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Reproductive performance and propagule pressure: Key drivers of *Rugulopteryx okamurae* (Ochrophyta, Dictyotales) invasion of a *Posidonia oceanica* meadow

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ABSTRACT

The invasive seaweed *Rugulopteryx okamurae* has rapidly spread along the Mediterranean and Atlantic coasts, displacing native species and causing unprecedented environmental and socioeconomic impacts. One of the threatened habitats are *Posidonia oceanica* meadows. In this habitat the vegetative performance of *R. okamurae* is already known, but the reproductive mechanisms that allow its continued dominance in space and time are still not known. Thus, the objective of this study is to investigate the reproductive performance of *R. okamurae* invading a *P. oceanica* meadow in Southern Spain, identifying and quantifying the reproductive structures, their temporal and intrapopulation changes and, the potential environmental factors triggering them. The results do not rule out the presence of sexual reproduction (only meiotic tetraspores have been observed, but no gametangia), suggesting that the population is mainly maintained by clonal mechanisms based on the formation of vegetative propagules and mitotic monospores that form throughout the thallus on both sides, more abundantly in larger individuals. Due to the greater ontogenetic maturity of the propagules and their larger presence throughout the year (only absent in January), we can say that the populations are mainly maintained thanks to them, since unicellular monospores were only observed in May and July. Estimates of propagule pressure indicate that it exceeds the carrying capacity of the species' benthic habitat and that, therefore, new individuals are exported to the water column. This fact would explain the enormous amount of biomass in suspension, facilitating the dispersal and colonization of the species and the colonization of neighboring areas, where it produces severe the socio-economic impacts.

1. Introduction

Traits related to reproduction are some of the most determinant for species' invasiveness (Jelbert et al., 2015). In particular, the ability to reproduce both sexually and asexually is a key attribute in highly invasive species (Colautti et al., 2006; Goncalves et al., 2023). The massive production of propagules and the effectiveness of dispersal mechanisms are identified as primary factors for invasion (Pyšek and Richardson, 2007; Moravcová et al., 2015), as evidenced by widely distributed terrestrial plants like *Agave sisalana* Perrine or *Asparagus asparagoides* (Linnaeus) Druce (Goncalves et al., 2023).

In the case of invasive seaweeds, the combination of asexual reproduction mechanisms and rapid growth rates facilitates the occupation of new areas and the maintenance of their populations (Schaffelke and Hewitt, 2007). Asexual mechanisms include vegetative processes such as fragmentation and vegetative propagules, asexual spores, and the parthenogenetic development of unfertilized gametes (Liu et al., 2017). For instance, the genus *Asparagopsis* Montagne propagates vegetatively by rhizoid regrowth, and in the case of *A. armata*, apical hook-like branches detach from the gametophytes and attach to new substrata, while sporophytes easily break up and continue to grow (Zanolla et al., 2018; Zanolla et al., 2022). Another widely distributed genus including

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invasive species, *Caulerpa* J. V. Lamoroux, reproduces vegetatively through stolon extension and fragmentation, resulting in clonal growth (Zubia et al., 2020). This diversification allows the establishment of extensive patches with high densities of clonal individuals, harming native species, including crustose Corallinaceae, *Cystoseira* spp. and the seagrass *Posidonia oceanica* (Linnaeus) Delile (Ceccherelli and Cinelli, 1999; Klein and Verlaque, 2008; Montefalcone et al., 2015).

The brown seaweed *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Dictyotaceae, Phaeophyceae) is the only seaweed included in the List of Invasive Alien Species of Union Concern (Commission Implementing Regulation (EU) 2022/1203 of 12 July 2022 amending Implementing Regulation (EU) 2016/1141) because of its dramatic environmental and socio-economic impacts (MITECO, 2022; Mogollón et al., 2024). Native to the Western Pacific coast, *R. okamurae* was first identified in the Thau Lagoon in 2002, without an invasive behavior (Verlaque et al., 2009). However, in 2015, the seaweed initiated an unprecedented cryptic invasion along the southern coast of Spain, where it quickly proliferated (Altamirano et al., 2016). Since then, the species rapidly spread, invading both Mediterranean and Atlantic waters of the Iberian Peninsula (Altamirano et al., 2017; Díaz-Tapia et al., 2025), and reaching the Macaronesian Islands (Faria et al., 2021; REDEXOS, 2022; Bernal-Ibáñez et al., 2022), France (Ruitton et al., 2021), Morocco (El Aamri et al., 2018; El Madany et al., 2024), and Italy (Bellisimo et al., 2024), continuing its expansion to Mediterranean and Atlantic waters. Projections suggest that *R. okamurae* could eventually occupy the entire Mediterranean Sea and part of the Atlantic coasts, considering the highly favorable conditions for its establishment (Muñoz et al., 2019). This expansion could be promoted by accidental human activities or sea currents (García-Lafuente et al., 2023; Mateo-Ramírez et al., 2023; Bellisimo et al., 2024), accelerating the spread of the species and amplifying its associated ecological impacts (Muñoz et al., 2019).

The rapid and extensive proliferation of *R. okamurae* has substantial environmental and socioeconomic impacts (Altamirano et al., 2016; García-Gómez et al., 2018; Mogollón et al., 2024). This species is considered a threat to human activities, particularly affecting the fishing sector, which has experienced substantial economic losses estimated in millions of euros due to diminished fish stocks, fishing gear clogging, and damages provoked by drifting biomass (MITECO, 2022; Mogollón et al., 2024). Additionally, local administrations face challenges related to the management of massive amounts of castaway biomass on beaches, especially in touristic areas (MITECO, 2022).

The sexual life cycle of *R. okamurae* is isomorphic haplodiplontic digenetic, typically taking over two years to complete in its native habitat, alternating between haploid gametophytes and diploid sporophytes (Sun et al., 2006; Hwang et al., 2009). Although sexual reproduction has not been observed in introduced areas (Verlaque et al., 2009; Altamirano et al., 2017; Bellisimo et al., 2024; Díaz-Tapia et al., 2025), the species employs other mechanisms to produce new individuals, including vegetative propagation by propagules (Kajimura, 1992) and asexual reproduction through mitotic monospores (Verlaque et al., 2009; Altamirano et al., 2017). These mechanisms generate six different cohorts in a population of *R. okamurae* invading a *Posidonia oceanica* meadow in southern Spain (Rosas-Guerrero et al., 2025). Hence, identifying the recruitment mechanisms that produce these cohorts is key to understand the role of reproduction in the species' invasiveness and the environmental and endogenous factors that shape it, which would allow us to identify temporal windows of invasiveness that are crucial for management strategies.

Therefore, this study aims to elucidate the reproductive mechanisms underlying the biomass and cohort production witnessed in a population of *R. okamurae* invading a *P. oceanica* meadow in southern Spain. For this, we conducted a seasonal study to assess the seaweed's ability to form vegetative propagation and asexual structures, and the environmental factors triggering these processes. These findings will be useful to test the hypotheses that propagule pressure and clonal propagation are responsible for the invasion of *R. okamurae*.

2. Methods

2.1. Study area and sampling procedure

The study was conducted on a population of *R. okamurae* invading a *P. oceanica* meadow at Cambriles Cliff, Granada, Spain (36° 44.0033′ N, 3° 20.6767′ W), at a depth of 10 m. The *P. oceanica* meadow covers 48 ha, spanning from 7 to 13 m in depth (Portal Ambiental de Andalucía, 2024). The samples were collected manually by scuba diving every two months from July 2021 to July 2022, using 30 cm × 30 cm quadrants (Rosas-Guerrero et al. (2025). Appropriate permits were obtained from the relevant authorities to conduct research on the *P. oceanica* habitat and with *R. okamurae*.

Sampling was carried out at three areas three areas of 8–10 m^2 with homogeneous biomass of the studied population of *R. okamurae*, separated by 5 m from each other. To ensure a sufficient and representative number of thalli for the measurements, four subsamples were taken at each area, separated at least by 1 m, and their values were averaged. *Rugulopteryx okamurae* thalli were thoroughly removed, avoiding damage to *P. oceanica* plants and the associated community, and placed in plastic bags, preventing accidental dispersal. Subsequently, samples were transported to the laboratory in insulated containers to maintain cold and dark conditions, preserving the integrity of the thalli for further analysis.

2.2. Reproductive analysis

During each sampling, all biomass within each replicate was categorized into nine size classes, with two-centimeter increments, measured from the most distal apex to the base of the thallus. The number of individuals with propagules (vegetative propagation) and spores (including monospores and tetraspores) was recorded for each sampling event (Fig. 1). Abundance of reproductive individuals was calculated both, in absolute terms of the mean number of individuals within a given size class and as frequency in relation to the total population (Rosas-Guerrero et al., 2025). Moreover, the minimum and maximum size class capable of generating reproductive structures was recorded in every sampling. Individuals that presented multiple reproductive structures were accounted for separately. The number of spores and propagules on individual reproductive thalli was counted on a single 4-mm-diameter (0.125 cm^2) area per individual. This was done aiming to standardize the density of propagules and spores. A total of ten individuals were analyzed per replicate, (120 individuals analyzed per month and size class). This area was placed where reproductive structures were most abundant. Density was expressed per cm^2 of thallus surface.

2.3. Reproductive output: Propagule pressure

Propagule pressure was defined as the number of potential new individuals that can be formed per square meter of seabed, and potentially settle on the meadow or be cast into other areas. Propagule pressure was calculated for each sampling time based on the number of individuals with propagules and spores and the propagule and spore densities during each sampling event as a value of abundance of these reproductive structures. As the total thallus surface area occupied by propagules and spores was not evaluated, propagule pressure was obtained by using the estimated density of propagules and spores for a single cm^2 of thallus in the calculations, in order to obtain a realistic and conservative measure. Although this reference area is larger than the measured thallus surface (0.125 cm^2), it is assumed to be smaller than the total surface area occupied by propagules and spores on reproductive thalli in this study. This approach provides an estimate that avoids overestimating propagule pressure, while allowing the minimum potential number of new

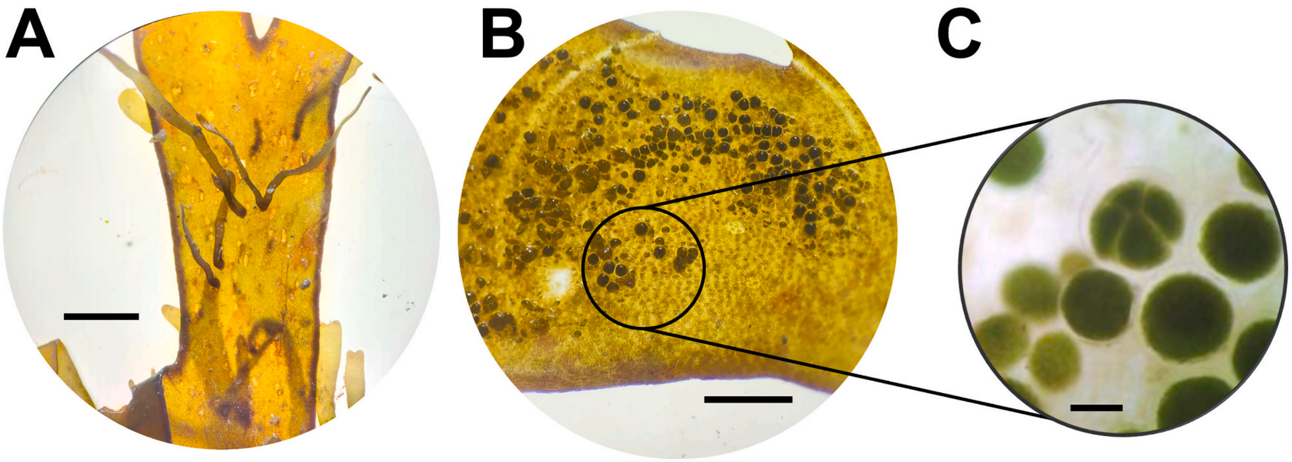

Fig. 1. *Rugulopteryx okamurae* reproductive structures. Propagules (A), spores (B), and monospores and tetraspores (C). Scale bars = 1 mm (A-B), 100 μM (C).

individuals that could be inferred to be produced. For this reason, the contribution of propagules and spores from individuals of each size class is considered separately when calculating propagule pressure. The following formula was used to estimate propagule pressure (Pp) at a given sampling time:

$$\text{Pp}\ \left(\text{individuals}\cdot\text{m}^{-2}\right) = \sum\nolimits_{i=1}^{9}\left[(\text{A}_\text{i}\ \text{x}\ \text{D}_\text{i}) + (\text{B}_\text{i}\ \text{x}\ \text{E}_\text{i})\right]$$

where A_i and B_i are the average abundances of individuals exhibiting vegetative propagules and spores, respectively, for each size class (i), and D_i and E_i are the average densities of propagules and spores, respectively, in one cm^2 of thallus surface.

2.4. Statistical analysis

A one-way ANOVA ($P < 0.05$) was conducted to verify temporal differences in the number of reproductive individuals and reproductive structures, their frequencies in the total population, and the propagule pressure. The frequency values (%) were subjected to the arcsine transformation to comply with ANOVA assumptions. The number of reproductive structures within each size class was analyzed using a two-way ANOVA ($P < 0.05$), with time and size class as fixed factors. Homoscedasticity and the normality of the data were checked before the ANOVAs, using Levene's and Shapiro-Wilks tests, respectively. The Student-Newman-Keuls test (SNK) was performed for post hoc comparisons when significant differences were found for a given biological variable. SigmaPlot 11.0 (Systat Software Inc., Chicago, IL, USA) was used to conduct the ANOVAs.

A principal component analysis (PCA) was performed to evaluate the relationship between environmental factors (average temperature, maximum and minimum temperature, salinity, photoperiod, ammonium, nitrate, nitrite and phosphate, as explained in Rosas-Guerrero et al., 2025), and the abundance of individuals with vegetative propagules and spores. The two main axes derived from the environmental space of the PCA from Rosas-Guerrero et al. (2025) were used to apply Pearson correlation against biotic variables, employing the PAST software (Hammer et al., 2001).

3. Results

Propagules and spores were observed along the whole surface of both sides of the thalli. Some individuals were able to produce propagules, monospores, and tetraspores simultaneously. Propagules were observed throughout the year, except for January. However, spores were only observed in May and July. Furthermore, gametangia were not detected in any thallus throughout the study period, despite careful observation.

3.1. Reproductive analysis

3.1.1. Propagules

Propagule structures were observed along the thallus surface, from the apex to the base, including broken parts of the thalli, where the highest densities were recorded. The number of individuals bearing propagules showed significant differences across months (Fig. 2A, Table 1), with the highest values observed in July, consistently exceeding 200 individuals per square meter. Moreover, these values were significantly higher in July 2022 than in 2021 and were fourteen-fold higher than in November, March, and May (Fig. 2A, Table 1). The frequency of individuals with propagules also showed marked temporal differences (Fig. 2B, Table 1). A peak was observed in July 2022, when nearly two of 10 individuals had propagules, significantly higher than in July 2021, when 10% of the individuals had these structures. By contrast, the lowest values were observed in November and March,

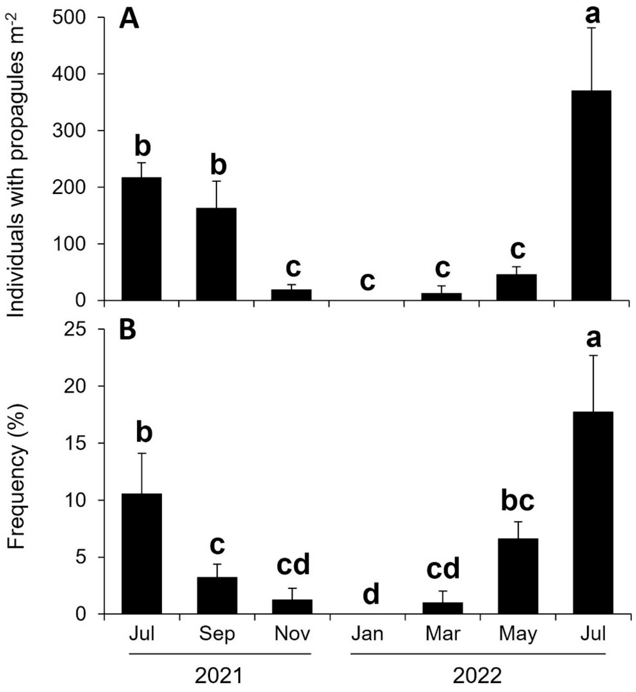

Fig. 2. *Rugulopteryx okamurae* individuals with propagules, per surface (m^{-2}) (A), and as frequency in the population (%) (B). Data are expressed as the mean ± SD ($n = 3$). Different letters denote significant differences across months following ANOVA ($P < 0.05$).

Table 1

Statistical analyses. One-way (month) ANOVA for abundance of reproductive individuals (m^{-2}) and their frequency (%) in relation to the total population, and propagule pressure data (m^{-2}) of *R. okamurae*. Two-way (month and size class) ANOVA for reproductive structures per size class (cm^{-2}). The asterisks indicate significant differences ($P < 0.05$).

	Variable	df	MS	F-value	*P* value
One-way ANOVA	Number of individuals with propagules	6	473	21.6	< 0.001*
	Frequency of individuals with propagules	6	0.06	30.1	< 0.001*
	Number of individuals with spores	6	484	12.0	0.008*
	Frequency of individuals with spores	6	0.002	0.8	0.493
	Propagule pressure	6	$6.05 \cdot 10^{10}$	112.7	< 0.001*
Two-way ANOVA	Density of propagules				
	Month	6	18,444	75.5	< 0.001*
	Size class	8	4088	16.7	< 0.001*
	Month x Size class		1763	7.2	< 0.001*
	Density of spores				
	Month	6	2,300,461	86.5	< 0.001*
	Size class	8	750,739	28.2	< 0.001*
	Month x Size class		189,896	7.1	< 0.001*

when only 1% of individuals showed propagules (Fig. 2B).

The minimum thallus size required to produce propagules varied depending on the month and ranged from 0 to 2 cm in September to 4–6 cm in March and May (Fig. 3), although the frequency of thalli with propagules was lower than 1% within these thallus sizes (Fig. 4). On the other side, throughout the study period, the frequency of individuals with propagules increased with increasing size class, with the highest frequencies observed in the highest size class found in each month, except for the months with the highest size classes found (16–18 cm) (May and July 22), when the frequency decreased (Fig. 4). For example, in July 2021, only 2 of 10 individuals in the 8–10 cm size class had propagules, but this number doubled in the 10–12 cm size class and increased to 7 of 10 individuals in the 14–16 cm size class (Fig. 4). The capacity of individuals in each size class to produce propagules also varied over time (Figs. 3 and 4). For example, the frequency of individuals with propagules of size 6–8 cm was approximately 20% in July and September 21, but decreased by an order of magnitude in March and May 22 (Fig. 4).

Propagule density showed significant variations among months and size classes, but these changes were time-dependent (Tables 1 and 2). The highest density (31–130 propagules) was recorded in July 2022, whereas November showed the lowest values (Table 2). Propagule density increased according to the size class in May, July 2021 and July 2022 (Tables 1 and 2). However, no significant differences were observed among size classes in September and November 2021, and March 2022, with an average of 26, 11, and 14 propagules, respectively (Table 2). Nevertheless, the ability to produce vegetative propagules varied substantially for each size class across months, but also among individuals within a given size class, as shown by the high standard deviations (Table 2). For instance, in July 2022, the density of propagules in the 10–12 cm size class was nearly tenfold higher than in March (Table 2).

3.1.2. Spores

Spores were observed along the thalli, excluding the apex. Tetraspores were not detected because of their minimal frequency compared to monospores (e.g., 0.07% of individuals with spores in May and 0.04% in July 2022). The spore distribution was not uniform because the highest density was observed between the fifth and ninth dichotomies. Individuals with spores appeared only in May and July and exhibited substantial temporal variations (Fig. 5A, Table 1). The highest values were recorded in July, but no differences were observed between 2021 and 2022. Furthermore, the values observed in July were three times higher than in May (Fig. 5A, Table 1). Nonetheless, the frequency of individuals with spores in the population remained similar along the study period (nearly 14%) (Fig. 5B).

As with propagules, the minimum and maximum thallus size classes

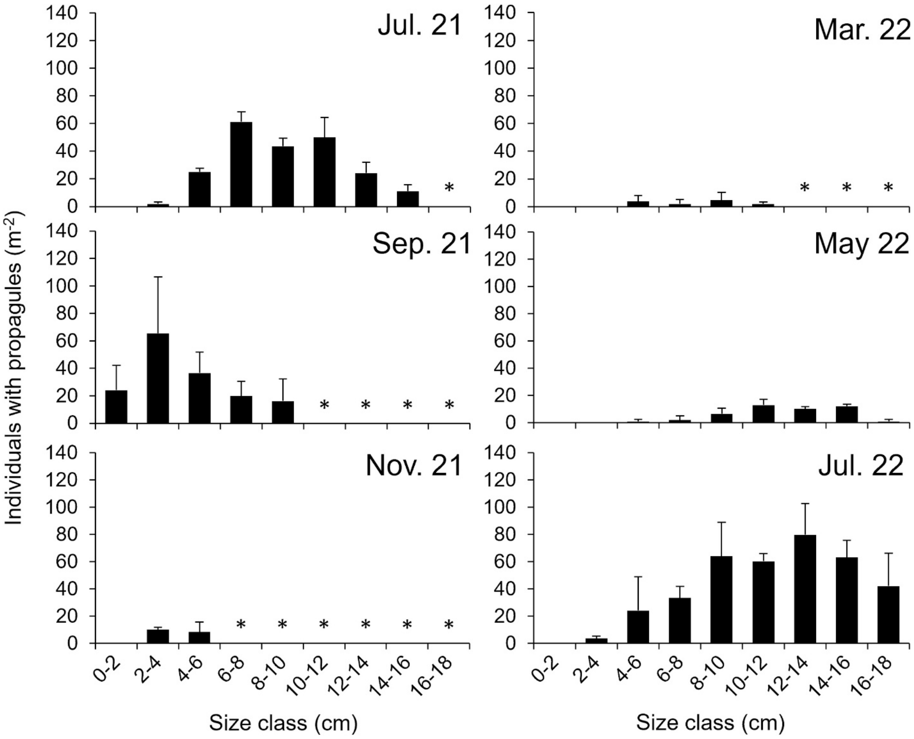

Fig. 3. *Rugulopteryx okamurae* individuals with propagules per size class (m^{-2}). Asterisks indicate the absence of individuals of a given size class. Data are expressed as the mean ± SD (n = 3).

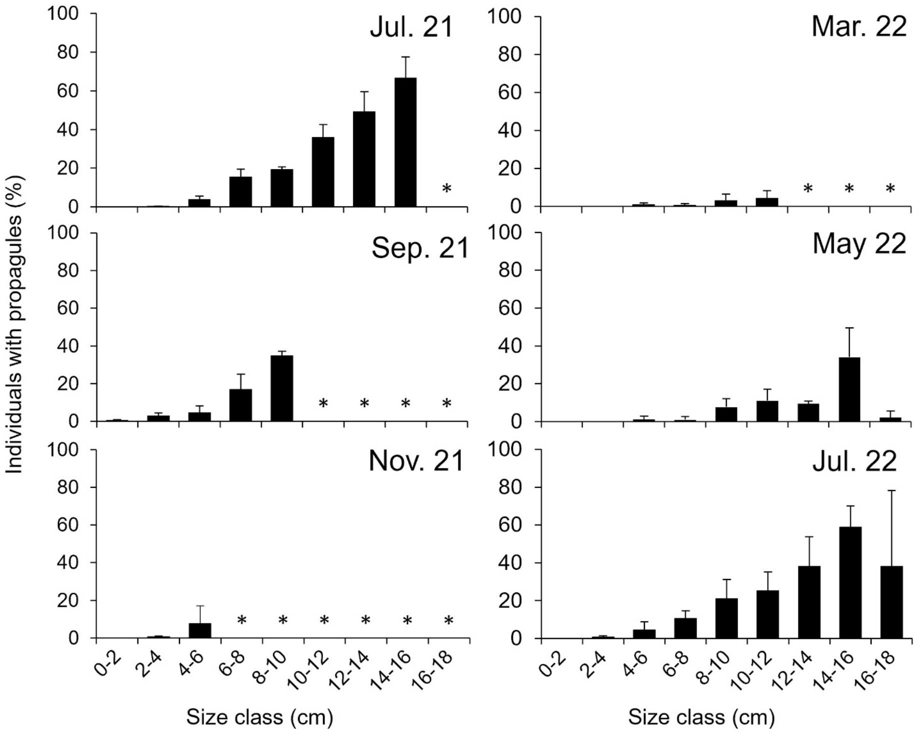

Fig. 4. Frequency (%) of *R. okamurae* individuals with propagules within a given size class. Asterisks indicate the absence of individuals of a given size class. Data are expressed as the mean ± SD (n = 3).

Table 2
Density of propagules per cm^2 in each size class and sampling event. Data are expressed as the mean ± SD ($n = 3$). Dashes indicate the absence of individuals of a given size class, whereas zeros indicate the presence of non-reproductive individuals. Superscript letters indicate significant differences among months for the same size class ($P < 0.05$). Subscript letters indicate significant differences among size classes within the same month ($P < 0.05$).

Size class (cm)	Jul. 21	Sep. 21	Nov. 21	Mar. 22	May 22	Jul. 22
0–2	${}_{d}0 \pm 0$	7.6 ± 12.4	0 ± 0	0 ± 0	${}_{c}0 \pm 0$	${}_{d}0 \pm 0$
2–4	${}_{cd}25.2 \pm 38.6^{ab}$	40.1 ± 10.5^{a}	10.0 ± 3.6^{ab}	0 ± 0^{b}	${}_{c}0 \pm 0^{b}$	${}_{c}31.2 \pm 11.0^{ab}$
4–6	${}_{bc}34.2 \pm 17.0$	28.8 ± 3.4	12.8 ± 11.2	8.3 ± 11.1	${}_{c}3.3 \pm 5.7$	${}_{c}37.4 \pm 29.3$
6–8	${}_{bc}39.6 \pm 5.6^{ab}$	21.8 ± 13.3^{ab}	–	10.0 ± 17.2^{bc}	${}_{c}17.9 \pm 31.0^{bc}$	${}_{c}52.0 \pm 22.3^{a}$
8–10	${}_{bc}50.8 \pm 8.7^{b}$	34.9 ± 20.0^{b}	–	21.6 ± 24.9^{bc}	${}_{bc}35.5 \pm 27.3^{b}$	${}_{b}84.2 \pm 5.2^{a}$
10–12	${}_{bc}50.9 \pm 11.9^{b}$	–	–	15.9 ± 13.8^{c}	${}_{a}76.1 \pm 46.1^{b}$	${}_{ab}106.4 \pm 36.3^{a}$
12–14	${}_{b}64.2 \pm 22.0^{b}$	–	–	–	${}_{ab}60.0 \pm 32.2^{b}$	${}_{ab}109.9 \pm 4.3^{a}$
14–16	${}_{a}101.6 \pm 10.0^{b}$	–	–	–	${}_{a}70.6 \pm 14.9^{c}$	${}_{a}130.4 \pm 16.9^{a}$
16–18	–	–	–	–	${}_{c}8.0 \pm 11.3^{b}$	${}_{ab}100.9 \pm 10.5^{a}$

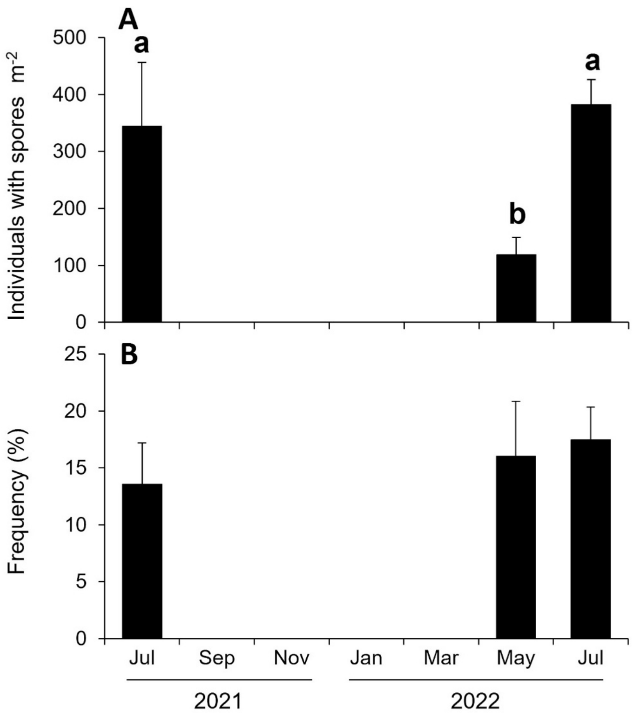

Fig. 5. *Rugulopteryx okamurae* individuals with spores, per surface (m^{-2}) (A) and as frequency in the population (%) (B). Data are expressed as the mean ± SD (n = 3). Different letters denote significant differences across months, following ANOVA ($P < 0.05$).

of spore-producing individuals varied across months. The minimum size was 2–4 cm in July and 6–8 cm in May, with no maximum size observed (Fig. 6). Like propagule-bearing individuals, the smallest individuals with spores accounted for less than 1% of that size class (Fig. 7). The frequency of individuals with spores fluctuated between May and July (Fig. 7). In July 2021, thalli in the 6–8 cm and 10–12 cm size classes together represented 75% of all individuals with spores (Fig. 7), with frequencies ranging from 38% to 52% (Fig. 7). In July 2022, the highest number of individuals was found in the 10–12 cm and 14–16 cm size classes, representing 73% of all individuals with spores (Fig. 7). In May, the highest number of individuals also belonged to the 10–12 cm and 14–16 cm size classes, accounting for 84% of all individuals (Fig. 7), with frequencies ranging from 21% to 34% of the total number of

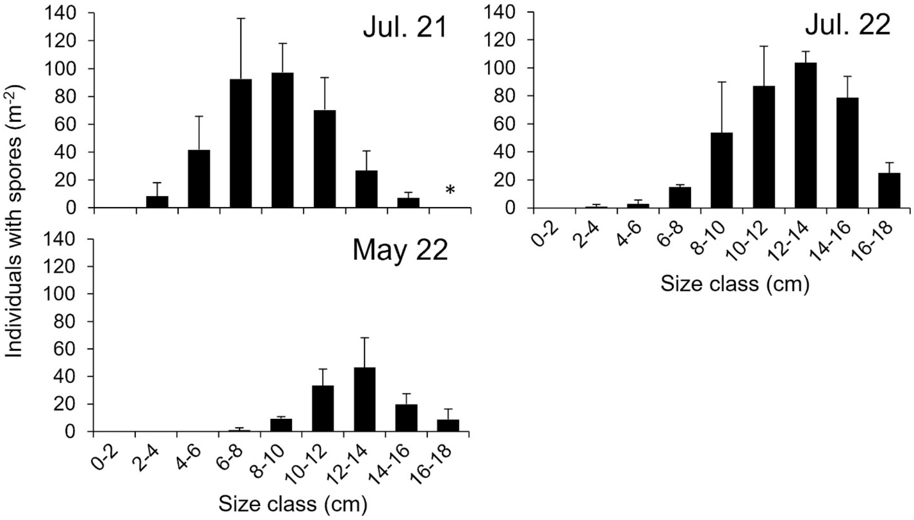

Fig. 6. *Rugulopteryx okamurae* individuals with spores per size class and surface (m^{-2}). Asterisks indicate the absence of individuals of a given size class. Data are expressed as the mean ± SD (n = 3).

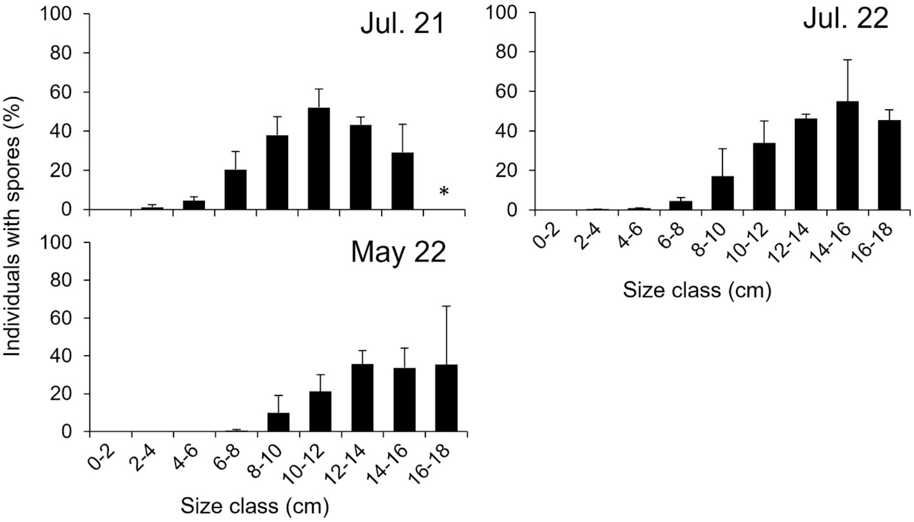

Fig. 7. Frequency (%) of *R. okamurae* individuals with spores within a given size class. Asterisks indicate the absence of individuals of a given size class. Data are expressed as the mean ± SD (n = 3).

individuals with spores (Fig. 7).

Significant variations in spore density were observed depending on the sampling month, size class, and their interaction (Tables 1 and 3).

Table 3

Density of spores per cm^2 in each size class and sampling event. Data are expressed as the mean ± SD ($n = 3$). Dash indicates the absence of individuals of a given size class, whereas zeros indicate the presence of non-reproductive individuals. Superscript letters indicate significant differences across months for the same size class ($P < 0.05$). Subscript letters indicate significant differences among size classes in the same month ($P < 0.05$).

Size class (cm)	Jul. 21	May 22	Jul. 22
0–2	0 ± 0	${}_{c}0 \pm 0$	${}_{e}0 \pm 0$
2–4	21.3 ± 8.2	${}_{c}0 \pm 0$	${}_{e}10.6 \pm 18.4$
4–6	76.2 ± 14.9	${}_{c}0 \pm 0$	${}_{de}260.1 \pm 238.2$
6–8	114.6 ± 39.9^{b}	${}_{c}43.1 \pm 74.7^{b}$	${}_{d}437.7 \pm 186.0^{a}$
8–10	85.8 ± 14.3^{b}	${}_{bc}291.3 \pm 69.6^{b}$	${}_{c}708.1 \pm 160.8^{a}$
10–12	272.2 ± 212.9^{b}	${}_{b}409.0 \pm 60.4^{b}$	${}_{ab}1131.7 \pm 200.7^{a}$
12–14	231.2 ± 105.5^{c}	${}_{a}773.4 \pm 211.5^{b}$	${}_{ab}1186.3 \pm 106.1^{a}$
14–16	173.8 ± 155.5^{c}	${}_{ab}555.6 \pm 177.2^{b}$	${}_{bc}970.2 \pm 210.7^{a}$
16–18	–	${}_{ab}556.9 \pm 497.0^{b}$	${}_{a}1416.3 \pm 290.5^{a}$

The highest density (11–1186 spores cm^{-2} thallus surface) was recorded in July 2022, followed by May of the same year (43–773 spores cm^{-2} thallus surface) (Table 3). The spore density varied greatly among individuals within a given size class and was higher in larger size classes during May and July 2022. By contrast, in July 2021, no significant differences were detected among size classes, with an average of 139 spores cm^{-2} thallus surface (Table 3). The highest spore density recorded throughout the study period was observed in July 2022 in the 10–12 cm and 16–18 cm size classes. For instance, in the 10–12 cm size class, the spore density in July 2022 was threefold higher than in July 2021 and May 2022 (Table 3).

3.2. *Propagule pressure*

The propagule pressure exhibited significant differences along the sampling period (Fig. 8, Table 1). The highest values were observed in July 2022 and were six times higher than in July 2021 and May 2022. In these months, spores contributed 90% more than propagules (Fig. 8). By contrast, in September and November 2021, and March 2022, the contribution shifted completely to propagules. The lowest propagule

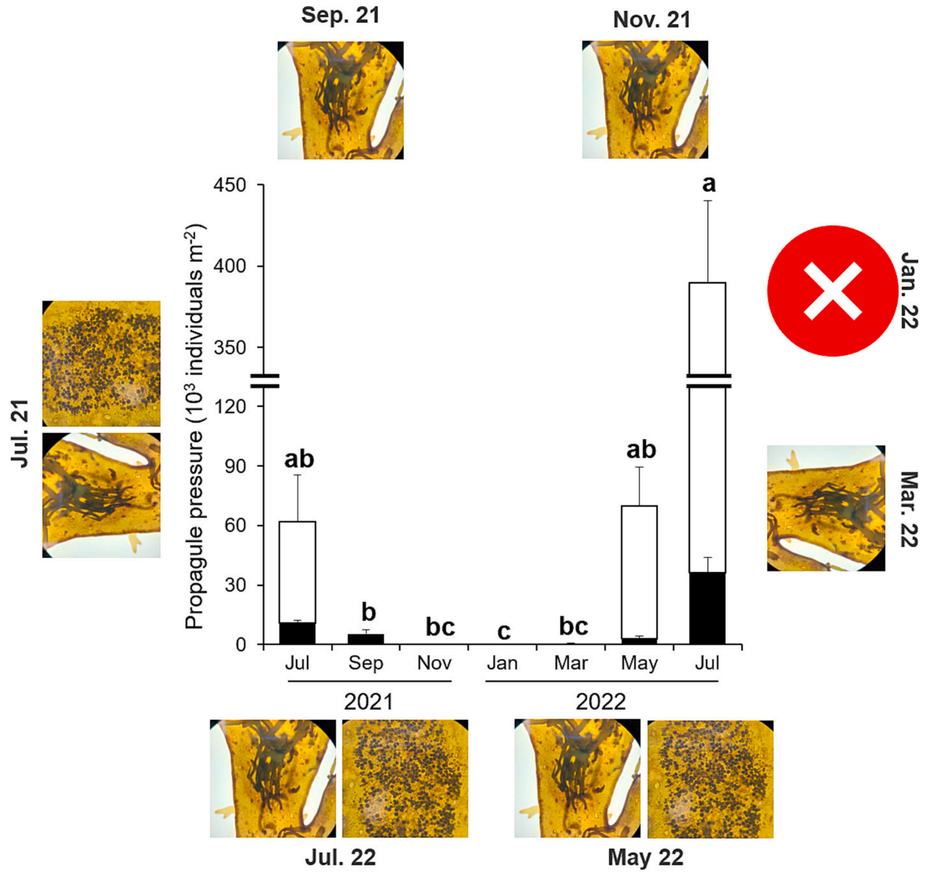

Fig. 8. Propagule pressure of *R. okamurae* exerted by vegetative propagules (black bars) and spores (white bars) in each sampling event. Data are expressed as the mean ± SD (n = 3). Different letters indicate significant differences across months ($P < 0.05$).

pressure was recorded in November and March (307 ± 71 new individuals per m^2). No propagule pressure was observed in January, with null values (Fig. 8). Overall, the total potential of new individuals throughout the study period in this area reached 527,431 ± 107,015 individuals per m^2 (Fig. 8).

3.3. *Principal component analysis*

A principal component analysis (PCA) of environmental factors in the study area revealed distinct contributions of specific abiotic factors along the two primary axes (PC 1 and PC 2), accounting for 79.8% of the total variance. Temperature, photoperiod, and salinity were the main contributors to PC 1. Nitrate and ammonium concentrations predominantly influenced PC 2 (as described in Rosas-Guerrero et al., 2025). Pearson correlation analysis between the number of individuals with propagules and their frequency along PC 1 showed positive correlations (Table 4). By contrast, the number of individuals bearing spores, and their frequency did not show any relationship with the environmental axes derived from the PCA (Table 4).

Table 4
Correlation analysis between the two primary axes (PC 1 and PC 2) and biological variables measured: number of *R. okamurae* individuals with propagules per m^2 and their frequency in relation to the population (%), and number of individuals with spores per m^2 and their frequency (%) ($n = 7$). The asterisks indicate significant differences ($P < 0.05$).

	PC 1		PC 2	
Variable	r	P value	r	P value
Ind. with veg. Propagules (m^{-2})	0.77	0.01*	0.01	0.81
Ind. with veg. Propagules (%)	0.67	0.03*	0.03	0.70
Ind. with spores (m^{-2})	0.41	0.12	0.03	0.69
Ind. with spores (%)	0.30	0.20	0.08	0.55

4. Discussion

The analysis of the reproductive phenology of *R. okamurae* reveals that vegetative propagation and asexual reproduction are the key mechanisms enabling the species to persist in the invaded *P. oceanica* meadow. This population is maintained primarily by the continuous presence of asexual and vegetative structures, driven by the high number of fertile individuals and high densities of spores and propagules. Additionally, this study confirmed the absence of gametangia throughout the year and agrees with previous observations on the lack of gametophytes in introduced areas (Verlaque et al., 2009; García-Gómez et al., 2018; Bellisimo et al., 2024; Díaz-Tapia et al., 2025; El Madany et al., 2024).

The scarcity of gametangia is frequent in the family Dictyotaceae in the Mediterranean Sea, suggesting that the presence of gametophytes is more of an exception than the rule, with populations likely being sustained primarily through asexual and vegetative mechanisms (Küpper et al., 2019). Nevertheless, although gametangia were not observed during the study period, the presence of gametophytes cannot be completely discarded because tetraspores were sparsely and occasionally found. Hwang et al. (2009) confirmed that thalli produce gametophytes under controlled conditions through tetraspore germination, which subsequently develop male and female gametangia after nine weeks, requiring up to 19 weeks to complete the full life cycle. Given that gametophytes and sporophytes are morphologically identical (isomorphic), confirming their presence without genetic tools requires observing the sexual reproductive structures (gametes). Therefore, it remains unclear whether gametophytes are absent because tetraspores are unable to germinate and/or grow, or because gametogenesis is restricted by environmental factors in the introduced area. Moreover, the absence of gametophytes may also be related to the longevity of individuals and their short life span in the introduced population (Rosas-Guerrero et al., 2025). Nonetheless, Agatsuma et al. (2005) noted that *R. okamurae* requires more than two years to complete its life cycle in native regions. The population of *R. okamurae* in the study area exhibited up to six cohorts within a year (Rosas-Guerrero et al., 2025), suggesting that the species may not be reaching the gametophytic phase in its incomplete life cycle. This observation is crucial because species with a short life span generally exhibit higher reproductive rates and can adapt quickly to new environments, a trait that may enhance their invasiveness (Pyšek and Richardson, 2007; Ni et al., 2021).

Although the production of asexual spores was limited to May and July, propagules were present throughout the year, except for January, indicating that *R. okamurae* may generate new individuals nearly year-round, primarily through vegetative propagation and asexual structures. Vegetative and asexual mechanisms are common among marine benthic organisms, particularly invasive seaweeds (Santelices, 1990; Liu et al., 2017). For example, *Hypnea musciformis* (Wulfen) J. V. Lamouroux, one of the most common invasive species in the Hawaiian Islands, relies on vegetative propagation to sustain its populations (Smith et al., 2002). Similarly, in the Mediterranean Sea, species of the genus *Caulerpa* maintain their populations predominantly via vegetative mechanisms (Klein and Verlaque, 2008; Ruiz et al., 2015). *Rugulopteryx okamurae* exhibits similar strategies to these species. However, although reproductive individuals did not exceed 20%, densities surpassing 3200 individuals per m^2 were observed in *P. oceanica* meadows (Rosas-Guerrero et al., 2025). This finding, combined with the higher densities of spores and propagules in elongating thalli, suggests that the population may be primarily sustained by larger individuals, which have larger thalli more susceptible to mechanical breakage. When these thalli break, the scarred areas exhibit the highest density of propagules (Rosas-Guerrero et al., 2020). Hence, the idea that larger individuals have greater reproductive capacities is supported by their ability to reallocate resources toward the development of reproductive structures (Arenas and Fernández, 1998; Zanolla et al., 2017). This mechanism is particularly relevant to their invasive potential and propagule pressure. By contrast, smaller individuals seem to prioritize resource allocation toward growth to enhance their chances of survival (Åberg, 1996). This hypothetical mechanism has been observed in preliminary studies by Rosas-Guerrero et al. (2020), suggesting that *R. okamurae* invests resources in elongation when growth is possible. However, when growth capacity is limited, these individuals shift resources toward the extensive production of propagules, especially in broken parts (Kajimura, 1992), optimizing their reproductive output, intensifying propagule pressure, and further reinforcing the invasive behavior of *R. okamurae*.

A conservative estimate of the propagule pressure exerted by *R. okamurae* was obtained, suggesting that over half a million new theoretical individuals per square meter could be produced in this habitat, implying an increment of 35 times the density of individuals inhabiting the meadow (Rosas-Guerrero et al., 2025). Although this discrepancy likely reflects the unknown survival rates of vegetative propagules and spores, the large number of potential new individuals indicates that the pressure *R. okamurae* poses in the *P. oceanica* habitat remains high throughout the year. This process may harm this habitat's associated biota, particularly the native flora, by limiting available substrate and displacing local species, as occurs in other regions invaded by *R. okamurae* (García-Gómez et al., 2021; Sempere-Valverde et al., 2021; Faria et al., 2022). Additionally, while some new recruits may remain in the source population, the substrate cannot host such a large number of potential individuals. Thus, a substantial proportion of these potential recruits remain in the water column, where they keep growing and are transported to new areas, contributing to the substantial amounts of drifting *R. okamurae* that cause negative socioeconomic impacts on beaches and clog fishing gears at sea (MITECO, 2022). Moreover, some of these new recruits may sink and form unattached aggregations, which are photosynthetically active on the deep-sea floor (Mateo-Ramírez et al., 2023). These outcomes align with the propagule pressure hypothesis, one of the key theoretical frameworks for understanding the success of invasive species (Lockwood et al., 2005; Enders et al., 2018; Gioria et al., 2023). However, the difference in propagule pressure between July 2021 and 2022 indicates that it may not stabilize over time, increasing the unpredictability of the species' invasion.

The reproductive mechanisms observed in the present study are generally influenced by environmental factors that trigger reproduction. Temperature, day length, light intensity, nutrient concentrations, and water movements are the primary abiotic factors regulating seaweed reproduction (de Bettignies et al., 2018; Chefaoui et al., 2019). For instance, the reproductive capacity of *Dictyota dichotoma* (Hudson) J. V. Lamouroux, a species within the Dictyotaceae family, correlates with the photoperiod, exhibiting the peak of reproductive activity during spring and summer (Gauna et al., 2013). In the case of *R. okamurae*, the number of individuals with propagules and their frequency in the population were increased by rising temperatures, longer photoperiods, and decreasing salinity, conditions associated with May and July (summer). By contrast, spore production was not affected by the environmental factors considered here. The lack of a clear relationship between nitrate and nitrite concentrations and the biological variables measured could stem from the low levels (generally below detection limits) of these compounds at the study site. However, Bogaert et al. (2016) reported that nutrient availability, particularly nutrient limitation, promoted the sporogenesis of *D. dichotoma*.

Finally, although vegetative propagation through thallus fragmentation in *R. okamurae* was not determined in this work, apical fragments detaching from the parent organism may disperse to new areas and exert propagule pressure by generating new propagules in the scarred zones of the thalli (Rosas-Guerrero et al., 2020). This ability to generate new individuals via fragmentation is shared with other Dictyotaceae members (Herren et al., 2006; Gauna et al., 2013) but is also reminiscent of the harmful invasive behavior of *Caulerpa taxifolia* and *C. cylindracea* in *P. oceanica* meadows, where accidental thallus fragmentation is one of the main mechanisms for maintaining monospecific populations (Ceccherelli and Cinelli, 1999; Ceccherelli et al., 2002). This fragmentation process increases propagule pressure, enhances invasiveness, and facilitates recruitment and colonization of new habitats by enabling rapid vegetative propagation (Sakai et al., 2001; Wright, 2005). Hence, it ultimately raises the propagule pressure of *R. okamurae* within the *P. oceanica* habitat and adjacent areas.

5. Conclusions

This study's findings highlight how *R. okamurae* maintains its population within *P. oceanica* meadows and expands through vegetative and asexual mechanisms throughout the year, especially during summer by larger individuals, and nearly halts in winter. The production of propagules and spores occurs along the entire thallus and is closely linked to thallus size. Propagules are influenced by abiotic environmental factors, while spores are not. The continuous potential production of new individuals implies high propagule pressure, with estimates surpassing half a million new individuals per square meter, greatly exceeding the capacity of the meadow to host them. Therefore, many new individuals could remain suspended in the water column or sink to deeper areas, facilitating dispersal, establishing new populations, and exerting negative socioeconomic impacts. This observation reinforces the central role of propagule pressure in determining invasiveness and underlines the importance of considering all reproductive mechanisms when assessing risks and management strategies for invasive seaweeds, identifying spring and summer as distinctive temporal windows of propagule pressure.

CRediT authorship contribution statement

Jesús Rosas-Guerrero: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Raquel Carmona:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Julio De la Rosa:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Conceptualization. **Marianela Zanolla:** Writing – review & editing, Methodology, Investigation, Formal analysis. **María Altamirano:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

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

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Data availability

Data will be made available on request.

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