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Evaluating fish foraging behaviour on non-indigenous *Asparagopsis taxiformis* using a remote video foraging system

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ABSTRACT

The proliferation of pest and invasive marine macroalgae threatens coastal ecosystems, with biotic interactions, including direct effects such as grazing and indirect effects such as the trophic cascades, where one species indirectly affects another through its interactions with a third species, play a critical role in determining the resistance of local communities to these invasions. This study examines the foraging behaviour and preference of native fish communities toward native (*Halopteris scoparia*, *Sargassum vulgare*) and non-indigenous (*Asparagopsis taxiformis*) macroalgae using the Remote Video Foraging System (RVFS). Fifty-four weedpops were deployed across three locations to present these macroalgae, while associated epifaunal assemblages were also collected. Video analysis revealed that four common fish species displayed preference towards native macroalgae, possibly due to by the presence of zoobenthos rather than herbivory. This observation suggests that these fish species identified the macroalgae as a habitat that harboured their preferred food items. In contrast, *A. taxiformis* was consistently avoided, suggesting limited integration into the local food web. Site-specific variations in fish-macroalgae interactions and epifaunal diversity highlighted the complexity of these dynamics. This study contributes to understanding of the ecological implications of invasive macroalgae and supports the use of RVFS as a tool for assessing local biotic resistance against non-indigenous species in coastal ecosystems globally.

1. Introduction

Oceanic islands are generally renowned for their distinctive ecosystems and genetic diversity, characterised by an array of unique species and substantial endemism (Gillespie, 2007; Ávila et al., 2018). The Macaronesian islands, in particular, serve as reservoirs of biodiversity, hosting a diverse assemblage of marine life, including a significant number of macroalgae species (Freitas et al., 2019). These islands act as offshore refuges for a diverse array of marine organisms, largely due to the stable climatic conditions that persisted through the Pleistocene glaciations, which fostered unique genetic lineages in these isolated habitats (Crowley, 1981; Pflaumann et al., 2003; Hayes et al., 2005; Xavier et al., 2010).

Despite their ecological importance, oceanic islands face significant threats from non-indigenous species (NIS) introductions (Micael et al., 2014; Castro et al., 2022). The vulnerability of these islands to marine NIS is closely linked to the isolation of their shallow-water ecosystems, which limits natural colonisation and recovery from disturbances (Parrish, 1989; Hachich et al., 2015). Although some marine populations on oceanic islands maintain occasional connections to coastal areas, this connectivity is highly variable and often species-specific, influenced by local oceanographic barriers such as deep ocean

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trenches, strong currents, and temperature gradients (Rocha et al., 2007; Hogan et al., 2012). These marine ecosystems often have lower native species richness, smaller populations, and simplified trophic structures, which reduce competition and biotic resistance to invaders (Vitousek, 1990; Micael et al., 2014). Furthermore, demographic isolation and resource limitations, such as restricted food and space, heighten the susceptibility of these ecosystems to NIS impacts (Micael et al., 2014). Consequently, oceanic islands typically exhibit lower functional diversity and simpler ecological networks than mainland counterparts, leaving them vulnerable to invasions (Pearson, 2009).

In the Macaronesian archipelagos, macroalgae are the most dominant NIS, with 31 identified species (Castro et al., 2022). The introduction of invasive macroalgae can disrupt the ecological balance and genetic integrity of these marine communities, leading to significant biodiversity losses and altered ecosystem functions (Katsanevakis et al., 2014; Geburzi and McCarthy, 2018).

Macroalgae are essential in the marine food web, as primary food source but also by providing habitat for diverse organisms that are prey for numerous higher-level consumers, including non-photosynthetic bacteria, protists, invertebrates, and fish (Potapova et al., 2005). In addition, there is also consideration of the cascading effect along the food web: macroalgae serve as a primary nutritional source for herbivorous invertebrates and fishes (Lim et al., 2016; Chen et al., 2021), which in turn, indirectly support higher-level consumers, such as invertivorous and piscivorous fishes (van Lier et al., 2018; Wenger et al., 2018). By consuming macroalgae-associated epifauna and being prey to meso- and apex predators, invertivorous fishes play a crucial role in facilitating the transfer of energy to the next trophic level. This process highlights the vital trophic links that connect primary producers to upper-level consumers, forming the “bedrock” of marine biodiversity and ecosystem functioning. These trophic interactions span across all trophic levels within marine food webs, creating a bi-directional dynamic with both top-down and bottom-up effects (Chen et al., 2021).

The introduction of NIS can lead to biological invasions that significantly disrupt the local ecosystems and promote phase shifts (Lesser and Slattery, 2011; Edelist et al., 2013), loss of food web complexity (Byrnes et al., 2007) and decline of native taxa or lineages (Micael et al., 2014; Thomsen et al., 2016; Geburzi and McCarthy, 2018). In particular, NIS macroalgae have the potential to outcompete or exclude native macroalgae and other sessile organisms (Gestoso et al., 2012; Palomo et al., 2016), as well as to have direct and indirect impacts on dietary habits, food availability, trophic interactions and, ultimately, on the local food webs (Katsanevakis et al., 2014; Thomsen et al., 2016). When exploring these processes involving NIS macroalgae, it is important to recognise the role of epifauna in the macroalgae-consumers interactions, since their role as a habitat providers can influence trophic interactions dynamics by affecting the strength of predator-prey relationships (i.e., enhancing predator foraging efficiency on epifauna or reducing prey vulnerability to predation due to habitat use traits) (Klecka and Boukal, 2013). In this context, the dynamics of consumer–food resource interactions assume increased significance, as macroalgae consumers and epifauna consumers can exert either facilitative or constraining influences on the proliferation of NIS: consumer preference for native macroalgae and associated epifauna can indirectly facilitate NIS proliferation by reducing the pressure on NIS, whereas preference for NIS macroalgae or epifauna may contribute to biotic resistance to invasions (Thomsen et al., 2016; Chebaane et al., 2024).

The potential influence of NIS macroalgae on local trophic interactions underlines the importance of ascertaining whether local consumers manifest selective, rejection, or generalist feeding behaviours that either promote or hinder the dominance of NIS macroalgae. These feeding behaviours constitute a pivotal mechanism and fundamental factors influencing the resistance, susceptibility and resilience of local communities to biological invasions (Santamaría et al., 2021; Chebaane et al., 2024). This study assesses whether local fish display preferences when presented with a selection of native and NIS macroalgae and their associated epifauna. Understanding these preferences is crucial to determining whether consumer feeding behaviours can contribute to biotic resistance against NIS. Additionally, this research examines the role of macroalgae both as a primary food source and as a habitat provider for specific epifauna assemblages, and how these factors may influence the diet of local fish, which were categorised as herbivorous, invertivorous or omnivorous. Our hypotheses were that fish would display a preference for native macroalgae and associated epifauna, potentially facilitating the proliferation of NIS macroalgae, and that these preferences would vary according to the feeding categories of fish (herbivorous, invertivorous, and omnivorous). The study’s findings aim to shed light on the potential role of consumer preferences in mediating the impacts of NIS macroalgae on local ecosystems.

2. Materials and methods

2.1. Experimental design and study site

In this pilot study, one non-indigenous macroalgal species (*Asparagopsis taxiformis*) (Castro et al., 2022) and two indigenous macroalgal species (*Halopteris scoparia* and *Sargassum vulgare*) were selected to conduct the herbivory preference experiment. The selection of these macroalgae was driven by their ecological significance, as they represent the dominant communities in the studied area, which is Madeira Island in the NE Atlantic (Fig. 1). The entire experimental procedure was conducted *in situ* in an underwater environment, employing scuba diving techniques. The water temperature was on average 18 °C (±1°), and the experiment was performed at a depth range of 7–8 m. Three different locations in the southern region of Madeira Island were chosen for replication of the experiment.

2.1.1. Remote video foraging system design

To ensure a uniform presentation of macroalgae to fish across all study locations, standard experimental units (Fig. 2) were constructed, inspired by the Herbivory Assay protocol known as “Weedpops,” which had been developed by The Marine Global Earth Observatory (MarineGEO) and adapted from the research of Hay (1981). Additionally, our study used the approach of the Remote Video Foraging System (RVFS) (Chebaane et al., 2022, 2024). While the RVFS experiment traditionally employed fouling communities, our adaptation utilises the conceptually similar weedpops as the experimental units, designating them as the ‘studied bait’ in this investigation. Despite the variances in the specific bait employed, we explicitly employ the RVFS protocol in our study for the assessment of foraging behaviour.

In this study, each experimental unit, referred to as a “weedpop Experimental unit,” consisted of three lines (1 m of round plait ropes made from polypropylene) called to as weedpop. To achieve the desired vertical orientation of each weedpop in the water, one end was equipped with 1-kg D-ring weights commonly used in scuba diving, while the opposite end featured a plastic sponge floater. Each line had four tags placed equidistantly, with an individual from each species of macroalgae randomly positioned adjacent to three tags, while the fourth space was left empty to serve as a control (as illustrated in Fig. 2).

The macroalgae specimens were collected on the very day of the experiment, within the same dive, from the exact location where the experimentation took place. At each site, a team of three scuba divers deployed a total of six weedpop experimental units, with three units deployed each day over two consecutive days. Each weedpop experimental unit was equipped with a tripod, supporting a video camera (PARALENZ Vaquita Underwater 4K Camera) set up to record videos for the weedpop experimental unit. To ensure the camera’s stability, every tripod was anchored with 2 kg of D-ring dive weights, a choice influenced by both its ease of transportation to the water and its proven efficacy in maintaining camera stability.

On the first day of the experiment, a team of three divers deployed three weedpop experimental units, including the weedpops and tripods

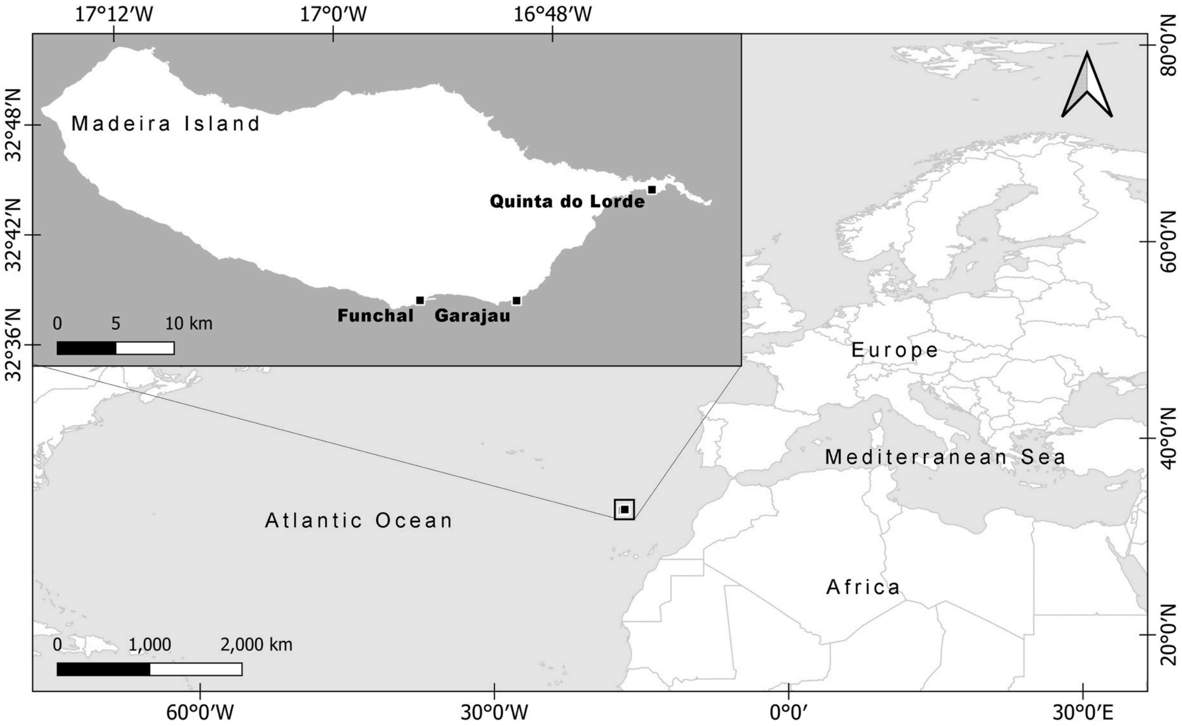


Fig. 1. Map showing the location of the study area in the southern region of Madeira Island, NE Atlantic. The map highlights the three sites where herbivory preference experiments were conducted.

equipped with cameras (Fig. 2, step 1). Following this, macroalgae were collected and attached to the weedpops (Fig. 2, steps 2 and 3). The position of each macroalga on every weedpop was documented by one diver using a pre-prepared sheet (Fig. 2, step 4). Afterward, the cameras were activated for video recording, and the team exited the site (Fig. 2, step 5). Two hours later, two divers returned to the site to turn off the cameras (Fig. 2, step 6). The presence or absence of macroalgae on the weedpops was then recorded by one diver on the same pre-prepared sheet (Fig. 2, step 7). The cameras and tripods were subsequently removed while the macroalgae remained affixed to the weedpops (Fig. 2, step 8).

After a 24-h interval, a team of three divers revisited the site. The presence or absence of macroalgae was recorded initially (Fig. 2, step 9), followed by the detachment of these macroalgae from the weedpops (Fig. 2, step 10). A new set of macroalgae was randomly positioned on each weedpop, and the procedures from the previous day were repeated on the next day at the same time (Fig. 2, step 1–10). This process spanned 2 days per location, equivalent to 48 h of experimentation.

Previous studies (Willis et al., 2006; Birt et al., 2012) have shown that factors such as time of day and substrate type significantly influence fish behaviour and abundance. These studies have also reported minimal day-to-day variability within our context. Therefore, we conducted the experiment at the same time each day to control for variability associated with time of day and exclude ‘day’ as a factor in our analysis. This approach resulted in six replicates per block rather than the initial planned three. By standardising the timing of the experiment, we minimised the impact of time-of-day variability, enabling a focused analysis of macroalgae removal, fish preference, and abundance across the three distinct locations.

2.1.2. *Epifaunal sampling design*

In parallel with RFVS deployment and trials, samples of *Halopteris scoparia*, *Sargassum vulgare*, and *Asparagopsis taxiformis* were collected from each of the three study locations: Funchal, Garajau, and Quinta do Lorde. Three replicates of each macroalga per location were collected, each separated by a few meters (Fig. 2, step 11). Macroalgae individuals at a depth of 7–8 m were carefully detached from the substrate, enclosed in a plastic zip bag to minimize organism loss, and promptly transported to the laboratory on the same day.

In the laboratory, each sample was rinsed through a 0.2 mm mesh sieve with fresh water to capture all mobile macrofauna. Subsequently, each macroalga was examined under a stereomicroscope to detach any remaining epifauna species that were still attached. Each sample from each macroalga was placed in a container and preserved with 70% ethanol. Organisms were identified to the order level, as this level of identification suffices for community distinction (Timms et al., 2013; Otero-Ferrer et al., 2019; Guerra-García et al., 2021). The quantification was done using a dissecting microscope.

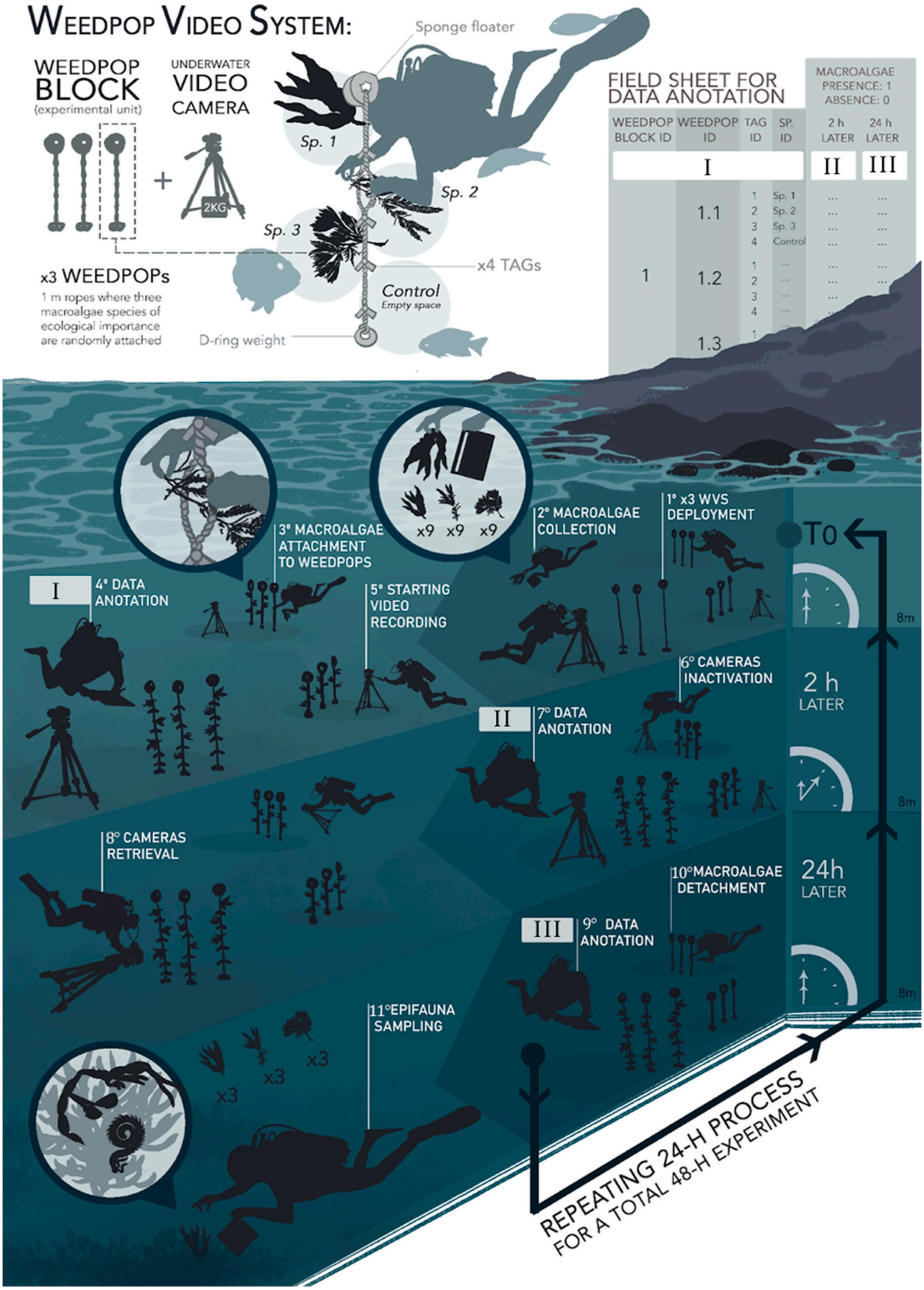
The macroalgae were placed on filter paper to drain the water. Subsequently, each sample of macroalga was weighed using a digital scale with milligram precision. Epifauna abundance was assessed by standardising the count to a number of individuals per 10 g of wet macroalgal weight.

2.2. *Data analysis*

The analysis was conducted using Primer 7, while data visualisation was carried out using both Primer 7 and R (version 4.2.1), utilising the “ggplot2” (Wickham, 2016) and “networkD3”) (Allaire et al., 2017) packages.

2.2.1. *Macroalgae removal across space*

To examine variations in macroalgae removal across different locations, presence-absence data were gathered from the weedpops, and a univariate mixed-effects PERMANOVA analysis was conducted, employing Euclidean distance matrices among the samples (Anderson and Robinson, 2003). The factor ‘Location’ was treated as a fixed factor with three levels, the factor ‘Block’ was a random factor nested within ‘Location’ with six replicates per location, and the factor ‘Macroalgae’ was a fixed factor with three levels. This analysis was first applied to the initial 2-h interval, which served as a baseline, and subsequently to the full 24-h period. Statistical significance was assessed through 9999



WEEDPOP BLOCK ID	WEEDPOP ID	TAG ID	SP. ID	MACROALGAE PRESENCE: 1 ABSENCE: 0 2 h LATER	24 h LATER
I				II	III
1	1.1	1	Sp. 1	...	...
		2	Sp. 2	...	...
		3	Sp. 3	...	...
		4	Control	...	...
	1.2	1	...	...	...
		2	...	...	...
		3	...	...	
		4	...	...	
	1.3	1	...		

Fig. 2. Experimental setup of the Remote Video Foraging System (RVFS) featuring weedpops as the experimental units. Each experimental unit comprises three polypropylene ropes equipped with D-ring weights and floaters (referred to as weedpop), accommodating macroalgae specimens. Utilising video camera on a tripod to record the fish interaction with the experimental units for 2 h, the protocol includes the following steps (1) deployment of the weedpop units with tripods and cameras, (2) collection and (3) attachment of macroalgae to the weedpops; (4) documentation of position at T0; (5) initiation of video recording; (6) stopping the video recording; (7) scoring of macroalgae presence or absence after 2 h (2h), (9) scoring and (10) detachment of macroalgae after 24-h interval (24h). (11) collection of macroalgae for epifaunal sampling. The entire process totals a 48-h experiment period.

permutations at a confidence level of $\alpha = 0.05$. If the count of unique permutations was insufficient for statistical inferences at a significance level of 0.05, Monte Carlo P-values were used (Anderson and Robinson, 2003; Anderson, 2008).

Similarity matrices were calculated using the Bray-Curtis index when comparing quantitative species composition and Euclidean distances in all other cases. This standardisation was used to streamline the description of similarity measures across the different analyses.

2.2.2. Fish abundance and composition

A sole observer employing a scan sampling technique documented fish species abundance, composition, and behaviours. The observer conducted scans second by second within intervals of approximately 4 min and 30 s due to the automatic splitting of video by the camera. However, all recorded seconds were included in the analysis to ensure comprehensive data coverage. A total of 24 h, 38 min, and 51 s of video footage were recorded across the three study locations, with approximately 1 h and 30 min of video content per weedpop experimental unit. Fish abundance was quantified using the MaxN analysis method (Cappo, 2010; Whitmarsh et al., 2017), which estimates the maximum number of individuals from a single species observed within an individual video frame. The derived MaxN data were then used to calculate the Bray-Curtis similarity matrix, followed by the application of a Multivariate One-way analysis of covariance PERMANCOVA (Anderson, 2001), with 'Location' as a fixed factor. The total duration in seconds per weedpop experimental unit was included in the design as a covariate. Subsequently, a Similarity Percentages Procedure (SIMPER) analysis was conducted to illustrate the contributions of fish species to the observed similarities in species composition across the various locations. Additionally, fish composition was assessed within each location using a presence-absence methodology. These data were used to calculate a Jaccard matrix. Once again, a PERMANCOVA analysis was applied, using the same design as the previous analysis, to investigate potential differences in species composition across the study locations. Trophic levels and diets for each fish species were determined based on the data provided by FishBase (Froese and Pauly, 2000).

2.2.3. Fish behaviour

To further explore fish behaviour dynamics, the analysis focused on three categories: presence, interest and biting. Presence was quantified as the amount of time (in seconds) a fish was visible on the video. Interest was defined as the duration (in seconds) during which a fish swam toward or paused in front of specific species of macroalgae, and biting was defined as the duration (in seconds) during which a fish fed on the macroalgae (Chebaane et al., 2022). The presence of fish per second across different locations was assessed using a univariate PERMANOVA analysis. This analysis employed a nested design, with the 'Location' factor being fixed, and the 'Weedpop experimental unit' nested within each location as a random factor. The total duration in seconds per weedpop experimental unit was included in the design as a covariate. To assess the preference of fish for specific macroalga species in terms of interest and biting, a univariate PERMANCOVA analysis was employed. This analysis followed a complete randomised block design, with the 'Location' factor fixed, the 'block' factor nested randomly within 'Location', and the 'macroalgae' factor fixed. The presence, interest, and biting behaviours of each fish species were then visualised in a Sankey diagram. These diagrams were created using the "networkD3" package in R (Allaire et al., 2017).

2.2.4. Epifauna associated with the macroalgae

The epifaunal abundance data from each sample were initially computed by dividing the epifauna count by the original weight of the macroalgae sample, standardising it to 10 g for comparability. Subsequently, normality was assessed using the Shapiro-Wilk test, and the homogeneity of variances was examined using Levene's test in IBM SPSS Statistics 27, with results indicating that normal data distribution and homogeneity in variances were achieved. A two-way PERMANOVA test was conducted after calculating the Bray-Curtis similarity matrix of epifauna abundance to investigate differences in epifauna community composition among the studied macroalgae species within each location. The factor 'location' was fixed with three levels (Funchal, Garajau, and Quinta do Lorde), and the factor 'macroalgae' was fixed with three levels (*Halopteris scoparia* and *Sargassum vulgare* and *Asparagopsis taxiformis*). Data were intentionally left untransformed to avoid magnifying rare epifaunal species; for example, The more complex morphology of *H. scoparia* compared to *A. taxiformis* and *S. vulgare* results in more available space, which could lead to a higher percentage of rare species. Principal Coordinates Analysis (PCO) was used to visualise the epifaunal composition by taxonomic class for each macroalgae species at each location. The same PERMANOVA design was used to test differences in the number of epifaunal taxa, total epifaunal abundance, and the Shannon-Wiener diversity index (H') between the studied macroalgae species in each location after calculating the Euclidean distance similarity matrix.

3. Results

3.1. Macroalgae removal across space

Site-specific macroalgae removal was observed, regardless of the duration of exposure to grazer. During the initial 2-h period, macroalgae were noticeably removed only from Funchal. Specifically, both native and brown macroalgae, *Halopteris scoparia* and *Sargassum vulgare*, were removed from the Funchal weedpop. However, statistical significance was not achieved due to the relatively low proportion of these removals (Table 1; Fig. 3).

Following a 24-h interval, the selectivity for *H. scoparia* and *S. vulgare* in Funchal became statistically significant as a greater proportion of these macroalgae were removed. As for the non-indigenous red macroalgae *Asparagopsis taxiformis*, removal was observed in a single weedpop located in Quinta do Lord. Furthermore, in Garajau, native brown macroalgae *H. scoparia* were also removed, but this was limited to a small proportion, resulting in statistical non-significance (Table 1; Fig. 3).

3.2. Fish abundance and composition

A total of 109 fish, representing 13 different species, were observed within the 18 weedpop experimental units across various locations (Fig. 4). These locations displayed significant differences in both fish compositions and abundance (Table S1). Due to a camera malfunction at the Garajau location, the recorded footage for one of the weedpops

Table 1

Results of the univariate PERMANOVA for the proportion of macroalgae removal across locations during the initial 2 h and after 24 h. Abbreviations used: EXP - Experimental unit; F - Funchal; Q - Quinta do Lorde; G - Garajau; A - *Asparagopsis taxiformis*; H - *Halopteris scoparia*; S - *Sargassum vulgare*. Bold font indicates statistical significance at the $\alpha = 0.05$ level. Df - degrees of freedom; MS - mean square sum; P (MC) - p-values for the permutation using the Monte-Carlo test. The permutation test was conducted with 9999 permutations.

Source	Df	2-h			24-h		
		MS	Pseudo-F	P (MC)	MS	Pseudo-F	P (MC)
Location	2	0.67	5.00	**0.02**	3.91	15.29	**0.001**
Macroalgae	2	0.17	1.67	0.20	1.19	7.11	**0.001**
EXP (Location)	15	0.13	1.33	0.24	0.26	1.53	0.15
Location x Macroalgae	4	0.17	1.67	0.18	1.32	7.94	**0.001**
Residuals	30	0.10			0.17		
Pairwise comparisons		F≠ (Q = G)			For F: A ≠ (S= H) Q and G: A = S = H		

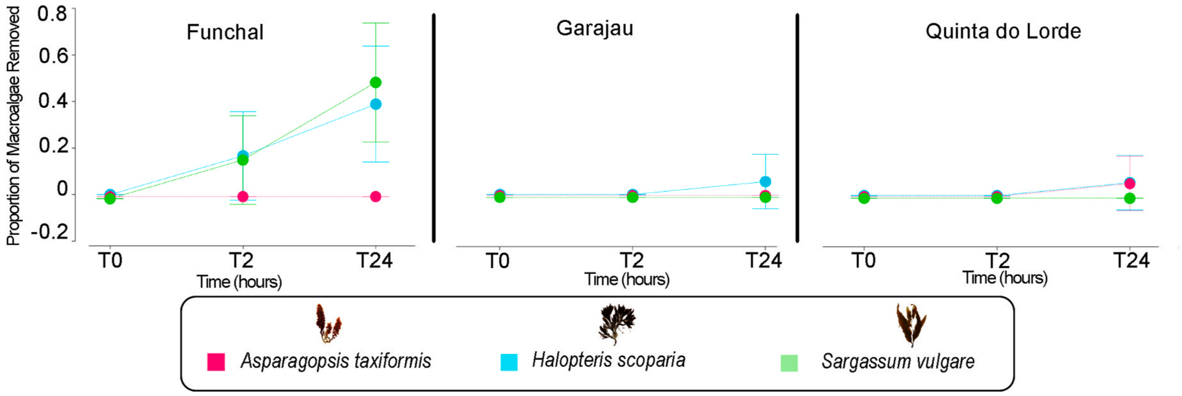


Fig. 3. Proportion of macroalgae removed from weedpops per location (Funchal, Garajau, and Quinta do Lorde) during the initial 2 h (T2) and after 24 h (T24). The x-axis represents the time intervals (T0: initial setup, T2: after 2 h, and T24: after 24 h), while the y-axis shows the proportion of macroalgae missing. Each point represents the mean proportion missing for each macroalga species (*Asparagopsis taxiformis*, *Halopteris scoparia*, and *Sargassum vulgare*), with error bars indicating the standard error.

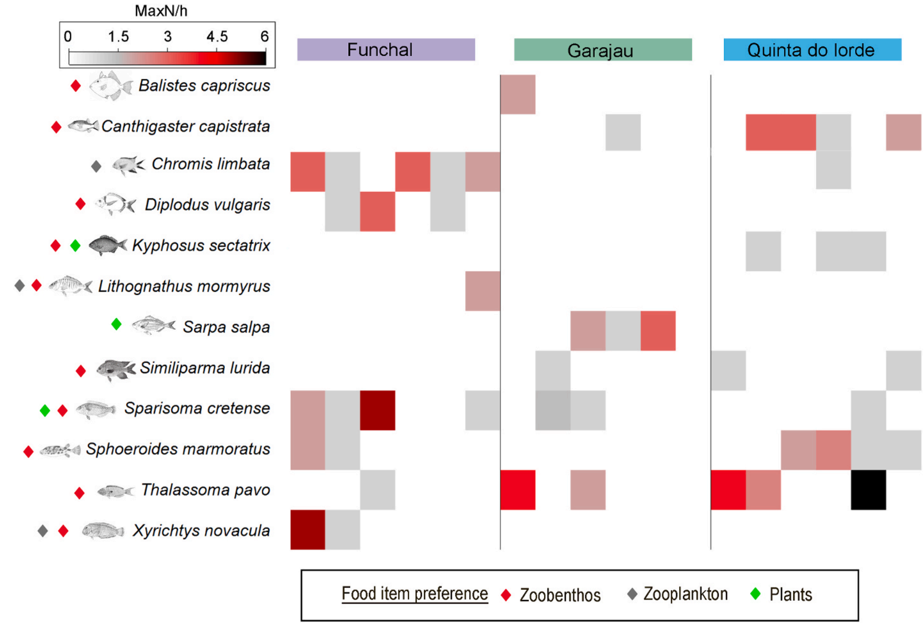


Fig. 4. Shade plot illustrates the average maximum number of individual fish per hour for each species, across video setups (n = 6 per location), at various locations.

blocks was shorter compared to the other samples. To account for this difference, video duration was included as a covariate in all subsequent analyses.

The statistical analysis carried out through PERMANOVA revealed differences in MaxN among the locations (Table S1), indicating variations in the maximum number of observed fish. However, PERMDISP analysis did not show any significant differences in dispersion across the locations ($F_{2,15} = 2.5809$; $p = 0.1$), suggesting a relatively consistent distribution pattern (Table S1).

Regarding species composition, the PERMANOVA analysis also demonstrated significant differences across the locations (Table S1), indicating variations in the species presence. Consistent with the MaxN analysis, PERMDISP analysis did not reveal significant differences in dispersion across locations ($F_{2,15} = 2.984$; $p = 0.1$), implying relatively uniform species distribution patterns (Table S1).

In Funchal, 45 individuals from 7 different fish species were observed, with an average observation rate of 5.5 individuals per hour. Notably, *Chromis limbata* and *Sparisoma cretense* were the most abundant species in this area (Fig. 4; Table S2).

In Garajau, 20 individual fish, representing 6 different species, were recorded, with an average observation rate of 2.8 individuals per hour. The dominant species observed in this location were *Thalassoma pavo* and *Sarpa salpa* (Fig. 4; Table S2).

Lastly, in Quinta do Lorde, 44 individual fish from 8 different species were documented, with an average observation rate of 5 individuals per hour. The dominant species in this area were *Canthigaster capistrata* and *Sphoeroides marmoratus* (Fig. 4; Table S2).

Most fish species observed in the three locations were classified as carnivorous, with a trophic level range of 3.0–4.0, predominantly feeding on zoobenthos. Among the fish identified, *Sarpa salpa* was the sole herbivorous species, with a trophic level 2.0. *Kyphosus sectatrix* has a trophic level range of 2.0–2.19, and *Sparisoma cretense* had a trophic level of 2.6, indicating that they consume macroalgae and small invertebrates.

3.3. Fish behaviour

Regardless of specific fish species, the temporal presence of fish displayed significant similarity across the three studied locations (Table S3; Fig. 5). *Chromis limbata* was the predominant species in terms of temporal presence in Funchal, while in Garajau, *Sarpa salpa* and *Sparisoma cretense* were the most frequently observed species. In Quinta do Lorde, the three most frequent fish species were *Canthigaster capistrata*, *Sphoeroides marmoratus*, and *Thalassoma pavo* (Table S4).

Significant differences in fish preferences were observed when identifying macroalgae species that attracted particular interest. *Sargassum vulgare* and *Halopteris scoparia* were preferred over *Asparagopsis taxiformis* across all locations (Table S5). Three fish species, *Chromis limbata*, *Thalassoma pavo*, and *Sparisoma cretense*, consistently interacted with all three presented macroalgae species. Only these three fish species showed interest to the non-indigenous red macroalgae *A. taxiformis*. Additionally, *Canthigaster capistrata* showed a distinct preference for *S. vulgare* along with the three mentioned fish species. For *H. scoparia*, all the previously mentioned fish, along with *Canthigaster capistrata*, *Similiparma lurida*, and *Balistes capriscus*, showed interest in this macroalga species.

Regarding biting behaviour, only *Sparisoma cretense*, *Canthigaster capistrata*, *Thalassoma pavo*, and *Similiparma lurida* were observed biting (Fig. 5). Among the three macroalgae species presented, both *H. scoparia* and *S. vulgare* were bitten, with *H. scoparia* being the most frequently bitten (Fig. 5; Table S5). On the other hand, *A. taxiformis*, was not bitten by any fish.

At Quinta do Lorde and Funchal, fish targeted only *H. scoparia*. Specifically, in Funchal, *Thalassoma pavo* showed preferred for *H. scoparia*, while in Quinta do Lorde, *Sparisoma cretense* displayed a similar preference. In Garajau, all four species were observed biting *H. scoparia*, and both *Sparisoma cretense* and *Canthigaster capistrata* were seen to biting not only *H. scoparia* but also *S. vulgare*.

In the context of the diet of the interacting fish species with the provided macroalgae, it was observed that all fish primarily fed on zoobenthos, except for *S. cretense*, which displayed a mixed dietary preference for both zoobenthos and macroalgae.

3.4. Epifauna associated with the macroalgae

A total of 3621 epifauna individuals were identified to the order level, encompassing 5 phyla, 13 classes, and 34 orders. The total epifaunal abundance was primarily composed of Arthropods, mainly Amphipoda (90%), followed by Harpacticoida (3%) and Decapoda (2.5%). Molluscs accounted for 10% of the total abundance, predominantly represented by Carditida (Bivalvia) at 36% and Caenogastropoda

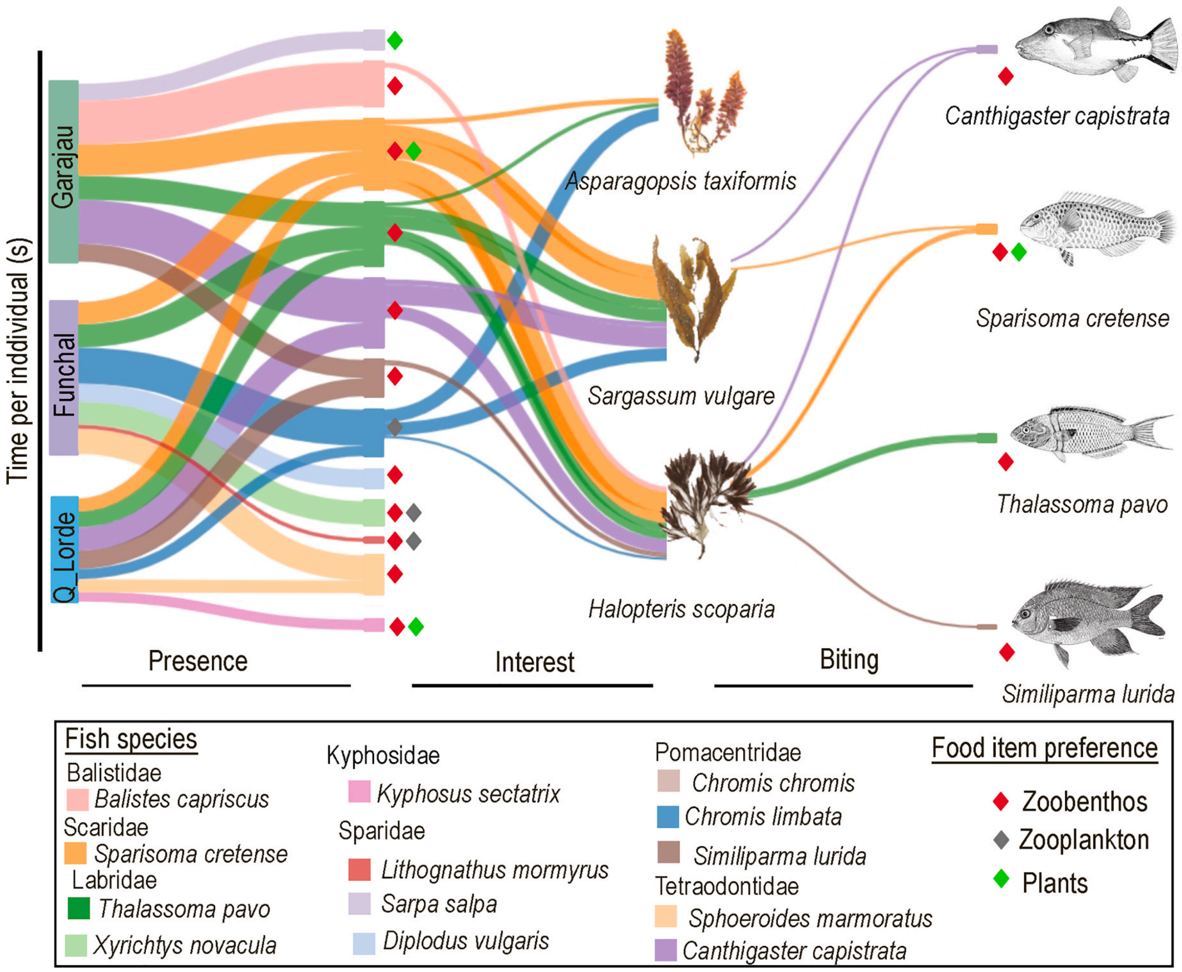


Fig. 5. Sankey diagram illustrating fish interactions with macroalgae across the three study locations (Garajau, Funchal, and Quinta do Lorde). The diagram shows flow of fish behaviours: Presence, Interest, and Biting; towards specific macroalgae species (*Asparagopsis taxiformis*, *Sargassum vulgare*, and *Halopteris scoparia*). The nodes represent locations, macroalgae, and fish species. Links between the nodes indicate how fish species interact with macroalgae, with the width of each link corresponding to the duration (in seconds) of each behaviour per individual fish. The colours of the links and nodes represent the specific fish species involved, while icons denote food item preferences: zoobenthos, zooplankton, and plants. The right side of the diagram highlights the fish species observed exhibiting biting behaviour, which were the only species recorded performing this action during the study.

(Gastropoda) at 36%. Annelida constituted 5.4% of the total, with Phyllodocida (57%) and Terebellida (34%). Echinoderms accounted for 0.5% primarily Ophiuroidea (68%). Cnidaria was minimally present, with Actiniaria representing 0.05% of the total abundance, observed in a single sample of *Sargassum vulgare* located in Funchal.

Epifauna associated with the three macroalgae at each studied location showed a significant difference among the macroalgae species, regardless of location (Table S6). *S. vulgare* had the highest relative abundance of epifauna, followed by *Halopteris scoparia* and *Asparagopsis taxiformis*. PERMANOVA results based on the epifaunal abundance indicated significant differences among macroalgae and locations, with an interaction between those factors. Subsequent pairwise comparisons revealed that the epifaunal communities associated with each macroalga species varied significantly across all locations (Table S6). In the

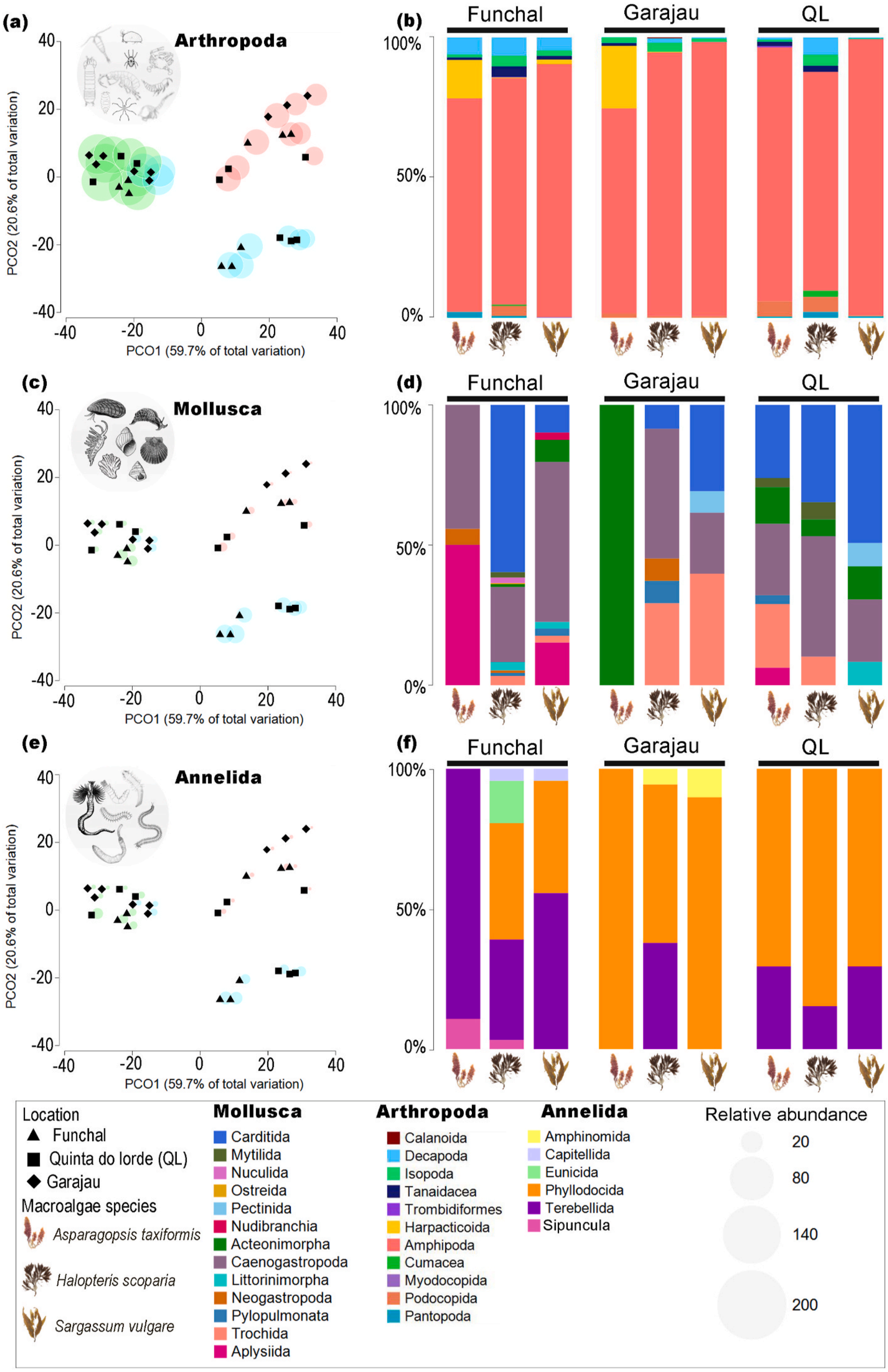


Fig. 6. Principal Coordinates Analysis (PCO) of epifauna taxonomic composition and abundance per 10 g of macroalgae species (*Asparagopsis taxiformis*, *Sargassum vulgare*, and *Halopteris scoparia*) across three study locations: Funchal, Garajau, and Quinta do Lorde (QL). Each location includes three replicate samples per macroalgae species, indicated by shapes, and macroalgae species are distinguished by colour. Panels (a), (c), and (e): PCO ordinations show Epifaunal community structure based on Bray-Curtis distance matrices, with the axes representing the main variation among samples: (a) Arthropoda, (c) Mollusca, and (e) Annelida. Bubble sizes reflect the relative abundance of each taxonomic group, as indicated in the legend. Panels (b), (d), and (f): Bar charts display the percentage contribution of each order to the total epifaunal abundance for each taxonomic group per macroalgae species within each location: (b) Arthropoda, (d) Molluscs, and (f) Annelids. The orders within each phylum are depicted with specific colours as listed in the legend.

Principal Coordinates Analysis (PCO) ordination based on epifaunal abundances per macroalga showed distinct groupings among samples representing different macroalgae species (Fig. 6). However, samples of *H. scoparia* in Garajau merged with those from all locations of *S. vulgare*. No distinct groupings emerged among the sampling sites, suggesting that the significant differences in epifaunal composition were contingent upon specific algal species, thought a site-specific effect was seen due to similarities between *H. scoparia* in Garajau and *S. vulgare* (Table S6; Fig. 6).

Regarding order richness and diversity, significant differences were observed among the macroalgae species, with the site-specific effect noted (Table S6; Fig. 7). In Funchal, *H. scoparia* hosted the highest number of orders, followed by *S. vulgare*, while *A. taxiformis* hosted the fewest. For diversity, *H. scoparia* displayed greater diversity than both *S. vulgare* and *A. taxiformis*, which displayed equal levels.

In Garajau, *H. scoparia* similarly hosted the highest number of orders, while *A. taxiformis* and *S. vulgare* displayed equivalent order richness. Concerning diversity, *A. taxiformis* and *H. scoparia* demonstrated the highest levels, in contrast to *S. vulgare*.

For Quinta do Lorde, *A. taxiformis* and *H. scoparia* hosted a higher number of orders compared to *S. vulgare*. In terms of diversity, *H. scoparia* showed greater diversity compared to *A. taxiformis* and *S. vulgare*, with *S. vulgare* displaying the lowest diversity.

With respect to taxonomic composition, arthropods were the most abundant phylum across all three studied locations and macroalgae, followed by molluscs and annelids. *S. vulgare* displayed the highest abundance of arthropods in all locations when compared to *A. taxiformis* and *H. scoparia* (Table S7: Fig. 6). However, in Funchal and Quinta do Lorde, there was no significant difference in the total abundance of arthropods between *A. taxiformis* and *H. scoparia*. In Garajau, *A. taxiformis* hosted the lowest total abundance of arthropods (Table S7: Fig. 6).

Interestingly, *S. vulgare* hosted the lowest number of arthropods orders across all locations (Funchal (5), Garajau (4), and Quinta do Lorde (5)), while *H. scoparia* displayed the highest number of arthropod orders (Funchal (8), Garajau (6), and Quinta do Lorde (7)). Only in Quinta do Lorde were the numbers of arthropod orders equal between *A. taxiformis* and *H. scoparia* (7) (Fig. 6).

Regarding molluscs, which constitute the phylum with the largest number of orders (13), the highest total abundance of molluscs across all locations was observed in *H. scoparia*, followed by *S. vulgare* and *A. taxiformis*. Notably, *A. taxiformis* hosted the lowest total abundance of molluscs in Funchal and Garajau. In Quinta do Lorde, both *A. taxiformis* and *S. vulgare* displayed an equal total abundance of molluscs (Table S7; Fig. 6).

H. scoparia also displayed the highest number of mollusc orders in both Funchal (10) and Garajau (5). In these locations, *S. vulgare* ranked second, hosting 5 orders of molluscs in Garajau and 8 in Funchal. Conversely, *A. taxiformis* had the lowest number of mollusc orders in these locations, with 3 in Funchal and 1 in Garajau. However, in Quinta do Lorde, *A. taxiformis* hosted the highest number of mollusc orders (7), surpassing *S. vulgare* (5) and *H. scoparia* (5).

Regarding the annelids, the total abundance of annelids was highest in *H. scoparia*, followed by *S. vulgare*, while *A. taxiformis* hosted the lowest abundance of annelids in Funchal. However, in Quinta do Lorde and Garajau, *S. vulgare* exhibited an equal total abundance of annelids as *H. scoparia* and *A. taxiformis*, with *H. scoparia* surpassing *A. taxiformis* in total annelid abundance (Table S7; Fig. 6).

H. scoparia, both in Funchal and Garajau, hosted the highest number of annelid orders, with 5 in Funchal and 3 in Garajau, in contrast to *A. taxiformis* (2 in Funchal and 1 in Garajau) and S. *vulgare* (3 in Funchal and 2 in Garajau). In Quinta do Lorde, all the macroalgae displayed an equal number of annelid orders, which amounted to 2 (Fig. 6).

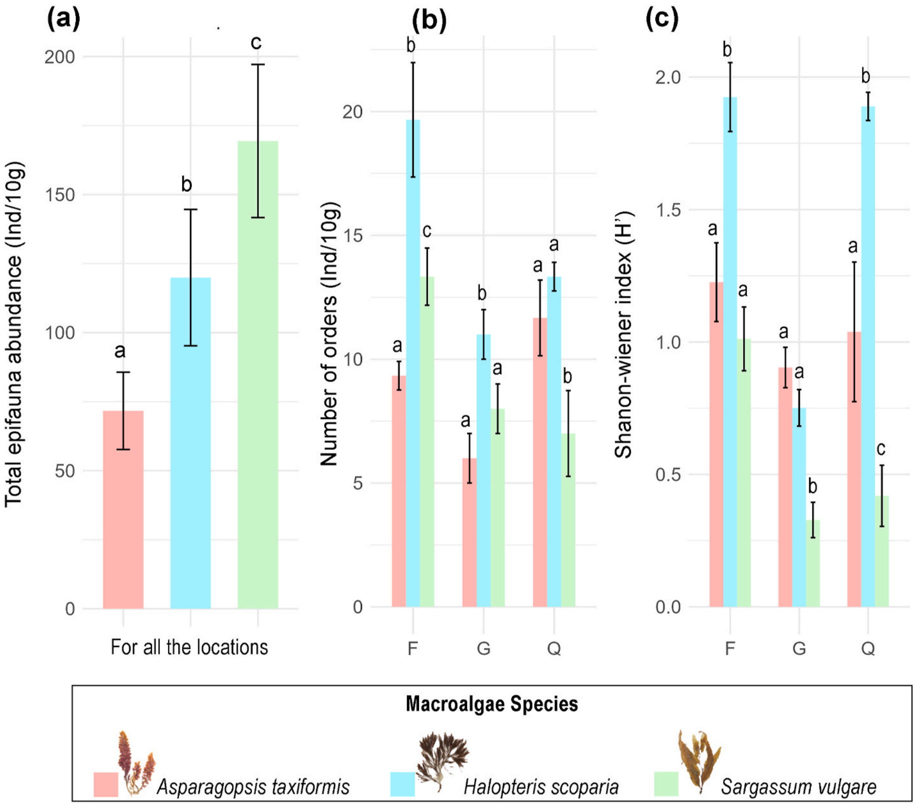


Fig. 7. (a) Total epifaunal abundance (density) per 10 g of macroalgae species across all locations. (b) Number of orders (taxonomic richness) identified per macroalgae species within each location. (c) Shannon-Wiener index (H′) per macroalgae species within each location (diversity). Letters (a, b, c) above bars indicate statistically significant differences between macroalgae species at the α = 0.05 level, based on pairwise comparison to PERMANOVAs (detailed results in Table S6). Locations: F: Funchal; G: Garajau; Q: Quinta do Lorde.

Regarding the other identified phyla, the minor taxa were Echinodermata and Cnidaria. Actiniaria (Cnidaria) and Forcipulatida (Echinodermata) were exclusively associated with *S. vulgare* in Funchal. Ophiuridae (Echinodermata) were detected in both *H. scoparia* samples from Funchal and Quinta do Lorde, and in *A. taxiformis* samples from Funchal. Comatulida (Echinodermata) was exclusively associated with *H. scoparia* in Garajau.

4. Discussion

This study employed the Remote Video Foraging System (RVFS) to assess the foraging preferences of fish communities towards three macroalgae species: the non-indigenous *Asparagopsis taxiformis*, and the native species *Sargassum vulgare* and *Halopteris scoparia*.

The results consistently showed that fish exhibited a clear preference for the native macroalgae (*S. vulgare* and *H. scoparia*), with *A. taxiformis* being consistently avoided across all study sites. Fish displayed no biting behaviour towards *A. taxiformis*, likely due to its low palatability caused by secondary metabolites that deter herbivory, as observed in other studies (Marić et al., 2016; Máximo et al., 2018; Gache et al., 2019). This avoidance reflects the learned avoidance of toxic prey by fish (Crossland, 2001).

During the initial 2 h observation period, no significant macroalgae removal was recorded, likely due to limited biting attempts observed in the video footage. However, a noticeable removal of macroalgae was observed after 24 h, suggesting that extended exposure increases the likelihood of interaction with grazers. Since video footage was only available for the first 2 h, the factors contributing to increased removal during the remaining 22 h remain unclear. The recorded detachment of macroalgae could have been influenced by factors other than fish foraging, such as ocean currents or invertebrates like crustaceans and molluscs, although their impact is less likely given the macroalgae's position 30 cm above the seafloor (Francis et al., 2019). This highlights the importance of video recordings in *in situ* experiments, as they provide detailed insights into fish and grazer behaviours that simple presence-absence assessments, like those from traditional weedpop experiments, cannot capture (Struthers et al., 2015; Chebaane et al., 2022). To better understand these dynamics, future studies should include nighttime recordings, as grazing activity can differ significantly between day and night (Harvey et al., 2012; Myers et al., 2016).

Fish communities varied significantly across the study locations, with notable differences in composition and abundance, even though the overall time the fish spent in the footage (presence) did not significantly differ. Garajau, a marine protected area with minimal human disturbance (Gestoso et al., 2017), displayed the highest feeding activity despite having the lowest fish abundance and diversity among the three locations. Fish-macroalgae interactions were primarily centred on *H. scoparia* and *S. vulgare*, with four species — *Sparisoma cretense*, *Canthigaster capistrata*, *Thalassoma pavo*, and *Similiparma lurida* — actively engaging in feeding behaviours.

Conversely, Funchal and Quinta do Lorde, which are more affected by coastal modifications and human activities (Bernal-Ibáñez et al., 2021), exhibited different patterns of fish feeding behaviour compared to Garajau. In Funchal, significant macroalgae removal occurred during the initial 2 h, primarily due to the feeding activity of a single *Thalassoma pavo* individual on *H. scoparia*. Although Funchal recorded the highest number of fish per hour, the removal of macroalgae was largely due to specific feeding events rather than overall fish abundance, highlighting the complex relationship between fish behaviour and macroalgae preference. At Quinta do Lorde, *Sparisoma cretense* was the sole species observed feeding, with biting behaviour limited to *H. scoparia*.

These findings highlight that fish abundance alone does not accurately reflect herbivory activity (Bejarano et al., 2017; Fox and Bellwood, 2008; Magneville et al., 2023).

Relying solely on weedpops without video analysis can lead to incomplete understanding of fish-macroalgae interactions. For example, *Sarpa salpa*, which is exclusively herbivorous as an adult, was expected to be a primary feeder but showed no interest in the macroalgae during the observed timeframe. This lack of engagement could be due to the timing of the recordings, as *S. salpa* is known to exhibit feeding activity later in the afternoon (Zemke-White et al., 2002; Magneville et al., 2023). These observations stress the importance of conducting experiments across different times of the day to capture the full spectrum of fish feeding behaviours.

Biting behaviour was primarily observed among zoobenthophagous fish, suggesting that these species targeted the epifauna associated with the macroalgae rather than the algae itself. *S. cretense*, which exhibits herbivorous feeding behaviour in the Eastern Mediterranean but adopting a more omnivorous tendency in the Atlantic Ocean (Tuya et al., 2004; Azzurro et al., 2007; Clemente et al., 2010; Alomar et al., 2016), also exhibited biting behaviour. This suggests that fish may recognise native macroalgae as hosts to viable feeding resources, such as small invertebrates like polychaetes, amphipods, copepods, and molluscs (Castriota et al., 2005; Warburton and Hughes, 2011).

Epifaunal assemblage analysis revealed distinct patterns across macroalgae species and locations, closely aligning with fish behaviour observations. *S. vulgare* and *H. scoparia* consistently supported significantly higher abundance and order-level diversity of epifauna compared to *A. taxiformis*. This pattern is likely due to the structural complexity of native macroalgae, which provides more niches and refuges for small invertebrates, supporting a more diverse epifaunal community (Taylor and Cole, 1994; Wernberg et al., 2004; McDonald and Bingham, 2010*)*. *H. scoparia* and *S. vulgare* were observed to have the same level of complexity (Chemello and Milazzo, 2002). In contrast, the non-indigenous *A. taxiformis*, characterised by its simpler structure and lower fractal complexity (Guerra-García et al., 2012), consistently hosted the lowest abundance, order richness, and diversity of epifauna. This aligns with previous findings indicating that *A. taxiformis* was typically hosts an impoverished faunal assemblage compared to native macroalgae, a trend also observed in our study (Mancuso et al., 2022).

Site-specific effects further influenced the order richness and diversity of epifauna, underscoring the complex interplay between macroalgal structure, location, and fish interactions even at small spatial scales (Guerra-García et al., 2012; Kelaher et al., 2001). Notably, in Garajau, where fish-macroalgae interactions were primarily focused on *H. scoparia* and *S. vulgare*, epifaunal diversity and species richness were significantly lower compared to Funchal and Quinta do Lorde. This suggests that increased fish interaction with these macroalgae may reduce epifaunal diversity due to increased higher predation pressure. Conversely, *A. taxiformis*, which experienced limited fish interactions, did not exhibit higher epifaunal diversity. This challenging the expectation that reduced fish predation could allow *A. taxiformis* to act as a refuge for epifauna, as suggested by previous studies on non-indigenous macroalgae (Chemello and Milazzo, 2002; Vázquez-Luis et al., 2010).

In ecosystems with limited predation, prey densities, such as epifauna, are expected to increase due to reduced predation pressure. However, when predators are present, complex habitats like macroalgae can act as refuges, stabilizing predator-prey interactions and allowing prey to thrive despite active predation (Menge and Sutherland, 1976; Orth, 1992; Moreno, 1995; Chemello and Milazzo, 2002). This dynamic is evident in our study, particularly in Garajau, where high levels of fish interaction with native macroalgae, such as *H. scoparia* and *S. vulgare*, were associated with reduced epifaunal diversity, suggesting that intense predation pressure can diminish the refuge benefits typically provided by these complex habitats. Conversely, in Funchal and Quinta do Lorde, where fish-macroalgae interactions were more limited, mainly involving *T. pavo* with *H. scoparia* in Funchal and *S. cretense* with *H. scoparia* in Quinta do Lorde, higher epifaunal diversity on native macroalgae was observed. This suggests that reduced predation pressure allowed these macroalgae to sustain richer epifaunal communities, highlighting the critical role of predation in shaping these assemblages.

The associated epifauna, such as crustaceans, molluscs, and polychaetes, are important food sources for higher trophic groups, including fish (Castriota et al., 2005; Valls, 2017). In our study, arthropods, particularly amphipods, were the most abundant group, with S. vulgare hosting the highest relative abundance, followed by H. scoparia, especially in Garajau. Conversely, *A. taxiformis* consistently displayed the lowest abundance of arthropods. This pattern underscores the influence of both macroalgal structure and fish interactions in shaping epifaunal communities. The absence of significant fish interactions with *A. taxiformis* across all locations did not lead to an increase in epifaunal diversity, challenging the hypothesis that reduced predation would allow *A. taxiformis* to act as a refuge. Instead, it highlights how the structural complexity of native macroalgae supports more abundant epifaunal assemblages, illustrating the interplay between habitat features and predator-prey dynamics in coastal ecosystems.

The widespread persistence of *A. taxiformis* in the Madeira Island ecosystem (Friedlander et al., 2017; Sangil et al., 2018; Bernal-Ibáñez et al., 2021), combined with its avoidance by local fish, suggests that this invasive species will continue to dominate without being controlled by natural consumers, unlike native macroalgae. This poses a significant threat to biodiversity in coastal areas in Madeira is implied (Martin et al., 1992; Heck et al., 2003). Our findings suggest that *A. taxiformis* not only fails to serve as a significant refuge for epifauna but also provides limited prey availability for fish, further disconnecting it from the native food web. If *A. taxiformis* were to become more dominant, it could lead to bottom-up effects on rocky shore ecosystems by altering the availability of food resources and reducing primary producer biomass (Mancuso et al., 2022; Bernal-Ibáñez et al., 2022a). However, these implications remain speculative, and further research is essential to fully understand the ecological consequences of *A. taxiformis* dominance and its impact on native species and ecosystem functions.

Besides these potential effects of *A. taxiformis*, the emergence of the NIS brown macroalgae, *Rugulopteryx okamurae*, characterised by invasive traits, was documented on Madeira Island one year before the initiation of our investigation (Bernal Ibáñez et al., 2022b). The proliferation of *R. okamurae* occurred after the conclusion of our study, during which the foraging preferences of fish for this algae were not assessed. The potential impact of this NIS macroalgae on the Madeira Island ecosystem, especially in terms of habitat alteration, is a cause for concern. This is prompted by the observed rapid spread of established populations in various island regions (Pers. obs.) and the documented ecological impacts in the shallow-water habitats from nearby Macaronesian islands (Faria et al., 2021, 2022). Despite the absence of an assessment of the interaction with the fish communities at invaded habitats, experimental studies have shown the defensive role of *R. okamurae* against generalist herbivores like sea urchins (Casal-Porras et al., 2021). Madeira island has experienced declines in key herbivorous species, as the case of the long-spined sea urchin *Diadema antillarum* (Gizzi et al., 2021; Alves et al., 2007). A decline in herbivory control, combined with the rapid proliferation and competitive superiority of *R. okamurae* at favourable habitats (Faria et al., 2021; García-Gómez et al., 2021) prompts speculations about the role of herbivory interactions as a biotic resistance mechanism in this region.

Moving forward, it is advised to conduct further investigations, spanning different seasons and times of the day, given the known variations in fish activities throughout the daily cycle. These investigations should assess trophic interactions involving invertebrate predators, such as sea hares (*Aplysia* sp.), crabs, and sea urchins. This approach will help determine their capacity to consume NIS macroalgae species like *R. okamurae* and *A. taxiformis*.

This study provided a detailed methodology that can be universally applied, offering a robust framework for studying NIS macroalgae and their trophic interaction in any location worldwide. Such research regarding the assessment of trophic interaction between this NIS algae that is well known to have a invasion characteristics and the native species, will be needed and it will provide a more comprehensive understanding of the complex ecological consequences of NIS macroalgae dominance in the region and inform managers for more effective NIS management.

CRediT authorship contribution statement

Sahar Chebaane: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Aschwin Hillebrand Engelen:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Miguel Pessanha Pais:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Rodrigo Silva:** Writing – review & editing, Investigation. **Francesca Gizzi:** Investigation. **Raül Triay-Portella:** Writing – review & editing, Investigation. **Marta Florido:** Writing – review & editing, Visualization. **João Gama Monteiro:** Writing – review & editing, Validation, Supervision, Resources, Methodology, 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.

Data availability

Data will be made available on request.

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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.2024.106766.

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