Regional Studies in Marine Science 99 (2026) 105127

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

Aphanius fasciatus as a geomorphological baseline indicator for salt marsh restoration in the Venice Lagoon

Luca Altavilla [*], Chiara Facca, Francesco Cavraro, Stefano Malavasi

Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University of Venice, Via Torino, 155, Venice Mestre (VE), 30170, Italy

ARTICLE INFO

Keywords:
Salt marsh restoration
Ecological indicators
Habitat preferences
Transitional waters ecosystems

ABSTRACT

Restoration is widely recognised as a key strategy to reduce biodiversity loss, especially in transitional water ecosystems. Yet, the absence of clear ecological baselines often makes it difficult to identify suitable reference conditions for habitat reconstruction. In this study, we investigated the habitat preferences of the resident killifish *Aphanius fasciatus*, a species closely tied to the morphological features of Mediterranean salt marsh creeks. Monthly sampling was carried out over one year in salt marshes of the Venice Lagoon, allowing us to assess the relationship between habitat characteristics and species abundance. Results revealed that *A. fasciatus* favours creeks that retain water at low tide, are nutrient-rich, and exhibit high structural complexity. The species therefore represents a valuable ecological indicator, providing a practical tool to define site-specific baselines for salt marsh restoration. More broadly, our findings suggest that salt marshes with high geomorphological heterogeneity support not only *A. fasciatus* but also other species of ecological and commercial importance, raising the possibility that this species could act as an umbrella species for conservation and management.

1. Introduction

Restoration is increasingly recognised as a crucial strategy for preventing biodiversity loss (Feola et al., 2022). Consequently, it has emerged as an important and expanding area within the environmental sciences (Airoldi et al., 2021; Billah et al., 2022; Cadier et al., 2020).

In restoration processes, the primary objective should be to reconstruct habitats as similar as possible to a target ecosystem, i.e. a natural and undisturbed reference system, considered natural and in good condition (Elliott et al., 2022). This target ecosystem is essential to create or regenerate habitats able to maximise species richness and, consequently, the ecosystem services they provide (Perry et al., 2023). Site selection and the initial ecological conditions are therefore key variables in these processes (Gann et al., 2019; Mason et al., 2006), substantially improving restoration outcomes [see for example Gann et al. (2019) and Mason et al., (2006)].

However, as pointed out by Maciel et al. (2024), a major obstacle in restoration or habitat requalification is the lack of accurate data describing the target ecosystem, often leading to the establishment of sliding baselines. In the context of Mediterranean salt marshes, particularly in the Venice Lagoon, quantitative data are currently lacking.

Salt marshes are among the most productive habitats in transitional water ecosystems, supporting high fish densities thanks to abundant trophic resources and refuge functions provided by their structural complexity (Airoldi & Beck, 2007; Franco et al., 2006,2006b; Kennish, 2002; Lowe and Peterson, 2014; Rountree & Able, 2007). Despite their ecological importance, these habitats have undergone severe global decline due to land claim, erosion, pollution, aquaculture, and sea-level rise (Airoldi & Beck, 2007; Fagherazzi, 2013). In the Venice Lagoon, salt marshes decreased from 149 km^2 in 1912–37 km^2 in 2003, mainly as a result of anthropogenic-induced erosion (Silvestri et al., 2003; Sarretta et al., 2010), and further losses are predicted over the next decades (Carniello et al., 2009; Scarascia & Lionello, 2013).

That said, the first step in restoration planning should be the definition of a target ecosystem, taking into account geomorphological variations among sites, as these are primary factors influencing habitat use by nekton and other taxa (Hixon and Beets, 1993; Sebens, 1991; Williams and Zedler, 1999)

Considering the ecological complexity of transitional habitats and the difficulty of quantifying their quality, ecological indicator species can provide practical, measurable, site-specific benchmarks (Siddig et al., 2016; Gann et al., 2019). A highly effective approach to assessing the conservation status of coastal lagoon habitats is the use of resident species. Spending the entire life cycle within transitional waters, these

---

[*] Corresponding author.
E-mail address: luca.altavilla@unive.it (L. Altavilla).

https://doi.org/10.1016/j.rsma.2026.105127
Received 2 February 2026; Received in revised form 4 June 2026; Accepted 4 June 2026

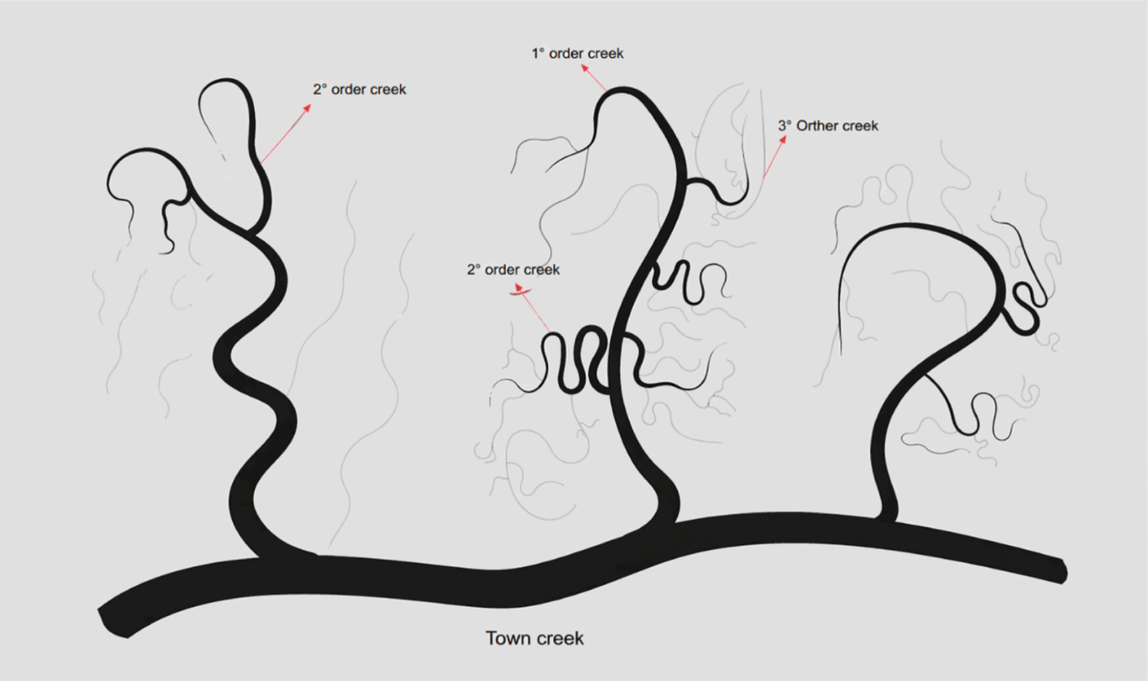

Fig. 1. Schematic representation of the three first-order creeks investigated in the study area, together with their associated second- and third-order tributaries.

species provide reliable insights due to their distribution and abundance, which are often strongly linked to the morphological features typical of lagoon systems, such as tidal creeks, salt marshes, and isolated pools (Bortone et al., 2005; Cavraro et al., 2019; Fiorin et al., 2007; Gilby et al., 2017; Habitats Directive 92/43/EEC; Zucchetta et al., 2012). Differences across locations in habitat use by nekton are frequently attributed to variations in habitat configuration and composition (Allen et al., 2007), making site selection and the initial ecological conditions key variables in these processes.

The Nature Restoration Law establishes binding and quantitative restoration targets, aiming to restore at least 20% of the EU's land and sea areas by 2030. It also mandates the implementation of restoration measures for all degraded ecosystems by 2050. Additionally, the law recommends the use of indicator species to standardise restoration practices (Regulation EU, 2024/1991). In this framework, the Mediterranean killifish *Aphanius fasciatus* (Valenciennes, 1821) represents a particularly suitable candidate. This resident species is strongly associated with habitat morphology and specific lagoonal structures, including salt marshes, small creeks, and shallow pools (Cavraro et al., 2014; Valdesalici et al., 2015). The inclusion of *A. fasciatus* in both the Habitats Directive (92/43/EEC) and the Bern Convention, owing to its strong association with the habitats it exploits, further strengthens its value as a resident species that can serve as a practical tool for identifying target ecosystems in restoration processes, thereby helping to overcome the lack of historical baselines. Therefore, *A. fasciatus* can be used as a indicator species to identify the type of habitats it preferentially occupies, under the assumption that these habitats reflect relatively favourable conditionsand can thus serve as realistic target ecosystems for restoration planning. An in-depth understanding of *A. fasciatus* habitat preferences is essential to support habitat management strategies (Kessabi et al., 2010) and to strengthen its role as an ecological indicator in Mediterranean transitional waters (Facca et al., 2020; Lionetto et al., 2023).

Although it is well recognised that the species can occur in good condition and at considerable densities within artificial habitats of the Venice Lagoon (Cavraro et al., 2013), its occurrence in natural habitats provides a more robust framework for assessing its ecological role and its value as an indicator of habitat quality under less altered conditions. In light of this, the primary objective of the present study is twofold. First, we aim to identify the specific geomorphological structures and physical features that compose the intertidal salt marsh creeks. Second, we seek to determine which of these preferred habitat structures maximise the relative abundance of *A. fasciatus* within the Venice Lagoon salt marshes.

Under the assumption that the habitats exhibiting the highest density of this resident species reflect high ecological quality and favourable conditions, the findings from this investigation will serve to establish quantitative and site-specific reference models (baselines). This will provide essential empirical support for habitat management strategies and future restoration planning aimed at maximising the ecological effectiveness of the reconstructed marsh creeks.

2. Material and methods

2.1. *The study species*

The Mediterranean killifish *Aphanius fasciatus* is a small cyprinodont species primarily found in the central-eastern Mediterranean region and has also established populations in the Suez Canal and Red Sea. According to the International Union for Conservation of Nature (IUCN), its distribution is limited to coastal areas. As stated in Annex II of the Habitats Directive of the European Union (Protocol ASPIM 92/43/EEC) and in Appendices II and III of the Bern Convention (Bern/Berne, September 19, 1979), the conservation status of this species is considered "unfavorable-inadequate." This classification is largely due to the loss of habitats that *A. fasciatus* relies on for survival. The European Habitat Directive (92/43/CEE) classifies *A. fasciatus* as a resident species that require the establishment of special conservation areas due to its strong dependency of specific morphological features (Cavraro et al., 2011; Franco et al., 2006; Franzoi et al., 2010), highlighting its possible role as indicator species of habitat structure.

2.2. *The study area*

Fish sampling was conducted in a natural salt marsh located along the margins of the northern Venice Lagoon. The area is characterised by

Table 1
List of variables included in the 5 models, with their labels and definitions. Measurements were conducted in situ, at different tide level as specified in the Definition column, or were derived from aerial photographs and GIS analyses (QGIS software). Variables in the first box were used to calculate some of the derived variables included in the models.

	Variable	Label	Definition
	Length	L	Length of the main creek plus its tributaries' length. Measured through QGis software from the creek's mouth to the points where the channel bottom rises to bank full elevation.
	Width	W	Mean width of the main creek. Width was measured in situ at bank full elevation every 10 m from the mouth to the end.
	Depth	D	Mean depth of creek. Measured in situ at bank full elevation, following the width transects.
	Cross-section	Cs	Area of the creek mouth. The cross-section was calculated in situ from multiple vertical measurements at bank full tide level.
	Surface Area	Sua	Surface Area of the main creek measured through QGis software from the creek's mouth to the points where the creek bottom rises to bank full elevation
Connectivity model	Drainage area	Da	Area of intertidal marsh drained by the creek. Drainage area was estimated from aerial photographs through QGis software.
	Distance	Ds	Shortest distance from the creek mouth to town creek mouth which correspond to the first connection of the salt marsh with the “open lagoon”.
	Tributaries volume	Tv	Volume of the main creek's tributaries at bank full tide level
Channel shape model	Branches	Br	Number of tributaries extending from the main creek. Measured in situ.
	Slope	S	Slope of the regression line based on bottom elevation. Measured in situ in the central point of the creek, every 10 m.
	Meander	Me	Ratio of the number of bends to main channel length. Higher ratio indicates greater channel sinuosity
	Steepness	St	Ratio of total volume to bottom area. Higher ratio indicates squares profiles and steeper banks.
	Bends	B	Number of points where the main channel changes direction by more than 30 °. Measured from aerial photographs through QGis software
Morphological model	Total/full Submerged Surface	Ss	Mean area of the surface submerged by water at bank full tide level. Measured in situ at bank full elevation every 10 m from the mouth to the end, following the width transects.
	Split	Sp	Ratio of the number of branches to main channel length. High ratio indicates greater channel branching
	Low-tide Submerged Area	Sa	Area of creek bottom covered by water at the mean low tide. Measured following the Submerged Surface transect.
	Axial dominance	Ad	Ratio of main creek length to total length of all tributaries. Higher ratio indicates a lower degree of branching
	Fringe	Fr	Ratio of the main Surface Area at bank full elevation to mean Low-tide submerged area. High ratios indicate more shallow fringing profile.
Hydrological model	Flow	Fl	Ratio of Cross-section area to the Total volume. Higher ratios indicates that the creek fills and empties slowly than others
	Conduit	Cn	Ratio of drainage area to Total/full submerged Surface. Higher ratio indicates a larger contributing catchment relative to the flooded area
	Total Volume	Av	Volume of the town creek plus its tributaries' volume.
	Volume	V	Volume of the main creek at bank full tide level
Chemical-physical model	Temperature	T	Water temperature expressed in °C, measured by means of a multiparametric probe
	Oxygen	O	Solute oxygen expressed in ppm. Measured by means of a multiparametric probe
	Turbidity	Turb	Expressed in FNU. Measured by means of a multiparametric probe
	pH	pH	Water pH measured by means of a multiparametric probe
	Salinity	Sal	Expressed in PSS. Measured by means of a multiparametric probe
	Sediment Chlorophyll	Chl	Measured fluorometrically as proposed by Lorenzen (1966)
	Water Chlorophyll	Chla	Measured fluorometrically as proposed by Lorenzen (1966)

a network of small-sized creeks shaped by semi-diurnal tidal excursions, which produce cyclic flooding and draining events. During high tide, these creeks are flooded, providing access to a variety of aquatic organisms that are forced to leave during ebb tide.

2.3. *Habitat characterisation*

Geomorphological and chemical-physical variables were collected to investigate whether creeks morphology and connectivity influence the relative abundance and distribution of the studied species within the salt marsh system. The entire study area encompasses a main town creek that connects 3 first other creeks with associated second and third other creeks (Fig. 1). For this study, we investigate the 3 first-order creeks and 8 s-order creeks (each representing a sampling station) with relative affluents (third-order creeks) covering an area of about 0.5 km^2. The tidal creeks ranged from about 27–230 m in length and from 0.19 and 3 m in width. Geomorphological variables were measured following the method proposed by Allen et al. (2007), adapted to the site under investigation as showed in Table 1. 22 geomorphological variables were directly measured on field or derived by aerial imagery. Chemical-physical variables were measured by means of a multiparametric probe (Hanna Instruments HI9829), while chlorophyll-a concentration in water and sediment were measured following the methodology proposed by Lorenzen (1966) (Table 1). All spatial analyses were performed within QGIS software (v. 3.14; QGIS Development Team, 2020) adopting the Monte Mario reference system (EPSG:3004).

2.4. *Fish sampling*

Fish were captured once a month from May 2023 to May 2024 by positioning a fyke net at the mouth of each creek during the high tide

Table 2

List of Generalised Mixed Effect Model (GLMMs) fitted with a Gamma distribution. For each model, the category, label, structure, and Akaike Information Criterion (AIC) value are reported. Within each category, the saturated model and progressively simplified models are presented. The model selected based on the lowest AIC value is shown in bold. Abbreviations: Ab = abundance, T = temperature, pH = potential hydrogen, Sal = salinity, O = dissolved oxygen, Turb = turbidity, Chl = chlorophyll-a, Ss =total/full submerged surface, Sp = split, Ad = axial dominance, Tv = tributaries, Sa = low-tide submerged area,Fr = fringe, V = volume, Fl = flow, Av = total volume, Cn = conduit, Ds = distance,Da = drainage area, B = bends, Me = meander, S = slope.

Model category	Model Label	Model Structure	AIC
Connectivity model	c1	Ab ~Ds + Da + Tv	830.81
Connectivity model	c2	Ab Da + Tv	829.65
Connectivity model	**c3**	**Ab ~Da**	**829.60**
Channel shape model	**s0**	**Ab ~B + Me + St + S**	**828.32**
Morphological model	m0	Ab ~Ss + Sp + Ad + Sa + Fr	843.96
Morphological model	m1	Ab ~Ss + Ad + Sa + Fr	843.27
Morphological model	**m2**	**Ab ~Ss + Ad + Sa**	**841.77**
Hydrological model	h0	Ab ~V + Fl + Av + Cn	832.91
Hydrological model	**h1**	**Ab ~Fl + Av + Cn**	**830.91**
Chemical-physical	cp0	Ab ~ Temp*O + pH + Sal + Turb + Chl + Chla	919.15
Chemical-physical	cp1	Ab ~ Temp + O + pH + Sal + Turb + Temp:O	917.28
Chemical-physical	**Cp3**	**Ab ~ Temp + O + pH + Turb + Chl + Temp:DO**	**916.50**

peak. The nets remained in place till the end of the ebb flow ensuring that all fish present in each creek segment were trapped within the net as water receded. Nets contents were placed in a plastic tray containing a millimetric laminated sheet to reference the fish measurements. All the fish were photographed for subsequent identification and total length measurements allowing the quick release to the wild. Species and sex were visually determined while abundance and length were measured using the free software ImageJ (ver. 1.51, W. S. Rasband, US National Institutes of Health, Bethesda, MD, USA, see https://imagej.nih.gov/ij/ Schneider et al., 2012)

2.5. *Data analysis*

Models were performed within the R environment (R Core Team 2014), and plotted using the ggplot2 package (Wickham, 2016). Geomorphological variables were grouped into four categories to generate four different Generalised Mixed Effect Model (GLMMs) plus an additional GLMM for the chemical-physical variables (Table 2), using the glmmTMB package. Chemical-physical model was fitted with a negative binomial distribution, including an interaction term between temperature and oxygen. No zero-inflation component was included (ziformula = ~0), as model diagnostics indicated that zero-inflation was not present in the dataset. Geomorphological models included “station nested within creeks’ order” as a random intercept to account for spatial dependency among sampling sites. Grouping the variables in different models allowed us to avoid overfitting and multicollinearity, maximising models’ performance. Statistical analyses were carried out following the protocol proposed by Zuur et al. (2009). In geomorphological models, all continuous predictor variables were standardised (mean = 0, standard deviation = 1) and the negative binomial distribution family were specified to align with the positive, right-skewed nature of the abundance (Ab) data. Starting from a saturated model, the most parsimonious combination of predictors was chosen based on Akaike’s Information Criterion (AIC), using the dredge() function procedure from the MuMin package (Barton, 2023). Residual diagnostics were checked using the DHARMa package to evaluate model fit, homogeneity, and dispersion. Finally, multicollinearity among predictors was assessed as proposed by Zuur et al. (2009), calculating the Variance Inflation Factor (VIF). None of the models presented predictors showing VIF above 5. Model-based predicted abundance plots were generated by varying one predictor across its observed range while holding all other predictors at their mean values.

3. Results

Statistical analysis revealed clear relationship between *A. fasciatus* abundance and geomorphological features. Chemical-physical parameters also showed significant influences on the species abundance. *A. fasciatus* was caught in the marsh system every month but December and January, when water temperature dropped between 3 and 10 °C. GLMM model reveal significant correlation between abundance and O, pH, Turb and Chl, as showed in Table 3. Oxygen and turbidity were negatively correlated with *A. fasciatus* abundance (Fig. 2a,c), while pH and sediment chlorophyll showed the opposite trend (Fig. 1b)

Table 3

Summary of significant predictors from the negative binomial GLMM assessing the effects of environmental variables on fish abundance (Dissolved oxygen (DO), turbidity (Turb), pH, Chlorophyll (Chl), and the interaction term Temp: DO). Asterisks indicate significance levels (* $p < 0.05$, ** $p < 0.01$).

Predictor	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
DO	−0.801688	0.254004	−3.156	0.00160 **
pH	0.738554	0.247938	2.979	0.00289 **
Turb	−0.009481	0.003693	−2.567	0.01026 *
Chl	0.034405	0.013294	2.588	0.00966 **
Temp:DO	0.026957	0.012432	2.168	0.03013 *

The inverse relationship between predicted abundance and dissolved oxygen is consistent with the seasonal oxygen–temperature dynamics shown in Fig. 3. As temperature increases from spring to summer, dissolved oxygen declines, while species abundance increases, reaching its peak during the warmest months. Conversely, during winter, high oxygen levels coincide with low temperatures and minimal abundance, supporting the observed negative association between abundance and dissolved oxygen.

3.1. *Morphological model*

Statistically significant relationship was found in the morphological model, as showed in Table 4. Predicted fish abundance decrease markedly when Total/full Submerged surface (Ss) and Axial dominance increase (Fig. 4). On the contrary, predicted fish abundance increase exponentially at higher values of Low-tide submerged area.

3.2. *Hydrological model*

Hydrological model showed significant positive relationship between fish abundance and Flow, Total volume, and Conduit, where predicted fish abundance growth exponentially at high value of the three variables, as showed in Fig. 5,f and Table 4.

3.3. *Connectivity model*

Connectivity model showed positive association between fish

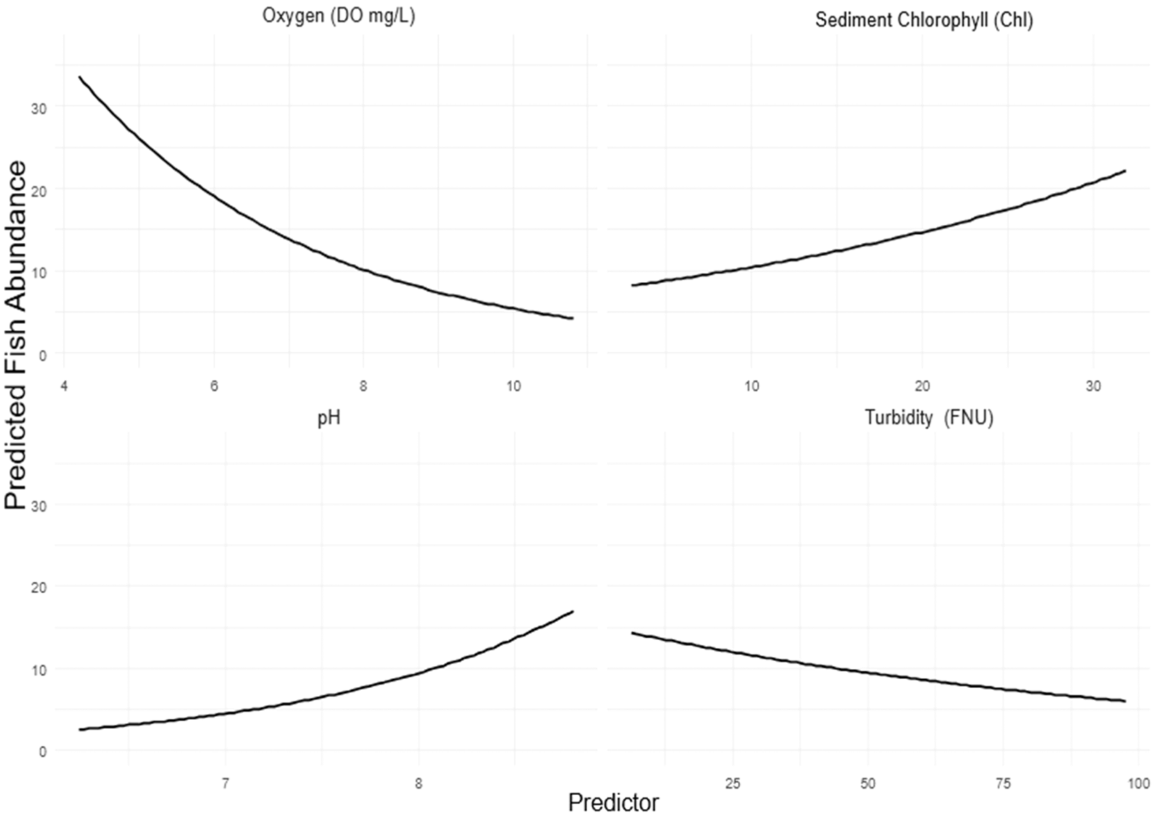

Fig. 2. Predicted abundance of *A. fasciatus* in relation to physicochemical variables included in the model: dissolved oxygen (DO, mg L^{-1}), sediment chlorophyll (Chl), pH, and turbidity (FNU).

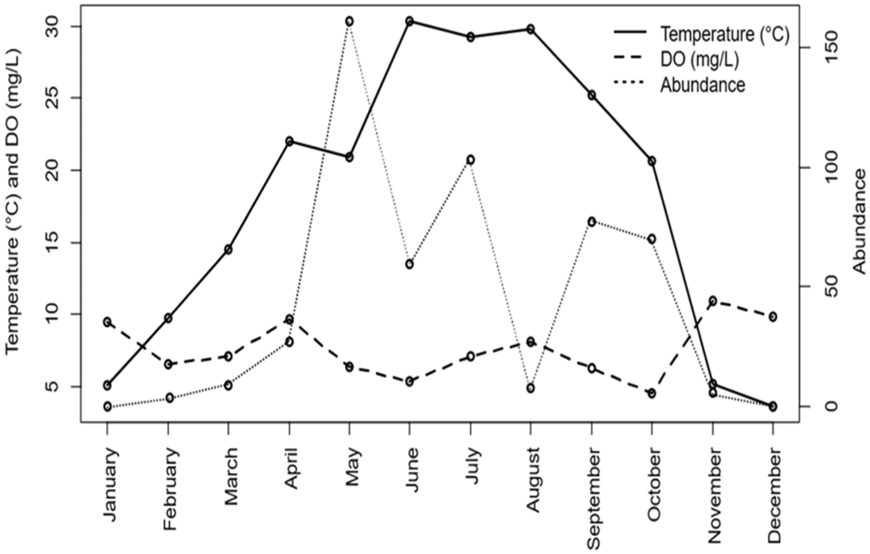

Fig. 3. Monthly mean values of water temperature (°C, solid line), dissolved oxygen (DO, mg L^{-1}, dashed line), and A. fasciatus abundance (dotted line, right axis) recorded in the study creeks during the sampling campaign.

abundance and Drainage area, showing a progressive increase of predicted abundance along the observed gradient (Fig. 6).

3.4. Channel shape model

Concerning the Channel shape model, Bend resulted strongly positively associated to fish abundance while Meander, Steepness and Slope showed the opposite trend as showed in Fig. 7.

4. Discussion

The present analysis of Mediterranean salt-marsh creeks revealed significant variation in fish abundance, highlighting the role of geomorphological features in habitat selection by *A. fasciatus* and underscoring its potential as an ecological indicator of habitat structure in these ecosystems.

Fish relative abundance was found to be strongly linked to specific

Table 4
Summary of significant predictors from the negative binomial GLMM assessing the effects of Geomorphological variables on fish abundance. Asterisks indicate significance levels (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

	Predictor	Estimate	Std. Error	t value	Pr(>|t|)
Morphological Model	Total/full Submerged Surface	−0.8055	0.2987	−2.697	0.00855 **
	Axial Dominance	−0.5895	0.2451	−2.405	0.01853 *
	Submerged Area	0.6845	0.3056	2.240	0.02793 *
Hydrological Model	Flow	0.4532	0.1901	2.384	0.019514 *
	Axial volume	0.4985	0.2227	2.239	0.027994 *
	Conduit	0.7841	0.2036	3.851	0.000238 ***
Connectivity Model	Drainage Area	0.6482	0.1627	3.983	0.000148 ***
Channel Shape Model	Bends	0.9712	0.2245	4.326	4.45e−05 ***
	Meander	−2.0537	0.5054	−4.063	0.000115 ***
	Steepness	−0.5580	0.1678	−3.325	0.001349 **
	Slope	−2.2425	0.4926	−4.553	1.92e−05 ***

habitat morphology as well as chemical and physical variables.

The Morphological model showed that the abundance of the species decreases as Axial dominance and Total/full submerged surface increase, while it tends to increase with a larger Low-tide submerged area. This indicates that *A. fasciatus* prefers smaller channels that do not fully empty during low tide. This preference may be attributed to the anti-predatory function of these habitats, which provide shelter for the species, as also observed in other congeneric species (Thompson, 2015).

The Hydrological model showed a positive relationship between fish abundance and factors such as Total volume, Conduit, and Flow. This indicates that the species prefers deep-water creeks that fill and empty slowly during tidal cycles. Similar patterns were found by Teo and Able (2003) in Delaware Bay, New Jersey. The significance of the Conduit (the ratio between Drainage area and Total/full submerged surface) aligns with the statistically significant relationship between fish abundance and chlorophyll levels. A larger drainage surface contributes to greater nutrient input into the channel, which in turn promotes phytoplankton growth (Custado, David, 2021). Additionally, the statistically significant correlation between fish abundance and Drainage area further supports this hypothesis.

The Channel shape model offered valuable insights into the preferred morphologies of the study species. The positive correlation with the number of bends indicates that greater structural complexity creates suitable habitats, increasing the availability of microhabitats and refuges. Conversely, the negative relationship with Meander, Steepness and Slope suggests that excessive tortuosity and steep profiles can reduce the usability of the system, likely limiting fish presence during the tidal cycle. These findings align with those of Gutierrez-Estrada et al. (2007), who reported similar habitat preferences for the ecological equivalent *Fundulus heteroclitus* in the Atlantic salt marshes of Spain.

From a chemical-physical perspective, *A. fasciatus* shows a preference for low-turbidity and nutrient-rich waters. Reduced turbidity likely enhances visual foraging efficiency and improves predator–prey interactions (Brodeur et al., 2003; Utne-Palm, 2002), which are key processes in shallow, structurally complex environments such as salt marsh creeks. Similarly, higher sediment chlorophyll (a proxy for microphytobenthic biomass) may indicate increased primary productivity and, consequently, greater food availability through benthic and detrital pathways (MacIntyre et al., 1996). The species' preference for a pH range of 7–9 is consistent with what is widely documented in the literature for other species due to physiological reasons [see, for example: Gibson et al., 2011; Ikuta et al., 2003; Kwong et al., (2014)].

Overall, these habitat preferences highlight the suitability of resident species as ecological indicators of habitat structure, thereby supporting their application in restoration planning and evaluation.

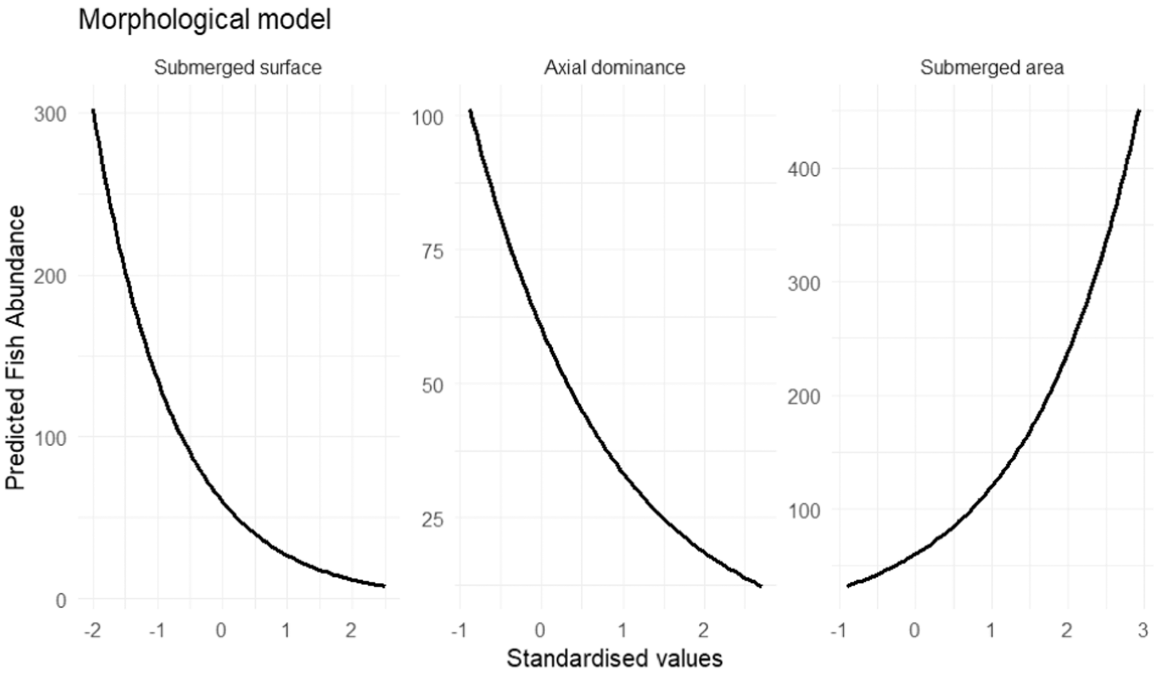

Fig. 4. Predicted fish abundance in response to standardised values of significant geomorphological, hydrological, connectivity, and channel-shape variables. Panels A–C represent the Morphological model, panels D–F depict the Hydrological model, panel G shows the Connectivity model, and panels H–K illustrate the Channel-Shape model. Predicted values are based on GLMM models fitted to standardised predictor variables. Fig. 4 Predicted fish abundance as a function of standardised significant predictors from the Morphological model Predictions are derived from GLMMs fitted using standardised covariates.

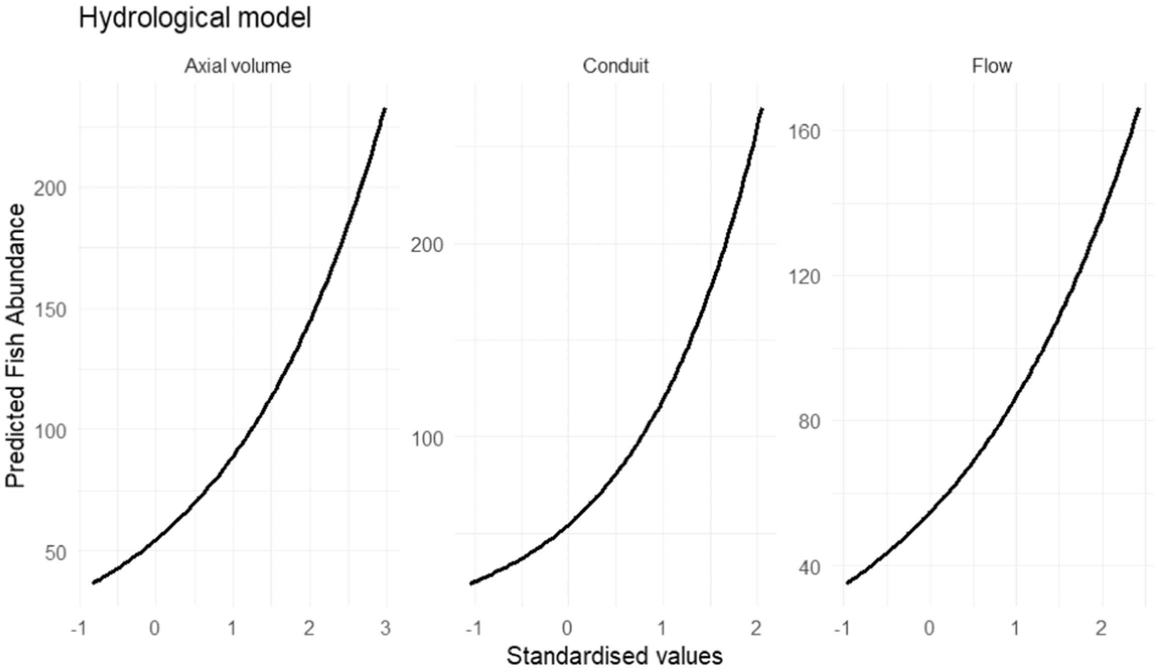

Fig. 5. Predicted fish abundance as a function of standardised significant predictors from the hydrological model. Predictions are derived from GLMMs fitted using standardised covariates.

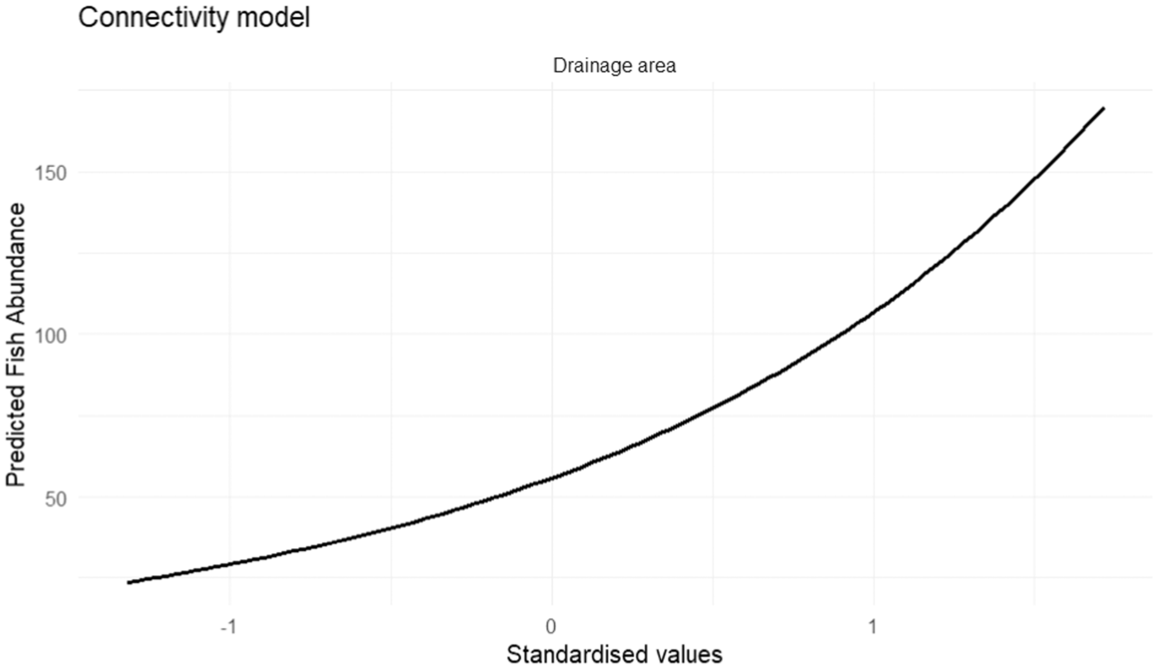

Fig. 6. Predicted fish abundance as a function of standardised significant predictors from the Connectivity model. Predictions are derived from GLMMs fitted using standardised covariates.

The use of a resident species to evaluate or planning restoration programs is a well-documented technique. Teo, Able (2003) investigate the population structure of *Fundulus heteroclitus*, the ecological equivalent of *A. fasciatus* in American salt marshes, to evaluate colonisation and restoration success in Delaware Bay, New Jersey. The diet composition of *F. heteroclitus* was examined in both natural and human-made habitats in Middletown to understand the resource availability of restored marshes (James-Pirri et al., 2001). The same species was studied by Able et al. (2012) to investigate connectivity between marsh creeks and the importance of subhabitats in restoration processes. Similarly to the present study, *Fundulus parvipinnis* was used as a study model to identify key variables for designing and mimicking the geomorphology of natural marshes and diversity in the restoration process (Williams and Zedler, 1999). More generally, fish assemblages were used to determine the quality of habitat restoration processes in coral reef and river ecosystems (Karr, 1987; Fausch et al., 1990; Bortone, Kimmel, 1991). Furthermore, Rozas et al. (2005) demonstrate that salt marsh morphology influences nekton assemblage and that different morphologies result in varying outcomes for fisheries support. Despite the numerous examples supporting the use of resident species to assess

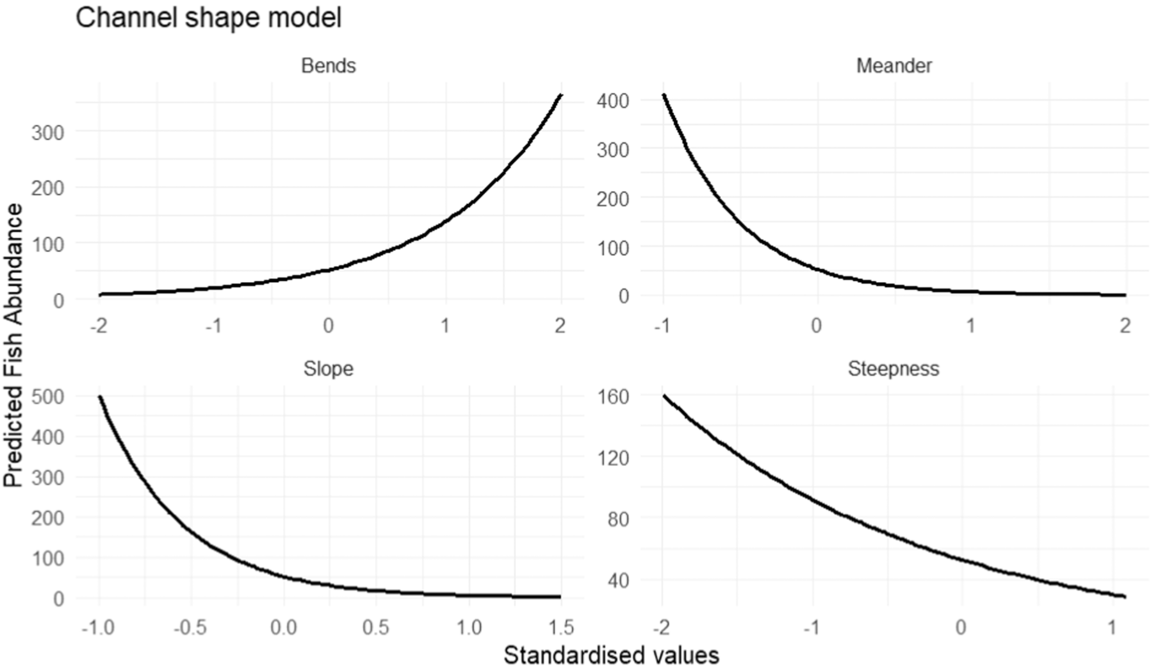

Fig. 7. Predicted fish abundance as a function of standardised significant predictors from the Channel shape model. Predictions are derived from GLMMs fitted using standardised covariates.

habitat quality, it is important to acknowledge that, while such species provide a robust and integrative proxy of local environmental conditions, they do not fully capture multi-taxa responses or broader ecosystem functioning. Consequently, both in the studies cited above and in the present case study, the implications drawn for restoration design should be interpreted as context-dependent and indicative, rather than strictly mechanistic or universally prescriptive

That said, considering the worldwide loss of salt marshes and the creation or restoration of marshes often undertaken without a proper understanding of their functional structure (Able et al., 2007; Dahl 1990; Kneib 2003; Minello et al., 1994; Peterson et al., 2008; Weinstein et al., 2001; Zedler 2001), the present work provides the basis for framing what can be defined as the baseline of a target ecosystem in the North Adriatic Sea, where typical Mediterranean salt marshes occur.

Although this study did not specifically address species co-occurrence, it is worth noting that catches of *A. fasciatus* were often accompanied by species of both commercial and community interest, such as *Sparus aurata*, *Knipowitschia panizzae*, *Chelon* spp., *Atherina boyeri*, and *Carcinus aestuarii*. While this aspect was beyond the original scope of the study, it represents an interesting emerging pattern that deserves further investigation. In particular, it opens the possibility of exploring whether *A. fasciatus* could serve as an umbrella species, a hypothesis that should be tested through dedicated quantitative analyses in future research.

In conclusion, our results underline that salt marshes with high structural heterogeneity maximise the colonisation of resident species, which can serve as proxies of habitat suitability for other species exploiting the same environment. Based on our findings, we recommend the construction of high-volume creeks sufficiently distant from each other to maximise the drainage area and enhance nutrient input from the land. Moreover, winding and slow-flowing creeks that do not fully empty during mean low tide appear to provide optimal conditions for supporting higher fish abundance.

Funding

This study was funded by the Italian Ministry of University and Research (MUR – ADIR funds).

CRediT authorship contribution statement

Altavilla Luca: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Malavasi Stefano:** Supervision, Funding acquisition. **Cavraro Francesco:** Writing – review & editing, Conceptualization. **Facca Chiara:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

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

Acknowledgments

The care and use of experimental animals complied with the Italian animal welfare laws, guidelines and policies as approved by the Article 18 of the Italian regional decree n. 54/2012. All the experimental activities are supervised by a certified veterinarian with expertise in captivity animal welfare (assignment REP 286/2022 PROT 74099 del July 29, 2022). The authors are thankful to the editors and the anonymous reviewers for their comments and suggestions.

Data availability

Data will be made available on request.

References

Able, K.W., Balletto, J.H., Hagan, S.M., Jivoff, P.R., Strait, K., 2007. Linkages between salt marshes and other nekton habitats in Delaware Bay. Rev. Fish. Sci. 15, 1–61. USA,(1-2).

Able, K.W., Vivian, D.N., Petruzzelli, G., et al., 2012. Connectivity among salt marsh subhabitats: residency and movements of the mummichog (Fundulus heteroclitus). Estuaries Coasts 35, 743–753. https://doi.org/10.1007/s12237-011-9471-x.

Airoldi, L., Beck, M., 2007. Status of Euromediterranean coastal marine habitats: loss and trends. Rapp. Comm. Int. Mer Médit 38, 410.

Airoldi, L., Beck, M.W., Firth, L.B., Bugnot, A.B., Steinberg, P.D., Dafforn, K.A., 2021. Emerging solutions to return nature to the urban ocean. Annu. Rev. Mar. Sci. 13, 445–477. https://doi.org/10.1146/annurev-marine-032020-020015Billah.

Allen, D.M., Haertel-Borer, S.S., Milan, B.J., Bushek, D., Dame, R.F., 2007. Geomorphological determinants of nekton use of intertidal salt marsh creeks. Mar. Ecol. Prog. Ser. 329, 57–71.

Barton K. 2023. MuMIn: multi–model inference. R package version 1.47.5. See https://CRAN.R-project.org/package=MuMIn. [Google Scholar.

Billah, M.M., Bhuiyan, M.K.A., Islam, M.A., Das, J., Hoque, A.R., 2022. Salt marsh restoration: an overview of techniques and success indicators. Environ. Sci. Pollut. Res. 29 (11), 15347–15363. https://doi.org/10.1007/s11356-021-18305-5.

Bortone, S.A., Dunson, W.A., Greenawalt, J.M., 2005. Fishes as estuarine indicators. In: Bortone, S.A. (Ed.), Estuarine indicators. CRC Press, Boca Raton.

Bortone, S.A., Kimmel, B.J., 1991. Environmental assessment and monitoring of artificial habitats. In: Seaman, In.W., Sprague, L.M. (Eds.), Artificial Habitats for Marine and Freshwater Fisheries. Academic Press, San Diego, California, pp. 177–234.

Brodeur, R., Veloza, A., Ryer, C., De Robertis, A., 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Can. J. Fish. Aquat. Sci. 60 (12), 1517–1526.

Cadier, C., Bayraktarov, E., Piccolo, R., Adame, M.F., 2020. Indicators of coastal wetlands restoration success: a systematic review. Front. Mar. Sci. 7, 600220. https://doi.org/10.3389/fmars.2020.600220.

Carniello, L., Defina, A., D'Alpaos, L., 2009. Morphological evolution of the Venice lagoon: Evidence from the past and trend for the future. J. Geophys. Res.: Earth Surf. 114 (4), 1–10. https://doi.org/10.1029/2008JF001157.

Cavraro, F., Bettoso, N., Zucchetta, M., D'Aietti, A., Faresi, L., Franzoi, P., 2019. Body condition in fish as a tool to detect the effects of anthropogenic pressures in transitional waters. Aquat. Ecol. 53 (1), 21–35.

Cavraro, F., Daouti, I., Leonardos, I., Torricelli, P., Malavasi, S., 2014. Linking habitat structure to life history strategy: Insights from a Mediterranean killifish. J. Sea Res. 85, 205–213. https://doi.org/10.1016/j.seares.2013.05.004.

Cavraro, F., Torricelli, P., Franzoi, P., Malavasi, S., 2013. Productivity in natural and artificial habitats in brackish water systems: An example from *Aphanius fasciatus* populations. Transit. Waters Bull. 7 (1), 23–31. https://doi.org/10.1285/i1825229Xv7n1p23.

Cavraro, F., Fiorin, R., Riccato, F., Zucchetta, M., Franzoi, P., Torricelli, P., Malavasi, S., Habitat, D. E., Aphanius, D. I., & Valenciennes, F. (2011). Distribuzione E Habitat Di. 134, 125–134.

Custado, M.J.G., David, C.P.C., 2021. Influence of runoff on coastal chlorophyll-a concentration in selected Philippine upwelling sites. SciEnggJ 14 (1), 108–118.

Elliott, B.B., Olds, A.D., Henderson, C.J., Rummell, A.J., Gilby, B.L., 2022. Optimising restoration and rehabilitation using environmental and spatial drivers of plant assemblages. Landsc. Urban. Plan. 226, 104484. https://doi.org/10.1016/j.landurbplan.2022.104484.

Facca, C., Cavraro, F., Franzoi, P., Malavasi, S., 2020. Lagoon resident fish species of conservation interest according to the Habitats Directive (92/43/EEC): A review on their potential use as ecological indicator species. Water (Switz.) 12 (7), 2059. https://doi.org/10.3390/w12072059.

Fagherazzi, S., Mariotti, G., Wiberg, P.L., McGLATHERY, K.J., 2013. Marsh collapse does not require sea level rise. Oceanography 26 (3), 70–77.

Fausch, K.D., Lyons, J., Karr, J.R., Angermeier, P.L., 1990. Fish communities as indicators of environmental degradation. In: Adams, In.S.M. (Ed.), Biological Indicators of Stress in Fish. American Fisheries Society, Bethesda, Maryland, pp. 123–144.

Feola, A., Ponis, E., Cornello, M., Brusà, R.B., Cacciatore, F., Oselladore, F., Matticchio, B., Canesso, D., Sponga, S., Peretti, P., Lizier, M., Maniero, L., Volpe, V., Sfriso, A., Ferla, M., Bonometto, A., 2022. An integrated approach for evaluating the restoration of the salinity gradient in transitional waters: monitoring and numerical modeling in the Life Lagoon Refresh case study. Environments 9 (3), 31. https://doi.org/10.3390/environments9030031.

Fiorin, R., Malavasi, S., Franco, A., Franzoi, P., 2007. Comparative energy allocation in two sympatric, closely related gobies: the black goby Gobius niger and the grass goby Zosterisessor ophiocephalus. J. Fish. Biol. 70, 483–496.

Franco, A., Franzoi, P., Malavasi, S., Riccato, F., Torricelli, P., 2006. Fish assemblages in different shallow water habitats of the Venice Lagoon. Hydrobiologia 555 (1), 159–174. https://doi.org/10.1007/s10750-005-1113-5.

Franco, A., Franzoi, P., Malavasi, S., Riccato, F., Torricelli, P., Mainardi, D., 2006b. Use of shallow water habitats by fish assemblages in a Mediterranean coastal lagoon. Estuar. Coast. Shelf Sci. 66, 67–83. https://doi.org/10.1016/j.ecss.2005.07.020 (1–2).

Franzoi, P., Franco, A., Torricelli, P., 2010. Fish assemblage diversity and dynamics in the Venice lagoon. Rend. Lincei 21 (3), 269–281. https://doi.org/10.1007/s12210-010-0079-z.

Gann, G.D., McDonald, T., Walder, B., Aronson, J., Nelson, C.R., Jonson, J., Hallett, J.G., Eisenberg, C., Guariguata, M.R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., Dixon, K.W., 2019. International principles and standards for the practice of ecological restoration. Second edition. Restor. Ecol. 27 (S1), S1–S46. https://doi.org/10.1111/rec.13035.

Gibson, R., Atkinson, R., Gordon, J., Smith, I., Hughes, D., 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. Ocean. Mar Biol Annu Rev 49, 1-42.

Gilby, B.L., Olds, A.D., Connolly, R.M., Yabsley, N.A., Maxwell, P.S., Tibbetts, I.R., Schoeman, D.S., Schlacher, T.A., 2017. Umbrellas can work under water: Using threatened species as indicator and management surrogates can improve coastal conservation. Estuar. Coast. Shelf Sci. 199, 132–140. https://doi.org/10.1016/j.ecss.2017.10.003.

Gutiérrez-Estrada, J.C., Silva, C., Yáñez, E., Rodríguez, N., Pulido-Calvo, I., 2007. Monthly catch forecasting of anchovy Engraulis ringens in the north area of Chile: non-linear univariate approach. Fish. Res. 86, 188–200 (2-3).

Hixon, M.A., Beets, J.P., 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol. Monogr. 63, 77–101.

Ikuta, K., Suzuki, Y., Kitamura, S., 2003. Effects of low pH on the reproductive behavior of salmonid fishes. Fish physiol. biochem. 28 (1), 407–410.

James-Pirri, M., Raposa, K., Catena, J., 2001. Diet composition of mummichogs, Fundulus heteroclitus, from restored and unrestricted regions of a New England salt marsh. Estuar. Coast. Shelf Sci. 53 (2), 205–213. https://doi.org/10.1006/ecss.2001.0807.

Karr, J.R., 1987. Biological monitoring and environmental assessment: a conceptual framework. Environ. Manag. 11, 249–256.

Kennish, M.J., 2002. Environmental threats and environmental future of estuaries. Environ. Conserv. 29 (1), 78–107. https://doi.org/10.1017/S0376892902000061.

Kessabi, K., Navarro, A., Casado, M., Saïd, K., Messaoudi, I., Piña, B., 2010. Evaluation of environmental impact on natural populations of the Mediterranean killifish *Aphanius fasciatus* by quantitative RNA biomarkers. Mar. Environ. Res. 70 (3–4), 327–333. https://doi.org/10.1016/j.marenvres.2010.06.005.

Kwong, R.W., Kumai, Y., Perry, S.F., 2014. The physiology of fish at low pH: the zebrafish as a model system. J. Exp. Biol. 217 (5), 651–662. https://doi.org/10.1242/jeb.091603.

Lionetto, M.G., Zonno, V., Schiavone, R., Giordano, M.E., Barca, A., Belmonte, G., Verri, T., 2023. The Mediterranean killifish Aphanius fasciatus (Valenciennes, 1821) (Teleostei: Cyprinodontidae) as a sentinel species for protection of the quality of transitional water environments: Literature, insights, and perspectives. Water 15 (15), 2721.

Lorenzen, C.J., 1966. A method for the continuous measurement of in vivo chlorophyll concentration. In Deep Sea Res. Oceanogr. Abstr. 13 (2), 223–227. Elsevier,April.

Lowe, M.R., Peterson, M.S., 2014. Effects of coastal urbanization on salt marsh faunal assemblages in the northern Gulf of Mexico. Mar. Coast. Fish. 6 (1), 89–107.

Maciel, E.B., Jovem-Azevêdo, D., Lima, C.S.D.S., Pessanha, A.L.M., 2024. Multiple habitats drive the functional diversity of fish assemblages in a tropical estuary. Mar. Environ. Res. 195, 106379. https://doi.org/10.1016/j.marenvres.2024.106379.

MacIntyre, H.L., Geider, R.J., Miller, D.C., 1996. Microphytobenthos: The Ecological Role of the "Secret Garden" of Unvegetated, Shallow-Water Marine Habitats. I. Distribution, Abundance and Primary Production. Estuaries 19 (2), 186–201. https://doi.org/10.2307/1352224.

Mason, T., French, K., Russell, K., 2006. Moderate impacts of plant invasion and management regimes in coastal hind dune seed banks. Biol. Conserv. 134 (3), 428–439. https://doi.org/10.1016/j.biocon.2006.08.032.

Minello, T.J., Zimmerman, R.J., Medina, R., 1994. The importance of edge for natant macrofauna in a created salt marsh. Wetlands 14 (3), 184–198.

Perry, H.J., Goodridge Gaines, L.A., Borland, H.P., Henderson, C.J., Olds, A.D., Mosman, J.D., Gilby, B.L., 2023. Identifying optimal values of coastal habitat condition for management and restoration. Estuar. Coast. Shelf Sci. 282, 108250. https://doi.org/10.1016/j.ecss.2023.108250.

Peterson, C.H., Able, K.W., DeJong, C.F., Piehler, M.F., Simenstad, C.A., Zedler, J.B., 2008. Practical proxies for tidal marsh ecosystem services: application to injury and restoration. Adv. mar. biol. 54, 221–266.

QGIS Development Team. (2020). QGIS Geographic Information System (Version 3.14) [Computer software]. Open Source Geospatial Foundation. https://qgis.org.

Regulation (EU) 2024/1991 of the European Parliament and of the Council of 12 July 2024 on nature restoration. Official Journal of the European Union, L 2024. ⟨https://eur-lex.europa.eu/eli/reg/2024/1991/oj⟩.

Rountree, R.A., Able, K.W., 2007. Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions. Aquat. Ecol. 41 (1), 25–45.

Rozas, L.P., Caldwell, P., Minello, T.J., 2005. The fishery value of salt marsh restoration projects. J. Coast. Res. 40, 37–50.

Sarretta, A., Pillon, S., Molinaroli, E., Guerzoni, S., Fontolan, G., 2010. Sediment budget in the Lagoon of Venice, Italy. Cont. Shelf Res. 30 (8), 934–949. https://doi.org/10.1016/j.csr.2009.07.002.

Scarascia, L., Lionello, P., 2013. Global and regional factors contributing to the past and future sea level rise in the Northern Adriatic Sea. Glob. Planet. Change 106, 51–63. https://doi.org/10.1016/j.gloplacha.2013.03.004.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. methods 9 (7), 671–675.

Sebens, K., 1991. Habitat structure and community dynamics in marine benthic systems. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman and Hall, New York, pp. 211–234.

Siddig, A.A., Ellison, A.M., Ochs, A., Villar-Leeman, C., Lau, M.K., 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. Ecol. Indic. 60, 223–230.

Silvestri, S., Marani, M., Marani, A., 2003. Hyperspectral remote sensing of salt marsh vegetation, morphology and soil topography. Phys. Chem. Earth 28, 15–25. https://doi.org/10.1016/S1474-7065(03)00004-4 (1-3).

Teo, S.L.H., Able, K.W., 2003. Growth and production of the mummichog (Fundulus heteroclitus) in a restored salt marsh. Estuaries 26, 51–63. https://doi.org/10.1007/BF02691693.

Teo, S.L.H., Able, K.W., 2003. Habitat use and movement of the mummichog (Fundulus heteroclitus) in a restored salt marsh. Estuaries 26 (3), 720–730.

Thompson, J.S., 2015. Size-selective foraging of adult mummichogs, Fundulus heteroclitus, in intertidal and subtidal habitats. Estuaries Coasts 38 (5), 1535–1544.

Utne-Palm, A.C., 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. Mar. Freshw. Behav. Physiol. 35 (1–2), 111–128. https://doi.org/10.1080/10236240290025644.

Valdesalici, S., Langeneck, J., Barbieri, M., Castelli, A., Maltagliati, F., 2015. Distribution of natural populations of the killifish Aphanius fasciatus (Valenciennes, 1821) (Teleostei: Cyprinodontidae) in Italy: past and current status, and future trends. Ital. J. Zool. 82 (2), 212–223. https://doi.org/10.1080/11250003.2014.1003418.

Weinstein, M.P., Teal, J.M., Balletto, J.H., Strait, K.A., 2001. Restoration principles emerging from one of the world's largest tidal marsh restoration projects. Wetl. Ecol. Manag. 9 (5), 387–407.

Wickham, H., 2016. Data analysis. In ggplot2: elegant graphics for data analysis. Cham: Springer international publishing, pp. 189–201.

Williams, G.D., Zedler, J.B., 1999. Fish assemblage composition in constructed and natural tidal marshes of San Diego Bay: relative influence of channel morphology and restoration history. Estuaries 22, 702–716. https://doi.org/10.2307/1353057.

Zucchetta, M., Cipolato, G., Pranovi, F., Antonetti, P., Torricelli, P., Franzoi, P., Malavasi, S., 2012. The relationships between temperature changes and reproductive investment in a Mediterranean goby: insights for the assessment of climate change effects. Est. Coast. Shelf Sci. 101, 15–23.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R, 574. springer, New York.