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Fish are more abundant in salt marsh creeks with a salinity gradient and low drainage capacity

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A R T I C L E I N F O

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A B S T R A C T

Salt marsh conditions and morphology influence the ecological function of marsh habitats. However, little is known about how the interplay between these factors impacts fish in the highly modified marshes typical of north-western Europe. We conducted a two-year survey at two salt marsh areas in the Dutch Wadden Sea to test the influence of marsh creek morphology on in-creek abiotic conditions and the abundance of four numerically dominating fish species representing the different life-history strategies of fish in the marshes. We measured fish abundance and several abiotic factors seasonally, and quantified the morphological attributes of each creek (such as volume), and of the creek basin (such as drainage density and bathymetry). Modelling results revealed a salinity gradient and/or a greater capacity for water retention (creek volume or drainage density) were associated with higher abundances of Atlantic herring (*Clupea harengus*), European eel (*Anguilla*), gobies (*Pomatoschistus* sp.) and the three-spined stickleback (*Gasterosteus aculeatus*) across most seasons. During recruitment months sticklebacks and gobies were more abundant in brackish water conditions with a higher capacity for water retention. Eels were more abundant in creeks with larger volumes and lower salinities. Larval and juvenile herring were more numerous in brackish water than in water with higher salinity, but an effect of creek morphology on herring abundance was not detected. While recruitment processes were important determinants in the seasonal abundance of most species, creek morphology and abiotic conditions affected the use of salt marsh habitat by the fish species studied. Intertidal marsh creeks that retain water during low tide and have a salinity gradient hold more fish than marshes lacking these characteristics. These findings highlight the effects of local salt marsh conditions on fish assemblages. Taking the specific marsh conditions and their effects on fish into account in salt marsh management can improve outcomes for fish.

1. Introduction

Salt marshes are highly productive ecosystems that stabilise coastlines, filter runoff and support marine biodiversity (Barbier et al., 2011). For fish, coastal marshes provide essential stop-over, spawning and nursery habitats for a wide variety of resident and transient species that benefit from access to food and shelter (Boesch and Turner, 1984; Deegan et al., 2002; Kneib, 1997). In many areas, marsh habitats are even essential for maintaining fish populations targeted by fisheries (Baker et al., 2020; Barbier et al., 2011; Beck et al., 2001). However, salt marshes across the world have undergone massive structural changes as a result of coastal development, leading to large losses and modifications (Crooks et al., 2011; Duarte et al., 2008). In northern Europe, large mainland areas are protected by seawalls and dykes which have created migratory barriers between fresh and saltwater habitats, leaving only a highly modified foreshore available for marsh development (Bakker et al., 2002; Vos and Knol, 2015). Together with dam construction and river modification, these developments have resulted in a 93 % decrease in migratory fish populations over the last 50 years (Deinet et al., 2020). By fundamentally changing the structure of salt marshes, marshscapes may no longer be incorporating values that are essential for fish species across their entire life cycle. It is therefore important we understand how coastal modification has altered the physical structure of salt marshes, and in turn, how this has affected their habitat value for fish.

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The physical structure of salt marshes is an important determinant in their value as a habitat for fish species (Allen et al., 2007). Marine species, especially small and juvenile fishes, access salt marshes from the seaside via a network of intertidal and/or subtidal creeks permeating the marsh surface (Friese et al., 2021a; Rozas et al., 1988). The morphological traits of these waterways, such as their length, width, depth, and connectivity to the sea, can influence their suitability as a habitat for fish by affecting the within-creek conditions (Allen et al., 2007; Gewant and Bollens, 2012; McIvor and Odum, 1988; Rozas, 1992; Visintainer et al., 2006; Williams and Zedler, 1999). For example, creeks with lower water velocity have been associated with higher biomass of fish and crustacean species (Allen et al., 2007). However, most research on this relationship has been conducted in the southern United States, where the marsh surface is inundated with water each tidal cycle (Allen et al., 2007; Cattrijsse and Hampel, 2006; Christian and Allen, 2014; Gewant and Bollens, 2012; McIvor and Odum, 1988; Visintainer et al., 2006; Williams and Zedler, 1999). While some studies have explored the relationship between marsh morphology and fish outside the southern United States (e.g. see Jin et al. (2014); Lechene et al. (2018); Lesser et al. (2020)), research is lacking in north-western Europe (but see de la Barra et al. (2022)) where the marsh surface only floods occasionally with very high water levels (Cattrijsse and Hampel, 2006). Given the differences in marsh tidal inundation between studies on partially and completely flooding marshes in north-western Europe and the southern United States, respectively, we might expect the effects of marsh morphology on fish to also differ.

The Wadden Sea is the largest wetland area in Europe, supporting a range of habitats including intertidal mudflats and salt marshes (Enemark, 2005). The present-day Wadden Sea salt marsh area is vastly reduced (~50–80 % wetland loss) compared to its historical extent because of ditching and damming for land reclamation (Airoldi and Beck, 2007; Elschot et al., 2020; Vos and Knol, 2015). Salt marshes can be found along the mainland and on the south sides of the barrier islands. Today the mainland Wadden Sea marsh habitats are characterised by artificially constructed drained foreshore marshes with uniformly structured tidal creeks cut off from the freshwater system by a dyke (Bakker et al., 2002; Friese et al., 2021a). More naturally developing and structured marshes mainly occur on the barrier islands separating the area from the North Sea (Bakker et al., 2002). While many European studies compare differences in species composition between natural and modified salt marshes and detail the use of marshes by fish (Cattrijsse et al., 1994; de la Barra et al., 2022; Drake and Arias, 1991; Friese et al., 2018; Green et al., 2009; Laffaille et al., 2000; Lechene et al., 2018), evidence of which characteristics are important for fish is limited (Garbutt et al., 2017), but see de la Barra et al. (2022) who showed water exchange volume to be an important marsh property affecting fish abundances. However, a comprehensive study on the different morphological elements affecting salt marsh fish communities in north-west Europe is missing. The aim of this research was to fill this knowledge gap. Our objective was to understand the relationships between salt marsh creek morphology, environmental conditions and fish abundance in a modified and a natural salt marsh in the Dutch Wadden Sea. By quantifying the morphological characteristics of the two different salt marshes, we explore the spectrum of marsh conditions

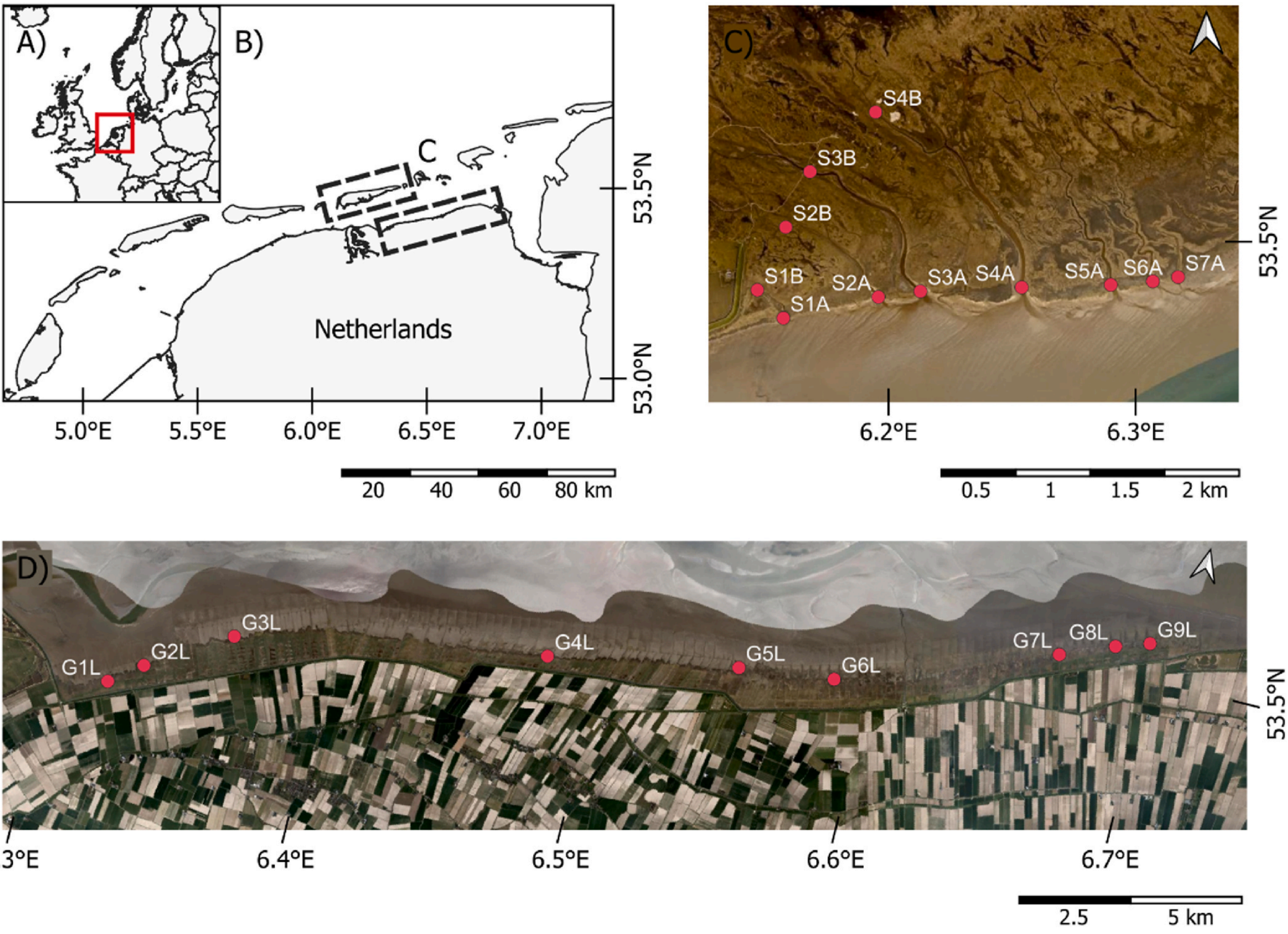

Fig. 1. Map of the study locations in the Dutch Wadden Sea in north-western Europe (A & B) where C) represents the natural island of Schiermonnikoog, and (D) shows the artificially constructed marsh on Groningen Coast. Points represent fyke net locations and fyke 'names'.

available for fish in the Wadden Sea. We hypothesised fish would be more abundant in creeks which retained water throughout a tidal cycle, as we expected this to create more stable habitat conditions.

2. Methods

2.1. Study sites

Sixteen salt marsh creeks were studied in the Dutch Wadden Sea, the Netherlands (Fig. 1). Two marsh areas were selected: the back-barrier salt marsh on the Wadden Island of Schiermonnikoog (total marsh area ~5400 ha (Schiermonnikoog info, 2024); n = 4 creeks) and the artificially constructed mainland marsh of Groningen coast (total marsh area ~1752 ha (Elschot et al., 2020); n = 9 creeks). Schiermonnikoog was selected because it is a naturally developing marsh, situated in a protected area, with low levels of livestock grazing from April–October, and unmodified creeks. Groningen coast was selected to represent a typical modified marsh along the Wadden Sea coast: an area of reclaimed agricultural land in front of a dyke (approx. 40 km) with mosaic livestock grazing from April–October. Creeks were included from both areas to represent the breadth of creek morphologies present in the Wadden Sea. The creeks are inundated during a standard tidal cycle, and the greatest tidal exchange occurs during spring tides (bimonthly), when partial flooding of the marsh surface is most likely to occur (Friese et al., 2018). Only very rarely during storm conditions is the marsh surface inundated entirely.

Biotic and abiotic variables were sampled at the creek mouth, where it opened to the sea (low sites) (Fig. 1). To represent upstream habitat missing from Groningen coast creeks, sampling occurred in the high salt marsh vegetation in four creeks on Schiermonnikoog (high sites; mean elevation above Normaal Amsterdams Peil (NAP): ~1.28 m) (Fig. 1C: fyke locations ‘B’). The high sampling sites were placed 320 m, 0.9 km, 1.3 km, and 1.7 km upstream in creeks 1, 2, 3 and 4, respectively (Fig. 1C) in the high marsh zone. Each upstream fyke was placed inland at a distance from the mouth approximately three quarters of the total length of the main creek to sample a different part of the creek habitat. In these upstream areas the water was predominantly brackish and harboured a distinct in-creek community, which was absent from the mainland marshes where the upstream extent of the creeks is cut-off by a sea dyke. The exact location of the upstream fykes was slightly modified in the field to avoid nesting birds.

2.2. Creek morphology

2.2.1. Field measurements

Creek width and bank slope were measured using a laser (Leica Disto X3) and the Trimble® R8 GNSS System (Global Navigation Satellite System) rtk-dGPS (dGPS) with a vertical resolution of 1 mm, for all creeks (Table 1). Three-point cross-sections were measured by taking one point at each edge and one at the deepest point in the creek. On average, 10 cross-sections were measured at each creek, evenly spread out along the entire length of the main channel. Width and slope calculations were subsequently made based on the field measurements using Pythagorean Theorem, and the mean width and slope of each creek was calculated by averaging the values across all cross-sections.

2.2.2. Digital terrain models

Creek attributes related to the properties of the larger channel network of a creek were derived from Digital Terrain Models (DTM) using a publicly available dataset of terrain in the Netherlands (Actueel Hoogtebestand Nederland, AHN). This refers to a number of larger scale variables such as tributary length, mean watershed elevation, total creek length, creek volume, creek drainage efficiency (drainage density) and how many smaller creeks enter the larger creek (bifurcation ratio) (see Table 1 for full list). The latest series of data acquired between 2020 and 2022 was selected with a pixel size of 0.5 m × 0.5 m (AHN4, https://www.arcgis.com/apps/mapviewer/index.html?layers=77da2e9eeea8427aab2ac83b79097b1a). To extract the channel network properties, the DTMs were analysed using the Python toolbox TidalGeoPro Version 0.4 available at https://doi.org/10.5281/zenodo.7071308 (Gourgue et al., 2022) (see Supplement 1: digital terrain models). This toolbox first applies a multi-window median neighbourhood analysis (Liu et al., 2015) to identify channel pixels based on an elevation threshold with respect to neighbouring pixels. From this, the channel edges are retrieved as polygons, and the channel network skeleton is extracted as the centrelines of the channel polygons and redefined at equidistant (0.5 m) points along the skeleton. At each skeleton point (equidistant points along the skeleton) and each skeleton node (confluence point between three or more skeleton sections), the basin surface areas are computed based on the Euclidean distance between each grid cell and the nearest channel (further detailed in Supplement 1: digital terrain models). For each skeleton section (connection between two skeleton nodes), the stream order is computed following Hack’s ordering system. The

Table 1
Outlines the creek morphology attributes measured with dGPS, laser or that were extracted from the digital terrain model (DTM), with a description of each variable and how it was calculated (further information is also available in Supplement 1: Digital Terrain Models).

Variable measured with dGPS or laser	
Creek width	The average horizontal distance between the two creek banks of the main channel, measured at 10 different cross-sections evenly spaced along the entire creek length. When width could not be measured due to unfavourable conditions, it was calculated from Google Earth.
Creek bank slope	The average slope (mean slope 1 + mean slope 2)/2)) of the main channel, measured at ~ 10 different cross-sections evenly spaced along the entire creek length. Slope was calculated as the horizontal distance between the lowest vegetation point (creek edge) to the deepest point of the creek, divided by the elevation change.
Variables extracted from the DTM	
Combined tributary length (m)	Sum of the length of all other tributaries (not including the main creek length) branching from the main creek.
Main creek length (m)	The length of the main creek from the mouth of the creek to the end of the longest tributary.
Total creek length (m)	Sum of the combined tributary length and main creek length.
Depth	The difference between the mean channel edge elevation and the lowest elevation within multiple cross-sections.
Tributary dominance	The combined tributary length divided by the main creek length.
Sinuosity	Ratio between the channel length along its centreline and the straight-line distance between its start and end point.
Bifurcation ratio	Number of creeks of the next higher order, relative to the current order (N_{i+1}/N_i) (Chirol et al., 2018). The stream orders were calculated by assigning a number to a creek segment to express the level of branching of a channel network. Following Hack’s ordering system, the main channel (with its mouth at the sea) has an order of 1 and side channels are given increasingly higher orders. *the higher it is, the higher is the degree of complexity and branching of the creek network (enhancing connectivity and water distribution through the network).
Elevation (m)	Mean elevation in the creek.
Bathymetry (m)	Mean watershed elevation; the mean elevation of the marsh plus the within creek elevation.
Total creek volume (m^3)	The mean creek elevation multiplied by the creek surface area.
Basin surface area (m^2)	Total area of the salt marsh surface that drains into a creek. Computed based on the Euclidean distance between each grid cell and the nearest channel.
Creek surface area (m^2)	Horizontal area within the creek boundaries, based on the location of the channel edges. Calculated as the area of each channel polygon.
Drainage density (m^{-1})	The total creek length (m) divided by the basin surface area (m^2) (the drainage area). *A higher drainage density indicates a more extensive channel network, which generally suggests the system is more efficient at draining water.

channel depth is calculated as the difference between the mean channel edge elevation and the lowest elevation within a cross-section. Channel width is measured as the distance between channel edges. Finally, the cross-sectional area is determined as the integral of the difference between the mean channel edge elevation and the cross-section elevation.

Creek lengths are computed for each skeleton point and skeleton node by measuring the distance along the channel to the downstream edge of the salt marsh (defined manually in GIS as a line shapefile). The creek length at the downstream node corresponds to the total creek length per channel (including the tributaries). The main creek length was measured as the total length of the channel sections classified as Hack order 1, while tributary length is the length of channels with Hack order >1.The creek surface area was calculated as the area of each channel polygon, based on the location of the channel edges. Bathymetry was calculated directly by averaging all elevation values from the DTM (including both the marsh platform and the creeks). Elevation was calculated by averaging the DTM values within the channel polygons, which delineate the channel edges. Total creek volume was obtained as the mean creek elevation multiplied by the creek surface area.

2.3. Fish collection

Fish were captured at both sampling sites every season from March 2021 until February 2023 using fyke nets (8 mm mesh size, 7m long) (Supplement 1: Table S1). Seasons were defined as: winter (December, January, February), spring (March, April, May), summer (June, July, August), and autumn (September, October, November). Fishing was carried out during spring tides when the tidal volume was highest (Friese et al., 2018). During spring tides, low tide occurred close to dawn and dusk. Thus, each fyke net was set at low tide and then emptied twice, once ~12h after initially being set, and again ~24h after the net was first set. This allowed us to separate catches into day and night activity, and minimised fish stress by limiting their time in the fyke nets. Fishing occurred in blocks where 3–4 nets were set in separate creeks at the same time. Each fyke was placed centrally in the deepest part of each creek: at low sites the fyke opening was set at a width of 3 m (Supplement 1: Fig. S1) and at high sites at a width of 2 m. High fykes had a smaller opening due to the creek narrowing with distance into the marsh. In all cases, the fyke opening faced landward, and was placed to allow fish to swim past the net with incoming tide, and be caught in the net with the outgoing tide. The fykes did not block off the entire width of creeks in any of the cases.

The catch was processed in the field. When the number of organisms in the catches were too large to count within 2 h (assessed at net lift based on catch size), a subsample of the overall catch was processed. Fish were identified to the lowest taxonomic level, counted and the total length of the first 50 fish of each species were measured. Fish were sampled randomly from the overall catch using a small scoop net to avoid size selectivity.

2.4. Environmental variables

Organic matter and chlorophyll *a* content of the sediment were sampled to investigate the relationship between organic matter accumulation, biofilm biomass and creek morphology. Sediment was sampled at each fishing event from the creek edge near the fyke using a modified 50 mL disposable syringe as a sediment corer (diameter: 2.6 cm) (methods from van der Ouderaa et al., 2021). For organic matter content, the sediment was sampled down to two different sediment depths (OM1: 0–1 and OM5: 0–5 cm). For chlorophyll *a*, the sediment was sampled down to 1 cm depth (0–1 cm) and immediately wrapped in aluminium foil to prevent further photosynthetic activity. All samples were collected in separate plastic bags and transported on ice to the laboratory where they were stored at −20 °C until processing. Organic matter content was calculated by measuring the Percent Loss on Ignition (LOI) using the following equation: $LOI(\%) = [(W1\text{-}W2)/W2] \times 100$ where W1 = dry weight (48 h at 75 °C) and W2 = dry weight after burning (4 h at 550 °C). The OM1 and OM5 samples were analysed separately. Chlorophyll *a* was extracted from freeze dried sediment using 90 % acetone (dark, −20 °C, 48 h) according to Jeffrey and Humphrey (1975). Chlorophyll *a* concentration was then measured with a fluorometer (Trilogy). At each fishing event we also measured salinity (conductivity, mS/cm) and water temperature (°C) using a multi-meter (Multi 3320®). Conductivity was converted to the practical salinity scale using the “ec2pss” function from the “wql” package in R, at a standardised temperature of 25 °C and pressure at sea level (0) (Jassby et al., 2016).

2.5. Data analysis

The following section details the data selection and model building process followed in this analysis. Briefly, a subset of the overall morphological and environmental variables were selected based on correlation analysis, followed by a two-step model selection process to determine which morphological and environmental variables affected the Catch Per Unit Effort (CPUE, per 24 h) separately for each of four fish species (*Pomatoschistus* sp., flatfish, three-spined stickleback, and eel) (Table 2).

2.5.1. Selecting fish data

The study was designed to evaluate the effects of morphological and abiotic variables on the abundance of individual fish species representing common ecological guilds found in the salt marshes. For this analysis four of the most abundant fish species were selected from different ecological guilds: estuarine residents, marine juveniles, and diadromous fish (anadromous and catadromous). Gobies, which included *Pomatoschistus microps, Pomatoschistus minutus* and *Pomatoschistus lozanoi* in our study, are estuarine residents and were the most common group of fish caught in both salt marshes (Supplement 1: Fig. S2) (Elliott et al., 2007). The second most common group was Atlantic herring (*Clupea harengus*), and our herring catches were dominated by larval and juvenile life stages (Fig. S2). Herring typically use the Dutch Wadden Sea as marine juveniles; spawning in the North Sea and entering the Wadden Sea in spring as larvae (Dickey-Collas et al., 2009), though recent evidence suggests there may still be small, localised herring populations spawning in the Wadden Sea (Maathuis et al., 2024). Anadromous fish migrate from marine conditions to brackish or freshwater to spawn, of the species in this group the three-spined stickleback was selected because it occurred consistently in our catches year-round. Catadromous species migrate from brackish or freshwater to marine conditions to spawn and were represented by eel in our dataset. Preliminary data analyses showed little to no sticklebacks present in August or September, herring in March, July, August, January and February, or eels present in the period January–April at either location. Thus, these months were excluded from the statistical analyses and figures for the respective species but included them in F igure S2 and F ig. 4. All catches were analysed as the total number per two tides (summed number of a day and night catch in 24 h).

2.5.2. Selecting morphological and environmental variables

All analyses were conducted in R v4.3.0 (R Core TeamR., 2013). To describe differences in morphological characteristics between the different creeks and locations, a Principal Component Analysis (PCA) was performed on all creek morphology variables using the ‘prcomp’ function from the ‘stats’ package (R Core TeamR., 2013), and the output was plotted with the ‘fviz_pca_biplot’ function from the ‘factoextra’ package (Kassambara and Mundt, 2017). A correlation analysis was then conducted with the ‘Pearson’ method using the ‘PerformanceAnalytics’ v2.0.4 package (Peterson et al., 2014) on all abiotic parameters including: environmental data (water temperature and salinity), sediment properties (organic matter to 1 and 5 cm depth, and chlorophyll *a* concentration to 1 cm depth), and creek morphology parameters (15

Table 2
Overview of the data analysis process used to assess the effects of morphological and environmental variables on species-specific CPUE.

Step	Action	Description	Rationale
1	Select fish data	Choose species data and transform raw data where required	Ensure data approximate normal distribution for linear model selection
2	Explore morphological characteristics	Use Principal Component Analysis to examine relationships between creeks and locations	Identify patterns and relationships
3	Select environmental and morphological variables	Conduct a correlation analysis and select a subset of uncorrelated variables	Avoid multicollinearity
4	Additive model	Build a base linear additive model and select variables based on MuMIn. For all species the base model was: lm (CPUE species #1 ~ sqrt_volume + sqrt_sinuosity + sqrt_slope + drainage density + bathymetry + bifurcation + elevation + salinity + chlorophyll *a* + temperature + Location + Season, data = df)	Identify key predictor variables per species
5	Interaction model	Test for interactions between variables and context (location and season) and select variables based on MuMIn, e.g. lm (CPUE species #1 ~ salinity × Location + salinity × Season + sqrt_volume × Location + sqrt_volume × Season + Location × Season, data = df)	Detect location-specific effects because variables were often highly correlated with location. Detect seasonally-specific responses, expected based on strong seasonal signal in the data
6	Manual model refinement	Fit species-specific mixed effects models which meet assumptions of the data (e.g. Poisson, negative binomial), and refine by comparing models using Analysis of Variance and AIC	Refine model performance

Notes: At steps 4 and 5, variable selection was guided by MuMIn (Barton and Barton, 2015), with variables and interactions chosen from the top three models with the lowest AIC values. At step 6, variable selection was guided by comparing models using Analysis of Variance and AIC values, ensuring that statistical significance (ANOVA) and model fit (AIC) informed model refinement.

variables describing different elements, see Table 1). Highly correlated variables ($R^2 \geq 0.80$) were identified, and one variable was selected to remain for analysis (Supplement 1: Table S2). The only exception was the morphological variable volume which remained in the analyses although it was highly correlated with bathymetry. To compare fish densities across areas, the general approach is to correct catch by sampled volume to arrive at Catch Per Unit Effort (CPUE). However, since we wanted to compare the morphological properties of different creeks (including differences in properties relating to volume) we analysed catches as numbers per 24 h. Therefore the effect of volume needed to be included in the model to understand the effects of other variables. The final morphology parameters included in the models were: bathymetry, sinuosity, bifurcation ratio, creek elevation, volume, average slope and drainage density. Sinuosity, volume and slope were square root transformed for analysis because of large differences in the magnitude of values between the two salt marsh areas. For the sediment properties, only kept chlorophyll *a* was kept, because it was significantly correlated with organic matter (1 and 5 cm depth, $p < 0.05$) and made the most biological sense (indicator for biofilm biomass). For the rest of the environmental variables both temperature and salinity were included as model parameters.

2.5.3. Model selection

The model selection and refinement process occurred in three steps. Firstly, an additive linear 'base' model was constructed from the morphological and environmental variables selected in the previous step (Section 2.5.2), to test which variables best described the abundance (# CPUE) for each fish species (Step 4 in Table 1). The variable 'Location' (Schiermonnikoog or Groningen coast) was also included in the base model to account for any effects relating to location itself, such as the distance from the sea or the island vs. mainland effect. 'Season' was also included in the model, since there was a strong seasonal signal in the data (Fig. S1). The raw CPUE for each fish species was cube root transformed (sticklebacks and eel) or log1p (gobies and herring) transformed, because the raw data did not fit a normal distribution. For herring, sticklebacks and eel, data transformations were not sufficient to achieve normality. However, running such a complicated model selection process using a non-linear model created issues with model convergence. Thus, the linear model selection process on the most normally transformed response was used to guide variable selection for these species. The variables which performed best were then selected from the top three models with the lowest AIC using the MuMIn package (v1.47.5) (Barton and Barton, 2015).

Secondly, these variables were then incorporated into a new model which tested for interactions between each variable and 'Location' and 'Season' (Step 5 in Table 2), because preliminary analysis revealed both these factors to have substantial effects on fish abundance. The interactions and variables which performed best were selected from the top three models, as above.

Thirdly, once the final variables and interactions had been determined, mixed effects models or a generalised additive model (GAM) were run for each species, with fyke code included as a random effect to control for pseudoreplication associated with repeated sampling at the same fyke. Independence between fykes within the same creek was assumed since 1) high and low fykes were located relatively far from each other, 2) had distinctly different in-creek communities, and 3) a complete tidal cycle (12 h 'rest' period) passed between fishing events. Because of the fundamental differences between the mainland and island locations, salt marsh location (Schiermonnikoog or Groningen coast) and season were always included in the final model, regardless of whether they emerged as significant predictors during model selection, to account for spatiotemporal effects. Where necessary, variables were scaled at this final model selection step. The best model type for each species was then selected based on AIC values and assumptions-testing (overdispersion, zero-inflation, normality of the residuals). The effects of each variable in each model (Chisq and p-values) were ascertained using the 'Anova' command from the 'car' package for mixed effects models (Fox and Weisberg, 2018), and the 'anova' command from base R for the GAM model outputs. Relative effects of variables and interactions (z-values and associated p-values) were retrieved using the 'summary' command from base R.

Goby abundance was best described by a linear mixed effects model from the "lme4" package on the log1p transformed response (the log1p transformed data met the assumptions of a linear model). Effects included main effects and interactions between drainage density × season, temperature × season, and location (Supplement 3: Goby model selection). Herring abundance was best described by a GAM, using the "gam" command from the "mgcv" package on raw (untransformed) data with a negative binomial family (Wood, 2017). The final herring model included fixed effects of elevation, sinuosity, location, season and a non-linear smoother for salinity (Supplement 3: Herring model selection). For sticklebacks a 'glmmTMB' model from the "glmmTMB" package with a poisson family and a zero-inflated component on raw data provided the best fit for the data (Brooks et al., 2017). The final model included interactions between drainage density × season, and salinity × season, fixed effects of temperature, location and chlorophyll *a*, along with a zero inflated model component containing chlorophyll *a*, location, and the interaction between drainage density and season (Supplement 3: Stickleback model selection). (Bates et al., 2014; Brooks et al., 2017)Eel abundance was best described by a 'glmmTMB' model from the "glmmTMB" package with a poisson family and zero-inflated model component (Brooks et al., 2017). The final eel model included interactions between creek water volume × location, and temperature × season, with salinity as a fixed effect and a constant assumption of zero-inflation in the zero-inflated model component (Supplement 3: Eel model selection). For each fish species the statistically significant relationships from the model outputs have been presented in figures. A detailed output of the results of each model selection step are shown in Supplement 3: Model Selection.

3. Results

3.1. Creek morphology

The Principal Component Analysis (PCA) on all 14 morphological variables showed a clear separation in the morphological attributes of creeks between the natural island marsh and the modified mainland marsh (Fig. 2). Creeks on the natural marsh tended to be longer, deeper, wider, and more curved (higher sinuosity) relative to those of the human-made marsh (Fig. 2; Supplement 2: Fig. S3). Conversely, the creeks on the modified marsh were higher in elevation and drainage density (Fig. 2; Supplement 2: Fig. S3). These two variables were positively correlated regardless of location ($r = 0.50$, $p = 0.05$; Fig. 2). This aligned with our field observations: most creeks on the modified marsh retained very little water at low tide (2–57 cm; average 17 cm water depth), while most creeks on the natural marsh retained a substantial amount of water throughout a tidal cycle (1–115 cm; average 39 cm water depth).

The creeks on the natural marsh had a wider range of morphological attributes compared with those of the modified marsh (shown as much larger variation within creeks in Fig. 2). Ordination axis one (PCA 1) was largely determined by depth, volume, length and width, which was driven by the relatively high values for the two largest natural creeks on the island (S3 and S4). PCA axis 2 was driven by the contrast of high sinuosity values of two smaller natural creeks (S1 and S7), and high elevation and drainage density for the majority of the creeks along the Groningen coast (Fig. 2; Supplement 2: Fig. S3).

3.2. Abiotics

The morphological attributes of salt marsh creeks were related to the within-creek conditions (Supplement 1: Table S2). Salinity was the variable most affected by creek morphology, showing strong negative correlations with bathymetry ($r = -0.51$, $p < 0.001$), bifurcation ($r = -0.40$, $p < 0.001$), and volume ($r = -0.57$, $p < 0.001$) (Supplement 1: Table S2). Salinity was lower in a marsh with greater complexity (bifurcation), greater volume and a higher mean watershed. These characteristics were associated with the island marsh, where creeks (except S1) were not cut-off from freshwater inputs by a dyke. Chlorophyll *a* showed weak negative correlations with sinuosity ($r = -0.15$, $p < 0.05$) and volume ($r = -0.24$, $p < 0.01$), and positively correlated with elevation ($r = 0.33$, $p < 0.001$) (Supplement 1: Table S2). Water temperature was least affected by any of the morphological attributes, only showing weak negative correlations with bathymetry ($r = -0.15$, $p < 0.05$) and volume ($r = -0.17$, $p < 0.05$) (Supplement 1: Table S2). In general, the creeks on the artificial mainland marsh were more saline and had higher levels of chlorophyll *a* than the natural island location, though the two areas experienced relatively similar temperatures, with the exception of spring when the average temperature on the mainland

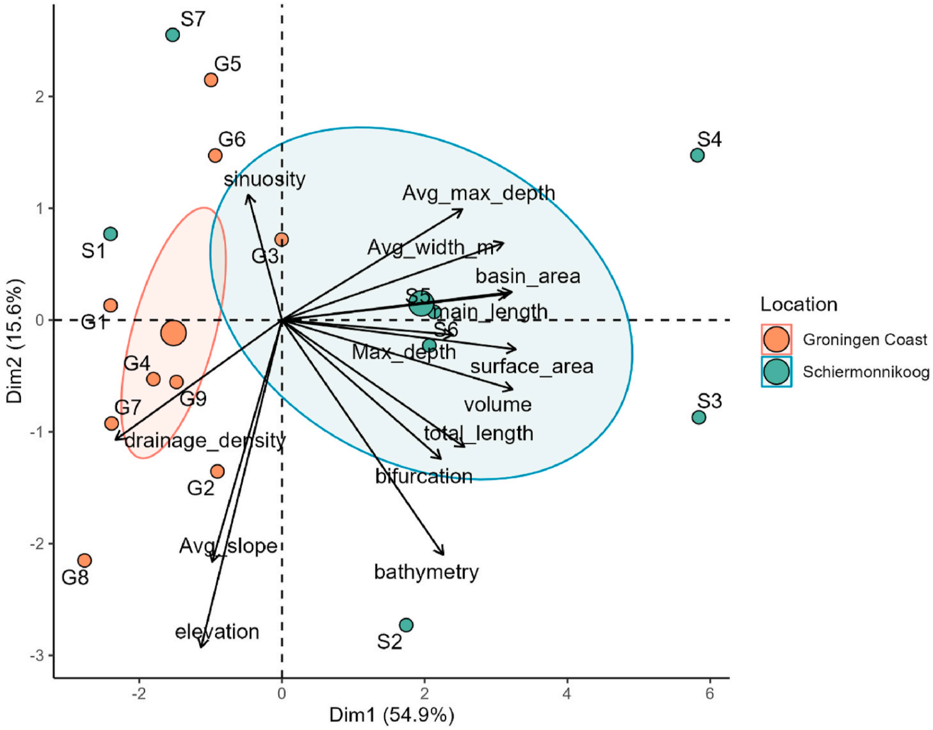

Fig. 2. PCA biplot showing the contribution (arrow length) of variables describing creek morphology to the principal components. Confidence ellipses (95 %) show grouping of each location: Groningen coast (mainland) and Schiermonnikoog (island). Points represent individual creeks and point labels are the individual creek names assigned in our study. Larger points represent the central value for each location.

was higher than the island (Table 3).

3.3. *Fish assemblages*

In total 139,165 fish were caught over the two sampling years. The most abundant fish species were *Pomatoschistus microps*, *Clupea harengus*, Goby sp. (most likely *Pomatoschistus lozanoi*), Flatfish sp. (which includes individuals of *Platichthys flesus*, *Solea*, and *Scophthalmus maximus*, and potentially *Pleuronectes platessa*) grouped because often they were too small to speciate in the field) and sand goby (*Pomatoschistus minutus*) (Fig. S2). Together they made up 98 % of the overall catch.

3.4. *Gobies*

Goby numbers were affected by season (Chisq = 102.78, $p < 0.001$); they increased in abundance through the summer and peaked in the autumn (Fig. 3A). The summer catches were characterised by larval and juvenile life stages of gobies, which grew to larger size ranges in the autumn (Fig. 4A). The peak in abundance on the natural island marsh (Schiermonnikoog) in the autumn was driven by larger numbers of juvenile gobies growing to larger sizes (Fig. 3A; Fig. 4A). Location did not have a significant effect on goby abundance (Chisq = 0.03, p = 0.86). Gobies occurred in higher numbers in creeks which retained more water throughout the tidal cycle particularly in the summer and autumn, reflected by the significant interaction between drainage density and season (Chisq = 11.2, p = 0.01). The strongest effects of drainage density were seen in autumn and summer, respectively, when gobies decreased in abundance as drainage density increased (Fig. 3B). Temperature and season also interacted significantly (Chisq = 8.78, p = 0.03). Goby abundance declined with increasing temperature in summer but increased with warmer temperatures in autumn (Fig. 3C).

3.5. *Herring*

Herring exhibited seasonal trends in abundance, and arrived as small juveniles/post-larvae in spring in high numbers, before decreasing in numbers throughout the summer (effect of season: Chisq = 27.0, $p < 0.001$) (Fig. 4B; Fig. 5A). Creek morphology did not emerge as an important determinant of herring abundance. Instead, higher herring numbers were associated with a salinity optimum (Chisq = 48.5, $p < 0.001$), an effect which was most pronounced at the island marsh location (Fig. 5B). Including sinuosity and elevation in the final model improved model fit, but both variables had a small and nonsignificant effect on herring abundance (Chisq <3, $p > 0.1$).

3.6. *Sticklebacks*

There was a significant effect of season on stickleback abundance (Chisq = 163.5, $p < 0.001$). In general, there was a spike in stickleback numbers in the summer associated with lower size ranges at the natural island marsh (1–3 cm), and again in winter with adult sticklebacks arriving to the mainland coast (Fig. 6A; Fig. 4C). Drainage density and salinity both interacted with season, and higher stickleback numbers were associated with both lower drainage densities, and lower salinities in summer and spring (drainage density interaction effect: Chisq = 41.6, <0.001; salinity interaction effect: Chisq = 65, $p < 0.001$) (Fig. 6B and C). Temperature also had a significant effect on stickleback numbers, reflecting the two 'peaks' occurring at warmer temperatures (typically in summer) and cooler temperatures in spring, autumn, and winter (Chisq = 11.4, $p < 0.001$) (Fig. 6A and D). In winter, stickleback (adult) numbers were much higher on the mainland marsh than the natural island location, though sampling did not occur in the same month and year at each location (Groningen coast: January 2022 and February 2023; Schiermonnikoog: January 2023, not sampled in 2022 due to logistical constraints) (Fig. 6A). During winter, higher numbers of adult sticklebacks were associated with higher drainage densities and salinities (Fig. 4C and. 6B and C). Overall, juvenile sticklebacks were more abundant in creeks which retained water (lower drainage density) and had lower salinities in the spring and summer, while in winter adult sticklebacks were more abundant under the opposite conditions.

3.7. *Eel*

Eel abundance was affected by season (Chisq = 16.3, $p < 0.001$), with lowest numbers detected in autumn (Fig. 7A). While elvers (juvenile eels) were not detected, a wide size range of adults was caught (Fig. 4D). The number of eels was affected by the interaction between location and creek volume (Chisq = 8.7, p = 0.003), with more eels found in high volume creeks at the natural island marsh (Schiermonnikoog) (Fig. 7B). Conversely, fewer eels were found at higher salinities (Chisq = 15.4, $p < 0.001$) (Fig. 7C). Eel abundance was affected by seasonal changes in temperature (Chisq = 9.3, p = 0.01), increasing as temperatures exceeded ~12 °C (Fig. 7D). Overall, eel numbers were higher in the natural island marsh with larger creek volumes, and present in greater abundance at lower salinities.

4. Discussion

4.1. *Creek morphology*

The two marsh locations in the Dutch Wadden Sea were selected to encompass the range of marsh habitats present in this area. In our study, the natural island marsh had larger creeks with greater variability in morphological characteristics than the mainland marsh. This is a pattern typical of Dutch salt marshes. Back-barrier marshes, such as those at the island location, make up ~40 % of the salt marshes found in the Netherlands (Esselink et al., 2017). They have developed in the shelter of sand dunes, and these marshes are considered 'natural' areas (Bakker et al., 2002). Conversely, uniformly structured drainage systems were dug into the majority of mainland marshes (found in the north-east Netherlands) (Bakker et al., 2002; Esselink et al., 2017), and natural creek systems could not develop. This explains the uniform morphological creek attributes which were typical of the mainland marsh in our study. Artificially created foreshore marshes make up 50 % of the Dutch Wadden Sea marshscape (Esselink et al., 2017). By including this type of marsh and a naturally occurring back-barrier salt marsh in our study, the full breadth of creek morphologies found in the Dutch Wadden Sea were represented. The differences observed between the larger, deeper creeks on the island relative to the more uniformly structured creeks on the mainland, is an artefact of how these areas have been 'created' or

Table 3
Values of the three environmental variables (mean ± SE) measured at each sampling location per season.

		Winter	Spring	Summer	Autumn
Salinity	Groningen coast	40.8 ± 0.9	33.8 ± 1.2	32.1 ± 0.8	37.8 ± 0.9
	Schiermonnikoog	19.4 ± 3.6	29.9 ± 1.7	28.3 ± 1.4	29.8 ± 1.5
Temperature (°C)	Groningen coast	7.4 ± 0.6	15.3 ± 0.7	20.4 ± 0.3	12.7 ± 0.5
	Schiermonnikoog	6.9 ± 0.2	10.7 ± 0.7	21.3 ± 0.4	13.1 ± 0.2
Chlorophyll *a* (μg/g)	Groningen coast	78.6 ± 16.3	66.4 ± 8.7	97.6 ± 16.3	93.7 ± 22.2
	Schiermonnikoog	17.1 ± 3.9	42.8 ± 8.3	31.8 ± 23	42.2 ± 8.8

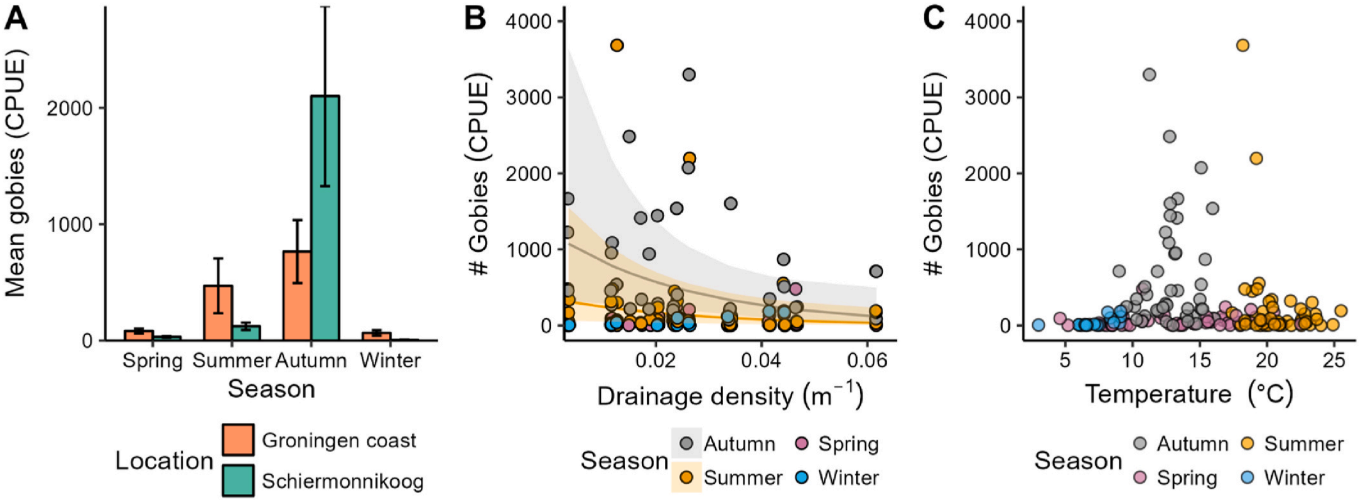

Fig. 3. The mean number of gobies (CPUE = catch per 24 h) by season and sampling location (A). The relationships between the number of gobies and drainage density where lines represent model fit of significant seasons (B) and temperature (C) are shown.

developed.

A key difference between the mainland and island marshes is the presence of a dyke along the entire range of the mainland salt marsh, severely restricting the inland marsh extent and tidal movement. The resulting tidal restriction can result in the loss of brackish water habitats, with negative consequences for estuarine and diadromous species (Bice et al., 2023; Moreno-Valcarcel et al., 2016). In our study, mainland marshes are severely tidally restricted by a dyke, and designed to drain almost completely each tidal cycle to prevent surface flooding for livestock grazing (Bakker et al., 2002). The mainland creeks were higher in salinity, muddier and exhibited greater extremes in temperature and salinity relative to the natural island marsh (Table 2). Our observations match those reported by other authors who have demonstrated that in-creek marsh conditions are more variable, and can exhibit greater extremes, in severely tidally restricted marshes (Raposa and Roman, 2003; Ritter et al., 2008). Such conditions can be unfavourable for certain fish or fish life stages (Raposa and Roman, 2003; Ritter et al., 2008). Furthermore, reductions in diadromous and brackish fish species, diversity loss, and lower species richness have been associated with increased salinity resulting from the loss of brackish habitat (Whitfield, 2005; Zampatti et al., 2010). Thus, in our study area, the dyke and high drainage efficiency marshes that are characteristic of the mainland do not provide an optimal brackish habitat necessary for diadromous and brackish fish.

4.2. Fish-habitat relationships

There are a wide range of morphological conditions that can affect fish abundance. In our study, drainage density and creek volume emerged as the two most important morphological variables affecting the abundance of gobies, sticklebacks and eels. The effects of morphology on fish appear to vary with local salt marsh conditions (such as edge modification and tidal restriction), and fish species or life stage (Bradley et al., 2020; Cattrijsse and Hampel, 2006; Raposa and Roman, 2003; Rozas, 1995; Ziegler et al., 2019, 2021). For example, in a frequently inundated marsh in the south-Eastern United States, drainage area did not emerge as an important factor for most shrimp and fish species, affecting the creek use of only a small subset of species (Allen et al., 2007). Meanwhile, in the United Kingdom, researchers found a higher number of fish and crustaceans associated with greater water exchange volume (de la Barra et al., 2022). The complexity of salt marshes, associated with local marsh conditions, and the resulting effects on their function for fish make it difficult to assess our findings against other research. However, the capacity of creeks to retain water (drainage density) emerged as a more significant predictor variable than other morphological characteristics such as length, width and slope (though these were correlated with volume, which was an important predictor of eel abundance), which have emerged elsewhere as important for fish (Gewant and Bollens, 2012; McIvor and Odum, 1988; Williams and Zedler, 1999). Thus, our study offers a new perspective on the morphological and environmental variables which may be important for fish species in marshes experiencing infrequent surface inundation.

4.3. Fyke catchability and performance

Many factors influence the efficiency with which fyke nets sample fish. These include tidal height (driven by diel, lunar, and seasonal cycles), submersion depth (linked to creek morphology and tidal variation), and environmental conditions such as temperature and salinity, which can affect fish behaviour and abundance (Hubert and Fabrizio, 2007; Kruse et al., 2016). To minimise variation in catchability, sampling was standardised across diel, lunar, and seasonal cycles in our study. Fixed fyke positions were maintained, and key environmental variables were measured to further account for variation in fyke performance. By incorporating a range of morphological and environmental variables into the abundance models, we accounted for the varying effects of season, fyke width, location, depth, flow, and potential differences in net performance. While tidal height was not explicitly included as a variable in our models, sampling was consistently conducted at dawn and dusk, during spring tide cycles, and across multiple seasons (season was included as a variable in the models). This design helped control for effects of varying tidal height on species abundance. Additionally, adjustments to fyke width opening accounted for creek narrowing further into the marsh, ensuring a comparable proportion of the creek was sampled between fyke positions in the same creek. Overall, while differences in fyke width (between high and low fykes) and tidal height may have influenced catchability and gear performance, these factors were largely accounted for in the study design or incorporated in the statistical design as controlling factors.

4.4. Overview fish community

Similar fish species were found in the Dutch salt marshes relative to those reported in other European and UK studies (Koutsogiannopoulou and Wilson, 2007; Laffaille et al., 2000; Maes et al., 1998; Mathieson et al., 2000). In terms of community composition, previous studies in the Netherlands have described similar salt marsh fish communities, though with slightly different dominating species. For example, in our study we

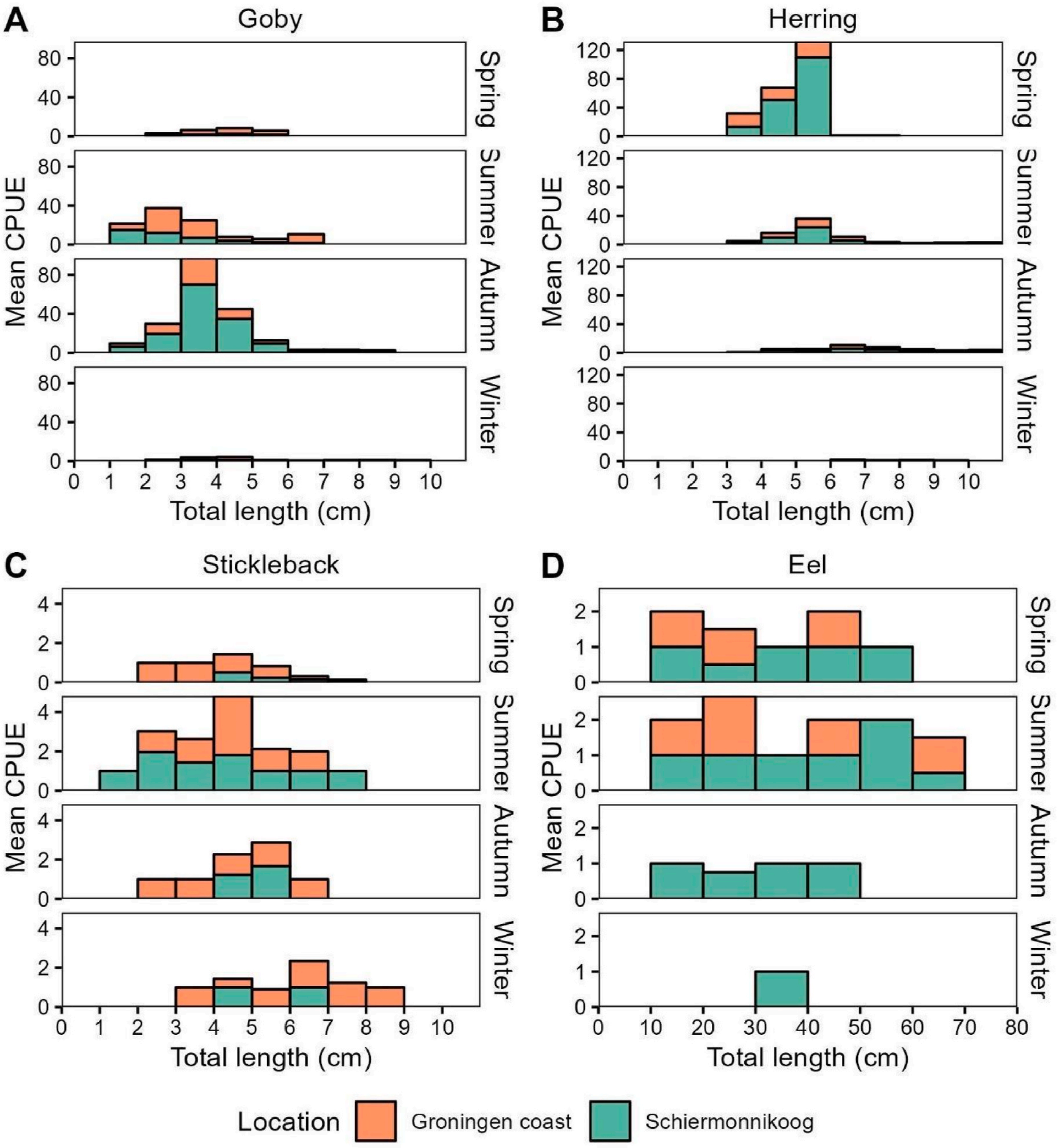

Fig. 4. Length frequency plots for gobies (A), herring (B), sticklebacks (C) and eel (D) by location (complete dataset), where mean CPUE represents average catch per unit effort (24 h).

found herring to dominate the spring marsh assemblages instead of the post-larval flounder which was described by Cattrijsse et al. (1994). Given that we captured similar species to those reported by other authors in the same, general, spatial area (Netherlands or Wadden Sea) (Cattrijsse et al., 1994; Friese et al., 2021b; Hamer et al., 2022), we feel our methods were effective at catching fish representative of the salt marsh creek assemblages in this area, with our catches giving a measure of true abundance and fish activity in the sampled study creeks.

4.4.1. Gobies

The ‘gobies’ group in our study was comprised of three different species: *Pomatoschistus microps* (the most abundant), *Pomatoschistus minutus*, and *Pomatoschistus lozanoi*, each with slightly different life histories (Laffaille et al., 1999; Leitao et al., 2006). In general, *Pomatoschistus* sp. are iteroparous nest-building fish, found in large numbers in the Wadden Sea (Friese et al., 2021b; Miller, 1975). Gobies, notably the common goby (P. microps), dominated our catches in the Dutch salt marshes, mirroring their widespread presence in European and UK salt marsh communities (Koutsogiannopoulou and Wilson, 2007; Mathieson et al., 2000). Lowest abundances occurred in winter and spring, with numbers increasing through summer to peak in autumn: a trend observed in other Europe and UK studies (Friese et al., 2021b; Koutsogiannopoulou and Wilson, 2007; Maes et al., 1998; Souza et al., 2014). This seasonal pattern is linked to recruitment processes. Both common and sand gobies reproduce from late-spring to late-summer, though the onset and duration of spawning for each species is slightly different (Koutsogiannopoulou and Wilson, 2007; Miller, 1975; Nellbring, 1993; Souza et al., 2014). In summer we observed a pulse in juveniles shown by smaller size ranges (0–3 cm) (Souza et al., 2014). In autumn, the length-frequency peak then shifted to 3–5 cm, when we likely detected juveniles as well as the previous year classes when males left the nests and became easier to catch (Souza et al., 2014). During both seasons, we

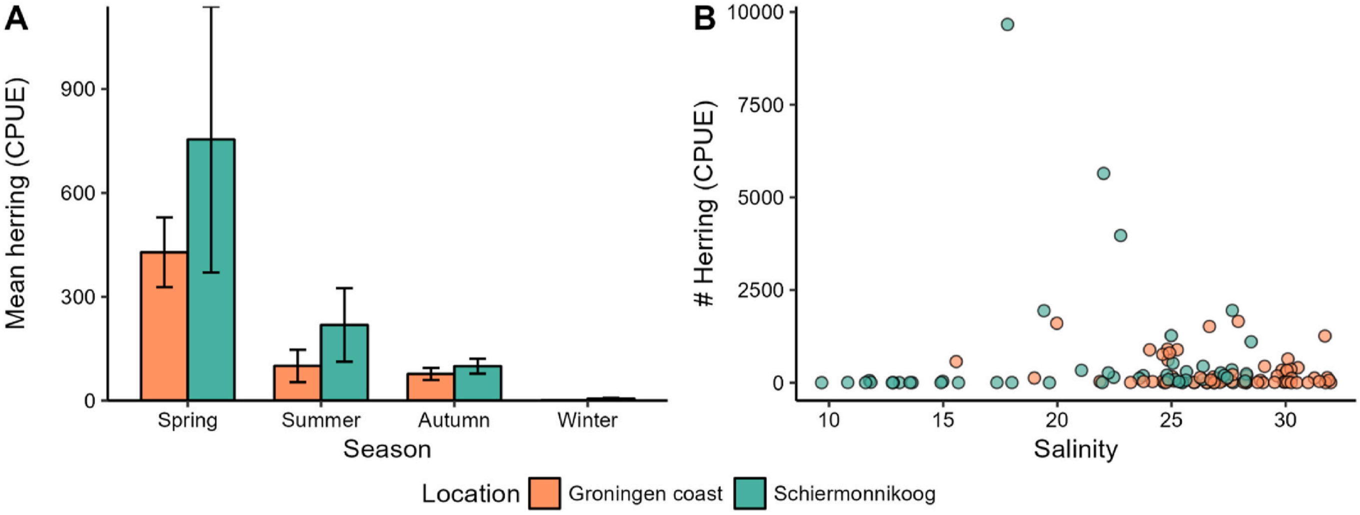

Fig. 5. The mean number of herring (catch per 24 h) by season and sampling location (A). The relationship between the number of herring and salinity are shown for each location (B).

detected the presence of two age classes when both juvenile recruits (~1.5–3 cm) and individuals from the previous year class (>3 cm) contributed, as was demonstrated by Miller (1975). The prevalence of juveniles in marshes through summer and autumn has been noted in other studies in the German Wadden Sea and south-west Netherlands (Cattrijsse et al., 1994; Friese et al., 2021b; Hampel et al., 2003). Thus, goby abundance in the salt marshes appears to be driven by recruitment processes, which is also affected by temperature.

Temperature had a seasonally dependent effect on goby abundance. Numbers decreased with rising temperatures in summer and increased with rising temperatures in autumn. Generally, temperature affects several life-processes of gobies, such as growth and spawning success, and the optimal temperature for the common goby is 20 °C (Fonds and Van Buurt, 1974; Freitas et al., 2010; Nellbring, 1993). Thus, gobies appear to have an optimal water temperature; they prefer cooler summer temperatures which are similar to the warmest temperatures in autumn, explaining the negative and positive temperature-abundance relationships in summer and autumn respectively.

Gobies were less abundant at higher drainage densities during the recruitment seasons of summer and autumn. A higher drainage density implies a more efficient water drainage system, resulting in minimal in-creek water retention at low tide. Water retention is important for gobies for several reasons, the most obvious being that they are an aquatic organism, requiring water for life processes. While many goby species can survive out of water for several hours (Graham, 1997), including the common goby (personal observation, 2022-23), a lack of water may have a negative influence on gobies during reproduction. Gobies build nests and care for the eggs until hatching, and it is favourable for them to select more stable habitats for nesting (Jones and Reynolds, 1999; Nellbring, 1993). This is perhaps why both species build nests in areas with consistently shallow waters (0.4–2.8 m) (Nellbring, 1993). These depths fall within the average depth range for the island marsh (Schiermonnikoog: 39 cm) in our study, but the water levels at low tide on the mainland marshes (Groningen coast: 17 cm) were likely too shallow for nest-building gobies. Thus, water retention in the creek system appears important for goby species during months when nesting and recruitment occur.

4.4.2. Sticklebacks

Similar to gobies, sticklebacks were more abundant at lower drainage densities (higher in-creek water retention) in spring and summer (recruitment seasons). As with gobies, sticklebacks are a nest-building species, and it is more favourable for them to build nests in stable habitats (Chung et al., 2023; Kynard, 1978; Moodie, 1972; Rushbrook et al., 2010)). They prefer deeper waters for nest-building, as shallower nests are more vulnerable to wave destruction and subsequent abandonment by guarding males (Kynard, 1978). Thus, the habitat quality of Dutch salt marshes could be improved for sticklebacks (as with gobies) by encouraging greater in-creek water retention throughout a tidal cycle.

Numbers of juvenile sticklebacks increased in summer, aligning with observations from North-Western Europe and Ireland (Friese et al., 2021b; Koutsogiannopoulou and Wilson, 2007). Stickleback juveniles typically have a maximum length of 2.7–3.5 cm (Bergström et al., 2015; Demchuk et al., 2015). Only the natural island marsh, with more brackish conditions, supported the lowest stickleback size ranges. Sticklebacks typically do not move seaward until they are 3–4 cm in size (Bergström et al., 2015; Friese et al., 2021b) and can spawn in brackish water (Arai et al., 2003). Thus, it is likely the juveniles hatched in the island salt marshes. We therefore infer the lower salinities and drainage densities on the natural island marsh during spring and summer make the island a more favourable spawning habitat, influencing recruitment success of sticklebacks in Dutch salt marshes.

In winter, adult three-spined sticklebacks were more abundant at the mainland compared to the island. Since sampling occurred during different months and years between the locations, consideration was given to whether the stochastic arrival of sticklebacks had been missed at the island location. However, the stable stickleback numbers reported in German Wadden Sea marshes during winter make this unlikely (Friese et al., 2021b). Instead, the high stickleback numbers at the mainland were likely driven by migratory and feeding behaviour. Migratory sticklebacks spend their late-juvenile life stage at sea, migrating to freshwater to spawn (Bergström et al., 2015; Ramesh et al., 2022). Previous research has shown three-spined sticklebacks feed on Orchestia flushed into the marsh creeks during winter and spring storms (Friese et al., 2018, 2021b). The mainland location in our study occurs in close proximity to the Ems-Dollard estuary, where the inland spring migration of sticklebacks has been detected (M. Nicolaus, personal communication, March 5, 2024; D.R.A.H. Mathijssen, personal communication, March 11, 2024). Thus, adult sticklebacks may forage opportunistically in the mainland marshes as they migrate to freshwater spawning areas. During winter, stickleback numbers were positively related to drainage density; conditions associated with the mainland marsh location. Adult sticklebacks likely use the marsh opportunistically in winter, where they move between salt marsh creeks and subtidal areas with high tides, as part of their migration to freshwater for spawning. This differed from

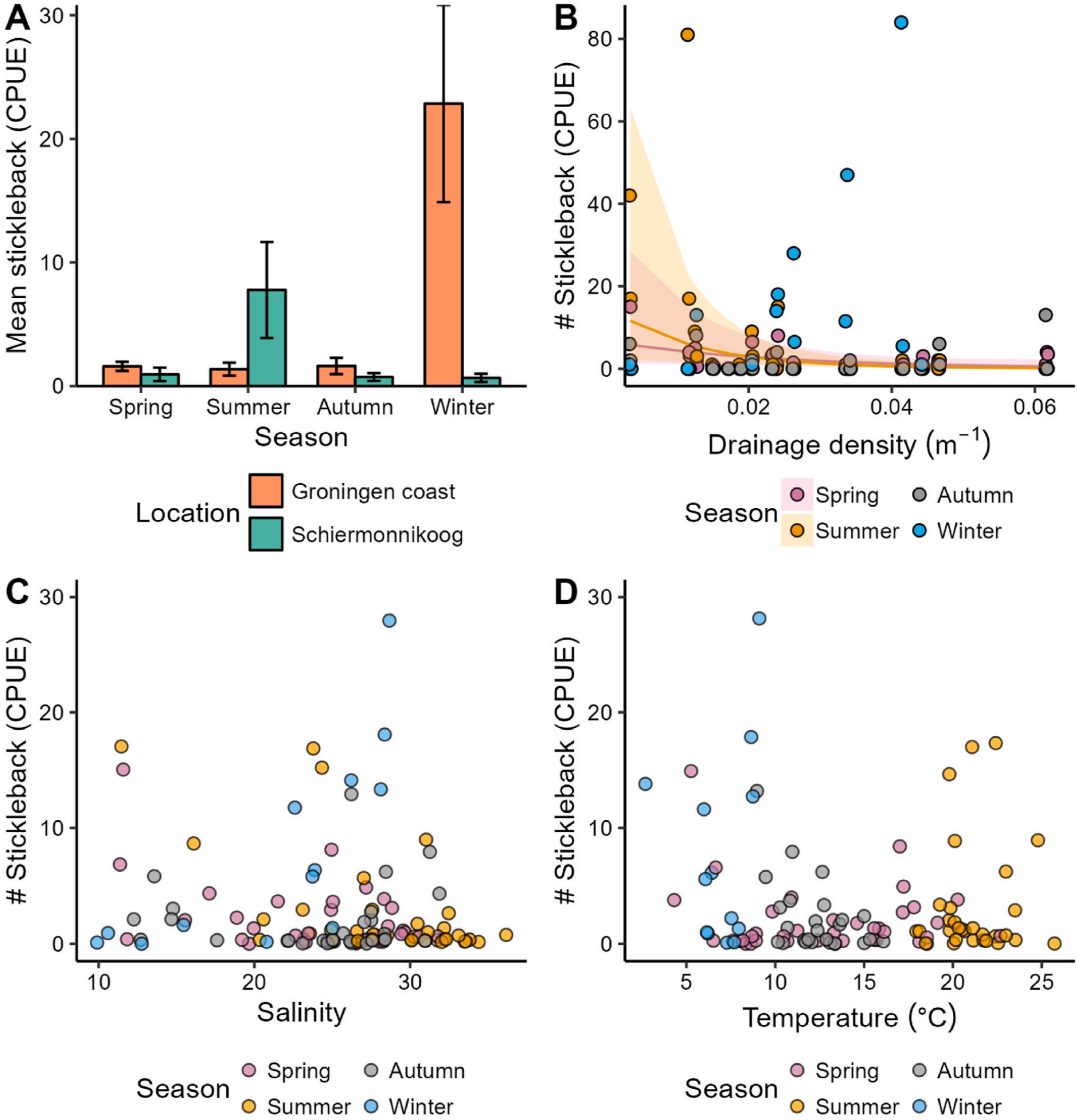

Fig. 6. The mean number of sticklebacks (catch per 24 h) by season and sampling location (A). The relationships between the number of sticklebacks and drainage density where lines represent model fit (B), salinity(C), and temperature (D) are shown.

their behaviour in spring and summer, when they appeared to take up residence in salt marshes with high water retention and lower salinity, which may provide more stable conditions for recruitment. Overall, it appears the mainland marshes provide a ‘stopover’ area for adult sticklebacks during cooler temperatures in winter, while low drainage and brackish water conditions at the island marshes support recruitment during warmer temperatures in spring and summer.

4.4.3. *Herring*

In spring, large numbers of post-larval herring arrived in the Dutch salt marshes. A similar spring influx has been observed in the German Wadden Sea salt marshes, and more generally in the Wadden Sea, when post-larval herring typically arrive in mid-April from the Downs spawning grounds in the southern North Sea (Dickey-Collas et al., 2009; Friese et al., 2021b). The numbers of post-larval herring in the marshes is largely driven by external factors, such as North Sea winter conditions and spawning stock biomass (Dickey-Collas et al., 2009; Nash and Dickey-Collas, 2005). Herring numbers declined in the marshes as the summer progressed, perhaps as warmer in-creek temperatures made growth conditions unfavourable (Maes et al., 2005). Juvenile herring abundance was low in autumn and winter, and we did not catch any adult herring in any season.

While spawning and North Sea conditions likely determined the magnitude of post-larval herring arrival in the Wadden Sea, salinity had a local effect on herring numbers. Herring numbers were highest at mid-range salinities; brackish conditions which were prevalent on the island. Brackish conditions can be energetically favourable. Herring can reduce the energetic costs of osmoregulation and buoyancy in more isotonic conditions, such as brackish water (Berg et al., 2020; Rao, 1968; Sundby and Kristiansen, 2015). For example, the metabolic rates of larval herring were lowest at 16 PSU (Berg et al., 2020), suggesting energetic advantages in seeking brackish waters during spring growth. Thus, herring abundance in Wadden Sea salt marshes is driven by the influx of larvae in the spring, with a preference for brackish water post-arrival, emphasising estuarine advantages for larval stages.

4.4.4. *European eel*

Eel was consistently caught at relatively low abundances throughout

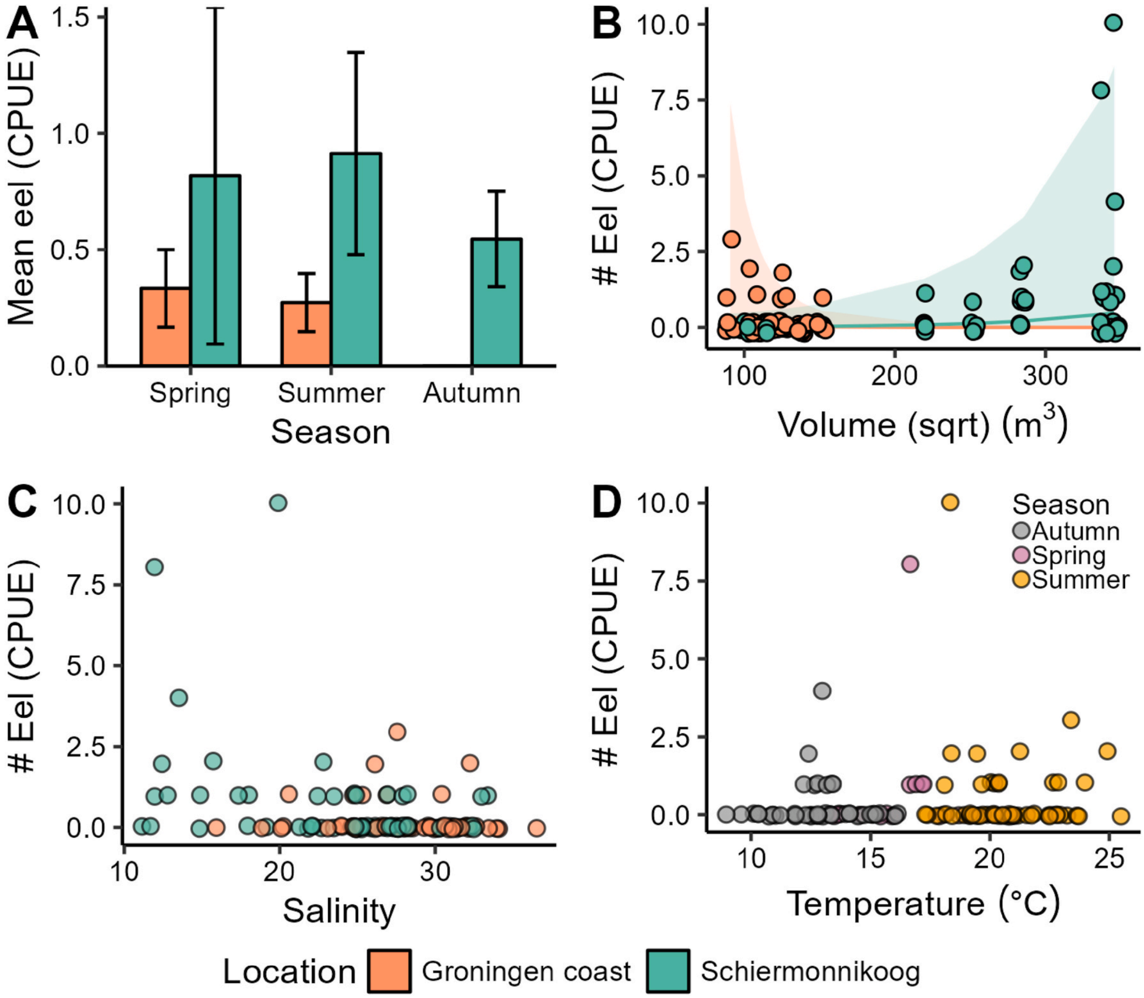

Fig. 7. The mean number of eel (catch per 24 h) by season and sampling location (A). The relationships between eel abundance and creek volume (where lines represent model fit) (B), salinity (C), and temperature (D) are shown.

our study compared to the other fish species in the salt marshes, reflecting findings in tidal marshes of the Netherlands and Belgium Westerschelde (Cattrijsse et al., 1994; Hampel et al., 2003, 2004), and broader Europe (Joyeux et al., 2017; Laffaille et al., 2000; Maes et al., 1998; Salgado et al., 2004). Despite being catadromous, known for migrating from freshwater to saltwater for spawning, eels exhibit plasticity when selecting their 'growth' habitats, with some selecting brackish coastal areas and wetlands instead of freshwater (Arai et al., 2006; Édeline and Élie, 2004). It is likely the eels we encountered in the Dutch salt marshes reside there for growth, a phenomenon documented in both European and US salt marsh literature (Eberhardt et al., 2015; Laffaille et al., 2005). Eel abundance increased with seasonal changes in temperature, aligning with observations in other salt marsh studies (Hampel et al., 2004; White and Knights, 1997). This temperature-related increase was likely because eels enter hibernation at cooler temperatures (≤10 °C), which explains our inability to detect them during the cooler months (November–March) (Riley et al., 2011; Rohtla et al., 2022). Overall, eels were more prevalent during warmer months.

Eels were more abundant in creeks with lower salinities and higher water volume, conditions primarily associated with the natural island marsh. However, both trends were consistent across the creeks on the island marsh and remained significant when including location as a factor in the models. This indicates the results were not driven by a location effect, but rather that the absence of lower salinities and high volume creeks on the mainland marsh contributed to the lower abundance of eels detected there. Eels are more abundant in freshwater or brackish water marsh systems relative to truly marine areas (Hampel et al., 2004; Maes et al., 1998; Mathieson et al., 2000; Weinstein et al., 1980). Eel will orientate towards odourless freshwater as opposed to seawater when given the choice (Tosi et al., 1990), emphasising the significance of freshwater in determining elver and juvenile eel migration (Laffaille et al., 2005; White and Knights, 1997). While we did not encounter any elvers, possibly due to our creeks lacking a connection to a freshwater body, our results highlight the importance of brackish habitat and freshwater input for eels.

The positive correlation between eels and higher volume creeks raised initial concerns during model building, as we considered whether this preference might be due to our analysis being based on fish numbers rather than fish densities (per unit area). To address this, the models were also trialled on CPUE corrected for creek volume. Despite this correction, creek volume still significantly influenced eel abundance at the island. During analysis and results interpretation, consideration was also given to whether creek volume influenced the catchability of eel. Given reasonable numbers of eel were still caught at relatively low water volumes, the catchability of this species was unlikely to have been significantly affected by creek volume. Literature searches revealed very little information about the factors driving habitat preferences of eel in salt marshes. However, studies like Jellyman and Ryan (1983) associated higher water volumes with peaks in elver migration, and Salgado et al. (2004) only caught eel during spring tides (not neap tides) when water volume was highest. While eel has been reported in European marshes elsewhere, these studies have also been conducted during spring tides, as was our research (Cattrijsse et al., 1994; Hampel et al., 2003, 2004). Notably, the highest eel catches at the island occurred in creeks with highest volumes, which always have water in them (per obs. 2021–2023). This leads us to suspect that higher eel abundances are more likely to occur in subtidal creeks, where the environment is more stable and the fish are less exposed to terrestrial predators.

5. Conclusions

The artificially created mainland marsh had different morphological and environmental conditions compared to the natural island marsh, which in turn affected fish numbers. Brackish conditions were important for herring, sticklebacks and eel. Potentially because brackish conditions act as a cue for upstream migration and post-larval settlement (Bice et al., 2023; Havel and Fuiman, 2016; O'Connor et al., 2017; Tosi et al., 1990), and offer lower energetic costs (related to osmoregulation and buoyancy). Lower drainage densities (greater in-creek water retention throughout a tidal cycle) were important for juvenile sticklebacks and gobies, and higher creek volumes (subtidal creeks on the island) supported larger numbers of eels. Increasing the water retention capacity of mainland marsh creeks would result in favourable outcomes for these species. While recruitment processes drove the abundance of all species (except eels) in the salt marshes, the morphology and conditions in the salt marsh creeks affected the quality of this habitat for fish.

CRediT authorship contribution statement

Hannah Charan-Dixon: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Loreta Cornacchia:** Writing – review & editing, Methodology, Formal analysis. **Nino van Hees:** Writing – review & editing, Investigation. **Stella Bos:** Writing – review & editing, Investigation. **Ingrid Tulp:** Writing – review & editing, Supervision, Funding acquisition. **Britas Klemens Eriksson:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Statement

During the preparation of this work the author(s) used ChatGPT in order to improve the readability of written work and for coding solutions in R. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2025.109362.

Data availability

Data will be made available on request.

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