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Short communication

Multiple introduction events expand the range of the invasive brown alga *Rugulopteryx okamurae* to northern Spain

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ABSTRACT

The brown alga *Rugulopteryx okamurae* is one of the most recent and aggressive marine invaders known, with a non-native range that spans from the western Mediterranean to the southern Iberian Peninsula, and the European Macaronesian archipelagos. Here, we provide the first record of its presence at three disjunct areas from northern Spain, supported by morphological and molecular evidence. *Rugulopteryx okamurae* was discovered in the port of Bilbao in the northeastern Atlantic of Spain, more than 1200 km away from the nearest invaded location previously known. It was also found at two separate areas in northwestern Spain: San Amaro, a small inlet at the entrance of the port of A Coruña, and Monteferro-Playa América, a site close to the port of Vigo. In two areas, *R. okamurae* was found to cover up to 100 % of the bottom, suggesting that it may behave as an aggressive invader in northern Spain. Our findings confirm the propensity of *R. okamurae* for long-distance dispersal and reveal that this invader is expanding its range northwards along the European Atlantic coast.

1. Introduction

The number of introduced seaweeds detected in Europe has been steadily increasing since 1970, and currently represents 4–10 % of the macrobenthic flora (van der Loos et al., 2024). Some of these species become invaders if they cause impacts on marine ecosystems or their services. The brown seaweed *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim is one of the most aggressive invaders reported in recent years, causing severe impacts in the Strait of Gibraltar and the Macaronesian archipelagos (García-Gómez et al., 2020; Faria et al., 2022b). Native to eastern Asia, it was first introduced to the Mediterranean in the Thau Lagoon in 2002, without showing any invasive behaviour (Verlaque et al., 2009). However, since 2015, it has become an invasive species on both sides of the Strait of Gibraltar (García-Gómez et al., 2020). Its range is expanding across the Mediterranean coasts of Spain, France and Italy, as well as the Atlantic coasts of southern Spain, Portugal and Morocco, including the Macaronesian archipelagos of the Canary Islands, Madeira, and Azores (Ruitton et al., 2021; Bernal-Ibáñez et al., 2022; Faria et al., 2022a; Bellisimo et al., 2024; Liulea et al., 2023; El Madany et al., 2024) (Fig. 1A). In the Atlantic Iberian Peninsula, *R. okamurae* has so far only been confirmed in southern Spain and Portugal (García-Gómez et al., 2020; Liulea et al., 2023). Projections based on species distribution models suggest that the expansion will persist in Europe, eastward across the Mediterranean and northward along the Atlantic up to Brittany (Sainz-Villegas et al., 2022). This predicted scenario highlights the necessity for continued vigilance with regard to any potential new occurrences.

Rugulopteryx okamurae has significantly impacted most regions

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where it has been recorded, causing drastic ecosystem shifts that include the near-eradication of native benthic species (García-Gómez et al., 2020; Faria et al., 2022b). In addition, its massive growth results in large amounts of drifting biomass, which severely affects human activities (Altamirano et al., 2021). On beaches, these large drifts pose problems for tourism, while in the subtidal, drifting material clogs fishing nets, reducing their efficiency (Altamirano et al., 2021). As a result, *R. okamurae* is included in the Spanish list of invasive species (MITECO, 2020), as well as in the list of invasive alien species of Union concern (European Union, 2022), and should be subject to continuous monitoring and management efforts.

It is virtually impossible to eradicate invasive seaweeds, so early detection in new locations is key to develop plans to prevent and mitigate their impacts. However, detecting *Rugulopteryx okamurae* in Europe early on is challenging because it is morphologically similar to the native *Dictyota dichotoma* (Hudson) J.V. Lamouroux (Verlaque et al., 2015). The only reliable way to distinguish between the two is by examining cross sections of the thallus (Hwang et al., 2009). As a result, *R. okamurae* often goes undetected until the invasion is well advanced and the resulting problems are already apparent.

We have recently identified materials suspected of being the invasive *Rugulopteryx okamurae* in three separate areas of the northern Iberian Peninsula: two in Galicia and one in the Basque Country. This study presents morphological and molecular evidence confirming the assignment to *R. okamurae* and provides an updated distribution of this problematic invasive seaweed.

2. Materials and methods

In total, 88 sites were surveyed in northern Spain between June 2023 and June 2024 as part of several algal studies (Fig. 1B-C, Supplemental Table 1). At these sites, specimens morphologically similar to *Dictyota dichotoma* were collected from intertidal and subtidal habitats down to 10 m depth, as well as drifted specimens.

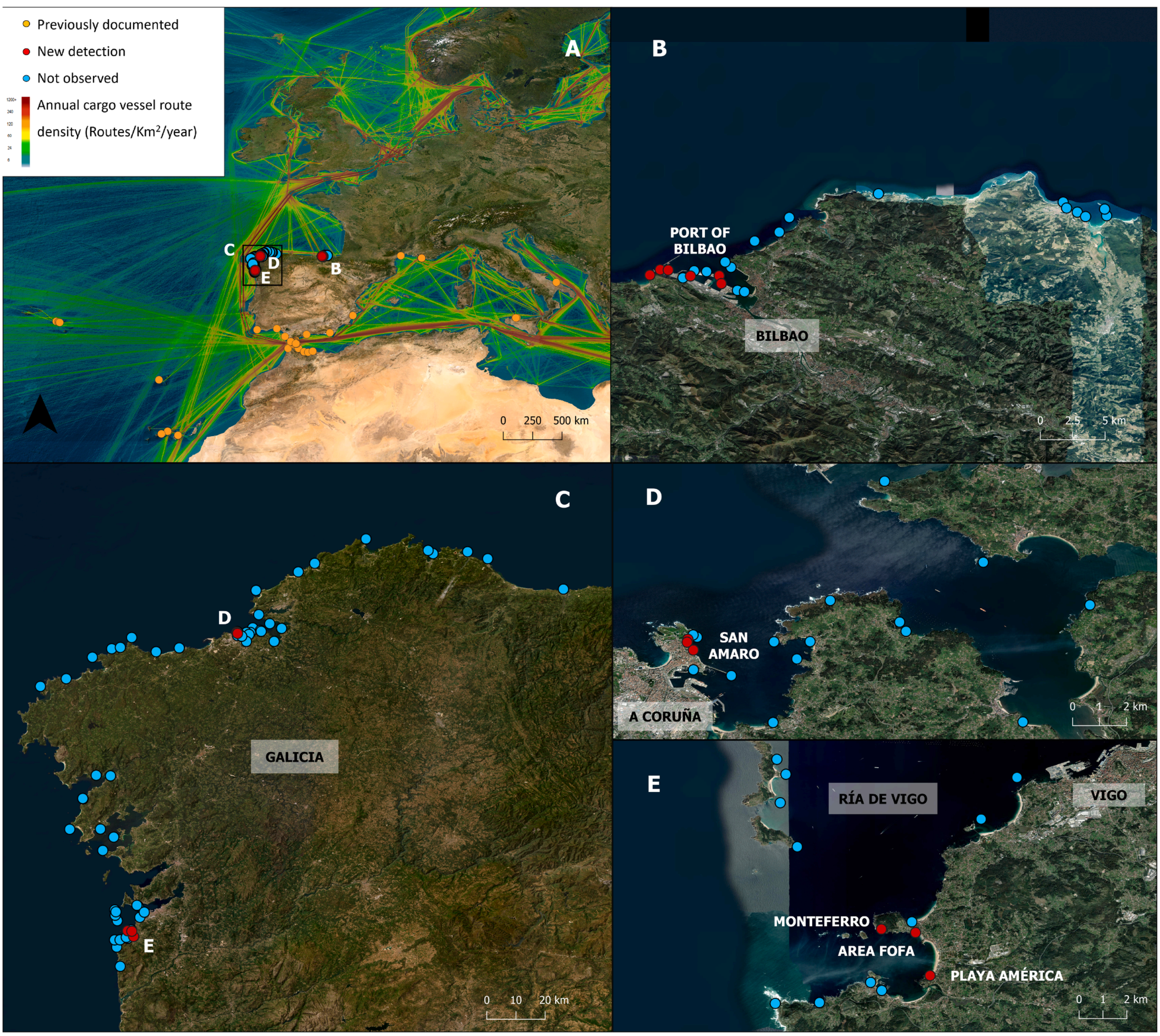

Fig. 1. Distribution of *Rugulopteryx okamurae* in Europe and northern Africa (A), Galicia (B), the Basque Country (C), Rías de A Coruña, Ares, Ferrol (D) and Ría de Vigo (E). Yellow circles show previous records of the species, red ones correspond to the new records, and blue circles indicate explored sites where *R. okamurae* was not observed. In Fig. A it is also represented the Route Density Map at 1 km resolution created by EMSA in 2019 and made available on EMODnet Human Activities, an initiative funded by the EU Commission. (https://monitor.emodnet.eu/resource/22?lang=en).

The identity of the specimens was investigated in fresh, initially by hand-made cross sections of the thallus to check whether the medulla was unicellular or multicellular at the thallus margin, the key character that distinguishes the native *Dictyota dichotoma* from the invasive *Rugulopteryx okamurae*. Specimens identified as *R. okamurae* were preserved in 4 % formalin and/or mounted as herbarium vouchers, which are housed in the herbarium of the University of Santiago de Compostela (SANT). Tissue samples from a selection of seven specimens were preserved (dry in silica gel or wet in ethanol) for molecular analysis. Finally, the vegetative and reproductive characters of *R. okamurae* specimens was studied.

DNA extractions and PCRs were carried out following protocols described in Díaz-Tapia et al. (2023). We selected the *psb*A molecular marker using primers as in Faria et al. (2022a). The PCR products were externally sequenced at the sequencing service of University of A Coruña. The resulting sequences were assembled and aligned with all *R. okamurae* sequences available in GenBank (Supplemental Table 2), and uncorrected p-distances were estimated using Geneious v.7.0.6.

3. Results and discussion

3.1. Morphological observations

The morphological study of the collected specimens unequivocally confirms the presence of *Rugulopteryx okamurae* in three areas of northern Spain (Fig. 1). Specimens identified as *R. okamurae* grew as dense, bushy, spherical clumps ca. 36 cm in diameter (Fig. 2A-C, Supplemental Video), had an erect thallus, up to 15 cm in length, flattened, ribbon-like and dichotomously branched (Fig. 2D), often with abundant vegetative proliferations (Fig. 2E) that were easily detached. Thalli were yellowish-brown and iridescent at the apices when submersed (Fig. 2B); iridescence was absent in drifted specimens. In cross-section, the thallus showed a central medulla composed of unpigmented cells and a layer of pigmented cortical cells (Fig. 2F-H). The medulla at the upper and mid parts of the thallus was composed of a single layer of cells in the center, but it had 2–6 layers of cells at the margins (Fig. 2F-H).

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Sporophytes have been found in northern Spain. Tetrahedrically divided tetrasporangia and asexual monospores were found in mid parts of the thallus (Fig. 2I), subspherical, 100–150 × 140–150 μm, subtended

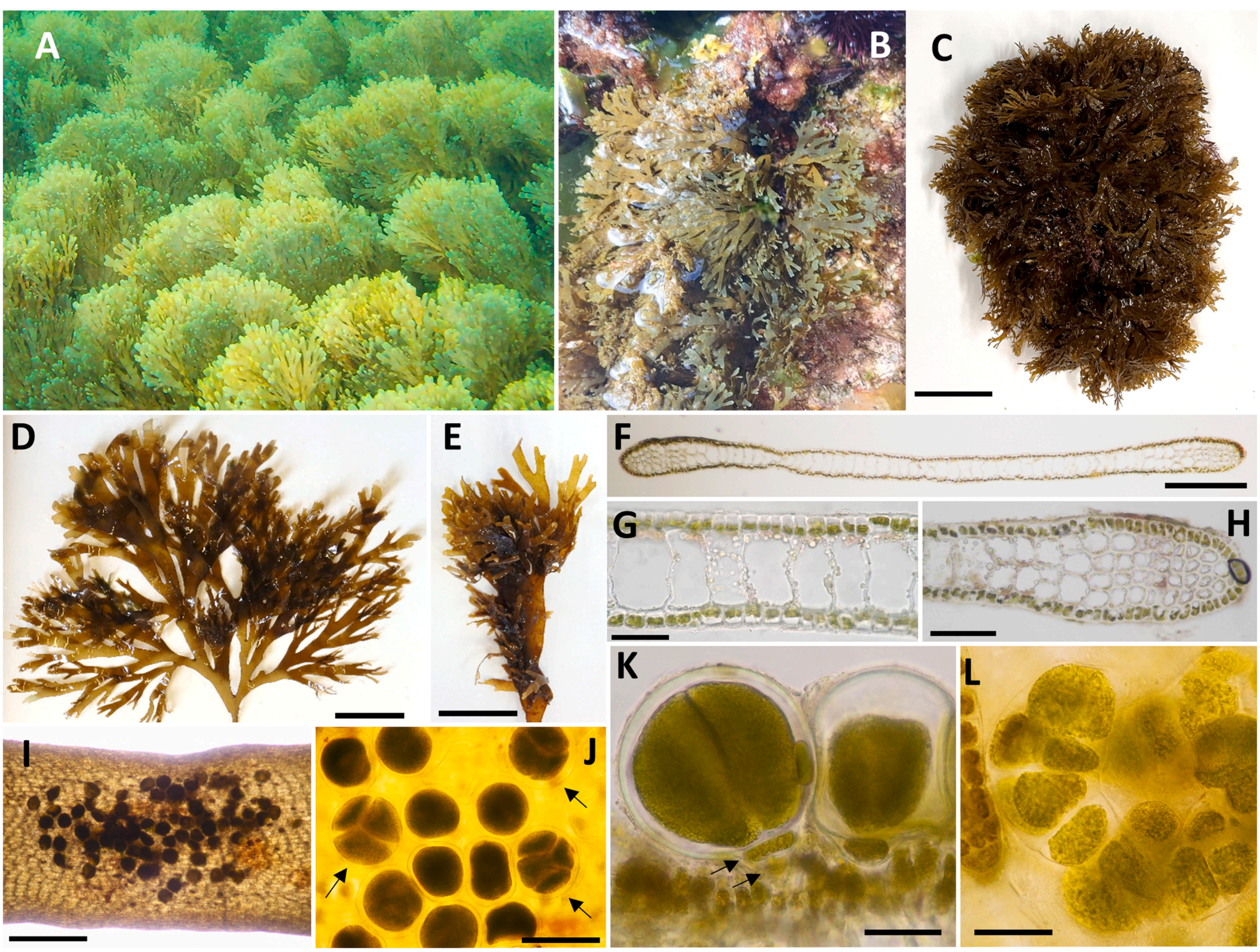

Fig. 2. *Rugulopteryx okamurae* from northern Spain. A, subtidal stand in San Amaro completely covering the rocky substratum. B, specimens in an intertidal rock pool at San Amaro. C, specimen growing as dense bushy spherical clump. D, fragment of a specimen dichotomously branched. E, fragment of a specimen bearing abundant proliferations. F, cross section of thallus showing a unilayered medulla centrally that becomes multi-layered at the margins. G, detail of a cross section of the thallus at the centre. H, detail of a cross section of the thallus at the margin. I, surface view of a thallus with sporangia. J, sporangia in surface view with some of them thetrahedrically divided (arrows). K, cross section of the thallus with sporangia with two subtended basal cells (arrows). L, young thallus germinating on an old specimen. Scale bars: C = 7 cm, D = 2.5 cm, E = 1.5 cm, F = 350 μm, G, K, L = 60 μm, H = 100 μm, I = 650 μm, J = 170 μm.

by two stalk cells (Fig. 2J-K). Spores were often found germinating on the sporophyte (Fig. 2L). They were observed in materials from Bilbao and San Amaro.

The morphological characters observed on our specimens were consistent with previous descriptions of *Rugulopteryx okamurae* in other introduced and native regions (Hwang et al., 2009, Verlaque et al., 2009). Upon inspecting the cross sections of the thalli of the collected specimens it was found that some of them did not correspond to *R. okamurae*, but to *Dictyota dichotoma*. The native *Dictyota dichotoma* has a very similar habit to *R. okamurae,* but the latter can be distinguished by the presence of a unicellular medulla all along the cross sections of the middle and apical parts of the thalli (Verlaque et al., 2009). In addition, *R. okamurae* has distinctive organoleptic characteristics because, unlike *D. dichotoma*, its taste is unpleasant, spicy and bitter. Another species introduced in to the region is *D. cyanoloma* Tronholm, De Clerck, A.Gómez-Garreta & Rull Lluch, which is characterised by a striking iridescence that distinguishes it from *R. okamurae.*

3.2. Molecular identification of Rugulopteryx okamurae

The identity of a selection of seven specimens morphologically identified as *Rugulopteryx okamurae* was further investigated using *psb*A. The alignment of all sequences available in GenBank and the ones newly determined revealed four haplotypes 0.27–0.5 % divergent. A single haplotype was found in the invaded region including northern Spain (this study), Azores, Madeira, and the Mediterranean (Spain, France and Italy). This same haplotype was also found in Japan, the native region. The other three haplotypes belong to specimens from Japan and Korea.

3.3. Distribution of Rugulopteryx okamurae in northern Spain, potential introduction vectors and implications

Our study confirms the presence of *Rugulopteryx okamurae* in three areas of northern Spain: two in Galicia (northwest coast) and one in the Basque Country (northeast coast) (Fig. 1). This is the first report of this invader in northern Spain, demonstrating that the northward expansion of *R. okamurae* continues in southern Europe.

On the Basque coast, *Rugulopteryx okamurae* was found at six sites (Fig. 1C): five within the port of Bilbao and one in a nearby natural coastal stretch that is exposed to strong swells. Within the port, *R. okamurae* was very abundant at two sites, covering 100 % of the riprap blocks from 0 to 10 m depth. At the other sites, isolated specimens were observed attached to rocks at depths of up to 6 m, with scattered patches observed at greater depths. In the natural site, only isolated specimens were recorded growing on rocky reefs. The species was first detected in June 2023 and has been confirmed to be present in 2024 after persisting through the winter. The study sites are part of a long-term monitoring program (Quintano et al., 2023), and this finding further serves to illustrate the value of such a program as a tool for early detection of invasive species. Regrettably, long-term monitoring is well-established in Spain for oceanic waters (https://www.seriestemporales-ieo.net/), but it is rare for coastal areas.

Rugulopteryx okamurae was also observed in two sites within Galicia: San Amaro in the north and Monteferro-Playa América in the south (Fig. 1B-E). San Amaro is a small inlet located near the entrance channel to the port of A Coruña, approximately 1 km from the latter. The site has a sandy beach surrounded by natural rocky reefs to the north and a breakwater to the south, and is exposed to waves. A survey conducted in June 2024 revealed that *R. okamurae* was extremely abundant, covering 80–100 % of the rocky substratum on transects ranging from 50 to 600 m on both the north and south sides of the embayment, at depths from 0 to 10 m (Fig. 2A). Some specimens were also found in intertidal rock pools, albeit at a markedly lower density (Fig. 2B). Additionally, a few drifted specimens were observed on the beach.

The coast between Monteferro and Playa América is a moderately wave-exposed bay within Ría de Vigo (Fig. 1E) where sandy beaches alternate with rocky reefs. In June 2024 isolated specimens of *Rugulopteryx okamurae* were discovered growing on rocky substrate in the low intertidal of Area Fofa and Playa América. Small quantities of drifted specimens were also collected at these two sites and at Monteferro. Additional surveying at sites further north and south did not yield any more specimens of *R. okamurae*. These sites included a marina situated nearly 2 km away from the initial discovery of the invader.

The discovery of stands of *Rugulopteryx okamurae* in different areas in northern Spain, separated by hundreds of km as well as from the closest invaded site in southern Portugal, strongly suggests multiple independent human-mediated introductions. Common introduction vectors for seaweeds are shipping and aquaculture activities (Piñeiro-Corbeira et al., 2020). Determining the introduction vector for marine species is challenging, so they are typically presumed based on exposure to vectors. The three sites where *R. okamurae* was detected in northern Spain are in or near ports with significant maritime traffic (Fig. 1A) related to both fishing and cargo activities, which strongly suggests that shipping is the primary introduction vector. Our findings, along with previous records from the Macaronesian archipelagos, indicate that *R. okamurae* exhibits a high capacity for long-distance dispersal.

Temperature is the primary environmental factor that determines the range of algae and other organisms at the biogeographical scale. The north coast of Spain has cooler waters than other regions invaded by *Rugulopteryx okamurae*, with a winter minimum of 11°C compared to 14°C in the Strait of Gibraltar (Puertos del Estado, 2024). In the native range, the winter minimum is even lower (9.2°C; Mercado et al., 2022), suggesting that temperature may not prevent the invader from expanding further north. This idea is supported by projections from species distribution models (Sainz-Villegas et al., 2022). Given the importance of shipping as a vector for the spread of the species and the high density of maritime traffic between northern Spain, northern France, and southern England (Fig. 1A), it is reasonable to assume that the latter two regions are at high risk of invasion by *R. okamurae*. In addition to human-mediated vectors, winter currents flow north along the Bay of Biscay (Pingree, 1993), which could facilitate the natural spread of the invader, despite the presence of a sandy stretch of ca. 500 km between southern France and Brittany, which interrupts the rocky coastline.

The high density of the local stands in northern Spain suggests that *Rugulopteryx okamurae* may have reached the establishment stage, characterised by the persistence and growth of stands based on internally produced propagules (Sakai et al., 2001). Specimens, collected in June produced abundant tetraspores, monospores and vegetative proliferations, which likely contributed to the rapid establishment of high density, high coverage populations. It remains to be seen whether the species will progress to the next stage, in which will spread to other sites in the region. Nevertheless, the considerable abundance of *R. okamurae* at several invaded sites, together with the observation that it is already producing a substantial number of propagules, suggests that spread is a likely outcome.

The distribution of *Rugulopteryx okamurae* in northern Spain, although probably wider than reported here, still appears limited given that it went unrecorded in the 73 other recently surveyed sites (Fig. 1B-E). This suggests that the spread and colonization of *R. okamurae* in northern Spain are at early stages. Spain has developed a strategy for the control of *R. okamurae,* that includes guidelines for the management, control, and possible eradication of the invader (MITECO, 2022). It is recommended that such a strategy be implemented without delay in the Basque Country and Galicia. The first steps that should be taken include an assessment of the actual distribution of the species, which is beyond the scope of this work, and the implementation of measures to prevent its human-mediated spread. These include management plans for biomass washed up on beaches and caught in fishing nets to ensure that it does not return to the water. Educating fishermen and the general public about this new ecological problem may also help prevent the spread of the invader.

It is uncertain whether *Rugulopteryx okamurae* will have an ecological impact in northern Spain similar to that observed in southern Spain and the Macaronesia (García-Gómez et al., 2020; Faria et al., 2022b). However, preliminary results indicate that algal richness has decreased significantly in one of the invaded sites in the port of Bilbao. There, 12 replicate squares are surveyed annually as part of a monitoring programme (Quintano et al., 2023), and a decline from 40 to 49 species in 2021–2022 to 12–16 species in 2023–2024 has been detected (unpublished results). Prior to the introduction of *Rugulopteryx okamurae*, the macroalgae community that thrived in this site presented a crustose layer of *Lithophyllum incrustans, Mesophyllum expansum* and *Zanardinia typus*, a basal layer of perennial species such as *Ellisolandia elongata* and *Halopteris filicina* partially covered by epiphytes (*Centroceras clavulatum*), and scattered specimens of the canopy species *Sargassum vulgare* and *Gongolaria usneoides*. Once the population of *R. okamurae* was fully developed, the presence of all these species became testimonial. This drastic shift in community composition and reduction in diversity indicates that *R. okamurae* may also be an aggressive invader also in northern Spain. No prior data are available on the diversity and community composition in San Amaro. However, the very high cover of *R. okamurae* at this site suggests that a similar effect is likely.

Degraded or stressed algal assemblages are generally more susceptible to invaders than healthy ones (Caselle et al., 2018). In northern Spain, these systems include kelp forests, Fucales canopies, and *Gelidium corneum* beds, which are being replaced by algal turfs in response to multiple stressors (Barrientos et al., 2024; Muguerza et al., 2024; Piñeiro-Corbeira et al., 2024). It remains to be seen whether the remaining healthy seaweed beds in northern Spain will be resilient to the invasive species, or whether the invasion will be an additional stressor that exacerbates their decline. Further research is needed in this area. It is also possible that degraded seaweed beds could facilitate the spread of *Rugulopteryx okamurae*. Beyond the ecological implications, the eventual spread of this aggressive invader could have significant socio-economic consequences in a region where fisheries and beach tourism are of great economic importance.

CRediT authorship contribution statement

Silvia Iglesias: Writing – review & editing, Resources, Investigation. **María del Carmen López-Rodríguez:** Writing – review & editing, Resources, Investigation. **Nahiara Muguerza:** Writing – review & editing, Resources, Investigation. **Cristina Piñeiro-Corbeira:** Writing – review & editing, Resources, Investigation. **Sara Barrientos:** Writing – review & editing, Resources, Investigation. **María Bustamante:** Writing – review & editing, Resources, Investigation. **Sara Carrasco:** Writing – review & editing, Resources, Investigation. **Javier Cremades:** Writing – review & editing, Resources, Investigation. **Pilar Díaz -Tapia:** Writing – original draft, Visualization, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nerea Alvite:** Writing – review & editing, Visualization, Resources, Investigation, Formal analysis, Data curation. **Rafael Bañón:** Writing – review & editing, Resources, Investigation. **Rodolfo Barreiro:** Writing – review & editing, Investigation, Conceptualization. **Endika Quintano:** Writing – review & editing, Resources, Investigation. **F. Javier Tajadura:** Writing – review & editing, Resources, Investigation. **Isabel Díez:** Writing – review & editing, Resources, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2024.103830.

Data availability

DNA sequences used in this study are available in GenBank.

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