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Suitability of compensatory saltmarsh habitat for feeding and diet of multiple estuarine fish species

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Abstract

Saltmarsh provides essential fish feeding and nursery habitat but has globally declined by 50%. We used a statistical block design to compare fish feeding activity within human-engineered or "re-aligned" saltmarsh to established saltmarsh. Linear and multivariate modelling highlighted that Thinlip Mullet (*Chelon ramada*) and European Bass (*Dicentrarchus labrax*) feeding rates were 16% and 31% lower within re-aligned than established saltmarshes, whereas Gobies (*Pomatoschistus* spp.) fed at the same rate as in both habitats. Analysis of European bass and Goby gut contents highlighted that important detritivorous prey species were up to 85.6% lower in re-aligned sites. Lower vegetation density may have negatively affected the feeding ecologies of fishes within re-aligned sites. However, due to the ecological value and potential for further improvement or habitat development, continued assessment of the beneficial effects of re-aligned sites for fisheries and net gain perspectives is needed.

KEYWORDS

essential fish habitat, habitat restoration, net gain, nursery, Re-aligned habitat, saltmarsh

1 | INTRODUCTION

Globally, estuaries provide important nursery habitats for commercially and ecologically important fishes (Stamp et al., 2022; Swadling et al., 2022). In particular, saltmarshes are highly productive habitats (Bouchard & Lefeuvre, 2000; Nixon, 1980), which are known to provide predation refuge (Allen et al., 1994; West & Zedler, 2000) and critical feeding opportunities for many species (Fonseca et al., 2011; Green et al., 2012; Kelley, 1988; Kneib, 1997; Laffaille et al., 2001; Swadling et al., 2022). The importance of saltmarsh as a feeding habitat for juvenile fish is well illustrated by Laffaille et al. (2001) & Fonseca et al. (2011), who reported that on average 33%–38% of juvenile European Bass (*Dicentrarchus labrax*) entering saltmarsh have empty stomachs, but only 2%–7% were empty when leaving. Similar results have also been reported for Thinlip Mullet (*Chelon ramada*) where it is estimated that in the brief 1–2 h tidal submersion of saltmarsh, they are capable of consuming 7%–8% of their total body weight (Laffaille et al., 2001).

Despite estuaries providing important habitat for many fish species, they are often modified by anthropogenic activities (Airoldi et al., 2008; Lotze et al., 2006; Stamp et al., 2022), either directly by removal or adaptation of intertidal habitat or agricultural activities (e.g. sheep grazing on saltmarsh Laffaille et al., 2000) or indirectly by management of adjacent land (e.g. agriculture, Almeida et al., 2014). Globally, approximately 50% of saltmarsh habitat has been lost or degraded (Adam, 2002; Barbier et al., 2011). More specifically, up to 85% of UK estuaries have been affected by historic land reclamation, with loss of intertidal habitat ranging from 50 to 64% (Attrill et al., 1999; Mclusky et al., 1992). Historic habitat loss is compounded by issues such as sea level rise, coastal squeeze and continuing human development of estuaries (e.g. port developments), which is predicted to result in 2% further loss of saltmarsh habitat per year till 2050 (Colclough et al., 2003; Dixon et al., 1998).

Over the past 20–30 years construction of compensatory habitat, or managed re-alignment, has increasingly been used to mitigate saltmarsh loss (Mossman et al., 2012). Managed re-alignment is a coastal management technique whereby sea defences are actively breached and tidal water is encouraged to flood low-lying coastal land (Lawrence et al., 2018). Alternatively, managed retreat may also occur where sea defences naturally breach and a decision is made to not re-inforce or repair damaged sea defences (Mossman et al., 2012). These processes create new intertidal areas, in which saltmarsh or mudflat may develop (Lawrence et al., 2018; Mossman et al., 2012). The construction of these sites is primarily driven by conservation legislation (e.g. the Habitat Directive, EU Council Directive 92/43/EEC & UK statutory instrument, 2017, 1012) but may also provide additional benefits such as coastal flood defence (Esteves, 2013; Kentula, 2000).

The benefits of coastal wetlands, such as saltmarsh, from a fishery and flood defence standpoint, are now being recognised as part of coastal and shoreline management plans in regions such as Australia (Burchett et al., 1999; Creighton et al., 2017), the United States (Byers & Chmura, 2007) and Europe (Esteves, 2013). In which national and regional authorities have committed to protect, restore and maintain saltmarsh via legislative instruments (e.g. USA: Sustainable Fisheries Act 1996 and Coastal Zone Management Act 1972; Australia: Commonwealth EPBC Act 2009, Europe: EU Council Directive 92/43/EEC & UK statutory instrument, 2017, 1012). In the UK specifically, authorities committed to "re-align" 10% of the coastline by 2030 and 15% by 2060 (CASB, 2013; Esteves, 2013). As a result, the number of restorative saltmarsh projects, including managed re-alignment, are likely to increase and the importance of these novel habitats from a fisheries perspective is of growing interest (Colclough et al., 2003; Fonseca et al., 2011).

Despite the common and growing use of managed re-alignment or managed retreat, it has been estimated that even after a period of 50–100 years these novel habitats do not resemble their natural/established counterparts (Garbutt et al., 2006; Mossman et al., 2012). In particular, within Northern Europe re-aligned sites often lack the biological complexity of established saltmarsh and are generally characterised by pioneer plant communities (Mossman et al., 2012). This is thought to be a result of the macrotidal environment combined with construction designs, in which re-aligned sites generally have lower topographic complexity and lower drainage creek density than established saltmarsh (Lawrence et al., 2018). Furthermore, these sites often retain compacted soil (characteristic of prior agricultural land use) with poor nutrient re-cycling (Spencer et al., 2008). It has therefore been argued that re-aligned saltmarsh does not typically provide habitats with comparable biological characteristics to established saltmarsh (Mossman et al., 2012).

Despite concerns about the comparability of re-aligned and established saltmarsh, these sites may provide valuable feeding opportunities for a wide variety of commercially and ecologically important fish (Colclough et al., 2005; Fonseca et al., 2011; Nunn et al., 2016; Stamp et al., 2022). Within the context of historic and modern habitat loss in estuaries, re-aligning the coastline to create new habitat is particularly important because without the process of re-aligning the coastline to create new habitat, feeding opportunities for coastal fishes may be reduced (Mclusky et al., 1992; Rochette et al., 2010). Even if these sites do not fully mitigate for historic habitat loss (Best et al., 2007), and while habitat loss on fish production remains difficult to quantify (Mclusky et al., 1992; Rochette et al., 2010), re-aligned sites likely provide fish feeding opportunities that would otherwise be absent.

The habitat provision that is required for feeding ecologies and the growth of dependent fishes is uncertain (Levin & Stunz, 2005). In particular, these sites are likely to host many juveniles (0–2 years) (Colclough et al., 2005; Fonseca et al., 2011; Nunn et al., 2016). Increased growth and survival of these age classes are likely to disproportionately affect long-term population dynamics (Levin & Stunz, 2005). Therefore, for commercially or ecologically important species, the effects of habitat restoration must be documented to inform conservation and fisheries management policies.

We sought to determine whether fish feeding rates and foraging/diet differed between re-aligned and established saltmarsh habitats. To achieve our objective, we compared feeding rates and foraging/diet of common estuarine fishes in re-aligned and established sites within three sites in the UK. Three species were selected based on their widespread distribution across Europe: European bass (*Dicentrarchus labrax*), Thinlip Mullet (*Chelon ramada*) and Common/Sand Goby (*Pomatoschistus* spp.).

2 | METHODS

2.1 | Sample sites

Using a statistical block design, juvenile fishes were collected at three re-aligned sites that were paired with nearby natural or established saltmarsh sites across the United Kingdom (Figure 1, Table 1). Fish sampling at paired re-aligned: established saltmarsh sites occurred over the same spring tidal cycle. This design allowed standardisation of environmental conditions, such as tidal inundation and weather, across both re-aligned and established saltmarshes at the time of sampling. All surveys were conducted during large spring tidal cycles, when complete tidal inundation of the marsh flat ranged from 1 to 2 h. Re-aligned sites were selected based on their large spatial extent, wide geographical distribution across the United Kingdom and relative age since the first tidal inundation. Established and re-aligned saltmarsh sites were assumed to be independent because fish could not feed within both sites during the same tidal inundation, and fish capture locations were either separated by several

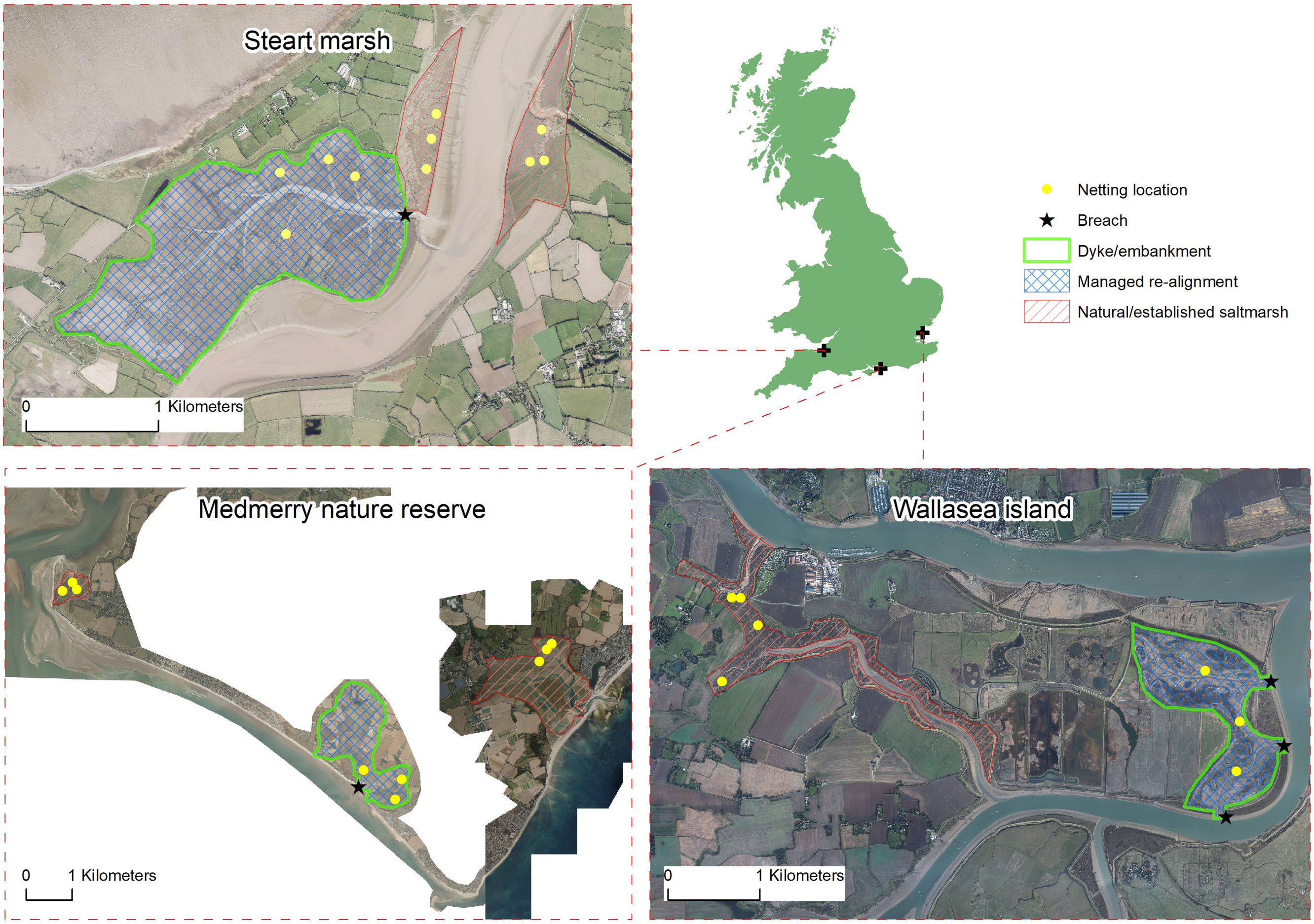

FIGURE 1 Juvenile fish sampling locations within re-aligned and established saltmarsh at Steart Marsh (sampled: 05/2017, 08/2017 & 06/2018), Medmerry Nature Reserve (sampled: 06/2017) and Wallasea Island (07/2017). Further site details are provided: Table 1. All sampling was conducted in the United Kingdom.

TABLE 1 Saltmarsh name (Medmerry Nature Reserve, Steart Marsh and Wallasea Island), sampling month/year, habitat type (RS = re-aligned saltmarsh; ES = established saltmarsh), latitude and longitude, tidal range, surface area and age of each re-aligned saltmarsh site when sampled in 2017–2018

Survey	Sampling dates	Habitat	Latitude	Longitude	Tidal range (m ACD)	Area (km^2)	Year of tidal inundation
Medmerry Nature Reserve	06/2017	RS	50.751	−0.8244	0.6 to 5.1	3.02	2013
		ES	50.78217	−0.91163		0.39	-
		ES	50.7619	−0.760567		2.93	-
Steart Marsh	05/2017, 08/2017, 06/2018	RS	51.2028	−3.0337	−0.2 to 13	2.62	2014
		ES	51.20568	−3.03005		0.41	-
		ES	51.20665	−3.015694		0.37	-
Wallasea Island	07/2017	RS	51.6046	0.859	0.2 to 5.7	1.65	2015
		ES	51.61569	0.782941		0.71	-

Note: All sampling was within the United Kingdom.

kilometres or adjoining re-aligned and established marshes were separated by an embankment and did not share creek networks.

At each saltmarsh, juvenile fishes were captured in 2.75-m-long winged fyke nets with two 5-m leaders and 53-cm openings. Mesh sizes were 10 mm in the leaders and 6.5–8 mm in the main body. A single net was deployed in at least three representative drainage channels distributed across each site (Figure 1). Creeks were selected based on expert opinion and the proportion of mud and vegetation within and surrounding each creek. Each net was deployed with leaders facing landward, thereby allowing fish to swim over the net on the flooding tide to feed within the saltmarsh, and then be captured on the ebbing tide.

Fyke nets were deployed at low tide and positioned to be fully immersed at mid and high tide but fully exposed to air at low tide. Each net was checked at low tide following each tidal inundation (referred to as a net deployment), for a minimum of three tidal inundations at each site. From each net deployment, a maximum of 30 age-0 individuals of each target species or taxa were randomly collected. Individual fish were immediately euthanized via overdose with Tricaine Methanesulfonate (MS-222), followed by the destruction of the brain (ASPA, 1986). Following confirmation of death, all specimens were stored in labelled containers filled with 80% Industrial Methylated Spirit (IMS) for later stomach content analysis in the laboratory.

Target species were selected because they are abundant in estuaries across Northern Europe (Laffaille et al., 2002; Leitão et al., 2006; Pickett & Pawson, 1994). European Bass and Common/Sand Goby are generalist predators (Leitão et al., 2006; Pickett & Pawson, 1994), whereas Thin Lipped Mullet feed predominantly on benthic phytoplankton and detritus (Almeida, 2003; Kasımoğlu & Yılmaz, 2012; Laffaille et al., 2002; Sá et al., 2006). These species therefore represent different feeding modes to compare habitat suitability between re-aligned and established saltmarshes.

2.2 | Gut content identification

Each fish was identified to species or genus, length measured (total length - mm) and weighed (g) using a digital balance. The full digestive tract (gut) was removed and weighed separately. The gut was dissected under light microscopy, and contents were enumerated and identified to the lowest possible taxon. Common (*Pomatoschistus microps*) and Sand Goby (*Pomatoschistus minutus*) were grouped as Common/Sand Goby, as they are difficult to distinguish and previous research suggested their feeding ecologies do not differ (Leitão et al., 2006).

2.3 | Data analysis

Within each survey, the length frequencies of each species were compared between habitats using a Kruskal–Wallis test. Fish capture rates were too low to compare feeding activity between creeks or tidal inundations among sites. Therefore, fish were pooled within "Re-aligned saltmarsh" or "Established saltmarsh" habitats.

2.3.1 | Feeding rate

The number of fish with empty stomachs was calculated for each species in each site, as a percentage of the total caught (Vacuity Index, V%). As a measure of foraging success, Gut weight (GW) was related to Total Length (TL) across re-aligned and established saltmarsh habitats and surveys (re-aligned site name and survey date), using a generalised linear model with a Gamma distribution and log link (R package "stats" v3.6.1; R Core Team, 2019). Statistical assumptions were visually assessed using model diagnostics (i.e. QQplot, residuals vs fitted plot).

For each fish species or genus, the most complex model included all variables and interactions. Each interaction and/or variable was then sequentially removed until the null model with no fixed effects was fitted. Models were ranked using Akaike Information Criterion (adjusted for small sample size -AICc), and the model with the lowest AICc score was selected. Models with AICc scores ≤2 and with the fewest fixed effects were selected (Zuur et al., 2013). Site-specific differences between re-aligned sites (e.g. tidal range or prevailing weather conditions), and their effect on foraging success were assessed by including "survey" as a fixed effect, the predictive ability of this model was then ranked against other models, which did not include survey using AICc. Analyses were performed with R version 3.6.0 (R Core Team, 2019).

2.3.2 | Diet

Fish foraging/diet between re-aligned and natural saltmarsh was compared for European Bass and Common/Sand Goby. Thinlip Mullet were not included because their diet was difficult to accurately identify (dominated by benthic phytoplankton and detritus). Diet data were converted to a Bray Curtis similarity matrix, with a dummy variable (1) to account for fish with empty stomachs (Clarke et al., 2006). Data were not transformed prior to analysis. A 2-way crossed multivariate PERMANOVA, and further pairwise testing, was used to test for differences in the diet of each species between surveys and habitats. All PERMANOVA tests were analysed using the statistical software PRIMER-E 7.0.13 with PERMANOVA+. Nonmetric Multi-Dimensional Scaling (nMDS) was used to visually illustrate the variability in diets between habitats and surveys. The average abundance of dominant prey species (>1% of overall abundance within stomachs) was used to identify prey species that drove differences in foraging/diet between habitats and surveys. Site-specific differences between re-aligned sites (e.g. tidal range or prevailing weather conditions) and their effect on fish feeding ecology were assessed by including "survey" as a fixed effect.

3 | RESULTS

Five surveys were completed, with 180 net deployments across three re-aligned and established saltmarsh sites. Across all net deployments, 487 individual fish were retained for feeding-rate and diet analysis, including 157 Thinlip Mullet (age-0), 128 European Bass (age-0) and 202 Common/Sand Goby (multiple age groups). Capture rates of fish taxa varied among surveys (Table 2), so feeding rates and diet could not be compared among all fish taxa for each survey. Where sample size was sufficient and balanced between re-aligned and established saltmarsh sites feeding rate and diet were compared (Table 2).

TABLE 2 Number of Thinlip Mullet (*Chelon ramada*), European Bass (*Dicentrarchus labrax*) and Common/Sand Goby (*Pomatoschistus* spp.) captured (*n*) within each survey and saltmarsh habitat (Est = established, ReS = Re-aligned) within Medmerry Nature Reserve, Steart Marsh and Wallasea Island saltmarshes in the United Kingdom during 2017–2018.

		Thinlip Mullet		*European Bass*		*Common/Sand Goby*	
Survey	**Hab type**	***n***	**V%**	***n***	**V%**	***n***	**V%**
Medmerry Nature Reserve, June 2017	Est	**15**	**100%**	1	-	8	-
	Est	**31**	**100%**	14	-	-	-
	ReS	**21**	**100%**	2	-	-	-
Steart Marsh May 2017	Est	-	-	-	-	**52**	**32%**
	ReS	-	-	-	-	**19**	**68%**
Steart Marsh August 2017	Est	**30**	**4%**	**17**	**0%**	-	-
	Est	**30**	**5%**	**1**	**0%**	-	-
	ReS	**30**	**13.3%**	**40**	**2.5%**	13	-
Steart Marsh June 2018	Est	-	-	-	-	**27**	**41%**
	ReS	-	-	-	-	**37**	**32%**
Wallasea Island July 2017	Est	-	-	**53**	**7%**	**46**	**19.5%**
	ReS	-	-	**9**	**11%**	**30**	**23.3%**

Note: The percentage of fish with empty stomachs (V%) is shown. Surveys selected for further analysis are emboldened.

Average total length was 70.1 mm (±0.83 mm SE) for Thinlip Mullet, 49.7 mm (±0.77 mm SE) for European Bass and 40.2 mm (±0.29 mm SE) for Common/Sand Goby. Common/Sand Goby was larger in re-aligned habitats for Steart Marsh May 2017 and Wallasea Island July 2017. European Bass did not differ in size between re-aligned and established saltmarshes in Steart Marsh August 2017 & Wallasea Island July 2017. Thinlip Mullet were larger in re-aligned habitats within Steart Marsh August 2017, and smaller within re-aligned habitat within the Medmerry June 2017 (Figure 2).

3.1 | Feeding rates

Vacuity index (V%) varied among surveys, sites and species. Guts of all Thinlip Mullet were empty (V% = 100%) at both established and re-aligned sites within the Medmerry Nature Reserve in June 2017. For remaining surveys and species V% was higher at re-aligned sites except *Pomatoschistus* sp. at Steart Marsh in June 2018 (Table 2). Feeding rates differed between habitats and among surveys for Thinlip Mullet, between habitats for European Bass and among surveys for Common/Sand Goby (Table 3). In general, Thinlip Mullet and European Bass fed at higher rates in established saltmarsh sites. Specifically, the gut weight of Thinlip Mullet was 0.12 g (16%) higher within established saltmarsh sites than re-aligned sites within Medmerry June 2017 and Steart Marsh August 2017. Similarly, the gut weight of European Bass was 0.15 g (31%) higher within an established saltmarsh than a re-aligned saltmarsh within Steart Marsh August 2017 and Wallasea island July 2017. By contrast, gut weight of Common/Sand Goby did not differ between re-aligned and established saltmarsh sites at Steart Marsh May 2017 and June 2018, and Wallasea Island July 2017 but rather differed between surveys (Table 4; Figure 3).

3.2 | Diet

3133 individual prey items from 24 species/taxa were identified from guts of European Bass and Common/Sandy Goby. Diets of European Bass and Common/Sand Goby differed between surveys (Table 5). European Bass diets differed significantly between established and re-aligned saltmarsh sites and among all surveys (Table 5, Figure 4). Common/Sand Goby diets differed between established and re-aligned saltmarsh in Steart Marsh May 2017 ($t = 3.066$, $p < 0.001$) and Wallasea Island July 2018 ($t = 3.1425$, $p < 0.001$) but not in Steart Marsh June 2017 ($t = 0.731$, $p = 0.610$) (Table 5 and Figure 4).

In general, the same prey species were found in the guts of fish captured at both re-aligned and established saltmarsh sites, but their relative abundances varied. Notably, *Orchestia gammarellus and Sphaeromatidae* together accounted for 50% of all prey species but were 85.6% and 49.5%, respectively, lower in guts of fish captured within re-aligned saltmarsh sites across all surveys. *Delphacoides* spp. accounted for 14.1% of all prey consumed by European Bass within established saltmarsh within Steart Marsh August 2017 survey, these were nearly absent in European Bass diets in the re-aligned saltmarsh site. Bivalve siphons accounted for 19.7% of Common/Sand Goby diets in the re-aligned site within the Wallasea Island July 2017 survey but were 16% lower in the established saltmarsh site.

4 | DISCUSSION

Here, we found that re-aligned saltmarshes do provide a feeding habitat for economically and ecologically important fish species. The results suggest that while there are similarities in fish prey availability between re-aligned and established saltmarshes, differences in the

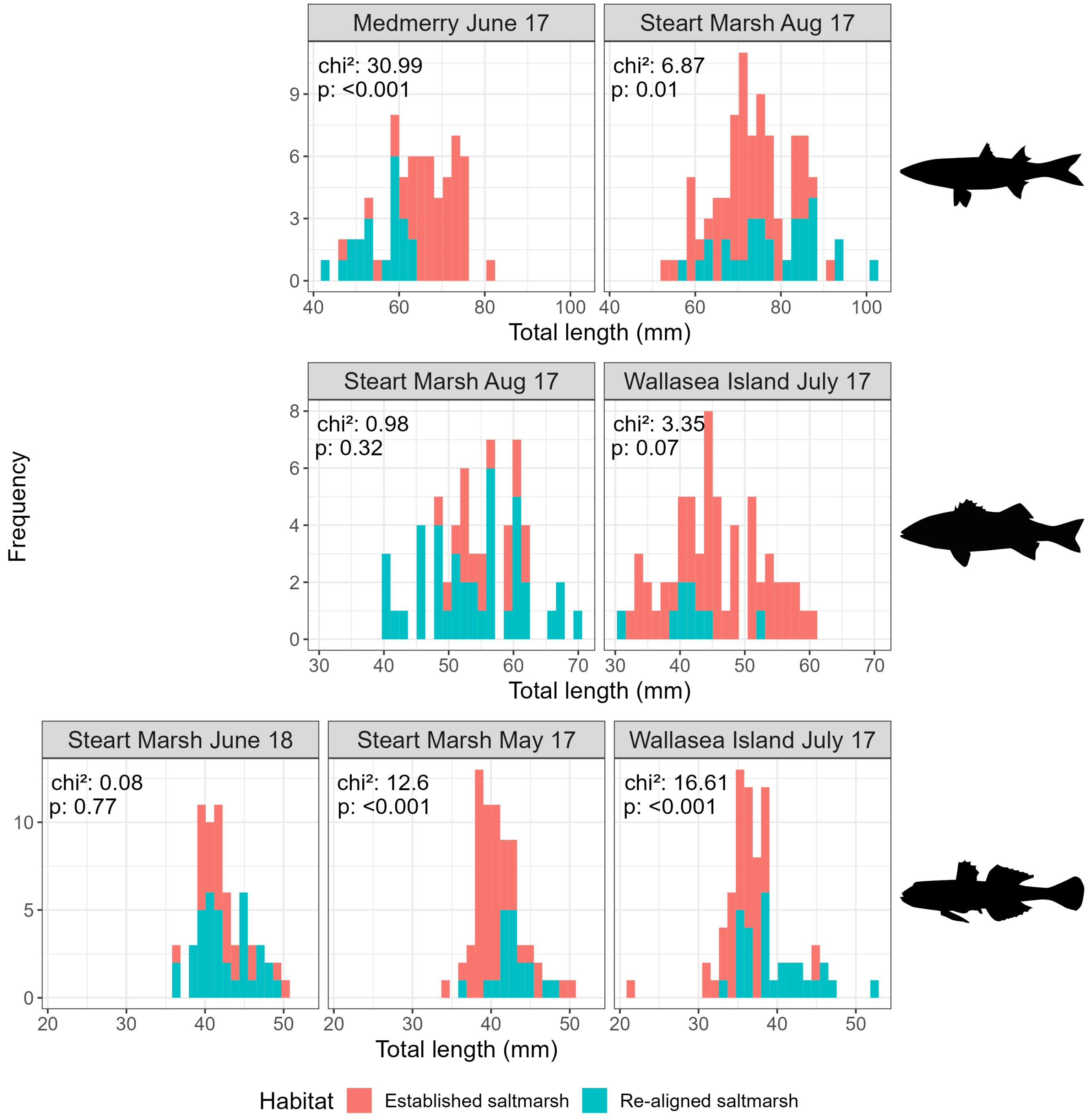

FIGURE 2 Length frequency of Thinlip Mullet (top), European Bass (middle) and Common/Sand Goby (bottom) sampled in established and re-aligned saltmarshes within Medmerry Nature Reserve, Steart Marsh and Wallasea Island saltmarshes in the United Kingdom during 2017–2018. Chi^2 test statistics comparing the total length of each species between habitats for each survey are shown in top right of each panel.

abundances of key prey species drive variation in feeding activity and foraging success within re-aligned and established saltmarsh sites.

4.1 | Benthic or detrital-feeding fish

Our results suggest that Thinlip Mullet feed less within re-aligned saltmarshes than within established saltmarshes. Typically, re-aligned saltmarshes are characterised by lower vegetation density, and open sections of unvegetated marsh flats are more common than in surrounding established saltmarsh (Mossman et al., 2012). Lower Thinlip Mullet feeding success within re-aligned sites may therefore be a result of increased predation risk caused by lower vegetation cover (Halpin, 2000). Low vegetation density also results in lower organic matter, plus higher pH and salinity within sediments (Kadiri et al., 2011), which has been shown to directly impact microbial

TABLE 3 Δ AICc scores for the top five candidate feeding-rate models for Thinlip Mullet (*Chelon ramada*), European Bass (*Dicentrarchus labrax*) and Common/Sand Goby (*Pomatoschistus* spp.) sampled in re-aligned and established saltmarshes at Medmerry Nature Reserve, Steart Marsh and Wallasea Island in the United Kingdom, 2017–2018.

Species	Fixed effects	AICc
Thinlip Mullet	**Gut weight ~ Total length + Habitat + Survey**	**0**
	Gut weight ~ Total length * Habitat * Survey	1
	Gut weight ~ Total length * Habitat + Survey	1.2
	Gut weight ~ Total length + Habitat * Survey	1.7
	Gut weight ~ Total length + Survey	9
European Bass	**Gut weight ~ Total length + habitat**	**0**
	Gut weight ~ Total length * Habitat + Survey	1
	Gut weight ~ Total length * Habitat * Survey	1.8
	Gut weight ~ Total length + Habitat + Survey	2.2
	Gut weight ~ Total length + Habitat * Survey	3.8
Common/Sand Goby	Gut weight ~ Total length + habitat * Survey	0
	Gut weight ~ Total length * Habitat * Survey	1.3
	Gut weight ~ Total length + Survey	**2**
	Gut weight ~ Total length + Habitat + Survey	3.4
	Gut weight ~ Total length * Habitat + Survey	3.9

Note: Selected models are highlighted by bold font.

TABLE 4 Model coefficients of selected feeding-rate models for European Bass (*Dicentrarchus labrax*), Thinlip Mullet (*Chelon ramada*) and Common/Sand Goby (*Pomatoschistus* spp.) sampled in re-aligned and established saltmarshes at Medmerry Nature Reserve, Steart Marsh and Wallasea Island in the United Kingdom, 2017–2018.

Fish species/taxa	Term	Estimate	Std. error	*T* value	*p* Value
TL Mullet	Intercept (Habitat: Established saltmarsh + Medmerry June 2017)	0.127	0.116	1.09	<0.01
	Total length (mm)	0.339	0.102	−3.31	<0.01
	Habitat: Re-aligned saltmarsh	0.055	0.0118	4.73	<0.01
	Survey: Steart Marsh August 2017	−5.44	0.507	−10.7	<0.01
European Bass	Intercept (Habitat: Established saltmarsh)	−0.374	0.078	−4.797	<0.01
	Total length (mm)	0.068	0.005	14.835	<0.01
	Habitat: Re-aligned saltmarsh	−5.492	0.226	−24.286	<0.01
Common/Sand Goby	Intercept	0.204	0.054	3.75	<0.01
	Total length (mm)	−0.178	0.05	−3.54	<0.01
	Survey: Steart March May 2017	0.043	0.003	16.8	<0.01
	Survey: Wallasea Island July 2017	−3.86	0.171	−22.6	0.275

biofilm communities within re-aligned sites (Burden et al., 2013). Thinlip Mullet, and grey mullets in general, are known to feed directly on biofilms and plant detritus (Carpentier et al., 2014), therefore, lower feeding rates may be a result of the lower plant density affecting the biofilm communities upon which Thinlip Mullet feed.

4.2 | Predator fish species

Our results suggest that habitats within re-aligned saltmarshes do not currently provide the same feeding opportunities for European Bass as established saltmarshes. Diets of European Bass within re-aligned saltmarshes sites contained fewer detritivores (e.g. *Orchestia gammarellus*, *Sphaeromatidae*; Marsden, 1976; Schrama et al., 2015) and herbivores (e.g. *Delphacoides*; Brantock & Botting, 2018), so the abundance of these prey species was likely linked to the availability of organic matter and vegetation (Sprung & Dias, 2003). Vegetation density and organic matter are generally lower within re-aligned saltmarsh habitat (Mossman et al., 2012), which may therefore result in a reduced availability of these prey.

Our results indicated that Common/Sand Goby fed at similar rates in re-aligned and established saltmarsh, although they fed on different proportions of the same prey species in each habitat. Unlike European Bass, prey species consumed by Common/Sand Goby were from a wide range of taxa and feeding groups, including detritivores (e.g. *O. gammarellus*), Polychaete worms and bivalves, that do not all directly depend on vegetation or organic matter (Cammen, 1976; Paramor & Hughes, 2004). Due to the wide variety

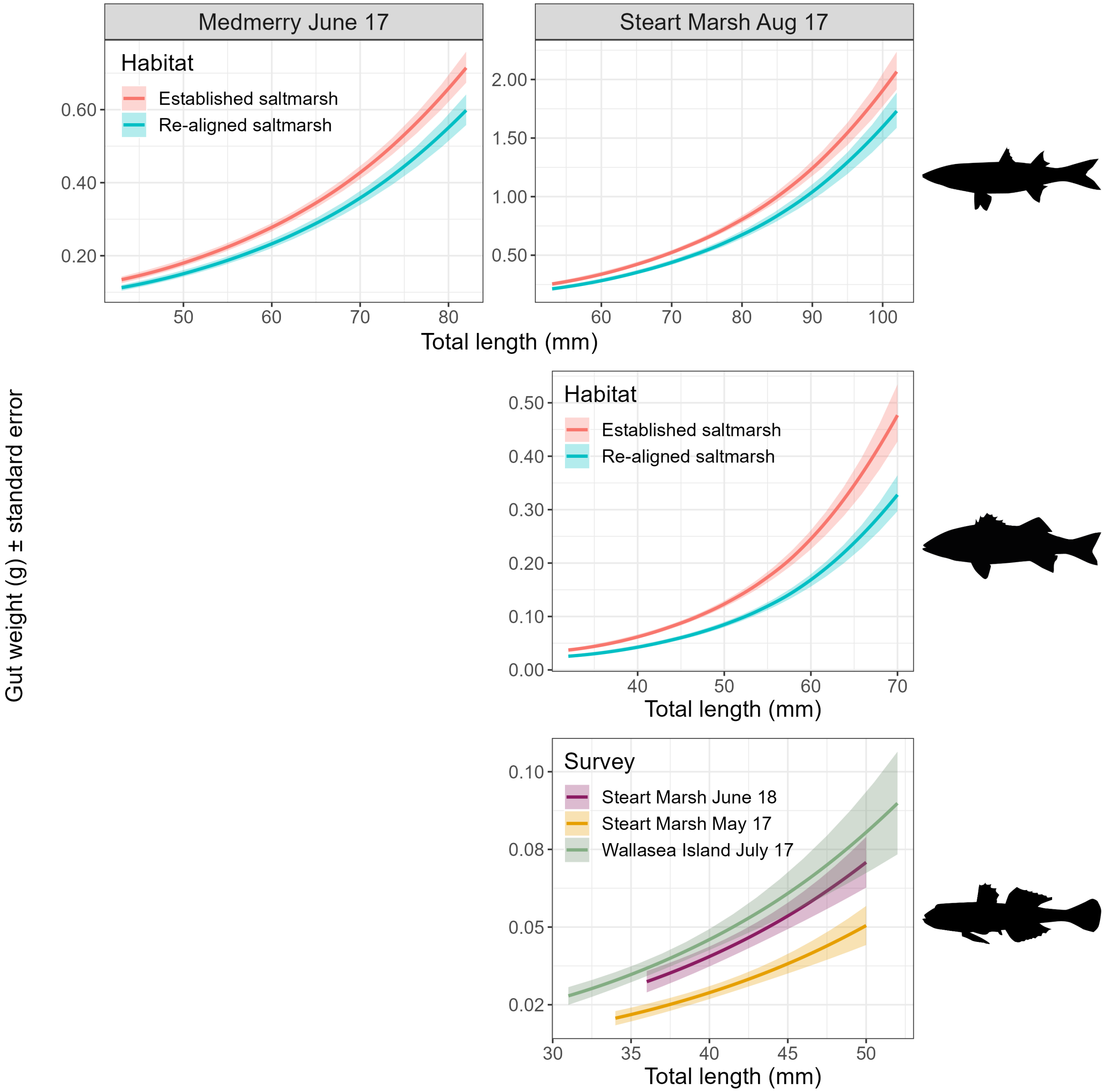

FIGURE 3 Relationships between gut weight and total length for Thinlip Mullet (top panel), European Bass (middle panel) and Common/Sand Goby (bottom panel) sampled in re-aligned and established saltmarshes at Medmerry Nature Reserve, Steart Marsh and Wallasea Island in the United Kingdom, 2017–2018.

of prey species and similar feeding rates, Common/Sand Goby may exploit re-aligned saltmarsh habitat more successfully than other species, such as Thinlip Mullet and European Bass.

4.3 | Vegetation and habitat/site development

Our results suggest the presence of vegetation or organic matter may be important for fish feeding success within re-aligned habitats. Globally, evidence suggests that the plant community within re-aligned sites can resemble the natural surrounding habitat within 10 years (USA—Byers & Chmura, 2007). However, as a result of variable construction design (Lawrence et al., 2018; Mossman et al., 2012) and possibly the macrotidal environment, re-aligned sites in Northern Europe may not achieve full biological equivalence to established saltmarsh within 50–100 years of tidal inundation (Mossman et al., 2012). Fully biologically equivalent saltmarsh habitat may, however, not be needed to provide valuable feeding habitat for dependent fish populations. Furthermore, novel habitats within re-aligned sites can provide functional fish

TABLE 5 PERMANOVA results assessing differences in diets of European Bass and Common/Sand Goby sampled in established and re-aligned saltmarsh sites (habitat) at Medmerry Nature Reserve, Steart Marsh and Wallasea Island in the United Kingdom, 2017–2018.

Taxa	Term	Df	SS	MS	Psuedo F	*p*
European Bass	Habitat	1	24,119	24,199	9.4699	<0.001
	Survey	1	34,741	34,741	13.641	<0.001
	Habitat: Survey	1	9633.6	9633.6	3.7825	<0.001
	Residual	115				
Common/Sand Goby	Habitat	1	23,251	23,251	17.251	0.001
	Survey	2	83,870	41,935	31.113	0.001
	Habitat: Survey	2	13,794	6896.9	5.117	0.001
	Residual	368		1347.8		

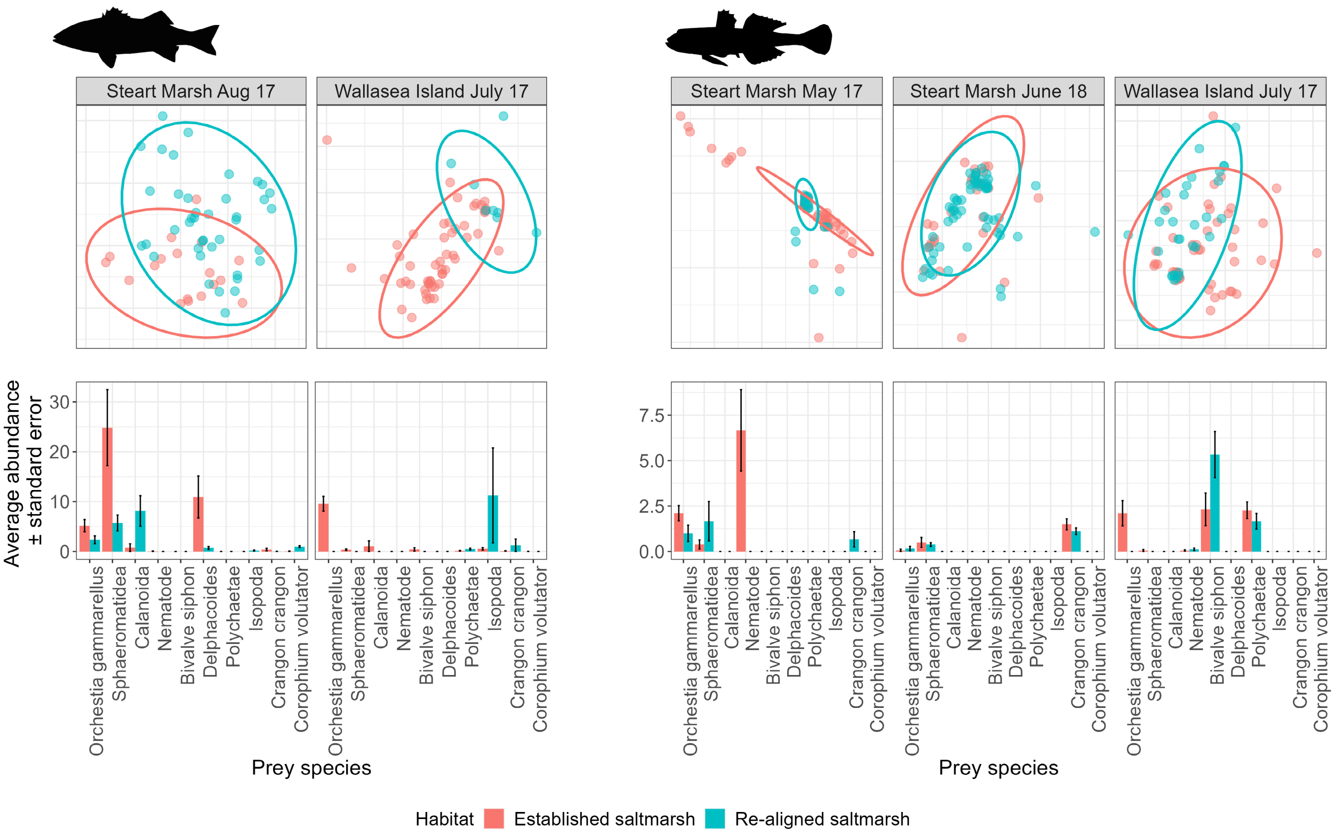

FIGURE 4 Nonmetric Multi-Dimensional Scaling (nMDS) plot demonstrating dietary similarity of European Bass (top left) and Common/Sand Goby (top right) captured within established and re-aligned saltmarsh sites sampled at Steart Marsh and Wallasea Island in the United Kingdom, 2017–2018. Points represent individual fish. 95% of ordinance ellipses show overlap in the diet. European Bass 2D stress value = 0.16, Common/Sand Goby 2D stress value = 0.12. Average abundance of predominant prey species per stomach for European Bass (bottom left) and Common/Sand Goby (bottom right) captured within established and re-aligned saltmarsh sites

feeding habitats that could help to maintain the productivity of coastal fish species through the provision of juvenile habitat (Colclough et al., 2003).

4.4 | Future research

Re-aligned sites are increasingly being designed to replicate or approximate characteristics of established saltmarsh habitats. Construction designs that facilitate floral and faunal colonisation should include: (1) avoiding the creation of fast-flow areas; (2) constructing irregular drainage creeks; (3) allowing shallow gradients between marsh flats; and (4) constructing features such as deep ponds (Burgess et al., 2019). However, few studies have assessed long-term colonisation of re-aligned sites or how fish interact with re-aligned habitats (in general) or specific construction design features within re-aligned sites (Colclough et al., 2003; Fonseca et al., 2011; Nunn et al., 2016). Each of the fish taxa included here is abundant in estuaries and saltmarshes, but their highly variable capture rates prevented spatial and temporal comparisons of fish habitat quality among all surveys. Such comparisons would help to identify mechanisms or design features that facilitate fish feeding in re-aligned sites. Time since tidal inundation (i.e. the age of re-aligned sites) likely influences fish feeding success and diet (Fonseca et al., 2011). Future survey work should target a range of re-aligned sites that vary in construction design and age to provide useful sites for monitoring and assessing habitat design and development (Gray et al., 2002; Mossman et al., 2012).

Future work should also include an assessment of abiotic and biotic factors influencing fish foraging activity, including inter- and intraspecific competition (Craig et al., 2007; Shoji & Tanaka, 2007). The energetic consequences of fish foraging within re-aligned sites should also be assessed, for example, the prey consumed by fish within re-aligned habitats may not have equivalent nutritional values to those within established saltmarsh or vise versa. This could be achieved by coupling future dietary surveys, with growth and condition assessments of fish captured within different habitats (Ciotti et al., 2013; 2014) or by collection of potential prey species and measuring their relative nutritional value.

5 | CONCLUSIONS

Globally, it is estimated that 50% of saltmarsh has been lost (Nordlie, 2003; Stamp et al., 2022; Swadling et al., 2022; Whitfield & Pattrick, 2015), and as much as 85% of coastal habitats are at continued risk from further human construction or development, e.g. land claim (Seitz et al., 2014). Re-alignment of coastal areas is not thought to provide completely biologically equivalent habitats to those that have been lost (Mossman et al., 2012). However, here we demonstrate that complete biological equivalence in terms of floral diversity and density, may not be required to provide a feeding habitat for fish. In the context of broad-scale historic and contemporary habitat loss within estuaries (Stamp et al., 2022; Swadling et al., 2022), we have highlighted that re-aligned habitats do provide feeding habitats that are being exploited by a range of fish species. Continued construction of re-aligned sites is advocated; however, further study is needed to identify how variability in construction design and habitat development influences fish exploitation of re-aligned habitats, and ultimately how these sites contribute towards fish production from estuarine systems.

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DATA AVAILABILITY STATEMENT

The data underlying this article will be shared upon reasonable request to the corresponding author.

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