



Understanding the invasion of the macroalga *Rugulopteryx okamurae* (Ochrophyta) in the northern Alboran Sea through the use of biogeographic models

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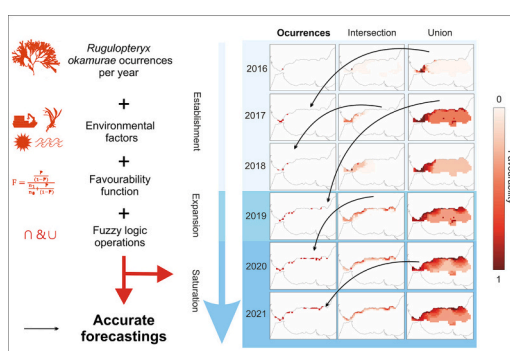
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HIGHLIGHTS

- Three different phases of the *Rugulopteryx okamurae* invasion were identified: establishment, expansion and saturation.
- Favourability functions based on yearly occurrences and fuzzy logic operations generated predictive invasion models.
- Establishment was driven by accessibility through dispersion and oceanographic characteristics.
- All factors (biotope, biocoenosis, coastal influence, dispersal accessibility, and oceanography) affected expansion.
- Saturation was driven by all environmental factors but coastal influence.

GRAPHICAL ABSTRACT

Invasion process of the macroalga *Rugulopteryx okamurae* (Ochrophyta) in the northern Alboran Sea.



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ABSTRACT

Rugulopteryx okamurae is a brown alga native to the northwestern Pacific and invasive elsewhere. It was first sighted in the southern Strait of Gibraltar in 2015, expanded to the northern Strait of Gibraltar in 2016, and had covered most of the northern Alboran Sea by 2021. Understanding the factors that may explain its different phases of colonisation is crucial for developing mitigation and control measures. We modelled the yearly distribution of *R. okamurae* in the northern Alboran Sea from 2016 to 2021 using the favourability function, which produces commensurable biogeographic models despite variations in species prevalence across years. This function also allows the use of fuzzy logic operations to combine previous environmental models based on different explanatory factors, namely biotope, biocoenosis, coastal influence, accessibility through dispersion, and oceanographic characteristics. Significant environmental models were assembled, and their fuzzy intersection and union applied. This resulted in two final biogeographic models for each year, which were used to predict the distribution of the species in following years. The biogeographic models exhibited a high predictive capacity, as most years accurately predicted colonisation in the following year or even multiple years ahead. Accessibility

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through dispersion and oceanographic characteristics were critical during the initial years of establishment, while complete establishment depended on all five factors together. Expansion to the whole northern Alboran coast was explained by favourable conditions for any of the explanatory factors, while all factors except coastal influence explained the saturation of the invasion. We conclude that the biogeographic models prove valuable in understanding the factors that contributed to the spread of *R. okamurai* in the northern Alboran Sea. This approach could help prevent further colonisation and mitigate the ecosystem and commercial consequences of *R. okamurai*'s invasion.

1. Introduction

Biological invasions pose significant challenges from a scientific and environmental perspective (Rizzo and Vega Fernández, 2023). Invasive species are defined as organisms that establish themselves in a new environment far from their original distribution, often as a result of human activities, and have a detrimental impact on the biodiversity, ecology and ecosystem services of the invaded region (Simberloff et al., 2013; Cassey et al., 2018).

Over 900 species have been introduced into the Mediterranean Sea since the beginning of the 20th century, about 10–15 % of which are invasive (Zenetos and Galanidi, 2020; Öztürk, 2021). The arrival of these marine organisms can be attributed to various factors, including ballast waters from maritime traffic (primarily fishing and commercial ships), habitat modification, climate change and fishing-related activities such as aquaculture (Bianchi and Morri, 2003; Claudet and Fraschetti, 2010; Coll et al., 2010).

The brown macroalga *Rugulopteryx okamurai* (E.Y. Dawson) Hwang et al., 2009, belongs to the Dictyotaceae family, and is native to the northwestern Pacific (Hwang et al., 2009; Verlaque et al., 2009). Its remarkable capacity for vegetative reproduction, including asexual strategies such as the production of mitotic monospores, and its survival under extreme temperature fluctuations, anthropised environments and low light availability, endow it with significant colonisation and invasion potential (Rosas-Guerrero et al., 2018; Altamirano-Jeschke et al., 2019; Mateo-Ramírez et al., 2023). Other species traits, such as its production of anti-herbivory metabolites, nitrogen-retention capacity, photosynthetic activity resilience, and ability to adapt to various orientations and depths, also contribute to the species' invasive ability (Casal-Porras et al., 2021). *R. okamurai* specimens mainly colonise rocky substrates, but have also been observed on mixed and sandy bottoms (Navarro-Barranco et al., 2019; García-Gómez et al., 2021a; Sempere-Valverde et al., 2021).

Ocaña et al. (2016) first reported massive proliferation of a dictyotalean seaweed in Spanish waters in Ceuta (southern Strait of Gibraltar) in 2015, which was identified as *R. okamurai* by Altamirano-Jeschke et al. (2016); Altamirano-Jeschke et al. (2017). It was likely introduced via ballast water, hull fouling or mariculture (Rosas-Guerrero et al., 2018; Ministry for Ecological Transition and Demographic Challenge, 2020). In 2016, it was first sighted in the north of the Strait of Gibraltar (Algeciras, Cádiz), and later spread throughout the northern region of the Alboran Sea, reaching the eastern limit of this sea (Almería province) in 2021 (García-Gómez et al., 2018, 2020; Ministry for Ecological Transition and Demographic Challenge, 2020; Bellissimo et al., 2024). This colonisation process was closely monitored by the Environmental Information Network of Andalusia (REDIAM). The species has now expanded further east in the Mediterranean Sea (Terradas-Fernández et al., 2023; Bellissimo et al., 2024).

Among the confirmed impacts of *R. okamurai* in the Alboran Sea are the displacement of native macroalgal and marine angiosperm meadows, such as those of *Posidonia oceanica* (Linnaeus) Delile, 1813 (a seagrass endemic to the Mediterranean), the homogenisation and impoverishment of substrates, and economic damage to sectors such as fishing and tourism (Verlaque et al., 2009; Ministry for Ecological Transition and Demographic Challenge, 2020; Báez et al., 2023; Mogollón et al., 2023). *R. okamurai* also significantly affects sessile

invertebrates, including sponges, tubular polychaetes and corals (notably gorgonians), leading to a reduction in species richness (El Aamri et al., 2018; García-Gómez et al., 2018, 2021a). Additionally, organisms such as ascidians and echinoderms may be impacted, as well as molluscs like *Charonia lampas* (Linnaeus, 1758) and *Patella ferruginea* Gmelin, 1791, both of which are threatened species in the region (Ministry for the Ecological Transition and Demographic Challenge, 2022).

In this context, it is imperative to analyse the sequence of colonisation locations of *R. okamurai* in the northern Alboran Sea. According to Shigesada and Kawasaki (1997), the encroachment of an invasive species into a new territory typically occurs in three phases: establishment, in which the species begins to colonise a new area; expansion, where the population starts to grow exponentially and the area occupied by the species increases; and saturation, when the species fills the distribution gaps and reaches its carrying capacity in the invaded territory. It would be useful to determine whether the invasion of *R. okamurai* in the northern Alboran Sea followed this pattern and what the environmental drivers of the colonisation process were over these years. To this aim, we need assessment tools that allow short- to medium-term forecasting of the colonisation process, which would facilitate the development of preventive measures in areas not yet colonised or where colonisation has just begun.

Biogeographic models have proved to be valuable tools for analysing species–environment relationships and predicting new invasion areas (Fischer et al., 2016; Aliaga-Samanez et al., 2022; Di Febbraro et al., 2023; Rodríguez et al., 2024), and are thus essential to conservation (Real et al., 2008; Acevedo et al., 2010; Romero et al., 2014; Baquero et al., 2021). Examples of their application in invasive macroalgae control include the use of generalised additive models (GAM) to successfully capture the spatial and temporal distribution of the invasive spread of *Caulerpa taxifolia* (M.Vahl) C.Agardh, 1817 in the Eastern Mediterranean (Katsanevakis et al., 2010). Another species, *Undaria pinnatifida* (Harvey) Suringar, 1873, was modelled using the favourability function to examine relationships between the seaweed's distribution and environmental variables in Northern Iberia (Báez et al., 2010). These biogeographic models were also previously utilised for our alien species of interest, with Muñoz et al. (2021) and Bellissimo et al. (2024) building a global biogeographic model that forecast the colonisation of the Mediterranean Sea by *R. okamurai* with coarse resolution.

The principal aim of this study was to biogeographically analyse the spatial and temporal colonisation of *R. okamurai* in the northern Alboran Sea, from the first sighting of the species in 2016 to the colonisation of the whole coastal fringe in 2021. We hypothesised that the colonisation process of *R. okamurai* occurred in distinct phases – establishment, expansion and saturation – each driven by a combination of environmental factors. We predicted that the influence of these factors would vary throughout the invasion process, reflecting the different ecological requirements and dispersal mechanisms at each stage. Using environmental and biogeographic modelling, we aimed to identify the environmental factors involved in the different phases of the colonisation. This could allow early identification of critical areas that specific management measures could be targeted towards to prevent further invasion in this affected region and elsewhere.

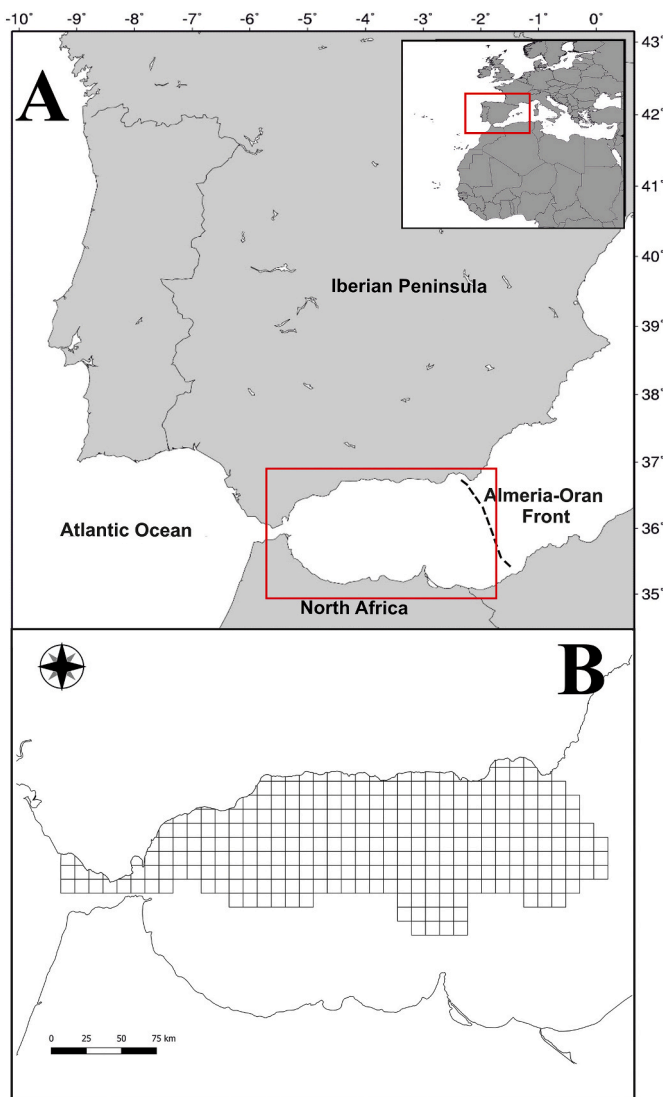


Fig. 1. Area of study (A). The northern Alboran Sea (B) divided into a grid of approximately 10 × 10 km. The grid was downloaded from the Ministerio para la Transición Demográfica (MITECO) website: <https://www.miteco.gob.es/>.

2. Materials and methods

2.1. Study area

The Alboran Sea is a marine basin situated in the western part of the Mediterranean Sea (Fig. 1A). It is bordered by the Iberian Peninsula to the north and northern Africa to the south, rendering it a geographically intricate and unique region (Bellido et al., 2020). From an oceanographic standpoint, the Alboran Sea experiences intense dynamics, influenced by two primary currents – the North Atlantic Current and the Western Mediterranean Current – that converge in this area (Rodríguez Martínez, 1989; Real et al., 2021). This interplay of currents impacts the physical and chemical properties of the water, generating temperature and salinity gradients that influence the distribution of marine biodiversity (Oguz et al., 2014; Bosso et al., 2022; Pearman et al., 2023).

We focused on the northern part of the Alboran Sea (Fig. 1B), as the data available on *R. okamurai* distribution are considerably more comprehensive there than in the southern part of the Alboran Sea.

2.2. Variable selection

We compiled an *R. okamurai* distribution dataset recorded by

REDIAM (https://portalrediam.cica.es/descargas?path=%2F08_AMBITOS_INTERES_AMBIENTAL%2F02_LITORAL_MARINO%2F03_BIOLOGIA%2FspeciesInvasorasLitoral%2FInfGeografica%2FInfVectorial%2FShapes), covering the period from 2016 to 2021. This dataset comprised 143 observations of the species, either directly observed attached to substrata, or as beach-cast algae. As these data were spatially and temporally autocorrelated, we latticed the study area spatially and temporally so that only the spatial structure due to population, community dynamics and biogeographic processes was maintained (Legendre, 1993), avoiding the effect of the local accumulation of data in space and time. We used a grid of approximately 10 × 10 km, comprising 305 cells, to divide the study area into Operational Geographic Units (OGUs). This grid can be downloaded from the Ministry for the Ecological Transition and Demographic Challenge (MITECO) website (<https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/bdn-cart-aux-descargas-marina.html>). We compiled a set of 1830 Operational Spatio-Temporal Units (OSTUs) resulting from crossing the 305 OGUs of the spatial coverage with the 6 years of the study period. The species was observed in a total of 65 OSTUs.

These data were transformed into a binary variable, with a value of 1 denoting occurrence of the species and a value of 0 indicating no occurrence in each OSTU. We selected 123 variables to potentially explain this distribution, which were divided into 5 explanatory factors: biotope (8 variables), biocoenosis (8 variables), coastal influence (11 variables), accessibility through dispersion (4 variables) and oceanographic characteristics (92 variables). The biotope factor grouped variables related to the percentage of seafloor substrate types (such as the percentage of rocky or sandy bottoms), while the biocoenosis factor encompassed the presence of other invasive species as well as the cover percentage of *P. oceanica* meadows. Coastal influence combined physicochemical and biological data from coastal inflows, including variables related to eutrophication. Accessibility through dispersion grouped variables that could explain the dispersal of *R. okamurai* in the northern Alboran Sea, such as maritime traffic. Lastly, the oceanographic characteristics factor comprised variables such as primary production, temperature, depth or currents. These variables were considered stable across the years, except for the presence of other invasive species, for which the data were specific to each year. The pool of variables, their source and their adscription to explanatory factors are shown in Suppl. Mat. Table I.

2.3. Building models

We built an explanatory model for each year and explanatory factor using the statistical software IBM SPSS Statistics version 28. The initial phase involved evaluating the independent explanatory capability of each predictor variable. This assessment was based on the significance of Rao score tests derived from univariate logistic regressions, where the probability of occurrence (or no occurrence) of the species was analysed against the variation in the values of each predictor variable separately. The relationship between a dependent variable (occurrence/absence of *R. okamurai*) and each predictor variable were analysed using logistic regressions:

$$P = \frac{e^y}{(1 + e^y)}$$

where P is the probability of occurrence of *R. okamurai* in a certain OSTU, e is the base of the natural logarithm and y is a polynomial 'logit function' like the one shown below:

$$Y = \beta_0 + \beta_{1x}$$

where β_0 is a constant and β_{1x} is the predictor variable coefficient x (Tabachnick and Fidell, 2013).

To address the potential rise in type I errors resulting from testing multiple variables, we assessed the False Discovery Rate (FDR) following the method proposed by Benjamini and Hochberg (1995). This

procedure orders the variables by decreasing importance (increasing the estimated p value for each one), with i being the position of each variable in this ordered list, and only accepts variables up to the highest position i whose p value is less than i^*q/V , where V is the total number of variables tested and q is the false discovery rate. Thus, we retained in our workflow the variables that were statistically significant in univariate logistic regressions after controlling for an FDR value lower than $q < 0.05$.

Then, to assess whether the combination of variables could have a higher explanatory power than the individual variables, we produced an ensemble model for each factor and year. We conducted a stepwise multivariate logistic regression of the occurrence of *R. okamurae* on all the retained variables of each factor, employing forward conditional selection. The parameters of the logit functions were estimated by a gradient ascent machine learning algorithm. To mitigate redundancy due to multicollinearity among predictor variables belonging to the same explanatory factor, we computed pairwise Spearman's correlation coefficients (r) among variables within each explanatory factor. Where two variables corresponding to the same explanatory factor and included in the multivariate logistic regression model were significantly correlated ($p < 0.01$), we selected the variable most significantly correlated with the occurrence of the species according to the univariate Rao score tests, removed the other variable, and the multivariate logistic regression was repeated. This process allowed us to derive progressively more complex and informative probability models for each factor and year.

Nevertheless, as the probability is contingent not only upon a species' response to the predictor variables but also upon its overall prevalence in an area (Cramer, 1999), the outcomes of these models are not amenable to direct comparison among years that differ in their prevalence of *R. okamurae* in the study area (Pulido-Pastor et al., 2018). To address this issue, in the final phase, we employed the favourability function (Real et al., 2006; Acevedo and Real, 2012) to obtain explanatory models. This function is derived from probability and yield values for each factor and year that are independent of the species prevalence in the study area in that particular year. As a result, it enables comparability of the species' response to the predictor variables (favourability for the species) over the years, even when they exhibit different prevalence.

The Favourability Function is described by the following formula:

$$F = \frac{\frac{P}{1-P}}{\left(\frac{n_1}{n_0}\right) + \left(\frac{P}{1-P}\right)}$$

where F is the degree of favourability of *R. okamurae* in every OSTU, P is the probability of the presence obtained using logistic regression, and n_1 and n_0 are the number of occurrences and absences, respectively. Favourability measures the degree to which local spatio-temporal conditions allow a spatio-temporal probability different to that expected by chance, defining this chance probability as the prevalence of the species in the study area at the given year (Acevedo and Real, 2012). In ecological terms, a favourability value of 0.5 would imply that local environmental conditions have no significant impact on the probability of *R. okamurae* being present. Essentially, this would signify that the probability of occurrence remained consistent with the overall prevalence of *R. okamurae* across the entire dataset. On the other hand, a local favourability value exceeding 0.5 would suggest that the environment is conducive to *R. okamurae* occurrence. Conversely, a value below 0.5 would indicate that the prevailing environmental conditions are unsuitable or detrimental for *R. okamurae* in the year analysed. This concept emphasises the critical relationship between a species' occurrence and the specific ecological conditions of its habitat (Acevedo and Real, 2012).

We built explanatory models for each of the five factors described above and per year (2016, 2017, 2018, 2019, 2020, 2021). In cases where the distribution of *R. okamurae* was explained by more than one factor, we performed fuzzy logic operators, namely fuzzy intersection (minimum favourability of the significant models at each OSTU) and fuzzy union (maximum favourability of the significant models at each OSTU), to obtain the two final biogeographic models (Barbosa and Real, 2012). Fuzzy logic is a mathematical approach that enables the handling of imprecision or uncertainty by representing the membership of elements to sets in a gradual, rather than dichotomous (full or no membership), manner. In other words, instead of setting absolute boundaries, fuzzy logic allows for defining transition zones where an element can partially belong to multiple sets (Olivero et al., 2013). Fuzzy intersection indicates the degree to which the OSTUs were favourable for the species due to all the significant factors together, whereas fuzzy union indicates

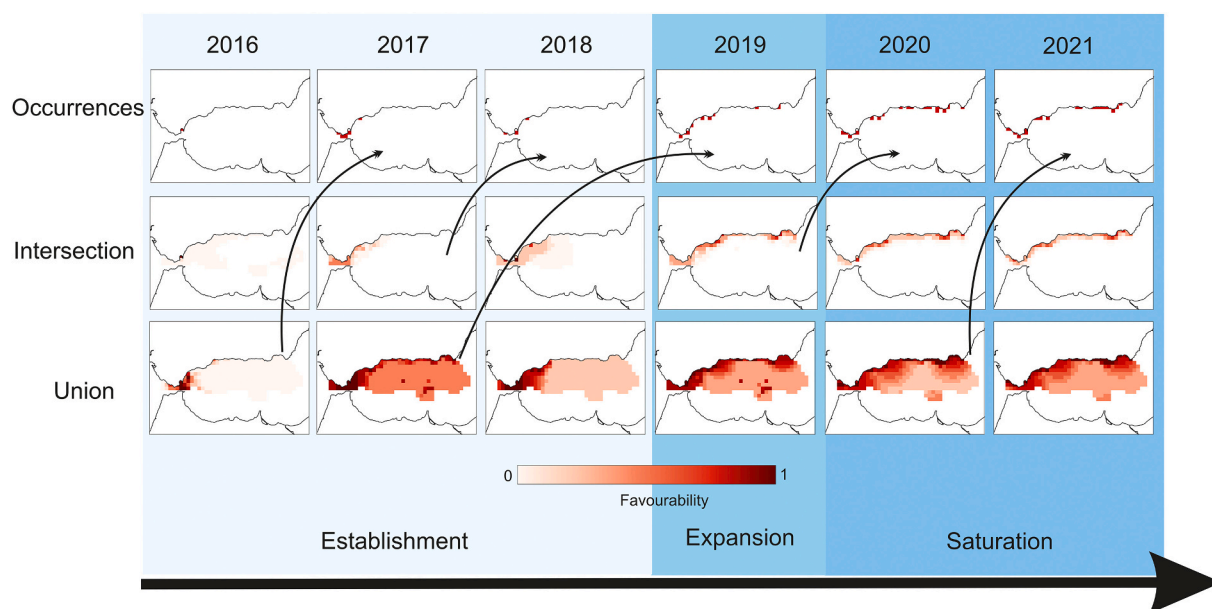


Fig. 2. Occurrence data and biogeographic models of *R. okamurae* (intersection and union) per year. The three phases of a successful invasion in only 6 years can be clearly observed: establishment (2016–2018 period), expansion (2019) and saturation (2020–2021 period). The arrows indicate the models that best predict the following years (Table 3). Union: Maximum of the favourability. Graphic scale and orientation as in Fig. 1.

Table 1

Explanatory variables along with the factor they are associated to, their slope (B) and significance of the Rao's score test for each significant explanatory model of the distribution of *R. okamurae* per year. Variable code definition can be consulted in supplementary Table 1.

Year	Factor	Variable	B	Rao's <i>P</i>	
2016	Accessibility through dispersion	Density of maritime traffic	4.489E-03	7.683E-30	
	Oceanographic characteristics	Photosynthetic Available Radiation	−52.434	5.971E-04	
2017	Biotope	Fine mud	−7.175	6.798E-05	
	Biocoenosis	Presence of <i>Caulerpa racemosa</i>	3.391	8.442E-05	
	Coastal influence	Mean Nitrates	15.113	6.444E-03	
		Mean O ₂ in surface	−0.665	1.884E-03	
2018	Accessibility through dispersion	Distance to the Strait of Gibraltar	−6.454E-05	3.993E-05	
	Oceanographic characteristics	Minimum nitrate in surface	2860.222	5.434E-13	
	Biocoenosis	Presence of <i>Asparagosis taxiformis</i>	6.400	4.909E-31	
	Accessibility through dispersion	Distance to the Strait of Gibraltar	−4.966E-05	4.852E-03	
	Oceanographic characteristics	Minimum nitrate in surface	1697.565	6.447E-06	
2019	Biotope	Fine mud	−6.831	1.709E-08	
	Biocoenosis	Posidonia meadows	41.922	9.189E-10	
	Accessibility through dispersion	Presence of <i>Asparagosis taxiformis</i>	3.021	7.473E-07	
		Distance to ports	−5.419E-05	2.840E-05	
		Oceanographic characteristics	Bathymetry	5.517E-03	4.566E-06
		Mean primary productivity in surface	2561.195	7.324E-06	
		Mean currents velocity in surface	4.992	2.683E-05	
		Biotope	Mixed coarse sediment	4.769	1.294E-13
			Distance to the coast	−3.344E-04	4.502E-09
	Biocoenosis	Posidonia meadows	92.934	1.902E-11	
Presence of <i>Asparagosis taxiformis</i>		4.903	1.619E-20		
2020	Accessibility through dispersion	Distance to ports	−3.256E-05	2.905E-04	
	Oceanographic characteristics	Bathymetry	0.0137	4.669E-10	
		Minimum nitrate in average depth	0.445	9.785E-12	
		Mean dissolved molecular oxygen in surface	1.190	6.629E-07	
	Biotope	Mixed coarse sediment	4.946	2.193E-12	
		Distance to the coast	−4.648E-04	1.107E-09	
		Biocoenosis	Posidonia meadows	87.131	1.268E-12
		Presence of <i>Asparagosis taxiformis</i>	4.781	5.830E-19	
		Presence of <i>Caulerpa racemosa</i>	23.662	3.601E-07	
		Distance to ports	−3.265E-05	2.092E-04	
2021	Oceanographic characteristics	Bathymetry	0.0109	1.185E-10	
		Mean dissolved molecular oxygen in surface	4.148	4.664E-07	
		Maximum salinity in average depth	1.377	4.996E-07	
		Minimum silicate in surface	31.267	1.509E-05	

the degree to which the OSTUs were favourable for the species due to any of the significant factors.

2.4. Model evaluation

We evaluated the explanatory capacity, in terms of discrimination and classification power, of the significant explanatory models and the biogeographic models on the occurrence or not of *R. okamurae* over the OSTUs during the years used to build the models (Abebe et al., 2024; Bosso et al., 2024). We also evaluated, in the same terms, the predictive capacity of the biogeographic models over the occurrence or not of *R. okamurae* over the OSTUs during the subsequent years to those used to build the models. We calculated the Area Under the Curve (AUC) to evaluate the discrimination capacity (Lobo et al., 2008). AUC is a widely used metric for assessing the discriminatory capacity in species distribution modelling. It measures how well a model can distinguish between occurrences and absences. An AUC value of 0.5 indicates a model with no discrimination power (random predictions), while a value of 1.0 indicates perfect discrimination. Typically, models with AUC values above 0.7 are considered to have acceptable performance, with values above 0.9 reflecting outstanding performance (Hosmer and Lemeshow, 2000; Jiménez-Valverde, 2012).

Classification ability was quantified using a favourability value of 0.5 as a classification threshold and seven different indices: sensitivity (proportion of OSTUs where the species occurred that were classified as favourable), specificity (proportion of OSTUs with no occurrence of the species that were classified as unfavourable), true skill statistics (TSS) (the degree to which both the sensitivity and the specificity were high), correct classification rate (CCR) (proportion of OSTUs with and without occurrence of the species that were correctly classified as favourable or

unfavourable, respectively), over-prediction rate (proportion of favourable OSTUs with no occurrence of the species), under-prediction rate (proportion of unfavourable OSTUs where the species occurred) and Cohen's Kappa coefficient (degree of good classification, taking into account the possibilities of random correct classification).

3. Results

3.1. Modelling *R. okamurae* colonisation potential

The occurrence of *R. okamurae* remained close to the Strait of Gibraltar during the three first model years (2016–2018). The distribution then leaped to the eastern limit of the Alboran Sea in 2019, and the gaps in distribution along the northern coast of the Alboran Sea began to be filled in 2020 and 2021 (Fig. 2). These three respective periods thus represent the phases of establishment, expansion and saturation of the invasion of the northern coast of the Alboran Sea (Fig. 2). The explanatory models produced for each year, and the variables involved in them, are shown in Table 1.

3.1.1. Explanatory and predictive models during the establishment phase

The distribution of *R. okamurae* in 2016 was explained by two factors, namely accessibility through dispersion (high vessel density) and oceanographic characteristics (low photosynthetically available radiation). The distribution of *R. okamurae* in 2017 was explained by the five factors considered for the study, grouping 6 variables: low cover of fine mud (biotope), presence of the invasive species *Caulerpa racemosa* (Forsskål) J. Agardh, 1873 (biocoenosis), high nitrates and low O₂ in surface water (coastal influence), short distance to the Strait of Gibraltar (accessibility through dispersion) and high values of minimum

concentration of nitrate in surface (oceanographic characteristics). In 2018 the algal distribution was explained by factors biocoenosis (presence of invasive species *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon, 1845), accessibility through dispersion (short distance to the Strait of Gibraltar) and oceanographic characteristics (high values of minimum concentration of nitrate in surface water) (Table 1).

The predictive biogeographic models resulting from the intersection of explanatory models were more conservative than those resulting from their union. While the intersection for the first three years exhibited intermediate favourability values for *R. okamurai* both in the Gibraltar Strait area and the western coastal zone of the Alboran Sea, the favourability values were higher and demonstrated greater potential distribution capacity for the algae in the union. Notably, the union of explanatory models for the year 2017 displayed medium-to-high favourability values across practically the entire northern coastal area of the Alboran Sea, as well as in the Alboran Island region (Fig. 2).

3.1.2. Explanatory and predictive models during the expansion phase

During 2019 a clear expansion of *R. okamurai* was observed throughout the entire study area. This was explained by 4 factors and 7 variables (see Table 1), namely biotope (low cover of fine mud), biocoenosis (presence of *P. oceanica* and *A. taxiformis*), accessibility through dispersion (short distance to ports) and oceanographic characteristics (shallow depth, high primary productivity in surface water and high velocity of currents in surface water).

The predictive biogeographic model resulting from the intersection of the explanatory models displayed moderate and moderately-high favourability values along the northern coast of the Alboran Sea. On the other hand, the biogeographic model resulting from the union of explanatory models predicted very high favourability values along the entire northern coastal zone of the Alboran Sea and around Alboran Island, with favourability decreasing with the increasing distance of OGUs from the coast (Fig. 2).

3.1.3. Explanatory and predictive models during the saturation phase

The final phase occurred during 2020–2021, and the algal distributions were explained by the same factors in both years, although they differed slightly in the predictor variables (Table 1). A high cover of mixed coarse sediment and short distance to the coast were the biotope characteristics that were significantly explanatory for the distribution of the species during both 2020 and 2021. Biocoenosis was explanatory through the presence of *P. oceanica* and *A. taxiformis* during the two years, and through that of *C. racemosa* in 2021. A short distance to ports was significantly related to the occurrence of *R. okamurai* in both years of saturation. The oceanographic characteristics related to the saturation during both years were shallow depth and high dissolved molecular oxygen in surface water, while high minimum nitrate at average depth was also explanatory in 2020, and high maximum salinity at average depth and minimum silicate in surface water in 2021.

The biogeographic models, either resulting from the intersection or

the union of explanatory models, were very similar for these two years. Both intersection models showed medium-to-high favourability values throughout the coastal area of the Strait of Gibraltar and the northern coast of the Alboran Sea, while the union models reached high favourability values in areas farther away from the coast.

3.2. Evaluation of models on data from the year used to build them

The capacity of each explanatory model to discriminate and classify the distribution data from the year used to build them can be found in Suppl. Mat. Table II, while that of the biogeographic models is shown in Table 2. All models demonstrated outstanding discrimination capacity ($AUC > 0.9$). The classification capacity varied according to the year and model type, although all models had very low underprediction values (< 0.1), indicating that they explained quite well the locations where *R. okamurai* was not found in particular years. On the other hand, overprediction was generally high, meaning that models tended to consider as favourable for the species locations where the species had not yet been found.

3.3. Predictive capacity of the models for subsequent years

The predictive ability of the models based on their AUC can be examined in Table 3 (for classification indices of predictions, see Suppl. Mat. Table III). The predictive model that best discriminated the occurrences of *R. okamurai* in 2017 was the union of explanatory models in 2016 ($AUC = 0.949$). For the year 2018, the predictive model with the best discrimination ability was the intersection of explanatory models in 2017 ($AUC = 0.982$). The distribution of the species in 2019 was best predicted by the union of explanatory models in 2017 ($AUC = 0.906$), while the predictive model that best discriminated the distribution data of *R. okamurai* in 2020 was the intersection of explanatory models of the year 2019 ($AUC = 0.930$). Finally, the occurrence and absence data for 2021 were best discriminated by the union of explanatory models of 2020 ($AUC = 0.960$). The cartographic representation of each biogeographic model is shown in Fig. 2.

4. Discussion

The alga *R. okamurai* has proven to be a highly invasive species in the northern Alboran Sea (García-Gómez et al., 2021a, 2021b; Mercado et al., 2022; Mateo-Ramírez et al., 2023), although the factors explaining its successful colonisation vary depending on the year and the invasion phase. These explanations are hypotheses based on correlational inferences, and are thus subject to the limitations of such statistical approaches. However, when they were used to predict the distribution of the species in subsequent years, the approach was hypothetico-deductive, and predictions were confronted with a new set of data. In any case, given the correlative nature of the inferences and predictions, the processes that connect the variables of the models with the

Table 2

Classification and discrimination indexes for intersection and union models built. AUC = Area Under Curve. CCR = Correct Classification Rate. TSS = True Skill Statistics. For the evaluation by factors, see Annex 2 of the supplementary material.

	Model year											
	2016		2017		2018		2019		2020		2021	
	Intersection	Union	Intersection	Union	Intersection	Union	Intersection	Union	Intersection	Union	Intersection	Union
AUC	0.997	0.997	0.990	0.964	0.974	0.957	0.936	0.948	0.953	0.968	0.962	0.977
Sensitivity	1.000	1.000	0.167	1.000	0.667	1.000	0.417	1.000	1.000	0.476	0.409	1.000
Specificity	0.997	0.944	1.000	0.702	0.997	0.811	0.976	0.648	0.630	0.979	0.986	0.636
CCR	0.997	0.944	0.984	0.708	0.993	0.813	0.954	0.662	0.656	0.944	0.944	0.662
Overprediction	0.500	0.944	0.000	0.937	0.333	0.950	0.583	0.896	0.833	0.375	0.308	0.824
Underprediction	0.000	0.000	0.016	0.000	0.003	0.000	0.024	0.000	0.000	0.038	0.045	0.000
Kappa	0.665	0.100	0.282	0.085	0.663	0.078	0.393	0.127	0.190	0.511	0.487	0.201
TSS	0.997	0.944	0.167	0.702	0.663	0.811	0.393	0.648	0.630	0.455	0.395	0.636

distribution of the species in the different phases of invasion must be carefully examined.

4.1. Key factors in the establishment and expansion of *R. okamurai* in the northern Alboran Sea

During the first year of the establishment phase (2016), our models suggest that only accessibility through dispersion and the oceanographic characteristics were key in the alga's settlement, predicting *R. okamurai*'s distribution quite well until 2018 (Fig. 2). Accessibility through dispersion was linked to high vessel density, which could be expected given that the most likely hypothesis for *R. okamurai*'s entry into the Strait of Gibraltar, and consequently into the Alboran Sea, is the immense maritime traffic historically present in this area (Cepillo Galvin, 2014; Rosas-Guerrero et al., 2018). However, the oceanographic characteristic favourable to settlement of the species was 'low values of photosynthetically available radiation', which seems contradictory since *R. okamurai* requires this radiation for its development. In fact, this variable was positively associated with the invasion of *Undaria pinnatifida* along the northern coast of Spain (Báez et al., 2010). However, a low level of photosynthetically available radiation would disfavour all the algal species in the area and, given that *R. okamurai* is known to be capable of surviving in very low- or no-light conditions – entering a state of metabolic inactivity to later reactivate when conditions become favourable (García-Lafuente et al., 2023; Mateo-Ramírez et al., 2023) – this situation may give it an advantage over its competitors. This seems to have been a critical factor in the initial phase of establishment.

By the year 2017, when *R. okamurai* had already spread throughout the Strait of Gibraltar and was beginning to colonise the westernmost area of the Alboran Sea, the models indicated that additional factors could explain the dispersion of the species (Table 1). In fact, the union of all the explanatory models for this year predicted expansion not only in the next two years (up to 2019) but also, to a lesser extent, in the subsequent years (Fig. 2 and Table 3). In 2019, *R. okamurai* experienced significant expansion in the northern area of the Alboran Sea, transitioning from being solely present in the Strait of Gibraltar and adjacent areas to spreading from west to east across the entire study area, and this was well predicted with models produced with data from 2017. The union of all these factors also predicted the invasion of the species around Alboran Island, which had not occurred up to 2021.

Our models suggest that the biotope factor that hindered the expansion of the species was the coverage of fine mud sediment, which is expected, as *R. okamurai* prefers to settle on hard or rocky bottoms (Navarro-Barranco et al., 2019; Sempere-Valverde et al., 2021). High nutrient input (particularly nitrates) from the mainland was also

influential, as were high values of nitrates in the surface (measured as oceanographic characteristics), possibly because they favoured algal growth, as hypothesised by Mercado et al. (2022). High irradiance exposure likely had an influence too, since the biomass productivity in Gibraltar strait waters is highest during summer time (Figuerola et al., 2023).

Furthermore, the Algeciras area and its surroundings (where the invasion started) are known for having high levels of eutrophication (Mercado et al., 2018). This is also in line with the low values of O₂ available in the surface water being favourable to the settlement and expansion of the species (Table 1). Concurrently, the results suggest that the presence of the invasive alga *C. racemosa* preceded the encroachment of *R. okamurai*. In subsequent models (2019–2021), the presence of another invasive species (*A. taxiformis*) also indicated favourable conditions for the settlement and expansion of *R. okamurai*. This aligns with two hypotheses: a) that the presence of previous invasive species creates disturbances in the habitats they colonise, leaving open niches for other invaders to more easily settle in (Shigesada and Kawasaki, 1997; MacDougall and Turkington, 2005; Altamirano-Jeschke et al., 2019), and b) that the same environmental factors that support one invasive species can also facilitate the establishment of another. Accessibility through dispersion also seems to have a role in the later part of settlement and during the expansion of the invasion, in this case only due to the distance to the initial location of the settlement area (the Strait of Gibraltar).

4.2. Key factors during the saturation phase

The intersection of explanatory models in 2019 best predicted the beginning of saturation in the following year (2020). Four out of the five considered factors (biotope, biocoenosis, accessibility through dispersion and oceanographic characteristics) accounted for the beginning of saturation, and the predictor variables were similar to those in models from previous years. However, within the biocoenosis factor, in addition to the presence of *A. taxiformis*, the saturation was also explained by the high cover of meadows of the angiosperm *P. oceanica*. This is noteworthy as *P. oceanica* settles in primarily sandy bottoms, while *R. okamurai* prefers rocky substrates (Fornes et al., 2006; Short et al., 2007; Sempere-Valverde et al., 2021). Nevertheless, the mere occurrence of *P. oceanica* (including dead mats) may also favour the alga's establishment, as it may find it easier to attach to the rhizomes of *P. oceanica* and the associated seabed (Rosas-Guerrero et al., 2022). There are indications that both species might compete for light availability, and given *R. okamurai*'s robust nature, it would likely have a competitive advantage over the marine angiosperm, which is more delicate and vulnerable to habitat alterations (Boudouresque et al., 2009; Solé et al., 2021; Mancini et al., 2023).

In 2020 and 2021, *R. okamurai* reached saturation levels in the study area, ultimately expanding along most of the coast of the Alboran Sea. Both years were characterised by the same factors, which, in turn, exhibited similar predictor variables (Table 1). The biotope factors favourable to saturation were the percentage of mixed coarse sediment and short distance from the coast. The explanatory biocoenosis factor once again involved the high cover of seagrass meadows and the presence of invasive species *C. racemosa* and *A. taxiformis* (their significance explained in the section above). Accessibility through dispersion, namely a short distance to ports, was also favourable to the establishment and dispersion of the invasive alga. This variable was also found to be important for this species by Bellissimo et al. (2024) at the scale of the Mediterranean Sea. Finally, the oceanographic characteristics factoring saturation were related to eutrophication and bathymetry, favourable to *R. okamurai* in shallow areas with abundant nutrients (Mercado et al., 2022). The final outcome is that this species has invaded nearly all of the northern coast of the Alboran Sea, which concurs with favourability models produced by Muñoz et al. (2021).

Table 3
Area Under the Curve (AUC) of the predictive models for both the intersection and the union ensembles. The models that best predicted a given year are highlighted in bold.

Year being predicted	Year when the predictive model was built	Predictive model AUC		Invasion phase
		Intersection	Union	
2017	2016	0.934	0.934	Establishment
2018	2016	0.905	0.905	
2019	2017	0.982	0.982	Expansion
	2016	0.777	0.752	
	2017	0.730	0.906	
2020	2018	0.722	0.773	Saturation
	2016	0.697	0.644	
	2017	0.661	0.879	
2021	2018	0.588	0.608	
	2019	0.930	0.918	
	2016	0.708	0.675	
	2017	0.683	0.896	
	2018	0.661	0.672	
	2019	0.926	0.937	
	2020	0.948	0.960	

4.3. Prevention and mitigation actions

Given the factors involved in this colonisation process, the future looks promising for the encroachment of this species in the rest of the Mediterranean Sea, where it could potentially colonise much of the coastal area, bringing potential ecological and economic impacts if control and mitigation measures are not implemented (Muñoz et al., 2021). In fact, there are already records of its occurrence in various regions beyond the Alboran Sea. In the Mediterranean Sea, it has been reported further eastward in Alicante (Spain) (Terradas-Fernández et al., 2023), in the Marseille region (France) (Ruitton et al., 2021) and the Gulf of Palermo (Italy) (Bellissimo et al., 2024). The species has also ventured into the Atlantic coasts of Portugal (Liulea et al., 2024), including the archipelagos of the Azores (Faria et al., 2022), Madeira (Bernal-Ibañez et al., 2022) and the Canary Islands (Haroun et al., 2023). The Mediterranean and Atlantic coasts of Morocco have also been affected by the species (El Aamri et al., 2018; El Madany et al., 2024).

We consider early action to be key to controlling this invasive species and preventing its colonisation of new areas as, once established, its eradication is almost impossible (Altamirano-Jeschke et al., 2019, 2022). In the case of the already-invaded areas of the northern Alboran Sea, the best current option is to implement actions to mitigate its effects on both native flora and fauna, and to monitor the possible gradual adaptation of other species towards cohabiting with the invasive algae, as well as the impact on the fishing and tourism sectors (Báez et al., 2023).

On the other hand, the valorisation of algal biomass, as a control strategy in areas with massive amounts of algae – especially beach-cast and free-floating algae – could help to reduce the impact of the bio-invasion (Barcellos et al., 2023; Vega et al., 2023), as has been proposed for other invasive seaweeds (Pinteus et al., 2018; Pereira et al., 2021).

For those high favourability-value areas not yet colonised by *R. okamurai*, early action programmes should be prioritised to detect the alga when densities are still low and remove it before it becomes too abundant to feasibly control.

5. Conclusion

We can conclude that our biogeographic models were a useful tool in understanding the factors that have contributed to the establishment of *R. okamurai* in the northern Alboran Sea, its subsequent expansion and, ultimately, the near-total colonisation of the entire study area in just 6 years. These factors are likely the same or very similar in other locations the species is beginning to invade, which should be helpful for focusing preventive and early-detection actions. The more direct application of our models to other regions should be made by applying the same or analogous methods to areas of new encroachment of the species, which should be conducted by local researchers who could benefit from our work to identify areas favourable to the invasion of the species.

CRedit authorship contribution statement

Lucrecia Souviron-Priego: Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ana Luz Márquez:** Writing – review & editing, Supervision, Methodology, Investigation, Data curation. **Nathalie Korbee:** Writing – review & editing, Supervision, Funding acquisition. **Félix L. Figueroa:** Writing – review & editing, Supervision, Funding acquisition. **Raimundo Real:** Writing – review & editing, Supervision, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.176851>.

Data availability

Data will be made available on request.

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