



# Challenges and opportunities of the exotic invasive macroalga *Rugulopteryx okamurae* (Phaeophyceae, Heterokontophyta)

Félix L. Figueroa<sup>1</sup> · Julia Vega<sup>1</sup> · Noelia Flórez-Fernández<sup>2</sup> · José Mazón<sup>2</sup> · María Dolores Torres<sup>2</sup> · Herminia Domínguez<sup>2</sup> · Leonel Pereira<sup>3</sup>

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## Abstract

The invasion of *Rugulopteryx okamurae* along the southern European coastline is producing significant ecological and socioeconomic impacts. Its rapid proliferation and high adaptability have caused severe ecosystem disruptions, displacing indigenous species and altering habitat structures. Various factors, including favorable environmental conditions and chemical defenses, have contributed to its rapid spread. This situation has prompted urgent interdisciplinary research and the implementation of management strategies. Regulatory frameworks have been established to address its invasive status, aiming to control the bio-invasion. Valorization strategies could contribute to sustainable marine ecosystem management and marine biotechnology advancements. *R. okamurae* presents a wide variety of valuable molecules in its internal composition, such as alginates, terpenoids or carotenoids, with potential biotechnological applications. Promising results have been obtained using *R. okamurae* in compost or biostimulants, as supplements in aquafeed or as part of biomaterial to develop eco-friendly products. Some molecules like terpenoids have shown anti-inflammatory properties with applications in the nutraceutical industry. However, significant challenges remain in fully understanding its biology, ecological impacts, and effective control measures. Coordinated efforts among scientists, politicians, companies and stakeholders are essential to mitigate its spread and explore its potential for sustainable resource utilization. The ecological and economic impacts are being studied but there is a still scarce number of studies to follow a strategy of control based in blue and circular economy.

**Keywords** Biomass valorization · Invasive species management · Marine biotechnology · Negative impacts · *Rugulopteryx okamurae*

## The bio-invasion and general perspectives

*Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Dictyotales, Phaeophyceae), initially identified as *Dilophus okamurae* E.Y. Dawson, is prevalent

in the temperate regions of the Northwest Pacific Ocean. *Rugulopteryx okamurae* is native to the northwestern Pacific Ocean, primarily found along the coasts of Japan, Korea, and China (Pereira 2024) (Fig. 1). Recently, this seaweed has become invasive along the southern European coastlines. Its ability to adhere to and thrive on various natural and artificial surfaces, combined with its prolific reproduction, has led to the displacement of indigenous species, resulting in significant ecological impacts (García-Gómez et al. 2018, 2020; 2021a). The bio-invasion of Mediterranean coasts by *R. okamurae* is part of the general high arrival of exotic species, mainly from tropical and subtropical areas (Wes-selmann et al. 2024).

Its introduction to Europe was first noted in 2002 in the Thau Lagoon (France), associated with oyster aquaculture (Verlaque et al. 2009). Subsequent sightings include the Atlantic coast near the Straits of Gibraltar in 2016 (Altamirano Jeschke et al. 2016), as well as along the Moroccan Mediterranean coast

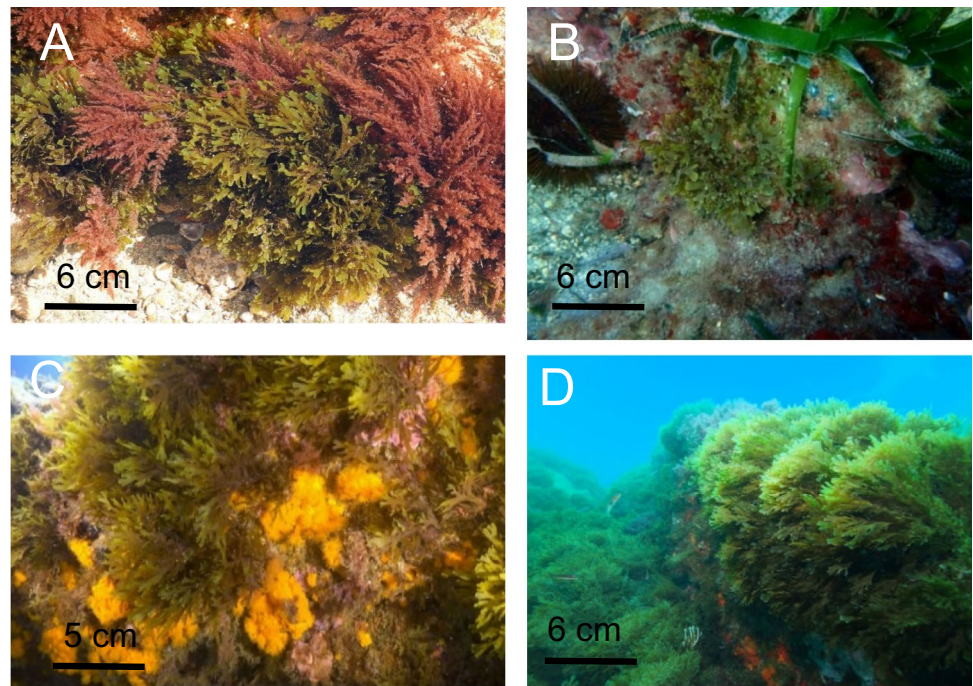
✉ Félix L. Figueroa  
felixlfigueroa@uma.es

<sup>1</sup> Andalusian Institute of Blue Biotechnology and Development (IBYDA), Experimental Center Grice Hutchinson, University of Malaga, Lomas de San Julián 2, 29004 Malaga, Spain

<sup>2</sup> Department of Chemical Engineering, Faculty of Science, CINBIO, University of Vigo, Campus Ourense, 32004 Ourense, Spain

<sup>3</sup> Department of Life Sciences, CFE - Center for Functional Ecology: Science for People & Planet Marine Resources, Conservation and Technology - Marine Algae Laboratory, University of Coimbra, 3000-456 Coimbra, Portugal

**Fig. 1** A) *Rugulopteryx okamurae* (Phaeophyceae) and *Asparagopsis armata* (Rhodophyta), two exotic species that can grow in the same subtidal habitat, B) *R. okamurae* growing in the *Posidonia oceanica* meadows, C-D) *R. okamurae* covering the orange coral *Astroides calycularis*. Photographs. A, C and D by Fernando Alarcón (Equilibrio Marino), and B) by Alejandra Pérez y Fernando Orri (Aquatours)



around the same time (El Aamri et al. 2018). Within a short span, *R. okamurae* has spread along rocky shores, colonizing depths ranging from 0 to 40 m, with peak coverage observed between 10–20 m (García-Gómez et al. 2020). This expansion occurred notably in coastal regions with high ecological significance (Bermejo et al. 2012, 2014), leading to a drastic reduction in the diversity of indigenous algae in affected areas, particularly in the Mediterranean. Some of the communities and species in risk due to the presence of *R. okamurae* are (MTERD 2020, 2022): (1) Impacted communities—Kelp forests, *Cystoseira* species communities, *Posidonia oceanica* meadows, eulittoral and infralittoral seaweed communities, maerl beds, and epiphytic invertebrate fauna. (2) Impacted species—*Laminaria ochroleuca*, *Saccorhiza polyschides*, various *Cystoseira* (sensu lato) species (e.g., *Gongolaria usneoides*) (Phaeophyceae), *Lithophyllum byssoides*, *Gymnogongrus crenulatus* (Rhodophyta), *Sphaerechinus granularis* (Echinodermata), *Leptogorgia sarmentosa*, *Eunicella* spp., *Paramuricea clavate* (Cnidaria), *Charonia lampas* (Gastropoda), *Astroides calycularis*, *Corallium rubrum* (Cnidaria), and *Patella ferruginea* (Gastropoda).

The spread of *R. okamurae* continues along the Spanish Mediterranean coast, with reports from Andalucía and Alicante (García-Gómez et al. 2020; Terradas-Fernández et al. 2023). Additionally, sightings have been reported along the Atlantic coast, including the Canary Islands, and Cantabric waters (Díaz-Tapia et al. 2025). In Portugal, it has been found in Algarve and Azores archipelago. Specifically in Azores, *R. okamurae* has become the dominant organism, causing significant ecological disruption through

the displacement of native species (Faria et al. 2022; Liu-lea et al. 2023; Pereira 2024). *Rugulopteryx okamurae* has been also identified along the coast of Marseille (France) (Ruitton et al. 2021) with high negative impacts on both fauna and algal communities (Borriglione et al. 2024) and in the north-western coast of Sicily (Italy) (Bellissimo et al. 2024) and of Adriatic sea (Bottalico et al. 2024).

Specimens of *R. okamurae* exhibit various vegetative propagules and tetra- monosporangia, being the dominant the vegetative propagules, which explains its rapid proliferation in the region (Altamirano Jeschke et al. 2016). The bio-invasion of *R. okamurae* is believed to be due to spreading through ballast waters of vessels navigating to the Strait of Gibraltar from other harbours (Williams et al. 1988; Werschkun et al. 2014; García-Gómez et al. 2020). The movement of this alga between northern and southern regions of the Strait of Gibraltar can be facilitated by horizontal currents at 100–150 m depth, where specimens of *R. okamurae* have been collected by fishermen (García-Lafuente et al. 2023). Laboratory experiments have demonstrated that this alga can survive extended periods in darkness, suggesting its high resilience and invasive potential (Mateo-Ramírez et al. 2023).

Furthermore, the swift expansion of this species can be attributed to the favorable temperature for its growth and reproduction throughout the entire photic zone (Verlaque et al. 2009). Consequently, the fragmented thalli, carried by tides and wave activity in the Strait of Gibraltar, act as a seeding source for new populations. The influx of water into the Mediterranean Sea aids in the eastward dispersion

of *R. okamurae* along the Mediterranean Coast, while the coastal counter-current along the Gulf of Cádiz contributes to its spread along the Cádiz coast (García-Lafuente et al. 2006; Muñoz et al. 2015). Particularly aggressive in the Strait of Gibraltar, the proliferation is likely exacerbated by factors such as global warming (García-Gómez et al. 2018, 2020). The increased temperatures in sea surface (SST) in the Mediterranean over the past two centuries, i.e., +1–2 °C, have likely contributed to the expansion and impacts of marine non-native species (Hellmann et al. 2008; Walther et al. 2009). Water temperature in the coastal area of Gibraltar strait is typically high during summer, and it has been increasing steadily for the last 40 years ( $T_{\text{mean}} = 0.029 \text{ °C year}^{-1}$ ;  $T_{\text{max}} = 0.028 \text{ °C year}^{-1}$ ) (Rodil et al. 2024). Additionally, algae species are altering their distribution ranges in response to warming (Pechl et al. 2017). This process is being accelerated by human activities (Blackburn et al. 2011). The annual sea temperature in the Strait of Gibraltar, with a monthly average of approximately 15 °C, is ideal for temperate to subtropical species such as *R. okamurae* (Verlaque et al. 2009; El Aamri et al. 2018).

Wesselmann et al. (2024) studied the relationships between the changes of SST in the Mediterranean and the temperature ranges of growing of the exotic species in the origin habitat. They observed that exotic macrophytes from regions where minimum SSTs are two to three degrees warmer than those in the Mediterranean exhibited the highest rates of spread. Over 80% of non-native macrophytes in the Mediterranean do not exceed the maximum temperature of their native habitats, whereas about half of these species experience lower minimum SSTs in the Mediterranean compared to their native range. This suggests that tropical/subtropical macrophytes could potentially expand into Mediterranean waters because their ability to adapt to a lower thermal limit (Wesselmann et al. 2024).

Among the 80 identified non-native macrophytes in the Mediterranean, *R. okamurae* holds an intermediate position in the gradient temperature to tropical origin, as other successful invasive algae as *Ulva ohnoi*, *Codium fragile* (Chlorophyta), *Dictyota cyanoloma* (Phaeophyceae), *Agardhiella subulata*, *Palisada maris-rubri* or *Asparagopsis armata* (Rhodophyta). These findings suggest that future warming trends will likely increase the thermal habitat available for thermophilic species in the Mediterranean Sea, facilitating their spread and establishment.

Beside temperature, elevated levels of nitrate and phosphate in surface waters have also been proposed as a contributing factor to bio-invasions (Mercado et al. 2022). The massive biomass production resulting from these conditions has significant impacts on biodiversity and human activities in affected region. *Rugolopteryx okamurae* can store nutrients, allowing it to resist oligotrophic conditions and exploit nutrient peaks, whether from natural sources like land runoff

and upwelling events or from anthropogenic factors such as population surges during the tourist season (García-Gómez et al. 2018, 2021b; Mercado et al. 2022). Moreover, this proliferation leads to the accumulation of considerable amounts of beach cast material (García-Gómez et al. 2020), greatly affecting fishing activities along the coast of the Gibraltar Strait (Mogollón et al. 2024). By using satellite images, Haro et al. (2024) observed an average coverage of 1.5 ha between 2018 and 2022 in “Los Lances” beach (Tarifa, Spain), with massive accumulations in summer and early autumn (i.e., in August 2019 the coverage reached 8 ha). In addition to beach-cast algae, a substantial amount of biomass have been observed accumulated in the seafloor, both in rocky platforms or sandy areas, where its thickness can reach 45–50 cm (MTERD 2022).

The strategy to counteract the widespread invasion requires an interdisciplinary approach, incorporating risk analysis methodologies and strategies for the eradication and/or control of the invasive species, in compliance with specific regulations, such as the Spanish Law on Invasive Alien Species (RD 630/2013). It is notable that *R. okamurae* was classified as an invasive alien alga in December 2020, mandating adherence to the principles, methodologies, and guidelines set forth by the Society for Ecological Restoration (SER) for the development and management of ecological restoration projects.

This species was formally categorized as an invasive (alien) species within the list of exotic species under Spanish Law (Order TED/1126/2020), prompting the publication of a control strategy for *R. okamurae* (Resolution 22/8/2022, BOE nº 196). Additionally, *R. okamurae* has been included in the list of worrisome invasive alien species of the European Union (Order of 12/7/2022 modifying the Implementing Regulation UE-2016/1141).

The Strategy for the Control of *R. okamurae* in Spain outlines several objectives for managing the bio-invasion. Risk assessments suggested that *R. okamurae* has the potential to spread along the coastlines of the Mediterranean, covering both European and African shores, as well as the Atlantic coast of Morocco and the eastern coast of the United States of America (Muñoz et al. 2019; Bellissimo et al. 2024).

Conducting fundamental research is crucial to comprehend the ecophysiology of this species in the coastal regions of the Strait of Gibraltar and the Mediterranean coast. An interdisciplinary approach is necessary, involving oceanographic studies, assessing its impacts on benthic algal communities and the pelagic trophic network, technological studies for harvesting, and biotechnological investigations aimed at resource valorization. This multifaceted strategy aims to slow its expansion, while simultaneously explore potential applications (Figuroa et al. 2023). The biomass of this species holds promise for various applications including agriculture (as biostimulants and compost), cosmeceuticals,

animal feed, biopolymers for diverse industries, and bioenergy, among others. However, understanding the biology of this species and elucidating the key environmental factors contributing to its remarkable success in colonizing the Mediterranean remains notably limited (Berti et al. 2023). Several reviews on the evolution of the bio-invasion of *R. okamurai* and its potential biomass applications have been published in recent years (Barcellos et al. 2023; Laamraoui et al. 2024). In this review, we are mainly focus on the biomass valorization and the management of the bio-invasion, considering the limited economic studies available within the context of sustainable and blue economy.

## Composition

The valorization of *R. okamurai* biomass is crucial to control its expansion, spread and further colonization. Brown seaweeds are rich in polysaccharides (such as alginates and fucoidans), phlorotannins, terpenoids or fatty acids. Their biological properties make them sustainable resources for generating valuable ingredients in the nutraceutical or cosmeceutical sector. Hence, different strategies should be explored, including the valorization of the entire seaweed for compost, biomaterials or bioenergy, as well as the valorization of specific components or molecules. The sequential utilization of different fractions, following a biorefinery approach should be considered (Park et al. 2023).

Table 1 summarizes the composition of *R. okamurai* obtained from different published articles. The percentage of total carbon is about 34% of the dry weight (DW), in the range of other seaweeds (Duarte 1992). The total content of N is very variable. Mercado et al. (2022) observed changing nitrogen values, reaching 4.5% of DW. Therefore, the total proteins are also very variable. However, in general *R. okamurai* is in the range of low-mid values of total proteins compared with other macroalgae (Holdt and Kraan 2011), although this species presents high-quality proteins as essential amino acids (primarily leucine, phenylalanine, and valine) account for 32% of the total amino acid profile (Cebrián-Lloret et al. 2024). The C:N ratio oscillates between 15 and 20. The total S content is in the range of 0.8–2.8%, probably related with the accumulation of fucoidans (a sulphated polysaccharide). Differences in the ash content has been observed (11.5 – 27.8%), that can be related with different pretreatment process. The ash content is similar to the values obtained in other macroalgae (Holdt and Kraan 2011). In contrast, the level of lipids in the Dictyotaceae is high compared to other macroalgae, reaching values of 8% (Holdt and Kraan 2011; Bogaert et al. 2020). In addition, *R. okamurai* mainly contains saturated fatty acids, with a notable portion (18%) being n3 polyunsaturated fatty

**Table 1** Composition of *Rugulopteryx okamurai* (% of dry weight, except the C:N ratio) obtained in different articles

Component	Content (%)	Reference
Carbon	30.29 ± 0.50	(de la Lama-Calvente et al. 2021)
	34.2 – 42.1	(Mercado et al. 2022)
	36.8 ± 0.2	(López-Hortas et al. 2023)
	35.3 ± 0.3	(Vega et al. 2023)
	34.2 – 41.4	(Córdoba-Granados et al. 2024)
Nitrogen	1.99 ± 0.03	(de la Lama-Calvente et al. 2021)
	1.4 – 4.5	(Mercado et al. 2022)
	2.7 ± 0.1	(López-Hortas et al. 2023)
	1.7 ± 0.1	(Vega et al. 2023)
	1.8 – 2.2	(Córdoba-Granados et al. 2024)
C:N	15.2 ± 0.4	(de la Lama-Calvente et al. 2021)
	19.9 ± 1.0	(Vega et al. 2023)
Sulphur	2.79 ± 0.07	(Ferreira-Anta et al. 2023)
	0.8 ± 0.1	(Vega et al. 2023)
	1.3 ± 0.0	(Córdoba-Granados et al. 2024)
Total proteins	16.43 ± 0.70	(Ferreira-Anta et al. 2023)
	14.7 ± 0.1	(López-Hortas et al. 2023)
	12.2 ± 0.2	(Cebrián-Lloret et al. 2024)
Ash	11.2 – 13.6	(Córdoba-Granados et al. 2024)
	11.56 ± 0.68	(Ferreira-Anta et al. 2023)
	27.8 ± 1.4	(Vega et al. 2023)
	11.30 ± 0.08	(Cebrián-Lloret et al. 2024)
Lipids	33.4 – 33.9	(Córdoba-Granados et al. 2024)
	6.17 ± 0.15	(Ferreira-Anta et al. 2023)
	8.0 ± 0.4	(Vega et al. 2023)
	17.3 ± 3.2	(Cebrián-Lloret et al. 2024)
Soluble carbohydrates	8.8 – 10.0	(Córdoba-Granados et al. 2024)
	75 ± 2.4	(Ferreira-Anta et al. 2023)
	8.8 ± 0.4	(Vega et al. 2023)
	60.4 ± 5.1	(Cebrián-Lloret et al. 2024)
Alginates	7.9 – 8.3	(Córdoba-Granados et al. 2024)
	2.3 - 3.2	(Ferreira-Anta et al. 2023)
	2	(López-Hortas et al. 2023)
	32 ± 4.8	(Cebrián-Lloret et al. 2024)
Fucose	6	(Córdoba-Granados et al. 2024)
	6.38 ± 0.02	(Ferreira-Anta et al. 2023)
	8	(Cebrián-Lloret et al. 2024)
	1	(Córdoba-Granados et al. 2024)
Phenolic compounds	3	(Ferreira-Anta et al. 2023)
	3.0 ± 0.3	(López-Hortas et al. 2023)
	8 ± 0.7	(Vega et al. 2023)
	4.5 ± 0.3	(Cebrián-Lloret et al. 2024)
	1.9 – 3.5	(Córdoba-Granados et al. 2024)

Date and place of collection: Lama-Calvente et al. (2021) – No information; Ferreira-Anta et al. (2023) - Los Lances beach (Tarifa, Spain) July 2021; López-Hortas et al. (2023) – Bolonia beach (Tarifa, Spain), July – November 2021; Vega et al. (2023) - La Caleta beach (Tarifa, Spain) June 2019; Cebrián-Lloret et al. (2024) – Granada; Córdoba-Granados et al. (2024): Punta Carnero (Algeciras, Spain) April 2022 and 2023

acids, resulting in a favorable n6/n3 ratio of 0.31 (Cebrián-Lloret et al. 2024). Córdoba-Granados et al. (2024) observed a higher content of saturated fatty acids (37–46%), being the main fatty acids the palmitic acid (16:0) and oleic acid (18:1n9). Soluble carbohydrates are one of the main components of *R. okamuræ*, being around 60–75% of its composition (Ferreira-Anta et al. 2023; Cebrian-Lloret et al. 2024). However, Vega et al. (2023) and Córdoba-Granados et al. (2024) observed lower proportions (7.9–8.8%), probably due to differences in the extraction process or methodology. The content of alginates, fucose and phenolic compounds is discussed below.

## Alginates

Alginate is a biopolymer of guluronic acid and mannuronic acid found in brown seaweeds. Alginates have commercial applications in the food, cosmetic or pharmaceutical industries due to their gelling capabilities (Reddy 2022). In addition, alginates also have diverse biological properties, e.g., anti-inflammatory or antitumoral with potential pharmacological activities (Fujihara et al. 1984; Borazjani et al. 2017).

The yield of alginate extracted from *R. okamuræ* after microwave hydrothermal treatment (Ferreira-Anta et al. 2023), and microwave hydro-diffusion and gravity (López-Hortas et al. 2021) was around 3.2 and 2.0% DW, respectively. In contrast, Cebrián-Lloret et al. (2024) observed a much higher content of alginates in *R. okamuræ*, reaching 32% DW. In other brown seaweeds the content of alginates is around 15–30%, e.g., *Ascophyllum nodosum* or *Laminaria digitata*, commercially used for alginate extraction, present values close to 30% (Holdt and Kraan 2011), whereas *Sargassum muticum* showed values of 15% (Flórez-Fernández et al. 2019).

## Fucoidans

Fucoidans are sulphated polysaccharides mainly composed of fucose, which can contain other monosaccharides, such as mannose, xylose, galactose or rhamnose, and glucuronic acids. The structure of fucoidans can vary among different species of brown algae, influencing their biological activities (Jayawardena et al. 2022). This polysaccharide can be found in different brown algae such as *Fucus vesiculosus*, *A. nodosum* or *Saccharina japonica*, with concentrations ranging from 10–30% DW (Rodríguez-Jasso et al. 2011; Hifney et al. 2016; Zhao et al. 2018). In *Dictyota dichotoma*, a species from the same family as *R. okamuræ* 38% fucoidan has been reported (El-Sheekh et al. 2024). In *R. okamuræ*, only the fucose content has been determined by HPLC, obtaining values around 6–8% DW (Ferreira-Anta et al. 2023; Cebrián-Lloret et al. 2024).

A broad range of biological activities have been described in fucoidans such as antioxidant, anticoagulant, antithrombotic, antiviral, anticancer, antidiabetic or immunomodulatory activities (De Zoysa et al. 2008; Li et al. 2008; Prokofjeva et al. 2013; Fitton et al. 2015; Zhang et al. 2015; Cotas et al. 2024).

## Terpenoids

Species of the Dictyotaceae, such as *R. okamuræ*, are a great source of terpenoids, including sesquiterpenoids, diterpenoids, and meroterpenoids (Cuevas et al. 2021). Terpenoids in algae acts as feeding deterrent, e.g., some of these compounds have shown feeding deterrent activity against young abalone or young sea urchin *Strongylocentrotus nudus* and even can inhibit the settlement and metamorphosis of the larvae of abalone (*Haliotis discus*) (Kurata et al. 1988, 1989, 1990; Suzuki et al. 2002).

More than twenty terpenoids have been identified in *R. okamuræ* (ex. *Dilophus okamuræ*) specimens (Table 2) collected in several locations of the Japanese coasts (Ochi et al. 1982; Kurata et al. 1988, 1989, 1990; Ninomiya et al. 1999). Recently, Cuevas et al. (2021) and Casal-Porras et al. (2021) identified different diterpenoids in *R. okamuræ* from the Spanish coast. In addition, new diterpenoids have been identified in this species: rugukadiol A (1), rugukamurals A–C, and ruguloptones A–F (Cuevas et al. 2021). Casal-Porras et al. (2021) observed a concentration of  $4.2 \pm 0.5\%$  dilkamural, a terpenoid with feed deterrent and toxic capabilities in *R. okamuræ* collected in the Strait of Gibraltar. However, the concentration of dilkamural in *R. okamuræ* collected in Japan was much lower, 1.9% (Ninomiya et al. 1999), indicating latitudinal influence related to the different environmental conditions in Japan compared to Strait Gibraltar waters. Regarding the content of terpenoids, only Córdoba-Granados et al. (2024) reported a concentration that vary from 2.2 to 29.4 mg g<sup>-1</sup> DW.

Different applications have been attributed to these compounds: anti-herbivore, anti-bacterial, anti-viral, anti-fungal, anti-tumoral, insecticide or anti-inflammatory activities (Fenical 1979; Suzuki et al. 2002; Tziveleka et al. 2005; Othmani et al. 2016).

## Polyphenols

Among the macroalgae, the highest concentration of phenolic compounds is observed in brown algae (Zubia et al. 2007; Guinea et al. 2012; Heffernan et al. 2014; Tenorio-Rodríguez et al. 2017). Phenolic compounds represent a big family of molecules, e.g., phlorotannins, bromophenols, flavonoids or phenolic acids, that are synthesized in response to environmental stress conditions like herbivory or UV radiation. *Rugulopteryx okamuræ* normally shows low values of

**Table 2** Examples of extraction/purification of terpenoids from *Rugulopteryx okamurae*

Extraction conditions	Yield	Compounds	References
A: MeOH (1:1); Hex/DE (90:10) W: EtOH (1:1; 1:4) W: MeOH (1:1; 1:4)	28.25% -	Dilkamural Sesquiterpene lactone, santonin, irofulven, xanthatin	Casal-Porras et al. (2021) Vega et al. (2023)
A: MeOH (1:1); LSR: 10.2/143 (v/w), mashed: 5 min, sonication: 8 min, 6 stages Pur: liquid: liquid extraction DE, 3 stages W: EtOH W: EtOH	1.55 g Fra. (mg) F: 512.4; G: 208.7; B: 65.6; C: 41.1 - -	Rugukadiol A, rugukamurals A-C, ruguloptones A-F Sesquiterpenes Dictyterpenoids A and B	Cuevas et al. (2021) de Paula et al. (2011) Suzuki et al. (2002)

DE: diethyl ether; EtOH: ethanol; Fra: fraction; Hex: *n*-Hexane; A: acetone; MeOH: methanol; Pur: purification; W: water.

phenols, around 3–9 mg g<sup>-1</sup> DW (Table 1). However, other brown macroalgae, such as *Fucus*, *Sargassum* or *Cystoseira* spp., have reported values above 50 mg g<sup>-1</sup> DW (Celis-Plá et al. 2016; Mekinić et al. 2019).

Different bioactivities have been attributed to polyphenols: antioxidant, UV photoprotection, cardiometabolic activity, neuroprotective, anticancer, antimicrobial modulation of activity of gut microbiota (Table 3). El Madany et al. (2023) found that the total phenolic content of *R. okamurae* extracts is decreasing in the following sequence: ethanol > chloroform > methanol, with the highest values around 17.7 mg g<sup>-1</sup> DW (quercetin equivalents).

### Fucoxanthin

The carotenoid fucoxanthin is an accessory photosynthetic pigment that is responsible of the characteristic color of brown algae. Usually, fucoxanthin concentration in brown algae is around 0.1–0.8% of dry weight (Fung et al. 2013; Shannon and Abu-Ghannam 2018). Fucoxanthin concentration in *R. okamurae* is very variable, from non detected to 8 mg g<sup>-1</sup> DW (Córdoba-Granados et al. 2024). This molecule exhibits several biological activities with benefits for human health such as antioxidant, antimicrobial, anti-inflammatory, antifungal and antitumoral activity (Miyashita et al. 2011; Din et al. 2022).

### Valorization strategies to contribute to the control of the bio-invasion

Pinteus et al. (2018) discuss the benefits of using invasive species like *R. okamurae* for extracting bioactive compounds. This approach presents two key advantages: (1) high availability of the biological material, and (2) through the collection, mitigating the negative effects caused by the invasive species, contributing to ecosystem restoration and sustainability at ecological, economic and social levels.

The tonnes of *R. okamurae* accumulations in touristic beaches, especially in summer, can cause severe losses in

local economy. Rodil et al. (2024) quantified the accumulated biomass of *R. okamurae* in 5 different sandy beaches of Tarifa (with high tourism interest) using transects and observed quantities that varied from 4 to 190 kg m<sup>-2</sup>. In addition, (Haro et al. 2024), using remote sensing, observed coverage values of this algae as beach-cast algae of 1.5 ha, with peaks that can reach 8 ha in Los Lances beach. These amounts are higher than those reported of average algal biomass of wrack on beaches worldwide, i.e. 0.1 to 325 kg wet weight m<sup>-1</sup> (Hyndes et al. 2022). In addition, this accumulation can become a globally significant contributor to greenhouse gases, Rodil et al. (2024) observed CO<sub>2</sub> average fluxes close to 20 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>, reaching maximum peaks of 290 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>.

Regarding economic impacts, (Mogollón et al. 2024) estimated the annual economic impact of these accumulations on 3.3 million Euros per year, being the most affected sector the artisanal fishing, as the catches of traditional fishes was drastically reduced (Báez et al. 2023). The fishermen collect a significant biomass of algae in their nets, which not only reduces their fish catch but also obstructs or even broke the nets (Báez et al. 2023). Public administration is the second most affected, since it must pay the cost derived from cleaning and maintaining beaches.

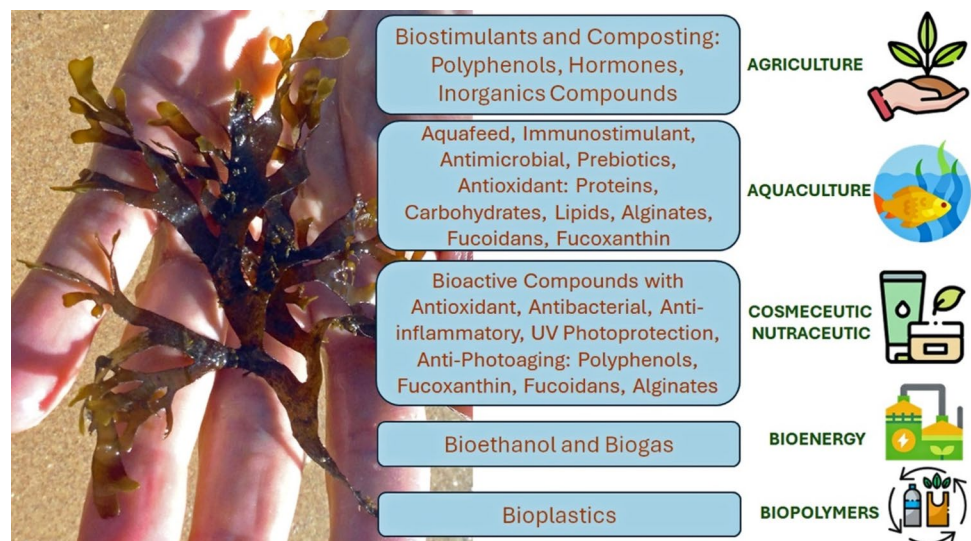
Efforts to find sustainable uses and exploitation strategies for the abundant biomass of *R. okamurae* can help to finance its removal from coastal areas by the municipalities (Patón et al. 2022; León-Marcos et al. 2024). This process, named “elimination for valorization” is a promising alternative to combat the negative effects caused by the spread of this invasive macroalgae (De la Lama-Calvente et al. 2023).

Optimizing harvest procedures and extraction techniques will allow high added-value compounds to be obtained by simple, economic, and industrially scalable processes. Beach-cast algae are the most problematic for municipalities as they negatively affect tourism, the use of this type of biomass for compost or aquafeed, for example, will reduce the cost of waste treatments since a commercial product can be produced (Patón et al. 2022; Patón and García-Gómez 2024; Vizcaíno et al. 2024). Therefore, the biotechnological

**Table 3** List of most abundant polyphenols presented in *Rugulopteryx okamurae* (adapted from Vega et al. (2023), from *R. okamurae* collected in “La Caleta” beach, Tarifa, Spain in June 2019)

Polyphenol	Chemical structure	Bioactivity	Reference
Eugenitin		Anti-leishmanial	(Andrioli et al. 2014)
Ferulic acid		Antioxidant, anti-inflammatory, apoptosis inhibitor, cardioprotective	(Raj and Singh 2022)
Fraxetin		Anti-inflammatory, anticancer, antioxidant, antibacterial	(Lee et al. 2022)
Hispolon		Anticancer	(Balaji et al. 2015)
Kojic acid		Skin lightening agent, antioxidant, antimicrobial, anti-inflammatory	(Zilles et al. 2022)
Maltol		Antioxidant	(Suh et al. 1996)
Marmesin		UV-A-filtering	(Joo et al. 2004)
Phenylacetic acid		Anticancer	(Balaji et al. 2015)
Pyrogallol		Anticancer, antiviral, antioxidant, bactericidal	(Su et al. 2021)
Resveratrol		Anti-aging, photoprotective, estrogen-like, skin-whitening, anti-acne, wound healing, anti-scarring, antimicrobial, anti-skin cancer	(Mascarenhas-Melo et al. 2023)
Scoparone		Anti-inflammatory, antioxidant, anti-apoptotic, anti-fibrotic, hypolipidemic, anticancer	(Kim et al. 2013)

**Fig. 2** Biocompounds of *Rugulopteryx okamurae* and the potential application in different fields



uses of invasive algal species can contribute to the control of bio-invasions, a concerning phenomenon linked to global change. *R. okamurae* present a high diversity of bio-compounds with potential applications in agriculture, aquaculture, cosmeceutics, nutraceuticals, bioenergy or biomaterials (Fig. 2). The current state of research on the potential application of *R. okamurae* biomass in different sectors is still at a technology readiness level (TRL) of 5–6. However, in the near future it is expected that the development and demonstration of system prototypes in operational environment advance the TRL, bringing it closer to market readiness.

### Compost and Biostimulants

Composting is a relatively simple and cost-effective process, in which organic matter is degraded by microorganisms and converted into a product with high fertilizing properties and other benefits for the agriculture industry.

Macroalgae normally have a high salt content or low C:N ratios that present difficulties to composting. Berti et al. (2023) tried to compost *R. okamurae* biomass in different ways, only *R. okamurae* and in combination with horticultural and garden pruning residues, in order to reduce peat in media for tomato seedlings. The substrates that contained 40% compost of only *R. okamurae* or in combination with garden pruning showed promising results. In these substrates, the high initial electrical conductivity and ion concentration were remarkably reduced thanks to the fast leaching of salt that occurred with customary irrigation. It was therefore concluded that composts based on *R. okamurae* could be used as a seedling growing medium for the valorisation of algae (Berti et al. 2023).

Another approach to obtain compost is vermicomposting, but traditional vermicomposting did not work appropriately with *R. okamurae* due to its high content of sesquiterpenoids

with high toxicity. In consequence, other alternatives are necessary. The use of insect farms has been proposed to eliminate the invasive algal biomass and to provide fertilizers and animal proteins. Patón et al. (2023) have analyzed vermicomposting with five invertebrate species, with *Dendrobaena veneta* and *Eisenia fetida*, blatticomposting with *Eublaberus* spp. “Ivory”, mealworms, such as *Tenebrio molitor*, and with *Hermetia illucens*. *Hermetia illucens* and the ivory cockroaches *Eublaberus* spp. can consume this seaweed and the high concentration of sesquiterpenes did not affect long-term survival, growth or reproduction. The experiments were performed with both desalted and non-desalted algae, obtaining successful degradation of *R. okamurae* in both cases. This species consumes the algae and is the easiest to maintain, allowing the creation of bioremediation plants on an industrial scale.

Composting this algae has been identified as a viable solution for agricultural use. Correa-Bustos et al. (2024) examined the composting of *R. okamurae* mixed with plant residues and evaluated the final compost for its potential as a substrate and nutrient source, aiming to determine the most effective mixture composition. The composting trials involved different proportions of seaweed (100%, 30–35%, and 15%) combined with plant waste (from vegetables, fruits, and gardens), using both washed and unwashed seaweed. Initial trials revealed challenges, such as a low C/N ratio and the effects of washing the algae. As a result, a second trial was conducted to optimize the mixtures, targeting a C/N ratio close to 30. Additionally, it was decided not to wash the algae to lower the electrical conductivity (EC) of the mixtures. The results showed that the composting process was not negatively affected by high EC levels when using unwashed algae. However, washing the algae prior to composting did influence compost quality, with washed algae composts combined with garden waste (SwP

34.0 dS m<sup>-1</sup>) having a lower EC than unwashed algae composts (SP 51.6 dS m<sup>-1</sup> and SFP 64.9 dS m<sup>-1</sup>). Compost made only from horticultural and garden waste (FHP 43.7 dS m<sup>-1</sup>) also had high EC, but the addition of low proportions of unwashed algae (15%) did not further increase EC (SFHP 47.6 dS m<sup>-1</sup>). Other quality parameters were not impacted by the absence of algae washing at the start of the composting process.

Some seaweeds have been proven to present high potential as plant protective agents. Zarraonaindia et al. (2023) analyzed the biostimulant capacity of a foliar application of *R. okamurae* and *U. ohonoi* extracts in grapevines. Aqueous extracts at 70 °C of *R. okamurae* biomass improved the defence mechanisms in grapevine plants, by inducing defence genes such as *PR10*, *PAL*, *STS48* and *GST1*, mainly 24 h after the first application. The increased expression level of these genes agreed with i) an increase in trans-piceid and trans-resveratrol content, observed in the leaves treated with the extract of *R. okamurae*, and ii) an increase in jasmonic acid and decrease in salicylic acid. Moreover, an induction of antioxidant enzyme activity was observed at the end of the experiment, with an increase in superoxide dismutase and catalase in the *R. okamurae* treated leaves.

## Aquafeed

Several authors have analyzed macroalgae as a promising supplementation in diets for feeding fish and demonstrated their potential benefits on growth, muscle proximate composition and digestive functionality (Wan et al. 2019). From a nutritional point of view, macroalgae can be used as an alternative source of proteins, carbohydrates or lipids, whereas in recent years they have acquired a great interest for their bioactive compounds such as polysaccharides, pigments, polyphenols, and vitamins (Vizcaíno et al. 2016; Sáez et al. 2020; Ferreira et al. 2021; Passos et al. 2021).

As mentioned above, *R. okamurae* present a high lipid content (8 – 17%), compared with other macroalgae, like *Gracilaria* or *Ulva* normally present less than 3% of lipids (Nunes et al. 2017; Susanto et al. 2019). Approximately, 18% of the lipids are n3 polyunsaturated fatty acids and the ratio n6/n3 is 0.31. On the other hand, the protein content in *R. okamurae* is not very high (around 12%), but presents a good amino acid profile; around 32% of total amino acids, are essential ones such as leucine, phenylalanine and valine (Cebrián-Lloret et al. 2024). Based on these results, *R. okamurae* could be a promising source for aquafeed. However, it is known that the use of *R. okamurae* in aquafeeds can negatively affect animal performance. Casal-Porras et al. (2021) reported that *R. okamurae* with 4.2% of dilkamural was not palatable for sea urchins and caused great toxic effects, exhibiting not only deterrent properties but also

causing harmful and even lethal effects on the sea urchins. The toxicity of dilkamural is concentration-dependent since mild deterrence, but not significant harmful effects, were observed on sea urchins whose diet contained a concentration of dilkamural lower than that found in the invasive specimens (Ninomiya et al. 1999). The results of this study have highlighted that both, the compound was highly deterrent and toxic.

Fonseca et al. (2023) and Vizcaíno et al. (2024) evaluated the potential of *R. okamurae* for use as dietary ingredients (5% supplementation) in juvenile seabass through three different approaches: raw, enzymatically hydrolyzed and fermented. The treatment of the biomass improved the digestibility and nutrients availability, while at the same time did decrease the content of undesirable and potentially harmful metabolites, such as dilkamural. Vizcaíno et al. (2024) observed that the content of dilkamural decreased from 0.55% in raw *R. okamurae* to 0.04, 0.18 and 0% after enzymatic hydrolysis, fermentation and both of them, respectively. The results revealed that the inclusion of raw *R. okamurae* caused adverse effects on fish growth and gut functionality, although these effects were not observed when algae were previously treated. In general, diets supplemented with algae (specially treated ones) induced an increase of protein, ARA and DHA in the muscle composition, and a significant reduction in muscle and liver lipid oxidation (Fonseca et al. 2023; Vizcaíno et al. 2024).

## Cosmeceutical and nutraceutical applications

*Rugulopteryx okamurae* boasts a promising array of cosmeceutical and nutraceutical properties due to its rich content of bioactive compounds with antioxidant, anti-inflammatory and hydrating properties. Regarding cosmeceutic properties, fucoxanthin has strong antioxidant properties that could protect the skin from oxidative stress and UV-induced damage, whereas polysaccharides such as alginates or fucoidans, could provide hydration as well as other benefits such as antioxidant or anti-inflammatory (López-Hortas et al. 2021; Lourenço-Lopes et al. 2021; Pajot et al. 2022). Besides, Vega et al. (2023) reported anti-acne activity in ethanol:water and methanol:water extracts of *R. okamurae*. The presence of these compounds equips *R. okamurae* with potent antioxidant properties, allowing it to effectively neutralize harmful free radicals and mitigate oxidative stress-induced damage to the skin (Aslam et al. 2021).

In relation to nutraceutical properties, some authors have reported antitumoral, antidiabetic or anti-inflammatory properties in *R. okamurae*. Harada and Kamei (1997) reported that extracts of *R. okamurae* exhibited strong cytotoxicity

against human leukemia cell lines (HL60 and MOLT-4) at  $50 \mu\text{g mL}^{-1}$ . According to Jiménez-González et al. (2019), the cytotoxic impact of *R. okamurae* extract was evident across all tested cell lines within the dose range of 10 to  $100 \mu\text{g mL}^{-1}$ . Among these cell lines, human breast carcinoma BT-474 cells exhibited the highest sensitivity to the algae extract, with an  $\text{IC}_{50}$  value of  $18.7 \pm 2.2 \mu\text{g mL}^{-1}$ . Conversely, the colorectal cancer cell line HT29 demonstrated the greatest resistance, with an  $\text{IC}_{50}$  value of  $220.0 \pm 131.0 \mu\text{g mL}^{-1}$ .

Jeong et al. (2012) have reported that *R. okamurae* extracts obtained with 70% ethanol for 24 h showed potent antidiabetic activity ( $\text{IC}_{50} = 50.63 \mu\text{g mL}^{-1}$  in inhibition of  $\alpha$ -glucosidase assays) among different brown and red macroalgae.

In addition, anti-inflammatory properties have been also described in *R. okamurae*. Cuevas et al. (2021) reported that the diterpenoid rugukadiol A and the secospatanes, ruguloptones A and F, significantly inhibited the production of the inflammatory mediator NO in LPS-stimulated microglial cells Bv.2 and macrophage cells RAW 264.7. Rugukadiol A and ruguloptone A also inhibited the expression of Nos2 and the pro-inflammatory cytokine Il1b in both immune cell lines. Rugukadiol A displays significant anti-inflammatory activity in immune cells, as inhibitor of the production of NO and of the expression of Nos2 and the cytokine Il1b (Cuevas et al. 2021).

### Biogas production by anaerobic digestion

During the anaerobic digestion, microorganism metabolize organic matter generating biogas composed mainly by methane and carbon dioxide. An important parameter in the digestion process is the C/N ratio, the optimum value is around 20–30 (Murphy et al. 2015). The anaerobic digestion of red and green macroalgae, in general, has limitations due to their low C/N ratios (Tabassum et al. 2016, 2017). Low C/N ratios can inhibit bacterial due to the excessive amount of ammonia that can accumulate in the anaerobic reactor (Allen et al. 2013). In addition, the salt levels in marine biomass are a major concern, particularly regarding the bacterial inhibition associated with salinity in the digester. Toxicity level increase as chloride concentration rises from 5 to  $20 \text{ g L}^{-1}$  (Lefebvre et al. 2007).

However, the co-digestion of seaweeds with other compounds, could enhance the digestibility of the process and the methane yield (Ganesh Saratale et al. 2018). De la Lama-Calvente et al. (2021) proposed the anaerobic co-digestion of *R. okamurae* with olive mill solid waste (OMSW), a solid by-product generated in the production of olive oil. The co-digestion of macroalgae with OMSW would balance the C/N ratio, and dilute the toxins and inhibitory substances for the process, such as salt (in the case of macroalgae) or phenols

and lignocellulosic (from OMSW) (Fernández-Rodríguez et al. 2022), resulting in an improvement in the kinetics of the process, higher methane performance coefficients, and an increase in the biodegradability of the substrates (Fernández-Rodríguez et al. 2019a, b). The highest methane production in the study was found in the 1*R. okamurae*–3 OMSW co-digestion mixture, with  $454 \text{ mL CH}_4 \text{ g}^{-1} \text{ VS}$  and the lowest methane yield values were obtained for the digestion of *R. okamurae* alone ( $177 \pm 15 \text{ mL CH}_4 \text{ g}^{-1} \text{ VS}$ ) (de la Lama-Calvente et al. 2021). The obtained methane yield of the mono-digestion of *R. okamurae* (de la Lama-Calvente et al. 2021) is within the range of the methane yields reported for anaerobic digestion of other marine macroalgae such as *Sargassum*, *Gracilaria*, *Laminaria*, *Asco-phylum* or *Ulva*, for which methane yields are between 140 and  $280 \text{ mL CH}_4 \text{ g}^{-1} \text{ VS}$  (Ganesh Saratale et al. 2018). The highest biodegradability was observed in the mixture *R. okamurae*–1OMSW. The co-digestion improved the methane yield of the macroalga alone by 157% as well as the biodegradability of the single *R. okamurae*, achieving an increase in its degradability of up to 11% (de la Lama-Calvente et al. 2021).

### Bioplastics

Macroalgae are rich in polysaccharides, such as carrageenan, agar or alginates, which are great materials for producing bioplastics. *Rugulopteryx okamurae* can be proposed as an useful biomass to offer an environmentally friendly solution to conventional plastics. Santana et al. (2022) analyzed the potential use of *R. okamurae* for the development of bio-based plastic materials using glycerol (GLY) as plasticizer in different proportions: RO/GLY 50/50, 60/40 and 70/30%. It was observed that the higher the content of *R. okamurae*, the greater the viscoelastic properties, rigidity and resistance the bioplastics display. The water uptake capacity (WUC) with the increasing percentage of seaweed in the mixture, varying from 262% for 50/50 to 181% for 70/30%. The mold temperature (90, 120 and  $150^\circ\text{C}$ ) for the 70/30 did not show significant differences on the final properties of the obtained bioplastic.

### Management of the bio-invasion following a sustainable strategy and the blue economy

The management of the control of an exotic and invasive species is extremely complex. The main objective would be the eradication, but this is very far to get in most bio-invasions. The case of *R. okamurae* is particularly severe due to the speed of its spread and the vast area it has covered in a short time (García-Gómez et al. 2020). Algae can float

near the seafloor and be carried long distance by horizontal and vertical marine currents (García-Lafuente et al. 2023), colonizing new substrata and contributing to the rapid progression of the bio-invasion.

Large quantities of *R. okamurae* reach the beaches, accumulating as beach-cast algae and causing considerable ecological damage to coastal ecosystems. These accumulations also negatively impact local economies, as municipalities are responsible for beach cleaning. A key issue is that this beach-cast algae is considered natural waste and transported to landfills. Although the blue and circular economy promotes waste valorization, there is currently no government-endorsed program to convert this waste into valuable products, such as compost, biomaterials or biostimulants.

Floating algae are often collected by fishermen, but they normally throw them back into the water. Currently, there are no protocols to prevent this, allowing the algae to return to the marine environment and continue its invasive potential. However, the collection of this type of algae could present an opportunity for valorization, turning it into a useful resource.

In comparison, the collection of beach-cast algae is generally easier compared to harvesting floating algae or algae attached to substrates. However, the methods used to clean beaches from beach-cast algae have significant negative effects on beach quality, as large amounts of sand are removed by the machinery employed. More research is needed to enhance harvesting techniques and minimize these environmental impacts.

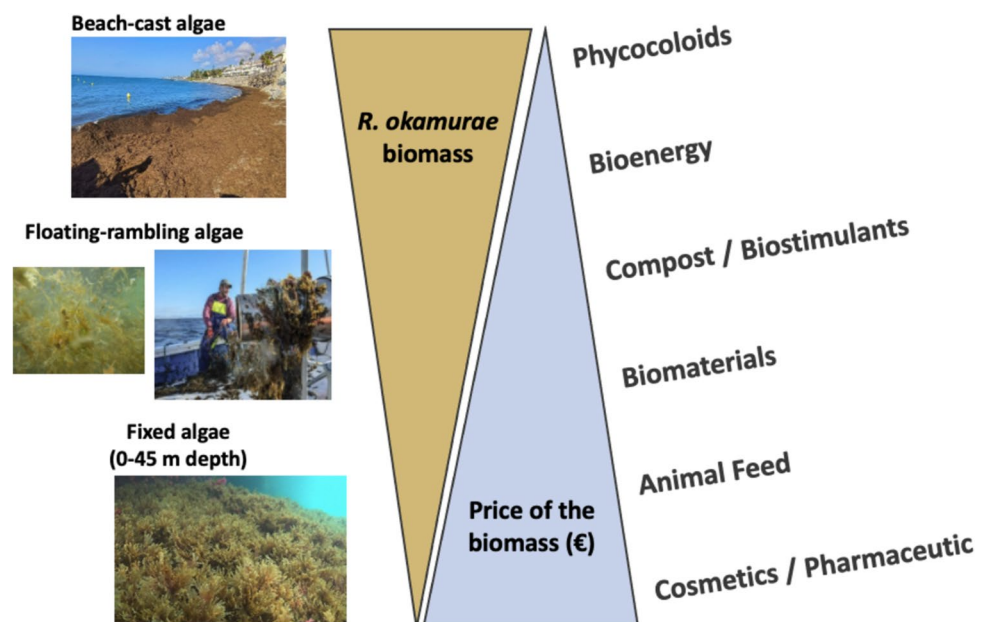
In terms of valorization, beach cast algae (considered a residual biomass) could potentially be used for the extraction of phycocolloids, as large quantities of biomass are needed, and the algae can retain sufficient quality for this purpose

(Fig. 3). Additionally, beach-cast algae could be used to produce bioenergy, such as ethanol or biogas. However, other products with higher economic value, like biomaterials or biostimulants, may require higher-quality biomass. This higher-quality biomass can be sourced from floating algae that are collected by fishermen in their nets (Fig. 3). Finally, high-value products such as food or cosmeceuticals, which require smaller amounts of biomass compared to phycocolloids or bioenergy, could be obtained from high-quality algae biomass, such as those fixed on rocks (Fig. 3). However, this remains a theoretical proposal due to the high costs involved. Additionally, harvesting algae from rocks would need to ensure sustainability from ecological, economic, and social perspectives.

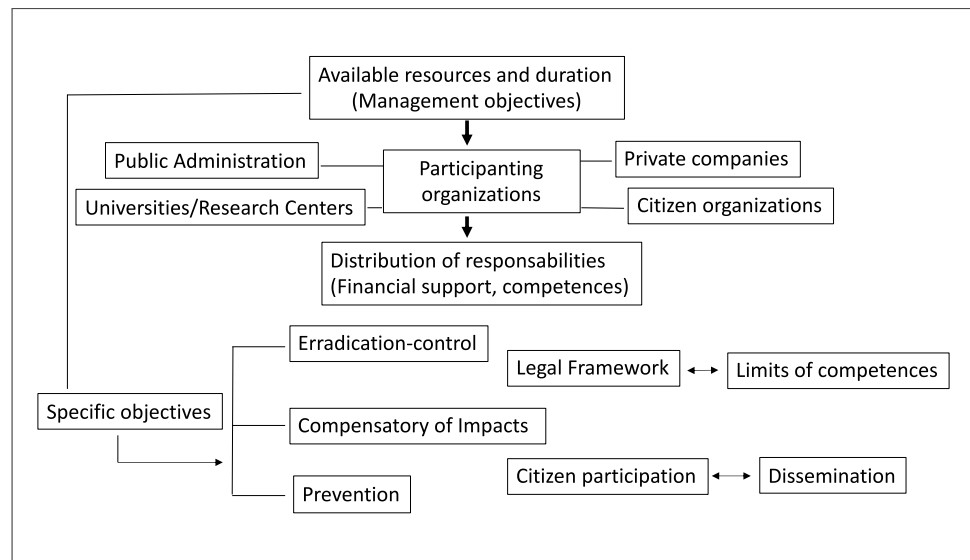
Currently, we are far from realizing the full valorization potential of these algae, as there have been no pilot studies to demonstrate the sustainability of the process or its relation to controlling the bio-invasion.

Any control or mitigation strategy requires significant financial support (Fig. 4). There have been successful cases of eradication of terrestrial invasive species in Spain, whereas there are currently no known instances of eradicating invasive marine algal species, except for the small-scale eradication of *Caulerpa racemosa* and *Caulerpa prolifera* in the Mediterranean (Vilà et al. 2008). In fact, it is more common for exotic species to become naturalized, integrating into coastal ecosystems at the expense of native biodiversity (Belando et al. 2021). The naturalization of *R. okamurae* in the Mediterranean is also a possibility, but it could lead to a drastic reduction in biodiversity and the loss of ecological services provided by native coastal organisms.

**Fig. 3** Tentative value of *Rugulopteryx okamurae* biomass, from lower values of beach cast algae followed by floating and rambling algae compared to higher values as algae attached to substrates. Different uses according to the type of biomass are suggested



**Fig. 4** Objectives and strategy for the management of exotic invasive species (modified from Vilà et al. (2008))



According to Vilà et al. (2008), it is crucial not only to have the necessary resources to manage and control bio-invasion but also to ensure the participation of relevant organizations. Firstly, local, regional, and national public administrations must collaborate within their respective areas of competence. In addition, public administrations must coordinate with researchers from universities and research centers through an interdisciplinary approach that integrates science, technology, and social engagement (Fig. 4).

The distribution of responsibilities in managing bio-invasions is critical. In the case of Spain, strategies for controlling *R. okamurae* and protecting threatened species are proposed by the national government. However, the implementation and further development of these national recommendations must be carried out by regional governments (Autonomous Communities), which are responsible for environmental conservation, particularly in inland coastal waters. The lack of financial support and poor communication between public administrations is delaying the solutions that the public, especially local authorities, fishermen, academia, and environmentalists, are demanding.

The ideal approach involves developing pilot projects funded by public funds and supported by private financial contributions. These projects should address various objectives, including developing low-impact harvesting techniques that take both environmental and economic costs into account. Furthermore, the participation of civil society organizations such as ecological, naturalist, and general public groups, is essential for the success of these control strategies (Kelly et al. 2020; Dionisio et al. 2022).

Citizen science, with the active involvement of civil society, has proven to be an excellent tool for marine observation, restoration, and habitat conservation. The model of

collaboration between public administrations, academia (universities and research centers), private companies, and civil society is known as the Quadruple Helix model. This model has been successfully applied to various crisis situations (Roman et al. 2020). The Helix models of innovation have been linked to sustainable development goals (König et al. 2021). The bio-invasion of *R. okamurae* provides an opportunity to apply this model.

The specific objective of managing the bio-invasion of exotic species includes eradication and control (Fig. 4). Some researchers have established that according to the characteristic of *R. okamurae* bio-invasion, its eradication results impossible (Altamirano Jeschke et al. 2016; García-Gómez et al. 2021b; Figueroa et al. 2023). Compensatory measures are being applied to most affected sectors. For instance, taxes for the use of landfills have been reduced, and fishermen have received compensation due to the decline in coastal fishery yields. However, both sectors (tourism and fisheries) have indicated that these measures are insufficient to offset the significant impact of the invasion. Municipal authorities aim to maintain clean beaches free from exotic algae, while fishermen would prefer to catch fish rather than large quantities of algae in their nets.

One potential way to get financial support could be to include the control of *R. okamurae* in the Blue Carbon Strategy. The valorization of *R. okamurae*, for biomaterials (i.e., bioplastics (Santana et al. 2022)) or bioenergy (Bibi et al. 2017; De la Lama-Calvente et al. 2023), can retire a high amount of carbon of the system, contributing to climate change mitigation (Rodil et al. 2024). The current state of knowledge about the potential of macroalgal cultivation in providing climate-related and other ecosystem services has been reviewed by the Eklipse expert working group of European Union (Fricke et al. 2024). Seaweed culture provide

ecosystem service in aquatic ecosystem (Duarte et al. 2017; Fricke et al. 2024). However there is a lack of quantitative evidence for some ecosystems services (e.g., blue carbon and role in C-sequestration), including the methods for its quantification (van den Burg et al. 2022).

## Conclusions

There is scientific evidence supporting the potential application of bio-compounds obtained from the *R. okamurae* in various fields such as agriculture, aquaculture, nutraceutical, biomaterial or energy (Pinteus et al. 2018; Pereira et al. 2021; Barcellos et al. 2023). However, the development of pilot projects that integrate the collection and the valorization at industrial level of this biomass is still pending. Currently, the Technology Readiness Level (TRL) for the utilization of *R. okamurae* biomass in different fields stands at 5–6. However, it is expected that it can reach higher TRL and finally the entry in the market. Then the bio-invasion can be converted in an opportunity to develop circular economy, contributing to the restoration of damaged ecosystems. Nevertheless, it is crucial to ensure that seaweed harvesting practices are sustainable, avoiding adverse impacts on beach sand, local species, and essential ecosystem services.

Complete eradication of *R. okamurae* is considered impossible by experts, but controlling its spread can help to reduce its negative impacts on expansion. Stronger collaboration among scientists, public administrations, companies and citizens is essential for developing control strategies. This strategy should be focus on the valorization of algal biomass in areas severely affected by the invasion, such as the Strait of Gibraltar. Reducing the biomass of invasive species in affected regions could offer numerous benefits, including ecosystem restoration and conservation, the creation of new job opportunities and the development of the blue economy.

Economic analysis of the cost of harvesting, processing and production of bioproducts for the market are still pending, including life cycle analysis (LCA). The potential exploitation of *R. okamurae* must take into account its ecological impacts and the effects on ecosystem services during biomass valorization. There is scarce information on socioeconomical analysis of the use of *R. okamurae* (Mogollón et al. 2024) nor any economical study on the valorization.

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## Declarations

**Competing interests** The authors declare no competing interests.

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