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A New Front in Marine Conservation: Addressing the Invasion of *Rugulopteryx okamurae*

Temporal Shifts in Subtidal Rocky Benthic Communities Associated With the Invasion of *Rugulopteryx okamurae* in a Port Environment

E. Quintano¹  | J. Tajadura²  | A. Santolaria¹  | M. Bustamante²  | O. Arriaga¹  | I. Uriarte¹  | I. Saiz-Salinas²  | N. Muguerza¹ 

¹Laboratory of Botany, Department of Plant Biology and Ecology, Fac. of Science and Technology & Research Centre for Experimental Marine Biology and Biotechnology PIE-EHU, University of the Basque Country (EHU), Bilbao, Spain | ²Department of Zoology and Animal Cell Biology, Fac. of Science and Technology & Research Centre for Experimental Marine Biology and Biotechnology PIE-EHU, University of the Basque Country (EHU), Bilbao, Spain

Correspondence: E. Quintano (endika.quintano@ehu.eus)

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ABSTRACT

The invasive brown alga *Rugulopteryx okamurae*, native to the northwestern Pacific, has rapidly expanded along the European Atlantic coast, reaching the Basque Coast in 2023, and was likely already present in 2022. Using annual data from a monitoring survey conducted between 2010 and 2025, this study assesses the spatio-temporal variability of subtidal rocky benthic communities at two locations within a port environment on the western Basque Coast affected by the presence of *R. okamurae*. Following its establishment, marked shifts in benthic community composition, structure and functioning were detected. Taxa richness, density and diversity declined sharply from 2022 onwards, whereas assemblages from both study locations became increasingly similar, indicating strong community homogenization. Multivariate analyses revealed a rapid reorganization of communities coinciding with the arrival of *R. okamurae*. The diverse native macroalgae and associated invertebrates present prior to the invasion were replaced by a single persistent community dominated by *R. okamurae* and the bryozoan *Tubulipora* spp. Functional and structural analyses showed a pronounced loss of calcareous and structurally complex macroalgae, together with the collapse of basal and crustose layers and a transition towards canopy-dominated assemblages largely associated with the dominance of the invasive species. Overall, our results suggest that *R. okamurae* acts as a strong habitat-modifying species in this port environment, rapidly transforming subtidal rocky communities and highlighting the urgent need for early detection, long-term monitoring and management strategies in newly invaded areas.

1 | Introduction

Invasive algae are species that, due to anthropogenic activities, spread beyond their native biogeographic range, often causing severe ecological and economic impacts (Williams and Smith 2007; Gurevitch et al. 2011). Indeed, biological invasions rank among the leading causes of marine biodiversity loss worldwide. The most harmful invasive species can displace native

taxa, reshaping community structures and food webs, and disrupting nutrient cycles and sedimentation processes (Molnar et al. 2008; Viard and Comtet 2015). Given these impacts, preventing and mitigating the introduction and spread of invasive species has become an essential scientific and policy challenge, requiring strategies to ensure that human-mediated introductions do not adversely alter marine ecosystems (European Parliament and Council 2008; European Commission 2020).

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Invasions generally progress through four distinct stages: transport, introduction, establishment and spread. The success of each stage depends on three key factors: propagule supply, biological traits and abiotic conditions (Papacostas et al. 2017). In addition, environmental stressors (e.g., pollution and anthropogenic modification) interact with invasion processes, with more degraded areas showing higher invasion success (Occhipinti-Ambrogi and Savini 2003). The rapid spread of invasive algae in marine environments over the last decades can be attributed to several factors. On the one hand, ocean warming driven by climate change increases the abundance of invasive species (Sorte et al. 2010). On the other hand, aquaculture and hull-fouling have been major pathways for the spread of invasive algal taxa (Williams and Smith 2007; Díaz-Tapia et al. 2025).

In temperate European coastal systems, and particularly in semi-enclosed and highly anthropogenically modified environments such as ports, biological invasions are strongly facilitated by intense maritime traffic, which promotes the transport of propagules through hull fouling and ballast water discharge (Carlton and Geller 1993; Williams and Smith 2007; Katsanevakis et al. 2013). Ports and marinas are therefore considered major introduction hubs and stepping-stones for the secondary spread of non-native marine species (Floerl et al. 2009; Airolidi et al. 2015). In addition, disturbed habitats and artificial coastal infrastructures often favour the establishment of opportunistic taxa, particularly under environmental conditions altered by climate warming and other anthropogenic stressors (Occhipinti-Ambrogi and Savini 2003; Sorte et al. 2010).

Although the most effective strategy to curb the expansion of invasive species is to prevent their initial introduction, predicting the invasive potential of each species is extremely difficult, as different organisms rely on distinct traits and mechanisms for dispersal (Valentine et al. 2007). Despite these differences, most invasive species tend to share a suite of common traits. They are generally fast-growing, opportunistic taxa with broad distributions in their native range, high reproductive output, short life cycles, early sexual maturity and the ability to reproduce asexually. Many also display gregarious behaviour, heteromorphic reproductive cycles and a strong capacity to adapt to varying environmental conditions (Ojaveer et al. 2015; Pereira 2024).

Rugulopteryx okamurai (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Dictyotales, Heterokontophyta) is a brown alga native to the north-western Pacific (Pereira 2024). It has a digenetic isomorphic life cycle, alternating between morphologically identical gametophytic and sporophytic stages. Morphologically, the species can reach up to 30 cm in length, exhibits dichotomous branching and has a greenish-brown coloration. No clear macroscopic traits have yet been identified to distinguish it reliably from *Dictyota dichotoma* (Hudson) J.V. Lamouroux (a native brown alga on the Basque Coast), and microscopic examination of thallus cross-sections is required for proper identification (Hwang et al. 2009). This morphological similarity limits precise taxonomic discrimination by visual surveys, thereby impeding early detection and subsequent mitigation efforts. *R. okamurai* can reproduce both sexually (via gametes and tetraspores) and asexually (via mitotic monospores or vegetative propagules). Moreover, it has been reported across a wide depth range, from tidal pools down to 50 m (MITECO 2022).

R. okamurai was first recorded in the Mediterranean in 2002 in the Thau lagoon, France, most likely following the importation of the oyster *Magallana gigas* Thunberg (Verlaque et al. 2009). Later, in 2016, the first records of its presence for both Spain and the Atlantic Ocean were reported in the Strait of Gibraltar (Ceuta and Tarifa) (Altamirano-Jeschke et al. 2016). Very quickly—within roughly 4 years—it appeared along the coasts of Málaga and Cádiz, and strandings reached Granada and Almería (MITECO 2022). Because of its recent rapid expansion and the damage it has caused, *R. okamurai* was included in Spain's Catalogue of Invasive Exotic Species in 2020, regulated under Royal Decree-Law 630/2013 of 2 August. It was also listed among the European Union's Invasive Alien Species of Union concern in 2022 (MITECO 2022). Thereafter, it has continued to spread northwards along the Atlantic, and in recent years it has been reported from several locations, including Morocco (El Madany et al. 2024), the Azores (Faria, Prestes, Moreu, Cacabelos, and Martins 2022), Madeira (Bernal-Ibáñez et al. 2022), Italy (Bellissimo et al. 2024) and Portugal (Liulea et al. 2023). In the Cantabrian Sea, *R. okamurai* was recorded for the first time on the Basque Coast in 2023 and subsequently in Galicia in 2024 (Díaz-Tapia et al. 2025).

The factors behind the invasion success of this alga are multiple. One plausible driver is its high capacity to assimilate nitrate—it can take up dissolved nitrogenous compounds from the water and store them within its cells. This allows the alga to maintain growth rates even in oligotrophic areas by utilizing stored nutrients (Bonomi-Barufi et al. 2025). Moreover, a chemical compound named Dilkamural has been identified in *R. okamurai* and appears to facilitate its spread and invasiveness. This compound confers resistance to intense herbivore pressure—for example, it deters grazing by sea urchins and can be harmful, in some cases lethal, to those invertebrates (Casal-Porras et al. 2021). In addition to these mechanisms, climatic conditions along the Mediterranean and North Atlantic coasts are suitable for the species' survival, which has greatly facilitated its ability to invade these environments (Verlaque et al. 2009).

Biological invasions cause both ecological and economic harm in invaded areas, and the case of *R. okamurai* is no exception (MITECO 2022). The species has been observed to alter the structure and composition of marine benthic communities in invaded sites, often accompanied by reduced natural variability and losses in species richness (García-Gómez et al. 2020; Faria, Prestes, Moreu, Martins G, et al. 2022). It affects a range of community types, including kelp forests, communities dominated by species of the genus *Cystoseira* C. Agardh (*sensu lato*), *Posidonia oceanica* (Linnaeus) Delile meadows and both intertidal and subtidal algal assemblages. Several species have been shown to suffer direct impacts, for example, the macroalgae *Laminaria ochroleuca* Bachelot Pylae, *Saccorhiza polyschides* (Lightfoot) Batters and *Gongolaria usneoides* (Linnaeus) Molinari & Guiry, as well as gastropods such as *Charonia lampas* Linnaeus and *Patella ferruginea* Gmelin (Figueroa et al. 2025). Conversely, some studies have reported a positive correlation between high epifaunal bryozoan diversity and the biomass of *R. okamurai* (Caballero-Herrera et al. 2025).

The primary objective of this study is to evaluate the spatio-temporal variability of subtidal rocky benthic communities in

a port environment from the western Basque Coast invaded by *R. okamurae*. Accordingly, the hypothesis tested is that subtidal rocky benthic communities in the port environment exhibit lower diversity and higher homogeneity in areas where *R. okamurae* is highly abundant.

2 | Materials and Methods

2.1 | Study Area and Data Collection

The study area is located on the western sector of the Basque Coast, within the southeastern Bay of Biscay (eastern Cantabrian Sea, northern Spain), specifically in the vicinity of the Nervión River estuary (43°22′08.6″ N, 3°05′20.0″ W) (Figure 1). Average sea surface temperature along the Basque Coast ranges from approximately 12°C in February to 22°C in August (Valencia et al. 2004), although since the 1980s, sea surface temperatures have increased at a rate of 0.15°C–0.25°C per decade (Chust et al. 2022). The region is exposed to long-fetch wave conditions, with swell predominantly originating from the northwest

(Galparsoro et al. 2010). Geomorphologically, the coastline is characterized by steep cliffs interspersed with sandy beaches and estuarine environments (Chust et al. 2011). Furthermore, the study area is subject to significant anthropogenic pressure, mainly associated with maritime traffic linked to the Port of Bilbao, where benthic habitats are sheltered from hydrodynamic exposure and dominated by artificial substrates of quarried rock, with high sediment accumulation and limited light penetration.

Sampling was carried out at two rocky subtidal locations: Punta Lucero (PL) and Punta Ceballos (PC) (Figure 1). PL functions as an active berthing area and is directly exposed to port operations, being subject to recurrent physical and anthropogenic disturbance. In contrast, PC is located in a comparatively less disturbed sector of the port, with reduced direct influence from shipping activities. The impact of the invasive macroalga *R. okamurae* on subtidal vegetation and macroinvertebrate benthic communities was evaluated using data collected between 2010 and 2025, allowing the assessment of long-term temporal variability. The assemblages analysed corresponded to the shallow subtidal zone (depth range, 2–6 m). Twelve surfaces (delimited



FIGURE 1 | Above: Map showing the two locations surveyed during the study within the Port of Bilbao (estuary of the Nervión River): Punta Lucero (PL: 43°21′51.6″ N 3°06′12.8″ W) and Punta Ceballos (PC: 43°21′45.0″ N 3°05′31.4″ W). Below: (A) Cross-section of the thallus of *D. dichotoma*. (B) Field appearance of *Dictyota/Rugulopteryx*-like specimens. (C–D) Cross-sections of *R. okamurae* showing groups of medullary cells in the apical region. White lines in the micrographs indicate 60 µm.

by a 40×40 cm quadrat) were studied per location and year, yielding a total of 384 sampling units across the entire study period. Within each surface, the composition and abundance of macroalgal and macroinvertebrate taxa were estimated in situ. The relative cover of each taxon was visually estimated using a 5% interval cover scale (from 5% to 100%). For taxa with a cover below 1%, a value of 0.5% was assigned. Taxa that could not be reliably identified in situ were collected and transported to the laboratory for subsequent identification. In the laboratory, samples were examined using a stereomicroscope and a light microscope. Organisms were taxonomically identified to the lowest possible level, generally to species level, although in a few cases, higher taxonomic levels were used when species-level identification was not feasible. Taxonomic nomenclature followed AlgaeBase (Guiry and Guiry 2026) for macroalgal taxa and WoRMS (Horton et al. 2026) for invertebrate taxa (Tables A1 and A2).

Following the first confirmed identification of *R. okamurai* in 2023 in the Basque Coast (Díaz-Tapia et al. 2025), earlier datasets were critically re-examined. Based on expert judgement and the unusually high cover values recorded, *Dictyota*-like records exceeding 15% cover in 2022 were conservatively reassigned to *R. okamurai*, as such abundances had never been observed for native *Dictyota* J.V. Lamouroux spp. in the historical dataset. From 2023 onwards, specimens resembling *Dictyota* spp. were collected to discriminate between the native species and the invasive *R. okamurai* (Figure 1B). For each specimen, thin cross-sections of the thallus were prepared to enable accurate species identification. Species determination was based on the organization of medullary cells: In *D. dichotoma*, medullary cells are isolated throughout the thallus section (Figure 1A), whereas in *R. okamurai*, numerous medullary cells form clusters in the apical medulla (Hwang et al. 2009) (Figure 1C,D).

2.2 | Response Variables and Statistical Analyses

The spatio-temporal variability of community taxonomic structure was analysed using a multivariate approach with PRIMER 7 (Plymouth Routines in Multivariate Ecological Research) software package (Clarke and Gorley 2015). A permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was conducted to test for differences in assemblage multivariate structure associated with time and location. The objective of this analysis was to compare community composition among annual sampling surveys and between the two study locations, rather than to model temporal trajectories or explicitly account for temporal autocorrelation. The experimental design included one random factor, time (16 levels; corresponding to the years 2010–2025) and one fixed factor, location (two levels; PL and PC). Time was treated as a random factor because the sampled years represent observations distributed across the study period for inference on temporal variability. Location was considered a fixed factor because the study focused on comparing these two specific port areas without extrapolating the results to a broader regional scale. Bray–Curtis similarity coefficients were calculated between all pairs of samples. Statistical significance of each term was assessed using 9999 permutations of appropriate units (Anderson et al. 2008). The a priori significance level was set at $\alpha = 0.01$.

Prior to analysis, data were square-root transformed to downweight the influence of dominant species. Given the large number of samples, data were represented multidimensionally using annual means for each location, and spatio-temporal variability was explored using non-metric multidimensional scaling (nMDS) ordination. Similarity percentage (SIMPER) analyses were subsequently conducted to identify the taxa contributing most to the dissimilarities between the detected groups in the nMDS diagram. Finally, a permutation test for homogeneity of multivariate dispersion was conducted (PERMDISP; Anderson 2006). In contrast to the PERMANOVA design, this analysis used the assemblage groups identified by the nMDS as a factor nested within time, enabling the assessment of spatial heterogeneity of assemblages within each group and location. Coherent plots combined with shade plots were constructed using data pooled from both locations to identify common temporal patterns in community structure across the study area (Somerfield and Clarke 2013). Coherent plots were used to assess significant associations among taxa and to identify groups of species exhibiting consistent covariation through time. Shade plots were generated concurrently to visualize interannual changes in species abundance, with increasing shading intensity representing higher relative abundance. Analyses were performed using the Index of Association. Only the 50 most abundant taxa were included. The resulting groups of taxa were tested for statistical significance using a Similarity Profile (SIMPROF). As increasing the significance level does not affect the overall grouping structure (Somerfield and Clarke 2013), a significance level of 5% was selected to facilitate the identification and visualization of taxa displaying similar temporal dynamics over the study period.

In addition to multivariate analyses, both taxonomic and morpho-functional trait-based approaches were applied to single response variables. Community-level metrics—including total taxa richness (*S*), taxon density (*n*; i.e., number of taxa per quadrat; Gotelli and Colwell 2001) and Shannon diversity index—were calculated integrating all recorded macroalgal and invertebrate taxa within each quadrat. To examine temporal dynamics from a morpho-functional perspective, the relative cover of taxa was aggregated into four morpho-functional traits (two traits for macroalgal taxa and two traits for invertebrates), allowing the assessment of functional changes in the community over time. For macroalgae, functional traits included morphology (as a proxy for structural complexity) and vertical distribution within the assemblage. Morphological categories followed Díez et al. (2012), comprising (i) simple (uniseriate, polysiphonous, foliose non-corticated and slightly corticated: cortex with one to two layers), (ii) complex (corticated algae: cortex with more than two layers, plus leathery macrophytes) and (iii) calcareous (articulated and crustose) forms. Vertical distribution was classified into four strata: canopy, epiphytic, basal and crustose layers. Biological traits of invertebrates represent fundamental ecological strategies, particularly in relation to habitat use (i.e., whether species develop as algal epibionts or as epibenthic forms not directly settling on algae) and to their primary trophic strategy (i.e., suspensivore, herbivore, detritivore, omnivore or carnivore), which rank among the most distinctive features of benthic invertebrates (Wahl 2009). Trait categories were defined following the BIOTIC catalogue (MarLIN 2006),

and trait information was supplemented by primary and secondary literature sources.

To evaluate the 15-year temporal trends (2010–2025) across both locations (PC and PL), time-series modelling was implemented based on the measurement scale of each parameter. For continuous macroecological metrics integrated as a single value per year and location (total accumulated richness and integrated community density), generalized additive models (GAMs) were applied across the 15 annual data points (Wood 2017). For quadrat-level cover metrics and descriptive indices (12 replicates per year), generalized additive mixed models (GAMMs) were performed (Zuur et al. 2014) to strictly prevent temporal pseudoreplication arising from the non-independence of spatial replicates sampled within the same year. Year was incorporated as a random-effect intercept, thereby accounting for intra-annual correlation structures. The smoothing spline basis dimension for the temporal predictor was conservatively restricted to $k=4$ to capture long-term macroecological trajectories while preventing the overfitting of transient noise (Wood 2017). However, for two highly variable faunal parameters (total faunal cover and suspensivore's cover), the intra-annual spatial patchiness prevented numerical convergence under the non-linear GAMM framework and, therefore, standard linear models (LMs) were applied to ensure analytically robust convergence and directly test for continuous long-term degradation. All non-linear models were fitted using restricted maximum likelihood (REML) under a Gaussian distribution, and assumptions were validated via the *gam.check* procedure (Wood 2017). All these analyses were conducted in R (R Core Team 2026).

3 | Results

3.1 | Multivariate Structure of Assemblages

The nMDS ordination (Figure 2A) showed a clear spatio-temporal structuring of the assemblages, consistent with the significant Time $\times$ Location interaction detected by PERMANOVA (Table A3). At a similarity level of 45%, two main groups of

samples were identified. Group A included samples from both locations (PL and PC) collected between 2010 and 2021, and samples from PC in 2022. Within this group, samples from PL and PC were generally separated in ordination space, and successive years within each location tended to cluster closely, forming a temporal sequence. Group B comprised samples collected from 2022 onwards, with the exception of samples from PC in 2022. In this group, there is a convergence of samples from both locations, indicating increasing similarity between PL and PC in recent years (2023–2025).

PERMDISP analyses revealed clear differences in multivariate dispersion between the two assemblage groups identified by the nMDS ordination (Figure 2B). Comparatively, samples from each of the two locations (PL and PC) were more spatially dispersed in Group A than in Group B, indicating higher within-group heterogeneity in assemblages associated with Group A. The reduction in multivariate dispersion from Group A to Group B was statistically significant at both locations, PC ($p=0.003$) and PL ($p=0.007$). These results indicate a decrease in assemblage heterogeneity.

Similarity percentage analysis (SIMPER) revealed an average dissimilarity of 75.61% between Groups A and B. The invasive macroalga *R. okamurae* was the main contributor to this dissimilarity, exhibiting substantially higher abundance in Group B. In contrast, Group A was characterized by greater abundances of native taxa such as *Centroceras gasparrinii* (Meneghini) Kützinger, *Ellisolandia elongata* (J.Ellis & Solander) K.R.Hind & G.W.Saunders, *Lithophyllum* Zanardini spp. and *Halopteris* Kützinger spp. (Table A4). Collectively, the first 11 taxa, each contributing more than 2% to the overall dissimilarity and including both algal and invertebrate species, explained more than 53% of the dissimilarity between groups. These results indicate that the observed differences in community structure, and the convergence patterns detected in the nMDS ordination, were largely driven by the dominance of *R. okamurae* and the concomitant reduction of native macroalgal assemblages. Faunal differentiation between groups was primarily driven by the bryozoans *Beania magellanica* Busk and *Tubulipora* Lamarck spp. In Group A, *B. magellanica* was the most abundant invertebrate,

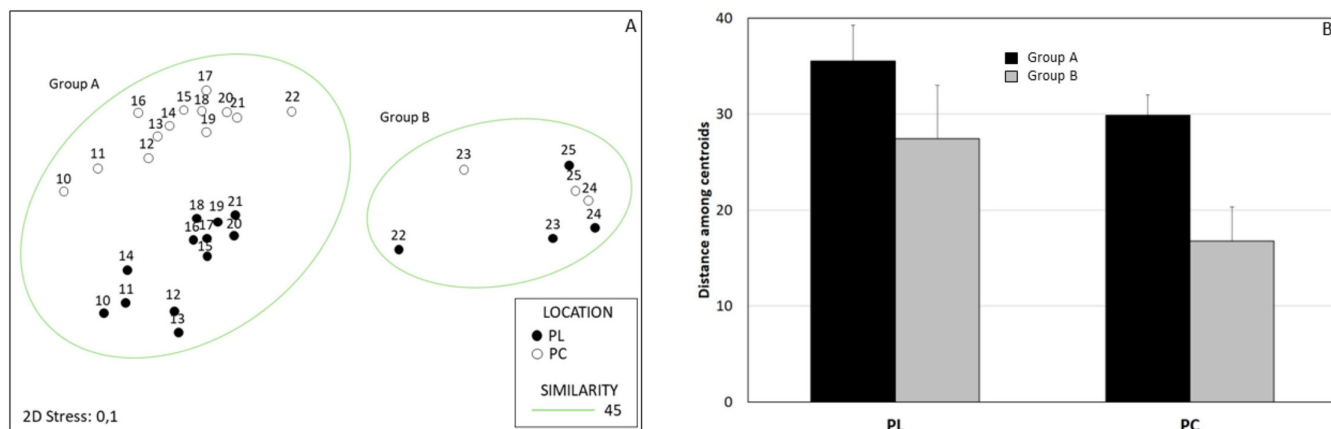


FIGURE 2 | (A) Non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis dissimilarities calculated from square-root-transformed data, showing centroids for each Time $\times$ Location combination. Green contours indicate clusters defined at 45% similarity (Groups A and B). (B) Average group heterogeneity (PERMDISP) for Group A and Group B at two locations (PL: Punta Lucero; and PC: Punta Ceballos). Results are shown as mean distance to centroid $\pm$ standard deviation.

whereas *Tubulipora* spp. was absent. Conversely, Group B was dominated by *Tubulipora* spp., with a markedly reduced presence of *B. magellanica*.

The agglomerative clustering of the interspecies association matrix, combined with the shade plot, revealed a clear and consistent pattern in community organization across the study period (Figure 3). Species associations (I–XII) were structured according to the two assemblage groups identified in the nMDS (Groups A and B), rather than following a strict chronological separation between years. Group A, which included samples from 2010 to 2021 together with the 2022 sample from one of the study locations (PC), was characterized by

the presence of multiple coherent groups or species associations (II–XII). These coherent groups involved combinations of native macroalgae such as *E. elongata*, *Lithophyllum* spp., *Codium* Stackhouse spp., *Dictyota* spp. and *Ceramium* Roth spp., together with a diverse assemblage of associated invertebrates, most notably the bryozoan *B. magellanica* and the bivalve *Rocellaria dubia* Pennant. In contrast, in Group B, comprising the 2022 sample from PL and all samples from 2023 to 2025, the community structure was dominated by a single, well-defined coherent association (I) characterized by the strong and recurrent co-occurrence of the invasive macroalga *R. okamurai* and the bryozoan *Tubulipora* spp. This species pair represented the only consistent interspecific

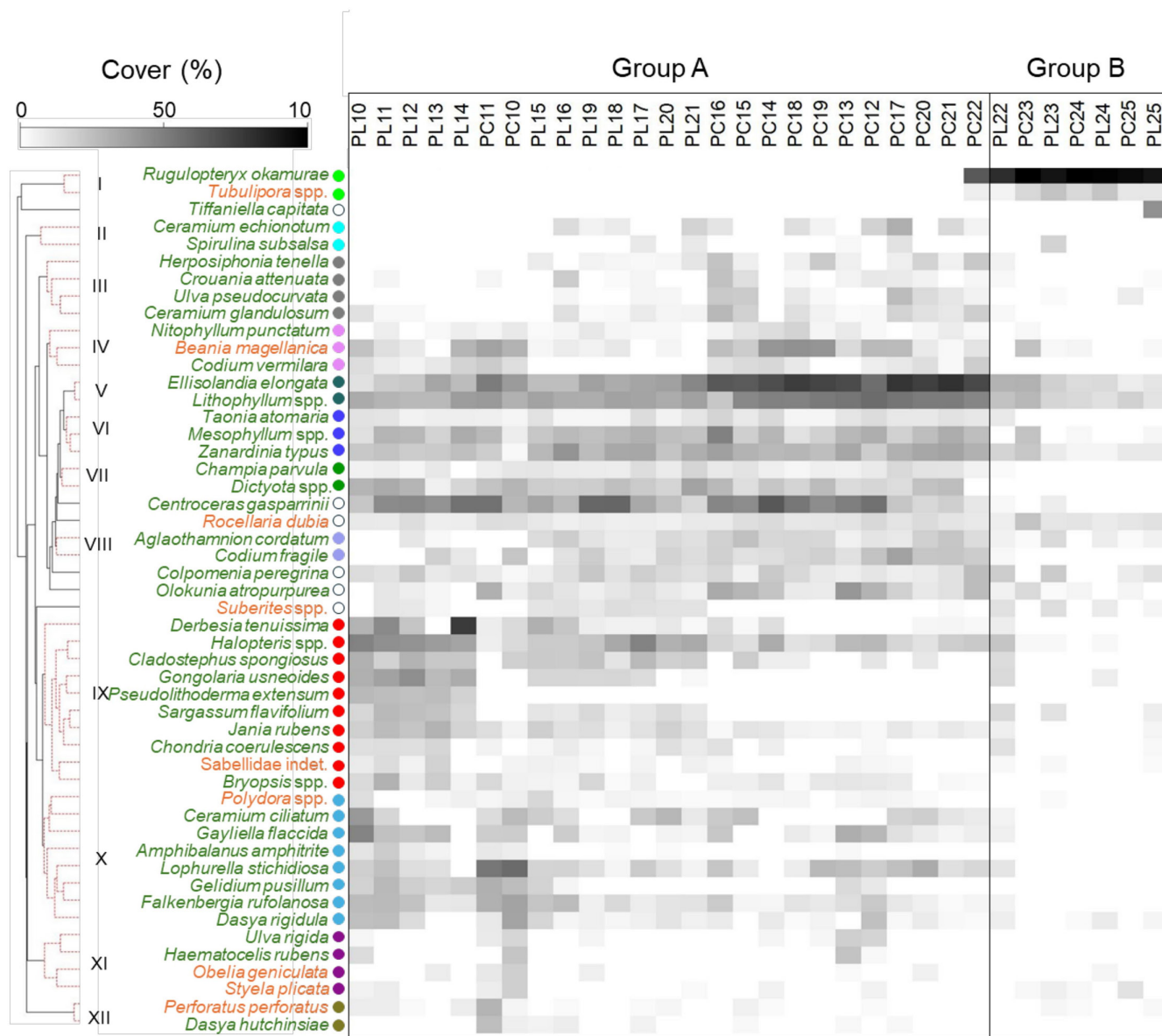


FIGURE 3 | Shade plot of the data matrix for the years studied and dendrogram based on the Index of Association between taxa showing 12 'coherent groups' in the community (I–XII). A blank space indicates the absence of that taxon in that year. Solid black lines indicate significant groups of variables ($p < 0.05$), and dashed red lines indicate groups of variables for which the null hypothesis cannot be rejected ($p > 0.05$). Green text represents algae taxa; brown text represents invertebrate taxa. Coloured circles indicate taxa belonging to the same coherent group and white circles refer to singletons. *Bryopsis* spp.: *B. hypnoides* and *B. plumosa*; *Dictyota* spp.: *D. dichotoma* and *D. cyanoloma*; *Halopteris* spp.: *H. scoparia* and *H. filicina*; *Lithophyllum* spp.: *L. incrustans* and *L. hibernicum*; *Mesophyllum* spp.: *M. lichenoides* and *M. expansum*; *Suberites* spp.: *S. domuncula*, *S. massa* and *S. sp.*; *Tubulipora* spp.: *T. liliacea* and *T. plumosa*.

association within Group B, clearly distinguishing these assemblages from those grouped within Group A. In addition to these coherent groups, the shade plot revealed the presence of several algal and invertebrate taxa occurring as singletons, defined as species recorded only sporadically or at a limited number of sampling times within Group A. These taxa did not form stable interspecific associations and showed no consistent temporal pattern, and most of them were absent from assemblages included in Group B.

3.2 | Single Response Variables

The structural and functional variations described below are visually represented in the time-series plots, whereas the comprehensive statistical outputs supporting these temporal trends are provided in Tables A5 and A6.

Response variables exhibited marked temporal variation across all community metrics examined. Total taxa richness and density (number of taxa per quadrat) were generally stable at both study locations between 2010 and 2021, although a noticeable decline was recorded in 2014 at both PL and PC. From 2022 onwards, a pronounced and sustained decrease in both metrics was observed (Figure 4A). Shannon diversity showed a similar temporal pattern, with moderate interannual variability prior to 2022 and a marked reduction thereafter. The period 2023–2025 was characterized by consistently lower values of species richness, taxon density and Shannon diversity at both locations (Figure 4B).

Total macroalgal cover exhibited location-specific patterns. At PL, algal cover peaked at the beginning of the study in 2010 and progressively declined until 2015, remaining relatively stable thereafter. In contrast, PC showed fluctuating algal cover

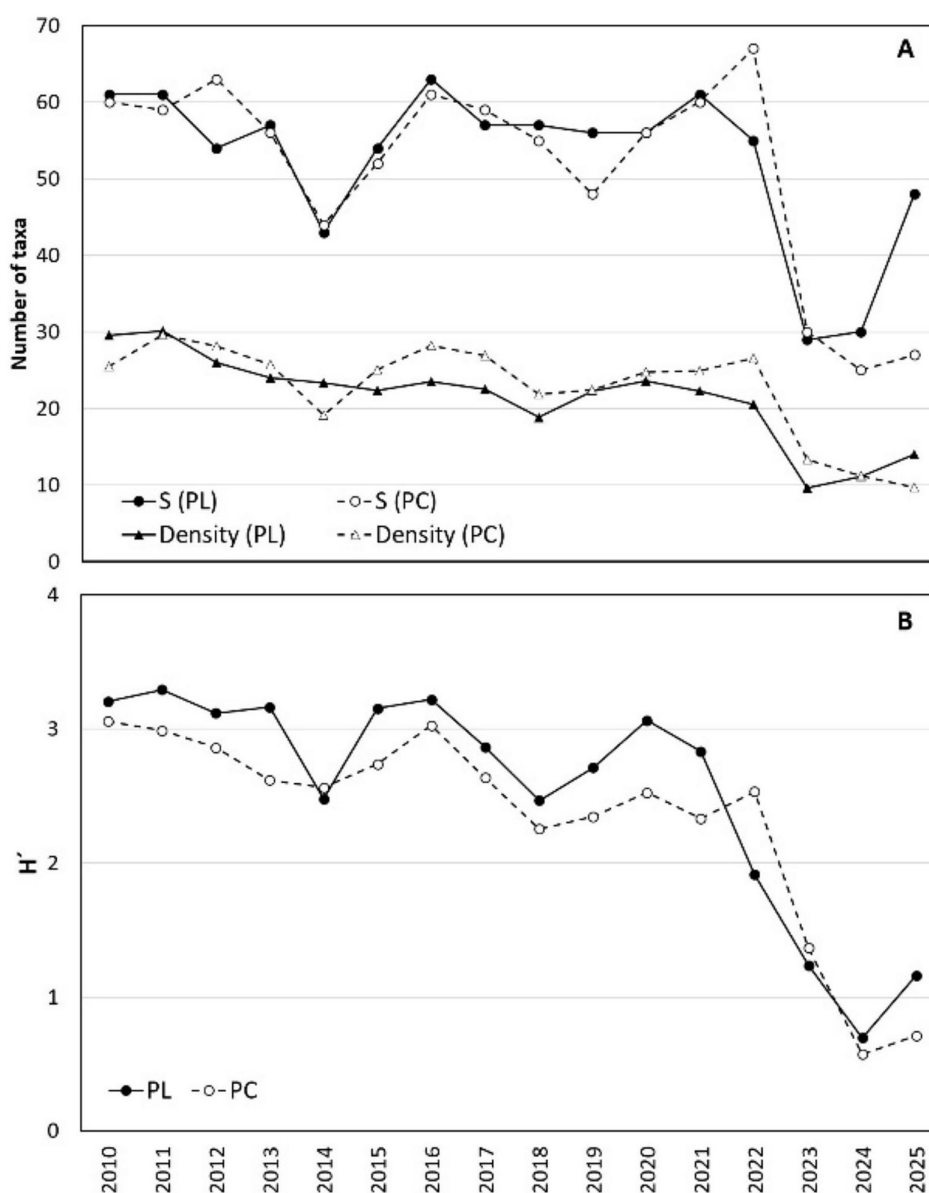


FIGURE 4 | Temporal variation of community descriptors for Punta Lucero (PL) and Punta Ceballos (PC). Panel (A) shows species richness (S , circles) and species density (triangles). Panel (B) shows the Shannon diversity index (H'). In both panels, solid lines and filled symbols represent PL, whereas dashed lines and open symbols represent PC.

between 2010 and 2022, followed by a drastic decline towards the end of the study period (2022–2025). This reduction was mainly associated with a pronounced loss of complex and calcareous algal forms, whose cover dropped drastically after 2022 at both locations. In contrast, morphologically simple algae followed an opposite trend; their abundance increased sharply from 2022 onwards, becoming the dominant functional group by the end of the study. This shift was largely driven by the proliferation of the invasive *R. okamurai*. Overall, these temporal trends indicate a clear structural shift in phytobenthic communities after 2022, consistent across both PL and PC (Figure 5A,B).

The vertical distribution of macroalgae followed a clear stratified organization, with species occupying distinct vertical layers within the community. The vertical structure of macroalgal communities showed clear temporal changes at both locations (Figure 5C,D). From 2010 to 2021, communities were dominated by basal and crustose strata, which together accounted for most of the total algal cover at PL and PC. Canopy-forming macroalgae remained at relatively low and stable values during this period, whereas epiphytic forms contributed marginally throughout the time series. From 2022 onwards, a pronounced shift in vertical layering was detected at both locations, with a sharp reduction in basal and crustose cover and a simultaneous increase in canopy-forming algae, driven mainly by the increase in the cover of *R. okamurai*. This structural reorganization resulted in a simplified vertical profile dominated by *R. okamurai* canopy, which persisted until the end of the study period.

Unlike the patterns observed in macroalgae, no consistent temporal trends were detected for the faunal response variables examined following the introduction of *R. okamurai* in 2022 (Figure 6). Although some changes following its introduction were abrupt, they remained within the range of previously observed variability. Faunal cover was the most fluctuating variable over time (Figure 6A,B), with epibionts fluctuating more than epibenthic taxa (Figure 6A,B). Among trophic strategies, suspensivores exhibited the largest temporal changes but remained dominant throughout the study period (Figure 6C,D).

4 | Discussion

This study evaluates the spatio-temporal variability of subtidal rocky benthic communities at two locations within the Port of Bilbao and provides evidence of a profound reorganization of these communities coincident with the establishment of the invasive macroalga *R. okamurai*. Overall, the results suggest a marked simplification of community structure, expressed through reduced diversity, loss of structural complexity, reduced heterogeneity and the breakdown of previously stable species associations. By combining a long-term time series with community-level structural and functional descriptors, this study provides one of the first integrative assessments of the potential early impacts of *R. okamurai* in a highly anthropized port environment.

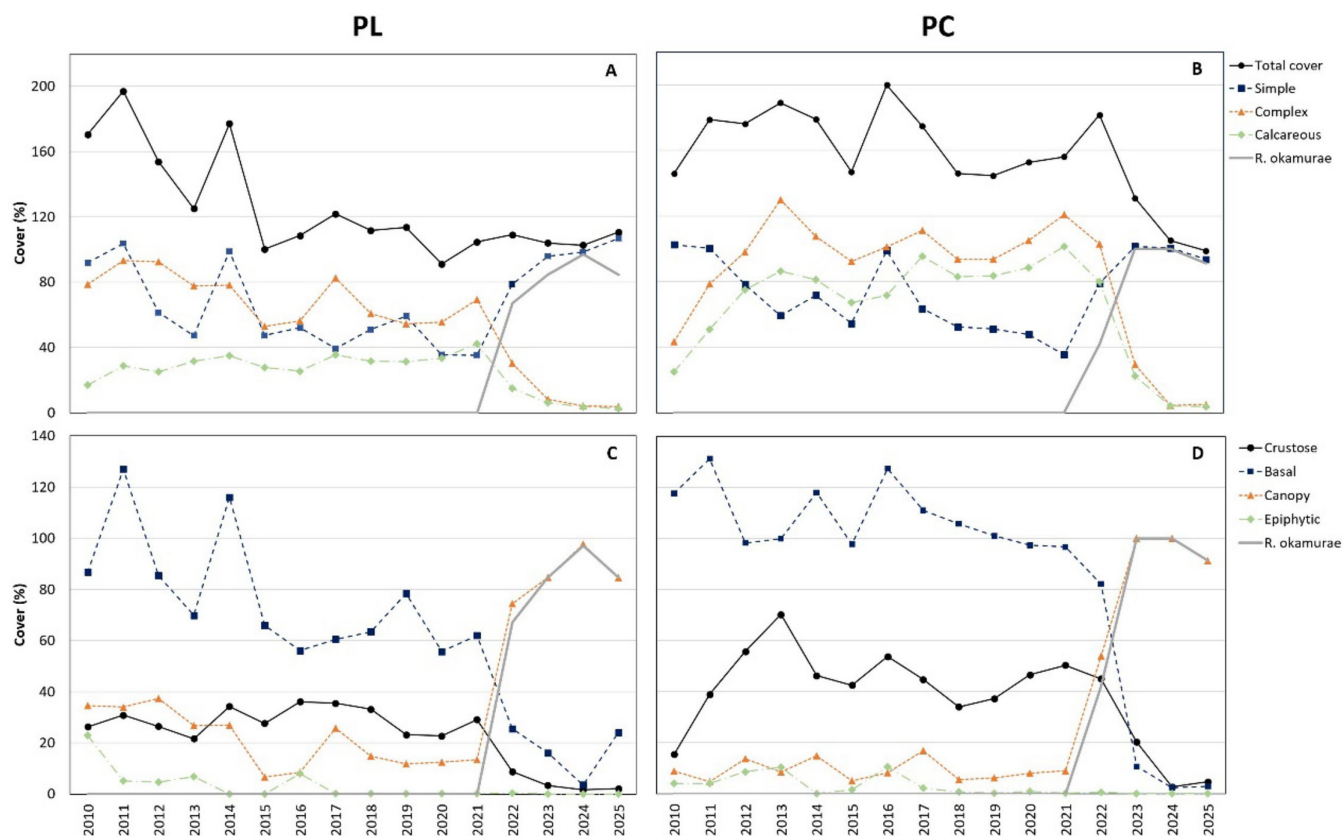


FIGURE 5 | Temporal variation of macroalgal single response variables for Punta Lucero (PL) and Punta Ceballos (PC). Panels (A) and (B) show the mean total macroalgal cover and the total cover for each of the three functional morphologies (simple, complex and calcareous). Panels (C) and (D) show the mean total macroalgal cover for each stratum in the vertical layering. In all cases, the total *R. okamurai* cover is shown.

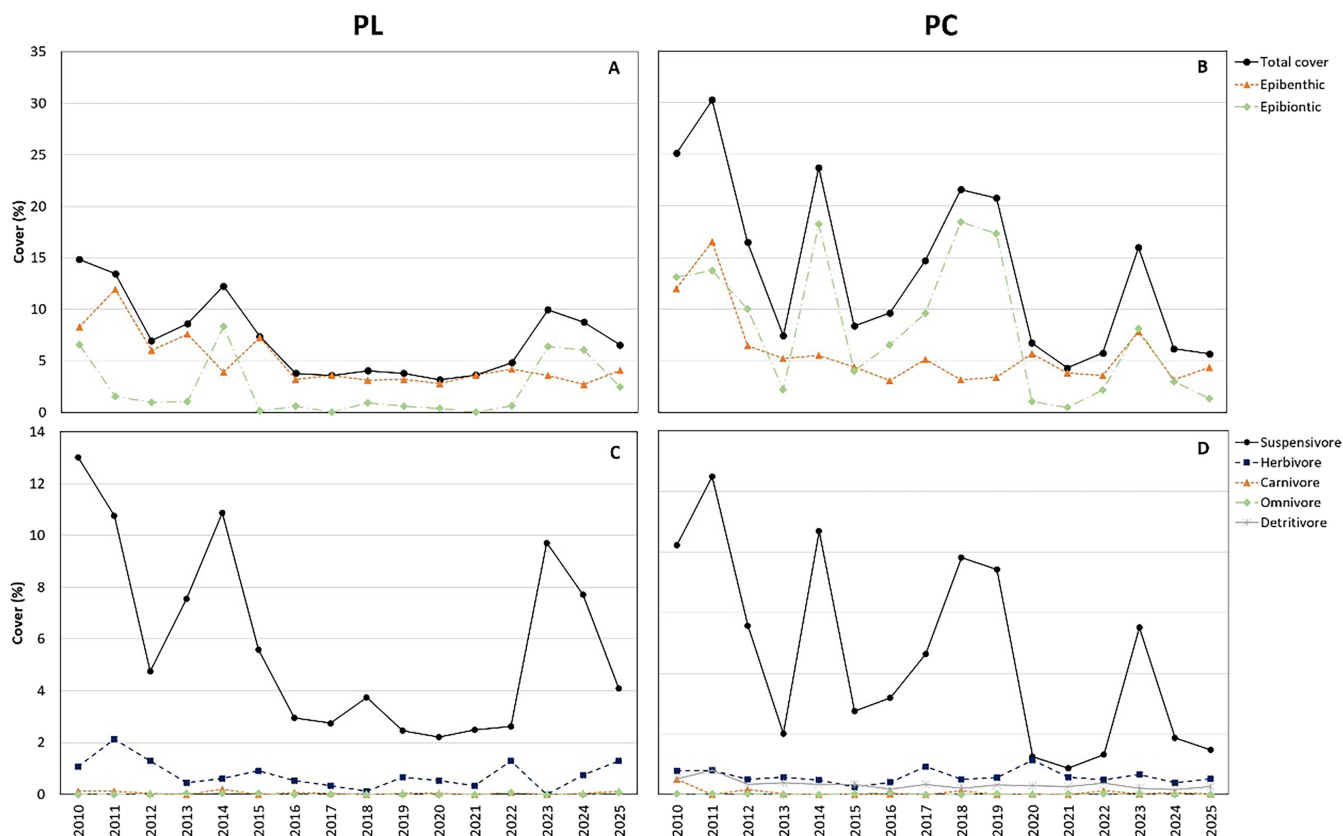


FIGURE 6 | Temporal variation of macroinvertebrate single response variables for Punta Lucero (PL) and Punta Ceballos (PC). Panels (A) and (B) show the mean total macroinvertebrate cover and the total cover for both living habits (epibenthic and epibiontic). Panels (C) and (D) show the mean total macroinvertebrate cover for each trophic strategy.

A significant shift in community composition was detected around 2022, shortly preceding the first formal record of *R. okamurai* in 2023 (Díaz-Tapia et al. 2025). Our results indicate that the community turnover began in 2022, a period when *R. okamurai* was probably incorrectly identified as the native *Dictyota dichotoma*. This misidentification likely masked the early expansion of the invasive alga, which was already competing for space and resources with other invertebrates and macroalgae.

Community composition exhibited decreased dispersion over time, signalling a temporal trend towards reduced structural heterogeneity. Although both locations initially displayed higher variability—both within and between them—the study period concluded with marked biotic homogenization. This resulted in a clear convergence of community structures of PL and PC, as the invasive species progressively dominated the local assemblages, revealing a marked contrast in community structure between the beginning and the end of the study period.

Changes in community organization were further reflected in the restructuring of species associations. Prior to the invasion, assemblages were characterized by multiple coherent groupings involving combinations of native macroalgae and associated invertebrates. These associations involved structurally complex algae such as *E. elongata* and *Lithophyllum* spp. and morphologically simpler taxa such as *Codium* spp. and *Dictyota* spp., together with invertebrates including the bryozoan *B. magellanica*

and the bivalve *R. dubia*. These groupings reflect a complex and functionally diverse community structure. Coincident with the establishment of *R. okamurai*, most of these coherent associations disappeared. Post-invasion assemblages were dominated by a single, persistent association formed by *R. okamurai* and *Tubulipora* spp., representing a novel species interaction absent from earlier years. In parallel, several taxa that had previously formed part of coherent associations persisted only sporadically or disappeared entirely, occurring as singletons without stable interspecific relationships, leading to community simplification.

Community-level diversity metrics also support this pattern of community simplification. Although total species richness remained relatively stable throughout much of the historical period, a clear decline was observed from 2022 onwards, accompanied by sharp reductions in Shannon diversity. Together, these trends indicate not only a loss of taxa but also a pronounced shift towards increasingly unbalanced assemblages dominated by a small number of species. Such diversity losses are a common outcome of biological invasions, where competitive exclusion and habitat monopolization reduce niche availability and constrain community assembly (Vilà et al. 2011). Decreased diversity has been widely linked to reduced functional redundancy, lower ecosystem stability and a diminished capacity to buffer environmental variability (Hooper D et al. 2005; Cardinale et al. 2012). In this context, the reduction in diversity documented in the Port of Bilbao suggests a potential link between the establishment of *R. okamurai* and changes extending beyond simple species turnover, with possible implications for

processes underpinning the resilience and long-term functioning of subtidal benthic communities.

The establishment of *R. okamurai* was also associated with changes in the vertical layering of the community structure. A well-structured community comprises four vertical layers: crustose, basal, canopy and epiphytic layers (Muguerza et al. 2017). Prior to 2022, assemblages in our study area displayed a multi-layered configuration characterized by a well-developed crustose and basal layer, together with low coverage of canopy and epiphytic species. Although the increase in canopy cover (formed by *R. okamurai*) could initially be interpreted as a positive structural response, a pronounced decline in basal and crustose layers was observed after the establishment of this invasive species, suggesting reduced substrate stability and habitat complexity. Since no well-developed native canopy layer was present in the study area prior to the invasion, direct comparisons regarding habitat-forming capacity and associated faunal assemblages cannot be made within the scope of this study. Nevertheless, the observed shift towards a *Rugulopteryx*-dominated canopy suggests a reorganization of the vertical structure of the assemblage, characterized by the replacement of persistent basal and encrusting components by a simplified canopy layer that could influence light penetration, space availability and the persistence of understory taxa. These patterns indicate a tendency towards structural simplification within the study system (Steneck et al. 2002), although the broader functional consequences of these changes were not directly assessed in the present study.

In addition to the alteration of the vertical layering, different native macroalgal species exhibited uneven responses following the establishment of *R. okamurai*. The calcareous species *E. elongata*, which previously exhibited high covers, declined substantially after the arrival of *R. okamurai*. Despite this reduction, *E. elongata*, together with the encrusting calcareous *Lithophyllum* spp., remained among the most persistent native taxa after invasion, suggesting some degree of resistance relative to other species. Comparable responses have been reported in other invaded regions, such as the Azores (Faria, Prestes, Moreu, Cacabelos, and Martins 2022) and the Mediterranean (Sempere-Valverde et al. 2020), where *R. okamurai* was associated with declines in native macroalgae and reduced the abundance of calcareous species, suggesting similar patterns across different biogeographic contexts.

Notably, the effects observed were not limited to macroalgae but also involved macroinvertebrate assemblages, although faunal responses were comparatively less pronounced. The introduction of *R. okamurai* coincided with simplified flora-fauna species associations, potentially reflecting changes in shelter and feeding opportunities for benthic fauna. In contrast, the bryozoan *Tubulipora* spp. showed a strong positive association with *R. okamurai*-dominated assemblages, suggesting that a limited number of invertebrate taxa may benefit from the new habitat conditions associated with the proliferation of the invader. In the absence of a consensus regarding faunal dynamics following macroalgal invasions (Thomsen et al. 2014), the faunal patterns described in this study are consistent with other research (Liuzzi and López Gappa 2011; Saarinen et al. 2018), showing shifts in the dominance of epiphytic species associated with changes in

macroalgal assemblages. More specifically, Caballero-Herrera et al. (2025) indicate a direct correlation between the expansion of *R. okamurai* and modifications in epiphytic bryozoan communities. Although that study did not investigate temporal changes, it did identify a high diversity of epiphytic bryozoans on *R. okamurai* fronds, including various species of the genera *Tubulipora* and *Beania*.

Because of the high temporal variability recorded for faunal cover throughout the study period, no substantial changes were detected before and after the introduction of *R. okamurai*. Conversely, other studies conducted in natural rocky shores have highlighted significant changes in faunal abundance rather than specific community composition (Navarro-Barranco et al. 2019). Given that anthropogenic activities in port environments significantly alter the structure of rocky-bottom benthic communities (Hawkins et al. 2016), the environmental conditions associated with the port setting may have partially masked potential faunal responses associated with the establishment of *R. okamurai*.

Furthermore, this study demonstrates that suspensivores maintained their dominance throughout the sampling period, suggesting that no other trophic guilds derived a competitive advantage following the introduction of *R. okamurai*. One plausible explanation involves the deterrent properties of *Dilcamural* (Caballero-Herrera et al. 2025), which may have buffered potential herbivore pressure on the newly available food supply.

The success of *R. okamurai* may result from the combined action of several reinforcing mechanisms. These include its ability to trap sediments, which may negatively affect native assemblages, the production of secondary metabolites that deter herbivory and an exceptional dispersal and reproductive capacity largely based on asexual propagation (García-Gómez J et al. 2021; Casal-Porras et al. 2021; MITECO 2022). In addition, the invasive potential of this species is strongly enhanced by its remarkable ecological plasticity, as it can colonize a wide range of depths and substrates, from shallow rocky reefs to soft sediments and artificial structures. *R. okamurai* has been reported down to 50-m depth and can reach very high cover values on subtidal rocky substrates (García-Gómez J et al. 2021). Together, these traits may alter trophic interactions, reduce community resilience and limit recovery potential following disturbance. The strong community-level changes observed in this study, despite its relatively sheltered conditions, are consistent with previous research documenting substantial ecological changes associated with *R. okamurai* in benthic assemblages (Faria, Prestes, Moreu, Cacabelos, and Martins 2022; Díaz-Tapia et al. 2025).

Port environments may have facilitated the establishment and spread of *R. okamurai* within the study area. Such environments are typically exposed to chronic anthropogenic pressures and often support benthic communities with reduced stability, structural complexity and resistance to disturbance (Bulleri et al. 2016), conditions that may increase susceptibility to biological invasions. In this context, the pronounced community reorganization documented in the Port of Bilbao may reflect both the high invasive capacity of *R. okamurai* and the pre-existing vulnerability of port-associated assemblages.

However, the invasion of *R. okamurai* did not produce a simultaneous response across both studied locations but instead progressed in a gradual and spatially asynchronous manner, likely reflecting differences in local environmental conditions and disturbance regimes between locations. PL, which functions as a vessel berthing area, is directly influenced by port activities and is therefore subject to chronic physical and anthropogenic disturbance. In contrast, PC experiences lower disturbance levels and historically supported more heterogeneous and structurally complex assemblages. In PL, the initial community composition showed lower abundance of crustose and complex species, and therefore a less developed encrusting and basal layer than that observed in PC. The earlier community shift observed at PL is consistent with the idea that pre-disturbed communities may be more susceptible to the establishment and spread of opportunistic invaders. Research indicates that less complex assemblages, characterized by reduced biotic resistance and a higher availability of empty niche space, are more susceptible to the successful recruitment and rapid expansion of opportunistic invaders (Bulleri and Chapman 2010). This pattern is further corroborated by observations in Alicante Bay, where *R. okamurai* has successfully colonized highly degraded areas impacted by desalination plants and sewage discharges. Notably, the invader was absent in healthy *P. oceanica* meadows, reinforcing the link between environmental degradation and the loss of biotic resistance against this invasive species (Terradas-Fernández et al. 2023). Although the magnitude of the changes observed within the port is evident, extending comparable analyses to open-coast environments and across broader environmental gradients will be essential to fully assess the invasive potential of this species under contrasting ecological conditions.

Despite its limited spatial scope, this study provides evidence of substantial community-level changes associated with the establishment of *R. okamurai* in subtidal rocky benthic communities. The invasion coincided with reduced diversity, simplified species associations and marked alterations in community structure. The contrasting responses observed between locations further suggest that anthropogenically disturbed and structurally simplified assemblages may be especially vulnerable to invasion, highlighting the importance of prioritizing surveillance efforts in ports, marinas and other artificial coastal infrastructures that can function as invasion hubs and secondary dispersal points. The spatially asynchronous invasion dynamics observed between locations further support the need for site-specific monitoring and management strategies adapted to local disturbance conditions. In this context, management actions should focus on early detection programs in high-risk areas, regular monitoring of artificial substrates and shipping-related infrastructures and minimization of secondary spread through biofouling and maritime traffic management. Recent studies have also highlighted the potential utility of remote sensing approaches, predictive dispersal models and spatial monitoring tools for improving detection and supporting rapid management responses (Roca et al. 2022; Laamraoui et al. 2024). Continued assessment of invaded and non-invaded habitats across broader environmental gradients will be critical to understanding the long-term ecological consequences associated with this invasion and to informing adaptive conservation and management strategies.

Author Contributions

E. Quintano: conceptualization, data curation, formal analysis, visualization, writing – original draft, writing – review and editing, project administration, supervision, investigation, methodology, software, validation, funding acquisition, resources. **J. Tajadura:** data curation, formal analysis, investigation, writing – original draft, writing – review and editing, software. **A. Santolaria:** writing – review and editing, investigation. **M. Bustamante:** investigation, writing – review and editing. **O. Arriaga:** investigation, writing – review and editing. **I. Uriarte:** investigation, writing – review and editing. **I. Saiz-Salinas:** validation, supervision, investigation. **N. Muguerza:** writing – original draft, visualization, formal analysis, data curation, conceptualization, methodology, investigation, supervision, project administration, writing – review and editing, software.

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Disclosure

No permission was required to reproduce material from other sources, as all figures, tables and graphical materials presented in this manuscript are original and were created by the authors.

Ethics Statement

This study did not involve experiments on legally protected species, and no ethical approval was required. All field sampling was conducted in accordance with applicable local regulations, under authorization from the Bilbao Port Authority, and was performed in a manner that minimized any disturbance to wildlife and the environment.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available in Zenodo repository ([10.5281/zenodo.21258356](https://doi.org/10.5281/zenodo.21258356)).

References

- Airolidi, L., X. Turon, S. Perkol-Finkel, and M. Rius. 2015. “Corridors for Aliens but Not for Natives: Effects of Marine Urban Sprawl at a Regional Scale.” *Diversity and Distributions* 21: 755–768. <https://doi.org/10.1111/ddi.12301>.
- Altamirano-Jeschke, M., J. Álamo, and F. J. Medina. 2016. “Arribazones de la Especie Exótica *Rugulopteryx okamurai* (E.Y. Dawson) en el Estrecho de Gibraltar.” *Algas*. 20. <http://hdl.handle.net/10630/12433>.

- Anderson, M. J. 2006. "Distance-Based Test for Homogeneity of Multivariate Dispersions." *Biometrics* 62: 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>.
- Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. "PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods." Plymouth. PRIMER-E.
- Bellissimo, G., M. Altamirano, A. Muñoz, et al. 2024. "The Invasive Brown Seaweed *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) Continues to Expand: First Record in Italy." *BioInvasions Records* 13, no. 2: 385–401. <https://doi.org/10.1101/2023.09.23.559131>.
- Bernal-Ibáñez, A., S. Chebaane, J. Sempere-Valverde, et al. 2022. "A Worrying Arrival: The First Record of Brown Macroalga *Rugulopteryx okamurae* in Madeira Island and Its Invasive Risk." *BioInvasions Records* 11, no. 4: 912–924. <https://doi.org/10.3391/bir.2022.11.4.10>.
- Bonomi-Barufi, J., F. L. Figueroa, J. Vega, et al. 2025. "Physiological Responses of the Alien Macroalga *Rugulopteryx okamurae* (Phaeophyceae, Heterokontophyta) to Changes in Nutrients and Temperature." *Journal of Phycology* 61, no. 1: 44–60. <https://doi.org/10.1111/jpy.13528>.
- Bulleri, F., F. Badalamenti, L. Iveša, et al. 2016. "The Effects of an Invasive Seaweed on Native Communities Vary Along a Gradient of Land-Based Human Impacts." *PeerJ* 4: e1795. <https://doi.org/10.7717/peerj.1795>.
- Bulleri, F., and M. G. Chapman. 2010. "The Introduction of Coastal Infrastructure as a Driver of Change in Marine Environments." *Journal of Applied Phycology* 47: 26–35. <https://doi.org/10.1111/j.1365-2664.2009.01751.x>.
- Caballero-Herrera, J. A., L. V. Ramalho, P. Marina, et al. 2025. "Highly Diverse Epifaunal Bryozoans on the Invasive Alien Species *Rugulopteryx okamurae* (Ochrophyta) in the Strait of Gibraltar Area, With the Description of a New Species." *Mediterranean Marine Science* 26, no. 4: 1017–1032. <https://doi.org/10.12681/mms.41517>.
- Cardinale, B. J., J. E. Duffy, A. Gonzalez, et al. 2012. "Biodiversity Loss and Its Impact on Humanity." *Nature* 486: 59–67. <https://doi.org/10.1038/nature11148>.
- Carlton, J. T., and J. B. Geller. 1993. "Ecological Roulette: The Global Transport of Nonindigenous Marine Organisms." *Science* 261: 78–82. <https://doi.org/10.1126/science.261.5117.78>.
- Casal-Porras, I., E. Zubía, and F. G. Brun. 2021. "Dilkamural: A Novel Chemical Weapon Involved in the Invasive Capacity of the Alga *Rugulopteryx okamurae* in the Strait of Gibraltar." *Estuarine, Coastal and Shelf Science* 257: 107398. <https://doi.org/10.1016/j.ecss.2021.107398>.
- Chust, G., A. Borja, A. Caballero, et al. 2011. "Climate Change Impacts on Coastal and Pelagic Environments in the Southeastern Bay of Biscay." *Climate Research* 48: 307–332. <https://doi.org/10.3354/cr00914>.
- Chust, G., M. González, A. Fontán, et al. 2022. "Climate Regime Shifts and Biodiversity Redistribution in the Bay of Biscay." *Science of the Total Environment* 803: 149622. <https://doi.org/10.1016/j.scitotenv.2021.149622>.
- Clarke, K. R., and R. N. Gorley. 2015. "PRIMER v7: User Manual/Tutorial." PRIMER-E. Plymouth.
- Díaz-Tapia, P., N. Alvite, R. Bañón, et al. 2025. "Multiple Introduction Events Expand the Range of the Invasive Brown Alga *Rugulopteryx okamurae* to Northern Spain." *Aquatic Botany* 196: 103830. <https://doi.org/10.1016/j.aquabot.2024.103830>.
- Díez, I., M. Bustamante, A. Santolaria, et al. 2012. "Development of a Tool for Assessing the Ecological Quality Status of Intertidal Coastal Rocky Assemblages, Within Atlantic Iberian Coasts." *Ecological Indicators* 12, no. 1: 58–71. <https://doi.org/10.1016/j.ecolind.2011.05.014>.
- El Madany, M., M. Hassoun, F. El Aamri, and N. El Mtili. 2024. "Recent Occurrence and Expansion of the Non-Indigenous Alga *Rugulopteryx okamurae* in Morocco (Mediterranean and Atlantic Shores)." *Aquatic Botany* 190: 103722. <https://doi.org/10.1016/j.aquabot.2023.103722>.
- European Commission. 2020. "EU Biodiversity Strategy for 2030: Bringing Nature Back Into Our Lives." Brussels. European Commission. https://environment.ec.europa.eu/strategy/biodiversity-strategy-2030_en.
- European Parliament and Council. 2008. "Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 Establishing a Framework for Community Action in the Field of Marine Environmental Policy (Marine Strategy Framework Directive)." *Official Journal of the European Union* L164: 19–40.
- Faria, J., A. C. L. Prestes, I. Moreu, E. Cacabelos, and G. M. Martins. 2022. "Dramatic Changes in the Structure of Shallow-Water Marine Benthic Communities Following the Invasion by *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in Azores (NE Atlantic)." *Marine Pollution Bulletin* 175: 113358. <https://doi.org/10.1016/j.marpolbul.2022.113358>.
- Faria, J., A. C. L. Prestes, I. Moreu, M. Martins G, A. I. Neto, and E. Cacabelos. 2022. "Arrival and Proliferation of the Invasive Seaweed *Rugulopteryx okamurae* in NE Atlantic Islands." *Botanica Marina* 65, no. 1: 45–50. <https://doi.org/10.1515/bot-2021-0060>.
- Figueroa, F. L., J. Vega, N. Flórez-Fernández, et al. 2025. "Challenges and Opportunities of the Exotic Invasive Macroalga *Rugulopteryx okamurae* (Phaeophyceae, Heterokontophyta)." *Journal of Applied Phycology* 37: 579–595. <https://doi.org/10.1007/s10811-024-03404-w>.
- Floerl, O., G. J. Inglis, K. Dey, and A. Smith. 2009. "The Importance of Transport Hubs in Stepping-Stone Invasions." *Journal of Applied Ecology* 46: 37–45. <https://doi.org/10.1111/j.1365-2664.2008.01540.x>.
- Galparsoro, I., A. Borja, I. Legorburu, et al. 2010. "Morphological Characteristics of the Basque Continental Shelf (Bay of Biscay, Northern Spain); Their Implications for Integrated Coastal Zone Management." *Geomorphology* 118: 314–329. <https://doi.org/10.1016/j.geomorph.2010.01.012>.
- García-Gómez J. C., M. Florido, L. Olaya-Ponzone, J. Sempere-Valverde, and C. Megina. 2021. "The Invasive Macroalga *Rugulopteryx okamurae*: Substrata Plasticity and Spatial Colonization Pressure on Resident Macroalgae." *Frontiers in Ecology and Evolution* 9: 631754. <https://doi.org/10.3389/fevo.2021.631754>.
- García-Gómez, J. C., J. Sempere-Valverde, A. R. González, et al. 2020. "From Exotic to Invasive in Record Time: The Extreme Impact of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in the Strait of Gibraltar." *Science of the Total Environment* 704: 135408. <https://doi.org/10.1016/j.scitotenv.2019.135408>.
- Gotelli, N. J., and R. K. Colwell. 2001. "Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness." *Ecology Letters* 4: 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Guiry, M. D., and G. M. Guiry. 2026. "AlgaeBase." Worldwide Electronic Publication. National University of Ireland. Galway. Retrieved January 8, 2026. <https://www.algaebase.org>.
- Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. "Emergent Insights From the Synthesis of Conceptual Frameworks for Biological Invasions: Conceptual Frameworks for Biological Invasions." *Ecology Letters* 14, no. 4: 407–418. <https://doi.org/10.1111/j.1461-0248.2011.01594.x>.
- Hawkins, S. J., A. J. Evans, L. B. Firth, et al. 2016. "Impacts and Effects of Ocean Warming on Intertidal Rocky Habitats." In *Explaining Ocean Warming: Causes, Scale, Effects and Consequences*, edited by D. Laffoley and J. M. Baxter, 147–176. IUCN. <https://doi.org/10.2305/IUCN.CH.2016.08.en>.

- Hooper D, U., S. Chapin F, J. J. Ewel, et al. 2005. "Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge." *Ecological Monographs* 75, no. 1: 3–35. <https://doi.org/10.1890/04-0922>.
- Horton, T., A. Kroh, S. Ah Yong, et al. 2026. "World Register of Marine Species (WoRMS)." WoRMS Editorial Board. Retrieved January 8, 2026. <http://www.marinespecies.org>.
- Hwang, I. K., W. J. Lee, H. S. Kim, and O. De Clerck. 2009. "Taxonomic Reappraisal of *Dilophus okamurai* (Dictyotales, Phaeophyta) From the Western Pacific Ocean." *Phycologia* 48, no. 1: 1–12. <https://doi.org/10.2216/07-68.1>.
- Katsanevakis, S., A. Zenetos, C. Belchior, and A. C. Cardoso. 2013. "Invading European Seas: Assessing Pathways of Introduction of Marine Aliens." *Ocean and Coastal Management* 76: 64–74. <https://doi.org/10.1016/j.ocecoaman.2013.02.024>.
- Laamraoui, M. R., B. Mghili, M. Roca, et al. 2024. "Rapid Invasion and Expansion of the Invasive Macroalgae *Rugulopteryx okamurai* in the Mediterranean and Atlantic: A 10-Year Review." *Marine Pollution Bulletin* 209: 117194. <https://doi.org/10.1016/j.marpolbul.2024.117194>.
- Liulea, S., E. A. Serrão, and R. Santos. 2023. "Spread and Impact of the Invasive Brown Algae *Rugulopteryx okamurai* on the Algarve Coast, Southern Portugal (NE Atlantic)." SSRN. <https://doi.org/10.2139/ssrn.4446622>.
- Liuzzi, M. G., and J. López Gappa. 2011. "Algae as Hosts for Epifaunal Bryozoans: Role of Functional Groups and Taxonomic Relatedness." *Journal of Sea Research* 65, no. 1: 28–32. <https://doi.org/10.1016/j.seares.2010.06.007>.
- MarLIN. 2006. "BIOTIC—Biological Traits Information Catalogue." Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. <https://www.marlin.ac.uk/biotic>.
- MITECO, Ministerio para la Transición Ecológica y el Reto Demográfico. 2022. "Estrategia de Control del Alga *Rugulopteryx okamurai*." Retrieved January 8, 2026. https://www.miteco.gob.es/content/dam/miteco/es/biodiversidad/publicaciones/estrategias/estrategia_rokamurai_cs_28072022_tcm30-543560.pdf.
- Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. "Assessing the Global Threat of Invasive Species to Marine Biodiversity." *Frontiers in Ecology and the Environment* 6, no. 9: 485–492. <https://doi.org/10.1890/070064>.
- Muguerza, N., I. Díez, E. Quintano, M. Bustamante, and J. M. Gorostiaga. 2017. "Structural Impoverishment of the Subtidal Vegetation of Southeastern Bay of Biscay From 1991 to 2013 in the Context of Climate Change." *Journal of Sea Research* 130: 166–179. <https://doi.org/10.1016/j.seares.2017.06.006>.
- Navarro-Barranco, C., B. Muñoz-Gómez, D. Saiz, et al. 2019. "Can Invasive Habitat-Forming Species Play the Same Role as Native Ones? The Case of the Exotic Marine Macroalga *Rugulopteryx okamurai* in the Strait of Gibraltar." *Biological Invasions* 21: 3319–3334. <https://doi.org/10.1007/s10530-019-02049-y>.
- Occhipinti-Ambrogi, A., and D. Savini. 2003. "Biological Invasions as a Component of Global Change in Stressed Marine Ecosystems." *Marine Pollution Bulletin* 46, no. 5: 542–551. [https://doi.org/10.1016/S0025-326X\(02\)00363-6](https://doi.org/10.1016/S0025-326X(02)00363-6).
- Ojaveer, H., B. S. Galil, M. L. Campbell, et al. 2015. "Classification of Non-Indigenous Species Based on Their Impacts: Considerations for Application in Marine Management." *PLoS Biology* 13, no. 4: e1002130. <https://doi.org/10.1371/journal.pbio.1002130>.
- Papacostas, K., E. Rielly-Carroll, S. Georgian, et al. 2017. "Biological Mechanisms of Marine Invasions." *Marine Ecology Progress Series* 565: 251–268. <https://doi.org/10.3354/meps12001>.
- Pereira, L. 2024. "Non-Indigenous Seaweeds in the Iberian Peninsula, Macaronesia Islands (Madeira, Azores, Canary Islands) and Balearic Islands: Biodiversity, Ecological Impact, Invasion Dynamics, and Potential Industrial Applications." *Algal Research* 78: 103407. <https://doi.org/10.1016/j.algal.2024.103407>.
- R Core Team. 2026. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing. Vienna, Austria. <https://www.R-project.org/>.
- Roca, M., B. Dunbar M, A. Román, et al. 2022. "Monitoring the Marine Invasive Alien Species *Rugulopteryx okamurai* Using Unmanned Aerial Vehicles and Satellites." *Frontiers in Marine Science* 9: 1004012. <https://doi.org/10.3389/fmars.2022.1004012>.
- Saarinen, A., S. Salovius-Laurén, and J. Mattila. 2018. "Epifaunal Community Composition in Five Macroalgal Species—What Are the Consequences if Some Algal Species Are Lost?" *Estuarine, Coastal and Shelf Science* 207: 402–413. <https://doi.org/10.1016/j.ecss.2017.08.009>.
- Sempere-Valverde, J., E. Ostalé-Valriberas, M. Maestre, and R. González. 2020. "Impacts of the Non-Indigenous Seaweed *Rugulopteryx okamurai* on a Mediterranean Coralligenous Community (Strait of Gibraltar): The Role of Long-Term Monitoring." *Ecological Indicators* 121: 107135. <https://doi.org/10.1016/j.ecolind.2020.107135>.
- Somerfield, P. J., and K. R. Clarke. 2013. "Inverse Analysis in Non-Parametric Multivariate Analyses: Distinguishing Groups of Associated Species Which Covary Coherently Across Samples." *Journal of Experimental Marine Biology and Ecology* 449: 261–273. <https://doi.org/10.1016/j.jembe.2013.10.002>.
- Sorte, C. J. B., S. L. Williams, and R. A. Zerebecki. 2010. "Ocean Warming Increases Threat of Invasive Species in a Marine Fouling Community." *Ecology* 91, no. 8: 2198–2204. <https://doi.org/10.1890/10-0238.1>.
- Steneck, R. S., M. H. Graham, B. J. Bourque, et al. 2002. "Kelp Forest Ecosystems: Biodiversity, Stability, Resilience and Future." *Environmental Conservation* 29, no. 4: 436–459. <https://doi.org/10.1017/S0376892902000322>.
- Terradas-Fernández, M., C. Pena-Martín, M. Valverde-Urrea, et al. 2023. "An Outbreak of the Invasive Macroalgae *Rugulopteryx okamurai* in Alicante Bay and Its Colonization on Dead *Posidonia oceanica* Matte." *Aquatic Botany* 189: 103706. <https://doi.org/10.1016/j.aquabot.2023.103706>.
- Thomsen, M. S., J. E. Byers, D. R. Schiel, et al. 2014. "Impacts of Marine Invaders on Biodiversity Depend on Trophic Position and Functional Similarity." *Marine Ecology Progress Series* 495: 39–47. <https://doi.org/10.3354/meps10566>.
- Valencia, V., J. Franco, Á. Borja, and A. Fontán. 2004. "Hydrography of the Southeastern Bay of Biscay." In *Oceanography and Marine Environment of the Basque Country*, edited by A. Borja and M. Collins, 159–194. Elsevier. [https://doi.org/10.1016/S0422-9894\(04\)80045-X](https://doi.org/10.1016/S0422-9894(04)80045-X).
- Valentine, J. P., R. H. Magierowski, and C. R. Johnson. 2007. "Mechanisms of Invasion: Establishment, Spread and Persistence of Introduced Seaweed Populations." *Botanica Marina* 50, no. 5–6: 351–360. <https://doi.org/10.1515/BOT.2007.040>.
- Verlaque, M., F. Steen, and O. De Clerck. 2009. "*Rugulopteryx* (Dictyotales, Phaeophyceae), a Genus Recently Introduced to the Mediterranean." *Phycologia* 48, no. 6: 536–542. <https://doi.org/10.2216/08-103.1>.
- Viard, F., and T. Comtet. 2015. "Applications of DNA-Based Methods for the Study of Biological Invasions." In *Biological Invasions in Changing Ecosystems*, edited by J. Canning-Clode, 411–435. De Gruyter Open. <https://doi.org/10.1515/9783110438666-025>.
- Vilà, M., J. L. Espinar, M. Hejda, et al. 2011. "Ecological Impacts of Invasive Alien Plants: A Meta-Analysis of Their Effects on Species, Communities and Ecosystems." *Ecology Letters* 14: 702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>.

Wahl, M. 2009. *Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change*. Springer-Verlag. <https://doi.org/10.1007/978-3-540-92704-4>.

Williams, S. L., and J. E. Smith. 2007. "A Global Review of the Distribution, Taxonomy, and Impacts of Introduced Seaweeds." *Annual Review of Ecology, Evolution, and Systematics* 38, no. 1: 327–359. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095543>.

Wood, S. N. 2017. *Generalized Additive Models: An Introduction With R*. 2nd ed. Chapman and Hall/CRC.

Zuur, A. F., A. A. Saveliev, and E. N. Ieno. 2014. *A Beginner's Guide to Generalized Additive Mixed Models With R*. Highland Statistics Ltd.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table A1.** Mean macroalgae cover for each year and location (PL: Punta Lucero, PC: Punta Ceballos). In the case of some heteromorphic species (*Asparagopsis armata*, *Bonnemaisonia hamifera* and *Derbesia tenuissima*), the gametophytic and sporophytic phases have been differentiated and recorded independently. Although these stages belong to the same biological species, they are presented as distinct functional units due to their contrasting morphologies and ecological roles. *Bryopsis* spp.: *B. hypnoides* and *B. plumosa*; *Dictyota* spp.: *D. dichotoma* and *D. cyanoloma*; *Halopteris* spp.: *H. scoparia* and *H. filicina*; *Lithophyllum* spp.: *L. incrustans* and *L. hibernicum*; *Mesophyllum* spp.: *M. lichenoides* and *M. expansum*. **Table A2.** Mean invertebrate cover for each year and location (PL: Punta Lucero, PC: Punta Ceballos). *Crisia* spp.: *C. denticulata* and *C. sp.*; *Spirobranchus* spp.: *S. triqueter* and *S. sp.*; *Suberites* spp.: *S. domuncula*, *S. massa* and *S. sp.*; *Tubulipora* spp.: *T. liliacea* and *T. plumosa*. **Table A3.** PERMANOVA results on assemblages. TI: time; Lo: location. **Table A4.** Summary of the results of the SIMPER routine. The average abundance (cover in %) and percentage contribution (contrib. %) of each taxon are presented. The 11 taxa listed contribute > 2% to the formation of groups. *Dictyota* spp.: *D. dichotoma* and *D. cyanoloma*; *Halopteris* spp.: *H. scoparia* and *H. filicina*; *Lithophyllum* spp.: *L. incrustans* and *L. hibernicum*; *Mesophyllum* spp.: *M. lichenoides* and *M. expansum*; *Tubulipora* spp.: *T. liliacea* and *T. plumosa*. **Table A5.** Summary of the statistical models applied to evaluate 15-year temporal trends for each ecological variable at Punta Lucero (PL). **Table A6.** Summary of the statistical models applied to evaluate 15-year temporal trends for each ecological variable at Punta Ceballos (PC).