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Exploring foraging preference of local fish species towards non-indigenous fouling communities near marinas: Insights from Remote Video Foraging System (RVFS) trials

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ABSTRACT

Non-indigenous species (NIS) spread from marinas to natural environments is influenced by niche availability, habitat suitability, and local biotic resistance. This study explores the effect of indigenous fish feeding behaviour on NIS proliferation using fouling communities, pre-grown on settlement plates, as two distinct, representative models: one from NIS-rich marinas and the other from areas outside marinas with fewer NIS. These plates were mounted on a Remote Video Foraging System (RVFS) near three marinas on Madeira Island. After 24-h, NIS abundance was reduced by 3.5 %. *Canthigaster capistrata*'s preference for marinas plates suggests potential biotic resistance. However, *Sparisoma cretense* showed equal biting frequencies for both plate types. The cryptogenic ascidian *Trididemnum cereum* was the preferred target for the fish. Our study introduces a global framework using RVFS for in-situ experiments, replicable across divers contexts (e.g., feeding behaviour, biotic resistance), which can be complemented by metabarcoding and isotopic analysis to confirm consumption patterns.

1. Introduction

Predation stands as a fundamental biological process that plays critical roles in maintaining the equilibrium and stability of marine ecosystems, namely in controlling marine organisms' abundance and distribution, promoting biodiversity and enhancing ecosystem functioning (Hammerschlag et al., 2019). However, in invaded ecosystems, the introduction of non-indigenous marine species (NIS) can disrupt this delicate balance by altering food web dynamics, which can lead to NIS out performing or outcompeting native species (Geburzi and McCarthy, 2018). This invasive behaviour of NIS can lead to significant ecological consequences, including reduced species diversity, altered community structure, and impaired ecosystem functioning (Carlton, 2000; Bax et al., 2003; García-Gómez et al., 2020).

Oceanic islands often exhibit a high proportion of relict island species and clades, which have displayed remarkable resistance to significant climatic changes that led to the extinction of their mainland counterparts (Cronk, 1997; Kier et al., 2009). This resilience is likely bolstered by the climatic buffering effect of the surrounding ocean (Cronk, 1997; Bell, 2008). The hight levels of insular endemism richness stem from persistent ancient lineages and adaptive diversification (Isaac et al., 2007; Whittaker and Fernández-Palacios, 2007; Kier et al., 2009). It is important to note that paleoendemic island lineages, representing taxonomically isolated species, possess a substantial amount of unique evolutionary history, surpassing closely related neoendemic lineages (Givnish, 1998; Schluter, 2000; Isaac et al., 2007; Whittaker and Fernández-Palacios, 2007). Island populations have been shown to be highly susceptible to factors inducing biotic perturbations, including the

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encroachment of human activities and infrastructure into marine environments, rapid shifts in climate conditions, and the introduction of NIS (Perrings, 2002; Tuya et al., 2002; Whittaker and Fernández-Palacios, 2007; Russell and Kueffer, 2019; Bernal-Ibáñez et al., 2021a). Oceanic islands, especially those with high intensity or frequency of marine traffic and maritime infrastructures, face an elevated risk of NIS introduction (Castro et al., 2020). Marinas and harbours are regarded as hot zones for NIS establishment due to the increased maritime activity inside them and compounded by the effects of the anthropogenic interventions and infrastructure development (Chebaane et., 2019; Martínez-Laiz et al., 2019; Castro et al., 2020). These locations can serve as 'steppingstones' for the introduction of NIS into nearby natural habitats due to their function as a refuge for newly arrived NIS (Canning-Clode et al., 2013; De Mesel et al., 2015; Chebaane et al., 2019; Castro et al., 2020). Additionally, the frequent traffic of local boats from inside the marina and harbours to the outside neighbouring areas facilitates the potential of NIS spread and establishment in natural habitats (Canning-Clode et al., 2013; Ferrario et al., 2017; Afonso et al., 2020; Parretti et al., 2020; Costello et al., 2022). The introduction and spread of NIS from marinas and harbours can increase the risk of invasion events that perturb the natural ecological dynamics and genetic diversity, potentially leading to the decline and even extinction of paleoendemic island lineages (Geburzi and McCarthy, 2018). In addition, on populated islands, the socio-economic consequences of NIS proliferation can be severe, causing harm to local industries, such as fisheries, aquaculture, and tourism (Çinar et al., 2014).

Fouling NIS (e.g., barnacles, tunicates, bryozoans, sponges) are known for forming densely packed colonies capable of outcompeting native species for space and resources (Byers, 2002; Oricchio and Muniz Dias, 2020). This competitive advantage is often due to their high resistance to abiotic stressors (Shea and Chesson, 2002; Geburzi and McCarthy, 2018). Invasive fouling NIS may also possess allelochemicals, which improve their competitive capacity against local fouling species in horizontal interactions, as well as protect them against potential consumers such as foragers and predators in vertical interactions (Mackenzie et al., 2001). In this context, predation can assume a pivotal role in fostering biotic resistance against invasion and expansion versus promoting NIS proliferation (deRivera et al., 2005; Dumont et al., 2011).

The function of predation varies based on the traits and composition of predators and prey (Carlsson et al., 2009; Kimbro et al., 2013). Native predators such as fish, crabs, and sea urchins can help control fouling NIS populations by feeding on them (Stachowicz et al., 1999; Stachowicz et al., 2002; Freestone et al., 2013; Simkanin et al., 2013; Santamaría et al., 2018). However, not all native species are capable of consuming NIS, in which case the selective consumption of native species can favour NIS establishment and expansion. In summary, regarding biotic resilience to NIS, the outcome of predation can vary depending on the interplay of predator and prey traits.

Trophic interactions are often complex, due to manifesting with direct and indirect effects, as well as negative and positive impacts for native communities (Thomsen et al., 2016; Katsanevakis et al., 2014). Positive effects (i.e., biotic resistance) occur when local consumers such as fish and benthic grazers prey on NIS, reducing NIS abundance and spread (Santamaría et al., 2018; Simkanin et al., 2013; Tiralongo et al., 2021). In contrast, negative effects (i.e., biotic facilitation) may occur when consumers selectively forage on native species over NIS, increasing NIS abundance and spread, a mechanism known as the Enemy Release Hypothesis (Keane and Crawley, 2002; Colautti et al., 2004). Therefore, the trophic effects of local consumers, such as foraging and grazing fish, are important elements in structuring fouling assemblages (Leclerc et al., 2020; Janiak and Branson, 2021).

Fouling communities have served as a model system in ecological research, facilitating investigations into a spectrum of theories and hypotheses within the field of marine ecology. These encompass the examination of principles such as the intermediate disturbance hypothesis, the latitudinal gradient of species richness, and the exploration of concepts related to biological invasions, including the biotic resistance hypothesis and the enemy release hypothesis (Lenz et al., 2004; Canning-Clode, 2009; Gestoso et al., 2018; Tamburini et al., 2022; Chebaane et al., 2023). Both the biotic resistance and biotic facilitation of NIS by predation/grazing have been previously assessed in artificial environments (Rogers et al., 2016; Gestoso et al., 2018; Leclerc et al., 2020), as well as in natural habitats (Ruesink, 2007; Gu et al., 2023).

Comparative studies between artificial and natural habitats consistently demonstrated that artificial habitats tend to exhibit a higher abundance of fouling NIS when compared to neighbouring natural habitats (Simkanin et al., 2013; Janiak and Branson, 2021; Rothäusler et al., 2022). However, the mechanisms behind the spread and infiltration of NIS into natural habitats remain poorly understood as they are likely to be influenced by compounding abiotic and biotic factors, including but not limited to building materials and grazing/foraging pressure (Glasby et al., 2007; Marins et al., 2010; Lambert, 2002; Simkanin et al., 2013; Simkanin et al., 2012).

To advance our understanding of the mechanisms influencing the spread of NIS from maritime infrastructures to natural habitats in the vicinity, it is necessary to conduct comprehensive studies or experimental trials that target specific factors. In this context, this study was designed to examine the foraging preferences of local fish communities in relation to the presence of NIS in an island ecosystem of Madeira Island, Portugal. Our focus lay in investigating whether local fish communities showed a preference for foraging on assemblages from marinas, where NIS are expected to be more abundant than native taxa, or from the assemblages from the natural area. We also assessed whether fish selectively remove or forage on NIS or native taxa within each assemblage and whether selective foraging promotes changes in the assemblage structure, potentially facilitating or suppressing the establishment and spread of NIS.

2. Materials and methods

2.1. Study location

This study was conducted on the southern coast of Madeira Island, NE Atlantic Portugal (Fig. 1), at Quinta do Lorde (32°44′26.80″N, 16°42′38.72″W), Funchal (32°38′27.59″N, 16°55′6.90″ W), and Calheta (32°42′49.27″N, 17° 9′56.77″ W). Funchal and Calheta are subject to varying degrees of anthropogenic activities, with Funchal experiencing highest anthropogenic influence (being the island's capital with higher population density). Conversely, Quinta do Lorde exhibits the lowest level of anthropogenic pressures due to its location in a low human population density. All three locations host touristic marinas, which have been identified as a hotspots for NIS introduction (Ramalhosa et al., 2017). The study involved two main phases: first, the recruitment of fouling communities both inside and outside each marina; and second, the observation of local foragers interacting with the recruited fouling communities in a natural setting - shallow waters (7 to 8 m depth) on rocky bottoms, which are dominated by small boulders within the vicinity of the marinas (Fig. 1).

The fish assemblages at these locations share species, such as *Thalassoma pavo*, *Similiparma lurida*, *Chromis limbata*, *Sparisoma cretense*, *Canthigaster capistrata* and *Sphoeroides marmoratus* (Friedlander et al., 2017; Chebaane et al., 2022).

2.2. Field and laboratory procedures

2.2.1. Fouling assemblage settlement

To obtain two different fouling assemblage types, one with a higher proportion of non-indigenous species (NIS) than the "second" (hereinafter referred to as "treatments"), 16 settlement plates were deployed by SCUBA divers inside each marina (where NIS richness and abundance is higher, (Ramalhosa et al., 2017)) and 16 outside the marinas. In both sites, the substrates were uniform, consisting of a mixed substrate of

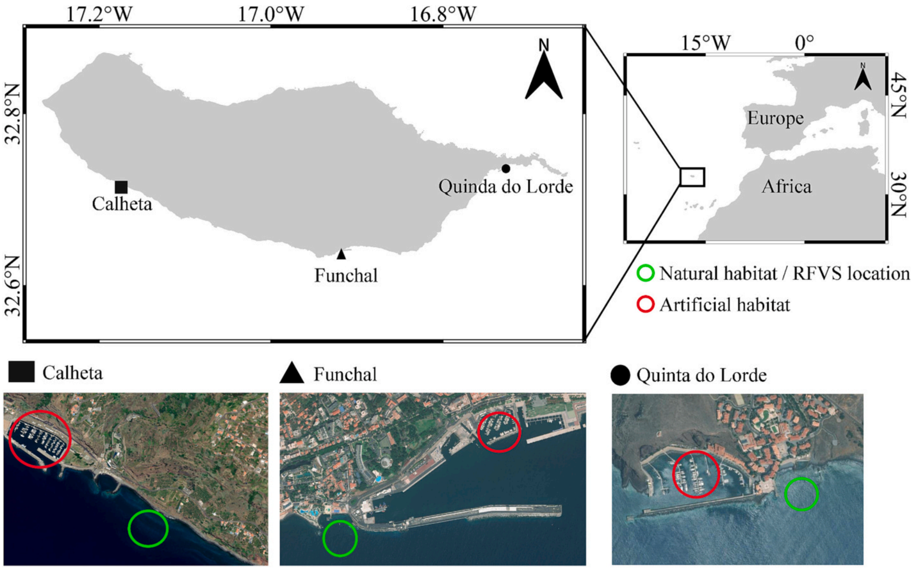

Fig. 1. Map of Madeira Island displaying the three study locations, the recruitment sites of baits for the Remote Video Foraging System (RVFS) and where the RVFS experiments were conducted.

sand and boulders (Figs. 1; A.1). Settlement plates were made from polyvinyl chloride (PVC) panels, each measuring 12 × 12 cm, and were attached to a custom deployment set up using polypropylene boxes. Each set up was composed of two superimposed boxes, with weights (two cement blocks, each weighing 8–10 kg) in the lower one and with four recruitment plates vertically attached in the upper one (as illustrated in Fig. A1). These deployment set-ups were positioned on the seafloor. At each site, four recruitment set ups (4boxes with 4 plates each) were deployed inside and outside the marina at 7–8 m depth and with 3–5 m distance between them (total of 16 recruitment plates per site and per treatment). Recruitment period in each treatment was six months, from April to October 2021, to maximise recruitment and coverage of fouling assemblages (Canning-Clode et al., 2009). After the recruitment period, each plate was photographed and fouling assemblage composition was assessed by visual inspection and with image analysis. Abundance was quantified through counts of individual and total plate coverage was estimated. These measurements were crucial in confirming the higher relative abundance of NIS in assemblages recruited inside marinas. More comprehensive details regarding the analysis can be found in Section 2.2.3 (Analysis of foraging effects on plates).

2.2.2. *Observation of foraging behaviour and preferences*

After the settlement period, SCUBA divers removed the plates from the boxes and placed each one on a previously labelled zip bag before bringing them to the surface. On shore, bags were placed in a container filled with seawater sourced from the corresponding site, with the intention of mitigating any harm and ensuring the survival of the organisms during transit. One of the four plates from each settlement box (4 plates per treatment, per location) was transported to the laboratory and then placed in a refrigerator with seawater for species identification using a stereo microscope. Plates stored in the refrigerator were inspected for taxa identification 3 days after the date of collection. The remaining 3 plates from each box were used in an in situ experimental trial, using RVFS - Remote Video Foraging Video System (Chebaane et al., 2022) to identify fishes interacting with the recruited assemblages. Plate assignment followed a randomised complete block design (Anderson and McLean, 1974) with 9 plates per RVFS: three settlement plates from a box inside the marina (IN), three plates from a box outside the marina (OUT) and three empty control plates (C) (Fig. A.1). Empty plates were used to ensure that foraging attempts were not motivated simply by the presence of plates, and that foragers were identifying and opting for fouling assemblages. The first batch of colonised plates (12 plates in total) was set up on two RVFS structures at each location within 1 h of collection from the settlement boxes. The remaining 12 colonised plates were stored in seawater to be used after 24 h. They were kept in separate buckets with an air pump during this period. Later, these plates were also mounted on the two RVFS structures, replacing the initial batch of plates (Fig. A.1 B). The structures were positioned approximately 3–5 m apart outside the marinas, at a distance ranging from 0.5Km to 1KM from the marina entrance. These structures were placed at a depth of 7–8 m above a sandy seabed. Both RVFS structures were deployed 24 h before starting the experiment by scuba divers, around 5 m from the original settlement site outside the marina (Fig. 1). No plates were transported between locations.

To minimise the attractive effect of novelty created by the presence of a foreign structure, RVFS structures were deployed without the plates 24 h before starting the experiments (Warburton and Hughes, 2011; Chebaane et al., 2022). After SCUBA divers fixed the plates on the structures for the start of the experiments (T0), remote cameras (Paralenz Vaquita) for each RVFS structure were placed on a weighted tripod on the ground, located approximately 2 m away from the RVFS structure and facing the plates, ensuring that all 9 plates were fully in frame (Fig. A.1 D).

Divers left the site to avoid interference and cameras recorded video continuously for approximately 3 h, after which (T3) the divers returned to carefully collect the cameras and tripods for video analysis in the laboratory.

The video analysis period was continuous and started immediately after fixing the plates to the RVFS structures (T0) to minimise the influence of SCUBA diver presence and ended after 3 h. Fish species and behaviours were annotated by a single observer using a scan sampling technique, and quantifying presence, interest, and foraging state.

Presence was quantified as the amount of time (in seconds) a fish is visible on the video. Interest was quantified as the amount of time (in seconds) a fish spends swimming towards or pausing in front of a plate. Foraging was quantified as the amount of time (in seconds) a fish spends biting on a plate, as well as the number of bites during each foraging period.

2.2.3. Analysis of foraging effects on plates

To evaluate the impact of foragers on each plate, all plates were systematically photographed underwater by SCUBA divers with an Olympus TG6 camera mounted onto a photoquadrat frame, without manipulating or interfering with the plates or structures. Photographs were taken after fixing the plates onto the RVFS structures (T0), before collecting the video cameras after 3 h (T3), and finally after 24 h (T24), followed by the removal of the RVFS structures from the sites (Fig. A.1, C).

Underwater photos of the plates were subject to colour and lens correction, perspective cropping, and resizing using Adobe Photoshop CS6. Coral Point Count with Excel extensions (CPCe V4.1) software was then used to randomly place 100 points on each plate. Taxa under each point were identified and registered to determine live cover (total number of points with live organisms) and taxa relative abundances (percent of points for each taxa) at T0 (when deploying), T2 (3 h after deployments) and T3 (24h after deployment, (Kohler and Gill, 2006; Chebaane et al., 2022). Furthermore, empty space and sediment were also considered during this assessment. As all photos were perspective cropped and resized to have the same dimensions, we devised a strategy to assess if organisms/taxa has been removed during exposure periods. CPCe files with random point coordinates used in T0 were saved a re-used for T3 and T24 so that the coordinates of the 100 points stored on the *.cpce file of each plate matched the same location on the plate in sequential images, allowing for repeated sampling of each randomly placed point (see Chebaane et al., 2022).

2.3. Data analysis

2.3.1. Settlement of fouling assemblages

To test our assumption that assemblages recruited inside marinas each settlement had significantly higher proportions of NIS than those recruited outside, two univariate permutational analysis of variance (PERMANOVA) were performed based on Euclidean distance matrices among samples (Anderson, 2008). One test used the total number of points with non-indigenous species (NIS) and another for the total coverage of the plate (number of points with taxa). A randomised block design was used, with the factors Location (random, 3 levels), Treatment (fixed, 2 levels) and settlement Box (random, 12 levels, nested in Location).

In addition, to test for differences in assemblage composition between settlement sites, the relative abundance per taxa on each plate at T0 was analysed through a multivariate PERMANOVA using the same design as in the univariate analysis above. Abundances were square root transformed to reduce the importance of dominant species before generating the Bray-Curtis similarity matrix for analysis (Anderson, 2008). The homogeneity of multivariate dispersions was tested using permutational analysis of multivariate dispersions (PERMDISP). Principal Coordinates Ordination (PCO) plots were created from the similarity matrix, with overlaid Spearman correlation vector representing the relative abundance of non-indigenous species (NIS) per sample to analyse the strength of NIS in the main species composition gradients.

Statistical analyses were performed in Primer-e v6 + PERMANOVA add-on (Anderson, 2008; Clarke and Gorley, 2015) and the software package R version 4.2.1 (R Core Team, 2022). using the ggplot2 package version 3.4.2 (Wickham, 2016).

2.3.2. Observation of foraging behaviour and preferences

A Sankey diagram was created to visualise and analyse interactions and preferences of fish in different behavioural categories, namely presence, interest, and foraging. This facilitated the identification of flows and patterns, providing insights into species-specific preferences, individual presence across locations, and the level of foraging activity displayed in different treatments. The colour-coded links in the diagram allowed for a visual representation of different species' contributions to the overall flow and behaviour. The diagrams were generated in R with the “networkD3” package (Allaire et al., 2017).

To confirm the results of the generated diagram, a univariate PERMANOVA analysis was conducted, employing the same randomised block design used in this study. This analysis specifically examined the preference differentiation between plates incubated inside or outside marinas.

There was little to no foraging on the control plates (usually 0 bites up to one event of 2 bites). This showed that foraging attempts were not motivated simply by the presence of plates, and that foragers chose to target fouling assemblages. This was enough evidence and required no further inclusion of control data on statistical analyses.

A comprehensive overview of bite occurrences for each species across different locations and within each treatment was attained by calculating descriptive statistics in the form of percentages. This approach provided a nuanced perspective on the distribution of bites. All graphical representations were produced using R version 4.2.1 software (R Core Team, 2022).

2.3.3. Analysis of foraging effects on plates

In order to assess the effect of foragers on the provided treatments, the Bray-Curtis similarity matrix was calculated using the species' relative abundance. The similarity values were then subjected to repeated measure permutational analysis of variance (PERMANOVA) with the factors Location (random, 3 levels), Treatment (fixed, 2 levels), and RVFS (Random, 4 levels, nested in location), as well as the factor Time (fixed, 2 levels, repeated measure) following the approach by Anderson (2008, page 66). The permutation of residuals under a reduced model was applied. Univariate PERMANOVAs were performed, using the same design as the multivariate analysis, with the species richness, total species coverage, and relative abundance of non-indigenous species. Pairwise analysis was conducted when interactions were observed. The statistical analyses were carried out using Primer-e v6+ PERMANOVA software. The predated percentage data were separately analysed using univariate analysis PERMANOVA for the removed taxa after 3 h and 24 h, following the same randomised block design. Pairwise analysis was performed, and the results were visualised in Fig. A.2.

Furthermore, to determine the selectivity of foragers for a specific fouling taxon, the initial mean coverage of biofouling was calculated for each taxon per treatment for each location to compute Ivlev's electivity index (Ei). Ivlev's electivity index (Ei) (Ivlev, 1961) was employed to analyse the foraging selectivity of the species after 3 h and 24 h of foraging. The Ei index was calculated using the ‘ivlev’ function within the selectapref R package (Richardson, 2020), and the analysis was conducted using R version 4.2.1 software. Ivlev's Ei index was computed using the formula:

$$\mathrm{E_i} = (\mathrm{a_i} - \mathrm{b_i})/(\mathrm{a_i} + \mathrm{b_i})$$

where a_i represents the relative proportion of taxon i removed by the foragers, and b_i represents the relative proportion of taxon i present in the RVFS structure for each treatment. The resulting index ranged from −1 to 1, with −1 indicating complete avoidance, 1 indicating preference, and 0 indicating indifference.

3. Results

3.1. NIS abundance and fouling assemblage differences

Settlement plates from inside the marinas exhibited, on average, 98 % to 67 % more NIS abundance when compared to plates from outside marinas, within each location, validating our assumption for treatments (Table A.1; Fig. 2 A). In terms of total coverage of the plates, Funchal plates had similar coverage, but Calheta and Quinta do Lorde had one RVFS structure each with dissimilar coverage per treatment, both with higher coverage inside than outside the marina (Table A.1).

Assemblage structure differed between the IN and OUT treatments

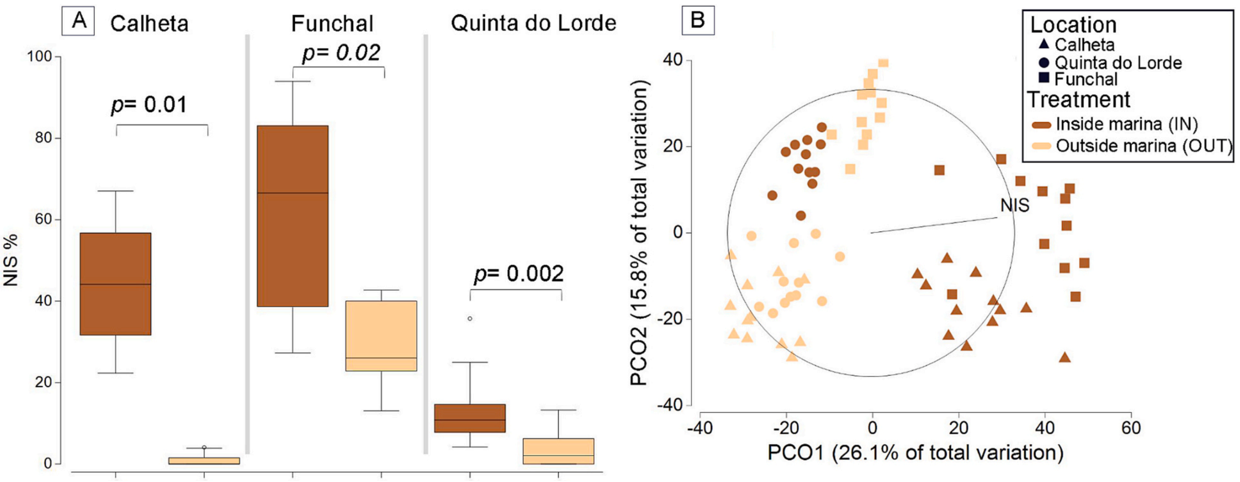

Fig. 2. A: Average total non-indigenous species percentage per treatment at each location after settlement (T0) with the *p*-value indicating the significant differences in univariate pairwise PERMANOVA. B: Principal Coordinates Analysis (PCO) plot of fouling taxa relative abundances at the three studied Locations (shapes) and treatments (colour) at T0, based on a Bray-Curtis similarities matrix and square root transformation. Vector represents the Spearman correlation (coefficient higher than 0.5) with the PCO axes for the relative abundance of all NIS (non-indigenous species) per plate.

(Table A.2). However, it is important to note that these treatment disparities were location-specific, both in terms of assemblage structure and the relative abundance of non-indigenous species (Tables A.1; A.2). The Principal Coordinate Analysis (PCO) plot illustrates these patterns (Fig. 2 B). In the case of Funchal and Calheta, the PCO plot indicated heterogeneous fouling assemblages, revealing clear dissimilarities between the IN and OUT treatments. On the other hand, Quinta do Lorde, exhibits a fouling assemblage that is more homogenous, despite the significant differences between the treatments (Table A.2), with fewer distinctions observed between the IN and OUT treatments (Fig. 2).

3.2. Observation of foraging behaviour and preferences

A total of 270 individual organisms belonging to ten different species were recorded in videos obtained from the Remote Video Foraging System (RVFS). The analysis revealed that six out of the ten observed species had the ability to consume sessile taxa present on the provided PVC-colonised settlement plates (Table A.3), based on existing literature.

The foraging behaviour observations revealed that among the seven observed species across different locations within the RVFS, certain fish species displayed a higher level of interest ($p = 0.045$) in the IN treatment compared to the OUT treatment (Fig. 3; Table 1). Specifically, both *Canthigaster capistrata* and *Sparisoma cretense* displayed a clear interest in the IN treatment (Fig.3). Additionally, among the seven species that showed interest, four species, namely *C. capistrata*, *Sphoeroides marmoratus*, *S. cretense*, and *Similiparma lurida*, were observed foraging from both the IN and OUT treatments (Fig. 3). It was observed that *C. capistrata* and *S. cretense* spent more time foraging from both the IN and OUT treatments, with *C. capistrata* demonstrating a preference for the IN treatment, while *S. cretense* had equal foraging times for both treatments (Fig. 3). While no statistically significant differences in the duration of foraging were found when comparing treatments, notable dissimilarities were observed in terms of location (Fig.3; Table 1).

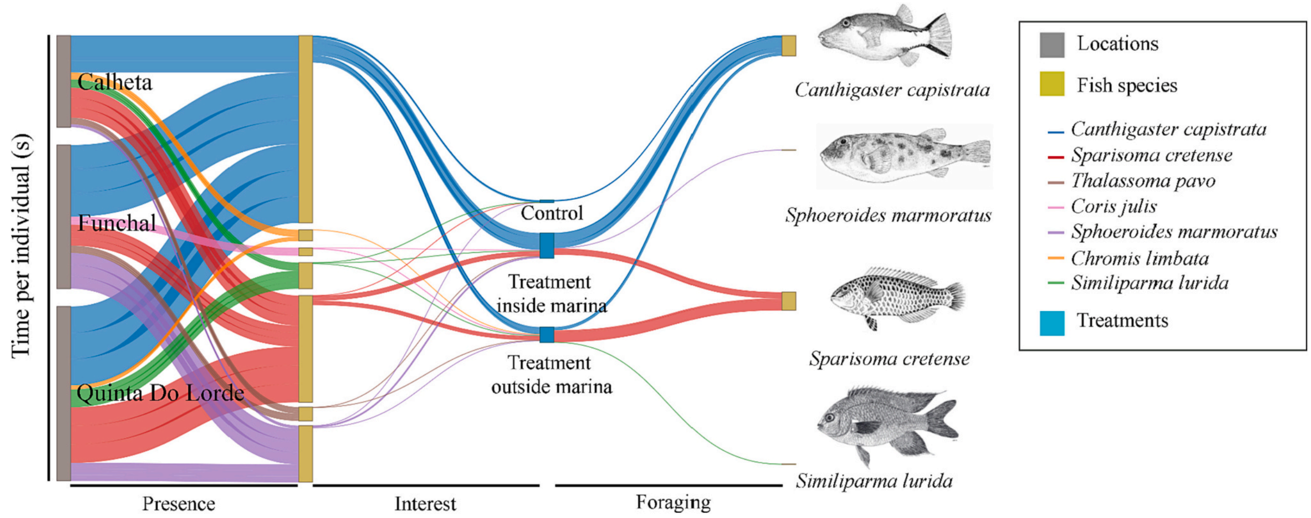

Fig. 3. Sankey diagram showing the patterns of presence, interest, and foraging behaviour of fish individuals. The nodes in the graph represent different entities: Location (Grey nodes), Species (Green nodes), and Treatment (Blue nodes). The connections between nodes, represented by the links, indicate the flow or transition of individuals from one category to another (e.g., the diagram first shows the presence of species per location, followed by the species showing interest in a specific treatment, and finally, the species engaging in foraging behaviour towards a specific treatment. The width of the links corresponds to the magnitude of the flow or the average duration in which individuals are present, interested, or foraging on a specific treatment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Univariate PERMANOVA results for the effects of location and treatment on fish preference, interest (seconds), and number of bites. Bold font indicates statistical significance at the α = 0.05 level. df: degrees of freedom; MS: mean square sum; *P* (prem): *p*-values for the permutation test. The permutation test was conducted with 9999 permutations.

Source	df	Interest (seconds)			Foraging (seconds)			Number of bites		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Location	2	13,654	0.982	0.424	21,325	3.221	0.040	30,577	4.210	0.019
Treatment	1	43,381	7.915	0.045	16,136	0.6152	0.577	25,220	1.210	0.388
RVFS (Location)	9	13,903	1.441	0.219	6619.9	0.4857	0.941	7261.2	0.6529	0.806
Location x Treatment	2	5480.7	0.5681	0.659	26,228	1.924	0.163	20,833	1.873	0.175
Residuals	9	9646.3			13,628			11,121		

When examining the number of bites per treatment in each location for the different species, it was observed that *S. lurida* and *S. marmoratus* exhibited only 2 and 1 bites, respectively (Fig. A.3). Conversely, regardless of location, *C. capistrata* and *S. cretense* displayed varying biting patterns. *Canthigaster capistrata* displayed more bites from treatment IN (109 bites) than from treatment OUT (19 bites). While, *S. cretense* showed approximately equal biting frequencies for both the IN treatment (40 bites) and the OUT treatment (32 bites) (Fig. A.3).

However, these preferences were partly location-dependent (Table 1). In Calheta, *S. cretense* demonstrated a higher number of bites (21 bites) and a clear preference for the IN treatment (80 %) (Fig. A.3). In Funchal, *C. capistrata* had the highest number of bites (100 bites), with a predominant focus on the IN treatment (90 %), while *S. cretense* displayed a comparable preference for the IN treatment, but with a lower overall frequency of bites (a total of 20 bites with approximately 70 % on IN treatment plates). In Quinta do Lorde, *C. capistrata* tended to bite slightly more on the IN treatment plates (64 %) compared to the OUT treatment, with a total of 28 recorded bites. On the other hand, *S.cretense* individuals foraged less from the IN treatment (29 %) than the OUT treatment, with a total of 31 recorded bites (Fig. A.3).

Overall, *C. capistrata* spent more time foraging and showed a higher number of bites on IN treatment plates, while *S. cretense* showed a similar preference, but only in Funchal and Calheta. These preferences were therefore location-specific. (Fig.3; Table 1).

3.3. Analysis of foraging effects on plates

The analysis of the percentage of biofouling coverage that was grazed upon during the initial 3 h of foraging revealed a significant difference between the IN and OUT treatments (Fig. A.2; Table A.4) The results confirm that the fish exhibited a greater preference for foraging from the IN treatment, aligning with the observations made in the video. Furthermore, notable variations specific to each location emerged after 24 h. Specifically, in Calheta, a higher proportion of biofouling was grazed upon on the IN treatment compared to the OUT treatment, whereas no significant difference was observed in Quinta do Lorde and Funchal (see Fig. A.2).

Subsequently, when assessing the impact of foraging on the structure of the biofouling community, significant changes were observed only after 24 h of foraging for the IN treatment, regardless of the location. In contrast, no significant impact was observed after 3 or 24 h for the OUT treatment (see Table 2).

The effect of foragers on the diversity of the biofouling community varied depending on the location. Only at Funchal there was a significant reduction in species richness observed on the IN treatment (Table 2). The total coverage of biofouling was significantly reduced on the IN treatment for both Calheta and Funchal, and on the OUT treatment for Funchal and Quinta do Lorde. This reduction in coverage was significant only after 24 h of foraging.

Furthermore, the IN treatment showed a significant decrease in the relative abundance of NIS, suggesting that foragers had a greater impact on reducing NIS in certain locations, primarily at Calheta and Funchal after 24 h of foraging.

Among the fouling species identified, it was observed that 44 % of non-indigenous species (NIS) were preyed upon by foragers, while only 33 % of the remaining native biofouling species served as prey (Table A.5). The most targeted species were *Trididemnum cereum* (Cryptogenic), *Lithophyllum incrustans* (Native), *Celleporaria inaudita* (NIS), and *Schizoporella pungens* (NIS).

When Ivlev's index was examined, which considered the initial relative abundance of fouling species, variations in species preferences and avoidance were observed across locations and treatments during the initial three-hour period and during the 24 h (Fig. 4; Table A.6).

Table 2

Summary of PERMANOVA tests for differences in biofouling taxa richness, percentage cover, and assemblage structure, considering Treatments (Tr) (IN: inside the marina, OUT: outside the marina), Time (Ti) of exposure to foragers (T0: before exposure; T3: 3 h of foraging; T24: after 24 h of foraging), and Location (Lo) (Calheta, Funchal, and Quinta Do Lorde). Bold font indicates statistical significance at α = 0.05. df: degrees of freedom; MS: mean squared distance; P (perm): *p*-values for the permutation test.*: Bray Curtis similarity; **: Euclidean distance; ∀: the universal quantifier.

Source	df	Assemblage structure*			Richness**			Total percentage cover**			NIS relative abundance**		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Treatment	1	31,571	1.8910	0.2156	0.0424	0.0128	0.9203	2.2892	2.3989	0.2564	14,403	7.9964	0.1122
Time	2	3.134	2.7817	0.1592	0.0033	10.0170	0.0254	0.0869	9.0804	0.0327	4.8894	2.464	0.2059
Location	2	25,741	8.5426	0.0001	3.9724	4.7877	0.0137	1.8972	4.0246	0.0212	8308.8	30.467	0.0001
Tr x Ti	2	1.6491	28.530	0.0127	0.0006	0.6825	0.5504	0.0130	1.1939	0.3966	2.2241	3.1263	0.1531
Tr x Ti x Lo	4	0.0578	0.0873	0.8385	0.0008	2.8648	0.0343	0.0109	6.0207	0.0007	0.7114	4.94	0.003
Res	36	0.6624			0.0003			0.0018			0.1441		
Pairwise comparisons		Tr x Ti IN: T3 = (T0 ≠ T24) OUT: T0 = T3 = T24			Trx Ti x Lo For Calheta ∀ Tr: T0 = T3 = T24 For Funchal IN: T3 = (T0 > T24) OUT: T0 = T3 = T24 For Quinta Do Lorde ∀ Tr: T0 = T3 = T24			Trx Ti x Lo For Calheta IN: T24 < (T3 = T0) OUT: T0 = T3 = T24 For Funchal ∀ Tr: T24 < (T3 = T0) For Quinta Do Lorde IN: T0 = T3 = T24 OUT: T3 = (T0 > T24)			Trx Ti x Lo For Calheta IN: T3 = (T24 < T0) OUT: T0 = T3 = T24 For Funchal Tr: T24 < (T3 = T0) OUT: T0 = T3 = T24 For Quinta Do Lorde ∀ Tr: T0 = T3 = T24		

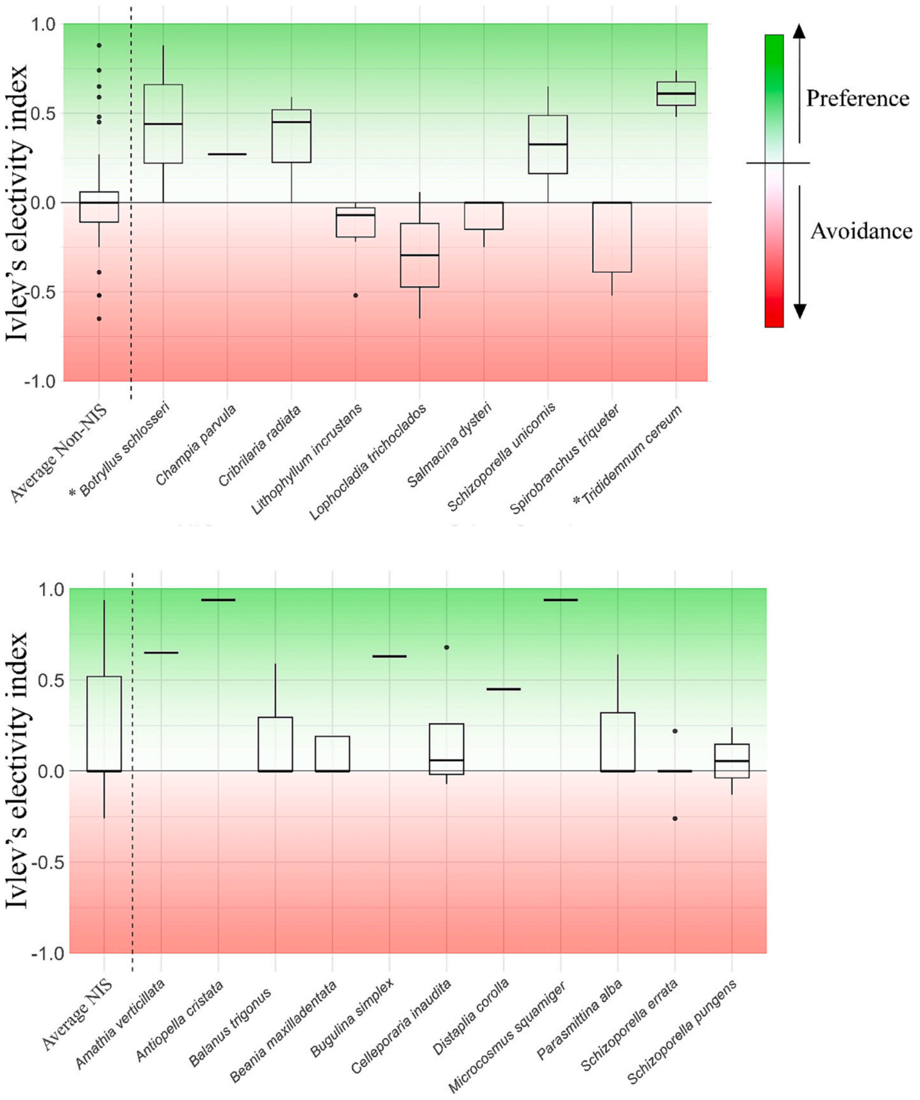

Fig. 4. Box plots illustrating the average Ivlev's electivity index for Non-Indigenous Species (NIS) and the average Ivlev's electivity index for Non-NIS (Native and cryptogenic species). * = Cryptogenic species.

At Calheta, during the initial 3-h period for the IN treatment, there was a preference for the cryptogenic ascidian *T. cereum*, alongside the non-indigenous bryozoans *Schizoporella errata* and *C. inaudita*, and the crustose algae *Nemoderma* sp. and *L. incrustans*. After 24 h, the preference consolidated around the ascidian species *T. cereum* (Cryptogenic). Concurrently, there was a decline in preference for the crustose alga L. *incrustans* and the encrusting bryozoans, with a noticeable shift towards the soft ascidian *Distaplia corolla* (NIS), *Botryllus schlosseri* (Cryptogenic), and the Porifera *Sycon* sp. (Table A.6).

Also at Calheta, but for the OUT treatment, the native calcareous bryozoan *Cribrilaria radiata* was selectively targeted throughout the entire 24-h period, encompassing both the initial 3-h period and subsequent hours, while the crustose algae (both species) were avoided.

At Funchal, for the IN treatment, during the initial three-hour period, preference was shown for the non-indigenous branched soft bryozoans *Bugulina simplex* and *Amathia verticillata*, along with crustose algae and the cryptogenic ascidian species *T. cereum*. After 24 h, the preference shifted to prefer more ascidian species and non-indigenous encrustant bryozoans *Parasmittina alba* and *S. pungens*. However, there was an avoidance of *S. errata* (Table A.6).

For the OUT treatment at Funchal, during the initial three-hour period, a preference for branched algae was observed, with no selectivity for encrusting bryozoans. The non-indigenous species *Balanus trigonus* was preferred. After 24 h, both crustose algae and Annelida were avoided.

At Quinta do Lorde, for IN treatment plates, during the initial three-hour period, a preference was observed for the calcareous tubeworm *Spirorbis* sp., while the branched algae *Champiaceae* sp. were avoided. After 24 h, there was an increased avoidance of the algae species (Table A.6).

Finally, also at Quinta do Lorde, but for the OUT treatment, during the initial three-hour period, preference was observed for algae and the native bryozoan *C. radiata*. After 24 h, there was an avoidance of crustose algae and Annelida, while the preference increased for the native bryozoans *C. radiata* and *Schizoporella unicornis*, and the non-indigenous bryozoan *C. inaudita* (Table A.6).

Overall, intriguing patterns were revealed through our analysis of foraging behaviour, shedding light on nuanced preferences displayed by fish across treatments and locations. Notably, a distinct preference towards NIS and a specific preference for the cryptogenic ascidian *T. cereum* were observed (Fig. 4).

The observed variations in biofouling coverage, community structure, and species richness within the studied locations warrant a careful interpretation of findings related to feeding preferences. Various factors likely contribute to differences in foraging preference and subsequent impacts on biofouling communities. The availability of prey, considering both quantity and quality, alongside local environmental conditions, may contribute to shaping foraging preferences. The unique characteristics of each location contribute to the observed variations in fouling communities and foraging preferences. These local factors can influence the abundance and composition of predators, thereby affecting the selection of prey species and shaping the overall structure of biofouling communities. In Quinta do Lorde, with the lowest human pressure compared to Calheta and Funchal, both IN and OUT treatments exhibit the lowest NIS abundance and more native species. Foragers in Quinta do Lorde were biting equally from both treatments. However, in locations with higher NIS abundance (Funchal and Calheta), foragers prefer the IN treatment, likely due to the increased presence of their preferred prey (NIS species). In this context, this suggests a gradient-like pattern: as NIS abundance increases, foragers show a clearer preference, while in locations with lower NIS abundance, the preference is less noticeable.

4. Discussion and conclusions

The results of this study suggest that at least some of the foragers, by preferring non-indigenous species (NIS), may contribute to same level of biotic resistance to NIS proliferation. The Remote Video Foraging System (RVFS) was utilised as a methodological tool to investigate the ability of foragers to suppress the establishment and spread of NIS from the inside of marinas and harbours to the neighbouring areas. By comparing the fouling assemblages from marinas where NIS abundance and diversity is generally higher (IN treatment) (Chebaane et al., 2019; Martínez-Laiz et al., 2019; Castro et al., 2020) and from neighbouring natural habitats (outside and within the vicinity of the marina: OUT treatment), the study aimed to assess whether foragers display a preference between the communities and evaluate their impact on different fouling assemblages, particularly on the relative abundance of NIS.

4.1. Forager species preferences and behaviour

Our findings suggest that different fish species may display varying preferences when interacting with fouling communities with different NIS ratios (i.e., assemblages colonised inside vs outside of marinas). *Canthigaster capistrata*, for example, displayed a greater interest in the fouling assemblages settled and grown inside marinas, spending more time foraging and with a higher number of bites than with fouling assemblages from substrates incubated outside marinas. On the other hand, *Sparisoma cretense* exhibited an overall preference towards the outside plates. However, this overall preference was mostly due to observations in one of the locations, where individuals displayed a higher relative interest for assemblages recruited outside marinas. These location-specific differences in *S. cretense* preferences explain why the overall interest and foraging selectivity was not significantly different and illustrate that foraging preference may vary according to local conditions. In addition to the species mentioned earlier, interactions with the fouling assemblages were also observed by *S.marmoratus* and *S. lurida.* However, it should be noted that these two species had only one or two recorded bites on the plates, indicating a limited ability to confirm their interest in the offered fouling assemblages.

Using a RVFS approach was an important step towards understanding fish foraging patterns within the area. This study highlighted the importance of foraging assemblage composition on determining the selective effects of foraging.

4.2. Foraging as biotic resistance to NIS proliferation

Results revealed a clear preference among foragers for NIS. These observed feeding preferences could potentially contribute to biotic resistance against the proliferation of NIS, as supported by previous studies (Dumont et al., 2011; Cheng et al., 2019; Price et al., 2021; Freestone et al., 2021). The preference for specific taxa exhibited site-specificity, indicating that forager choices are influenced by the compositions of fouling communities in their respective locations. Building upon the insights gained from the RVFS experiments, the study further observed the foraging behaviour of different identified forager species within the studied area, along with their preferences and their impact on different fouling assemblages, during the initial 3 h of foraging. In this study, the Macaronesian sharp nose-puffer, *C. capistrata*, preferred biofouling assemblages that harboured a greater relative abundance of NIS, suggesting prior exposure to such patches and their recognition as viable food sources. However, this engaging in biofouling foraging behaviour is considered a novel finding regarding its previously known diet of zoobenthos and primarily sea urchins in the Canary Islands (Clemente et al., 2010). Notably, this recognition and selection process occurred within a remarkably short time frame of 3 h. Considering the fish's capacity to learn and discern specific food sources based on their nutritional needs (Aranda et al., 2000; Vivas et al., 2006), these findings suggest that the pufferfish recognise NIS-rich patches as a valuable food resource (Warburton and Hughes, 2011).

In the case of the Mediterranean parrotfish *S. cretense*, a generalist feeder (Flecker and Taylor, 2004), no preference for any specific treatments was observed. Nonetheless, it's important to note that results from a previous study have indicated that this particular fish engages in bulldozing behaviour, characterised by deliberate and sweeping movements as it grazes on the biofouling within the Quinta do Lorde marina. This distinctive feeding behaviour significantly influences the composition of fouling assemblages within the marina, consequently fostering greater diversity among fouling communities (Chebaane et al., 2022). Yet, previous studies found that generalistic grazers can prevent the dominance of specific fouling species and help to maintain higher benthic diversity levels (Steele et al., 2018). As large omnivorous fish foragers are characterised by their broad diets and simultaneous effects on multiple trophic levels, parrotfish may play a significant role in slowing the invasion process of fouling NIS communities within the vicinity of the marinas (Humphries et al., 2020). Therefore, the parrotfish may provide biotic resistance against the establishment and spread of NIS, as observed in previous studies (Chebaane et al., 2022; Cheng et al., 2019). During the initial three-hour period, both fish species, *C. capistrata* and *S. cretense*, effectively removed a larger proportion of total biofouling from plates with a higher relative abundance of non-indigenous species (NIS) in the IN treatment compared to plates with lower NIS abundance in the OUT treatment, despite the absence of a significant preference in their foraging behaviour. This suggests that these fish species preferred plates with fouling assemblages containing a higher NIS content within the marinas, considering them as a primary food source patch (Warburton and Hughes, 2011). Consequently, this feeding behaviour is generally not advantageous for NIS, as it does not specifically target native-rich assemblages. However, despite the heightened foraging activities observed during the 3-h video recording, there were no discernible changes in fouling assemblages within this short time. It is important to highlight that the foraging did not have an immediate impact on the total fouling coverage on the plates. This lack of immediate impact on the composition of biofouling communities suggests that fouling structural modifications may occur at a slower pace.

Notably, our findings align with this notion, as after 24-h exposure to predation, significant changes were observed in fouling assemblages, but only in the plates from inside marinas (IN treatment), by the significant reduction in the abundance of NIS, primarily in Funchal and Calheta. These changes are in accordance with the observations previously described, where foraging fishes exhibited preference for plates with fouling assemblages from inside the marinas (see above). Although 24 h is still a relatively short period, findings suggest that the foraging selectively for assemblages with higher relative abundance of NIS can exert effective pressure on them. The reduction in NIS abundance and the distinct preference for NIS over native species within this time frame can be interpreted as an indicative sign that fish foraging can act as a local biotic resistance mechanism to fouling NIS proliferation (Skein et al., 2021).

4.3. Most targeted species on fouling assemblages

Foragers showed a preference towards tunicates, bryozoans, and crustose algae, although the selectivity observed varied depending on the location. This variability is likely attributable to the differences in fouling communities at each studied site, as well as variations in predation pressure by fish and mobile invertebrate forager populations, which could have shaped the fouling communities through time (Friedlander et al., 2017; Gestoso et al., 2018; Castro et al., 2022; Sempere-Valverde et al., 2023; Chebaane et al., 2023). Ascidians, known as fast-growing colonial organisms, are typically consumed first by predators due to their lack of structural defences (Freestone and Osman, 2011; Dias et al., 2020). In our study, the non-indigenous ascidians *D. corolla* and *Microcosmus squamiger*, along with the cryptogenic species *B. schlosseri*, were selected in the IN treatment after 24 h. Notably, during the initial 3 h of predation, a stronger preference was displayed by foragers for a specific species, the cryptogenic tunicate *T. cereum*.

Regardless of location, this study has shown an apparent preference for ascidians by foragers over other fouling species, these findings align with the results of other research (e.g., Freestone et al., 2011; Vieira et al., 2012; Hiebert et al., 2019; Giachetti et al., 2022; Chebaane et al., 2023). In locations where bryozoans dominated, the foragers exhibited a preference not only for ascidians, but also for arborescent bryozoans and less mineralised encrusting bryozoans, such as the non-indigenous *C. inaudita* and *P. alba*, as well as species lacking calcification like *A. verticillata*. These findings align with previous research (Dias et al., 2020; Vieira et al., 2021).

4.4. Limitations and further research

Having been affixed to boxes at each location for six months without cages to exclude predators, the susceptibility of plates to potential predation raises questions regarding its consequential impacts on resulting assemblages and the learning behaviours of fish. Predation exposure could disrupt the growth and progress of settling organisms, thereby influencing the subsequent composition of fouling communities and inducing adjustments in fish foraging behaviours that establish links between the settlement boxes and food resources (Warburton and Hughes, 2011). Consequently, this interconnectedness might contribute to forming preferences for specific fouling communities. Furthermore, it's worth noting that fish memory can play a significant role in shaping such foraging behaviours and preferences in response to environmental cues (Broglio et al., 2003).

Furthermore, it is crucial to carefully consider the temporal interval between deploying settlement boxes outside marinas and introducing the RVFS structures. If the same fish encounter both scenarios in close proximity, the memories associated with their experiences at the settlement boxes could introduce bias into the behaviours observed at the RVFS structures (Broglio et al., 2003; Odling-Smee and Braithwaite, 2003; Warburton and Hughes, 2011). Therefore, a meticulous approach to maintaining temporal separation becomes imperative for accurate interpretation of fish responses to various fouling assemblages. To mitigate these potential confounding factors, several strategies could be explored. One approach involves relocating the settlement plates from the boxes to an ex-situ facility equipped with an air pump. This relocation could occur over an extended period, allowing the fouling settlement plates to remain viable. Subsequently, these plates could be affixed onto the RVFS structure for the preference experiment. Alternatively, careful consideration of the placement of the boxes could ensure they are positioned in an area distinct from the designated site for the RVFS experiment.

The video records for 3 h per RVFS facilitated the identification of the foraging species as well as to determine preference of fouling assemblages from inside marinas. However, the inspection of plates after the three-hour exposure period showcased no significant alterations in fouling assemblages, underscoring the inadequacy of the initial three-hour foraging period to induce significant shifts in community composition or structure. Additionally, during the initial 3-h observation period, only fish species were observed interacting within the treatments, and the observations were conducted during the daytime. However, when considering the remaining 21 h, which include the nocturnal period, other feeders could potentially contribute to the observed changes in fouling assemblages within the treatments. An array of organisms, including annelids, sea stars, sea urchins, chitons and various invertebrates with the capacity to feed from the RVFS structure, might have played a role. These organisms have been documented to consume settlers and adults of NIS sessile invertebrates (Edgar et al., 2011; Young and Bellwood, 2011; Lavender et al., 2014; Rogers et al., 2016).

Furthermore, it is important to acknowledge that this experiment was conducted during a single season, and there is a possibility that certain fish species were not reported due to their absence in the area. As a result, caution should be exercised when deriving definitive conclusions based on these findings. Additional experiments conducted across different seasons are necessary to develop a comprehensive understanding of fish species that can forage on fouling communities in general. Specifically, analysis of stomach contents, environmental DNA (e.g., for the fouling species on the plates and for the stomach contents of the identified forager species), and stable isotope analysis must be carried out to confirm the consumption of fouling species (Kadye and Booth, 2012; Chebaane et al., 2022; Mofu et al., 2023).

The impact and preference of foragers during the observed time intervals displayed location-specific patterns. The study locations were selected randomly, primarily based on their convenient proximity and easy access to water bodies. However, these three chosen locations demonstrated significant variations in the composition and abundance of sessile invertebrate communities, as well as fish communities and mobile invertebrate species (Friedlander et al., 2017; Castro et al., 2022; Sempere-Valverde et al., 2023). It is worth noting that these locations were located in the southern region of Madeira Island, which is known for its high degree of coastal urbanisation (Bernal-Ibáñez et al., 2021b). The ecosystem in these areas is influenced by the presence of coastal constructions, resulting in complex effects that vary across different organisms and geographical scales (Gittman et al., 2016; Sedano et al., 2020a; Sedano et al., 2020b; Guerra-García et al., 2021; Chebaane et al., 2023). Thus, it is likely that the fouling community experiences different biotic and abiotic pressures, resulting in distinct structures and compositions particularly in terms of the NIS and native species across different locations. Consequently, these variations may also influence the abundance and composition of grazers, resulting in differences in foraging activities and preferences. Moreover, the higher richness of native species could have potentially reduced the relative abundance of NIS, thereby contributing to biotic resistance alongside the predation (Gestoso et al., 2018; Leclerc et al., 2020).

Standardisation methods during analysis can, to some extent, minimise the potential effects of foraging pressure (e.g., one location has significantly higher foraging activity than other), however, follow up and future work should also include independent surveys/studies to assess differences in foraging intensity (Gestoso et al., 2018; Leclerc et al., 2020; Tamburini et al., 2022; Gauff et al., 2022).

By employing video monitoring of target assemblages with different NIS content as foraging choices, this study provides a benchmark to better understand how fish species may favour NIS proliferation or contribute to local biotic resistance (Struthers et al., 2015; Chebaane et al., 2022). Biotic resistance in marine environments is complex, and influenced by diverse factors such as latitude, habitat characteristics, and the taxonomic identity of the invader and it involves discerning between competition with and consumption by native species (Kimbro et al., 2013).

Our finding provide supporting evidence that foragers can play a significant role in controlling or favouring the local proliferation of NIS. In this study, even without major evidence of foragers exhibiting strong preference for NIS (i.e., exhibited only in two locations), foraging has resulted in a higher decrease in NIS than in native taxa, favouring the survival of the latter. Our observations suggest that some local fish species have the ability to identify NIS-rich patches as valuable food resources. They appear to exhibit selective feeding habits towards ascidians and some bryozoan species which are common in these NIS-rich patches. Even thought is not completely clear why they are targeting these patches and taxa, the end results is still the same: they contribute to the suppression of NIS and, consequently, their local proliferation. Recognising the contribution of specific species to biotic resistance (due to their feeding behaviour and preferences) is crucial to better understand local control/facilitating mechanisms for NIS proliferation and potential invasions, which can be key when managing biological invasion risks in areas adjacent to ports and recreational marinas, but also in mitigating ongoing NIS proliferation.

CRediT authorship contribution statement

Sahar Chebaane: Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Conceptualization, Validation. **Miguel Pessanha Pais:** Methodology, Supervision, Validation, Writing – review & editing. **Aschwin Hillebrand Engelen:** Methodology, Supervision, Validation, Writing – review & editing. **Patrício Ramalhosa:** Investigation, Validation, Writing – review & editing. **Rodrigo Silva:** Investigation, Writing – review & editing. **Francesca Gizzi:** Investigation. **João Canning-Clode:** Funding acquisition, Resources, Validation, Writing – review & editing. **Alejandro Bernal-Ibáñez:** Investigation. **João Gama Monteiro:** Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Validation, 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

Data will be made available on request.

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Appendix A. Supplementary data

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