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Oysters at work: How Europe's reef engineers shape species diversity

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ABSTRACT

European flat oyster (*Ostrea edulis*) populations are collapsed, and wild habitats are now exceedingly rare. The present study is the most comprehensive species diversity study of wild *Ostrea edulis* habitats to date, documenting 290 species across five remnant, restored and fished oyster reefs in Scotland. By examining both epibiotic and infaunal assemblages from hand-gathered box cores, the role of native oysters in shaping benthic species diversity and functional community structure was evaluated. In oyster habitats, significantly higher epibiotic diversity and greater abundance of habitat-structuring traits (e.g. sessility and habitat creation) were observed. On average, epibiotic diversity was ~50% higher where oysters were present and 80% higher in shallow, undisturbed habitats, compared to where they were absent, with statistical models confirming oyster presence as a significant predictor of species diversity. In contrast, infaunal assemblages showed weak and non-significant responses, with only modest functional shifts and a slight increase in species diversity. These findings provide rare empirical evidence of the importance of *O. edulis* as an ecosystem engineer, enhancing surface habitat complexity and supporting functionally rich and diverse epibiotic communities. Trait-based analyses further indicate that many associated epibiotic species contribute to this structure reinforcing biodiversity through positive feedback. These findings demonstrate that oyster habitats consistently deliver enhanced species diversity, highlighting the need to prioritise such habitats for restoration, whilst providing rare reference data for international restoration efforts such as those stimulated by the recent European Restoration Regulation.

1. Introduction

Biodiversity is in global decline, with many habitats being affected by climate change and anthropogenic activities (Hooper et al., 2012; O'Hara et al., 2021; Hajji and Lucas, 2024; Wiens and Zelinka, 2024; Keck et al., 2025). Due to global biodiversity loss, governments have developed international agreements, national policy and domestic legislation to protect and restore biodiversity (Santamaría and Méndez, 2012; Ortiz et al., 2021; European Parliament, 2024; Scottish Government, 2024). The Kunming-Montreal Global Biodiversity Framework (2022) of the Convention on Biological Diversity now sets out restorative goals (CBD, 2022; Obura et al., 2023, Hughes and Grumbine, 2023) that cascade through most European countries via the Nature Restoration Regulation (European Parliament, 2024) and regional policies, such as the Scottish Biodiversity Strategy and the Nature Conservation Act of the Netherlands (Government of the Netherlands, 2017; Scottish Government, 2024).

Restoration initiatives put a strong emphasis on ecosystem services, the benefits that humans derive from nature, including provisioning (e.g., food and water), regulating (e.g., climate and disease control), cultural (e.g., spiritual and recreational) and supporting services (e.g., nutrient cycling and soil formation) (zu Ermgassen et al., 2020; CIEEM,

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2025; Danovaro et al., 2025). By acknowledging the potential benefits that ecosystem services provide, governments and industries are more effectively motivated to curb biodiversity loss (Costanza, 2020; Kubiszewski et al., 2020; van der Schatte Olivier et al., 2020). Consequently, effective conservation management must assess and account for the specific ecosystem services supported by target habitats and species (Tallis and Polasky, 2009).

Global assessments indicate that up to 85%% of oyster reefs have declined from historic levels due mostly to overfishing but also pollution, habitat destruction and climate change (Beck et al., 2009; Thurstan et al., 2024). In the North-East Atlantic, European native oyster (*Ostrea edulis*) habitats are collapsed (see zu Ermgassen et al., 2025a, 2025b): once having formed extensive reefs and now persistent only in small remnant populations and a handful of managed fisheries (Eagling et al., 2015; Fariñas-Franco et al., 2018; Thurstan et al., 2024; Kennon et al., 2023; zu Ermgassen et al., 2025a, 2025b). It is probable that the decline of these reefs has led to the loss of multiple ecosystem services including carbon storage (Lee et al., 2020, 2024) and the enhancement of biodiversity (Kennon et al., 2023).

At a meso-scale, the structural complexity of oyster habitats likely creates a mosaic of microhabitats, offering shelter, feeding grounds and breeding sites for a diverse range of marine organisms, including fish, crustaceans, molluscs and echinoderms (Karp et al., 2018; Lown et al., 2021; Kennon et al., 2023, 2025). Increased surface area also promotes the colonisation of sessile species such as algae, sponges and bryozoans, which in turn provide resources for higher trophic levels (Smyth and Roberts, 2010). By offering physical refuges, particularly for juvenile and smaller organisms, biogenic shellfish habitats potentially reduce predation pressure and contribute to enhanced survival and species richness (Coen et al., 1999; Kennon et al., 2023). Infaunal species diversity, may also be influenced by sediment stabilisation and the accumulation of biodeposits (e.g., faeces and pseudofaeces; Haven and Morales-Alamo, 1966) which have the potential to enhance secondary production and food availability around the oyster bed. Organic matter not incorporated into food webs may subsequently accumulate and modify sediment in adjacent habitat. *Ostrea edulis* has been shown to treble the flux of sediments and organic material to the seabed in laboratory experiments (Lee et al., 2024).

Biological traits, such as body size, feeding mode, mobility and burrowing depth, determine how species interact with their environment and contribute to ecosystem functions (Díaz et al., 2013). These traits are directly linked to the provision of ecosystem services such as nutrient cycling, sediment bioturbation and water filtration. As ecosystem engineers, oysters are thought to modify habitat structure and local conditions, thereby shaping the trait profiles of associated communities. For instance, the introduction of hard substrate and structural complexity may favour traits associated with sessile suspension feeders or surface-dwelling organisms, while discouraging deep-burrowing deposit feeders typically dominant in soft sediments (Bremner et al., 2006). In this way, oysters potentially, not only enhance species richness but also alter the functional diversity of ecosystems, an important consideration when evaluating the success and resilience (Kennon et al., 2025) of restoration efforts.

The growing recognition of the vital ecosystem services provided by *Ostrea edulis* has led to a surge in restoration initiatives (Nordheim, 2019; Preston et al., 2020; zu Ermgassen et al., 2025b), aimed at reintroducing or enhancing native oyster populations as a 'nature-based solution' (see WWF, n.d.) to enhance biodiversity (Kennon et al., 2023), improve water quality (Fabra et al., 2025) and store carbon (Lee et al., 2024). These projects seek not only to recover a lost habitat but also the ecosystem services; in particular biodiversity enhancement (zu Ermgassen et al., 2020). However, because *O. edulis* reefs have been largely absent in many places over the past century (Beck et al., 2009; Thurstan et al., 2024; zu Ermgassen et al., 2025a, 2025b), it is crucial that restoration practitioners are equipped with a robust ecological understanding to guide decision-making and manage expectations among funders and policymakers. While some studies have assessed species diversity at a 'reef scale', i.e. over 10's of square metres, (Korringa, 1954; Smyth and Roberts, 2010; Fariñas-Franco et al., 2018; Lown et al., 2021; Kennon et al., 2023), how oysters influence their immediate environment has yet to be comprehensively assessed in *O. edulis* communities. This finer-scale biodiversity knowledge is particularly relevant to restoration practitioners, especially in the early-stages of restoration projects because full reef development may take more than a decade to establish (Kennon et al., 2023).

1.1. Aims

The present study set out to investigate how various components of species diversity are directly influenced by the presence of *Ostrea edulis*, with the goal of generating insights to support more effective restoration management. Such insights could include greater understanding of how reintroducing *O. edulis* will affect their immediate surroundings in terms of species diversity as well as provide evidence for setting expectations for funders and stakeholders.

The following hypotheses were tested:

Hypothesis 1. Infaunal diversity is enhanced due to the presence of oysters.

Hypothesis 2. Epibiotic diversity is enhanced due to the presence of oysters.

In addition, the study aimed to explore how the presence of oysters may influence the biological traits of associated fauna, particularly those contributing to key ecosystem functions such as habitat creation, which are critical to the delivery of ecosystem services in restored oyster habitats.

2. Methods

2.1. Site selection

Two of the study sites in the present work were in Loch Ryan where the only remaining wild oyster fishery in Scotland has operated since 1701 (see Kennon et al., 2023). Two study sites were small, undisturbed, remnant populations, discovered by the authors, in hard-to-reach locations off the west coast of Scotland (Table 1; Fig. 1). In addition, one of the study sites was undergoing oyster restoration by the Dornoch Environmental Enhancement Project (DEEP; Fariñas-Franco et al., 2018). In all cases, oyster habitats were considered sufficiently mature (various size classes including adults, associate shell material, and physical complexity) to be potentially influenced by the presence of oysters (see also Kennon et al., 2023, 2025).

Shallow sites were sampled by snorkelling, and deeper sites were sampled by SCUBA. At each site four areas with an oyster abundance of $>5/m^2$, the OSPAR definition of an oyster bed (OSPAR Commission, 2009), were selected. In the adjacent habitat, with similar environmental characteristics (e.g. depth and sediment type), four control areas were also selected that had an oyster abundance of $0/m^2$. For each sample, a 25 cm × 25 cm × 10 cm box core was randomly placed in an area with live oysters (treatment) or in an area containing no oysters (control) (Fig. 2). Each treatment quadrat captured 1–2 live oysters.

2.2. Species diversity surveys

Epibiota was recorded in situ within each 25 cm × 25 cm × 10 cm box core (Fig. 2). Trained surveyors used the SACFOR abundance scale (Hiscock, 1996) to record conspicuous epibiotic species efficiently in the field, collecting voucher specimens to confirm identity back at the laboratory, as necessary. The sediment from within the box was then carefully collected to a depth of 10 cm, using a trowel and transferred into a 5 L bucket. Once returned to the shore, sediment was sieved

Table 1
Study sites in the present work. Deeper sites were 4.5–5.5 m below chart datum. Shallower sites were 0-1 m below chart datum. Definitions of 'sheltered' (ie restricted, <20 km, fetch) and 'moderately strong' currents (ie 1-3kn) and zones follow JNCC (2022).

Site	Size of site	Average oyster density /m^2	Estimated Size Range (edge-umbo) mm	Depth category	Zone	Environmental notes	Management
Loch Ryan 1[a]	4 km^2	25	30–90	Deeper	Upper Circalittoral	Moderate tidal currents	Self-sustaining, Fished four years earlier
Loch Ryan 2	2 km^2	15	20–70	Shallower	Upper Infralittoral	Wave sheltered shoreline	Self-sustaining, Undisturbed[c]
Isle of Mull	1 km^2	5	40–60	Shallower	Upper Infralittoral	Wave sheltered shoreline	Self-sustaining, Undisturbed[c]
Isle of Skye	0.5 km^2	5	50–70	Shallower	Upper Infralittoral	Wave sheltered shoreline	Self-sustaining, Undisturbed[c]
Dornoch Firth[b]	0.5 km^2	20	50–70	Deeper	Upper Circalittoral	Moderate tidal currents	Four years of restoration

[a] Loch Ryan Oyster Fishery.
[b] Dornoch Environmental Enhancement Project.
[c] No recorded fishing activity.

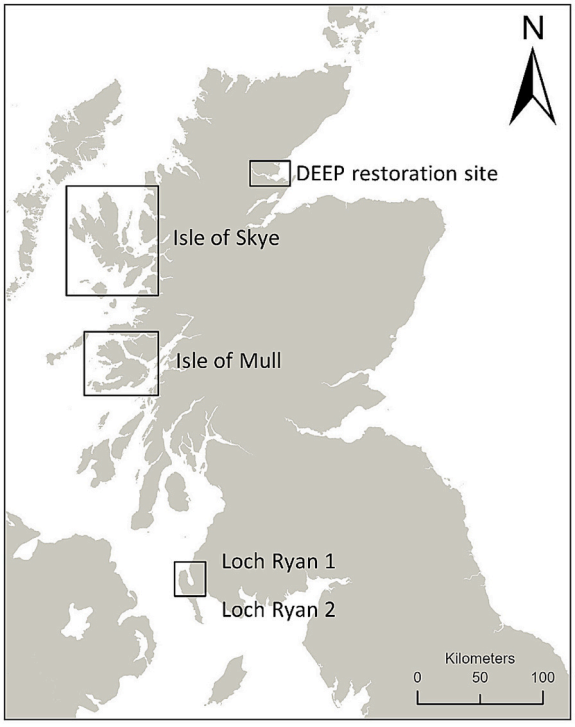

Fig. 1. Site map: Five survey locations in the present study across Scotland. (Loch Ryan 1 – Within the Loch Ryan oyster fishery; Loch Ryan 2 – Outside oyster fishery). Given the rarity of oyster habitat (zu Ermgassen et al., 2025a, 2025b) and the risk of poaching, precise locational information is redacted on the advice of the statutory nature conservation agency, NatureScot (https://www.nature.scot/).Basemap source: Esri. "UK Coastline". Data from Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors and the GIS user community. Used under license.

through a 0.5 mm mesh to separate infauna and fixed with 4% formaldehyde solution. Infauna were subsequently identified in the laboratory to the lowest possible taxonomic level and enumerated by Shalla Benthic Identification Services.

2.3. Statistical analysis

Epibiotic and infaunal sampling involved different methods and captured different components of species diversity, therefore the analyses for each were conducted separately. Analyses primarily focused on differences between Oyster and No Oyster treatments, with Location and Depth included as additional explanatory factors to account for spatial variability.

Species abundance data were used to calculate Shannon-Wiener's diversity indices (H′), using Primer v7 (Clarke and Gorley, 2015). Epibiotic data were transformed from SACFOR scale into numerical data using the methods set out in Strong and Johnson (2020). This method takes percentage cover and body size into account allowing for a more unified dataset, accounting for highly abundant species. Sources such as www.marlin.ac.uk were used to determine a standard size category for species in the data transformation.

R (R Core Team, 2025) was used to perform a general linear model (GLM) to examine the effects of Location, Treatment and Depth and their interaction on Shannon-Wiener's diversity, using the following model:

$$\text{Location}^{*}\ \text{Treatment} + \text{Treatment}^{*}\ \text{Depth}$$

Where: Treatment = Oyster vs No oyster; Location = Dornoch vs Loch Ryan 1 vs Loch Ryan 2 vs Mull vs Skye; Depth = Deeper vs Shallower.

Depth and Location were included as explanatory variables to account for spatial and environmental variation among sites, which spanned a wide geographic range and encompassed both subtidal and infralittoral areas. Due to relatively low replication, the statistical power to detect interaction effects within the GLM analyses may have been limited.

2.4. Biological trait analysis

A biological trait analysis (BTA; Paganelli et al., 2012), was used to investigate how the presence of oysters influenced the functional traits present in the biotic community. Again, separate analyses were carried out for the epibiotic and infaunal data sets. In both cases only species identified to a minimum of family level were used.

The epibiotic data were compared against four biological traits with twelve characteristic modalities (Table 2) and for the infaunal data, three biological traits subdivided into 13 characteristic modalities (Table 3) were used to describe the important functional attributes of the macrobenthic faunal community associated with the oyster reef (Paganelli et al., 2012; Kent, 2015; Beauchard et al., 2017). Traits were chosen that could potentially assist the enhancement of species diversity either through further habitat creation (e.g. tube forming) or modification (e.g. bioturbation). Online sources such as Marlin (www.Marlin.ac.uk) and WoRMs (www.marinespecies.org) as well as academic literature were used to inform on trait categories for each species. Trait values 0 or 1 were assigned where 1 is the highest affinity and 0 where there is low or no affinity in a "Species x Trait" matrix.

The "Species x Trait" matrix was combined with the species abundance table to create an "Sample x Trait" matrix which showed the

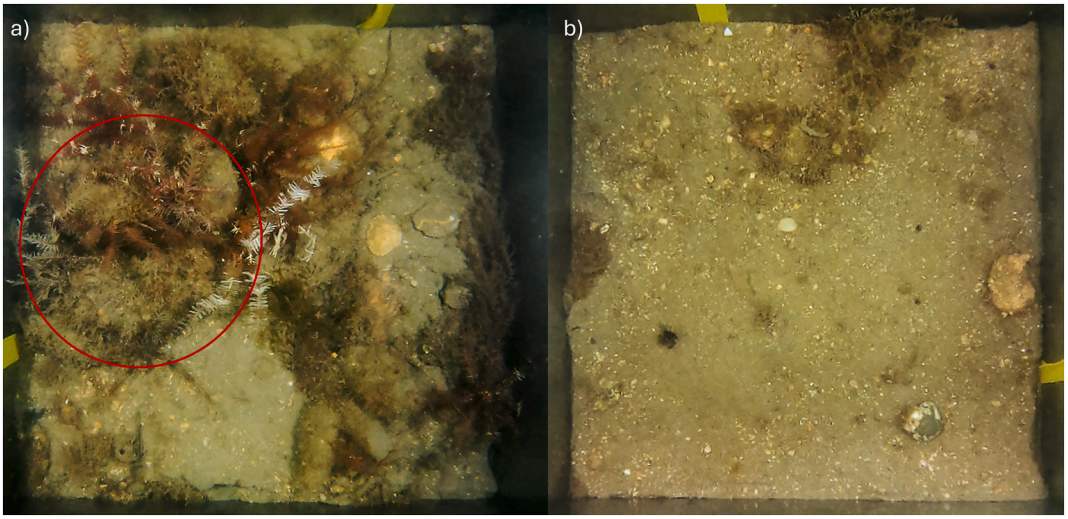

Fig. 2. Example Box cores: An overhead view of a typical box core. a) Loch Ryan 1 treatment 'Oyster" (two live oysters indicated in red circle). b) Loch Ryan 1 control "No oyster". Box core area was 25 × 25 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Epibiota biological trait categories for BTA (Paganelli et al., 2012; Kent, 2015; Beauchard et al., 2017).

Trait	Characteristic	Label	Justification
Living habit	Sessile	L1	Oyster presence may influence habitat structure and spatial niche availability (Grabowski et al., 2005; Ysebaert et al., 2019; Reeves et al., 2020).
	Tube/burrow	L2	
	Errant	L3	
Feeding habit	Active suspension	F1	Resource acquisition strategies and contributions to nutrient cycling may vary with oyster presence (Grabowski et al., 2005).
	Passive suspension	F2	
	Primary producer	F3	
	Other	F4	
Degree of attachment	Permanent	D1	Assessing how strongly organisms attach to substrates indicates the role of oysters as a stable physical structure for settlement (Royer et al., 2006; Ysebaert et al., 2019; Reeves et al., 2020).
	Temporary	D2	
	None	D3	
Habitat creation ability	Above sediment 3D structures	H1	Oyster presence may enhance secondary habitat formation as species modify their environment (e.g. tube-building) (Grabowski et al., 2005; Ysebaert et al., 2019; Reeves et al., 2020).
	None	H2	

Table 3
Infaunal biological trait categories for BTA (Paganelli et al., 2012; Kent, 2015; Beauchard et al., 2017).

Trait	Characteristic	Label	Justification
Living habit	Surface	L1	Oyster presence may influence habitat structure and spatial niche availability (Grabowski et al., 2005; Ysebaert et al., 2019; Reeves et al., 2020).
	Burrow dwelling	L2	
	Tube dwelling	L3	
	Burrower/ Crawler	L4	
Feeding habit	Suspension	F1	Resource acquisition strategies and contributions to nutrient cycling may vary with oyster presence (Grabowski et al., 2005).
	Deposit	F2	
	Scavenger	F3	
	Predator	F4	
	Scraper/grazer	F5	
	Parasitic	F6	
Degree of Bioturbation	None	B1	Oyster presence may influence organic carbon availability in the sediment. (Lee et al., 2024)
	Passively	B2	
	Actively	B3	

abundance of each trait in each sample. A permutational multivariate analysis of variance (PERMANOVA), using Bray–Curtis dissimilarities, was used to determine if significant differences in trait composition were due to Treatment, Location or an interaction between both Treatment and Location (Primer v7; Clarke and Gorley, 2015). Depth was not included as a factor in this model as it is confounded with Location. SIMPER was used to compare traits between the treatments to determine if there were any functional differences within the infaunal and epibiotic communities between the "Oyster" and "No Oyster" samples. Where significant trends in the biological traits were detected a Principal Component Analysis (PCA) of biological trait data performed in PRIMER was performed. Overlaid vectors were used to represent the biological traits that exhibit the strongest correlations with the ordination axes, highlighting the principal contributors to variation in trait composition among samples.

3. Results

3.1. Species diversity

A total of 71 epibiotic species were recorded across the sites. Although spatial variation among locations was detected, the primary objective of this study was to quantify differences associated with oyster presence. Consequently, results are presented with emphasis on treatment-level patterns. The highest average Shannon Wiener's diversity index was from the Loch Ryan 1 (Fishery) "Oyster" and the lowest average Shannon Wiener's diversity index from the Skye "No Oyster" (Fig. 3). The samples with oysters present at the deeper (4.5–5.5 m) sites showed on average 17% greater epibiotic diversity and the shallower (0-1 m) sites had 84% greater epibiotic diversity.

The GLM showed significant main effects of Treatment, Location and Depth on epibiotic Shannon-Wieners diversity. Treatment had a significant effect ($F_{1,34} = 40.47$, P-value <0.001), as did Location ($F_{4,35} = 45.50$, $P < 0.001$) and Depth ($F_{1,37} = 1.38$, $P < 0.001$). However, there was no significant effect observed from either of the interaction terms, with no significant Location: Treatment interaction ($F_{4,\ 30} = 1.38$, P-value = 0.215) and no significant Depth: Treatment interaction ($F_{1,36} = 1.38$, P-value = 0.247). A total of 219 species were recorded from infaunal samples. The Loch Ryan 'Oyster' samples were found to have the highest average species diversity whereas the Skye 'No Oyster' samples had the lowest average species diversity (Fig. 4). Overall, the samples with oysters present at the deeper sites, showed a small increase

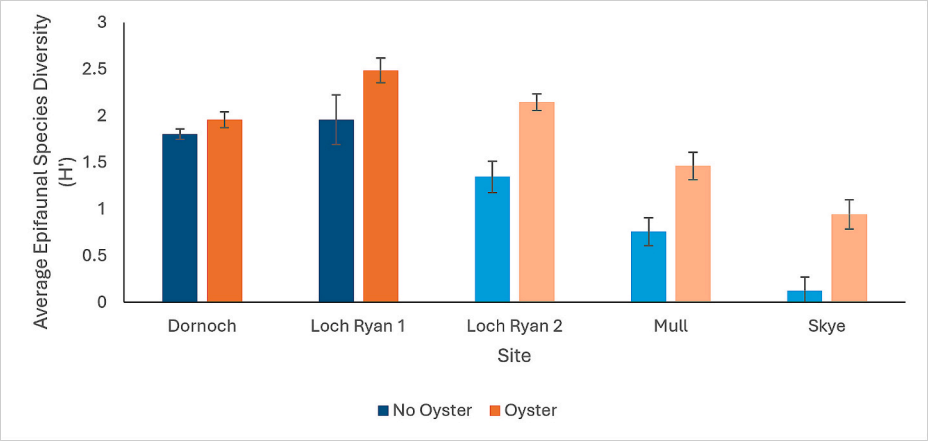

Fig. 3. Epibiotic Diversity: Average Epibiotic Shannon Wiener's diversity (H′) for "Oyster" and "No Oyster" at each site. Sites at a shallower depth (<2 m) denoted in lighter colours. Error bars are Standard Error. *Indicates significant differences between treatments at each location.

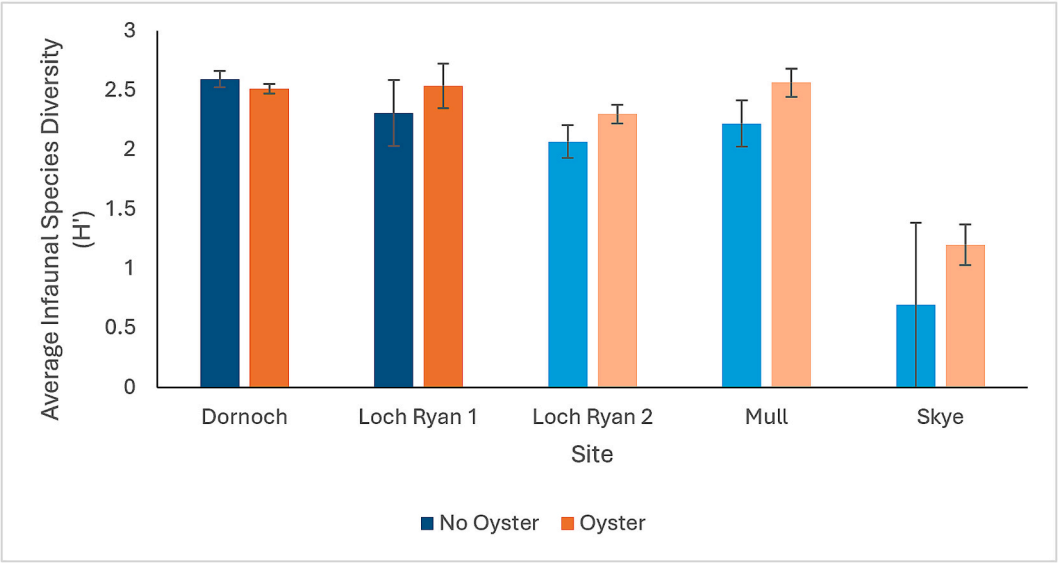

Fig. 4. Infaunal Diversity: Average Infauna Shannon Wieners diversity (H′) for "Oyster" and "No Oyster" at each site. Sites at a shallower depth < 2 m denoted in lighter colours. Error bars are Standard Error.

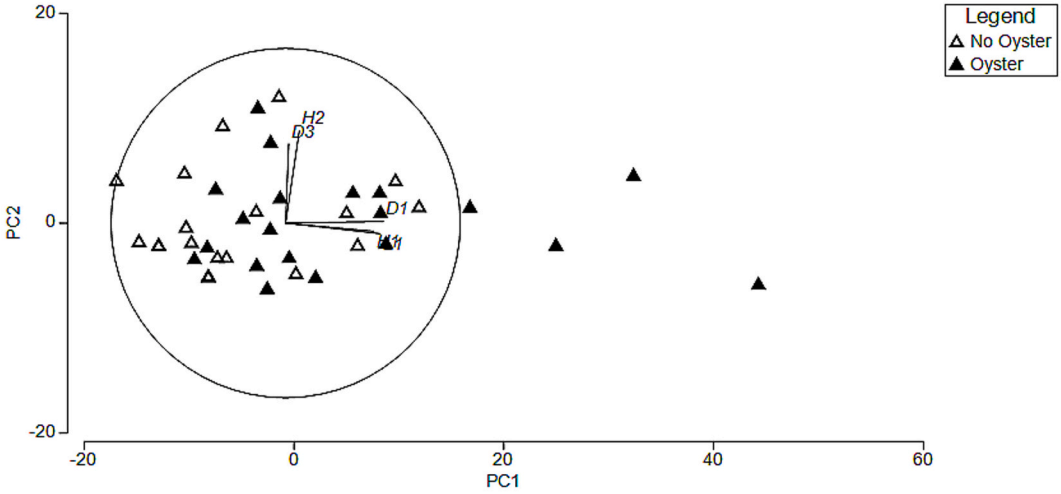

Fig. 5. Epifaunal Biological Traits: PCA of Epifaunal biological trait data performed in PRIMER. Overlaid vectors represent the biological traits most strongly correlated with the ordination axes, with vector length proportional to the strength of the correlation.

of 3% in infaunal diversity and samples at the shallower sites showed a increase of 9% in infaunal diversity.

The GLM showed no significant effect of Treatment on infaunal Shannon-Wiener's diversity ($F_{1,32}$ = 3.9816, P-value = 0.06512) and there was no significant effect observed from the interaction of Location: Treatment ($F_{4,28}$ = 0.6112, P-value = 0.65799) or Depth: Treatment ($F_{1,34}$ = 0.0578, P-value = 0.811429). However as with the epibiotic data, Depth ($F_{1,35}$ = 8.2790, *P*-value = 0.006882) and Location ($F_{4,33}$ = 18.8497, P-value <0.001) were each significant as factors.

3.2. Biological trait analysis

PERMANOVA showed a significant difference in epibiotic traits between 'Oyster' and 'No Oyster' treatments ($F_{1,30}$ = 4.6855, R^2 = 0.07973, *P*-value = 0.01). Location was also a significant factor ($F_{4,30}$ = 4.6892, R^2 = 0.31917, P-value = 0.001), whereas the interaction of Treatment and Location was not significant ($F_{4, 30}$ = 1.3312, R^2 = 0.09061, P-value = 0.201). PCA supported these patterns, with samples separating according to treatment and vectors indicating that the traits most strongly associated with the ordination were permanent attachment, sessile, and habitat creation (Fig. 5). SIMPER analysis (Table 4) showed that the epibiotic traits contributing most to the dissimilarity between 'Oyster' and 'No Oyster' treatments were "permanent attachment", "sessile" and "habitat creation". These traits were all more abundant when oysters were present and together accounted for approximately half of the dissimilarity between treatments. Overall, the average dissimilarity in trait abundance between the 'Oyster' and 'No Oyster' treatments was 37.8%.

PERMANOVA analysis revealed Location significantly affected trait abundance ($F_{4,26}$ = 10.3059, R^2 = 0.58156, P-value = 0.001) however there were no significant differences in infaunal traits between Treatments ($F_{1,26}$ = 0.9189, R^2 = 0.01296, P-value = 0.447) or the interaction of Location and Treatment ($F_{4,26}$ = 0.6856, R^2 = 0.03869, P-value = 0.779).

4. Discussion

The present work is the most detailed biodiversity study of European native oyster habitats to date; documenting 290 species across five locations within remnant, restored and fished oyster habitats. The presence of oysters was associated with increased epibiotic diversity and greater representation of traits associated with structural complexity. In contrast, infaunal communities did not exhibit significant biodiversity increase at the scale considered. These findings provide rare empirical evidence that *Ostrea edulis* is an important ecosystem engineer in temperate benthic environments; primarily through the provision of niches for epibiota. Furthermore, this study provides reference data for the biodiversity, community composition and functional traits associated with rare remnant European native oyster habitats, enabling restoration practitioners to support evidence-based restoration targets and assess restoration trajectories. A total of 71 epibiotic species were identified, with significantly higher Shannon-Wiener diversity (H′) recorded at sites where oysters were present. The presence of oysters was a significant predictor of epibiotic diversity, aligning with previous studies linking enhanced species diversity to structurally complex biogenic bivalve reefs (Kent, 2015; Ysebaert et al., 2019; zu Ermgassen et al., 2020; Zempléni et al., 2025; Kennon et al., 2023, 2025), even at low shellfish densities (Fariñas-Franco et al., 2023). Overall, epibiotic diversity was 17% greater in the deeper (4.5–5.5 m bcd) sites and 80% greater in the shallower (0–1 m bcd) sites, this difference is likely reflects a combination of restoration history and environmental variation. The deeper sites included restored and previously fished reefs that may still be developing structural complexity (Kennon et al., 2023, 2025) whilst the shallower sites were largely undisturbed, with no recorded fishing activity. Inherent differences between shallow infralittoral macroalgal communities and deeper circalittoral faunal turf communities likely influenced the benthic assemblage structure (JNCC, 2022). The lack of significant interaction effects between Treatment and Location or Depth in the GLM suggests that the positive influence of oysters on epibiotic diversity is broadly consistent across environmental settings. However, Depth and Location each had significant independent effects when modelled separately, indicating that local environmental conditions also play an important role in shaping this response.

The presence of oysters in an otherwise structurally homogenous environment facilites the settlement of sessile organisms, such as barnacles (*Balanus* sp.), keel worms (*Spirobranchus* sp.), bryozoans, hydroids and algae. These taxa are often dependent on hard substrata and further enhance habitat complexity themselves, creating positive feedback that supports greater epibiotic diversity. Biological trait analysis supports this interpretation with traits such as "permanent attachment," "sessile," and "habitat creation" consistently more abundant in samples containing oysters. SIMPER analysis showed that these traits accounted for 38% of the observed dissimilarity between treatments. This pattern is particularly evident in both Loch Ryan Locations, where trait abundance in 'Oyster' samples was significantly greater for sessile, attached organisms and habitat-creating species. PERMANOVA further underscores the significance of oyster presence on epibiotic trait composition, with both treatment and location explaining a significant proportion of the variation. However, the interaction term was not significant, again suggesting additive rather than synergistic effects. The overall explanatory power of the model (22.9%) suggests that while oysters have a strong influence, other unmeasured factors, such as sediment type, hydrodynamic conditions, or associated algal turfs may also contribute to the trait composition of the community (Grabowski et al., 2005; Reeves et al., 2020).

Contrary to the epibiotic data, the infaunal results were inconclusive. While a total of 219 infaunal species were recorded, substantially more than the epibiotic total, the presence of oysters only resulted in a small and insignificant 7% average increase in Shannon-Wiener diversity. GLM models found no significant effect, suggesting that oyster presence had very little influence on infaunal diversity at this scale. The differing responses of epibiotic and infaunal communities highlight the multifaceted role of oyster habitats in benthic ecosystems. This aligns with findings from other temperate regions where different species of oyster support higher trophic levels, increase recruitment of associated fauna and promote community stability (Grabowski and Peterson, 2007; Zu

Table 4
SIMPER analysis of differences in epibiotic biological traits between 'oyster' and 'no oyster' treatments. (Permanent attachment (D1) Sessile (L1) Above sediment 3D habitat creation (H1) Primary Producer (F3) Active suspension feeder (F1) No habitat creation (H2)) (Diss/SD = Average dissimilarity/Standard Deviation).

Site	Trait	Average Abundance		Average Dissimilarity	Diss/SD	Contribution %
		No Oyster	Oyster			
Dornoch	H2	5.25	5.75	3.51	1.3	10.96
	D3	3.5	3.75	3.42	1.24	10.67
	L1	6.5	6.5	3.22	1.39	10.06
Loch Ryan 1	D1	14	27	7.45	1.55	20.12
	H1	12.5	24	6.59	1.61	17.79
	L1	13	24.25	6.56	1.57	17.71
Loch Ryan 2	D1	8	16.25	7.27	2.39	19.25
	H1	8	16.25	7.27	2.39	19.25
	L1	5	11.75	5.84	2.25	15.46
Skye	D1	5.25	10.75	8.58	3.69	22.16
	L1	3.25	7.75	7.33	1.37	18.95
	H1	5.25	9.5	6.76	2.72	17.47
Mull	D1	6.25	11.5	8.18	1.5	18.8
	H1	4.25	9.5	6.72	1.45	15.43
	L1	3.25	7.75	6.36	1.58	14.62

Ermgassen et al., 2012; Cranfield et al., 2004). Longer timescales or more mature reefs may yield stronger infaunal responses, as biodeposition and organic enrichment processes accumulate (Haven and Morales-Alamo, 1966; Gadeken et al., 2021; Lindenbaum et al., 2008; Rees et al., 2008; Fariñas-Franco et al., 2023). Alternatively, oyster effects may primarily influence the sediment surface and associated epibiota, while the infaunal community remains largely unaffected. This suggests that the ecological value of sediment habitats may be retained even where oysters are absent, highlighting that both oyster reefs and adjacent soft sediments contribute to overall benthic biodiversity. While statistical models explained a moderate proportion of variance, unmeasured factors such as sediment grain size, organic content, water quality and fishing pressure could influence the observed patterns. Additionally, while trait-based analyses provide functional insights, they are inherently limited by the resolution and accuracy of trait categorization and abundance estimates.

The present work highlights the importance of *Ostrea edulis* as an ecosystem engineer capable of supporting diverse and functionally rich epibiotic assemblages. Restoration efforts that reintroduce oysters to historical sites aim to re-establish such ecosystem services (Hughes et al., 2023). However, the scale of such effects has been elusive and likely dependant on environmental conditions and restoration design (zu Ermgassen et al., 2020). By improving our understanding of the biodiversity consequences of oyster reef restoration, this study provides evidence to inform restoration targets and evaluate ecological outcomes. The demonstrated enhancement of epibiotic diversity highlights the ecological benefits of restoring habitat-forming specie as such as *O. edulis* and supports their inclusion in marine conservation strategies (Cavanagh et al., 2016; Hillebrand et al., 2026). Field-based ecological data, such as these, provide an important evidence base for prioritising interventions and guiding legislation, by explicitly linking structural habitat provisioning with biodiversity outcomes. This is particularly relevant in the context of current global biodiversity goals, where ecosystem restoration is a cornerstone of long-term environmental resilience (Díaz et al., 2020; CBD, 2022; European Parliament, 2024).

CRediT authorship contribution statement

Naomi Kennon: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alex Robertson-Jones:** Investigation. **Gurjameer Ramday:** Investigation. **Michela Iodio:** Investigation. **Magnus Janson:** Investigation. **Salma Shalla:** Investigation, Data curation. **Debbie McGregor:** Investigation, Data curation. **Francis Bunker:** Investigation, Data curation. **Owen Paisley:** Investigation. **Brodie Thomas:** Writing – review & editing. **Cass Bromley:** Writing – review & editing. **James Mair:** Writing – review & editing, Investigation. **Michael C. Bell:** Writing – review & editing, Supervision, Methodology, Conceptualization. **William G. Sanderson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2026.120179.

Data availability

Data will be made available on request.

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