Estimating production of finfish in saltmarshes on the South Wales coast

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Comisiynwyd y prosiect hwn gan Cyfoeth Naturiol Cymru (CNC) i ddarganfod a allai adfer cynefinoedd morfa heli wella cynhyrchiant poblogaethau pysgod morol ac aberol yn effeithiol, gan fynd i'r afael ag anghenion tystiolaeth hanfodol o dan Reoliadau Cadwraeth Cynefinoedd a Rhywogaethau 2017. Gan fod creu morfeydd heli yn cael ei gynnig fwyfwy i wrthbwyso effeithiau gweithgareddau dynol fel cloddio am agregau a dal mewn systemau dŵr oeri, bydd yr ymchwil hon yn darparu data hanfodol i werthuso hyfywedd creu morfeydd heli a chefnogi gwneud penderfyniadau sy'n seiliedig ar dystiolaeth.

Mae morfeydd heli yn hysbys fel cynefinoedd magu pwysig i bysgod ifanc, ond nid yw eu rôl wrth gefnogi cynhyrchiant pysgod wedi'i deall yn llawn eto. Yn fyd-eang, bu dirywiad o 50% mewn cynefinoedd morfeydd heli, sydd wedi arwain at gynnydd mewn prosiectau adfer. Mae'r astudiaeth hon yn amcangyfrif cynhyrchiant pysgod mewn tri math o gynefinoedd aberol: morfa heli naturiol, adlinio a reolir (morfa heli wedi'i hadfer), a glannau heb lystyfiant.

Dull gweithredu
Dros gyfnod o 12 mis, cynhaliwyd arolygon misol gan ddefnyddio rhwydi sân a *fyke* ar draws 17 safle yn aberoedd Bae Caerfyrddin. Cofnodwyd rhywogaethau, niferoedd a meintiau pysgod i gyfrifo cyfanswm y cynhyrchiant pysgod. Amcangyfrifwyd cynhyrchiant pysgod gan ddefnyddio'r Dull Crynhoi Cynyddrannol.

Canlyniadau allweddol

- Roedd morfeydd heli naturiol yn cynnal dwysedd, biomas a chynhyrchiant pysgod uwch na chynefinoedd heb lystyfiant neu gynefinoedd adlinio a reolir.
- Ar gyfer penwaig, llymrïaid, crethyll tri phigyn, lledod mwd a physgod ystlys arian, dim ond yn y cynefin morfa heli naturiol y gellid mesur cynhyrchiant.
- Ar hyn o bryd, rydym yn cael chwe rhywogaeth ym morfeydd heli naturiol De Cymru drwy gydol y flwyddyn.
- Defnyddiwyd mathau o gynefinoedd yn wahanol gan bysgod ar wahanol gyfnodau eu bywydau, gan ddangos pwysigrwydd mosaig o gynefinoedd.

Casgliad a goblygiadau
Mae canfyddiadau'r ymchwil hon yn tynnu sylw at rôl hanfodol morfeydd heli naturiol wrth gynnal poblogaethau pysgod amrywiol. Nid yw'r safle adlinio a reolir wedi cyflawni swyddogaeth ecolegol lawn morfeydd heli naturiol eto, fel y dangosir gan ddwyseddau, biomas a chynhyrchiant pysgod is.

Arwyddocâd y canfyddiadau
Dyma'r astudiaeth gyntaf yn y DU i amcangyfrif cynhyrchiant pysgod mewn cynefinoedd morfa heli. Mae'r canlyniadau'n darparu data sylfaenol hanfodol ar gyfer deall cymunedau pysgod morfa heli yn Ne Cymru. Mae'r canfyddiadau hyn yn pwysleisio pwysigrwydd morfeydd heli ar gyfer cynhyrchiant pysgod ac yn awgrymu bod angen datblygu'r adlinio a reolir ymhellach i efelychu manteision ecolegol llawn

morfeydd heli naturiol. Bydd yr ymchwil hon yn helpu i arwain ymdrechion adfer yn y dyfodol ac yn llywio arferion rheoli.

Mae canfyddiadau allweddol yn ymwneud â natur dymhorol mewn dwysedd ac amrywiaeth pysgod ifanc mewn morfeydd heli wedi'u cyhoeddi yn Shute, S.L., Pennack, L.M., Scorey, A., Nielsen, I.A., Unsworth, R.K.F., Esteban, N., 2025. Mae dwysedd pysgod mewn morfa heli yng ngogledd-ddwyrain Cefnfor yr Iwerydd dair gwaith yn uwch na glannau heb lystyfiant. Estuar. Coast. Shelf Sci. 327, 109599. https://doi.org/10.1016/j.ecss.2025.109599.

Executive summary

Background

Natural Resources Wales (NRW) commissioned this project to investigate whether saltmarsh habitat restoration can effectively improve productivity of marine and estuarine fish populations, addressing critical evidence needs under the Conservation of Habitats and Species Regulations 2017. As saltmarsh creation is increasingly proposed to offset impacts from human activities like aggregate extraction and cooling water entrapment, this research will provide essential data to evaluate the viability of saltmarsh creation and support evidence-based decision-making.

Saltmarshes are known to be important nursery habitats for juvenile fish, yet their role in supporting fish production is still not fully understood. Globally, there has been a 50% decline in saltmarsh habitats, which has led to a rise in restoration projects. This study estimates fish production in three types of estuarine habitats: natural saltmarsh, managed realignment (restored saltmarsh), and unvegetated shores.

Approach

Over the course of 12 months, monthly surveys were conducted using seine and fyke nets across 17 sites in the Carmarthen Bay estuaries. Fish species, numbers, and sizes were recorded to calculate total fish production. Fish production was estimated using the Increment Summation Method.

Key Results

- Natural saltmarshes supported higher fish density, biomass, and production than unvegetated or managed realignment habitats.
- For Atlantic herring, lesser sandeel, three-spined stickleback, European flounder, and sand smelt production was only measurable in the natural saltmarsh habitat.
- We find six species present in the South Wales natural saltmarshes year-round.
- Habitat types were used differently by different life stages of fish evidencing the importance of a mosaic of habitats.

Conclusion and implications

The findings of this research highlight the essential role of natural saltmarshes in supporting diverse fish populations. The managed realignment site has not yet achieved the full ecological functionality of natural saltmarshes, as shown by lower fish densities, biomass, and production.

Significance of findings

This is the first UK study to estimate fish production in saltmarsh habitats. The results provide crucial baseline data for understanding saltmarsh fish communities in South Wales. These findings emphasise the importance of saltmarshes for fish production and suggest that the managed realignment needs further development to replicate the full ecological benefits of natural saltmarshes. This research will help guide future restoration efforts and inform management practices.

Key findings relating to seasonality in density and diversity of juvenile fish in saltmarsh have been published in Shute, S.L., Pennack, L.M., Scorey, A., Nielsen, I.A., Unsworth, R.K.F., Esteban, N., 2025. Fish density in NE Atlantic saltmarsh is three-fold higher than unvegetated shores. Estuar Coast Shelf Sci 327, 109599. https://doi.org/10.1016/j.ecss.2025.109599.

Introduction

Saltmarshes are dynamic and highly productive intertidal habitats (Townend *et al.*, 2011). The topography of saltmarshes is varied, consisting of three main features: creeks, pools, and flats; the pools and creeks are devoid of vegetation and have soft, muddy benthic substrates that are the first to be submerged on a flooding tide, while the vegetated flats sit above the creeks and pools, typically becoming submerged only towards the higher end of the tidal cycle (Zedler *et al.*, 1999). These combined topographies create a unique environment. Saltmarshes provide ecosystem services including coastal defence, carbon sequestration, water filtration, nutrient cycling, habitat for endangered species, and fish nurseries (McKinley et al., 2018).

The habitat has been listed both as an Annex I natural habitat type of community interest under the Habitats Directive and Conservation of Habitats and Species Regulations 2017, a habitat of principal importance under the Environment (Wales) Act 2016 and a feature of Sites of Special Scientific Interest under the Wildlife and Countryside Act 1981. However, with the combination of sea level rise and anthropogenic developments involving land reclamation, the UK has lost 85% of its saltmarshes over the last 200 years, while globally at least 50% of saltmarsh cover has been lost (Barbier *et al.*, 2011; Hansen and Reiss, 2015).

Natural Resources Wales (NRW) commissioned this project to address one of their priority marine evidence gaps, specifically investigating whether saltmarsh habitat creation and/or restoration can effectively mitigate impacts on marine and estuarine fish populations. The motivation for this research stems from the need for robust evidence to support the use of saltmarsh creation as a compensatory measure for impacts to fish under the Conservation of Habitats and Species Regulations 2017. Given proposals for saltmarsh creation to offset impacts upon fish, NRW requires detailed evidence to ensure that such measures are sufficient to maintain the overall coherence of the National Site Network (NSN). The findings will form part of the evidence base used by NRW to assess the effectiveness of saltmarsh habitat creation as a compensation measure for fish loss, providing a comparison with global data and contributing to evidence-based decision-making in marine habitat management.

Objectives of Study

The overall aim of the study is to advance knowledge of fish assemblages in UK saltmarshes, for four saltmarshes along the coast of South Wales which have not been included in previous studies. This study is the first in the UK to quantify productivity of finfish species from saltmarsh habitat with objectives of (1) assessing variation in fish assemblage between (i) native saltmarsh, (ii) restored saltmarsh and (iii) unvegetated estuarine coastline; (2) analysing spatio-temporal trends in fish assemblages in South Wales; (3) comparing fish assemblage data interannually (October 2022 and 2023); and (4) estimating finfish biomass and production from each habitat surveyed.

1. Ecosystem functioning in UK saltmarshes

UK saltmarshes produce 400 - 500 g/m^2 of organic carbon annually (Boorman, 2003). This production stems from a diverse array of organisms, including plants like sea purslane and cord grass, algae such as water felt and bladderwrack, along with phytoplankton, and microphytobenthos (Polderman, 1978; Svensson *et al.*, 2007).

Invertebrate species are the primary consumers of the resulting production and detritus (Créach *et al.*, 1997). Production from the vegetation and the benthic community provides a range of food sources for juvenile fish as they develop, and their diets change (Boesch and Turner, 1984). For juveniles of predatory fish species such as European bass (*Dicentrarchus labrax*) and European flounder (*Platichthys flesus*), invertebrates are a significant prey source in saltmarshes, comprising amphipods, ragworms, crabs, and shrimp (Hampel *et al.*, 2005). Grey mullets (*Chelon ramada, Chelon labrosus,* and *Chelon aurata*) as detritivores feed on the detritus and algae of saltmarshes (Cardona, 2015).

In addition to provision of food/prey to juvenile fish species, the vegetation and complex topographic structures of saltmarshes provide shelter from predators and strong currents for the juvenile fish (James *et al.*, 2019). Due to the benefits afforded to juvenile fish by the saltmarsh habitat it was theorised that they would serve as optimal nursery grounds for some fish species (Vernberg, 1993).

The drive to create and restore saltmarshes in the UK is partly founded on this exceptional productivity and crucial role as fish habitats. With their high carbon sequestration potential, ability to reduce flood risk by slowing and absorbing storm surge waters and wave energy, and their capacity to support diverse food webs that benefit commercially and ecologically important species, saltmarsh restoration represents a nature-based solution that delivers multiple ecosystem services (McKinley et al., 2018).

2. Research progress on fish use of saltmarshes

Successful recruitment rates are crucial to maintaining a fish population (Caley *et al.*, 1996). Optimal nursery habitats enhance fish populations by offering conditions that favour the growth, development, and protection of the recruiting juveniles (Munro and Bell, 1997). Fish often have R-selected life cycles which means they produce many offspring providing little to no parental care with high juvenile mortality rates (Adams, 1980). Juvenile survival is a critical factor in fish population sustainability, as early life stages are particularly susceptible to environmental pressures and predation (Jørgensen and Holt, 2013). Investigating the nursery habitats contributing to a fish stock is key to understanding how to sustain and protect them (Beck *et al.*, 2001). However, the qualification of what makes a "fish nursery habitat" is highly debated and the current agreed-upon definition stands at "a habitat where a species exhibits higher than average juvenile density, growth, survival or movement to adult habitat" (Lefcheck *et al.*, 2019). Loss of fish nursery habitats reduces the already low juvenile survival rates, significantly impacting the recruitment of adult populations (Rochette *et al.*, 2010; Sundblad *et al.*, 2014).

Fish use of saltmarshes in North America have been extensively researched since the 1970s (Cain and Dean, 1976). Numerous fish species have been identified using North American saltmarshes as a nursery habitat (Endresz, 2020; Rogers *et al.*, 1984; Whitfield, 2017).

Investigation into the saltmarsh fish assemblages in Europe began in the 1980s (Boesch and Turner, 1984; Cattrijsse *et al.*, 1994; Costa *et al.*, 1994; Laffaille *et al.*, 2000). The nursery value of European saltmarshes has not explicitly been assessed, and fish assemblages in UK saltmarshes were not studied until the early 2000s and are spatially limited to southern England (Colclough *et al.*, 2005, 2004; Green *et al.*, 2012, 2009; McCormick *et al.*, 2021; Pickett *et al.*, 2004; Stamp *et al.*, 2023).

Studies in Europe concurs with the North American studies that most fish entering the systems are juveniles (Costa *et al.*, 2001; Joyeux *et al.*, 2017; Lafage *et al.*, 2021; Mathieson *et al.*, 2000; Veiga *et al.*, 2006). However, due to the geographical and geological differences between North American and European saltmarshes, findings on “fish habitat use” in one region may not directly apply to the other, although they still provide valuable insights into the broader trends (Allen, 2000).

Some species like European bass, European flounder, and grey mullet are consistently present in saltmarsh fish assemblages in Europe and the UK (Cattrijsse *et al.*, 1994; Cattrijsse and Hampel, 2006; Colclough *et al.*, 2005), indicating the importance of saltmarshes as a nursery habitat for these species. However, a wider range of species would also be expected to utilise the habitat as juveniles.

3. Development and application of fish production models

Models are useful tools for translating biological complexities into meaningful insights (Allman and Rhodes, 2004) and the first fish production models were developed in the 1970s and include size-based models, age-structured models, and production/biomass (P/B) ratios (Allen, 1971; Cowley and Whitfield, 2002; Dolbeth *et al.*, 2010, 2008; Gillespie and Benke, 1979; MacLeod *et al.*, 2022; Randall and Minns, 2000; Wong and Dowd, 2016). Calculating finfish productivity from a habitat provides a quantitative measure of the ecosystem service provided for both commercial stocks and stocks of conservation species, which can then be compared between different habitats (Seitz *et al.*, 2014). Metrics like productivity translates ecosystem services into understandable terms, making it a useful tool to inform and encourage investment in the conservation and protection of the habitat (Syukur *et al.*, 2021).

Fish productivity in European estuaries and coastal lagoons has been extensively studied, with the Increment Summation Method (ISM) being a prominent approach (Dolbeth *et al.*, 2010, 2008; Erzini *et al.*, 2022; Franco *et al.*, 2010; Pihl and Rosenberg, 1982a). The approach is based on size and categorises fish into distinct cohorts based on lengths and tracks the cohort’s growth over time. The output of this model is in grams (wet weight) produced per square meter annually (g WW m^{-2} $year^{-1}$) (Winberg, 1971). ISM provides a detailed approach to assessing production, where each cohort’s production is assessed individually from one sample event to the next. Through ISM, monthly, seasonal, and annual changes in productivity can be observed on a species level. However, this model only provides insight to the production over the time the study takes place, it does not estimate future production based on growth or mortality values.

In the Minho and Mondego estuaries of Portugal, (Dolbeth *et al.*, 2010) reported production ranging from 0.66 to 6.73 g WW m^{-2} $year^{-1}$ for the five most abundant species. Similarly, Franco et al. (2010) estimated production of European flounder in the Venice Lagoon marshes, Italy, at 0.21 to 0.52 g WW m^{-2} $year^{-1}$.

Another method used to estimate fish production is the Instantaneous Growth method. This method estimates fish production by applying growth rate coefficients (derived from measured changes in weight between sampling events) to the average standing biomass over a time period, rather than directly tracking biomass changes between cohorts as done in ISM (Chapman, 1978). This approach calculates how much new tissue is generated based on how quickly the existing biomass is growing, making it particularly useful when cohort boundaries are unclear or when sampling frequency is limited. This approach was applied to estimate production in the Ria de Aveiro coastal lagoon, Portugal, which ranged from 0.9 to 2.5 g WW m^{-2} $year^{-1}$ (Pombo *et al.*, 2007).

In this study we have used ISM to estimate productivity of commercial and conservation species in saltmarshes, managed realignment, and unvegetated estuarine shores in South Wales for the period of the study. ISM was selected because it allows for direct comparisons between these three estuarine habitats and because of the level of detail it provides, such as high temporal resolution and species-specific insights. It is particularly well-suited for open systems like estuaries, as the model inherently accounts for mortality, emigration, and immigration without requiring additional estimates. Furthermore, ISM offers highly accurate biomass estimations and is a well-established method, making the results comparable to similar studies.

4. Sampling techniques for fish in saltmarshes: fyke and seine nets

As saltmarsh consists of varied terrains, sampling the fish assemblages can be challenging (Adam, 1993). Therefore, to effectively sample fish assemblages in the habitat, a combination of methods is required to account for the full complexity of the environment. Popular methods are drop samplers, pop nets, fyke nets, seine nets, beam trawls, mark and recapture, and acoustic tracking (Harrison-Day *et al.*, 2020; Pickett *et al.*, 2004; Ricci *et al.*, 2017). This study uses a combination of fyke and seine netting, replicating the same methods used in studies based on other UK saltmarshes for direct comparability (Colclough *et al.*, 2005; Elliott and Hemingway, 2002).

Both fyke and seine net techniques have their advantages and disadvantages. Fyke nets generally catch a wider diversity of fish species with lower abundances, while seine nets catch fish in higher frequencies with lower diversity (Crinall and Hindell, 2004). Seine nets are active nets deployed from shore, relatively nonselective but may target mid-water species (Lyons, 1986). Seine nets are also versatile so can be used creatively to suit the topography, which is useful in a dynamic environment (Johnson *et al.*, 2007). Fyke nets are static nets deployed in the creeks of the saltmarsh, filtering the water of the creek through the net on the ebbing tide (Harrison-Day *et al.*, 2020). Fyke nets target benthic species best (Breen and Ruetz, 2006), and may be better than seine netting for capturing highly mobile species, as the movement from seine netting can alert the fish and cause them to move before they are captured. Using these techniques in conjunction maximises data collected in abundance and diversity (Clark *et al.*, 2007; Franco *et al.*, 2022). Seine nets provide reliable density estimates because they sample a clearly defined area, whereas fyke nets yield less precise density data due to their extended deployment periods and continuous water flow (Harrison-Day *et al.*, 2020).

Materials and Methods

1. Study location

This research focuses on the saltmarshes of South Wales' Burry Inlet/Loughor Estuary and Three Rivers (Tywi, Taf, Gwendraeth) estuaries (Figure 1). Natural saltmarsh sites were surveyed over three clusters: North Gower, Llanelli Wetlands, and Laugharne Castle. Cwm Ivy is a managed realignment (recently restored saltmarsh) within the Burry Inlet that was surveyed as a separate cluster. Sea defences at Cwm Ivy have breached, allowing saltmarsh to re-establish. Control sites were selected within the same estuaries, on shores with no saltmarsh vegetation and sandy or muddy benthos (hereafter referred to as "unvegetated"). Two unvegetated clusters were surveyed; one in the Burry inlet at Llanelli Beach, and one in the Three Rivers estuaries at St Ishmael. Each cluster was sampled over a 24 hour period with two fyke netting sites and one seine netting site (except from Llanelli Wetlands with only one fyke netting site). In total seventeen sites were sampled monthly, eight in saltmarshes, three in the managed realignment site, and six in unvegetated sites. From September 2023 to September 2024 surveys were carried out each month. In October 2022, 2023, and 2024 saltmarsh sites, Laugharne and Crofty, were surveyed by seine net (Figure 1).

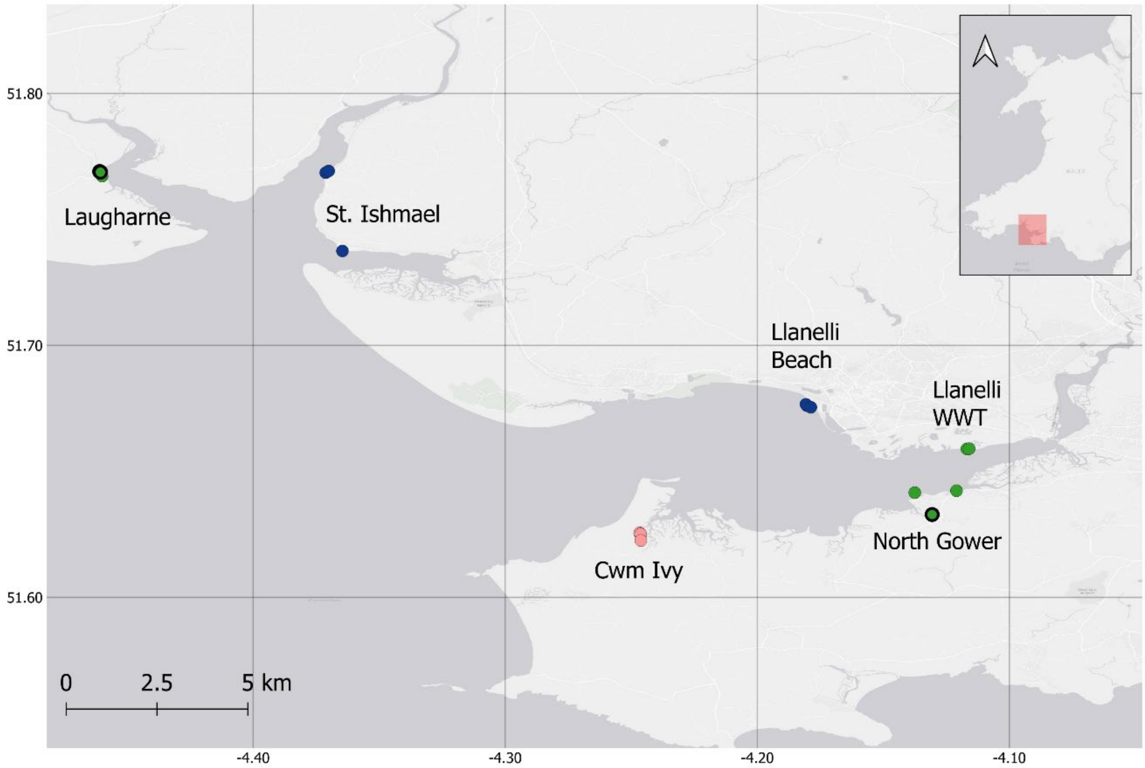


Figure 1 Locations of sites sampled in October 2022, 2023, 2024 (bold black outlines) and sites sampled from October 2023 to September 2024, in South Wales' Carmarthen Bay. Sampling across three habitat types: saltmarsh (green), managed realignment (pink), and unvegetated (blue). Sampling was conducted with both seine nets and fyke nets.

2. Sampling technique: Fyke netting

In saltmarsh creeks, winged fyke nets were deployed: 10 mm mesh wings 5 m long, 8 mm mesh D-ring trap 50 cm high, with a 6.5 mm mesh cod end net (as used in other saltmarsh assessments in the UK e.g. Colclough, 2018). The small mesh sizes ensure juveniles are accounted for in the samples (Stamp *et al.*, 2023). Due to the distinct topographies of saltmarsh habitats, each fyke netting site required a unique sampling plan. Appropriate fyke netting sites were determined by several factors: accessibility, maximising area sampled, and position in relation to other sites. Using local tidal graphs and in-person observations, a fixed tidal height was determined at which the nets were to be deployed on the flooding tide, and a fixed tidal height at which they were to be removed (see tidal heights in Appendix B).

The theory of selective tidal stream transport (STST) is that fish which use STST enter the saltmarsh on the upper water layers of the flooding tide and exit in the deeper water on the ebbing tide (Gibson *et al.*, 2001). The wings of the net face upstream, so that as the tide floods the saltmarsh water (and marine organisms) flow around the net up into the saltmarsh and as the water exits through the creeks the organisms are channelled into the cod end. Nets were retrieved on the ebbing tide when 50 cm of water was left in the creek (top of D-ring visible), to minimise fish mortality by limiting the fish's time out of water and exposure to predation by common shore crab (*Carcinus maenas*). However, nets would occasionally fill with large numbers of crabs in the cod end making it difficult to avoid losses of sampled fish. Fyke nets were placed at the bottom of the creeks on the edge of the saltmarsh to maximise the area sampled. To avoid the entrapment of protected air-breathing animals, such as the Eurasian otter (*Lutra lutra*) and common scoter (*Melanitta nigra*), otter guards were used to cover the mouth of the nets (Larocque *et al.*, 2012).

In unvegetated habitats, fyke nets were set up so that they submerged at the same tidal height as the nearest saltmarsh fyke nets submerged, with the wings set at a 40º angle.

To calculate fish density the area sampled by the fyke net must be known. Flats and creeks higher up the intertidal drain into the fyke nets, all contributing to the area sampled. Using QGIS, a polygon was drawn from the position of the fyke up to the high-water point including all tributaries into the creek (Butcher *et al.*, 2005). The area sampled was estimated as the area within the polygon, this was repeated for each fyke net, see Appendix C.

3. Sampling technique: Seine netting

Seine netting was carried out during the high tide between the set up and retrieval of fyke nets. Site selection ensured no pseudo-replication by choosing areas that would not later drain into the creeks with the previously deployed fyke nets. Seine net sampling took place 30 mins before high tide to 30 mins after, using a 15 m x 2 m, 3 mm knotless mesh net with poles for manoeuvring the net at either end (as used in other saltmarsh fish surveys in the UK e.g. Colclough, 2018). Seine netting was scheduled according to tidal stages, resulting in surveys conducted during both daylight and nighttime hours, depending on the tide times on each survey day. At each seine site, three replicates were taken. When sampling over vegetated saltmarsh flats the standard beach seine methods were employed, ensuring the lead line was tight to the seabed to be effective in pushing the vegetation out of the way (for details see Johnson et al., 2007; Franco et al., 2022). When seine netting in saltmarsh pools both poles started close together at the back of the pool with the lead line sitting on the bottom, the poles were pulled around closely to the sides, with operators joining up at the other end of the pool. Saltmarsh pools were less frequently sampled as they are often entirely covered at high tides. Unvegetated sites were sampled 30 mins before high tide to 30 minutes after, the seine net was used as a typical beach seine. Sites at Llanelli WWT and St Ishmael were not accessible at the full height of a high tide so were sampled on the flooding tide as close to the high tide as possible.

The area sampled in each seine haul was calculated as approximately $36m^2$, assuming the 15m net length formed the arc length for the semi-circle.

4. Data collection

Coordinates of sites were taken in the field using “pin my location” function in Google Maps, later verified with Google Maps satellite imaging. Timings of each netting were recorded, at deployment and retrieval of each net.

Once captured, fish were transferred into a 40 L bucket. Using a hand net, fish were retrieved from the bucket. Individuals were identified to a species level based on photo identification guides. Any individuals that were not identified with certainty in the field were photographed and later identified. The first 15 individuals of each species were measured with a 60 cm WaterMark Ultimate Fish Board. Once measured fish were immediately placed into a filled 40 L bucket and then released back into the water they were taken from (Bertelli & Unsworth, 2014). Fish spent a maximum of 1 minute out of the water. Abundance, lengths, date, gear, habitat type, site name, and timing of deployments were recorded in one data sheet for each sample taken.

5. Data analysis

a) Data organisation

Raw data was entered into Microsoft Excel spreadsheets, with separate sheets for abundance data and length data. Date, gear used, habitat type, site name, area sampled, and timing of deployments were entered in the data sheets for each sample taken. Abundance data was imported into R studio (R Core Team, 2021).

b) Data visualisation

Density was calculated by dividing total abundance by the total area sampled to give number of individuals per hectare. Descriptive statistics for density measures such as total, mean, standard deviation, Standard Error of the Mean (SEM), and range were extracted for each subgrouping (e.g. by habitat or net type).

To assess community composition across the three habitats, sites, and season, non-Metric Multidimensional Scaling (nMDS) was performed using the Bray-Curtis dissimilarity matrix in PRIMER7. The nMDS plot generated during the analysis visually represents the similarity of species composition in each sample. Each point corresponds to a sampling instance, with points that are closer together representing more similar species compositions.

c) Statistical testing

To assess habitat associations of fish species across three distinct habitat types (saltmarsh, managed realignment, and unvegetated), chi-square tests with simulated p-values were employed. Raw abundance data from seine and fyke net sampling were first converted to presence/absence format to standardise comparisons between gear types. For each species, contingency tables showing presence or absence across the three habitat categories were constructed. Due to low occurrence counts for several species, Monte Carlo simulations (10,000 replicates) were used to generate more accurate p-values than traditional chi-square approximations would provide. Habitat association was determined by comparing the percentage occurrence of each species across habitat types, with statistical significance assessed at $\alpha = 0.05$.

Community composition analyses were conducted using PRIMER7 (version 7;Clarke and Gorley, 2015). These analyses were restricted to seine net data to maintain consistency in gear efficiencies and area covered across all samples. 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, month, and season on community composition. Homogeneity of multivariate dispersions was assessed using PERMDISP to test an assumption of PERMANOVA. The PERMDISP analysis revealed heterogeneous dispersion among groups. Multiple data transformations were attempted but did not resolve the dispersion issue. Despite this violation of assumptions, we proceeded with PERMANOVA analysis as it still provides valuable insights when interpreted alongside visualisation methods (Anderson and Walsh, 2013). The nMDS ordination plots derived from the same Bray-Curtis similarity matrices were used to visually confirm patterns identified in the PERMANOVA results, with stress values reported to indicate goodness of fit.

Fish density and Shannon diversity index were calculated for each sample from the interannual data (October 2022, 2023, 2024). Both data sets met normality assumptions, allowing the use of one-way ANOVAs to test the differences in means of each measure throughout the three years. When ANOVA results were significant, Tukey's HSD post-hoc tests were performed to identify specific differences between years.

For the interannual analysis of community composition (October 2022, 2023, 2024 samples from Crofty and Laugharne), an nMDS ordination was generated from a Bray-Curtis similarity matrix. The resulting plot included overlay clusters at 40% and 60% similarity levels. A PERMANOVA was conducted to test the effects of year and site on community composition, with pairwise comparisons performed when significant differences were detected. Homogeneity of multivariate dispersions was tested using PERMDISP, which confirmed that the assumption of homogeneous dispersion was met for the analysis. This validation of PERMANOVA assumptions strengthens the reliability of the statistical results for the interannual comparisons.

d) Estimating fish biomass

The biomass estimation employed a comprehensive approach combining fish abundance data with length-weight relationships. Length measurements were converted to weights using established species-specific length-weight conversion parameters. For species requiring preliminary length-type conversions (fork length to total length), an additional transformation was applied.

The biomass calculation used a proportional approach where length frequencies within each species, site, and month were determined. These proportions were applied to the total abundance counts to estimate the number of individuals at each weight. Biomass was then calculated by multiplying these estimated counts by their corresponding weights. Finally, biomass density (g WW m^{-2}) was derived by dividing the total biomass by the area sampled, allowing for standardised comparisons across sites, habitats, and months. Annual mean biomass, standard errors, and cumulative totals were calculated to summarise temporal patterns in fish biomass distribution.

e) Estimating fish production using increment summation method

Length data was subset by species and habitat type. Data sets were transformed into length frequency files. Length-frequency histograms were generated for each month of sampling for each species in each habitat. Cohorts were identified by significant peaks in the length frequency data. Peaks in the distribution were identified based on two key parameters: (1) minimum threshold - a point in the frequency data was considered for peak evaluation only if its value was at least two; and (2) minimum prominence - a peak was considered significant if it was at least one individual higher than the surrounding values.

Mean length, standard deviation of length, and proportion were calculated for each identified cohort. Cohorts in consecutive months were assessed to determine if they could belong to one cohort, using water temperatures and known growth rates. Once a cohort has been traced through two or more months it can be used to calculate production using the following equations.

To calculate the total abundance of each cohort the proportion of the cohort in the length sample was multiplied by the total abundance of the species in that subset.

$$Total\ of\ cohort\ in\ month\ t = Proportion\ of\ cohort\ in\ measured\ individuals\ in\ month\ t \times total\ number\ of\ species\ recorded\ in\ month\ t$$

Density of a cohort was determined by using the previously calculated “area sampled” and the total abundance of the cohort.

$$Density\ of\ cohort\ in\ month\ t = Total\ of\ cohort\ in\ month\ t \div Total\ area\ sampled\ in\ month\ t$$

The mean length of each cohort each month was extracted and converted into wet weight (g) using species-specific length-weight equations published on FishBase.se (see Appendix E for values and references). All calculations were repeated for the same cohort in the consecutive month. Density and mean wet weight were then inputted to the Increment Summation Equation.

$$P_{cn} = \sum_{t=1}^{t=0} \left(\frac{N_t + N_{t+1}}{2}\right) \times (W_{t-1} - W_t)$$

The resulting value is production in grams per square metre for the time between the first sample event to the second. This was repeated for every consecutive month for each identifiable cohort. All months were summed together to give a value in grams per metre squared annually (g WW m^{-2} year $^{-1}$) for that species.

Only seine netting data was used for both biomass and production calculations due to uncertainty with fyke net area estimations and efficiencies. All individuals considered in the production estimation were juveniles, as adults were rarely present and when they were numbers were too low for cohort detection.

Results

Over one year of monthly surveys and 3 years of October surveys, totalling 82 days of field work and 373 netting events, 10,999 individual finfish across 21 species were recorded. Of these, 7,270 were from seven commercially and recreationally important species: Atlantic herring (*Clupea harengus*), European sprat (*Sprattus sprattus*), European bass (*Dicentrarchus labrax*), Thinlip mullet (*Chelon ramada*), Thicklip mullet (*Chelon labrosus*), Golden mullet (*Chelon aurata*), and European flounder (*Platichthys flesus*). Additionally, 350 individuals were recorded from three species of conservation importance: lesser sandeel (*Ammodytes tobianus*), sea trout (*Salmo trutta*), and European eel (*Anguilla anguilla*) (Table 1). Juveniles comprised 83% of all individuals recorded during the study. Five species were observed exclusively as juveniles: grey mullet, Atlantic herring, lesser sandeel, sea trout, and European eel (as yellow eels).

For subsequent analyses, all mullet species are grouped under 'grey mullet,' as they all belong to the genus Chelon and are not distinguished at the species level in either commercial or recreational fisheries. Similarly, common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*) are combined as 'goby species' for the analysis.

Table 1 Summary of fish recorded at saltmarsh habitats from October 2023 – September 2024, totals (N), estimated mean densities (ind/ha) per sample with ± SE and size ranges (cm). Data are presented separately for seine net and fyke net sampling methods to highlight habitat-specific and method-specific variations. Species with < 10 total counts were excluded, with the exception of species of conservation interest, marked with an *. Grey mullet group comprises three species (*Chelon labrosus, Chelon ramada*, and *Chelon aurata*), while Goby spp. group includes common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*).

Species	**Net**	**Saltmarsh Mean Density(ind/ha)**	**+/- SE**	**Saltmarsh Size range (cm)**	**Saltmarsh *N***
Grey mullet species	S	3811	±775	1.1-18.7	1427
Grey mullet species	F	5.58	±2.77	1.8-10.6	275
Atlantic herring	S	4869	±2737	3.2-8.5	1823
Atlantic herring	F	1.55	±0.84	4.5-10.5	186
European bass	S	3309	±1341	0.3-20.8	1239
European bass	F	4.77	±1.95	3.2-55	186
Goby spp.	S	2334	± 623	0.8-6	874
Goby spp.	F	5.57	± 2.27	1.2-9.2	408
Lesser sandeel	S	886	±447	3.5-10.8	332
Lesser sandeel	F	0	-	-	0
Three-spined stickleback	S	838	±408	1-8.2	315
Three-spined stickleback	F	0.03	±0.03	4.1-4.7	2
European flounder	S	483	±358	1.1-32.5	181
European flounder	F	0.07	±0.03	10-23	10
Sand smelt	S	40	±17	4.5-11	15
Sand smelt	F	0	-	-	0
European sprat	S	104	±91	3.5-7.6	39
European sprat	F	0.01	±0.01	7.5-7.5	1
European eel*	S	2	±2	8 - 8	1
European eel*	F	0	-	-	0
Sea trout*	S	2	±2	12.2 - 12.2	1
Sea trout*	F	0.07	±0.07	22.8-22.8	1

Table 2 Summary of fish recorded at unvegetated habitats from October 2023 – September 2024, totals (N), estimated mean densities (ind/ha) per sample with ± SE and size ranges (cm). Data are presented separately for seine net and fyke net sampling methods to highlight habitat-specific and method-specific variations. Species with < 10 total counts were excluded, with the exception of species of conservation interest, marked with an *. Grey mullet group comprises three species (*Chelon labrosus, Chelon ramada*, and *Chelon aurata*), while Goby spp. group includes common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*).

Species	Net	Unvegetated Mean Density (ind/ha)	+/- SE	Unvegetated Size range (cm)	Unvegetated *N*
Grey mullet species	S	1517	±551	1.9-13	377
Grey mullet species	F	1.48	±0.89	3.6-19	8
Atlantic herring	S	285	±269	4.7- 9	71
Atlantic herring	F	0			0
European bass	S	1702	±486	1.5-33	423
European bass	F	8.94	±4.22	3.4-20	56
Goby species	S	793	± 271	1.6-6.6	197
Goby species.	F	1.48	± 0.89	3.5-7.5	22
Lesser sandeel	S	0	-	-	0
Lesser sandeel	F	0	-	-	0
Three-spined stickleback	S	4	±4	4.5-4.5	1
Three-spined stickleback	F	0	-		0
European flounder	S	48	±18	3 - 11	12
European flounder	F	0.73	±0.52	5.2-9.6	7
Sand smelt	S	120	±66	2.3-8.8	30
Sand smelt	F	0	-	-	0
European sprat	S	0	-	-	0
European sprat	F	0	-	-	0
European eel*	S	0	-	-	0
European eel*	F	0	-	-	0
Sea trout*	S	4	±4	24.6-24.6	1
Sea trout*	F	0	-	-	0

Table 3 Summary of fish recorded at managed realignment habitats from October 2023 – September 2024, totals (N), estimated mean densities (ind/ha) per sample with ± SE and size ranges (cm). Data are presented separately for seine net and fyke net sampling methods to highlight habitat-specific and method-specific variations. Species with < 10 total counts were excluded, with the exception of species of conservation interest, marked with an *. Grey mullet group comprises three species (*Chelon labrosus, Chelon ramada*, and *Chelon aurata*), while Goby spp. group includes common goby (*Pomatoschistus microps*) and sand goby *Pomatoschistus minutus*).

Species	Net	Managed Realignment Mean Density (ind/ha)	+/- SE	Managed Realignment Size range (cm)	Managed Realignment *N*
Grey mullet species	S	574	± 453	1.4-7.4	62
Grey mullet species	F	0.56	± 0.15	3.4-22.5	46
Atlantic herring	S	0	-	-	0
Atlantic herring	F	0	-	-	0
European bass	S	1500	± 551	1.5-6.2	162
European bass	F	2.05	± 1.28	2.5-38	109
Goby spp.	S	675	± 225	0.9-3.8	73
Goby spp.	F	5.50	± 2.86	2.5-5.3	548
Lesser sandeel	S	0	-	-	0
Lesser sandeel	F	0	-	-	0
Three-spined stickleback	S	0	-	-	0
Three-spined stickleback	F	0	-	-	0
European flounder	S	0	-	-	0
European flounder	F	0.06	± 0.04	5-10	4
Sand smelt	S	0	-	-	0
Sand smelt	F	0	-	-	0
European sprat	S	0	-	-	0
European sprat	F	0	-	-	0
European eel*	S	0	-	-	0
European eel*	F	0.14	± 0.05	21.5-38	13
Sea trout*	S	0	-	-	0
Sea trout*	F	0	-	-	0

1. Fish density by habitat

When comparing seine net samples across habitats, saltmarsh habitat had higher mean monthly densities for nine out of eleven species (Table 1). Notably, grey mullet species (3811 ind/ha, SE ± 775), Atlantic herring (4869 ind/ha SE ± 2737), and European bass (3309 ind/ha, SE ± 1341) reached their greatest densities in saltmarsh. Only sand smelt (40 ind/ha, SE ± 17) and sea trout (4 ind/ha, SE ± 4) exhibited highest densities in unvegetated habitat. No species reached their highest density in the managed realignment.

Mean monthly densities from fyke net samples showed a different pattern for some species. Saltmarsh still supported the highest densities for six species: grey mullet (5.58 ind/ha, SE ± 2.77), Atlantic herring (1.55 ind/ha, SE ± 0.84), goby species (5.57 ind/ha, SE ± 2.27), and three-spined stickleback (0.03 ind/ha, SE ± 0.03). However, European bass and European flounder showed higher densities in unvegetated habitat (8.94 ind/ha, SE ± 4.22 and 0.73 ind/ha, SE ± 0.52, respectively) than in saltmarsh. Managed realignment showed the highest density only for European eel (0.14 ind/ha, SE ± 0.05).

Based on exclusively seine net data, the total density of fish species was highest in saltmarsh habitat, with 16,700 ind/ha (6255 individuals caught), followed by the unvegetated habitat at 4490 ind/ha (1116 individuals caught), and the managed realignment at 2750 ind/ha (297 individuals caught). All species had higher total densities in the saltmarsh than in any other habitat (Figure 2). In species which were recorded in all three habitats (grey mullet species, European bass and goby species) all had the highest density in saltmarsh, then unvegetated and the lowest density in the managed realignment.

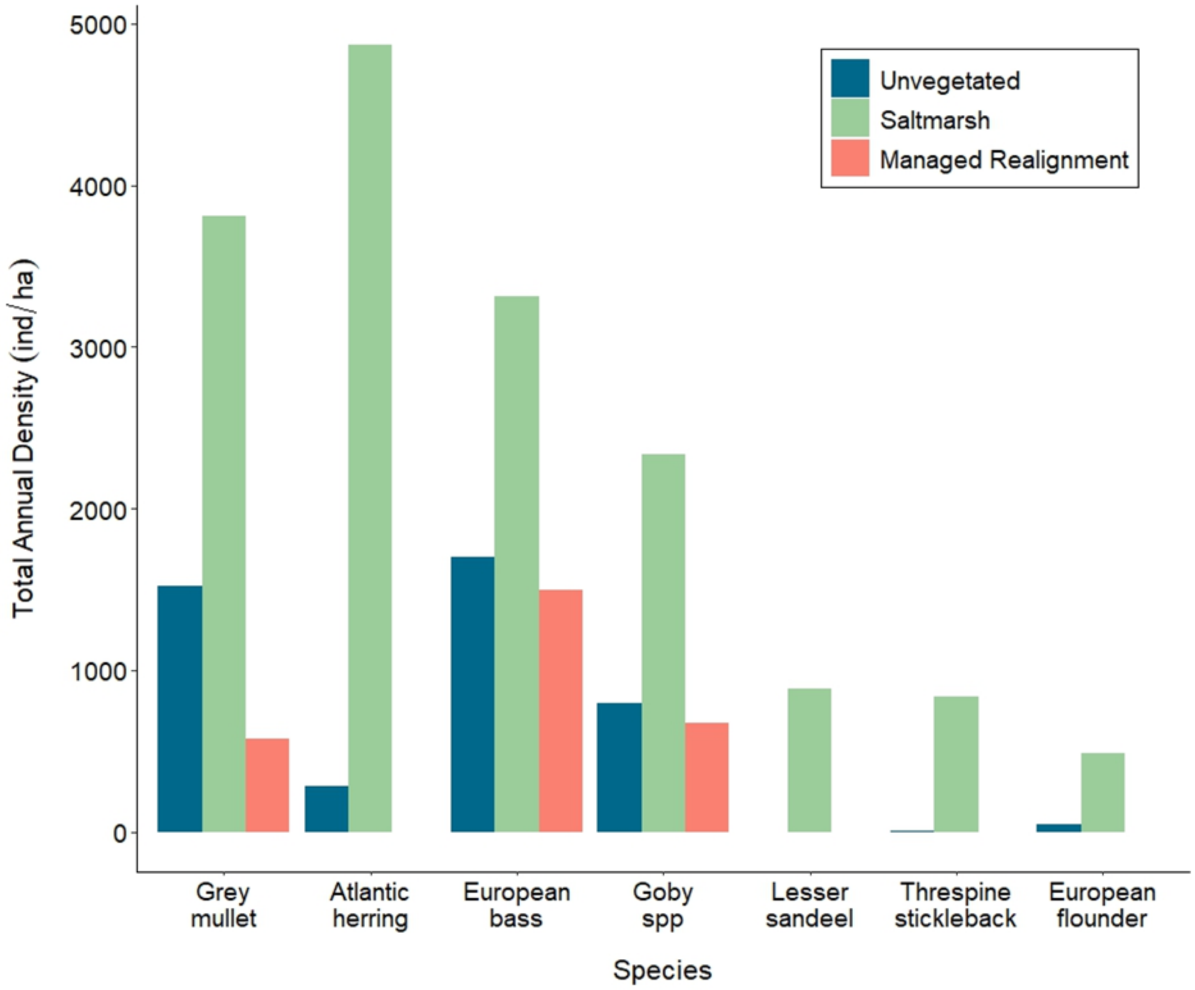


Figure 2 European bass and grey mullet species showed particularly high densities across all habitat types, with Atlantic herring demonstrating the highest overall density in natural saltmarsh. Some species (lesser sandeel, three-spined stickleback, and European flounder) were recorded at very low densities or were absent entirely from unvegetated and managed realignment habitats. The total annual density (individuals per ha) of the 7 most abundant species across three habitat types. This data is representative of seine netting only.

2. Species-specific habitat associations

Four of the eleven species were significantly more likely to be caught in saltmarsh habitat: Atlantic herring ($\chi^2 = 20.2$, $p < 0.001$), three-spined stickleback ($\chi^2 = 15.6$, $p = 0.001$), lesser sandeel ($\chi^2 = 9.4$, $p = 0.01$), and grey mullet ($\chi^2 = 7.7$, $p = 0.02$). European eel was the only species significantly more likely to be caught at the managed realignment site than the other habitats ($\chi^2 = 31.6$, $p < 0.001$). The remaining six species showed no habitat associations ($p > 0.05$). In unvegetated habitats while some species had higher densities, no species were significantly more likely to be caught here, than in other habitats (Table 2).

Table 4 Species-specific habitat associations based on chi-square analysis. Habitat preferences of eleven fish species sampled using seine and fyke nets from October 2023 to September 2024. Four species showed significant preference for saltmarsh habitat, one species significantly preferred the managed realignment site, and none showed significant preference for unvegetated habitats.

Species	Chi Square	P Value	Preferred Habitat
Grey mullet	7.7	0.02	Saltmarsh
Atlantic herring	20.2	<0.001	Saltmarsh
European bass	1.5	0.5	-
Goby species	1.6	0.5	-
Lesser sandeel	9.4	0.01	Saltmarsh
Three-spined stickleback	15.6	0.001	Saltmarsh
European flounder	3.7	0.2	-
Sand smelt	3.0	0.2	-
European sprat	4.6	0.1	-
Sea trout	0.6	1	-
European eel	31.6	<0.001	Managed realignment

3. Drivers of community composition

Overall fish communities showed no distinct separation between habitat types ($F = 1.02$, $p = 0.424$). However, site and season influenced species composition, with site accounting for 15% of variation and season accounting for 30% (site: $F = 2.99$, $p = 0.001$; season: $F = 3.92$, $p = 0.001$).

While habitat types did not exhibit distinct species compositions, saltmarsh habitats demonstrated greater variability than either managed realignment or unvegetated habitats (mean dispersion: saltmarsh = 1.1, unvegetated = 0.8, managed realignment = 0.7). These patterns are reflected in the nMDS plot (Figure 3), which shows substantial overlap in species composition across all habitats, with saltmarsh points displaying a noticeably wider spread than unvegetated and managed realignment habitats. Heterogeneity of these dispersions were confirmed ($p < 0.05$). The nMDS ordination provided a good representation of the data, with a stress value of 0.18.

Pairwise tests revealed differences in community compositions across all seasons ($p \leq 0.003$). The greatest dissimilarity was observed between winter and summer ($t = 5.49$, $p = 0.001$), followed by spring and summer ($t = 4.89$, $p = 0.001$). While still significant, winter and spring showed the least dissimilarity ($t = 1.92$, $p = 0.003$).

Most individual sites exhibited distinct compositions, with 11 out of 15 possible site comparisons showing differences ($p < 0.05$). Non-significant differences were found between: Llanelli Wetlands and Ferryside ($p = 0.675$), Llanelli Wetlands and Cwm Ivy ($p = 0.095$), Llanelli Beach and Cwm Ivy ($p = 0.743$), and Llanelli Wetlands and Llanelli Beach ($p = 0.047$, marginally significant). The site comparisons with the strongest differences were Laugharne and Cwm Ivy ($t = 3.10$, $p = 0.001$) and Laugharne and Llanelli Beach ($t = 3.16$, $p = 0.001$).

Additionally, a significant interaction was detected between site and month ($F = 4.08$, $p = 0.001$), suggesting that seasonal effects on species composition varied among sites. The interaction between habitat and season was not significant ($F = 1.02$, $p = 0.461$).

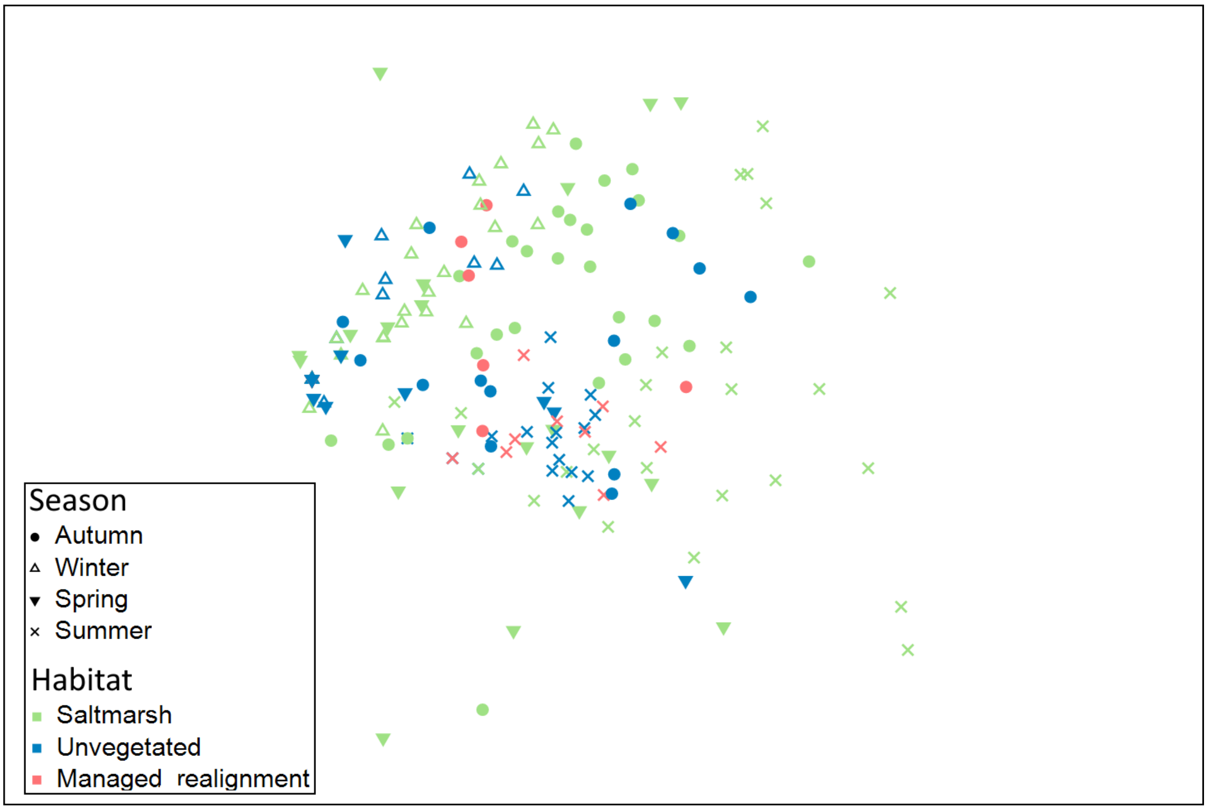


Figure 3 Fish assemblages recorded within 200 seine net samples from October 2023 – September 2024, at six locations in South Wales. Data are presented as an nMDS plot with Bray-Curtis similarity. The species composition of all habitats shows considerable overlap, indicating similar species compositions. The saltmarsh habitat species composition show a wider spread indicating more variation in species composition.

4. Temporal and spatial trends in fish density

Spatial and temporal patterns in fish density varied considerably across the study area. At the site level, saltmarsh locations showed the highest species-specific densities, with saltmarsh site Laugharne supporting peak densities for four species (Atlantic herring, grey mullet species, European bass, and lesser sandeel) and Crofty supporting peak densities for three species (goby species, three-spined stickleback, and European flounder) (Figure 4). For Atlantic herring and lesser sandeel, the Laugharne site alone accounted for more than 80% of their total recorded densities across all habitats. Similarly, three-spined stickleback and European flounder showed similar concentration patterns at Crofty (>80% of total densities).

Among non-saltmarsh sites, Ferryside (unvegetated) had the highest density for sea trout, while Cwm Ivy (managed realignment) supported the highest density of European eels.

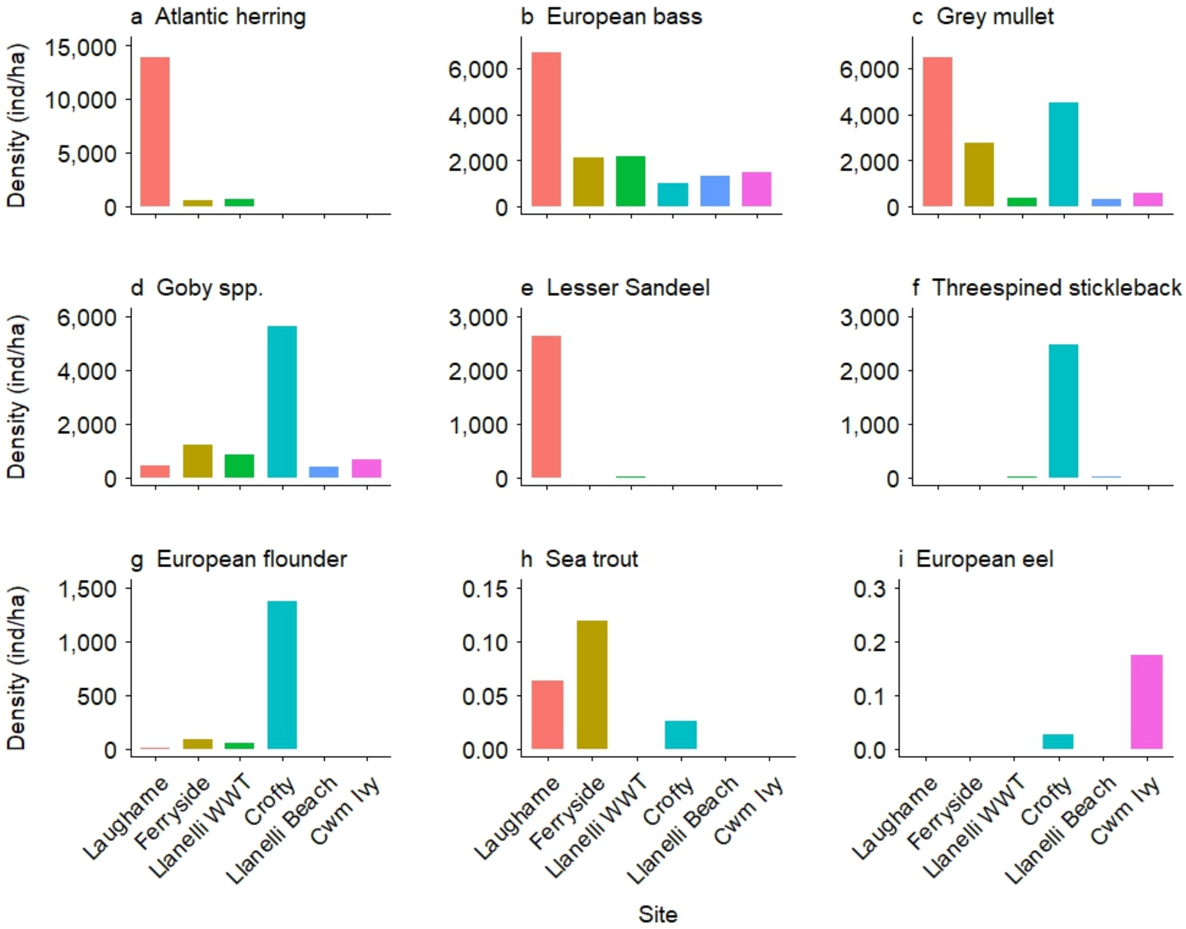


Figure 4 The saltmarsh site at Laugharne had the highest overall density for four species. European eel density peaked at the Cwm Ivy site. Saltmarsh sites include Laugharne (red), Llanelli WWT (green), and Crofty (turquoise). Unvegetated sites include Ferryside (yellow) and Llanelli Beach (blue). The managed realignment site consists solely of Cwm Ivy (pink). The densities shown represent the total annual density at each site. Please note the variability in y axis scale. Data for plots a – g are from seine netting only. Data for plots h and i are from both seine and fyke netting, as there would only be 1-2 data points for these species without fyke netting data.

Temporally, fish species exhibited distinct seasonal density patterns across all sites, habitats and estuaries (Figure 5). Atlantic herring, European bass, and grey mullet species densities peaked during summer months, while goby species, three-spined stickleback, and sea trout showed density maxima in autumn. Lesser sandeel and European flounder densities both peaked in spring. Three-spined stickleback density peaked in early Autmn and Sea trout peaked later in Autumn.

Species-specific density magnitudes varied considerably. Atlantic herring reached the highest monthly density of any species, exceeding 100 individuals per ha in July, while sea trout had the lowest maximum at just 0.15 individuals per ha. Most species showed elevated densities for only one to three months annually, followed by relatively low values during the remainder of the year. Exceptions included grey mullet, goby species, and European eel, which maintained more consistent densities throughout the annual cycle.

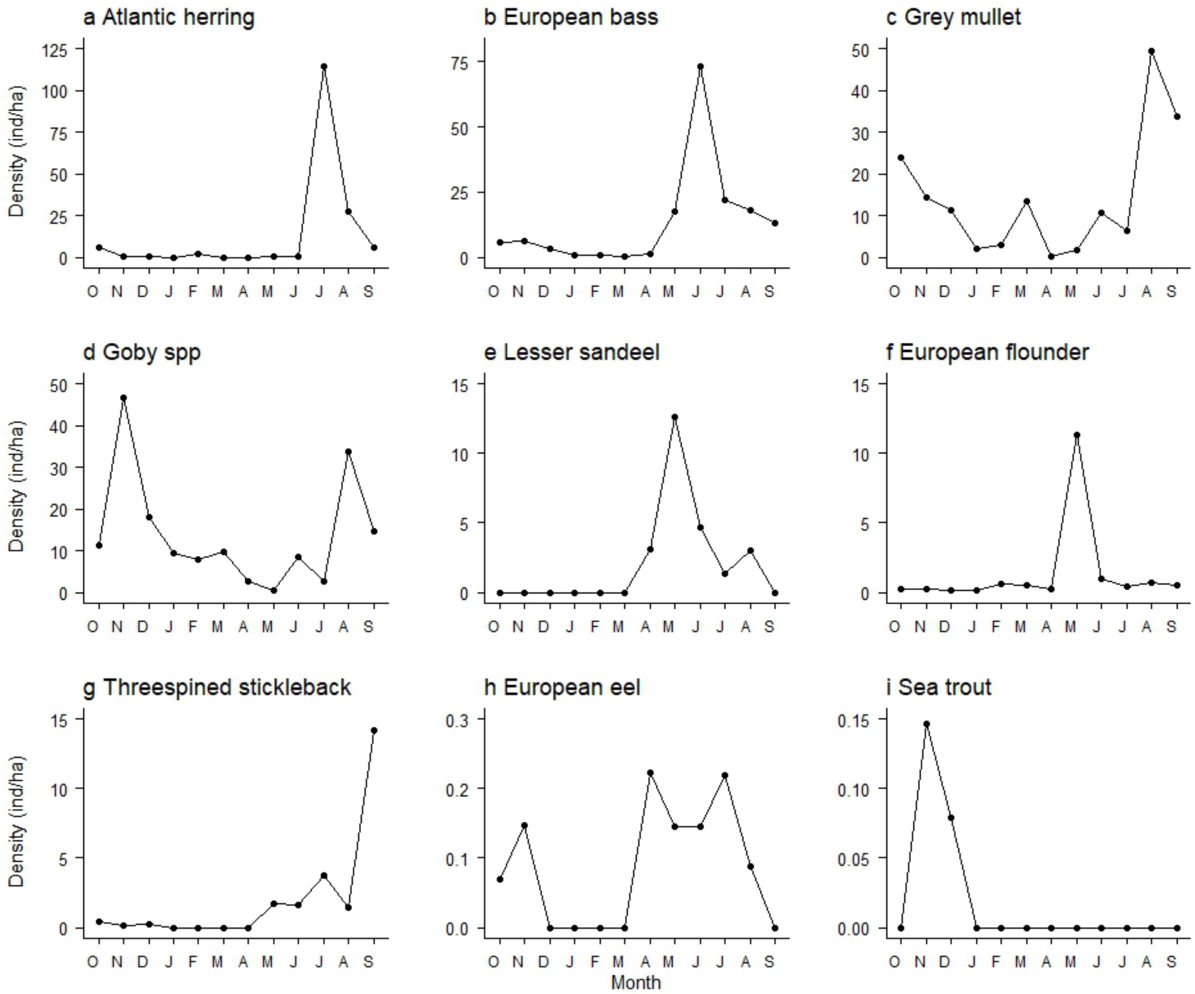


Figure 5 Atlantic herring had the highest monthly density of any species surpassing 100 individuals per ha in July, while sea trout had the lowest peak at just 0.15 individuals per ha. Total monthly densities for each species are shown from October 2023 to September 2024. Species exhibited distinct seasonal peaks, with some reaching maximum density in the summer (e.g., Atlantic herring, European bass), while others peaked in autumn (e.g., three-spined stickleback, goby species, sea trout). Data are compiled across all three habitat types, and both netting types to give an overview of species density trends in the estuaries South Wales. Please note the variability in y axis.

Monthly densities analysed by habitat type revealed distinct variations in the timing of peak densities for the same species (Figure 6). This habitat-specific seasonality was evident across multiple species. For example, goby species reached peak density at different times in each habitat: June in managed realignment, August in saltmarsh, and September in unvegetated habitat. European bass densities peaked synchronously in June in both saltmarsh and managed realignment habitats, but earlier (May) in unvegetated habitat. Grey mullet species showed the opposite pattern, with synchronous peaks in September in unvegetated and managed realignment habitats, but an earlier peak (August) in saltmarsh. Notably, no species exhibited simultaneous density peaks in both saltmarsh and unvegetated habitats.

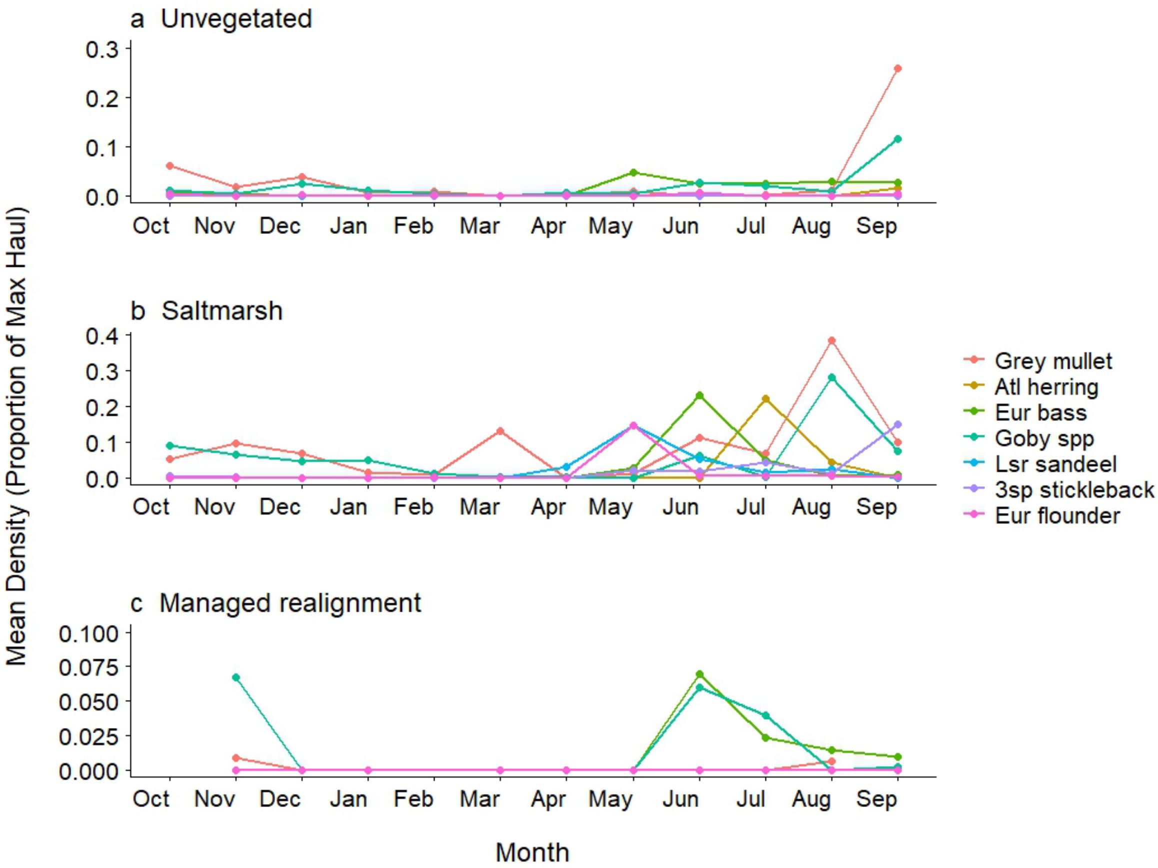


Figure 6 In each species maximum total density for a seine haul was normalised to 1 to enhance visualisation of density trends across all months in all habitats. Mean density for each month in each habitat was calculated as a proportion of the maximum total density for that species. The timing of peak densities for the same species varies between habitats, with consistently higher densities observed in the saltmarsh habitat, even during winter. 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*). Please note the variability in y axis. This data is representative of seine netting only.

5. Year-on-year fish abundance comparison

For two of the saltmarsh sites, Crofty and Laugharne, data is available allowing a comparison of abundances in October 2022, 2023 and 2024. Overall, fish diversity in October increased over the study period ($F(2, 16) = 10.77$, $p = 0.001$). Diversity was highest in 2024 ($H = 1.1$), followed by 2023 ($H = 0.87$) and 2022 ($H = 0.27$). Both 2023 and 2024 had higher diversity than 2022 (mean differences = 0.597 and 0.786; $p = 0.01$ and $p = 0.001$, respectively), while diversity levels between 2023 and 2024 were not different (mean difference = 0.189, $p = 0.58$).

Total mean fish density varried across the three years with 1,865 individuals/ha (SE ± 2058) in 2022, 8,611 individuals/ha (SE ± 7,301) in 2023, and 9,259 individuals/ha (SE ± 4893) in 2024. Fish density was significantly higher in 2024 compared to 2022 ($F = 4.32$, $p = 0.032$; Tukey $p = 0.046$), while no other pairwise differences were significant. Although individual species exhibited year-to-year fluctuations in density (Figure 7), these differences were not statistically significant ($p > 0.08$).

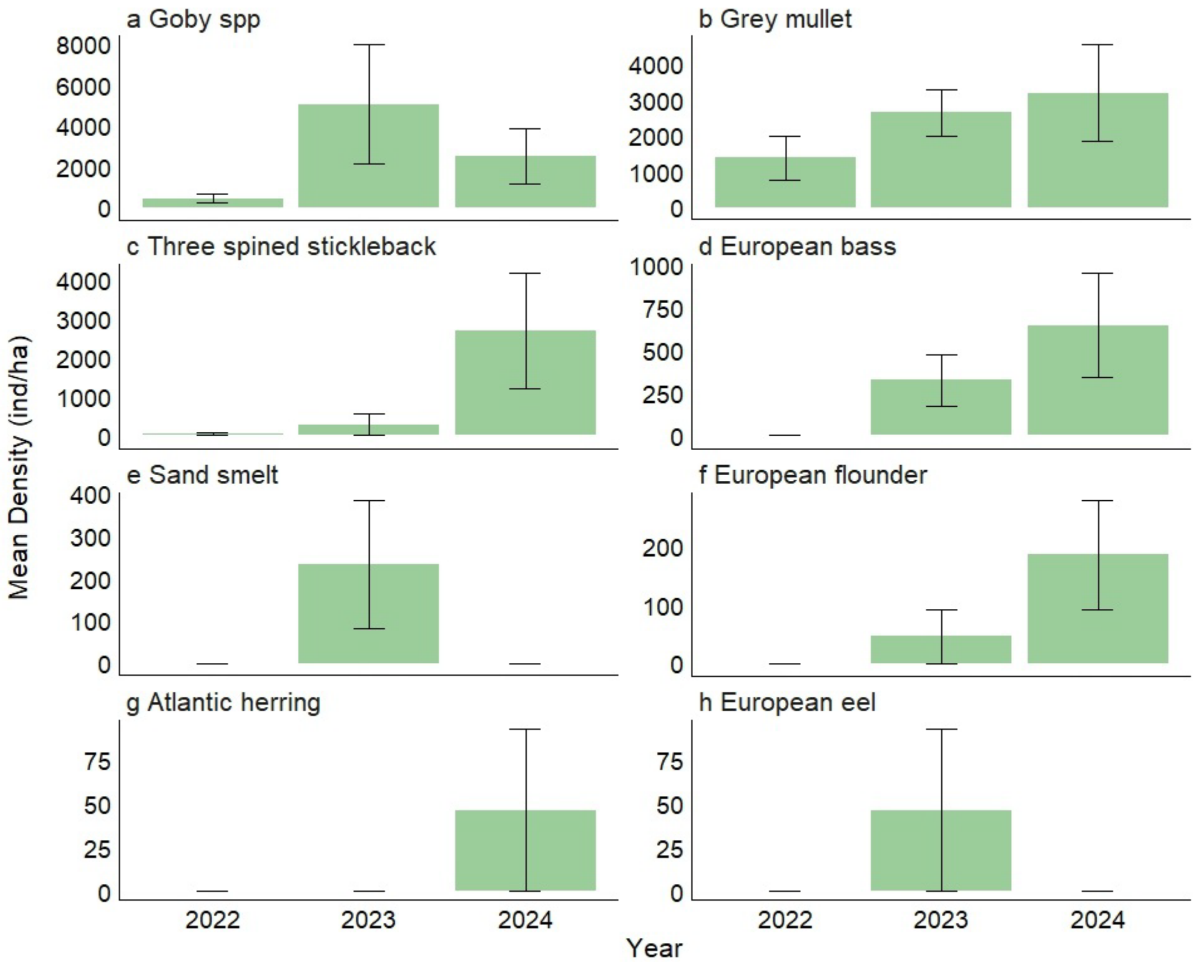


Figure 7 Grey mullet species exhibited consistently high mean densities, remaining above 1,000 individuals/ha across the three years in October. In contrast, other species demonstrated more notable variation in mean densities across years, with gobies showing a pronounced peak in 2023 at 5,000 individuals/ha but only reaching 436 individuals/ha in 2022. Standard error bars indicate variability within the datasets for each year. 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*). This data is representative of seine netting only.

Fish assemblages showed distinct spatial and temporal clustering patterns (stress = 0.12; Figure 8). Strong within-year similarities characterised the community structure, particularly in 2022 where most samples (80%) formed a tight cluster at 60% similarity. Site-specific patterns emerged at Laugharne, where consecutive years (2023-2024) formed a distinct group at 40% similarity. Crofty exhibited particularly consistent community composition in 2024 (all samples clustering at 60% similarity), while showing broader similarity patterns across all study years at the 40% threshold.

Both temporal and spatial factors shaped fish assemblage composition (Year: Pseudo-F = 6.56, $p = 0.001$; Site: Pseudo-F = 11.02, $p = 0.001$). Temporal changes in fish communities remained consistent across sites, as indicated by the Year × Site interaction (Pseudo-F = 1.77, $p = 0.111$).

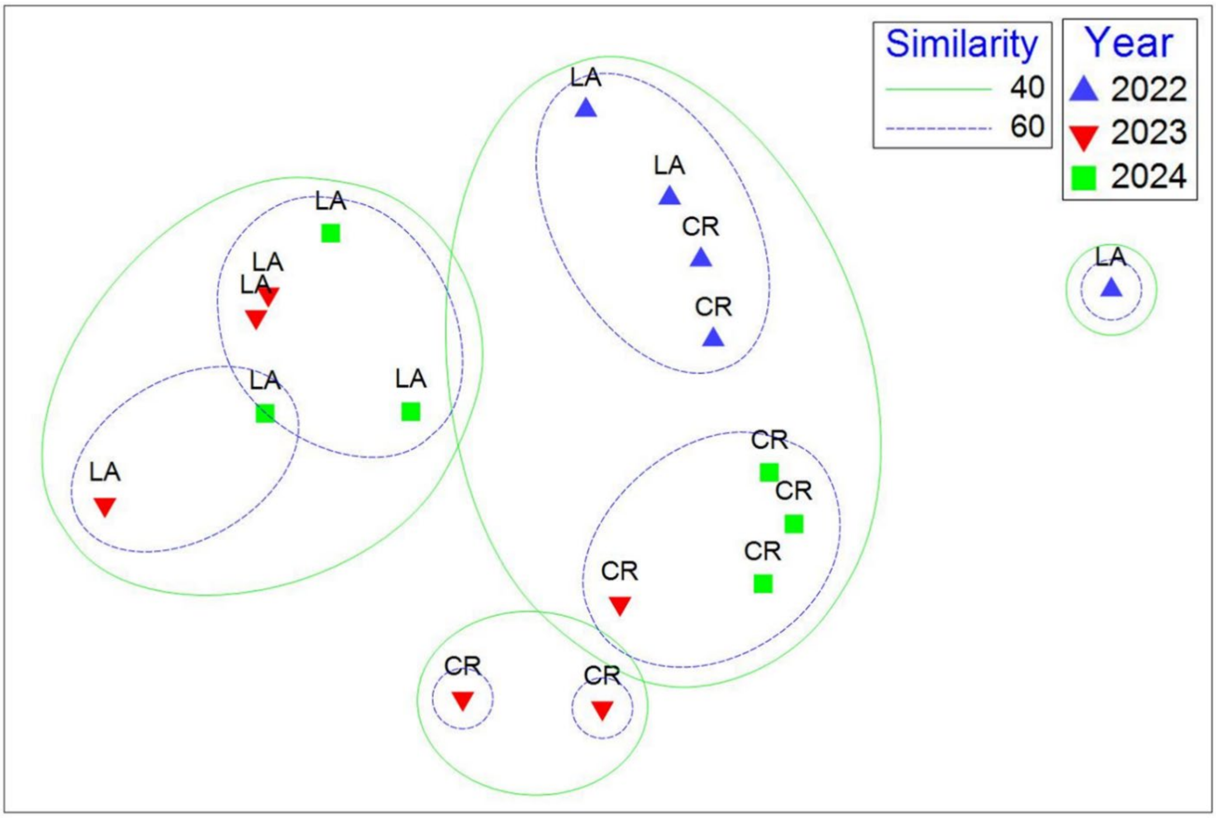


Figure 8 Fish assemblages recorded within 30 seine net samples in saltmarsh habitats sampled in October 2022, 2023, and 2024 across two locations in South Wales (CR: Crofty, LA: Laugharne). Data are presented as an nMDS plot with Bray-Curtis similarity clusters at the 40% and 60% levels.

6. Fish biomass and production estimates

The saltmarsh habitat had the highest annual mean biomass at 12.06 ± 3.055 g WW m^{-2}, with 11 different species present (Table 3). Within the saltmarsh, grey mullet species (24.48%), European bass (23.06%), Atlantic herring (19.11%), and European flounder (16.48%) were the dominant species, collectively accounting for approximately 83% of the biomass. The unvegetated habitat had an annual mean biomass of 3.525 ± 1.318 g WW m^{-2}, with European bass being the most dominant species (55.4%), followed by grey mullet (19.7%) and Sea trout (9.5%).
The managed realignment habitat showed the lowest an annual mean biomass, almost six times smaller than that of the saltmarsh habitat (2.021 ± 1.347 g WW m^{-2}), with European bass contributing most significantly (89.3%) to this total, while goby species and grey mullet contributed minimally (1.2% and 9.6% respectively). Cumulatively, the saltmarsh habitat supported the highest total biomass (144.723), substantially exceeding both the unvegetated habitat (42.297) and managed realignment (24.247).

Table 5 Annual mean biomass (g WW m^{-2}) was calculated from October 2023 to September 2024 with relevant standard error (SE) values. Total cumulative biomass from the year was calculated for each habitat as g WW m^{-2}. Saltmarsh habitat had the highest total annual mean biomass and cumulative biomass. Note managed realignment did not have data collected in October 2023 so cumulative biomass is one month short of the other two habitats. 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*).

Habitat	Species	Annual Biomass (mean)	Plus/ minus	SE	Cumulative Biomass
Managed realignment	Grey mullet species	0.193	±	0.133	2.318
Managed realignment	European bass	1.804	±	1.343	21.649
Managed realignment	Goby spp.	0.023	±	0.019	0.281
Managed realignment	**Total**	**2.021**	**±**	**1.347**	**24.247**
Saltmarsh	Grey mullet species	2.953	±	1.165	35.432
Saltmarsh	Atlantic herring	2.305	±	1.429	27.658
Saltmarsh	European bass	2.761	±	1.096	33.137
Saltmarsh	Goby species	0.261	±	0.092	3.129
Saltmarsh	Lesser sandeel	1.076	±	0.872	12.908
Saltmarsh	Three-spined stickleback	0.355	±	0.207	4.254
Saltmarsh	European flounder	1.989	±	0.701	23.861
Saltmarsh	European sprat	0.109	±	0.108	1.307
Saltmarsh	Sand smelt	0.209	±	0.134	2.503
Saltmarsh	Sea trout	0.043	±	0.043	0.521
Saltmarsh	European eel	0.001	±	0.001	0.015
Saltmarsh	**Total**	**12.060**	**±**	**3.055**	**144.723**
Unvegetated	Grey mullet species	0.697	±	0.289	8.362
Unvegetated	Atlantic herring	0.204	±	0.186	2.447
Unvegetated	European bass	1.953	±	1.004	23.434
Unvegetated	Goby species	0.168	±	0.068	2.015
Unvegetated	Three-spined stickleback	0.003	±	0.003	0.034
Unvegetated	European flounder	0.125	±	0.049	1.503
Unvegetated	Sand smelt	0.042	±	0.022	0.507
Unvegetated	Sea trout	0.333	±	0.333	3.996
Unvegetated	**Total**	**3.525**	**±**	**1.318**	**42.297**

Saltmarsh habitat yielded the highest overall production at 3.724g WW m^{-2} $year^{-1}$ (Table 4). The unvegetated habitat produced 1.443g WW m^{-2} $year^{-1}$, which is approximately 2.5 times lower than that of the saltmarsh habitat. Managed realignment habitat had the lowest production value of the three at 0.289g WW m^{-2} $year^{-1}$, equivalent to about one-thirteenth of the saltmarsh production and one-fifth of the unvegetated habitat.

Saltmarsh habitat also had the highest total cumulative production for seven of the eight species. In contrast, unvegetated habitat showed lower total productivity across all species apart from European bass. In managed realignment habitat, measurable production was limited to just three species (grey mullet, European bass, and goby species), and in all cases these values were lower than those recorded in other habitats for the same species.

The highest species-specific cumulative production in any habitat was recorded for grey mullet species in saltmarsh (1.338 g WW m^{-2}), closely followed by Atlantic herring in saltmarsh (1.24g WW m^{-2}). European bass represented a substantial proportion (36.5%) of the total cumulative production across all species and habitats, contributing 1.884 g WW m^{-2} $year^{-1}$ to the overall total of 5.167g WW m^{-2} $year^{-1}$.

Production exhibited strong seasonal patterns, with autumn (2.089 g WW m^{-2} $season^{-1}$) and summer (2.943 g WW m^{-2} $season^{-1}$) representing the periods of highest productivity. Winter and spring showed markedly lower production (0.243 and 0.181g WW m^{-2} $season^{-1}$ respectively).

All production estimates were derived exclusively from juveniles, as adults were rarely present and when observed, their abundance was insufficient for effective cohort detection.

Table 6 The saltmarsh habitat had the highest cumulative production for seven species, while the unvegetated habitat had the highest production for European bass. Managed realignment had measurable production for three species. Production was calculated for all species possible. Dashes represent where no measurable production was detected. Total cumulative production represents survey year only (October 2023 – October 2024). Grey mullet species (comprises three species (*Chelon labrosus, Chelon ramada*, and *Chelon aurata*), while Goby spp. includes common goby (*Pomatoschistus microps*) and sand goby (*Pomatoschistus minutus*).

Species	Habitat	Production Autumn (g WW m^{-2})	Production Winter (g WW m^{-2})	Production Spring (g WW m^{-2})	Production Summer (g WW m^{-2})	Total Production (g WW m^{-2} $year^{-1}$)
Grey Mullet species	Managed realignment	0.117	-	-	-	0.117
Grey Mullet species	Saltmarsh	0.393	0.098	0.125	0.721	1.338
Grey Mullet species	Unvegetated	0.187	0.045	-	-	0.231
Atlantic herring	Managed realignment	-	-	-	-	-
Atlantic herring	Saltmarsh	0.688	-	-	0.555	1.24
Atlantic herring	Unvegetated	-	-	-	-	-
European bass	Managed realignment	-	-	-	0.168	0.168
European bass	Saltmarsh	0.124	-	-	0.462	0.586
European bass	Unvegetated	0.328	-	-	0.799	1.13
Goby spp.	Managed realignment	-	-	-	0.004	0.004
Goby spp.	Saltmarsh	0.148	0.082	0.018	0.09	0.337
Goby spp.	Unvegetated	0.05	0.018	-	0.013	0.082
Lesser sandeel	Managed realignment	-	-	-	-	-
Lesser sandeel	Saltmarsh	-	-	-	0.007	0.007
Lesser sandeel	Unvegetated	-	-	-	-	-
Three -spined stickleback	Managed realignment	-	-	-	-	-
Three-spined stickleback	Saltmarsh	0.054	-	0.038	-	0.092

Three-spined stickleback	Unvegetated	-	-	-	-	-
European flounder	Managed realignment	-	-	-	-	-
European flounder	Saltmarsh	-	-	-	0.011	0.011
European flounder	Unvegetated	-	-	-	-	-
Sand smelt	Managed realignment	-	-	-	-	-
Sand smelt	Saltmarsh	-	-	-	0.113	0.113
Sand smelt	Unvegetated	-	-	-	-	-
Sub total	Managed realignment	0.117	-	-	0.172	0.289
Sub total	Saltmarsh	1.407	0.18	0.181	1.959	3.724
Sup total	Unvegetated	0.565	0.063	-	0.812	1.443
Total for all habitats	-	2.089	0.243	0.181	2.934	5.456

Fish production varied considerably across species, habitats, and seasons (Figure 9). Atlantic herring (Figure 9a) showed no measurable production in unvegetated and managed realignment habitats, but sharply peaked in saltmarsh during August and September, reaching 0.658 WW m^{-2} $month^{-1}$ in September.

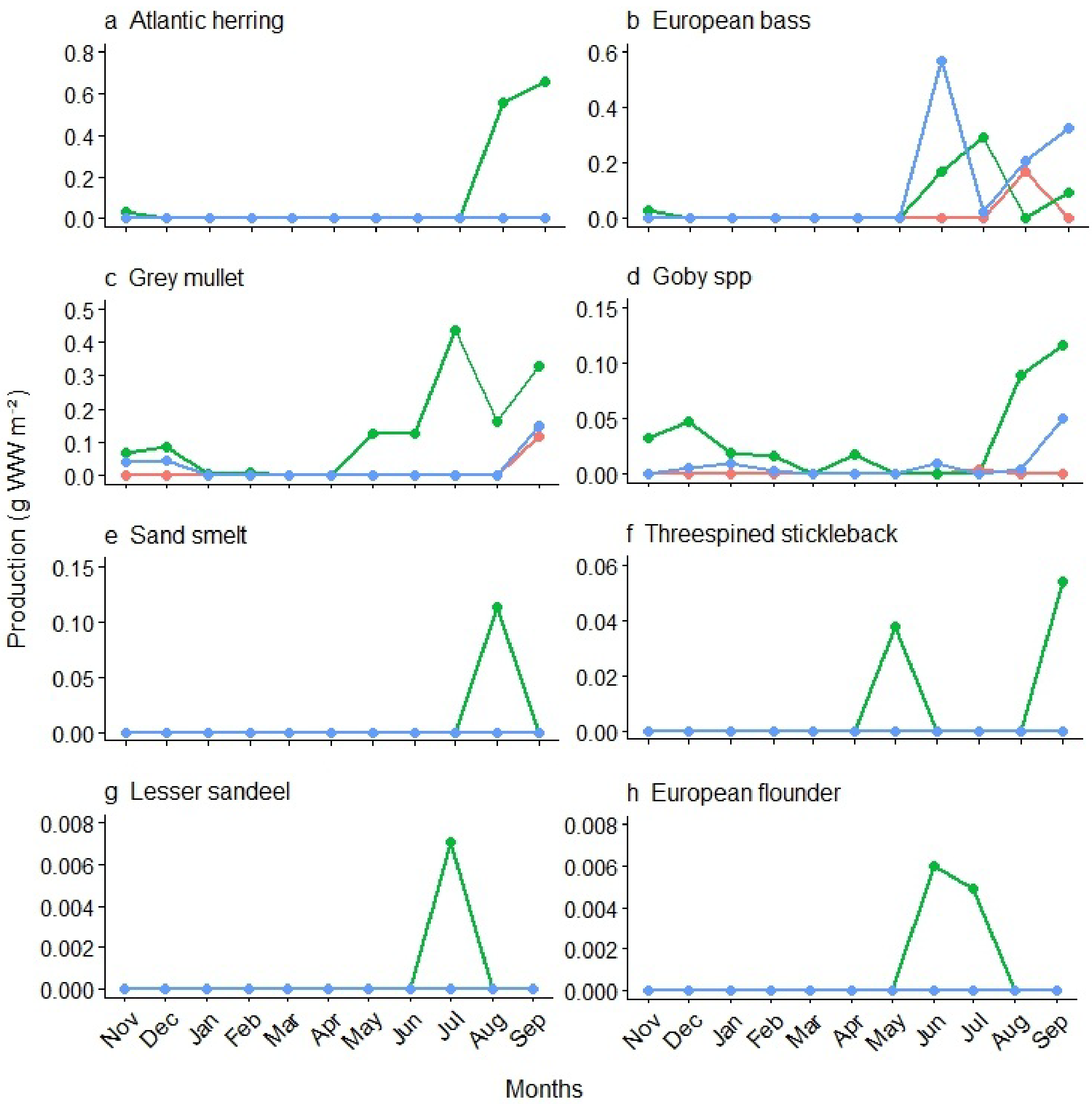
European bass (Figure 9b) showed high production in unvegetated habitat with a peak in June (0.569 g WW m^{-2} $month^{-1}$), followed by an increase in September (0.328 g WW m^{-2} $month^{-1}$). In saltmarsh, European bass production peaked in June peaking at 0.569 g WW m^{-2} $month^{-1}$. Managed realignment showed minimal bass production except for a peak in September (0.168 g WW m^{-2} $month^{-1}$).

Grey mullet exhibited production peaks at different times across habitats (Figure 9c). The largest peak in grey mullet productivity occurred in the saltmarsh during July (0.435 g WW m^{-2} $month^{-1}$). The largest peaks in both the unvegetated and managed realignments habitats was seen in September (0.146 and 0.117 g WW m^{-2} $month^{-1}$, respectively).

Goby species (Figure 9d) showed the most consistent production across months and habitats, with measurable production across nine months. In unvegetated habitats, production fluctuated throughout the year with an early peak in January (0.01 g WW m^{-2} $month^{-1}$) and a larger peak in September (0.05 g WW m^{-2} $month^{-1}$). Saltmarsh habitat goby production peaked in December (0.047 g WW m^{-2} $month^{-1}$) and August (0.115 g WW m^{-2} $month^{-1}$). Managed realignment goby production peaked in July at 0.004 g WW m^{-2} $month^{-1}$.

For several species, productivity was restricted in temporal and spatial distribution. Sand smelt, three-spined stickleback, lesser sandeel, and European flounder each showed production in only one or two months, and all exclusively in the saltmarsh habitat. Overall, saltmarsh habitat supported the highest production for all but one species, particularly during summer months.

Figure 9 Throughout the study period European bass have been the most productive species overall. The most significant peak in production of European bass is in the unvegetated habitat in June 2024. All of the measured production for Atlantic herring was seen between July and August 2024. Three habitats productivity are depicted using different coloured lines; blue- unvegetated, green- saltmarsh, and pink- managed realignment. Note the variability of the y axis.



To provide context for these findings, production estimates were compared across European coastal habitats (Table 5).

The estuarine saltmarsh habitat in Carmarthen Bay showed the most similar community production (3.72 g WW $m^{-2}year^{-1}$) to that found in the Forth estuary (4.3 g WW $m^{-2}year^{-1}$) estimated using instantaneous growth rates.

The saltmarsh habitat in this study exhibited higher production rates than those reported for two Portuguese estuaries, the Rio de Aveiro (2.10 - 2.48 g WW $m^{-2}year^{-1}$) and the Mondego Estuary (0.66 - 2.26 g WW $m^{-2}year^{-1}$), but lower rates than the minimum production recorded for the Minho Estuary (4.32 - 6.73 g WW $m^{-2}year^{-1}$).

The unvegetated estuarine shores in Carmarthen Bay (1.44 g WW $m^{-2}year^{-1}$) yielded lower production values than in any Portuguese estuaries, but higher values than those reported for Swedish coastal bays (0 - 0.95 g WW $m^{-2}year^{-1}$).

The managed realignment site had the lowest production value among the Carmarthen Bay habitats (0.29 g WW $m^{-2}year^{-1}$), similar to production levels in the coastal bays in Sweden (0 - 0.95 g WW $m^{-2}year^{-1}$).

Table 7 Comparison of total community production estimates in European marine coastal habitats ordered from highest productivity to lowest.

Study area	**Estimation method**	**Habitat**	**Production (g WW m^{-2} $year^{-1}$)**	**Study**
Minho Estuary, Portugal	Increment summation method	Estuary	4.32 - 6.73	Dolbeth *et al*., 2010
Forth Estuary	Instantaneous growth	Estuary	4.3	Elliot & Taylor 1989
Carmarthen Bay, Wales	Increment summation method	Estuarine saltmarsh	3.72	Present study
Ria de Aveiro, Portugal	Instantaneous growth	Estuary	2.10 - 2.48	Pombo *et al*., 2007
Mondego Estuary, Portugal	Increment summation method	Estuary	0.66 - 2.26	Dolbeth *et al*., 2010
Carmarthen Bay, Wales	Increment summation method	Estuarine unvegetated shore	1.44	Present study
Gullmarsvik, Sweden	Increment summation method	Coastal bay	0.24 - 0.95	Pihl & Rosenberg 1982
Sandvik, Sweden	Increment summation method	Coastal bay	0 - 0.43	Pihl & Rosenberg 1982
Carmarthen Bay, Wales	Increment summation method	Estuarine managed realignment	0.29	Present study

Discussion

This study provides first insights into how saltmarsh and managed realignment sites support finfish stocks in South Wales. Saltmarsh habitats showed substantially higher fish densities, biomass, and productivity compared to unvegetated and managed realignment habitats. Nine species exhibited higher monthly densities in saltmarshes, including species of both conservation and commercial importance. These findings suggest saltmarshes function as critical habitats for estuarine fish communities.

1. Fish habitat preferences highlight saltmarsh dominance

Our findings revealed substantially higher total fish densities in saltmarsh compared to both unvegetated and managed realignment habitats - with densities more than three times greater in saltmarshes than in unvegetated habitats. This pattern aligns with broader evidence of saltmarshes functioning as critical fish habitats throughout temperate regions worldwide, likely due to their structural complexity providing both refuge from predators and enhanced food resources (Boesch and Turner, 1984; Crinall and Hindell, 2004; Joyeux *et al.*, 2017). Notably, all monitored species demonstrated highest total annual densities in saltmarshes. Additionally, the higher mean monthly densities observed for nine species in saltmarsh signifies consistently favourable conditions across taxonomic groups. In contrast, unvegetated habitat hosted higher densities for only two species, sea trout and sand smelt. The managed realignment sites demonstrated reduced capacity to sustain fish assemblages, with only five species recorded and just one (European eel fyke netting) at higher abundances, possibly reflecting the site's early successional stage and limited number of creek entries.

Four fish species demonstrated significant associations with saltmarsh habitat - grey mullet species, Atlantic herring, lesser sandeel, and three-spined stickleback - further highlighting the habitat's ecological value. European eel, notably, exhibited an association with the managed realignment site, while no species showed an association to unvegetated sites over other habitats. Importantly, three species with a preference for saltmarsh (grey mullet species, Atlantic herring, and lesser sandeel) were observed exclusively as juveniles, reinforcing the theory that saltmarshes may function as critical nursery grounds for species of both ecological and commercial significance. While further research monitoring juvenile growth and survival rates would be needed to establish definitive nursery function (Lefcheck *et al.*, 2019), these observations align with and extend previous studies that have documented juvenile fish utilisation of saltmarshes across various regions (Franco *et al.*, 2010; Joyeux *et al.*, 2017; Rogers *et al.*, 1984; Whitfield, 2017).

Saltmarsh habitats appeared particularly important for Atlantic herring and lesser sandeel, with lesser sandeel found exclusively in saltmarsh and Atlantic herring showing near-exclusive use of saltmarsh, only appearing in the unvegetated habitat in one month. These findings contrast interestingly with previous studies. In Essex saltmarshes, Atlantic herring was reported as the second most abundant species, while lesser sandeel was recorded in low numbers (<10 individuals) (Green *et al.*, 2009). Neither species were documented in Dublin Bay (Koutsogiannopoulou and Wilson, 2007), indicating regional variations in habitat use patterns across the British Isles possibly reflecting proximity to suitable adult habitat. Although lesser sandeel are typically associated with soft, sandy substrates for burrowing (Hùines and Bergstad, 2000), these findings point to juvenile lesser sandeel using nearby saltmarsh habitats, for shelter from predators or foraging. This habitat association has ecological implications, as lesser sandeel are an important food source regionally for a variety of marine predators, including seabirds such as puffins and kittiwakes, and marine mammals such as harbour porpoise, seals, and even minke whales, where they can comprise up to 54% of the whale’s diet (Engelhard *et al.*, 2014; García-Vernet *et al.*, 2021; Staudinger *et al.*, 2020). Similarly, our findings on Atlantic herring, which is among the UK’s most commercially important fish species (Pauly *et al.*, 2020; Peverley and Stewart, 2021), provide evidence that saltmarshes may play an underappreciated role in contributing to commercially valuable fisheries. Understanding these strong habitat associations reinforces the value of saltmarshes in coastal ecosystems and highlights the need to incorporate these habitats into both fisheries management frameworks and marine conservation planning.

Throughout this study, the critically endangered European eel was the only species to indicate preference for the managed realignment habitat (Ben Ammar *et al.*, 2021; Lyach, 2022; Richards *et al.*, 2020). European eels were consistently recorded in managed realignment from April to August, with fewer individuals found in the saltmarsh habitat, appearing only once in October. This difference in European eel densities between the two habitats may be related to the managed realignment sites’ proximity to the sea, as it is the closest site in the estuary. European eel colonisation densities are often highest in habitats nearer to the sea, as these areas are the first encountered during their upstream migration (Degerman *et al.*, 2019; Domingos *et al.*, 2006). Additionally, European eels in the yellow stage (in which all captured individuals were) have been known to exhibit site fidelity (Verhelst *et al.*, 2018). Therefore, the proximity of the managed realignment site to the sea could explain the higher densities observed. Other factors, such as water depth, vegetation cover, and burrowing substrate, also influence habitat preference and may vary between the managed realignment and saltmarsh habitats (Laffaille *et al.*, 2009, 2004, 2003; Verhelst *et al.*, 2018). Notably, European eels were never recorded in the unvegetated habitat. While many studies have focused on European eels in estuaries, establishing their presence in these environments, our site-specific observations suggest a potential preference for vegetated habitats, though broader spatial sampling would be needed to determine whether this pattern holds across different estuarine systems.

2. Fish communities on a spatial and temporal scale

The estuarine fish assemblage documented in South Wales broadly aligns with patterns observed across the UK and continental Europe. Several species - gobies, grey mullet, and European bass - dominant in our study are consistently recorded as dominant species in saltmarshes throughout Europe (Cattrijsse *et al.*, 1994; Koutsogiannopoulou and Wilson, 2007; Lafage *et al.*, 2021; Laffaille *et al.*, 2000; Veiga *et al.*, 2006). However, our findings also reveal biogeographical distinctions, particularly the dominance of Atlantic herring in South Wales. This pattern appears characteristic of UK saltmarshes, as Atlantic herring was similarly abundant in Essex saltmarshes (Green *et al.*, 2009), but is recorded in lower abundances or entirely absent in continental European saltmarsh studies. These differences may reflect varying biogeographical factors between UK and continental European coastal systems, particularly the distribution patterns of Atlantic herring populations (Brunel and Dickey-Collas, 2010). Specifically, the North Sea and waters around the UK contain major Atlantic herring spawning grounds, potentially explaining their higher abundance in UK saltmarshes compared to continental European sites (Haegele and Schweigert, 1985).

The species composition analysis reveals that the three habitat types do not display distinctly different species compositions. This overlap is consistent with previous estuarine studies where habitat differentiation is often expressed through differences in relative abundance, density, and size distribution of fish rather than complete turnover in species presence (França *et al.*, 2009). Fish species in estuaries typically use multiple intertidal habitats while showing quantitative preferences that reflect habitat-specific ecological functions. Despite this overlap in species composition, a clear difference emerges in the variability observed across habitats. Saltmarsh habitats exhibited more variable species compositions compared to both unvegetated and managed realignment habitats. This increased variability is likely driven by the presence of species such as lesser sandeel and European sprat that were primarily or exclusively recorded in saltmarsh areas. These findings establish that while core species assemblages overlap across all three habitat types, saltmarsh environments provide conditions that support a broader range of species, including those that appear infrequently in the other habitats, highlighting their distinctive contribution to estuarine biodiversity. However, the overlapping species compositions also highlight the complementary roles that different habitats play within estuarine ecosystems, evidencing that the maintenance of a mosaic of habitat types is essential for sustaining the full spectrum of fish diversity in coastal regions (Freeman *et al.*, 2024; Henriques *et al.*, 2017).

While fish communities did not differ distinctly by habitat type, clear site-specific compositions emerged across our study locations. These site-specific patterns are likely driven by local factors such as proximity to spawning grounds, freshwater input gradients, or position within the broader estuarine system (Kimmerer, 2002; Pereira *et al.*, 2015). The lesser sandeel, for instance, was exclusively present at the Laugharne saltmarsh site, which indicates that it may be in proximity to a lesser sandeel burrowing site where these fish retreat during the night and hibernate during winter (Henriksen *et al.*, 2024). European eel showed strong preference for the Cwm Ivy managed realignment site, which may be attributed to its position near the mouth of the estuary or freshwater influence from nearby tributaries. Similarly, the three-spined stickleback was observed almost exclusively at the Crofty saltmarsh site, which is directly influenced by a river running through the sampling area, providing improved water flow, higher oxygenation levels, potentially a more favourable habitat for the species than other sites (Walton *et al.*, 2007). These observations highlight how fine-scale spatial factors can influence fish distribution patterns within the same habitat type and emphasises why preserving diverse locations of the same habitat within a single estuary is vital for robust, thriving fish communities.

Temporally, we also saw distinct species compositions. As expected, most species densities peaked from late spring to early autumn (Greenwood and Hill, 2003; Hagan and Able, 2003). However, species did not all peak in the same months; there appears to be a sequential trend in the density peaks of the seven most dominant species, with lesser sandeel and European flounder peaking in May, European bass in June, Atlantic herring and grey mullet in August, three-spined stickleback in September, and goby species in November. These staggered peaks align with known spawning and recruitment periods and the pattern reflects how many species have evolved temporally separated early life stages that minimise competition for resources. This 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 peaks 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 often relied on quarterly or seasonal sampling, our high-resolution, monthly data demonstrate that these coarser approaches may overlook finer-scale habitat use patterns. The rapid changes observed in species dominance highlight the dynamic nature of estuarine fish assemblages, emphasising the importance of temporal resolution when designing monitoring programs. The habitat-use patterns documented here provide valuable insights for species-specific management strategies and monitoring, helping to identify the periods when key species are most abundant.

Across habitat types, species' density peaks showed clear temporal differences, indicating both spatial and temporal partitioning in estuarine usage. The absence of synchronous density peaks between saltmarsh and unvegetated habitats for any species indicates these habitats serve different purposes at various life stages. Previous research has established that complex habitats like saltmarshes primarily serve as nursery grounds, providing crucial refuge from predation and abundant food resources for vulnerable juveniles (Boesch and Turner, 1984). As fish develop, their habitat requirements often shift, with many species moving to unvegetated areas where reduced structural complexity facilitates more efficient foraging for larger individuals that are less susceptible to predation (Grønkjær *et al.*, 2007; Perry *et al.*, 2018). Our findings provide compelling evidence for this life-stage dependent habitat-use pattern. For example, grey mullet peak in saltmarshes during August but in unvegetated areas during September. European bass displayed an opposite trend, with earlier peaks in unvegetated habitats and later peaks in saltmarshes. However, closer examination revealed this pattern still aligns with life-stage habitat preferences. The May peak in unvegetated habitats comprised exclusively of European bass between 5.5-11.5 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, with saltmarshes catering to earlier life stages while unvegetated habitats accommodate larger, less vulnerable individuals. The observed size-specific habitat partitioning demonstrates that fish populations utilise multiple habitats sequentially as they develop, with saltmarshes primarily supporting earlier developmental stages while unvegetated areas accommodate larger juveniles, a pattern that underscores the need for preserving complementary habitat types within connected estuarine seascapes (Nagelkerken *et al.*, 2015; Perry *et al.*, 2018).

A striking pattern emerges when examining year-round habitat usage: saltmarshes consistently supported higher mean fish densities across all seven of the most abundant species compared to unvegetated and managed realignment habitats. Saltmarshes continued to host high densities even during winter periods, when managed realignment and unvegetated habitats showed marked declines.

Notably, our study observed the year-round presence of six species in saltmarshes (European bass, goby species, grey mullet species, Atlantic herring, European flounder, and three-spined stickleback), when compared to the lower numbers reported in other UK saltmarshes: Essex (two species) and Dublin Bay (four species) (Green *et al.*, 2009; Koutsogiannopoulou and Wilson, 2007). This higher species persistence indicates particularly favourable conditions in these South Wales systems, though the underlying mechanisms require further investigation. When examining species richness across latitudes, from Ireland to Portugal, a general pattern emerges where warmer regions accommodate a greater number of species (Koutsogiannopoulou and Wilson, 2007; Laffaille *et al.*, 2000; Veiga *et al.*, 2006). This latitudinal gradient confirms that temperature plays a key role in shaping estuarine fish assemblages, as is also seen on a seasonal scale demonstrated in this study. The observation that warmer climates support higher overall species richness suggests that milder winter conditions in south Wales may also enable more species to persist year-round by reducing seasonal constraints on growth or survival.

While our study primarily focused on habitat preferences and community structure, we also examined inter-annual compositions in saltmarshes to provide initial insights into population dynamics over time. Between October 2022 and 2024, no significant changes were detected in specific species densities, however overall fish density increased from 2022 to 2024. Species diversity also increased across the study period. Studies in other estuarine systems have shown that changes in species assemblages can be linked to climate-driven warming, altered freshwater inflows, and habitat modifications (Dolbeth *et al.*, 2008; Veiga *et al.*, 2006). However, since environmental conditions and breeding dynamics were not directly measured in this study, the specific drivers of these interannual shifts remain uncertain. Future research incorporating long-term environmental monitoring (e.g. salinity, dissolved oxygen, nutrients) the detailed physical site characteristics, as well as recruitment studies could help disentangle the mechanisms underlying these patterns and provide deeper insight into how estuarine fish communities respond to environmental change. Alternatively, the increase in both density and diversity may be due to increased netting skill throughout the study period.

3. Higher fish biomass and production in saltmarshes

Biomass calculations revealed that saltmarsh habitat maintained the highest values, followed by unvegetated habitat, with managed realignment exhibiting the lowest biomass values. The difference between managed realignment and unvegetated habitat is, however, relatively minor compared to the substantial differences between these habitats and saltmarshes. Saltmarsh annual mean biomass (12.06 ± 3.055 g WW m^{-2}) exceeded that of either other habitat by more than three-fold, with unvegetated habitats at 3.525 ± 1.318 g WW m^{-2} and managed realignment at 2.021 ± 1.347 g WW m^{-2}. These biomass values are comparable to those reported for other estuarine systems globally. Thus, our saltmarsh biomass values fall within the range reported for estuarine bays in Queensland (2.9-25.3 g WW m^{-2}; Blaber *et al*., 1989) and our unvegetated and managed realignment habitat biomass values are similar to those reported for estuarine bays and lagoons in Mexico and various sites in the USA (Flores-Verdugo *et al*., 1990; Thayer *et al*., 1987; Yáñez-Arancibia *et al*., 1980). These comparisons demonstrate that temperate saltmarshes in South Wales yield fish biomass values comparable to and in some cases exceeding, those documented in various estuarine habitats worldwide, including some tropical systems, highlighting the considerable capacity of these temperate habitats to sustain productive fish communities despite seasonal limitations.

Saltmarsh habitat facilitated the highest levels of production for all species except European bass, which showed highest production values in the unvegetated habitat. When considering total cumulative production, saltmarsh habitats demonstrated the highest overall productivity. Unvegetated habitat ranked second most productive with a value approximately two and a half times smaller than that of the saltmarsh, but almost five times larger than the production value of the managed realignment. When compared with other European coastal systems, our saltmarsh production estimate falls within the higher middle range, with a lower value than the Minho estuary, Portugal (Dolbeth *et al.,* 2010) and the Forth estuary (Elliott and Taylor, 1989), but exceeding estimates reported for Ria de Aveiro, Portugal, (Pombo *et al*., 2007) and Mondego estuary, Portugal (Dolbeth *et al*., 2010). Unvegetated habitat estimate in our study was found to be lower than all above estimates, but was higher than those found for Swedish coastal bays (Pihl and Rosenberg, 1982). The managed realignment habitat falls towards the lower end of reported values, comparable to values from the Swedish coastal bays.

The higher productivity in saltmarsh habitat highlights their critical ecological role in estuarine systems, aligning with its well-established ecological role in providing structural complexity and rich invertebrate communities, creating ideal conditions for juvenile fish (Boesch and Turner, 1984; Cabral and Costa, 2001; Joyeux *et al.*, 2017; Lafage *et al.*, 2021; Vernberg, 1993; Whitfield, 2017). In contrast, the managed realignment is still in an early successional stage, likely limiting its capacity to support fish populations to the same extent as fully established saltmarshes (Colclough *et al.*, 2005; Garbutt *et al.*, 2006; Tupper and Able, 2000). This indicates that it may not yet be fully integrated into the broader estuarine system, which could be currently limiting its functionality for fish. Tupper and Able (2000), estimated that full ecosystem functioning in managed realignment projects may take 12 to 21 years to develop. Given that the managed realignment site was only breached in 2014, and is non-engineered (Dale *et al.*, 2021), the observed lower productivity is likely due to ongoing ecological succession, as the habitat continues to integrate into the estuarine system. Continual monitoring will be crucial to determine whether community composition and productivity converge with natural habitats as the managed realignment site matures, and to assess when, or if, full ecosystem functionality is achieved (Garbutt *et al.*, 2006). While unvegetated habitats provide some benefits through easier foraging (Freeman *et al.*, 2024; Whitfield, 2020) overall productivity remains lower than in saltmarshes.

European bass were the overall most productive species (1.88 g WW m^{-2} $year^{-1}$), followed by grey mullet (1.69 g WW m^{-2} $year^{-1}$) and then Atlantic herring (1.24 g WW m^{-2} $year^{-1}$). European bass accounted for the highest proportion of production in both the unvegetated habitat (78%) and managed realignment (58%); however, in the saltmarsh, grey mullet (36%) and Atlantic herring (33%) both had higher production values than European bass (16%). The production values for European bass observed across all habitat types in south Wales estuaries are higher than those found in European mainland studies. In the Ria de Aveiro, an estuary heavily influenced by anthropological pressures, European bass contributed 27% of total production (Pombo *et al.*, 2007), and in another Portuguese estuary its highest value reached 54% of total production (Dolbeth *et al.*, 2010).

Five of eight species with detectable production exclusively had measurable production in the saltmarsh habitat (Atlantic herring, lesser sandeel, three-spined stickleback, European flounder, and sand smelt). These production patterns reveal a compelling contrast: while European bass dominates productivity metrics in unvegetated and managed realignment habitats, saltmarshes facilitate a more balanced distribution of production across multiple species, thereby maintaining higher overall ecosystem productivity through taxonomic diversification rather than single-species dominance.

As anticipated, production exhibited strong seasonal patterns, with notably lower values during winter and spring months. This seasonality is primarily driven by reduced fish abundances during colder periods, which impedes reliable cohort detection. When winter cohorts are identifiable, their low abundance results in fewer individuals being incorporated into biomass calculations, consequently reducing production estimates. For most species, continuous cohorts were only detectable between May and September. This pronounced seasonal variation contrasts with production estimates from the Portuguese Mondego estuary (Dolbeth *et al.*, 2008), however it is likely that milder winter temperatures in Portugal which do not constrain production to the same extent as the colder UK winters accounts for the observed difference. Only grey mullet and goby species maintained measurable production throughout all seasons in our study, albeit with markedly lower values during winter and spring. Interestingly, goby species in the Mondego estuary did not display strong seasonal patterns in production, instead showing more variable interannual fluctuations (Dolbeth *et al.*, 2008), suggesting that gobies may generally maintain more consistent production throughout the year across different geographic regions.

4. Limitations and areas for future research

A key area for future research is enhancing the quantification methods for fish data collected using fyke and seine nets in saltmarshes. Fyke nets, though widely used in saltmarsh creeks, are inherently subject to variable flow conditions which influence catch rates (Breen and Ruetz, 2006; Harrison-Day *et al.*, 2020). Future studies could focus on refining species-specific catch efficiencies for fyke nets. Similarly, further work could explore species-specific catch efficiencies for seine netting in densely vegetated habitats, where physical obstructions substantially reduce sampling effectiveness (Pierce *et al.*, 1990), and so reporting fish biomass and production values may be an underestimate. Complementary environmental DNA (eDNA) analysis could serve as a valuable validation tool to identify species present in the ecosystem but potentially missed by traditional capture methods, thereby providing a more comprehensive assessment of fish community composition.

Discrepancies exist between fish density estimates derived from seine nets versus fyke nets, with fyke netting consistently yielding lower density values. This disparity likely stems from either methodological limitations in density estimation or inherent differences in catch efficiency and selectivity between the two gear types. The current approach to estimating the area sampled by fyke nets may produce overly conservative density estimates, as it typically overestimates the effective sampling area. Accurately determining this parameter remains challenging because fyke nets are deployed over extended periods with variable water flow through the net. Currently, calculations rely on maximum potential area sampled, which may artificially deflate density estimates. Future methodological improvements could focus on developing standardised protocols for determining more precise measurements of effective sampling area for fyke nets. Incorporating flowmeters could potentially refine these area calculations by quantifying water volume passing through the nets during deployment. Consequently, due to these quantification uncertainties associated with fyke net data, our analysis limited their use to presence-absence tests for habitat preference assessment and inclusion in the summary table.

The Increment Summation Method provides detailed insight into productivity over a specific time period; however, these findings represent only that discrete timeframe and cannot be extrapolated to predict longer-term productivity patterns. A more extensive temporal dataset spanning a wider range of habitat types would enhance understanding of interannual variations and better quantify the contributions of younger cohorts to overall ecosystem productivity (Dolbeth *et al.*, 2008; Pombo *et al.*, 2007). The continuation of regular fish surveys across saltmarshes, unvegetated shores, and managed realignments, particularly as the latter mature through succession, could contribute to a valuable long-term dataset, enabling more precise estimates of annual production and species composition. Expanding surveys to include a greater diversity of connected estuarine habitats would further illuminate how fish populations utilise the broader seascape throughout their life cycles.

To establish definitive nursery function of saltmarshes for key species identified in this study, particularly Atlantic herring and lesser sandeel, future research should specifically track juvenile growth, survival rates, and movement patterns between habitats (Lefcheck *et al.*, 2019).

Additionally, research should investigate the differences in species composition among saltmarsh sub-habitats, such as pools, creeks, and flats. Previous studies document how sub-habitats may be used differently depending on species and life stage (MacKenzie and Dionne, 2008; Virgin *et al.*, 2020). Notably, pools offer refuge and feeding opportunities during low tide, unlike creeks and flats, which drain completely (Able *et al.*, 2005; Allen *et al.*, 2017). This study focused primarily on vegetated flats using seine nets and creeks using fyke nets, while push nets may be better suited for sampling in smaller tidal pools. Including these sub-habitats in future studies could offer further insights into how fish use the diverse topography of saltmarshes, and influence design of re-created saltmarsh habitat going forward to maximise benefits.

Another important consideration is identification of the drivers behind high fish production in saltmarsh ecosystems, as shown by the variation between saltmarsh sites Laugharne and North Gower. Factors such as water quality, salinity, vegetation structure, and prey availability are likely to play crucial roles (Green *et al.*, 2009; Mathieson *et al.*, 2000). Understanding these influences would enhance our knowledge of saltmarshes role within estuarine ecosystems and guide more effective conservation and management strategies.

Conclusion

Our comprehensive analysis of fish communities across three habitat types in South Wales reveal the substantial ecological value of saltmarshes in estuarine ecosystems. Across multiple metrics - species density, biomass, and production - saltmarshes consistently outperformed both unvegetated and managed realignment habitats. This superior performance likely stems from saltmarshes' structural complexity, which provides both refuge from predation and enhanced food resources, creating ideal conditions for a diverse array of fish species (Boesch and Turner, 1984).

A key finding of this study is that saltmarshes promote a more balanced distribution of production across multiple species, whereas production in unvegetated and managed realignment habitats is characterised by the dominance of a single species (European bass). This diversification of productivity likely enhances ecosystem resilience by preventing over-reliance on individual species' success. The ability of saltmarsh habitats to support species rarely found elsewhere further underscores its importance for maintaining biodiversity in estuarine systems (Laffaille *et al.*, 2000).

Despite the clear benefits of saltmarshes, our results also demonstrate the importance of habitat mosaics within estuaries. Not all species showed preference for saltmarsh habitats, with European eel notably favouring managed realignment and European bass showing more complex patterns of habitat use. Additionally, the size-specific habitat partitioning observed in species like European bass highlights how fish utilise different habitats sequentially as they develop. These patterns emphasise that no single habitat type can support all species at all life stages, and so effective conservation requires preserving complementary habitat types within connected estuarine seascapes (Freeman *et al.*, 2024).

The managed realignment site, while sustaining fewer species than the other habitats, showed promising ecological function despite being in an early successional stage. Its particular importance for critically endangered European eel suggests it provides valuable habitat for some species, even as it continues to develop toward fuller integration with the estuarine ecosystem. Continued monitoring will be essential to track how this habitat evolves over time and whether it converges functionally with natural saltmarshes as it matures (Garbutt *et al.*, 2006) or whether further action is needed to optimise the site for use by fish.

Collectively, these findings emphasise the need for integrated management approaches that recognise both the exceptional value of saltmarshes and the complementary roles of diverse habitat types in safeguarding coastal fish communities.

References

Able, K.W., Smith, K.J., Hagan, S.M., 2005. Fish composition and abundance in New Jersey salt marsh pools: sampling technique effects. Northeast Nat (Steuben) 12, 485–502.

Adam, P., 1993. Saltmarsh ecology. Cambridge University Press. https://doi.org/https://doi.org/10.2307/5632

Adams, P.B., 1980. Life history patterns in marine fishes and their consequences for fisheries management. Fishery Bulletin 78.

Allen, D.M., Ogburn-Matthews, V., Kenny, P.D., 2017. Nekton use of flooded salt marsh and an assessment of intertidal creek pools as low-tide refuges. Estuaries and Coasts 40, 1450–1463. https://doi.org/10.1007/s12237-017-0231-4

Allen, J.R.L., 2000. Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and Southern North Sea coasts of Europe. Quaternary Science Reviews 1155–1231.

Allen, K.R., 1971. Relation Between Production and Biomass. Journal of Fisheries Research Board of Canada 1573–1581. https://doi.org/10.1139/f71-236

Allman, E.S., Rhodes, J.A., 2004. Mathematical models in biology: an introduction. Cambridge University Press., United Kingdom.

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

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol Monogr 81, 169–193. https://doi.org/10.1890/10-1510.1

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

Ben Ammar, I., Cornet, V., Houndji, A., Baekelandt, S., Antipine, S., Sonny, D., Mandiki, S.N.M., Kestemont, P., 2021. Impact of downstream passage through hydropower plants on the physiological and health status of a critically endangered species: The European eel Anguilla anguilla. Comp Biochem Physiol A Mol Integr Physiol 254. https://doi.org/10.1016/j.cbpa.2020.110876

Blaber, S.J.M., Brewer, D.T., Salini, J.P., 1989. Species composition and biomasses of fishes in different habitats of a tropical Northern Australian estuary: Their occurrence in the adjoining sea and estuarine dependence. Estuar Coast Shelf Sci 29, 509–531. https://doi.org/10.1016/0272-7714(89)90008-5

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

Boorman, L., 2003. Saltmarsh Review: An overview of coastal saltmarshes, their dynamic and sensitivity characteristics for conservation and management (JNCC Report No. 334).

Breen, M.J., Ruetz, C.R., 2006. Gear bias in fyke netting: evaluating soak time, fish density, and -predators. N Am J Fish Manag 26, 32–41. https://doi.org/10.1577/m05-013.1

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
Butcher, A., Mayer, D., Smallwood, D., Johnston, M., 2005. A comparison of the relative efficiency of ring, fyke, fence nets and beam trawling for estimating key estuarine fishery populations. Fish Res 73, 311–321. https://doi.org/10.1016/j.fishres.2005.01.014
Cabral, H., Costa, M.J., 2001. Abundance, feeding ecology and growth of 0-group sea bass, Dicentrarchus labrax, within the nursery areas of the Tagus estuary. Journal of the Marine Biological Association of the UK 81, 679–682. https://doi.org/10.1017/S0025315401004362
Cain, R.L., Dean, J.M., 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Mar Biol 36, 369–379. https://doi.org/10.1007/BF00389199
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 Syst 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.
Cardona, L., 2016. Food and feeding of Mugilidae. https://doi.org/https://doi.org/10.1201/b19927-10.
Cardona, L., 2015. Biogeography and distribution of Mugilidae in the Mediterranean and the Black Sea, and North-East Atlantic., in: Biology, Ecology and Culture of Grey Mullets (Mugilidae). CRC Press, pp. 126–137. https://doi.org/10.1201/b19927-10
Cattrijsse, A., Hampel, H., 2006. European intertidal marshes: A review of their habitat functioning and value for aquatic organisms. Mar Ecol Prog Ser 324, 293–307. https://doi.org/10.3354/meps324293
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/109.10.3354/meps109195.
Chapman, D., 1978. Production, in: Bagenal, T. (Ed.), Methods for Assessment of Fish Production in Fresh Waters. Blackwell Scientific Publications, Oxford, pp. 202–2017.
Clark, S.J., Jackson, J.R., Lochmann, S.E., 2007. A Comparison of Shoreline Seines with Fyke Nets for Sampling Littoral Fish Communities in Floodplain Lakes. N Am J Fish Manag 27, 676–680. https://doi.org/10.1577/m06-197.1
Clarke, K.R., Gorley, R.N., 2015. Primer: User manual/tutorial. Primer-E Ltd., Plymouth, UK 93.
Colclough, S., Coates, S., Dutton, C., Cousins, T., Astley, T., 2004. The potential for fisheries enhancements associated with managed realignment, Working Paper - Centre for Social and Economic Research on the Global Environment.
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/https://doi.org/10.1111/j.1365-2400.2005.00467.x

Costa, M.J., Catarino, F., Bettencourt, A., 2001. The role of salt marshes in the Mira estuary (Portugal). Wetl Ecol Manag 9, 121–134. https://doi.org/10.1023/A:1011193421035
Costa, M.J., Costa, J.L., Raposo De Almeida, P., Assis, C.A., 1994. Do eel grass beds and salt marsh borders act as preferential nurseries and spawning grounds for fish? An example of the Mira estuary in Portugal.
Cowley, P.D., Whitfield, A.K., 2002. Biomass and production estimates of a fish community in a small South African estuary. J Fish Biol 61, 74–89. https://doi.org/10.1006/jfbi.2002.2069
Créach, V., Schricke, M.T., Bertru, G., Mariotti, A., 1997. Stable Isotopes and Gut Analyses to Determine Feeding Relationships in Saltmarsh Macroconsumers, Estuarine, Coastal and Shelf Science.
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
Dale, J., Burgess, H.M., Berg, M.J., Strong, C.J., Burnside, N.G., 2021. Morphological evolution of a non-engineered managed realignment site following tidal inundation. Estuar Coast Shelf Sci 260, 107510. https://doi.org/10.1016/j.ecss.2021.107510
Day, J.W., Crump, Byron.C., Kemp, Michael.W., Yanez-Arancibia, A., 2012. Estuarine Ecology, Estuarine Ecology. Wiley. https://doi.org/10.1002/9781118412787
Degerman, E., Tamario, C., Watz, J., Nilsson, P.A., Calles, O., 2019. Occurrence and habitat use of European eel (Anguilla anguilla) in running waters: lessons for improved monitoring, habitat restoration and stocking. Aquat Ecol 53, 639–650. https://doi.org/10.1007/s10452-019-09714-3
Dolbeth, M., Martinho, F., Freitas, V., Costa-Dias, Ś., Campos, J., Pardal, M.Â., 2010. Multi-year comparisons of fish recruitment, growth and production in two drought-affected Iberian estuaries. Mar Freshw Res 61, 1399–1415. https://doi.org/10.1071/MF10002
Dolbeth, M., Martinho, F., Viegas, I., Cabral, H., Pardal, M.A., 2008. Estuarine production of resident and nursery fish species: Conditioning by drought events? Estuar Coast Shelf Sci 78, 51–60. https://doi.org/10.1016/j.ecss.2007.11.021
Domingos, I., Costa, J.L., Costa, M.J., 2006. Factors determining length distribution and abundance of the European eel, Anguilla anguilla, in the River Mondego (Portugal). Freshw Biol 51, 2265–2281. https://doi.org/10.1111/j.1365-2427.2006.01656.x
Elliott, M.., Hemingway, Krystal., 2002. Fishes in estuaries. Blackwell Science , Iowa. https://doi.org/10.1002/9780470995228
Elliott, M., Taylor, C.J.L., 1989. The structure and functioning of an estuarine/marine fish community in the Forth estuary, Scotland., in: Proceedings of the 21st European Marine Biology Symposium, Gdánsk. Polish Academy of Sciences, Institute of Oceanology, pp. 14–19.
Endresz, K., 2020. Understanding the ecological linkages between salt marsh ecosystems and nearshore fisheries.
Engelhard, G.H., Peck, M.A., Rindorf, A., C. Smout, S., 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 Journal of Marine Science 71, 90–104. https://doi.org/10.1093/icesjms/fst087

Erzini, K., Parreira, F., Sadat, Z., Castro, M., Bentes, L., Coelho, R., Gonçalves, J.M.S., Lino, P.G., Martinez-Crego, B., Monteiro, P., Oliveira, F., Ribeiro, J., de los Santos, C.B., Santos, R., 2022. Influence of seagrass meadows on nursery and fish provisioning ecosystem services delivered by Ria Formosa, a coastal lagoon in Portugal. Ecosyst Serv 58. https://doi.org/10.1016/j.ecoser.2022.101490

European Commission, 2021. The Habitats Directive [WWW Document]. European Commission. URL https://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm (accessed 1.18.23).

Flores-Verdugo, F., González-Farías, F., Ramírez-Flores, O., Amezcua-Linares, F., Yáñez-Arancibia, A., Alvarez-Rubio, M.,, Day, J.W., 1990. Mangrove ecology, aquatic primary productivity, and fish community dynamics in the Teacapán-Agua Brava Lagoon-Estuarine system (Mexican Pacific).

França, S., Costa, M.J., Cabral, H.N., 2009. Assessing habitat specific fish assemblages in estuaries along the Portuguese coast. Estuar Coast Shelf Sci 83, 1–12. https://doi.org/10.1016/j.ecss.2009.03.013

Franco, A., Elliott, M., Franzoi, P., Nunn, A., Hänfling, B., Colclough, S., Young, M., 2022. Study Methods: Field Equipment, Sampling and Methods, 1st ed, Fish and Fisheries in Estuaries: A Global Perspective. 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

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

Garbutt, R.A., Reading, C.J., Wolters, M., Gray, A.J., Rothery, P., 2006. Monitoring the development of intertidal habitats on former agricultural land after the managed realignment of coastal defences at Tollesbury, Essex, UK. Mar Pollut Bull 53, 155–164. https://doi.org/10.1016/j.marpolbul.2005.09.015

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

Gibson, R.N., Barnes, M., Atkinson, R.J.A., 2001. Selective tidal-stream transport of marine animals. Oceanography and Marine Biology, an Annual Review 39, 305–353.

Gillespie, D.M., Benke, A.C., 1979. Methods of calculating cohort production from field data-some relationships. Limnol Oceanogr. https://doi.org/10.4319/lo.1979.24.1.0171

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., Grey, J., Underwood, G.J.C., 2012. High site fidelity and low site connectivity in temperate salt marsh fish populations: A stable isotope approach. Oecologia 168, 245–255. https://doi.org/10.1007/s00442-011-2077-y

Greenwood, M.F.D., Hill, A.S., 2003. Temporal, spatial and tidal influences on benthic and demersal fish abundance in the Forth estuary. Estuar Coast Shelf Sci 58, 211–225. https://doi.org/10.1016/S0272-7714(03)00071-4
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. Canadian Journal of Fisheries and Aquatic Sciences 42, s39–s55. https://doi.org/10.1139/f85-261
Hagan, S.M., Able, K.W., 2003. Seasonal changes of the pelagic fish assemblage in a temperate estuary. Estuar Coast Shelf Sci 56, 15–29. https://doi.org/10.1016/S0272-7714(02)00116-6
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. Helgol Mar Res 59, 151–162. https://doi.org/10.1007/s10152-004-0214-2
Hansen, V.D., Reiss, K.C., 2015. Chapter 16 - Threats to Marsh Resources and Mitigation, in: Shroder, J.F., Ellis, J.T., Sherman Risks, and Disasters, D.J.B.T.-C. and M.H. (Eds.), Hazards and Disasters Series. Elsevier, Boston, pp. 467–494. https://doi.org/https://doi.org/10.1016/B978-0-12-396483-0.00016-9
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
Henriksen, O., Moran, N.P., Veilex, L.A., Behrens, J.W., Nielsen, A., Mildenberger, T.K., Wright, P.J., Jensen, H., van Deurs, M., 2024. Effects of sediment type and light availability on the burying behaviour of small sandeel (Ammodytes tobianus). J Exp Mar Biol Ecol 577. https://doi.org/10.1016/j.jembe.2024.152020
Henriques, S., Cardoso, P., Cardoso, I., Laborde, M., Cabral, H.N., Vasconcelos, R.P., 2017. Processes underpinning fish species composition patterns in estuarine ecosystems worldwide. J Biogeogr 44, 627–639. https://doi.org/10.1111/jbi.12824
Hùines, A.Ê.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, 2007. UK Biodiversity Action Plan: List of UK BAP priority marine species. Joint Nature Conservation Committee 1–6.
Johnson, D.H., Shrier, B.M., O'Neal, J.S., Knutzen, J.A., Augerot, X., O'Neil, T.A., Pearsons, T.N., 2007. Salmonid Field Protocols Handbook: Techniques for Assessing Status and Trends in Salmon and Trout. Salmonid Field Protocols Handbook: Techniques for Assessing Status and Trends in Salmon and Trout 267–324. https://doi.org/10.47886/9781888569926.fmatter
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
Kimmerer, W., 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? Mar Ecol Prog Ser 243, 39–55. https://doi.org/10.3354/meps243039
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., Baisez, A., Rigaud, C., Feunteun, E., 2004. Habitat preferences of different European eel size classes in a reclaimed marsh: a contribution to species and ecosystem conservation. Hal Open Science 24, 642–651. https://doi.org/10.1672/0277-5212(2004)024[0642:HPODEE]2.0.CO;2ï
Laffaille, P., Feunteun, E., Baisez, A., Robinet, T., Acou, A., Legault, A., Lek, S., 2003. Spatial organisation of European eel (Anguilla anguilla L.) in a small catchment. Ecol Freshw Fish 12, 254–264. https://doi.org/10.1046/j.1600-0633.2003.00021.x
Laffaille, P., Feunteun, E., Lefeuvre, J.C., 2000. 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., Lasne, E., Baisez, A., 2009. Effects of improving longitudinal connectivity on colonisation and distribution of European eel in the Loire catchment, France. Ecol Freshw Fish 18, 610–619. https://doi.org/10.1111/j.1600-0633.2009.00378.x
Laffaille, P., Lefeuvre, J.-C., Schricke, M.-T., Feunteun, E., 2001. Feeding Ecology of 0-Group Sea Bass, Dicentrarchus labrax, in Salt Marshes of Mont Saint Michel Bay (France). Estuaries 24, 116–125. https://doi.org/https://doi.org/10.2307/1352818
Larocque, S.M., Cooke, S.J., Blouin-Demers, G., 2012. A breath of fresh air: Avoiding anoxia and mortality of freshwater turtles in fyke nets by the use of floats. Aquat Conserv 22, 198–205. https://doi.org/10.1002/aqc.1247
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
Lyach, R., 2022. The Effect of Fishery Management on the Yield of the Critically Endangered European Eel Anguilla anguilla in Mesotrophic Rivers and Streams in Central Europe. Fishes 7, 1–17. https://doi.org/10.3390/fishes7010042
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

MacKenzie, R.A., Dionne, M., 2008. Habitat heterogeneity: Importance of salt marsh pools and high marsh surfaces to fish production in two Gulf of Maine salt marshes. Mar Ecol Prog Ser 368, 217–230. https://doi.org/10.3354/meps07560
MacLeod, H.A., Shuter, B.J., Minns, C.K., Rennie, M.D., 2022. Productivity of Fish Populations: Environmental and Ecological Drivers, in: Encyclopedia of Inland Waters, Second Edition. Elsevier, pp. 207–224. https://doi.org/10.1016/B978-0-12-819166-8.00198-5
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
McCormick, H., Salguero-Gómez, R., Mills, M., Davis, K., 2021. Using a residency index to estimate the economic value of coastal habitat provisioning services for commercially important fish species. Conserv Sci Pract 3, 1–12. https://doi.org/10.1111/csp2.363
McKinley, E., Ballinger, R.C., Beaumont, N.J., 2018a. Saltmarshes, ecosystem services, and an evolving policy landscape: A case study of Wales, UK. Mar Policy 91, 1–10. https://doi.org/https://doi.org/10.1016/j.marpol.2018.01.021
McKinley, E., Ballinger, R.C., Beaumont, N.J., 2018b. Saltmarshes, ecosystem services, and an evolving policy landscape: A case study of Wales, UK. Mar Policy 91, 1–10. https://doi.org/10.1016/j.marpol.2018.01.021
Munro, J.L., Bell, J.D., 1997. Enhancement of marine fisheries resources. Reviews in Fisheries Science 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 and Fisheries 16, 362–371. https://doi.org/10.1111/faf.12057
Pauly, D., Zeller, D., Palomares, M.L.D., 2020. Sea Around Us Concepts, Design and Data (seaaroundus.org). [WWW Document].
Pereira, H.H., Neves, L.M., da Costa, M.R., Araújo, F.G., 2015. Fish assemblage structure on sandy beaches with different anthropogenic influences and proximity of spawning grounds. Marine Ecology 36, 16–27. https://doi.org/10.1111/maec.12113
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
Peverley, M., Stewart, J.E., 2021. Fisheries Research & Management Plan: Atlantic Herring (Clupea harengus) in the North of Devon & Severn IFCA's District. Devon and Severn Inshore Fisheries and Conservation Authority & North Devon Biosphere.
Pickett, G.D., Kelley, D.F., Pawson, M.G., 2004. The patterns of recruitment of sea bass, Dicentrarchus labrax L. from nursery areas in England and Wales and implications for fisheries management. Fish Res 68, 329–342. https://doi.org/10.1016/j.fishres.2003.11.013
Pierce, C.L., Rasmussen, J.B., Leggett, W.C., 1990. Sampling littoral fish with a seine: corrections for variable capture efficiency. Canadian Journal of Fisheries and Aquatic Sciences 47, 1004–1010. https://doi.org/10.1139/f90-115
Pihl, L., Rosenberg, R., 1982a. Production, Abundance, and Biomass of Mobile Epibenthic Marine Fauna in Shallow Waters, Western Sweden. Mar. Biol. Ecol 51, 273–301. https://doi.org/10.1016/0022-0981(82)90197-6

Pihl, L., Rosenberg, R., 1982b. Production, abundance, and biomass of mobile epibenthic marine fauna in shallow waters, Wester Sweden. Mar. Biol. Ecol 51, 273–301. https://doi.org/https://doi.org/10.1016/0022-0981(82)90197-6

Polderman, P.J.G., 1978. Algae of saltmarshes on the south and southwest coasts of england. British Phycological Journal 13, 235–240. https://doi.org/10.1080/00071617800650281

Pombo, L., Rebelo, J.E., Elliott, M., 2007. The structure, diversity and somatic production of the fish community in an estuarine coastal lagoon, Ria de Aveiro (Portugal). Hydrobiologia 587, 253–268. https://doi.org/10.1007/s10750-007-0687-5

R Core Team, 2021. R: A language and environment for statistical computing. . R Foundation for Statistical Computing.

Randall, R.G., Minns, C.K., 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Canadian Journal of Fisheries and Aquatic Sciences 57, 1657–1667. https://doi.org/10.1139/cjfas-57-8-1657

Rees, S., Angus, S., Creer, J., Lewis, H., Mills, R., 2019. Guidelines for the selection of biological SSSIs. Part 2 Detailed guidelines for Habitats and Species. Chapter 1a Coastlands (coastal saltmarsh, sand dune, machair, shingle, and maritime cliff and slopes, habitats), JNCC.

Ricci, S.W., Eggleston, D.B., Bohnenstiehl, D.W.R., 2017. Use of passive acoustic monitoring to characterize fsh spawning behavior and habitat use within a complex mosaic of estuarine habitats. Bull Mar Sci 93, 439–453. https://doi.org/10.5343/bms.2016.1037

Richards, J.L., Sheng, V., Wing Yi, C., Lai Ying, C., Sin Ting, N., Sadovy, Y., Baker, D., 2020. Prevalence of critically endangered European eel (Anguilla anguilla) in Hong Kong supermarkets. Sci Adv 6. https://doi.org/10.1126/sciadv.aay0317

Rochette, S., Rivot, E., Morin, J., Mackinson, S., Riou, P., Le Pape, O., 2010. Effect of nursery habitat degradation on flatfish population: Application to Solea solea in the Eastern Channel (Western Europe). J Sea Res 64, 34–44. https://doi.org/10.1016/j.seares.2009.08.003

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, 595–606. https://doi.org/10.1577/1548-8659(1984)113<595:fuigse>2.0.co;2

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. https://doi.org/10.1093/icesjms/fst152

Shimadzu, H., Dornelas, M., Magurran, A.E., 2015. Measuring temporal turnover in ecological communities. Methods Ecol Evol 6, 1384–1394. https://doi.org/10.1111/2041-210X.12438

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

Shute, S.L., Pennack, L.M., Scorey, A., Nielsen, I.A., Unsworth, R.K.F., Esteban, N., 2025. Fish density in NE Atlantic saltmarsh is three-fold higher than unvegetated shores. Estuar Coast Shelf Sci 327, 109599. https://doi.org/10.1016/j.ecss.2025.109599.

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 and Fisheries 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 and Coasts 38, 268–284. https://doi.org/10.1007/s12237-014-9801-x
Sundblad, G., Bergström, U., Sandström, A., Eklöv, P., 2014. Nursery habitat availability limits adult stock sizes of predatory coastal fish. ICES Journal of Marine Science 71, 672–680. https://doi.org/10.1093/icesjms/fst056
Svensson, C.J., Hyndes, G.A., Lavery, P.S., 2007. Food web analysis in two permanently open temperate estuaries: Consequences of saltmarsh loss? Mar Environ Res 64, 286–304. https://doi.org/10.1016/j.marenvres.2007.02.002
Syukur, A., Al-Idrus, A., Zulkifli, L., 2021. Seagrass-associated fish species' richness: Evidence to support conservation along the south coast of Lombok Island, Indonesia. Biodiversitas 22, 988–998. https://doi.org/10.13057/biodiv/d220255
Thayer, G.W., Colby, D.R., Hettler, W.F., 1987. Utilization of the red mangrove prop root habitat. Marine Ecological Progress Series 35, 25–38.
Townend, I., Fletcher, C., Knappen, M., Rossington, K., 2011. A review of salt marsh dynamics. Water and Environment Journal 25, 477–488. https://doi.org/10.1111/j.1747-6593.2010.00243.x
Tupper, M., Able, K.W., 2000. Movements and food habits of striped bass (Morone saxatilis) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh. Mar Biol 137, 1049–1058. https://doi.org/https://doi.org/10.1007/s002270000421

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/https://doi.org/10.1016/j.ecss.2006.05.037
Verhelst, P., Reubens, J., Pauwels, I., Buysse, D., Aelterman, B., Van Hoey, S., Goethals, P., Moens, T., Coeck, J., Mouton, A., 2018. Movement behaviour of large female yellow European eel (Anguilla anguilla L.) in a freshwater polder area. Ecol Freshw Fish 27, 471–480. https://doi.org/10.1111/eff.12362
Vernberg, F.J., 1993. Salt-marsh processes: A Review. Environ Toxicol Chem 12, 2167–2195. https://doi.org/10.1002/etc.5620121203
Virgin, S.D.S., Beck, A.D., Boone, L.K., Dykstra, A.K., Ollerhead, J., Barbeau, M.A., McLellan, N.R., 2020. A managed realignment in the upper Bay of Fundy: Community dynamics during salt marsh restoration over 8 years in a megatidal, ice-influenced environment. Ecol Eng 149. https://doi.org/10.1016/j.ecoleng.2020.105713
Walton, W.E., Wirth, M.C., Workman, P.D., 2007. Environmental factors influencing survival of threespine stickleback (Gasterosteus aculeatus) in a multipurpose constructed treatment wetland in southern California. Journal of Vector Ecology 32, 90–105. https://doi.org/10.3376/1081-1710(2007)32[90:efisot]2.0.co;2

Whitfield, A.K., 2020. Littoral habitats as major nursery areas for fish species in estuaries: a reinforcement of the reduced predation paradigm. Marine Progress Series 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
Winberg, G.G., 1971. Methods for the Estimating of Production of Aquatic Animals., in: Academic Press Inc, London. p. 175.
Wong, M.C., Dowd, M., 2016. A Model Framework to Determine the Production Potential of Fish Derived from Coastal Habitats for Use in Habitat Restoration. Estuaries and Coasts 39, 1785–1800. https://doi.org/10.1007/s12237-016-0121-1
Yáñez-Arancibia, A., Linares, F.A., Day, J.W., 1980. Fish community structure and function in terminos lagoon, a tropical estuary in the southern gulf of mexico, in: Estuarine Perspectives. Elsevier, pp. 465–482. https://doi.org/10.1016/B978-0-12-404060-1.50044-7
Zedler, J.B., Callaway, J.C., Desmond, J.S., Vivian-Smith, G., Williams, G.D., Sullivan, G., Brewster, A.E., Bradshaw, B.K., 1999. Californian Salt-Marsh Vegetation: An Improved Model of Spatial Pattern. Ecosystems 2, 19–35. https://doi.org/10.1007/s100219900055

Appendices

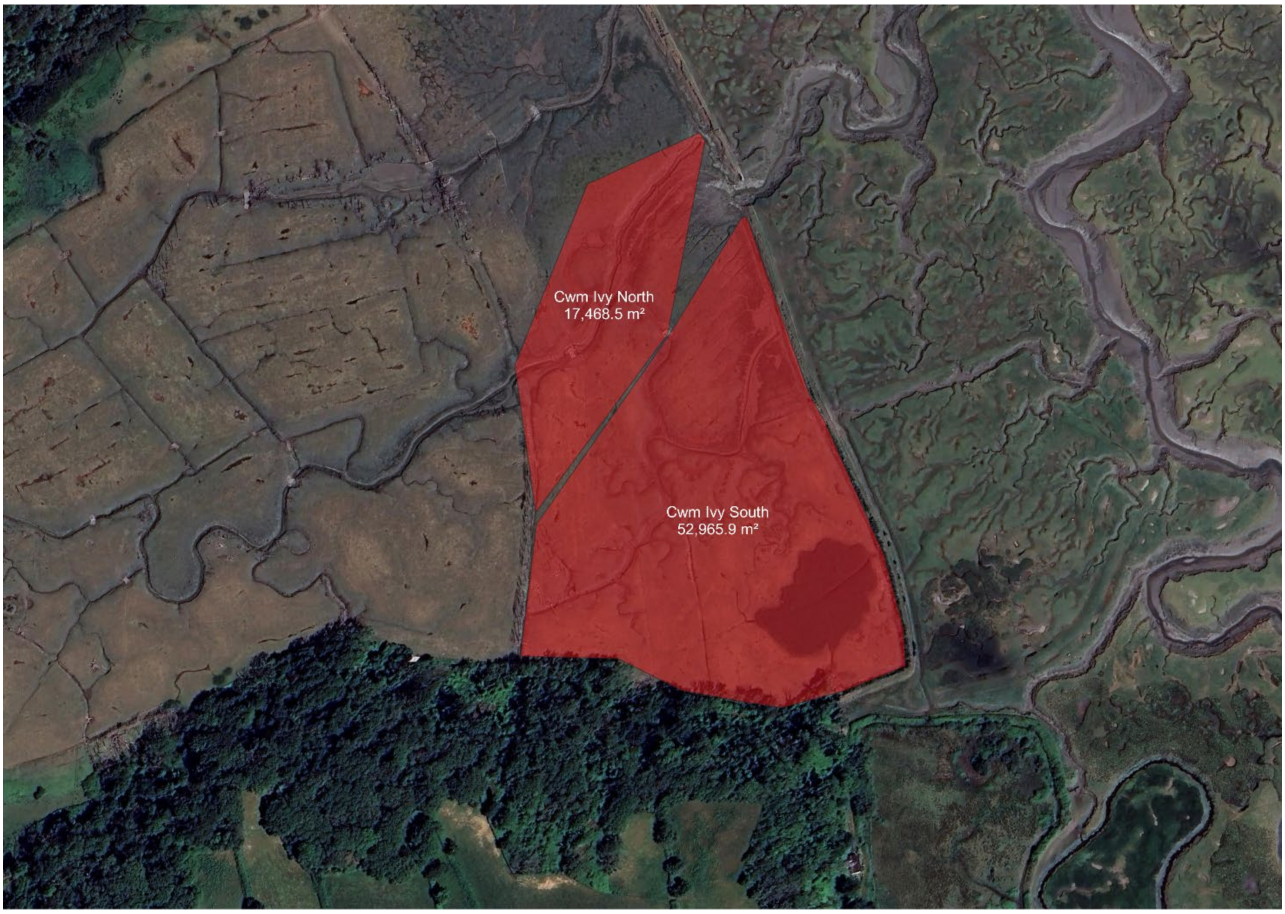
Appendix A: Site survey characteristics including gear type, sampling period and location. The year 2022 is represented by October only, 2023 by October-December and 2024 by January-August.

Cluster	Site name	Method	Year	Coordinates (Decimal Degrees)
Cwm Ivy	Middle Creek	Fyke	2023, 2024	51.625573, -4.246668
Cwm Ivy	South Creek	Fyke	2023, 2024	51.625094, -4.246295
Cwm Ivy	Cwm Ivy	Seine	2023	51.622601, -4.246206
Cwm Ivy	Cwm Ivy	Seine	2024	51.627215, -4.248690
N/A	Weobely Castle	Seine	2022	51.62898, -4.20786
North Gower	Crofty playground	Seine	2022, 2023, 2024	51.632471, -4.131028
North Gower	Crofty	Fyke	2023, 2024	51.64156, -4.13755
North Gower	Pen-Clawdd	Fyke	2023, 2024	51.64233, -4.12101
N/A	Pen-Clawdd	Seine	2022	51.63288, -4.13066
N/A	Loughor	Seine	2022	51.64501, -4.09508
Llanelli WWT	Llanelli WWT	Fyke	2023, 2024	51.65894, -4.11688
Llanelli WWT	Llanelli WWT	Seine	2023, 2024	51.659019, -4.114064
Llanelli Beach	Llanelli Beach	Seine	2023, 2024	51.675450, -4.178758
Llanelli Beach	South	Fyke	2023, 2024	51.676077, -4.180313
Llanelli Beach	North	Fyke	2023, 2024	51.676635, -4.180732
St Ishmael	Kidwelly	Fyke	2023, 2024	51.737064, -4.363060
St Ishmael	Ferryside	Fyke	2023, 2024	51.768557, -4.371200
St Ishmael	Ferryside	Seine	2023, 2024	51.769244, -4.370037
Laugharne	Castle North	Fyke	2023, 2024	51.768967, -4.460058
Laugharne	Castle South	Fyke	2023, 2024	51.76718, -4.45993
Laugharne	Castle	Seine	2022, 2023, 2024	51.770735, -4.458806

Appendix B: Tidal heights of deployment and retrieval for each fyke net placed across all habitat types.

Site name	Habitat type	Deployment height (m)	Retrieval height (m)
Cwm Ivy – Middle Creek	Managed realignment	5.63	6.25
Cwm Ivy – South Creek	Managed realignment	6.00	7.19
Crofty	Saltmarsh	6.25	7.5
Pen-Clawdd	Saltmarsh	6.75	8.13
Llanelli WWT	Saltmarsh	5.65	6.7
Llanelli Beach South	Unvegetated	5.07	6.8
Llanelli Beach North	Unvegetated	5.07	6.8
Kidwelly	Unvegetated	4.25	4.5
Ferryside	Unvegetated	4.5	5
Laugharne Castle North	Saltmarsh	4.25	5.25
Laugharne Castle South	Saltmarsh	4.5	5.5

Appendix C: Areas sampled by fyke net.



Cwm Ivy Cluster with 2 fyke nets set up in two different creeks, North and south.

North Gower cluster with two fyke nets set up in two different creeks, one at Crofty and one at Pen-clawdd.

Llanelli WWT cluster with one fyke net set up at the bottom of a saltmarsh creek.

Llanelli Beach cluster with two fyke nets set up either side of the beach groin, North and South.

St Ishmael cluster with two fykes set up on different sandy/muddy beaches, one at Kidwelly and one at Ferryside.

Laugharne cluster with two fyke nets set up in different creeks, North and South.

Appendix D: Full species list with habitat and netting occurrences.

Species	Gear	Saltmarsh (*N*)	Unvegetated (*N*)	Managed Realignment (*N*)
Atlantic herring	Seine	1823	71	0
Atlantic herring	Fyke	186	0	0
European bass	Seine	1239	423	162
European bass	Fyke	186	56	109
Common goby	Seine	836	167	73
Common goby	Fyke	403	17	548
Grey mullet	Seine	1427	377	62
Grey mullet	Fyke	275	8	46
European flounder	Seine	181	12	0
European flounder	Fyke	10	7	4
Lesser sandeel	Seine	332	0	0
Lesser sandeel	Fyke	0	0	0
Three-spined stickleback	Seine	315	1	0
Three-spined stickleback	Fyke	2	0	0
Sand goby	Seine	38	30	0
Sand goby	Fyke	5	5	0
European sprat	Seine	39	0	0
European sprat	Fyke	1	0	0
Sand smelt	Seine	15	30	0
Sand smelt	Fyke	0	0	0
European eel	Seine	1	0	0
European eel	Fyke	0	0	13
Greater pipefish	Seine	0	4	0
Greater pipefish	Fyke	0	1	0
Sea trout	Seine	1	1	0
Sea trout	Fyke	1	0	0
Fifteen-spine stickleback	Seine	0	0	0
Fifteen-spine stickleback	Fyke	0	1	0
Fivebeard rockling	Seine	0	0	0
Fivebeard rockling	Fyke	1	0	0
Rudd	Seine	0	0	0
Rudd	Fyke	1	0	0
Topmouth gudgeon	Seine	1	0	0
Topmouth gudgeon	Fyke	0	0	0
Worm pipefish	Seine	1	0	0
Worm pipefish	Fyke	0	0	0

Appendix E: Conversion values from length measurements to wet weight.

Conversion from lengths to weights.

Species	Length measurement In field	Length measurement In equation	a	b	Reference
Atlantic herring	FL	TL	0.00497	3.192	Coull *et al.*, 1989
European bass	FL	FL	0.0123	2.955	Dorel, 1986
Grey mullet	FL	FL	0.008	3.15	Moreno-Valcarcel *et al.*, 2012
Golden grey mullet	FL	FL	0.008	3.14	Veiga *et al.*, 2009 and Moreno-Valcarcel *et* 2012
European flounder	TL	TL	0.0116	2.963	Dorel, 1986
Lesser sandeel	FL	TL	0.0015	3.169	Reay, 1973
European eel	TL	TL	0.00056	3.313	Mann & Blackburn, 1991
Sand smelt	FL	TL	0.0069	3	Bauchot and Bauchot, 1978
Three-spined stickleback	TL	TL	0.0239	2.611	Wilhelms 2013
European sprat	FL	TL	0.00219	3.479	Coull *et al.*, 1989
Goby species	FL	FL	0.01	2.898	Wilhelms 2013
Thinlip mullet	FL	FL	0.008	3.15	Moreno-Valcarcel *et al.*, 2012
Golden mullet	FL	FL	0.008	3.14	Moreno-Valcarcel *et al.*, 2012
Grey mullet	FL	FL	1.008	3.145	Moreno-Valcarcel *et al.*, 2013
Sea trout	FL	FL	0.131	2.905	Crisp & Beaumount, 1995

Conversion from total lengths to fork lengths for species where no conversion from fork length to weight was found.

Species	a	b	Reference
Atlantic herring	0	1.09	Ojaveer, 2003
Lesser sandeel	0	1.04	Reay, 1973
Sand smelt	0	1.102	Fishbase
European Sprat	0	1.09	Ojaveer, E. and R. Aps, 2003

Data Archive Appendix

No data outputs were produced as part of this project.

Further copies of this report are available from library@cyfoethnaturiolcymru.gov.uk