Research Article

Nataly Quiroz-González, Luis G. Aguilar-Estrada*, Julio A. Acosta-Calderón, Lucía Álvarez-Castillo and Fernando Arriola-Álvarez

Biodiversity of epiphytic marine macroalgae in Mexico: composition and current status

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Abstract: Marine epiphyte studies in Mexico, including macroalgae, are lacking in the published literature. Floristic studies have been mainly focused on identifying the algae growing on rocky substrata, and epiphytic algae have been recorded, but only occasionally. The aim of this work is to establish the current state of knowledge of the epiphytic macroalgae and their hosts on the Mexican coasts. A systematic revision of the literature published from 1950 to 2021 is also reported, the literature information is included, and the composition, species richness, current state of knowledge of the epiphytic marine macroalgae, and their relationship with the various marine Mexican ecoregions are reported. Sixty-one publications since 1950 included at least one record of epiphytic macroalgae. In this study, 615 species of epiphytic macroalgae and 224 species of hosts for Mexico are reported. This checklist will provide a baseline for future taxonomic and biogeographic studies of the epiphytic marine algae in the country.

Keywords: algae; epibiosis; inventory of species; species richness; taxonomy.

***Corresponding author: Luis G. Aguilar-Estrada**, Facultad de Ciencias, UNAM Av. Universidad 3000, Circuito Exterior S/N Delegación Coyoacan, C.P. 04510 Ciudad Universitaria, D.F., Mexico,
E-mail: lgae@ciencias.unam.mx
Nataly Quiroz-González and Fernando Arriola-Álvarez, Facultad de Ciencias, UNAM Av. Universidad 3000, Circuito Exterior S/N Delegación Coyoacan, C.P. 04510 Ciudad Universitaria, D.F., Mexico
Julio A. Acosta-Calderón, Instituto de Ecología, Universidad del Mar, Campus Puerto Ángel, Ciudad Universitaria s/n, Col. El Faro, C.P. 70902, Puerto Ángel, San Pedro Pochutla, Oaxaca, Mexico
Lucía Álvarez-Castillo, Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Ciudad Universitaria 3000, C.P. 04510, Ciudad de México, Coyoacán, Mexico

1 Introduction

In order to attach themselves and survive, benthic marine macroalgae require a suitable substratum; these substrata are diverse, such as rock, mud, sand, animals, vascular plants, and even other algae (Báez and Flores-Moya 2003; Darley 1987; Galicia-García 2017). When the substratum is a living organism, it is called a basibiont, and the interaction is named epibiosis; in particular, when the substratum is a plant, it is called epiphytism (Álvarez-Álvarez et al. 2020; Borowitzka and Lethbridge 1989). In marine communities, the most common living substrata are phanerogams and macroalgae. Their epiphytes depend on their development and, to a large extent, on the characteristics of the basibiont, such as its size, longevity, life cycle, and chemical defenses (Harder 2009; Mateo-Cid et al. 1996; Ortuño-Aguirre and Riosmena-Rodriguez 2007; Williams and Seed 1992).

Epiphytism is an ecological strategy where the epiphyte obtains a substratum for its establishment and development, while the host may benefit from protection against solar radiation, desiccation, and direct exposure to air (Littler and Littler 1999; Mateo-Cid et al. 2014; Nava-Olvera et al. 2017).

The phycological knowledge in Mexico has focused mainly on studies of the local flora attached to rocky substrata. Epiphytic species are only occasionally indicated as part of the floristic inventory. Most of the known information for algal epiphytism in Mexico has been reported under this format. The number of specific studies undertaken to identify the macroalgae that grow as epiphytes of seagrasses, other algae, or mangroves, is noticeably less common.

In Mexico, studies focused on this interaction have been carried out to evaluate the epiphytic species on a particular basibiont, such as seagrasses or brown algae, or as part of floristic inventories that seek to register only the epiphytic species (Álvarez-Álvarez et al. 2020; Galicia-García 2017; Nava-Olvera et al. 2017; Ortuño-Aguirre and Riosmena-Rodriguez 2007; Quang-Young et al. 2006; Ramírez-Rodríguez et al. 2011). For example, Ortuño-Aguirre and Riosmena-Rodríguez (2007) recognized the epiphytism on *Padina concrescens* for the coasts of Baja California. Mateo-Cid et al.

(2014) determined the epiphytic species on *Sargassum sinicola* in the Magdalena and Margarita islands in Baja California Sur. Recently, Álvarez-Álvarez et al. (2020) determined the epiphytic algae on species of *Padina* of the Mexican tropical Pacific. Ramírez-Rodríguez et al. (2011) and Galicia-García (2017) reported the epiphytic algae from Veracruz. For the Mexican Caribbean, Quang-Young et al. (2006) developed an exclusive floristic inventory of epiphytic marine algae for a locality of Quintana Roo. Nava-Olvera et al. (2017) examined the epiphytic species growing on *Thalassia testudinum* from the States of Veracruz and Quintana Roo.

As Álvarez-Álvarez et al. (2020) pointed out, the study of the epiphytism is a crucial variable to consider in marine environments; it increases the species richness of marine algae and can be used to analyze the structure of benthic marine communities. Unfortunately, most of the data on epiphytism is found in floristic studies developed for the different states of the Mexican Republic, but no work has compiled these data from old works into the most recent studies, nor has an analysis by region been carried out. This study aims to include old and recent studies by compiling data on epiphytic macroalgal species recorded along the coasts of Mexico, as well as data on their basibionts.

2 Materials and methods

Sixty-one published articles were reviewed that included records of epiphytic species from Mexico, North Pacific, Gulf of California, Tropical Mexican Pacific, Gulf of Mexico, and the Mexican Caribbean (Acosta-Calderón et al. 2016; Aguilar-Rosas and Aguilar-Rosas 1994; Aguilar-Rosas and Machado-Galindo 1990; Aguilar-Rosas and Pacheco-Ruiz 1985; Aguilar-Rosas et al. 1998, 2000, 2002, 2007, 2010; Álvarez-Álvarez et al. 2020; Dawson 1944, 1950, 1953, 1960, 1962, 1966; Dreckmann et al. 1990; Galicia-García et al. 2013; Galindo-Villegas et al. 1997; García-López et al. 2017; Garduño-Solórzano et al. 2005; Godínez-Ortega et al. 2019; González-Gándara et al. 2007; Huerta and Tirado 1970 Landa-Cansigno et al. 2019; Martinell and Gold 1997; Mateo-Cid et al. 1996, 2006, 2013, 2020; Mateo-Cid and Mendoza-González 1991a, 1991b, 1992, 1997, 2001, 2012; Mendoza-González and Mateo-Cid 1992, 1994, 1996, 1998, 1999, 2007; Mendoza-González et al. 1994, 2011, 2016, 2017, 2018, 2020; Nava-Olvera et al. 2017; Norris 2010, 2014; Ortuño-Aguirre and Riosmena-Rodriguez 2007; Pedroche and González-González 1981; Pérez-Jiménez et al. 2020; Quang-Young et al. 2006; Quiroz-González et al. 2017, 2018; Ramírez-Rodríguez et al. 2011; Robinson et al. 2020; Senties 1990; Stout and Dreckmann 1993). The reference search was carried out using the Google academic algorithm with keywords such as epiphytic algae, epiphytic seaweed, epiphytism in algae, epiphytism in mangroves, epiphytism in seagrasses, marine algae in Mexico, marine basibiont, marine macroalgae, phycoflora. The lists of species were reviewed, focusing on the epiphytes and their substratum type. Scientific names were nomenclaturally updated utilizing AlgaeBase (Guiry and Guiry 2022). The morpho-functional groups to which each species belongs according to the classification of Steneck and Dethier (1994) were included (microscopic, filament, foliose, corticated foliose, articulated calcareous, crusts). Additionally, each epiphytic species was recorded in the corresponding ecoregion proposed by Spalding et al. (2007).

3 Results

In total, 61 published articles were reviewed with data on epiphytes on algae, seagrasses, and mangroves from all of Mexico's coasts. The oldest studies date back to 1950, most recent were in 2021.

From the 61 works reviewed, 2520 epiphytic algal records were obtained for the coasts of Mexico. According to Spalding et al. (2007), there are 1092 records for the Atlantic (corresponding to the Northern Gulf of Mexico, Southern Gulf of Mexico, and Western Caribbean), with 830 epiphytes recorded for the tropical Pacific (Mexican Tropical Pacific and Chiapas-Nicaragua) and 598 for the North Pacific and Gulf of California (Southern California Bight, Cortezian, and Magdalena Transition). After curatorial work on the nomenclatural data, 398 valid species records were gathered for the Atlantic, 241 for the North Pacific and Gulf of California, and 223 for the tropical Pacific.

In total, 615 epiphytic species have been reported for Mexico. These taxa are distributed among 216 genera, 75 families, 33 orders, and 3 phyla (Supplementary Table S1). An inventory of orders, families, genera and species of epiphytic algae in each algal division is presented in Table 1. The number of basibiont algal species was 224, distributed in 100 genera, 51 families, 24 orders, and 3 phyla (Supplementary Table S1). The inventory for basibionts in each division is also presented in Table 1. Four species of seagrasses were also recorded (*Phyllospadix scouleri*, *P. torreyi*, *Ruppia maritima*, and *Thalassia testudinum*). However, the terms mangrove and seagrass were used in some articles but without specification of the species of the basibiont.

Twenty-two species of epiphytic algae were recorded growing on more than six different basibiont species. Of these, *Erythrotrichia carnea, Stylonema alsidii*, and *Ulva australis* were found as epiphytes on the largest number of basibionts (13 spp.).

The most frequently recorded basibiont species were *Padina durvillei* (with 67 epiphytic species), *Thalassia testudinum* (50 epiphytic species), *Sargassum sinicola* (49 epiphytic species) and *Sargassum muticum* (37 epiphytic species). On the other hand, 249 species of epiphytic algae were recorded without information on the basibiont.

Table 1: Inventory of orders, families, genera and species by algal division for epiphytic algae and basibionts.

	Orders	Families	Genera	Species	Most representative orders	Most representative families	Most representative genera
Ephiphytic algae							
Rhodophyta	19	43	143	415	Ceramiales (243) Corallinales (43)	Rhodomelaceae (98) Ceramiaceae (64)	*Ceramium* (31) *Chondria* and *Laurencia* (15)
Chlorophyta	5	19	39	121	Cladophorales (60) Bryopsidales (30)	Cladophoraceae (40) Caulerpaceae (9)	*Cladophora* (23) *Chaetomorpha* (12)
Ochrophyta	9	13	34	79	Ectocarpales (44) Asterocladales (21)	Dictyotaceae (20) Chordariaceae (17)	*Dictyota* (13) *Ectocarpus* (9)
Basibionts							
Rhodophyta	12	26	62	118	Ceramiales (33) Gigartinales (20)	Rhodomelaceae (23) Gracilariaceae (13)	*Gracilaria* (11) *Hypnea* (6) *Gelidium* (6)
Chlorophyta	4	14	19	63	Bryopsidales (33) Cladophorales (23)	Cladophoraceae (15) Codiaceae (7)	*Cladophora* (7) *Codium* (7)
Ochrophyta	8	11	19	37	Dictyotales (14) Fucales (11)	Dictyotaceae (14) Sargassaceae (8)	*Padina* (8) *Sargassum* (8)

The number of species is presented in parentheses.

Regarding the number of epiphytic species per ecoregion, the highest value presented was in the ecoregion 68 (Western Caribbean) with 120 species, followed by ecoregion 166 (Tropical Mexican Pacific) with 98 species, and ecoregion 59 (Southern California Bight) with 85 species (Figure 1). Twenty-one species of epiphytic algae were found in more than three ecoregions proposed for Mexico. *Erythrotrichia carnea* and *Stylonema alsidii* were found in most ecoregions except for ecoregion 43, which includes part of the coast of Tamaulipas state. Meanwhile, *Erythrocladia irregularis*, *Sahlingia subintegra*, *Chaetomorpha linum*, *Asparagopsis taxiformis*, *Spyridia filamentosa*, *Centroceras clavulatum*, *Anotrichium tenue*, *Jania tenella*, and *Champia parvula* were reported in more than four ecoregions.

4 Discussion

Sixty-three published works were reviewed, and only seven included data focused on epiphytism. The remaining

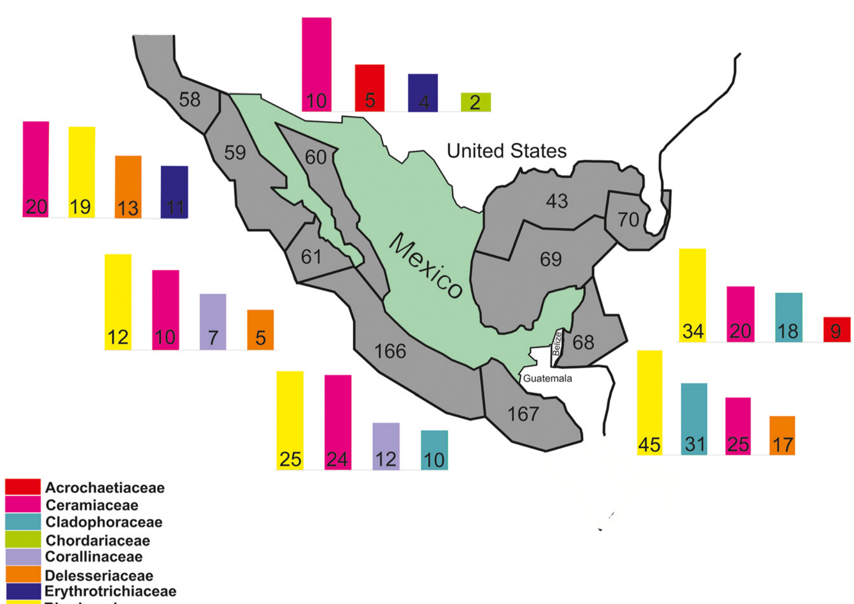

Figure 1: Numbers of algal species in each of the families that are best represented in each biogeographical ecoregion around Mexico, as defined by Spalding et al. (2007).

contributions were mostly floristic inventories where epiphytism is mentioned only occasionally and not as part of the main research. This contribution represents the first effort to compile all data regarding macroalgal epiphytism from Mexico (similar efforts have been carried out in Spain, Cuba and other countries García-Redondo et al. 2019; Jover et al. 2020).

The marine macroalgal diversity in Mexico includes 1698 taxa (Pedroche and Sentíes 2020). In this study, 618 species of epiphyte macroalgae were reported for the Mexican coasts. This number represents 37 % of the total diversity of algae known in the country. The percentage of epiphytic species with respect to the total diversity of algae known for Mexico corresponds to 36 % for Rhodophyta, 39 % for Chlorophyta, and 33 % for Ochrophyta. According to Bolton (1994), the species richness of marine macroalgae can be separated into distinct areas. For instance, an area with less than 200 marine algal species can be considered an area with a poor flora, moderately poor areas have 200–400 algal species, and rich areas have more than 900–1100 species. The Mexican coast does not fall into one of these proposed categories. According to this study, Mexican waters have between 400 and 900 macroalgal species. This difference can be explained as being due to the subtropical latitudes of Mexico, our study also contrasts with that of Bolton (1994), which was done in a country in a temperate zone. According to Barlow et al. (2018), it is well-known that tropical and subtropical environments harbor more diversity than temperate environments. Thus, it is important to establish a baseline of diversity from poorly studied groups such as the macroalgal epiphytes.

The epiphytic phycoflora in México is well represented by Rhodophyta (418 spp.), followed by Chlorophyta (122 spp.) and Phaeophyceae (79 spp.) The dominance of the red algae followed by the chlorophytes has been reported in other algal studies and seagrasses from different marine environments. This pattern also matches the dominance observed in other ecosystems in tropical areas (Jover et al. 2020; Montañés et al. 2003; Phang et al. 2016). For example, in a similar review study from Indonesia, Malaysia, Philippines, Singapore, Thailand, and Vietnam, Phang et al. (2016) reported similar diversity and dominance of the epiphytic macroalgal taxa.

On the other hand, the orders Ceramiales and Corallinales have been identified in the literature for harboring an elevated number of epiphytic species, representing almost 50 % of the total species (Aguilar-Rosas and Machado-Galindo 1990; Álvarez-Álvarez et al. 2020; Diez-García et al. 2013; García-Redondo et al. 2019; Mateo-Cid et al. 2014; Montañés et al. 2003; Soares and Fujii 2012). These data were corroborated by this study because the orders with the highest number of registered epiphytic species were Ceramiales, Cladophorales, Ectocarpales, and Corallinales.

However, in general, the genera *Chaetomorpha*, *Jania*, *Ceramium*, *Ulva*, and *Cladophora* are important due to the high number of epiphytic species, in the present study. In addition to these genera, *Chondria*, *Laurencia*, *Dictyota* and *Ectocarpus* also stand out for their number of epiphytic species. Still, it is important to mention that most of the studies are localized and do not include a larger geographic area (i.e., a whole country) (García-Redondo et al. 2019; Jover et al. 2020). In this work, the taxa best represented included annual algae with reproductive strategies based upon the formation and dispersion of spores, which allow them to remain on the basibiont and be successful as epiphytes (Albis Salas 2010; Darley 1987; Mateo-Cid et al. 1993). Also, the main basibiont species reported for Mexican waters were the seagrass *Thalassia testudinum* and the brown algae *Padina. durvillei, Sargassum. sinicola* and *Sargassum muticum*. This information corresponds to that reported by other authors (Álvarez-Álvarez et al. 2020; Mateo-Cid et al. 2014; Nava-Olvera et al. 2017).

A high number of studies around the world have focused on seagrasses, and fewer studies have focused on algae as basibionts. Epiphytic algae can comprise between 24 % and 67 % of the total biomass of a seagrass bed (Saunders et al. 2003). According to Saunders et al. (2003) and Nava-Olvera et al. (2017), seagrass leaves function as excellent substrata for epiphytes because they provide a suitable habitat for their development, as they are in conditions of high light and water flow. On the other hand, for basibiont algae, it is known that some brown algae such as *Cystoseira*, *Laminaria, Padina, Sargassum*, *Stypopodium*, and *Zonaria* usually harbor complex assemblages of epiphytes. This was also observed in the present study, where the genera *Padina* and *Sargassum* were reported as important basibionts (Álvarez-Álvarez et al. 2020; Jover et al. 2020; Mateo-Cid et al. 2014; Montañés et al. 2003; Pedersen et al. 2014; Ramdani et al. 2015). Authors such as Montañés et al. (2003), Mendoza-González et al. (2011), Álvarez-Álvarez et al. (2020) and Jover et al. (2021) have mentioned that the reason these genera are successful basibionts could be due to their longevity, which allows the epiphytes to complete their life cycles on the host.

Also, these same authors hypothesized that the quality of a basibiont could be attributed to thallus characteristics, like hardness, texture, shape, leaf surface, stipes, and attachment structures. Aguilar-Rosas and Machado-Galindo (1990) pointed out that unevenness in the surface of basibionts will provide spaces for the attachment of epiphytes. Those algal genera and marine phanerogams whose morphological architecture have made them excellent hosts for other epiphytic algae have been called “nurse” species (Álvarez-Álvarez et al. 2020; Jover et al. 2020; Ortuño-Aguirre and Riosmena-Rodríguez 2007).

It has been observed that those algae that produce antifouling substances have fewer epiphytic species on their surface. In particular, this effect has been reported in brown algae such as *Sargassum* and *Padina*, that produce substances such as dimethylsulfopropionate (DMSP) and proline (Dahms and Dobretsov 2017), which prevent the development of bacteria, diatoms, and other groups of algae.

The species of epiphytic macroalgae most frequently recorded in Mexico could be classed as filamentous algae, followed by crustose and coralline algae, according to the morphofunctional groups proposed by Steneck and Dethier (1994). These observations agreed with other authors, who have mentioned the dominance of filamentous groups as epiphytes. This success has been attributed to their short life cycles, the morphological simplicity of the thallus, and the high photosynthetic rates of filamentous epiphytic algae. Some authors have also mentioned that filamentous algae may be successful epiphytes because they have a high tolerance to harsh environmental factors, a high supply of propagules, and a high capacity to settle (Álvarez-Álvarez et al. 2020; Barrios and Díaz 2005; Dawes 1998; Montañés et al. 2003; Pedersen et al. 2014).

Darley (1987) pointed out that epiphytic algal species have low attachment specificity because they can also be found as epizoic and epilithic. The association of many epiphytic species with more than one basibiont can be explained as suggested by Eminson and Moss (1980) and Tsioli et al. (2021), who associated the low specificity with eutrophic environments, where the elevated nutrients mask the chemical interactions between epiphytes and basibionts. On the other hand, some epiphytic algae show a substratum preference; these algae have been termed strict epiphytes (Jover et al. 2020; Santelices 1977). The epiphytic species *Stylonema alsidii* and *Erythrotrichia carnea* were recorded in this study on a low number of basibionts and were considered to be in this category (Aguilar-Rosas et al. 2007; Quiroz-González et al. 2018; Zuccarello et al. 2008).

According to Haritonidis and Tsekos (1976), Reyes et al. (1998), Bàrbara et al. (2005), Diez-García et al. (2013), Nava-Olvera et al. (2017) and García-Redondo et al. (2019), the species richness of Chlorophyta and Ochrophyta-Phaeophyceae can be categorized among tropical, subtropical, and temperate regions. The Cheney index (IC = 6.8) establishes that the epiphytic phycoflora in Mexico has a tropical affinity. Because the coast of Mexico is on a tropical/subtropical boundary with the surface temperature of the seawater between 30 °C and 15 °C, the Cheney index makes sense (Lalli and Parsons 1997). Spalding et al. (2007) acknowledged eight marine ecoregions for Mexico: Southern California Bight, Cortezian, Magdalena Transition, Revillagigedos, Mexican tropical Pacific, Chiapas-Nicaragua, Northern Gulf of Mexico, Southern Gulf of Mexico and Western Caribbean. In this study, the vast majority of marine epiphytic algae were recorded in the Western Caribbean (286 spp.) followed by the Southern Gulf of Mexico (209 spp.), Mexican Tropical Pacific (208 spp.), and the Southern California Bright (138 spp.). This may be explained by the different environmental conditions in each ecoregion, their diversity, host availability, sampling effort, or the specialized studies of basibionts, and/or the complex taxonomy of the epiphyte and basibiont taxa.

Epiphytic algae represent an important source of food for a high number of marine invertebrates, such as mollusks, crustaceans, and echinoderms, among many others. Also, epiphytic algae contribute to the primary productivity, nutrient flux, sediment accumulation, and species richness of marine ecosystems (Borowitzka et al. 2006). Besides, they can provide long-term data about water and environmental quality (Michael et al. 2008). They have an important potential in the development of monitoring programs for polluted ecosystems. Although the value and importance of epiphytic algae are clear, their studies remain poorly developed, as has been pointed out by several authors worldwide (García-Redondo et al. 2019).

In Mexico, it is important to emphasize the study of epiphytism, mostly because, historically, it has been considered only as circumstantial information from larger phycofloristic inventories. Looking into the condition of algal epiphytism is of great importance because it may give us information regarding the environmental conditions of the studied marine ecosystems and the value of this ecological interaction, and its effect on the littoral community as a whole.

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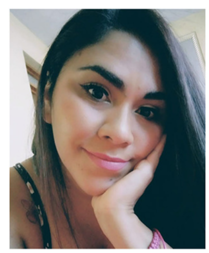
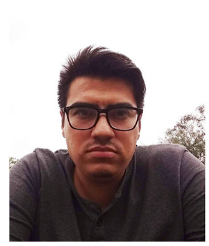
Bionotes



Nataly Quiroz-González
Facultad de Ciencias, UNAM Av. Universidad 3000, Circuito Exterior S/N Delegación Coyoacan, C.P. 04510 Ciudad Universitaria, D.F., Mexico

Nataly Quiroz-González is a professor at the Facultad de Ciencias, Universidad Nacional Autónoma de México. Her lines of research are systematics, taxonomy and ecology of marine algae. She currently focuses on molecular systematics of red marine algae and algal ecological interactions such as epibiosis.



Luis G. Aguilar-Estrada
Facultad de Ciencias, UNAM Av. Universidad 3000, Circuito Exterior S/N Delegación Coyoacan, C.P. 04510 Ciudad Universitaria, D.F., Mexico
lgae@ciencias.unam.mx

Luis G. Aguilar-Estrada is a PhD student at the Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México (UNAM). His doctoral research focuses on biogeography of marine gastropods (Vetigastropoda). He collaborates with Laboratorio de Ficología (Biodiversidad Marina) at UNAM. His current research interests are ecological interactions of marine benthos, such as seaweeds, seagrasses and mangroves.

Julio A. Acosta-Calderón
Instituto de Ecología, Universidad del Mar, Campus Puerto Ángel, Ciudad Universitaria s/n, Col. El Faro, C.P. 70902, Puerto Ángel, San Pedro Pochutla, Oaxaca, Mexico

Julio A. Acosta-Calderón is a seaweed biologist at Universidad del Mar. His research focuses on the systematics, taxonomy and ecology of tropical seaweeds with emphasis in intertidal and brackish habitats. Recent work has characterized the chemical properties of seaweeds from coastal lagoons of the Mexican tropical Pacific.

Lucía Álvarez-Castillo
Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Ciudad Universitaria 3000, C.P. 04510, Ciudad de México, Coyoacán, Mexico

Lucía Álvarez-Castillo is a marine biologist and current PhD candidate specializing in marine benthic environments. Her experience lies in the study of invertebrates and meiofauna. As a scientist she possesses research and analytical skills, which she has applied to various projects. Her areas of interest include taxonomy, ecology, statistics, evolution, and systematics. She is passionate about applying scientific knowledge to address modern biological problems, and she is committed to personal and professional growth.

Fernando Arriola-Álvarez
Facultad de Ciencias, UNAM Av. Universidad 3000, Circuito Exterior S/N Delegación Coyoacan, C.P. 04510 Ciudad Universitaria, D.F., Mexico

Fernando Arriola-Álvarez is a biologist and professor at Facultad de Ciencias of Universidad Nacional Autónoma de México (UNAM). He has worked with molluscs associated with macroalgae. His recent interests are focused on the biodiversity of macroscopic epiphytic algae.