Estuarine, Coastal and Shelf Science 327 (2025) 109599

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Fish density in NE Atlantic saltmarsh is three-fold higher than unvegetated shores

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ARTICLE INFO

Keywords:
Estuary
Fish assemblage
Wetland
Teleost
Essential fish habitat
Habitat restoration

ABSTRACT

Atlantic saltmarshes are widely recognised as important and productive estuarine habitats, yet their role in supporting fish populations in northern Europe remains understudied. We used fyke and seine nets to assess fish assemblages at 14 sites across two estuaries in Carmarthen Bay, South Wales. Sampling took place in both saltmarshes and unvegetated estuarine shores monthly from October 2023 to September 2024. The age composition of the catch was predominantly juvenile (83 %). Fish density was significantly higher in saltmarshes (5972 ind/ha) compared to unvegetated shores (1806 ind/ha; $p < 0.001$). Six species were present in saltmarshes across all seasons, including Atlantic herring (*Clupea herrangus*) and European flounder (*Platichthys flesus*) not previously documented year-round in UK saltmarshes. Several species, were significantly more likely to be caught within saltmarsh, including lesser sandeel (*Ammodytes tobianus*) and grey mullet species (*Chelon ramada, Chelon labrosus, Chelon aurata*), while no species were significantly more likely to be caught in unvegetated shores, demonstrating saltmarshes enhanced nursery function. In total, 19 fish species were recorded in saltmarshes, representing the highest species richness documented for UK saltmarshes. Clear seasonal shifts in community composition were observed, with peaks in European flounder (*Platichthys flesus*) in May, European bass (*Dicentrarchus labrax*) in June and Atlantic herring (*Clupea herrangus*) in July, likely reflecting staggered recruitment strategies that minimise competition during early life stages. These findings provide the first year-round assessment of saltmarsh fish assemblages on the west coast of the UK and highlight the ecological value of saltmarshes in supporting coastal fish communities.

1. Introduction

Saltmarshes are dynamic and highly productive intertidal habitats, that provide crucial ecosystem services such as flood protection, carbon sequestration and nutrient cycling (Doolan and Hynes, 2023; King and Lester, 1995; McKinley et al., 2018). These habitats also play a vital but often overlooked role supporting fish production serving as nursery and foraging grounds for many species of commercial and conservation importance (Boesch and Turner, 1984; Taylor et al., 2018). At least sixteen commercially important species and five conservation-sensitive species have been recorded in European saltmarshes (Laffaille et al., 2000a).

Maintaining any healthy fish stock relies fundamentally on successful recruitment rates (Caley et al., 1996). Fish are most vulnerable as juveniles and must survive to adulthood to be able to contribute to the stock (Heck et al., 2003; Jørgensen and Holt, 2013). Nursery habitats enhance fish populations by offering protection and foraging opportunities favouring growth and development of juvenile fish (Munro and Bell, 1997). Understanding these contributing habitats is essential for effective fish population conservation (Beck et al., 2001). A nursery habitat is defined as an area "where a species exhibits higher than average 1) juvenile density, 2) growth, 3) survival or 4) movement to adult habitat" (Beck et al., 2001; Ciotti et al., 2025; Lefcheck et al., 2019).

Since the 1800s, England has lost more than 85 % of its saltmarsh habitat (Green et al., 2021). The UK is projected to lose a further 5,262

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https://doi.org/10.1016/j.ecss.2025.109599
Received 27 June 2025; Received in revised form 1 November 2025; Accepted 1 November 2025
Available online 2 November 2025

ha by 2060 (ONS and Defra, 2016). This dramatic decline, combined with growing recognition of the habitats' ecological value, has led to saltmarsh being designated as both an Annex I habitat under the EU Habitats Directive (transposed into UK law through the Conservation of Habitats and Species Regulations, 2017) and a habitat of principal importance under the Environment (Wales) Act 2016. These protections have driven increased investment in saltmarsh restoration, making comprehensive understanding of their ecological functions a key priority (Pétillon et al., 2023).

Saltmarsh fish assemblages are influenced by numerous biotic and abiotic factors including tidal cycles, seasonal variability, freshwater regime, grazing intensity, and site characteristics (de la Barra et al., 2022; Hampel et al., 2004; Lafage et al., 2021; Laffaille et al., 2000a; Veiga et al., 2006). For instance, intense grazing can alter invertebrate composition, directly affecting prey availability and decreasing growth rates of juvenile European bass (Laffaille et al., 2000b). Studies across Ireland, UK, Netherlands, France, Portugal, and Spain consistently record core species including European bass (*Dicentrarchus labrax*), European flounder (*Platichthys flesus*), grey mullet (*Chelon* spp.), and gobies (*Pomatoschistus* spp.) in saltmarsh habitats (Cattrijsse et al., 1994; Koutsogiannopoulou and Wilson, 2007; Mathieson et al., 2000; Ribeiro et al., 2012; Stamp et al., 2023). However, current understanding of saltmarsh fish ecology in the UK shows significant geographic bias. Research in southeast England, where tidal ranges rarely exceed 6 m and wave exposure is relatively low, has documented up to 14 fish species during summer months (Colclough et al., 2005; Freeman et al., 2024; Green et al., 2009; Mathieson et al., 2000). Year-round assessments of UK and Irish saltmarsh fish assemblages have been limited to Essex and Dublin, both systems with moderate physical conditions (Green et al., 2009; Koutsogiannopoulou and Wilson, 2007).

In contrast, western UK saltmarshes experience much greater tidal fluctuations (up to 12 m) and higher wave energy (Burrows et al., 2009), yet remain comparatively understudied. The limited research on west coast fish assemblages, restricted to two seasonal sampling events in Bangor, revealed that there is a tidal influence on species composition but left year-round patterns unexplored (de la Barra et al., 2022). This research gap is particularly significant given current conservation priorities. With growing recognition of saltmarsh ecological importance and increasing investment in habitat restoration (UK Centre for Ecology and Hydrology., 2022; Wildfowl and Wetlands Trust, 2023), comprehensive understanding across diverse environmental conditions is essential for effective conservation strategies.

We conducted a comprehensive assessment of fish communities within South Wales, Carmarthen Bay's estuarine high tide habitats, comparing saltmarsh and unvegetated shores. Using seine nets and fyke nets, completing monthly surveys over a year, we aimed to: 1) characterise the saltmarsh fish assemblages for the first time in South Wales, 2) quantify differences between fish assemblages in vegetated saltmarsh habitats versus adjacent unvegetated shores to understand comparative nursery functioning, and 3) determine fine-scale spatial and temporal distribution patterns of fish species throughout Carmarthen Bay's two major estuarine systems (Loughor estuary and Three Rivers estuaries).

2. Methods

2.1. Study site

Carmarthen Bay, South Wales, United Kingdom is home to one of the most varied assemblage of coastal features in the British Isles, with a large tidal range of 8 m (May and Hansom, 2003). Carmarthen Bay is designated as a Special Area of Conservation (SAC) partly due to the full composition of Atlantic salt meadows species (Glauco-Puccinellietalia maritimae), the presence of the saltmarsh species *Salicornia* spp. is also a contributing factor to the designation (JNCC, 2015). Our study was conducted across the two major estuarine systems in Carmarthen Bay: the Burry Inlet (Loughor estuary) and the Three Rivers estuaries (Taf, Tywi and Gwendraeth estuaries). Loughor estuary contains 2886 ha of saltmarsh while the Three Rivers estuaries contains 1134 ha (Fig. 1). Saltmarshes in Carmarthen Bay make up 69 % of all Welsh saltmarshes and 9 % of all UK saltmarshes (ONS and Defra, 2016).

Sampling sites were situated across five clusters: three clusters were in saltmarsh (Crofty, Llanelli Wetlands, and Laugharne), and two clusters were in unvegetated estuarine shores (Llanelli Beach and Ferryside) (Fig. 1). A total of 14 sampling sites were established (8 saltmarsh, 6 unvegetated) across the five clusters, with the aim of deploying two fykes at independent sites and a seine net at a third independent site per cluster (Llanelli Wetlands only had one fyke netting site due to accessibility). Sites were selected to represent two dominant high-intertidal habitat types in the region: saltmarsh characterised by vegetated flats and muddy creeks, and unvegetated estuarine shores consisting of high-intertidal sand and mud banks. Sites were also selected based on accessibility, maximum sampling coverage and spatial distribution across the study area. Monthly sampling of all clusters were conducted between October 2023 and September 2024. Naturally the sites were exposed to differing environmental factors such as level of wave exposure and freshwater input. Each saltmarsh cluster was exposed to varying grazing regimes: Laugharne remained ungrazed, Llanelli WWT experienced seasonal cattle grazing, while Crofty had year-round grazing by cattle, sheep, and horses.

2.2. Fish sampling

Fish were sampled using a combination of beach seine netting and winged fyke netting, to best capture the abundances and diversity of species using the habitat (Crinall and Hindell, 2004; Franco et al., 2015). Fyke nets are static and can be more effective at capturing benthic and highly mobile species, but often low in abundance (Harrison-Day et al., 2020). While seine nets are active nets targeting mid water species and generally catching a higher abundance of fish, providing a quantitative measure (Lyons, 1986).

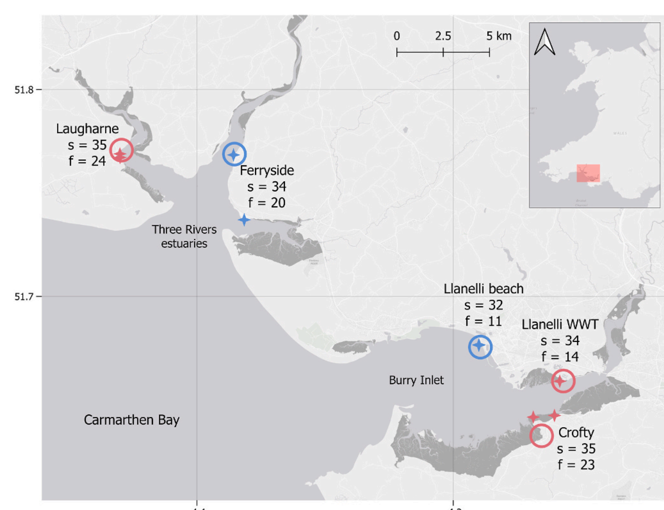

Fig. 1. The Three Rivers estuaries and Burry Inlet in Carmarthen Bay, South Wales, United Kingdom. Sampling sites within saltmarsh habitats are shown in red, and unvegetated shore sites in blue. Seine netting sites are marked with circles, and fyke netting sites with stars. Each site cluster is labelled by name, with the corresponding numbers of seine and fyke net samples completed between October 2023 and September 2024 indicated for each cluster. The extent of saltmarsh within the bay is shown in dark grey, derived from data obtained from DataMap Wales, an open-source geoportal maintained by Natural Resources Wales. Contains Natural Resources Wales information © Natural Resources Wales and Database Right. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fyke nets were deployed in saltmarsh creeks. Each net had 5 m long wings with 10 mm mesh, a D-ring trap (50 cm height) with 8 mm mesh, and a cod end with 6.5 mm mesh (Colclough and Cucknell, 2018; Franco et al., 2022). These mesh sizes were selected to effectively sample fish across all size classes, including juveniles (Stamp et al., 2023).

Given the complex and diverse topography of saltmarsh, sampling protocols were tailored to each fyke netting site. A set tidal height was determined for each fyke net using a combination of in person observations and graphs obtained from https://tides4fishing.com/, this was usually about 2 h before the high tide (Table S2). At unvegetated sites, fyke nets were positioned to submerge at tidal heights matching those of the adjacent saltmarsh sites in the same estuary, with wings set at 40° angles.

Seine netting was conducted during high tide between fyke net deployment and retrieval. To prevent pseudo-replication, seine sites were positioned outside the drainage areas of fyke nets. Three replicate hauls were carried out per site per month. Sampling used a 15 m × 2 m knotless mesh net (3 mm mesh size) within a 1-h window around high tide (±30 min; Colclough and Cucknell, 2018). At saltmarsh sites, the net was deployed in a semicircular shape from the shoreline over the vegetated flat (not within creeks). One end was fixed on the shore while the other was walked out to a maximum depth of approximately 1 m and swept in an arc to land, with both ends hauled onto shore (Hahn et al., 2007). At unvegetated sites, the same technique was applied over the bare sandy or muddy bank. Due to site-specific constraints at Llanelli WWT and Ferryside, sampling occurred during the flooding tide at the nearest feasible time to high tide.

Captured fish were transferred to 40 L buckets and sampled using hand nets. All fish were identified to species level, with fork length measurements recorded for the first 15 individuals of each species using a 60 cm WaterMark Ultimate Fish Board. Measured fish were immediately moved to recovery buckets containing 40 L of water before release (Bertelli and Unsworth, 2014).

For each sample, we recorded species abundance, individual fork lengths, sampling date, gear type, site location, and deployment timing.

2.3. Data analysis

Statistical analyses were primarily performed in R (Version 4.4.1; R Core Team, 2024), with plots created using the ggplot2 package (Wickham, 2016). Community composition analyses, including nMDS ordinations and PERMANOVA tests, were conducted using PRIMER7 (version 7; Clarke and Gorley, 2015). Fyke netting data only contributed to diversity values and qualitative analysis, data obtained from fyke nets was not used in density estimates, as calculating the area sampled by a fyke net is unreliable (Harrison-Day et al., 2020).

2.3.1. Density and diversity analysis

Seine haul area was calculated as approximately 36 square meters, assuming the 15 m net length formed the arc length for the semi-circle (Pierce et al., 1990). Density values were standardised to individuals per hectare by dividing abundance by area sampled. Diversity was calculated as Shannon's diversity index as it accounts for both species' richness and evenness (Ortiz-Burgos, 2016). All data were tested for normality using Shapiro-Wilks tests ($\alpha = 0.05$). To compare total density and diversity values between habitat types, non-parametric Wilcoxon tests were employed due to non-normal distributions, and median values are presented alongside.

2.3.2. Species specific habitat analysis

Mean densities were calculated from seine-net data only for each species in each habitat to provide a descriptive summary of relative abundance patterns, and are presented with standard error and the length range of each species. Median values were not used, as the frequency of zero counts across species rendered them uninformative for comparative purposes. To assess habitat associations of different species, we analysed presence/absence data across saltmarsh and unvegetated habitats (Neu et al., 1974). Abundance data were converted to binary presence/absence (1/0) values for each seine netting event. Fisher's exact tests were performed for each species to determine whether their occurrence differed significantly between habitat types, generating odds ratios that indicated relative habitat preference. Odds ratios greater than 1 indicated higher occurrence in saltmarsh habitat, while values less than 1 indicated higher occurrence in unvegetated. Statistical significance was determined using p-values from the Fisher's exact tests.

2.3.3. Investigating fish composition

To examine age composition of fish populations across habitat types, individuals were classified as either juvenile or adult based on species-specific length thresholds obtained from the literature (Table S3). The proportion of juveniles and adults was calculated for each species within both saltmarsh and unvegetated habitats. Results were visualised as stacked bar charts displaying the percentage of juveniles and adults, only species with more than 10 total counts from seine netting were included in the visualisation. This contains both seine and fyke netting data, as they may better target different life stages.

Community composition analyses were conducted using PRIMER7. These analyses were restricted to seine net data to maintain consistency in abundance measurements. A Bray-Curtis similarity matrix was constructed and used to generate non-metric Multidimensional Scaling (nMDS) ordinations.

PERMANOVA tests (999 permutations) were performed on the Bray-Curtis matrices to assess the effects of habitat, site, and month on community composition. The model included interaction terms for habitat × month and site × month. PERMDISP was used to test for differences in the variability of assemblage composition within groups. The analysis revealed heterogeneous multivariate dispersions among groups, even when data were transformed using square-root, fourth-root, and log(x+1) transformations. We proceeded with PERMANOVA analysis with cautious interpretation, using nMDS ordination plots derived from the same Bray-Curtis similarity matrices to visually validate the identified patterns (Anderson and Walsh, 2013), with stress values reported to indicate goodness of fit.

For direct temporal comparison between habitats, monthly mean densities for each species were standardised as a proportion of that species' maximum observed density across all samples. This approach enabled visualisation of seasonal patterns while facilitating inter-species comparisons independent of absolute abundance differences. Only species with more than 100 total counts were included in the visualisation.

To analyse temporal patterns in fish community composition within saltmarsh habitats, we aggregated abundance data by month. To simplify analysis species with fewer than 50 total individuals captured were grouped as "Others". Monthly species composition was calculated as the proportion of each species' abundance relative to the total catch for that month. Results were visualised as stacked bar charts showing the percentage contribution of each species to the total catch across all months (October 2023 through September 2024). This approach allowed for examination of seasonal shifts in community structure within saltmarsh habitats throughout the annual cycle.

3. Results

3.1. Habitat differences

We recorded 8525 fish from 21 species across 262 net deployments (170 seine nets, 92 fyke nets) between October 2023 and September 2024 (Table S4). Of the 21 species, 19 occurred in saltmarsh habitats, seven of them unique to saltmarsh, and 14 in unvegetated habitats, with two unique species. Focusing on seine net data fish density and diversity varied among habitat types (Fig. 2). Fish density was significantly higher in saltmarsh (5972 ind/ha) than in unvegetated shores (1806 ind/ha) ($W = 4672$, $p < 0.001$). Diversity was also higher in saltmarsh (0.637)

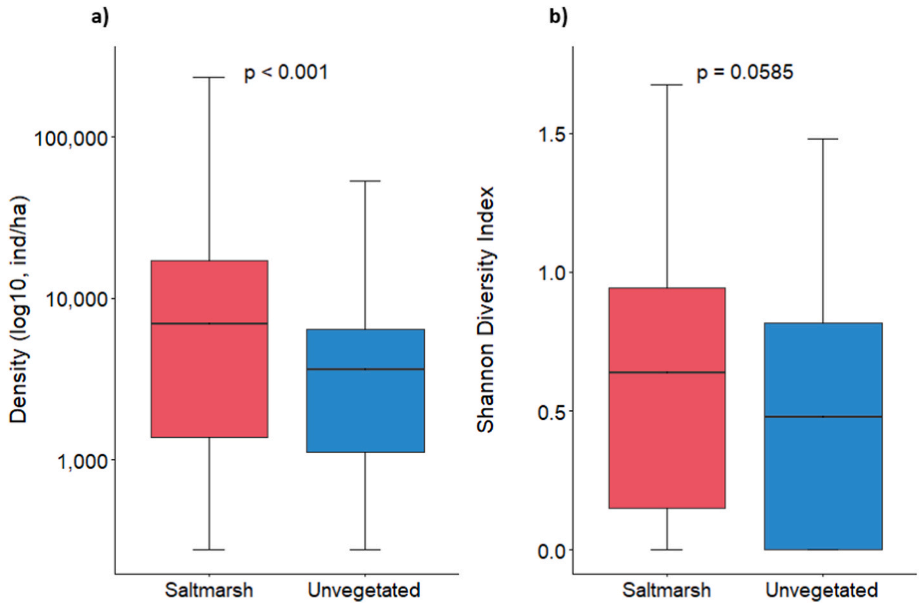

Fig. 2. Box plot of fish density and b) diversity across saltmarsh (red) and unvegetated (blue) habitats, from monthly seine net samples from October 2023 to September 2024. P values are included from Wilcoxon tests. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

than in unvegetated shores (0.478), but not significantly (W = 6914, p = 0.06).

Habitat did not have a significant effect on overall fish assemblage composition (Pseudo-F = 1.08, p = 0.3). Although fish communities exhibited no distinct separation between habitats, composition was considerably more variable in saltmarsh compared to unvegetated (mean dispersion 1.1 and 0.8 respectively, PERMDISP, $p < 0.05$). This pattern was visually supported by the nMDS ordination (stress = 0.19; Fig. 4), which showed a similar central tendency for both habitats but a greater spread of samples from saltmarsh.

3.2. Species habitat associations

Of the 15 species groups captured using seine nets, six were recorded exclusively in saltmarsh, and an additional six were more abundant in saltmarsh compared to unvegetated habitat (Table 1). In contrast, greater pipefish were captured only in unvegetated habitats, while sand smelt and sea trout exhibited higher densities in unvegetated. Three species were significantly more likely to be caught in saltmarsh: grey mullet (p = 0.028, OR = 2.04), lesser sandeel (p = 0.007, OR = ∞), and three-spined stickleback (p = 0.001, OR = 13.47) (Table 2). No species were significantly more likely to be caught in the unvegetated habitat than in saltmarsh (Table 2).

3.3. Age structure

Combining both seine and fyke netting data juveniles comprised 83 % of all fish recorded during the study. Three species were observed exclusively as juveniles: grey mullet, Atlantic herring, and lesser sandeel (Fig. 3). European bass largely consisted of juveniles, with adults representing just 0.5 % of individuals in the saltmarsh. The piscivorous fish species European bass, European flounder, and sand smelt had a higher proportion of adults in saltmarsh than in the unvegetated habitat.

Fyke netting caught higher proportions of adults than seine netting (26 %–16 %: Fig. S1). The largest European bass caught in a seine net was 33 cm, fyke netting captured a 55 cm European bass.

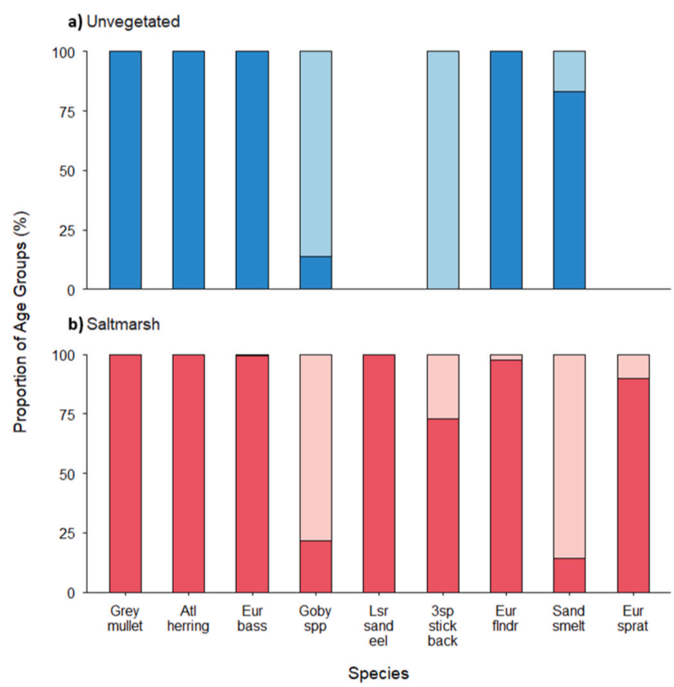

Fig. 3. Representation of juvenile (dark colour) and adult (pale colour) showed that species age compositions differed between a) unvegetated and b) saltmarsh habitats. Empty bars reflect where no data was recorded for the species. Note that there is a small proportion of adult European bass in saltmarsh (0.5 %) not visible on plot. Species with less than 10 total counts were not included. Grey mullet comprises three species (*Chelon labrosus*, *Chelon ramada*, and *Chelon aurata*), while Goby spp. includes common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

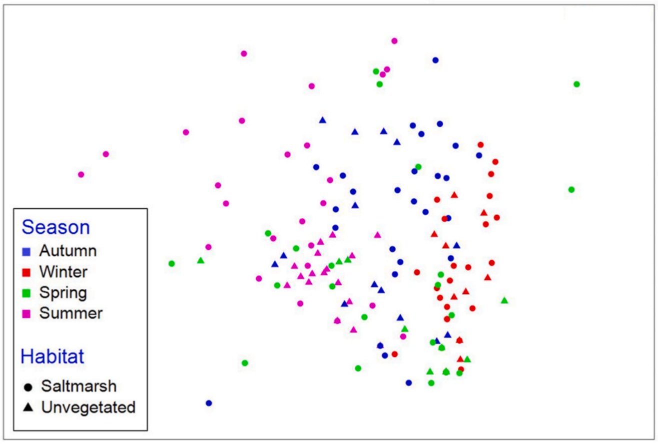

Fig. 4. Fish assemblage data are presented as an nMDS plot with Bray-Curtis similarity. Data were recorded over 170 seine net samples in saltmarsh and unvegetated habitats at five sites between October 2023–September 2024.

3.4. Seasonal patterns

Fish assemblages were significantly affected by season (Pseudo-F = 2.66, $p = 0.001$) and site (Pseudo-F = 2.91, $p = 0.001$). Seasonal changes contributed 24 % of variation, while site differences explain 17 %. The effects of season varied by site (Season x Site: Pseudo-F = 3.83, $p = 0.001$). PERMDISP found the site factor to be heterogenous ($p < 0.05$) and season to be homogenous ($p = 0.1$).

Clear temporal patterns emerged, with pairwise tests revealing differences in community compositions across all seasons ($p \leq 0.01$). The greatest dissimilarity was observed between winter and summer (t = 4.71, $p = 0.001$), while winter and spring were most similar, though still significantly different (t = 1.92, $p = 0.006$).

3.5. Habitat use over time

At the species level, temporal patterns in density exhibited habitat-specific differences (Fig. 5). Peak densities occurred at different times in saltmarsh and unvegetated habitats, with consistently higher relative peaks recorded in saltmarsh. Mean relative densities remained low in the unvegetated habitat throughout most of the year, with only grey mullet and goby species exceeding 10 % of their maximum observed density. In contrast, all species reached densities above 10 % of their respective maxima in saltmarsh.

A pattern emerged in which abundance peaks tended to occur earlier in saltmarsh than in unvegetated shores. For example grey mullet, goby species, and European flounder, peaks in saltmarsh preceded those in unvegetated habitats by a month. Although the unvegetated peak in European bass occurred before the saltmarsh peak, closer examination revealed this pattern still aligns with life-stage habitat preferences: the May peak in unvegetated habitats comprised exclusively of European bass between 5.5 and 11.5 cm, while the June saltmarsh peak consisted predominantly (88 %) of much smaller individuals (1.2–3 cm). This size distribution confirms these are different cohorts.

Saltmarsh assemblage composition varied throughout the year, with no single species dominating across all months. Six species were recorded in saltmarsh during all four seasons (Fig. 5c): grey mullet, Atlantic herring, European bass, goby species, European flounder and three-spined stickleback. Lesser sandeel exhibited a more seasonal pattern, recorded exclusively between April and August. Goby species were most prevalent in the winter months, comprising >45 % of the total catch from November through February. Species composition shifted markedly through spring and summer, with successive dominance of grey mullet (March), lesser sandeel (April), European bass (June), and Atlantic herring (July). The late summer and early autumn months (August, September, and October) exhibited a more balanced assemblage, with no species exceeding 50 % of the total catch. The equivalent monthly assemblage composition for the unvegetated habitat is provided in Fig. S2. As PERMDISP indicated significantly greater multivariate dispersion among saltmarsh samples, the saltmarsh assemblage was retained as the primary focus in the main figure to illustrate the higher compositional variability characteristic of this habitat.

4. Discussion

Our study is the first to examine the fish assemblages of saltmarshes along the west coast of the UK, addressing a notable gap in our understanding of these habitats. We found that fish density was consistently higher in saltmarshes than unvegetated estuarine shores, highlighting their ecological value for coastal fish communities. Systematic sampling revealed the highest fish diversity yet reported from a UK saltmarsh and provided the first evidence of year-round residence by juvenile Atlantic herring and European flounder.

4.1. Importance of saltmarshes for fish communities

Saltmarsh in Carmarthen Bay supported a three-fold higher fish

Table 1
Summary of mean density and size ranges of each recorded species in seine hauls across saltmarsh and unvegetated habitats from October 2023–September 2024. Grey mullet comprises three species (*Chelon labrosus*, *Chelon ramada*, and *Chelon aurata*), while Goby spp. includes common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*). Species are ordered by mean density in saltmarsh.

Species	Saltmarsh					Unvegetated				
	Mean density	SE	Length range		N	Mean density	SE	Length range		N
	ind/ha		(cm)			ind/ha		(cm)		
Atlantic herring (*Clupea herrangus*)	4869	±2737	3.2	−8.5	1823	299	±282	4.7	−9	71
Grey mullet (*Mugilidae spp.)*	3811	±775	1	−18.7	1427	1570	±576	1.9	−44	373
European bass (*Dicentrarchus labrax*)	3309	±1341	0.3	−20.8	1239	1755	±507	1.5	−33	417
Goby (*Pomatoschistus* spp.)	2334	±623	0.8	−6	874	825	±283	1.6	−6.6	196
Lesser sandeel (*Ammodytes tobianus*)	887	±448	3.5	−10.8	332	0	±0			0
Three-spined stickleback (*Gasterosteus aculeatus*)	839	±408	1	−8.2	314	4	±4	4.5	−4.5	1
European flounder (*Platichthys flesus*)	483	±359	1.1	−32.5	181	42	±17	3	−11	10
European sprat (*Sprattus sprattus*)	104	±91	3.5	−7.6	39	0	±0			0
Sand smelt (*Atherina presbyter*)	40	±17	4.5	−11	15	126	±70	2.3	−9	30
European eel (*Anguilla anguilla*)	3	±3	8	−8	1	0	±0			0
Sea trout (*Salmo trutta*)	3	±4	12.2	−12.2	1	4	±4	24.6	−24.6	1
Fifteen-spined stickleback (*Spinachia spinachia*)	3	±5			1	0	±0			0
Topmouth gudegeon (*Pseudorasbora parva*)	3	±6	4.7	−4.7	1	0	±0			0
Worm pipefish (*Nerophis lumbriciformis*)	3	±7			1	0	±0			0
Greater pipefish (*Syngnathus acus*)	0	±0			0	17	±17	6.5	−8.5	4

Table 2
Habitat association between saltmarsh and unvegetated shores of 15 fish species in Carmarthen Bay estuaries. Seine netting presence/absence data were analysed using Fishers exact. Odds ratios are not shown for species that were only present in one habitat, as this generates a ratio of infinity. Grey mullet comprises three species (*Chelon labrosus*, *Chelon ramada*, and *Chelon aurata*), while Goby spp. includes common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*). Species are ordered by mean density in saltmarsh (Table 1).

Species	Odds Ratio	Direction	P Value	Significance
Atlantic herring	2.64	Saltmarsh	0.133	
Grey mullet	2.04	Saltmarsh	0.028	*
European bass	0.93	Unvegetated	0.875	
Goby spp.	1.05	Saltmarsh	1.000	
Lesser sandeel	–	Saltmarsh	0.007	*
Three-spined stickleback	13.47	Saltmarsh	0.001	*
European flounder	1.53	Saltmarsh	0.492	
European sprat	–	Saltmarsh	0.158	
Sand smelt	0.83	Unvegetated	0.780	
European eel	–	Saltmarsh	1.000	
Sea trout	0.63	Unvegetated	1.000	
Fifteen-spined stickleback	–	Saltmarsh	1.000	
Topmouth gudegeon	–	Saltmarsh	1.000	
Worm pipefish	–	Saltmarsh	1.000	
Greater pipefish	0.00	Unvegetated	0.388	

density than adjacent unvegetated habitat. Although overall diversity and species composition did not differ significantly between habitats, the saltmarsh assemblage was significantly more variable, with seven species recorded exclusively in saltmarsh. These findings reinforce the widely accepted ecological principle that structured estuarine habitats like saltmarsh, seagrass, and mangroves enhance fish communities respective to unvegetated habitats (Green et al., 2012; Whitfield, 2017).

Carmarthen Bay saltmarshes support high fish species richness among UK saltmarshes. A total of 19 species were recorded, exceeding the 14 species previously reported (Green et al., 2009). Six species were present year-round, a higher number than those reported in Essex and eastern Ireland, which only recorded two and four species respectively (Green et al., 2009; Koutsogiannopoulou and Wilson, 2007). Notably, this includes the first evidence of Atlantic herring and European flounder using UK saltmarshes as year-round juvenile habitats. This elevated species richness may reflect regional ecological differences, although it could also be influenced by the high frequency sampling approach using the combination of both seine and fyke netting, compared to more limited sampling regimes employed in previous studies. In the Celtic Sea, Baited Remote Underwater Video surveys of kelp and seagrass habitats recorded 22 fish species in kelp and 36 in seagrass (Furness and Unsworth, 2020). Our recorded richness for saltmarshes reached approximately 86 % of that in kelp and 52 % of that in seagrass. Similar patterns have been reported elsewhere, with saltmarshes supporting fish assemblages comparable in density to macroalgal habitats but lower than those of seagrass (Minello et al., 2003).

Across both habitats, juveniles heavily dominated the catch, consistent with the well-documented role of estuaries as nurseries (James et al., 2019; Sheaves et al., 2006, 2015; Whitfield, 2020). However, three species showed strong association with saltmarsh relative to the unvegetated estuarine shores. Among these, grey mullet and lesser sandeel were recorded exclusively as juveniles, suggesting a particularly important nursery function of saltmarsh for these species, as reflected in their significantly higher juvenile presence (Beck et al., 2001). These observations align with previous documentation that saltmarshes provide important resources for juvenile fish (Franco et al., 2010; Joyeux et al., 2017; Rogers et al., 1984; Whitfield, 2017). The absence of any species associations with the unvegetated habitat indicates that they offer comparatively limited value to juvenile fish in Carmarthen Bay.

4.2. Role of saltmarshes for key species

In this study, lesser sandeel were found exclusively in saltmarsh, despite the species being typically associated with soft, sandy substrates suitable for burrowing (Hùines and Bergstad, 2000). Our findings

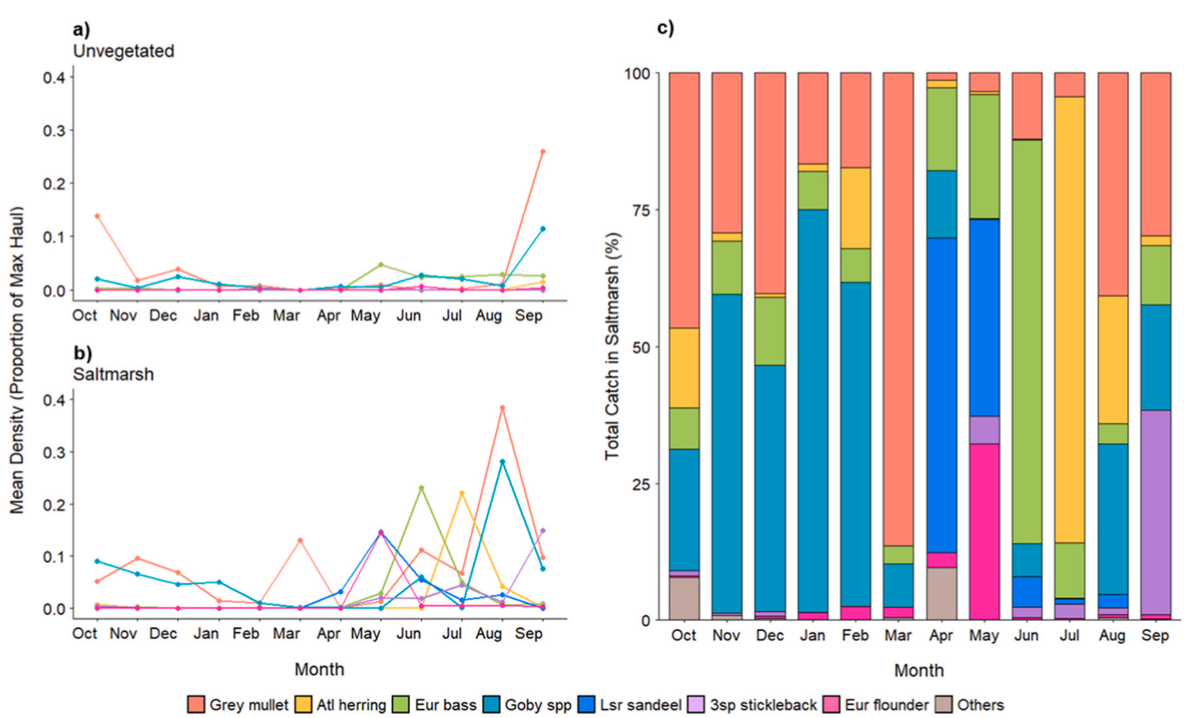

Fig. 5. Maximum total density for a seine haul was normalised to 1 to enhance visualisation of species specific density trends across all months in a) unvegetated and b) saltmarsh habitats. Mean density for each month in each habitat was calculated as a proportion of the maximum total density. c) Monthly saltmarsh fish composition proportionally. Grey mullet comprises three species (*Chelon labrosus, Chelon ramada, and Chelon aurata*), while Goby spp. includes common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*).

suggest that juveniles may use nearby saltmarsh at high tide, potentially for foraging or predator avoidance. Lesser sandeel are a key prey species for a wide range of marine predators (Engelhard et al., 2014; García-Vernet et al., 2021; Staudinger et al., 2020), and their ecological importance has recently led to the closure of the North Sea fishery (UK Government, 2024). Sandeel have not previously been recorded in saltmarshes within the British Isles (Green et al., 2009; Koutsogiannopoulou and Wilson, 2007), suggesting that this may be the first evidence of sandeel using saltmarsh habitats in the region. This may reflect regional variation in habitat use, or alternatively, methodological differences. Our seine net sampling targeted vegetated flats rather than creek systems, and lesser sandeel were captured exclusively by this gear type. This pattern may therefore reflect how sandeel use saltmarshes rather than broader geographical trends.

Saltmarsh habitat also appeared particularly important for Atlantic herring in Carmarthen Bay, with the species largely restricted to saltmarsh throughout the study period, occurring in saltmarsh samples 11 of the 12 months and in unvegetated habitat in only one month. Atlantic herring were recorded exclusively as juveniles. A key distinction of UK saltmarshes compared with other northern European systems is the notable dominance of this species (Green et al., 2009), which is typically recorded at lower abundances or absent elsewhere (Mathieson et al., 2000). These differences likely reflect regional variation in Atlantic herring population distributions and spawning grounds (Brunel and Dickey-Collas, 2010; Haegele and Schweigert, 1985). Given that Atlantic herring are among the UK's most commercially important fish species (Pauly et al., 2020; Peverley and Stewart, 2021), understanding the role of saltmarshes in supporting their early life stages reinforces the ecological and economic value of these habitats and highlights the need to include them in broader fisheries management and conservation strategies.

4.3. Fish assemblage drivers

The fish assemblage documented in this study broadly aligns with patterns observed across the UK and continental Europe, where gobies, grey mullet, and European bass consistently dominate (Cattrijsse et al., 1994; Koutsogiannopoulou and Wilson, 2007; Lafage et al., 2021; Laffaille et al., 2000a; Veiga et al., 2006). Season and site emerged as the primary drivers of community composition.

Site acted as a secondary determinant of fish community composition, suggesting that spatial heterogeneity among saltmarshes influenced assemblage structure in Carmarthen Bay. This indicates that recurring site-specific patterns may underlie the high compositional variation observed across saltmarsh habitats. For example, lesser sandeel were exclusively recorded at Laugharne, between April and August, consistent with their known winter hibernation behaviour (van der Kooij et al., 2008; Winslade, 1974). Similarly, a large influx of post-larval European flounder was observed settling in creeks at Crofty in May. These observations illustrate how seasonal life history traits, local recruitment events, and estuarine connectivity may collectively shape site-level community structures. As no two sites were exposed to identical environmental conditions, site-specific differences likely contributed to the observed spatial variability in fish assemblages (Friese et al., 2018; Garcia et al., 2017; Laffaille et al., 2000a; Sheaves and Johnston, 2008). Comparable patterns have been reported elsewhere, with saltmarsh assemblages in Mont-Saint-Michel Bay also strongly influenced by site characteristics (Lafage et al., 2021).

All seasons differed significantly from one another, reinforcing the strong seasonal structuring of coastal fish assemblages (Laffaille et al., 2000a; Maes et al., 2004; Selleslagh and Amara, 2008). Monthly sampling revealed distinct temporal patterns, with different species reaching peak abundance at specific times during spring and summer. These staggered peaks align with known spawning and recruitment periods, suggesting that many of these species may have evolved temporally separated early life stages that minimises direct competition for resources, although sampling across multiple years would be needed to verify this. Such temporal separation is particularly important during critical developmental phases, when access to food and suitable habitat can strongly influence survival rates, a pattern well documented in estuarine systems worldwide (Day et al., 2012; Shuai et al., 2016; Strydom, 2015). The timing of these shifts is consistent with established life history strategies; for instance, lesser sandeel spawns in winter, leading to peak juvenile abundance in April and May (Campanella and Van Der Kooij, 2021), whereas European bass recruits slightly later, reaching highest densities in June (Lincoln et al., 2024). While previous studies have typically relied on quarterly or seasonal sampling, our high-resolution monthly data reveal that coarser temporal approaches may overlook finer-scale habitat use patterns. The rapid shifts observed in species dominance highlight the dynamic nature of estuarine fish assemblages and emphasise the importance of temporal resolution when designing monitoring programmes. However, as with any sampling regime, large incidental catches of schooling species such as mullet and Atlantic herring may obscure true seasonal trends, reinforcing the need for multi-year datasets to distinguish consistent temporal patterns from short-term variability.

4.4. Age structured habitat use

Species density peaks showed clear temporal differences between the two habitats, indicating both spatial and temporal partitioning. The absence of synchronous density peaks between saltmarsh and unvegetated habitats for any species suggests these habitats serve different purposes at various life stages. As fish develop, their habitat requirements often shift, with many species moving to areas where reduced structural complexity facilitates more efficient foraging by larger individuals that are less susceptible to predation (Grønkjær et al., 2007; Perry et al., 2018). In our study, grey mullet densities peaked in saltmarsh during August but in unvegetated shores during September. For European bass, the saltmarsh peak represented young-of-the-year fish, whereas the unvegetated peak corresponded to year-one individuals. This size-specific habitat partitioning demonstrates that fish populations use multiple habitats sequentially as they develop, with saltmarshes primarily supporting early developmental stages and unvegetated shores accommodating larger juveniles; a pattern that underscores the need to preserve habitat mosaics within connected estuarine seascapes (Nagelkerken et al., 2015; Perry et al., 2018). Collectively, these findings provide strong evidence for life stage dependent habitat-use patterns in coastal fish communities.

In apparent contrast to the ontogenetic habitat shift, we observed higher proportions of adult carnivorous fish, including European bass, European flounder, and sand smelt, in saltmarsh compared with the unvegetated habitat. The presence of larger predatory fish in saltmarsh may seem unexpected given the generally low levels of predation reported for estuarine systems (Whitfield, 2020). However, larger piscivores are known to use shallow marsh habitats (Rountree and Able, 1997) and are likely attracted to areas of high prey availability (Baker and Sheaves, 2021). The traditional focus on saltmarshes as nursery habitats may have led to an underrepresentation of adult predatory fish in previous studies. Future research explicitly targeting adult use of UK coastal nursery habitats would help clarify the extent to which these environments also support larger predatory individuals.

4.5. Conclusions

Our study demonstrates that saltmarshes support higher density of juvenile fish compared with adjacent unvegetated habitats. Clear habitat preferences for saltmarsh were identified among several species. While the importance of saltmarsh habitat for juvenile fish is evident, our findings also reveal an ontogenetic shift in habitat use away from saltmarsh towards unvegetated shores as fish increase in size, highlighting the ecological significance of habitat mosaics within estuarine systems for supporting multiple life stages.

This study provides the first year-round assessment of saltmarsh fish assemblages on the west coast of the UK, including direct comparison with adjacent unvegetated habitats, and contributes valuable baseline evidence for the ecological value of saltmarshes. Future research into the nursery function of saltmarshes and their connectivity with adult populations will further enhance understanding of their contribution to fisheries sustainability and coastal ecosystem functioning (Ciotti et al., 2025).

CRediT authorship contribution statement

Sasha L. Shute: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Lauren M. Pennack:** Writing – review & editing, Investigation. **Alex Scorey:** Writing – review & editing. **Ida A. Nielsen:** Writing – review & editing, Funding acquisition, Conceptualization. **Richard K.F. Unsworth:** Writing – review & editing, Validation, Supervision, Methodology. **Nicole Esteban:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author used Claude.ai in order to improve readability. After using this tool/service, the author reviewed and edited the content as needed and takes full responsibility for the content of the published article.

Funding

We acknowledge support from Natural Resources Wales (NRW) (contract number IN/marine fish/2023).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to the Wetlands and Wildfowl Trust (WWT) and National Trust for allowing us to access their sites in Llanelli and North Gower. All sampling was approved by a Welsh Government dispensation (reference DISP092 (23/10/2019-15/10/2024)). We appreciated support and guidance from Steve Colclough to standardise sampling protocols with other studies in the UK. We thank the MarCEL interns and students from Swansea University that assisted with field work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109599.

Data availability

Data will be made available on request.

References

Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol. Monogr. 83, 557–574. https://doi.org/10.1890/12-2010.1.

Baker, R., Sheaves, M., 2021. Predation in littoral habitats is a complex process: comment on Whitfield (2020). Mar. Ecol. Prog. Ser. 662, 205–208. https://doi.org/10.3354/meps13677.

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., Sheridan, P.F., Weinstein, M.P., 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51, 633–641. https://doi.org/10.1641/0006-3568(2001)051[0633:TICAMO]2.0.CO;2.

Bertelli, C.M., Unsworth, R.K.F., 2014. Protecting the hand that feeds us: Seagrass (Zostera marina) serves as commercial juvenile fish habitat. Mar. Pollut. Bull. 83, 425–429. https://doi.org/10.1016/j.marpolbul.2013.08.011.

Boesch, D.F., Turner, R.E., 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7, 460–468. https://doi.org/10.2307/1351627.

Brunel, T., Dickey-Collas, M., 2010. Effects of temperature and population density on von Bertalanffy growth parameters in Atlantic herring: a macro-ecological analysis. Mar. Ecol. Prog. Ser. 405, 15–28. https://doi.org/10.3354/meps08491.

Burrows, R., Yates, N.C., Hedges, T.S., Li, M., Zhou, J.G., Chen, D.Y., Walkington, I.A., Wolf, J., Holt, J., Proctor, R., 2009. Tidal energy potential in UK waters. Proc. Inst. Civ. Eng.: Marit. Eng. 162, 155–164. https://doi.org/10.1680/maen.2009.162.4.155.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. Annu. Rev. Ecol. Systemat. 27, 477–500. https://doi.org/10.1146/annurev.ecolsys.27.1.477.

Campanella, F., Van Der Kooij, J., 2021. Spawning and Nursery Grounds of Forage Fish in Welsh and Surrounding Waters Distribution of Adult and Juvenile Forage Fish Species During Autumn and Winter.

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. Mar. Ecol. Prog. Ser. 109, 195–208. https://doi.org/10.3354/meps109195.

Ciotti, B.J., Brown, E.J., Colloca, F., Eggleston, D.B., Hyman, A.C., Le Pape, O., Lipcius, R. N., Maathuis, M.A.M., Poiesz, S.S.H., Rose, K.A., Seitz, R.D., Ventura, D., van de Wolfshaar, K.E., 2025. Measuring juvenile habitat quality for fishes and invertebrates. Biol. Rev. 100. https://doi.org/10.1111/brv.70050, 000–000.

Clarke, K.R., Gorley, R.N., 2015. PRIMER v7 : User Manual/Tutorial.

Colclough, S., Cucknell, A., 2018. Estuary Edges 2018 - a Survey of Fish Populations Associated with a Series of Artificial Habitat Structures in the Thames Estuary. London.

Colclough, S., Fonseaca, T., Astley, T., Thomas, K., Watts, W., 2005. Fish utilisation of managed realignments. Fish. Manag. Ecol. 1–10. https://doi.org/10.1111/j.1365-2400.2005.00467.x.

Crinall, S.M., Hindell, J.S., 2004. Assessing the use of saltmarsh flats by fish in a temperate Australian embayment. Estuaries 27, 728–739. https://doi.org/10.1007/BF02907656.

Day, J.W., Crump, ByronC., Kemp, MichaelW., Yanez-Arancibia, A., 2012. Estuarine Ecology, Estuarine Ecology. Wiley. https://doi.org/10.1002/9781118412787.

de la Barra, P., Skov, M.W., Lawrence, P.J., Schiaffi, J.I., Hiddink, J.G., 2022. Tidal water exchange drives fish and crustacean abundances in salt marshes. Mar. Ecol. Prog. Ser. 694, 61–72. https://doi.org/10.3354/meps14118.

Doolan, G., Hynes, S., 2023. Ecosystem service valuation of blue carbon habitats: a review for saltmarshes and seagrasses. J. Ocean Coast. Econ. 10. https://doi.org/10.15351/2373-8456.1174.

Engelhard, G.H., Peck, M.A., Rindorf, A., Smout, S.C., Van Deurs, M., Raab, K., Andersen, K.H., Garthe, S., Lauerburg, R.A.M., Scott, F., Brunel, T., Aarts, G., Van Kooten, T., Dickey-Collas, M., 2014. Forage fish, their fisheries, and their predators: who drives whom? ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 71, 90–104. https://doi.org/10.1093/icesjms/fst087.

Franco, A., Elliott, M., Franzoi, P., Nunn, A., Hänfling, B., Colclough, S., Young, M., 2022. Study methods: field equipment, sampling and methods. Fish and Fisheries in Estuaries: a Global Perspective, first ed. John Wiley & Sons Ltd. https://doi.org/10.1002/9781119705345.app1.

Franco, A., Fiorin, R., Zucchetta, M., Torricelli, P., Franzoi, P., 2010. Flounder growth and production as indicators of the nursery value of marsh habitats in a Mediterranean lagoon. J. Sea Res. 64, 457–464. https://doi.org/10.1016/j.seares.2010.01.006.

Franco, A., Quintino, V., Elliott, M., 2015. Benthic monitoring and sampling design and effort to detect spatial changes: a case study using data from offshore wind farm sites. Ecol. Indic. 57, 298–304. https://doi.org/10.1016/j.ecolind.2015.04.040.

Freeman, H.A., Hepburn, L.J., Taylor, M.I., Hunter, E., Dumbrell, A.J., Gregson, B.H., Smith, A.J., Lamphierre, A., Cameron, T.C., 2024. What makes a habitat a home? Habitat associations of juvenile European sea bass, Dicentrarchus labrax, in estuarine nurseries. J. Fish. Biol. 105, 539–556. https://doi.org/10.1111/jfb.15791.

Friese, J., Temming, A., Dänhardt, A., 2018. Grazing management affects fish diets in a Wadden Sea salt marsh. Estuar. Coast Shelf Sci. 212, 341–352. https://doi.org/10.1016/j.ecss.2018.07.014.

Furness, E., Unsworth, R.K.F., 2020. Demersal fish assemblages in ne atlantic seagrass and kelp. Diversity 12, 1–13. https://doi.org/10.3390/d12100366.

Garcia, A.M., Winemiller, K.O., Hoeinghaus, D.J., Claudino, M.C., Bastos, R., Correa, F., Huckembeck, S., Vieira, J., Loebmann, D., Abreu, P., Ducatti, C., 2017. Hydrologic pulsing promotes spatial connectivity and food web subsidies in a subtropical coastal ecosystem. Mar. Ecol. Prog. Ser. 567, 17–28. https://doi.org/10.3354/meps12060.

García-Vernet, R., Borrell, A., Víkingsson, G., Halldórsson, S.D., Aguilar, A., 2021. Ecological niche partitioning between baleen whales inhabiting Icelandic waters. Prog. Oceanogr. 199, 102690. https://doi.org/10.1016/j.pocean.2021.102690.

Green, A.E., Unsworth, R.K.F., Chadwick, M.A., Jones, P.J.S., 2021. Historical analysis exposes catastrophic seagrass loss for the United Kingdom. Front. Plant Sci. 12. https://doi.org/10.3389/fpls.2021.629962.

Green, B.C., Smith, D.J., Earley, S.E., Hepburn, L.J., Underwood, G.J.C., 2009. Seasonal changes in community composition and trophic structure of fish populations of five salt marshes along the Essex coastline, United Kingdom. Estuar. Coast Shelf Sci. 85, 247–256. https://doi.org/10.1016/j.ecss.2009.08.008.

Green, B.C., Smith, D.J., Underwood, G.J.C., 2012. Habitat connectivity and spatial complexity differentially affect mangrove and salt marsh fish assemblages. Mar. Ecol. Prog. Ser. 466, 177–192. https://doi.org/10.3354/meps09791.

Grønkjær, P., Carl, J.D., Rasmussen, T.H., Hansen, K.W., 2007. Effect of habitat shifts on feeding behaviour and growth of 0 year-group flounder Platichthys flesus (L.) transferred between macroalgae and bare sand habitats. J. Fish. Biol. 70, 1587–1605. https://doi.org/10.1111/j.1095-8649.2007.01447.x.

Haegele, C.W., Schweigert, J.F., 1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Can. J. Fish. Aquat. Sci. 42, s39–s55. https://doi.org/10.1139/f85-261.

Hahn, P.K.J., Bailey, R.E., Ritchie, A., 2007. Beach seining. In: Salmonid Field Protocols Handbook: Techniques for Assessing Status and Trends in Salmon and Trout Populations. American Fisheries Society, Bethesda, Maryland, pp. 267–323.

Hampel, H., Cattrijsse, A., Mees, J., 2004. Changes in marsh nekton communities along the salinity gradient of the Schelde river, Belgium and the Netherlands. Hydrobiologia 515, 137–146. https://doi.org/10.1023/B:HYDR.0000027325.16156.6c.

Harrison-Day, V., Prahalad, V., Kirkpatrick, J.B., McHenry, M., 2020. A systematic review of methods used to study fish in saltmarsh flats. Mar. Freshw. Res. 72, 149–162. https://doi.org/10.1071/MF20069.

Heck, K.L., Hays, G., Orth, R.J., 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. Mar. Ecol. Prog. Ser. 253, 123–136. https://doi.org/10.3354/meps253123.

Hùines, A.È.S., Bergstad, O.A., 2000. Density of wintering sand eel in the sand recorded by grab catches. Fish. Res. 49, 295–302.

James, N.C., Leslie, T.D., Potts, W.M., Whitfield, A.K., Rajkaran, A., 2019. The importance of different juvenile habitats as nursery areas for a ubiquitous estuarine-dependent marine fish species. Estuar. Coast Shelf Sci. 226, 106270. https://doi.org/10.1016/j.ecss.2019.106270.

JNCC, 2015. Carmarthen Bay and Estuaries/Bae Caerfyrddin ac Aberoedd: Standard Data Form (Site UK0020020). UK National Site Network of European Sites [WWW Document]. https://sac.jncc.gov.uk/site/UK0020020. (Accessed 18 October 2025).

Jørgensen, C., Holt, R.E., 2013. Natural mortality: its ecology, how it shapes fish life histories, and why it may be increased by fishing. J. Sea Res. 75, 8–18. https://doi.org/10.1016/j.seares.2012.04.003.

Joyeux, E., Carpentier, A., Corre, F., Haie, S., Pétillon, J., 2017. Impact of salt-marsh management on fish nursery function in the bay of Aiguillon (French Atlantic coast), with a focus on European sea bass diet. J. Coast Conserv. 21, 435–444. https://doi.org/10.1007/s11852-017-0501-0.

King, S.E., Lester, J.N., 1995. The value of salt marsh as a sea defence. Mar. Pollut. Bull. 30, 180–189. https://doi.org/10.1016/0025-326X(94)00173-7.

Koutsogiannopoulou, V., Wilson, J.G., 2007. The fish assemblage of the intertidal salt marsh creeks in North Bull Island, Dublin Bay: seasonal and tidal changes in composition, distribution and abundance. Hydrobiologia 588, 213–224. https://doi.org/10.1007/s10750-007-0664-z.

Lafage, D., Carpentier, A., Duhamel, S., Dupuy, C., Feunteun, E., Lesourd, S., Pétillon, J., 2021. Site characteristics more than vegetation type influence food web structure of intertidal salt marshes. Front. Mar. Sci. 8, 669759. https://doi.org/10.3389/fmars.2021.669759.

Laffaille, P., Feunteun, E., Lefeuvre, J.C., 2000a. Composition of fish communities in a European macrotidal salt marsh (the Mont Saint-Michel Bay, France). Estuar. Coast Shelf Sci. 51, 429–438. https://doi.org/10.1006/ecss.2000.0675.

Laffaille, P., Lefeuvre, J.-C., Feunteun, E., 2000b. Impact of sheep grazing on juvenile sea bass, Dicentrarchus labrax L., in tidal salt marshes. Biol. Conserv. 96, 271–277. https://doi.org/10.1016/S0006-3207(00)00081-1.

Lefcheck, J.S., Hughes, B.B., Johnson, A.J., Pfirrmann, B.W., Rasher, D.B., Smyth, A.R., Williams, B.L., Beck, M.W., Orth, R.J., 2019. Are coastal habitats important nurseries? A meta-analysis. Conserv. Lett. 12, 1–12. https://doi.org/10.1111/conl.12645.

Lincoln, H., Robins, P.E., Wilmes, S.B., Pérez-Mayol, S., Moore, A., Simpson, S., Goward-Brown, A., Heney, C., Malham, S., Morales-Nin, B., Hold, N., McCarthy, I.D., 2024. Predicting potential spawning areas of European bass, Dicentrarchus labrax, in the Irish and Celtic seas. Fish. Res. 270, 106884. https://doi.org/10.1016/j.fishres.2023.106884.

Lyons, J., 1986. Capture efficiency of a beach seine for seven freshwater fishes in a north-temperate lake. N. Am. J. Fish. Manag. 6, 288–289. https://doi.org/10.1577/1548-8659(1986)6<288:ceoabs>2.0.co;2.

Maes, J., Van Damme, S., Meire, P., Ollevier, F., 2004. Statistical modeling of seasonal and environmental influences on the population dynamics of an estuarine fish community. Mar. Biol. 145, 1033–1042. https://doi.org/10.1007/s00227-004-1394-7.

Mathieson, S., Cattrijsse, A., Costa, M.J., Drake, P., Elliott, M., Gardner, J., Marchand, J., 2000. Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. Mar. Ecol. Prog. Ser. 204, 225–242. https://doi.org/10.3354/meps204225.

May, V.J., Hansom, J.D., 2003. Carmarthen Bay. In: Clayton, K.M., Bird, E.C.F. (Eds.), Coastal Geomorphology of Great Britain, Geological Conservation Review Series. JNCC, Peterborough.

McKinley, E., Ballinger, R.C., Beaumont, N.J., 2018. Saltmarshes, ecosystem services, and an evolving policy landscape: a case study of Wales, UK. Mar. Pol. 91, 1–10. https://doi.org/10.1016/j.marpol.2018.01.021.

Minello, T., Able, K., Weinstein, M., Hays, C., 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar. Ecol. Prog. Ser. 246, 39–59. https://doi.org/10.3354/meps246039.

Munro, J.L., Bell, J.D., 1997. Enhancement of marine fisheries resources. Rev. Fish. Sci. 5, 185–222. https://doi.org/10.1080/10641269709388597.

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 Fish. 16, 362–371. https://doi.org/10.1111/faf.12057.

Neu, C.W., Byers, C.R., Peek, J.M., 1974. A technique for analysis of utilization-availability data. J. Wildl. Manag. 38, 541–545. https://doi.org/10.2307/3800887.

ONS and Defra, 2016. Food and Rural Affairs. In: Scoping UK coastal margin ecosystem accounts. Office for National Statistics, Newport, UK.

Ortiz-Burgos, S., 2016. Shannon-Weaver diversity index. In: Kennish, M.J. (Ed.), Encyclopedia of Estuaries. Encyclopedia of Earth Sciences Series, pp. 572–573. https://doi.org/10.1007/978-94-017-8801-4_233.

Pauly, D., Zeller, D., Palomares, M.L.D., 2020. Sea Around Us Concepts, Design and Data (seaaroundus.org). [WWW Document].

Perry, D., Staveley, T.A.B., Gullström, M., 2018. Habitat connectivity of fish in temperate shallow-water seascapes. Front. Mar. Sci. 4, 1–12. https://doi.org/10.3389/fmars.2017.00440.

Pétillon, J., McKinley, E., Alexander, M., Adams, J.B., Angelini, C., Balke, T., Griffin, J. N., Bouma, T., Hacker, S., He, Q., Hensel, M.J.S., Ibáñez, C., Macreadie, P.I., Martino, S., Sharps, E., Ballinger, R., de Battisti, D., Beaumont, N., Burdon, D., Daleo, P., D'Alpaos, A., Duggan-Edwards, M., Garbutt, A., Jenkins, S., Ladd, C.J.T., Lewis, H., Mariotti, G., McDermott, O., Mills, R., Möller, I., Nolte, S., Pagès, J.F., Silliman, B., Zhang, L., Skov, M.W., 2023. Top ten priorities for global saltmarsh restoration, conservation and ecosystem service research. Sci. Total Environ. 898. https://doi.org/10.1016/j.scitotenv.2023.165544.

Peverley, M., Stewart, J.E., 2021. Fisheries Research & Management Plan: European Sea Bass (*Dicentrarchus labrax*) in the North of Devon and Severn IFCA's District. Devon and Severn Inshore Fisheries and Conservation Authority & North Devon Biosphere. 57 pp + appendices.

Pierce, C.L., Rasmussen, J.B., Leggett, W.C., 1990. Sampling littoral fish with a seine: corrections for variable capture efficiency. Can. J. Fish. Aquat. Sci. 47, 1004–1010. https://doi.org/10.1139/f90-115.

R Core Team, 2024. R: a Language and Environment for Statistical Computing.

Ribeiro, J., Carvalho, G.M., Gonçalves, J.M.S., Erzini, K., 2012. Fish assemblages of shallow intertidal habitats of the Ria Formosa lagoon (South Portugal): influence of habitat and season. Mar. Ecol. Prog. Ser. 446, 259–273. https://doi.org/10.3354/meps09455.

Rogers, S.G., Targett, T.E., Van Sant, S.B., 1984. Fish-Nursery use in Georgia Salt-marsh estuaries: the influence of springtime freshwater conditions. Trans. Am. Fish. Soc. 113 (2), 595–606. https://doi.org/10.1577/1548-8659(1984)113<595:fuigse>2.0.co.

Rountree, R.A., Able, K.W., 1997. Nocturnal fish use of New Jersey Marsh creek and adjacent Bay Shoal habitats. Estuar. Coast Shelf Sci.

Selleslagh, J., Amara, R., 2008. Environmental factors structuring fish composition and assemblages in a small macrotidal estuary (eastern English Channel). Estuar. Coast Shelf Sci. 79, 507–517. https://doi.org/10.1016/j.ecss.2008.05.006.

Sheaves, M., Baker, R., Johnston, R., 2006. Marine nurseries and effective juvenile habitats : an alternative view. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps318303.

Sheaves, M., Baker, R., Nagelkerken, I., Connolly, R.M., 2015. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. Estuaries Coasts 38, 401–414. https://doi.org/10.1007/s12237-014-9846-x.

Sheaves, M., Johnston, R., 2008. Influence of marine and freshwater connectivity on the dynamics of subtropical estuarine wetland fish metapopulations. Mar. Ecol. Prog. Ser. 357, 225–243. https://doi.org/10.3354/meps07292.

Shuai, F., Li, X., Li, Y., Li, J., Yang, J., Lek, S., 2016. Temporal patterns of larval fish occurrence in a large subtropical river. PLoS One 11. https://doi.org/10.1371/journal.pone.0146441.

Stamp, T., West, E., Colclough, S., Plenty, S., Ciotti, B., Robbins, T., Sheehan, E., 2023. Suitability of compensatory saltmarsh habitat for feeding and diet of multiple estuarine fish species. Fish. Manag. Ecol. 30, 44–55. https://doi.org/10.1111/fme.12599.

Staudinger, M.D., Goyert, H., Suca, J.J., Coleman, K., Welch, L., Llopiz, J.K., Wiley, D., Altman, I., Applegate, A., Auster, P., Baumann, H., Beaty, J., Boelke, D., Kaufman, L., Loring, P., Moxley, J., Paton, S., Powers, K., Richardson, D., Robbins, J., Runge, J., Smith, B., Spiegel, C., Steinmetz, H., 2020. The role of sand lances (Ammodytes sp.) in the Northwest Atlantic Ecosystem: a synthesis of current knowledge with implications for conservation and management. Fish Fish. 21, 522–556. https://doi.org/10.1111/faf.12445.

Strydom, N.A., 2015. Patterns in larval fish diversity, abundance, and distribution in temperate South African estuaries. Estuaries Coasts 38, 268–284. https://doi.org/10.1007/s12237-014-9801-x.

Taylor, M.D., Gaston, T.F., Raoult, V., 2018. The economic value of fisheries harvest supported by saltmarsh and mangrove productivity in two Australian estuaries. Ecol. Indic. 84, 701–709. https://doi.org/10.1016/j.ecolind.2017.08.044.

UK Centre for Ecology & Hydrology, 2022. Unlocking billion-pound investment in restoration of saltmarshes [WWW Document]. URL. https://www.ceh.ac.uk/news-and-media/news/unlocking-billion-pound-investment-restoration-saltmarshes. (Accessed 8 April 2025).

UK Government, 2024. The Sandeel (Prohibition of Fishing) (Scotland) Order 2024.

van der Kooij, J., Scott, B.E., Mackinson, S., 2008. The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. J. Sea Res. 60, 201–209. https://doi.org/10.1016/j.seares.2008.07.003.

Veiga, P., Vieira, L., Bexiga, C., Sá, R., Erzini, K., 2006. Structure and temporal variations of fish assemblages of the Castro Marim salt marsh, southern Portugal. Estuar. Coast Shelf Sci. 70, 27–38. https://doi.org/10.1016/j.ecss.2006.05.037.
Whitfield, A.K., 2020. Littoral habitats as major nursery areas for fish species in estuaries: a reinforcement of the reduced predation paradigm. Mar. Progr. Ser. 649, 219–234. https://doi.org/10.3354/meps13459.
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. Rev. Fish Biol. Fish. 27, 75–110. https://doi.org/10.1007/s11160-016-9454-x.
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis.
Wildfowl & Wetlands Trust, 2023. WWT awarded £21 million to restore coastal saltmarsh in UK [WWW Document]. URL. https://www.wwt.org.uk/news-and-stories/news/wwt-awarded-21-million-to-restore-coastal-saltmarsh-in-uk. (Accessed 8 April 2025).
Winslade, P., 1974. Behavioural studies on the lesser sandeel Ammodytes marinus (Raitt) II. The effect of light intensity on activity. J. Fish. Biol. 6, 577–586. https://doi.org/10.1111/j.1095-8649.1974.tb05100.x.