



Review

Rapid invasion and expansion of the invasive macroalgae *Rugulopteryx okamurae* in the Mediterranean and Atlantic: A 10-year review

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ABSTRACT

This review seeks to establish a baseline on the current knowledge and gaps in the scientific literature on the invasive macroalgae *Rugulopteryx okamurae*. Through a systematic literature analysis we summarize the insights regarding distribution and potential impacts as non-indigenous species associated with its expansion from the Strait of Gibraltar since first detected by 2015. After 10 years, this invasive alien macroalgae has broadly expanded across the Mediterranean Sea (France, Spain, Morocco and Italy) and the Atlantic coasts (Morocco, Spain, Portugal, Madeira, Azores and Canary Islands). The developed research mainly shows early new detections of *R. okamurae*, the negative effects including both economic and ecological impacts on native biota, monitoring efforts, as well as potential applications of the biomass generated. Most of the research is mainly focused on the Strait of Gibraltar adjacent waters, making other vulnerable regions impacted unknown. These findings demonstrate *R. okamurae* highly invasive behavior, the need of more research regarding its spatial monitoring, impacts and potential uses, as well the complexity of cross-border coastal management. The potential invasion of broader areas in both Mediterranean and Atlantic coasts from the European and African continent requires international efforts to monitor and mitigate its ecological and economic impact, developing both scientific applications stretching efforts with specialized private companies and adapting public policies. The gaps identified in the current knowledge of *R. okamurae* as an invasive alien species reveal as a priority the development and implementation of an international monitoring program, integrating public participation to identify early-warnings, that could be used to quantify impacts transferable to public policies and cross-border coastal management between both continents, filling the identified management gaps opening management opportunities in the industrial sector.

1. Introduction

The introduction of Non-Indigenous Species (NIS) is today considered as one of the major threats to global marine biodiversity (Zenetos et al., 2022a), representing macroalgae more than 40 % of the NIS in Europe (Schaffelke et al., 2006; Williams and Smith, 2007). The frequency in which NIS are introduced into new marine ecosystems has achieved an unprecedented level and will continue to increase in the coming years (Tsirintanis et al., 2022). By establishing new ecological contexts, invasive alien species can radically change the structure and

functioning of the marine environment, with considerable negative impacts on the ecosystem services (Tsirintanis et al., 2022; Castro et al., 2024). With a semi-enclosed configuration influenced by oceanic, physical and atmospheric processes, the Mediterranean Sea is marked by well-defined mosaics of contrasting ecosystems, an ideal living laboratory to study anthropogenic impacts in marine ecosystems (Aurelle et al., 2022). The Mediterranean Sea is the world's most affected region by biological invasions, already facing more than 1000 introduced species (Zenetos et al., 2022b), among which macroalgae are the more represented and with the highest invasive behavior (Zenetos et al.,

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2022b; Muguerza et al., 2022).

Among all the NIS introduced in the Mediterranean, *Rugulopteryx okamurae* (E.Y.Dawson) (Hwang et al., 2009) has shown a highly invasive behavior against native sessile organisms, showing an extraordinary expansion capacity in speed, density and distance (García-Gómez et al., 2020). This macroalgae is native from the temperate Northwest Pacific Ocean (Hwang et al., 2009), and it was first recorded as alien species in the Mediterranean Thau lagoon (France) but without an invasive behavior, probably introduced through oyster *Crassostrea gigas* farming (Verlaque et al., 2009). However, its behavior once introduced in the Strait of Gibraltar was completely different, showing a fast spread helped by the strong currents with high density and rocky bottom coverage ending in a huge floating and beached biomass (Altamirano et al., 2016; García-Gómez et al., 2018; Roca et al., 2022). Since first detected, in the last 10 years (2015–2024) this alga showed an extensive and impactful expansion from the Strait of Gibraltar to Sicily, in the Mediterranean Sea, with spots on the coast of Alicante, Spain and to the Azores islands in the Atlantic Ocean (García-Gómez et al., 2018; Bernal Ibáñez et al., 2022; CADRECTE, 2023; Bellisimo et al., 2024; El Madany et al., 2024). While attached in the rocky bottoms of the subtidal euphotic zone up to 45 m of depth, this macroalgae shows the highest coverage (80–90 %) between 10 and 20 m of depth (García-Gómez et al., 2018; Florido et al., 2023). Recently, drifted thalli were observed on the circalittoral and bathyal bottoms of the Alboran Sea, between 50 and 450 m depth (Rueda et al., 2023). The highly invasive potential of *R. okamurae* is enhanced by its prolific vegetative reproduction, dispersal pathway and high survival in unfavorable environmental conditions (Altamirano et al., 2019; Mateo-Ramírez et al., 2023).

The invasion of *R. okamurae* is leading to many ecological, namely a reduction in native biodiversity in the intertidal and subtidal zone (Sempere-Valverde et al., 2021; Faria et al., 2022a; Florido et al., 2023; Liulea et al., 2023), and economic impacts in the Straits of Gibraltar, the

Mediterranean Sea and the Atlantic Ocean (Mogollón et al., 2024). This macroalgae caused significant ecological impacts, both on fisheries and tourism, although the economic impacts have not been well studied yet (García-Gómez et al., 2018; Altamirano et al., 2019; Báez et al., 2023; Mogollón et al., 2024). The rapid expansion and massive potential occupation showed by probabilistic modelling highlights the *R. okamurae* as one of the most dangerous and threatening NIS macroalgae in Mediterranean waters (García-Gómez et al., 2020, 2021). Despite the increasing interest in the invasion of this species in the Mediterranean, studies on the ecology, distribution and impacts of *R. okamurae* in affected and potentially affected areas are urgently needed to accordingly implement management measures, as the current knowledge is still in its early stage. These impacts emphasize the relevance of prevention, rapid action measure and early detection to mitigate the impacts of the spread of this species in the Mediterranean.

To detect knowledge gaps and needs in the study of this invasion, we conducted a systematic literature review including habitat preferences, associated biota and environmental tolerances, as well as its dispersal strategies, monitoring efforts, and potential applications. Hence, this review presents an overview of the drivers behind the proliferation of *R. okamurae* and the ecological and economic implications associated with the invasion, including the valorization methods available, as well as possible management strategies and eradication techniques to inform discussions on the projected expansion in the Mediterranean basin and the Atlantic Ocean.

2. Material and methods

This review was conducted using a systematic literature review to identify all empirical research on the occurrence, impact, monitoring techniques and applications of *R. okamurae* between 2015 and 2024. This review was performed following the Preferred Reporting Items for

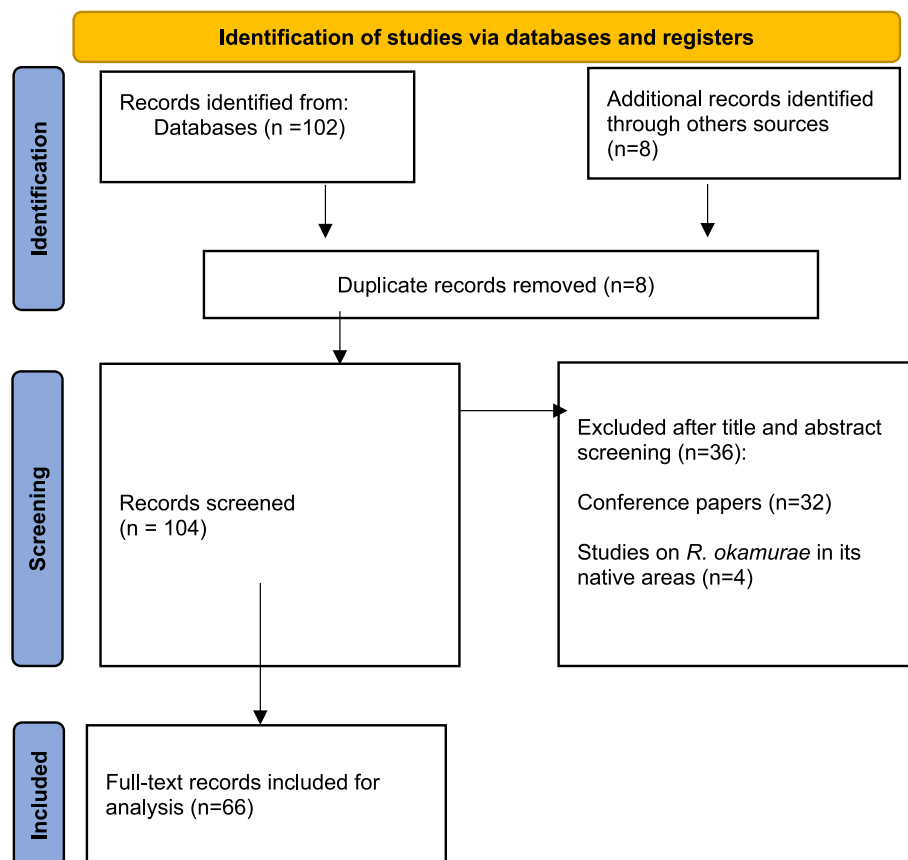


Fig. 1. Search flow for full-text articles included in this review (based on PRISMA flow - Moher et al., 2009).

Systematic Reviews and Meta-Analyses (PRISMA) (Moher et al., 2009) (Fig. 1). Scopus and Google Scholar were used to search the terms “*Rugulopteryx okamuræ*”, “invasion” and “monitoring” within the different Mediterranean and Atlantic countries. All papers were assessed on the basis of title, keywords and abstract, and papers appearing to contain data on the biology, ecology, reproduction, monitoring, ecological and economic impacts and possible valorization methods of *R. okamuræ* were reviewed. Only articles reporting the presence of *R. okamuræ* outside its native distribution were included in this review. According to these criteria, papers dealing exclusively with the presence of *R. okamuræ* in their native distribution were excluded.

After the full text review, a content analysis was conducted by collecting and extracting data from each of the included publication. In particular, the data concern: dates, locations, depths, frequency, monitoring method, environmental parameters, recorded impacts and possible valorization methods. The scientific literature review was analyzed to address seven research questions covering aspects related to the invasion of *R. okamuræ* in the Strait of Gibraltar, the Mediterranean Sea and the Atlantic Ocean: 1) What is the spatial coverage of *R. okamuræ* research? 2) What was the temporal trend of studies? 3) What are the habitat preferences of *R. okamuræ*? 4) What factors favor the invasion of *R. okamuræ*? 5) What was the economic and ecological impact of *R. okamuræ*? 6) What are the methods for valorizing the biomass of this algae? 7) What are the gaps in research about *R. okamuræ*?

3. Results and discussion

3.1. Publication trend

The number of studies concerning *R. okamuræ* has increased rapidly in recent years; from the 66 papers published between 2015 and 2024, there is a notable peak in 2023 (Fig. 2A). *R. okamuræ* was first observed in the Strait of Gibraltar in 2015 under the name *Dictyota* due to its similarity (Ocaña et al., 2016) and was formally identified and recorded as *R. okamuræ* in 2016 by Altamirano et al. (2016). Despite the peak in published papers in the last ten years, there is still many knowledge gaps about the *R. okamuræ* invasion. Research has been conducted mainly in countries adjacent to the Strait of Gibraltar, where it was first detected, due to the undergoing significant impacts in those shorelines. As indicated in Table 1, most of the studies were carried out in Spain, followed by Morocco, Portugal, France and Italy. Since its first record in the Strait of Gibraltar, this alga has been expanding both towards the Mediterranean Sea and the Atlantic Ocean (Fig. 3), being reported in southern, eastern and, also recently, northern Spain (Altamirano et al., 2016; Terradas-Fernández et al., 2023; Diaz-Tapia et al., 2024), Morocco (El Aamri et al., 2018), France (Ruitton et al., 2021), and southern Portugal (Faria et al., 2022a; Liulea et al., 2023). Additionally, this invasive

species has even extended to several islands in Macaronesia, such as the Azores (Faria et al., 2022a, 2022b), the Canary Islands (Fernández-Herrera, 2023) and Madeira Island (Bernal Ibáñez et al., 2022). Studies have recently reported a new record of the invasive species *R. okamuræ* in the eastern Mediterranean. A total of three records of this species were recorded in Italian waters, the Ionian Sea (Marletta et al., 2024), the Tyrrhenian Sea (Bellissimo et al., 2024) and the Adriatic Sea (Tursi et al., 2023), indicating a continuing process of expansion of this alga in the central Mediterranean. Although the algae was recorded in the central Mediterranean (Italy) (Marletta et al., 2024), data on its presence in the adjacent water to the strait of Gibraltar is considerably lacking, particularly from Algeria, Tunisia and Libya (Fig. 3).

From the 66 examined documents, 50 % dealt with biomass valorization, followed by monitoring (spatial distribution) and impacts of *R. okamuræ* (45.56 %) (Fig. 2B). 10 publications specified the abundance and coverage of this algae, while the other studies only reported the presence of the species. Regarding valorization studies, the most discussed application with a 70.5 % was the use of composting as a source of biomolecules, followed by the generation of bioplastics and biogas (25.50 %), as well as fertilizers (3.98 %). However, few studies addressed the economic and ecological impact of *R. okamuræ*. Studies focused on the role of the environmental variables affecting the algal bloom are very limited, only representing a 4.54 % of the published studies.

3.2. Life cycle

The plant body of *R. okamuræ* is dichotomously to anisotomously, branched, flattened with obtuse apices showing a distinctly apical cell, and rhizoids in the basal parts (Terradas-Fernández et al., 2023; Bellissimo et al., 2024). Thallus fixed to the substrate by several hyaline, multicellular rhizoids, with stolon like segments on which novel fronds grow. The thallus is membranous, erect, with 3–20 cm in diameter, composed of flattened, straplike fronds. Thalli were yellowish-brown in colour, iridescent at the apices when submersed, which was absent in drifted specimens (Bellissimo et al., 2024). In cross section, the thallus demonstrated a central medulla formed by unpigmented cells and a layer of pigmented cortical cells. The medulla at 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, which is the key character for morphological identification of *R. okamuræ* (Diaz-Tapia et al., 2024). The morphological and anatomical characteristics of the specimens cited above are generally in line with the descriptions reported in their native regions (Hwang et al., 2009).

The life cycle of *R. okamuræ* is an isomorphic digenetic cycle, with two morphologically equal but physiologically independent phases: gametophytic and sporophytic phases (Altamirano et al., 2019). This macroalgae displays all three types of reproduction in both native and

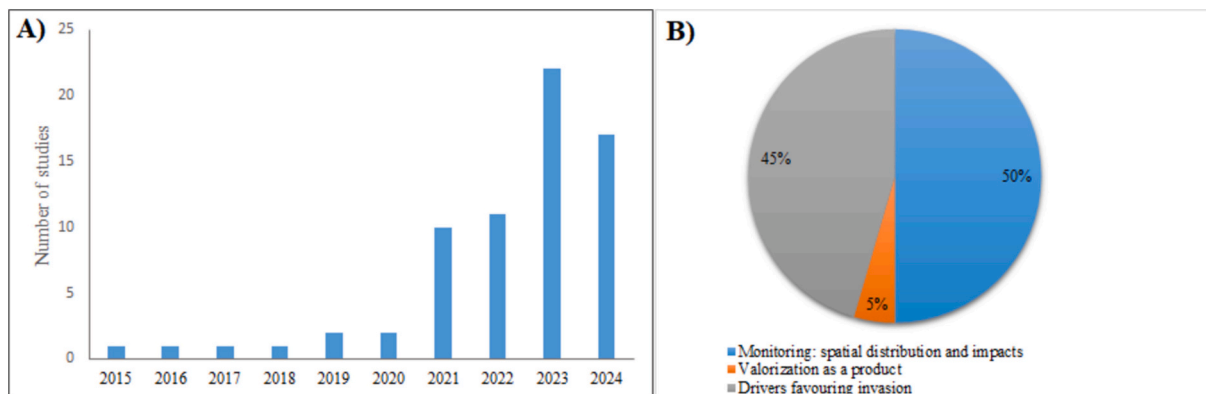


Fig. 2. Number of scientific publications on *R. okamuræ* since 2015 (A) and topics addressed by the studies (B).

Table 1

Studies reporting the presence of *R. okamurai* in the Mediterranean Sea and the Atlantic Ocean.

Country	Regions	Date	Coverage	Depth	References
Spain	Jbel Moussa, Ceuta, Andalusia	2018–2019	80–90 %	0–40 m	García-Gómez et al. (2020)
Spain	Alboran sea	2017–2020	100 %	0–10 m	García-Gómez et al. (2021)
Spain	Tarifa	2021	–	0–5 m	Roca et al. (2022)
Spain	Tarifa	2022	–	–	Haro et al. (2024)
Spain	Granada	2021	–	30–48 m	Estévez et al. (2022)
Spain	Gulf of Cádiz	2019–2021	65–90 %	258–823 m ^a	Mateo-Ramírez et al. (2023)
Spain	Alboran Sea	2021	3.8–65 %	50–450 m ^a	Rueda et al. (2023)
Spain	Alicante	2023	–	6.5–15.8 m	Terradas-Fernández et al. (2023)
Spain	Bilbao and Galicia	2023	80–100 %	0–10 m	Díaz-Tapia et al. (2024)
Portugal	Azores	2019	97 %	5 m	Faria et al. (2022a)
Portugal	Madeira	2021	–	–	Bernal Ibáñez et al. (2022)
Portugal	Algarve	2020–2021	–	–	Liulea et al. (2023)
Morocco	Ksar Sghir, Md'iq, Oued Laou, Jebha, Cal Iris	2019–2021	–	10–20 m	El Madany et al. (2024)
Morocco	Tangier, Asillah	2019–2021	–	10–20 m	El Madany et al. (2024)
Morocco	Tangier, Belyounech, M'diq	2017	–	–	El Aamri et al. (2018)
Morocco	Jbel Moussa	2015–2019	10.39 %	20 m	Sempere-Valverde et al. (2021)
France	Thau ^b	2002	–	–	Verlaque et al. (2009)
France	Marseille	2018–2019	69–85 %	3–15 m	Ruitton et al. (2021)
Italy	Gulf of Palermo	2023	60 %	2–4 m	Bellisimo et al. (2024)
Italy	Gulf of Palermo	2024	–	3–30 m	Marletta et al. (2024)
Italy	Bari	2023	–	–	Tursi et al. (2023)

^a Floating thalli.

^b With no invasive behavior.

introduced areas: vegetative (propagules), asexual (monospores) and sexual. This burn alga is generally present all year-round as a sporophyte in invaded areas, and it establishes and maintains novel populations by fragmentation, asexual monospores and/or vegetative propagules. The asexual and vegetative strategies of the established populations

(propagules and monospores) have led to the massive proliferation of *R. okamurai* in the Strait of Gibraltar and the adjacent waters (Altamirano et al., 2019). From each propagule of *R. okamurai*, a new clonal individual can be produced. One square centimeter of thallus generates more than 25 vegetative propagules and more than 100 asexual monospores (Altamirano et al., 2019). Recently, female gametophytes were found for the first time in introduced areas (Bilbao, Spain) by Díaz-Tapia et al. (2024). Oogonia were found in sori in middle to upper parts of the thallus, with subspherical oogonia. However, these results suggest that *R. okamurai* can reproduce sexually in invaded regions. The importance of sexual reproduction on the persistence and growth of *R. okamurai* populations in the Mediterranean and Atlantic is not well understood. Hwang et al. (2009) emphasized that it is only sporophytes that found in native regions, since they appear to fail to undergo meiosis to produce gametophytes. In its indigenous range, this macroalgae reproduces throughout the year. Maximum reproductive development and growth occur above 15 °C, whereas the thallus is limited to a basal system of perennial rhizoids in winter (Hwang et al., 2009).

3.3. Habitat preferences

In its native environment, *R. okamurai* is present on rocky bottoms between the lower eulittoral and infralittoral zones, with shallow populations between 0 and 7 m depth, reaching depths of 15 m and 35 m (Hwang et al., 2009). In its native habitats, the maximal density recorded in the literature is ca. 50 g FW m⁻² and the highest coverage percentage is less than 5 % (Jung and Choi, 2020; Jung et al., 2020). In introduced areas, *R. okamurai* was observed at depths from 0 to 40 m, but the most frequent depth range was 10–20 m (García-Gómez et al., 2020; Sempere-Valverde et al., 2021). This species was found growing both in well-lit environments, on rocks exposed to light (sandstone and limestone bottoms), and in more shaded regions. It also grows epiphytically on coralligenous organisms, cold-water corals and *Posidonia oceanica* (Terradas-Fernández et al., 2023; Bellisimo et al., 2024). It has been demonstrated that *R. okamurai* shows strong preference for artificial substrates. The species was common on tires, ceramics and discarded fishing material including nets and ropes (García-Gómez et al., 2021). However, they were also found on a wide variety of substrates, including cement and concrete, breakwater boulders close to sandy bottoms, glass bottles, plastics and metal surfaces (García-Gómez et al., 2021). These anthropogenic structures can provide ecological functions similar to those of the natural habitat, notably by providing habitat for *R. okamurai*. The range of temperature where this invasive species was observed is from 11 to 23 °C.

Although *R. okamurai* is not an abundant species in communities on the native grounds, it shares habitat with species such as *Ulva pertusa*, *Chondria crassicaulis*, *Corallina* spp., the algae Melobesioidean, *Gelidium divaricatum*, *Ralfsia verrucosa*, *Sargassum thunbergii*, *Chondracanthus intermedia*, *Cladophora sakaii*, *Codium adhaerens*, *Dictyota dichotoma*, *Pterocladia capillacea* and *Acrosorium yendoii* (Choi et al., 2010). Among invertebrates, different species have been found to be associated with *R. okamurai* in their native range, including gastropods, bivalves, chitons, annelids, abalone and sea urchins. In the settled populations of *R. okamurai* after being introduced in the Strait of Gibraltar and adjacent waters, *R. okamurai* induces a decrease in species richness of the community, composed by few species, mainly other invasive macroalgae such as *Asparagopsis armata*, *Asparagopsis taxiformis* and *Caulerpa cylindracea*. García-Gómez et al. (2021) observed the interaction of *R. okamurai* with 43 resident macroalgae species at generally illuminated rocky habitats of the northern Strait of Gibraltar shores. The faunal assemblage associated with *R. okamurai* was studied in the Strait of Gibraltar, resulting in a total of 96 different taxa of invertebrates (Navarro-Barranco et al., 2019), mainly belonging to the phyla Arthropoda, Annelida (polychaetes), Mollusca and Echinodermata (Navarro-Barranco et al., 2019) and in several common coastal fishes (García-

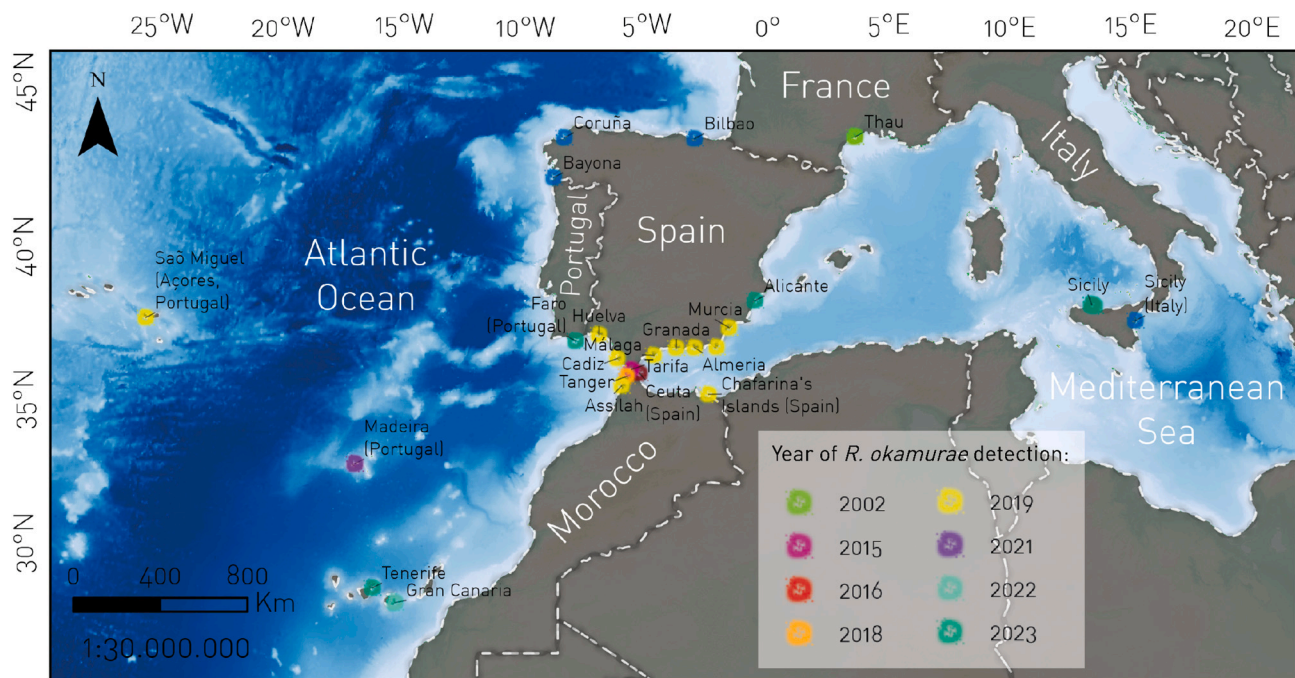


Fig. 3. Current spatial distribution of *R. okamurae* in the Mediterranean Sea and Atlantic Ocean according to first detection reports in scientific studies across time. Please note that the only non-invasive behavior of *R. okamurae* was recorded in Thau (France) in 2002, the other locations report an invasive behavior.

Gómez et al., 2018). Other animals observed in introduced populations of *R. okamurae* in the Strait of Gibraltar include octopus (*Octopus vulgaris*), cuttlefish (*Sepia officinalis*), crustaceans and vagile echinoderms (*Galathea strigosa*, *Palaemon* sp., *Periclimenes* sp. or *Sphaerechinus granularis*), as well as some scorpion fish (*Scorpaena scrofa*), blennids (*Tripterygion tripteronotum*, *Parablennius gattorugine* and *P. rouxi*), conger eels (*Conger conger*), moray eels (*Muraena helena*) and labrids (*Labrus bergylta*, *Symphodus roissali*, *Coris julis*), without the presence of exotic species seeming to affect them (García-Gómez et al., 2018). Additionally, this species hosts a various epifaunal community than native ecosystem (Navarro-Barranco et al., 2021). While herbivores represent one of the predominant trophic groups in *R. okamurae*, this is due to the high density of species from the genera *Tricolia*, *Rissoella* and *Cymodoc*. The paucity of herbivorous species may be linked to the high production of secondary metabolites by *R. okamurae*, acting as allelochemical deterrents against sessile epiphytes and herbivorous species (Casal-Porras et al., 2021). These compounds were found to inhibit the settlement of some predators and to possess foraging deterrent against them, thus indicating that natural products *R. okamurae* could play a chemical defense role (Casal-Porras et al., 2021).

3.4. Factors contributing to the success of the *R. okamurae* invasion

The high invasive capacity of *R. okamurae* in the invaded regions is probably due to its high capacity of vegetative reproduction and survival in unfavorable environmental conditions (Rosas-Guerrero et al., 2018; Altamirano et al., 2019). These unattached thalli can ultimately accumulate on rocks or other hard substrates (artificial or natural) and then begin a new invasion far from their original site. One square centimeter of thallus generates more than 25 vegetative propagules and more than 100 asexual monospores (Altamirano et al., 2019). A propagule is a multicellular structure that spontaneously detaches from the parental thallus and produces a new individual. The huge productivity of *R. okamurae* in coastal areas represents a significant source of drifted thalli towards the coast, the adjacent coastal regions and the deep sea areas. The possibilities of *R. okamurae* spreading out to other areas of the Mediterranean via deep detached thalli are potentially high and a raise

concern. Rueda et al. (2023) already reported the presence of the drifted thalli in the deep waters of Alboran, the zone with maximum values of density and biomass is dominated by intense surface currents associated with the Alboran Sea gyral circulation system. Bellisimo et al. (2024) showed that most of the western Mediterranean (the Balearic archipelago, Sardinia and Corsica), the central Mediterranean (the north coast of Africa and Sicily) as well as the eastern Mediterranean basin, are highly favorable to the invasion by *R. okamurae*.

While rising temperatures is one of the environmental drivers favoring the growth and competitiveness of macroalgal invaders (Mannino et al., 2017; Li et al., 2023), *R. okamurae* have a wide temperature tolerance and it has an exceptionally high temperature tolerance in its gametophyte form (Mercado et al., 2022). Studies suggest that temperature and nutrients are factors that can influence on growth and photosynthesis of *R. okamurae* (Mercado et al., 2022). Moreover, it has been reported that low temperatures reduce growth and photosynthetic activity, or that opposing nutrient conditions resulting in antagonistic responses in thallus growth. Annual population monitoring suggests that high temperatures favor the reproduction and vegetative proliferation of this invasive macroalgae in the Strait of Gibraltar, with a higher presence of fertile individuals, as well as propagules and monospores during the summer period (Salido and Altamirano, 2021). Comparisons between the native habitats of *R. okamurae* and the Strait of Gibraltar suggest that mean and maximum temperatures in two regions are similar, but that the temperature winter minimum is higher in the Strait (14.0 °C vs. 9.2 °C; Jung et al., 2020). The warmer winters suggest that the active growth annual period of this species could be longer in the introduced area than in its native habitat. In its native regions, accumulated precipitation and lower temperatures during the winter probably limit the growth of *R. okamurae* (Hwang et al., 2009). As in its native regions, high abundances of *R. okamurae* along invaded regions were observed during the summer seasons, coinciding with the hot and dry periods (García-Gómez et al., 2020; Haro et al., 2024). Marletta et al. (2024) found larger specimens in May than those collected in March. This could be due to the difference in water temperature, which was 17 °C in May and 14 °C in March. However, maintained temperature peaks in summer may be a crucial factor for its blooming, where climate

change is a key factor inducing its proliferation and success in invaded areas (García-Gómez et al., 2020; Mercado et al., 2022).

Furthermore, *R. okamurai* displays a high adaptation capacity to a wide range of environmental factors such as nutrients and light, that makes it colonizing a large bathymetric and community range (Salido and Altamirano, 2021). High rates of nitrogen incorporation (Mercado et al., 2022), as well as photosynthesis capacity with increasing nutrients in seawater (Merchán et al., 2020), could also explain the massive proliferation of this invasive species in the Strait and the Mediterranean waters. It is also highly tolerant of high salinity levels, which raises concerns about its penetration of hypersaline coastal lagoons (Mercado et al., 2022). Rosas-Guerrero et al. (2020) highlighted the importance of the synergistic effect of temperature and nutrients on the seasonality of the *R. okamurai* population. It seems that the success of the invasion of this species is also linked to its ability to tolerate unfavorable conditions. In laboratory experiments, Mateo-Ramírez et al. (2023) reported that unattached specimens collected in deep waters were alive and healthy, and retained intact photosynthetic capacity after long periods of darkness, indicating considerable resilience and invasive potential for this macroalgae. Additionally, this invasive alga contains a chemical weapon (dilkamural), helping to explain the great expansion of *R. okamurai* in the Mediterranean and the Atlantic (Casal-Porras et al., 2021). In the laboratory, the generalist herbivore *Paracentrotus lividus* exhibited lower consumption on the *R. okamurai* than on the native seaweed *Ulva* sp. This low consumption was attributed to the presence of dilkamural in *R. okamurai*, which exhibited not only deterrent characteristics but also produced detrimental and even lethal effects on the sea urchins (Casal-Porras et al., 2021). However, another study by Hachero-Cruzado et al. (2024) showed that sea urchins accepted *R. okamurai* as food under laboratory conditions, enhancing their consumption after a long exposure period.

This alga has once again demonstrated its capacity to spread long distances across open sea to reach remote islands, in this case the island of Sicily in Italy (Bellisimo et al., 2024; Marletta et al., 2024). Similarly, the species succeeded in crossing large distances and reaching the Macaronesian islands: the Azores (Faria et al., 2022a), Madeira (Bernal Ibáñez et al., 2022) and the Canary Islands (Fernández-Herrera, 2023). There are several main explanations for the rapid expansion of *R. okamurai* in the Mediterranean and Atlantic. Common introduction pathways for *R. okamurai* are shipping. This brown macroalga probably arrived in the Strait of Gibraltar via the ballast water of large Asian ships that moored in TangierMed ports or in Algeciras Bay (García-Gómez et al., 2020). Interestingly, the three locations where *R. okamurai* was recorded in northern Spain are situated in or near ports with high maritime traffic, which clearly supports shipping as the main introduction vector (Díaz-Tapia et al., 2024). In Palermo (Italy), *R. okamurai* was first reported near an important port, which is the final destination of fishing activities conducted in other areas of the Mediterranean invaded by *R. okamurai* (Bellisimo et al., 2024). Given the importance of the Strait of Gibraltar as a shipping route between the Atlantic and the Mediterranean, it seems reasonable to consider shipping as a vector for the introduction of *R. okamurai* into the Mediterranean and the Atlantic. Another possible route of arrival could be associated with the arrival of the thalli of this macroalgae via anthropogenic pathways, such as professional and recreational fishing and commercial transport (Bellisimo et al., 2024). *R. okamurai* thallus can remain entangled in trawls or hooked into trammel or longlines nets, which commonly clog the nets. This is probably the pathway by which *R. okamurai* arrived in several regions of the Mediterranean. The propagation of this alga by hydrodynamic processes has also been reported by García-Lafuente et al. (2023). These authors observed that the vertical velocity field in the Strait of Gibraltar, which exceeds the small sedimentation velocity of *R. okamurai*, permit their vertical displacements throughout the water column. Recently, Mateo-Ramírez et al. (2023) reported for the first time large quantities of detached *R. okamurai* thalli on deep-sea bottoms of the Gulf of Cadiz. Outflow from the Mediterranean appears to be the

main vector for the spread of these unattached thalli into the bathyal zones of the Gulf of Cadiz basin (Atlantic) (Mateo-Ramírez et al., 2023). The surface circulation associated with the Atlantic jet penetrating the Alboran Sea could favor the rapid expansion of this invasive alga to other regions in the Mediterranean. The variety of artificial substrates colonized by *R. okamurai* attracted attention to the potential capacity of this alga to take advantage of habitat degradation, which rises the likelihood of its successful establishment (García-Gómez et al., 2021; Florido et al., 2023). These structures enhance the total area for recruitment surface of *R. okamurai* (García-Gómez et al., 2021). The heavy colonization of artificial structures and litter can facilitate the spread of this macroalgae over natural rocky substrates. The role of marine litter in the introduction of invasive species has recently received more attention (Mghili et al., 2023), but their role in the ecology and invasion of *R. okamurai* remains unclear.

3.5. Ecological and economic impacts

The impacts of the invasion of *R. okamurai* are varied and include social, economic and ecological impacts (Fig. 4). However, there are much fewer works to determine specific impacts of *R. okamurai* on native communities. Once established on the rocky substrates, these algae appears to be much more efficient in competing for the resources and space than most native species (García-Gómez et al., 2018, 2020). The resident benthic community has undergone damage parallel to the expansion of *R. okamurai*. After its first record in Jbel Moussa (Morocco) in 2017, this macroalgae became the most common species in just one year (Sempere-Valverde et al., 2021), followed by the significant change in the coralligenous community structure and a decline of the bio-indicator species *Mesophyllum expansum* (Philippi) Cabioch & M.L. Mendoza and *Paramuricea clavata* (Risso, 1826). It quickly invaded a large part of the coast of the island of São Miguel, in the Azores (Faria et al., 2022a). This was followed by major changes in the structure of shallow marine benthic communities, with significant losses of species richness and natural variability. Faria et al. (2022b) reported a spectacular reduction in the abundance of corticated algae, articulated coralline algae and corticated foliose algae in invaded sites, even substituting previous dominant species (e.g. *Ellisolandia elongata*, *Dicthyota* spp. *Halopteris* spp.), reducing diversity assemblage compared to control sites (Faria et al., 2022b). These findings are in accordance to the ones reported in the Strait of Gibraltar, where *R. okamurai* has also quickly affected the structure of marine benthic communities by displacing previously dominant assemblages (García-Gómez et al., 2021). This macroalgae displays a high competitive capacity against indigenous species and communities, such as seagrass beds like *Posidonia oceanica* and *Cymodocea nodosa*, fucalcan and kelp forests and gorgonians (Terradas-Fernández et al., 2023; Bellisimo et al., 2024). Similarly, the coverage of sessile species on Tarifa Island decreased in terms of percentage of species coverage until 2020, with the exception of *R. okamurai* and the coral *Astroides calycularis* (García-Gómez et al., 2021).

The invasive alga *R. okamurai* was widely recorded in circalittoral and bathyal bottoms of the Strait of Gibraltar and the Alboran Sea in the form of detached thalli, that sometimes were highly entangled in certain benthic sessile invertebrates (Rueda et al., 2023). Generally, small benthic organisms (encrusting hydrozoans, sponges, etc.) showed low coverage-entanglement levels of drifted thalli (Rueda et al., 2023). Conversely, large sessile and colonial benthic species with a complex three-dimensional morphology (e.g. colonial scleractinians and gorgonians) displayed high levels of *R. okamurai* thalli entangled in various parts of their colonies (Rueda et al., 2023). The thalli entangled in these colonial suspension foraging species may interfere with their foraging capability in the long-term, leading to habitat degradation in the near future (Rueda et al., 2023). Some of these invertebrates generally have moderate to slow growth rates and are therefore considered vulnerable species.

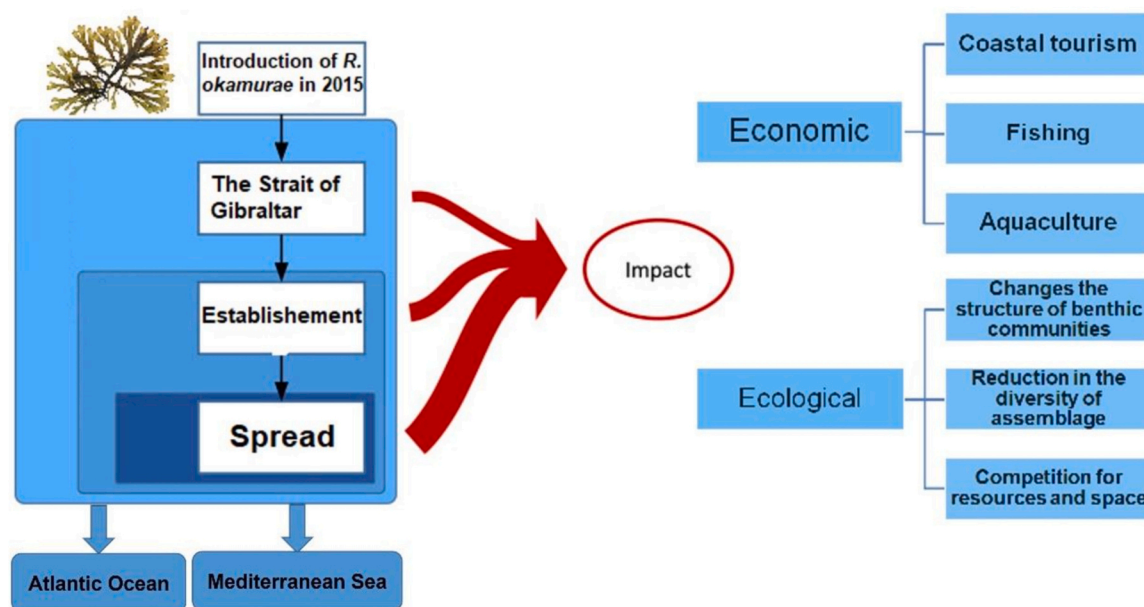


Fig. 4. Ecological and economic impacts of the invasive alga *R. okamuræ*.

The large biomass of *R. okamuræ* interfere recreational activities and the aesthetics of coastal areas (Mogollón et al., 2024). As a result, blooms of this algae can affect tourism revenues and need from biomass removal interventions (Ocaña et al., 2016). The decomposition of this stranded algae can have negative effects on human health, coastal tourism and beach access. For instance, *R. okamuræ* wrack deposits, mostly during the summer, have caused discomfort due to their unpleasant smell. More than 5000 t of biomass were extracted from the beaches of Ceuta in 2015 (Ocaña et al., 2016) and 6.213 t from Los Lances beach (Tarifa, Spain) in the summer of 2021 (Roca et al., 2022). High beached *R. okamuræ* biomass was also observed in Moroccan beaches (El Madany et al., 2024). Massive numbers of drifted thalli of this alga have been reported along the coasts of Spain and Morocco, where nowadays they constitute a major issue for coastal tourism (Altamirano et al., 2019; Mogollón et al., 2024). Bathing areas in Spain and Morocco, that were known for their crystal clear waters, were already invaded by turbid waters filled with detached debris of *R. okamuræ* (Mghili et al., 2024).

In regard to economic losses, fishermen reported significant economic losses due to negative interaction with *R. okamuræ* (Báez et al., 2023). The fishermen community still claims high algae biomass in their fishing nets reducing catchability (Báez et al., 2023). In particular, the bloom of *R. okamuræ* causes strong “golden tides” obstructing fishing nets, needing to spend more time to render the net operational again (Báez et al., 2023). Most of the works have focused on the events linked to the stranding of *R. okamuræ* biomass, but exact costs to the tourism and fisheries sectors are still difficult to assess (Ocaña et al., 2016; El Madany et al., 2024). However, some studies calculated their impact. Mogollón et al. (2024) estimated the annual economic impact of *R. okamuræ* in the municipality of Tarifa, Spain. The economic impacts were valued at than three million euros per year, concentrated mainly in the fishing sector and public administration (Mogollón et al., 2024). In the strait of Gibraltar, economic impacts were estimated at $0,4 \times 10^6$ € in nine months due to the removal of derived material beached on the shores and $0,8 \times 10^6$ € to the fishing industry in the same period due reduced catches of many species of commercial value (Altamirano et al., 2019). Not only fisheries were affected by *R. okamuræ* blooms, but also aquaculture activity (Mghili et al., 2024). During *R. okamuræ* blooms, large quantities of biomass can be produced, often causing significant clogging of aquaculture cages and other equipment as observed by Mghili et al. (2024). These large blooms can deplete oxygen in the water

and release harmful toxins, which can be adversely affect fish health.

3.6. Algal biomass valorization

To date, there are few studies on the valorization of *R. okamuræ* biomass (Agabo-García et al., 2023; Berti et al., 2023; El Madany et al., 2023). This macroalgae seems to display many attributes, with remarkable potential for uses in different industries (Barcellos et al., 2023). The proliferation of *R. okamuræ* in the Mediterranean also represents a major socio-economic problem linked to the high quantities of density and biomass accumulated as waste. Several studies have investigated the potential uses of *R. okamuræ*, centering on its use in bioplastics, biogas production and composting. Additionally, potential antioxidant, antimicrobial and anti-inflammatory activities have been investigated, as the ability to inhibit α -glucosidase (Barcellos et al., 2023; Casal-Porras et al., 2021; De la Lama-Calvente et al., 2023), which may have attractive properties for the pharmaceutical, biomedical or food industries. Further research should be performed to identify the metabolites and the real contribution of the constituents of this species for medicinal applications. *R. okamuræ* could find future uses in the cosmeceutical field via the production of bioproducts beneficial for the medical textiles industry and for skin care (cream) (Barcellos et al., 2023). Studies that aim to identify the potential of *R. okamuræ* as a functional anti-diabetic food have already taken the first steps (El Madany et al., 2023), but are remain in their infancy and need additional investigation.

3.7. Management of the invasive macroalgae *R. okamuræ*

Given the current distribution and invasive potential of *R. okamuræ*, the implementation of extensive and coordinated long-term monitoring programs to track new invasions and some strategies to prevent its spread, becomes essential. The brown alga *R. okamuræ* is listed in the Spanish list of invasive species (MITECO, 2020), as well as in the list of invasive species of Union concern (European Union, 2022). Among the countries invaded by *R. okamuræ*, Spain has launched a strategy to combat this invasive alga (MITECO, 2022), which emphasizes the necessity of preventing new arrivals, control and management of existing populations, and the coordination among the agents responsible for such management. While other countries have reported the ecological and economic impacts of this invasive species, these are often not fully

integrated across government. Management protocols are based on prevention, early detection, rapid response and control should be the main concepts that regional governments should apply when managing *R. okamurae*. Early detection of *R. okamurae* in novel sites is the first step in developing action plans to prevent and attenuate their impacts. However, early detection of *R. okamurae* in the Mediterranean and Atlantic is challenging given its morphological similarity with the indigenous species *Dictyota dichotoma* (Altamirano-Jeschke et al., 2017). It is necessary to develop a specific action plan for each region depending on the stage of establishment of *R. okamurae*. Eradicating invasive macroalgae from their new habitats is most probably to be successful if attempted before they become largely established (Anderson, 2007). Therefore, eradication actions are only recommended when they can be launched quickly after the early detection of *R. okamurae* (minimum thallus density). On the north coast of Sicily, *R. okamurae* is at the beginning of its invasion based on observations by Bellisimo et al. (2024). Diaz-Tapia et al. (2024) suggested that the propagation and colonization of *R. okamurae* in northern Spain is still in its infancy. Unfortunately, it is probably that *R. okamurae* cannot be eradicated in highly affected areas. There is general agreement among researchers about impossibility of eradicating invasive algae once they become well established (Anderson, 2007; Marks et al., 2017). To date, efforts to eradicate largely distributed alien macroalgae have failed, with the exception of *Caulerpa taxifolia*, which has been successively eradicated (Anderson, 2005). In Southern California, the combination of early detection and rapid management response was behind the apparently successful eradication of *C. taxifolia* (Anderson, 2005). This invasive algae is an excellent example of multi-agency cooperation, with the presence of early detection systems in the field and the rapid response of managers. Monitoring programs for *R. okamurae* in invaded areas are generally limited. Besides, existing monitoring programs are poorly coordinated with managers. It will be crucial to develop well-coordinated research projects in the Mediterranean and Atlantic regions that focus on early identification of this species and habitat features that facilitate invasions, as well as possible technologies for effective control and eradication. A detailed analysis of control and management approaches could be discussed in one or more workshops with participants from several disciplines (marine ecology and phyecology). Developing a management protocol in different countries can be challenging due to many issues, including differences in political systems, economic interests, cultural norms, and varying scientific expertise and infrastructure capacities. However, measures and actions could help limit the expansion and impact of this macroalgae. The potential spread capacity of *R. okamurae* must be reduced immediately as a first response by focusing on the vectors of introduction of this species. Eliminating floating *R. okamurae* is essential for the management of this invasive algae, as it prevents the propagation of highly invasive and photosynthetically active fragments to other regions. Biotechnological valorization of *R. okamurae* has been identified as a management strategy for waste biomass, aiding in the reduction of costs related to beach cleaning (Barcellos et al., 2023).

To effectively manage its propagation, a multidisciplinary approach integrating ecological knowledge is required. Most published studies of predation on *R. okamurae* are rare and anecdotic. This macroalgae is known to be consumed by generalist and specialist mesograzers like abalones (*Haliotis discus hannai*) and sea urchins (*Strongylocentrotus nudus*) in its natural range (Agatsuma et al., 2005). In terms of biological control, recent progress has been achieved in identifying biocontrol species for *R. okamurae* in invaded regions. Specifically, the sea urchin *Paracentrotus lividus* is a generalist herbivore largely distributed along the coasts of the Mediterranean and northeastern Atlantic, and has high potential to regulate the abundance, distribution and diversity of indigenous and non-indigenous algae (Pusceddu et al., 2021). Recent studies have shown that *P. lividus* feeds on *R. okamurae*, under laboratory conditions, and could therefore be considered a biological regulator of this invasive species (Hachero-Cruzado et al., 2024). However, further

research is needed, as previous studies have shown that consumption rates of *R. okamurae* are low due to the toxic effects of this algae (Casal-Porras et al., 2021). Knowledge of predation intensity on this algae seems to be a key element in regulating *R. okamurae* populations. Other studies showed that manual removal of invasive macroalgae, in combination with implantation of juvenile urchins, can be an efficient method of minimizing the benthic cover of invasive macroalgae. Consequently, the effectiveness of this approach for *R. okamurae* necessitated proper testing at small experimental scale before application in the field, in addition to long-term financial support for testing this approach.

3.8. Critical considerations

Despite the growing number of studies on the presence of *R. okamurae* as an invasive species in the Mediterranean Sea and Atlantic Ocean, there are some worrying gaps.

There are numerous aspects of the ecology of *R. okamurae* that remain unclear or little-examined. Initially, there is a significant gap in knowledge about the life cycle of *R. okamurae* in introduced areas. Another aspect that is still poorly understood concerns reproductive structures. Most of the reproductive structures reported in introduced areas are mainly sporophytes while gametophytes are poorly documented (Altamirano et al., 2019). A better understanding of the reproductive mechanisms of *R. okamurae* will be essential for understanding the invasion process of this algae. The habitat limits of *R. okamurae* resulting from light availability, temperature and salinity and their interactions with depth are also unknown. Additionally, little is known about the interaction of *R. okamurae* with native fauna. The roles of diatoms in *R. okamurae* and their effects on its associated fauna are poorly understood, partly due to contradictions between the results obtained by Hachero-Cruzado et al. (2024) and Casal-Porras et al. (2021).

However, our understanding of *R. okamurae* distribution in the Mediterranean and Atlantic remains insufficient. It is worth highlighting that only few studies undertake empirical research on the monitoring of this macroalgae, which reflects the scarcity of studies on this species in some parts of the Mediterranean and the Atlantic. Despite the increase in qualitative research, data on the abundance and coverage of *R. okamurae* are unfortunately still scarce. Moreover, the restricted number of papers estimating the abundance and coverage of *R. okamurae* and their methodological inconsistencies hamper the comparison of results. While the majority of reviewed studies focus on the Strait of Gibraltar, the Atlantic and Mediterranean coasts would also benefit from similar investigative efforts. Studies are particularly lacking for the regions closest to the Strait of Gibraltar, which are highly exposed to invasion by *R. okamurae*.

More detailed studies are needed to understand the underlying factors that are responsible for the proliferation of this species in introduced areas. There are significant inconsistencies when focusing on environmental conditions between regions invaded. In the Mediterranean and Atlantic, *R. okamurae* can be exposed to a variety of environmental conditions that affect the growth rate and proliferation of this algae. Reports on the impact of temperatures on the proliferation of *R. okamurae* in introduced areas are generally limited to the Strait of Gibraltar, with little information on the Mediterranean and the Atlantic. Future research should focus on understanding the role of temperature on the success of *R. okamurae* invasion in different invaded regions. While data are available for understanding the role of nutrients in the proliferation of *R. okamurae* in the Strait of Gibraltar (Mercado et al., 2022), less is known for other regions. The invaded areas are situated in different ecoregions with different primary productivity. These differences in nutrient concentration could limit the proliferation of biomass by *R. okamurae* in some regions. However, further research is needed on the role of nutrients in the proliferation of this macroalgae in introduced areas.

Future interactions among environmental stressors such as

eutrophication, high levels of modification and ocean warming could give *R. okamurae* a significant advantage compared to native species in the Mediterranean and the Atlantic, needing from further research (Mercado et al., 2022).

The current lack of methods and tools to eradicate or control *R. okamurae*, mean that removal or interception of pathways of introduction the only effective method to limiting the impacts of this macroalgal invasion. Additional works should comprehensively be performed to investigate the role of shipping as a vector for invasion in other regions. The potential to limit the propagation of *R. okamurae* through commercial and recreational vessels movements, which often expose coastal region across the Mediterranean and the Atlantic to invasion by this macroalgae, could be vital for the conservation of marine biodiversity in the Mediterranean and the Atlantic. Future work should further examine in greater depth role of ocean currents as a potential environmental factors in the introduction of *R. okamurae* to other regions in the Mediterranean and Atlantic, which could be important in developing management measures. Any data describing the type of substrates colonized by this algae could contribute to the development of management measures to prevent potential dispersal vectors and reduce the expansion of this species in the Mediterranean Sea and the Atlantic Ocean.

Further studies are required in the form of manipulative and empirical experiments, including studying community-level interactions, such as impacts on local flora and fauna and food webs. Studies should cover a variety of marine environments and extend over long periods of time, with a focus on areas of particular ecological value. Understanding ecological consequences of the *R. okamurae* invasion needs quantitative data. There are challenges in terms of quantifying the impacts of the *R. okamurae* invasion for many sites, due to the lack of baseline data, such as detailed location investigations pre-invasion, hinders a robust understanding of the impacts of the invasion of this macroalgae. Monitoring programs such as the Sessile Bioindicators in Permanent Quadrats (SBPQ) should be implemented to obtain information on the current state of deep water habitats before and after the massive invasion of *R. okamurae* in these areas, in order to understand the potential impacts caused by the drifted thalli (García-Gómez, 2015). In addition, experimental research on the impacts of the drifted thalli on key habitat-forming organisms and on carbon sequestration in marine sediments could also be useful in identifying potential changes in the deep sea habitat.

Understanding the impact of *R. okamurae* on different economic sectors (e.g. coastal tourism and fishing) remains a key area of research in the invaded region (Morocco and Spain). While it is acknowledged that these *R. okamurae* biomasses have caused an important impacts in the coastal tourism and fisheries sectors, there have been no quantitative analyses to estimate the economic losses. This is critical data, as this socio-economic knowledge is required to induce the change and to support the implementation and development of a coordinated regional response to *R. okamurae* biomass. In addition, it is important that all stakeholders, in particular scientists, decision-makers and fishermen, participate in the elaboration of management measures.

The development of an international and cross-border database in the invaded countries by *R. okamurae* is crucial, as the potential solutions to manage the influx of *R. okamurae* in the future would need from geolocated data and local management strategies. Long-term records of *R. okamurae* are required to track spatial and temporal changes and their impacts on the benthic community. While some efforts have been developed using drones and satellites in a local scale (Roca et al., 2022; Haro et al., 2024), this type of data is needed to better understand how to manage this species effectively and develop early-warning tools in a broader scale, where the engagement of NGOs and citizen participation can be crucial (Price-Jones et al., 2022; Liulea et al., 2023).

Knowing the role that meteorological conditions (wind and currents) play in the spatio-temporal dynamics of *R. okamurae* biomass along the shoreline is therefore crucial to designing successful management

strategies to minimize its negative impacts on the ecosystem services sector (tourism and fisheries) and to establish protocols for collecting these biomass. Unfortunately, the algal biomass collected mechanically is not consistently measured and quantified in the different countries. Moreover, mechanical removal activities are more intense during the summer period. Therefore, recording the amount of algal biomass collected could improve our understanding and knowledge of the seasonal trend of *R. okamurae* and the possibilities for recycling this biomass (Haro et al., 2024). This quantification is especially important considering that *R. okamurae* biomass can be potentially used in the generation of bioplastics, biomaterials, biogas, composting, and cosmetic and pharmaceutical uses (Barcellos et al., 2023). The potential value of *R. okamurae* cannot be quantified or evaluated with only few studies available. To effectively valorize the biomass of *R. okamurae*, an essential piece of data is the biochemical composition of this macroalga. The analysis of *R. okamurae* composition has not yet been studied, and in this respect, some questions remain unanswered.

4. Conclusions

This article presents a review of the scientific literature regarding the populations of the invasive alga *R. okamurae* in introduced regions. The rapid increase in the number of publications on *R. okamurae* in recent years is a welcome step towards understanding blooms of this invasive algae, their geographical distribution and ecological, potential applications and economic impacts. This species has many number of life history characteristics that make it well-established in many areas of the Mediterranean and Atlantic. The common characteristics of *R. okamurae* include rapid reproduction and growth, broad environmental tolerance and high dispersal capacity. The high persistence and abundance of *R. okamurae* in introduced areas has raised the awareness of its invasion potential and heightened concerns about its possible harmful impacts on ecosystems and biota. Despite this progress, there remain several knowledge gaps regarding the ecology of *R. okamurae*, many of which concern its life cycle and the impact of environmental factors on reproductive mechanisms in invaded areas. With the majority of articles focusing on coastal zone monitoring, research on ecological and economic impacts is limited, thus hindering detailed analysis of the interaction of *R. okamurae* with other communities. As there is no regional management strategy to prevent the establishment of *R. okamurae* in other regions, international collaborative efforts should focus on managing the spread of this macroalgae. Management protocols are based on prevention, early detection, rapid response and control should be the main concepts that regional governments should apply when managing *R. okamurae*.

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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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2024.117194>.

Data availability

No data was used for the research described in the article.

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