diversity

MDPI

Article

Spatial Distribution and Potential Impact of Drifted Thalli of the Invasive Alga *Rugulopteryx okamurae* in Circalittoral and Bathyal Habitats of the Northern Strait of Gibraltar and the Alboran Sea

José L. Rueda [1,*], Ana Mena-Torres [1], Marina Gallardo-Núñez [1], Emilio González-García [1], Alejandro Martín-Arjona [1], Javier Valenzuela [1], Cristina García-Ruiz [1], María González-Aguilar [1], Ángel Mateo-Ramírez [1], Marga García [2], Miriam Sayago-Gil [2] and Juan Tomás Vázquez [1]

1 Oceanographic Centre of Málaga (Centro Oceanográfico de Málaga), Instituto Español de Oceanografía—CSIC, Puerto Pesquero s/n, 29640 Fuengirola, Spain; ana.mena@ieo.csic.es (A.M.-T.); marina.gallardo@ieo.csic.es (M.G.-N.); emilio.gonzalez@ieo.csic.es (E.G.-G.); alejandro.martin@ieo.csic.es (A.M.-A.); javiervalenzuelajimenez@hotmail.com (J.V.); cristina.garcia@ieo.csic.es (C.G.-R.); maria.gonzalez@ieo.csic.es (M.G.-A.); angel.mateo@ieo.csic.es (Á.M.-R.); juantomas.vazquez@ieo.csic.es (J.T.V.)

2 Oceanographic Centre of Cádiz (Centro Oceanográfico de Cádiz), Instituto Español de Oceanografía—CSIC, MuellePesquero S/N, 11006 Cádiz, Spain; marga.garcia@ieo.csic.es (M.G.); miriam.sayago@ieo.csic.es (M.S.-G.)

* Correspondence: jose.rueda@ieo.csic.es

check for updates

Citation: Rueda, J.L.; Mena-Torres, A.; Gallardo-Núñez, M.; González-García, E.; Martín-Arjona, A.; Valenzuela, J.; García-Ruiz, C.; González-Aguilar, M.; Mateo-Ramírez, Á.; García, M.; et al. Spatial Distribution and Potential Impact of Drifted Thalli of the Invasive Alga *Rugulopteryx okamurae* in Circalittoral and Bathyal Habitats of the Northern Strait of Gibraltar and the Alboran Sea. *Diversity* **2023**, *15*, 1206. https://doi.org/10.3390/d15121206

Academic Editor: Juan J. Vergara

Received: 29 September 2023
Revised: 17 November 2023
Accepted: 29 November 2023
Published: 7 December 2023

Abstract: The arrival of a new invasive alga, *Rugulopteryx okamurae*, in the Strait of Gibraltar (SoG) in 2015 marked an unprecedented milestone in the North African and, later, in the European marine ecosystems. Nowadays, it is colonising vast infralittoral areas and significantly modifying some habitats and associated communities of the southern Iberian Peninsula. In recent expeditions, a high amount of free drifted thalli of this alga has been detected in different circalittoral and bathyal habitats of the northern SoG and the Alboran Sea. The present study combines quantitative data of this alga obtained with the use of a remotely operated vehicle (ROV) and a bottom otter trawl. The coverage–entanglement level of the drifted thalli on circalittoral and bathyal benthic invertebrates (e.g., not covering, covering only the basal part, covering one-third of the invertebrate, etc.) was also annotated from picture frames taken in locations with abundant drifted thalli. In underwater images, drifted thalli were mainly detected in circalittoral and bathyal bottoms of the northern SoG and the north-western Alboran Sea, between 50 to ca. 450 m depth. Nevertheless, abundant drifted thalli were also detected in bottom otter trawl samples from circalittoral bottoms of the north-central and north-eastern Alboran Sea. Small benthic organisms (e.g., encrusting sponges, hydrozoans, etc.) generally displayed low coverage–entanglement levels of drifted thalli. Nevertheless, large sessile and colonial benthic organisms with a complex three-dimensional morphology (e.g., gorgonians, colonial scleractinians) reached high levels of *R. okamurae* thalli entangled in different parts of their colonies. The drifted *R. okamurae* thalli entangled in these colonial suspension feeding organisms may hinder their feeding capability in the long term, resulting in habitat deterioration in the near future.

Keywords: benthic invertebrates; alien species; invasive species; drifted algae; Mediterranean Sea; coverage; biomass

1. Introduction

The Strait of Gibraltar (SoG) and the Alboran Sea represent areas of oceanographic and biological confluence, which are located between the Mediterranean Sea and the Atlantic Ocean [1–3]. This sector of the Western Mediterranean Sea presents complex submarine geomorphology, with a high diversity of habitats, species (including a wide variety of threatened ones), and commercially exploited marine resources [1,2,4–6]. Unfortunately, it is also an area exposed to high anthropogenic pressures, harbouring widely urbanized coastal areas, intense maritime traffic, and high activity of industrial and artisanal fishing fleets, which require complex spatial and temporal management.

In 2015, the arrival of a new alien and highly invasive alga, *Rugulopteryx okamurae* (E.Y. Dawson), to the SoG marked an unprecedented milestone in North African and European marine ecosystems [7–13]. From 2015 to date, *R. okamurae* has colonised most of the infralittoral rocky bottoms (5–30 m deep) of the SoG and is currently expanding towards adjacent Atlantic and Mediterranean coastal areas, including the southern and eastern Iberian Peninsula [14,15], southern Portugal [16], north Africa [17] and some Macaronesian Islands (e.g., Madeira, Azores Islands) [18,19], where it is currently modifying the infralittoral habitats and associated communities. In Europe, this alga was firstly detected in 2002 in the Thau lagoon (southern France), but it became highly dominant along the Marseille coasts during 2018–2020 [20,21]. The great invasive capacity of *R. okamurae* is enhanced by its dispersion pathway (through unattached thalli–free drifted thalli), prolific vegetative reproduction, and high survival in adverse environmental conditions [9,10,22]. Moreover, the very high productivity of this alga is transported via drifted thalli that can accumulate on beaches, rocks, or other hard substrates, and may generate a significant impact on human socioeconomic activities, tourism, and, of course, on marine habitats, not just where the algae develop but also in adjacent coastal locations (Figure 1). In the case of the invasion of *R. okamurae*, its high vegetative growth can sometimes lead to the algae covering 80–100% of the infralittoral and shallow circalittoral bottoms of the SoG and the Alboran Sea, which unfortunately results in (1) a regression of many native algae and invertebrate species and (2) the reduction in the typical benthic heterogeneity of infralittoral rocky coasts [11,12,14]. Moreover, large amounts of detached thalli can be transported by the currents (drifted thalli) not just to the shores but also to deep areas, where they can cause a negative impact on some fragile habitat-forming species (e.g., the bamboo coral *Isidella elongata*) [22].

This study documents for the first time the massive presence of drifted *R. okamurae* thalli in the deep circalittoral and bathyal bottoms of the northern SoG and the Alboran Sea. The drifted thalli seem to be transported and dispersed by bottom currents as already documented in the nearby Gulf of Cádiz [22]. In this new study, the potential impact that the drifted thalli may have on different habitat-structuring/forming species of circalittoral and bathyal habitats has been based on the coverage–entanglement of the drifted thalli on those sessile organisms. The main aims of the present study are (1) to detect and quantify the accumulations of drifted thalli of *R. okamurae* on the shelf and slope of the northern SoG and the Alboran Sea and (2) to study the interaction of drifted thalli of *R. okamurae* with habitat-structuring/forming species of circalittoral and bathyal bottoms in this area of transition between the Atlantic Ocean and the Mediterranean Sea. The starting hypothesis is that the drifted thalli may be abundant in deepareas close to infralittoral areas colonised by this alga, and that the coverage–entanglement by the drifted thalli will be higher in large and three-dimensionally complex organisms. The importance of the present study is to document the potential impact that this new biological threat can generate not only in infralittoral habitats, but also in circalittoral and bathyal habitats to undertake rapid actions that may serve to improve knowledge of those deep-sea areas and species mostly affected by this invasive alga and/or implement actions for documenting and mitigating this impact in the near future.

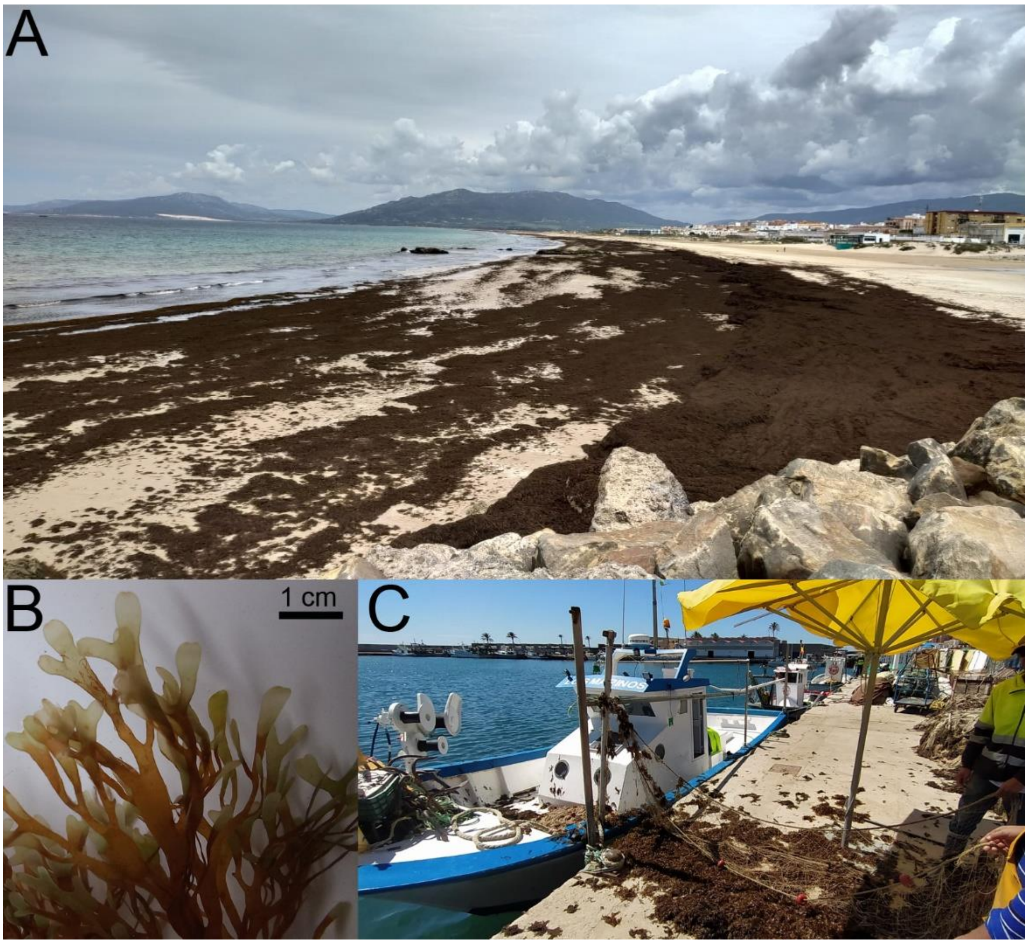

Figure 1. (**A**) Massive accumulation of drifted thalli of the invasive alga *Rugulopteryxokamurae* on *Los Lances* beach (Tarifa, Cádiz) in the northern part of the Strait of Gibraltar (photo taken by Luis Miguel Fernández-Salas). (**B**) Detail of a drifted thalli of *R. okamurae* collected off Calaburras (Málaga) in the northern Alboran Sea (36.4791 N, 4.6461 W) (scale: 1 cm) (photo taken by José L. Rueda). (**C**) Cleaning of fishing nets covered with entangled drifted thalli of *R. okamurae* at the fishing harbour of Fuengirola (Málaga) (photo taken by Ángel Mateo Ramirez).

2. Materials and Methods

Data on presence, coverage, and biomass of *Rugulopteryx okamurae* in Spanish waters of the northern margin of the Strait of Gibraltar (SoG) and the Alboran Sea have been obtained during different expeditions carried out by Instituto Español de Oceanografía—CSIC. The first one was the CIRCAESAL 0721 expedition carried out between July and August 2021, with the aim of assessing the health status of the circalittoral and bathyal benthic habitats of this basin. The CIRCAESAL 0721 expedition was carried out within the framework of the Marine Strategy Framework Directive (Directive 2008/56/CE) and the monitoring activities of circalittoral and bathyal benthic habitats under the Descriptor 1 (Biodiversity) and Descriptor 6 (Seabed). During the CIRCAESAL 0721 expedition, 35 transects of underwater imageswere obtained with a remotely operated vehicle (ROV) and an underwater camera sled (UCS) in 14 sectors of the northern SoG and the Alboran Sea (Figure 2, Table S1). Several of these transects were located in Marine Protected Areas (from the Natura 2000 Network or Marine Reserves—e.g., the insular shelf of the Alboran Ridge) while others where located in areas with a moderate-high degree of anthropic and fishing pressure (e.g., Bay of Málaga). High-resolution and georeferenced underwater images obtained with these two devices were analysed for identifying and quantifying key benthic and demersal species, drifted thalli of *R. okamurae*, and substrate types. The underwater images were obtained with high-precision submarine navigation using a HiPAP device, being captured between 0.5 and 2.5 m from the seafloor, during ca. 1–8 h transects. The mean distances explored were ca. 2000 m for ROV transects and ca. 1000 m for UCS transects at depths between 17 and 718 m. Some of the biological (e.g., colonies, organisms) and seafloor characteristics observed in each transect could be measured using laser pointers for scaling (with 10 cm separation in both ROV and TASIFE). In photo frames along the underwater image transects, coverage measurements (%) of drifted thalli of *R. okamurae* on the seabed were taken by using the grid option in the software ImageJ and counting those grids where the drifted thalli were present (Figure S1).

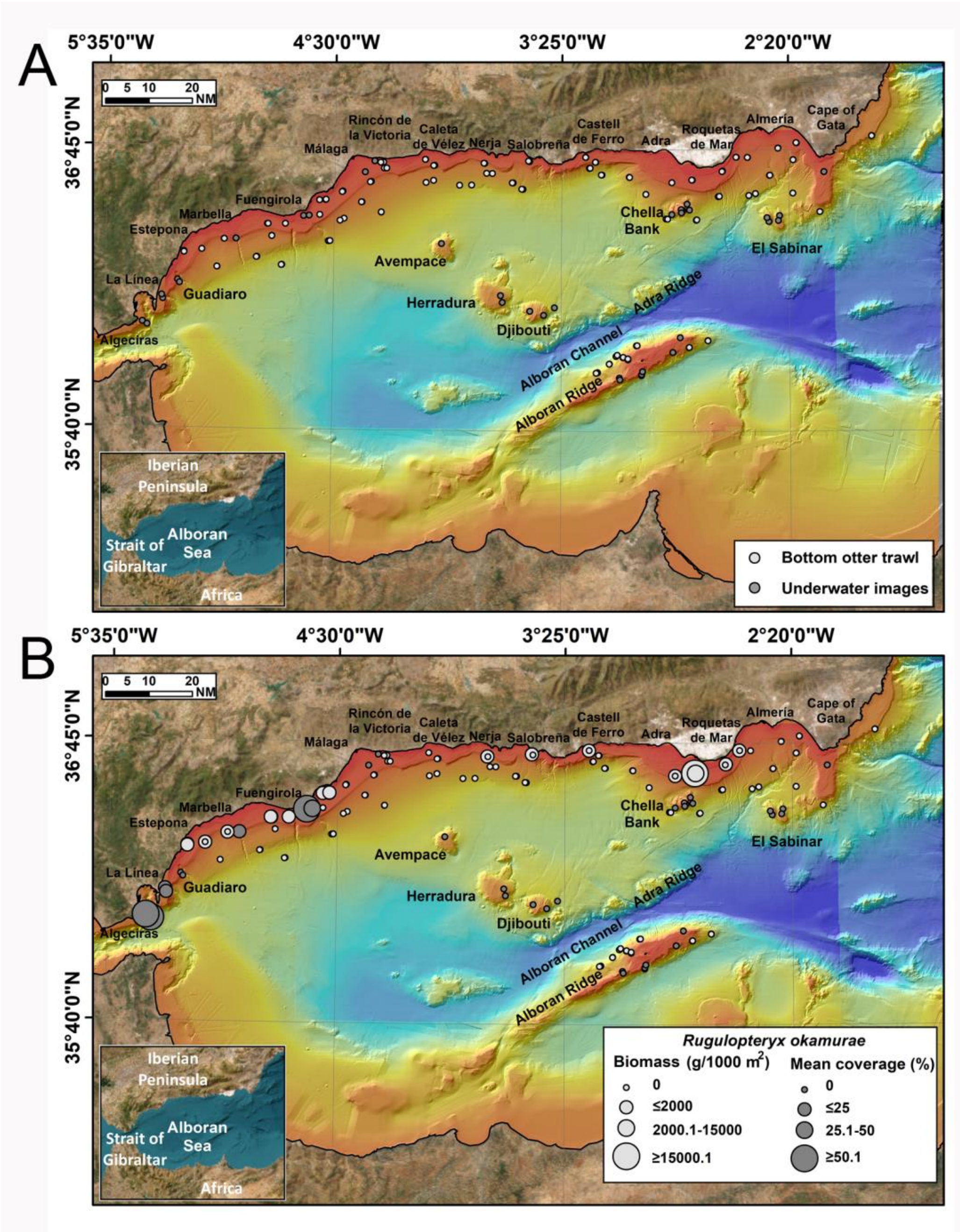

Figure 2. (**A**) Location of bottom trawl samples obtained during the MEDITS expeditions (white circles) and underwater image transects obtained with the ROV LIROPUS 2000 and UCS TASIFE during the CIRCAESAL 0721 expedition (grey circles) in the northern Strait of Gibraltar and the Alboran Sea. Detailed positioning data of each sample and transect are listed in Tables S1 and S2

(Supplementary Materials). (**B**) Biomass (g/1000 m^2) (white circles) and mean coverage (%) (grey circles) of drifted thalli of *Rugulopteryx okamurae* detected in bottom otter trawl samples and underwater images, respectively, in different circalittoral and bathyal areas of the northern Strait of Gibraltar and the Alboran Sea. Size of the circle denotes increasing biomass and coverage of drifted thalli, with the smallest circles indicating absence of drifted thalli in the sample or underwater image transects (below).

Additional data on the distribution of drifted thalli of *R. okamurae* in circalittoral and bathyal bottoms of the northern SoG and the Alboran Sea was obtained from several MEDITS surveys (International Bottom Trawl Surveys in the Mediterranean) carried out in spring from 2016 to 2023 (Figure 2). Haul duration was determined as a function of depth, with 30 min hauls for those stations located <200 m depth (mostly continental shelf) and 60 min hauls for those located at depths greater than 200 m (continental slope) [23]. The geographical position of each haul was recorded using a global positioning system device. A GOC-73 bottom trawl (average horizontal opening: 21.5 m; average vertical opening: 2.5 m; cod end mesh size: 20 mm) was used for collecting the samples [24]. Thalli of *R. okamurae* were separated from other collected organisms and weighed (i.e., wet weight) on board. Finally, biomass data was standardised to grams per 1000 m^2.

For studying the interaction of the drifted thalli of *R. okamurae* with some key benthic organisms (e.g., habitat-forming species, dominant species) of circalittoral and bathyal bottoms, each organism was identified to the lowest possible taxonomic level. In some cases, when the organisms could not be identified to species or genus level (e.g., encrusting sponges, hydrozoans, globular bryozoan, etc.), then they were treated as operational taxonomic units (OTUs) (as commonly done in underwater imagery studies) because the identification in underwater images is generally complex ([25] and references therein). Although the designation of OTUs in genetics is related to taxa that share the same type of genetic code, in this study the designation of OTUs was based on morphological and colour features that sometimes even different species may share. In several cases, the identification of some organisms to species and genus level was possible from samples collected with the ROV sampling device in the same locations during this expedition and in adjacent areas in previous expeditions using rock dredges. In some cases, the same OTU (e.g., encrusting sponges) may contain different species and, on the contrary, phenotypes of the same species could occasionally have been assigned to different OTUs and/or species, but this is a common problem when analysing underwater images. For this reason, some analyses were later based on the biological traits of those species and OTUs in order to know which groups, forms, and sizes of organisms could be more vulnerable to drifted thalli covering–entangling on their colonies. Drifted thalli of *R. okamurae* and other organisms collected have been deposited in the biological reference collection of the Centro Oceanográfico de Málaga (Oceanographic Centre of Málaga) from Instituto Español de Oceanografía—CSIC.

Interaction data of drifted thalli of *R. okamurae* with the OTUs was taken in photo frames (taken 1–2 m from the seabed) along the underwater image transects. During the quantification of OTUs, the abundance of individuals and colonies was annotated with respect to the different coverage–entanglement levels of *R. okamurae* drifted thalli as follows: (A) absence of *R. okamurae* drifted thalli on such OTU–species; (B) presence of *R. okamurae* drifted thalli just in the basal part of the individual–colony of each OTU-species; (C) presence of *R. okamurae* drifted thalli in less than 1/3 of the individual–colony; (D) presence of *R. okamurae* drifted thalli between 1/3 and 2/3 of the individual–colony; (E) presence of *R. okamurae* drifted thalli between 2/3 and 3/3 of the individual–colony; (F) total coverage of *R. okamurae* drifted thalli in the individual–colony.

With the data obtained, the densities of individuals and colonies with each level of coverage–entanglement in each OTU were estimated per square metre and also as percentage of individuals of each level within each OTU, with the aim of finding which OTUs displayed the maximum levels of coverage–entanglement of drifted thalli. Moreover, four biological traits of the top dominant OTUs were considered in order to know which ones were mainly related to the amount of detached thalli of *R. okamurae* that hook to the OTUs. In this sense, a one-way PERMANOVA was used for testing each biological trait based on the Bray–Curtis similarity index and using square root transformed data of the abundance of the top-dominant OTUs in relation to the different coverage–entangling levels by *R. okamurae* drifted thalli, in order to achieve homogeneity in the variance. Biological traits were analysed as fixed factors and included (1) *benthic position* with 3 levels: surface, 2–20 cm height from the seabed, and >20 cm; (2) *body form* with 4 levels: flattened, globulose, erect but not branched, and erect and branched; (3) *size* with 4 levels: small (<2 cm), medium (2–10 cm), medium-large (>10 and <50 cm), and large (>50 cm); and (4) *flexibility* with 3 levels: none, low (between 10° and 45°), and high (>45°). Levels of biological traits were similar to those used by [26]. Finally, principal component analysis (PCA) was performed to graphically explore differences between OTUs in relation to the quantity of *R. okamurae* drifted thalli covering–entangling on them and the relationships of the different biological traits considered. Multivariate routines were implemented in PRIMER 6.0 + PERMANOVA [27].

3. Results

The alien and invasive alga *Rugulopteryx okamurae* was extensively detected in circalittoral and bathyal bottoms of the northern Strait of Gibraltar (SoG) and the Alboran Sea as drifted detached thalli that sometimes were heavily entangled in some benthic sessile invertebrates (Figures 2–5). In the underwater images, drifted thalli were mainly detected in the northern SoG (Algeciras and La Línea) and the north-western Alboran Sea (Calaburras) at depths between 40 (Calaburras) and ca. 400 m (Algeciras Submarine Canyon) (Figure 2). The mean coverage of *R. okamurae* drifted thalli was moderate-high in Calaburras (42.7–65.6%) and Algeciras Submarine Canyon (54.6–57.8%), and moderate-low in La Línea (4.0–5.8%) and Placer de las Bóvedas (3.8%). Drifted thalli of this alga were also detected in several samples from the MEDITS expedition otter trawls in the north-western Alboran Sea (from Estepona to Fuengirola) and the north-central and north-eastern Alboran Sea (from Nerja to Roquetas de Mar), but always in continental shelf locations (depth < 120 m) (Figure 2). In general, accumulations of drifted thalli were detected in both underwater images and bottom trawl samples in the north-western part of the Alboran Sea, but not in the north-eastern part of the Alboran Sea, where only the bottom trawl samples displayed presence of drifted thalli. Biomass of drifted thalli of *R. okamurae* collected in otter trawls was high in Punta Entinas (14,049–40,128.5 g/1000 m^2), moderate in Fuengirola, Castell de Ferro, and Roquetas de Mar (1319.0–1766.6 g/1000 m^2), and low in Estepona and Marbella (7.8–75.5 g/1000 m^2). No drifted thalli of *R. okamurae* were detected in the circalittoral or bathyal bottoms of the Alboran Ridge and the banks of Avempace, La Herradura, Ville of Djibouti, El Sabinar, and Chella, among others. It is important to highlight the absence of drifted thalli of this invasive alga on the insular shelf bordering the Alboran Island (Alboran Ridge), where a large number of vulnerable benthic habitats and species occur.

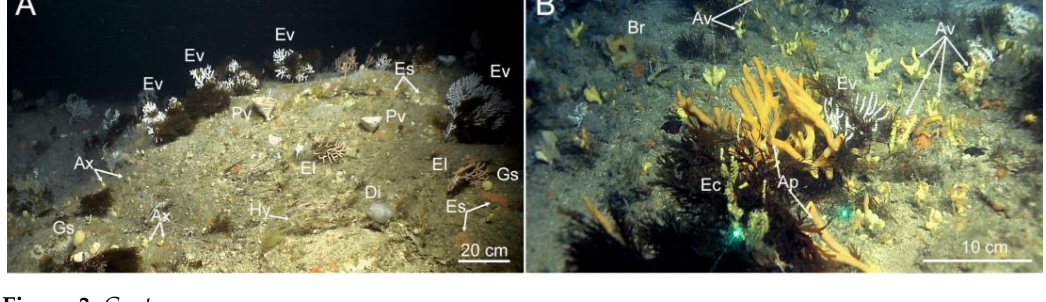

Figure 3. *Cont.*

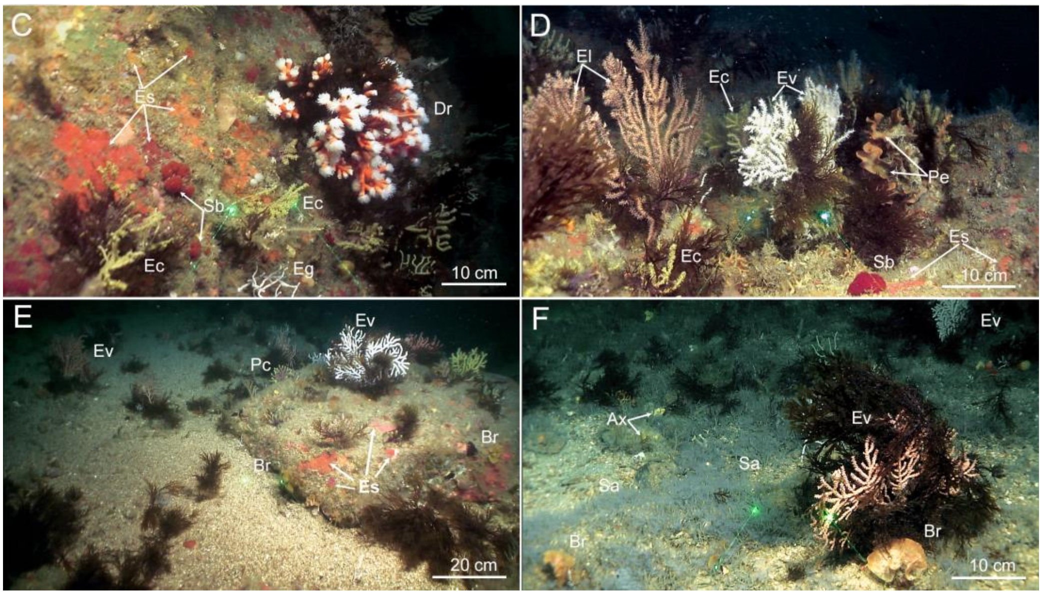

Figure 3. Drifted thalli of *Rugulopteryx okamurae* on some circalittoral habitats from hard (**A**–**D**) and mixed bottoms (**E**–**F**) in the northern Strait of Gibraltar and the Alboran Sea displaying different levels of coverage–entanglement on key benthic organisms. Ap: *Axinella polypoides*; Ax: *Axinellidae*; Av: *Axinella verrucosa*; Br: Bryozoan; Di: *Diazona* sp.; Dr: *Dendrophyllia ramea*; Ec: *Eunicella cavolini*; Eg: *Eunicella gazella*; El: *Eunicella labiata*; Es: Encrusting sponges; Ev: *Eunicella verrucosa*; Gs: Globular sponges; Pc: *Paramuricea clavata*; Pv: *Phakellia ventilabrum*; Sa: Sabellidae; Sb: *Synoicum blochmanni*.

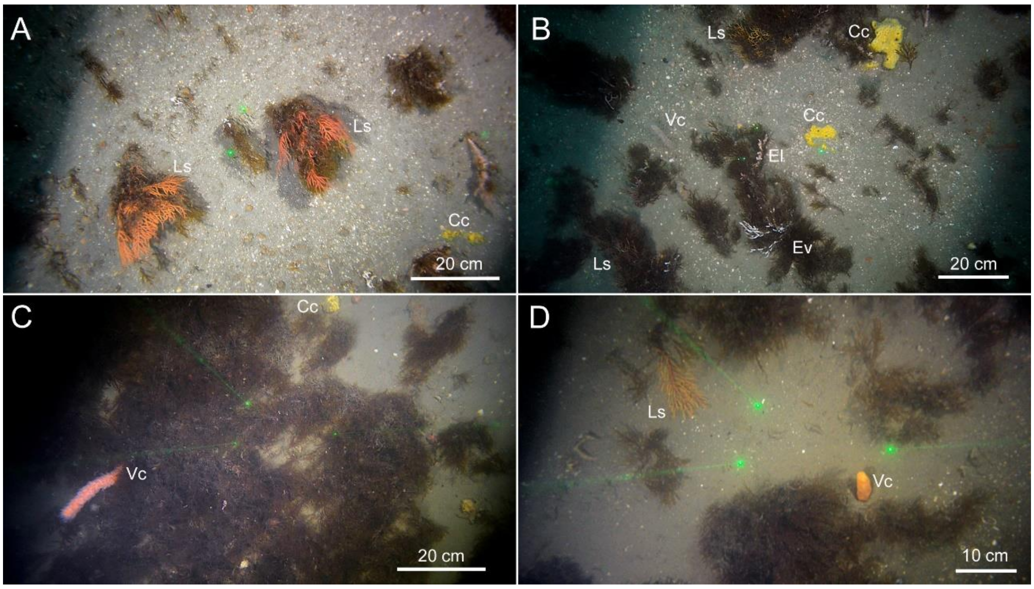

Figure 4. Drifted thalli of *Rugulopteryx okamurae* on some circalittoral habitats with gorgonians (**A**), sponges (**B**) and sea-pens (**C**,**D**) in the northern Strait of Gibraltar and the Alboran Sea displaying different levels of coverage–entanglement on those key benthic organisms. Cc: *Cliona celata*; El: *Eunicella labiata*; Ev: *Eunicella verrucosa*; Ls: *Leptogorgia sarmentosa*; Vc: *Veretillum cynomorium*.

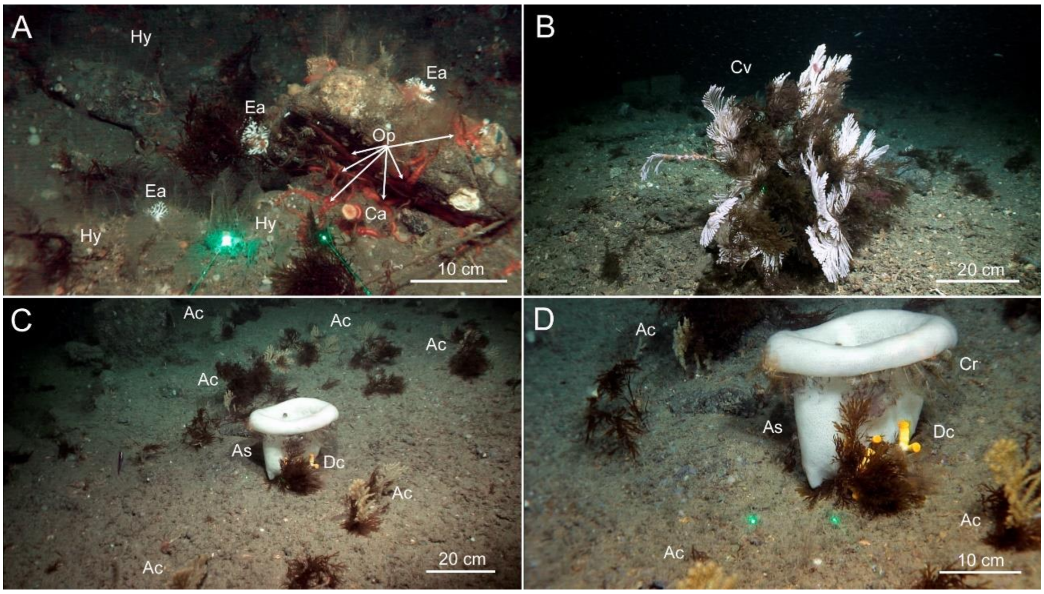

Figure 5. Drifted thalli of *Rugulopteryx okamurae* on some bathyal habitats with solitary scleractinians and hydrozoans (**A**), large gorgonians (**B**) and large sponges (**C**,**D**) in the northern Strait of Gibraltar and the Alboran Sea displaying different levels of coverage–entanglement on those key benthic organisms. Ac: *Acanthogorgia* spp.; As: *Asconema setubalense*; Ca: *Caryophyllia* spp.; Cr: Crinoids; Cv: *Callogorgia verticillata*; Dc: *Dendrophyllia cornigera*; Ea: *Errina aspera*; Hy: Hydrozoans; Op: *Ophiothrix* spp.

In underwater images, drifted thalli of *R. okamurae* were detected on some individuals and colonies of different species and OTUs, and displaying different coverage–entanglement levels (Figures 3–8). Regarding sponges, the encrusting and/or globular sponges together with large and small cup-shaped sponges (e.g., *Asconema setubalense, Phakellia ventilabrum*) generally did not present high levels of coverage–entanglement of *R. okamurae* drifted thalli, with most colonies displaying levels A (absence of drifted thalli) and B (presence of drifted thalli in the basal part of the individual–colony) (Figures 3, 5, 6 and 8). Nevertheless, the branched forms of the genus *Axinella* (e.g., *Axinella polypoides* and *A. verrucosa*) sometimes reached higher levels of coverage–entanglement of drifted thalli, with specimens reaching level D (presence of drifted thalli between 1/3 and 2/3 of the individual–colony) (Figures 3, 6 and 8). In relation to other groups, sessile colonial annelids (e.g., *Filograna implexa*), bryozoans (e.g., *Reteporella* sp., *Pentapora* sp.), calcareous hydrozoans (e.g., *Errina aspera*), and urochordates (e.g., *Synoicum blochmanni*) generally reached low coverage–entanglement levels of drifted thalli (levels A and B), but occasionally some calcareous hydrozoans and bryozoans with branched foliose forms reached level C (presence of drifted thalli in less than 1/3 of the individual–colony) (Figures 3, 5, 6 and 8).

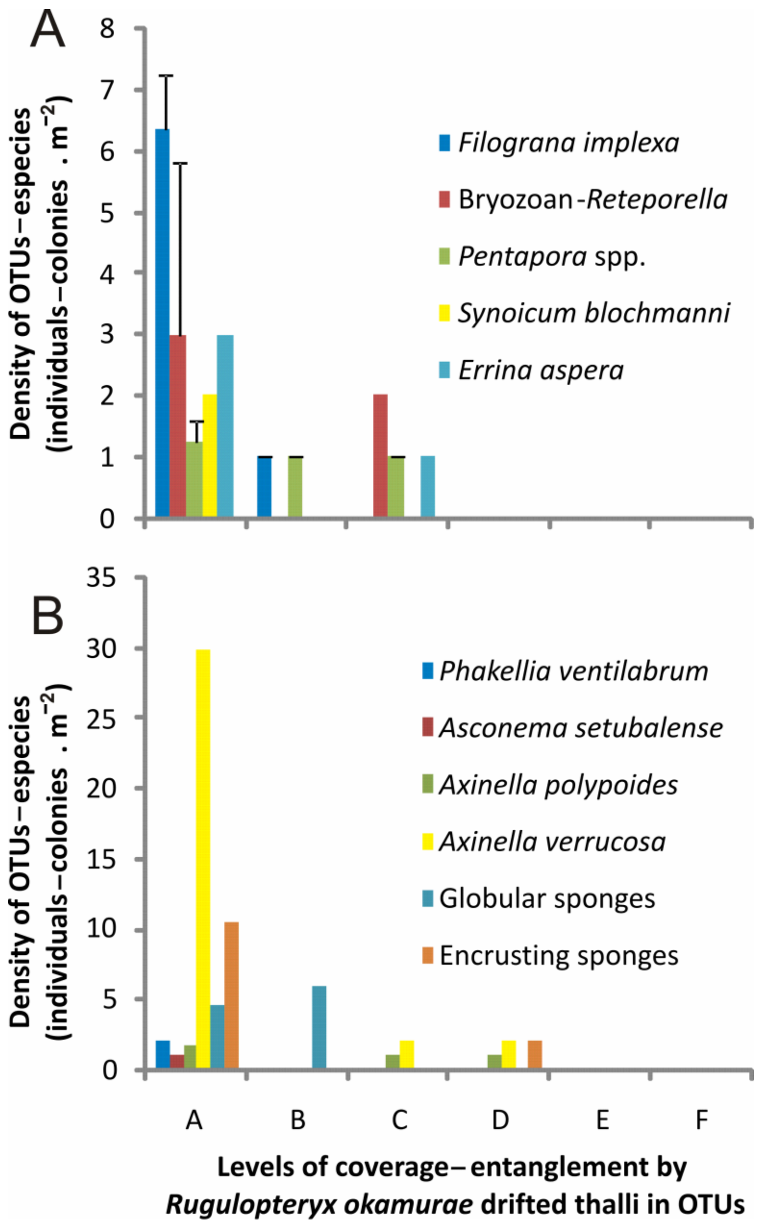

Figure 6. Mean density (+standard deviation) of different (**A**) hydrozoan, polychaete, bryozoan, and ascidian as well as (**B**) sponge species and OTUs with different levels of coverage–entanglement by drifted thalli of *Rugulopteryx okamurae* in circalittoral and bathyal bottoms of the northern Strait of Gibraltar and the Alboran Sea. A: absence of *R. okamurae* drifted thalli; B: presence of *R. okamurae* drifted thalli in the basal part of the individual–colony; C: presence of *R. okamurae* drifted thalli in less than 1/3 of the individual–colony; D: presence of *R. okamurae* drifted thalli between 1/3 and 2/3 of the individual–colony; E: presence of *R. okamurae* drifted thalli between 2/3 and 3/3 of the individual–colony; F: total coverage of *R. okamurae* drifted thalli in the individual–colony.

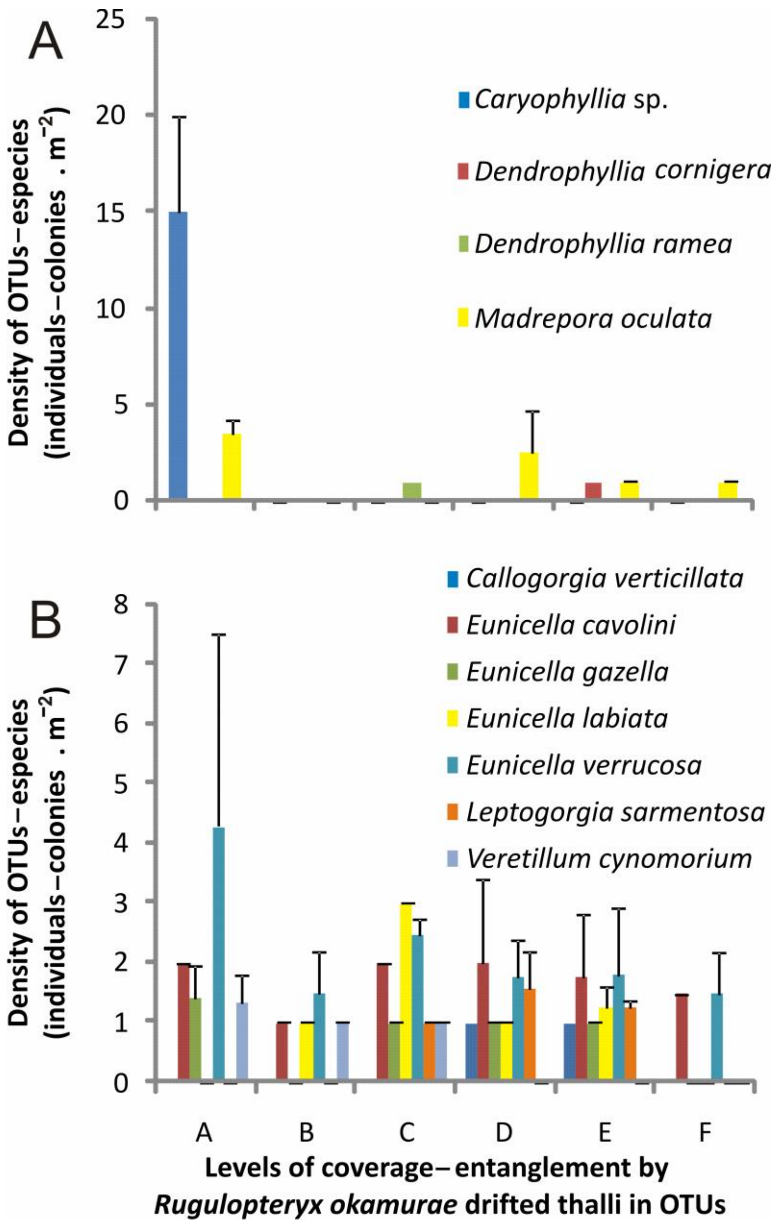

Figure 7. Mean density (+standard deviation) of different scleractinian (**A**) and octocoral (**B**) species with different levels of coverage–entanglement by drifted thalli of *Rugulopteryx okamurae* in circalittoral and bathyal bottoms of the northern Strait of Gibraltar and the Alboran Sea. A: absence of *R. okamurae* drifted thalli; B: presence of *R. okamurae* drifted thalli in the basal part of the individual–colony; C: presence of *R. okamurae* drifted thalli in less than 1/3 of the individual–colony; D: presence of *R. okamurae* drifted thalli between 1/3 and 2/3 of the individual–colony; E: presence of *R. okamurae* drifted thalli between 2/3 and 3/3 of the individual–colony; F: total coverage of *R. okamurae* drifted thalli in the individual–colony.

		Levels of coverage– entanglement by ***Rugulopteryx okamurae*** **drifted thalli in OTUs**					
		A	B	C	D	E	F
Annelids, bryozoans, Urochordates, Hydrozoans	*Filograna implexa*	86	14				
	Bryozoan-*Reteporella*	60		40			
	Pentapora spp.	38	31	31			
	Synoicum blochmanni	100					
	Errina aspera	75		25			
Cnidarians Scleracti-nians	*Caryophyllia* sp.	100					
	Dendrophyllia cornigera					100	
	Dendrophyllia ramea			100			
	Madrepora oculata	44			30	13	13
Cnidarians Octocorals	*Callogorgia verticillata*				50	50	
	Eunicella cavolini	18	10	20	20	17	15
	Eunicella gazella	31		23	23	23	
	Eunicella labiata		16	48	16	20	
	Eunicella verrucosa	32	12	18	13	14	11
	Leptogorgia sarmentosa			26	41	33	
	Veretillum cynomorium	40	30	30			
Sponges	*Phakellia ventilabrum*	100					
	Asconema setubalense	100					
	Axinella polypoides	46		27	27		
	Axinella verrucosa	88		6	6		
	Globular sponges	43	57				
	Encrusting sponges	84			16		

Figure 8. Percentage of individuals–colonies of top-dominant OTUs and species in relation to different levels of coverage–entanglement by drifted thalli of *Rugulopteryx okamurae* in circalittoral and bathyal bottoms of the northern Strait of Gibraltar and the Alboran Sea. A: absence of *R. okamurae* drifted thalli; B: presence of *R. okamurae* drifted thalli in the basal part of the individual–colony; C: presence of *R. okamurae* drifted thalli in less than 1/3 of the individual–colony; D: presence of *R. okamurae* drifted thalli between 1/3 and 2/3 of the individual–colony; E: presence of *R. okamurae* drifted thalli between 2/3 and 3/3 of the individual–colony; F: total coverage of *R. okamurae* drifted thalli in the individual–colony. Intensity of the red colour indicates higher percentage values.

Regarding cnidarians, scleractinians displayed different levels of coverage–entanglement of drifted thalli of *R. okamurae*, with some of the large colonial species (e.g., *Madrepora oculata, Dendrophyllia cornigera*) generally reaching the highest levels (E: presence of drifted thalli between 2/3 and 3/3 of the individual–colony; F: total coverage of drifted thalli in the individual–colony) (Figures 5, 7 and 8). Nevertheless, the solitary and small scleractinians (e.g., *Caryophyllia* spp.) did not display thalli entangled on their skeletons (level A) (Figures 5, 7 and 8). Regarding octocorals, almost all the large and highly branched gorgonians (e.g., *Callogorgia verticillata, Leptogorgia sarmentosa, Eunicella cavolini, Eunicella verrucosa*, etc.) reached moderate to high levels of coverage–entanglement of drifted thalli (levels D, E and F) (Figures 4, 5, 7 and 8). Nevertheless, the flexible and large sea-pen *Veretillum cynomorium*, only reached low to moderate levels of coverage–entanglement of drifted thalli (levels A, B and C) (Figures 4, 7 and 8).

In relation to the four biological traits of the top-dominant OTUs and species, PERMANOVA analyses showed that their *body form* and *size* were the main biological traits related to the different levels of *R. okamurae* drifted thalli that covered–entangled on their individuals and colonies (Table 1, Figure 9). Those invertebrates with an erect and branched body form and with a medium-large size (mostly gorgonians and colonial scleractinians) were those that presented the highest levels of *R. okamurae* drifted thalli (Table 1).

Table 1. Results of one-way PERMANOVA examining the relationships of some biological traits on the abundance of top-dominant invertebrates with different levels of coverage–entanglement of drifted thalli of *Rugulopteryx okamurae* on them.

Source of Variation	df	SS	MS	F	*p*
Benthic position	2	7740.4	3870.2	2.0215	0.0656
Res	19	36,375	1914.5		
Total	21	44,115			
Body form	3	17,993	5997.6	4.1327	**0.0006**
Res	18	26,123	1451.3		
Total	21	44,115			
Size	3	12,543	4181	2.3837	**0.0204**
Res	18	31,572	1754		
Total	21	44,115			
Flexibility	2	3267.4	1633.7	0.75991	0.6128
Res	19	40,848	2149.9		
Total	21	44,115			

Pairwise tests
Globulose ≠ Erect and branched *; Erect and branched ≠ Erect but not branched **
Medium ≠ Medium
large **

Bold values indicate significant values; * $p < 0.05$; ** $p < 0.01$.

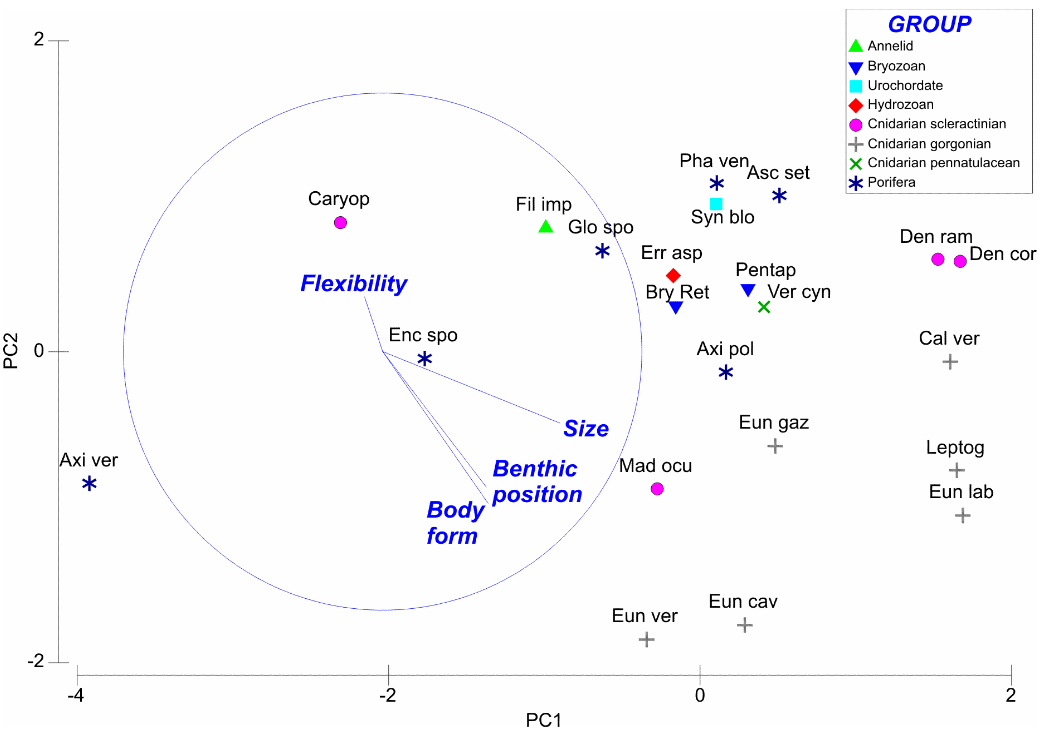

Figure 9. Principal component analysis (PCA) of the abundance of top-dominant OTUs and species in relation to their coverage–entanglement levels of *Rugulopteryx okamurae* drifted thalli and their biological traits. Fil imp: *Filograna implexa*; Bry Ret: Bryozoan—*Reteporella*; Pentap: *Pentapora* spp.; Syn blo: *Synoicum blochmanni*; Err asp: *Errina aspera*; Caryop: *Caryophyllia* sp.; Den cor: *Dendrophyllia cornigera*; Den ram: *Dendrophyllia ramea*; Mad ocu: *Madrepora oculata*; Cal ver: *Callogorgia verticillata*; Euncav: *Eunicella cavolini*; Eungaz: *Eunicella gazella*; Eun lab: *Eunicella labiata*; Eunver: *Eunicella verrucosa*; Leptog: *Leptogorgia sarmentosa*; Ver cyn: *Veretillum cynomorium*; Phaven: *Phakellia ventilabrum*; Asc set: *Asconema setubalense*; Axi pol: *Axinella polypoides*; Axiver: *Axinella verrucosa*; Glo spo: Globular sponges; Enc spo: Encrusting sponges. PC1 and PC2 explained 52.9 and 21.5% of the variance, respectively.

PCA ordination displayed a similar trend to that of the PERMANOVA analyses, with small and flattened to globular invertebrates (e.g., globular and encrusting sponges, *Filograna implexa*, etc.; generally displaying low levels of drifted thalli, levels A–C) on the left and top part of the ordination plot (Figure 9). Moreover, the large, erect, and branched invertebrates such as scleractinians and gorgonians (generally displaying moderate-high levels of drifted thali, levels C–E) were located on the right and bottom part of the ordination plot (Figure 9). Axes I and II of the PCA ordination explained 74.4% of the variance. The most correlated biological traits with this ordination were (1) *size* with a positive correlation with the PC1 (Spearman correlation = 0.68, $p < 0.05$), (2) *body form* with a negative correlation to PC2 (Spearman correlation = −0.59, $p < 0.05$), and (3) *benthic position* with a negative correlation to PC2 (Spearman correlation = −0.52, $p < 0.05$) (Figure 9). In the PCA, the vectors of these biological traits generally pointed to colonial scleractinians and gorgonians, which were those invertebrates with the medium and large sizes, erected from the seafloor and with a branched morphology. Those invertebrates reached the highest levels of coverage by drifted thalli of *R. okamurae* (Figure 9).

4. Discussion

Drifted thalli of the invasive alga *Rugulopteryx okamurae* in circalittoral and bathyal bottoms were mainly detected in the northern Strait of Gibraltar (SoG) and the north-westernAlboran Sea (underwater images from CIRCAESAL 0721), but also along the continental shelf of the north-central and north-easternAlboran Sea (bottom otter trawl samples from MEDITS expeditions). In general, accumulations of drifted thalli were detected in both underwater images and bottom trawl samples in the northwestern part of the Alboran Sea, but not in the northeastern part of the Alboran Sea, where only the bottom trawl samples displayed presence of drifted thalli. No drifted thalli were detected in sectors disconnected from the continental margin such as the Alboran Ridge (Alboran Island and its insular shelf); the banks of Avempace, La Herradura, and Ville de Djibouti (located, respectively, at ca. 20, 30, and 33 nautic miles away from the continental margin of the southern Iberian Peninsula); and even the banks Chella (also known as Seco de los Olivos) and El Sabinar, located only ca. 3 nautic miles from the continental shelf break. The spatial trend detected for drifted thalli of this invasive alga is very similar to that described for the infralittoral bottoms where it occurs as a dominant component of photophilous algal communities from the northern SoG to Almería coastal locations in the northeastern sector of the Alboran Sea [7–10,13–15,21,28]. The massive productivity of this invasive alga in those coastal locations represents an important source of drifted thalli towards the shores, the adjacent coastal locations eastwards and also the deep areas located nearby. Coastal current circulation in the northern SoG and the Alboran Sea is driven by the Atlantic surficial waters, which flow towards the Mediterranean Sea, favouring the transport of *R. okamurae* drifted thalli eastwards into the Mediterranean Sea, as also detected in some distribution models [3,29]. The present study provides one of the first records of large accumulations of drifted thalli of this highly invasive alga in circalittoral and bathyal bottoms of the Alboran Sea, as previously detected in the Gulf of Cádiz (GoC). Massive occurrence of drifted thalli of *R. okamurae* has been recorded along the coasts of southern Spain (e.g., coasts of the Andalusian region) where nowadays they represent a serious problem for tourism (e.g., high amount of drifted thalli on beaches) and fisheries (Figure 1) [13]. In the GoC, drifted thalli were detected in circalittoral and bathyal bottoms, due to the action of some coastal currents and the Mediterranean outflow water current (MOW), which are the main driving mechanisms for thalli dispersal towards the deep-sea [22]. In the northern Alboran Sea, the area with maximum values of biomass (located on the continental shelf off Roquetas de Mar), is characterised by intense surface currents associated with the Alboran Sea gyral circulation system [3]. Nevertheless, the process of dispersal towards deep locations has not yet been described, but it is expected that further massive colonisation of infralittoral bottoms by this invasive alga will be followed by high amounts of drifted thalli in those circalittoral and bathyal bottoms located nearby.

In the northern SoG and the Alboran Sea, some circalittoral and bathyal areas displayed no or low occurrence of drifted thalli of *R. okamurae*, and this is partly explained by the absence and/or low occurrence of infralittoral rocky bottoms in those areas (e.g., Bay of Málaga, [6]), which are needed for the establishment of large living populations of this alga [13]. In other areas with abundant infralittoral rocky bottoms (e.g., around the Alboran Island, Alboran Ridge [6]), the absence of drifted thalli of *R. okamurae* in circalittoral and bathyal bottoms probably indicates that this invasive macroalge has not yet arrived or become a dominant component of the infralittoral photophilous macroalgal communities. The physiographical isolation of the Alboran Island from the continental shelf and from the main naval traffic routes could represent an advantage against invasion of *R. okamurae*.

Coverage of drifted thalli of *R. okamurae* in circalittoral and bathyal bottoms of the northern SoG and the Alboran Sea ranged between 3.8% and 65.6% for circalittoral bottoms and 4.0% and 57.8% for bathyal bottoms. Regarding biomass, the values ranged between 7.8 and 40,128.5 g/1000 m^2. These values are lower than those reported in infralittoral bottoms (sometimes reaching 100% coverage), and this is because some of the drifted thalli are exported upwards to the shores or horizontally to similar depths along the continental shelf and slope, so the amount of drifted thalli exported downwards is then lower than that from the infralittoral source [11,28]. Biomass values obtained in the MEDITS expeditions were always higher on the continental shelf (<120 m depth) than on slope bottoms (>120 m depth), indicating a higher presence of drifted thalli in the circalittoral bottoms. Nevertheless, no bathymetric pattern was detected in coverage data obtained in the underwater images, with high and low values occurring in both circalittoral and bathyal bottoms, especially in the Algeciras and La Línea submarine canyons. Some submarine structures such as submarine canyons could explain some of the high values detected on the slope bottoms located nearby as those of Algeciras and La Línea submarine canyons. The role of submarine canyons and some erosive channels in transporting sediment, organic particles, organisms, and even litter from the shelf to the slope is widely known [30], and this has already been pointed out by [22] when understanding the dispersal of drifted thalli to deep locations of the north-eastern GoC. Indeed, remains of other algae (e.g., *Gelidium, Codium bursa*) and even seagrass species (e.g., *Zostera noltii*) were sometimes detected in samples of deep-sea sediments from erosive channels and submarine canyons in the Alboran Sea and GoC before the arrival of *R. okamurae* (Rueda, pers. com.). There is also evidence of massive presence of drifted thalli of *R. okamurae* in submarine canyons of the southern SoG (e.g., Ceuta Submarine Canyon; Juan and Rueda, pers. com.), which may be the result of the downslope transport of the abundant production of this alga in the southern SoG coastal areas, where recurrent massive strandings (up to 5000 tonnes) have been removed from the shores since 2016 [31].

Drifted thalli of *R. okamurae* displayed different levels of coverage–entanglement in different top-dominant and habitat-forming invertebrates of circalittoral and bathyal bottoms of the northern SoG and the Alboran Sea. Generally, invertebrates with small size, not emerging significantly from the seabed (benthic position close to the seabed), and with a flat or globular morphology (noncomplex body form) displayed low levels of *R. okamurae* drifted thalli. Some of these invertebrates were the encrusting and globular sponges and urochordates, the small solitary scleractinians (e.g., *Caryophyllia* spp.) and some colonial annelids (e.g., *Filograna implexa*). These species generally have a small capacity for entangling drifted algae, especially if not occurring in a high abundance as it has also been found for small aquatic plants displaying noncomplex body forms and occurring at low-moderate densities [15,32]. As commented by [32], drifting algal mats are conglomerates detached from their parent algal source areas that can be moved by winds or hydrodynamic forces, generally forming clumps or mats that may disintegrate or aggregate, which in some cases can cover wide extensions of the sea floor. Drifted algae are often gathered close to the areas where living populations occur, and in these areas they can have major impacts on seafloor dynamics [15,22,32]. Nevertheless, they can also be transported by strong currents and reach distant areas, affecting the health status, distribution, and temporal dynamics of different key organisms and even whole habitats [15,22,32]. In this sense, the impact of the drifted thalli of *R. okamurae* on these small and non-three-dimensionally complex benthic components (mostly filter feeding invertebrates) is expected to be low, except if the drifted thalli may occasionally form stable large clumps that no longer move with the currents. The degradation of these clumps on top of these small filter-feeding invertebrates may cause an increase in nutrients and hypoxia, together with a physical barrier for capturing food particles from the water column, causing a decline in their population [32]. Indeed, some authors have detected an increase in deposit feeders together with declines in filter feeders and photosynthetic organisms in areas with large clumps of drifted algae [32–35].

Some circalittoral and bathyal bottoms of the northern SoG and the Alboran Sea have high densities of sessile invertebrates that are large, emerge from the seafloor, and have a complex body form (highly branched) [1,2]. In the present study, some of these invertebrates have been found to retain a large amount of drifted thalli of *R. okamurae* around their bodies. These invertebrates are mainly gorgonians and colonial scleractinians that have polyps that capture small food particles [2,36,37]. Moreover, some of these invertebrates generally have moderate to slow growth rates and can build vulnerable and threatened habitats that are included in regional and international conservation lists under different conventions and directives (e.g., OSPAR, Habitats Directive) [2]. Previous studies found that the complex morphologies and densities of some seagrass species may increase the retention capacity of drifted algae [38,39]. A similar condition may also occur for those mentioned invertebrates in relation to their retention capacity of *R. okamurae* drifted thalli. In the present study, it was not possible to detect if some *R. okamurae* thalli were living and attached to the gorgonians and scleractinians, but it is expected that most of the thalli were free drifted and sometimes entangled and covered whole colonies. Colonisation of living *R. okamurae* on gorgonians (e.g., *Paramuricea clavata*) and colonial scleractinians (e.g., *Dendrophyllia ramea*) in infralittoral and shallow circalittoral bottoms of the Alboran Sea and the SoG has previously been documented as epiphytes growing on dead skeletons of those sessile suspension feeders [28,40]. In this case, the combined effect of global warming and other anthropic pressures (e.g., fisheries) seem to cause weakness in the polyps of those cnidarians and a subsequent increase in diseases and epibionts [41,42]. In the present study, some polyps of the colonial scleractinians and gorgonians with high levels of drifted thalli were detected closed, so it is expected that negative impacts could occur on the gorgonians and scleractinians if thalli are constantly entangled around their branches. The entanglement of drifted algae in complex body form organisms or less complex ones but occurring at high densities is explained by their higher retention capacity, not only for drifted algae but also for lost fishing lines and nets, plastics, and other drifted materials through the seafloor [43]. Some of these drifted materials can cause a physical abrasion to delicate invertebrate colonies, which a priori may not be the case for the drifted thalli of *R. okamurae* on the invertebrates of this study. Nevertheless, this was the case for other bathyal invertebrates such as the large, fragile, and three-dimensionally complex bamboo coral colonies (*Isidella elongata*) that were severely damaged when large amounts of drifted thalli entangled on the apical and easy-to-break branches of their colonies containing the polyps [22]. An interesting case in the present study was that of some large and emerging invertebrates that have the ability to retract to the seafloor (e.g., the pennatulacean *Veretillum cynomorium*) [44]. The burial and emerging process of this soft bottom sea pen could help them to be clean of drifted thalli, resulting in low levels of drifted thalli around their bodies (generally levels A or B). Another interesting case is that of some highly flexible and moderately branched invertebrates (e.g., the sponge *Axinella polypoides*) that generally displayed less coverage of drifted thalli than that of gorgonians with similar size and body form (e.g., *Eunicella gazella*). Probably the higher flexibility and lower three-dimensional complexity of *A. polypoides* than that of gorgonians is beneficial against accumulating high levels of entanglement.

The potential impacts of the entanglement of drifted *R. okamurae* thalli on some of the studied invertebrates could include a lower capacity for capturing food particles, if the entangled thalli are constantly touching and disturbing structures involved on feeding such as polyps, zooids, or sensitive apertures (e.g., urochordates). It is expected that the fitness will be reduced in those organisms that are experiencing a constant disturbance in some of their feeding structures. Some of these organisms are important habitat-forming species and their decline could involve a decrease in the environmental status of the habitats as already detected in infralittoral and shallow circalittoral coralligenous communities colonised by *R. okamurae* in the northern and southern sector of the Alboran Sea [28,40]. In general, macroalgal blooms end up displacing several aquatic organisms including seagrasses, corals, or brown and red algae in the areas that they occupy [45]. This competition for space with other photophilous species and invertebrates has been previously documented for *R. okamurae* and other invasive algae [11,40]. Other effects of large amounts of drifted thalli of *R. okamurae* could be similar to that of other algae and may include the reduction in the photosynthetic capacity of photophilous species, including seagrasses [32], and the depletion of oxygen due to decomposition of the algal tissues in areas with abundant thalli, leading to the potential release of toxic metabolites to consumers [46]. Experimental studies should be performed in order to understand how different levels of coverage by drifted thalli of *R. okamurae* affect the physiology and biology of these key habitat-forming species of the Mediterranean Sea and nearby Atlantic Ocean.

The dispersion of the drifted thalli of *R. okamurae* may have uncertain ecological consequences that could affect not only the intertidal and infralittoral areas, which are already experiencing large loads of drifted thalli, but also the deep compartments of the ecosystem, as detected in the present study and in the GoC [22]. Therefore, the living population of *R. okamurae* from infralittoral areas act as a source of drifted thalli for adjacent deep-sea areas, so further algal colonisation to new infralittoral areas may result in further arrival of drifted thalli to those adjacent deep-sea areas. In order to detect and understand the potential impacts caused by the drifted thalli in the deep-sea areas, it is important to carry out monitoring programs for obtaining information on the present-day health status of the deep-sea habitats before and during periods with massive *R. okamurae* development occurring in adjacent infralittoral areas. Moreover, experimental studies on the effects of the drifted thalli on key habitat-forming species and on carbon sequestration in marine sediments could also be helpful for understanding potential changes in the deep-sea ecosystem.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d15121206/s1, Figure S1: Coverage measurements by ImageJ software; Table S1: Coordinates of the underwater images transects; Table S2: Coordinates of the bottom otter trawl samples.

Author Contributions: Conceptualisation, J.L.R., A.M.-T., M.G.-N., E.G.-G., Á.M.-R. and J.T.V.; methodology, J.L.R., A.M.-T., M.G.-N., E.G.-G., Á.M.-R., J.V. and J.T.V.; data acquisition: J.L.R., E.G.-G., A.M.-A., M.G., M.S.-G., J.T.V., C.G.-R., J.V. and M.G.-A.; formal analysis, J.L.R., A.M.-T., M.G.-N., E.G.-G., Á.M.-R. and J.T.V.; writing—original draft preparation, J.L.R., A.M.-T., E.G.-G., A.M.-A. and Á.M.-R.; writing—review and editing, J.L.R., A.M.-T., M.G.-N., E.G.-G., Á.M.-R., J.V., J.T.V., A.M.-A., M.G., M.S.-G., J.T.V., C.G.-R. and M.G.-A.; visualisation, A.M.-T., M.G.-N., E.G.-G., Á.M.-R., J.V. and J.T.V. All authors have read and agreed to the published version of the manuscript.

Funding: This study has been funded by the projects 18-ESMARES2-CIRCA (IEO and Ministerio de Transición Ecológica y Reto Demográfico—MITERD of the Spanish government for the application of the Marine Strategy Framework Directive in Spanish waters) and DEMALBORAN (Evaluación de Recursos Demersales por Métodos Directos en el Mar de Alborán, IEO and the European Maritime and Fisheries Fund).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Data supporting the reported results will be available following publication of the manuscript.

Acknowledgments: We really appreciate the help provided by the captains, crew, and scientific colleagues of the R/V Ángeles Alvariño (IEO-CSIC) and Miguel Oliver (SGP, MAPA) during the CIRCAESAL and MEDITS expeditions, respectively. We appreciate the sampling permits provided by the Dirección General de Biodiversidad, Bosques y Desertificación (Secretaría de Estado de Medio Ambiente, Ministerio para la TransiciónEcológica y el Reto Demográfico) and Subdirección General de Investigación Científica y Reservas Marinas (Secretaría General de Pesca, Ministerio de Agricultura, Pesca y Alimentación) from the Spanish government for conducting research on some Marine Protected Areas. We are grateful for the detailed English grammar review of the manuscript by Terence W. Edwards, a native English grammar teacher from the prestigious English school "Sunny View School" (Málaga, Spain). We deeply appreciate the reviews made by two anonymous reviewers and the editor on previous drafts of this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Rueda, J.L.; Gofas, S.; Aguilar, R.; de la Torriente, A.; García Raso, J.E.; Iacono, C.L.; Luque, Á.A.; Marina, P.; Mateo-Ramírez, Á.; Moya-Urbano, E.; et al. Benthic fauna of littoral and deep-sea habitats of the Alboran Sea: A hotspot of biodiversity. In *Alboran Sea—Ecosystems and Marine Resources*; Báez, J.C., Vázquez, J.T., Camiñas, J.A., Malouli Idrissi, M., Eds.; Springer: Cham, Switzerland; Dordrecht, The Netherlands, 2021; pp. 285–358. ISBN 978-3-030-65515-0.
2. Templado, J.; Luque, Á.A.; Moreno, D.; Tierno de Figueroa, J.M.; Sánchez Tocino, L.; Aguilar, R.; de la Torriente, A. Invertebrates: The realm of diversity. In *Alboran Sea—Ecosystems and Marine Resources*; Báez, J.C., Vázquez, J.T., Camiñas, J.A., Malouli Idrissi, M., Eds.; Springer: Cham, Switzerland; Dordrecht, The Netherlands, 2021; pp. 359–430. ISBN 978-3-030-65515-0.
3. Vargas-Yáñez, M.; García-Martínez, M.; Moya, F.; Balbín, R.; López-Jurado, J. The oceanographic and climatic context. In *Alboran Sea—Ecosystems and Marine Resources*; Báez, J.C., Vázquez, J.T., Camiñas, J.A., Malouli Idrissi, M., Eds.; Springer: Cham, Switzerland; Dordrecht, The Netherlands, 2021; pp. 85–109. ISBN 978-3-030-65515-0.
4. Baro, J.; García, T.; Serna Quintero, J.M. Description of artisanal Fisheries in northern Alboran Sea. In *Alboran Sea—Ecosystems and Marine Resources*; Báez, J.C., Vázquez, J.T., Camiñas, J.A., Malouli Idrissi, M., Eds.; Springer: Cham, Switzerland; Dordrecht, The Netherlands, 2021; pp. 521–542. ISBN 978-3-030-65515-0.
5. González-Aguilar, M.; García-Ruiz, C.; García Jiménez, T.; Serna Quintero, J.M.; Ciércoles Antonell, C.; Baro Domínguez, J. Demersal Resources. In *Alboran Sea—Ecosystems and Marine Resources*; Báez, J.C., Vázquez, J.T., Camiñas, J.A., Malouli Idrissi, M., Eds.; Springer: Cham, Switzerland; Dordrecht, The Netherlands, 2021; pp. 589–628. ISBN 978-3-030-65515-0.
6. Ercilla, G.; Vázquez, J.T.; Alonso, B.; Bárcenas, P.; Casas, D.; d'Acremont, E.; Estrada, F.; Fernández-Salas, L.M.; Galindo-Zaldívar, J.; Juan, C.; et al. Seafloor Morphology and Processes in the Alboran Sea. In *Alboran Sea—Ecosystems and Marine Resources*; Báez, J.C., Vázquez, J.T., Camiñas, J.A., Malouli Idrissi, M., Eds.; Springer: Cham, Switzerland; Dordrecht, The Netherlands, 2021; pp. 157–205. ISBN 978-3-030-65515-0.
7. Altamirano-Jeschke, M.; de la Rosa Álamos, J.; Martínez Medina, F.J. Arribazones de la especia exótica *Rugulopteryx okamurae* (E.Y. Dawson) en el estrecho de Gibraltar. In Proceedings of the Sesión Científica de la Sociedad Española de Ficología, Madrid, Spain, 11 November 2016.
8. Altamirano-Jeschke, M.; de la Rosa Álamos, J.; Martínez Gil, F.J.; Román Muñoz Gallego, A. Prolifera en el estrecho un alga nunca citada en nuestro litoral: De origen asiático," *Rugulopteryx okamurae*" ocupa ya una gran extensión. *Quercus* **2017**, *374*, 32–33.
9. García-Gómez, J.C.; Sempere-Valverde, J.; Ostalé-Valriberas, E.; Martínez, M.; Olaya-Ponzone, L.; González, A.R.; Espinosa, F.; Sánchez-Moyano, E.; Megina, C.; Parada, J.A. *Rugulopteryx okamurae* (E.Y. Dawson) I.K. hwang, W.J. Lee & H.S. Kim (Dictyotales, ochrophyta), alga exótica "explosiva" en el estrecho de Gibraltar. Observaciones preliminares de su distribución e impacto. *Almoraima* **2018**, *48*, 97–113.
10. García-Gómez, J.C.; Sempere-Valverde, J.; González, A.R.; Martínez-Chacón, M.; Olaya-Ponzone, L.; Sánchez-Moyano, E.; Ostalé-Valriberas, E.; Megina, C. From exotic to invasive in record time: The extreme impact of *Rugulopteryx okamurae* (Dictyotales, ochrophyta) in the Strait of Gibraltar. *Sci. Total Environ.* **2020**, *704*, 135408. [CrossRef] [PubMed]
11. García-Gómez, J.C.; Florido, M.; Olaya-Ponzone, L.; Rey Díaz de Rada, J.; Donázar-Aramendía, I.; Chacón, M.; Quintero, J.J.; Margariño, S.; Megina, C. Monitoring extreme impacts of *Rugulopteryx okamurae* (Dictyotales, ochrophyta) in El estrecho natural park (Biosphere reserve). Showing radical changes in the underwater seascape. *Front. Ecol. Evol.* **2021**, *9*, 639161. [CrossRef]
12. Sempere-Valverde, J.; García-Gómez, J.C.; Ostalá-Valriberas, E.; Martínez, M.; Olaya-Ponzone, L.; González, A.R.; Sánchez-Moyano, E.; Megina, C.; Parada, J.A.; Espinosa, F. Expansion of the exotic brown algae *Rugulopteryx Okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim in the Strait of Gibraltar. In Proceedings of the 1st Mediterranean Symposium on the Non-Indigenous Species, Antalya, Turkey, 17–18 January 2019.
13. MITECO (2022). Estrategia de control del alga Rugulopteryx okamurae en España. Available online: https://www.miteco.gob.es/content/dam/miteco/es/biodiversidad/publicaciones/estrategia_rokamurae_cs_28072022_tcm30-543560.pdf (accessed on 20 June 2023).

14. Martín-Arjona, A.; Urra, J.; Marina, P.; Caballero, J.A.; González-Duarte, M.; Cuadros, A.; Silva, L. Caracterización de comunidades algales e identificación de hábitats presentes en los fondos infralitorales rocosos del estrecho de Gibraltar tras el asentamiento del alga invasora *Rugulopteryx okamurae*. In Proceedings of the XXV Bienal de la Real Sociedad Española de Historia Natural, Málaga, Spain, 4–5 September 2023; pp. 135–136.
15. Terradas-Fernández, M.; Pena-Martín, C.; Valverde-Urrea, M.; Gran, A.; Blanco-Murillo, F.; Leyva, L.; Abellán-Gallardo, E.; Beresaluze, E.; Izquierdo, A.; del Pilar-Ruso, Y.; et al. An outbreak of the invasive macroalgae *Rugulopteryx okamurae* in Alicante Bay and its colonization on dead *Posidonia oceanica* matte. *Aquat. Bot.* **2023**, *189*, 103706. [CrossRef]
16. Liulea, S.; Serrão, E.A.; Santos, R. Spread and impact of the invasive brown algae *Rugulopteryx Okamurae* on the Algarve Coast, Southern Portugal (Ne Atlantic). *SSRN* **2023**, in press. [CrossRef]
17. El Aamri, F.; Idhalla, M.; Tamsouri, M.N. Occurrence of the invasive brown seaweed *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Dictyotales, Phaeophyta) in Morocco (Mediterranean Sea). *MedFAR* **2018**, *1*, 92–96.
18. Bernal Ibáñez, A.; Chebaane, S.; Sempere Valverde, J.; Faria, J.; Ramalhosa, P.; Kaufmann, M.; Florido, M.; Albert-Fonseca, A.; Canning-Clode, J.; Gestoso, I.; et al. A worrying arrival: The first record of brown macroalga *Rugulopteryx okamurae* in Madeira Island and its invasive risk. *BioInvasions Rec.* **2022**, *11*, 912–924. [CrossRef]
19. Faria, J.; Prestes, A.C.L.; Moreu, I.; Cacabelos, E.; Martins, G.M. Dramatic changes in the structure of shallow-water marine benthic communities following the invasion by *Rugulopteryx okamurae* (Dictyotales, ochrophyta) in Azores (NE Atlantic). *Mar. pollut. Bull.* **2022**, *175*, 113358. [CrossRef]
20. Verlaque, M.; Steen, F.; De Clerck, O. Rugulopteryx (Dictyotales, Phaeophyceae), a genus recently introduced to the Mediterranean. *Phycologia* **2009**, *48*, 536–542. [CrossRef]
21. Ruitton, S.; Blanfuné, A.; Boudouresque, C.-F.; Guillemain, D.; Michotey, V.; Roblet, S.; Thibault, D.; Thibaut, T.; Verlaque, M. Rapid spread of the invasive brown alga *Rugulopteryx okamurae* in a National Park in Provence (France, Mediterranean Sea). *Water* **2021**, *13*, 2306. [CrossRef]
22. Mateo-Ramírez, Á.; Iñiguez, C.; Fernández-Salas, L.M.; Sánchez-Leal, R.F.; Farias, C.; Bellanco, M.; Gil, J.; Rueda, J.L. Healthy thalli of the invasive seaweed *Rugulopteryx okamurae* (Phaeophyceae) being massively dragged into deep-sea bottoms by the Mediterranean Outflow Water. *Phycologia* **2023**, *62*, 99–108. [CrossRef]
23. Bertrand, J.A.; Gil de Sola, L.; Papaconstantinou, C.; Relini, G.; Souplet, A. The general specifications of the Medits surveys. *Sci. Mar.* **2002**, *66*, 9–17. [CrossRef]
24. Fiorentini, L.; Dremière, P.Y.; Leonori, I.; Sala, A.; Palumbo, V. Efficiency of the bottom trawl used for the Mediterranean international trawl survey (MEDITS). *Aquat. Living Resour.* **1999**, *12*, 187–205. [CrossRef]
25. Puerta, P.; Mosquera-Giménez, A.; Reñones, O.; Domínguez-Carrió, C.; Rueda, J.L.; Urra, J.; Carreiro-Silva, M.; Blasco-Ferre, J.; Santana, Y.; Gutiérrez-Zárate, C.; et al. Variability of deep-sea megabenthic assemblages along the western pathway of the Mediterranean outflow water. *Deep. Sea Res. Part I Oceanogr. Res. Pap.* **2022**, *185*, 103791. [CrossRef]
26. González-Irusta, J.; De la Torriente, A.; Punzón, A.; Blanco, M.; Serrano, A. Determining and mapping species sensitivity to trawling impacts: The BEnthos Sensitivity Index to Trawling Operations (BESITO). *ICES J. Mar. Sci.* **2018**, *75*, 1710–1721. [CrossRef]
27. Clarke, K.R.; Warwick, R.M. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd ed.; Natural Environment Research Council: Plymouth, UK, 1994; ISBN 9781855311404.
28. Estévez, R.M.; Palacios, M.; Cervera, J.L.; González-Duarte, M.M. Expansion of the invasive alga *Rugulopteryx okamurae* (Dictyotaceae, Ochrophyta) in the Mediterranean Sea: First evidence as epiphyte of the cold-water coral *Dendrophyllia ramea* (Cnidaria: Scleractinia). *BioInvasions Rec.* **2022**, *11*, 925–936. [CrossRef]
29. Román-Muñoz, A.; Martín-Taboada, A.; de la Rosa, J.; Carmona, R.; Zanolla, M.; Altamirano, M. La modelación de la distribución de especies como herramienta en la gestión de invasiones biológicas en el medio marino: El caso de *Rugulopteryx okamurae* (Dictyotaceae, ochrophyta) en el mediterráneo. *Algas* **2019**, *55*, 37–40.
30. Cerrillo-Escoriza, J.; Lobo, F.J.; Puga-Bernabéu, Á.; Rueda, J.L.; Bárcenas, P.; Sánchez-Guillamón, O.; Serna Quintero, J.M.; Gil, J.L.P.; Murillo, Y.; Caballero-Herrera, J.A.; et al. Origin and driving mechanisms of marine litter in the shelf-incised Motril, Carchuna, and Calahonda canyons (northern Alboran Sea). *Front. Mar. Sci.* **2023**, *10*, 1098927. [CrossRef]
31. Ocaña, O.; Afonso-Carrillo, J.; Ballesteros, E. Massive proliferation of a dictyotalean species (Phaeophyceae, Ochrophyta) through the Strait of Gibraltar. *Rev. Acad. Canar. Cienc.* **2016**, *28*, 165–170.
32. Arroyo, N.L.; Bonsdorff, E. The role of drifting algae for marine biodiversity. In *Marine Macrophytes as Foundation Species*; Olafsson, E., Ed.; CRC Press: Boca Raton, FL, USA; Taylor & Francis Group: Abingdon, UK, 2016; p. 285. ISBN 978-1-4987-2324-4.
33. Bonsdorff, E. Drifting algae and zoobenthos—Effects on settling and community structure. *Neth. J. Sea Res.* **1992**, *30*, 57–62. [CrossRef]
34. Raffaelli, D. Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland. *Helgol. Mar. Res.* **2000**, *54*, 71–79. [CrossRef]
35. Correia, K.M.; Alford, S.B.; Belgrad, B.A.; Darnell, K.M.; Darnell, M.Z.; Furman, B.T.; Hall, M.O.; Hayes, C.T.; Martin, C.W.; McDonald, A.M.; et al. Drift macroalgae positively influence seagrass-associated nekton communities of the northern Gulf of Mexico. *Front. Environ. Sci.* **2022**, *10*, 939296. [CrossRef]
36. Roberts, M.J.; Wheeler, A.J.; Freiwald, A.; Cairns, S.D. *Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats*; Cambridge University Press: Cambridge, UK, 2009; pp. 1–336. ISBN 978-0-521-88485-3.

37. Rossi, S.; Bramanti, L.; Gori, A.; Orejas, C. *Marine Animal Forests. The Ecology of Benthic Biodiversity Hotspots*, 1st ed.; Springer: Dordrecht, The Netherlands, 2017; ISBN 978-3-319-21011-7.
38. Virnstein, R.W.; Carbonara, P.A. Seasonal abundance and distribution of drift algae and seagrasses in the mid-Indian River Lagoon, Florida. *Aquat. Bot.* **1985**, *23*, 67–82. [CrossRef]
39. Bell, S.S.; Hall, M.O. Drift macroalgal abundance in seagrass beds: Investigating large-scale associations with physical and biotic attributes. *Mar. Ecol. Prog. Ser.* **1997**, *147*, 277–283. [CrossRef]
40. Sempere-Valverde, J.; Ostalé-Valriberas, E.; Maestre, M.; González Aranda, R.; Bazairi, H.; Espinosa, F. Impacts of the non-indigenous seaweed *Rugulopteryx okamurae* on a Mediterranean coralligenous community (Strait of Gibraltar): The role of long-term monitoring. *Ecol. Indic.* **2021**, *121*, 107135. [CrossRef]
41. Garrabou, J.; Coma, R.; Bensoussan, N.; Bally, M.; Chevaldonné, P.; Cigliano, M.; Díaz, D.; Harmelin, J.G.; Gambi, M.C.; Kersting, D.K.; et al. Mass mortality in Northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. *Glob. Change Biol.* **2009**, *15*, 1090–1103. [CrossRef]
42. Linares, C.; Doak, D.F. Forecasting the combined effects of disparate disturbances on the persistence of long-lived gorgonians: A case study of *Paramuricea clavata*. *Mar. Ecol. Prog. Ser.* **2010**, *402*, 59–68. [CrossRef]
43. Angiolillo, M.; Fortibuoni, T. Impacts of marine litter on Mediterranean reef systems: From shallow to deep waters. *Front. Mar. Sci.* **2020**, *7*, 581966. [CrossRef]
44. Williams, G.C. The global diversity of Sea Pens (Cnidaria: Octocorallia: Pennatulacea). *PLoS ONE* **2011**, *6*, e22747. [CrossRef] [PubMed]
45. Valiela, I.; McClelland, J.; Hauxwell, J.; Behr, P.J.; Hersh, D.; Foreman, K. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.* **1997**, *42*, 1105–1118. [CrossRef]
46. Casal-Porras, I.; Zubía, E.; Brun, F.G. Dilkamural: A novel chemical weapon involved in the invasive capacity of the alga *Rugulopteryx okamurae* in the Strait of Gibraltar. *Estuar. Coast. Shelf Sci.* **2021**, *257*, 107398. [CrossRef]