



# The Invasive Macroalga *Rugulopteryx okamurae*: Substrata Plasticity and Spatial Colonization Pressure on Resident Macroalgae

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## OPEN ACCESS

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### Specialty section:

This article was submitted to  
Biogeography and Macroecology,  
a section of the journal  
Frontiers in Ecology and Evolution

**Received:** 20 November 2020

**Accepted:** 09 April 2021

**Published:** 08 June 2021

### Citation:

García-Gómez JC, Florido M,  
Olaya-Ponzone L,  
Sempere-Valverde J and Megina C  
(2021) The Invasive Macroalga  
*Rugulopteryx okamurae*: Substrata  
Plasticity and Spatial Colonization  
Pressure on Resident Macroalgae.  
*Front. Ecol. Evol.* 9:631754.  
doi: 10.3389/fevo.2021.631754

The present study constitutes the first evaluation of the space colonization strategies performed by *Rugulopteryx okamurae* when co-occurring with the resident macroalgal community in the introduced areas. Since the first apparition of the nonindigenous macroalga in the Strait of Gibraltar, its high propagation capacity together with its colonization ability has enhanced the establishment success of the species in detriment of the resident biota. In this study, we carried out observational surveys during 2017–2020 in order to assess the coverage levels of *R. okamurae* on different lighting conditions, surface orientations, and substrata types (artificial and natural). Results revealed that, beyond the high percent coverages already reported at illuminated and semi-illuminated natural rocky habitats, *R. okamurae* is able to settle on a wide variety of artificial substrata. The settlement performance of the species was also investigated and different mechanisms underlying the space colonization were proposed. Thus, *R. okamurae* was observed interacting with 43 resident macroalgal species at generally illuminated rocky habitats of the northern Strait coasts. Six colonization mechanisms were proposed for spatial growth scenarios. Overall, results pointed out that, in most of the cases where the invasive species co-occur with the resident community, *R. okamurae* would be favored as regards spatial growth success. Competitive interactions and environmental factors which influence results obtained must be addressed in order to fully predict impacts on resident communities. Moreover, together with previous scientific works, overall data provided in this study highlight the need to urgent implement management measures focused on habitats susceptible to be invaded, as well as studies on the ecology and dispersal vectors of *R. okamurae* in the Strait of Gibraltar and adjacent areas.

**Keywords:** *Rugulopteryx okamurae*, macroalgae, biological invasions, invasive macroalga, space colonization, Strait of Gibraltar

## INTRODUCTION

The introduction and spread of nonindigenous marine species (NIS) are within the major threats to global biodiversity, natural resources, and human health and constitute a priority for the protection and management of coastal areas (Bax et al., 2003; Galil et al., 2018). When an introduced NIS acclimates and expresses an aggressive ecological behavior, its status progresses from established NIS to invasive NIS. In such cases, NIS competes with the resident community for resources like space, so the ecosystem and its services can be altered. In the case of macroalgae, the establishment of the introduced species may lead to competitive interactions with the resident macroalgal community through lateral and epiphytic growth, which can be facilitated by a higher thermal tolerance than its competitors and the production of secondary metabolites for allelopathic defense (Tronholm et al., 2012). Secondary metabolites can ease lateral competition but also impede predation by native consumers, thus increasing the ecological competitiveness of the species in the introduced environments (Pereira and Da Gama, 2008). Consequently, NIS may severely affect the marine ecosystems by modifying the local habitats, community structure, and food webs (Viard and Comtet, 2015; Marks et al., 2018). To meet EU regulation on the prevention and management of NIS, it is highly necessary to establish standard methodologies and monitoring plans in sensitive and little-studied areas (Galil et al., 2018).

The Strait of Gibraltar is a biodiversity hotspot located in the convergence of three biogeographic provinces within the Atlantic–Mediterranean subregion (Ekman, 1953). This area is highly sensitive to environmental changes (Coll et al., 2010), and it experiences an intense maritime traffic, which is a major vector for the introduction of NIS (Papacostas et al., 2017). The benthic communities of the Strait of Gibraltar may have already suffered the cumulative impacts from the invasive NIS *Asparagopsis armata*, *Asparagopsis taxiformis*, and *Caulerpa cylindracea* (Boudouresque and Verlaque, 2002; Andreakis et al., 2004; Rivera-Ingraham et al., 2010). In such vulnerable geographical area, the detection and monitoring of potential invasive species can provide valuable information. Mechanisms that can influence the invasion success of marine macroalgae remain misunderstood, even though they are critical for the successful mitigation and conservation of the ecosystems affected (Noè et al., 2018).

In 2015, the brown macroalga *Rugulopteryx okamuræ*, native to the Northwestern Pacific (Hwang, 1994), was detected for the first time on both shores of the Strait of Gibraltar (Altamirano-Jeschke et al., 2016; Ocaña et al., 2016). In the Mediterranean Sea, this species was previously recorded on the coastal lagoon of Thau (French Mediterranean coast), presumably introduced through the commerce of Japanese oysters for aquaculture (Verlaque et al., 2009). Nevertheless, in Thau lagoon, this species did not show a critical invasive behavior as it happened in the Strait coasts (Verlaque et al., 2009; García-Gómez et al., 2018). During 2015–2016, *R. okamuræ*

quickly colonized most of the shoreline of this Strait, requiring municipal cleaning machines to remove more than 5,000 tons of detached biomass from the touristic beaches of Ceuta, North Africa (Ocaña et al., 2016; El Aamri et al., 2018). The massive algal wracks detected (**Supplementary Figure 1**), together with the huge coverages identified when the species is attached to the rocky bottoms (García-Gómez et al., 2018, 2020), suggest that this case is worryingly unusual because of the large amounts of biomass produced in such a small geographical area. Beyond the ecological impacts, social and economic consequences of the invasive behavior of *R. okamuræ* can be also assumed (e.g., the massive biomass released on the coasts threatens the tourist inflow and the fishing sector as it becomes entangled in nets, hindering the fish extraction).

On its native distributional range, *R. okamuræ* is abundant throughout the year. The maximum growth and reproductive development occurs above 15°C, while the thallus is reduced to a basal system of perennial rhizoids in winter (Kajimura, 1992; Hwang et al., 2009). Agatsuma et al. (2005) suggests that the biological cycle of the species in the Pacific waters is completed in 2 years, but it is still unknown if the species is able to complete its life cycle in the Mediterranean and Atlantic waters (Verlaque et al., 2009; Altamirano-Jeschke et al., 2016, 2017). Despite that sexual reproduction is still unperceived in the introduced habitats, the vegetative and asexual strategies of the established populations (propagules and monospores) have led to the massive occupation of most of the rocky bottoms (Altamirano-Jeschke et al., 2017 and Altamirano et al., 2019), becoming present all-year round in the southern and northern coasts of the Strait of Gibraltar.

The extreme propagation capacity of the species, combined with a high survival capability, would make the impact magnitude high and any secondary spread events worrisome. In fact, shortly after delimiting the distributional range of *R. okamuræ* in 2017 (see García-Gómez et al., 2020), massive wrack deposits of the species were sighted at points beyond its eastern and western limits along the northern coasts of the Strait of Gibraltar, in Granada and Almería (Altamirano et al., 2019; Figueroa et al., 2020). Moreover, preliminary models predicting suitable areas for the incoming establishment of *R. okamuræ* populations have evidenced the risk of nearby areas along the entire southern and eastern Iberian Peninsula, where protected areas and others of great conservation interest are included (Muñoz et al., 2019).

This study aims to perform a preliminary evaluation of the establishment potential of *R. okamuræ* in the introduced habitats, as well as the vulnerability of the resident benthic macroalgae facing its spatial growth and propagation through the coasts of the Strait of Gibraltar. Specifically, the following objectives were raised (1) to estimate the coverage of *R. okamuræ* on different substrata, orientations, and lighting conditions and (2) to assess the implications on the resident macroalgal community when *R. okamuræ* is established in the same substrata, highlighting apparent colonization strategies underlying the spatial growth of the invasive species.

## MATERIALS AND METHODS

### Sampling Locations

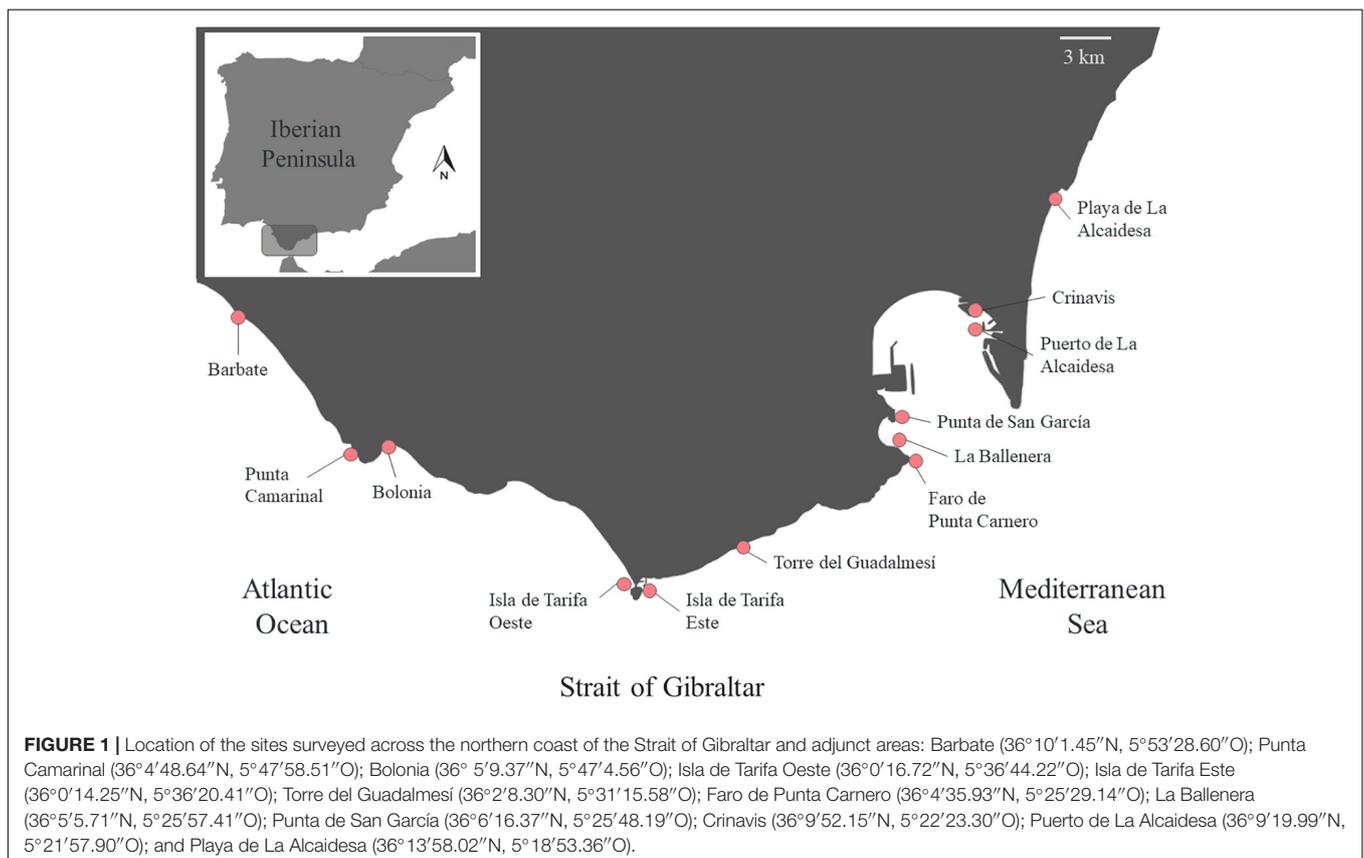
Observational studies were performed in 12 surveys (period from June to September, during 2017–2020), comprehending all the ranges of distribution of *R. okamuræ* on the northern coasts of the Strait of Gibraltar and adjacent areas. Each survey corresponded to one sampling site where the invasive species was present and attached to the rocky bottom and located less than 20 km from each other (Figure 1). This area hosts the Marine Protected Area “El Estrecho Natural Park,” included within The Intercontinental Biosphere Reserve of the Mediterranean. The study sites were the following: Barbate, Punta Camarinal, Bolonia, Isla de Tarifa Oeste, Isla de Tarifa Este, Torre del Guadalmesí, Faro de Punta Carnero, La Ballenera, Punta de San García, Crinavis, Puerto de La Alcaidesa, and Playa de La Alcaidesa.

### Coverage of *R. okamuræ* on Different Substrata and Lighting Conditions

In each sampled site, an estimation of *R. okamuræ* coverage was carried out by direct visual observations in three 50-m-long and 4-m-wide transects. When necessary, *in situ* observations were supported by video- and photographic data taken in the same survey. Transects were located parallel to the shoreline between 0 and 10 m depth. In the case of sites where the

considered substrata limited the sampling area (i.e., artificial structures at Puerto de La Alcaidesa and Crinavis), transects were located parallel to the shoreline but distributed along the horizontal plane. Thus, the coverage of *R. okamuræ* was assessed considering the following substrata conditions: inclination (i.e., vertical and horizontal), lighting conditions (i.e., highly illuminated, moderately illuminated, poorly illuminated and unlit areas), and substrata nature (i.e., natural and artificial substrata). Natural substrata were represented by maërls and pebbles, limestone, sandstone, slate, and wood. Meanwhile, artificial substrata considered were breakwater boulders near sandy bottoms, cement and concrete, ceramics, breakwater limestone boulders, abandoned fishing nets and ropes, glass bottles, metallic surfaces, metallic surfaces on boats and ships, plastics, and car tires.

The total percent cover of *R. okamuræ* per substratum was estimated as the overall coverage occupied at each abovementioned condition within the 200 square meters of each transect. Because some anomalous artificial substrata are not frequently found while crucial considering space availability in marine habitats, a selective exploration was carried near the limits of the sampling transects when considering components of the marine debris (i.e., plastics, ceramics, abandoned fishing nets and ropes, glass bottles, and car tires). Overall *R. okamuræ* coverage values were included within a 0 to 3 scale attending to different ranges. Thus, if the coverage ranged between 1 and 30% for all aforementioned transects at one specific substratum, the



species was classified as “present” (1) for that substratum; percent coverages between 31 and 60% were classified as “abundant” (2) and coverages over 61% as “dominant” (3). Resident macroalgal coverage was not included since competitive scenarios were not contemplated for this objective.

## Substrata Types and Colonization Strategies Associated With *R. okamuræ* Establishment

In order to better understand how *R. okamuræ* is spatially growing on the coastal habitats, the presence of the invasive macroalga was examined in, at least, one of all aforementioned sampling sites by direct—*in situ*—or indirect observation (photographs and/or videos). In surveys, we recorded the spatial growth scenarios where *R. okamuræ* co-occurred with other macroalgal species when established at different recipient habitats. Habitats were differentiated attending to rocky substrata nature (natural and artificial), tide exposition (intertidal areas, tide pools, and subtidal areas), illumination (illuminated and shadow habitats), and bottom composition (sandy bottoms). The resident macroalgal community was identified to the lowest taxonomic level possible, and the percentage of co-occurring scenarios at different habitats was recorded. Because preliminary surveys revealed different coexistence patterns, the spatial colonization strategies by which *R. okamuræ* seems to become established on generally illuminated rocky habitats were proposed.

To synthesize all the information obtained about the spatial growth of *R. okamuræ*, Venn diagrams were created using Venny 2.1 online software (Oliveros, 2007). Venn diagrams allow to visualize and analyze relationships between different data groups by representing all possible combinations and elements contained in each one of them. Identifying the spatial growth strategies described as groups, displayed diagrams allow the identification of shared (overlapped circles) and unique species (independent regions of circles) performing each interaction described and/or their different combinations. No more than four group combinations were displayed in each analysis to comply with the requirements of the exotic geometries of the software (Oliveros, 2007).

## RESULTS

### Coverage of *R. okamuræ* on Different Substrata and Lighting Conditions

*Rugulopteryx okamuræ* dominated (i.e., 100% coverage) at highly illuminated areas (vertical and horizontal) and moderately illuminated horizontal surfaces (0–10 m depth) (Table 1). The species was abundant (31–60%) at vertical moderately illuminated areas, present (1–30%) at horizontal surfaces of the entrance of caves and crevices, and totally absent (0% coverage) at unlit areas and vertical poorly illuminated habitats. Concerning substrata nature, 100% of coverage was obtained for limestone and sandstone (natural rocky substrata), and limestone rip-rap boulders (artificial rocky substrata). The species was abundant

(31–60% coverage) at ceramics, tires, and abandoned fishing nets and ropes, while present (1–30% coverage) on a wide variety of substrata, including breakwater boulders close to sandy bottoms, cement and concrete, glass bottles, metallic surfaces (including those from the upper zone of boats and ship hulls), and plastics.

### Habitats and Colonization Strategies Underlying *R. okamuræ* Establishment

Forty-three macroalgal species were detected in relation to possible implications inferred by the spatial establishment of *R. okamuræ*, including four NIS (*A. armata*, *A. taxiformis*, *C. cylindracea*, and *Dictyota cyanoloma*). Species which spatially co-occurred with *R. okamuræ* at each habitat type are listed in Table 2 (left section). In 22 and 23% of the cases, the invasive species co-occurred with the macroalgal community at natural and illuminated habitats, respectively (Figure 2A). Sublittoral habitats harbored 17% of the spatial growth scenarios, while tide pools, artificial structures, and intertidal zones recorded 10, 10, and 9%, respectively. Sandy (5%) and shadow bottoms (4%) were less represented, being the habitats where *R. okamuræ* was rarely observed spatially growing and interacting with the resident community.

Six spatial growth strategies by which *R. okamuræ* becomes established at generally illuminated rocky habitats were proposed regarding possible effects on the resident macroalgae (right section of Table 2 and Figures 2B, 3). In two of the strategies identified, we suggest the space colonization as a result of the direct interaction with the resident macroalgae. Thus, competition by lateral compression (LAT) and overgrowth as epiphyte (EPI) were proposed for 28% and 16% of the total cases, respectively, where *R. okamuræ* was established on the substrata interacting (i.e., co-occurring) with the resident macroalgal community. Other settlement scenarios did not show signs of direct macroalgal interaction although the final occupancy by the invasive species was expected to occur. Thus, the invasive species was observed to grow and develop on the resident macroalgae without being attached on the adult thalli (GRO) (9%) and, in 28% of the cases, the resident species were surrounded by *R. okamuræ*, which remained abundantly established around the resident macroalgal populations (OCC). In this last strategy, and according to overall observations, *R. okamuræ* became established on the space left by the previously established populations with the resident macroalgae death, as a consequence of its biological cycle or another unidentified factors (e.g., abiotic stressors, predation).

Surveys revealed other cases where, despite that biological interactions between both macroalgae were apparently perceived, no direct evidences of negative impacts on the resident community were observed. However, it must be taken into account that physicochemical factors, physiological impacts, or other indirect effects from *R. okamuræ* competitiveness have not been examined here, so results obtained for the latter mechanisms must constitute just the preliminary basis to further investigate patterns observed if they happened (impacts). Two main processes needed to be differentiated in this case: on the one hand, we described spatial growth events where disturbance/stress processes may be occurring

**TABLE 1** | Coverage of *Rugulopteryx okamuræ* under different lighting conditions and substrata nature (natural and artificial substrata).

Light exposition and surface orientation	Unlit (dark) areas	Vertical	Horizontal
	Poorly illuminated areas (entrance of caves and crevices)	Vertical	Horizontal
	Moderately illuminated areas	Vertical	Horizontal
	Highly illuminated areas	Vertical	Horizontal
Natural substrata	Maerl and pebbles (<5 cm of diameter)		
	Limestone		
	Sandstone		
	Slate		
	Wood		
Artificial substrata	Breakwater boulders near sandy bottom		
	Cement and concrete		
	Ceramics		
	Limestone rip-rap boulders		
	Abandoned fishing nets and ropes		
	Glass bottles		
	Metallic surfaces		
	Metallic surfaces from boats and ships		
	Plastics		
	Tires		
	Coverage categories	0	1
		2	3

Grey bars represent the percentage ranges of observed coverage of *R. okamuræ* during the visual samplings (0–10 m depth). The absence of grey bars reveals that *R. okamuræ* was absent in all locations surveyed. Coverage categories correspond to the following coverage ranges: 0: Absent (0% coverage); 1: Present (1–30% coverage); 2: Abundant (31–60% coverage); 3: Dominant (61–100% coverage).

even though they are not perceived yet. Despite the lack of negative evidences of resident species death or damaged tissues in our surveys, this strategy was assumed to lead to disturbance events in the species involved since indirect implications derived from similar competitive scenarios have been obtained and could be likely to occur in the study area (e.g., indirect implications like shading, chemical alteration, bioturbation). In this regard, only one strategy was proposed for the 13% of the overall co-occurrence cases. It was described for those cases where *R. okamuræ* mats, detached from the rocky bottom and dispersed in the water column, become free-floating on the resident species thallus without being totally attached on them (FLO). On the other hand, we also perceived colonization strategies led by the resident macroalgae. Unless *R. okamuræ* was established on the substrata, the resident macroalgae seemed to take advantage from the spatial growth (e.g., epiphytes of the invasive macroalga) in the 6% of the cases surveyed. Hence, *R. okamuræ* was observed as a basibiont (i.e., host to a macroalgal epibiont) (BAS) (Figures 4A–C) of *A. armata* (Figure 4A), *Colpomenia sinuosa*, *Halopteris scoparia*, *Plocamium cartilagineum* (Figure 4B), *Titanoderma pustulatum*, and *Sphaerococcus coropifolius*.

Mechanisms underlying spatial exclusion were those expected to seriously compromise resident species survival,

so they were selected to be explored with Venn diagrams. Thus, relations between LAT, EPI, GRO, and OCC were together examined (Figure 5A). Besides, GRO, EPI, FLO, and BAS were independently studied in order to check possible relations in terms of disturbance/stress and overgrowth strategies (Figure 5B). Most of species displaced by LAT were also observed to suffer spatial pressure by OCC (seven common species were involved in LAT and OCC strategies: *D. cyanoloma*, *Dictyota dichotoma*, *Dictyota dichotoma* var. *intricata*, *Dictyota fasciola*, *Dictyopterus polypodioides*, *Stoechospermum polypodioides*, and *Ulva rigida*). In fact, despite that LAT was perceived to only affect two of the resident species in an exclusive way, it was the mechanism most combined with remaining interactions. In contrast, OCC was more exclusive in terms of species affected by only one spatial growth strategy of *R. okamuræ* (i.e., five species were displaced only by OCC processes).

GRO was also poor combined with other interactions of spatial exclusion. Overall, macroalgae suffering overgrowth interactions by this strategy included the macroalgal species *Codium vermilara*, *C. sinuosa*, *Lithophyllum incrustans*, *Mesophyllum alternans*, *Mesophyllum lichenoides*, *Halopithys incurva*, *Peyssonnelia* ssp., and *Taonia atomaria*. Venn diagrams revealed that six species were observed to be affected by *R. okamuræ* establishment only by epiphytic strategies:

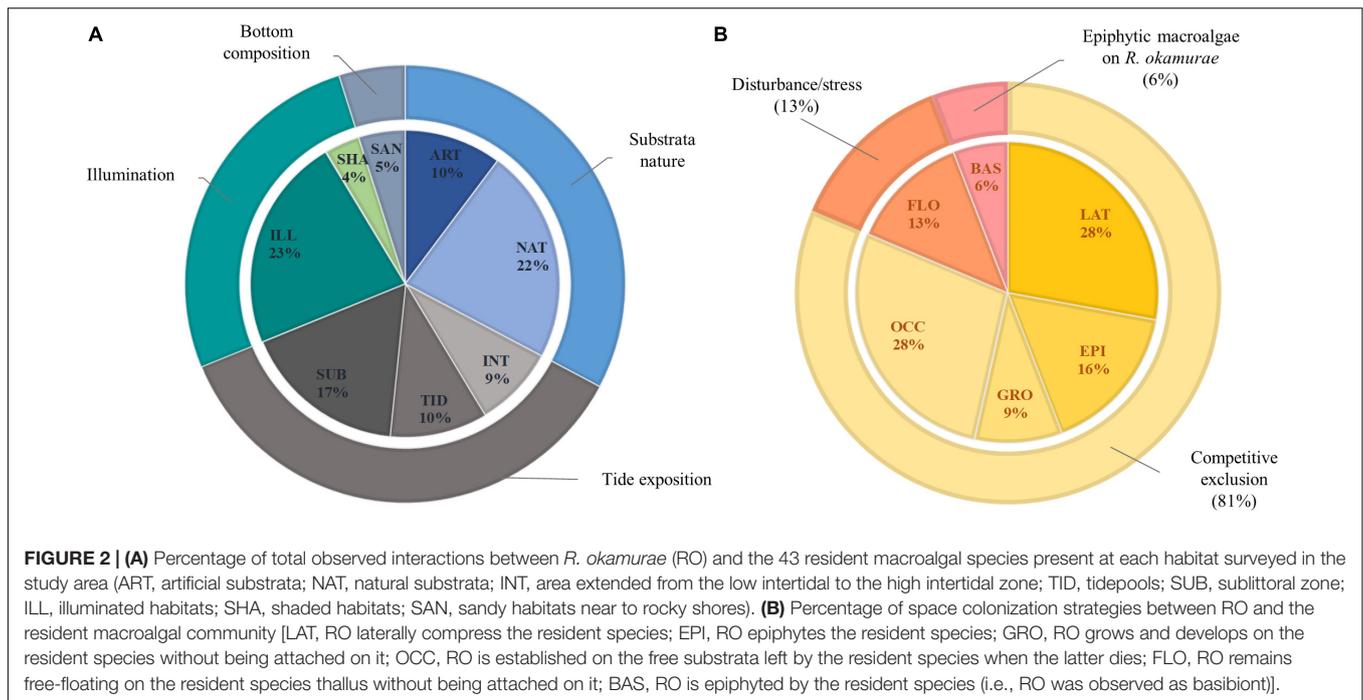
**TABLE 2** | Presence (shaded quadrats) of perceived interactions between *R. okamuræ* and resident macroalgal species at introduced habitats.

	Habitats								Space colonization strategies					
	ART	NAT	INT	TID	SUB	ILL	SHA	SAN	LAT	EPI	GRO	OCC	FLO	BAS
<i>Amphiroa rigida</i> J. V. Lamouroux														
<i>Asparagopsis armata</i> Harvey														
<i>A. taxiformis</i> (Delle) Trevisan de Saint-Léon														
<i>Caulerpa cylindracea</i> Sonder														
<i>Caulacanthus</i> sp./ <i>Gelidium</i> sp. Turf														
<i>Chaetomorpha</i> sp.														
<i>Cladophora laetevirens</i> (Dillwyn) Kützing														
<i>Codium adhaerens</i> C. Agardh														
<i>C. bursa</i> (Oliv) C. Agardh														
<i>C. vermilara</i> (Oliv) Delle Chiaje														
<i>Cladostephus spongiosus</i> (Hudson) C. Agardh														
<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbès and Solier														
<i>Cystoseira tamariscifolia</i> (Hudson) Papenfuss														
<i>Dictyopteris polypodioides</i> (A. P. De Candolle) J. V. Lamouroux														
<i>Dictyota cyanoloma</i> Tronholm, De Clerck, A.Gómez-Garreta and Rull Lluich														
<i>D. dichotoma</i> (Hudson) J. V. Lamouroux														
<i>D. dichotoma</i> var. <i>intricata</i> (C. Agardh) Greville														
<i>D. fasciola</i> (Roth) J. V. Lamouroux														
<i>Ellisolandia elongata</i> (J. Ellis and Solander) K. R. Hind and G. W. Saunders														
<i>Fucus spiralis</i> Linnaeus														
<i>Gelidium corneum</i> (Hudson) J. V. Lamouroux														
<i>G. spinosum</i> (S. G. Gmelin) P. C. Silva														
<i>Halophthys incurva</i> (Hudson) Batters														
<i>Halopteris filicina</i> (Grateloup) Kützing														
<i>H. scoparia</i> (Linnaeus) Sauvageau														
<i>Jania rubens</i> (Linnaeus) J. V. Lamouroux														
<i>Laurencia obtusa</i> (Hudson) J. V. Lamouroux														
<i>Lithophyllum byssoides</i> (Lamarck) Foslie														
<i>L. incrustans</i> Philippi														
<i>Mesophyllum alternans</i> (Foslie) Cabioch and M. L. Mendoza														
<i>M. lichenoides</i> (J. Ellis) Me. Lemoine														
<i>Osmundea pinnatifida</i> (Hudson) Stackhouse														
<i>Peyssonnelia</i> ssp.														
<i>Plocamium cartilagineum</i> (Linnaeus) P. S. Dixon														
<i>Sargassum</i> f. c. C. Agardh														
<i>Sphaerococcus coronopifolius</i> Stackhouse														
<i>Stoechospermum polypodioides</i> (J. V. Lamouroux) J. Agardh														
<i>Taonia atomaria</i> (Woodward) J. Agardh														
<i>Titanoderma pustulatum</i> (J. V. Lamouroux) Nägeli														
<i>Treptacantha usneoides</i> (Linnaeus) Orellana and Sansón														
<i>Ulva rigida</i> C. Agardh														
<i>Valonia utricularis</i> (Roth) C. Agardh														
<i>Zonaria tournefortii</i> (J. V. Lamouroux) Montagne														

"Habitats" columns refer to the different habitats where *R. okamuræ* (RO) has been observed interacting with the resident macroalgal species (ART, artificial substrata; NAT, natural substrata; INT, area extended from the low intertidal to the high intertidal zone; TID, tidepools; SUB, sublittoral zone; ILL, illuminated habitats; SHA, shaded habitats; SAN, sandy habitats near to rocky shores). "Space colonization strategies" columns refer to the observed interactions between *R. okamuræ* and the resident species on generally illuminated rocky habitats [LAT, RO laterally compress the resident species; EPI, RO epiphytes the resident species; GRO, RO grows and develops on the resident species without being attached on it; OCC, RO is established on the free substrata left by the resident species when the latter dies; FLO, RO remains free-floating on the resident species thallus without being attached on it; BAS, RO is epiphyted by the resident species (i.e., RO was observed as basibiont)].

*Amphiroa rigida*, *C. cylindracea*, *Codium bursa* (Figure 6), *Ellisolandia elongata* (Figures 4D,E), *Valonia utricularis*, and *Zonaria tournefortii*. Species epiphyted by *R. okamuræ* did not experience GRO events during the sampling process. Contrarily, spatial occupancy by free-floating mats on resident species thalli (FLO) involved the species *Cladostephus spongiosus*,

*E. elongata*, *A. taxiformis*, *Halopteris filicina*, *P. cartilagineum*, and *Treptacantha usneoides*. The latter three species were also observed to be epiphyted by *R. okamuræ*. Contrarily, epibiosis on *R. okamuræ* (BAS) was less frequent and relegated to few species: *A. armata*, *C. sinuosa*, *H. scoparia*, *S. coronopifolius*, and *T. pustulatum*.



## DISCUSSION

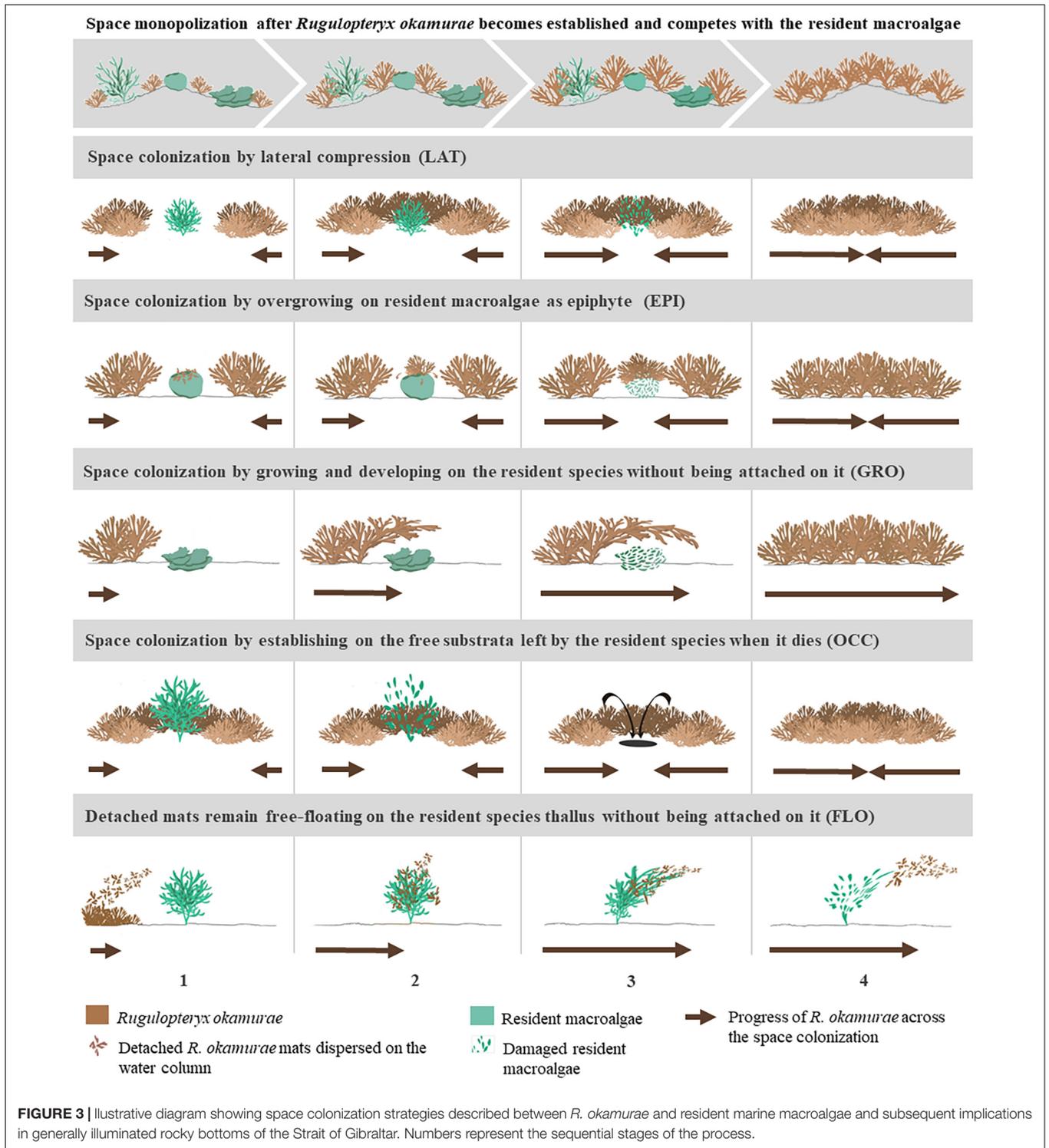
It is crucial to perform observational studies to obtain full ecological characterizations in environmental assessments (Moschella et al., 2005). In this regard, this study evidences the high establishment success and preliminary spatial colonization strategies underlying the invasive potential of *R. okamuræ* for the first time at the northern coasts of the Strait of Gibraltar. Although findings reflect a difficult scenario for mitigation strategies on the invaded areas, information about the invasibility of the resident communities could result useful in the development of early detection and rapid responses in areas not yet invaded (Lodge et al., 2006; Williams and Smith, 2007). In this respect, these preliminary results aim to advance our understanding in marine community ecology, targeting conservation efforts on the present bioinvasion case.

### Substrata Conditions and Establishment Success

Results obtained for natural habitats agree with those from previous contributions (see García-Gómez et al., 2020) that well-illuminated hard rocky bottoms may present a major propagule pressure at the local range expansion of *R. okamuræ* in the Strait of Gibraltar. Likewise, shelter conditions from subtidal rocky habitats may also facilitate the presence of introduced species even if detrimental to light availability (Piazzi and Ceccherelli, 2002), as observations performed in this study and the high coverages of *R. okamuræ* at coralligenous (Sempere-Valverde et al., 2020) and precoralligenous habitats reflect (García-Gómez et al., 2020).

Acclimation capacity plays a key role in the success over the native communities, particularly at scenarios of environmental

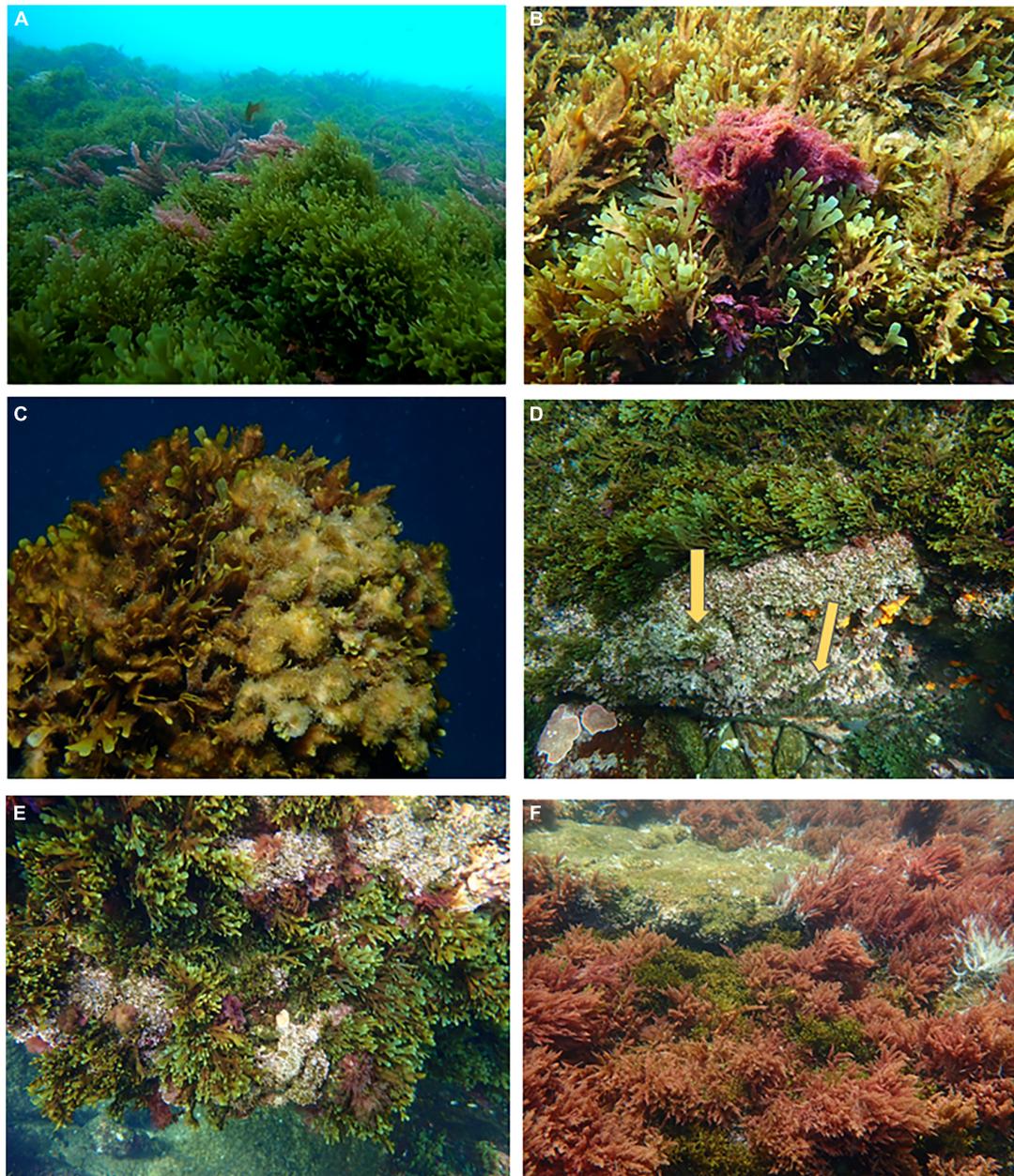
change (Tronholm et al., 2012; Papacostas et al., 2017). In this regard, any knowledge about the type of substrata colonized could help to better develop management actions to prevent potential dispersal vectors and to minimize the range expansion of the invasive species (Checoli-Mantelatto et al., 2020). According to our surveys, *R. okamuræ* was present and even abundant in a number of artificial surfaces, from harbor infrastructures (e.g., breakwaters, limestone rip-rap boulders and metallic surfaces of boats) to marine litter (abandoned fishing nets, ropes, plastics, tires, and glass bottles). The diversity of artificial substrata colonized led to give attention to the potential ability of the species to take advantage to ecosystem degradation, which increases the scale of the impact on recipient communities (Occhipinti-Ambrogi and Savini, 2003). The development and survival through time and distance on different substrata nature must complement results obtained in this work for futures researches. Furthermore, raised awareness must be adopted to those sectors which may be involved in the accidental dispersion of the invasive species (e.g., correct cleaning of fishing and diving equipments). In this regard, beyond the socioeconomic impacts reported in fisheries (see García-Gómez et al., 2018; Altamirano et al., 2019), the spatial growth of *R. okamuræ* on materials related to artificial coastal defense structures, commercial shipping, recreational boats, and even fishing equipment could imply the establishment and dispersion of the species at short (<1 km) and/or long (>1 km) distances (Ruitton et al., 2005; Lord et al., 2015). In the same way, most of materials derived from marine litter also showed to constitute adequate substrata for the invasive species, and thus the permanence or increase in marine litter in the area could become another key donor habitat for secondary spread events (Kießling et al., 2015).



### Habitat Conditions Associated With General *R. okamurae*–Resident Macroalgae Interactions

Once established on the rocky substrata, *R. okamurae* seems to be much more effective in competing for the space than most

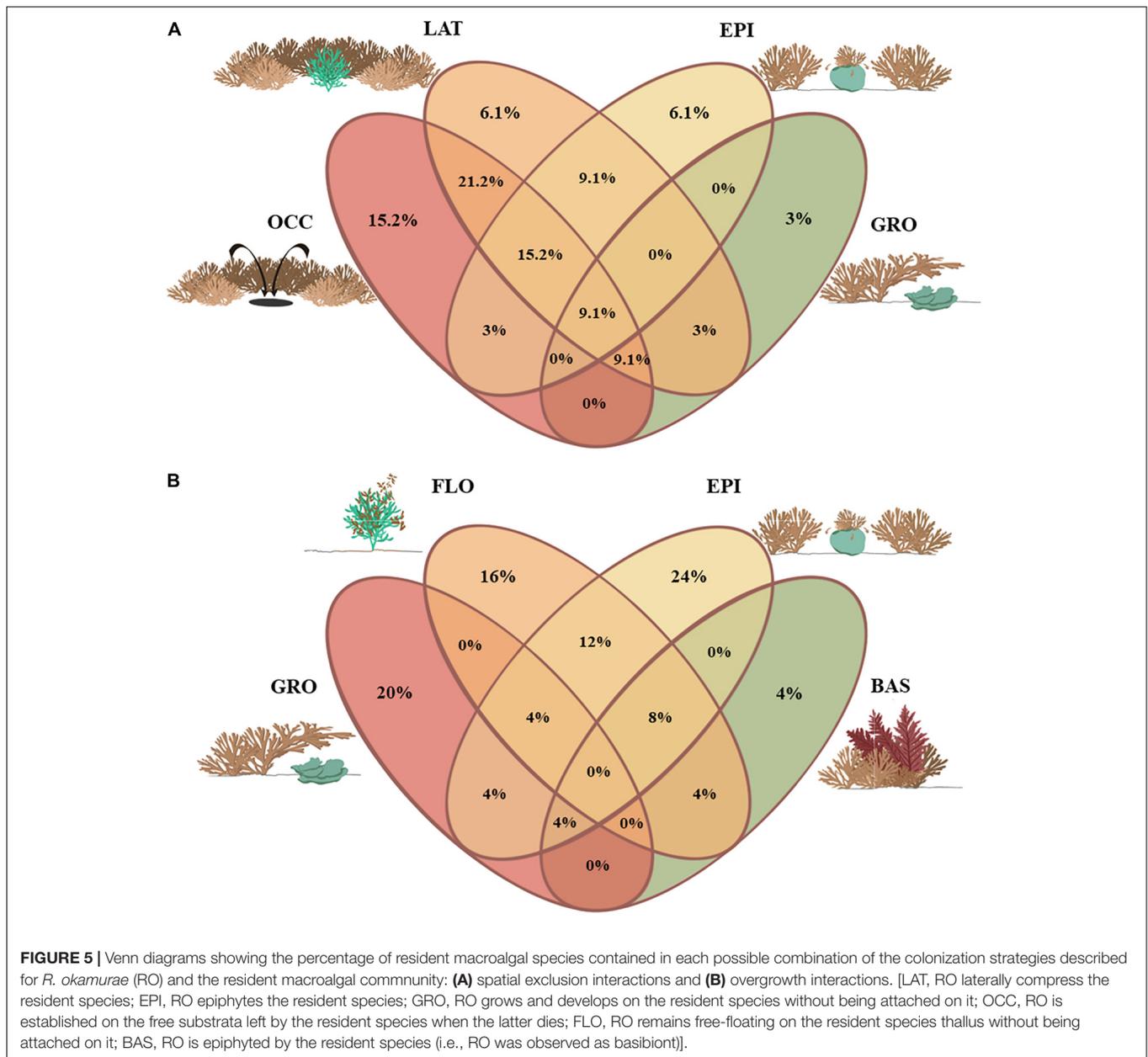
of the resident species (García-Gómez et al., 2018, 2020). Thus, competing with the photophilous community, it usually becomes dominant over other benthic taxa (García-Gómez et al., 2020; Figure 7). Parallel schemes were perceived in this study, since illuminated and natural habitats harbored most of the interactive scenarios between *R. okamurae* and the resident macroalgae.



**FIGURE 4 | (A)** Overgrowth of *Asparagopsis armata* on *Rugulopteryx okamurae* in the Strait of Gibraltar (1–5 m depth) after 2017. **(B)** Overgrowth of *Plocamium cartilagineum* and **(C)** generalist algae on *R. okamurae*. **(D)** *Ellisolandia elongata* surrounded by *R. okamurae* fronds with small specimens already inserted on *E. elongata* specimens (arrows). **(E)** Expansion of *R. okamurae* in detriment of *E. elongata* in rocky illuminated habitats. **(F)** *Asparagopsis armata* laterally compressed by *R. okamurae* before 2017.

However, particular caution is required interpreting spatial competitive interactions and direct consequences on recipient communities, as other factors not considered can influence distribution patterns (McCook et al., 2001). More exposed habitats may compromise the adequate development of macroalgae due to abiotic stressors (i.e., canopy erosion by hydrodynamics and/or sediment abrasion) (Ruitton et al., 2005), which also makes difficult the direct observation of interactions with the recipient biota. Even more, spatial competition due

to invasive macroalgae establishment may be enhanced in habitats where resources are limited (light, nutrients, or space) (Ólafsson, 2017). For example, good adaptation to low-light conditions may endow competitive advantages over other resident macroalgae in introduced habitats (e.g., the study case of the invasive *Agarophyton vermiculophyllum*) (Zi-Min and Lopez-Bautista, 2014). In accordance, co-occurring events detected at shadow environments stress effects already reported on endangered sciaphilic taxa by *R. okamurae* (Ocaña et al.,



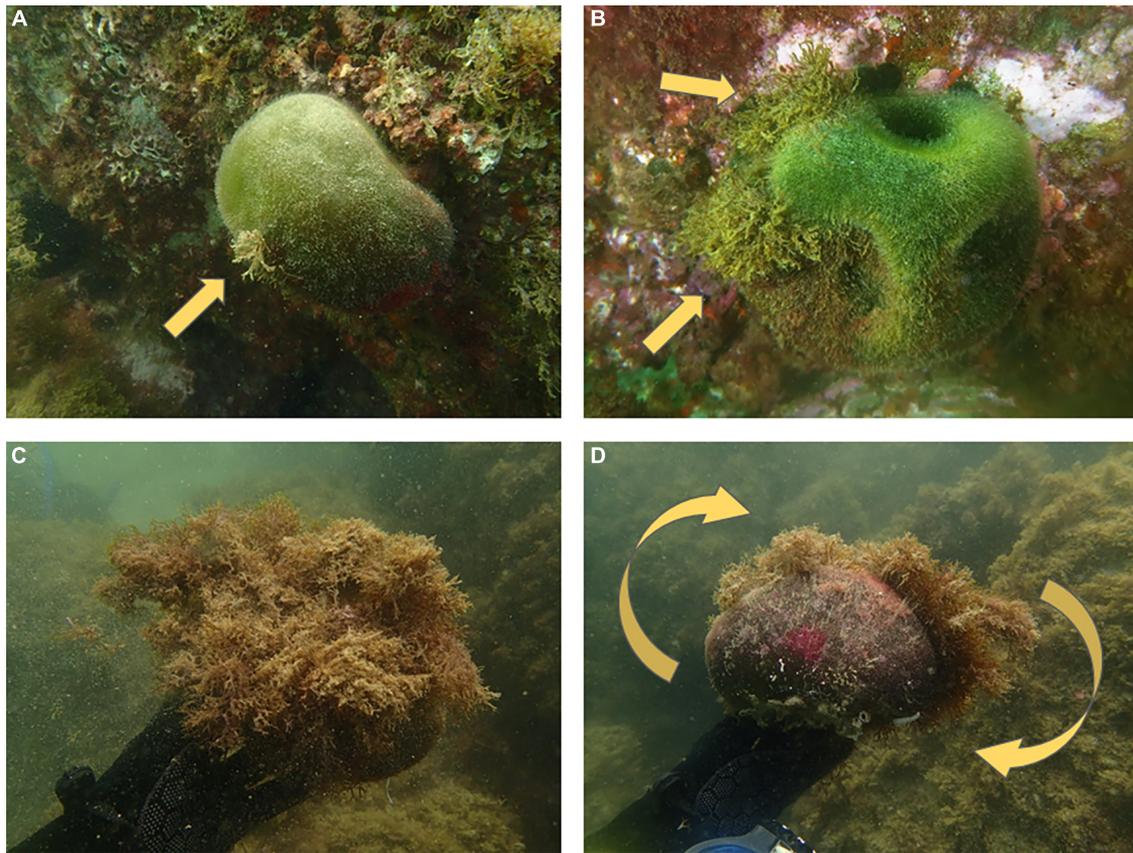
2016; García-Gómez et al., 2018; Sempere-Valverde et al., 2020).

## Colonization Strategies Underlying *R. okamuræ* Establishment

Despite that the recent loss of resident macroalgal habitats has been associated with the spread of *R. okamuræ* in the Strait coasts to a large extent (Ocaña et al., 2016; García-Gómez et al., 2018, 2020; Altamirano et al., 2019), mechanisms underlying the invasion success of *R. okamuræ* remain misunderstood. In this study, the spatial collision between the invasive species and the resident macroalgae allowed to better understand the spatial colonization strategies at generally illuminated rocky

habitats, driving different patterns in the settlement of the introduced species.

Eighty-one percent of the scenarios observed were conceived as negative for the resident community, and thus the total displacement of the resident macroalgae was conceived as the most common consequence of the spatial establishment of *R. okamuræ*. The strategies most addressed for scenarios perceived were the spatial exclusion by LAT and the total occupancy of the space when the resident species dies because of unidentified factors (e.g., natural death). Species exclusion and replacement can become critical in terms of habitat modification in rocky environments, especially when talking about engineered species (Buschbaum et al., 2006; Alomar et al., 2016). Indirect consequences of species replacement are



**FIGURE 6** | Example of progressive epibiosis of *Codium bursa* by *Rugulopteryx okamuræ*. **(A)** Incipient occurrence after *R. okamuræ* establishment. **(B)** Progress of *R. okamuræ* spatial growth. **(C)** *C. bursa* extremely epiphyted by *R. okamuræ*. **(D)** Opposite side of the same individual of *C. bursa* showing depigmented tissue in lateral and basal areas.

not contemplated here. However, habitat changes derived from *R. okamuræ* displacement could promote cascade effects on benthic ecosystems (e.g., associated fauna and higher trophic levels), even when habitat complexity is not compromised because species competing are morphologically similar (e.g., Navarro-Barranco et al., 2019). Together with impacts already reported on macroalgal communities (e.g., García-Gómez et al., 2018; 2020), potential implications in associated biota enhance the need to encompass the percentage cases of total exclusion found in this study to ecological repercussions under a more holistic view of the impacts at nonnative habitats.

With thermal tolerance, allelopathic defense in macroalgal communities (mainly on tropical areas) constitutes an important factor in the success of marine bioinvasions (Pereira and Da Gama, 2008; Tronholm et al., 2012). Settlement inhibition by chemical defenses does not necessarily imply significant negative impacts at community level when considering faunal taxa, because settling larvae can usually settle on other substrata (Ólafsson, 2017). Otherwise, it could become crucial for the establishment success of sessile or sedentary species dispersing by passive mechanisms (e.g., macroalgal propagules). In this regard, *R. okamuræ* contains bioactive compounds which may limit settlement inhibition from the sesquiterpene family and

spatane and seco-spatane skeleton diterpenes (Kurata et al., 1988; Ninomiya et al., 1999; De Paula et al., 2011). Indeed, epibiosis on the invasive species was an event scarcely represented when compared with other strategies of space colonization. However, epibiosis on *R. okamuræ* must also be attributed when considering impacts on the recipient communities, especially taking into account that dense populations of the invasive macroalga have colonized wide surfaces through its bathymetric range of distribution in the northern and southern coasts of the Strait of Gibraltar (e.g., over 90% coverage at 10–20 m depth) (García-Gómez et al., 2020; Sempere-Valverde et al., 2020).

Resident species able to take advantage of the spatial growth of other species can also exist depending on the environmental conditions (Ólafsson, 2017). The established invasive species *A. armata* has been to overgrow *R. okamuræ* populations in shallow subtidal bottoms after 2018 (1–5 m depth) (Figures 4A,F). It could be expected that certain competitors can limit the invasion success through time (Levine et al., 2004). Otherwise, *R. okamuræ* could be contributing to provide habitat for other invasive species, facilitating the establishment when available space is inaccessible (Olyarnik et al., 2009). Biotic resistance in marine environments is often not strong enough (Papacostas et al., 2017), and scenarios of facilitation



**FIGURE 7 |** Resident benthic species exclusion and subsequent monopolization of the space by *R. okamurae* in the rocky bottoms of the Strait of Gibraltar. **(A)** First scheme of *R. okamurae* establishment on rocky substrata of the Strait of Gibraltar (~10 m depth) in the presence of resident species, as *Sphaerococcus coronopifolius* (arrows). **(B)** *S. coronopifolius* expressing signs of degeneration (arrow) after/while interacting with the introduced species. **(C)** Resident species lost and subsequent monopolization of rocky bottoms by *R. okamurae*.

between invaders could make this susceptibility to progressively increase by altering the competitive landscape (Simberloff and Von-Holle, 1999). In the Strait of Gibraltar, different notorious invasions by macroalgae have happened in the latter years (e.g., *A. armata*, *A. taxiformis*, *Lophocladia lallemandii*, *C. taxifolia*, *C. cylindracea*) (Boudouresque and Verlaque, 2002; Andreakis et al., 2004; Rilov and Galil, 2009; Rivera-Ingraham et al., 2010). These successive scenarios, together with other drivers of global change (e.g., changing temperature conditions), destabilize not only the current species distribution but also the structure and function of resident communities in the Mediterranean Sea (Occhipinti-Ambrogi, 2007). On the other hand, it has not been tested yet if the reproductive and vegetative behavior of *R. okamurae* varies throughout time, leading other species to take advantage of those moments of minimum biomass production. As in its native habitats, *R. okamurae* can be observed all year round in the Strait coasts, but whether the species is able to complete its life stage is still unknown (Verlaque et al., 2009; Altamirano-Jeschke et al., 2016, 2017). Studies carried out during the months of maximum algal expansion (2016–2017) have shown that *R. okamurae* achieves coverages greater than

30% even in the winter months at 15-m depth (García-Gómez et al., 2020), periods when it would be expected that the low temperatures make the species reduces its maximum biomass. Also, experiences on *C. taxifolia* by (Glasby et al., 2005a,b) show that even when the total disappearance of the algal populations occur over relatively short periods of time, recovers in the native biota may not occur. Further studies on mentioned interactions will elucidate the capability of resident species (invasive or native) to buffer against *R. okamurae* displacement. Meanwhile, according to Piazzini et al. (2001), it is possible that only when resident species are able to be invaded but not displaced can the macroalgal community be said to resist the invasion of the introduced macroalga.

A different pattern is perceived when *R. okamurae* grows on other species thalli, as direct overgrowth often results in the total displacement of the basibiont. One example is the interaction between *R. okamurae* and *C. bursa*, represented in **Figure 6**. Unlike this growth strategy, the rest of observed overgrowth conditions did not imply the direct attachment of *R. okamurae* rhizomes or thallus. In this respect, it was noteworthy that the macroalgal species affected by the horizontal

elongation of *R. okamuræ* thallus were highly characterized by flattened and encrusting taxa, where crustose macroalgae are included. According with other marine bioinvasion cases, it should be verified whether habitat type (Piazzi et al., 2001; Ceccherelli et al., 2002) and allelopathic substances from coralline macroalgae (Vermeij et al., 2011) influence interactions by which *R. okamuræ* rhizomes remain attached to other species.

Yet the consequences of the introduction of *R. okamuræ* are not necessarily limited to interactions performed when attached to the rocky substrata. Mats of *R. okamuræ* can be released after being established on the bottom becoming free-floating on the water column. It has not been clarified yet if the wrack depositions of the invasive macroalga are due to the thorough water agitation in specific geographic areas (e.g., high tidal coefficient or groundswell), the result after completing the natural life cycle, or the combination of all mentioned processes. Meanwhile, results indicate that disturbances by floating mats trapped on the thallus of resident erect macroalgae could be minimal because, at least in current areas, these mats shed shortly afterward. However, albeit negative impacts were not perceived, consequences on the macroalgal community can be wide and diverse. For example, physical damages can occur since contact can reduce light levels by shading (Kennelly, 1989), abrasion, chemical effects, and the facilitation of direct overgrowth (McCook et al., 2001). Also, overall floating mats may serve as physical barriers for settling larvae (Zi-Min and Lopez-Bautista, 2014) or pelagic organisms, whose behavior can result as modified due to the decreased visibility nearshore (Kirby et al., 2000). Figueroa et al. (2020) have pointed out that *R. okamuræ* mats detached from the rocky bottoms and transported by currents to a certain depth are capable of maintaining high photosynthetic activity and physiologically viable spores. Because the easy dispersion of *R. okamuræ* constitutes a threat facing other European marine areas (Altamirano et al., 2019), the role of released mats needs to be accounted also considering potential secondary spread events.

## CONCLUSION

All the available data clarify that the high propagation capacity of *R. okamuræ*, in combination with its competitive and spatial establishment capacity, enhances the settlement of the species once having entered an area that presents favorable biotic and abiotic factors (Altamirano et al., 2019; García-Gómez et al., 2020). Results obtained in this study reinforces the high ability of *R. okamuræ* to grow on different substrata types, formed by not only abiotic but also biotic compounds, since macroalgal species also constitute suitable substrata and thus they could facilitate the invasion in a similar way than hard bottoms (Olyarnik et al., 2009). The high representation of strategies which implied the spatial exclusion of the resident macroalgae, together with other interactions of potential disturbance, claims the development of major biodiversity assessments in the Strait of Gibraltar. This, combined with the high propagation capability of the species (Altamirano-Jeschke et al., 2017 and Altamirano et al., 2019), makes the dispersion to habitats susceptible to be invaded, an alarming phenomenon that needs to be managed.

So far, the life history of *R. okamuræ* remains uncertain in the Mediterranean and Atlantic waters, more change the future of this bioinvasion represents. The spatial establishment capability observed in this work enhances the performance of observational and experimental investigations including environmental factors which influence patterns obtained. This could help to fully understand those elements which favor the establishment success of the species on lit and semi-lit rocky substrata and thus to lend further urgency for management actions focused on *R. okamuræ* impacts.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

JG-G: investigation, obtaining data *in situ*, data analysis, supervision, validation, funding acquisition, and project administration. MF: investigation, data analysis, and data curation. JG-G and MF cowrote the manuscript. All the authors contributed substantially to revisions. LO-P: investigation, obtaining of data *in situ*, and data curation. JS-V: investigation. CM: investigation and supervision.

## FUNDING

This study was funded by CEPESA Foundation and Red Eléctrica de España (REE). Additional financial support was provided by the Organization of Fish Producers of Almadrabas (OPP-51), ENDESA, ACERINOX, and Diputación Provincial de Cádiz. This project has also benefited from scientific equipment and infrastructures financed by the Autoridad Portuaria (AP) of Seville and the Aquarium of Seville.

## ACKNOWLEDGMENTS

We are deeply grateful to the city of La Línea, particularly to the logistical support provided by Puerto La Alcaidesa, the Yacht Club (RCNLL), and the Maritime Club, as well as by the town halls of La Línea and Tarifa. Special thanks are given to Darren Fa and Stephen for facilitating information from Gibraltar shores. Thanks are also given to Campo de Gibraltar (La Línea) and to the CIES (Algeciras) diving clubs. Finally, we express our gratitude to Antonio Vegara, Juanjo Quintero, Salvador Magariño, Juan Antonio Parada, José Fosela, Isabel Cárdenas, Candela Sánchez, and José Cantera for their continued collaboration.

## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.631754/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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