



How the invasive algae *Rugulopteryx okamurae* affect coastal biodiversity? Insights from coastal fish communities of gran Canaria (NE Atlantic Ocean)

Xavier Bachot, Rodrigo Riera*

Biodiversity and Conservation Group (BIOCON), IU-ECOQUA, 35001 Las Palmas de Gran Canaria, Canary Islands, Spain

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ABSTRACT

Biological invasions present significant threats to global biodiversity and ecosystem functioning. The introduction of invasive species can lead to ecosystem homogenization, altering community dynamics and negatively impacting native species and habitats. *Rugulopteryx okamurae*, a brown seaweed native to the Northwest Pacific, has rapidly invaded marine ecosystems in Europe, transforming coastal habitats. This study examines the impact of *R. okamurae* on fish communities across different zones of Gran Canaria, with a particular focus on the invasion gradient. We observed significant variations in fish species abundance and richness across sites, with a noticeable trend towards reduced diversity and a higher prevalence of opportunistic species in areas heavily invaded by *R. okamurae*. The invasion gradient, rather than typical edge effects, appeared to play a more substantial role in shaping community structure, suggesting that the pervasive spread of *R. okamurae* leads to habitat homogenization. Ongoing monitoring and adaptive management strategies are crucial to fully understand and mitigate the impacts of *R. okamurae* on marine biodiversity in Gran Canaria.

1. Introduction

The impact of biological invasions on biodiversity loss is widely recognized, underscoring their profound ecological and economic consequences (Clavero and García-Berthou, 2005; Simberloff et al., 2013; Bellard et al., 2016; Bacher et al., 2018; Pyšek et al., 2020). Globally, there are over 37,000 established alien species, of which over 3,500 are invasive and have documented impacts (Roy et al., 2023). Approximately one-quarter of these species are found in aquatic environments, with freshwater ecosystems accounting for 14 % and marine environments for 10 % (Roy et al., 2023). In marine environments, the introduction of non-native species carries the risk of becoming invasive (Ruiz et al., 1999; Byers, 2002; Jeschke et al., 2014; Iacarella et al., 2019; Geraldí et al., 2020). Such invasions have been linked to the displacement of indigenous species, loss of genetic diversity, habitat alterations, shifts in community dynamics and ecosystem functioning, potential impacts on human health, and significant economic consequences (Groszholz, 2002; Perrings, 2002; Wallentinus and Nyberg, 2007; Molnar et al., 2008; Vilà et al., 2010; Katsanevakis et al., 2014). For example, the introduction of the sea walnut (*Mnemiopsis leidyi*) in the Black Sea has drastically depleted zooplankton, the primary food source for anchovies, contributing to the collapse of anchovy populations in the

region (Knowler, 2005; Oguz et al., 2008; Roy et al., 2023). This example illustrates how invasive species can disrupt ecosystems by directly affecting native species and indirectly altering food webs, leading to cascading ecological consequences.

Invasive species, specifically, large seaweeds found in marine environments have had a notable impact on the worldwide spread of aquatic organisms, with their ecological impacts extensively reviewed in recent decades (Schaffelke et al., 2006; Williams and Smith, 2007; Thomsen et al., 2016). Invasive macroalgae globally assert dominance within ecosystems by seizing space and altering competitive dynamics, depriving native species of essential resources such as light and nutrients (Schaffelke and Hewitt, 2007; Davidson et al., 2015). This competition often results in the exclusive proliferation of invasive species and the homogenization of habitats (Schaffelke and Hewitt, 2007, Davidson et al., 2015). However, the documented impacts predominantly revolve around a handful of extensively researched and prominent algal species, including Green seaweed (*Caulerpa taxifolia*), Green sea fingers (*Codium fragile* subsp. *fragile*), Japanese wireweed (*Sargassum muticum*), and Wakame (*Undaria pinnatifida*) (Cacabelos et al., 2013; Salvaterra et al., 2013).

Marine macroalgae are extensively known as pivotal actors in various ecosystems (Macreadie et al., 2017). They possess the unique

* Corresponding author.

E-mail address: rodrigo.riera@ulpgc.es (R. Riera).

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ability to convert unassuming surfaces into intricately structured habitats capable of sustaining diverse arrays of species, spanning from mobile to sessile forms (Bruno et al., 2005; Dijkstra et al., 2012). While not all non-native species exhibit ecological detriment, many harbor traits that enable them to competitively displace indigenous marine flora, thereby reshaping community dynamics (Miller et al., 2007). The introduction of *Rugulopteryx okamuræ* (E. Y. Dawson) I.K. Hwang, W.J. Lee, and H.S. Kim, into Europe, a brown seaweed native to the Northwest Pacific, is an example of a significant marine invasive species event. Initially detected in the French Mediterranean coast, particularly in the Thau coastal lagoon, this introduction was linked to the presence of the Japanese oyster (*Crassostrea gigas*) (Verlaque et al., 2009). However, its invasive behavior did not become apparent until 2015 when large quantities of this seaweed were found on beaches in Ceuta, North Africa (Ocaña et al., 2016), and subsequently in Andalusian waters in 2016, reporting the first records of this macroalgae in the Atlantic Ocean (García-Gómez et al., 2018; García-Gómez et al., 2021; Faria et al., 2022a). From 2016 onwards, the invasive behavior of *R. okamuræ* escalated, leading to its colonization on both sides of the Strait of Gibraltar (El Aamri et al., 2018; García-Gómez et al., 2018). In this location, it became the dominant species, covering up to 90 % of the rocky seabed between 10 and 20 m depth (Ocaña et al., 2016; Altamirano et al., 2017; García-Gómez et al., 2018; Sempere-Valverde et al., 2021). This extensive colonization has caused a significant alteration in the structure of benthic communities, with notable reductions observed in other macroalgae species such as *Ellisolandia* sp., *Sphaerococcus coronopifolius*, *Codium bursa*, and *Dyctiota dychotoma* (Guerra-García et al., 2007; García-Gómez et al., 2018). Multiple factors contribute to the invasive success of *R. okamuræ*. Indeed, the invasive success of *R. okamuræ* is facilitated by its robust capabilities to colonize, detach quickly, float easily, and reattach to solid substrates with ease (García-Gómez et al., 2020; Ruitton et al., 2021; Faria et al., 2022a). This species also demonstrates elevated reproductive rates, generating hundreds of offspring from a solitary specimen via vegetative propagules and asexual monospores (Bernal-Ibáñez et al., 2022). Additionally, *R. okamuræ* thrives in diverse environmental conditions, storing nitrogen and capitalizing on nutrient surges, including those from upwelling events and coastal eutrophication, including urban or industrial wastewater discharge (Bernal-Ibáñez et al., 2022). The invasive spread of *R. okamuræ* has extended beyond the Strait of Gibraltar, with documented invasions in various other regions. Notably, in 2018, an invasion was reported along the Mediterranean coast of Provence, France (Ruitton et al., 2021; Bellissimo et al., 2024; Marletta et al., 2024). This was followed by the first recorded invasions in the Macaronesia region, located in the North Atlantic Ocean, including the Azores, Madeira, and the Canary Islands in 2019, 2021, and 2022 (Bernal-Ibáñez et al., 2022; Castro et al., 2022; Faria et al., 2022b; Faria et al., 2022a). These archipelagos are situated near the African continent, with the invasion particularly notable on the island of Gran Canaria, where this study was conducted (Castro et al., 2022).

The Port of Las Palmas, situated in Gran Canaria, is one of the principal nodes for global maritime traffic, linking with over 180 ports worldwide, connecting Europe, Africa and America thus solidifying its status as one of the foremost commercial hubs in Spain (Canaryports, 2021; Castro et al., 2022). Furthermore, over the past decade, the Port of Las Palmas has emerged as a pivotal hub or the maintenance and servicing of oil rigs and drilling vessels in the Atlantic region (Pajuelo et al., 2016; Ports of Las Palmas, 2021). In areas like archipelagos, where port connections serve as core in vast oceans, they have become key points for species invasions, especially macroalgae (Morente-López et al., 2023). These invasions arise from two distinct mechanisms, mainly transferred in ballast waters and hull fouling of commercial shipping (Guala et al., 2003; Kölzsch and Blasius, 2011; Castro et al., 2022). It is reasonable to assume that many of these introductions, such as *R. okamuræ*, are linked to the current high level of marine traffic in the Canary Islands (Pajuelo et al., 2016). Moving forward, it is essential to consider the implications

of these activities on associated marine communities, including epifauna and fish, to ensure the preservation of biodiversity and ecosystem health.

The main aim of this study was to examine the potential disparities in fish communities along the invasion gradient of *Rugulopteryx okamuræ* in coastal regions where this seaweed has established colonies. While diverse macroalgal habitats typically support abundant fish communities, regions with varying coverage of *R. okamuræ* increasingly dominated by *R. okamuræ* may experience reduced habitat complexity and availability due to its invasive nature and the presence of secondary metabolites, particularly terpenes, which have bioactive properties such as herbivory inhibition and cytotoxicity, rendering the algae unpalatable (García-Gómez et al., 2018). However, the potential effects of this species on the composition of benthic fish communities in the Canary Islands remain largely unknown. Martín-Jiménez & Riera (2024) have highlighted the impact of *R. okamuræ* expansion on epifaunal communities, revealing significant alterations in abundance and species richness across different levels of invasion. These findings emphasize the importance of considering the broader ecological implications of *R. okamuræ* invasion beyond its direct effects on macroalgal communities. Therefore, by investigating the diversity of fish communities along the invasion gradient of *R. okamuræ*, we aim to gain valuable insights into the overall ecological consequences of this invasive seaweed.

2. Materials and methods

2.1. Study area

The island of Gran Canaria, situated in the Atlantic Ocean at coordinates 28° 05' 59.03" N and 15° 24' 48.35" W was the study area (Fig. 1). This island belongs to the Canary archipelago, which consists of eight islands and several islets spanning between 27° and 30°N across 500 km, with the nearest eastern island approximately 100 km from the African coastline (Riera and Delgado, 2018). In 2024, a prospective survey was conducted on the outskirts of Las Palmas de Gran Canaria to identify the presence of *R. okamuræ* (Martín-Jiménez and Riera, 2024). Subsequently, our study focused on five specific coastal sites along the island's eastern coast that represents the northern, central, and southern populations respectively, i.e., San Cristóbal, La Puntilla, Tufia, Ojos de Garza, and Risco Verde. Importantly, the northern sites, San Cristóbal and La Puntilla, constitute the current invasion front of *R. okamuræ* on the island and are therefore considered the edge of the population in the island of Gran Canaria.

The study encompasses several coastal sites around Las Palmas and Telde, each with unique environmental characteristics that shape local marine ecology. San Cristóbal (hereafter, SC1) and La Puntilla Beach sites (hereafter, SC2), experiences strong NE trade winds and southward ocean currents, shaping its coastal dynamics and species distribution. The intertidal zones here are rocky with nearly 100 % coverage of *R. okamuræ* seaweed at depths around 2.5 m, reflecting its status as the invasion edge. In Telde, Tufia (hereafter, TF) and Ojos de Garza (hereafter, OG) exhibit similar wind conditions but are partially sheltered by natural formations, reducing exposure and leading to rocky substrates with moderate coverage (40–50 %) of *R. okamuræ*. At Risco Verde (hereafter, RV), cliffs provide further protection from winds and tides, creating steeper terrain with predominantly rocky substrates; however, *R. okamuræ* was absent during our surveys despite initial expectations, as it had previously been recorded at that coastal site (E. Soler, pers. obs). These varied coastal environments illustrate the influence of wind, currents, and geological features on marine ecosystems in the island.

2.2. Data collection

Between February and May 2024, data were collected across five coastal sites—San Cristóbal, La Puntilla, Tufia, Ojos de Garza, and Risco



Fig. 1. Geographic location of the Canary Islands. The surveyed sites are shown in the map, San Cristóbal (A), La Puntilla (B), Tufia (C), Ojos de Garza (D) and Risco Verde (E).

Verde—to assess changes in fish communities in relation to the coverage of *R. okamuræ*. At each site, twenty 50-m transects were conducted, with 10 transects in the northern part (hereafter right (L)) and 10 in the southern part (hereafter right (R)), totaling 100 transects. The study employs a one-way factorial design to test the hypothesis that the distribution and abundance of *R. okamuræ* influence the composition and abundance of fish communities. The primary factor investigated is the comparison of fish assemblages across the invasion gradient (northern edge, central and southern edge) of the seaweed's distribution. In this context, “edge” regions are defined as the northern sites of San Cristóbal and La Puntilla, where *R. okamuræ* coverage is nearly 100 %, and the southern site of Risco Verde, where the coverage is very sparse. These edge regions represent the peripheries of the seaweed's distribution. In contrast, “central” regions are located at Ojos de Garza and Tufia, where *R. okamuræ* coverage is consistently between 40 % and 50 %. This classification allows for a direct comparison of fish communities between regions with different levels of *R. okamuræ* abundance. The Edge and Central regions were not fully replicated along the coast, as the study focused on a single invasion gradient. While the study allocated ten 50-m visual transects to both the Northern and Central parts of the gradient, sampling was conducted at two sites in these regions, providing some spatial replication. In contrast, only a single site was sampled in the Southern region, limiting the ability to fully capture variability across this area. This design means that conclusions are specific to the studied gradient and may not be broadly generalizable across other geographic locations.

This sampling design resulted in 20 transects per site (San Cristóbal,

La Puntilla, Tufia, Ojos de Garza and Risco Verde), making up a total of 100 transects. Across all five sites, this approach yielded a total of 60 transects in edge regions (3 sites, 2 in the northern edge (San Cristóbal and La Puntilla) and 1 in the southern edge (Risco Verde)) and 40 transects in the central region (2 sites, Tufia and Ojos de Garza). For each transect, fish community data were collected to evaluate potential correlations between *R. okamuræ* abundance and changes in species richness and abundance of fish. This systematic design, with consistent replication and sample size allocation across both edge and central regions, provides a robust framework for analyzing the influence of *R. okamuræ* on marine ecosystems in these coastal environments. Additionally, the study examines differences between the northern and southern parts of each site, using the transects as replicates for each factorial level. This approach enables the analysis of fish community responses to high and low *R. okamuræ* coverage, as well as different environmental conditions across these sites.

The sampling collection was performed using a Reef Life Survey (RLS) method. This method applies globally standardized underwater visual census (UVC) over 30 years of shallow reef biodiversity research (Edgar et al., 2020). The census was done at a depth of ca. 2.5 m, where 50 m transects were placed along *R. okamuræ* meadows using snorkeling equipment. After a waiting period of approximately 5 min to allow the fish to cease being alert and return to its natural state, we moved about 5 m to the right of the transect to conduct the outbound at a speed of 0.5 m s^{-1} , and similarly for the return, while recording the diversity and abundance of fishes. Once in the laboratory, all the data obtained on the diversity and abundance of the fishes for each transect

are stored in a datasheet where the corresponding siet is also outlined.

2.3. Data analysis

Data analysis was conducted using R software. Species richness and individual abundances were visualized using boxplots. Permutational Multivariate Analysis of Variance (PERMANOVA) was employed to assess differences in fish community composition in relation to multiple spatial scales. The study incorporated *Region* as a fixed factor with three levels—Northern edge, Central, and Southern edge—to evaluate broader-scale variability in community composition across different regions of the study area. Nested within each region, *Site* represents specific coastal sites: San Cristóbal, La Puntilla, Tufia, Ojos de Garza, and Risco Verde. To account for local-scale variability, an additional fixed factor, *Orientation* (with two levels: Right and Left), was nested within each Site to analyze fine-scale spatial patterns in community distribution. PERMANOVA was performed to determine the significance of these factors on community composition, with results highlighting significant differences across the levels of Region, Site within Region, and Orientation within Site, as reported in Table 1. Prior to this analysis, the data were transformed using a logarithmic scale ($\log x + 1$) to stabilize variances and meet the test assumptions. The analysis provided F values and the probability of F, with significance indicated by $p < 0.05$.

To address potential limitations of sampling heterogeneity, particularly the single site in the southern edge, we implemented two additional steps to strengthen the analysis. First, we conducted pairwise PERMANOVA post-hoc comparisons between regions within each spatial gradient level to verify that observed patterns were consistent across sites. Additionally, a PERMDISP test was used to assess homogeneity of dispersion among groups, ensuring that differences detected by PERMANOVA were due to differences in centroid sites rather than dispersion variability. These steps enhance the robustness of our findings, minimizing the potential impact of unequal representation across spatial gradient levels.

All statistical analyses were carried out using a suite of R software packages. The *vegan* package (Oksanen et al., 2024) was primarily used for performing n-MDS and PERMANOVA, while *ggplot2* (Wickham et al., 2024) facilitated the creation of graphs, including boxplots. Additional packages such as *tidyverse* (Wickham, 2023), *janitor* (Firke et al., 2023), *flextable* (Gohel et al., 2024), and *readxl* (Wickham and Bryan, 2023) were employed for data reading and generating high-quality graphs and tables.

3. Results

A total of 8018 fish were censused, comprising 33 species (Suppl. Table 4). Among these, the five most abundant species were identified i. e. *Similiparma lurida* (Canary damsel) was the most abundant species in the fish community (2172 individuals, 27.1 % of the total abundance), followed by *Thalassoma pavo* (Ornate wrasse) (1731 ind., 21.6 %), *Sarpa salpa* (Salema porgy) (1612 ind., 20.1 %), *Sparisoma cretense* (Mediterranean parrotfish) (1200 ind., 15 %), and *Pomadasys incisus* (Bastard grunt) (240 ind., 3 %). In our fish census, we have identified several species that represent less than 0.5 % of the overall abundance. These

Table 1

PERMANOVA results of the fish assemblages using the study factors. df: degrees of freedom; SS: Sum of squares. Bold letters denote significant differences ($p < 0.05$).

	df	SS	R2	F	p
Region	2	2.721	0.022	7.083	0.001
Region(Site)	2	1.109	0.009	2.888	0.033
Region(Site(Orientation))	5	2.905	0.023	3.024	0.005
Residual	613	117.761	0.946		
Total	622	124.496	1		

species were *Aulostomus strigosus* (Atlantic trumpetfish), *Boops boops* (Bogue), *Chelon labrosus* (Thicklip grey mullet), *Diplodus puntazzo* (Sharpnose seabream), *Diplodus vulgaris* (Common two-banded sea bream), *Epinephelus marginatus* (Dusky grouper), *Mycteroperca fusca* (Island grouper), *Mullus surmuletus* (Striped red mullet), *Scorpaena maderensis* (Madeira rockfish), *Sphoeroides marmoratus* (Guinean puffer), *Synodus saurus* (Atlantic lizardfish) and *Trachinotus ovatus* (Pompano). Additionally, species such as *Serranus cabrilla* (Comber), *Xyrichtys novacula* (Pearly razorfish), *Squatina squatina* (Angel shark), *Auluterus scriptus* (Scrawled filefish), and *Muraena augusti* (Moray eel) were scarce, being represented by a single or two individuals.

The maximum number of individuals was found in the central region (4257 ind.) whilst the minimum abundance was found in the northern edge (1737 ind.). The abundance found in the southern edge was 2024 individuals. The maximum number of species was found in the central region (25 species) and southern edge (24 species) obtained richness values over 25 taxa, whilst the northern edge was characterized by a low fish diversity (19 species) (Suppl. Table 1).

The highest abundance of *Similiparma lurida* (1138 ind.), *Thalassoma pavo* (949 ind.), *Sarpa salpa* (1013 ind.) and *Sparisoma cretense* (682 ind.) were recorded in the central region. In contrast, *Pomadasys incisus* was the most abundant in the northern edge with 234 individuals. Conversely, the lowest abundance of *Similiparma lurida* (163 ind.) and *Thalassoma pavo* (299 ind.) was found at the northern edge. The southern edge had the lowest abundance of *Sarpa salpa* (82 ind.), *Sparisoma cretense* (190 ind.) and *Pomadasys incisus* (6 ind.) (Fig. 2).

Ojos de Garza Right (OGR) and San Cristóbal (Castle) Right (SC1R) consistently exhibited low abundance, with most values clustered near zero, indicating minimal fish presence in these sites. In contrast, San Cristóbal (La Puntilla Beach) Right SC2R, San Cristóbal (La Puntilla Beach) Left (SC2L) and San Cristóbal (Castle) Left (SC1L) showed higher abundance levels, occasionally marked by outliers suggesting localized peaks in fish populations. Meanwhile, Tufia Right (TFR), Tufia Left (TFL) and Ojos de Garza Left (OGL) demonstrated moderate to high abundance levels, occasionally punctuated by outliers suggesting significant local concentrations of fish. Risco Verde Right (RVR) and Risco Verde Left (RVL) exhibited moderate abundance with comparatively less variability across their distributions (Fig. 3).

Regarding species richness, SC1R and SC1L displayed low species richness, typically around 4–5 species, indicating a limited diversity of fish communities in these areas. In contrast, OGR and OGL showed higher species richness, ranging from 7 to 8 species, suggesting a more diverse fish community compared to SC1. RVR and RVL exhibited wide-ranging species richness with occasional outliers, highlighting areas of high diversity within these regions. TFR and TFL demonstrated moderate richness levels compared to SC1. SC2R and SC2L also showed moderate species richness, occasionally marked by outliers indicating localized peaks in species diversity (Fig. 4).

Based on the nMDS and PERMANOVA analyses (Fig. 5), significant spatial variation in the fish community composition among the surveyed transects was evident. The nMDS ordination plot clearly showed distinct grouping of the surveyed zones, indicating pronounced spatial heterogeneity across the study area. Specifically, transects in the Northern edge form a separate group, indicating different species dissimilarities and proportions compared with those in the Central region and Southern edge. This pattern aligns with the observation that *R. okamurae* showed the highest abundances in the Northern edge, which may drive localized ecological dynamics distinct from other regions. Despite the high *R. okamurae* density, the Northern edge also exhibited greater point dispersion in the ordination plot, suggesting more heterogeneous fish community composition compared to the Central and Southern zones.

The PERMANOVA results revealed that the fish assemblages varied significantly across several hierarchical levels (Table 1). At the broadest scale, Region (Northern edge, Central region and Southern edge) had a significant effect on community composition ($F = 7.083$, $p = 0.001$). Within Regions, Site (San Cristóbal, La Puntilla in the Northern edge,

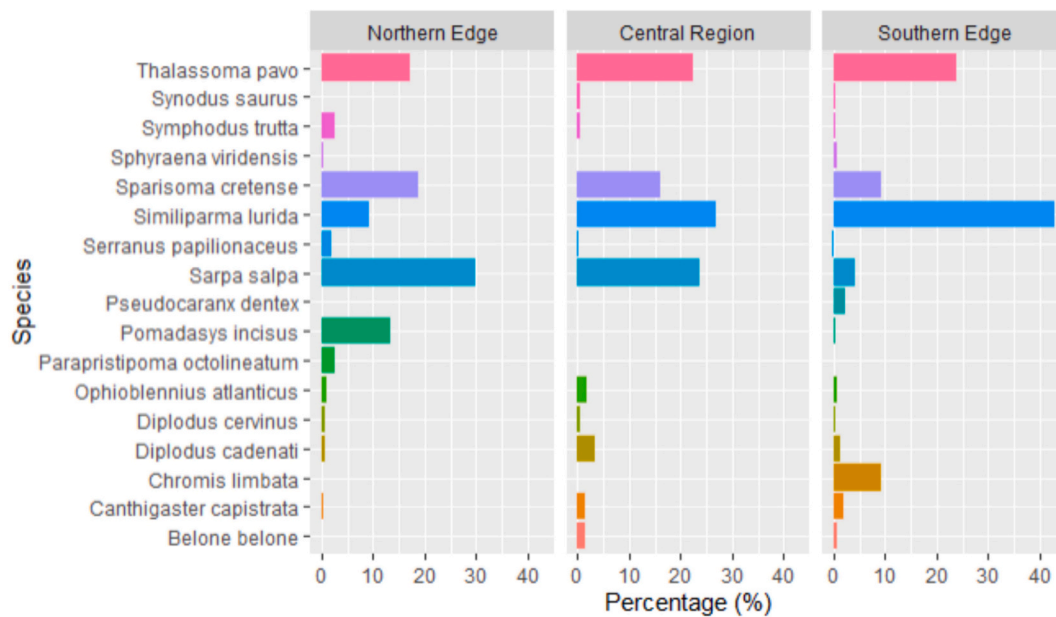


Fig. 2. Most abundant fish species (>0.5 % of the overall abundance) at each studied region (northern edge, central region and southern edge).

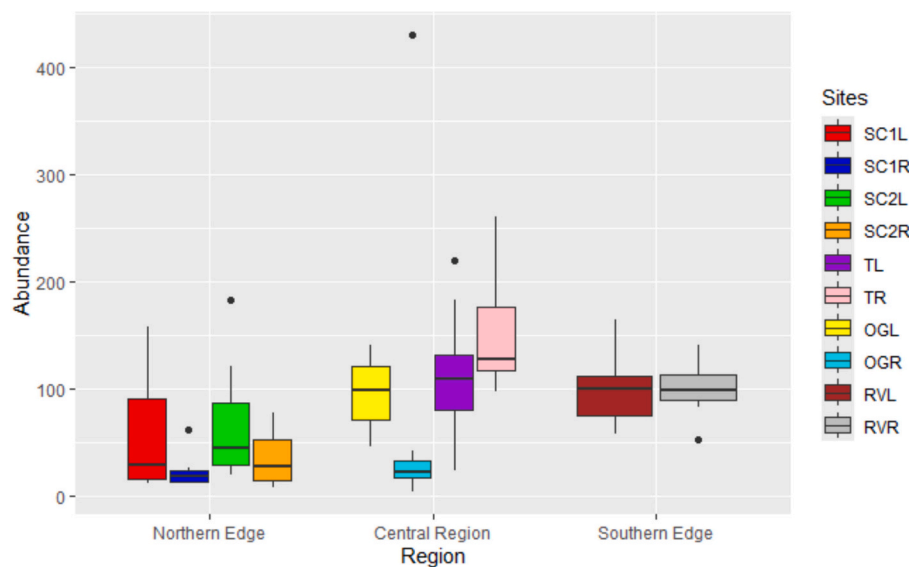


Fig. 3. Fish community abundance in each studied site (northern edge, central region and southern edge). The boxplot shows the median (black line) and the first and the third quartile (colored bar).

Tuffia, and Ojos de Garza in the Centre and Risco Verde in the Southern edge) differences also significantly influenced fish assemblages ($F = 2.888, p = 0.033$). Additionally, Orientation (Right or Left) was also a significant factor, showing variation across orientations ($F = 3.024, p = 0.005$). Together, these results highlight that community composition differences are structured across multiple spatial scales, with Region being the most influential factor (Table 1).

The analysis of species composition revealed marked dissimilarities between the northern edge, central region, and southern edge, with specific species contributing substantially to these differences (Table 2). Between the northern edge and centre, *Similiparma lurida* contributed to 25.6 % of the dissimilarity, followed by *Sarpa salpa* (19.7 % dissimilarity) and *Thalassoma pavo* (19.3 % dissimilarity); and to a lesser extent by *Sparisoma cretense* and *Diplodus cadenati* (14.2 % and 4.6 %, respectively). The species *Similiparma lurida* showed the greatest difference between northern and southern edges, contributing to 38.4 % of the

dissimilarity. *Thalassoma pavo* contributed 17.5 % of the dissimilarity, while *Sarpa salpa*, *Chromis limbata* and *Sparisoma cretense* each contributed between 7.7 % and 11.0 %. Between the centre and southern edge, *Similiparma lurida* again contributed the most to dissimilarity, accounting for 28.1 % of the difference. *Thalassoma pavo* and *Sarpa salpa* also contributed substantially (18.2 % and 15.6 %, respectively). Lesser contributors included *Sparisoma cretense* (10.9 %) and *Chromis limbata* (9.1 %).

4. Discussion

The presence of the invasive seaweed *Rugulopteryx okamurae* in the surveyed areas has significant implications for the local ichthyofauna. Two main observations highlight the distinctiveness of the northern region compared to the central and southern regions. The most notable difference is in the densities of key species such as *Similiparma lurida*,

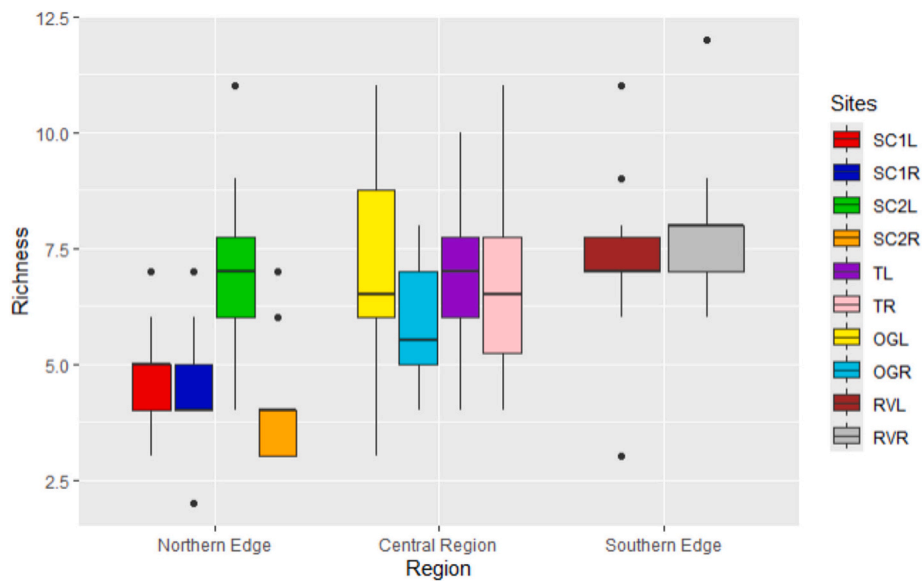


Fig. 4. Boxplot of the fish community richness in each studied site (northern edge, central region and southern edge). The boxplot shows the median (black line) and the first and the third quartile (colored bar).

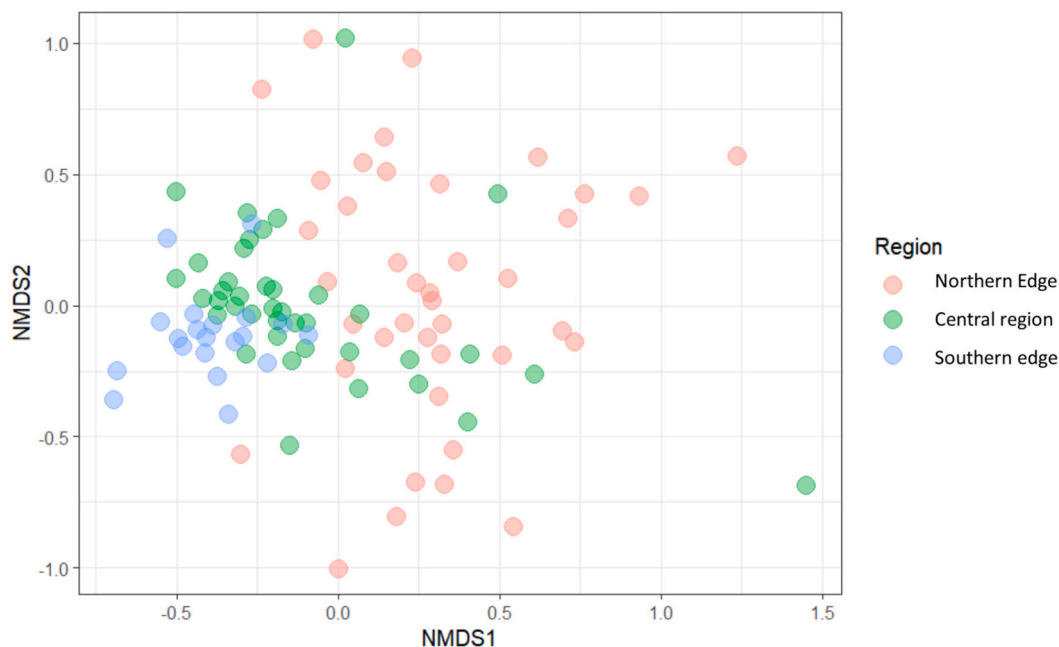


Fig. 5. NMDS ordination of the fish community considering the three studied regions. (Stress = 0.12).

Thalassoma pavo, *Sparisoma cretense*, and *Sarpa salpa*, which vary significantly by region. Additionally, some species, like *Chromis limbata* and *Pomadasys incisus*, were found only in specific sites, emphasizing the varied responses of different fish species to *R. okamuræ* presence.

The fish species diversity is slightly lower in the heavily invaded northern edge compared to the central region. This reduction in diversity suggests that *R. okamuræ* may lead to a homogenization of fish communities, as the dense mats of the seaweed create a more uniform habitat that supports fewer specialized species. Structurally complex habitats are essential for maintaining high biodiversity by providing various niches for different species (Castro et al., 2022; Faria et al., 2022a). The invasion of *R. okamuræ* likely simplifies the habitat, reducing niche availability and thus contributing to lower species diversity. Our study captures an invasion gradient from north to south, where the northern sites represent areas with high *R. okamuræ* coverage

and a more uniform habitat, while the central and southern sites exhibit varying levels of seaweed presence and associated habitat complexity. This gradient showed how increased invasion intensity affects fish communities differently across sites, with significant ecological consequences.

Moreover, the role of macroalgae as nursery habitats is highlighted by studies such as those conducted in Mediterranean *Cystoseira* forests, which have shown that these complex habitats support diverse and abundant juvenile fish populations due to their provision of both shelter and food (Bernal-Ibáñez et al., 2022; Faria et al., 2022a, 2022b; Castro et al., 2022). Additionally, *R. okamuræ* competes aggressively for space and resources, altering habitat structure and often outcompeting native species like *Paramuricea clavata* (soft coral colony) in the Mediterranean Sea (Sempere-Valverde et al., 2021) or *Jania rubens* (red algae) and *Codium adhaerens* (green algae) in the Atlantic Ocean (Liulea et al.,

Table 2

Dissimilarity in the composition of fish species between regions of study. Cumsum: Cumulative contribution of this and all previous species in list.

Northern Edge-Centre				
Species	North	Centre	Cumsum	% dissimilarity
<i>Similiparma lurida</i>	4.075	28.45	0.256	25.6
<i>Sarpa salpa</i>	12.925	25.325	0.453	19.7
<i>Thalassoma pavo</i>	7.475	23.725	0.646	19.3
<i>Sparisoma cretense</i>	8.20	17.050	0.788	14.2
<i>Diplodus cadenati</i>	0.325	3.475	0.834	4.6
Northern Edge-Southern Edge				
Species	North	South	Cumsum	% dissimilarity
<i>Similiparma lurida</i>	4.075	43.55	0.384	38.4
<i>Thalassoma pavo</i>	7.475	24.15	0.559	17.5
<i>Sarpa salpa</i>	12.925	4.10	0.669	11.0
<i>Chromis limbata</i>	0	9.30	0.757	8.8
<i>Sparisoma cretense</i>	8.2	9.50	0.834	7.7
Centre-Southern Edge				
Species	Centre	South	Cumsum	% dissimilarity
<i>Similiparma lurida</i>	28.45	43.55	0.281	28.1
<i>Thalassoma pavo</i>	23.725	24.15	0.463	18.2
<i>Sarpa salpa</i>	25.325	4.10	0.619	15.6
<i>Sparisoma cretense</i>	17.05	9.50	0.728	10.9
<i>Chromis limbata</i>	0	9.30	0.819	9.1

2023). This competitive exclusion likely reduces the availability of critical resources such as food and shelter for fish, leading to lower fish densities. Furthermore, the allelopathic compounds produced by *R. okamurae*, which deter herbivory and have cytotoxic properties (García-Gómez et al., 2018), may further inhibit the presence of fish that feed on or associate with macroalgae.

The composition of fish species varied notably between regions with different levels of *R. okamurae* coverage. While *R. okamurae* invasion has been associated with shifts in fish community composition, the relationship is not uniform across species. For instance, generalist species such as *Similiparma lurida* and *Thalassoma pavo* were more abundant in regions with lower *R. okamurae* densities. This suggests that these species may not exclusively thrive in highly invaded areas but instead occupy habitats with varying levels of disturbance. Conversely, regions with high *R. okamurae* densities tended to support species like *Sparisoma cretense* and *Sarpa salpa*, which are known to tolerate altered environments. In less invaded regions, a greater variety of specialized species that depend on more complex and diverse habitats were observed. This nuanced shift in species composition highlights the broader ecological impacts of *R. okamurae*, which not only affects individual species but also the overall structure and function of the fish community. Although the edge effect has been shown to influence community structure in some studies (Debinski and Holt, 2000; Holway, 2005; Willmer et al., 2022), its impact is not universally consistent. In our study, the edge effect was not significant in structuring the fish community associated with this invasive alga. This could be due to the high coverage of *R. okamurae* in the Northern edge, which may have homogenized habitat conditions and reduced the typical differences driven by edge effects. Additionally, the presence of resilient generalist species that adapt well to invaded environments might obscure any potential edge-related patterns. Consequently, our findings suggest that, in the case of *R. okamurae*, the edge effect does not play a crucial role in determining the structure of fish communities, highlighting the importance of considering other ecological factors and interactions when assessing the impact of invasive species.

The findings of the present study align with previous research on the impacts of invasive macroalgae. Namely, Martín-Jiménez & Riera (2024) observed that *R. okamurae* significantly alters marine ecosystems, using epifaunal communities as a proxy. These consistent patterns across different taxa highlight the widespread and profound effects of *R. okamurae* invasion. Future research should focus on filling several key knowledge gaps to better understand and mitigate the impacts of *R. okamurae* on marine ecosystems. Firstly, studies are needed to assess

the long-term effects of *R. okamurae* invasion on fish populations and community dynamics, including how these effects may change over time. Secondly, investigating the interactions between *R. okamurae* and other environmental stressors, such as nutrient runoff from agriculture and coastal urbanization in the Canary Islands, could provide insights into potential synergistic impacts on fish communities. Thirdly, more research is needed on effective control techniques that have been used in other areas facing the similar environmental problems, this includes manual removal efforts to directly reduce *R. okamurae* biomass (Klein and Verlaque, 2011; Savio et al., 2021), the use of biological control agents such as native herbivores that can selectively graze on *R. okamurae* (Pearson and Callaway, 2003), and habitat restoration techniques (Fuente et al., 2019), like reintroducing native seaweeds and enhancing structural complexity to outcompete *R. okamurae*. Addressing these research priorities will be essential for developing informed conservation and management strategies in areas affected by invasive macroalgae.

5. Conclusions

This study aimed to understand the impact of the invasive algae *Rugulopteryx okamurae* on fish communities across different coastal sites of Gran Canaria. We observed significant variations in fish communities along the invasion gradient, with a trend towards homogenization in areas heavily dominated by *R. okamurae*. This invasion promotes the proliferation of opportunistic species like *Similiparma lurida*, *Sparisoma cretense*, *Thalassoma pavo*, and *Sarpa salpa*, particularly in highly invaded areas, while these generalist species are also present in regions with lower *R. okamurae* densities. However, the invasion occurs at the expense of a greater diversity of specialized species that depend on more complex habitats. Hence, the invasion gradient itself is the primary driver structuring the studied fish communities. These findings highlight the need for ongoing monitoring and control to understand the future implications of this invasion in Gran Canaria. Furthermore, as the algae have already affected similar island ecosystems in the Azores and Madeira, tracking developments in these regions are crucial for predicting potential impacts in Gran Canaria. Future research should focus on assessing the long-term effects of *R. okamurae* invasion, its interactions with other environmental stressors, and effective control strategies to develop informed conservation and management approaches in regions affected by invasive macroalgae.

CRedit authorship contribution statement

Xavier Bachot: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Rodrigo Riera:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.seares.2025.102568>.

Data availability

Data are available upon request from the first author (XB).

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