Tidal water exchange drives fish and crustacean abundances in salt marshes

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Abstract

Coastal salt marshes provide an important habitat for fishes and crustaceans, including species of commercial value that feed or take refuge in the marsh. Yet, population abundances vary considerably between sites, often without clear explanation. We hypothesised that faunal abundance and mean size would be positively related to two physical properties that govern marsh accessibility to water dependent species, as has been found on the Southeastern coast of the USA: (i) the volume of water exchanged by tidal flooding, which gives access to the marsh, and (ii) edge amount, the length of the water-vegetation borderline per unit area where species can take refuge and feed. Digital terrain models and tidal information were used to select five marshes in Wales, UK, that differed in edge amount and water exchange (52° N, 4° W). Fishes and crustaceans were sampled using baited traps, fyke nets and seine nets. Fifteen species were caught, including commercially valuable brown shrimp, European eel and sea bass. We found water exchange volume, but not edge amount, boosted fish and crustacean abundances. Crab and sea bass sizes were both

negatively affected by water exchange, while shrimp and fish sizes were unaffected. Our findings show how the mechanisms that drive fish and crustacean abundances and sizes vary between geographical regions. Feasibly, fisheries associations with marsh hydrogeomorphology might operate differently in as well.

Keywords Landscape effects, salt marsh nekton, *Pomatoschistus microps, Carcinus maenas, Dicentrachus labrax*

1. Introduction

Coastal salt marshes provide valuable ecosystem services, including 'blue-carbon' sequestration, natural coastal protection, human wellbeing and habitat for the life-cycle maintenance of fish and invertebrates of commercial value (Liquete et al. 2013, Himes-Cornell et al. 2018, Rendón et al. 2019). However, some of the patterns and processes underpinning salt marsh ecosystem services are not fully understood and are often based on patchily distributed information (Himes-Cornell et al. 2018). Paradigmatically, although salt marshes are thought to be globally important for commercial fish and shellfish species, for much of the world there is scant information on which commercial species occur where, in what densities and whether some marshes are more important to fisheries than others and why that may be (Ziegler et al. 2021a). Salt marshes present a wide variety of morphologies as a consequence of different exposure to open water, sediment composition (i.e. mud to gravel), fresh water input (Allen 2000) and vegetation composition (Vaate et al. 2020), which varies substantially around the world (Allen 2000, Cattrijsse & Hampel 2006, Friess et al. 2012). These differences are likely to affect salt marsh ecosystem functioning, for example the selection of the salt marsh habitat by crustaceans depends on flooding duration (Minello et al. 2012), and the geomorphology of the salt marsh mediates the flux of its production to the aquatic habitat (Lesser et al. 2020). However, the relative importance of each of these drivers to inter-site variability in the provision of ecological functions are still poorly understood (Ziegler et al. 2021a). Here we investigate how a suite hydrogeomorphic properties on a landscape scale influence habitat provisioning for saltmarsh fishes and crustaceans.

Two salt marsh hydrogeomorphic characteristics may regulate fishes and crustaceans' use of marshes: 'edge amount' and 'water exchange' (Simenstad et al. 2002, Kneib 2003, Allen et al. 2007) (Fig 1). Edge amount is defined as the length of edge between creek and vegetated marsh per salt marsh unit area (Fig 1 A) (Minello & Rozas 2002). The water-to-vegetation interface is key to fish survival and growth, as it provides enhanced protection from predation and is the main foraging area for juvenile fish (Simenstad et al. 2002) (Fig 1 B). As fish and crustacean production can correlate with salt marsh edge amount (Kneib 2003) this hydrogeomorphic feature is a probable predictor of marsh habitat provisioning for fish.

Water exchange is the volume of water that enters and leaves the salt marsh area (creeks and vegetated marsh) in every tidal cycle; it is a product of the tidal regime and marsh geomorphological features (Fig 1 C). Geomorphology, such as elevation and creek abundance, determine local inundation patterns during tidal flooding, which in turn determine habitat functioning (e.g. Kneib 2003, Baker et al. 2013), including saltmarsh access to fishes and crustaceans. Water exchange may affect the species composition, total abundance and size distribution of fish and crustacean communities inhabiting marshes. This is because the phase of the tide used for entering and exiting the marsh differs between species and life stages (Kneib & Wagner 1994). Sites with greater water exchange should recruit higher abundances and a greater variety of life stages of fishes and crustaceans, because water exchange extends the temporal and spatial niches of flood and ebb conditions. High water exchange might also increase top-down trophic forcing within a marsh, given that greater average water depths can boost the abundances of larger fish predators, at the detriment of smaller prey individuals (Fig 1 C) (e.g. Ruiz et al. 1993, Paterson & Whitfield 2003).

So far, the influence of edge amount and water exchange has mainly been tested on the Southeastern coast of the United States, where most of our understanding on how salt marshes sustain fishes and crustaceans comes from. There, salt marshes are micro- (<2 m tidal range) or mesotidal (2-4 m tidal range), the lower limit of the vegetated marsh occurs at mean tide level (Cattrijsse & Hampel 2006) and, in particular in the Gulf of Mexico area, their inundation pattern can be highly affected by meteorological events (Minello et al. 2012). In contrast, Northwestern European salt marshes are subject to macrotidal regimes (>4 m tidal range) and the lower limit of their vegetated marsh occurs at mean high water of neap tides (Cattrijsse and Hampel 2006). As a consequence, the regime of inundation of the vegetated marsh in Southeastern USA is very different from that of Northwestern European salt marshes, that are only substantially inundated during spring tides, ~6-8 days per month, when the vegetated marsh can be covered by up to a meter of water (e.g. Möller & Spencer 2002). This difference in frequency and area of tidal exchange affects how fishes and crustaceans interact with the vegetated marsh (Cattrijsse & Hampel 2006). Despite their clear differences, salt marshes at both sides of the Atlantic are thought to sustain fish and crustacean populations through the provision of refuge and foraging opportunities (e.g. Cattrijsse et al. 1997, Laffaille et al. 2001, Minello et al. 2003, Colombano et al. 2021a).

We investigated how salt marsh hydrogeomorphology affects the abundance and size of fishes and crustaceans, sampling five sites in the United Kingdom. We focused on faunal responses to edge amount and water exchange volume, given the importance of these hydrological characteristics to fish and crustacean use Southeastern USA marshes (Simenstad et al. 2002, Kneib 2003, Allen et al. 2007). Despite the differences in salt marshes in the two regions, there is no evidence showing that the function of UK salt marshes will be fundamentally different from those of Southeastern USA, as the relationship between salt marshes' hydrogeomorphology and their function as fish and crustacean habitat has not been extensively studied outside North America. Therefore, we expect that abundances would be greater (P1) and individuals would be larger (P2) at more interspersed marshes and at marshes with greater tidal exchange of water. We expected this given the importance of the vegetated marsh-creek edge to the nourishment, production and protection of fishes and crustaceans, and because greater exchange of tidal volume results in more habitat available for these animals.

2. Materials and Methods

2.1. Salt marsh selection and study sites

The study first set out to identify a set of candidate salt marshes that varied optimally in edge amount and water exchange, but where these two parameters were not correlated. To do this, edge amount and water exchange were estimated for 16 candidate salt marshes across north Wales (Table S1). The extent of 13 of these 16 salt marshes had previously been GIS-mapped and measured (Ladd et al. 2019). The three remaining salt marshes were delineated following Ladd et al. (2019) by placing vertices on aerial images every 5 m along the marsh edge at a scale of 1:7500, to complete the pool of pre-candidate sites. For all the pre-candidate marshes, edge amount and water exchange were calculated as explained below. Using edge amount and water exchange scores, five representative salt marshes were selected from the pool (Table 1, Fig 2). All of the selected study sites had semidiurnal tidal cycles with similar tidal ranges (Table 1) and all were located within estuaries, with some influence of riverine input. Sites were within the same biogeographical region for marsh vegetation (Dijkema 1984) and as a result had very similar plant composition, with *Sporobolus* (*Spartina*) *anglica* as the lowest intertidal, stand-forming species. Four of the five sites were subject to livestock grazing (mainly sheep).

2.2 Edge amount and water exchange estimation

To calculate edge amount, we summed the creeks' length per area of marsh extent, using one meter resolution digital terrain models acquired from EDINA LIDAR Digimap Service (2016). The creeks' central path were delineated using the flow accumulation function of package "whitebox" in R (function "flow_accumulation_full_workflow", Qiusheng 2019). This function calculates the accumulated flow of all cells flowing into each downslope cell. At an adequate threshold of flow accumulation, salt marsh creeks can be identified. A threshold set at 1000 cells appeared as an adequate and conservative estimate of creek network as also found by Lawrence et al. (2018). The resulting creek networks were cropped to the extent of the marshes using the GIS-maps mentioned in the previous section. To calculate edge amount from these data, we summed the total length of the creek network and divided it by the area of the salt marsh. This is a proxy to edge amount as we did not measure the length of creeks' edges but their central path.

To estimate water exchange, we calculated the volume of water per area that inundates marshes (creeks and vegetated platform) during an average spring high tide, which equates to the average water depth over the marsh during spring flooding. We used mean high water spring height to account for the moment when more aquatic environment is available within the salt marsh area, however, similar results were obtained when using mean high water. Digital terrain models were cropped to the extent of each marsh and the average elevation of water per cell was calculated. Mean high water spring tidal height was obtained from the National Tidal and Sea level Facility (https://www.ntslf.org/tides/predictions). For each salt marsh the tidal information from the nearest gauge was used (Table 1).

2.3 Biological sampling

Fishes and crustaceans were sampled at the five study sites from June 1st to October 21st 2020. Each marsh was visited once in summer and once in autumn, seasons during which the abundance and richness of fish is highest in UK salt marshes (Green et al. 2009). For logistic reasons, marshes had to be surveyed on different days. To minimize the effect on catches from variation in tidal amplitude between survey days, sampling took place around spring tide (Table 1). We used three fishing methods to capture a broad representation of the fish and crustacean communities: crab traps, fyke nets and seine nets. Crab traps (n = 5) measuring 30 cm diameter × 69 cm long, with 17 mm mesh were baited with herring and placed in the shallow water of subtidal creeks (Fig S1. A). To capture highly mobile fish > 5 cm in total length, we deployed four fyke nets of two different sizes: three 'small' and one 'large'. Small fykes had 0.5 m diameter openings, 5 hoops and one 5 m wing, with mesh of 30 mm (wings) and 15 mm (cod end) (Fig S1 B). Small fyke nets were set in creeks of less than 3 m width. The large fyke had 1 m diameter opening, 7 hoops and two 5 m wings with 30 mm mesh and was set in creeks wider than 3 m (Fig S1 C). All fykes were deployed facing the mouth of the creeks to catch fish moving up the marsh with the incoming tide and covered the total width of the creek. To calculate fyke nets' catch per unit effort, we measured the width of the creek were a fyke was deployed in aerial images of the marshes, and multiplied it by the height of the net, as an indication of the area covered by each fyke.

For each marsh, all nine (crab traps n = 5, small fyke n = 3 and large fyke n = 1) were deployed during the afternoon low tide and recovered at the next low tide. During daylight hours, at low tide, an additional 6 m long, 5 mm mesh seine net was swept for 5 m over the creek bed (n = 5 sweeps) to target resident fishes and crustaceans smaller than 5 cm in total length. The seine was only used in creeks wider than 2 m to ensure its correct handling. All fishing was done in the lower marsh, as identified through the presence of the plants *Sporobolus* spp., *Salicornia* sp., *Suaeda* sp., *Puccinellia* sp., *Aster* sp., *Atriplex* spp. (Boorman 2003) (Fig S2). The traps and swipes of the seine were distributed across the lower marsh with the aim of capturing the widest extent possible (Fig S2). At least two independent water entrances were sampled for every marsh. For Fairbourne and Pont Briwet this meant all water entrances were covered. Traps of the same type were used in independent creeks branching from the main channels. The seine was used opportunistically where the local conditions allowed. This generally was on the main channels. The locations for traps and swipes of the seine were repeated in summer and autumn.

Samples were frozen immediately after field sampling and returned to the laboratory, for identification to species level following Hayward and Ryland (2012). All fish and shrimp from the sampling were then measured with callipers from head to tail for total length. For crabs, their carapace width was measured.

2.4. Statistical analysis

2.4.1. Abundance

From the biological sampling we derived four indicators of abundance of fishes and crustaceans: number of crabs caught in a trap per tidal cycle (12 hours), number of fish caught in a fyke per opening area, number of fish caught per meter swept with the seine, and the number of shrimp caught per meter swept with the seine. We used generalized linear mixed models (GLMMs) to test for the effect of 'edge amount' and 'water exchange' on each of these indicators. For crab traps and seine catches, a negative binomial distribution with log link function was used, as the data showed overdispersion. For fykes, catches were log transformed and then a Gaussian distribution was used. As the same sampling locations within marsh were used in both autumn and summer, 'location' within marsh and 'season' were evaluated as random factors, but only retained if they explained a significant amount of variation (Zuur 2009). Four nested models including a null model (Table S2) were compared using Akaike's information criterion corrected for small sample size (AICc, Burnham & Anderson 2002). Model comparisons were made with ∆AICc, which is the difference between the lowest AICc value (i.e. best of suitable models) and AICc from all other models. A model was considered better than the null model when ∆AICc > 2. We also calculated the AICc weight of models (w_i), which signifies the relative likelihood that a specific model is the best of the suite of all models. Finally, to supplement parameter-likelihood evidence of important effects, we also calculated 95% confidence intervals (CI).

2.4.2. Specimen size

We evaluated the effects of edge amount and water exchange on the mean size of the most abundant species found in our samples: *Carcinus maenas* (common shore crab), *Crangon crangon* (brown shrimp), *Pomatoschistus microps* (common goby) and *Dicentrarchus labrax* (sea bass). For sea bass, we only analysed specimens caught by fyke nets, as those caught in seine nets were much smaller and not comparable with fyke catches. Linear mixed models were used to estimate the effect of 'edge amount' and 'water exchange' on the carapace width (common shore crab), carapace length (brown shrimp) and total length (common goby and sea bass). These measures of size are the more commonly used for these species. The number of days since the first sampling date was used as a covariate ('sampling day'), in order to account for any age gain incurred from marshes being sampled at different dates (sampling later means individuals caught are older). 'Location' within marsh was used as random factor and its inclusion in the model was assessed following Zuur (2009). For each response variable, four nested models were compared to evaluate fixed effects (Table S2). Model selection and parameter estimation were done as for abundance data.

3. Results

3.1. Catches composition

Salt marshes were used by four species of crustaceans and 11 species of fish. In crab traps, only common shore crabs were caught and this was the only crab species found at the sites (Table 2). Highest catches of crabs occurred at Dwynant and lowest at Malltraeth (Table 2). For seine net catches, at all salt marshes common goby and brown shrimp were the dominant species. Other species caught with seine net were much less abundant (Table 2). Shrimp caught by the seine net included brown shrimp and *Palaemonetes varians*, the Atlantic ditch shrimp. Mysids were found at all sites but not in all hauls, and were more abundant at Ynys Hir. Young of the year sea basses were found at four of the five salt marshes in seine net catches. Dwynant presented the higher abundance of common goby and brown shrimp, but it was also the salt marsh with lowest number of species caught (Table 2). We found the highest number of species at Ynys Hir (Table 2) with half of the seine net hauls performed there catching 5 or more species while most of the hauls in other marshes only caught between 2 and 4 different species.

In fyke nets, sea bass and the European eel, *Anguilla anguilla*, were the most abundant species (Table 2). For fyke net catches, sea bass were found in all salt marshes, with highest abundance at Dwynant and lowest at Ynys Hir (Table 2). European eels were found at all salt marshes but Fairbourne. Two to three species per salt marsh were caught with fykes (Table 2) and most fyke deployments caught below 3 fish m^{-2}.

Sea bass and flounder, *Platichthys flesus,* were the only two species caught in both seine and in fyke nets, however the size of the animals caught by each gear was very different. Sea bass caught by the seine net were between 19 and 44 mm in total length, while the ones caught by fykes were between 116 and 450 mm. Total length of flounders caught by the seine net was between 13 and 140 mm, those caught by the fyke were 35 – 245 mm.

3.2 Abundance relative to water exchange and edge amount

'Water exchange' had a positive effect on the abundance of crabs caught in traps and on fish and shrimp caught by seine nets, but not on the abundance of fish caught by fyke nets (Table 3). 'Edge amount' only had a small negative effect on the abundance of fish caught by seine net (Table 3).

Common shore crab abundance was positively affected by 'water exchange', but less likely by 'edge amount', with the best model explaining 39% of the deviance observed (Table S2). Catches of common shore crab in the salt marsh with the highest 'water exchange' were 86% higher than the marsh with lowest 'water exchange' (Table 3, Fig 3).

The best model explaining total shrimp abundance only retained 'water exchange' as explanatory variable and explained 13% of the total deviance (Table S2). Increase in water exchange lifted shrimp catches by 34% between the lowest and highest water exchange marsh (Table 3, Fig 3).

‘Water exchange’ and ‘edge amount’ explained 48% of the deviance in the best model for the total number of fishes caught by the seine net (Table S2). However, the 95% CI for the edge amount parameter included zero (Table 3), meaning this effect could not be distinguished from no effect. Fish catches increased 22% from the lowest to the highest water exchange marsh (Fig 3).

Variations in fyke catches overall could not be explained by marsh ‘edge amount’ or ‘water exchange’ (Table S2).

3.3. Specimen size relative to water exchange and edge amount

Crab carapace width differed by 9% between ‘edge amount’ distribution limits and 8% between ‘water exchange’ extremes, with the model explaining 22% of the observed deviance (Fig. 4). The best models explaining size variation in common shore crab and common goby could not be clearly distinguished from those that did not include any of the hydrogeomorphic variables ($\Delta AIC_c < 2$, Table S2). ‘Edge amount’ had a small effect on brown shrimp size but the confidence intervals for its parameter included zero (Table 3) indicating that there was insufficient evidence to support this effect. On the other hand, we found a negative effect of ‘water exchange’ on sea bass size, with specimens at the salt marsh with highest water exchange being 51% smaller than those at the highest water exchange site (Figure 4).

4. Discussion

Our results highlight the importance of hydrogeomorphic characteristics on the functioning of ecosystems. The study shows that water exchange boosts fish and crustacean abundances in Northwestern European salt marshes, while edge amount makes only minor contributions. The effects of salt marsh hydrogeomorphic features on the body sizes of fauna were very minor or non-detectable, except for the common shore crab and the sea bass, whose sizes were both negatively related to water exchange and, in the case of the common shore crab, also to edge amount.

The positive association of fishes and crustaceans numbers with water exchange might simply be caused by the exchange of water effectively enlarging the intertidal area that becomes accessible to fauna through the incursion of water. Species such as the common goby, young of the year sea bass, and juvenile brown shrimp, all follow the rising tide into the marsh to forage in the intertidal areas and leave shortly before low water (Cattrijsse et al. 1997, Laffaille et al. 2001, Hampel & Cattrijsse 2004). For the shore crab, the availability of intertidal areas regularly in contact with the tide also represent an important resource as they mainly burrow in this part of the marsh (Wasson et al. 2019). Therefore, the positive association of fishes and crustaceans with water exchange might explained by larger intertidal areas granted by higher water exchange, operating through the provision of increased resources, such as foraging or refuging opportunities.

Water exchange can be perceived as the average depth of water over the marsh during spring high tides and, as such, as an indicator of how much aquatic environment (in terms of volume) becomes available per salt marsh area during tidal flooding. We expected this higher availability of aquatic environment to particularly benefit the abundance of larger fish, which we targeted by fyke net catches. However, water exchange did not translate into a higher abundance of larger fish (i.e. higher fyke catches). Fyke net catches varied little between marshes, with a few deployments accounting for much of the fyke net catch per marsh. This patchiness in catch suggests local characteristics, such as creek depth and distance to channel mouth (e.g. Colombano et al. 2021a), might be more important predictors of the distribution of larger individuals’ than hydrogeomorphological characteristics. Indeed, piscivorous fish are associated with deeper, subtidal channels and do not travel far into the salt marsh creeks to forage, preferring areas closer to the mouth (Colombano et al. 2021a).

Edge amount strongly benefits the abundance of free-swimming species in microtidal systems of Southeastern USA (Minello et al. 1994, Webb & Kneib 2002), as moving among vegetation within the vegetated marsh–creek boundary habitat provides refuge and better foraging opportunities for fishes and crustaceans (Zimmerman et al. 2002). While European marshes do provide foraging opportunities and refuge to fish and crustacean communities (e.g. Laffaille et al. 2001, Hampel et al. 2005), our edge amount results suggest that faunal transgression into the vegetation is not as important in Northwestern European compared to Southeastern USA saltmarsh settings. This could be in part due to different vegetation structure. Southeastern USA salt marshes are dominated by *Sporobolus* (*Spartina*) *alterniflora* that presents a reed-like structure and low stem density (8-550 stems m-^{2}; Zengel et al. 2020) which may result in a better habitat for invertebrate benthic species to burrow and wider spaces for fish to access the vegetated marsh, move among plants and forage while using the vegetation as refuge. In the UK, the lower marsh is dominated by *Sporobolus* (*Spartina*) *anglica* in a sward-like structure with high stem density (e.g. Tempest et al. 2015; 130-1800 stems m^{-2}) which may prevent fish and benthic invertebrates from using this area of the marsh in the same way. In Eastern USA, differences in salt marsh stem density and height did not affect fish incursion into the vegetated salt marsh (Ziegler et al. 2021b), but the question remains if at the even higher densities found in the UK, stem density becomes a limiting factor for fish to enter the vegetated marsh.

Animal size was only affected by the hydrogeomorphic variables assessed for the shore crab and sea bass. For brown shrimp and the common goby, we only found weak evidence that edge amount may play a role in determining their size (positive for shrimp, negative for goby).

Contrary to what we were expecting, water exchange and edge amount presented a small negative effect on the size distribution of the shore crab. This could be explained by size-dependent predation of the common shore crab (Crothers 1968): crabs smaller than 10 mm carapace width are prey for aquatic predators, while larger sizes are mainly preyed upon by shore birds (Thiel & Dernedde 1994 and references therein). It is possible that salt marshes with higher water exchange or higher edge amount benefit the abundance of avian predators, as salt marsh hydrogeomorphology modulates the density, use and community composition of its shore birds (e.g. Darnell & Smith 2004, Trocki & Paton 2006). Furthermore, crabs of smaller sizes find predation refuge by keeping to the high intertidal, inaccessible to marine predators (Thiel & Dernedde 1994), given that water exchange grants larger intertidal areas, higher water exchange could mean greater extent of refuge for smaller size classes, moving the population average towards smaller sizes. Water exchange also had a negative effect on sea bass size. Markings in their scales allowed us to age sea basses and conclude that differences in the mean size of sea basses were mainly due to a higher proportion of younger sea basses (Fig S3). This implies that sea basses are not necessarily growing faster at shallower salt marshes but rather, that older, probably higher trophic level sea basses are using these marshes while younger animals prefer deeper marshes. This negative relationship was contrary to what we were expecting, as generally higher trophic levels are expected to be benefited by salt marshes with higher tidal range, deeper water or longer inundation times (e.g. Ruiz et al. 1993, Nelson et al. 2015, Ziegler et al. 2019). As ours was a natural experiment, it is possible that some confounding effects existed. For example, as water exchange was derived from aerial images, and not from in-situ measurements of water depth, it is possible that geomorphologic characteristics down the shore line (e.g. barriers), climatic events or changes in rivers’ discharges during the sampling period could be affecting the effective salt marsh inundation. More research is needed to better understand this pattern.

Our study could only focus on a small range in edge amount and water exchange. These two variables can easily take values outside the range studied here, even within the UK. For example, using our methods, the edge amount of salt marshes at the Kent and Leven estuaries present values of 0.015 – 0.022 m m^{-2}. In the Gulf of Mexico, values of edge amount that we could find go from 0.002m m^{-2} to 0.15 m m^{-2} (Minello & Rozas 2002, Kneib 2003). Comparisons between numerical values between studies should be taken with care as these numbers were obtained through different methods. Considering this, it is likely that the relationships that we found (and did not find) will change outside the studied geographical range, as hydrogeomorphic variables interact with other elements of the landscape and the broader coastal context (Bradley et al. 2020). The importance of these interactions between in determining habitat value for aquatic species has not been sufficiently explored (e.g. see Ziegler et al. 2021a). Our results suggest that the importance of edge amount for promoting fish and crustacean abundance might be dependent on tidal range: important at micro and meso tidal systems, but not at macrotidal systems, such as those studied here. This would mean that edge amount might still be important for salt marshes at southern Europe (e.g. Cavraro et al. 2017) or South Africa (e.g. Leslie et al. 2017). On the other hand, water exchange might be important at salt marshes that rarely get their vegetated flat flooded, such as those in the rest of northern Europe, Australia and South America (e.g. Laffaille et al. 2000, Saintilan & Adams 2009, Valiñas et al. 2012).

There are possible caveats to our study. First, we did not measure edge amount directly, but used a proxy. Instead of measuring the length of creek edges we measured the lengths of creeks’ central path. Although these two measures are not identical, the length of the creek path to marsh area ratio is a very similar, repeatable and automatable proxy. The marshes we surveyed did not contain large ponds or very pronounced meanders (Fig S2) and therefore we considered the creek central path to be proportional to the length of its edges. A second caveat is that we only fished with the seine net during spring tide low water, in the residual water of the creeks. An important fraction of brown shrimp and young of the year sea bass enter the marsh with the flooding tide and leave with the ebbing tide (Cattrijsse et al. 1997, Laffaille et al. 2001), so our observations might underestimate the numbers that may be found during high water. Thirdly, we do not have local estimates of water velocity which affects the performance of swimming animals (e.g. Brodersen et al. 2008) and therefore might determine their distribution within and across salt marshes as well as their biological interactions (Friese et al. 2021).

Finally, it is important to note that climate change is affecting salt marsh hydrogeomorphology and therefore the process at the core of saltmarsh functioning (Fagherazzi et al. 2012) including their habitat value for aquatic species (Colombano et al. 2021b). Without better value judgments of individual marshes, the threat posed by climate change could be sever. There are numerous examples around the globe of rapid salt marsh loss, from various tidal regimes in a matter of years (e.g. Day Jr et al. 1998, Kennish 2001, Van der Wal & Pye 2004, Gu et al. 2018). Sea level rise pushes salt marshes landwards and artificial structures on the coast line prevent salt marsh migration in a process called coastal squeezing (Doody 2013). Coastal squeeze results in turn in the inundation and loss of formally mid marsh areas vital for hydrodynamic functioning as they contain complex topography, shallows, hillocks and relatively low distances to creeks (Lawrence et al. 2018). Increased storminess, wave and tidal action, as predicted by most climate change scenarios will also change salt marsh structure, as most theories and creek development models predict that higher depth and energy results in the incision and widening of creeks (Fagherazzi & Furbish 2001, Moffett & Gorelick 2016, Wiberg et al. 2020). At the scale of our study, this would mean a decrease in edge amount.

Here, we have shown that water exchange consistently and positively affects the total abundances of saltmarsh communities, while edge amount has no effect, despite being an important driver of secondary production in other regions of the world (e.g. Minello et al. 1994, Webb & Kneib 2002). Our findings suggest that Northwestern European marshes function through different mechanisms than the more studied microtidal salt marshes of the Southeastern USA. Links between fisheries production and salt marsh habitat (e.g. Rozas et al. 2005, Meynecke et al. 2008) might also be different. This is of paramount importance when scaling up assessments using remote sensing and furthers the need for collaborative research to better understand the geographic boundaries of the drivers that control the distribution and growth of species.

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Tables

Table 1: Environmental characteristics of the five study sites and high tide following the deployment of traps and fykes during summer and autumn.

Salt marsh	Water exchange (m^3 m^{-2})	Edge amount (m m^{-2})	Area (km^{-2})	Nearest tidal gauge	Tidal range (m)	High tide summer (m)	High tide autumn (m)
Dwynant	0.909	0.032	0.39	Barmouth	7.8	4.9	5.2
Fairbourne	0.652	0.026	0.53	Barmouth	7.8	4.6	5.1
Malltraeth	0.371	0.031	1.85	Holyhead	8.0	4.9	5.1
Pont Briwet	0.221	0.031	0.44	Barmouth	7.8	4.6	4.8
Ynys Hir	0.396	0.027	1.05	Barmouth	7.8	5.2	4.9

Table 2: Catches (mean ± standard error) for the three fishing methods and the five study sites. For crab traps the number of individuals caught per trap per tidal cycle are shown, for fykes number of fishes caught per net opening area (m^{-2}), for seine nets the number of individuals caught per m sweep. Hyphens (-) indicate a species was not caught at the site.

Species	Dwynant	Fairbourne	Malltraeth	Pont Briwet	Ynys Hir
Crab trap (n = 10)					
Carcinus maenas (common shore crab)	61.70 ± 16.78	11.70 ± 2.36	8.70 ± 2.62	9.10 ± 3.38	17.50 ± 2.91
Fyke net (n = 8)					
No crustaceans observed					
Fish					
Anguilla anguilla (European eel)	0.13 ± 0.13	-	0.01 ± 0.01	0.46 ± 0.23	0.14 ± 0.14
Atherina presbyter (sand smelt)	-	0.12 ± 0.12	-	-	-
Chelon ramada (thinlip grey mullet)	-	-	0.03 ± 0.03	-	-
Dicentrarchus labrax (sea bass)	1.26 ± 0.57	1.04 ± 0.60	0.68 ± 0.36	0.51 ± 0.34	0.06 ± 0.05
Platichthys flesus (flounder)	0.17 ± 0.17	-	-	0.33 ± 0.22	0.35 ± 0.20
Seine net (n = 10)					
Crustaceans					
Crangon crangon (brown shrimp)	127.12 ± 35.99	32.74 ± 10.73	73.69 ± 25.95	17.58 ± 3.98	65.49 ± 15.18
Mysida (mysids)	24.07 ± 9.84	11.70 ± 8.58	18.26 ± 14.56	72.42 ± 26.86	173.56 ± 113.76
Palaemonetes varians (Atlantic ditch shrimp)	-	0.14 ± 0.14	1.03 ± 0.51	-	1.94 ± 0.95
Fishes					
Ammodytes tobianus (lesser sand eel)	-	-	-	-	0.04 ± 0.04
Atherina presbyter (sand smelt)	-	0.12 ± 0.09	-	-	0.04 ± 0.04
Chelon auratus (golden grey mullet)	-	-	-	-	0.44 ± 0.40
Chelon labrosus (thicklip grey mullet)	-	-	-	0.04 ± 0.04	0.50 ± 0.37
Chelon ramada (thinlip grey mullet)	-	5.60 ± 5.60	-	-	-
Clupea harengus (herring)	-	-	-	-	0.24 ± 0.24
Dicentrarchus labrax (sea bass)	-	0.20 ± 0.16	0.06 ± 0.06	0.04 ± 0.04	3.78 ± 2.12
Platichthys flesus (flounder)	0.24 ± 0.16	0.20 ± 0.14	-	0.08 ± 0.08	0.60 ± 0.60
Pomatoschistus microps (common goby)	247.91 ± 130.81	61.53 ± 8.15	13.68 ± 4.46	28.18 ± 5.77	119.88 ± 56.61
Sprattus sprattus (sprat)	-	-	-	-	0.08 ± 0.08

<u>Table 3:</u> Parameter estimates and 95% confidence intervals (CI) for explanatory variables accounting for variation in the catches of crabs (traps), shrimp (seine nets) and fish species (seine and fyke nets), and for variation in the sizes of common shore crab (*Carcinus maenas)*, brown shrimp (*Crangon crangon*), common goby (*Pomatoschistus microps*) and sea bass (*Dicentrarchus labrax*). In bold, explanatory variables with CI excluding zero. See main text for model details.

Response variable	Explanatory variable	Parameter estimate ± SE	CI lower	CI upper
Crab abundance	**Intercept**	**1.51 ± 0.28**	**0.99**	**2.04**
	Water exchange	**2.61 ± 0.49**	**1.73**	**3.53**
Shrimp abundance	**Intercept**	**3.20 ± 0.35**	**2.52**	**3.91**
	Water exchange	**1.76 ± 0.62**	**0.56**	**3.08**
Fish abundance (seine)	**Intercept**	**6.54 ± 1.67**	**2.00**	**11.17**
	Edge amount	-132.03 ± 56.03	-290.17	21.45
	Water exchange	**2.33 ± 0.73**	**0.85**	**3.83**
Fish abundance (fyke)	**Intercept**	**-0.40 ± 0.12**	**-0.64**	**-0.17**
Common shore crab size	**Intercept**	**68.79 ± 3.60**	**61.72**	**75.87**
	Edge amount	**-701.16 ± 129.61**	**-955.73**	**-446.60**
	Water exchange	**-9.27 ± 1.27**	**-11.77**	**-6.77**
	Sampling day	**-0.03 ± 0.01**	**-0.04**	**-0.01**
Brown shrimp size	**Intercept**	**13.00 ± 4.50**	**4.21**	**21.79**
	Edge amount	254.50 ± 155.33	-48.64	557.34
	Sampling day	**0.03 ± 0.01**	**0.01**	**0.04**
Common goby size	**Intercept**	**25.35 ± 0.73**	**23.89**	**26.81**
	Sampling day	**0.03 ± 0.01**	**0.01**	**0.04**
Sea bass size	**Intercept**	**273.75 ± 36.29**	**200.57**	**346.93**
	Water exchange	**-176.07 ± 46.95**	**-270.75**	**-81.39**
	Sampling day	**1.28 ± 0.43**	**0.42**	**2.15**

Figures

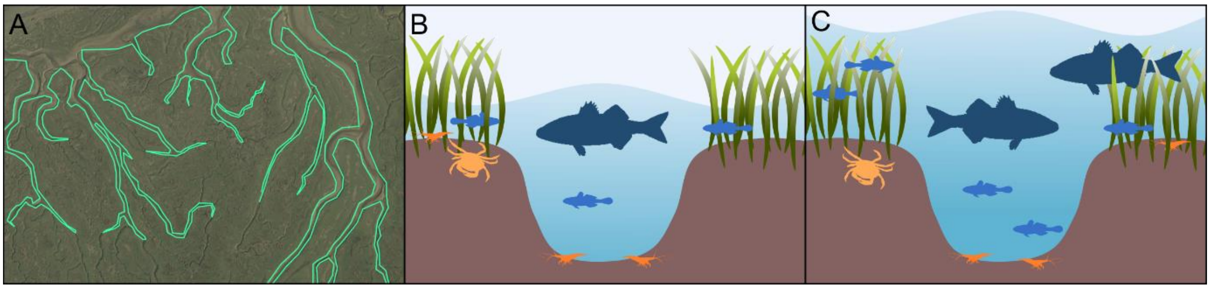

Fig 1: **A.** Aerial view of a salt marsh where the edge between creeks and the vegetated marsh has been delineated. Edge amount is defined as the total length of this edge amount. **B.** The creek-marsh edge provides refuge and foraging opportunities for smaller fishes and crustaceans. **C.** With greater water exchange there is more aquatic environment per unit area, which could attract more large fish.

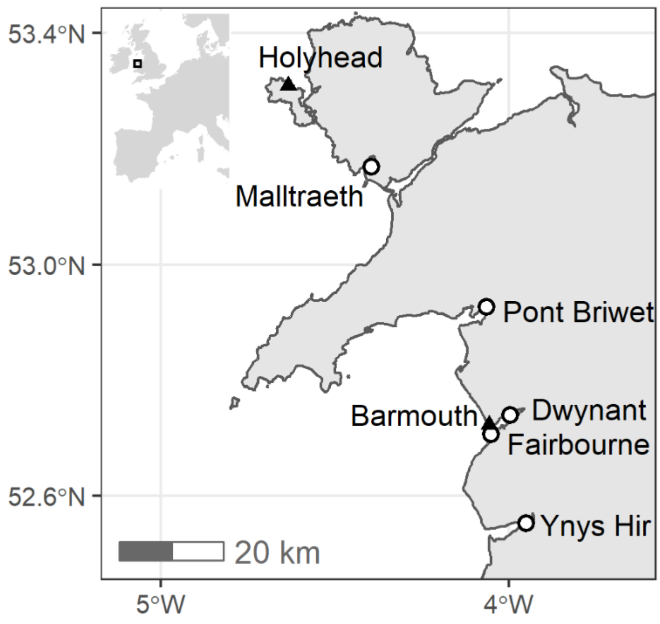

Fig 2: Locations of the five selected study sites (circles) and tidal gauges (triangles) on the west coast of Wales, UK.

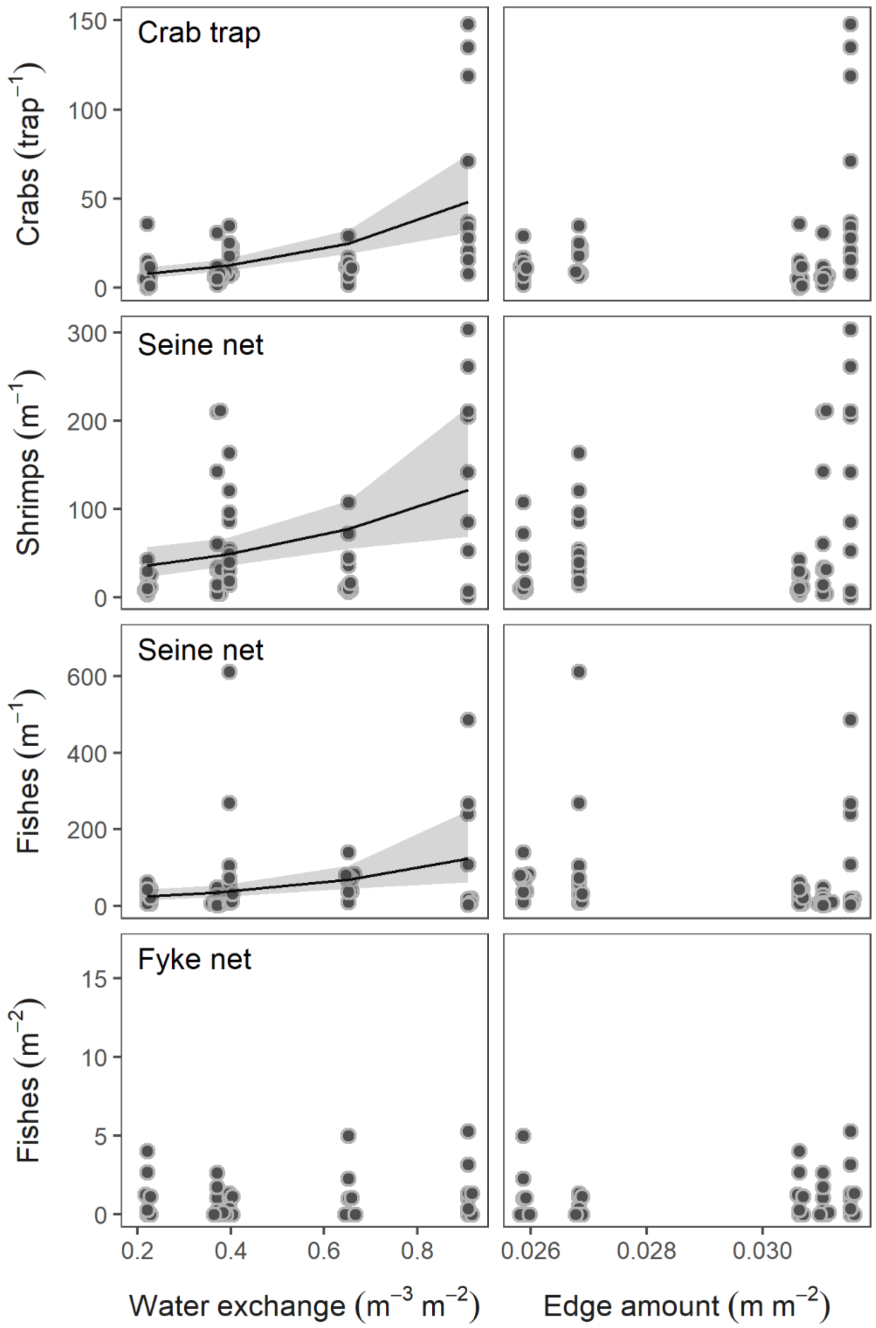

Fig 3: Relations of total crab (traps), shrimp (seine net) and fish (seine and fyke) catches with marsh edge amount and water exchange. Dots show catches. Black lines show best model predictions with grey standard error ribbons.

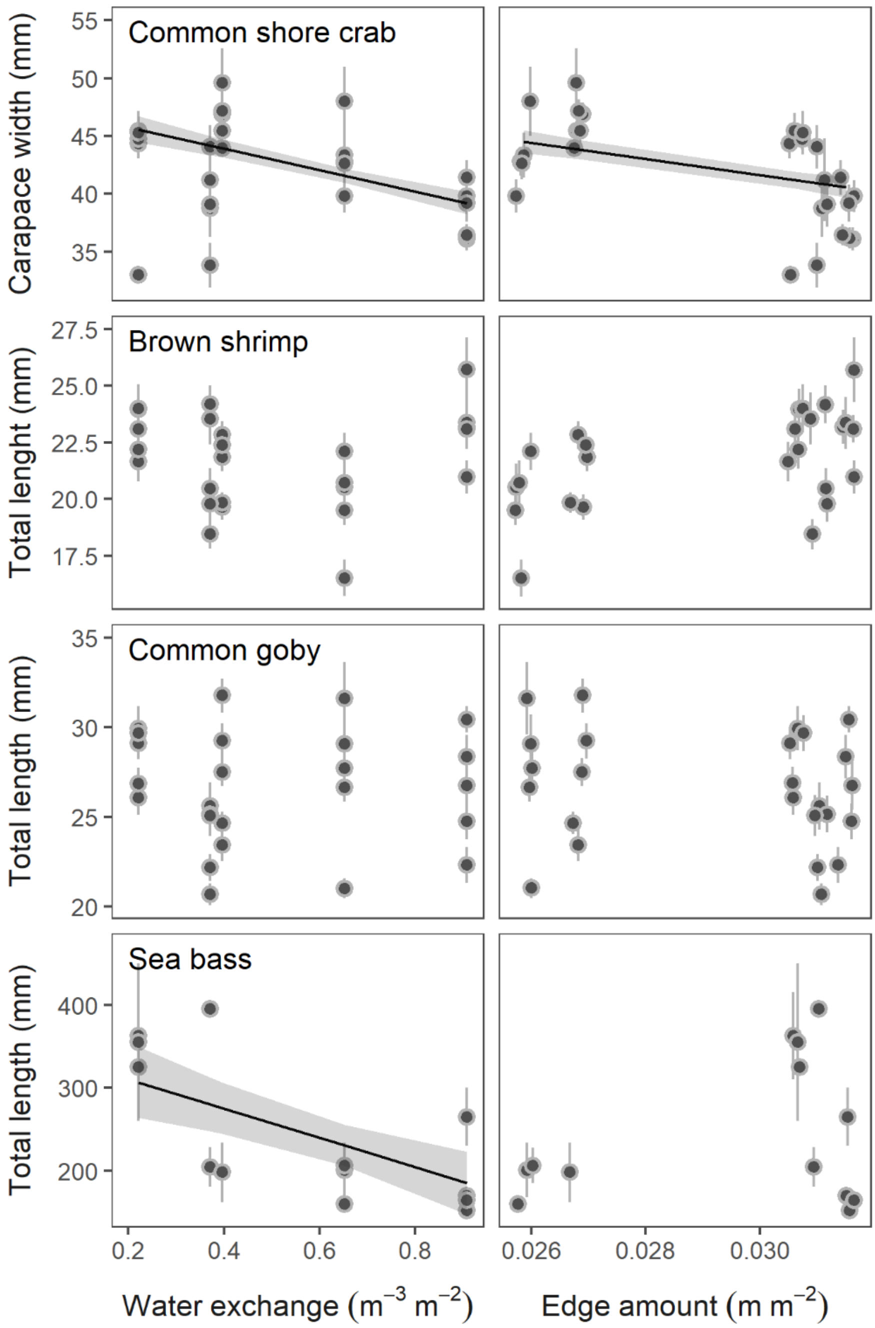

Fig 4: Mean sizes of individuals relative to edge amount and water exchange. Dots and vertical lines show the mean ± s.e. individual size for sampling locations within marshes. For common shore crab (*Carcinus maenas)* and brown shrimp (*Crangon crangon*), all individuals caught were considered; for common goby (*Pomatoschistus microps*) and sea bass (*Dicentrachus labrax*), only individuals of year-1 class were considered. Black lines show best model predictions with grey-ribbon standard errors.

Electronic supplementary material

Tidal water exchange drives fish and crustacean abundances in salt marshes

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Table S1: Edge amount and water exchange, extent and location for 16 candidate salt marshes across north Wales. Selected study sites are shown in bold.

Salt marsh	Edge amount (m m^{-2})	Water exchange (m^3 m^{-2})	Area (km^2)	Longitude	Latitude
Dwynant	**0.032**	**0.909**	**0.391**	**52.734**	**-4.016**
Fairbourne	**0.026**	**0.652**	**0.528**	**52.708**	**-4.043**
Garth Isaf	0.029	1.172	0.430	52.727	-3.999
Glaslyn Cob	0.027	0.966	0.341	52.918	-4.114
Glastraeth	0.028	0.180	1.351	52.910	-4.073
Malltraeth	**0.031**	**0.371**	**1.851**	**53.169**	**-4.395**
Mochras	0.031	0.552	0.710	52.820	-4.134
Penmaen Isa	0.025	0.074	0.963	52.559	-3.937
Penmaenpool	0.030	0.258	0.505	52.748	-3.953
Pont Borthwnog	0.030	0.504	0.215	52.750	-3.956
Pont Briwet	**0.031**	**0.221**	**0.445**	**52.925**	**-4.065**
Traeth Bach	0.033	0.628	0.995	52.897	-4.118
Traeth Maelgwyn	0.027	0.752	1.389	52.526	-4.018
YForyd	0.029	1.064	0.629	53.105	-4.323
Ynys Greigiog	0.027	0.792	1.465	52.540	-3.983
Ynys Hir	**0.027**	**0.396**	**1.053**	**52.552**	**-3.954**

Table S2: Summary of model-selection results for models explaining variation in abundance and size of fish and crustaceans in relation to interspersion and water exchange, *k* is the number of estimated parameters. See Methods for details. Models are listed in decreasing order of relevance.

Response variable	Candidate Model	*k*	AICc	ΔAICc	w_i
Crab abundance (crab trap)	Water exchange	3	389.49	0.00	0.66

	Edge amount + Water exchange	4	390.82	1.33	0.34
	Edge amount	3	410.06	20.57	0.00
	Null	2	414.26	24.77	0.00
Shrimp abundance (seine)	Water exchange	3	505.69	0.00	0.58
	Edge amount + Water exchange	4	506.86	1.17	0.32
	Edge amount	3	510.24	4.55	0.06
	Null	2	511.31	5.62	0.03
Fish abundance (seine)	Edge amount + Water exchange	5	497.97	0.00	0.52
	Water exchange	4	498.34	0.37	0.43
	Null	3	503.79	5.82	0.03
	Edge amount	4	504.03	6.06	0.02
Fish abundance (fyke)	Null	2	92.10	0.00	0.52
	Edge amount	3	93.73	1.63	0.23
	Water exchange	3	94.27	2.17	0.18
	Edge amount + Water exchange	4	96.04	3.94	0.07
Common shore crab (*Carcinus maenas*) size	Sampling day + Water exchange + Edge amount	5	3833.83	0.00	0.96
	Water exchange + Edge amount	4	3840.09	6.26	0.04
	Sampling day + Water exchange	4	3860.53	26.70	0.00
	Water exchange	3	3869.94	36.11	0.00
	Edge amount	3	3882.01	48.18	0.00
	Sampling day + Edge amount	4	3883.03	49.20	0.00
	Null	2	3940.47	106.64	0.00
	Sampling day	3	3941.23	107.39	0.00
Brown shrimp (*Crangon crangon*) size	Sampling day + Edge amount	5	5518.37	0.00	0.43
	Sampling day	4	5519.12	0.74	0.30
	Sampling day + Water exchange + Edge amount	6	5520.34	1.97	0.16
	Sampling day + Water exchange	5	5521.08	2.70	0.11
	Edge amount	4	5534.40	16.02	0.00
	Water exchange + Edge amount	5	5536.40	18.02	0.00
	Null	3	5538.01	19.63	0.00
	Water exchange	4	5540.00	21.62	0.00
Common goby (*Pomatoschistus microps*) size	Date	4	6439.07	0.00	0.40

	Date + Edge amount	5	6439.48	0.41	0.33
	Date + Water exchange	5	6441.08	2.02	0.15
	Date + Water exchange + Edge amount	6	6441.51	2.44	0.12
	Null	3	6448.07	9.00	0.00
	Edge amount	4	6449.23	10.16	0.00
	Water exchange	4	6450.04	10.97	0.00
	Water exchange + Edge amount	5	6451.20	12.13	0.00
Sea bass (*Dicentrachus labrax*) size	Date + Water exchange	4	527.53	0.00	0.58
	Date + Water exchange + Edge amount	5	528.39	0.87	0.38
	Water exchange	3	533.87	6.34	0.02
	Water exchange + Edge amount	4	535.19	7.67	0.01
	Date	3	538.14	10.61	0.00
	Date + Edge amount	4	539.51	11.98	0.00
	Null	2	544.20	16.67	0.00
	Edge amount	3	545.85	18.32	0.00

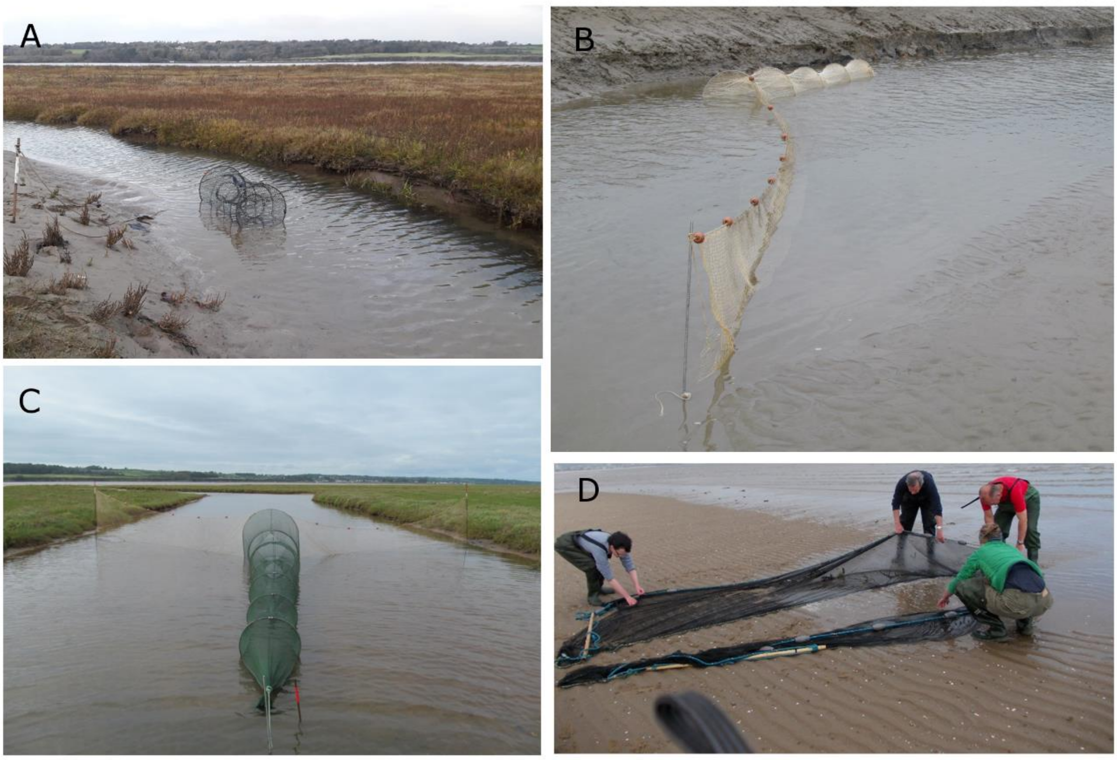
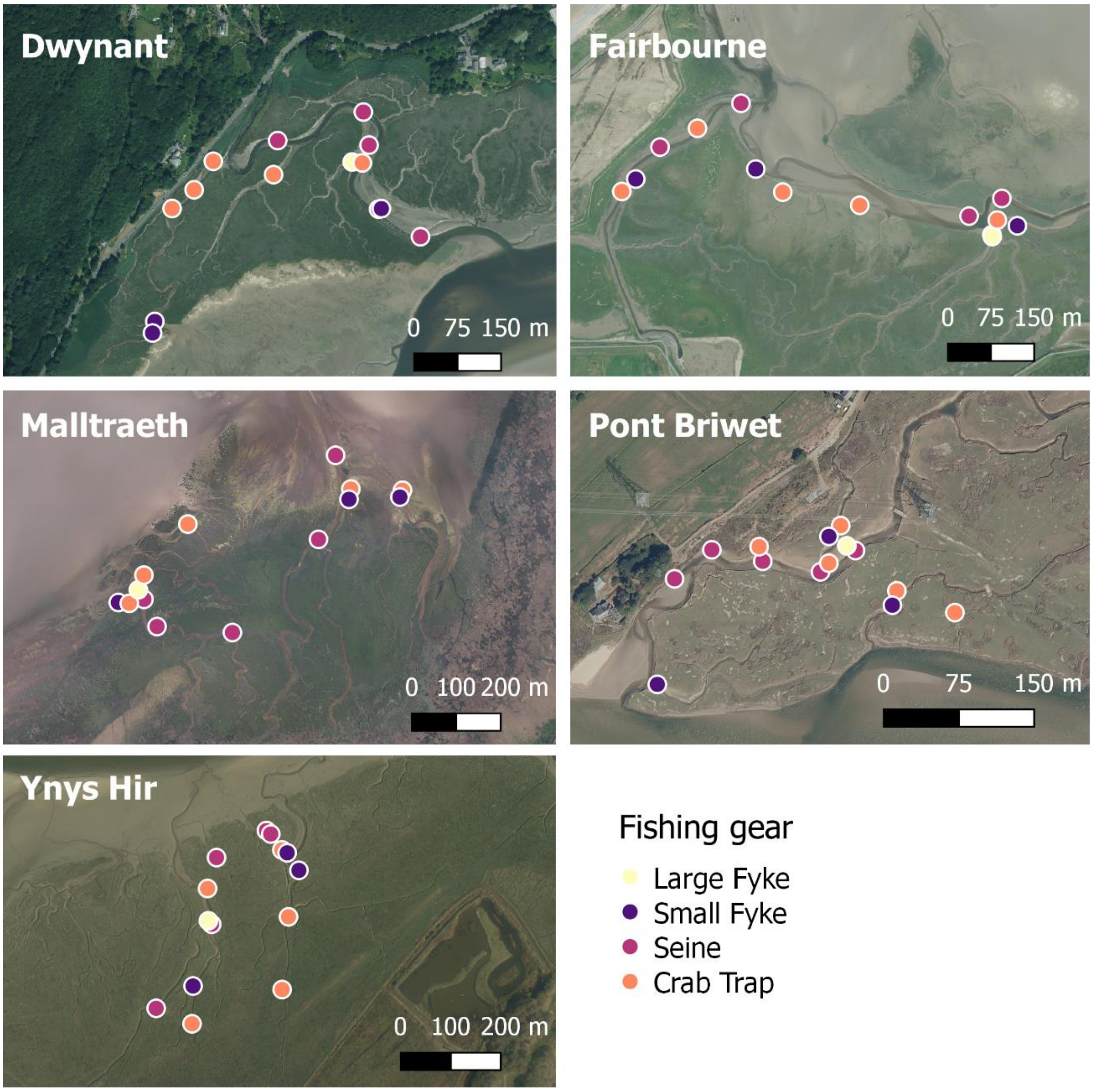


Fig S1: Fishing gear used during biological sampling. **A** crab trap, **B** small fyke, **C** large fyke, **D** seine net.



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665 **Fig S2**: Full schematic of the sampling locations within the five study marshes.

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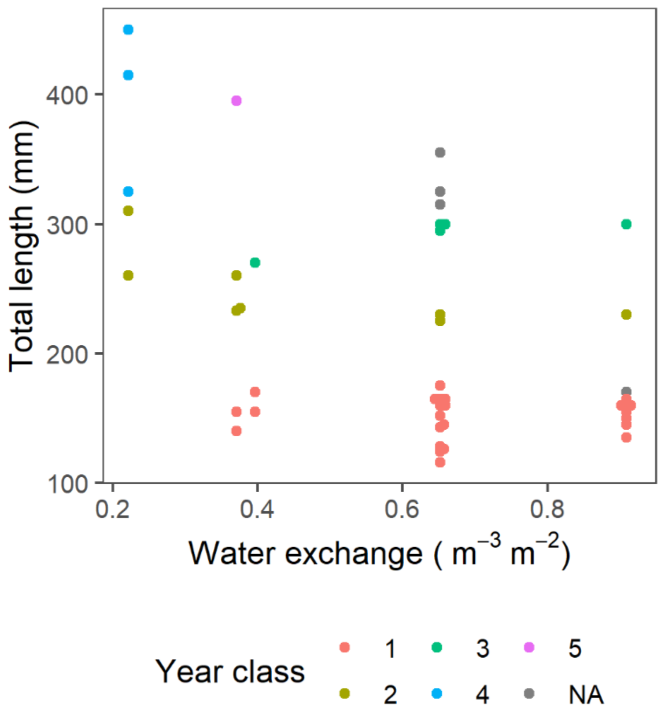

Fig S3: Sea bass (*Dicentrachus labrax*) total length relative to water exchange, showing the year class of each individual. Specimens which year class could not be determined are shown as NA.

Electronic supplementary material

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Table S1: Edge amount and water exchange, extent and location for 16 candidate salt marshes across north Wales. Selected study sites are shown in bold.

Salt marsh	Edge amount (m m^{-2})	Water exchange (m^3 m^{-2})	Area (km^2)	Longitude	Latitude
Dwynant	**0.032**	**0.909**	**0.391**	**52.734**	**-4.016**
Fairbourne	**0.026**	**0.652**	**0.528**	**52.708**	**-4.043**
Garth Isaf	0.029	1.172	0.430	52.727	-3.999
Glaslyn Cob	0.027	0.966	0.341	52.918	-4.114
Glastraeth	0.028	0.180	1.351	52.910	-4.073
Malltraeth	**0.031**	**0.371**	**1.851**	**53.169**	**-4.395**
Mochras	0.031	0.552	0.710	52.820	-4.134
Penmaen Isa	0.025	0.074	0.963	52.559	-3.937
Penmaenpool	0.030	0.258	0.505	52.748	-3.953
Pont Borthwnog	0.030	0.504	0.215	52.750	-3.956
Pont Briwet	**0.031**	**0.221**	**0.445**	**52.925**	**-4.065**
Traeth Bach	0.033	0.628	0.995	52.897	-4.118
Traeth Maelgwyn	0.027	0.752	1.389	52.526	-4.018
YForyd	0.029	1.064	0.629	53.105	-4.323
Ynys Greigiog	0.027	0.792	1.465	52.540	-3.983
Ynys Hir	**0.027**	**0.396**	**1.053**	**52.552**	**-3.954**

Table S2: Summary of model-selection results for models explaining variation in abundance and size of fish and crustaceans in relation to interspersion and water exchange, *k* is the number of estimated parameters. See Methods for details. Models are listed in decreasing order of relevance.

Response variable	**Candidate Model**	***k***	**AICc**	**ΔAICc**	**w_i**
Crab abundance (crab trap)	Water exchange	3	389.49	0.00	0.66
	Edge amount + Water exchange	4	390.82	1.33	0.34
	Edge amount	3	410.06	20.57	0.00
	Null	2	414.26	24.77	0.00
Shrimp abundance (seine)	Water exchange	3	505.69	0.00	0.58
	Edge amount + Water exchange	4	506.86	1.17	0.32
	Edge amount	3	510.24	4.55	0.06
	Null	2	511.31	5.62	0.03
Fish abundance (seine)	Edge amount + Water exchange	5	497.97	0.00	0.52
	Water exchange	4	498.34	0.37	0.43
	Null	3	503.79	5.82	0.03
	Edge amount	4	504.03	6.06	0.02

Fish abundance (fyke)	Null	2	92.10	0.00	0.52
	Edge amount	3	93.73	1.63	0.23
	Water exchange	3	94.27	2.17	0.18
	Edge amount + Water exchange	4	96.04	3.94	0.07
Common shore crab (*Carcinus maenas*) size	Sampling day + Water exchange + Edge amount	5	3833.83	0.00	0.96
	Water exchange + Edge amount	4	3840.09	6.26	0.04
	Sampling day + Water exchange	4	3860.53	26.70	0.00
	Water exchange	3	3869.94	36.11	0.00
	Edge amount	3	3882.01	48.18	0.00
	Sampling day + Edge amount	4	3883.03	49.20	0.00
	Null	2	3940.47	106.64	0.00
	Sampling day	3	3941.23	107.39	0.00
Brown shrimp (*Crangon crangon*) size	Sampling day + Edge amount	5	5518.37	0.00	0.43
	Sampling day	4	5519.12	0.74	0.30
	Sampling day + Water exchange + Edge amount	6	5520.34	1.97	0.16
	Sampling day + Water exchange	5	5521.08	2.70	0.11
	Edge amount	4	5534.40	16.02	0.00
	Water exchange + Edge amount	5	5536.40	18.02	0.00
	Null	3	5538.01	19.63	0.00
	Water exchange	4	5540.00	21.62	0.00
Common goby (*Pomatoschistus microps*) size	Date	4	6439.07	0.00	0.40
	Date + Edge amount	5	6439.48	0.41	0.33
	Date + Water exchange	5	6441.08	2.02	0.15
	Date + Water exchange + Edge amount	6	6441.51	2.44	0.12
	Null	3	6448.07	9.00	0.00
	Edge amount	4	6449.23	10.16	0.00
	Water exchange	4	6450.04	10.97	0.00
	Water exchange + Edge amount	5	6451.20	12.13	0.00
Sea bass (*Dicentrachus labrax*) size	Date + Water exchange	4	527.53	0.00	0.58
	Date + Water exchange + Edge amount	5	528.39	0.87	0.38
	Water exchange	3	533.87	6.34	0.02
	Water exchange + Edge amount	4	535.19	7.67	0.01

Date	3	538.14	10.61	0.00
Date + Edge amount	4	539.51	11.98	0.00
Null	2	544.20	16.67	0.00
Edge amount	3	545.85	18.32	0.00

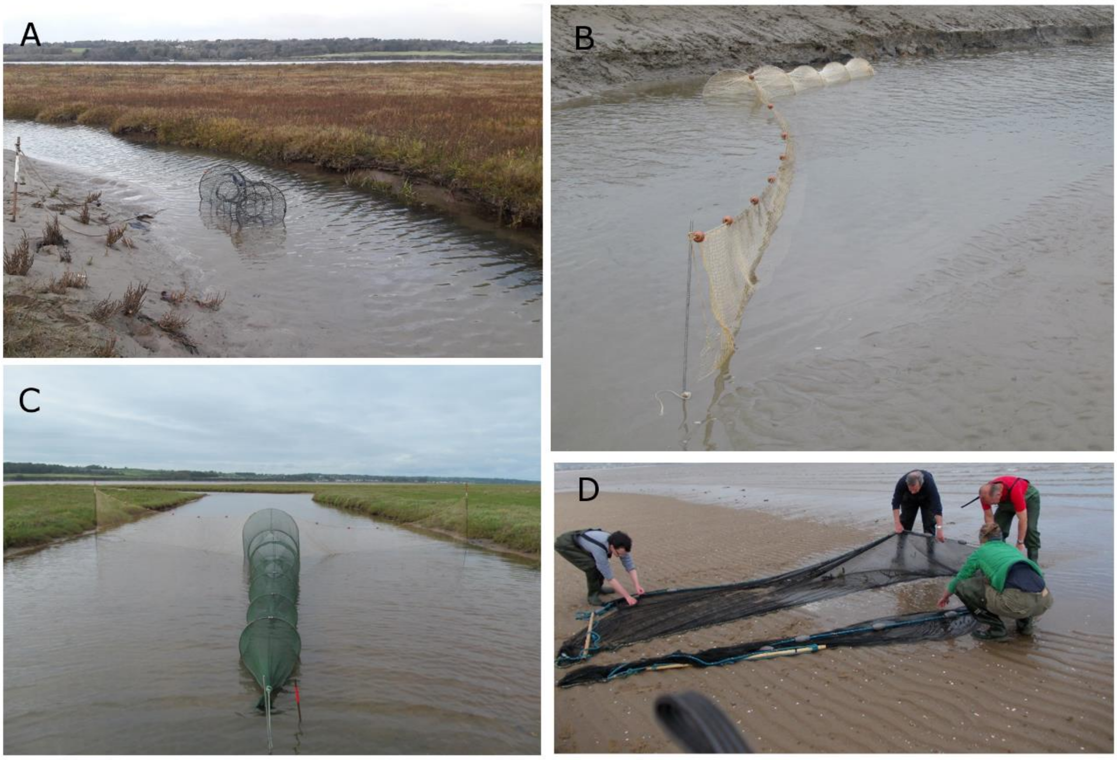

Fig S1: Fishing gear used during biological sampling. **A** crab trap, **B** small fyke, **C** large fyke, **D** seine net.

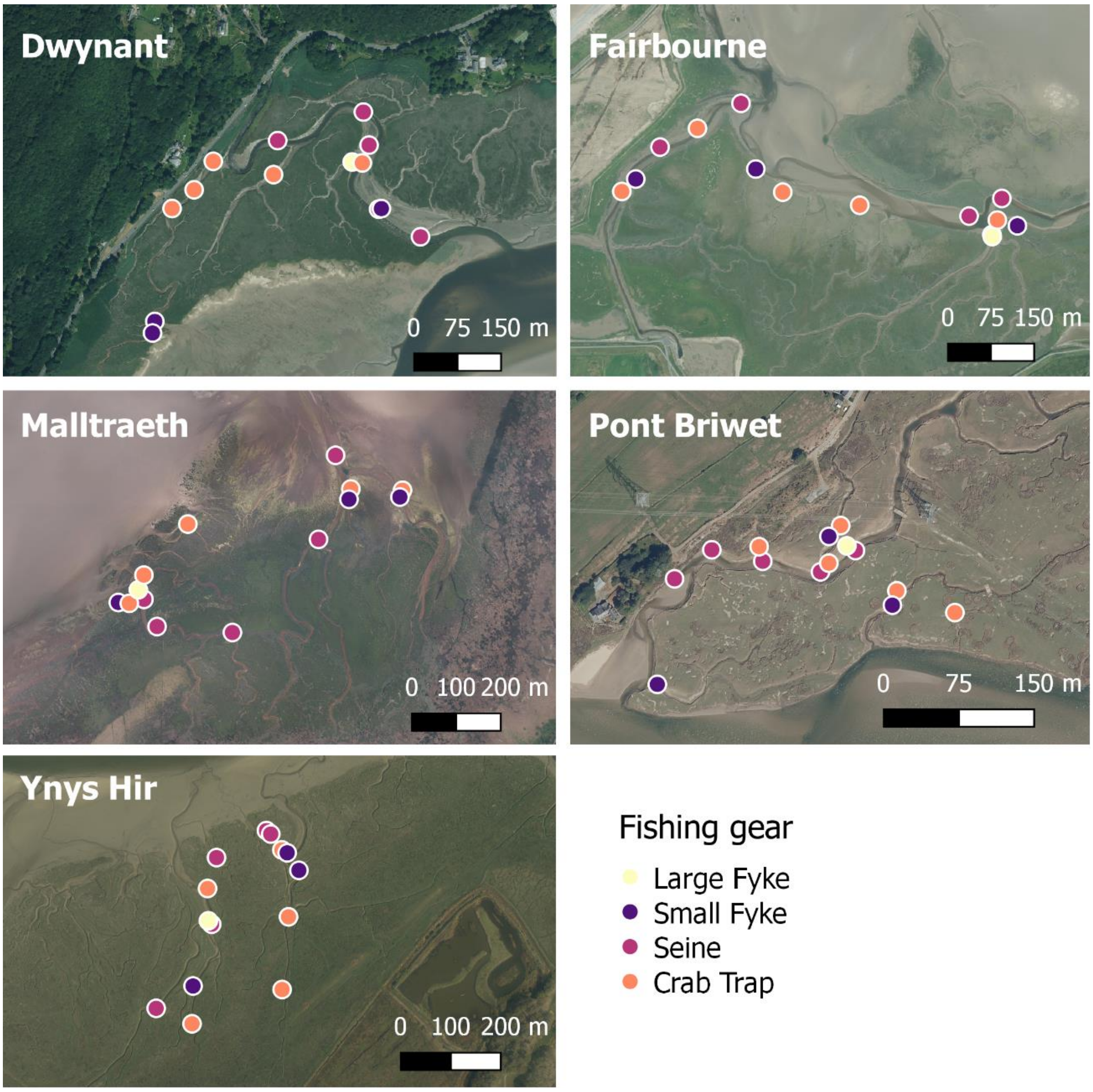

Fig S2: Full schematic of the sampling locations within the five study marshes.

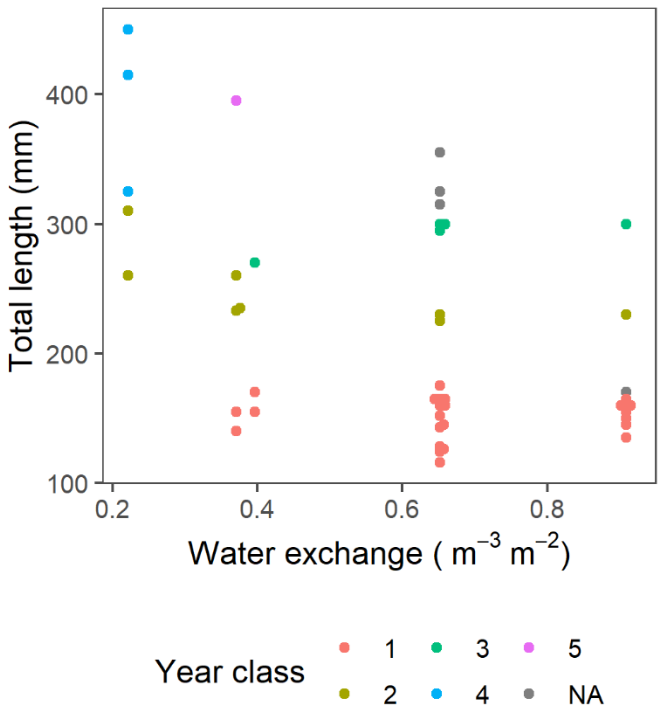

Fig S3: Sea bass (*Dicentrachus labrax*) total length relative to water exchange, showing the year class of each individual. Specimens which year class could not be determined are shown as NA.