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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

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Abstract

The invasive brown alga *Rugulopteryx okamurae* (Ochrophyta) has undergone a rapid expansion in the Strait of Gibraltar since its introduction in 2015, significantly altering coastal habitats. This study focused on analyzing the composition and structure of epifaunal bryozoan assemblages associated with *R. okamurae* populations on infralittoral rocky bottoms in the Strait of Gibraltar and adjacent areas (southern Spain). Seven samples were collected, each from one sampling station, using scuba diving techniques. A total of 49 bryozoan taxa were recorded, 45 of which were identified at the species level. This level of biodiversity makes this area a hotspot for bryozoans. One cyclostomatid species, *Favosipora infrarockensis* Ramalho n. sp., is described here as new to science; three other species are recorded here for the first time in Spanish waters, and nine are newly recorded in the Strait of Gibraltar and the Alboran Sea. Multivariate analyses revealed the presence of two distinct sample groups, primarily influenced by the geographical location within the Strait of Gibraltar. The species richness per sample ranged from 4 to 29, showing a positive trend with the wet biomass of *R. okamurae*. Most species have a wide biogeographic distribution across the Atlantic and Mediterranean, while only 15.6% of them are endemic to the Mediterranean Sea. This study highlights the high diversity of epibiont bryozoans in the Strait of Gibraltar area, in this case associated with *R. okamurae,* which is an invasive species that represents a severe threat to local biodiversity and is causing profound changes to habitats and associated communities.

Keywords: epibionts; biofouling; Bryozoa; biodiversity; western Mediterranean Sea.

Introduction

Macroalgae, commonly known as seaweeds, establish extensive and highly productive beds in coastal environments worldwide (Hurd *et al.,* 2014). Seaweeds have significant phylogenetic and functional diversity, playing a crucial role in the ecology of rocky shores, due to their role as primary producers and habitat providers for a wide variety of species, and their contribution to blue carbon sequestration (Chung *et al.,* 2011; Griffiths *et al.,* 2016; Miranda *et al.,* 2017). Seaweeds act as a substrate for the attachment of both sessile and mobile organisms, offering essential surface area for sheltering while serving as temporary or permanent habitats for many species (Urra *et al*., 2013; Mateo-Ramírez *et al*., 2022). Moreover, macroalgae also have a role as sediment traps (Stamski & Field, 2006), attracting a diverse array of organisms. They also serve as a direct food source for herbivores and, indirectly, for detritus-feeders species that feed on microbial films (Hayward, 1980). Macroalgae-associated species often show complex trophic interactions and may also act as additional secondary habitat-forming species; therefore, macroalgae initiate both trophic and habitat cascades that greatly increase coastal biodiversity (Seed & O'Connor, 1981).

Unfortunately, the escalating impact of human activities on the environment has led to significant changes in the composition of macroalgal communities (Benedetti-Cecchi *et al*., 2001; Macreadie *et al*., 2017). Notable community transformations include the retreat of species towards polar regions due to rising water temperatures, which is coupled with the expansion of species from warmer waters and non-native species (Harley *et al*., 2012; Koch *et al.,* 2013) and the regression of *Cystoseira* (*sensu lato*) populations in the Mediterranean Sea. These key benthic components of shallow rocky bottom have suffered a general degradation due to anthropogenic pressure (Thibaut *et al.,* 2005; Iveša *et al.,* 2016). The restructuring of macroalgal communities and the subsequent ecological consequences have altered the composition and structure of the associated epibionts, with potential effects on the trophic structure of the whole community (Saarinen *et al*., 2018; Navarro-Barranco *et al*., 2019).

Invasions are one of the major threats to biodiversity and ecosystem functioning in coastal habitats (Schaffelke *et al*., 2006; Williams & Smith, 2007). In this context, since its introduction in the Strait of Gibraltar area (southern Spain) in 2015 (Altamirano *et al*., 2016; Ocaña *et al*., 2016), the brown alga *Rugulopteryx okamurae* (Ochrophyta, Phaeophyceae, Dictyotales) has widely invaded the infralittoral rocky bottoms across the Atlantic Ocean, the Mediterranean Sea and adjacent areas (García-Gómez *et al*., 2018; 2020), and some Macaronesian Islands including the Azores Islands (Faria *et al*., 2022) and Madeira (Bernal Ibáñez *et al*., 2022). This colonization has led to a drastic modification of habitats and their associated communities (García-Gómez *et al.,* 2020; Sempere-Valverde *et al.,* 2021), expanding to southern Portugal (Liulea *et al*., 2023), the Moroccan coast (El Madany *et al.,* 2024), Alicante (eastern Spain) (Terradas-Fernández *et al.,* 2023), northern Spain (Díaz-Tapia *et al*., 2024), the Marseille coast (France) (Borriglione *et al.,* 2024), and Sicily (Italy) (Bellissimo *et al*., 2023; Marletta *et al.,* 2024, the easternmost report of the Mediterranean Sea so far).

The invasion of *R. okamurae* has had a local high environmental and socioeconomic impact, causing severe losses to ecosystem services and disrupting native coastal ecosystems (García-Gómez *et al.,* 2020; Estévez *et al.,* 2022). The introduction of *R. okamurae* into the Strait of Gibraltar and adjacent areas has also led to homogenisation of local macroalgae populations, resulting in a taxonomic composition dominated by a limited number of species, primarily other invasive macroalgae such as *Asparagopsis armata* and *A. taxiformis* (pers. obs.).

The fauna associated with the introduced populations of *R. okamurae* has been poorly studied in southern Spain (Navarro-Barranco *et al.,* 2019), particularly in the case of bryozoans. Bryozoans are one of the major groups of sessile epifaunal communities associated with macroalgae and filter-feeding organisms such as hydroids, serpulids, sponges, and tunicates (Saarinen *et al*., 2018; Rossbach *et al.,* 2022). These invertebrates play a significant role in benthic marine biodiversity (Appeltans *et al*., 2012; Lombardi *et al.,* 2014), as they represent crucial components of the food web for several organisms such as nudibranchs, pycnogonids, turbellarians, polychaetes, small arthropods, and nematodes (Lidgard, 2008). Furthermore, several bryozoan species act as important habitat builders, constructing colonies with intricate structures that provide shelter for other invertebrates and serve as vital nursery grounds for juvenile fish, thus enhancing overall biodiversity (Wood *et al.,* 2012; Bastos *et al.,* 2018; Ramalho *et al.,* 2018; Giampaoletti *et al*., 2020; Lombardi *et al*., 2021; Rosso *et al.,* 2023). In this context, the aims of the present study are: (1) to investigate the composition and structure of the epifaunal bryozoan assemblages associated with the invasive alga *R. okamurae* on rocky bottoms in the Strait of Gibraltar area, and (2) to analyse the affinities of the bryozoan species with its biogeographical context.

Material and Methods

Study area

The Strait of Gibraltar, with its complex geological history (Loget & Van Den Driessche, 2006), is of considerable biological significance due to its unique geographical and oceanographic characteristics (Báez *et al.,* 2021).

Its geographical location, as the waterway connecting the Atlantic Ocean and the Mediterranean Sea, makes the Strait of Gibraltar a biogeographical transition zone that influences the distribution of marine organisms (Real *et al.,* 2021). The complex interaction between water masses in the area promotes strong oceanic tidal currents and upwelling phenomena, influencing nutrient cycling and creating favourable conditions for primary producers, which ultimately influence the entire food chain (Echevarría *et al.,* 2002). Moreover, its location between three biogeographical regions (the Lusitanian, the Mauritanian and the Mediterranean Sea) allows the coexistence of species from the north Atlantic Ocean, and species from northwestern subtropical Africa and the Mediterranean Sea area (Ekman, 1953; Real *et al.,* 2021; Caballero-Herrera *et al.,* 2022), together with a high number of endemic marine species (Gofas, 1998).

Due to its singularity, the Strait of Gibraltar is a very interesting area for marine taxonomists; biogeographical studies have been published on sponges (Carballo *et al.,* 1997), ascidians (Naranjo *et al.,* 1998), molluscs (Gofas, 1998), amphipods (Conradi & López-González, 1999; Guerra-García & Takeuchi, 2004), isopods (Castelló & Carballo, 2001), and polychaetes (Sánchez-Moyano *et al.,* 2002). Several studies on bryozoans have been carried out in the last few decades, through sampling expeditions performed in deep-sea areas such as the historical BALGIM (Harmelin & d'Hondt, 1992a, b, 1993) and FAUNA I (Álvarez, 1992, 1994), and using material collected from local fishing gears (López de la Cuadra & García-Gómez, 1988, 1994). However, the information regarding the bryozoan fauna associated with photophilous macroalgal beds on shallow rocky bottoms is very scarce.

Sample collection and laboratory procedures

Seven samples were collected from infralittoral rocky bottoms between Bolonia (Cádiz), Ceuta, and Placer de las Bóvedas (Málaga) (Fig. 1), using scientific SCUBA diving techniques. Samples were collected in areas containing extensive rocky bottoms characterized by relatively homogeneous canopy-forming macroalgae. Specifically, sampling was conducted on rocky substrates dominated by the invasive alga *Rugulopteryx okamurae*, at depths ranging from 9 to 20 meters (Table 1, Fig. 1). The samples were collected during the INFRAROCK3D_0521 and INFRAROCK3D_0522 expeditions on board of the R/V SOCIB (July 2021) and R/V Francisco de Paula Navarro (May 2022), respectively, within the framework of the 17-ESMARES2-INFRA project under the Marine Strategy Framework Directive (MSFD) in Spanish waters.

An area of 25×25 cm was scraped above the rocky substrate for standardized identification of macrophytes and fauna. For each 25×25 cm quadrat, a photographic record was taken immediately prior to sampling. All macrophytes and fauna within the quadrat were carefully removed and placed in plastic zip-lock bags. Hand scrapers were used to facilitate the removal of attached organisms. Once on board the vessel, samples were labelled and preserved by freezing until processed in the laboratory.

Macrophytes and fauna were sorted using trays and small containers, and the small epibiont bryozoans were carefully detached from the fronds of *R. okamurae* using soft entomological tweezers under a stereomicroscope (Leica MZ12). Encrusting species that required taxonomic identification using optical or scanning electron microscopy were preserved together with the small portion of the frond to which they were attached, to minimize the removal of algal biomass. Bryozoan specimens were preserved in 70% ethanol.

For each sample, the volume, wet biomass, and dry biomass of all the algae were recorded. After shaking the sample to remove surface water, the individuals were cleaned of sand and epibionts; wet biomass (WB, in grams) of all species (all organisms were pooled) was measured using a Radwag Instrument WLC 1/A2/C/2 scale.

Algae samples were then transferred into a P-Selecta Digitheat-TFT Scientific drying oven and dried for 24 h at 60 °C until a constant dry biomass (DB) ± 0.01 g was reached, according to Edgar (1983). Volume (V) was measured in cm^3 by water displacement following the method described by Bussell *et al*. (2007).

Bryozoans were studied using an optical microscope and a Scanning Electron Microscope (SEM) (JEOL JSM-840) at the Centro de Microscopía of the Universidad de Málaga, and identified to the lowest possible taxonomic level using the available literature. Measurements (usually length = L and width = W) were taken in µm from SEM images using the software ImageJ (Abramoff *et al.,* 2004) and are presented in the text as [min–mean–max, Standard Deviation (SD), Number of measurements made (N)]. Vouchers were deposited in the invertebrate collection at the Museo Nacional de Ciencias Naturales – CSIC (MNCN) in Madrid (Spain).

Data analysis

The epifaunal bryozoan assemblages of *R. okamurae* were characterized based on frequency of occurrence (%F, percentage of samples in which a particular taxon was present), growth form (UE, uniserial encrusting; ME, multiserial encrusting; E, erect uniserial), distribution range (At, Atlantic; Me, Mediterranean; Ma, Macaronesian; Bo, Boreal; Ws, Widespread; En, Endemic of the Strait of Gibraltar), and substrate preference (Veg, plant; Roc, rocky; Bio, bioclasts; Fau, sessile fauna; Art, artificial substrate) for each taxon.

Multivariate analyses based on qualitative similarities among bryozoan taxa were performed to assess the similarity between samples. A group-average sorting classification (CLUSTER) of the samples was obtained using the Jaccard similarity index and the unweighted

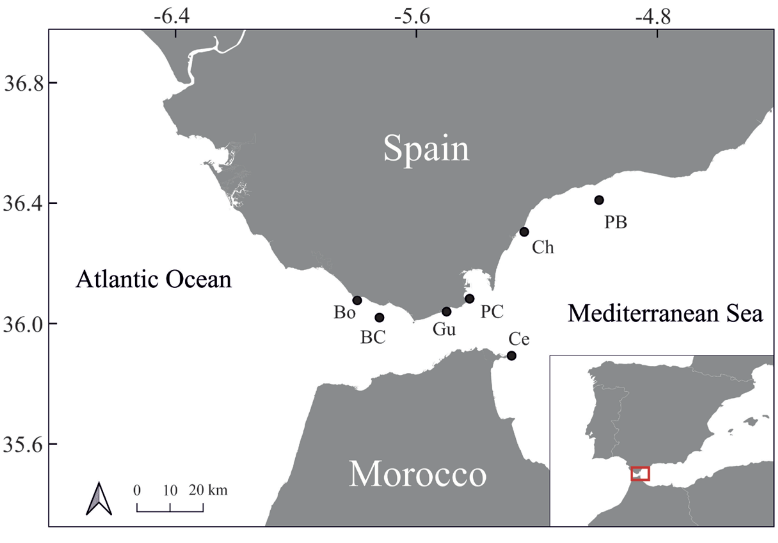

Fig. 1: Map of the study area indicating the geographical location of the Strait of Gibraltar, and the location of the samples: Bo, Bolonia; BC, Bajo Cabezos; Gu, Guadalmesí; PC, Punta Carnero; Ce, Ceuta; Ch, Chullera; PB, Placer de las Bóvedas.

Table 1. Location of the sampling stations in the Strait of Gibraltar area where the epifaunal bryozoan species of *R. okamurae* were analysed.

Sample	Code	Expedition	Latitude	Longitude	Depth (m)
Bolonia	Bo	INFRAROCK3D_0522	36.0766°N	5.7968°W	10
Bajo Cabezos	BC	INFRAROCK3D_0521	36.0196°N	5.7229°W	10
Guadalmesí	Gu	INFRAROCK3D_0522	36.0429°N	5.4999°W	9
Punta Carnero	PC	INFRAROCK3D_0521	36.0830°N	5.4231°W	13
Ceuta	Ce	INFRAROCK3D_0522	35.8928°N	5.2839°W	13
Chullera	Ch	INFRAROCK3D_0521	36.3070°N	5.2419°W	12
Placer de las Bóvedas	PB	INFRAROCK3D_0521	36.4100°N	4.9931°W	20

pair group method with an arithmetic mean agglomerative algorithm (UPGMA) (Sneath & Sokal, 1973). A permutation procedure, the similarity profile routine test (SIMPROF), was used to check the significance of sample groupings (Clarke *et al.,* 2008). These analyses were carried out with the PRIMER v.6 software (Plymouth Routines in Multivariate Ecological Research) (Clarke & Gorley, 2006).

Species richness (S) was recorded as the number of bryozoan taxa present in each sample. Statistical comparisonsof S values between groups identified by SIMPROF tests were performed using one-way ANOVA. The normality and homogeneity of the residuals were checked with the Shapiro-Wilk and Fligner tests, respectively. These data were analysed using the statistical program R version 4.4.0 (R Core Team, 2024), with graphs made using the ‘ggplot2’ package (Wickham, 2016).

Results

Bryozoan diversity

A total of 49 bryozoan taxa were recorded as epibionts of *R. okamurae*, 45 of which were identified to the species level (Table 2). One taxon is recognized as a new species and is described below. Twelve additional species are new records for the Strait of Gibraltar and the Alboran Sea area, known as ESAL (from the Spanish Estrecho y Alborán) within the framework of the MSFD in Spanish waters. Three of these 12 species are reported here for the first time in Spanish waters.

The taxa recorded here correspond to the three living orders: 33 taxa (67%) belong to Cheilostomatida, 15 taxa (31%) to Cyclostomatida, and a single taxon (2%) to Ctenostomatida. A total of 23 families were recorded, most of which were represented by a single taxon (56.6%). The families Bugulidae and Candidae were the best represented with five taxa each, followed by the families Tubuliporidae and Aeteidae with four taxa each (Table 2). The most frequent taxa were *Aetea truncata* and *Crisia eburnea harmelini*, both present in all samples (100% frequency of occurrence, %F), followed by *Chorizopora* sp. (71.4%F). The other 10 species with frequencies of occurrence over 50%F were *A. sica, Caberea boryi, Celleporina decipiens*, and *Filicrisia geniculata* (Table 2).

The number of epibiont bryozoan taxa of *R. okamurae* per sample ranged from four at Placer de las Bóvedas to 29 at Punta Carnero (Table 3). However, algal biomass values were highly variable between samples. High biomass values were observed at samples from Bolonia (140 g wet biomass, WB; and 17.3 g dry biomass, DB) and Bajo Cabezos (118.3 g WB, 14.62 g DB) (Table 3). In contrast, the lowest biomass values were observed at Chullera (53.8 g WB, 9.8 g DB) and Placer de las Bóvedas (30.9 g WB, 3.73 g DB), both located on the eastern side of the Strait of Gibraltar. Regarding algal volume (V), a similar spatial trend was observed, with the highest values at Bolonia (135 cm^3) and Bajo Cabezos (130 cm^3), and the lowest values at Chullera (50 cm^3) and Placer de las Bóvedas (40 cm^3) (Table 3). The biomass and volume values of *R. okamurae* were positively correlated with the number of epibiont bryozoan species per sample. Only WB showed a significant positive correlation with taxa richness ($R_{Spearman} = 0.77$; $p < 0.05$). Consequently, taxon richness (S) was standardized as bryozoan taxa per biomass unit of *R. okamurae.* According to this standardization, Punta Carnero and Guadalmesí were the samples with the highest richness of epibiont bryozoan taxa per unit of *R. okamurae* WB, while the lowest richness was observed at Chullera and Placer de las Bóvedas (Table 3). Similar results were obtained for *R. okamurae* dry biomass (DB).

In terms of growth form, multiserial encrusting colonies were predominant with 24 taxa (49% of the total), followed by erect colonies with 19 taxa (39%) and uniserial encrusting colonies with six taxa (12%). Similarly, from the 13 most frequently observed species (> 50%F), 46% corresponded to multiserial encrusting, 31% to erect colonies, and 23% to uniserial encrusting.

Table 2. List of bryozoan taxa found as epibionts on fronds of the invasive macroalga *R. okamurae* from the Strait of Gibraltar and adjacent areas. The sample where the taxa were collected (BC, Bajo Cabezos; Bo, Bolonia; PC, Punta Carnero; Gu, Guadalmesí; Ce, Ceuta; Ch, Chullera; PB, Placer de las Bóvedas), frequency of occurrence (%F), distribution range (At, Atlantic; Me, Mediterranean; Ma, Macaronesian; Bo, Boreal; Ws, Widespread; En, Endemic of the Strait of Gibraltar), substrate preference (Veg, plant; Roc, rocky; Bio, bioclasts; Fau, sessile fauna; Art, artificial substrate) and growth form (UE, uniserial encrusting; ME, multiserial encrusting; Er, erect are indicated. New records for the Strait of Gibraltar and Alboran Sea area are indicated with *; new records for Spanish waters are indicated with **.

Taxa	BC	Bo	PC	Gu	Ce	Ch	PB	%F	Distribution range	Substrate	Growth form
Class Gymnolaemata											
Order Cheilostomatida											
Family Aeteidae											
Aetea anguina (Linnaeus, 1758)	1	1	1					42.86	At, Me, Ma; Ws	Veg	UE
*Aetea lepadiformis*** Waters, 1906			1					14.29	Me	Veg	UE
Aetea sica (Couch, 1844)		1	1	1	1			57.14	At, Me, Ma	Veg, Bio	UE
Aetea truncata (Landsborough, 1852)	1	1	1	1	1	1	1	100	At, Me, Ma	Roc, Bio	UE
Family Beaniidae											
*Beania cylindrica** (Hincks, 1886)		1						14.29	Me	Fau	Er
Family Bugulidae											
Bicellariella ciliata (Linnaeus, 1758)	1							14.29	At, Me, Ma	Veg	Er
Bugula calathus calathus (Norman, 1868)			1			1		28.57	At, Me	Art	Er
Bugulina flabellata (Thompson in Gray, 1848)		1						14.29	At, Me, Ma	Art	Er
Bugulina fulva (Ryland, 1960)			1					14.29	At, Me, Ma	Roc, Art	Er
*Crisularia serrata** (Lamarck, 1816)					1			14.29	Me	Art	Er
Family Calloporidae											
Callopora rylandi Bobin & Prenant, 1965	1					1		28.57	At, Me	Roc	ME
Family Candidae											
Caberea boryi (Audouin, 1826)	1	1	1	1				57.14	At, Me, Ma	Bio	Er
*Cradoscrupocellaria ellisi** (Vieira & Spencer Jones, 2012)		1	1		1			42.86	At, Me, Ma	Bio, Roc	Er
Scrupocellaria delilii (Audouin, 1826)	1			1				28.57	At, Me, Ma	Art	Er
Scrupocellaria scrupea Busk, 1851			1	1	1			42.86	At, Me	Bio, Fau	Er
Scrupocellaria scruposa (Linnaeus, 1758)		1	1		1	1		57.14	At, Me	Roc, Bio, Fau	Er

Continued

Table 2 continued

Taxa	BC	Bo	PC	Gu	Ce	Ch	PB	%F	Distribution range	Substrate	Growth form
Family Celleporidae											
Cellepora pumicosa (Pallas, 1766)			1			1		28.57	At, Me, Bo	Roc, Art	ME
Celleporina decipiens Hayward, 1976	1	1	1	1				57.14	At, Me	Fau	ME
*Celleporina mediterranea*** Souto, Reverter-Gil & De Blauwe, 2014			1	1				28.57	Me	Roc, Fau	ME
Turbicellepora avicularis (Hincks, 1860)	1	1	1					42.86	At, Me, Ma; Bo, Ws	Roc, Bio	ME
Family Chorizoporidae											
Chorizopora sp.	1	1	1	1	1			71.43	Me		ME
Family Exochellidae											
Escharoides coccinea (Abildgaard, 1806)			1		1			28.57	At, Me	Bio, Art, Roc	ME
Family Fenestrulinidae											
Fenestrulina barrosoi Alvarez, 1993			1					14.29	At, Me	Veg	ME
Family Flustridae											
Chartella papyracea (Ellis & Solander, 1786)	1					1		28.57	At, Me	Roc	Er
Chartella tenella (Hincks, 1887)	1							14.29	Me	Bio, Fau, Roc	Er
Family Haplopomidae											
*Haplopoma bimucronatum occiduum** (Waters, 1879)				1				14.29	At, Me, Ma	Veg	ME
Haplopoma impressum (Audouin, 1826)	1	1	1	1				57.14	At, Me, Ma	Veg	ME
Family Hippothoidae											
Celleporella hyalina (Linnaeus, 1767)	1	1		1				42.86	At, Me, Ws	Bio, Roc	ME
Family Microporellidae											
*Microporella modesta*** Di Martino, Taylor & Gordon, 2020	1	1	1	1				57.14	Me	Bio, Fau, Art	ME
Family Savignyellidae											
Savignyella lafontii (Audouin, 1826)			1				1	28.57	Me	Art	Er
Family Scrupariidae											
Scruparia ambigua (d'Orbigny, 1841)	1	1		1				42.86	At, Me, Ws	Bio, Roc, Art	UE
*Scruparia chelata** (Linnaeus, 1758)	1	1	1	1				57.14	At, Me, Ws	Fau, Bio, Art	UE

Continued

Table 2 continued

Taxa	BC	Bo	PC	Gu	Ce	Ch	PB	%F	Distribution range	Substrate	Growth form
Family Vesiculariidae											
Amathia lendigera (Linnaeus, 1758)			1					14.29	At, Me, Ma, Ws	Veg	Er
Class Stenolaemata											
Order Cyclostomatida											
Unidentified sp. 1			1					14.29			ME
Family Annectocymidae											
*Annectocyma arcuata** (Harmelin, 1976)			1					14.29	Me	Bio	ME
Annectocyma major (Johnston, 1847)			1					14.29	At, Me, Ma	Veg	ME
Family Crisiidae											
Bicrisia gibraltarensis Harmelin, 1990	1							14.29	E	Bio	Er
Crisia eburnea harmelini (d'Hondt, 1988)	1	1	1	1	1	1	1	100	At, Me, Ws	Fau, Art	Er
Filicrisia geniculata (Milne Edwards, 1838)		1	1		1		1	57.14	At, Me	Bio	Er
Family Densiporidae											
Favosipora infrarockensis n. sp. Ramalho, 2025	1							14.29			ME
Family Entalophoridae											
*Mecynoecia delicatula** (Busk, 1875)					1			14.29	At, Me, Ws	Art	Er
Family Lichenoporidae											
*Disporella hispida** (Fleming, 1828)		1			1			28.57	At, Me, Ma, Bo, Ws	Fau, Roc, Bio	ME
Patinella distincta (Alvarez, 1993)		1	1	1	1			57.14	Me	Veg	ME
Patinella radiata (Audouin, 1826)	1	1	1	1				57.14	At, Me, Bo, Ws	Veg	ME
Family Plagioeciidae											
Plagioecia sarniensis (Norman, 1864)	1							14.29	At, Me, Ws	Bio, Fau	ME
Family Tubuliporidae											
Tubulipora liliacea (Pallas, 1766)	1				1			28.57	At, Me, Ma, Bo, Ws	Bio, Fau	ME
Tubulipora sp. 1					1			14.29			ME
Tubulipora sp. 3						1		14.29			ME
*Tubulipora ziczac** Harmelin, 1976				1				14.29	Me	Veg	ME

Table 3. Total number of taxa of epibiont bryozoans per sample, together with volume and biomass of *R okamurae*, in each sample. S, number of epibiont bryozoan taxa per sample; Vol., volume (cm^3) of *R. okamurae*; WB, wet biomass (g) of *R. okamurae*; DB, dry biomass (g) of *R. okamurae*; S/g WB, taxa richness/g of WB of *R. okamurae*; S/g DB, taxa richness /g of DB of *R. okamurae*.

Sample	S	Vol.	WB	DB	S/g WB	S/g DB
Bolonia	21	135	140	17.3	0.15	1.21
Bajo Cabezos	22	130	118.32	14.62	0.19	1.50
Guadalmesí	18	58	60.38	5.06	0.30	3.56
Punta Carnero	29	65	68.56	8.26	0.42	3.51
Ceuta	15	88	90.5	10.08	0.17	1.49
Chullera	8	50	53.83	9.84	0.15	0.81
Placer de las Bóvedas	4	40	30.9	3.73	0.13	1.07

New taxa and remarks on some new records

Of the 49 bryozoan taxa found in the present study, one is new to science (*Favosipora infrarockensis* Ramalho n. sp.). Three species (*A. lepadiformis, Microporella modesta,* and *C. mediterranea*) were recorded for the first time in Spanish waters, and nine species represent new records for the Strait of Gibraltar and Alboran Sea area (*Scruparia chelata, Crisularia serrata, Beania cylindrica, Cradoscrupocellaria ellisi, Haplopoma bimucronatum, Tubulipora ziczac, Annectocyma arcuata, Mecynoecia delicatula,* and *Disporella hispida*). One of the new records, *C. serrata*, is considered non-indigenous to the Mediterranean Sea.

Below, we present the description of the new species *F. infrarockensis* Ramalho n. sp. A short description and ecology of those species that represent new or noteworthy records for the study area are provided in the Supplementary Material.

Class STENOLAEMATA
Order CYCLOSTOMATIDA
Family DENSIPORIDAE Borg, 1944
Genus *Favosipora* MacGillivray, 1885
Favosipora infrarockensis Ramalho, n. sp.
urn:lsid:zoobank.org:pub:49D1DB27-82A6-4A32-8EE7-6E00D8570781

Material examined: Holotype: **MNCN 25.02/255**, Bajo Cabezos; one colony alive and fertile, used for SEM.

Etymology: Named after the INFRAROCK expeditions that are carried out every year throughout the Spanish coastal waters within the monitoring programme derived from the Marine Strategy Framework Directive, which is performed by the *Instituto Español de Oceanografía (IEO), CSIC.*

Description: Encrusting colony, almost circular (4.6 x 3.7 mm diameter), exposed basal lamina variable in size with fine ridges perpendicular to the margin indicating incipient zooids (Fig. 2A, B). Autozooidal apertures arranged in uniserial rows of three to seven apertures, connate or non-connate, peristome unicuspidate, apertures more or less oval [73-**100**-111 (SD = 16; N = 5) x 119-**139**-158 µm diameter (SD = 15; N = 5)], variable in size, decreasing in diameter distally to the growing edge; surface smooth to slightly rugose, with some tiny pores and granules on the internal wall; apertures occasionally with a terminal diaphragm (Fig. 2B-D). Nanozooids absent. Kenozooids polygonal, often hexagonal, usually larger than autozooids [93-**149**-208 (SD = 37; N = 15) x 110-**145**-178 µm diameter (SD = 22; N = 15)], with granules on internal wall (Fig. 2 B-D). Gonozooid irregularly lobate (1.18 x 1.46 mm diameter), roof formed by an external wall perforated by numerous tiny pseudopores, bordered by a raised rim; ooeciostome simple, inclined slightly towards the centre of the gonozooid, exterior walled, located near the gonozooid border inside the pseudoporous roof (Fig. 2 A, E-F); ooeciopore subcircular (90 x 111 µm diameter).

Remarks: Recent *Favosipora* species are recorded, mainly from the Indian and Pacific oceans (Bock, 2024). Only a single fossil species, *F. ichnusae* Toscano & Taylor, 2008, is recorded from Europe, collected from lower Miocene sediments of Sardinia (Italy) (Toscano & Taylor, 2008). Souto *et al.* (2015) described for the first time a *Favosipora* species in the Atlantic Ocean (Madeira Island), *F. purpurea*. This species differs from the new one, *F. infrarockensis*, mainly by the ooeciostome situated near the outer margin of the gonozooid, the smaller diameter (79-**98**-126 µm) of the autozooidal apertures, which have bicuspidate peristomes, and kenozooids which are smaller in diameter (28-**45**-58 µm) and have numerous pinhead spinules on their interior walls.

The sole fossil Mediterranean species, *F. ichnusae*, has autozooids disposed biserially in alternating long rows of 13–14 autozooids, with smaller apertural diameter (70–111 µm), smaller kenozooids (80–110 µm diameter), and gonozooids lobate and elongated, parallel to the colony (or subcolony) perimeter (2 mm long by 0.5–1 mm wide).

The most similar species to *F. infrarockensis* Ramalho n. sp. is *F. tincta* Gordon & Taylor, 2001, described from New Zealand, and characterized by simple and circular colonies, autozooids arranged uniserially (sometimes partly biserially), kenozooidal apertures larger than the

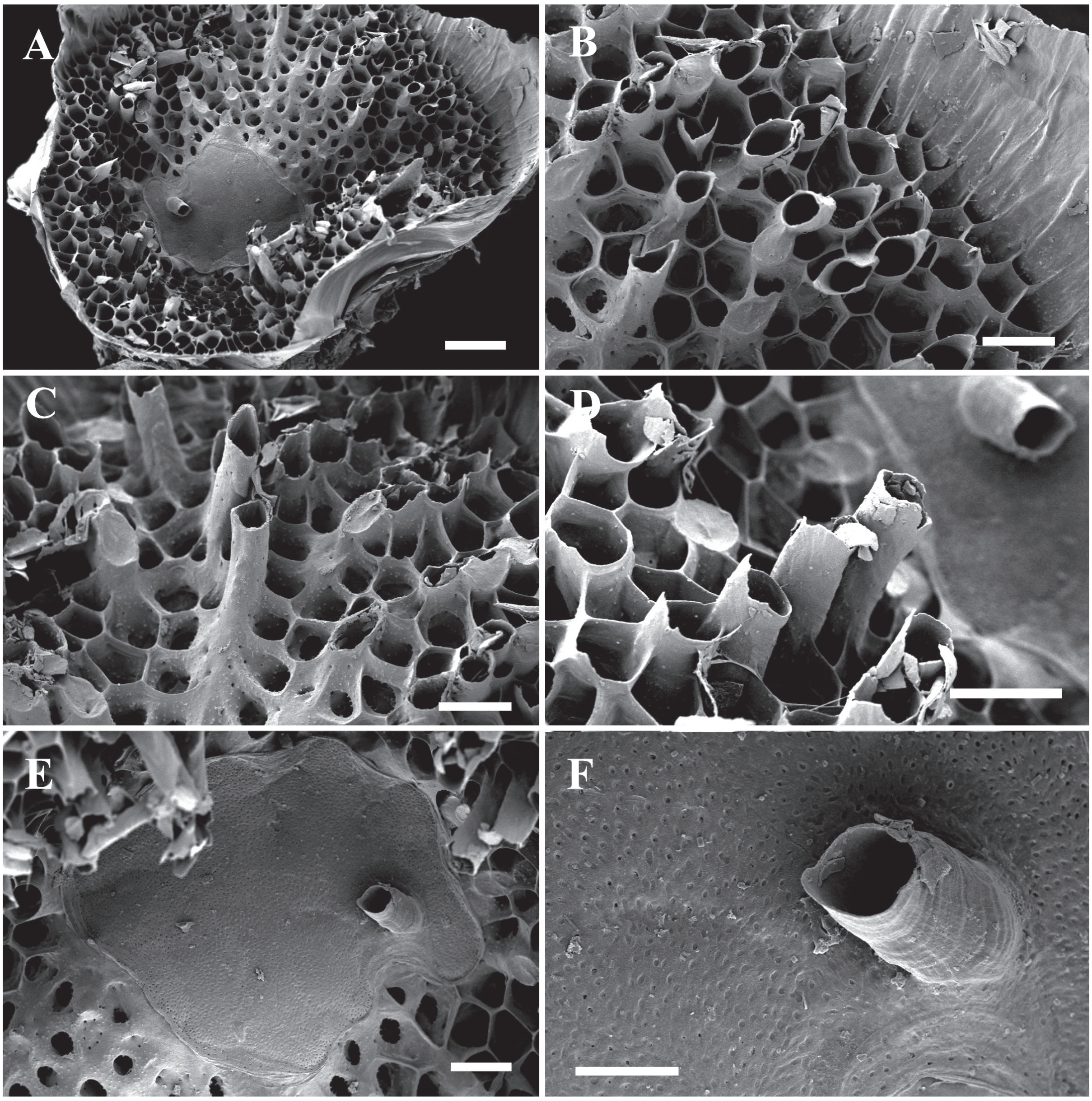

Fig. 2: *Favosipora infrarockensis* Ramalho, n. sp., holotype: MNCN 25.02/255. A., General view of the colony; B., detail of the marginal region of the colony showing autozooids, kenozooids (or alveoli), and edge of basal lamina; C., detail of some zooids and kenozooids; D., detail of some zooids near the gonozooid; E., general view of the gonozooid; F, detail of the ooeciostome and the gonozooid roof surface. Scale bars: 500 µm (A); 200 µm (B-E); 100 µm (F).

autozooidal aperture, gonozooid excentric, and nanozooids absent. But it differs in autozooidal aperture size (75–130 x 55–57 µm), rounded kenozooids with a somewhat different size (94–150 µm diameter), and ooeciostome slightly elevated with a smaller, slightly flared aperture (57–75 µm diameter).

Similarity between samples

Two groups of samples were identified through similarity (> 30% similarity, supported by SIMPROF tests) in multivariate analyses of the epibiont bryozoans found on *R. okamurae* (Fig. 3A). Group A corresponds to samples taken along the northern margin of the Strait of Gibraltar (Bolonia, Bajo Cabezos, Guadalmesí, and Punta Carnero), with no significant differences within groups (SIMPROF test: $\pi = 2.74$; $p = 0.149$). Group C corresponds to samples taken on the northeastern margin of the Strait of Gibraltar (Chullera and Placer de las Bóvedas), which formed a genuine cluster (SIMPROF test: $\pi = 0$; $p = 1$) that was significantly different from Group A (SIMPROF test: $\pi = 8.45$; $p = 0.001$). The sample taken from the southern margin of the Strait of Gibraltar (northern Africa), Ceuta, did not show similarity to either Group A or C (Fig.3A).

Taxon richness varied between the two groups. An ANOVA test revealed significant differences ($F_2 = 10.04$, $p = 0.02$) between groups A and C; samples clustered in Group A exhibiting the highest taxon richness (22.5 ± 4.65, mean ± SD) and those in Group C the lowest richness (6 ± 2.83) (Fig. 3B). The sample collected in Ceuta, with 15 species, showed an intermediate richness value. A total of 10 epibiont bryozoans were found exclusively in Group A (*A. anguina, C. boryi, Celleporella hyalina, C. decipiens, H. impressum, M. modesta, Patinella radiata, S. ambigua, S. chelata*, and *Turbicellepora avicularis*) and were frequently found in these samples (> 75%F). On the other hand, three species were exclusively collected at Ceuta (*C. serrata, M. delicatula,* and *Tubulipora* sp. 1). No exclusive taxa were found in Group C.

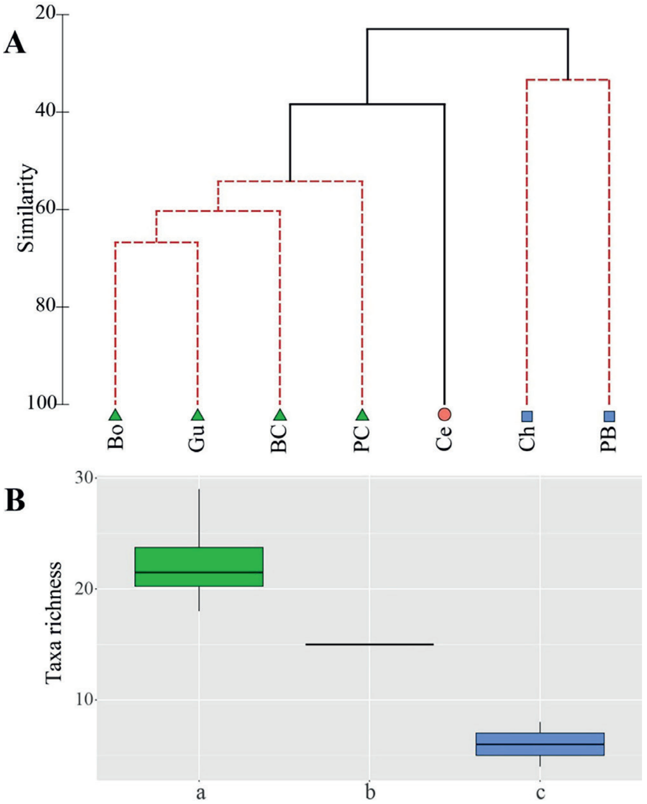

Fig. 3: A) Cluster analysis of samples based on the Jaccard similarity index. A SIMPROF test was conducted to determine significant differences ($p < 0.05$) between clusters/groups, marked by continuous lines. Samples: Bo, Bolonia; BC, Bajo Cabezos; Gu, Guadalmesí; PC, Punta Carnero; Ce, Ceuta; Ch, Chullera; PB, Placer de las Bóvedas. Samples were coded with a) green triangles (northern margin of the Strait of Gibraltar), b) red circles (southern margin of the Strait of Gibraltar), and c) blue squares (eastern margin of the Strait of Gibraltar). B) Box plot showing taxa richness for each group identified in panel A.

Biogeographic affinity of the bryozoan fauna

The bulk of the epibiont bryozoan taxa (35 species, 77.8% of the total) found on *R. okamurae* exhibited a wide distribution range along the Atlantic Ocean and the Mediterranean Sea. Twelve of these taxa (26.7% of the total) have a wide biogeographical distribution, inhabiting other seas. Sixteen species (34.8%) are also present in the Macaronesia archipelagos, including the Canary Islands, Madeira, and Azores (Table 2). Five species (11.1% of the total) reach boreal latitudes (Table 2). On the other hand, only eight species (15.6% of the total) are reported in the Mediterranean Sea but not in the Atlantic Ocean (*B. cylindrica, A. lepadiformis, T. ziczac, M. modesta, Savignyella lafontii, Chartella tenella, A. arcuata, C. mediterrenea*).

Affinity with the substrate

Twelve species (27.3 % of the total) were exclusively associated with plant substrates (seaweeds or seagrass leaves) (Table 2). The rest of the species did not show a very close (strict) preference for a given type of substrate, being able to adhere to rocky substrates (31.8%); to other sessile invertebrates such as sponges, ascidians, or even other larger bryozoans, or to bioclasts (calcareous structures of animal origin or calcareous algae) (43.2 %). In addition, 13 species (29.5%) are reported in the literature to colonize artificial substrates (Table 2).

Discussion

This study represents the first detailed analysis of the epibiont bryozoan fauna inhabiting the invasive Asian alga *R. okamurae* in the western Mediterranean Sea. The list of bryozoan species compiled here is surprisingly diverse, considering the extension of the sampling area (7 samples for a total of ca. 0.44 m^2) and the nature of the host substrate (an invasive macroalga). A total of 49 epibiont bryozoan taxa were associated with *R. okamurae*. These observations suggest that the richness of bryozoan species in infralittoral rocky habitats of the Strait of Gibraltar and adjacent areas might be higher if other types of habitats were taken into account, which makes this faunal group one of the most diverse in photophilic habitats within the study area. These species richness values are similar to those reported by Rosso *et al.* (2019) in central Mediterranean waters, where a total of 59 bryozoan species were found associated with native *Cystoseira* communities (a fucoid algae of high ecological value).

Although information on the diversity of bryozoan species associated with different habitats is very limited, a 2016 checklist of bryozoan species in the Mediterranean Sea includes 134 species in the biocenosis of infralittoral photophilic algae (Rosso & Di Martino, 2016). This observation suggests that, in the present study, over 36% of the known species inhabiting rocky photophilic infralittoral bottoms throughout the Mediterranean Sea basin were identified in a relatively small area dominated by an invasive alga. This highlights the ecological importance of the Strait of Gibraltar as a biodiversity hotspot, as has been previously documented for other faunal groups (Rueda *et al.*, 2021 and references therein), and the adaptability or opportunism/flexibility of some organisms (e.g. bryozoans) to colonise new surfaces provided by other organisms, in this case an invasive algal species (Jones & Thornber, 2010).

Since its introduction in the Strait of Gibraltar area, the invasion of *R. okamurae* along the southern coast of Spain and northern Morocco has involved the almost complete displacement of native macrophytes in the photophilic communities of rocky infralittoral bottoms, leading to the alteration of native habitats and a significant loss of biodiversity at the local scale (García-Gómez *et al.,* 2018, 2020). Regarding the epibiont fauna associated with macroalgae, various studies have attempted to analyse the ecological consequences of the alteration of algal communities resulting from biological invasions. However, there are no generalizations on how different faunal groups respond to such invasions (Thomsen *et al.,* 2014). The natural complexity of the ecosystem and the heterogeneity of the approaches considered in previous studies make it difficult to identify a general response pattern (Thomsen *et al.,* 2011). Some studies suggest that changes in epifauna associated with introduced macroalgae primarily affect abundance, rather than species composition, and strict host-symbiont associations are rarely observed (Viejo, 1999; Gestoso *et al.,* 2010; Mateo-Ramírez *et al.,* 2022). This was also observed by Navarro-Barranco *et al.* (2019) when analysing the invertebrates associated with native populations of *Dictyota dichotoma* and invasive populations of *R. okamurae* in Ceuta (southern Strait of Gibraltar).

This study was conducted within the monitoring program carried out for the Marine Strategy Framework Directive (Directive 2008/56/EC), and the oceanographic expeditions began in 2021, when the invasive alga *R. okamurae* had already colonized and transformed the infralittoral habitats around the Strait of Gibraltar. Therefore, there is no historical baseline before the invasion to analyse the potential effects on epibiont bryozoan communities. However, despite the lack of data on epifauna associated with native macroalgae, the results presented here show that epifaunal bryozoans have higher richness values compared to other invertebrate groups found in the same samples, such as molluscs or arthropods. Similarly, Borriglione *et al.* (2024) recently analysed the impact of *R. okamurae* on benthic communities along the Marseille coast; they observed an increase in copepod abundance in areas invaded by *R. okamurae*. This finding is attributed to the increase in algal biomass, which provides greater refuge from predators to meiofaunal organisms. Nevertheless, the high algal biomass could negatively impact species associated with the rocky substrate, such as polychaetes and sipunculids, through the dense canopy formed by the invasive *R. okamurae*. This canopy can alter water column parameters and sedimentation, reducing dissolved oxygen levels through algal respiration and the decomposition of algal detritus beneath the canopy (Borriglione *et al*., 2024).

Regardless of their taxonomic affiliation, herbivorous organisms tend to show a higher preference for native macrophytes (Gollan & Write*,* 2006; Monteiro *et al.,* 2009; Veiga *et al.,* 2018), possibly because of the coevolutionary relationship established with native epifauna. However, filter-feeders, detritus-feeders, and epibiont scavengers, which do not rely on algal hosts for food, may be favored by the availability of a new substrate, as it reduces grazing pressure (Jumars *et al.,* 2015; Veiga *et al.,* 2018). It has been hypothesised that the presence of defensive chemicals, common in invasive macrophytes (Máximo *et al.,* 2018), could contribute to the protection of epifaunal organisms against their predators (Hay *et al.,* 1990) and may favor certain epibiont invertebrates (Veiga *et al.,* 2018; Navarro-Barranco *et al.,* 2019). In line with this hypothesis, six secondary metabolites have been isolated from *R. okamurae* individuals sampled in the Strait of Gibraltar area; the compound dilkamural stands out among them due to its high concentration (Casal-Porras *et al*., 2021). Casal-Porras *et al.* (2021) observed that dilkamural not only had deterrent properties but also caused harmful and even lethal effects on the generalist native herbivore *Paracentrotus lividus* (Lamarck, 1816) in a set of feeding deterrent assays. Based on these observations, the authors suggested that the high invasive capacity of *R. okamurae* in the Strait of Gibraltar and adjacent areas could be favoured by this chemical weapon, as dilkamural has not been described previously here and has a defensive role against generalist herbivores in the invaded area. The deterrent capacity of dilkamural may promote the high richness observed for epibiont bryozoans, as it may reduce herbivore and predator pressure on the algal substrate. This information should be treated with caution, as it has not been possible to compare the composition and structure of current epibiont bryozoans with that of native algal communities before the invasion.

The interaction between bryozoans and macrophytes can vary between different hosts and epibionts. For some macrophytes, this interaction may provide a beneficial effect, such as the supply of CO_2 for photosynthesis (Mercado *et al.,* 1998), while for others it may have a negative impact, including defoliation and reduction of incident light (Muñoz *et al*., 1991; Saunders & Metaxas, 2008). Consequently, some macrophytes have developed antifouling mechanisms including mechanical inhibition, through cuticle peeling (i.e. the algae sloughs off the outermost cell layer to remove the associated epibiota) (Nylund & Pavia, 2005), and chemical inhibition by antifouling secondary metabolites (furanones) placed on the surface of some algae that deter the settlement and growth of many fouling organisms (Dworjanyn *et al.,* 2006).

Previous studies focusing on the interactions between epiphytic bryozoans and macrophytes with varying levels of structural complexity have concluded that changes in the composition of algal species alter the dominance patterns within coastal epifaunal communities and impact ecosystem functions (Liuzzi & Gappa, 2011; Saarinen *et al.,* 2018). However, few algal species appear to be essential for the survival of a specific taxon or functional group of epifauna, suggesting that other algal species may partially compensate for habitat degradation and loss (Bates & DeWreede, 2007; Liuzzi & Gappa, 2011). Furthermore, Liuzzi & Gappa (2011) found significant differences between bryozoan colony morphotypes and algal structural groups. Encrusting and multiserial bryozoan colonies were more frequent in foliose algae, which are a suitable substrate for approximately circular colonies. In contrast, runner species (i.e., uniserial stolons) were epibionts characteristic of filamentous algae. These conclusions are in line with our observations, as most epibionts and the most frequent taxa on the fronds of the foliose *R. okamurae* were multiserial encrusting species.

The high species richness of epibionts attached to an invasive algal host makes this area worth considering as a biodiversity hotspot for this faunal group. These assemblages include species with a wide biogeographical distribution, species restricted to the Mediterranean Sea, and endemic species restricted to the Strait of Gibraltar. The strategic location of the Strait of Gibraltar between the Atlantic Ocean and the Mediterranean Sea, and the proximity of the African and European biotic regions, facilitate the convergence of species with different distribution patterns (Ekman, 1953; Caballero-Herrera *et al.,* 2022). This biogeographical trend resembles that seen in molluscs from other coastal and circalittoral habitats in the Alboran Sea (Rueda *et al.*, 2009, Urra *et al.,* 2017, Caballero-Herrera *et al.*, 2023).

Bicrisia gibraltarensis was originally described based on material collected from the Strait of Gibraltar and the Gulf of Cádiz at depths ranging from 120 to 526 meters (Harmelin, 1990). Since its original description, no new records or areas of occurrence had been documented (Harmelin & d'Hondt, 1992b, 1993) until the present study. Harmelin & d'Hondt (1993) reported that this species does not extend beyond the Strait of Gibraltar area, despite being found in an area influenced by the Atlantic Ocean current entering the Mediterranean Sea. Similarly, in the present study, *B. gibraltarensis* was only found in Bajo Cabezos, which could reinforce its endemism in this area. On the other hand, *B. gibraltarensis* has been reported as a deep-water species (Harmelin & d'Hondt, 1992b); however, in our case, all colonies were collected at a depth of 10 meters. All colonies were alive, and most of them were fertile, indicating that they are adapted to this depth. The difference in depth between the original population and the present record raises some important questions about the similarity between both populations and the difficulty in finding this species (is it restricted to the Gibraltar area? Is it a rare species?). Further analyses of new samples collected in the area and detailed molecular studies could help to answer these questions.

Another important contribution of the present study is the observation of *C. serrata* in the Strait of Gibraltar area, as it is a species native to the Indo-Pacific Ocean (Australia) and considered non-indigenous in the Mediterranean Sea with records from Italy, Greece, and Spain (Catalonia) (Zabala, 1986; Chimenez Gusso *et al.*, 2014; Gerovasileiou & Rosso, 2016, and the references therein; Zenetos *et al.*, 2018; Servello *et al.,* 2019). In the present study, *C. serrata* was found only in Ceuta, which extends its reported geographical distribution. The fact that only one infertile colony was found could indicate 1) a recent and punctual introduction, or 2) that this species has been colonizing the area using a substrate other than *R. okamurae*. To answer this question, new samples collected on different substrates should be analysed, and monitoring of the area surrounding the location of the Ceuta sample and the commercial harbour (with a route connecting Ceuta, Barcelona, and Italy by ferry) should be carried out to confirm this possible introduction.

Our study also contributes to our knowledge on the genus *Favosipora*, with the description of a new species (*F. infrarockensis* n. sp., Fig. 2) that has been found only at Bajo Cabezos, a rocky outcrop located off the coast of Punta Paloma (10 km west of Tarifa island). Similarly, to *C. serrata*, only one colony was found growing on the fronds of *R. okamurae*. The frequent lack of gonozooids or other brood chambers impedes the determination of some families and genera of Cyclostomatida. When in an infertile form, *Favosipora* can be mistaken for other genera such as *Patinella*, *Disporella,* or *Lichenopora* (Gordon & Taylor, 2001), especially when observed by non-specialists. Previous studies have reported species belonging to *Favosipora* colonising substrates such as rocks, pebbles, undersides of boulders, and fragments of bivalve shells (Taylor & Grischenko, 2015; Souto *et al*., 2015). Thus, before considering *F. infrarockensis* a rare species, or a species restricted to only one sample, new samples must be analysed, as this species may prefer other substrates.

Multivariate analysis revealed a spatial continuity in sample similarity across the Strait of Gibraltar, with four samples from the northern sector of the Strait of Gibraltar clustering together and two other samples located further northeast forming a second group. The single sample collected from the southern sector of the Strait of Gibraltar fell outside these two groups. The diversity of epibiont bryozoans varied greatly between the samples, with the highest values found at the northern sector of the Strait of Gibraltar and the lowest at the northeastern one, which also exhibited lower biomass values of *R. okamurae* per sampled area. Notably, the sample from Placer de las Bóvedas was collected slightly deeper (ca. 20 m depth) than the other samples (ca. 11 m depth). The rocky bottom at Chullera, despite being colonized by *R. okamurae*, was characterized by high turbidity with strong currents and a dense population of gorgonians such as *Eunicella singularis* and *Leptogorgia sarmentosa.* These spatial variations in epibiont bryozoans could also be attributed to differences in the age of algal populations across locations, particularly in annual species such as *R. okamurae*, which cause periodic shifts in space availability for epifauna. In fact, fronds collected from the same sample exhibited different degrees of colonization, with some fronds being fully covered by bryozoans and others completely bare. This is in line with observations by Seed & O'Connor (1981), who noted that the large surface area of macroalgae creates microhabitat gradients, allowing for fine-scale variability in colonization by small invertebrates.

Long-term monitoring programmes, such as those performed in Spanish waters within the Marine Strategy Framework Directive (Directive 2008/56/EC) for the evaluation of habitats and associated biological communities, are crucial in the current context of climate change, habitat degradation and the invasion of non-native species, as they allow the tracking of variations in animal populations and their behaviour as a result of these environmental challenges. Climate change leads to alterations in the migratory, breeding, and distribution patterns of many species, while habitat degradation threatens the survival of countless ecosystems. In turn, non-native species (such as *R. okamurae*) can displace or compete with local species and disrupt trophic interactions, upsetting the natural balance of ecosystems in highly biodiverse areas such as the Alboran Sea basin (García-Gómez *et al*., 2020; Borriglione *et al*., 2024). In this context, microfaunal analysis and laboratory sorting are essential in order to obtain a complete assessment of species richness and diversity, as previously reported by Albano *et al.* (2011) and Gofas *et al.* (2014). Most of this fauna would be overlooked if the assessment were based only on mega and macro-fauna, easily sampled by visual census or limited to shipboard observations. These programs thus provide essential scientific data to identify long-term trends, playing a critical role in understanding ecological shifts and supporting evidence-based conservation policies within dynamic marine ecosystems.

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Supplementary Data

The following supplementary information is available online for the article:
New Records of bryozoans for the Alboran Sea and the area of the Strait of Gibraltar Spanish marine subdivisions, Spanish and Mediterranean waters found epiphytizing fronds of the invasive Asian alga *Rugulopteryx okamurae* in the Strait of Gibraltar, updated descriptions and ecology, biogeographical distribution and taxonomic remarks.