BioInvasions Records (2022) Volume 11, Issue 4: 925–936

Rapid Communication

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)

Rocío M. Estévez[1], Marina Palacios[2], Juan Lucas Cervera[1,3] and Manuel M. González-Duarte[4,*]

[1]*Departamento de Biología, Facultad de Ciencias del Mar y Ambientales, Campus de Excelencia Internacional del Mar (CEIMAR), Universidad de Cádiz, Avenida República Saharaui s/n, Apartado 40, Puerto Real (Cádiz), 11510 Spain*

[2]*Coral Soul, Paseo Andrés Segovia, Nº67, La Herradura (Granada), 18697 Spain*

[3]*Instituto Universitario de Investigación Marina (INMAR), Campus de Excelencia Internacional del Mar (CEIMAR), Universidad de Cádiz, Avenida República Saharaui s/n, Apartado 40, 11510 Puerto Real (Cádiz), Spain*

[4]*Centro Oceanográfico de Cádiz, CN - Instituto Español de Oceanografía (IEO-CSIC), Muelle de Levante, Puerto Pesquero s/n, Cádiz, 11006, Spain*

**Corresponding author*

E-mails: *manuel.gonzalez@ieo.csic.es*, *mangonduarte@gmail.com*

Citation: Estévez RM, Palacios M, Cervera JL, González-Duarte MM (2022) 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 Records* 11(4): 925–936, https://doi.org/10.3391/bir.2022.11.4.11

Received: 6 April 2022

Accepted: 21 July 2022

Published: 8 November 2022

Handling editor: Javier Atalah

Thematic editor: April Blakeslee

Copyright: © Estévez et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS

Abstract

The Mediterranean Sea is one of the main hotspots for the introduction of nonindigenous species in the world. The invasive alga *Rugulopteryx okamurae* was detected in 2015 along the coasts of the Strait of Gibraltar, the Atlantic entrance to the Mediterranean Sea. This brown seaweed of Asian origin, with an enormous expansion capacity and high survival rate, has spread rapidly across the Alboran Sea (western Mediterranean). Nevertheless, this species continues to show its highest abundance in areas close to the Strait of Gibraltar. We recorded *R. okamurae* in Punta de la Mona (Granada, northern coast of the Alboran Sea), one of the zones with the highest marine biodiversity in the Alboran Sea. This record is the easternmost point within the Spanish coasts where abundance data for this invasive species are available. *Rugulopteryx okamurae* demonstrated its highest abundance values at 48 m, an unusual record for this species in the Mediterranean Sea. We found *R. okamurae* growing on rocky bottoms, multiple coralligenous organisms, artificial substrates and epiphyting the coral *Dendrophyllia ramea* (an important habitat-forming species). Cold-water corals provide substrate, shelter and habitat for other species and play a critical role in deep water ecosystems. It is crucial to study and quantify the possible effects of invasive species on habitat-forming species, especially in the Mediterranean Sea, where the arrival of exotic organisms is striking; a better understanding of their dispersal capacities is urgently needed, as they can affect key organisms. The results obtained in this study validate the prolific capacity of *R. okamurae* to colonize new areas, affecting both littoral and deeper coastal areas. This behaviour, coupled with the ability to grow on a wide variety of suitable substrates, creates a strong threat to natural environments.

Key words: Alboran Sea, Asian algae, bathymetric range, epibiont, habitat-forming species, invasive species

Introduction

Nonindigenous species (NIS) are considered by many researchers to constitute major threats to biodiversity in marine environments (Bax et al. 2001; Galil et al. 2014). NIS have a powerful impact on the conservation

and function of ecosystems and the management of marine environments and may negatively impact human health and the economy (Bax et al. 2003; Galil et al. 2014; Ojaveer et al. 2014; González-Duarte et al. 2016; Kourantidou et al. 2021). The study of these species is crucial for maintaining biodiversity and ecosystem functions in a given area (Byers et al. 2002). NIS can dramatically alter the diversity and productivity of ecosystems (Carlton 2009) and the biotic relationships among native species (Byers et al. 2002), potentially leading to their local extinction (Haugom et al. 2002). Furthermore, the alteration of an ecosystem by NIS can subsequently facilitate the introduction of additional new exotic species (Simberloff and Holle 1999; Floerl et al. 2004; Wonham and Lewis 2009).

The Mediterranean Sea is a worldwide hot spot of marine diversity (Coll et al. 2010; Katsanevakis et al. 2014) and harbours between 4% and 18% of the world's marine species (Lejeusne et al. 2010). However, it is one of the most impacted seas in the world due to global warming, biological invasions, high human impacts and many other disturbances (Lejeusne et al. 2010; Katsanevakis et al. 2014; Galil et al. 2018; Giakoumi et al. 2019). The Mediterranean Sea has one of the highest introduction rates of marine NIS in the world (Streftaris et al. 2005; Galil et al. 2018). Indeed, the number of NIS in the Mediterranean Sea is increasing and has reached 821 species (Zenetos et al. 2017; Zenetos et al. 2020). Mediterranean biodiversity is significantly threatened by NIS, and many of changes in Mediterranean marine communities can be attributed to their effects (Galil and Zenetos 2000; Galil 2008; Zenetos et al. 2012, 2017).

The invasive alga *Rugulopteryx okamurae* (E. Y. Dawson) I. K. Hwang, W. J. Lee & H. S. Kim, is a brown algal species native to the western Pacific Ocean and present in the temperate waters of the Philippines, Taiwan, China, Korea and Japan (Huang 1994), where it can be found between 0.5 and 15 m depth (Hwang et al. 2009). This species is characterized by the presence of a dichotomously branched thallus and is recognized by the presence of a medulla that is one cell thick in its centre and two to three cells thick near its margins (Hwang et al. 2005).

In the Mediterranean Sea, this alga was first recorded in 2002 in Thau Lagoon (France), where it was accidentally introduced into a Japanese oyster farm of *Crassostrea gigas* (Thunberg, 1793) (Verlaque et al. 2009). In 2015, *R. okamurae* was recorded in Ceuta (African coast of the Strait of Gibraltar), and one year later, it covered most well-lit rocky bottoms (Ocaña et al. 2016). This region of the Strait of Gibraltar experiences intense maritime traffic (Piniella and Walliser 2013) and is considered a hotspot for biological invasions (Drake and Lodge 2004). Between 2015 and 2016, *R. okamurae* colonized most of the rocky shore of the Strait of Gibraltar, including the northern coast of the Strait (Altamirano-Jeschke et al. 2016; García-Gómez et al. 2018). Later, El Aamri et al. (2018) recorded *R. okamurae* between Cabo Negro and Tangier (Morocco). Since then, due to its extreme

propagation capacity and high survival rate, it has spread at high speeds throughout the Andalusian coasts from the Gulf of Cádiz (Atlantic Sea) (García-Gómez et al. 2021) to Málaga (northern coast of the Alboran Sea) (García-Gómez et al. 2020).

In this study, we update and discuss the distribution of *R. okamurae* in the Mediterranean, focusing on the Alboran Sea and recording its rapid expansion. In addition, we document the occurrence of *R. okamurae* in deep zones as an epiphyte of the coral *Dendrophyllia ramea* (Linnaeus, 1758), a very important habitat-forming species that has been classified as "vulnerable" in the Red List of Threatened Species of the Mediterranean by the International Union for Conservation of Nature (IUCN 2021), to provide valuable information to generate appropriate conservation plans for this coral.

Materials and methods

Specimens of *R. okamurae* were recorded growing on substrate associated with the coral communities of *D. ramea* in Punta de la Mona (Granada, Spain; PM hereafter), on the northern coast of the Alboran Sea (Figure 1). In the study area, the surveys were carried out by SCUBA diving and videos. Video transects 50 m long and 1.5 m wide were performed at a constant speed, 1 m above the seabed and parallel to the coast line, for every 6 m in depth, from 30 to 48 m. Three random video transects were recorded by depth. The survey took place in the spring (April 2021). To estimate the abundance of *R. okamurae* in the study area, the cover percentage of each algal bunch was calculated by analysing images obtained from the videos using the ImageJ program (version 1.4.3.67). For this purpose, a special support for the scooter was designed, with two lasers pointing at a known distance of 1.5 m to have a spatial scale in the photograph. In addition, the number of *R. okamurae* was counted, distinguishing between those specimens that were attached to the substrate (and type of substrate) and those that were detached from the bottom. To ensure that the specimens studied belonged to the species *R. okamurae*, different samples were taken and fixed in 80% ethanol for their identification based on recognition by the structure of the cortical and medullary layers.

Due to its ecosystem importance, PM was added to the list of "Lugares de Importancia Comunitaria" (Places of Community Importance) in Andalusia (Spain) and catalogued among the "Zonas Especiales de Conservación con Hábitats Marinos del Litoral Andaluz" (Special Conservation Zones with Marine Habitats on the Andalusian Coast). This site hosts endangered species, such as the mollusc *Patella ferruginea* Gmelin, 1791, and communities of the coral *D. ramea.* The latter is a habitat-forming species, also called fundamental species, which can establish community structures by generating stable conditions for other species and modulating the processes that take place in these ecosystems (Roberts et al. 2009).

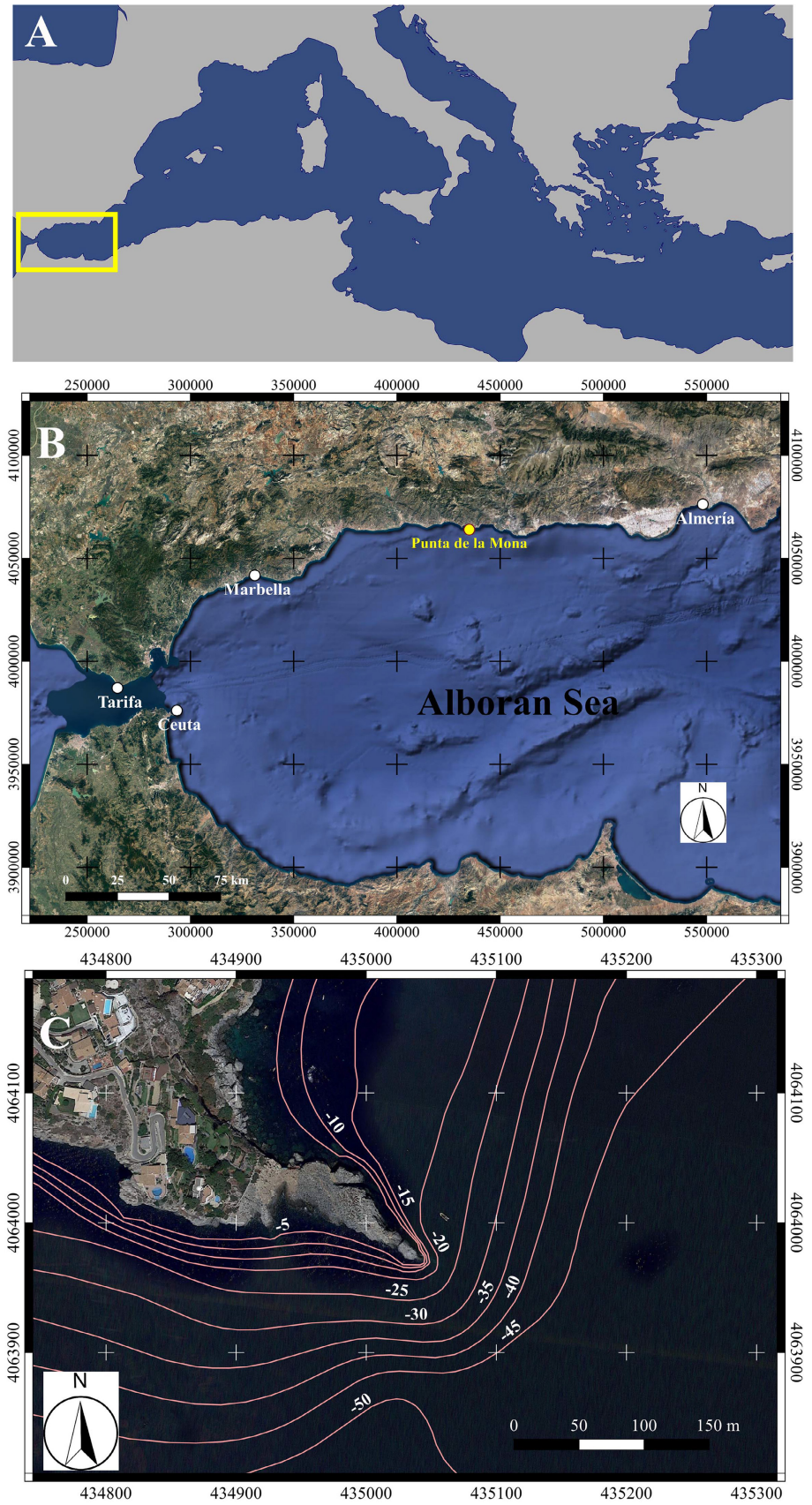

Figure 1. Records of *R. okamurae* in the Alboran Sea. A) Alboran Sea (Western Mediterranean); B) Records of *R. okamurae*: Tarifa (36.0152778°N; −5.6055555°W), Ceuta (35.8883333°N; −5.3161111°W), Marbella (36.5113889°N; −4.8833333°W), Almería (36.8402778°N; −2.4680555°W) and Punta de la Mona (present paper) (36.7236111°N; −3.7322222°W); C) Punta de la Mona and bathymetry (−5 to −50 m).

Although *D. ramea* is a dominant species in PM below depths of 20 m (Cebrián and Ballesteros 2004), the distribution patterns of this population and the size structure are not yet well described, and the possible effects of *R. okamurae* on this community are still unknown.

Data analysis

To determine if there were differences in the abundance of *R. okamurae* by depth, we selected the cover percentage as the response variable and the factor "Depth" (fixed, with four levels: 30; 36; 42 and 48 m). For this purpose, we used an ANOVA analysis. The normality and homogeneity of the residuals were checked with Shapiro–Wilk and Bartlett's tests, respectively. Square-root transformation was applied to the data to meet the assumptions of the models. While analysing the number of specimens fixed or detached from the substrate, we contemplated a similar experimental design considering the number of individuals of *R. okamurae* per transect as a response variable and "Depth" (fixed, with the same levels as described above) and "State" (fixed, two levels: detached and fixed). We used a Generalized Linear Model. All data were analysed using the statistical program R version 4.1.0 (R Core Team 2021).

Results and discussion

We found large proliferations of the species *R. okamurae* associated with the forests of the cold-water coral *D. ramea* in PM, growing on both rocky bottoms and as epiphytes of *D. ramea.* This record represents the easternmost point within the Spanish coasts where abundance data of this invasive species are available. The distribution of *R. okamurae* has been observed along the Spanish coasts in the Mediterranean Sea, and until now, the easternmost record in the Alboran Sea of *R. okamurae* is from Almería (Altamirano et al. 2019). However, there are still no quantitative data of this species in the eastern zone of the Alboran Sea; therefore, it is important to continue studying the dispersion of *R. okamurae* to provide accurate information for the monitoring, conservation and management of the Mediterranean Sea.

The results of the ANOVA analysis showed that the abundance of *R. okamurae* was lower at depths of 30–36 m and significantly different at 42 and 48 m, which in turn differed from each other ($F_{3,8}$=32.32, p-value < 0.001, Figure 2). The bathymetric distribution of this alga has been recorded in the Alboran Sea from the intertidal zone to 50 m in depth (Altamirano et al. 2016), presenting a higher density between 5 and 30 m (García-Gómez et al. 2021). In our sampling area, the cover percentage of *R. okamurae* increased with depth, showing the highest values at 48 m, an unusual depth record for this species in the Mediterranean Sea.

Normally, *R. okamurae* may be present as floating bushes, i.e., suspended in the water above the substrate but not attached to it (García-Gómez et al.

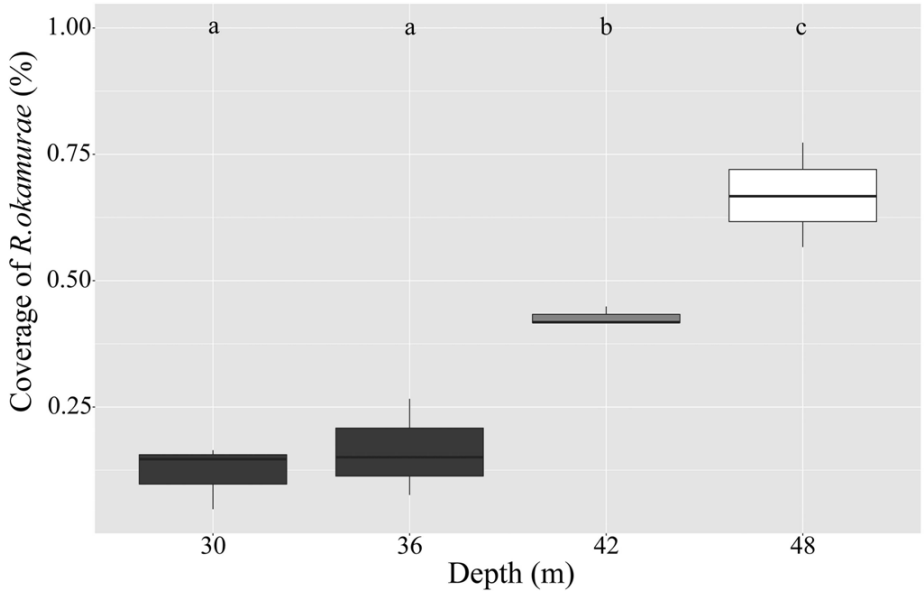

Figure 2. Average cover percentage of *Rugulopteryx okamurae* per transects by depth (30, 36, 42 and 48 m); showing the results of the ANOVA analysis.

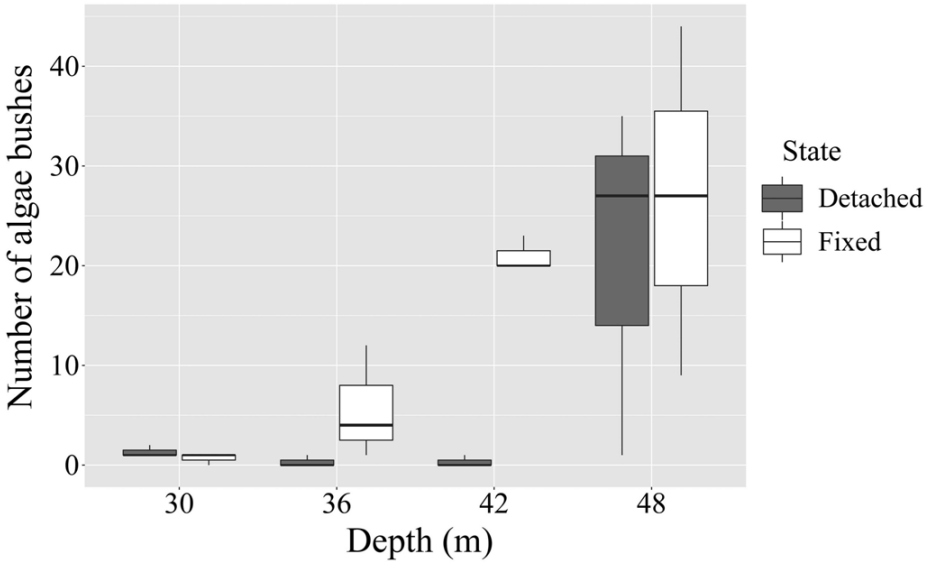

Figure 3. Average number of algal clump of *Rugulopteryx okamurae* per transects by depth (30, 36, 42 and 48 m) and differentiating between species fixed and detached from the substrate.

2020). This alga can live for long periods of time without being fixed to the bottom, thus increasing its dispersal capacity and ability to colonize a wide variety of substrates (García-Gómez et al. 2020). This fact, and their ability to survive outside the photic zone (Rosas-Guerrero et al. 2018), may be the reason for their high and rapid dispersion rates in the Mediterranean Sea (García-Gómez et al. 2020).

Our study noted a similar pattern between the numbers of bunches of *R. okamurae* and the cover percentage of this species, where both increased with depth, particularly for the ones attached to the hard bottom (Figure 3). At depths of 36 and 42 m, the number of bunches attached to the substrate was statistically higher than the number detached (Figure 3, Table 1). In contrast, at depths of 30 and 48 m, the number of *R. okamurae* clumps

Table 1. Generalized linear model of the number of algal clump of *Rugulopteryx okamurae* per transects by depth (30, 36, 42 and 48 m) and differentiating between specimens fixed and detached from the substrate.

	Estimate	SE	z value	Pr(>|z|)
(Intercept)	0.288	0.500	0.575	0.565
Depth(36)	−13.863	11.180	−1.240	0.215
Depth(42)	−13.863	11.180	−1.240	0.215
Depth(48)	27.568	0.516	5.347	< 0.001*
State (Fixed)	−0.693	0.866	−0.800	0.423
Depth(36) × State (Fixed)	35.264	13.449	2.622	0.009*
Depth(42) × State (Fixed)	48.363	13.288	3.639	0.001*
Depth(48) × State (Fixed)	0.932	0.882	1.056	0.291

* = significant differences; SE = Standard Errors; Null deviance: 388.63 on 23 degrees of freedom; Residual deviance: 86.948 on 16 degrees of freedom.

showed no significant difference between those attached and those detached from the substrate (Figure 3, Table 1). In addition, it can be assumed that the high presence of *R. okamurae* detached from the bottom in the deepest zone (48 m) was probably due to the specimens coming from the upper depths and dragged by marine currents.

According to our surveys, *R. okamurae* settled on a large number of organisms with calcareous skeletons, including gorgonians (genus *Leptogorgia*), hexacorals [*Parazoanthus axinellae* (Schmidt, 1862) and *Dendrophyllia ramea*] and bryozoans [*Pentapora fascialis* (Pallas, 1766) and *Myriapora truncata* (Pallas, 1766)]. The diversity of organisms colonized by *R. okamurae* highlighted the potential ability of the species to exert a severe impact on sessile native macrobiota (García-Gómez et al. 2020). In addition, the alga was growing on artificial substrates, from fishing waste (e.g., fishing lines, ropes, fishing nets) to debris (e.g., concrete structures, plastics pollution). In this regard, even though artificial substrates are common sites where this species attaches (García-Gómez et al. 2021) and which could contribute to the establishment and dispersion of NIS (Ruitton et al. 2005), in our study, most of the alga were growing on the rocky natural bottom.

The massive deposits of *R. okamurae* have substantial consequences for local biodiversity, as vast quantities have been found to occupy more than 90% of the horizontal surfaces between 10 and 20 m deep in the Alboran Sea (García-Gómez et al. 2020). This species preferentially establishes itself on hard substrates, so it has a large competitive advantage against other species, especially sessile species (García-Gómez et al. 2018). Additionally, the alga has the ability to grow on other sessile organisms, endangering key ecosystems such as *Posidonia oceanica* (Linnaeus) Delile, 1813 meadows, octocorals (gorgonians) or scleractinian corals such as *Astroides calycularis* (Pallas, 1766) (Figueroa et al. 2020; Sempere-Valverde et al. 2021).

In the Strait of Gibraltar, this alga has become a dominant species damaging fishing gear and nets and depositing tons of organic matter on tourist beaches (Casal-Porras et al. 2021). In fact, the massive expansion of this alga caused the accumulation of more than 5000 tons of algal biomass on

the African coast (Ocaña et al. 2016). The aggressive invasion process generates unprecedented ecological and landscape impacts in European waters (García-Gómez et al. 2020), causing large economic losses to the detriment of fishing and tourism activities (Altamirano-Jeschke et al. 2016).

Dendrophyllia ramea is a coral affected by diverse anthropogenic impacts; for example, when a colony is fractured by fishing lines, the injured area is generated where the living tissue is necrotic and the calcium carbonate skeleton is exposed (Orejas et al. 2019). In this area, opportunistic organisms, such as algae, barnacles, polychaetes and even the parasitic anthozoan *Alcyonium coralloide* (Pallas, 1766), can grow epiphyting colonies of *D. ramea*, preventing the living tissue from regenerating and even causing the death of the entire colony (Jiménez et al. 2016; Orejas et al. 2019). In the population of *D. ramea* studied in this contribution, we found the first case of *R. okamurae* epiphyting colonies of *D. ramea* (Figure 4), which adds a new disturbance agent to the PM ecosystem.

Invasive species have a substantial ecological impact because they threaten native flora and fauna, which reduces the biodiversity of many ecosystems (Molnar et al. 2008) and especially affects habitat-forming species such as *D. ramea,* a keystone species in the studied area and in the Alboran Sea environment (Zibrowius 1980; Ocaña et al. 2000; Cebrián and Ballesteros 2004). The invasion of *R. okamurae* on coralligenous habitats could possibly cause a decrease in the number of species and a taxonomic and functional homogenization of the epifaunal community (Navarro-Barranco et al. 2021).

The distribution and bathymetric range of *R. okamurae* in the Alboran Sea remain unclear, but the evidence provided here shows the importance of monitoring this species because they can affect key species, such as habitat-forming species, in deep waters. Localities such as PM are in danger due to this invasive species; therefore, precautionary measures against these events are necessary to prevent them from happening again.

The results obtained in this study highlight the high capacity of *R. okamurae* to colonize new areas, affecting not only the upper sublitoral zones but also the deeper ones. This, coupled with its ability to grow on a wide variety of suitable substrates, creates a strong threat to natural environments affecting unique ecosystems.

Acknowledgements

This work was supported by the project S.O.S. Corales and NGOs Coral Guardian, Coral Soul and Equilibrio Marino, and ESMARES2 from the Instituto Español de Oceanografía (IEO-CSIC), under the framework ordered to the IEO-CSIC by the Ministerio de Transición Ecológica y Reto Demográfico (MITECO) of the Spanish government for the application of the Marine Strategy Framework Directive (MSFD) in Spanish waters. We thank the scientific divers from S.O.S. Corales who assisted us in sampling expeditions and the underwater photographers Rafael Camacho (Figure 4A), Lolo García (Figure 4B) and Javier Sánchez (Figure 4C). We would also like to thank the BioInvasion Records reviewers who have contributed to the improvement of this article.

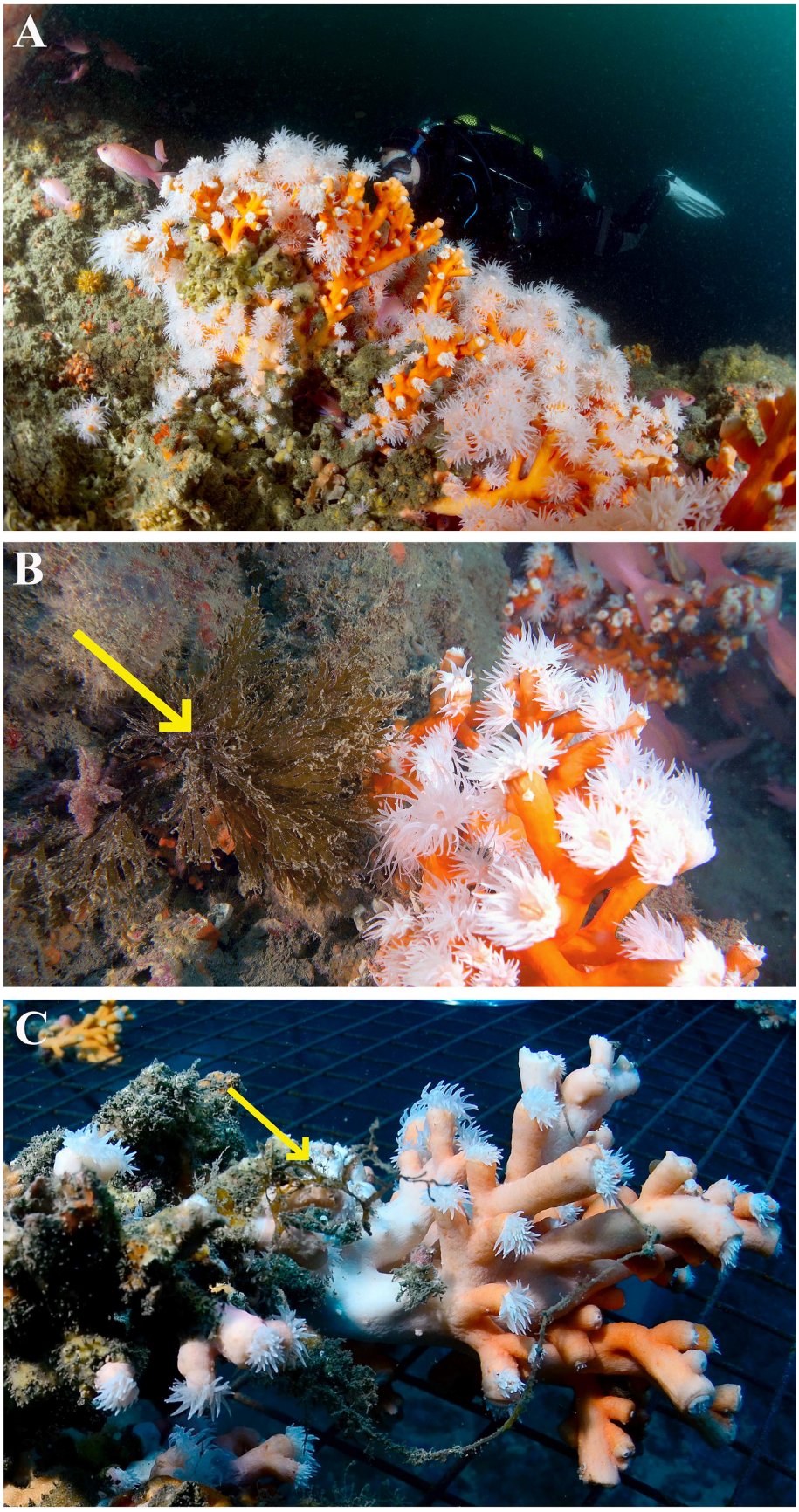

Figure 4. *Rugulopteryx okamurae* (pointed by arrows) epyphyting the coral *Dendrophyllia ramea*. A) Colony of the coral *D. ramea*; B) specimen of *D. ramea* epiphyted by *R. okamurae*; C) fragment of *D. ramea* epiphyted by *R. okamurae*. Photograph 4A by Rafael Camacho; 4B by Lolo García and 4C by Javier Sánchez.

Funding declaration

The NGO Coral Guardian, Coral Soul and Equilibrio Marino, with the SOS Coral project, multiannual funds of the research group "Marine and Fisheries Biology" (PAIDI RNM-213) and MITECO with the ESMARES2-INFRA project financed our work supporting study design, collection, analysis of the samples and data, as well as preparation of manuscript and article processing charge.

Authors' contributions

MMGD, RME and JLC conceived the idea, sample design and methodology; RME and MP conducted the samplings; RME and MMGD analyzed the samples; RME and MMGD data analysis; RME, MMGD, JLC and MP interpreted the results; RME wrote the paper with MMGD, JLC and MP.

References

Altamirano M, De la Rosa J, Martínez FJ (2016) Arribazones de la especia exótica *Rugulopteryx okamurae* (EY Dawson) I.K. Hawang, W.J. Lee and H.S Kem (Dictyotales, Ochorophyta) en el Estrecho de Gibraltar: primera cita para el Atlántico y España. *Algas* 52: 20

Altamirano M, De la Rosa J, Carmona R, Zanolla M, Muñoz AR (2019) Macroalgas invasoras en las costas andaluzas. *Algas* 55e: 10–13

Bax N, Carlton JT, Mathews-Amos A (2001) The control of biological invasions in the world's oceans. *Conservation Biology* 15: 1234–1246, https://doi.org/10.1111/j.1523-1739.2001.99487.x

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy* 27: 313–323, https://doi.org/10.1016/S0308-597X(03)00041-1

Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impacts of non-indigenous species. *Conservation Biology* 16: 630–640, https://doi.org/10.1046/j.1523-1739.2002.01057.x

Carlton JT (2009) Deep Invasion Ecology and the Assembly of Communities in Historical Time. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems. Ecological Studies, vol 204. Springer, Berlin, Heidelberg, pp 13–56, https://doi.org/10.1007/978-3-540-79236-9_2

Casal-Porras I, Zubía E, Brun FG (2021) Dilkamural: A Novel Chemical Weapon Involved in the Invasive Capacity of the Alga *Rugulopteryx okamurae* in the Strait of Gibraltar. *Estuarine, Coastal and Shelf Science* 257: 107398, https://doi.org/10.1016/j.ecss.2021.107398

Cebrián E, Ballesteros E (2004) Zonation patterns of benthic communities in an upwelling area from the western Mediterranean (La Herradura, Alboran Sea). *Scientia Marina* 68: 69–84, https://doi.org/10.3989/scimar.2004.68n169

Coll M, Piroddi C, Steenbeek J, Kaschner K, Lasram FBR, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T, Danovaro R, Estrada M, Froglia C, Galil BS, Gasol JM, Gertwagen R, Gil J, Guilhaumon F, Kesner-Reyes K, Kitsos M, Koukouras A, Lampadariou N, Laxamana E, López-Fé de la Cuadra CM, Lotze,Daniel Martin HK, Mouillot D, Oro D, Raicevich S, Rius-Barile J, Saiz-Salinas JI, San Vicente C, Somot S, Templado J, Turon X, Vafidis D, Villanueva R, Voultsiadou E (2010) The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE* 5: e11842, https://doi.org/10.1371/journal.pone.0011842

Drake JM, Lodge DM (2004) Global Hot Spots of Biological Invasions: Evaluating Options for Ballast-Water Management. *Proceedings of the Royal Society B: Biological Sciences* 271: 575–580, https://doi.org/10.1098/rspb.2003.2629

El Aamri F, Idhalla M, Tamsouri MN (2018) 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). *Mediterranean Fisheries and Aquaculture Research* 1: 92–96

Figueroa FL, Vega J, Gómez-Valderrama M, Korbee N, Mercado JM, Bañares E, Flores-Moya A (2020) Invasión de la especie exótica *Rugulopteryx okamurae* en Andalucía I: estudios preliminares de la actividad fotosintética. *Algas* 56: 35

Floerl O, Pool TK, Inglis GJ (2004) Positive interections between non-indigenous species facilatate transport by human vectors. *Ecological Applications* 14: 1724–1736, https://doi.org/10.1890/03-5399

Galil BS (2008) Alien species in the Mediterranean Sea-which, when, where, why? *Hydrobiologia* 606: 105–116, https://doi.org/10.1007/978-1-4020-8808-7_10

Galil BS, Zenetos A (2000) A sea under siege-alien species in the Mediterranean. *Biological Invasion* 2: 177–186, https://doi.org/10.1023/A:1010057010476

Galil BS, Marchini A, Occhipinti-Ambrogi A, Minchin D, Narščius A, Ojaveer H, Olenin S (2014) International arrivals: widespread bioinvasions in European Seas. *Ethology, Ecology & Evolution* 26: 152–171, https://doi.org/10.1080/03949370.2014.897651

Galil BS, Marchini A, Occhipinti-Ambrogi A (2018) East Is East and West Is West? Management of Marine Bioinvasions in the Mediterranean Sea. *Estuarine, Coastal and Shelf Science* 201: 7–16, https://doi.org/10.1016/j.ecss.2015.12.021

García-Gómez JC, Sempere-Valverde J, Ostalé-Valriberas E, Martínez M, Olaya-Ponzone L, González AR, Espinosa F, Sánchez-Moyano E, Megina C, Parada JA (2018) *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W.J. Lee & H.S. Kim (Dictyotales, Ochrophyta), alga exótica "explosiva" en el Estrecho de Gibraltar. Observacion espreliminares de sudistribución e impacto. *Almoraima* 49: 97–113

García-Gómez JC, Sempere-Valverde J, González AR, Martínez-Chacón M, Olaya-Ponzone L, Sánchez-Moyano E, Ostalé-Valriberas E, Megina C (2020) From exotic to invasive in record time: The extreme impact of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in the strait of Gibraltar. *Science of the Total Environment* 704: 135408, https://doi.org/10.1016/j.scitotenv.2019.135408

García-Gómez JC, Florido M, Olaya-Ponzone L, Sempere-Valverde J, Megina C (2021) The Invasive Macroalga *Rugulopteryx okamurae*: Substrata Plasticity and Spatial Colonization Pressure on Resident Macroalgae. *Frontiers in Ecology and Evolution* 9: 259, https://doi.org/10.3389/fevo.2021.631754

Giakoumi S, Katsanevakis S, Albano PG, Azzurro E, Cardoso AC, Cebrian E, Deidun A, Edelist D, Francour P, Jimenez C, Mačić V, Occhipinti-Ambrogi A, Rilov G, Ramzi Sghaie Y (2019) Management priorities for marine invasive species. *Science of the Total Environment* 688: 976–982, https://doi.org/10.1016/j.scitotenv.2019.06.282

González-Duarte MM, Megina C, López-González PJ, Galil B (2016) Cnidarian alien species in expansion. In: Goffredo S, Dubinsky Z (eds), The Cnidaria, Past, Present and Future. Springer, Cham, pp 139–160, https://doi.org/10.1007/978-3-319-31305-4_10

Haugom GP, Behrens H, Andersen AB (2002) Risk based methodologies to assess invasive aquatic species in ballast water. In: Leppäkoski E, Gollasch S, Olenin S (eds), Invasive aquatic species of Europe. Distribution, impacts and management. Springer, Dordrecht, pp 467–476, https://doi.org/10.1007/978-94-015-9956-6_46

Huang ZG (1994) Marine Species and their distributions in China's Seas. China Ocean Press, Beijing, 764 pp

Hwang IK, Kim HS, Y Lee WJ (2005) Polymorphism in the brown alga *Dictyota dichotoma* (Dictyotales, Phaeophyceae) from Korea. *Marine Biology* 147: 999–1015, https://doi.org/10.1007/s00227-005-1623-8

Hwang IK, Wook JL, Kim HS, De Clerck O (2009) Taxonomic Reappraisal of *Dilophus okamurae* (Dictyotales, Phaeophyta) from the Western Pacific Ocean. *Phycologia* 48: 1–12, https://doi.org/10.2216/07-68.1

IUCN (2021) International Union for Conservation of Nature. Red list of threated species. https://www.iucnredlist.org/ (accessed 20 October 2021)

Jiménez CE, Achilleos K, Abu Alhaija R, Gili JM, Orejas C (2016) Living in close quarters: epibionts on *Dendrophyllia ramea* deep-water corals (Cyprus and Menorca channel). *Rapport Commission International Mer Méditerranée* 41: 466

Katsanevakis S, Coll M, Piroddi C, Steenbeek J, Ben Rais Lasram F, Zenetos A, Cardoso AC (2014) Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. *Frontiers in Marine Science* 1: 32, https://doi.org/10.3389/fmars.2014.00032

Kourantidou M, Cuthbert R, Haubrock P, Novoa A, Taylor N, Leroy B, Leroy B, Capinha C, Renault D, Angulo E, Diagne C, Courchamp F (2021) Economic costs of invasive alien species in the Mediterranean basin. *NeoBiota* 67: 427–458, https://doi.org/10.3897/neobiota.67.58926

Lejeusne C, Chevaldonné P, Pergent-Martini C, Boudouresque CF, Pérez T (2010) Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in Ecology & Evolution* 25: 250–260, https://doi.org/10.1016/j.tree.2009.10.009

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6: 485–492, https://doi.org/10.1890/070064

Navarro-Barranco C, Moreira J, Espinosa F, Ros M, Rallis I, Sempere-Valverde J, Ostalé-Valriberas E, Altamirano M, García-Gómez JC, Guerra-García JM (2021) Evaluating the vulnerability of coralligenous epifauna to macroalgal invasions. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 2305–2319, https://doi.org/10.1002/aqc.3633

Ocaña A, Tocino LS, González PL (2000) Consideraciones faunística y biogeográficas de los antozoos ("Cnidaria: Anthozoa") de la costa de Granada (Mar de Alborán). *Zoologica baetica* 11: 51–66

Ocaña O, Alfonso-Carrillo JM, Ballesteros E (2016) Massive proliferation of a dictyotalean species (Phaeophyceae, Ochrophyta) through the Strait of Gibraltar. *Revista de la Academia Canaria de Ciencias* 28: 165–170

Ojaveer H, Galil BS, Minchin D, Olenin S, Amorime A, Canning-Clode J, Chainho P, Copp GH, Gollasch S, Jelmert A, Lehtiniemi M, McKenzie C, Mikuš J, Miossec L, Occhipinti-

Ambrogi A, Pećarević M, Pederson J, Quilez-Badia G, Wijsman JWM, Zenetos A (2014) Ten recommendations for advancing the assessment and management of non-indigenous species in marine ecosystems. *Marine Policy* 44: 160–165, https://doi.org/10.1016/j.marpol.2013.08.019

Orejas C, Jiménez C, Gori A, Rivera J, Iacono CL, Aurelle D, Achilleos K (2019) 23 Corals of Aphrodite: *Dendrophyllia ramea* Populations of Cyprus. In: Orejas, C., Jiménez, C. (eds) Mediterranean Cold-Water Corals: Past, Present and Future. Coral Reefs of the World, vol 9. Springer, Cham, pp 257–260, https://doi.org/10.1007/978-3-319-91608-8_23

Piniella F, Walliser J (2013) Maritime Safety in the Strait of Gibraltar: Taxonomy and Evolution of Emergencies Rate in 2000-2004 Period. *Journal of Maritime Research* 10(1): 25–29

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Roberts JM, Wheeler A, Freiwald A, Cairns, S (2009) Cold-water corals: the biology and geology of deep-sea coral habitats. Cambridge University Press, New York, 334 pp, https://doi.org/10.1017/CBO9780511581588

Rosas-Guerrero J, Meco YE, Altamirano M (2018) Could *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) have been introduced by ballast waters? *Algas* 54: 52

Ruitton S, Javel F, Culioli JM, Meinesz A, Pergent G, Verlaque M (2005) First assessment of the *Caulerpa racemose* (Caulerpales, Chlorophyta) invasion along the French Mediterranean coast. *Marine Pollution Bulletin* 50: 1061–1068, https://doi.org/10.1016/j.marpolbul.2005.04.009

Sempere-Valverde J, Ostalé-Valriberas E, Maestre M, Aranda RG, Bazairi H, Espinosa F (2021) Impacts of the non-indigenous seaweed *Rugulopteryx okamurae* on a Mediterranean coralligenous community (Strait of Gibraltar): The role of long-term monitoring. *Ecological Indicators* 121: 107135, https://doi.org/10.1016/j.ecolind.2020.107135

Simberloff D, Von Holle B (1999) Positive interactions of non-indigenous species: invasional meltdown? *Biological Invasions* 1: 21–32, https://doi.org/10.1023/A:1010086329619

Streftaris N, Zenetos A, Papathanassiou E (2005) Globalization in Marine Ecosystems: The Story of Non-Indigenous Marine Species across European Seas. *Oceanography and Marine Biology* 43: 429–464, https://doi.org/10.1201/9781420037449-10

Verlaque M, Steen F, De Clerck O (2009) *Rugulopteryx* (Dictyotales, Phaeophyceae), a genus recently introduced to the Mediterranean. *Phycologia* 48: 536–542, https://doi.org/10.2216/08-103.1

Wonham MJ, Lewis M (2009) Modeling Marine Invasions: Current and Future Approaches. In: Rilov G, Crooks JA (eds), Biological Invasions in Marine Ecosystems. Ecological Studies, vol 204. Springer, Berlin, Heidelberg, pp 71–105, https://doi.org/10.1007/978-3-540-79236-9_4

Zenetos A, Gofas S, Morri C, Rosso A, Violanti D, Garcia Raso J, Cinar M, Almogi-Labin A, Ates A, Azzurro E, Ballesteros E, Bianchi C, Bilecenoglu M, Gambi M, Giangrande A, Gravili C, Hyams-Kaphzan O, Karachle PK, Katsanevakis S, Lipej L, Mastrototaro F, Mineur F, Pancucci-Papadopoulou M, Ramos Espla A, Salas C, San Martin G, Sfriso A, Streftaris N, Verlaque M (2012) Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science* 13: 328–352, https://doi.org/10.12681/mms.327

Zenetos A, Çinar ME, Crocetta F, Golanic D, Rosso A, Gianna S, Shenkargh N, Turoni X, Verlaquej M (2017) Uncertainties and validation of alien species catalogues: The Mediterranean as an example. *Estuarine, Coastal and Shelf Science* 191: 171–187, https://doi.org/10.1016/j.ecss.2017.03.031

Zenetos A, Karachle P, Corsini-Foka M, Gerovasileiou V, Simboura N, Xentidis NJ, Tsiamis K (2020) Is the trend in new introductions of marine non-indigenous species a reliable criterion for assessing good environmental status? The case study of Greece. *Mediterranean Marine Science* 21: 775–793, https://doi.org/10.12681/mms.25136

Zibrowius H (1980) Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental. *Memoires del'Institut Oceanographique Fondation Albert 1er, Prince de Monaco* 11(1): 169–172