The brown alga *Rugulopteryx okamurae*: Insights into epifaunal diversity across marginal populations in Gran Canaria

Mónica Martín Jiménez , Rodrigo Riera [*]

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

ARTICLE INFO

ABSTRACT

Biological invasions pose significant threats to biodiversity, primarily through the depletion of natural resources and the disruption of local ecosystems. Our study focuses on *Rugulopteryx okamurae* (E. Y. Dawson) I·K. Hwang, W.J. Lee, and H.S. Kim, an invasive alga proliferating in the Macaronesia and Mediterranean regions. This research examines the epifaunal assemblages associated with *R. okamurae* across eastern and northeastern zones in Gran Canaria, Canary Islands. A total of 11,398 individuals from 63 species within five taxonomic groups were collected, with Arthropoda dominating the samples (88.68 % of the overall abundance), particularly the amphipods *Apohyale perieri* and *A. stebbingi*. Significant differences in species richness and individual abundance were observed between populations from San Cristóbal, Jinámar and Ojos de Garza. The central populations exhibited the highest species richness, while the northern populations showed the lowest. Multivariate analyses revealed distinct community compositions between the edge and central populations, underscoring the invasive alga's capacity to support diverse and abundant epifaunal assemblages. Moreover, *R. okamurae* demonstrated remarkable dominance in the study area, achieving total coverage of up to 100 % at certain sampling sites. This extensive coverage highlights the alga's ability to sustain a rich and varied epifaunal community, characterized by both species abundance and high biodiversity. The findings emphasize the need for targeted conservation and management strategies to mitigate the spread of *R. okamurae* and protect local biodiversity from further disruption.

1. Introduction

Biological invasions have profound ecological and economic consequences (Bacher et al., 2018; Faria et al., 2022a; Simberloff et al., 2013). But when we talk about invasive species, what do we really mean? The invasion process starts with the transport and introduction of a species into a new ecosystem, followed by its subsequent response, which will determine if this species becomes exotic or invasive (Colautti and MacIsaac, 2004; Manchester and Bullock, 2000; Rilov and Crooks, 2009). Some authors stated that a species can be considered exotic if it can maintain its population through recruitment and reproduction without the introduction of new individuals. (Colautti and MacIsaac, 2004; Devin and Beisel, 2007). On the other hand, if the species proliferates at high densities and spreads throughout the ecosystems, it becomes invasive. In recent decades, human activities and global change have led to an increase in biological invasions. Global change included both environmental (climate changes species exploitation, the transformation of land and water) and economic factors (Bellard et al., 2016;

Perrings et al., 2010; Sax and Gaines, 2003). Notably, globalisation is one of the main drivers of species dispersal due to the growth in trade that affects the number and frequency of new introductions (Perrings et al., 2010). The introduction of invasive species might serve as a pathway for changes and impacts on communities and ecosystems. Although most of the well-known impacts of these species have been negative, it must be considered that these impacts should be classified according to the response of the incipient ecosystem and native biota. In this sense, we will have a positive, negative, or no impact (Manchester and Bullock, 2000). In terms of negative impacts, we can highlight the loss of habitat and biodiversity (reducing its distribution, richness, and abundance) (Pyšek et al., 2012), loss of native genotypes and changes in food web structure (Faria et al., 2022a). While invasive species have spread across various environments (freshwater, marine, terrestrial, and brackish) only 10 % of studies focus on the marine environment (Mačic et al., 2018). Marine invasive species are mostly associated with anthropogenic vectors such as vessels, aquaculture, and ornamental activities (Rilov and Crooks, 2009). Such associations are evident in the

Mediterranean Sea (which is known as a hotspot for marine invasions), with notable instance of marine invasions. The most well-reported instance is the case of the alga *Caulerpa taxifolia*, which was the first macrophyte invasion to draw widespread public attention (Klein and Verlaque, 2008). Similarly, the alga *Caulerpa racemosa* var. *cylindracea* can also be highlighted, along with the algae *Undaria pinnatifida*, and *Codium fragile* (Li et al., 2023; Schaffelke and Hewitt, 2014; Tiralongo et al., 2022).

Invasive macroalgae, exemplified by these species pose a significant threat to marine biodiversity because they may alter both ecosystem structure and function by monopolizing space, leading to the loss of native space and changes in the food webs (Petrocelli and Cecere, 2015; Schaffelke et al., 2006). Additionally, their rapid spread could result in the monopolisation of space, leading to the loss of native species (Blanco et al., 2021). Introduced species can compete with resident macroalgal communities through lateral and epiphytic growth (Blanco et al., 2021; Faria et al., 2022b). Moreover, they often exhibit high reproductive rates, facilitated by the lack of predators in the new environment or by their ability to thrive in a broad range of environmental conditions (Blanco et al., 2021; Li et al., 2023; Metabolites et al., 2018). Alien marine macroalgae are particularly prone to becoming invasive due to specific characteristic enhancing their competitiveness, including short life cycles, spatial growth capacity, high reproductive capacity, successive outbreaks and the production of toxic metabolites (Metabolites et al., 2018). Invasive algae may produce secondary metabolites for allelopathic defense (Li et al., 2023). These metabolites not only reduce horizontal competition but also prevent predation, enhancing the ecological competitiveness of the species in the introduced environment (Pereira and Perez Da Gama, 2007). On the other hand, phenotypic plasticity - defined as the ability of organism to alter their morphology and/or physiology in response to varying environmental conditions - can explain why some species are invasive while others are not, the

ecological impact and possible extent of the invasive species and how native species may respond to introductions (Funk, 2008; Li et al., 2023; Rilov and Crooks, 2009).

Focusing on invasive macroalgae, *R. okamurae* stands out as a noteworthy introduction in Europe, Africa and Asia (Fig. 1). This brown seaweed, native to the Northwest Pacific (Japan, China, Korea, Taiwan and Philippines), was initially reported by Verlaque et al. (2009) in 2002 on the French Mediterranean coast, however in this region the alga did not present invasive behaviour. It is thought that this introduction was probably associated with the Japanese oyster *Magallana gigas* in the Thau coastal lagoon (northwestern Mediterranean), one of the enclaves most affected by invasive species. Some years later, in 2015 and 2016, this alga was first detected in the Strait of Gibraltar in the city of Ceuta (North Africa) and in Andalusian waters respectively (southern Iberian Peninsula (Spain)) (Altamirano et al., 2016, 2017; Ocaña et al., 2016). Between these two years *R. okamurae* covered most of the shallow rocky seabeds, resulting in the removal of 5000 tons of wrack algae material from Ceuta's beaches (García-Gómez et al., 2020; Ocaña et al., 2016). Since these years, its invasive behaviour has been intensified colonisingboth sides of the Strait of Gibraltar and, covering 90 % of the rocky seabed between 10 and 20 m depth (García-Gómez et al., 2018, 2020; Sempere-Valverde et al., 2019). The invasive success of *R. okamurae* is the result of various aspects, including its colonization ability, high rates of detachment and its floating have the capacity to reattach to hard substrata (Altamirano et al., 2017, 2019; García-Gómez et al., 2021). Moreover, this macroalgae exhibits a broad tolerance for varying depths, light conditions, and possesses the capacity to store nitrogen (Mercado et al., 2022). These attributes contribute significantly to its resistance to oligotrophic conditions, enabling it to thrive in nutrient-poor environments. Furthermore, the macroalgae demonstrates an adaptive advantage by capitalizing on nutrient peaks, which may arise from local upwelling events, seasonal coastal eutrophication, or anthropogenic
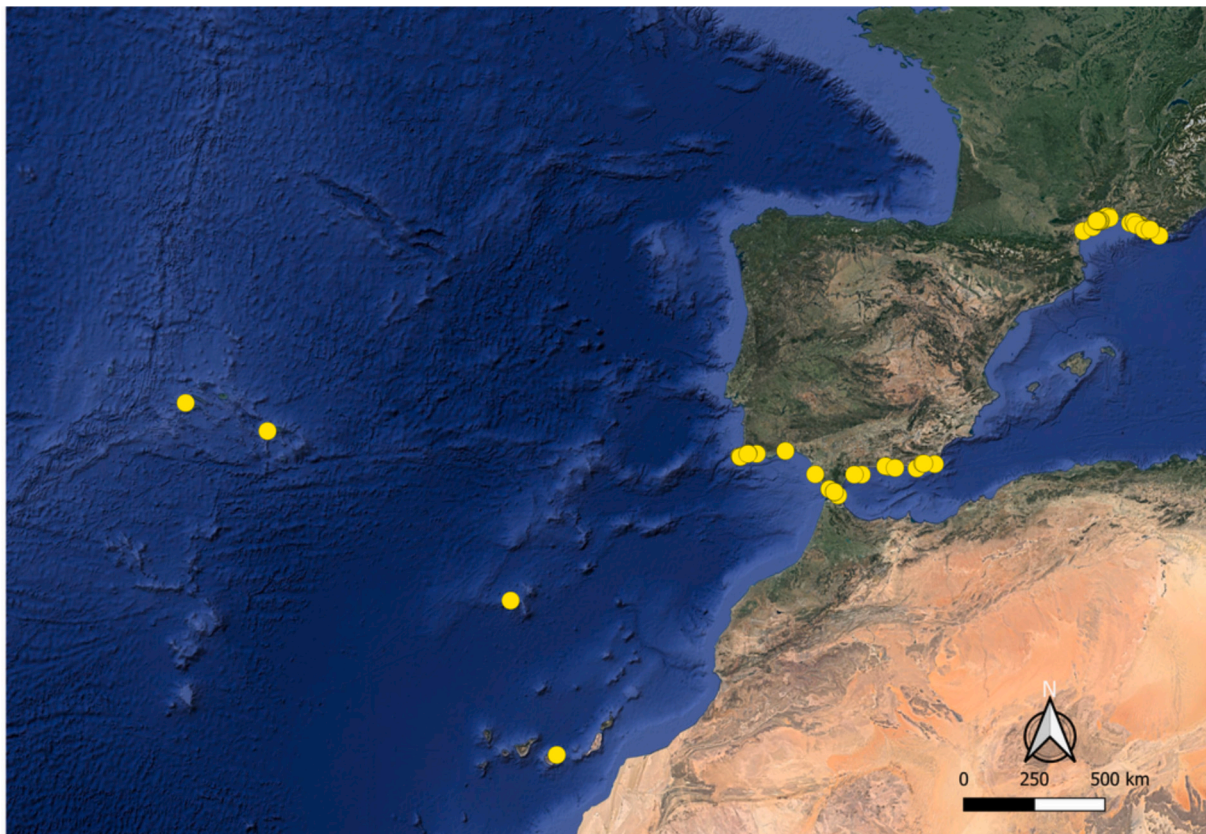

Fig. 1. Non-native occurrence record of *Rugulopteryx okamurae* in the Macaronesia and the western Mediterranean areas.

sources (Bernal-Ibáñez et al., 2022; Mercado et al., 2022). This adaptability allows the macroalgae to efficiently exploit environmental fluctuations and contribute to its overall ecological resilience (Bernal-Ibáñez et al., 2022). The occurrence of this invasive alga is not restricted to the Strait of Gibraltar, as it has been identified in various locations. In 2017, it was discovered at Belyounech Beach (Morocco) (El Aamri et al., 2018). A year later, in 2018, it was documented in Provence (France) (Ruitton et al., 2021). In 2019, it was observed in the Azores (Portugal) (Faria et al., 2022a; Faria et al., 2022b) and in 2021, it was found in Madeira (Portugal) (Bernal-Ibáñez et al., 2022). More recently, in 2022, it was detected in our study area, Gran Canaria, (Canary Is., Spain) (R. Haroun, *pers. comm.*).

Maritime traffic globally poses a threat to communities and ecosystems by facilitating the introduction of species with invasive potential (Ojaveer et al., 2018; Seebens et al., 2016). Cargo and recreational ships transport a diverse array of organism, including algae, bacteria, microorganisms, sponges and spores of different species, between ports worldwide through ballast water exchange and hull attachment (Guala et al., 2003; Kölzsch and Blasius, 2011; Liu et al., 2021). In our study, this factor is crucial because the main hypothesis of the introduction and subsequent presence of *R. okamurae* in Gran Canaria resulted from maritime traffic. This island experiences high-intensity maritime traffic, especially through the Port of Las Palmas de Gran Canaria, one the most important in the Atlantic Ocean due to its strategic geographical location connecting Europe, Africa and America, which could justify the island's high sensitivity to the introduction of non-native species (Canaryports, 2021; Castro et al., 2022).

The main objective of this study was to analyse differences in the epifauna between edge and central populations of *Rugulopteryx okamurae* in coastal areas of Gran Canaria colonised by this invasive alga. Central populations refer to those located in the core or interior regions of the algal patches, where conditions are typically more stable, with less exposure to external stressors such as wave action, desiccation, or human disturbances, allowing for robust growth of the alga and potentially supporting a more diverse or abundant epifaunal community. In contrast, edge populations are situated at the periphery or margins of the distribution of this alga in Gran Canaria, where conditions can potentially result in differences in the composition and abundance of epifauna. By comparing the epifaunal communities between these two spatial zones, the study aims to explore biodiversity differences, assess how varying environmental conditions impact these organisms, and understand the broader ecological roles of edge and central populations in structuring habitat dynamics and supporting associated marine life.

To this end, species richness and abundance of individuals were evaluated. In this context, the epifauna (the assemblage of organism, both sessile and mobile, residing on or affixed to the seabed or other substrates) was used as a model to test the ecological conditions between the *R. okamurae* patch and the surrounding macroalgae in epibenthic communities associated with this seaweed. This make sense as the associated communities are significantly influenced by marine macroalgae along the coast, serving as habitats and refuge from physical stress and predators for invertebrates (Gestoso et al., 2012). Although the idea of edge effect is well known in terrestrial and marine environments, it has not received enough attention when it comes to invasive macroalgae and the communities that surround them. Moreover, when these macroalgae become invasive, they jeopardize the structure and functioning of the ecosystem, resulting in alterations to the associated epibenthic communities. Prior research on the Mediterranean Sea has demonstrated that *Rugulopteryx okamurae* supports distinct epifaunal assemblages compared to native species such as *Dictyota dichotoma,* despite their morphological similarities (Navarro-Barranco et al., 2019). These differences may be associated with secondary metabolites, such as terpenes, as demonstrated in previous studies (Agatsuma et al., 2005; Yamase et al., 1999). Based on these previous studies, we also tested whether the invasive alga *R. okamurae* can host epifaunal communities in the study area.

2. Material and methods

2.1. Study area

The study was carried out on the island of Gran Canaria (Fig. 2) ubicated in the Atlantic Ocean (28° N, 15° W) This island belongs to the Canary archipelago, made up of eight islands and several islets located between 27° and 30°N, and distributed over 500 km, with the eastern island about 100 km from the African coast. A previous prospective survey was carried out in the edge populations of Gran Canaria to check the presence of *R. okamurae*. After this research, our study has been focused on three coastal sites of Gran Canaria, i.e., San Cristóbal, Jinámar and Ojos de Garza. The coastal site of San Cristóbal is characterized by an extensive intertidal platform (160 m) and numerous tide pools that are exposed to waves. During the dates when this sampling period, a wide distribution of *Rugulopteryx okamurae* was observed on the rocky substrate, displacing other algae such as *Asparagopsis taxiformis* (Delile) Trevisan 1845 and representing a high percentage of the total coverage. Jinámar, also presents an intertidal platform, with a length of ca. 45 m. This area is characteristically windy and exposed to waves. At this point, the distribution of *Rugulopteryx* was different, as in this case, it was more distributed on the rocky and sandy substrates. The third coastal site, Ojos de Garza (Fig. 6), lies further south of Las Palmas de Gran Canaria. This coastal site presents mainly a rocky substrate but is also sandy because it is located on the beach. In fact, wracking algae material from *Rugulopteryx okamurae* was observed. Unlike the other two sampling sites, this site was characterized by less exposure to waves. In this area, the distribution of the alga is widely distributed throughout the intertidal zone, presenting a lower percentage of total coverage compared to that of San Cristóbal.

2.2. Sampling design

A total of 60 samples were collected between February and June 2023 (Table 1), of which 20 represent each coastal site, 10 from the upper eulittoral (Area A) and 10 from the lower eulittoral (Area B) (Fig. 3A). These areas were carefully selected based on the specific characteristics of each sampling site with the aim of maintaining a minimum distance between the two areas, ensuring they were not too closely situated. All selected quadrats were chosen for their exceptional algal density, ensuring that each site had a consistent and high coverage of *R. okamurae* above 95 %. This targeted approach was employed to guarantee the accurate representation of high-cover areas, maximizing the study's relevance to regions heavily impacted by this species. This high-density criterion was also chosen to ensure uniformity across samples and to specifically focus on areas where *R. okamurae* is most prevalent, thereby minimizing variability in its abundance across quadrats. Given this selection process, the abundance of *R. okamurae* was not expected to be a variable factor influencing the abundance and diversity of epifauna within the sampled quadrats. This collection was performed using a destructive random sampling technique with a 25 × 25 cm^2 grid and a scraper to separate the algae from the substrate to which they were attached (Fig. 3B), and then they were placed in a zip bag with sea water and frozen to ensure the proper conservation of the epifauna.

Once in the lab, the samples were sorted out. The entire samples were put into a tray and with the help of thin tweezers all the epifauna was separated. The organisms were placed in a jar with 70° alcohol and then counted and separated into groups, using a Petri dish and finally introducing them into vials according to the taxonomic groups. Afterwards the taxonomic identification to the lowest level possible was performed, mainly to the species. These species were identified by visualizing them under a binocular microscope and using taxonomic identification guides and specialized bibliography (Lincoln, 1979; Riera et al., 2003).

Fig. 2. This figure shows the study area's geolocation. The distribution of Rugulopteryx okamurae is shown by the shaded area. The coastal locations of San Cristobal, Jinámar, and Ojos de Garza are denoted by A, B, and C, respectively.

Table 1
Characteristic of the sampling sites.

Sites	Zone	Coordinates (Latitude, Longitude)	Date	Orientation
San Cristóbal	A	28°04′55.3″N, 15°24′52.7″W	21/02/2023 09/03/2023 25/03/2023	Northern edge
	B	28°04′56.4″N, 15°24′53.5″W		
Jinámar	A	28°01′45.9″N, 15°23′21.7″W	06/05/2023 03/06/2023	Central
	B	28°01′46.0″N, 15°23′19.9″W		
Ojos de Garza	A	27°57′05.3″N, 15°22′48.6″W	22/04/2023 05/05/2023	Southern edge
	B	27°57′05.4″N, 15°22′48.1″W		

2.3. Data analysis

The data distribution of epibiont species richness and individual abundances were represented using boxplots. ANOVA analysis was performed considering the fixed factor of population location (predictor variable), and the dependent variable were epibiont species richness and abundance. Tukey post-hoc test was performed when significant effects were detected in the location factor. ANOVA assumptions were evaluated using the Shapiro-Wilk test to evaluate normality distribution of data, and the Cochran test was utilized to evaluate homocedasticity of variances. When normal distribution and/or homogeneity of the variances were not achieved, data were subjected to the Kruskal–Wallis non-parametric test, followed by a Games-Howell non-parametric multiple comparison test (Zar, 1999).

We performed a Permutational Multivariate Analysis of Variance (PERMANOVA) to examine significant changes in epifaunal assemblages. PERMANOVA is performed considering the following factors, population (northern edge, central and southern edge). As a result, we obtain the F value and the probability of F. The latter being significant must have a value of $p < 0.05$. Posteriorly, we used the Similarity percentage analysis (SIMPER) to identify the contribution of each species to overall dissimilarities, due to variations in abundance at each population. Finally, non-metric multidimensional scaling (n-MDS) was performed to assess patterns of epifaunal community structure among the sampled locations, n-MDS (non-metric multidimensional scaling) procedure was conducted based on Bray-Curtis similarity index on square-rooted transformed data.

The statistical analyses mentioned above were carried out by means of a set of R software packages. Primarily the *vegan* (Oksanen et al., 2022) package contains the codes to perform the n-MDS and PERMANOVA, *ggplot2* (Wickham, 2016) makes it possible to make graphs, among them the boxplot. Other packages like *tidyverse* (Wickham et al., 2019), *janitor* (Firke, 2023), *flextable* (Gohel and Skintzos, 2023) and *readxl* (Wickham and Bryan, 2022) are also used to read the data and make graphs and tables with higher quality.
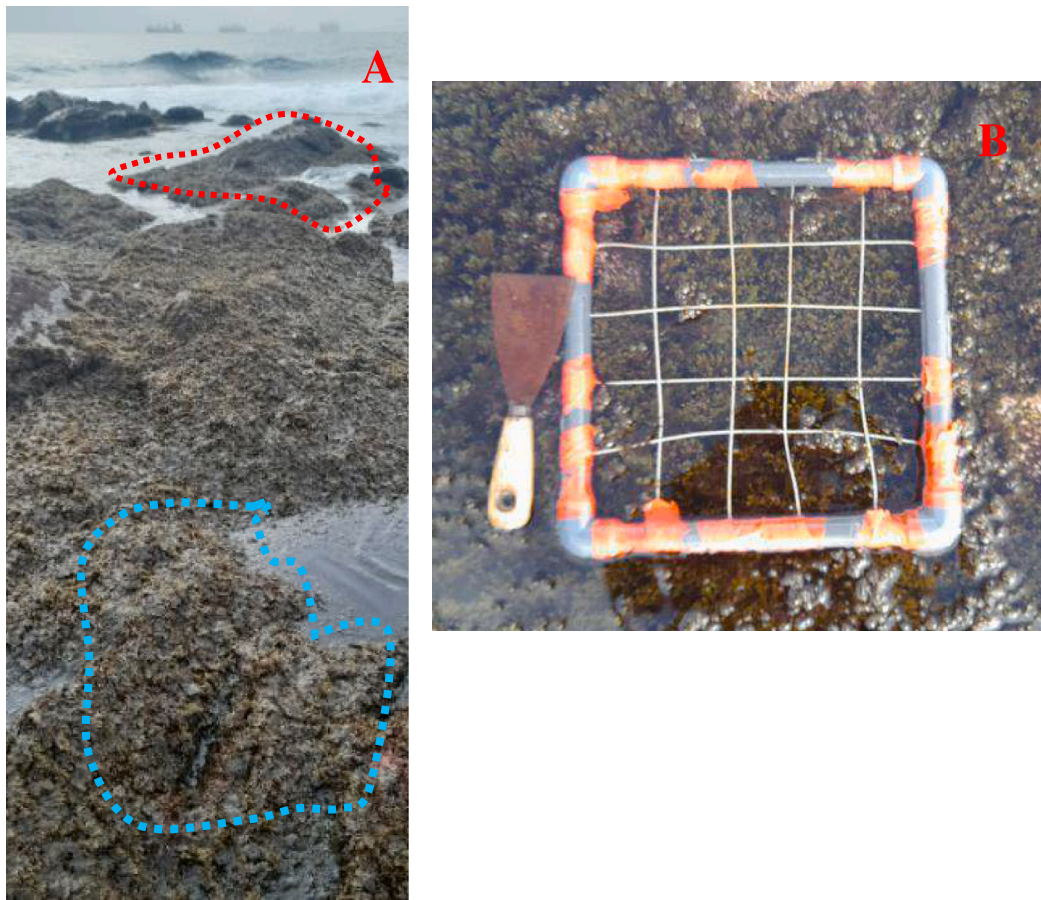
Fig. 3. A: Area A (red) and Area B (blue) patch distribution. **B:** 25 × 25 cm³ square grid. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

A total of 11,398 individuals were collected, belonging to 63 species distributed in five taxonomic groups (Annelida, Arthropoda, Chordata, Echinodermata, and Mollusca. Among these, Arthropoda was the most abundant taxa (10,108 individuals, 88.68 % of the overall abundance), followed by Annelida (695 ind., 6.10 %), Mollusca (363 ind., 3.18 %),

Echinodermata (167 ind., 1.47 %), and Chordata (1 ind., 0.00 %). Of the 63 species identified, the ten most abundant (Fig. 4) belonged to arthropods, annelids, and molluscs. Among the arthropods, four species of amphipods stand out for their high abundance: *Apohyale perieri (*Lucas, 1846), with 4096 individuals (35.26 %), was the most abundant species followed by *A. stebbingi* (Chevreux, 1888) with 2276 individuals (19.96 %), and *Elasmopus rapax* (A. Costa, 1853) with 1208 individuals (10.60
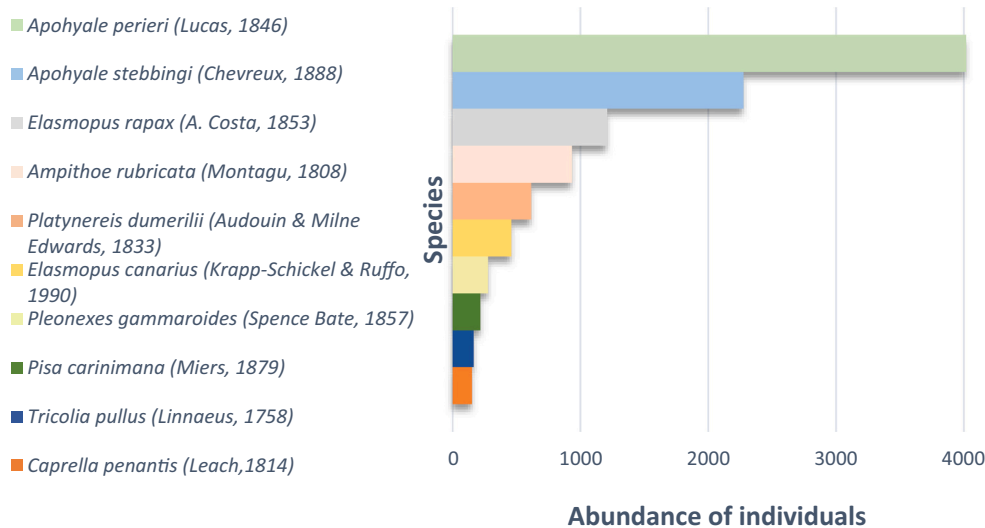

Fig. 4. The most abundant epifaunal species from the sampling sites.

%).

The abundance of individuals (Fig. 5A, Table 2) was maximum in the central and southern edge population (mean ± SD, 257.4 ± 129.2 individuals and 220.2 ± 119.7 ind. respectively), whereas in the northern population, abundances decreased notably, showing a minimum abundance (92.3 ± 71.7 ind.) (Fig. 5A), being highly significant these differences (One-way ANOVA, F = 12.45, p < 0.001).

In general, the number of species observed was similar, ranging from 10 to 18 taxa. The central edge (16.95 ± 4.1 spp.) was the site with the highest richness. In the southern edge (15.35 ± 4.5 spp.), however, the species richness was not as high as in the central population but was richer than the northern (12 ± 2.8 spp.), which had the lowest species richness of the three edge populations studied (Fig. 5B). This was confirmed by the values obtained in the ANOVA (One-way ANOVA, F = 8.14, p = 0.00076), which showed significant differences, especially between the northern edge and the central and southern edge (Tukey post-hoc test, northern edge-central, p = 0.013; northern edge-southern edge, p = 0.008).

The variability in the individual abundance was notable in the central population because Zone B (299.6 ± 165.6 ind.) was more abundant than Zone A (215.2 ± 62.2 ind.). In contrast, in the southern population, the opposite trend occurred, i.e., Zone A (295.4 ± 109.1 ind.) was more abundant than zone B (145 ± 75.9 ind.). The same occurred in the northern edge population (Zone A: 123 ± 90.3 ind., Zone B: 61.6 ± 24.4 ind.), however, these differences were not as high as in the other populations (Fig. 6A). On the other hand, for species richness (Fig. 6B), it was observed that Zone B of the central (19.7 ± 3.8 spp.) was higher than the rest, followed by the southern (18.6 ± 4.6 spp.) and northern (11.3 ± 2.5 spp.) edges. However, Zone A showed lower species richness, especially in the southern (12.1 ± 1.9 spp.) and northern (12.7 ± 3.0 spp.) edge populations. Due to the disparity of above-mentioned trends, no significant differences were found between zones (A and B)
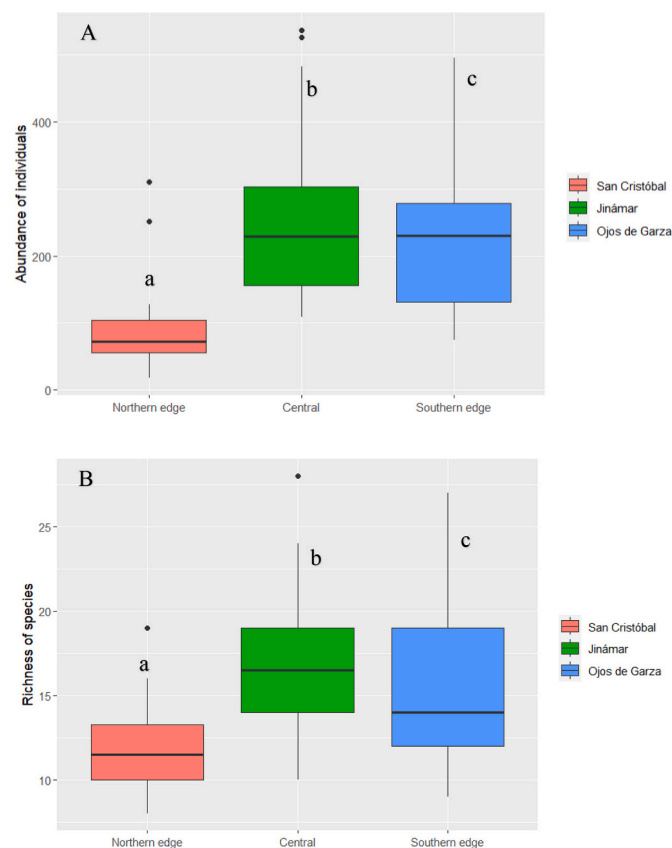

Fig. 5. A. Epifaunal abundance of the edge populations studied. **B.** Epifaunal richness of the edge populations studied.

Table 2
Species abundance at each coastal site.

Group	Species	San Cristóbal	Jinámar	Ojos de Garza
Picnogonida	*Achelia vulgaris* (Costa, 1861)	1	0	0
Polychaeta	*Alitta virens* (M. Sars, 1835)	6	0	2
Echinodermata	*Amphiura chiajei* (Forbes, 1843)	0	29	29
Amphipoda	*Ampithoe ramondi* (Adouin, 1826)	3	0	0
Amphipoda	*Ampithoe rubricata* (Montagu, 1808)	207	576	151
Isopoda	*Anthura gracilis* (Montagu, 1808)	3	8	7
Amphipoda	*Aora typica* (Krøyer, 1845)	0	1	1
Mollusca	*Aplysia sp* (Linnaeus, 1767)	0	0	1
Amphipoda	*Apohyale perieri* (Lucas, 1846)	514	1358	2147
Amphipoda	*Apohyale stebbingi* (Chevreux, 1888)	180	1674	422
Tanaidacea	*Apseudes talpa* (Montagu, 1808)	0	2	0
Amphipoda	*Atylus? sp* (Leach, 1815)	0	0	1
Mollusca	*Bittium latreillii* (Payraudeau, 1826)	21	0	2
Amphipoda	*Caprella acanthifera* (Leach, 1814)	19	4	16
Amphipoda	*Caprella cavediniae* (Krapp-Schickel & Vader, 1998)	2	47	80
Amphipoda	*Caprella equilibra* (Say, 1818)	14	5	5
Amphipoda	*Caprella penantis* (Leach, 1814)	32	60	59
Isopoda	*Carpias minutus* (Richardson, 1902)	0	5	14
Polychaeta	*Cirratulus cirratus* (O. F. Müller, 1776)	0	1	0
Polychaeta	*Cirriformia tentaculata* (Montagu, 1808)	1	0	3
Decapoda	*Clibanarius aequabilis* (Dana, 1851)	0	12	22
Mollusca	*Columbella adansoni* (Menke, 1853)	18	29	88
Amphipoda	*Corophium volutator* (Pallas, 1766)	0	2	0
Isopoda	*Cymodoce truncata* (Leach, 1814)	2	1	3
Hexapoda	Diptera larvae	1	0	0
Isopoda	*Dynamene bidentata* (Adamas, 1800)	4	0	0
Isopoda	*Dynamene edwardsi* (Lucas, 1849)	3	0	5
Amphipoda	*Elasmopus canarius* (Krapp-Schickel & Ruffo, 1990)	129	172	157
Amphipoda	*Elasmopus rapax* (A. Costa, 1853)	238	512	458
Amphipoda	*Ericthonius punctatus* (Spence Bate, 1857)	2	0	0
Decapoda	*Eriphia verrucosa* (Forskål, 1775)	1	16	2
	Eusirus sp. (Krøyer, 1845)	1	0	0
Amphipoda	*Hyale* sp. (Rathke, 1836)	2	0	0
	Lepadogaster candolii (Riso, 1810)	0	0	1
Amphipoda	*Leucothoe spinicarpa* (Abildgaard, 1789)	1	2	2
Mollusca	*Littorina littorea* (Linnaeus, 1758)	2	0	0
Polychaeta	*Lysidice unicornis* (Grube, 1840)	1	0	0
Amphipoda	*Maera grossimana* (Montagu, 1808)	0	0	1
Polychaeta	*Malmgrenia lunulata* (Delle Chiaje, 1830)	2	0	0
Echinodermata	*Marthasterias glacialis* (Linnaeus, 1758)	0	3	0

Table 2 (*continued*)

Group	Species	San Cristóbal	Jinámar	Ojos de Garza
Amphipoda	*Neoamphitrite edwardsii* (Quatrefages, 1866)	2	12	5
Echinodermata	*Ophiothrix fragilis* (Abildgaard in O.F. Müller, 1789)	0	93	13
Decapoda	*Pachygrapsus marmoratus* (Fabricius, 1787)	0	41	29
Decapoda	*Pachygrapsus transversus* (Gibbes, 1850)	6	25	6
Decapoda	*Pagurus anachoretus* (Risso, 1827)	0	0	7
Decapoda	*Palaemon elegans* (Rathke)	0	46	15
Echinodermata	*Paracentrotus lividus* (Lamarck, 1816)	1	34	4
Polychaeta	*Perinereis oliveirae* (Horst, 1889)	13	28	0
Mollusca	*Phorcus atratus* (W. Wood, 1828)	0	0	7
Decapoda	*Pisa carinimana* (Miers, 1879)	67	90	59
Polychaeta	*Platynereis dumerilii* (Audoin &Milne Edwards, 1833)	148	42	424
Amphipoda	*Pleonexes gammaroides* (Spence Bate, 1857)	95	135	47
Amphipoda	*Podocerus variegatus* (Leach, 1814)	1	6	0
Polychaeta	*Polyophthalmus pictus* (Dujardin, 1839)	19	26	19
Polychaeta	*Psamathe fusca* (Johnston, 1836)	0	0	1
Mollusca	*Pusia zebrina* (d'Orbigny, 1840)	17	0	14
Amphipoda	*Quadrimaera inaequipes* (A. Costa in Hope, 1851)	0	6	3
Polychaeta	*Scoletoma funchalensis* (Kinberg, 1865)	2	0	1
Isopoda	*Stenosoma capito* (Rathke, 1836)	0	0	1
Amphipoda	*Sunamphitoe pelagica* (H. Milne Edwards, 1830)	0	2	6
Polychaeta	*Syllis cornuta* (Rathke, 1843)	1	0	0
Mollusca	*Tricolia pullus* (Linnaeus, 1758)	64	40	60
Amphipoda	*Tryphosella sarsi* (Bonnier, 1893)	0	3	4

considering individual abundances (Kruskal-Wallis, H = 1.89, $p = 0.12$) nor species richness (H = 3.98, $p = 0.078$).

The epifaunal community at the northern edge, central and southern edge locations differed significantly according to the permutational multivariate analysis (PERMANOVA) (Pseudo-F = 6.95, $p = 0.0002$). Specifically, the edge populations (both northern and southern) were found to be statistically distinct from the central population, as indicated by the post-hoc tests (northern edge-central, $p < 0.023$; southern edge-central, $p < 0.034$). The MDS highlighted considerable heterogeneity between the southern and northern edge populations, distinguishing them from the central population (Fig. 7). Notably, the northern edge samples were clustered on the left side of the ordination plot, while the remaining samples were grouped toward the center and right side, reflecting the observed differences.

The amphipod *Apohyale perieri* was the species that contributed the most to the northern (25.20 %) and southern edge (45.80 %), also contributing to the central (20.68 %), but with a lower percentage than the other populations. The most abundant species in the central population was the amphipod *Apohyale stebbingi* (28.51 %). On the other hand, there were also specific species, such as the polychaete *Platynereis dummerilli,* in both the northern and southern edge populations (8.41 % and 7.70 %, respectively), and the amphipod *Elasmopus canarius* in the northern edge population (6.16 %) (Table 3). Among the north-south boundaries, the amphipod *Apohyale perieri* (38.2 %) stood out with a high contribution rate, followed by the south-central boundaries (32.6 %), in contrast to the north-central boundary, where it reflected a low contribution rate (24.10 %). Another species that contributed to these differences was the amphipod *Apohyale stebbingi*, which contributed the northern edge-central dissimilarities (25.90 %) and southern edge-central differenes (25.6 %). Other species that contributed to explain these differences were the amphipods *Elasmopus rapax* and *Amphitoe rubricata*, and the polychaete *Platynereis dummerilli*, but with low contribution percentages (6–9 %) (Table 4).

4. Discussion

The present study demonstrated that the invasive seaweed *Rugulopteryx okamurae* supports epifaunal communities with a high individual abundance, a finding consistent with previous research highlighting the capacity of invasive macrophytes to act as ecosystem engineers by providing complex habitats for associated fauna (Gallardo et al., 2016). Our results also revealed spatial variation in abundance and species richness across populations, with the central population exhibiting the highest values, followed by the southern edge and northern edge populations. This trend aligns with studies suggesting that edge effects in marine habitats often result in reduced habitat quality or stability at boundaries, which may influence local biodiversity (Boström et al., 2011). The observed spatial variability in individual abundance and species richness within each population further emphasizes the role of
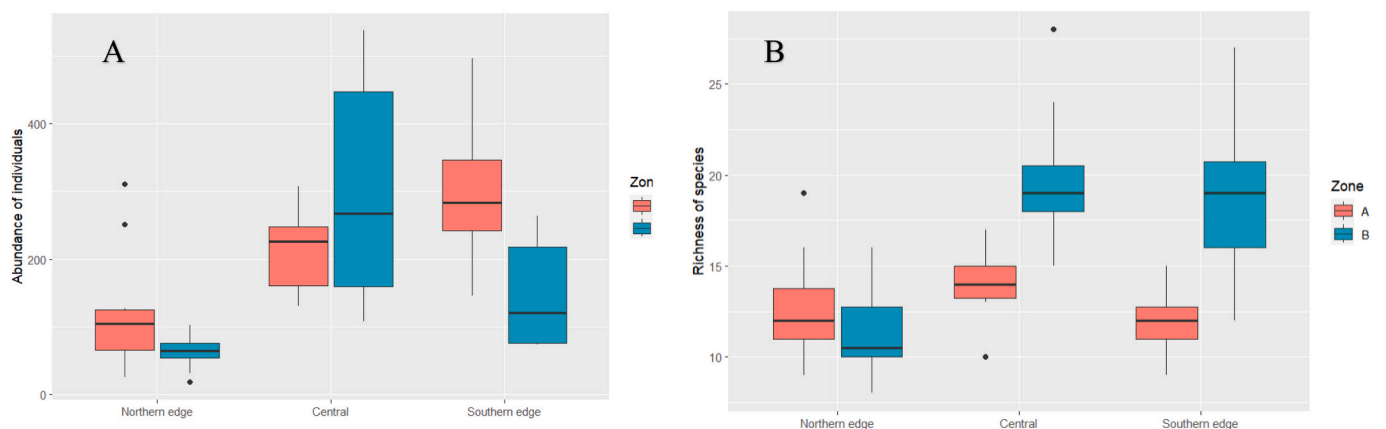

Fig. 6. A. Abundance of individuals according to the spatial variability of the edge population studied. **B.** Richness of species according to the spatial variability of the edge populations studied.
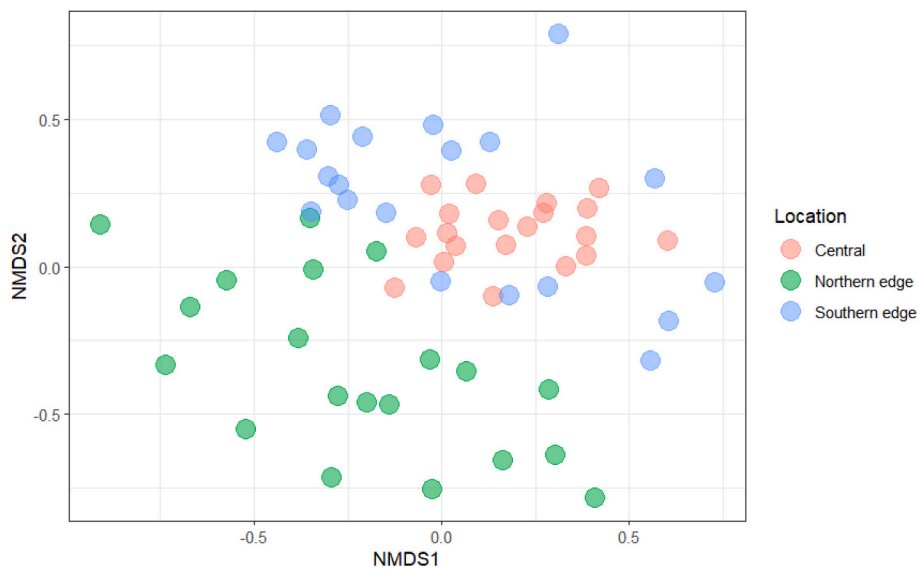
Fig. 7. N-MDS showing the distribution of the samples according to their orientation (stress: 0.017).

Table 3
Species contribution to community composition (SIMPER analysis).

Factor	Species	% Contribution	% Cumsum
Northern edge	*Apohyale perieri* (Lucas, 1846)	25.25	25.25
	Elasmopus rapax (A, Costa, 1853)	38.41	13.16
	Apohyale stebbingi (Chevreux, 1888)	48.90	10.49
	Ampithoe rubricata (Montagu, 1808)	57.50	8.60
	Platynereis dumerilii (Audoin & Milne Edwards, 1833)	65.91	8.41
	Elasmopus canarius (Krapp-Schickel & Ruffo, 1990)	72.07	6.16
Central	*Apohyale stebbingi* (Chevreux, 1888)	28.52	28.52
	Apohyale perieri (Lucas, 1846)	49.2	20.68
	Ampithoe rubricata (Montagu, 1808)	59.9	10.70
	Elasmopus rapax (A, Costa, 1853)	68	8.10
	Elasmopus canarius (Krapp-Schickel & Ruffo, 1990)	71.5	3.50
Southern edge	*Apohyale perieri* (Lucas, 1846)	45.8	45.80
	Apohyale stebbingi (Chevreux, 1888)	54.6	8.80
	Platynereis dumerilii (Audoin & Milne Edwards, 1833)	62.3	7.70
	Elasmopus rapax (A, Costa, 1853)	69.6	7.30
	Ampithoe rubricata (Montagu, 1808)	73.7	4.10

small-scale environmental factors, such as hydrodynamic conditions or substrate heterogeneity, in shaping community structure. For example, Zone B of the central population exhibited higher individual abundance and species richness compared to Zone A, a pattern reversed in the northern and southern edge populations. This heterogeneity may reflect local variations in the physical or biological characteristics of the habitat, such as nutrient availability or algal density (Benedetti-Cecchi and Cinelli, 1995; Whalen et al., 2016). Additionally, the distinct epifaunal compositions between edge and central populations, driven by differences in the densities of key species such as *Apohyale perieri* and *A. stebbingi*, highlight the influence of *R. okamurae* in modulating community structure. These findings are consistent with studies showing that amphipod assemblages are particularly responsive to habitat-forming invasive species due to their reliance on vegetative complexity for shelter and feeding opportunities (Navarro-Barranco et al., 2020).

This study demonstrated the invasive success of *R. okamurae* in the study area, with total coverage of up to 100 % at some sampling sites. This success can be attributed to the absence of functionally similar or taxonomically related species to this invasive macroalgae (Ricciardi and

Atkinson, 2004). Similar studies conducted in Japan, within the native range of *R. okamurae,* have also identified epifaunal communities characterized by a high diversity, including gastropods, bivalves, annelids, and sea urchins (Agatsuma et al., 2005; Omori et al., 2000). However, this study revealed differences in abundance at different sampling sites, indicating that species respond differently depending on the type of edge habitat they inhabit. The observed differences between the northern edge populations and the other studied populations (central and southern) may be attributed to various factors. These factors may include abiotic or abiotic changes in the environment (Murcia, 1995), alterations in interspecific interactions, or a combination of these and other factors (Ries and Sisk, 2004). Another contributing possible factor may be the structural complexity of the alien invasive macroalga *R. okamurae*. Non-indigenous seaweeds are known to alter the composition and structure of associated epifaunal assemblages compared to native macroalgae (Gestoso et al., 2010, 2012; Navarro-Barranco et al., 2019; Veiga et al., 2014). In agreement with Gestoso et al. (2010), the response of epifauna to the introduction of macroalgae was often reflected in terms of abundance rather than species composition. Our results support this hypothesis, however this trend was not clear discernible at the northern edge, where the lowest number of individuals and species richness was reported.

However, at the coastal site (San Cristóbal) of the northern population, it was observed that the invasive alga coexisted with other algal species, altering the magnitude of its effect and the ability of epifaunal communities to colonize non-native species (Gestoso et al., 2010; Wikström and Kautsky, 2004). This observation highlights the different responses of the effects of invasion depending on habitat complexity. As demonstrated in previous studies, higher epifauna densities typically occur in degraded or unproductive ecosystems, which could also explain the high abundances in the central and southern populations (Navarro-Barranco et al., 2021; Vázquez-Luis et al., 2009). Additionally, these disparities in the composition of epifaunal communities may also stem from mobile epifaunal species utilizing the edges as a refuge and a source of food (Arponen and Boström, 2012). However, a noteworthy consideration emerges, particularly in relation to the risk of predation, concerning *R. okamurae*, this risk is not very high since secondary metabolites (terpenes) associated with it have been found, which act as herbivore repellents (Yamase et al., 1999). This would explain the high abundance of active swimmers, such as amphipods or other species, which are suspension feeders that do not rely on algae to obtain their food (Navarro-Barranco et al., 2019; Vázquez-Luis et al., 2009).

Nevertheless, the results obtained were inconclusive due to the

Table 4
Species contribution to dissimilarity between sites (SIMPER analysis).

Populations	Species	Average		% Contribution	% Cumsum
Northern-Southern edge populations	*Apohyale perieri* (Lucas,1846)	16 %	24.32 %	38.2	38.2
	Apohyale stebbingi (Chevreux, 1888)	7 %	4.69 %	49.3	11.1
	Elasmopus rapax (A, Costa, 1853)	8 %	3.87 %	58.1	8.8
	Platynereis dumerilii (Audoin & Milne Edwards, 1833)	5 %	4.07 %	66.3	8.2
	Ampithoe rubricata (Montagu, 1808)	5 %	2.19 %	72.1	5.8
Northern-edge population and Central population	*Apohyale stebbingi* (Chevreux, 1888)	7 %	10.77 %	25.90	25.90
	Apohyale perieri (Lucas,1846)	16 %	7.83 %	50.00	24.10
	Elasmopus rapax (A, Costa, 1853)	8 %	3.08 %	59.20	9.20
	Ampithoe rubricata (Montagu, 1808)	5 %	4.01 %	68.00	8.80
	Platynereis dumerilii (Audoin & Milne Edwards, 1833)	5 %	0.49 %	72.40	4.40
Central population and Southern edge population	*Apohyale perieri* (Lucas,1846)	10.77 %	24.32 %	32.6	32.6
	Apohyale stebbingi (Chevreux, 1888)	7.83 %	4.69 %	53.8	21.20
	Ampithoe rubricata (Montagu, 1808)	3.08 %	3.87 %	61.5	7.7
	Platynereis dumerilii (Audoin & Milne Edwards, 1833)	4.01 %	4.07 %	68.1	6.6
	Elasmopus rapax (A, Costa, 1853)	0.49 %	2.19 %	74.7	6.6

limitations of this study. The main shortcoming is the absence of temporal replication, which is justified by the limited time available to conduct this study. In addition, the limited sampling effort, which resulted in a low number of sampled localities, restricts the representativeness of the results as they correspond only to a specific area within the study area, analysing only the epifauna of *R. okamurae*. However, it must be considered that the sampling was limited by external factors, given the dependence of the nature of the algae on tidal conditions, which made it difficult to establish a fixed sampling periodicity. Additionally, it would be interesting to analyse the epifauna associated with the algae that coexist with *R. okamurae* in the sampling area, such as the red algae species *Asparagopsis taxiformis*. For future research, a more comprehensive study of the epifauna should be conducted, considering not only the associated invertebrate communities, but also sessile species, epiphytes and fish. Taking a step forward, it is important to compare the epifauna of *R. okamurae* with other invasive algae species and with other species of the same family especially those with similar structural complexity, e.g., *Dictyota* spp. Finally, it would be valuable to consider the spatial variability of algae by expanding the study and sampling efforts to other regions, such as other islands in the Canary Islands, and adjacent archipelagos, e.g., Azores and Madeira.

CRediT authorship contribution statement

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.

Acknowledgements

Data availability

Data will be made available on request.

References

Agatsuma, Y., Kuwahara, Y., Taniguchi, K., 2005. Life cycle of *Dilophus okamurae* (Phaeophyceae) and its associated invertebrate fauna in Onagawa Bay, Japan. Fish. Sci. 71 (5), 1107–1114. https://doi.org/10.1111/j.1444-2906.2005.01070.x.

Altamirano, M., De la Rosa Álamos, J., Martínez Medina, F.J., 2016. Arribazones de la especie exótica *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Dictyotales, Ochrophyta) en el Estrecho de Gibraltar: primera cita para el Atlántico y España. Algas 52 (February 2021), 20. http://hdl.handle.net/10630/12433.

Altamirano, M., De La Rosa Álamos, J., Muñoz, A.-R., 2017. Prolifera en el Estrecho un alga nunca citada en nuestro litoral. In: Quercus. Observación, Estudio y Defensa de La Naturaleza, April, pp. 32–33.

Altamirano, M., De la Rosa, J., Carmona, R., Zanolla, M., Muñoz, A.-R., 2019. Macroalgas invasoras en las costas andaluzas (December).

Arponen, H., Boström, C., 2012. Responses of mobile epifauna to small-scale seagrass patchiness: is fragmentation important? Hydrobiologia 680 (1), 1–10. https://doi.org/10.1007/s10750-011-0895-x.

Bacher, S., Blackburn, T.M., Essl, F., Genovesi, P., Heikkilä, J., Jeschke, J.M., Jones, G., Keller, R., Kenis, M., Kueffer, C., Martinou, A.F., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Richardson, D.M., Roy, H.E., Saul, W.C., Scalera, R., Kumschick, S., 2018. Socio-economic impact classification of alien taxa (SEICAT). Methods Ecol. Evol. 9 (1), 159–168. https://doi.org/10.1111/2041-210X.12844.

Bellard, C., Cassey, P., Blackburn, T.M., 2016. Alien species as a driver of recent extinctions. Biol. Lett. 12 (2). https://doi.org/10.1098/rsbl.2015.0623.

Benedetti-Cecchi, L., Cinelli, F., 1995. Habitat heterogeneity, sea urchin grazing and the distribution of algae in littoral rock pools on the west coast of Italy (western Mediterranean). Mar. Ecol. Prog. Ser. 126, 203–212. https://doi.org/10.3354/meps1262023.

Bernal-Ibáñez, A., Chebaane, S., Sempere-valverde, J., Faria, J., Ramalhosa, P., 2022. A worrying arrival : the first record of brown macroalga *Rugulopteryx okamurae* in Madeira Island and its invasive risk a worrying arrival : the first record of brown macroalga Rugulopteryx okamurae in Madeira Island and its invasive risk. Bioinvasions Records 11 (4). https://doi.org/10.3391/bir.2022.11.4.10.

Blanco, A., Larrinaga, A.R., Neto, J.M., Troncoso, J., Lemos, L., Olabarria, C., 2021. Spotting intruders : species distribution models for managing invasive intertidal macroalgae. J. Environ. Manag. 281 (111861). https://doi.org/10.1016/j.jenvman.2020.111861.

Boström, C., Pittman, S.J., Simenstad, C., Kneib, R.T., 2011. Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Mar. Ecol. Prog. Ser. 427, 191–217. https://doi.org/10.3354/meps09051.

Canaryports, 2021, May 27. Las Palmas, cuarto puerto con mayor conectividad de España y 24 de Europa, según Naciones Unidas. https://www.eldiario.es/canariasahora/economia/palmas-cuarto-puerto-mayor-conectividad-espana-24-europa-naciones-unidas_1_7873362.html.

Castro, N., Carlton, J.T., Costa, A.C., Marques, C.S., Hewitt, C.L., Cacabelos, E., Lopes, E., Gizzi, F., Gestoso, I., Monteiro, J.G., Costa, J.L., Parente, M., Ramalhosa, P., Fofonoff, P., Chainho, P., Haroun, R., Santos, R.S., Herrera, R., Marques, T.A., Canning-Clode, J., 2022. Diversity and patterns of marine non-native species in the archipelagos of Macaronesia. Divers. Distrib. 28 (4), 667–684. https://doi.org/10.1111/ddi.13465.

Colautti, R.I., MacIsaac, H.I., 2004. A neutral terminology to define "invasive" species. Divers. Distrib. 10 (2), 135–141. https://doi.org/10.1111/j.1366-9516.2004.00061.x.

Devin, S., Beisel, J.N., 2007. Biological and ecological characteristics of invasive species: a gammarid study. Biol. Invasions 9 (1), 13–24. https://doi.org/10.1007/s10530-006-9001-0.

El Aamri, F., Idhalla, M., Tamsouri Naoufal, M., 2018. Occurrence of the invasive brown seaweed *Rugulopteryx okamurae* in Morocco occurrence of the invasive brown seaweed *Rugulopteryx okamurae* (E. Y. Dawson) I. K. Hwang, W. J. Lee & H. S. Kim (Dictyotales, Phaeophyta) in Morocco (Mediterranean Sea). In: Mediterranean Fisheries and Aquaculture Research, May.

Faria, J., Prestes, A.C.L., Moreu, I., Cacabelos, E., Martins, G.M., 2022a. Dramatic changes in the structure of shallow-water marine benthic communities following the invasion by *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in Azores (NE Atlantic). Mar. Pollut. Bull. 175. https://doi.org/10.1016/j.marpolbul.2022.113358.

Faria, J., Prestes, A.C.L., Moreu, I., Martins, G.M., Neto, A.I., Cacabelos, E., 2022b. Arrival and proliferation of the invasive seaweed *Rugulopteryx okamurae* in NE Atlantic islands. Bot. Mar. 65 (1), 45–50. https://doi.org/10.1515/bot-2021-0060.

Funk, J.L., 2008. Differences in plasticity between invasive and native plants from a low resource environment. J. Ecol. 96 (6), 1162–1173. https://doi.org/10.1111/j.1365-2745.2008.01435.x.

Gallardo, B., Clavero, M., Sánchez, M.I., Vilà, M., 2016. Global ecological impacts of invasive species in aquatic ecosystems. Global change biology 22 (1), 151–163.

García-Gómez, J.C., Sempere-Valverde, J., Ostalé-Valriberas, E., Martínez, M., Olaya-Ponzone, L., González, A.R., Espinosa, F., Sánchez-Moyano, E., Megina, C., Parada, J. A., 2018. *Rugulopteryx okamurae* (EY Dawson) IK Hwang, WJ Lee & HS Kim (Dictyotales, Ochrophyta), alga exótica "explosiva" en el estrecho de Gibraltar. Observaciones preliminares de su distribución e impacto. Almoraima. Revista de Estudios Campogibraltareños 49, 97–113.

García-Gómez, J.C., Sempere-Valverde, J., González, A.R., Martínez-Chacón, M., Olaya-Ponzone, L., Sánchez-Moyano, E., Ostalé-Valriberas, E., Megina, C., 2020. From exotic to invasive in record time: the extreme impact of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in the strait of Gibraltar. Sci. Total Environ. 704, 0–2. https://doi.org/10.1016/j.scitotenv.2019.135408.

García-Gómez, J.C., Florido, M., Olaya-Ponzone, L., Díaz, Rey, de Rada, J., Donázar-Aramendía, I., Chacón, M., Quintero, J.J., Magariño, S., Megina, C., 2021. Monitoring extreme impacts of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in El Estrecho Natural Park (biosphere reserve). Showing radical changes in the underwater seascape. Front. Ecol. Evol. 9. https://doi.org/10.3389/fevo.2021.639161.

Gestoso, I., Olabarria, C., Troncoso, J.S., 2010. Variability of epifaunal assemblages associated with native and invasive macroalgae. Mar. Freshw. Res. 61 (6), 724–731. https://doi.org/10.1071/MF09251.

Gestoso, I., Olabarria, C., Troncoso, J.S., 2012. Effects of macroalgal identity on epifaunal assemblages: native species versus the invasive species *Sargassum muticum*. Helgol. Mar. Res. 66, 159–166. https://doi.org/10.1007/s10152-011-0257-0.

Guala, I., Flagella, Maria, M., Andreakis, N., Procaccini, G., Kooistra, Wiebe, H.C.F., Buia, Maria, C., 2003. Aliens - algal introductions to European shores. Biogeographia – J. Integrative Biogeogr. 24 (1). https://doi.org/10.21426/b6110143.

Klein, J., Verlaque, M., 2008. The *Caulerpa racemosa* invasion: a critical review. Mar. Pollut. Bull. 56 (2), 205–225. https://doi.org/10.1016/j.marpolbul.2007.09.043.

Kölzsch, A., Blasius, B., 2011. Indications of marine bioinvasion from network theory: an analysis of the global cargo ship network. Eur. Phys. J. B 84, 601–612. https://doi.org/10.1140/epjb/e2011-20228-5.

Li, H., Geng, Y., Shi, H., Wu, C., Yu, Z., Zhang, H., Chen, L., 2023. Biological mechanisms of invasive algae and meta-analysis of ecological impacts on local communities of marine organisms. Ecol. Indic. 146, 109763. https://doi.org/10.1016/j.ecolind.2022.109763.

Lincoln, R.J., 1979. British marine amphipoda: Gammaridea. British Museum (Natural History) 818, 658 pages. doi: LK - https://worldcat.org/title/6367234.

Liu, L., Jia, J., Chu, Q., Zhang, K., Peng, S., 2021. Research status of ship's ballast water detection. IOP Conf. Series: Earth Environ. Sci. 621 (1), 012088. https://doi.org/10.1088/1755-1315/621/1/012088.

Mačic, V., Albano, P.G., Almpanidou, V., Claudet, J., Corrales, X., Essl, F., Evagelopoulos, A., Giovos, I., Jimenez, C., Kark, S., Marković, O., Mazaris, A.D., Ólafsdóttir, G., Panayotova, M., Petović, S., Rabitsch, W., Ramdani, M., Rilov, G., Tricarico, E., Katsanevakis, S., 2018. Biological invasions in conservation planning: a global systematic review. Front. Mar. Sci. 5. https://doi.org/10.3389/fmars.2018.00178.

Manchester, S.J., Bullock, J.M., 2000. The impacts of non-native species on UK biodiversity and the effectiveness of control. J. Appl. Ecol. 37 (5), 845–864. https://doi.org/10.1046/j.1365-2664.2000.00538.x.

Mercado, J.M., Gómez-Jakobsen, F., Korbee, N., Aviles, A., Bonomi-Barufi, J., Muñoz, M., Reul, A., Figueroa, F.L., 2022. Analyzing environmental factors that favor the growth of the invasive brown macroalga *Rugulopteryx okamurae*

(Ochrophyta): the probable role of the nutrient excess. Mar. Pollut. Bull. 174 (December 2021). https://doi.org/10.1016/j.marpolbul.2021.113315.

Metabolites, S., Máximo, P., Ferreira, L.M., Branco, P., Lima, P., Lourenço, A., 2018. Secondary metabolites and biological activity of invasive macroalgae of southern Europe. Mar. Drugs 16 (8), 265. https://doi.org/10.3390/md16080265.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10 (2), 58–62. https://doi.org/10.1016/S0169-5347(00)88977-6.

Navarro-Barranco, C., Muñoz-Gómez, B., Saiz, D., Ros, M., Guerra-García, J.M., Altamirano, M., Ostalé-Valriberas, E., Moreira, J., 2019. Can invasive habitat-forming species play the same role as native ones? The case of the exotic marine macroalga *Rugulopteryx okamurae* in the Strait of Gibraltar. Biol. Invasions 21 (11), 3319–3334. https://doi.org/10.1007/s10530-019-02049-y.

Navarro-Barranco, C., Ros, M., de Figueroa, J.M.T., Guerra-García, J.M., 2020. Marine crustaceans as bioindicators: amphipods as case study. Fisheries Aquacult. 9, 435–463.

Navarro-Barranco, C., Moreira, J., Espinosa, F., Ros, M., Rallis, I., Sempere-Valverde, J., Ostalé-Valriberas, E., Altamirano, M., García-Gómez, J.C., Guerra-García, J.M., 2021. Evaluating the vulnerability of coralligenous epifauna to macroalgal invasions. Aquat. Conserv. Mar. Freshwat. Ecosyst. 31 (9), 2305–2319 doi: 101002/aqc.3633.

Ocaña, O., Afonso-Carrillo, J., Ballesteros, E., 2016. Massive proliferation of a dictyotalean species (Phaeophyceae, Ochrophyta) through the strait of Gibraltar. Revista de La Academia Canaria de Ciencias 28, 165–169.

Ojaveer, H., Galil, B.S., Carlton, J.T., Alleway, H., Goulletquer, P., Lehtiniemi, M., Marchini, A., Miller, W., Occhipinti-Ambrogi, A., Peharda, M., Ruiz, G.M., Williams, S.L., Zaiko, A., 2018. Historical baselines in marine bioinvasions: implications for policy and management. PLoS One 13 (8). https://doi.org/10.1371/journal.pone.0202383.

Omori, M., Taniguchi, K., Shiraishi, K., Seki, T., 2000. Distribution of benthic invertebrates in relation to zonal structure of algal communities in a rocky sublittoral area, Tomari-hama, Oshika Peninsula, Northern Japan. Benthos Res. 55 (2), 69–83. https://doi.org/10.5179/benthos1996.55.2_69.

Pereira, R.C., Perez Da Gama, B.A., 2007. Macroalgal chemical defenses and their roles in structuring tropical marine communities. In: Algal Chemical Ecology. Springer, Berlin, pp. 25–55. https://doi.org/10.1007/978-3-540-74181-7_2.

Perrings, C., Mooney, H., Williamsom, M., 2010. The problem of biological invasions. In: Bioinvasions and Globalization: Ecology, Economics, Management, and Policy. https://doi.org/10.1093/acprof:oso/9780199560158.003.0001.

Petrocelli, A., Cecere, E., 2015. Invasive seaweeds: impacts and management actions. In: Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions, December, pp. 253–275. https://doi.org/10.1515/9783110438666-016.

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U., Vilà, M., 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob. Chang. Biol. 18 (5), 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x.

Ricciardi, A., Atkinson, S.K., 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecol. Lett. 7 (9), 781–784. https://doi.org/10.1111/j.1461-0248.2004.00642.x.

Riera, R., Guerra-garcía, J.M., Brito Castro, M., Núñez Fraga, J., 2003. Estudio de los caprélidos de Lanzarote, Islas Canarias (Crustacea: Amphipoda: Caprellidea). Vieraea: Folia Scientarum Biologicarum Canariensium 31 (31), 157–166.

Ries, L., Sisk, T.D., 2004. A Predictive Model Of Edge Effects, pp. 2917–2926.

Rilov, G., Crooks, J.A., 2009. Ecological Studies, Vol. 204.

Ruitton, S., Blanfuné, A., Boudouresque, C.-F., Guillemain, D., Michotey, V., Roblet, S., Thibaut, D., Thibaut, T., Verlaque, M., 2021. Rapid spread of the invasive Brown alga *Rugulopteryx*. Water 13 (2306).

Sax, D.F., Gaines, S.D., 2003. Species diversity: from global decreases to local increases. Trends Ecol. Evol. 18 (11), 561–566. https://doi.org/10.1016/S0169-5347(03)00224-6.

Schaffelke, B., Hewitt, C.L., 2014. Impacts of introduced seaweeds impacts of introduced seaweeds. June. https://doi.org/10.1515/BOT.2007.044.

Schaffelke, B., Smith, J.E., Hewitt, C.L., 2006. Introduced macroalgae - a growing concern. J. Appl. Phycol. 18 (3–5), 529–541. https://doi.org/10.1007/s10811-006-9074-2.

Seebens, H., Schwartz, N., Schupp, P.J., Blasius, B., 2016. Predicting the spread of marine species introduced by global shipping. Proc. Natl. Acad. Sci. USA 113 (20), 5646–5651. https://doi.org/10.1073/pnas.1524427113.

Sempere-Valverde, J., García-Gómez, J.C., Ostalé-Valriberas, E., Martínez, M., Olaya-Ponzone, L., González, A.R., Sánchez-Moyano, E., Megina, C., Parada, J.A., Espinosa, F., 2019. Expansion of the Exotic Brown Algae Rugulopteryx Okamurae (E. Y Dawson) I.K Hwang W. J. Lee & H.S. Kim in the strait of Gibraltar. January, 17–18. https://www.researchgate.net/publication/330925784.

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M., 2013. Impacts of biological invasions: What's what and the way forward. Trends Ecol. Evol. 28 (1), 58–66. https://doi.org/10.1016/j.tree.2012.07.013.

Tiralongo, F., Hall-Spencer, J.M., Giovos, I., Kleitou, P., 2022. Editorial: biological invasions in the Mediterranean Sea. Front. Mar. Sci. 9 (September), 1–4. https://doi.org/10.3389/fmars.2022.1016168.

Vázquez-Luis, M., Guerra-García, J.M., Sanchez-Jerez, P., Bayle-Sempere, J.T., 2009. Caprellid assemblages (Crustacea: Amphipoda) in shallow waters invaded by Caulerpa racemosa var. cylindracea from southeastern Spain. Helgol. Mar. Res. 63 (2), 107–117. https://doi.org/10.1007/s10152-008-0129-4.

Veiga, P., Rubal, M., Sousa-Pinto, I., 2014. Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species. Mar. Environ. Res. 101 (1), 115–123. https://doi.org/10.1016/j.marenvres.2014.09.007.

Verlaque, M., Steen, F., Clerck, O.De., 2009. Rugulopteryx (Dictyotales, Phaeophyceae), a genus recently introduced to the Mediterranean Rugulopteryx (Dictyotales, Phaeophyceae), a genus recently introduced to the Mediterranean. January 2017. https://doi.org/10.2216/08-103.1.

Whalen, M.A., Aquilino, K.M., Stachowicz, J.J., 2016. Grazer diversity interacts with biogenic habitat heterogeneity to accelerate intertidal algal succession. Ecology 97 (8), 2136–2146. https://doi.org/10.1890/15-1633.1.

Wikström, A.S., Kautsky, L., 2004. Beyond the individual : toward a Nomological network of organizational empowerment beyond the individual : toward a Nomological network of organizational empowerment. Biol. Invasions 6 (June 2004), 141–150. https://doi.org/10.1023/B:BINV.0000022132.00398.14.

Yamase, H., Umetoto, K., Ooi, T., Kusumi, T., 1999. Structures and absolute stereochemistry of five new Secospatanes and a Spatane isolated from the Brown alga Dilophus okamurai Dawson. Chem. Pharm. Bull. 813–818. http://www.mendeley.com/research/geology-volcanic-history-eruptive-style-yakedake-volcano-group-central-japan/.

R packages

Firke, S., 2023. janitor: Simple Tools for Examining and Cleaning Dirty Data. R package version 2.2.0. https://CRAN.R-project.org/package=janitor.

Gohel, D., Skintzos, P., 2023. Flextable: Functions for Tabular Reporting. R package version 0.9.1. https://CRAN.R-project.org/package=flextable.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. *vegan: Community Ecology Package*. R package version 2.6-4. https://CRAN.R-project.org/package=vegan.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wickham, H., Bryan, J., 2022. readxl: Read Excel Files. R package version 1.4.1. https://CRAN.R-project.org/package=readxl.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Software 4 (43), 1686. https://doi.org/10.21105/joss.01686.

Zar, J.H., 1999. Biostatistical analysis. Pearson Education India.