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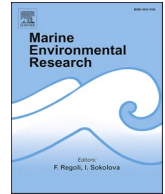
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Unveiling functional linkages between habitats and organisms: Macroalgal habitats as influential factors of fish functional traits

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ABSTRACT

Understanding the relationship between the characteristics of habitats and their associated community is essential to comprehend the functioning of ecological systems and prevent their degradation. This is particularly relevant for in decline, habitat-forming species, such as macroalgae, which support diverse communities of fish in temperate rocky reefs. To understand the link between the functional habitats of macroalgae and the functional dimension of their associated fish communities, we used a standardized underwater visual census to quantify the macroalgal functional diversity, as well as the functional diversity, redundancy, and richness of fish communities in 400 sites scattered in three southern temperate marine realms. Our findings reveal that functional macroalgal habitats can be classified into three groups that shape the functional diversity, redundancy, and richness of fish when considering trait commonness. These results enhance our comprehension of the functional connections between the habitat and coexisting fish within marine ecosystems, providing valuable insights for the preservation of these habitats.

1. Introduction

Functional habitats are physical and ecological characteristics or components that provide the structural amenities for an associated community of organisms, shaping the distribution and survival of species. (Harper et al., 1992; Kemp et al., 1999; Buffagni et al., 2000). These functional habitats can be defined by the traits of the ecosystem engineering organisms that provide habitat structure refuge space and foraging resources for other organisms (McGill et al., 2006). For instance, corals can be characterized by volume compactness or surface complexity (Zawada et al., 2019), whereas for macroalgae, differences in the consistency and complexity of the thallus distinguish different functional groups, e.g., leathery, corticated, or foliose that present important differences for reef fish and invertebrates utilizing these resources (Steneck and Dethier 1994; Jänes et al., 2016; Cresswell et al., 2017). High functional diversity in traits related to structural morphology results in structurally complex habitats, which offer a more diverse range of refuges and feeding resources for organisms from millimeter-size to large life forms (Kovalenko et al., 2012).

Unsurprisingly, numerous studies have demonstrated that these habitats play a crucial role in determining many aspects of the associated community, including its productivity, the size of individuals, as well as the species composition and richness (MacArthur and MacArthur 1961; Gardner et al., 1995; Downes et al., 1998; Srednick and Steele 2022). Anticipating the consequences of the ongoing global changes in marine communities requires understanding how these functional habitats shape their associated communities (Madin et al., 2016).

Here we investigate the link between the functional habitats of macroalgae and the functional characteristics of their associated fish communities in the temperate rocky reefs of the Southern hemisphere. Several studies have explored the relationship between functional habitats and the taxonomy of their associated community in multiple ecosystems (Tews et al., 2003; Buffagni et al., 2000; Anderson and Millar 2004; Thiriet et al., 2016). However, understanding the mechanisms of these associations requires to adopt a functional approach that links the functional characteristics of the habitats (here, functional groups of macroalgae), to the traits of the organisms living within it (Nooten et al., 2019; De Bello et al., 2021) – a perspective that has received limited

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attention in the literature on marine communities (Darling et al., 2017; Sgarlatta et al., 2022). Studying the traits of organisms living in functional habitats has several benefits. First, it allows us to go beyond the traditional taxonomic approach and promote a better understanding of the variety of functional roles played by species within a community (Petchey and Gaston 2006). Second, it is known that functional richness, diversity, and redundancy of a community are associated with fundamental properties, such as resilience and stability of ecosystems (Folke et al., 2004; Schmitt et al., 2020; Biggs et al., 2020). Therefore, this functional approach can help preserve and enhance the health of the ecosystem and the services provided. Finally, this functional perspective has a unifying ability to predict functional associations between habitats and species, regardless of the particular biogeography of species (Stuart-Smith et al., 2013; Helder et al., 2022). Thus, the use of a functional approach appears particularly appropriate for comprehending the functional links between habitats and the ecological traits of associated fish communities.

Macroalgal habitats have declined worldwide by 61% in the last 20 years, due to multiple stressors, such as climate change (Duffy et al., 2019), sediment and nutrient loading (Foster and Schiel 2010), or direct harvesting (Vásquez et al., 2014). As expected, declines in functional habitats such as macroalgae can affect the organisms living in them, as well as their functions. Recently, Duarte et al. (2020) found that the structural complexity of the macroalgal habitat influenced the functional traits of the mollusk community, such as feeding strategy, body size, and larval development. However, results have been more variable for fish communities. While recent studies showed a positive relationship between the density of juvenile fish and heightened macroalgal structural complexity (Cheminné et al., 2017), additional studies, such as Sgarlatta et al. (2022), did not observe discernible differences in the functional composition of fish across habitats characterized by varying levels of macroalgal complexity, specifically comparing rocky reefs and kelp forests. Thus, while macroalgal cover losses imply a reduction in structural functional habitat, with most likely negative consequences for the associated biodiversity and ecosystem services provided (Eger et al., 2023), there appears to be considerable variation in the magnitude of this effect. Improved assessments of the functional connections between the habitat and the coexisting species within it are essential to enable informed predictions about how ecosystems will respond to future scenarios.

This study presents a large-scale empirical assessment of trait-based relationships between macroalgal functional habitats (hereafter, macroalgal habitat) and functional dimensions of fish in temperate rocky reefs. We use Reef Life Survey underwater visual census data (Edgar et al., 2020) across an extensive gradient of macroalgal functional diversity and fish functional metrics (diversity, redundancy, richness, and composition) in three temperate realms of the world: Australasia, Southern Africa, and South America. We hypothesized that macroalgal habitats conditioned the functional dimension of marine fish. Our findings show that macroalgal habitats shape fish functional diversity, redundancy, and richness when considering fish trait frequency. Macroalgal habitats also modulate the functional composition of the fish community. Through this research, we emphasize the study and monitoring of functional relationships between habitats and organisms. Understanding these relationships will eventually allow us to identify which functions of coexisting organisms would be affected by the disappearance of functional habitats.

2. Material and methods

2.1. Study area and underwater visual census

We utilized a standardized quantitative dataset of macroalgal cover and fish density from Reef Life Survey (RLS, hereafter; Edgar et al., 2020). The macroalgal cover dataset collated 649 underwater visual, 50-m long transects, and the fish dataset collated 1459 visual transects

at 400 sites sampled collected between 2014 and 2019. These sites were distributed in three temperate marine realms around the Southern hemisphere: Australasia, Southern Africa, and South America (Fig. 1 and Table 2S; Spalding et al., 2007).

RLS methodology quantifies the macroalgal cover by taking 20 high-quality pictures of the seafloor every 2.5 m along the 50 m of the belt transect. Full details of the standardized methods are available online (Reef Life Survey Foundation, 2023). The density of fish was quantified by visually counting them within an area of 500 m² (2 × 250-m² blocks), and sizes were converted into biomass metrics using species-specific length-weight relationships available in FishBase (Froese and Pauly 2000).

2.2. Quantifying macroalgal functional diversity

In each photoquadrat image, five points (in a quincunx pattern) were overlaid using Squidle+ (a centralized marine image data management platform) and labelled according to the underlying biota. Each point was classified into one of five functional groups of macroalgae: Articulated calcareous, Corticated foliose, Corticated macrophytes, Foliose, and Leathery macrophytes (Steneck and Dethier 1994). We selected these functional traits of macroalgae because they provide essential components for habitat formation, including structural complexity, providing shelter, food resources, and protection against predation (Steneck and Dethier 1994; Duarte et al., 2020). We then applied the arcsine square root transformation to the percentage of macroalgal functional cover in each transect to approach normal distributions. Using the transformed data, we calculated the macroalgal functional diversity based on the inverse of the Simpson's index in each transect (i.e., a sample of 20 quadrats) using the *diversity()* function of the R vegan package. Finally, we averaged the transect diversity indices to obtain the macroalgal functional diversity score at each location.

2.3. Classifying macroalgal habitats

We used the *modetest()* function of the multimode package to investigate the number of modes in the distribution of macroalgal functional diversity. Because this suggested the presence of three modes meaning three distinct and broad ranges of functional diversity. Subsequently, we utilized a Gaussian mixture model-based classification algorithm applying the *Mclust()* function of the Mclust package, unveiling three macroalgal habitats characterized by low, intermediate, and high functional diversity (Fig. 2).

2.4. Functional traits, frequency, and biomass-related fish functional metrics

To understand how macroalgal habitats can influence the functional roles of fish, their interactions, and the contributions of different species to ecosystem processes, we classified fish species into four pivotal functional traits: gregariousness (forming schools, solitary, and paired); substrate preference (hard bottom or soft sediment); trophic level (browsing herbivore, benthic invertivore, higher carnivore, planktivore, and scraping herbivore); and water position (benthic, demersal, and pelagic), (Fishbase; Froese and Pauly 2000; Table S1). Analyzing these traits within a fish community is crucial for understanding functional patterns, niche differentiation, and trophic interactions, providing valuable insights into the functional diversity and dynamics that contribute to the structure and functioning of the community. Moreover, these traits offer information about physiological, reproductive, behavioral, and ecological attributes that influence how species interact with their environment and perform ecological functions (Stuart-Smith et al., 2013, Lazzari et al., 2020). We also investigated whether the commonness (i.e., the number of times they appear across the entire study area) of functional traits influenced the functional characteristics of the fish community at each macroalgal habitat. For that purpose, we



Fig. 1. Map of the study area, representing the sampled sites as dots. Dots indicate the sampling sites. Darkness in the shading intensifies as more sites overlap (N = 400).

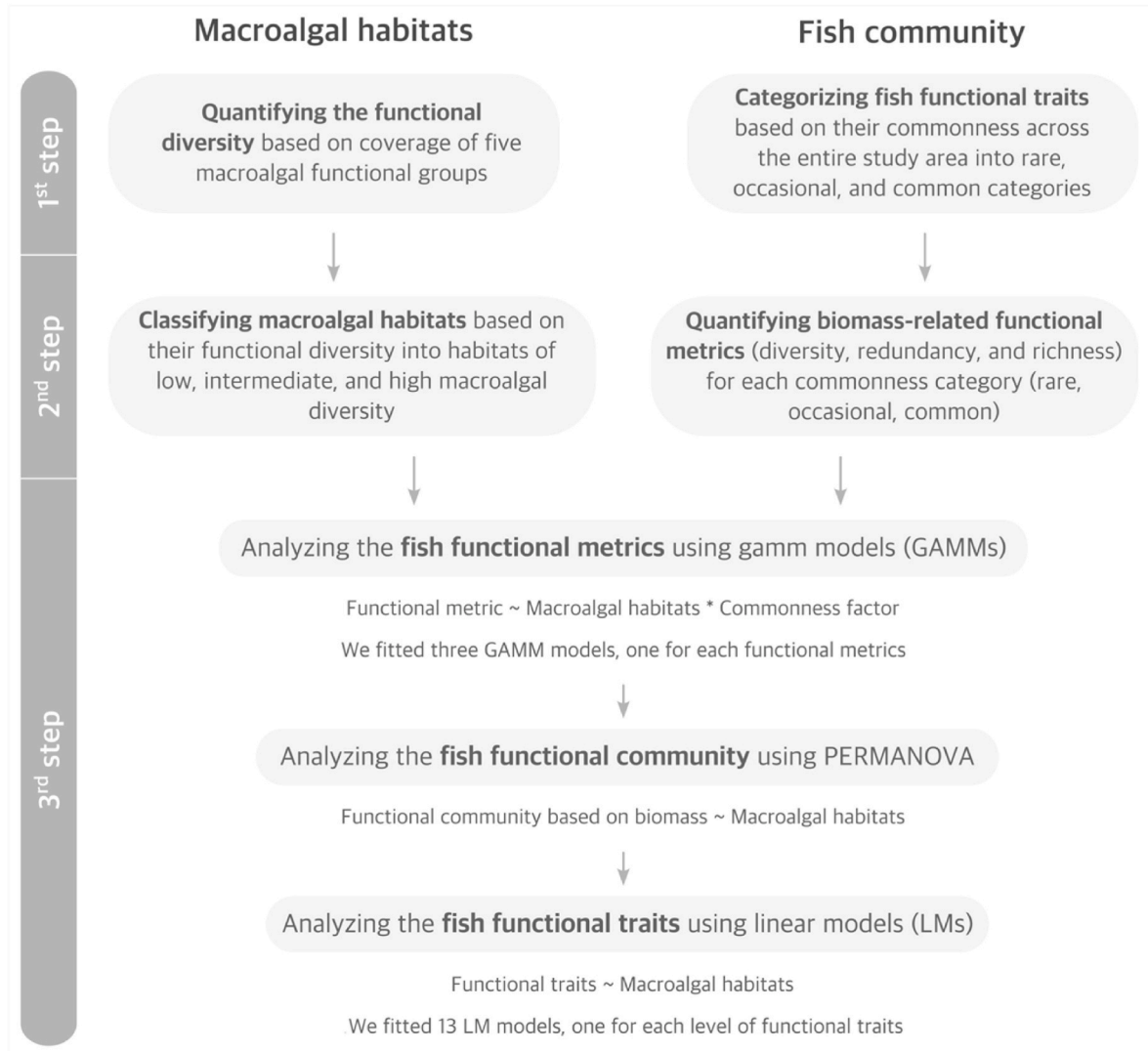


Fig. 2. Workflow of our study with the three essential methodological steps.

categorized fish trait levels into rare, occasional, and common traits levels based on the number of sites sampled in which trait levels were found (Fig. 2). Out of the 400 sites sampled, we defined rare trait levels as those occurring in $\leq 30\%$ of the sites (i.e., 120 sites or less), common trait levels as those occurring in $\geq 70\%$ of the sites (i.e., 280 sites or more), and occasional trait levels as those that occurred between $>30\%$ and $<70\%$ of the sites (i.e., 121 and 279 sites). We have selected these percentages because they ensure representation of the diverse functional levels of fish, allowing us to uncover patterns and underlying characteristics of each frequency group (Sanabria-Fernández et al., 2018). This

approach allows taking into account the commonness of traits in the fish community, which is important as not all environmental filters or ecological disturbances affect the functional trait of fish equally. It is important to note that the commonness category classified trait levels regardless of the number of species and biomass at each site.

Before calculating fish functional indicators, we also transformed fish biomass using $\log(x+1)$. Using the transformed biomass of fish species, we computed three fish functional metrics at each commonness category (i.e., rare, occasional, and common, Fig. 2). First, we calculated the functional diversity metric based on Rao's quadratic entropy of the

fish community, applying the *rao.diversity()* function available in the SYNCSA package. Functional diversity refers to the variety and range of functional traits and characteristics exhibited by different species within a community. Second, we computed the functional redundancy metric as $1-(Fdiv/Taxdiv)$ where *Fdiv* is the functional diversity measured by the Rao quadratic entropy index and *Taxdiv* is the taxonomic diversity measured by Simpson's index (De Bello et al., 2021). Functional redundancy informs us of species that perform similar functions, which are, from a purely functional point of view, interchangeable with little impact on ecosystem processes (Walker 1992; De Bello et al., 2021). Third, we also estimated the functional richness as the total number of present trait levels across all four traits in a community, representing the diversity and range of traits maintained by different fish species (Mayfield and Daily 2005). We computed these three functional metrics at the transect levels (i.e., in 1459 transects) and obtained the site means by averaging the transects according to their respective sites (i.e., 400).

2.5. Effects of the macroalgal habitat on the fish functional dimension

We followed three analytical approaches to evaluate the effect of macroalgal habitats on the functional characteristics of the fish community. First, we fitted the first set of Generalized additive mixed effect models (GAMMs, hereafter), consisting of three models i.e., one for each fish metric (diversity, redundancy, and richness), with the functional metric as the response variable, and macroalgal habitat as the sole fixed factor, i.e., without considering the commonness of fish traits. We then fitted a second set of GAMMs, where we tested the effects both for macroalgal habitats and commonness of fish traits. To this end, we included the fish metrics as the response variable and the macroalgal habitats and commonness of fish traits as a fixed factor. In both sets, we used the *gamm()* function of the *mgcv* package, including the sampling sites as a random factor to consider the spatial pseudoreplication and the latitude and longitude as covariates to take into account the spatial autocorrelation (Wood, 2017).

In the second set of analyses, we used PERMANOVA to test whether the biomass-based fish functional community depended on the macroalgal habitats. This approach extends the previous analyses because it estimates multivariate relationships between macroalgal habitats and fish functional structure. We used the *adonis()* function in the *vegan* package with 999 permutations. Specifically, we fitted the permanova model by including the Bray-Curtis distance of biomass of fish functional traits as response variables and macroalgal habitats as a fixed factor.

In the third set of analyses, we explored the effects of macroalgal habitats on fish functional traits from a univariate perspective. We

looked for fish traits changing their biomass when comparing between macroalgal habitats. To do this, we fitted a set of linear models to the multivariate biomass of fish functional traits using the *manyglm()* function in the *Mvabund* package. In these linear models, fish trait biomass was the response variable, and we included macroalgal habitats as a fixed factor.

We performed data processing and statistical analyses in R programming language (R Core Team, 2023). We used the following packages: *Mclust* (Scrucca et al., 2016), *Mvabund* (Wang et al., 2016), *mgcv* (Wood 2011), *multimode* (Ameijeiras-Alonso et al., 2021), *rfishbase* (Boettiger et al., 2012), *SYNCSA* (Debastiani and Pillar 2012), and *vegan* (Oksanen et al., 2022).

3. Results

3.1. Identifying the macroalgal habitats

We identified three macroalgal habitats based on the trimodal distribution of the functional diversity metric (ARC-test, $p < 0.001$; Fig. 3). The first macroalgal habitat had low-diversity scores between 0 and 0.33 (average \pm standard error; 0.05 ± 0.02). The second habitat gathered intermediate-diversity scores, between 0.65 and 2.13 (1.51 ± 0.03). Lastly, the third habitat showed high-diversity scores, between 2.15 and 3.87 (2.65 ± 0.03).

3.2. Effects of macroalgal habitats on the fish functional dimension

We found no statistical differences in fish functional diversity across macroalgal habitats (GAMMs, $df = 2$, $F = 1.66$, $p\text{-value} = 0.19$). However, when we fitted the model by adding the commonness of fish traits, we found that the two-way interaction between macroalgal habitats and commonness was significant (Fig. 4a; Table 1a). For rare and common traits, fish functional diversity scores were higher in low-diversity habitats (0.06 for rare and 2.64 for common traits), intermediate in high-diversity habitats (0.04 and 2.63), and lower in intermediate-diversity habitats (0.03 and 2.56). Low-diversity habitats decreased their contribution to functional diversity as commonness increased (44.42%, 37.61%, and 33.74% for rare, occasional, and common traits, respectively, Fig. 4a).

Fish functional redundancy was not found to differ between macroalgal habitats (GAMMs, $df = 2$, $F = 1.19$, $p\text{-value} = 0.3$). However, when we fitted the model by adding the commonness of fish traits, the two-way interaction between macroalgal habitats and commonness was significant (Fig. 4b; Table 1b). Specifically, habitats with intermediate-

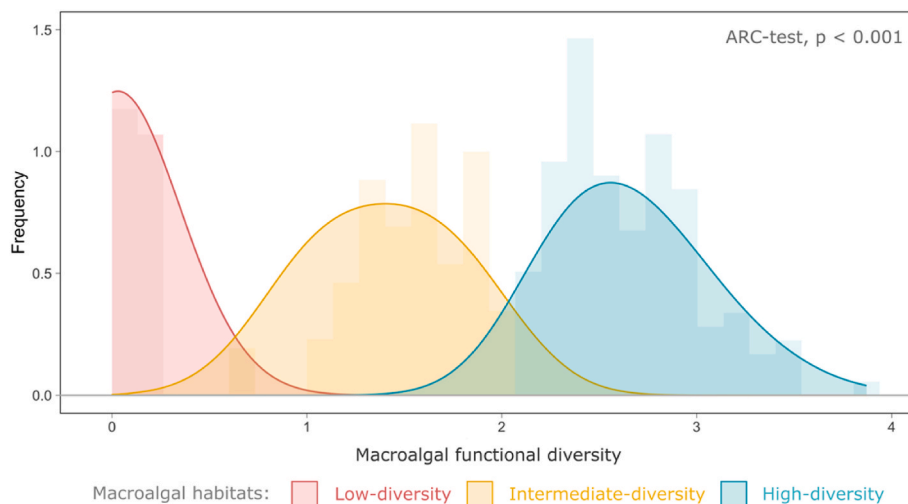


Fig. 3. Multimodality frequency (bars) and density distribution graph of the functional diversity of macroalgae. The colors represent the classification of bins, determined by the three macroalgal habitats identified using the McClust model.



Fig. 4. Percentage of functional a) diversity, b) redundancy and c) richness found in macroalgal habitats according to the commonness of fish functional traits (rare, occasional, and common). Numbers within bars are the average of fish functional a) diversity, b) redundancy, and c) richness pooled across macroalgal habitats as a function of fish trait commonness factor (rare, occasional, and common).

Table 1
Summary of the GAMMs models on fish functional metrics: a) diversity, b) redundancy, and c) richness.

Functional metric	Factors	df	F	p-value
a) Diversity	Macroalgal habitat	2	3.17	<0.05
	Commonness	2	252.24	<0.001
	Macroalgal habitat * Commonness	4	9.55	<0.001
b) Redundancy	Macroalgal habitat	2	1.91	0.15
	Commonness	2	478.63	<0.001
	Macroalgal habitat * Commonness	4	7.99	<0.001
c) Richness	Macroalgal habitat	2	2.6	0.07
	Commonness	2	996.59	<0.001
	Macroalgal habitat * Commonness	4	2.98	<0.05

diversity in macroalgal traits decreased their functional redundancy contribution as commonness increases (83.54%, 38.65%, and 32.92% for rare, occasional, and common traits, respectively, Fig. 4b). Conversely, we found an opposite pattern in high-diversity habitats, increasing their redundancy contribution as commonness increases (16.46% for rare, 22.53% for occasional, and 33.12% for common traits, Fig. 4b).

Functional richness did not show statistical differences between macroalgal habitats (GAMMs, $df = 2$, $F = 0.01$, p -value = 0.98). But once again, the two-way interaction was significant when we fitted the model with the macroalgal habitats and the commonness of fish traits (Fig. 4c; Table 1c). For rare and common traits, the functional richness was higher in low-diversity habitats (0.06 for rare and 9.42 for common traits), intermediate in high-diversity habitats (0.04 and 8.9), and lower in intermediate-diversity habitats (0.03 and 8.8).

Our second set of analyses revealed that the biomass-based fish functional composition depended on macroalgal habitats (Permanova; Pseudo-F = 3.93, $df = 2$, p -value = 0.008). From the results revealed by the third set of analyses, we found that nine of the 13 levels of functional traits, including gregariousness, substrate preference, trophic level, and position in the water, reflected a significant relationship with macroalgal habitats (Fig. 5; Table 2).



Fig. 5. Bar plots representing the fish biomass of trait levels pooled across macroalgal habitats, with error bars corresponding to standard errors. Asterisks denote a statistical difference ($p < 0.05$) in fish trait biomass between macroalgal habitats (Table 2).

Table 2
Summary of the Linear models on the biomass fish traits levels.

Trait	Trait level	Factor	F	p-value
Gregariousness	Forming schools	Macroalgal habitat	5.85	<0.001
	Solitary	Macroalgal habitat	3.04	<0.05
	Paired	Macroalgal habitat	2.43	0.07
Substrate preference	Hard bottom	Macroalgal habitat	3.54	<0.05
	Soft sediment	Macroalgal habitat	6.99	<0.001
Trophic level	Browsing herbivore	Macroalgal habitat	0.48	0.59
	Benthic invertivore	Macroalgal habitat	3.68	<0.05
	Top predator	Macroalgal habitat	4.24	<0.05
	Planktivore	Macroalgal habitat	8.82	<0.001
	Scraping herbivore	Macroalgal habitat	0.44	0.62
Water position	Benthic	Macroalgal habitat	4.13	<0.05
	Demersal	Macroalgal habitat	3.61	<0.05
	Pelagic	Macroalgal habitat	2.03	0.13

4. Discussion

Habitats play a crucial role in determining many aspects of the associated community, including its productivity, the size of individuals, as well as the species composition and richness (MacArthur and MacArthur 1961; Gardner et al., 1995; Downes et al., 1998; Srednick and Steele 2022). However, the linkages between the functional characteristics of the marine habitats and the organisms living within them are poorly explored in temperate rocky reefs (Sgarlatta et al., 2022). We investigated whether and how macroalgal habitats shaped the functional dimension of fish communities. Our findings show that macroalgal habitats can be classified into three groups that shape the functional diversity, redundancy, and richness of fish when considering trait frequency, and modulate the functional structure of fish communities. Most fish traits responded to changes in macroalgal habitat, suggesting the presence of non-random associations of fish traits with macroalgal habitats. Taken altogether, these results support the view that the functional characteristics of macroalgal habitats are fundamental drivers of the functional dimension and composition of fish communities.

The diversity of functional groups of ecosystem engineers determines macroalgal habitats (Steneck and Dethier 1994; Berke 2010). One potential way to measure habitat functionality is by quantifying the diversity of these functional groups of the ecosystem engineers, i.e., the macroalgae in this study. Here, we use two components to detect macroalgal habitat types: functional groups coverage and the functional diversity of macroalgae. This approach not only unveils the diversity of functions present but also emphasizes how these functions uniquely contribute to the habitat's functionality. Therefore, the functional diversity of macroalgae enables a precise characterization of the heterogeneity and complexity of biological communities, emphasizing the importance of functional attributes in the structure and dynamics of the described macroalgal habitats. An alternative way to identify habitats was developed by Cresswell et al. (2017), using the coverage of macroalgal functions together with ecosystem engineering animals (e.g., sponges or corals) and the type of substrate, broadly revealing four marine habitats (i.e., canopy algae, barren, epiphytic algae-understorey, and turf) in the Australian temperate realm. Despite using different

methods to characterize habitats, in both studies hypothesize that an increased functional structural diversity of macroalgae made the habitat more functionally heterogeneous, providing an array of multiple refugia and food resources for resident organisms (Kovalenko et al., 2012). These macroalgal habitats may condition the functional dimension of the coexisting organisms, as shown here. The study of the functional relationship between habitats and traits of the associated biological community allows us to understand the functioning of communities beyond the taxonomic perspective (Helder et al., 2022). While the results are significant, it's crucial to acknowledge potential limitations and address them in future research. For example, addressing the heterogeneity in sampling effort and ensuring equitable representation across each marine realm is imperative for guaranteeing the generalizability of our findings. Additionally, our study utilized five functional traits of macroalgae to describe the functional habitat. Expanding this number by incorporating new traits, such as filamentous or turf, could provide a more complete view. Another consideration is the potential limitation of not accounting for intraspecific variability in fish species' traits across different life stages. Although we selected traits predominant throughout the life cycle, future research might benefit from integrating traits exhibited at various life stages or establishing generic categories accommodating intraspecific variability.

Nine trait levels out of the 13 included in this study, corresponding to the four traits: gregariousness, substrate preference, trophic level, and water position, showed a significant relationship with the macroalgal habitats (Fig. 5). Overall, the habitat with the lowest macroalgal functional diversity presented higher biomass scores for all fish functional traits (Fig. 5). Worthy of mention are the results of top predators, as 45% of the biomass for this trait was found in low-diversity habitats, 32% in intermediate-diversity habitats, and 23% in high-diversity habitats. One possible explanation for these results is that the structure and complexity of the habitat can hinder the efficiency of predators in finding and capturing prey by restricting prey detection and limiting predator movement (Crowder and Cooper 1982; Rilov et al., 2007). Another additional explanation could arise from their behavior, as they typically exhibit remarkable swimming ability (Stuart-Smith et al., 2013). This makes them ideal candidates to act as temporary visitors in low-complexity macroalgal habitats. Although these results could also be derived from the fishing pressure, as this trait is closely linked to fishing, reducing, or even disappearing with high fishing intensity (Pauly et al., 1998). Nevertheless, Helder et al. (2022) found a positive relationship between the presence of solitary, cryptic, and nocturnal predators, and large-scale coral reef complexity. Therefore, further exploration of this relationship is needed to better understand the causal link between habitat and abundance of top predators. Surprisingly, the biomass of browsing herbivores showed similar contributions between macroalgal habitats (35%, 33%, and 31% for low-diversity, intermediate-diversity, and high-diversity habitats, respectively). We expected a larger biomass of browsing herbivores in habitats with higher macroalgal cover, matching higher food availability. However, recent studies are aligned with our results, as they have shown that the abundance and biomass of herbivorous fish is unaffected by increasing habitat complexity (Oakley-Cogan et al., 2020; Helder et al., 2022). Similarly, Suchley et al. (2016) demonstrated that the biomass of herbivorous fish did not correlate with the coverage of fleshy macroalgae. Potential factors influencing the abundance and biomass of herbivores may include hard reef surfaces and benthic surfaces covered in turfs (Oakley-Cogan et al., 2020). However, a likely explanation for these results is that herbivorous fish can generally feed on different functional groups of macroalgae, irrespective of their functional characteristics (Sura et al., 2021; Burkepile et al., 2022). Although there are herbivorous species that are more generalist than others, the presence of these species may influence the grazing surfaces available for specialist herbivorous species. In turn, this could contribute to the configuration of the identified functional habitats.

We also found that macroalgal habitats shape the functional

diversity, richness, and redundancy of fish communities when considering the trait frequency. Regarding the functional diversity, our results are in line with recent studies, which confirm that the structure of the habitat influences the functional diversity. For example, Madgett et al. (2023) in coral reefs and Cheminée et al. (2017) in rocky reefs concluded that the structural habitat conditions the functional diversity of fish. This is because the structural habitat provides different microhabitats and niches for fish to inhabit, increasing their morphological diversity (Velasco-Charpentier et al., 2021). Simultaneously, habitats with different complexities offered varied feeding opportunities, allowing fish to occupy diverse trophic roles and utilize different resources within the habitat (Rilov et al., 2007).

The present findings arise from an extensive dataset covering a wide geographic area, revealing a predominant influence of habitats on the functional composition of fish communities. However, it is crucial to acknowledge that in specific areas, as noted by Sgarlatta et al. (2022), this relationship may occasionally be elusive. We found that functional redundancy increased its contribution (more than double, *i.e.*, from 16.46% to 33.12%) in high-diversity habitats from low to high frequency. This finding indicates a positive relationship between macroalgal habitats and the functional redundancy of fish (Fig. 4). Functional redundancy is essential to understand resilience since it informs us about the presence of fish species that play similar roles in the marine ecosystem (De Bello et al., 2021). This redundancy can work as a buffer against disturbances by increasing the likelihood that other species of the same functional group will be present to compensate for possible losses (Walker 1992; McLean et al., 2019). Therefore, the presence of high redundancy in high-complexity habitats has significant implications for the functioning of ecosystems, as it suggests that functional habitats could maintain a higher resilience of fish communities. Recent studies conducted in the Galapagos Islands showed that the functional redundancy of fish was independent of bioregions and geographic strata (McKinley et al., 2023), suggesting a more central role of functional habitat as shown in this work.

The macroalgal habitat also conditions functional richness of fish. Richardson et al. (2017) obtained similar results when comparing the functional richness of fish between coral reefs habitats. These findings can be attributed to the fact that habitat complexity offers physical structures like crevices, reefs, and vegetation, which establish micro-environments and promote the coexistence of species with diverse habitat preferences, ultimately leading to an increase in functional richness (Darling et al., 2017). However, Brandl et al. (2016) also found that the functional richness of fish is sensible to habitat degradation. Therefore, habitat conservation is a key factor to maintain the functional dimension of the fish community.

Research conducted to date reveals that habitats are one of the factors that influence the functional dimension of organisms residing in the habitat (Anderson and Millar 2004; Thiriet et al., 2016). However, these studies do not consider the functional diversity of the habitat for its classification. For example, Richardson et al. (2017) determined the habitats based on coral species, and Sgarlatta et al. (2022) based on the habitat complexity, disregarding the functional dimension of the habitat itself. Here, we have considered the macroalgal functional groups of the habitat and studied their effect on the functional dimension of the marine fish community. Our results demonstrate that habitats of macroalgae can act as drivers for the functional dimension of fish, shaping functional metrics, such as diversity, redundancy, richness, and composition, together with specific traits. Simultaneously, we unveiled the key role of trait frequency in understanding the effects of habitats on coexisting organisms. These results highlight the importance of considering habitat functions in conservation strategies, as it will help preserve the structure of the associated community. Macroalgae management should minimize physical and chemical impacts on the functional diversity of macroalgae, such as harvesting for food and phycocolloid industry (Buschmann et al., 2017), aquaculture activities (Yang et al., 2015) or pollution by heavy metals and organic chemicals

(Coleman et al., 2008). By preserving macroalgal habitats, we contribute to maintaining functional linkages between the habitat and coexisting fish in temperate rocky reefs.

CRedit authorship contribution statement

José A. Sanabria-Fernández: Conceptualization, Data curation, Formal analysis, Funding acquisition, Writing – original draft, Writing – review & editing. **Alexandre Génin:** Formal analysis, Supervision, Writing – original draft, Writing – review & editing. **Vasilis Dakos:** Supervision, Writing – original draft, Writing – review & editing.

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.

Data availability

The data that support the findings of this study are openly available in Reef Life Survey web page (www.reeflifesurvey.com; Edgar & Smith, 2014, <https://doi.org/10.1038/sdata.2014.7>).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2023.106305>.

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