HAL open science

Rapid Spread of the Invasive Brown Alga Rugulopteryx okamurae in a National Park in Provence (France, Mediterranean Sea)

Sandrine Ruitton, A. Blanfuné, Charles F. Boudouresque, Dorian Guillemain, Valerie Michotey, Sylvain Roblet, Delphine Thibault, Thierry Thibaut, Marc Verlaque

► To cite this version:

Sandrine Ruitton, A. Blanfuné, Charles F. Boudouresque, Dorian Guillemain, Valerie Michotey, et al.. Rapid Spread of the Invasive Brown Alga Rugulopteryx okamurae in a National Park in Provence (France, Mediterranean Sea). Water, 2021, 13 (16), pp.2306. 10.3390/w13162306 . hal-03342953

HAL Id: hal-03342953
https://hal.science/hal-03342953

Submitted on 14 Sep 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution 4.0 International License

water

MDPI

Article

Rapid Spread of the Invasive Brown Alga *Rugulopteryx okamurae* in a National Park in Provence (France, Mediterranean Sea)

Sandrine Ruitton [1,*], Aurélie Blanfuné [1], Charles-François Boudouresque [1], Dorian Guillemain [2], Valérie Michotey [1], Sylvain Roblet [1], Delphine Thibault [1], Thierry Thibaut [1] and Marc Verlaque [1]

[1] Aix Marseille Univ., Université de Toulon, CNRS, IRD, MIO, 13288 Marseille, France; aurelie.banfune-thibaut@mio.osupytheas.fr (A.B.); charles.boudouresque@mio.osupytheas.fr (C.-F.B.); valerie.michotey@mio.osupytheas.fr (V.M.); sylvain_roblet@yahoo.fr (S.R.); delphine.thibault@univ-amu.fr (D.T.); thierry.thibaut@mio.osupytheas.fr (T.T.); marc.verlaque@mio.osupytheas.fr (M.V.)

[2] OSU Institut Pythéas, CNRS, IRD, Aix Marseille University, Université de Toulon, 13288 Marseille, France; dorian.guillemain@osupytheas.fr

* Correspondence: sandrine.ruitton@univ-amu.fr; Tel.: +33-684871765

Abstract: The temperate Northwest Pacific brown alga *Rugulopteryx okamurae* (Dictyotales, Phaeophyceae) was first discovered in 2002 in the Mediterranean Sea in the Thau coastal lagoon (Occitania, France) and then again in 2015 along the southern side of the Strait of Gibraltar, where it was assigned with invasive status. We report here on the first occurrence of the species in the Northwest Mediterranean Sea in Calanques National Park (Marseille, France) in 2018. By 2020, a large population had developed, extending over 9.5 km of coastline, including highly protected no-take zones. The seafood trade, with *R. okamurae* used as packing material for sea urchin *Paracentrotus lividus* shipments from Thau Lagoon, could be the vector of its introduction into the Marseille area. As observed in the Strait of Gibraltar, *R. okamurae* is spreading rapidly along the Marseille coasts, suggesting an invasive pathway. The subtidal reefs are densely carpeted with *R. okamurae*, which overgrows most native algal species. Fragments of the alga are continuously detached by wave actions and currents, sedimenting on the seabed and potentially clogging fishing nets, and thus, impacting artisanal fishing or washing up on the beaches, where they rot and raise concern among local populations.

Keywords: invasive species; NIS; Mediterranean Sea; *Rugulopteryx okamurae*; global change

check for updates

Citation: 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. https://doi.org/10.3390/w13162306

Academic Editor: María Pilar Cabezas Rodríguez

Received: 6 July 2021
Accepted: 16 August 2021
Published: 23 August 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Non-indigenous species (NIS) are a part of global change. The Mediterranean Sea is considered the worldwide hotspot of biological invasions; it harbours almost 1000 NIS, more than 600 of which are definitively established (introduced or invasive) [1–4]. They originate from different source regions, both warm waters (e.g., the Red Sea) and cold waters (e.g., the Northwest Pacific) [5,6]. The Mediterranean can also function as a hub, exporting NIS; for example, the seagrass *Halophila stipulacea* (Forsskål) Ascherson, native to the Red Sea, transited through the Mediterranean Sea before being exported towards the Caribbean [6–9]. This highlights the fact that each new locality where an NIS is found can constitute a possible source for future introductions, even in distant localities and between oceans.

Originating from the temperate Northwest Pacific Ocean, in particular Japan and Korea, *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee and H.S. Kim (Dictyotales, Ochrophyta, kingdom Stramenopile) was reported for the first time outside its native area in European waters in 2002, in the coastal lagoon of Thau (Occitania, France, Mediterranean, [10]). In view of the extent of the colonized area when it was discovered, totalling a dozen kilometres of shoreline, its introduction probably preceded 2002. This first introduction is probably linked to the oyster farming facilities of *Magallana gigas* (Thunberg, 1793) regularly importing spat from Japan. Since then, *R. okamurae* has established a large population within this lagoon, mixed with many other algae introduced from the Northwest Pacific [11]. In 2015, *R. okamurae* was, for the first time, recorded in the Mediterranean open sea in the southern (Ceuta, Spain, and Morocco) and northern (Spain) sides of the Strait of Gibraltar, where it quickly became invasive [12–15]. From 2015 to 2020, *R. okamurae* exhibited extensive northerly and southerly geographical expansion from these two initial locations, along both the Atlantic and the Mediterranean coasts, ranking among the most invasive NIS in the Mediterranean Sea [14,16].

In its native area, the alga dwells on sublittoral rocky substrata from 0.5 to 35.0 m deep [17], while it can occur down to 40.0 m deep in the northern Bay of Ceuta (southern sector of the Strait of Gibraltar) [14]. Here, we report on the first sighting of *R. okamurae* in the Northwest Mediterranean open sea, in the marine protected area (MPA) of Calanques National Park (hereafter—CNP, Provence, France), and its rapid spread, with findings on its distribution and life cycle and hypotheses regarding its origin.

2. Materials and Methods

The CNP was established in 2012. It includes both terrestrial and marine areas and stretches from La Ciotat (east) to Marseille (west) (Figure 1). The land area covers 85 km^2 (land core area) and 26 km^2 (surrounding area). The marine area covers 435 km^2 (marine core area, including 58 km^2 of no-take zones (NTZ) and a small reinforced protection zone) and 977 km^2 (adjacent marine area—AMA) [18,19]. It is important to emphasize that the regulations of the CNP are effectively implemented and are well respected by users.

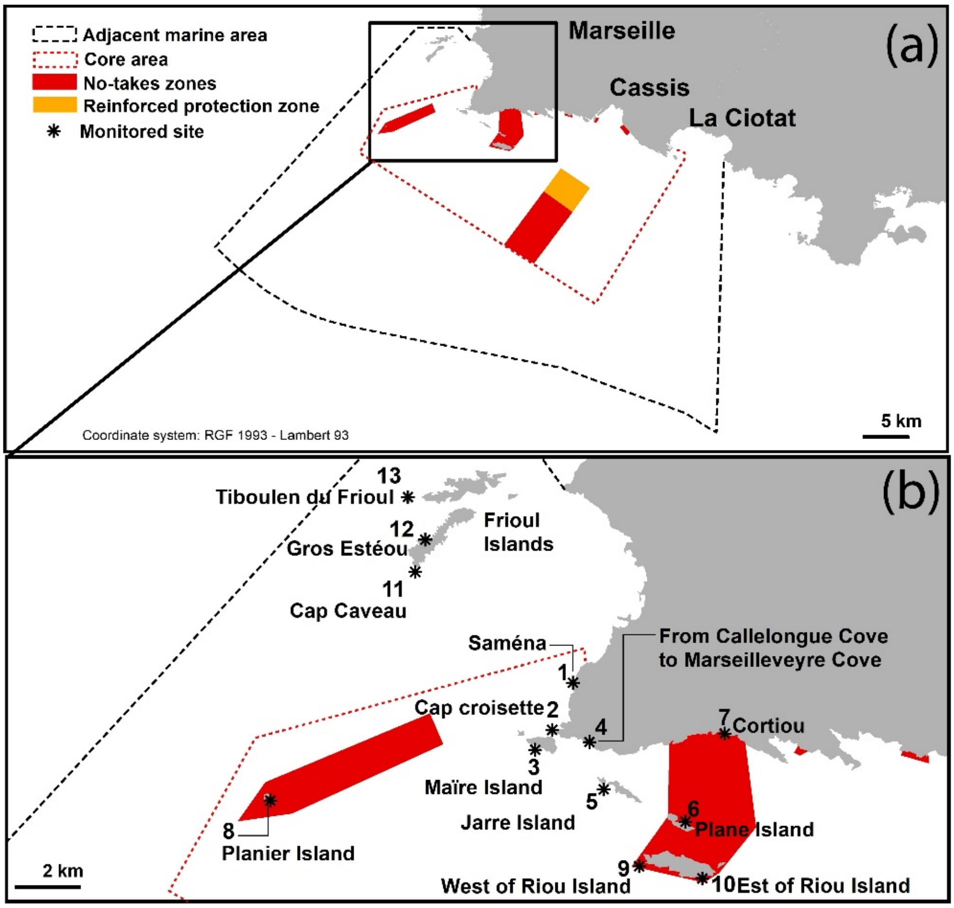

Figure 1. Calanque National Park (CNP), with boundaries and zoning (**a**) and monitored sites (**b**).

Field surveys on the benthic macroalgae and organisms as well as fish communities have been carried out by SCUBA diving within the framework of several research programmes aimed at monitoring the ecological status of the marine ecosystems of Calanques National Park. A compilation of all the macroalgae found within CNP is available [20].

Since the early 2000s, yearly routines on the benthic ecosystems and fish surveys have been conducted in several sites from the Frioul Islands (Site 13) to the Riou Island (Site 10) (Figure 1). Sites 11 through 13 are located within the AMA of CNP, 1 through 5 in the marine core area and 6 through 10 in the NTZs of CNP. In 2018 (first sighting of *Rugulopteryx okamurae*), 2019 and 2020, the 13 sites were thoroughly monitored (Figures 1 and 2), enabling the mapping of occurrence of *R. okamurae* and the building of a photographic database. In addition to these 13 sites, a few occasional observations were made at additional sites. The monitoring consisted of visiting each site on a yearly basis between April and September (a period of widespread development of *R. okamurae*). At each site, an area of about 150 m long, and between 0 and 20 m deep, was covered by 3 scientific divers where *R. okamurae* was searched for over the rocky substratum. About twenty photographs were taken at each site to document the whole algal community's coverage and composition with depth. Where *R. okamurae* was present, 5 photos were taken at 50 cm from the substrate to estimate the alga coverage using an image analysis tool. At Sites 2, 3 and 4, where *R. okamurae* was strongly established, wider explorations of the area were conducted to determine the limits of its range, and GPS positions were noted. All the results were implemented on a geographical information system (ArcGIS pro 2.7 ESRI®) to estimate the distance of coastline impacted by the alga.

In February 2019, at Site 3 (43°12.680° N, 05°20.385′ E; rocky substrate, Figure 2), the first site where *Rugulopteryx okamurae* was discovered, the surface covered by this alga was estimated (%) by the visual examination of twenty 1 m^2 quadrats, at 5 and 12 m deep. In September 2020, the wet and dry biomass of *R. okamurae* was assessed by collecting attached specimens within 5 quadrats of 400 cm^2 at 6 m deep, corresponding to the maximum development of *R. okamurae*. The wet biomass was measured by weighing the algae on an Ohaus Navigator XT scale to the nearest 0.1 g after placing them on absorbent paper for 10 min. Algae were then placed in a drying oven at 60 °C until a constant weight was reached, and the dry weight was then measured.

Morphological identification of *R. okamurae* was done according to the methods of [10,21]. It is worth emphasizing that the authors, who participated in the discovery of *R. okamurae* in the Thau Lagoon [10,11] and were very familiar with this species and all the macroalgae in the region, were easily alerted at the first sight of this species in Marseille.

3. Results

3.1. Observation and Species Expansion

Analysis of the photographic database between the early 2000s and 2017 did not reveal the presence of *R. okamurae* at any site; the first observation of clumps of this species was dated July 2018 (Site 3, Figure 2). Dense populations (covering up to 85%) were reported, in February 2019 only, all around Maïre Island (Site 3) and along the adjacent mainland coast (Site 4), between 3 m and 15 m deep, on rocky reefs (Figures 3 and 4). The impacted coastline was then estimated to be 5978 m long. By the end of 2020, newly invaded sites were detected (Sites 1, 2, 5 and 6; Table 1) and the affected coastline reached 9569 m. Only sublittoral reefs have been colonized so far; *R. okamurae* was not observed either on sandy habitats or in the seagrass *Posidonia oceanica* (Linnaeus) Delile meadows.

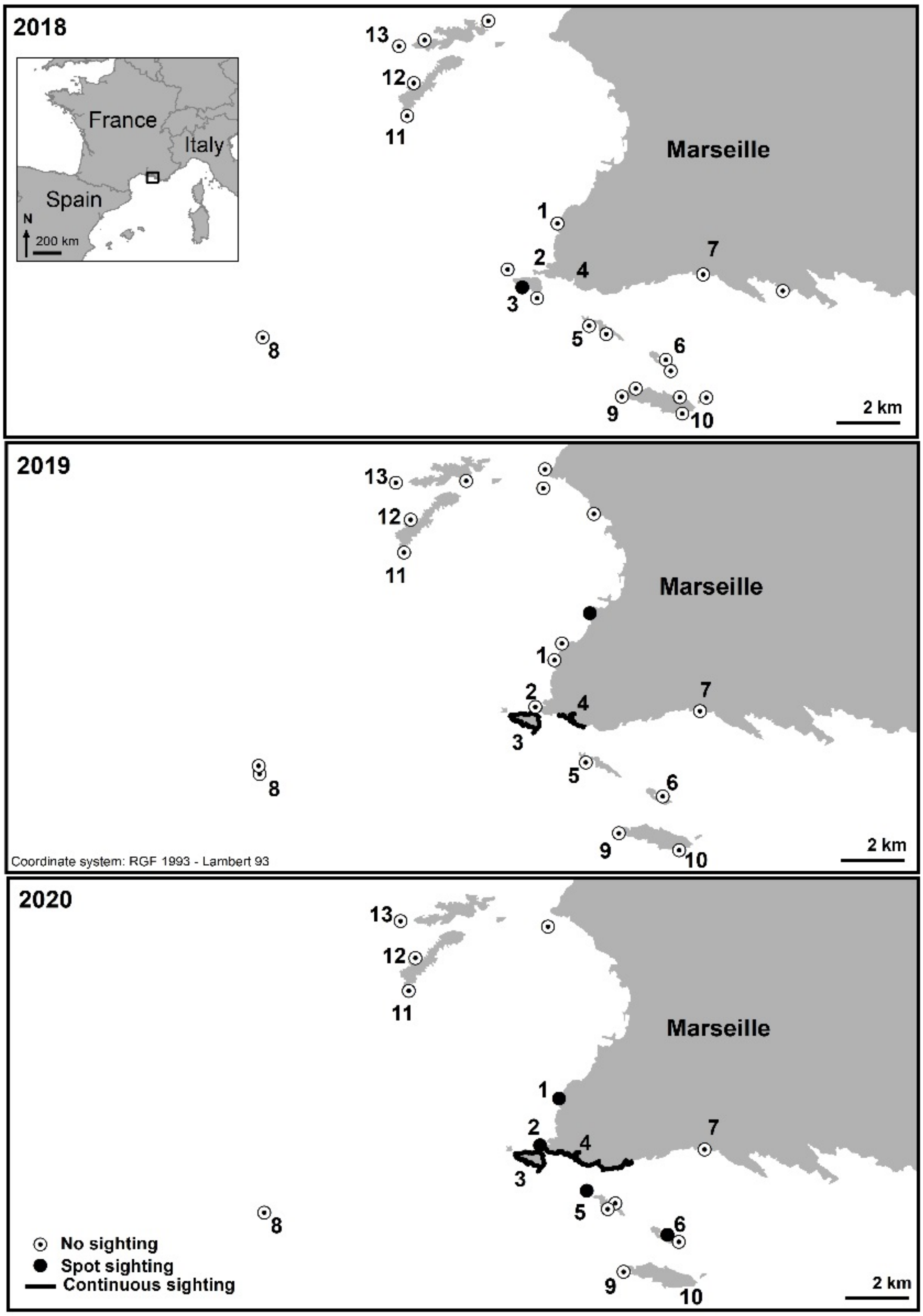

Figure 2. Maps of the extension of *Rugulopteryx okamurae* in 2018, 2019 and 2020. Numbers correspond to the monitored sites. Unnumbered points are additional sites that were visited occasionally.

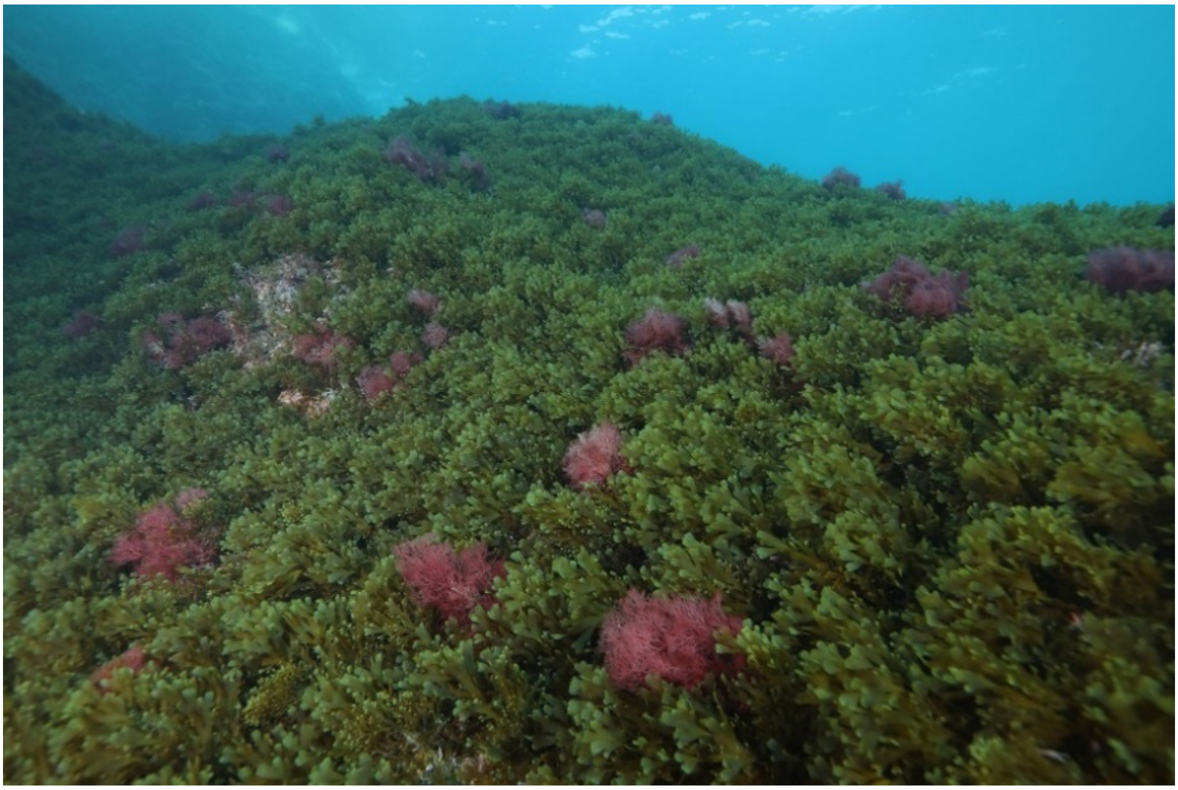

Figure 3. A rocky reef carpeted with *Rugulopteryx okamurae* in February 2019. Red seaweeds are *Sphaerococcus coronopifolius* Stackhouse, a native species. Photo © Sandrine Ruitton.

Figure 4. *Rugulopteryx okamurae* in February 2019. Photo © Sandrine Ruitton.

Table 1. *Rugulopteryx okamurae* presence and the main characteristics of distribution (% cover, depth) at the study sites. See Figure 1 for the locations of the sites with their number (No.).

No.	Sites	2018	2019	2020
1	Saména	No sighting	No sighting	Spot sighting, from 3 to 4 m deep. Percentage cover < 1%.
2	Cap Croisette	No sighting	No sighting	Spot sighting. Percentage cover < 1% from 1.4 to 3 m deep, reaching 20% at 3–6 m deep.
3	Maïre Island	No in situ sighting but spot sighting in the south of the island (a posteriori photo analysis).	Continuous sighting all around the island. Percentage cover reaching 85% at 5 m deep and 69% at 12 m deep. Maximum sighted depth: 20 m.	Continuous sighting all around the island. Maximum sighted depth: 25 m.
4	Coast from Callelongue Cove to Marseilleveyre Cove	No sighting	Continuous sighting, from 3 to 12 m deep. Percentage cover reaching 60% at this depth.	Continuous sighting. Percentage cover reaching 80% in some areas, around 6 m deep.
5	Jarre Island	No sighting	No sighting	Spot sighting only on the north side of the island, at 3 to 5 m deep. Percentage cover < 1%.
6	Plane Island	No sighting	No sighting	Spot sighting only on the northwest side of the island, at 3 to 5 m deep. Percentage cover around 2%.
7	Cortiou	No sighting	No sighting	No sighting
8	Planier Island	No sighting	No sighting	No sighting
9	West of Riou Island	No sighting	No sighting	No sighting
10	East of Riou Island	No sighting	No sighting	No sighting
11	Cap Caveau, Frioul Island	No sighting	No sighting	No sighting
12	Gros Estéou, Frioul Island	No sighting	No sighting	No sighting
13	Tiboulen du Frioul, Frioul Island	No sighting	No sighting	No sighting

Since 2018, the expansion of *R. okamurae* has been rapid and overwhelming (Figure 2) and the species seems to have settled durably in the Marseille area. The NTZ (Site 6) does not constitute a barrier to its spread.

3.2. Life Cycle and Impact

Dense populations of *R. okamurae* have been observed year-round since mid-2018, with maximums occurring during spring to late summer. In September 2020, off the south coast of the Maïre Island, the mean wet and dry biomass weights at 6 m deep were 1131.5 g.m^{-2} (SD = 201.7) and 149.0 g.m^{-2} (SD = 31.1), respectively. From spring to autumn, fragments break off from the substrate even without strong hydrodynamism and form large accumulations of drifting litter over the bottom (layers of up to 60 cm thick have been reported), while other fragments remain floating in the water column. Some of these drifting algae are swept away by currents and can pile up in protected areas, such as in the Callelongue Cove (between Sites 2 and 4), where they wash ashore (Figure 5). In winter, *R. okamurae* is still far spread. At the most colonized site, it covered up to 85% (SD = 13) of the substrate at 5 m deep and 69% (SD = 21) at 12 m deep in February 2019 (Table 1).

In Marseille, sublittoral reef canopy-forming *Cystoseira* (sensu lato) forests have been almost eradicated within the last century, as in many other Mediterranean areas, because of pollution, overfishing, and the resulting overgrazing [22,23]. The native reef communities are now bush-like stands dominated by *Corallina ferreyrae* E.Y. Dawson, Acleto, and Foldvik (syn. *C. caespitosa* R.H. Walker, J. Brodie, and L.M. Irvine) and *Halopteris scoparia* (Linnaeus) Sauvageau. In areas invaded by *R. okamurae*, the main native algal species that still remain are, in order of decreasing abundance, *Corallina ferreyrae*, *Sphaerococcus coronopifolius* Stackhouse (Figure 3), and *Codium bursa* (Linnaeus) C. Agardh.

All individuals of *R. okamurae* attached to the substrate were intact without epibionts or any evidence of grazing, which could be an indication of chemical defence. In autumn, during the senescence period, that is, when fragments of individuals break away from the substrate, a few epibionts were observed colonizing the alga.

Figure 5. A heap of dry fragments of *Rugulopteryx okamurae* cast ashore at the head of the Callelongue Cove (between Sites 2 and 4, see Figure 2), early June 2021. The girl (Emma Thibaut, 140 cm tall) gives the scale. Photo © Thierry Thibaut.

4. Discussion

4.1. Spread

Since its first observation in the Marseille area in July 2018, *Rugulopteryx okamurae* has rapidly established an extensive population, from Cap Croisette to Marseilleveyre Cove and around Maïre Island, showing a steady increase in its spatial distribution. Despite occurring for 20 years or more in the Thau Lagoon, *R. okamurae* has not displayed such invasive behaviour there as in the Strait of Gibraltar and in Marseille [10]. This might be due to its drastic regression during winter, which is probably linked to the low surface temperature of the lagoon during this period (down to 4–5 °C in January; [24]). Conversely, in Marseille, with the winter sea surface temperature usually above 13 °C, this alga persists throughout the winter, and therefore, rapidly spreading when conditions are favourable. A similarly rapid spread and invasive behaviour have also been reported in the Strait of Gibraltar [14].

The question of how *Rugulopteryx okamurae* spreads remains unresolved. In Thau Lagoon, Marseille (France) and Spain, no gametophytes have ever been observed so far [10,13,16], as they were in its source area (Japan [25]). Asexual reproduction with vegetative propagation by forming propagules (proliferous branchlets arising on the thallus surface) that grow into new plants appeared to be the main mode of reproduction in sink areas [17]. The absence of sexual reproduction is a common feature of invasive macroalgae in the Mediterranean [26]. This has been observed, in particular, for the green algae *Codium fragile* (Suringar) Hariot subsp. *tomentosoides* (Van Goor) P.C. Silva [27] and *Caulerpa* *taxifolia* (M. Vahl) C. Agardh [28,29] and the red alga *Womersleyella setacea* (Hollenberg) R.E. Norris [30–32].

In Marseille, the discovery of *Rugulopteryx okamurae* was made through routine and long-term monitoring of the marine environment. Field surveys and environmental monitoring by scientists allow for the early detection of NIS as well as the ability to carry out studies to identify the drivers of biological invasions and their consequences.

4.2. Origin

In the Thau Lagoon, the introduction of *R. okamurae* was linked to the import of spat of the Japanese oyster *Magallana gigas* from Japan and Korea for aquaculture [10,11]. In the Strait of Gibraltar (Spain), it is presumed that the vector of introduction could be maritime transportation by ballast waters from Asian vessels that transit through the Strait of Gibraltar [14,33]. According to [14], the large bloom in the south of the Iberian Peninsula is probably linked to a temperature peak in July 2015 (23.9 °C) and, more generally, with global climate change, while the species may have already been present but unnoticed in the region for several years due to possible confusion with *Dictyota pinnatifida* Kützing. Under these conditions, this invasion could be described as cryptic in its early stages.

In France, the probability of a natural spread from Thau to Marseille (150 km in a straight line), is very low, considering the dominant westwards Northwest Mediterranean current systems [34] and the absence of known intermediate populations. A few clumps of the alga were seen at Cap d'Agde (Occitania, France), in 2013 (T. Thibaut and M. Verlaque, personal communication), a few kilometres west of the Thau Lagoon, a location coherent with the dominant current. In Marseille, the introduction of *R. okamurae* by ships coming from the Pacific Ocean is possible (due to a potential release of ballast water upon arrival at the port of Fos, west of Marseille, which is strictly forbidden) but unlikely; no *R. okamurae* has been observed near or inside the harbour. Its introduction is more probably related to the importing of live shellfish or sea urchins (*Paracentrotus lividus* (Lamarck, 1816)) for human consumption since fresh specimens of *R. okamurae*, used as packing material for *P. lividus* from Thau Lagoon, were found at a local fish market in Marseille (M. Verlaque, personal communication, 10 January 2021). Sea urchins are considered a delicacy and their consumption is very popular in Provence. Our hypothesis is that sea urchins were carried to sea by recreational boaters as food supply, and that tests and packing material were then thrown overboard. Introductions related to seafood packing material have already been reported (see e.g., [35]).

Overall, the Thau, Gibraltar and Marseille populations could result from distinct introduction events. The Marseille population corresponds either to a distinct introduction event or to a dispersal via a secondary vector from Thau (e.g., seafood trade) illustrated by the hopscotch jump model. Once in a region (Thau, Strait of Gibraltar and Marseille), the spread of *R. okamurae* follows the diffusion dispersal pattern (wave of the advance model) (see [36] for dispersal models).

4.3. Impact

In Ceuta (south sector of the Strait of Gibraltar), large biomasses of *R. okamurae* have resulted in recurrent massive strandings on the beaches since 2017, localised downstream of the prevailing current [15]. More than 5000 metric tonnes of stranded *R. okamurae* has been removed from the beaches, and fishermen have reported the clogging of fishing nets resulting in a decline in fish catches [15]. In Marseille, the same has been occurring, with artisanal fishermen complaining that drifting *R. okamurae* clog their nets (September/October 2020), making them less efficient and heavier to lift back onboard the boat (Sandrine Ruitton, personal communication). Invaded areas are becoming unsuitable for fishing, down to 10 m deep. In semi-enclosed, very shallow and small coves, such as the Callelongue Cove, *R. okamurae* accumulated over the shore in long wide mats, which rotted and produced H_2S, bothering local inhabitants and sea-goers (Figure 5).

In the Strait of Gibraltar (Spain and Morroco), *R. okamurae* has become the dominant alga on the coastal rocky bottoms and replaced the native species *Dictyota dichotoma* (Hudson) J.V. Lamouroux [37], leading to a major change in the macrofaunal assemblages with a higher number of species and abundance of individuals and profound alteration of the species composition of autochthonous macroalgal communities. When the other invasive algae *Asparagopsis armata* Harvey, *A. taxiformis* (Delile) Trevisan and *Caulerpa cylindracea* Sonder were also present, *R. okamurae* appeared to be the most competitive and displaced the three former species [13]. No herbivory has been reported on this alga, which is strongly linked to the presence of anti-herbivory diterpenes [38].

Rugulopteryx okamurae caused a shift in the coralligenous habitat of Jbel Moussa (southern Strait of Gibraltar, west of Ceuta). In only one year, *R. okamurae* became the most abundant species and carpeted the native community, leading to an increase in the number of dead colonies of the red gorgonian *Paramuricea clavata* (Risso, 1826) and a significant decline in the cover of the red alga key species *Mesophyllum expansum* (Philippi) Cabioch and M.L. Mendoza (Corallinaceae) [16,39,40].

Both in the Strait of Gibraltar and in Marseille, *R. okamurae* does not respect the boundaries of marine protected areas, and its impact is as strong within as outside them. This has been demonstrated in many introduced species in the Mediterranean and worldwide [41–45], and once again contradicts the old theory of Charles Elton [46] regarding the resistance of pristine ecosystems to biological invasions (ecological resistance theory) [47].

5. Conclusions

Clearly, *R. okamurae* can induce significant changes in benthic assemblages and the functioning of marine ecosystems. Therefore, it is important to monitor the fate of this invasion (spread, stabilization, or natural decline; see [47]), which is part of the current dynamics of global change. *Rugulopteryx okamurae* can also cause discomfort (unpleasant smells) for the inhabitants and impact the activity of artisanal fishing. The boundaries of a national park (MPA) do not restrict its expansion. Finally, seafood trade should be subject to precautionary measures regarding their capacity as a vector in the dispersal of introduced species, which is not currently the case.

Author Contributions: Conceptualization, S.R. (Sandrine Ruitton), A.B., C.-F.B., T.T. and M.V.; methodology, S.R. (Sandrine Ruitton) and T.T.; fieldwork, S.R. (Sandrine Ruitton), A.B., D.G., D.T., S.R. (Sylvain Roblet) and T.T.; writing, S.R. (Sandrine Ruitton), A.B., C.-F.B., V.M. and D.T. All authors have read and agreed to the published version of the manuscript.

Funding: Many thanks to FR ECCOREV funding for the financial support. The project leading to this publication has received funding from the European FEDER Fund under project 1166-39417 and from the Excellence Initiative of Aix-Marseille University—A*MIDEX, a French "Investissements d'Avenir" programme.

Institutional Review Board Statement: Not applicable.

Informed Content Statement: Not applicable.

Data Availability Statement: The data presented in this study are available upon request from the corresponding author.

Acknowledgments: This work was carried out through field surveys with marine facilities using surface vessels and support teams from OSU Institut Pythéas and Institut National des Sciences de l'Univers. The authors would also like to thank the Calanques National Park's field teams for their observations. The authors are indebted to Michael Paul, a native English speaker, for proofreading the text and to two anonymous reviewers for their valuable suggestions.

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

Studied Specimens: Voucher dried specimens of *Rugulopteryx okamurae* (E.Y. Dawson) I.K Hwang, W.J. Lee and H.S. Kim were deposited in the Marseille University herbarium (HCOM), Marseille, France, with the following references: H8334-H8338, Marseille, Maïre Island, Les Fromages (Provence), 6 February 2019, 6 m deep, Coll. S. Ruitton. H8339, Marseille (Provence), January 2010, on a fishmonger's stall, mixed with sea urchins (*Paracentrotus lividus*) from the Thau Lagoon, Coll. M. Verlaque. H. 8340-H8341, Cap d'Agde, Roche Longue Môle (Occitania), 16 July 2013, Coll. M. Verlaque and T. Thibaut.

References

1. Galil, B.S. A sea under siege-alien species in the Mediterranean. *Biol. Invasions* **2000**, *2*, 177–186. [CrossRef]
2. Zenetos, A. Trend in alien species in the Mediterranean. An answer to Galil, 2009 "Taking stock: Inventory of alien species in the Mediterranean Sea". *Biol. Invasions* **2010**, *12*, 3379–3381. [CrossRef]
3. Ulman, A.; Ferrario, J.; Occhipinti-Ambrogi, A.; Arvanitidis, C.; Bandi, A.; Bertolino, M.; Bogi, C.; Chatzigeorgiou, G.; Çiçek, B.A.; Deidun, A.; et al. A massive update of non-indigenous species records in Mediterranean marinas. *PeerJ* **2017**, *5*, 1–59.
4. Galil, B.S.; Marchini, A.; Occhipinti-Ambrogi, A. East is east and West is west? Management of marine bioinvasions in the Mediterranean Sea. *Estuar. Coast. Shelf Sci.* **2018**, *201*, 7–16. [CrossRef]
5. Boudouresque, C.F.; Verlaque, M. Is global warming involved in the success of seaweed introductions in the Mediterranean Sea? In *Seaweeds and Their Role in Globally Changing Environments*; Israel, A., Einav, R., Seckbach, J., Eds.; Springer Publisher: Dordrecht, The Netherlands, 2010; pp. 31–50.
6. Boudouresque, C.F.; Perret-Boudouresque, M.; Verlaque, M. Donor and recipient regions for exotic species of marine macrophytes: A case of unidirectional flow, the Mediterranean Sea. *Rapp. Comm. Intl. Mer Méditerr.* **2016**, *41*, 426.
7. Ruiz, H.; Ballantine, D.L. Occurrence of the seagrass *Halophila stipulacea* in the tropical West Atlantic. *Bull. Mar. Sci.* **2004**, *75*, 131–135.
8. Willette, D.A.; Ambrose, R.F. The distribution and expansion of the invasive seagrass *Halophila stipulacea* in Dominica, West Indies, with a preliminary report from St. Lucia. *Aquat. Bot.* **2009**, *91*, 137–142. [CrossRef]
9. Maréchal, J.P.; Meesters, E.H.; Vedie, F.; Hellio, C. Occurrence of the alien seagrass *Halophila stipulacea* in Martinique (French West Indies). *Mar. Biodiv. Rec.* **2013**, *6*, 1–5. [CrossRef]
10. Verlaque, M.; Steen, F.; De Clerck, O. *Rugulopteryx* (Dictyotales, Phaeophyceae), a genus recently introduced to the Mediterranean. *Phycologia* **2009**, *48*, 536–542. [CrossRef]
11. Boudouresque, C.F.; Klein, J.; Ruitton, S.; Verlaque, M. Biological invasion: The Thau lagoon, a Japanese biological island in the Mediterranean Sea. In *Global Change: Mankind-Marine Environment Interactions*; Ceccaldi, H.J., Dekeyser, I., Girault, M., Stora, G., Eds.; Springer Publisher: Dordrecht, The Netherlands, 2011; pp. 151–156.
12. Ocaña, O.; Alfonso-Carrillo, J.M.; Ballesteros, E. Massive proliferation of a dictyotalean species (Phaeophyceae, Ochrophyta) through the Strait of Gibraltar. *Rev. Acad. Canaria Cienc.* **2016**, *28*, 165–169.
13. 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. *Rev. Estud. Campogibraltareños* **2018**, *49*, 97–113.
14. 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*, 1–9. [CrossRef] [PubMed]
15. Sempere-Valverde, J.; García-Gómez, J.C.; Ostalé-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, Proceedings of the 1st Mediterranean symposium on the non-indigenous species, Antalya, Turkey, 18 January 2019*; Langar, H., Ouerghi, A., Eds.; RAC/SPA Publisher: Tunis, Tunisia, 2019; pp. 107–108.
16. García-Gómez, J.C.; Florido, M.; Olaya-Ponzone, L.; Díaz de Rada, J.R.; Donázar-Aramendia, I.; Chacón, M.; Quintero, J.J.; Magariño, 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*, 1–18. [CrossRef]
17. Hwang, I.K.; Lee, W.J.; Kim, H.S.; De Clerck, O. Taxonomic reappraisal of *Dilophus okamurae* (Dictyotales, Phaeophyta) from the western Pacific Ocean. *Phycologia* **2009**, *48*, 1–12. [CrossRef]
18. Meinesz, A. Les Aires marines naturelles protégées du Parc national des Calanques. In *Méditerranée mer Vivante*, 20th ed.; Meinesz, A., Ed.; Lions Club Nice Doyen Publisher: Nice, France, 2020; pp. 232–234.
19. Parc National des Calanques. Available online: www.calanques-parcnational.fr.2021 (accessed on 12 May 2021).
20. Blanfuné, A.; Boudouresque, C.F.; Perret-Boudouresque, M.; Ruitton, S.; Sevaux, L.; Verlaque, M.; Thibaut, T. *Inventaire des Macroalgues du Parc national des Calanques*; Parc national des Calanques and MIO Publisher: Marseille, France, 2017; pp. 1–33.
21. Verlaque, M.; Ruitton, S.; Mineur, F.; Boudouresque, C.F. CIESM Atlas of exotic species. In *4. Macrophytes*; Briand, F., Ed.; CIESM Publisher: Monaco, Monaco, 2015; pp. 1–362.
22. Thibaut, T.; Pinedo, S.; Torras, X.; Ballesteros, E. Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean). *Mar. Pollut. Bull.* **2005**, *50*, 1472–1489. [CrossRef]

23. Thibaut, T.; Blanfuné, A.; Boudouresque, C.F.; Verlaque, M. Decline and local extinction of Fucales in the French Riviera: The harbinger of future extinctions Mediterr. *Mar. Sci.* **2015**, *16*, 206–224.
24. Ifremer. Réseau Velyger-Observatoire de la Reproduction et du Recrutement de l'huître en France. *Lagune de Thau.* 2021. Available online: https://wwz.ifremer.fr/velyger/Acces-aux-Donnees/Lagune-de-Thau/Temperature (accessed on 13 April 2021).
25. Agatsuma, Y.; Kuwahara, Y.; Taniguchi, K. Life cycle of *Dilophus okamurae* (Phaeophyceae) and its associated invertebrate fauna in Onagawa Bay, Japan. *Fish. Sci.* **2005**, *71*, 1107–1114. [CrossRef]
26. Ribera, M.A.; Boudouresque, C.F. Introduced marine plants, with special reference to macroalgae: Mechanisms and impact. In *Progress in Phycological Research*; Round, F.E., Chapman, D.J., Eds.; Biopress Ltd. Publisher: Bristol, UK, 1995; Volume 11, pp. 187–268.
27. Feldmann, J. Sur la parthénogénèse du *Codium fragile* (Sur.) Hariot dans la Méditerranée. *C.R. Acad. Sci.* **1956**, *243*, 305–307.
28. Meinesz, A. Modes de dissémination de l'algue *Caulerpa taxifolia* introduite en Méditerranée. *Rapp. Comm. Intl. Mer Méditerr.* **1992**, *33*, 44.
29. Žuljević, A.; Antolić, A. Synchronous release of male gametes of *Caulerpa taxifolia* (Caulerpales, Chlorophyta) in the Mediterranean Sea. *Phycologia* **2000**, *39*, 157–159. [CrossRef]
30. Verlaque, M. Contribution à la flore des algues marines de Méditerranée. Espèces rares ou nouvelles pour les côtes françaises. *Bot. Mar.* **1989**, *32*, 101–113. [CrossRef]
31. Cormaci, M.; Furnari, G.; Alongi, G.; Serio, D. On three interesting marine red algae (Ceramiales, Rhodophyta) from the Mediterranean Sea. *G. Bot. Ital.* **1994**, *128*, 1001–1006. [CrossRef]
32. Nikolić, V.; Žuljević, A.; Antolić, B.; Despalotović, M.; Cvitković, I. Distribution of invasive red alga *Womersleyella setacea* (Hollenberg) R.E. Norris (Rhodophyta, Ceramiales) in the Adriatic Sea. *Acta Adriatica* **2010**, *51*, 195–202.
33. Verdú Baeza, J. España y los problemas de aplicación del convenio de aguas de lastre en el área del estrecho de gibraltar. A propósito del alga invasora *Rugulopterix okamurae*. *Rev. Esp. Derecho Intl. Sección Estudios* **2020**, *72*, 261–287. [CrossRef]
34. Guihou, K.; Marmain, J.; Ourmières, Y.; Molcard, A.; Zakardjian, B.; Forget, P. A case study of the mesoscale dynamics in the North-Western Mediterranean Sea: A combined data–model approach. *Ocean Dynam.* **2013**, *63*, 793–808. [CrossRef]
35. Miller, R.L. *Ascophyllum nodosum*: A source of exotic invertebrates introduced into west coast near-shore marine waters. *Veliger* **1969**, *12*, 230–231.
36. Mineur, F.; Davies, A.J.; Maggs, C.A.; Verlaque, M.; Johnson, M.P. Fronts, jumps and secondary introductions suggested as different invasion patterns in marine species, with an increase in spread rates over time. *Proc. Roy. Soc. B Biol. Sci.* **2010**, *277*, 2693–2701. [CrossRef]
37. Navarro-Barranco, C.; Muñoz-Gómez, B.; Guerra-García, J.M.; Altamirano, M.; Ostalé-Valriberas, E.; Moreira, J. Can invasive habitat-forming species play the same role as native ones? The case of the exotic marine macroalga *Rugulopteryx okamurae* in the Strait of Gibraltar. *Biol. Invasions* **2019**, *21*, 3319–3334. [CrossRef]
38. Paula, J.C.D.; Vallim, M.A.; Teixeira, V.L. What are and where are the bioactive terpenoids metabolites from *Dictyotaceae* (Phaeophyceae). *Rev. Bras. Farmacogn.* **2011**, *21*, 216–228. [CrossRef]
39. García-Gómez, J.C.; Floridon, M.; Olaya-Ponzone, L.; Sempere-Valverde, J.; Megina, C. The invasive macroalga *Rugulopteryx okamurae*: Substrata plasticity and spatial colonization pressure on resident macroalgae. *Front. Ecol. Evol.* **2021**, *9*, 1–15. [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*, 1–5. [CrossRef]
41. Simberloff, D. No reserve is an island: Marine reserves and nonindigenous species. *Bull. Mar. Sci.* **2000**, *66*, 567–580.
42. Katsanevakis, S.; Issaris, Y.; Poursanidis, D.; Thessalou-Legaki, M. Vulnerability of marine habitats to the invasive green alga *Caulerpa racemosa* var. *cylindracea within a marine protected area. Mar. Environ. Res.* **2010**, *70*, 210–218.
43. Carlton, J.T.; Keith, I.; Ruiz, G.M. Assessing marine bioinvasions in the Galápagos Islands: Implications for conservation biology and marine protected areas. *Aquat. Invasions* **2019**, *14*, 1–20. [CrossRef]
44. Giakoumi, S.; Pey, A.; Di Franco, A.; Francour, P.; Kizilkaya, Z.; Arda, Y.; Raybaud, V.; Guidetti, P. Exploring the relationships between marine protected areas and invasive fish in the world's most invaded seas. *Ecol. Appl.* **2019**, *29*, 1–12. [CrossRef]
45. Mannino, A.M.; Balistreri, P. Invasive alien species in Mediterranean Marine Protected Areas: The Egadi Islands (Italy) case study. *Biodiversity* **2021**, *10*, 1–11. [CrossRef]
46. Elton, C.S. *The Ecology of Invasions by Animals and Plants*; Methuen: London, UK, 1958.
47. Boudouresque, C.F.; Verlaque, M. An overview of species introduction and invasion processes in marine and coastal lagoon habitats. *Cah. Biol. Mar.* **2012**, *53*, 309–317.