Vol. 694: 61–72, 2022
https://doi.org/10.3354/meps14118

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 11

Tidal water exchange drives fish and crustacean abundances in salt marshes

Paula de la Barra[1,3,*], Martin W. Skov[1], Peter J. Lawrence[1,2], Juan I. Schiaffi[3], Jan G. Hiddink[1]

[1] School of Ocean Sciences, Bangor University, Menai Bridge LL59 5AB, UK

[2] *Present address:* Institute of Science and Environment, University of Cumbria, Ambleside LA22 9BB, UK

[3] *Present address:* Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, Texel 1790 AB, The Netherlands

ABSTRACT: Coastal salt marshes provide 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 2 physical properties that govern marsh accessibility to water-dependent species, as has been found on the southeastern coast of the USA: (1) the volume of water exchanged by tidal flooding, which gives access to the marsh, and (2) 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 5 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. In total, 15 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 as well.

KEY WORDS: 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 well-being 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 information from only a few regions around the world (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), freshwater input (Allen 2000) and vegetation composition (Bij de Vaate et al. 2020), which varies substantially around

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*Corresponding author: delabarrapaula@gmail.com

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 is still poorly understood (Ziegler et al. 2021a). Here, we investigated how a suite of 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. 1A) (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. 1B). 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 geomorphological features of the marsh (Fig. 1C). 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 for fishes and crustaceans. Water exchange may affect the species composition, total abundance and size distribution of fish and crustacean communities inhabiting marshes because the phase of the tide used for entering and exiting the marsh differs among 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, to the detriment of smaller prey individuals (Fig. 1C) (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 USA, where most of our understanding of 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, particularly 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 & Hampel 2006). As a consequence, the regime of inundation of the vegetated marsh in the southeastern USA is very different from that of northwestern European salt marshes that are only substantially inundated during spring tides (~6–8 d mo^{-1}), when the vegetated marsh can be covered by up to 1 m 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 on both sides of the Atlantic are thought to sustain fish and

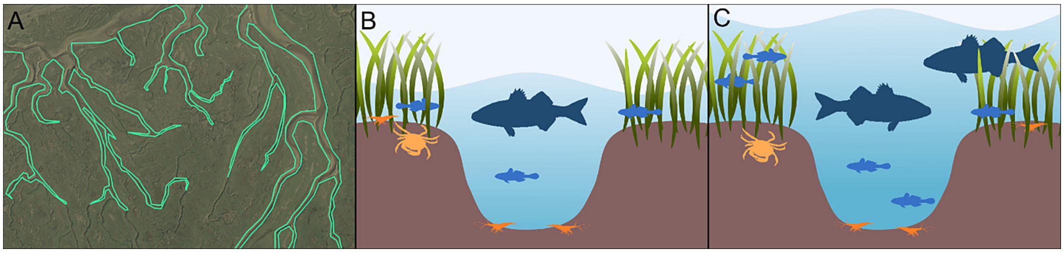

Fig. 1. (A) Aerial view of a salt marsh; the edge between creeks and the vegetated marsh has been delineated. Edge amount is defined as the total length of this edge per salt marsh unit area. (B) The creek–marsh edge provides refuge and foraging opportunities for smaller fishes and crustaceans. (C) With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

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 5 sites in the UK. We focused on faunal responses to edge amount and water exchange volume, given the importance of these hydrological characteristics to fish and crustacean use in southeastern USA marshes (Simenstad et al. 2002, Kneib 2003, Allen et al. 2007). Despite the differences in salt marshes in the 2 regions, there is no evidence showing that the function of UK salt marshes will be fundamentally different from those of the southeastern USA, as the relationship between salt marsh hydrogeomorphology and its function as fish and crustacean habitat has not been extensively studied outside North America. Therefore, we expect that abundances would be greater (Prediction 1) and individuals would be larger (Prediction 2) at more interspersed marshes and those with a greater tidal exchange of water. We expected this to occur 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 2 parameters were not correlated. To determine these features, edge amount and water exchange were estimated for 16 candidate salt marshes across north Wales (Table S1 in the Supplement at www.int-res.com/articles/suppl/m694p061_supp.pdf). The extent of 13 of these 16 salt marshes had previously been GIS-mapped and measured (Ladd et al. 2019). The 3 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 pre-candidate marshes, edge amount and water exchange were calculated as explained below. Using edge amount and water exchange scores, 5 representative salt marshes were selected from the pool (Table 1, Fig. 2). All 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 5 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 1 m resolution digital terrain models acquired from EDINA LIDAR Digimap Service (2016). The central path of each creek was delineated using the flow accumulation function of package 'whitebox' in R (function 'flow_accumulation_full_workflow'; Wu 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 proved to be 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.

Table 1. Environmental characteristics of the 5 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

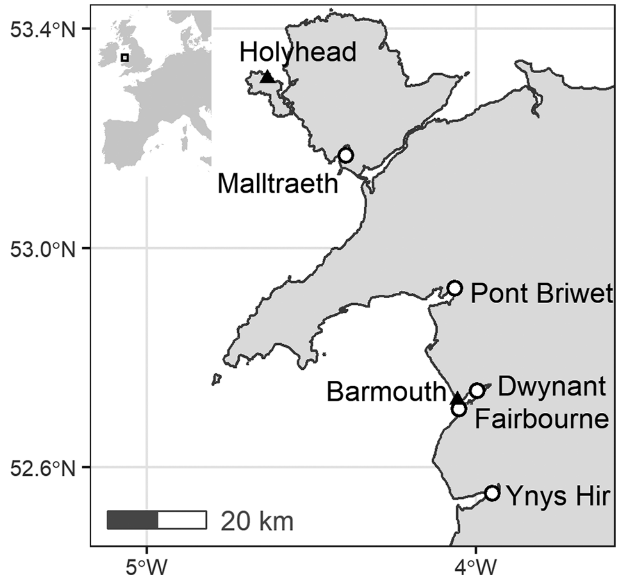

Fig. 2. The 5 selected study sites (circles) and tidal gauges (triangles) on the west coast of Wales, UK

This metric is a proxy to edge amount, as we did not measure the length of creek 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 the maximum amount of 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 5 study sites from 1 June to 21 October 2020. Each marsh was visited once in summer and once in autumn, which are the 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 variations in tidal amplitude between survey days, sampling took place around spring tide (Table 1). We used 3 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. S1A). To capture highly mobile fish >5 cm in total length, we deployed 4 fyke nets of 2 different sizes: 3 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. S1B). Small fyke nets were set in creeks less than 3 m in width. The large fyke had a 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. S1C). 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 where 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 9 (crab traps, n = 5; small fyke, n = 3; 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. and *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 2 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 local conditions allowed; generally, this 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 & 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

All statistical analyses and plots were generated in R version 4.1.1 (R Core Team 2021). Linear models were run using functions 'glmer' and 'lmer' of package 'lme4' (Bates et al. 2015). Plots were done with package 'ggplot2' (Wickham 2016).

2.4.1. Abundance

From the biological sampling, we derived 4 indicators of the abundance of fishes and crustaceans: number of crabs caught in a trap per tidal cycle (12 h), 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 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 a 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 a 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 ΔAICc, 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 $\Delta AICc > 2$. We also calculated the AICc weight of models, 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% CIs.

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 a random factor, and its inclusion in the model was assessed following Zuur (2009). For each response variable, 4 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. Catch composition

Salt marshes were used by 4 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, common goby and brown shrimp were the dominant species in all salt marshes. Other species caught with seine net were much less abundant (Table 2). Shrimp caught by the seine net included brown shrimp and *Palaemonetes varians* (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 bass were found at 4 of the 5 salt marshes in seine net catches. Dwynant had a higher abundance of common goby and brown shrimp, but it was also the salt marsh with the 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 catching 5 or more species; most of the hauls in other marshes only caught 2–4 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 3 species per salt marsh were caught with fykes (Table 2), and most fyke deployments caught less than 3 fish m^{-2}.

Table 2. Mean (±SE) catches for the 3 fishing methods and 5 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. (–) species not caught at that 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)					
Crustaceans (none 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
Fish					
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

Sea bass and flounder *Platichthys flesus* were the only 2 species caught in both seine and 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 those caught by fykes were 116–450 mm. Total length of flounders caught by the seine net was between 13 and 140 mm, while 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 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 the lowest water exchange (Table 3, Fig. 3).

The best model explaining total shrimp abundance only retained water exchange as an 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).

Table 3. Parameter estimates and 95 % CIs 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*. Explanatory variables with CIs excluding zero are in **bold**. See Section 2.4 for model details

Response variable	Explanatory variable	Parameter estimate ± SE	Lower CI	Upper CI
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**

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 CIs 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 the highest water exchange being 51 % smaller than those at the highest water exchange site (Fig. 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 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 fish and crustacean 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 represents 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 be explained by larger intertidal areas granted by higher water exchange operating

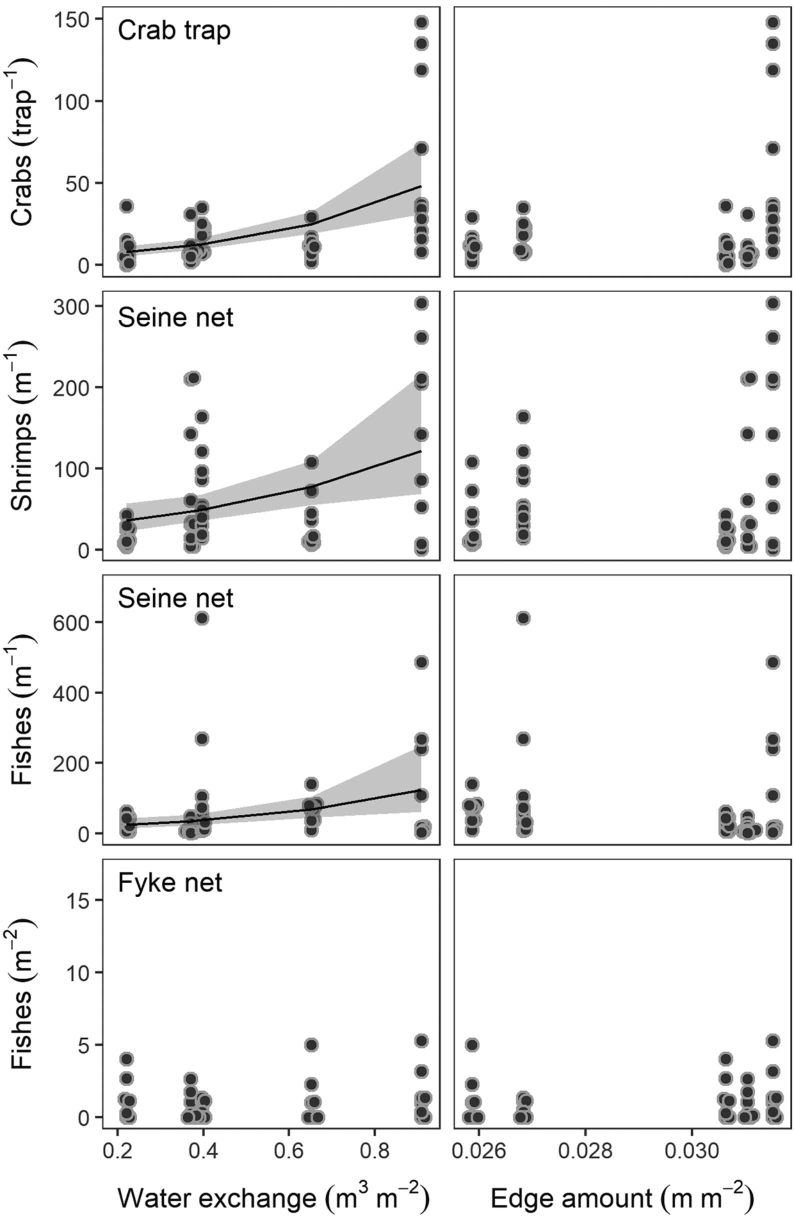

Fig. 3. Relations of total crab (traps), shrimp (seine net) and fish (seine and fyke) catches with marsh edge amount and water exchange. Dots: catches; black lines: best model predictions; grey shading: SE

through the provision of increased resources, such as foraging or refuge 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 the microtidal systems of the 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 has 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 a refuge. In the UK, the lower marsh is dominated by *S.* (*S.*) *anglica* in a sward-like structure with high stem density (130–1800 stems m^{-2}; e.g. Tempest et al. 2015) which may prevent fish and benthic invertebrates from using this area of the marsh in the same way. In the eastern USA, differences in salt marsh stem density and height did not affect fish incursion into the vegetated

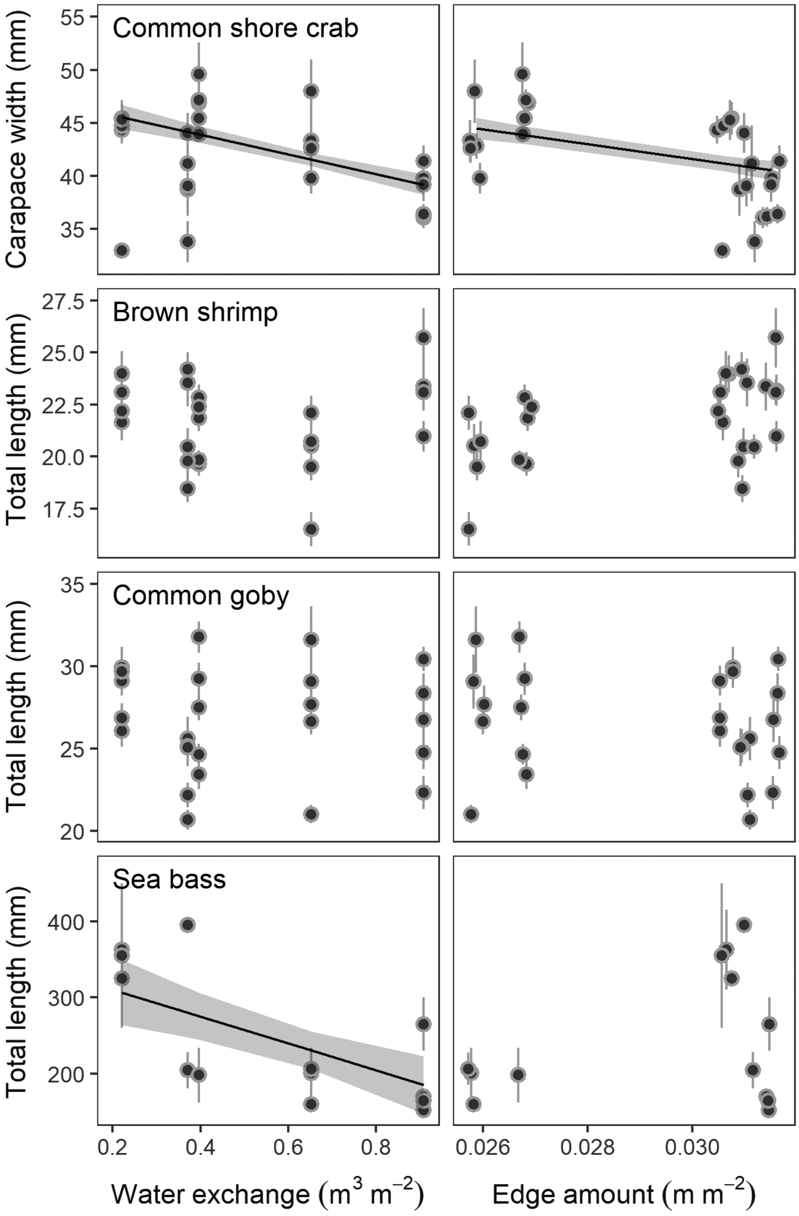

Fig. 4. Mean sizes of individuals relative to edge amount and water exchange. Dots and vertical lines show the mean ± SE individual size for sampling locations within marshes. For common shore crab *Carcinus maenas* and brown shrimp *Crangon crangon*, all individuals caught were considered; for common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

salt marsh (Ziegler et al. 2021b), but the question remains if stem density becomes a limiting factor for fish to enter the vegetated marsh at the higher densities found in the UK.

Animal size was only affected by the hydrogeomorphic variables assessed for 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 had 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 bass individuals and conclude that differences in the mean size of this species were mainly due to a higher proportion of younger individuals (Fig. S3). This implies that sea basses are not necessarily growing faster at shallower salt marshes; rather, that older, probably higher trophic level sea basses use 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 benefit from 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, some confounding effects may have 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 river 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 2 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 range from 0.002–0.15 m m^{-2} (Minello & Rozas 2002, Kneib 2003). Comparisons of numerical values between studies should be taken with care as these numbers were obtained through different methods. Considering this difference, it is likely that the relationships that we found (and did not find) will differ 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 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 in micro and meso tidal systems but not in macrotidal systems such as those studied here. This would mean that edge amount might still be important for salt marshes in 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 for salt marshes in which the vegetated flat is rarely flooded, such as those in the rest of northern Europe, Australia and South America (e.g. Laffaille et al. 2000, Saintilan et al. 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 the creeks' central paths. Although these 2 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 central path of the creek 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 saltmarsh functions (Fagherazzi et al. 2012), including habitat provision for aquatic species (Colombano et al. 2021b). Without better quantitative assessments of individual marshes, the threat posed by climate change could be severe. There are numerous examples around the globe of salt marsh being lost in a matter of years under various different tidal regimes (e.g. Day et al. 1998, Kennish 2001, van der Wal & Pye 2004, Gu et al. 2018). Sea level rise pushes salt marshes landwards while artificial structures on the coastline prevent salt marsh migration in a process called coastal squeezing (Doody 2013). Coastal squeeze in turn results in the inundation and loss of formally mid-marsh areas vital for hydrodynamic functioning, as they contain complex topography, shallows and hillocks, along with relatively low distances to creeks (Lawrence et al. 2018). Increased storminess, and 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 greater depths and higher energy environments result 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 salt marsh 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) may also be different. This information 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.

Acknowledgements. We thank Harriet Lincoln and Samantha Simpson for assistance in fish identification. We kindly thank Natural Resources Wales, The National Trust and RSPB Ynys-Hir for granting access to the sites. This project received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 663830.

LITERATURE CITED

Allen JR (2000) Morphodynamics of Holocene salt marshes: a review sketch from the Atlantic and southern North Sea coasts of Europe. Quat Sci Rev 19:1155–1231

Allen DM, Haertel-Borer SS, Milan BJ, Bushek D, Dame RF (2007) Geomorphological determinants of nekton use of intertidal salt marsh creeks. Mar Ecol Prog Ser 329:57–71

Baker R, Fry B, Rozas LP, Minello TJ (2013) Hydrodynamic regulation of salt marsh contributions to aquatic food webs. Mar Ecol Prog Ser 490:37–52

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:i01 doi:10.18637/jss.v067.i01

Bij de Vaate I, Brückner MZM, Kleinhans MG, Schwarz C (2020) On the impact of salt marsh pioneer species-assemblages on the emergence of intertidal channel networks. Water Resour Res 56:e2019WR025942

Boorman L (2003) Saltmarsh review. An overview of coastal saltmarshes, their dynamic and sensitivity characteristics for conservation and management. JNCC Report No. 334. Joint Nature Conservation Committee, Peterborough

Bradley M, Nagelkerken I, Baker R, Sheaves M (2020) Context dependence: a conceptual approach for understanding the habitat relationships of coastal marine fauna. Bioscience 70:986–1004

Brodersen J, Nilsson PA, Ammitzbøll J, Hansson LA, Skov C, Brönmark C (2008) Optimal swimming speed in head currents and effects on distance movement of winter-migrating fish. PLOS ONE 3:e2156

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York, NY

Cattrijsse A, Hampel H (2006) European intertidal marshes: a review of their habitat functioning and value for aquatic organisms. Mar Ecol Prog Ser 324:293–307

Cattrijsse A, Dankwa HR, Mees J (1997) Nursery function of an estuarine tidal marsh for the brown shrimp *Crangon crangon.* J Sea Res 38:109–121

Cavraro F, Zucchetta M, Malavasi S, Franzoi P (2017) Small creeks in a big lagoon: the importance of marginal habitats for fish populations. Ecol Eng 99:228–237

Colombano DD, Handley TB, O'Rear TA, Durand JR, Moyle PB (2021a) Complex tidal marsh dynamics structure fish foraging patterns in the San Francisco Estuary. Estuar Coast 44:1604–1618

Colombano DD, Litvin SY, Ziegler SL, Alford SB and others (2021b) Climate change implications for tidal marshes and food web linkages to estuarine and coastal nekton. Estuar Coast 44:1637–1648

Crothers JH (1968) The biology of the shore crab *Carcinus maenas* (L.). 2. The life of the adult crab. Field Stud 2: 579–614

Darnell TM, Smith EH (2004) Avian use of natural and created salt marsh in Texas, USA. Waterbirds 27:355–361

Day JW Jr, Scarton F, Rismondo A, Are D (1998) Rapid deterioration of a salt marsh in Venice Lagoon, Italy. J Coast Res 14:583–590

Dijkema KS (ed) (1984) Salt marshes in Europe. European Committee for the Conservation of Nature and Natural Resources, Strasbourg

Doody JP (2013) Coastal squeeze and managed realignment in southeast England, does it tell us anything about the future? Ocean Coast Manage 79:34–41

EDINA LIDAR Digimap Service (2016) Lidar composite digital terrain model Wales 1 m resolution. https://digimap.edina.ac.uk/

Fagherazzi S, Furbish DJ (2001) On the shape and widening of salt marsh creeks. J Geophys Res Oceans 106:991–1003

Fagherazzi S, Kirwan ML, Mudd SM, Guntenspergen GR and others (2012) Numerical models of salt marsh evolution: ecological, geomorphic, and climatic factors. Rev Geophys 50:RG1002

Friese JDS, Temming A, Dänhardt A (2021) Another piece of the puzzle: abiotic habitat properties of salt-marsh creeks benefit small fishes and crustaceans. Estuar Coast Shelf Sci 260:107498

Friess DA, Krauss KW, Horstman EM, Balke T, Bouma TJ, Galli D, Webb EL (2012) Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. Biol Rev Camb Philos Soc 87:346–366

Green BC, Smith DJ, Earley SE, Hepburn LJ, Underwood GJ (2009) Seasonal changes in community composition and trophic structure of fish populations of five salt marshes along the Essex coastline, United Kingdom. Estuar Coast Shelf Sci 85:247–256

Gu J, Luo M, Zhang X, Christakos G, Agusti S, Duarte CM, Wu J (2018) Losses of salt marsh in China: trends, threats and management. Estuar Coast Shelf Sci 214:98–109

Hampel H, Cattrijsse A (2004) Temporal variation in feeding rhythms in a tidal marsh population of the common goby *Pomatoschistus microps* (Kroyer, 1838). Aquat Sci 66: 315–326

Hampel H, Cattrijsse A, Elliott M (2005) Feeding habits of young predatory fishes in marsh creeks situated along the salinity gradient of the Schelde estuary, Belgium and The Netherlands. Helgol Mar Res 59:151–162

Hayward PJ, Ryland JS (eds) (2012) Handbook of the marine fauna of North-West Europe (reprint with corrections). Oxford University Press, Oxford

Himes-Cornell A, Pendleton L, Atiyah P (2018) Valuing ecosystem services from blue forests: a systematic review of the valuation of salt marshes, sea grass beds and mangrove forests. Ecosyst Serv 30:36–48

Kennish MJ (2001) Coastal salt marsh systems in the US: a review of anthropogenic impacts. J Coast Res 17:731–748

Kneib RT (2003) Bioenergetic and landscape considerations for scaling expectations of nekton production from intertidal marshes. Mar Ecol Prog Ser 264:279–296

Kneib RT, Wagner SL (1994) Nekton use of vegetated marsh habitats at different stages of tidal inundation. Mar Ecol Prog Ser 106:227–238

Ladd CJT, Duggan-Edwards MF, Bouma TJ, Pagès JF, Skov MW (2019) Change in saltmarsh extent for six regions across Great Britain (1846–2016). NERC Environmental Information Data Centre. https://doi.org/10.5285/03b62fd0-41e2-4355-9a06-1697117f0717

Laffaille P, Feunteun E, Lefeuvre JC (2000) Composition of fish communities in a European macrotidal salt marsh (the Mont Saint-Michel Bay, France). Estuar Coast Shelf Sci 51:429–438

Laffaille P, Lefeuvre JC, Schricke MT, Feunteun E (2001) Feeding ecology of 0-group sea bass, *Dicentrarchus labrax*, in salt marshes of Mont Saint Michel Bay (France). Estuaries 24:116–125

Lawrence PJ, Smith GR, Sullivan MJP, Mossman HL (2018) Restored saltmarshes lack the topographic diversity found in natural habitat. Ecol Eng 115:58–66

Leslie T, James NC, Potts WM, Rajkaran A (2017) The relationship between habitat complexity and nursery provision for an estuarine-dependent fish species in a permanently open South African Estuary. Estuar Coast Shelf Sci 198:183–192

Lesser JS, Bechtold CA, Deegan LA, Nelson JA (2020) Habitat decoupling via saltmarsh creek geomorphology alters connection between spatially-coupled food webs. Estuar Coast Shelf Sci 241:106825

Liquete C, Piroddi C, Drakou EG, Gurney L, Katsanevakis S, Charef A, Egoh B (2013) Current status and future prospects for the assessment of marine and coastal ecosystem services: a systematic review. PLOS ONE 8:e67737

Meynecke JO, Lee SY, Duke NC (2008) Linking spatial metrics and fish catch reveals the importance of coastal wetland connectivity to inshore fisheries in Queensland, Australia. Biol Conserv 141:981–996

Minello TJ, Rozas LP (2002) Nekton in Gulf coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. Ecol Appl 12:441–455

Minello TJ, Zimmerman RJ, Medina R (1994) The importance of edge for natant macrofauna in a created salt marsh. Wetlands 14:184–198

Minello TJ, Able KW, Weinstein MP, Hays CG (2003) Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. Mar Ecol Prog Ser 246:39–59

Minello TJ, Rozas LP, Baker R (2012) Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. Estuar Coast 35:501–514

Moffett KB, Gorelick SM (2016) Alternative stable states of tidal marsh vegetation patterns and channel complexity. Ecohydrology 9:1639–1662

Möller I, Spencer T (2002) Wave dissipation over macrotidal saltmarshes: effects of marsh edge typology and vegetation change. J Coast Res 36:506–521

Nelson JA, Deegan L, Garritt R (2015) Drivers of spatial and temporal variability in estuarine food webs. Mar Ecol Prog Ser 533:67–77

Paterson AW, Whitfield AK (2003) The fishes associated with three intertidal salt marsh creeks in a temperate southern African estuary. Wetlands Ecol Manage 11:305–315

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Rendón OR, Garbutt A, Skov M, Möller I and others (2019) A framework linking ecosystem services and human well-being: saltmarsh as a case study. People Nat 1: 486–496

Rozas LP, Caldwell P, Minello TJ (2005) The fishery value of salt marsh restoration projects. J Coast Res (Spec Issue) 40:37–50

Ruiz GM, Hines AH, Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar Ecol Prog Ser 99:1–16

Saintilan N, Rogers K, Howe A (2009) Geomorphology and habitat dynamics. In: Saintilan N (ed) Australian saltmarsh ecology. CSIRO publishing, Collingwood, p 53–74

Simenstad CA, Hood WG, Thom RM, Levy DA, Bottom DL (2002) Landscape structure and scale constraints on restoring estuarine wetlands for Pacific Coast juvenile fishes. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Springer, New York, NY, p 597–630

Tempest JA, Möller I, Spencer T (2015) A review of plant-flow interactions on salt marshes: the importance of vegetation structure and plant mechanical characteristics. WIREs Water 2:669–681

Thiel M, Dernedde T (1994) Recruitment of shore crabs *Carcinus maenas* on tidal flats: mussel clumps as an important refuge for juveniles. Helgol Meeresunters 48: 321–332

Trocki CL, Paton PWC (2006) Assessing habitat selection by foraging egrets in salt marshes at multiple spatial scales. Wetlands 26:307–312

Valiñas MS, Molina LM, Addino M, Montemayor DI, Acha EM, Iribarne OO (2012) Biotic and environmental factors affect Southwest Atlantic saltmarsh use by juvenile fishes. J Sea Res 68:49–56

van der Wal D, Pye K (2004) Patterns, rates and possible causes of saltmarsh erosion in the Greater Thames area (UK). Geomorphology 61:373–391

Wasson K, Raposa K, Almeida M, Beheshti K and others (2019) Pattern and scale: evaluating generalities in crab distributions and marsh dynamics from small plots to a national scale. Ecology 100:e02813

Webb SR, Kneib RT (2002) Abundance and distribution of juvenile white shrimp *Litopenaeus setiferus* within a tidal marsh landscape. Mar Ecol Prog Ser 232:213–223

Wiberg PL, Fagherazzi S, Kirwan ML (2020) Improving predictions of salt marsh evolution through better integration of data and models. Annu Rev Mar Sci 12:389–413

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, New York, NY. https://ggplot2.tidyverse.org

Wu Q (2019) whitebox: 'WhiteboxTools' R frontend. R package version 0.1.0. https://github.com/giswqs/whiteboxR

Zengel S, Mendelssohn I, Graham S, Fleeger JW, Johnson DS, Deis DR (2020) Synthesis of wetland vegetation response to oiling. Gulf of Mexico Research Initiative Information and Data Cooperatibe (GRIIDC), Harte Research Institute, Texas A&M University, Corpus Christi, TX

Ziegler SL, Able KW, Fodrie FJ (2019) Dietary shifts across biogeographic scales alter spatial subsidy dynamics. Ecosphere 10:e02980

Ziegler SL, Baker R, Crosby SC, Colombano DD and others (2021a) Geographic variation in salt marsh structure and function for nekton: a guide to finding commonality across multiple scales. Estuar Coast 44:1497–1507

Ziegler SL, Miller MD, Smith CS, Fodrie FJ (2021b) Abiotic cycles mediate the strength of cross-boundary consumption within coastal food webs. Estuar Coast 44: 1147–1156

Zimmerman RJ, Minello TJ, Rozas LP (2002) Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Springer, New York, NY, p 293–314

Zuur AF (ed) (2009) Mixed effects models and extensions in ecology with R. Springer, New York, NY

Editorial responsibility: Jana Davis,
Annapolis, Maryland, USA
Reviewed by: S. L. Ziegler and 1 anonymous referee

Submitted: January 6, 2022
Accepted: June 30, 2022
Proofs received from author(s): August 5, 2022