nursery role hypothesis. This can be expanded to consider the seascape of interconnected habitats that contribute to nursery functions (Sheaves et al., 2006). For many coastal systems, anthropogenic disturbance through farming, maritime activities, and wastewater treatment has resulted in habitat loss and fragmentation of these seascapes (Amorim et al., 2017; Aranda et al., 2022; Doody, 2008; Douglas et al., 2022; Eggleston et al., 1999; Montefalcone et al., 2010; Stamp et al., 2022; Swadling et al., 2023; Xue et al., 2016). Therefore, a vital management goal is to identify, maintain, and restore habitats that support large numbers of juvenile fish and contribute to their growth and survival through adulthood. This is particularly important in environments under immense anthropogenic pressure, such as coastal wetlands.

A focus on saltmarshes alone presents a barrier to the identification of key habitats providing nursery roles across seascapes in the United Kingdom, particularly regarding species such as European sea bass (Brady et al., 2020; Cabral & Costa, 2001; Cariou et al., 2021; Day et al., 2021; Dufour et al., 2009; Green et al., 2009, 2012; Huusko et al., 2007; Lilley & Unsworth, 2014; Selleslagh et al., 2012; Warren et al., 2010). Whereas these are highly productive systems that support juvenile fishes and their prey (Halpin, 2000; Stolen et al., 2009; Whitfield, 2017), and have experienced immense losses due to anthropogenic pressures (Amorim et al., 2017; Cooper et al., 2001; Doody, 2008; Harmsworth & Long, 1986), estuarine systems are a complex mosaic of structurally diverse habitats such as mud and sand bays, shingle beds, oyster reefs, and seagrass meadows, all of which could equally be fish nurseries. In many cases, beyond saltmarshes, habitats such as seagrasses (Heck et al., 1989; Sogard & Able, 1991; Coles et al., 1993; Connolly, 1994; Gray et al., 1996; Lazzari et al., 2003; Leslie et al., 2017; Rozas & Minello, 1998; Shoji et al., 2007) are compared against a single control habitat, whereas the seascape of other habitat types in these coastal systems is not explored. With little consideration for the value of these different but connected habitat types, there is a danger that the role of multiple habitats in contributing to recruitment success of juvenile fishes is being missed.

Juvenile European sea bass (*Dicentrarchus labrax*, Moronidae) utilize estuarine nurseries throughout their range. Sea bass are a commercially important species in the United Kingdom, though stocks have been declining as a result of increased fishing pressure and high variation in interannual recruitment (ICES, 2015). An improved understanding of what constitutes a quality nursery habitat for juvenile sea bass could inform deliverable actions to support increased recruitment and contribute to an ecosystem-based approach to their sustainable fisheries management. Previous research on sea bass nurseries has focused almost only on saltmarshes and summer habitats (Cabral & Costa, 2001; Cattrijsse et al., 1994; Cattrijsse & Hampel, 2006; Dufour et al., 2009; Green et al., 2009, 2012; Jennings & Pawson, 1992; Jin et al., 2007; Kelley, 1986, 1988; Laffaille et al., 2000, 2001; Pickett & Pawson, 1994). A substantial body of evidence suggests that sea bass in UK estuaries are highly abundant in saltmarshes throughout the summer months, across much of the United Kingdom, where they forage on macroinvertebrates and zooplankton (Green et al., 2009, 2012; Kelley, 1986, 1988; Laffaille et al., 2000; Jennings & Pawson, 1992; Pickett & Pawson, 1994), whereas in the Mediterranean they appear to be present in shallow coastal lagoons (Cabral & Costa, 2001; Dufour et al., 2009). However, the factors that determine habitat choice or differential growth and survival between potential nursery habitats are poorly understood. For example, it is unclear whether foraging potential, prey acquisition, refuge, or predation risk best predicts the nursery role of an estuarine habitat. Foraging potential and predation risk are thought to be influenced by habitat characteristics such as structural complexity, which is thought to reduce prey visibility (Baker & Sheaves, 2021; Canion & Heck Jr, 2009; Cheminée et al., 2016; Diehl & Eklov, 1995; Fullerton & Lamberti, 2006; Leslie et al., 2017; MacRae & Jackson, 2001; Sheaves et al., 2015; Tatrai & Herzig, 1995; Thiriet et al., 2014) and increase the abundance of macroinvertebrate prey taxa (Attrill et al., 2000; Hu et al., 2016; Wolters et al., 2018). Depth may also play a role in relative predation risk as shallow water is less accessible to larger piscivorous predatory fish (Harvey, 1991; Paterson & Whitfield, 2000; McIvor & Odum, 1988; Whitfield, 2017, 2020).

Direct measurements of contribution rates from different habitats to adult populations are challenging, if not impossible, in highly mobile species such as sea bass. However, we can assess factors that influence contribution, such as survival and habitat quality. This can be achieved by measuring multiple proxies, including juvenile fish abundance, growth rates, and conditional indices, as well as foraging potential and dietary differences. Although it is arguable that the use of high-quality habitat may support the survival of juvenile fish, it must be noted that survival is unlikely to be determined within the first 2 years of life alone, and multiple other processes may underpin the contribution of fish to adult populations.

This study provides a better understanding of which habitats support post-settlement habitat usage of 0-group (YoY) sea bass by examining how the distribution, age structure, condition, stomach fullness, and diet of juveniles vary across estuarine habitats. In particular, we (1) determine patterns of juvenile sea bass abundance across different estuarine habitats, (2) assess the condition of these sea bass and investigate whether their condition provides evidence of differences in habitat quality, (3) use measures of stomach fullness to determine whether differences in foraging activity are present in fish
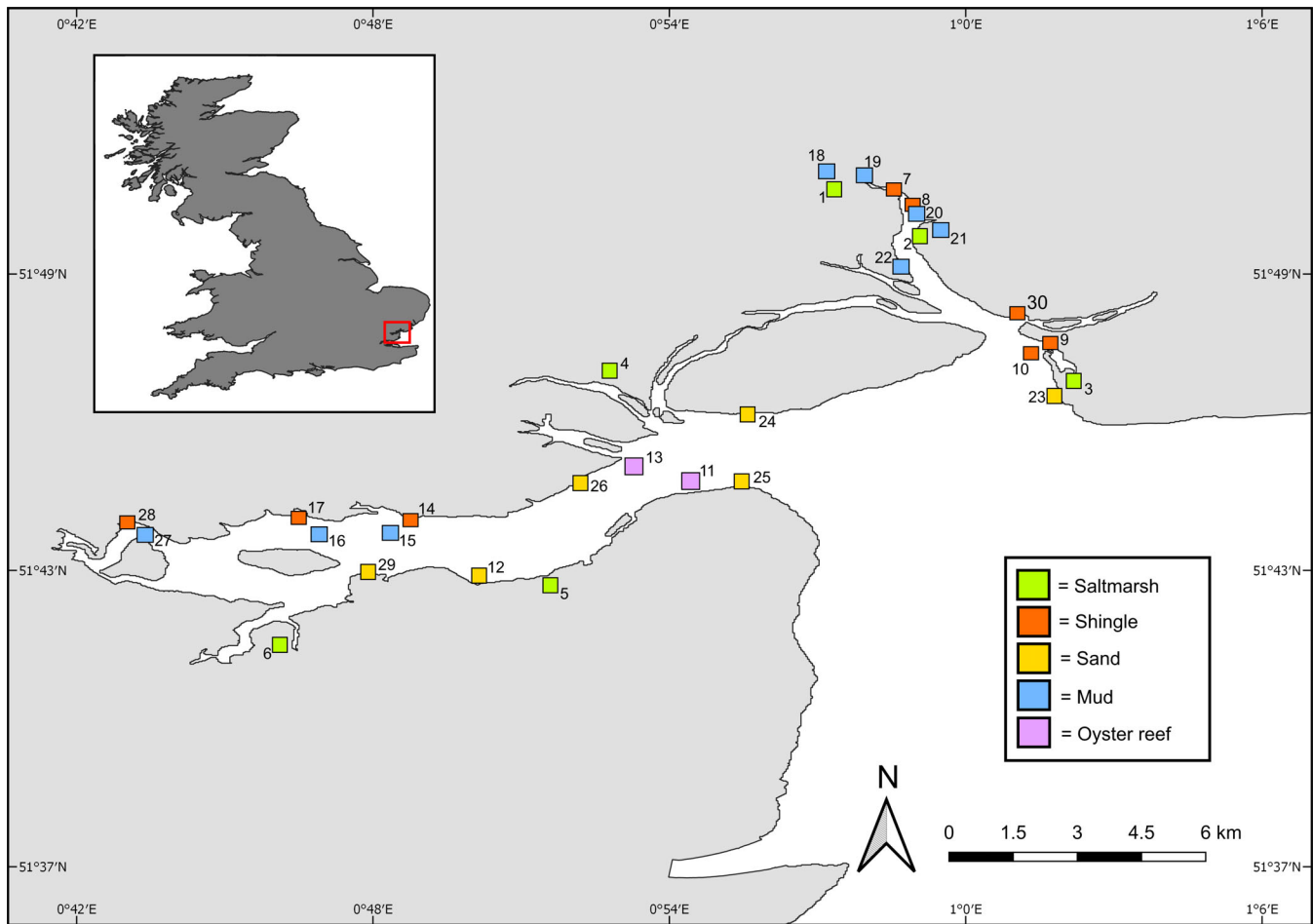
FIGURE 1 Map of sampling sites in the Colne and Blackwater estuaries (highlighted within red box), Essex, United Kingdom, between July and September 2020. Total sites = 30. Made using QGIS, version 3.2.3.

between 0-group and 1-group and discuss the implications for drivers of juvenile habitat usage, and (4) use dietary DNA metabarcoding to catalog the relative contributions of different prey to juvenile sea bass diets across habitats. Advances in dietary DNA metabarcoding allow parallel identification of multiple taxa simultaneously, including soft-bodied and rare prey taxa with little genetic material, which does not require taxonomic expertise (Jakubavičiūtė et al., 2017; Pompanon et al., 2012).

2 | MATERIALS AND METHODS

2.1 | Sampling site

The present study focused specifically on the Colne (51.800518, 1.012061) and Blackwater estuaries (51.757927, 0.932978), located on the Essex coastline, United Kingdom. The Colne and Blackwater form a single confluence where they meet at the sea (Figure 1) and are important for commercial inshore fish and shellfish industries, but also recreational fishing use. These estuaries were selected based on their accessibility and representation of different estuarine

habitats in an area situated toward the northern-range margin of *D. labrax*.

Both estuaries are relatively shallow systems (Blackwater maximum depth: 15.4 m, Colne maximum depth: 12.4 m at low tide), and both experience substantial tidal shifts in habitat availability, where the intertidal habitat and estuary creeks are exposed at low tide and fully drained on the lowest tides. Tidal flows also present changes in temperature and salinity, with a stronger salinity gradient found in the Blackwater estuary compared to the Colne.

A total of 30 sites were sampled across both estuaries between July and September 2020 (Figure 1), when juvenile sea bass numbers reach their peak (Green et al., 2009). Sampled sites were chosen based on tide, habitat type, and estuary position. Tide was included such that it could be inferred whether habitats that are important at high tide remain so at low tide, acknowledging that far less habitat by area and accessibility is available at low tide. Sites were sampled once within the summer sampling window, apart from sites 5 and 7 that required second visits to sample fully.

Five habitat types were surveyed in this study, saltmarshes, oyster reefs, intertidal beaches and subtidal bays composed of shingle, sand, or mud, which were well represented across the two estuaries

and sampled. Habitats were classified and selected based on a priori criteria, based primarily on substrate type (Table 1). For each habitat, sites were selected from three horizontal locations within the estuary, determined to be at the lower, middle, or upper estuary. A minimum of three sites per habitat in each estuary were sampled, except for oyster reefs, which could be accessed safely only in the Blackwater estuary at two sites (Table 1).

2.2 | Ethics statement

The care and use of fish in all aspects of this study, including capture and dispatch, complied with dispensations from the Kent and Essex Inshore Fisheries Conservation Authority (IFCA) to retain and dispatch juvenile sea bass (20200713AP) and under the Schedule 1 exemption for lethal sampling by authorized persons (ASPA 1986). All work was carried out with permission from the Kent and Essex IFCA, and the Marine Management Organisation.

2.3 | Sampling methodology

A combination of beach seine and barrier fyke netting was used to measure abundance of juvenile sea bass present in each habitat at high and low tides. Beach seines were used in relatively open habitat types, oyster reefs and bays composed of sand, mud, and shingle, whereas barrier fyke nets similar to those employed by Cattrijsse et al. (1994) and Green et al. (2009) were used on saltmarsh systems. Barrier fyke nets allow an entire creek to be barricaded and so sample a large, fixed area of habitat that can be quantified, with little scope for escapes. They were deployed at the mouth of creeks at high tide and removed when the tide had drained sufficiently. Three creeks were sampled per saltmarsh. Beach seines were used during high and low tides with either a 25 × 1.5 or a 30 × 3-m seine net, with a 9-mm mesh-size. Three beach seines were used per site, except for two sites where the yield was either extremely high, and therefore sampling was stopped on welfare grounds, or zero where sampling continued to confirm a zero value. The upstream area captured by fykes and the area captured by the arc of seine nets were used to standardize catches to catch per unit of effort (CPUE).

Netted fish were immediately identified, counted, and placed in an oxygenated recovery tank or, where appropriate, immediately returned to the sea. Length and weight were measured for all fish, except very large catches, where we measured a subsample of 20 fish per net and estimated the rest as they were returned to the sea. A maximum of 20 juvenile sea bass were dispatched per net and retained for future assessment of stomach contents, in accordance with permissions (see Section 2.2). Fulton's condition index (K) was calculated based on the following equation (Bacon et al., 2009; Cammilleri et al., 2018; Kerambrun et al., 2011, 2012; Springer & Murphy, 1990; Sutton et al., 2000):

$$K = \frac{W_f}{L_f^3} \times 100 \qquad (1)$$

where W is the mass of fish f (mg) and L is the length of fish f (mm). In the majority of cases, weight was measured from live individuals before release, such that we were unable to remove and account for gut contents.

The age group a fish belonged to was based on its length and compared to a priori thresholds determined from well-established length at age curves (Pickett & Pawson, 1994). Fish were assigned to 0-group (YoY: 0–79 mm), 1-group (first winter: 80–149 mm), or 2-group (second winter: 150–180 mm). This was cross-validated using length–frequency distributions plotted for the fish caught in this study. The resulting curve suggested that fish up to 95 mm could be considered 0-group fish. Models of CPUE and condition were performed for both length at age designations, and no differences in model outputs were found. Therefore, length at age designations from Pickett and Pawson (1994) were used, as these incorporated scale ageing.

To measure stomach fullness, gut contents were evacuated and weighed (to the nearest 0.01 g) from retained fish, and the stomach fullness index (SFI) was calculated using the following equation (Magnussen, 2011):

$$SFI = \frac{Wst_f}{L_f^3} \times 100 \qquad (2)$$

where Wst is the mass of stomach contents for fish f (mg) and L is the length of fish f (mm).

2.4 | Dietary analysis

2.4.1 | DNA extraction

Where possible, a maximum of six fish per age group were selected from each site with captured sea bass ($n = 18$ per habitat per tide) and used for analysis of stomach fullness and gut content using DNA metabarcoding. The skin of the fish to be dissected was cleaned using a 70% ethanol solution to remove estuarine contaminants on the fish's surface. Stomach digesta and lining were then squeezed out and transferred to a sterile 2-mL cryogenic vial, which were stored at −20°C for further analysis. Stomach samples were weighed separately to confirm enough material had been collected for DNA extractions. Dietary DNA extractions were performed using the DNEasy Blood and Tissue Kit (Qiagen) following the manufacturer's instructions. DNA extracts were then used for DNA metabarcoding.

2.4.2 | Polymerase chain reaction and high-throughput sequencing

Extracted DNA from stomach contents was polymerase chain reaction (PCR) amplified using the Leray–Geller primer set, which targets a 313-bp region of the cytochrome c oxidase subunit I (herein referred to as COI) gene (Geller et al., 2013; Leray et al., 2013). COI is highly conserved between most metazoans and eukaryotes, yet variation is

TABLE 1 Descriptions of habitat types by tide and site, with summaries of data collected.

Habitat type	Tide	Sites	Dates	Latitude/longitude	Total sites	Description	Gear type	Number of bass	Size range (mm)	Age range
Saltmarsh	High	1	July 29, 2020	51.85174, 0.95558	6	Low lying, vegetated, network of intertidal creeks, mud sediment, high tide. JNCC LS.LMp.Sm	Fyke	37	24–44	0
		2	August 5, 2020 September 24, 2020	51.83491, 0.98748				583	23–200	0–2+
		3	September 8, 2020	51.78067, 1.04411				155	23–83	0–1
		4	August 31, 2020	51.78561, 0.87273				54	33–62	0
		5	September 7, 2020	51.71485, 0.85398				321	10–87	0–1
		6	September 1, 2020 September 30, 2020	51.69706, 0.77072				178	37–119	0–1
Shingle	High	8	August 20, 2020	51.84306, 0.98127	6	Mud/clay sediment, large cobbles embedded into substrate, often macrophytes attached, high and low tides. JNCC LS. LCS	30 m seine	63	30–173	0–2+
		9	July 16, 2020	51.79444, 1.03149				38	28–155	0–2+
		14	September 4, 2020	51.73881, 0.83816				5	46–64	0
		17	September 16, 2020	51.73904, 0.77446				35	34–89	0–1
		28	September 17, 2020	51.73404, 0.72636				45	27–89	0–1
		30	August 24, 2020	51.80638, 1.02111				81	32–140	0–1
	Low	7	July 27, 2020	51.84800, 0.97890	4		25-m seine	23	23–45	0
		10	July 16, 2020	51.79485, 1.02893				17	105–153	1–2+
		15	September 15, 2020	51.73832, 0.84893				54	48–87	0–1
		16	September 11, 2020	51.73678, 0.77692				437	43–174	0–2+
Sand	High	12	September 21, 2020	51.71559, 0.83215	4	Mud/clay sediment, large cobbles embedded into substrate, often macrophytes attached, high and low tides. JNCC LS.LSa	30 m Seine	352	30–101	0–1
		24	September 29, 2020	51.77419, 0.94001				66	41–82	0–1
		26	August 18, 2020	51.75213, 0.87350				0	–	–
		29	August 28, 2020	51.704300, 0.7734				2	35–42	0
	Low	25	August 11, 2020	51.74872, 0.92057	1		25-m seine	16	21–57	0
Mud	High	18	July 31, 2020	51.85201, 0.95387	3	Soft mud sediment, flat, structurally simple high and low tides. JNCC LS.LMu	30 m seine	11	23–55	0
		22	August 3, 2020	51.82582, 0.97573				4	28–41	0
		27		51.73428, 0.72329				44	27–89	0–1

(Continues)

TABLE 1 (Continued)

Habitat type	Tide	Sites	Dates	Latitude/longitude	Total sites	Description	Gear type	Number of bass	Size range (mm)	Age range
			September 17, 2020							
	Low	19	July 15, 2020	51.85420, 0.95808	4			3	23–55	0
		20	July 14, 2020	51.84063, 0.98457				0	–	–
		21	July 17, 2020	51.83848, 0.98781				1	–	–
		23	July 31, 2020	51.78367, 1.03039				5	117–161	1–2+
Oyster reef	Low	11	September 10, 2020	51.74606, 0.89334	2	Live and dead oyster shell matrix embedded in mud sediment, high rugosity, low tide. JNCC SS.SBR	30 m Seine	27	37–77	0
		13	September 10, 2020	51.75528, 0.88403				66	49–91	0–1

sufficient for identification to genus level. Leray–Geller primers were selected as it has been shown that they capture a wide variety of invertebrate species, including many of the expected prey species that have previously been found in the stomachs of *D. labrax* (Green et al., 2009; Leray et al., 2013).

DNA extracts were diluted 1:10 in Milli-Q water to reduce PCR inhibition. PCR amplification occurred in 25-μL reactions consisting of 2.5 μL of diluted DNA, 12.5 μL of Taq, 9 μL of H_2O, and 0.5 μL of both forward (mICOIintF 5′-GGWACWRGWTGRACWITITA YCCYCC-3′; Leray et al., 2013) and reverse (jgHCO2198 5′-TAIACYTCIGGRTGICCRAARAAYCA-3′; Geller et al., 2013) primers (10 μM). Primers were modified to contain Illumina-specific overhang adapters. Reverse primers also contained a 12-base Golay barcode to distinguish samples during multiplexing. Thermal cycling for COI amplification consisted of an initial annealing stage of 95°C for 3 min; 16 cycles of 95°C for 10 s, a touchdown of 62–58°C for 30 s, and 72°C for 1 min; and a final 25 cycles of 95°C for 10 s, 46°C for 30 s, and 72°C for 1 min, with a final extension step held at 72°C for 7 min.

Following the first PCR, samples were purified using Ampure XP beads (Beckman Coulter) following the manufacturer's instructions. After purification, a short secondary PCR reaction was performed to attach Nextera XT indices, which consisted of 2.5 μL of purified PCR product, 2.5 μL of Nextera i5 and i7 index, 12.5 μL of Taq, and 5 μL of H_2O. Thermal cycling conditions consisted of an initial denaturation step of 3 min at 95°C followed by eight cycles each of 30 s at 95°C, 30 s at 55°C, and 30 s at 72°C. PCR products were purified again using the Ampure XP beads, and DNA was quantified using PicoGreen double-stranded DNA quantification assays (Thermo Fisher Scientific) on a POLAR star Omega (BMG Labtech) plate reader, as per the manufacturer's instructions. Indexed amplicons were then pooled in equimolar concentration. The Illumina-overhang-adapted DNA concentration was determined using the NEBNext Library Quant Kit for

Illumina (New England BioLabs). DNA libraries were sequenced on an Illumina NovaSeq 6000 with 2 × 250-bp paired-end chemistry at the Earlham Institute (Norwich, UK).

2.4.3 | Sequencing and bioinformatics

Sequence reads were processed following Dumbrell et al. (2016) and Gregson et al. (2022). Quality filtering was carried out using Sickle (Joshi & Fass, 2011). Sequence reads were trimmed when the average Q score, a measure of read accuracy, dropped below Q20 across a moving 35-bp window. Error correction was carried out in SPAdes (Bankevich et al., 2012), which uses the BayesHammer algorithm to correct for misidentified bases during sequencing (Nikolenko et al., 2013). Paired-end reads were merged into single contigs using the PEAR algorithm (Zhang et al., 2014) implemented via PANDAseq (Masella et al., 2012). Further quality filtering was carried out in the open-source bioinformatics package MOTHUR (Schloss et al., 2009) to remove homopolymer inserts longer than 12.

Sequences were dereplicated using VSEARCH, which removes singleton sequences, sorts by abundance, and clusters sequences around an operational taxonomic unit (OTU) centroid at a 97% similarity threshold (Rognes et al., 2016). Taxonomy was assigned OTU centroids using the "classify-consensus-vsearch" method of the q2-feature classifier in QIIME2 (Bolyen et al., 2019) against COI databases generated from NCBI using RESCRIPt (Robeson et al., 2021). OTU tables were decontaminated using the "microDecon" package (McKnight et al., 2019) in R (version 4.2.2, R Core Team, 2022), which removes a representative number of reads from contaminant species OTUs present in negative controls. OTU counts were normalized using the cumulative sum scaling method in the "metagenomeSeq" package (Paulson et al., 2013) to account for differences in

sequencing depth between samples. The "phyloseq" package (McMurdie & Holmes, 2013) was used to transform counts into relative abundances and analyse the taxonomic composition of diets.

2.5 | Statistical analysis

All statistical analyses were carried out in "R," version 4.2.2 (R Core Team, 2022). Figures were produced using "ggplot2" package (Wickham & Wickham, 2016). To determine whether abundance, condition of 0-group sea bass, and stomach fullness of 0-1 group sea bass differed across estuarine habitats at high and low tides, we used mixed effects models using the "glmmTMB" package (Brooks et al., 2017). 0-Group fish alone were used for analysis of abundance and condition, as very few fish of 1-2+ groups were caught to be representative of those age classes. Repeated measurements of sites provided by multiple fyke nets and seines performed within the same site were treated as random effects. Models for condition and stomach fullness used a nested random effect structure, considering both repeat measures of sites and individual fish taken from each seine or fyke. Heteroscedasticity produced by differences in the number of replications of each habitat was accounted for by using habitat replication as a dispersion parameter.

Disentangling whether differences in distribution patterns between high and low tides result from fish habitat selection or hydrological forces is challenging. On ebbing tides, large amounts of water leave the estuary and drastically reduce the amount of available shallow habitat to utilize, reducing the scope for habitat selection compared to high tide. Furthermore, the swimming ability of 0-group sea bass may not be sufficient to overcome strong tidal currents, which again may reduce the ability of fish to select habitats. Therefore, it is difficult to determine whether low-tide distributions are the result of fish selectively moving into habitats or if they are the result of hydrological deposition, such that it may not be appropriate to compare CPUE across habitats and between tides. Therefore, separate models were constructed for low and high tides. Pair-wise comparisons were performed using Tukey's post hoc test using the "lsmeans" package (Russell & Lenth, 2016).

To examine the differences in the diet composition of 0-1 group sea bass diets across habitats, redundancy analysis (RDA) was performed using the "phyloseq" package (McMurdie & Holmes, 2013). 0-1 Group sea bass were included in the diet analyses to investigate the full breadth of diets exhibited by juvenile sea bass. Size and age group were not included as variables in dietary analysis as the dietary constituents of sea bass are relatively well conserved within the first years of life. Green et al. (2009) and Laffaille et al. (2001) found both zooplanktonic species such as copepods and amphipods, as well as benthic invertebrates such as decapods and polychaetes, in the diets of both 0-group and 1-group sea bass. The RDA performed multiple regressions of the effect of habitat and tide on the community composition of the fish diets between sites. The resultant fitted distance matrix was then used to construct an ordination biplot. A permutation test based on 1000 random permutations was then performed to

understand whether a significant relationship exists between the response variables (community composition) and the environmental variables (habitat and tide). p-Values were determined based on the proportion of similarity between the permuted values and the "true" values (Borcard et al., 2011).

Due to the relatively small sample size, to determine the effects of habitat on the percentage contribution of prey species to sea bass gut contents, based on visual identification, individual Kruskal–Wallis tests were used for each species identified, over low and high tides separately. Tide was not considered when assessing differences in relative abundances between habitats, as the RDA revealed large amounts of overlap within diets between tides.

3 | RESULTS

3.1 | Catch per unit of effort

0-Group sea bass were found at 26 of the 30 sites at either low or high tide. At high tide, no significant difference in 0-group sea bass CPUE was found across habitats ($\chi^2_{(3,16)} = 2.00$, $p < 0.05$). Mean CPUE across habitats was similar, but the largest individual CPUE values were found on sand, at site 12, and on saltmarshes (Figure 2). Site 12 exhibited a 587% increase in CPUE compared to the mean for sand habitats, and 400% compared to the highest CPUE for saltmarshes and shingle.

At low tide differences in 0-group sea bass CPUE across habitats were found to be significant ($\chi^2_{(3,10)} = 12.14$, $p < 0.01$). Significantly more fish were found in oyster reefs ($p = 0.04$) and shingle ($p = 0.04$) compared to sand. It is also worth noting that although no significant difference was found when oyster reefs and shingle were compared to mud, considerable increases in mean CPUE were observed. Shingle exhibited the largest mean CPUE, increasing by 597% compared to the mean CPUE of mud, whereas oyster reefs exhibited a 214% increase compared to the mean CPUE of mud. For information on mean CPUE of other species caught across high- and low-tide habitats, see Table A1.

Size distributions of 0-2+ group sea bass were relatively similar across all habitats at both low and high tides, with the highest frequency appearing about 50–60 mm (Figure 3). However, at high tide, the largest individuals were found in saltmarshes, shingle, and sand, whereas at low tide they were found on mud, oyster reefs, and shingle. Saltmarsh, shingle, and mud also exhibit the largest range of sizes.

3.2 | Condition

No significant difference in 0-group sea bass condition was found across habitats at high tide ($\chi^2_{(3,16)} = 4.93$, $p = 0.176$) (Figure 4). The mean fish condition was very similar across all habitat types, though the highest-condition indices were found in saltmarsh and sand. However, at low tide, condition differed significantly across habitats ($\chi^2_{(3,10)} = 27.34$, $p < 0.01$) and was significantly lower on oyster reefs
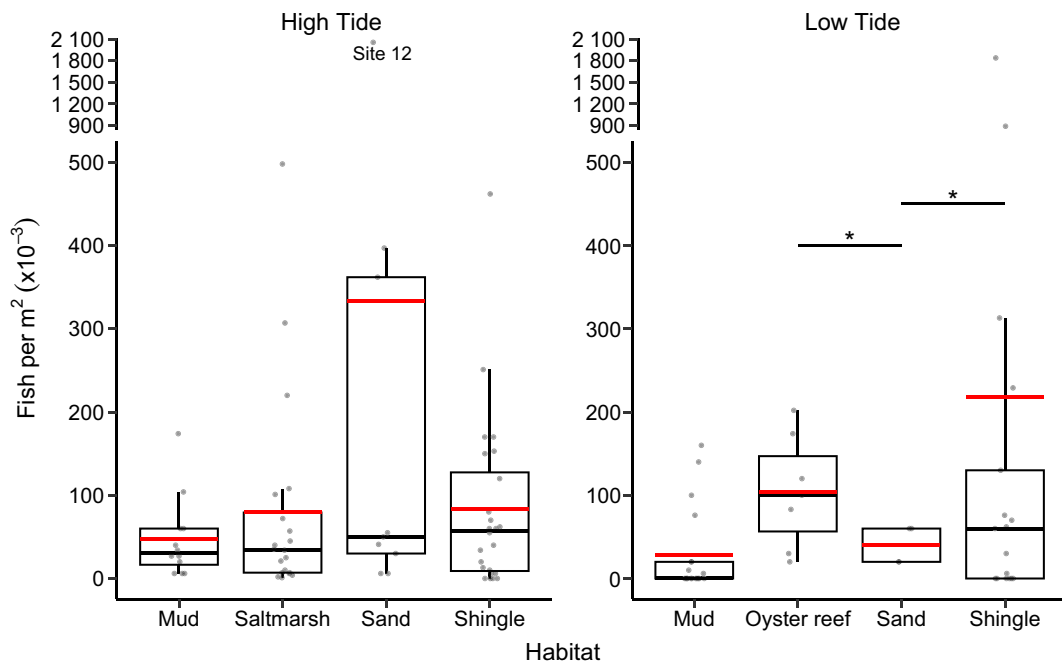
FIGURE 2 Box plots for the average catch per unit of effort (CPUE) of 0-group *Dicentrarchus labrax*, across estuarine habitats at high (left) and low (right) tides. Habitats are mud, saltmarsh, sand, shingle, and oyster reefs. CPUE is expressed as the number of fish per $m^2 \times 10^{-3}$. Points represent individual data points for each site. Whiskers represent maximum data points within 1.5× the interquartile range. Red line indicates the mean, and black line represents the median. Significant differences: $***p < 0.01$ and $*p < 0.05$.
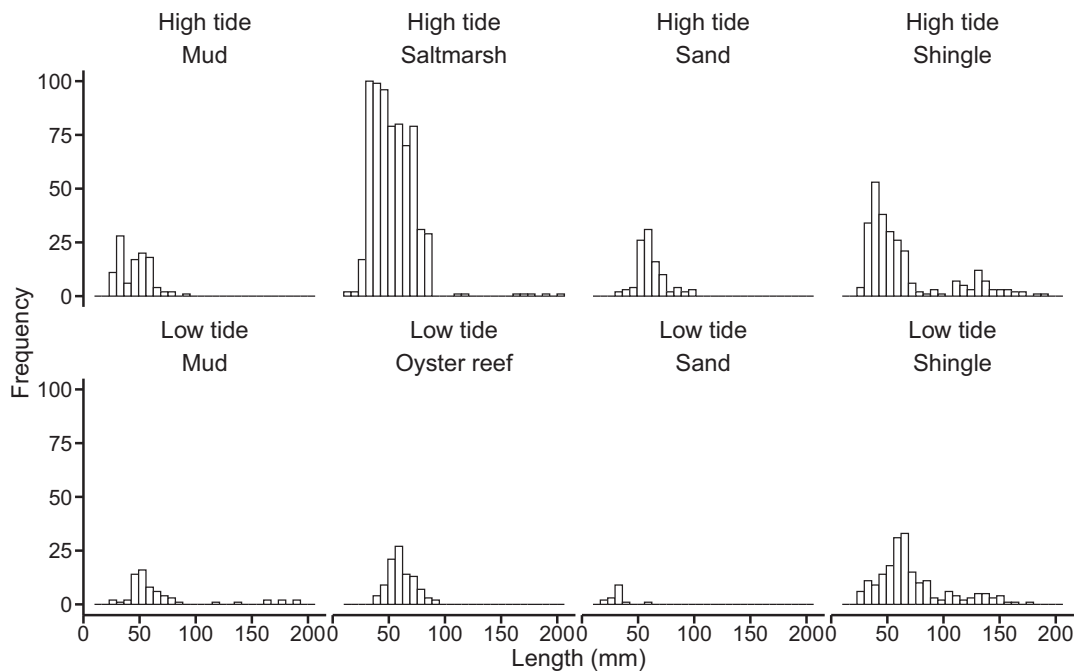

FIGURE 3 Size frequency distributions of 0-2+ group *Dicentrarchus labrax* length (mm), across estuarine habitats at high (top) and low (bottom) tides. Habitats are mud, saltmarsh, sand, shingle, and oyster reefs.

($p = 0.04$) compared with mud, and on shingle compared with sand or mud ($p = 0.01$), where sea bass abundance was highest. Condition on shingle was also significantly lower than that on sand ($p = 0.02$).

Mean condition increased by 22% on mud compared to that of oyster reefs and 25% compared to that of shingle. Similarly, sand exhibited an increase of 27% in mean condition from the mean condition of
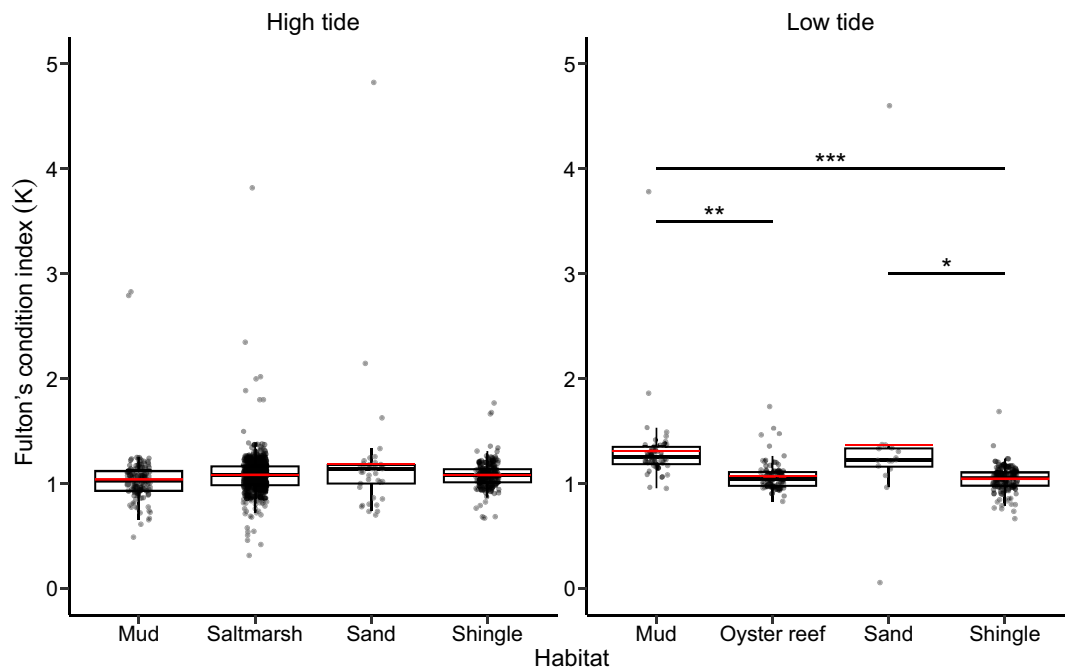
FIGURE 4 Box plots for the average Fulton's condition index (K) of 0-group *Dicentrarchus labrax*, across estuarine habitats at high (left) and low (right) tides. Habitats are mud, saltmarsh, sand, shingle, and oyster reefs. Condition index is the product of weight (mg)/length^3 (mm) $\times$ 100. Points represent individual data points for each fish. Whiskers represent maximum data points within 1.5$\times$ the interquartile range. Red line indicates the mean, and black line represents the median. Significant differences: ***$p < 0.01$ and *$p < 0.05$.

oyster reefs and 30% from that of shingle. No significant difference was found between mud and sand, or sand and oyster reefs, which exhibited similar mean conditions.

3.3 | Stomach fullness

At high tide differences in stomach fullness of 0-1 group sea bass between habitats were found to be significant ($\chi^2_{(3,14)} = 14.06$, $p < 0.01$). Fish exhibited significantly lower SFI in muddy habitats compared with saltmarshes ($p = 0.01$) and sandy habitats ($p < 0.01$). Mean SFI was highest on saltmarsh and sand compared with mud but was comparable to shingle (Figure 5). The largest individual SFI values were also found on saltmarsh systems and shingle. Mud exhibited the largest variability in SFI, and the smallest SFIs were found here. There are also significant differences in SFI between low-tide habitats ($\chi^2_{(3,11)} = 52.36$, $p < 0.01$). For example, SFI was significantly larger on sand compared to mud ($p = 0.01$), oyster reef ($p < 0.01$), and shingle ($p < 0.01$) but generally similar between shingle, oyster reef, and mud. Shingle showed the largest amount of variability and the lowest SFIs.

3.4 | Stomach content

The relative abundance of the most dominant eukaryotic genera present in the stomach contents of juvenile 0-1 group sea bass changed across habitats (Figure 6). For mud-dominated habitats ($n = 39$), diets

were primarily composed of copepods of the genus *Acartia*, mysids of the genus *Mesopodopsis* and *Neomysis* (46.2%), *Carcinus* decapods (15.0%), and *Hediste* polychaetes (7.1%). On oyster reefs ($n = 16$), diets consisted of *Ampelisca* amphipods (32.9%), *Carcinus* decapods (17.2%), *Hippolyte* shrimps, and *Dexamine* (27.1%). Diets over saltmarsh (44) consisted of *Hediste* polychaetes, which contributed the largest proportion of the diet at 59.4%, which was far larger than any other habitat, as well as *Carcinus* decapods (17.9%), *Idotea* (4.9%), and *Nephtys* polychaetes (3.7%). Similarly, diets of fish using sand habitats (35) consisted of *Hediste* (33.8%), *Carcinus* (15.6%), and *Nephtys* (10.4%). On shingle ($n = 95$), diets consisted of *Carcinus* decapods, which accounted for the largest relative abundance of 51.2%, as well as *Hediste* (3.4%), *Idotea* (2.6%), and *Neomysis* (3.6%). A relatively large representation of *Solea* (10.9%) was also found here, which was the only fish genera identified in the gut contents. It is also noteworthy that insects of the family *Dolichopodidae* (13.8%) and *Nymphalidae* (5%) were found in the stomachs of fish on mud bays and shingle bays, respectively. However, neither family could be identified to genus level and so were not considered in the relative abundance estimates.

RDA showed that there was considerable overlap in the diets of 0-1 group sea bass across habitat types and tide (Figure 7). The model significantly explained 2.31% ($F_{(6,222)} = 1.09$, $p < 0.01$) of the variation in diet composition. Diet composition was significantly correlated with habitat type ($F_{(4,222)} = 2.21$, $p < 0.01$), whereas tide had no significant effect ($F_{(1,222)} = 1.36$, $p = 0.153$). The interaction between habitat and tide also had no significant effect on diet composition
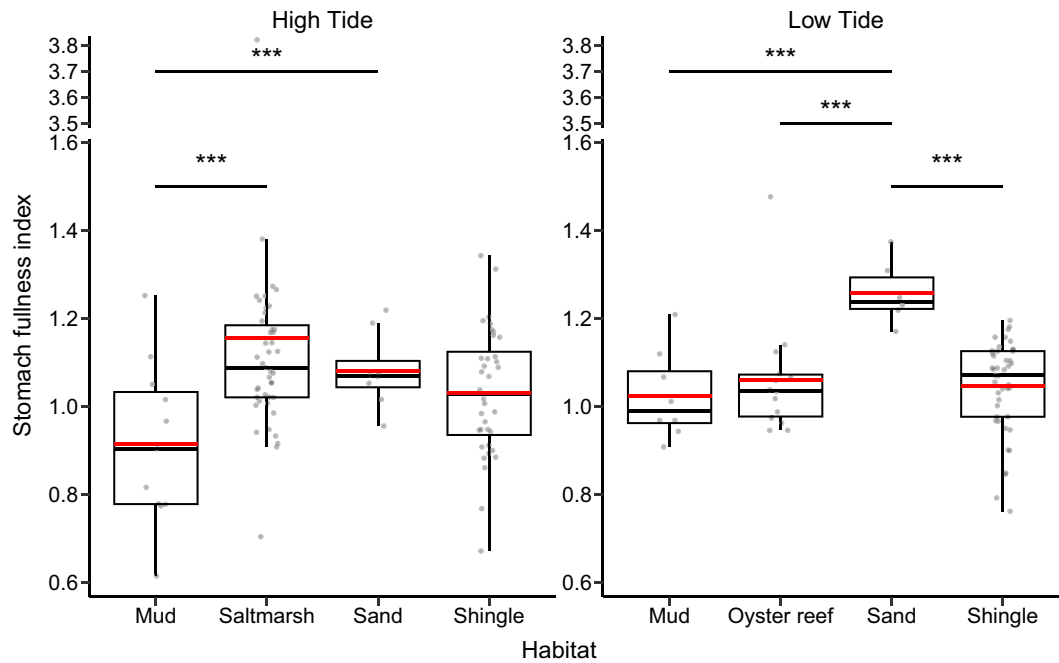
FIGURE 5 Box plots for the average stomach fullness (SFI [stomach fullness index], mg mm^{-3}) of 0-2+ group *Dicentrarchus labrax*, across estuarine habitats at high tide (left) and low (right) tides. Habitats are mud, saltmarsh, sand, shingle, and oyster reefs. Whiskers represent maximum data points within 1.5× the interquartile range; red bars represent means, and black bars represent medians. Thick black line represents the median, and red line indicates mean stomach fullness. Significant differences: ***$p < 0.01$ and *$p < 0.05$.
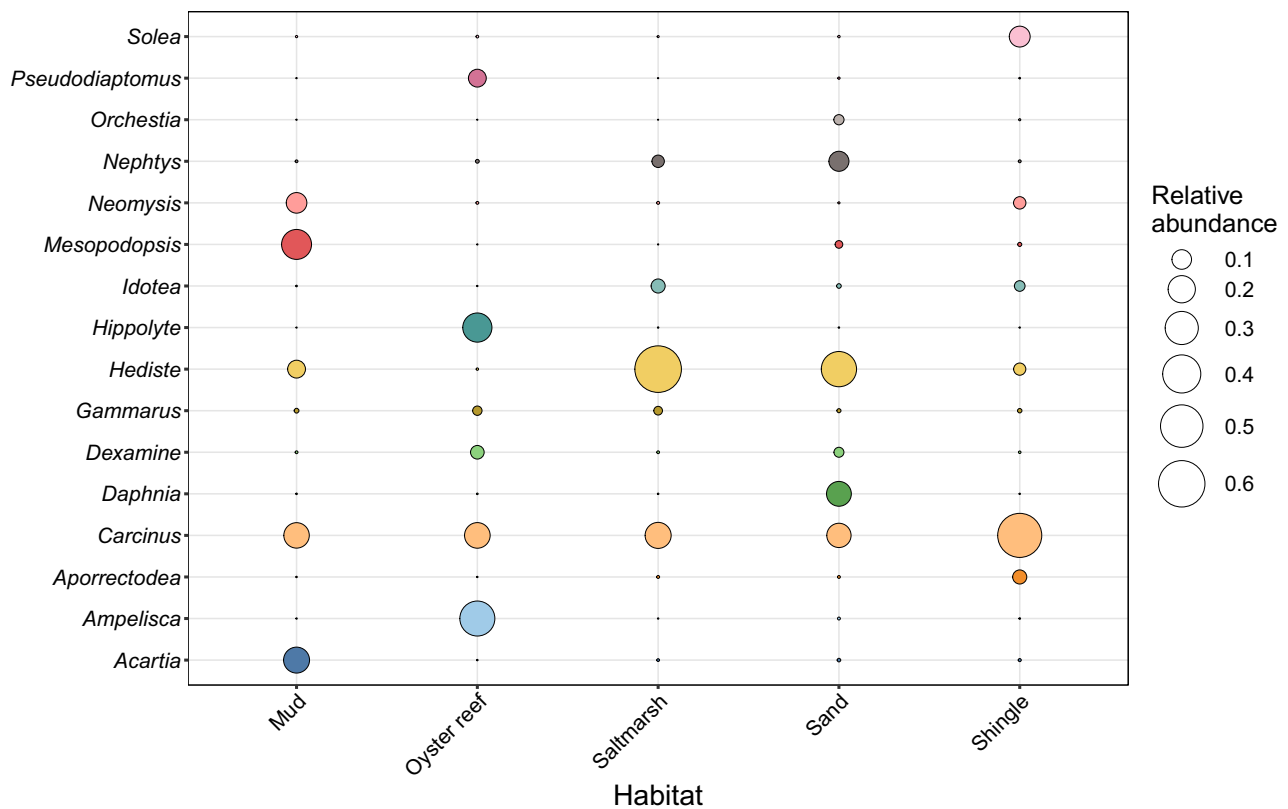

FIGURE 6 Bubble plots showing the relative abundance (depicted by size) of the most abundant (top 5) eukaryotic genera present in the stomach contents of 0-2+ group *Dicentrarchus labrax* across different estuarine habitats: mud, oyster reef, saltmarsh, sand, and shingle based on COI (cytochrome c oxidase subunit I) sequences, identified to genus level.
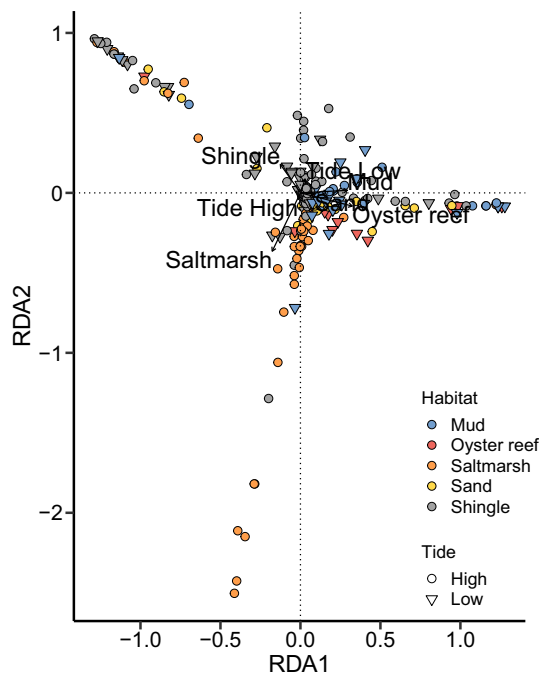
FIGURE 7 RDA (redundancy analysis) biplots for 0-2+ group *Dicentrarchus labrax* diets, amplified by COI (cytochrome c oxidase subunit I), constrained by habitats: mud (blue), oyster reefs (red), saltmarsh (orange), sand (yellow), and shingle (gray); tides: high (dots) and low (triangles). Scaling = 1.

$(F_{(1,222)} = 1.20, p = 0.225)$. For mud, shingle, and sand there was considerable overlap in diet composition between high- and low-tide points, suggesting that diets were similar between habitats and within habitats between tides. However, some differentiation in diet composition occurred between shingle beds and saltmarshes, with points scattering in opposing directions. The diet composition of fish using mud habitats somewhat differed from that of fish using shingle and saltmarshes, though large amounts of overlap still occurred, especially with shingle. This suggests that the strongest differences in diet composition were driven by the use of saltmarsh and shingle habitats, and to a lesser extent mud, whereas all other habitats were very similar across tides.

4 | DISCUSSION

An important criterion for establishing whether a habitat is a nursery is the contribution of juvenile fish to the next life-history stage compared to other habitats where juveniles are found (Beck et al., 2001; Dahlgren et al., 2006). Differences in contribution rates between habitats within the same system are difficult to measure, so proxies such as habitat quality are often used, as we have done in this study. In recent years, increased focus is being placed on the role of connected habitats, referred to as seascapes (Nagelkerken et al., 2015), and how these contribute to the nursery function of coastal systems (Amorim et al., 2017; Litvin et al., 2018; Nagelkerken et al., 2015; Olson

et al., 2019; Sheaves, 2009; Sheaves et al., 2006; Waltham et al., 2020). However, the majority of juvenile fish research in the United Kingdom has focused on saltmarsh systems alone (Cattrijsse et al., 1994; Cattrijsse & Hampel, 2006; Green et al., 2009, 2012; Jennings & Pawson, 1992; Jin et al., 2007; Kelley, 1986; Kelley, 1988; Laffaille et al., 2000, 2001; Pickett & Pawson, 1994), which has determined their importance a priori, by not sampling other habitats. This has hindered our ability to identify the full breadth of habitats that are important to juvenile fish on European coasts. The present study provides new insights into habitat utilization by juvenile sea bass across estuarine seascapes. When habitat utilization is considered, we find several habitats, such as sand and shingle edge habitats, are as if not more important than saltmarsh creeks for juvenile sea bass. Given the likelihood that fish are highly motile with tidal flows (Bretsch & Allen, 2006; Potthoff & Allen, 2003; Rangeley & Kramer, 1995; Reis-Filho et al., 2016), multiple habitat types likely contribute to the nursery function of temperate coastal estuaries.

At high tide, juvenile sea bass showed similar CPUE across all habitat types, suggesting either that all habitats are similarly desirable or that no differential selection occurred. This could be a result of all the habitats assessed in this study being relatively shallow, which is thought to provide refuge from predation, as it may be less accessible to larger piscivorous predators (Paterson & Whitfield, 2000; Whitfield, 2017, 2020). The value of shallow habitats as refuge has been demonstrated across many different habitats, including saltmarshes of South Africa (McIvor & Odum, 1988; Paterson & Whitfield, 2000; Rypel et al., 2007; Whitfield, 2017, 2020), mangroves (Gannon et al., 2015; Hindell & Jenkins, 2004; Vance et al., 1996; Whitfield, 2017, 2020), and the littoral zones of freshwater lakes and rivers (Harvey, 1991; Whitfield, 2017, 2020). It is unlikely that size segregation between habitat types occurs for 0-group sea bass at high tide. The size ranges of 0-group fish between high-tide habitats were relatively similar, with the majority of fish falling within 30–60 mm.

It is possible that the similarities in CPUE between habitats at high tide are the result of sampling artifacts where it was necessary to use different methodologies on different habitats, where fyke nets used on saltmarshes are considerably more efficient at trapping fish than seine nets in bays and open habitats. However, the higher efficiency of fyke nets creates a bias toward marshes, and still we find that all habitats are similarly utilized. Therefore, we suggest that the results presented in this study should be considered as conservative estimates of habitat use between estuarine habitats that indicate that a range of shallow coastal habitats are as important as, or more important than, saltmarshes.

Fish of both high and low conditions were found across all habitats, suggesting that all shallow high-tide habitats are similarly desirable to fish of both high and low conditions, which could suggest they are of similar quality. Condition is unlikely to change over the course of a single tidal cycle, during which a fish might occupy a specific habitat or indeed move between them. It is also unclear to what degree 0-group sea bass exhibit site fidelity over tidal cycles. Therefore, condition is unlikely to be the result of utilizing a particular habitat; rather, fish of a given condition select that habitat or interact with

hydrological processes in different ways, which may affect their distribution at high and low tides.

A subset of sand-dominated habitats (site 12) exhibited a CPUE close to 587% higher than the mean of sand habitats and 400% higher than the maximum CPUE of saltmarsh and shingle. Sand habitats were broadly characterized by the presence of a short sandy beach fringing intertidal flats composed of sandy-mud or mixed sediment. Uniquely, site 12 was a highly vegetated sand-dominated habitat fringed by cord grass (*Spartina* spp.) and an intertidal seagrass meadow, with rafts of filamentous algae that inundated the intertidal area, creating a complex matrix of coastal vegetation and macroalgae. Vegetative complexity is thought to decrease the efficiency and maneuverability of visual predators, and therefore provide refuge to juvenile fish (Heck Jr & Thoman, 1981; Savino & Stein, 1982; Stunz & Minello, 2001). It is possible that vegetative complexity also plays an important role in habitat desirability, which is masked by our habitat definitions. We defined habitat types based on the dominant structural characteristics observed at that site, primarily related to substrate types. However, this broad definition is limiting, in that it does not sufficiently consider structural differences within habitat types.

Alternatively, the similar abundance of 0-group sea bass between saltmarshes and bay habitats could be an artifact of habitat loss. Many of the bay and edge habitats sampled in this study would have likely bordered a saltmarsh in the past. Increased anthropogenic land reclamation and hard sea wall defenses combined with sea-level rise have resulted in large reductions in saltmarsh habitat (Amorim et al., 2017; Cooper et al., 2001; Doody, 2008), with a loss of 25% in Essex even in contemporary years (Cooper et al., 2001). It is possible that if fish are simply moving into any shallow water habitat on high tides, either actively or passively with tidal currents, were these saltmarshes still present, fish may continue to move into the shallow creek habitats beyond the limited fringe bays that they are today. It is also possible that abundance of bass varies temporally over the summer settlement period, which may mask differences in CPUE if different habitats are sampled in different months. However, this is unlikely to be the case as CPUE did not appear to differ between months, and most habitat types were represented throughout the sampling season.

Increased stomach fullness in sea bass using saltmarsh and sand habitats at high tide suggests these habitats may convey increased foraging opportunities. All diets exhibited a high representation of *Carcinus* crabs, likely *Carcinus maenas*. However, whereas saltmarsh diets primarily consisted of benthic taxa, sand and mud habitats exhibited more zooplanktonic taxa in diets. This is particularly the case for mud habitats, where fewer benthic species were present in the diet. This suggests that juvenile sea bass exhibit more, or increased, success in zooplanktivory, in mud and sand habitats and reduced benthic foraging on mud. The presence of terrestrial insects in the diet of sea bass using mud further supports this. However, the primary diet constituent of sea bass using sand and saltmarshes, where stomach fullness was highest, was *Hediste* polychaetes (likely *Hediste diversicolor*), which is an important part of the diet of many coastal fish species (Cabral, 2000; Hampel et al., 2005; Maia et al., 2009; Selleslagh et al.,

2012), including sea bass (Green et al., 2009; Hampel et al., 2005; Laffaille et al., 2000).

Mudflats have been found to have increased abundance and diversity of benthic macroinvertebrate taxa compared to saltmarshes in multiple studies (Bloomfield & Gillanders, 2005; Salgado et al., 2007; Sueiro et al., 2011). However, saltmarshes generally exhibit increased juvenile fish foraging rates and usage (Deegan et al., 2000; Hampel et al., 2005; Laffaille et al., 2001; West & Zedler, 2000). It is possible that important prey species such as *H. diversicolor* are easier to forage in saltmarshes and sand compared to mud habitats, where it may be more difficult to forage for benthic or infaunal species. This could suggest that whereas all habitats are well used by sea bass at high tide, saltmarshes and sand may provide better foraging habitat for key prey species and, therefore, provide better-quality habitat. However, to what degree sea bass depend on the presence of *H. diversicolor* and whether this increased foraging results in increased growth and nutrition are not known.

At low tide it is difficult to be certain whether habitat selection by the fish or hydrodynamic forces are more important in determining distribution patterns. The amount of available shallow habitat is severely reduced at low tide, and therefore, the scope for habitat selection is constrained to a smaller area (Childs et al., 2008; Gannon et al., 2015; Gibson, 2003; Krumme et al., 2015; Rangeley & Kramer, 1995; Raposa et al., 2009). However, as a diverse range of shallow habitats are still available, we decided to investigate abundance and habitat use patterns, and found that 0-group sea bass were more abundant in oyster reef and shingle habitats and that generally these fish were of lower condition and stomach fullness. Again, no size segregation seemed to occur between the majority of low-tide habitats, with the majority of 0-group fish falling within similar size ranges to high-tide habitats. This could indicate that 0-group sea bass actively select habitats with a 3D benthic structure compared to sand and mud habitats. The lower stomach fullness also suggests a lower foraging rate, which may indicate that these fish of lower condition utilize oyster reef and shingle as predation refuge more so than foraging habitat. Alternatively, if distribution patterns are more influenced by hydrological forces than active habitat selection, then a higher abundance in shingle and oyster reef could simply suggest that these habitats cover a larger area of depositional regions of the estuary at low tide. More so than at high tide, sampling bias could influence this result as many shallow habitats over low tide such as creek beds and subtidal mudflats were inaccessible.

Although fewer fish utilized sand and mud over low tides, these fish were of a higher condition, and those fish using sand habitats exhibited higher stomach fullness. This could indicate that fitter fish are better able to use habitats such as sand, which may be riskier but easier to forage on, due to the absence of complex structures that may provide refuge for macroinvertebrate prey. Alternatively, lower stomach fullness over oyster reef and shingle could be density dependent, where there are more fish present and, therefore, there may be increased competition for those food resources compared to sand. Diets of fish using oyster reef and shingle typically consisted of benthic taxa, such as decapods (e.g., *C. maenas* and *Hippolyte*) and

amphipods (e.g., *Dexamine* and *Ampelisca*). It is also possible that the dietary compositions and stomach fullness of fish in a given habitat are actually indicative of where a fish has been previously, for example, at high tide. Movements over tidal cycles that we cannot account for may be masking differences in foraging behavior and diet composition.

The contribution of fish to adulthood is unlikely to be determined by processes only in the first 2 years of life, nor can we say with any certainty that greater numbers of fish in better condition will provide enhanced contribution. To that end we cannot say whether, based on fish abundance and quality alone and inferred habitat quality therein, habitats are likely to be better nurseries. Processes that act throughout ontogeny and the annual cycle must also be considered, such as hydrodynamics and migrations (Litvin et al., 2018; Secor, 2015), and overwinter temperatures (Houde, 2016).

In conclusion, our work suggests that juvenile sea bass make use of a broad range of shallow littoral habitats ranging from saltmarshes to bays fringing subtidal channels. This is possibly due to the refugia provided from shallow water and habitat complexity, or alternatively, the use of bays could be an artifact of a behavioral syndrome, where fish attempt to move into shallower water and would have eventually traversed onto marshes that have now been lost. The highest abundance was found on a sand habitat but uniquely fringed by intertidal vegetation. Diets were similarly diverse across all habitats, suggesting that sea bass exhibit a generalist diet. However, saltmarsh and sand habitats likely present better foraging habitats for key prey species. We believe that shallow littoral habitats may underpin the distribution patterns of juvenile sea bass found in estuarine nurseries. Attempting to assign saltmarsh systems alone as targeted management areas, effectively becoming a "savior habitat," is potentially dangerous and risks the loss of connected habitats that are equally as valuable. The high abundance of sea bass across all estuarine habitats at high tide suggests that it is important to consider the protection of a mosaic of interconnected habitats to support nursery functions rather than focusing on individual habitat types.

AUTHOR CONTRIBUTIONS

Project conceptualization was undertaken by Howard A. Freeman, Tom C. Cameron, Leanne J. Hepburn, Martin I. Taylor, and Ewan Hunter. Research was undertaken by Howard A. Freeman, Benjamin H. Gregson, Albert J. Smith, Aaron Lamphierre, Alex J. Dumbrell, and Tom C. Cameron. Statistical analysis and the preparation of figures and tables were undertaken by Howard A. Freeman and Benjamin H. Gregson. Data interpretation and writing were performed by Howard A. Freeman, Benjamin H. Gregson, Leanne J. Hepburn, Ewan Hunter, Alex J. Dumbrell, and Tom C. Cameron.

ACKNOWLEDGMENTS

ORCID

Howard A. Freeman https://orcid.org/0000-0002-8520-0698
Leanne J. Hepburn https://orcid.org/0000-0002-5109-7127
Martin I. Taylor https://orcid.org/0000-0002-3858-0712
Ewan Hunter https://orcid.org/0000-0003-0140-2928
Alex J. Dumbrell https://orcid.org/0000-0001-6282-3043
Benjamin H. Gregson https://orcid.org/0000-0001-8337-227X
Tom C. Cameron https://orcid.org/0000-0002-5875-1494

REFERENCES

Amorim, E., Ramos, S., Elliott, M., Franco, A., & Bordalo, A. A. (2017). Habitat loss and gain: Influence on habitat attractiveness for estuarine fish communities. *Estuarine, Coastal and Shelf Science*, 197, 244–257.

Aranda, M., Peralta, G., Montes, J., Gracia, F. J., Fivash, G. S., Bouma, T. J., & van der Wal, D. (2022). Salt marsh fragmentation in a mesotidal estuary: Implications for medium to long-term management. *Science of the Total Environment*, 846, 157410.

Attrill, M. J., Strong, J. A., & Rowden, A. A. (2000). Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography*, 23(1), 114–121.

Bacon, P. J., Palmer, S. C. F., MacLean, J. C., Smith, G. W., Whyte, B. D. M., Gurney, W. S. C., & Youngson, A. F. (2009). Empirical analyses of the length, weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006. *ICES Journal of Marine Science*, 66(5), 844–859.

Baker, R., & Sheaves, M. (2021). Predation in littoral habitats is a complex process: Comment on Whitfield (2020). *Marine Ecology Progress Series*, 662, 205–208.

Bankevich, A., Nurk, S., Antipov, D., Gurevich, A. A., Dvorkin, M., Kulikov, A. S., Lesin, V. M., Nikolenko, S. I., Pham, S., Prjibelski, A. D., & Pyshkin, A. V. (2012). SPAdes: A new genome assembly algorithm and its applications to single-cell sequencing. *Journal of Computational Biology*, 19(5), 455–477.

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., & Orth, R. J. (2001). The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. *Bioscience*, 51(8), 633–641.

Bloomfield, A. L., & Gillanders, B. M. (2005). Fish and invertebrate assemblages in seagrass, mangrove, saltmarsh, and nonvegetated habitats. *Estuaries*, 28(1), 63–77.

Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., & Bai, Y. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology*, 37(8), 852–857.

Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical ecology with R* (Vol. 2, p. 688). Springer.

Brady, M. E., Chione, A. M., & Armstrong, J. B. (2020). Missing pieces in the full annual cycle of fish ecology: A systematic review of the

phenology of freshwater fish research. *bioRxiv*. https://doi.org/10.1101/2020.11.24.395665

Bretsch, K., & Allen, D. M. (2006). Tidal migrations of nekton in salt marsh intertidal creeks. *Estuaries and Coasts*, 29, 474–486.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400.

Cabral, H., & Costa, M. J. (2001). Abundance, feeding ecology and growth of 0-group seabass, *Dicentrarchus labrax*, within the nursery areas of the Tagus estuary. *Journal of the Marine Biological Association of the United Kingdom*, 81(4), 679–682.

Cabral, H. N. (2000). Comparative feeding ecology of sympatric Solea solea and S. Senegalensis, within the nursery areas of the Tagus estuary, Portugal. *Journal of Fish Biology*, 57(6), 1550–1562.

Cammilleri, G., Costa, A., Graci, S., Buscemi, M. D., Collura, R., Vella, A., Pulvirenti, A., Cicero, A., Giangrosso, G., Schembri, P., & Ferrantelli, V. (2018). Presence of anisakis pegreffii in farmed seabass (*Dicentrarchus labrax* L.) commercialized in southern Italy: A first report. *Veterinary Parasitology*, 259, 13–16.

Canion, C. R., & Heck, K. L., Jr. (2009). Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. *Marine Ecology Progress Series*, 393, 37–46.

Cariou, T., Dubroca, L., Vogel, C., & Bez, N. (2021). Comparison of the spatiotemporal distribution of three flatfish species in the seine estuary nursery grounds. *Estuarine, Coastal and Shelf Science*, 259, 107471.

Cattrijsse, A., & Hampel, H. (2006). European intertidal marshes: A review of their habitat functioning and value for aquatic organisms. *Marine Ecology Progress Series*, 324, 293–307.

Cattrijsse, A., Makwaia, E. S., Dankwa, H. R., Hamerlynck, O., & Hemminga, M. A. (1994). Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Marine Ecology Progress Series*, 109, 195–208.

Cheminée, A., Merigot, B., Vanderklift, M. A., & Francour, P. (2016). Does habitat complexity influence fish recruitment? *Mediterranean Marine Science*, 17(1), 39.

Childs, A. R., Cowley, P. D., Næsje, T. F., Booth, A. J., Potts, W. M., Thorstad, E. B., & Økland, F. (2008). Do environmental factors influence the movement of estuarine fish? A case study using acoustic telemetry. *Estuarine, Coastal and Shelf Science*, 78(1), 227–236.

Coles, R. G., Long, W. L., Watson, R. A., & Derbyshire, K. J. (1993). Distribution of seagrasses, and their fish and penaeid prawn communities, in Cairns harbour, a tropical estuary, northern Queensland, Australia. *Marine and Freshwater Research*, 44(1), 193–210.

Connolly, R. M. (1994). A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. *Marine and Freshwater Research*, 45(6), 1033–1044.

Cooper, N. J., Cooper, T., & Burd, F. (2001). 25 years of salt marsh erosion in Essex: Implications for coastal defence and nature conservation. *Journal of Coastal Conservation*, 7, 31–40.

Couillard, C. M., Maltais, D., Lazartigues, A., & Sirois, P. (2022). Combined use of otolith morphometry and microchemistry to study the origin of spring-spawning Atlantic herring in the St. Lawrence estuary and the Gulf of St. Lawrence. *Marine and Coastal Fisheries*, 14(1), e10189.

Dahlgren, C. P., Kellison, G. T., Adams, A. J., Gillanders, B. M., Kendall, M. S., Layman, C. A., Ley, J. A., Nagelkerken, I., & Serafy, J. E. (2006). Marine nurseries and effective juvenile habitats: Concepts and applications. *Marine Ecology Progress Series*, 312, 291–295.

Day, L., Brind'Amour, A., Cresson, P., Chouquet, B., & Le Bris, H. (2021). Contribution of estuarine and coastal habitats within nursery to the diets of juvenile fish in spring and autumn. *Estuaries and Coasts*, 44(4), 1100–1117.

Deegan, L. A., Hughes, J. E., & Rountree, R. A. (2002). Salt marsh ecosystem support of marine transient species. In M. P. Weinstein, & D. A. Kreeger (Eds.), *Concepts and controversies in tidal marsh ecology* (pp. 333–365). Springer. https://doi.org/10.1007/0-306-47534-0_16

Diehl, S., & Eklov, P. (1995). Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. *Ecology*, 76(6), 1712–1726.

Doody, J. P. (2008). *Saltmarsh conservation, management and restoration* (Vol. 12). Springer Science & Business Media.

Douglas, T. J., Schuerholz, G., & Juniper, S. K. (2022). Blue carbon storage in a northern temperate estuary subject to habitat loss and chronic habitat disturbance: Cowichan estuary, British Columbia, Canada. *Frontiers in Marine Science*, 9, 857586.

Dufour, V., Cantou, M., & Lecomte, F. (2009). Identification of seabass (*Dicentrarchus labrax*) nursery areas in the north-western Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 89(7), 1367–1374.

Dumbrell, A. J., Ferguson, R. M., & Clark, D. R. (2016). Microbial community analysis by single-amplicon high-throughput next generation sequencing: Data analysis–from raw output to ecology. In *Hydrocarbon and lipid microbiology protocols* (pp. 155–206). Springer.

Eggleston, D. B., Elis, W. E., Etherington, L. L., Dahlgren, C. P., & Posey, M. H. (1999). Organism responses to habitat fragmentation and diversity: Habitat colonization by estuarine macrofauna. *Journal of Experimental Marine Biology and Ecology*, 236(1), 107–132.

Fullerton, A. H., & Lamberti, G. A. (2006). A comparison of habitat use and habitat-specific feeding efficiency by Eurasian ruffe (*Gymnocephalus cernuus*) and yellow perch (*Perca flavescens*). *Ecology of Freshwater Fish*, 15(1), 1–9.

Gannon, R., Payne, N. L., Suthers, I. M., Gray, C. A., van der Meulen, D. E., & Taylor, M. D. (2015). Fine-scale movements, site fidelity and habitat use of an estuarine dependent sparid. *Environmental Biology of Fishes*, 98, 1599–1608.

Garcia, A. F. S., Garcia, A. M., Vollrath, S. R., Schneck, F., Silva, C. F. M., Marchetti, Í. J., & Vieira, J. P. (2018). Spatial diet overlap and food resource in two congeneric mullet species revealed by stable isotopes and stomach content analyses. *Community Ecology*, 19, 116–124.

Geller, J., Meyer, C., Parker, M., & Hawk, H. (2013). Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Molecular Ecology Resources*, 13(5), 851–861.

Gibson, R. N. (2003). Go with the flow: Tidal migration in marine animals. In M. B. Jones, A. Ingólfsson, E. Ólafsson, G. V. Helgason, K. Gunnarsson, & J. Svavarsson (Eds.), *Migrations and dispersal of marine organisms* (Vol. 174, pp. 153–161). Springer. https://doi.org/10.1007/978-94-017-2276-6_17

Gray, C. A., McElligott, D. J., & Chick, R. C. (1996). Intra-and inter-estuary differences in assemblages of fishes associated with shallow seagrass and bare sand. *Marine and Freshwater Research*, 47(5), 723–735.

Green, B. C., Smith, D. J., Earley, S. E., Hepburn, L. J., & Underwood, G. J. (2009). Seasonal changes in community composition and trophic structure of fish populations of five salt marshes along the Essex coastline, United Kingdom. *Estuarine, Coastal and Shelf Science*, 85(2), 247–256.

Green, B. C., Smith, D. J., & Underwood, G. J. (2012). Habitat connectivity and spatial complexity differentially affect mangrove and salt marsh fish assemblages. *Marine Ecology Progress Series*, 466, 177–192.

Gregson, B. H., Bani, A., Steinfield, L., Holt, D., & Whitby, C. (2022). Anaerobes and methanogens dominate the microbial communities in water harvesting ponds used by Kenyan rural smallholder farmers. *Science of the Total Environment*, 819, 153040.

Halpin, P. M. (2000). Habitat use by an intertidal salt-marsh fish: Trade-offs between predation and growth. *Marine Ecology Progress Series*, 198, 203–214.

Hampel, H., Cattrijsse, A., & Elliott, M. (2005). Feeding habits of young predatory fishes in marsh creeks situated along the salinity gradient of the Schelde estuary, Belgium and The Netherlands. *Helgoland Marine Research*, 59(2), 151–162.

Harmsworth, G. C., & Long, S. P. (1986). An assessment of saltmarsh erosion in Essex, England, with reference to the Dengie peninsula. *Biological Conservation*, 35(4), 377–387.

Harvey, B. C. (1991). Interactions among stream fishes: Predator-induced habitat shifts and larval survival. *Oecologia*, 87, 29–36.

Heck, K. L., Jr., & Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habitats. *Journal of Experimental Marine Biology and Ecology*, 53(2–3), 125–134.

Heck, K. L., Able, K. W., Fahay, M. P., & Roman, C. T. (1989). Fishes and decapod crustaceans of Cape Cod eelgrass meadows: Species composition, seasonal abundance patterns and comparison with unvegetated substrates. *Estuaries*, 12, 59–65.

Hindell, J. S., & Jenkins, G. P. (2004). Spatial and temporal variability in the assemblage structure of fishes associated with mangroves (*Avicennia marina*) and intertidal mudflats in temperate Australian embayments. *Marine Biology*, 144, 385–395.

Houde, E. D. (2016). Recruitment variability. In T. Jakobsen, M. J. Fogarty, B. A. Megrey & E. Moksness (Eds.), *Fish reproductive biology* (pp. 98–187). Wiley-Blackwell. https://doi.org/10.1002/9781118752739.ch3

Hu, Z., Sun, X., Cai, Y., Guo, L., Chen, Q., Liu, T., Shi, F., & Yang, L. (2016). The habitat type and trophic state determine benthic macroinvertebrate communities in lowland shallow lakes of China. *Journal of Limnology*, 75(2), 330–339.

Huusko, A. R. I., Greenberg, L., Stickler, M., Linnansaari, T., Nykänen, M., Vehanen, T., Koljonen, S., Louhi, P., & Alfredsen, K. (2007). Life in the ice lane: The winter ecology of stream salmonids. *River Research and Applications*, 23(5), 469–491.

ICES. (2015). Report of the working group for the Celtic Seas Ecoregion (WGCSE). ICES CM 2015/ACOM: 12, Copenhagen, Denmark. 1432 pp.

Jakubavičiūtè, E., Bergström, U., Eklöf, J. S., Haenel, Q., & Bourlat, S. J. (2017). DNA metabarcoding reveals diverse diet of the three-spined stickleback in a coastal ecosystem. *PLoS ONE*, 12(10), e0186929.

Jennings, S., & Pawson, M. G. (1992). The origin and recruitment of seabass, *Dicentrarchus labrax*, larvae to nursery areas. *Journal of the Marine Biological Association of the United Kingdom*, 72(1), 199–212.

Jin, B., Fu, C., Zhong, J., Li, B., Chen, J., & Wu, J. (2007). Fish utilization of a salt marsh intertidal creek in the Yangtze River estuary, China. *Estuarine, Coastal and Shelf Science*, 73(3–4), 844–852.

Joshi, N. A., & Fass, J. (2011). Sickle: A sliding-window, adaptive, quality-based trimming tool for FastQ files (Version 1.33) [Software].

Kelley, D. (1986). Seabass nurseries on the west coast of the UK. *Journal of the Marine Biological Association of the United Kingdom*, 66(2), 439–464.

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

Kerambrun, E., Le Floch, S., Sanchez, W., Guyon, H. T., Meziane, T., Henry, F., & Amara, R. (2012). Responses of juvenile seabass, *Dicentrarchus labrax*, exposed to acute concentrations of crude oil, as assessed by molecular and physiological biomarkers. *Chemosphere*, 87(7), 692–702.

Kerambrun, E., Sanchez, W., Henry, F., & Amara, R. (2011). Are biochemical biomarker responses related to physiological performance of juvenile seabass (*Dicentrarchus labrax*) and turbot (*Scophthalmus maximus*) caged in a polluted harbour? *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 154(3), 187–195.

Krumme, U., Grinvalds, K., Zagars, M., Elferts, D., Ikejima, K., & Tongnunui, P. (2015). Tidal, diel and lunar patterns in intertidal and subtidal mangrove creek fish assemblages from southwest Thailand. *Environmental Biology of Fishes*, 98(6), 1671–1693.

Laffaille, P., Feunteun, E., & Lefeuvre, J. C. (2000). Composition of fish communities in a European macrotidal salt marsh (the Mont saint-Michel Bay, France). *Estuarine, Coastal and Shelf Science*, 51(4), 429–438.

Laffaille, P., Lefeuvre, J. C., Schricke, M. T., & Feunteun, E. (2001). Feeding ecology of o-group seabass, *Dicentrarchus labrax*, in salt marshes of Mont Saint Michel Bay (France). *Estuaries*, 24(1), 116–125.

Lazzari, M. A., Sherman, S., & Kanwit, J. K. (2003). Nursery use of shallow habitats by epibenthic fishes in Maine nearshore waters. *Estuarine, Coastal and Shelf Science*, 56(1), 73–84.

Leray, M., Yang, J. Y., Meyer, C. P., Mills, S. C., Agudelo, N., Ranwez, V., Boehm, J. T., & Machida, R. J. (2013). A new versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity: Application for characterizing coral reef fish gut contents. *Frontiers in Zoology*, 10(1), 1–14.

Leslie, T., James, N. C., Potts, W. M., & Rajkaran, A. (2017). The relationship between habitat complexity and nursery provision for an estuarine-dependent fish species in a permanently open south African estuary. *Estuarine, Coastal and Shelf Science*, 198, 183–192.

Lilley, R. J., & Unsworth, R. K. (2014). Atlantic cod (*Gadus morhua*) benefits from the availability of seagrass (*Zostera marina*) nursery habitat. *Global Ecology and Conservation*, 2, 367–377.

Litvin, S. Y., Weinstein, M. P., Sheaves, M., & Nagelkerken, I. (2018). What makes nearshore habitats nurseries for nekton? An emerging view of the nursery role hypothesis. *Estuaries and Coasts*, 41(6), 1539–1550.

MacRae, P. S., & Jackson, D. A. (2001). The influence of smallmouth seabass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(2), 342–351.

Magnussen, E. (2011). Food and feeding habits of cod (*Gadus morhua*) on the Faroe Bank. *ICES Journal of Marine Science*, 68(9), 1909–1917.

Maia, A., Vinagre, C., & Cabral, H. N. (2009). Impact of a predator in the foraging behaviour of Solea senegalensis. *Journal of the Marine Biological Association of the United Kingdom*, 89(3), 645–649.

Masella, A. P., Bartram, A. K., Truszkowski, J. M., Brown, D. G., & Neufeld, J. D. (2012). PANDAseq: Paired-end assembler for illumina sequences. *BMC Bioinformatics*, 13(1), 1–7.

McIvor, C. C., & Odum, W. E. (1988). Food, predation risk, and habitat selection in a marsh fish assemblage. *Ecology*, 69(5), 1341–1351.

McKnight, D. T., Huerlimann, R., Bower, D. S., Schwarzkopf, L., Alford, R. A., & Zenger, K. R. (2019). microDecon: A highly accurate read-subtraction tool for the post-sequencing removal of contamination in metabarcoding studies. *Environmental DNA*, 1(1), 14–25.

McMurdie, P. J., & Holmes, S. (2013). Phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS ONE*, 8(4), e61217.

Montefalcone, M., Parravicini, V., Vacchi, M., Albertelli, G., Ferrari, M., Morri, C., & Bianchi, C. N. (2010). Human influence on seagrass habitat fragmentation in NW Mediterranean Sea. *Estuarine, Coastal and Shelf Science*, 86(2), 292–298.

Nagelkerken, I., Sheaves, M., Baker, R., & Connolly, R. M. (2015). The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries*, 16(2), 362–371.

Nash, R. D. M., & Geffen, A. J. (2000). The influence of nursery ground processes in the determination of year-class strength in juvenile plaice *Pleuronectes platessa* L. in port Erin Bay, Irish Sea. *Journal of Sea Research*, 44(1–2), 101–110.

Nikolenko, S. I., Korobeynikov, A. I., & Alekseyev, M. A. (2013). BayesHammer: Bayesian clustering for error correction in single-cell sequencing. *BMC Genomics*, 14(1), 1–11.

Olson, A. M., Hessing-Lewis, M., Haggarty, D., & Juanes, F. (2019). Nearshore seascape connectivity enhances seagrass meadow nursery function. *Ecological Applications*, 29(5), e01897.

Parsons, D. M., Middleton, C., Spong, K. T., Mackay, G., Smith, M. D., & Buckthought, D. (2015). Mechanisms explaining nursery habitat association: How do juvenile snapper (Chrysophrys auratus) benefit from their nursery habitat? *PLoS ONE*, 10(3), e0122137.

Paterson, A. W., & Whitfield, A. K. (2000). Do shallow-water habitats function as refugia for juvenile fishes? *Estuarine, Coastal and Shelf Science*, 51(3), 359–364.

Paulson, J. N., Stine, O. C., Bravo, H. C., & Pop, M. (2013). Differential abundance analysis for microbial marker-gene surveys. *Nature Methods*, 10(12), 1200–1202.

Pickett, G. D., & Pawson, M. G. (1994). *Seabass: Biology* (Vol. 12). Springer Science & Business Media.

Pihl, L., Modin, J., & Wennhage, H. (2005). Relating plaice (*Pleuronectes platessa*) recruitment to deteriorating habitat quality: Effects of macroalgal blooms in coastal nursery grounds. *Canadian Journal of Fisheries and Aquatic Sciences*, 62(5), 1184–1193.

Pompanon, F., Deagle, B. E., Symondson, W. O., Brown, D. S., Jarman, S. N., & Taberlet, P. (2012). Who is eating what: Diet assessment using next generation sequencing. *Molecular Ecology*, 21(8), 1931–1950.

Potthoff, M. T., & Allen, D. M. (2003). Site fidelity, home range, and tidal migrations of juvenile pinfish, *Lagodon rhomboides*, in salt marsh creeks. *Environmental Biology of Fishes*, 67, 231–240.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rangeley, R. W., & Kramer, D. L. (1995). Tidal effects on habitat selection and aggregation by juvenile pollock *Pollachius virens* in the rocky intertidal zone. *Marine Ecology Progress Series*, 126, 19–29.

Raposa, K. B., McKinney, R. A., & Beaudette, A. (2009). Effects of tide stage on the use of salt marshes by wading birds in Rhode Island. *Northeastern Naturalist*, 16(2), 209–224.

Reis-Filho, J. A., Giarrizzo, T., & Barros, F. (2016). Tidal migration and cross-habitat movements of fish assemblage within a mangrove ecotone. *Marine Biology*, 163, 1–13.

Robeson, M. S., O'Rourke, D. R., Kaehler, B. D., Ziemski, M., Dillon, M. R., Foster, J. T., & Bokulich, N. A. (2021). RESCRIPt: Reproducible sequence taxonomy reference database management. *PLoS Computational Biology*, 17(11), e1009581.

Rognes, T., Flouri, T., Nichols, B., Quince, C., & Mahé, F. (2016). VSEARCH: A versatile open source tool for metagenomics. *PeerJ*, 4, e2584.

Rozas, L. P., & Minello, T. J. (1998). Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bulletin of Marine Science*, 63(3), 481–501.

Russell, V., & Lenth, M. R. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69(1), 1–33.

Rypel, A. L., Layman, C. A., & Arrington, D. A. (2007). Water depth modifies relative predation risk for a motile fish taxon in Bahamian tidal creeks. *Estuaries and Coasts*, 30(3), 518–525.

Salgado, J. P., Cabral, H. N., & Costa, M. J. (2007). Spatial and temporal distribution patterns of the macrozoobenthos assemblage in the salt marshes of Tejo estuary (Portugal). *Hydrobiologia*, 587(1), 225–239.

Savino, J. F., & Stein, R. A. (1982). Predator-prey interaction between largemouth seabass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society*, 111(3), 255–266.

Schloesser, R. W., & Fabrizio, M. C. (2019). Nursery habitat quality assessed by the condition of juvenile fishes: Not all estuarine areas are equal. *Estuaries and Coasts*, 42(2), 548–566.

Schloss, P. D., Westcott, S. L., Ryabin, T., Hall, J. R., Hartmann, M., Hollister, E. B., Lesniewski, R. A., Oakley, B. B., Parks, D. H., Robinson, C. J., & Sahl, J. W. (2009). Introducing mothur: Open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Applied and Environmental Microbiology*, 75(23), 7537–7541.

Secor, D. H. (2015). *Migration ecology of marine fishes*. JHU Press.

Seitz, R. D., Wennhage, H., Bergström, U., Lipcius, R. N., & Ysebaert, T. (2014). Ecological value of coastal habitats for commercially and ecologically important species. *ICES Journal of Marine Science*, 71(3), 648–665.

Selleslagh, J., Lesourd, S., & Amara, R. (2012). Comparison of macrobenthic assemblages of three fish estuarine nurseries and their importance as foraging grounds. *Journal of the Marine Biological Association of the United Kingdom*, 92(1), 85–97.

Sheaves, M. (2009). Consequences of ecological connectivity: the coastal ecosystem mosaic. *Marine Ecology Progress Series*, 391, 107–115.

Sheaves, M., Baker, R., & Johnston, R. (2006). Marine nurseries and effective juvenile habitats: An alternative view. *Marine Ecology Progress Series*, 318, 303–306.

Sheaves, M., Baker, R., Nagelkerken, I., & Connolly, R. M. (2015). True value of estuarine and coastal nurseries for fish: Incorporating complexity and dynamics. *Estuaries and Coasts*, 38(2), 401–414.

Shoji, J., Sakiyama, K., Hori, M., Yoshida, G., & Hamaguchi, M. (2007). Seagrass habitat reduces vulnerability of red sea bream Pagrus major juveniles to piscivorous fish predator. *Fisheries Science*, 73, 1281–1285.

Sogard, S. M., & Able, K. W. (1991). A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuarine, Coastal and Shelf Science*, 33(5), 501–519.

Springer, T. A., & Murphy, B. R. (1990). Properties of relative weight and other condition indices. *Transactions of the American Fisheries Society*, 119(6), 1048–1058. https://doi.org/10.1577/1548-8659-119.6.1048

Stamp, T., West, E., Robbins, T., Plenty, S., & Sheehan, E. (2022). Large-scale historic habitat loss in estuaries and its implications for commercial and recreational fin fisheries. *ICES Journal of Marine Science*, 79(7), 1981–1991.

Stolen, E. D., Collazo, J. A., & Percival, H. F. (2009). Vegetation effects on fish distribution in impounded salt marshes. *Southeastern Naturalist*, 8(3), 503–514.

Stunz, G. W., & Minello, T. J. (2001). Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 260(1), 13–25.

Sueiro, M. C., Bortolus, A., & Schwindt, E. (2011). Habitat complexity and community composition: Relationships between different ecosystem engineers and the associated macroinvertebrate assemblages. *Helgoland Marine Research*, 65(4), 467–477.

Sutton, S. G., Bult, T. P., & Haedrich, R. L. (2000). Relationships among fat weight, body weight, water weight, and condition factors in wild Atlantic salmon parr. *Transactions of the American Fisheries Society*, 129(2), 527–538.

Swadling, D. S., West, G. J., Gibson, P. T., Laird, R. J., & Glasby, T. M. (2023). Don't go breaking apart: Anthropogenic disturbances predict meadow fragmentation of an endangered seagrass. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 33(1), 56–69.

Tableau, A., Brind'Amour, A., Woillez, M., & Le Bris, H. (2016). Influence of food availability on the spatial distribution of juvenile fish within soft sediment nursery habitats. *Journal of Sea Research*, 111, 76–87.

Tatrai, I., & Herzig, A. (1995). Effect of habitat structure on the feeding efficiency of young stages of razor fish (*Pelecus cultratus* (L.)): An experimental approach. *Hydrobiologia*, 299(1), 75–81.

Thiriet, P., Cheminée, A., Mangialajo, L., & Francour, P. (2014). How 3D complexity of macrophyte-formed habitats affect the processes structuring fish assemblages within coastal temperate seascapes? In *Underwater seascapes* (pp. 185–199). Springer.

Vance, D. J., Haywood, M. D. E., Heales, D. S., Kenyon, R. A., Loneragan, N. R., & Pendrey, R. C. (1996). How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns Penaeusmerguiensis and fish in a tropical mangrove forest in northern Australia. *Marine Ecology Progress Series*, 131, 115–124.

Vollrath, S. R., Possamai, B., Schneck, F., Hoeinghaus, D. J., Albertoni, E. F., & Garcia, A. M. (2021). Trophic niches and diet shifts of juvenile mullet species coexisting in marine and estuarine habitats. *Journal of the Marine Biological Association of the United Kingdom*, 101(2), 431–441.

Waltham, N. J., Elliott, M., Lee, S. Y., Lovelock, C., Duarte, C. M., Buelow, C., Simenstad, C., Nagelkerken, I., Claassens, L., Wen, C. K., & Barletta, M. (2020). UN decade on ecosystem restoration 2021–2030—What chance for success in restoring coastal ecosystems? *Frontiers in Marine Science*, 7, 71.

Warren, M. A., Gregory, R. S., Laurel, B. J., & Snelgrove, P. V. R. (2010). Increasing density of juvenile Atlantic (*Gadus morhua*) and Greenland

cod (*G. Ogac*) in association with spatial expansion and recovery of eelgrass (*Zostera marina*) in a coastal nursery habitat. *Journal of Experimental Marine Biology and Ecology*, *394*(1–2), 154–160.

West, J. M., & Zedler, J. B. (2000). Marsh-creek connectivity: Fish use of a tidal salt marsh in southern California. *Estuaries*, *23*(5), 699–710.

Whitfield, A. K. (2017). The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Reviews in Fish Biology and Fisheries*, *27*(1), 75–110.

Whitfield, A. K. (2020). Littoral habitats as major nursery areas for fish species in estuaries: A reinforcement of the reduced predation paradigm. *Marine Ecology Progress Series*, *649*, 219–234.

Wickham, H., & Wickham, H. (2016). Data Analysis. In *Data analysis* (pp. 189–201). Springer International Publishing.

Wolters, J. W., Verdonschot, R. C., Schoelynck, J., Verdonschot, P. F., & Meire, P. (2018). The role of macrophyte structural complexity and water flow velocity in determining the epiphytic macroinvertebrate community composition in a lowland stream. *Hydrobiologia*, *806*(1), 157–173.

Wright, P. J., Tobin, D., Gibb, F. M., & Gibb, I. M. (2010). Assessing nursery contribution to recruitment: Relevance of closed areas to haddock *Melanogrammus aeglefinus*. *Marine Ecology Progress Series*, *400*, 221–232.

Xue, S., Sun, T., Zhang, H., & Shao, D. (2016). Suitable habitat mapping in the Yangtze River estuary influenced by land reclamations. *Ecological Engineering*, *97*, 64–73.

Zhang, J., Kobert, K., Flouri, T., & Stamatakis, A. (2014). PEAR: A fast and accurate Illumina paired-end reAd mergeR. *Bioinformatics*, *30*(5), 614–620.

APPENDIX A

TABLE A1 Mean catch per unit of effort (CPUE) of the most abundant fish species, sea bass (*Dicentrarchus labrax*), mullet (*Chelon* sp.), sand smelt (*Atherina presbyter*), and Atlantic herring (*Clupea harengus*), caught across high- and low-tide habitats.

Tide	Habitat	Species	Mean CPUE (fish per m^2)
High	Saltmarsh	Sea bass	0.085
		Mullet	0.004
		Sand smelt	0.027
		Herring	0.000
	Shingle	Sea bass	0.118
		Mullet	0.060
		Sand smelt	0.317
		Herring	0.004
	Mud	Sea bass	0.048
		Mullet	0.001
		Sand smelt	0.012
		Herring	0.009
	Sand	Sea bass	0.238
		Mullet	0.001
		Sand smelt	0.243
		Herring	0.027
Low	Oyster reef	Sea bass	0.111
		Mullet	0.862
		Sand smelt	0.000
		Herring	0.000
	Shingle	Sea bass	0.269
		Mullet	0.039
		Sand smelt	0.026
		Herring	0.009
	Mud	Sea bass	0.037
		Mullet	0.085
		Sand smelt	0.000
		Herring	0.017
	Sand	Sea bass	0.040
		Mullet	0.118
		Sand smelt	0.000
		Herring	0.108