Marine Environmental Research 207 (2025) 107093

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Assessment of the *Rugulopteryx okamurae* invasion in Northeastern Atlantic and Mediterranean bioregions: Colonisation status, propagation hypotheses and temperature tolerance thresholds

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A R T I C L E I N F O

Keywords:
Rugulopteryx okamurae
Colonisation
Non-indigenous species
North atlantic coasts
Mediterranean Sea

A B S T R A C T

The recent proliferation of the invasive macroalga *Rugulopteryx okamurae* in the Mediterranean and Northeastern Atlantic regions poses significant ecological and socioeconomic threats. This study analyses the current state of knowledge on the invasion, assesses the primary dispersal vectors, and evaluates its invasive potential through temperature tolerance. Using Web of Science and Google Scholar databases, publications from 2004 to 2024 were reviewed and categorized into five key areas: physiology, distribution and spread, ecological impacts, socioeconomic consequences, and management strategies. The bibliographic search evidenced a significant increase in studies concerning *R. okamurae* over the last years (from 1 in 2020 to 38 in 2024). The results also indicated a certain agreement regarding the vector of introduction of this alga into the Strait of Gibraltar in 2015–2016 (ballast waters of merchant ships) but the rapid spread towards Mediterranean and Atlantic areas remains unclear. Nonetheless, aquaculture activities and currents were pointed out as significant dispersal vectors. The temperature analyses highlighted the broad thermal tolerance range of *R. okamurae*, from 10 °C to 30 °C, which contribute to its extensive colonisation. Therefore, this study underscores the need for urgent management actions to limit the expansion of *R. okamurae* and mitigate the negative effects observed on coastal ecosystems and economies of colonised areas.

1. Introduction

The appearance of non-native species modifies the natural ecosystem stability of the colonised area. The introduction of alien organisms into new areas constitutes one of the greatest threats to the global biodiversity but this issue is even more critical in the marine environment due to its higher connectivity and the absence of physical barriers (Hewitt et al., 2007). However, if the non-native organisms become an invasive species, the associated impacts not only affect the ecological status of the colonised ecosystem but also could lead to socioeconomic consequences (Davidson et al., 2015; Fidai et al., 2020).

Although often supported by global climate change, invasion events are mainly driven by a large number of anthropogenic factors such as aquaculture activities, maritime traffic, agriculture run-off and overfishing (Hewitt et al., 2007; Seebens et al., 2016; Houngnandan et al., 2022). All of them are related with habitat degradation or transport of species around the globe which are the main vectors of invasiveness. It was the case of the macroalga *Rugulopteryx okamurae* (E.Y.Dawson) I.K. Hwang, W.J.Lee & H.S.Kim (Dictyotales, Heterokontophyta) that arrived into the Mediterranean bioregion from the Western Pacific, its native area. Firstly, the exotic brown macroalga was introduced in the French Thau Lagoon in 2002 along with seeds of the Japanese oyster *Magallana gigas* (Thunberg, 1793), most likely imported from Japan for aquaculture purposes (Verlaque et al., 2009). Although this first introduction did not result in a significant invasion, likely due to local environmental characteristics such as low winter temperatures, typical salinity gradients of estuarine areas, and a predominantly muddy substrate, a second introduction was noted in 2015 in the Strait of Gibraltar (Ocaña et al., 2016). In this case, the introduction vector remains unclear, but most theories point toward the release of ballast water of merchant ships that often cross the Strait of Gibraltar (García-Gómez et al., 2020) because it is one of the main shipping traffic lines within Europe (115,708 ships/year; www.gibraltarport.com).

Once established in the Strait of Gibraltar (South of Spain and North

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https://doi.org/10.1016/j.marenvres.2025.107093
Received 16 January 2025; Received in revised form 16 March 2025; Accepted 17 March 2025
Available online 18 March 2025
0141-1136/

of Morocco), *R. okamurae* has rapidly spread its population into the Eastern North Atlantic and Mediterranean bioregions in the last 10 years (e.g. García-Gómez et al., 2020; Bellissimo et al., 2024), highlighting a huge invasive potential. In addition to the local habitat degradation, the colonisation ability of this macroalga could be enhanced by different large-scale environmental events derived from global climate change (i.e. heat waves, changes in local and global marine circulation and eutrophication) which often accelerate the invasion events (Occhipinti-Ambrogi, 2007; Houngnandan et al., 2022).

In fact, the first appearance of *R. okamurae* in Ceuta coincided with the record high temperature registered in the Strait of Gibraltar in July 2015 (around 24°C; García-Gómez et al., 2020). In this line, the literature suggests that in a warming climate, *R. okamurae* could develop an important biomass year-round in regions where the historical maximum temperatures were above 15 °C; a threshold at which this species experiences peak growth (Hwang et al., 2009). *Rugulopteryx okamurae* has continued to proliferate into new regions in both Mediterranean and Atlantic waters. In the various studies conducted to date, no clear pattern has been identified regarding the spread of *R. okamurae* to the newly located regions. Among the possible hypotheses, the transport of the alga through trawl nets to new regions stands out. Another possible hypothesis could be related to the Atlantic-Mediterranean circulation itself (García-Lafuente et al., 2023). However, it is still unclear in the literature whether the new colonisations of *R. okamurae* are associated with anthropogenic factors, such as the transport of the alga through ships and sea-food packaging, or if the alga is being distributed to other regions via Mediterranean-Atlantic circulation.

Despite some studies have revealed the presence of this macroalga in different areas (e.g. El Aamri et al., 2018; Bernal-Ibáñez et al., 2022) and others have shed light on different aspects of this biological invasion (e.g. García-Gómez et al., 2020; Berti et al., 2023), there is not any review synthesising the main causes of spread. However, literature reviews have historically been crucial in describing similar invasions (Davidson et al., 2015). For example, Fidai et al. (2020) carried out a broad systematic review on *Sargassum* monitoring studies published from 1960 to 2019 where identified several research gaps and proposed a unique definition for a "*Sargassum*" event to standardise and improve the related documentation. In addition, the magnitude and intensity of the current invasion is still poorly addressed, and it is crucial to apply management actions in order to reduce the spread and mitigate the invasion impacts.

Considering this research gap, this study applies an extensive review of peer-reviewed scientific studies and other well documented publications on the drastic ecological invasion conducted by *R. okamurae* since its introduction in 2015 in the Strait of Gibraltar. Thus, the main goals of this study were (1) to analyse the current state of knowledge on the invasion, (2) to synthesise the invasion dynamic along the Northeastern Atlantic and Mediterranean bioregions, (3) to assess the main dispersal vectors and (4) to reveal its invasive potential through temperature tolerance.

2. Material and methods

2.1. Study selection criteria

A systematic literature review was performed to understand the current knowledge about the invasion. The search was general in order to register all the available studies that have investigated any aspect related with the invasive macroalga *R. okamurae*. With that purpose, the literature review, carried out by using the Web of Science Core Collection and the period 2004–2024, was based on a single search applied to title, abstract and keywords: ((TI=(Rugulopteryx okamurae)) OR AB=(Rugulopteryx okamurae)) OR KW=(Rugulopteryx okamurae). Moreover, a broader search was performed on Google Scholar considering all the studies that mention "*Rugulopteryx okamurae*" within the same period.

Once ran this search, the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA, Moher et al., 2010) was followed to select the final list of publications assessed in this review (Fig. 1). First, the studies were screened by their titles and abstracts to remove duplicates found in both methods. Second, the full texts were examined to exclude publications that focused on other topics and provided limited information about *R. okamurae*. Given the novelty of this invasion, this study considered not only peer-reviewed publications (e.g. research articles and short communications) but also the available grey literature (e.g. conference papers, preprints, bachelor and master's theses), as the latter's greater speed could be advantageous in promoting management actions against this rapid invasion (Adams et al., 2017). Nonetheless, the inclusion of this type of literature is specified along the present review where they constitute the 29 % of the final list of publications ($n_{total} = 118$; see Fig. 1 and Text S1).

Moreover, after reading the full texts of the publications included in this review, five fields of interest were defined to classify the studies and investigate potential temporal dynamics. The proposed categories are: physiology, distribution and spread, ecological impacts, socio-economic consequences, and management and potential uses.

2.2. Dataset

To evaluate the thermal conditions experienced by this macroalga, ten points were strategically selected along the distribution area of *R. okamurae* (regions where the highest and/or lowest temperatures were observed). These ten points are: Thau Lagoon (first place of colonisation), Al Hoceima (northern Morocco), Alicante, Azores Islands, Bilbao, Calanques National Park (southeast France), Ceuta, Dona Ana Beach (Algarve), Madeira Islands and Palermo.

The GLORYS12V1 product was used in order to collect because it offers global ocean reanalysis with eddy-resolving resolution (0.083° × 0.083°) across 50 vertical levels. This product is primarily based on the real-time global forecasting system of the Copernicus Marine Environment Monitoring Service (CMEMS). The underlying model is the NEMO platform, which is forced at the surface using ECMWF's ERA-Interim reanalysis data, transitioning to ERA5 reanalysis for more recent years. Observations are assimilated through a reduced-order Kalman filter, incorporating along-track altimeter data (Sea Level Anomaly), satellite sea surface temperature, sea ice concentration, and *in situ* temperature and salinity vertical profiles. Additionally, a 3D-VAR scheme is employed to correct for slowly evolving large-scale biases in temperature and salinity (Drévillon et al., 2018).

With the aim of evaluating the temperature time series at each of the previously specified points, we obtained daily temperature data both at the surface and at a depth of 20 m (which is mostly the bottom at almost all points) from January 2010 to December 2024. That depth was chosen based on previous studies that demonstrated that most of the *R. okamurae* populations inhabit between 0 and 20 m depth (García-Gómez et al., 2020; Sempere-Valverde et al., 2021). Once the data were extracted, we calculated the monthly maxima and minima at each point and depth to assess the temperature range in which *R. okamurae* typically proliferates and colonises.

3. Results and discussion

3.1. Description of the published papers

Since in 2009 a study indicated the presence of *R. okamurae* within the French coastal lagoon of Thau, there has been a gap of five years without publications about this invasive macroalga (Fig. 2). Then, a transitional period was found between 2015 and 2020 when some studies were published almost every year, but the cumulative number of studies was still very small ($n_{total} = 11$). Indeed, most studies included in the literature review were published within the last four years ($n_{total} = 107$) when the number of studies increased every year until 2024 (n_{total}

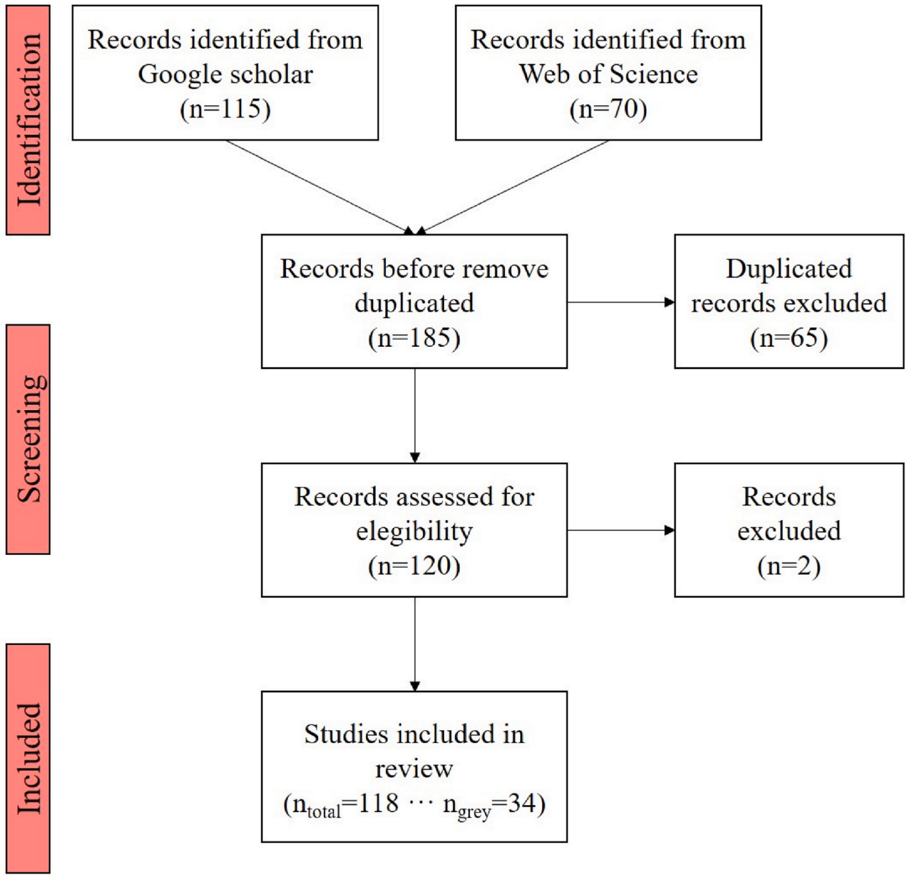

Fig. 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram of the screening process for the present study. Publications related to the invasion of *R. okamurae* were identified in Web of Science and Google Scholar (see main text). Number of grey publications is specified as "n_{grey}".

= 38). This rapid growth in the number of publications related to a crucial marine bioinvasion was also observed when the *Sargassum* blooms increased in frequency and magnitude. Fidai et al. (2020) demonstrated that the number of studies addressing these events increased from 8 to 64 in one decade (from 2000 to 2009 to 2010–2019). Therefore, it seems clear that research interest increases only when invasions become an ecological and socio-economic threat to coastal areas.

Regarding the comparison between peer-reviewed studies and grey literature, it is obvious that both types of publications increased at the same time although the greatest number of grey literature was registered in 2022 ($n_{grey} = 12$) instead of 2024 ($n_{grey} = 5$). The notable percentage of grey literature (29 %) makes this difficult to access literature a crucial resource to understand this rapid invasion in agreement with previous reviews about invasive macroalgae where the percentage of grey literature exceeded the 60 % (Klein and Verlaque, 2008). It is key to understand that the colonisation of new areas, as well as the coastal impacts and management actions in such drastic invasions, occurs at a high speed, which often is not coupled with the slow process of traditional publications in peer-reviewed journals. Given that, the recently observed increase of peer-reviewed studies and the reduction of grey literature could mean that the scientific community is paying more attention to this invasion, and the initial delay in publications has already been mitigated.

A clear temporal pattern was also observed among the fields of interest of those publications (Fig. 2). The few studies published until 2019 focused on the distribution and spread of *R. okamurae* but since then, several studies have investigated the ecological impacts of this invasion. Also in 2019, the first study addressing the management and potential uses of the invasive *R. okamurae* was published. This study opened a research gap that became the primary field of interest in 2023 and 2024 when more than 50 % of publications were added to this category. This trend is typical in drastic invasions, as several publications assessing opportunities to use *Sargassum* biomass appeared between 2015 and 2020, when the macroalgae had already spread across several tropical regions (Milledge et al., 2016; Thompson et al., 2020). By contrast, management actions are not always taken to attempt to cope with the spread of invasive species. For instance, *Caulerpa taxifolia* (M.Vahl) C. Agardh and *Caulerpa racemosa* (Forsskål) J.Agardh are invasive macroalgae with a similar capacity to colonise and modify native communities but the latter has received less scientific and public attention and most management actions have been focused on the eradication of *C. taxifolia* (Klein and Verlaque, 2008).

In 2021 a couple of studies from grey literature focused on the physiology of *R. okamurae* and since then, some studies assess the physiological characteristics of this invasive macroalga every year. Finally, it is worth noting that, as usual in these drastic biological invasions, after the ecological impacts there are also significant socio-economic consequences. For instance, after the invasive *Sargassum hystrix* var. *fluitans* colonised the coastal areas of Nigeria, the fishing communities evidenced several negative impacts such as limited access to fishing ground and clogged fishing gears which resulted in loss of effectiveness and catches (Solarin et al., 2014). The first study considering the economic consequences of *R. okamurae* bioinvasion was published in 2022, three years later than the first assessing its ecological impacts (Fig. 2), and it will likely become a growing field of interest in the next few years. In fact, the increasing number of publications related with the spread of *R. okamurae* suggest the constant colonisation of new areas and, thus, the appearance of future socio-economic impacts on these areas.

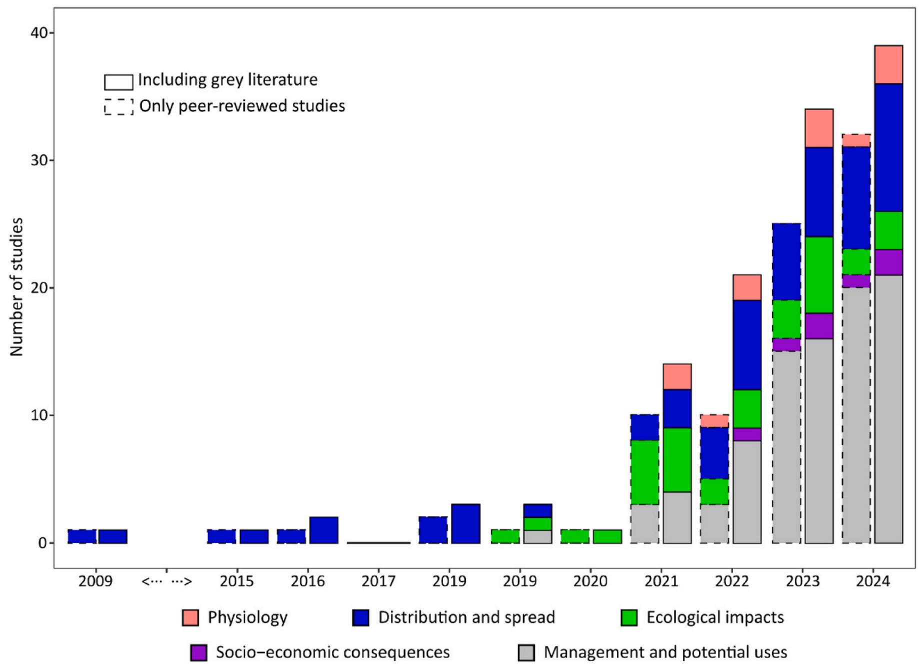

Fig. 2. Temporal dynamics in the number of studies assessing the invasion of *R. okamurae*. Publications by year and field of interest where the inclusion of grey literature is also specified.

This systematic literature review also revealed the existence of: (1) a concise mini-review focused on the potential applications of this invasive macroalga (Barcellos et al., 2023) and (2) a very recently published general review mainly assessing the biological aspects and management/uses of this invasion (Laamraoui et al., 2024). Given this, the present review aims to shed light on the spread mechanisms that have facilitated the rapid colonisation.

3.2. *Invasion dynamic*

Since *R. okamurae* was first identified in the French Mediterranean region in 2002 (Verlaque et al., 2009), more than a decade passed without any signs of this alga being recorded in Mediterranean regions. This changed in 2015, when a proliferation of *R. okamurae* was identified within the Strait of Gibraltar (Ceuta; Ocaña et al., 2016), which coincided with the highest recorded temperature between 2010 and 2017 (average of 24 °C and maximum of almost 28 °C; García-Gómez et al., 2020), marking the beginning of its exponential expansion and colonisation both in the Mediterranean and in Northeastern Atlantic bioregions (see Fig. 3).

Specifically, around the Strait of Gibraltar is where the higher proliferation of this alga has been detected, and since 2016, the surrounding areas (both in African and European regions; e.g. Altamirano-Jeschke et al., 2016) have been the most studied, with more than 20 regions found to be colonised by *R. okamurae*. The studies primarily focused on Mediterranean regions in Andalusia and Morocco (see Fig. 3). However, in recent years, several publications have shown that *R. okamurae* has reached the Italian (Bellissimo et al., 2024; Marletta et al., 2024; Bottalico et al., 2024) and French coasts (Ruitton et al., 2021; Borriglione et al., 2024). This last French region is particularly interesting because the algae was previously found nearby (close to Marseille; Verlaque et al., 2009) in 2002. This macroalga has also spread to Atlantic regions, being found in the Algarve (Liulea et al., 2024), Madeira Islands (Bernal-Ibáñez et al., 2022), Azores Islands (Faria et al., 2022a), and even along the North Atlantic coasts of Spain (Díaz-Tapia et al., 2025).

3.3. *Main drivers of propagation*

3.3.1. *Aquaculture*

Sea farming activities constitute one of the riskiest human-mediated global transfers of marine species (Hewitt et al., 2007). Indeed, the invasive *R. okamurae* reached the Mediterranean Sea as a result of an inadequate decontamination and quarantine process in the importation of M. *gigas* from the North Pacific with aquaculture purposes (Verlaque et al., 2009). The arrival of approximately 65 non-native seaweed species to the Mediterranean Sea is directly or indirectly linked to shellfish aquaculture (Boudouresque et al., 2020). For instance, Wolf et al. (2018) established the transport of shellfish species as the cause of the arrival of *Aglaothamnion halliae* (Collins) Aponte, Ballantine & Norris, 1997 and *Melanothamnus japonicus* (Harvey) Díaz-Tapia & Maggs, 2017 to the Venice Lagoon, a hotspot for marine invasions. The success of that unintentional movement of associated organisms mainly relies on the similarity in physiological tolerances between the target and associated species since transport and destination conditions should be optimum for the target species. In recent decades, measures have been implemented to limit the accidental transport of species via maritime routes, including regulations on ballast water (Gollasch and David, 2006), control of biofouling on vessels (Carrier et al., 2023), regulation of marine species trade (Simberloff and Rejmánek, 2011), inspection and disinfection protocols establishing quarantine zones (Hewitt and Campbell, 2010), as well as educational and awareness campaigns within the fishing sector (Piola and McDonald, 2012). Despite the risk mitigation measurements have improved over the last decades, the recently described introduction of *R. okamurae* in the Adriatic Sea was associated with the discharge of empty bivalve shells in recreational areas and the cultivation of M. *gigas* using seeds from French hatcheries (Bottalico et al., 2024).

Moreover, marine macrophytes are often used as packing material in order to transport live bait and seafood (e.g. clams, oysters, sea urchins). That macrophyte biomass is sometimes directly or indirectly discharged into the sea which is the main hypothesis proposed by Ruitton et al. (2021) to explain the introduction of *R. okamurae* in the Calanques National Park (France). The danger of wrapping bait with seaweeds was largely demonstrated in the past. For instance, this vector caused the

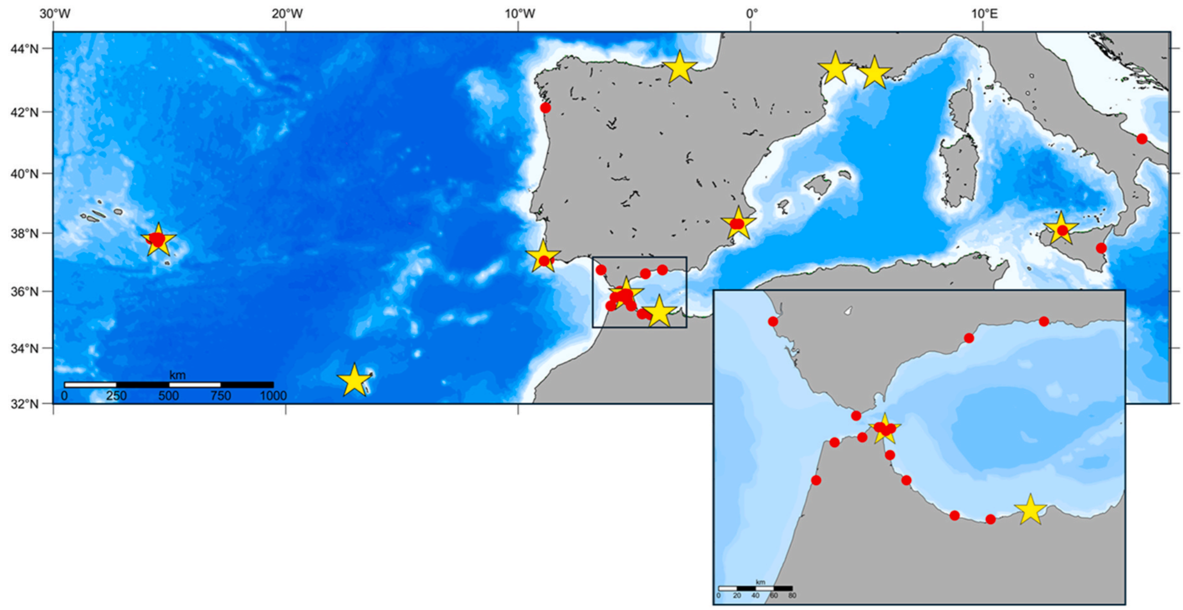

Fig. 3. Map showing the spread of *R. okamurae*. Regions where previous studies have recorded the presence of *R. okamurae* are indicated with red dots while yellow stars mark the points selected to analyse the temperature range experienced by the invasive alga.

introduction of *Codium fragile* (Suringar) Hariot into the San Francisco Bay (USA: Cohen et al., 2001) and *Fucus spiralis* Linnaeus in the Gruissan Lagoon (France: Sancholle, 1988). Therefore, shellfishing activities and the use of seaweeds as packing material are confirmed as two important drivers of colonisation. Nonetheless, multiple vectors have transported *R. okamurae* over long distances since a phylogenetic analysis has revealed great differences among near *R. okamurae* populations while sequence similarity was found among far populations (e.g. Madeira, Sicily and Adriatic Sea; Bottalico et al., 2024).

3.3.2. Maritime transports

The second and decisive introduction of *R. okamurae* in the studied bioregions was probably a consequence of the intense maritime traffic registered in the Strait of Gibraltar. García-Gómez et al. (2020) suggested this hypothesis due to the presence of two of the most important ports of Europe (Algeciras) and Africa (Tanger Med) where they often anchor Asian vessels. Invasive species can be unintentionally transported by maritime traffic in different ways (i.e. hull boring, hull fouling, dry and semi-dry ballast and ballast waters). Based on the morphological and biological characteristics of *R. okamurae* and its tolerance to large dark periods, several authors have also pointed out the ballast waters as the main introduction vector (e.g. Faria et al., 2022a; Terradas-Fernández et al., 2023). In agreement, the appearance of alien species in areas with intense maritime traffic has been reported worldwide (Seebens et al., 2016; Castro et al., 2020) and, consequently, several mitigation measurements have been adopted. In this regard, the International Convention for the Control and Management of Ships' Ballast Water and Sediments entered into force in September 2017, but the non-compliance or ineffectiveness of the proposed measures means that ballast water continues to be an active vector for the introduction of invasive species (Rak and Reuland, 2024).

Despite this second introduction event provoked a rapid eastward and westward expansion from the Strait of Gibraltar (García-Gómez et al., 2020), the colonisation of very far areas evidence different introduction events. Multiple invasions have been proved to favour the establishment of alien species, enhancing their invasiveness (Paolacci et al., 2021). In this line, maritime traffic has been proposed as the main propagation driver in areas such as the Azores archipelago (Faria et al., 2022a), Alicante Bay (Terradas-Fernández et al., 2023), the Atlantic and Mediterranean Moroccan shores (El Madany et al., 2024), and the north coast of Spain (Díaz-Tapia et al., 2025). However, the other drivers assessed in this study might have also contributed to the colonisation of these areas. It is worth highlighting, among other vectors of propagation, the use of fishing nets in areas colonized by the alga, which transport viable fragments of it (Ruiz and Carlton, 2003; Gollasch and David, 2006; Piola and McDonald, 2012), as well as the effect of transporting new species through hulls or anchors on fishing vessels (Hewitt and Campbell, 2010; Simberloff and Rejmánek, 2011).

3.3.3. Ocean circulation

The issues related to aquaculture and maritime traffic could be partially controlled through restrictive policies that ensure the prevention of algae transport. Nevertheless, the Atlantic-Mediterranean circulation itself also serves as a vector for transporting *R. okamurae* to new regions for colonisation. In this regard, García-Lafuente et al. (2023) demonstrated in a study in the Strait of Gibraltar that the Mediterranean Outflow Waters (MOW) are responsible for transporting *R. okamurae* from Mediterranean waters to the Gulf of Cádiz, finding thalli of the alga on the Atlantic shelf. However, the recent appearance of this species in regions such as the Algarve, Vigo, Bilbao, Madeira, and the Azores could be associated with the transport of these MOW along the Portuguese coast to northern Spain (the circulation of the MOW is shown in Fig. 4). Additionally, the fact that the main routes of the Meddies (Mediterranean Water Eddies) are directed towards the Azores and Madeira suggests that these anticyclonic gyres of Mediterranean water may carry *R. okamurae* thalli to these regions.

The finding by Mateo-Ramírez et al. (2023) of *R. okamurae* alive thalli at depths greater than 1000 m suggests that the alga can survive in darkness at temperatures around 10-15 °C, and that when this biomass reach a suitable region for reproduction, they are in good condition to colonise it. This fact gives *R. okamurae* a high invasion potential, making it possible for it to spread at great depths, not just at the surface, thus positioning the MOW as potential propagators of *R. okamurae*. However, from the Strait of Gibraltar to new colonisation areas, there are other possible transport routes for *R. okamurae*, such as the Canary Current moving southward or the influence of local winds that could move it to new regions.

In the case of the Mediterranean basin, the alga may have reached different Andalusian (e.g. Malaga and Almeria: Figueroa et al., 2020; Rueda et al., 2023) and Moroccan regions from Ceuta through the two

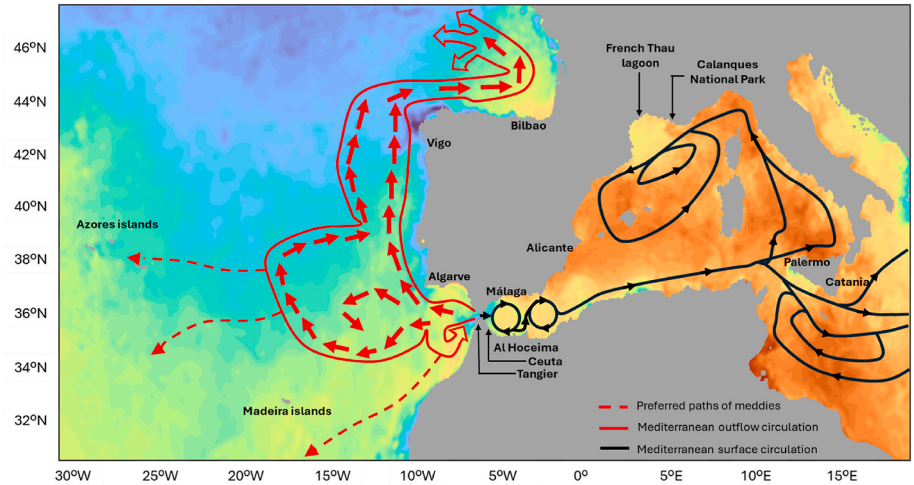

Fig. 4. Schematic map of the surface Mediterranean circulation (black lines, modified from Parras-Berrocal et al., 2020), the Mediterranean outflow circulation (red lines, modified from Izquierdo and Mikolajewicz, 2019), and the preferred paths of meddies (dashed red lines, modified from Izquierdo and Mikolajewicz, 2019). Additionally, some of the locations mentioned in the text as areas colonised by *R. okamurae* were added.

Alboran cyclonic gyres (Fig. 4). Moreover, from this gyre, the Algerian current extends to Sicily, where colonisation studies were carried out in Palermo and Catania in 2023 and 2024, even recently reaching the Adriatic Sea (Bottalico et al., 2024). Although the Mediterranean circulation would suggest that the alga has reached Sicily before Calanques National Park, this is not the case. *Rugulopteryx okamurae* was found in the surrounding open sea in 2013 and its settlement in the rocky shores was confirmed in 2016 within a No Take Zone of the Calanques National Park (Borriglione et al., 2024 and references therein), while it was confirmed in 2023 in Sicily (Bellissimo et al., 2024). This could be due to the fact that although the Mediterranean circulation continues from the north of Sicily to the Gulf of Lion, *R. okamurae* was found near this region in 2002, but it was not until 2015 in Ceuta that invasion studies began. Therefore, this macroalga might have reached France long before arriving in Ceuta, which is why it was found in this region in the period 2013. From France to the Spanish coasts (Alicante: Terradas-Fernández et al., 2023), the alga may has dispersed via the Mediterranean northern current. It is worth noting that although Mediterranean circulation may contribute to the propagation of *R. okamurae*, the alga itself tends to settle within the water column, and therefore, it is not necessarily being always transported.

Without diminishing the importance of other vectors of propagation, we propose further studies aimed at understanding the potential propagation routes supported by currents. Various studies have proposed this dispersal vector for *R. okamurae* in the literature such as the work of Tursi et al. (2023) in the Adriatic Sea, Bernal-Ibáñez et al. (2022) in Madeira, and the studies by García-Lafuente et al. (2023) and García-Gómez et al. (2020) in the Strait of Gibraltar.

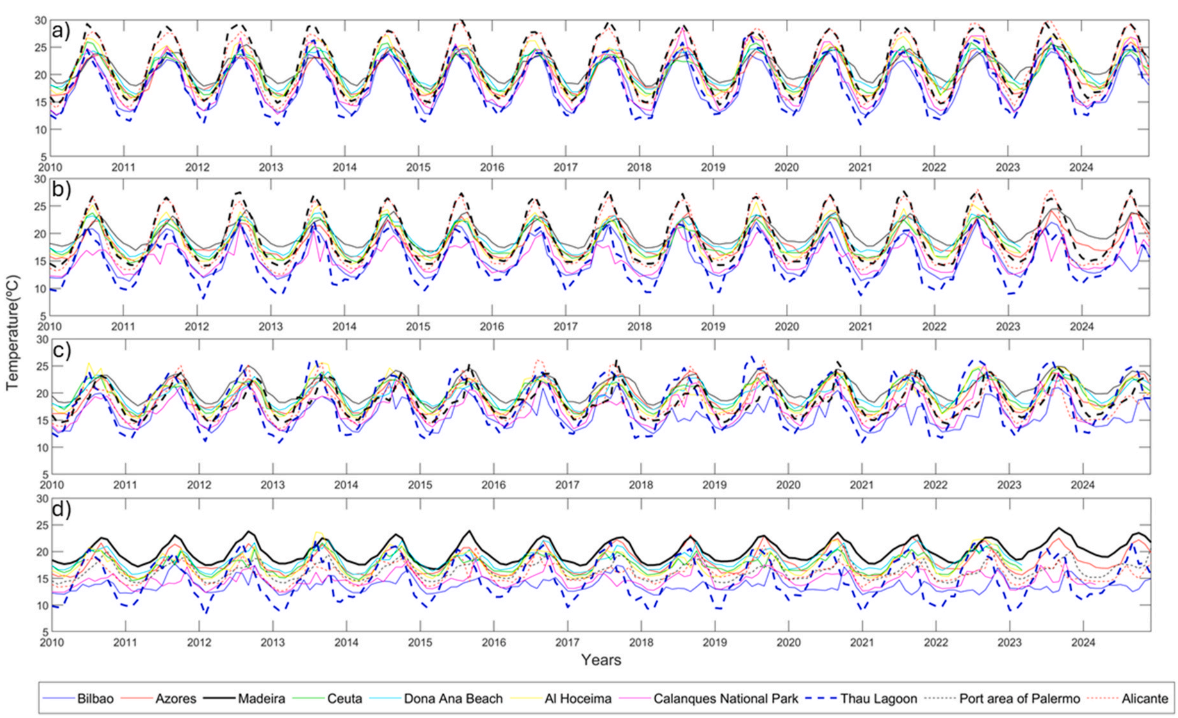

Fig. 5. Time series from 2010 to 2024 of the maximum surface temperatures (a), minimum surface temperatures (b), maximum temperatures at 20m (c), and minimum temperatures at 20m (d), calculated using daily data for each month in the 9 selected regions.

3.4. Temperature range on invaded areas

The fact that the thermal characteristics of the Mediterranean and Atlantic surface waters are so different makes the proliferation range of *R. okamurae* very broad. Therefore, we conducted a comparison using the GLORYS dataset of maximum and minimum temperatures from 2010 to 2024, selecting ten points (see methodology) to study the thermal range of *R. okamurae* (Fig. 5).

In this regard, we found that the highest surface temperatures reached up to 30 °C during the summer months in the easternmost region of our Mediterranean study area (Port of Palermo), while these maximum temperatures do not exceed 15 °C in northern Spain during the winter months (Bilbao), even reaching nearly 10 °C in Thau Lagoon (Fig. 5a). The fact that maximum temperatures do not fall below 15 °C (including the winter months), provides an opportunity for *R. okamurae*, as this is the temperature at which peak growth occurs (Hwang et al., 2009).

Regarding minimum surface temperatures, these same regions again showed the widest ranges, with Bilbao standing out with a minimum of 10 °C and Thau lagoon reaching 7 °C (Fig. 5b). As for the temperature range found at 20 m depth, we observed that the northern region of Morocco (Al Hoceima: El Madany et al., 2024) and Alicante recorded the highest temperatures, showing an annual cycle with temperatures very similar to those at the surface, with maximums shifted to 25 °C (Fig. 5c). In terms of minimums, Bilbao again recorded the lowest temperatures, where it seems that the annual cycle is not as pronounced as at the surface, with minimum temperatures barely exceeding 15 °C (Fig. 5d). This fact highlights the thermal range of colonisation of *R. okumurae*, as it remains present in regions with temperatures below 10 °C to areas with a maximum of 30 °C. These temperatures are consistent with Díaz-Tapia et al. (2025), who highlight that the optimal temperatures for *R. okamurae* are well above the range found in northern Spain, where minimums can even fall below 10 °C (Mercado et al., 2022). However, previous studies have shown that *R. okamurae* can survive at temperatures below its optimal growth range (under 15 °C: Mateo-Ramírez et al., 2023), taking advantage of spring and summer seasons to reproduce exponentially. This is the case in some regions with seasonal minimums close to 10 °C, such as Bilbao, Calanques National Park or Thau lagoon.

To evaluate the thermal conditions of each colonised region, the maximum and minimum temperatures both at the surface and at 20 m depth were calculated in the year when colonisation was observed (Table S1). Notably, the Calanques National Park in 2016 showed extreme values with surface temperatures exceeding 28 °C and minimums below 13 °C, similar to the cases of the Sicily regions (Port of Palermo and Bandita) or Alicante, where temperatures nearly reached 30 °C with minimums of 15 °C, standing out above all, the Adriatic Sea region with temperatures reaching 12 and 31 °C. These temperature ranges demonstrate the suitability of most regions colonised by *R. okamurae*, as even though the minimum temperatures in some areas (e.g., northern Spain) are lower than the minimum growth temperature for *R. okamurae*, this species can persist in those temperature ranges and take advantage of summer periods to grow and reproduce (García-Gómez et al., 2020). Therefore, this situation only heightens concerns about the potential for colonisation in adjacent regions, making it highly likely that the macroalga is already present. In the context of climate change and considering recent perspectives on the relationship between temperature and the spread of *R. okamurae*, an exponential colonisation of the algae towards northern regions could be expected. It is worth noting that this review was conducted up until the year 2024 and that, during the publication period, new colonisation regions have already been detected. For instance, studies such as Jiménez and Riera (2025) show the presence of *R. okamurae* in the Canary Islands since 2022.

4. Conclusions

The invasion of *R. okamurae* has sparked growing scientific interest in recent years, as shown by the increase in publications, particularly since 2020. This trend underscores the importance of understanding and managing bioinvasions in marine ecosystems, especially in vulnerable areas like the Mediterranean and northeastern Atlantic. Research has evolved from initially focusing on the distribution and spread of *R. okamurae* to examining its ecological and socioeconomic impacts, as well as exploring potential uses for the biomass it generates—an approach that may help alleviate some of its negative consequences.

Rugulopteryx okamurae's ability to adapt to a broad temperature range, from 10 °C in the northern Atlantic to 30 °C in the Mediterranean, has facilitated its spread across multiple regions. Literature suggests that the colonisation of new areas is mainly driven by human-induced aquaculture and maritime traffic activities and environmental factors such as ocean circulation and global warming. Thus, *R. okamurae*'s wide thermal tolerance, its capacity for rapid reproduction in favourable conditions and the presence of different dispersal vectors, explains its persistence and expansion along the studied areas. However, the present review shows that there are still great uncertainties regarding the main propagation routes of *R. Okamurae*, and that the exponential publication of studies on new regions should be accompanied by research analyzing the arrival routes of the alga. The thermal range of colonisation of *R. Okamurae* should not only serve as prior knowledge but also as a warning to protect new regions from colonisation and to develop measures to reduce the alga's propagation routes to new ecosystems.

The ecological impacts of *R. okamurae* include the displacement of native species, habitat degradation, and adverse physiological effects on key fauna (e.g. Navarro-Barranco et al., 2019; Casal-Porras et al., 2021; Borriglione et al., 2024). In terms of socio-economy, the invasion has negatively affected sectors like fishing and tourism, resulting in considerable economic losses due to reduced catches (Mogollón et al., 2024) and the accumulation of *R. okamurae* along beaches, which diminishes tourist appeal (Altamirano-Jeschke et al., 2022; Faria et al., 2022b). Aquaculture and maritime traffic constitute vectors where the dispersal of *R. okamurae* could be avoided or mitigated implementing risk mitigation measurements such as appropriate quarantine standard and different cleaning methods (Hewitt et al., 2007). By contrast, the potential ability of *R. okamurae* to disperse viable thalli through currents makes it impossible to prevent the arrival of this algae. The most efficient measure to avoid its establishment might be to maintain a healthy ecosystem.

In short, the invasion of *R. okamurae* highlights the need for an integrated response that spans scientific research, effective policy implementation, and public awareness. Promoting a circular economy and local initiatives to utilize *R. okamurae* biomass represent opportunities to mitigate the invasion's impacts and strengthen social cohesion (Vegara, 2024). Finally, preventing the general habitat degradation and implementing long-term monitoring programs is recommended to reduce the arrival of *R. okamurae*, understand the dynamics of this invasion and anticipate potential future consequences.

CRediT authorship contribution statement

Salvador Román: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Rubén Vázquez:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

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

Acknowledgements

Rubén Vázquez was supported by the Spanish Ministry of Science, Innovation and Universities, Through Grants (I + D + I PID2021-128656OB-I00).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107093.

Data availability

The data is openly available at https://marine.copernicus.eu/

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