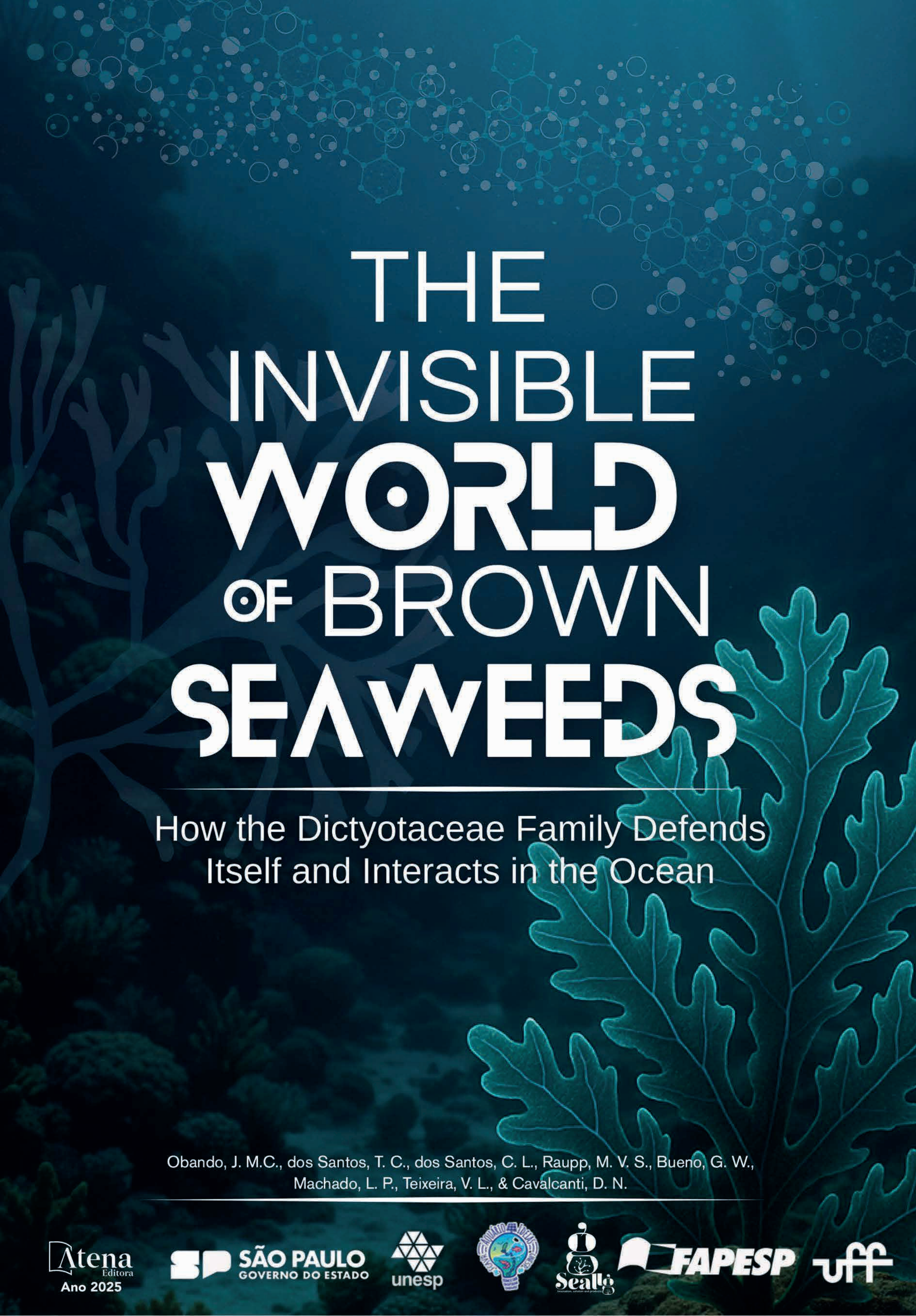


THE INVISIBLE WORLD OF BROWN SEAWEEDS

How the Dictyotaceae Family Defends Itself and Interacts in the Ocean

Obando, J. M.C., dos Santos, T. C., dos Santos, C. L., Raupp, M. V. S., Bueno, G. W.,
Machado, L. P., Teixeira, V. L., & Cavalcanti, D. N.

Atena
Editora
Ano 2025

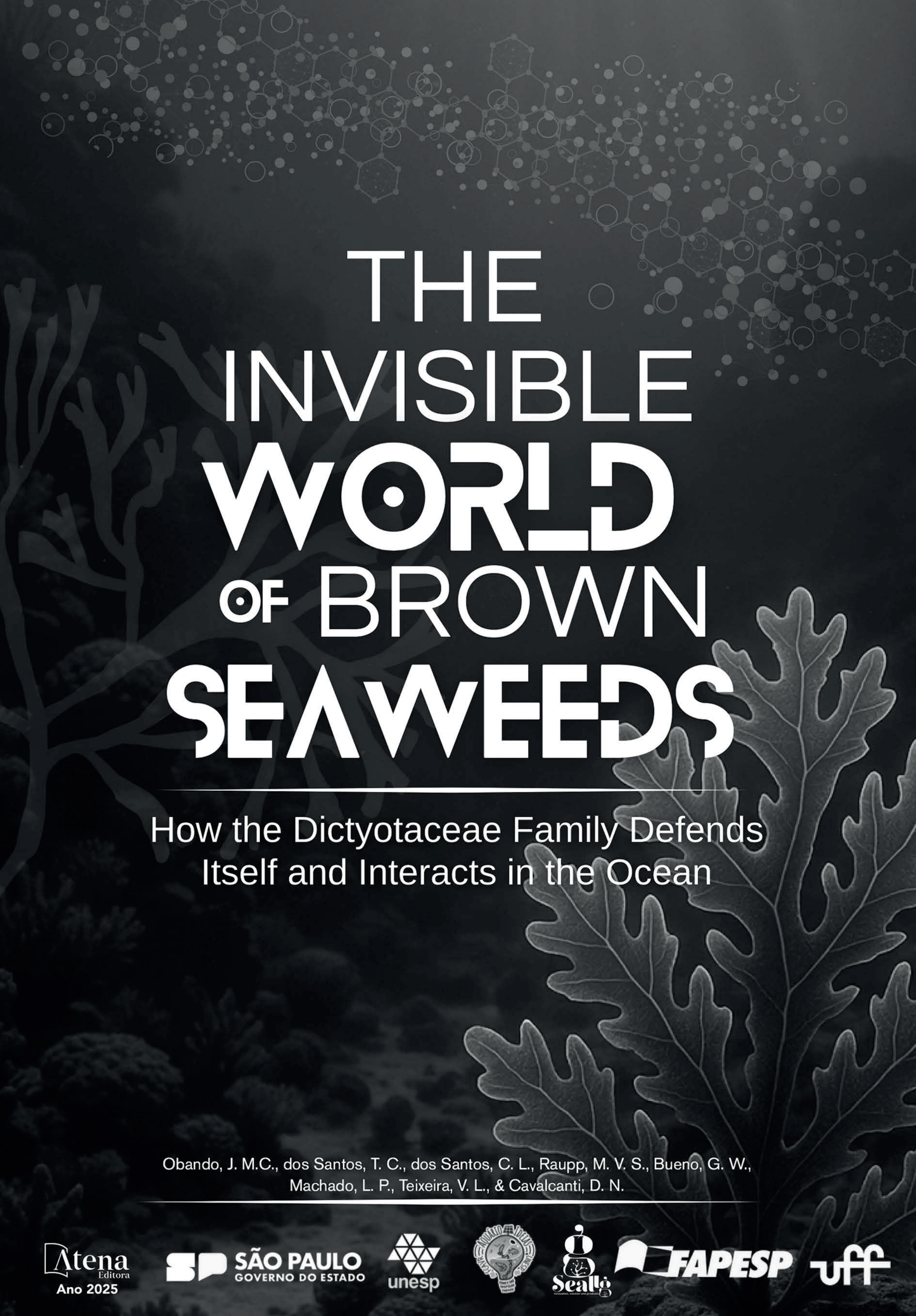
SÃO PAULO
GOVERNO DO ESTADO

unesp

Sealg

FAPESP

uff



THE INVISIBLE WORLD OF BROWN SEAWEEDS

How the Dictyotaceae Family Defends Itself and Interacts in the Ocean

Obando, J. M.C., dos Santos, T. C., dos Santos, C. L., Raupp, M. V. S., Bueno, G. W.,
Machado, L. P., Teixeira, V. L., & Cavalcanti, D. N.

Atena Editora
Ano 2025
SÃO PAULO
GOVERNO DO ESTADO
unesp
Sealg
FAPESP
uff

Editora chefe
Profª Drª Antonella Carvalho de Oliveira
Editora executiva
Natalia Oliveira Scheffer
Imagens da capa
iStock
Edição de arte
Yago Raphael Massuqueto Rocha

A Atena Editora mantém um compromisso firme com a integridade editorial em todas as etapas do processo de publicação, assegurando que os padrões éticos e acadêmicos sejam rigorosamente cumpridos. Adota políticas para prevenir e combater práticas como plágio, manipulação ou falsificação de dados e resultados, bem como quaisquer interferências indevidas de interesses financeiros ou institucionais.

Qualquer suspeita de má conduta científica é tratada com máxima seriedade e será investigada de acordo com os mais elevados padrões de rigor acadêmico, transparência e ética.

O conteúdo da obra e seus dados, em sua forma, correção e confiabilidade, são de responsabilidade exclusiva do autor, não representando necessariamente a posição oficial da Atena Editora. O download, compartilhamento, adaptação e reutilização desta obra são permitidos para quaisquer fins, desde que seja atribuída a devida autoria e referência à editora, conforme os termos da Licença Creative Commons Atribuição 4.0 Internacional (CC BY 4.0).

Os trabalhos nacionais foram submetidos à avaliação cega por pares, realizada pelos membros do Conselho Editorial da editora, enquanto os internacionais passaram por avaliação de pareceristas externos. Todos foram aprovados para publicação com base em critérios de neutralidade e imparcialidade acadêmica.

The invisible world of brown seaweeds

| Autores:
Johana Marcela Concha Obando
Thalisia Cunha dos Santos
Clara Lopes dos Santos
Maria Vitória Raupp Sebastião
Guilherme Wolff Bueno
Levi Pompermayer Machado
Valéria Laneuville Teixeira
Diana Negrão Cavalcanti

| Revisão:
Os autores

International Cataloguing-in-Publication Data (CIP)

I62 The invisible world of brown seaweeds / Johana Marcela Concha Obando, Thalisia Cunha dos Santos, Clara Lopes dos Santos, et al. – Ponta Grossa - PR: Atena, 2025.

Other authors:
Maria Vitória Raupp Sebastião
Guilherme Wolff Bueno
Levi Pompermayer Machado
Valéria Laneuville Teixeira
Diana Negrão Cavalcanti

Format: PDF
System Requirements: Adobe Acrobat Reader
Access mode: World Wide Web
Includes bibliography
ISBN 978-65-258-3660-7
DOI: https://doi.org/10.22533/at.ed.607252508

1. Macroalgae. 2. Chemical Interactions. 3. Abiotic. 4. Factors influence. 5. Dictyotales-Phaeophyta. I. Concha Obando, Johana Marcela. II. Santos, Thalisia Cunha dos. III. Santos, Clara Lopes dos. IV. Title.

CDD 579.8

Prepared by Librarian Janaina Ramos – CRB-8/9166

Atena Editora
☎ +55 (42) 3323-5493
☎ +55 (42) 99955-2866
www.atenaeditora.com.br
contato@atenaeditora.com.br

CONSELHO EDITORIAL

CONSELHO EDITORIAL

Prof. Dr. Alexandre Igor Azevedo Pereira – Instituto Federal Goiano
Profª Drª Amanda Vasconcelos Guimarães – Universidade Federal de Lavras
Prof. Dr. Antonio Pasqualetto – Pontifícia Universidade Católica de Goiás
Profª Drª Ariadna Faria Vieira – Universidade Estadual do Piauí
Prof. Dr. Arinaldo Pereira da Silva – Universidade Federal do Sul e Sudeste do Pará
Prof. Dr. Benedito Rodrigues da Silva Neto – Universidade Federal de Goiás
Prof. Dr. Cirênio de Almeida Barbosa – Universidade Federal de Ouro Preto
Prof. Dr. Cláudio José de Souza – Universidade Federal Fluminense
Profª Drª Daniela Reis Joaquim de Freitas – Universidade Federal do Piauí
Profª Drª. Dayane de Melo Barros – Universidade Federal de Pernambuco
Prof. Dr. Eloi Rufato Junior – Universidade Tecnológica Federal do Paraná
Profª Drª Érica de Melo Azevedo – Instituto Federal do Rio de Janeiro
Prof. Dr. Fabrício Menezes Ramos – Instituto Federal do Pará
Prof. Dr. Fabrício Moraes de Almeida – Universidade Federal de Rondônia
Profª Drª Glécilla Colombelli de Souza Nunes – Universidade Estadual de Maringá
Prof. Dr. Humberto Costa – Universidade Federal do Paraná
Prof. Dr. Joachin de Melo Azevedo Sobrinho Neto – Universidade de Pernambuco
Prof. Dr. João Paulo Roberti Junior – Universidade Federal de Santa Catarina
Profª Drª Juliana Abonizio – Universidade Federal de Mato Grosso
Prof. Dr. Julio Candido de Meirelles Junior – Universidade Federal Fluminense
Profª Drª Keyla Christina Almeida Portela – Instituto Federal de Educação, Ciência e Tecnologia do Paraná
Profª Drª Miranilde Oliveira Neves – Instituto de Educação, Ciência e Tecnologia do Pará
Prof. Dr. Sérgio Nunes de Jesus – Instituto Federal de Educação Ciência e Tecnologia
Profª Drª Talita de Santos Matos – Universidade Federal Rural do Rio de Janeiro
Prof. Dr. Tiago da Silva Teófilo – Universidade Federal Rural do Semi-Árido
Prof. Dr. Valdemar Antonio Paffaro Junior – Universidade Federal de Alfenas

Preface

This brief e-book is the result of the personal motivation of two researchers, Johana Marcela Concha Obando and Thalisia dos Santos, who worked in close collaboration throughout their Master's and Ph.D. studies over approximately eigth years. Their research focused on brown algae of the Dictyotaceae family as model organisms—species that have also been the subject of extensive investigation by the ALGAMAR research group at Fluminense Federal University (UFF), a group with a solid and longstanding trajectory in studying the chemical profiles and potential bioactives of brown seaweeds. This work also serves as a tribute to this remarkable group of algae, which provided us with a specific and scientifically rich focus that contributed significantly to our growth as natural products researchers—particularly through the exploration of diterpenes, a class of compounds that deepened our understanding of the natural products found in *Dictyota menstrualis* and *Canistrocarpus cervicornis*, two native species of the Brazilian coast.

With this e-book, we aim to provide an updated narrative review of the scattered literature on the chemical ecology of these algae and the role of various abiotic factors in shaping their metabolite production. This work brings together ecological, biochemical, and environmental perspectives, consolidating knowledge that is often fragmented across different sources—particularly for some of the most studied genera of the Dictyotaceae family that are part of Brazilian biodiversity.

The authors believe that the publication of accessible scientific material through open access platforms, such as Editora Atena, is a powerful tool for both scientific communication and national academic dissemination. This initiative is intended not only to support researchers and students, but also to broaden the visibility of marine chemical ecology as an evolving and interdisciplinary field.

Acknowledgements

We gratefully acknowledge the Aquário de Ideias (UNESP) for supporting our commitment to accessible and educational scientific dissemination, and for embracing the idea that innovation is inseparable from scientific dissemination. We would like to thank the Center for Research on Biodiversity Dynamics and Climate Change - CBioClima Fapesp and Secretariat of Science, Technology, and Innovation of the State of São Paulo - SCTI, SPAI Network; Cetma Project. The INCT Nanotechnology for Sustainable Agriculture, the Coordination for the Improvement of Higher Education Personnel – Brazil (MEC-CAPES INCTNanoAgro #88887.986628/2024-00) for the postdoctoral fellowship (Obando JMC).

Special thanks go to the ALGAMAR Laboratory, which has supported our research over the years. We are especially grateful to Professor Valéria Laneuville Teixeira, whose dedication and leadership have been fundamental to the development of a Brazilian research line focused on natural products from marine algae—an area of great value to the national academic community—and for her trust in supporting this publication.

Funding

The authors would like to thank the Foundation for the Improvement of Higher Education Personnel (CAPES); the INCT Nanotechnology for Sustainable Agriculture, National Council for Scientific and Technological Development (MCTI-CNPqINCTNanoAgro #405924/2022-4; CNPq Productivity development technological grant 302711/2023-6 and 303653/2022-1 MEC-CAPES INCTNanoAgro #88887.953443/2024-00); and São Paulo Research Foundation (FAPESP) process nº 2021/10639-5; 2022/02756-4 and 2024/03203-4 for the financial support to perform this study. This work was also supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (Grants No. 443930/2014-7 and Productivity Fellowship No. 304070/2014-9).

ABSTRACT

The Dictyotaceae family is one of the most representative families of brown algae and includes several important genera, such as *Dictyota*, *Dictyopteris*, *Padina*, *Stypopodium*, and *Lobophora*, all of which play crucial roles in marine ecosystems. Due to their high chemical diversity and relevant bioactivity of their primary and secondary metabolites, such as terpenes, polyphenols, steroids, fatty acids, and pigments, these macroalgae have become promising sources of bioactive molecules. With a wide range of effects at the molecular and cellular levels, these molecules are intrinsically linked to the metabolic complexity of algae, which manifests through interactions with various environmental pressures present in the complex marine ecosystem. Thus, the intrinsic chemistry of algae plays a fundamental role in modulating two essential aspects of its ecology: (1) reproduction and (2) survival. This work provides an up-to-date overview of the classification and diversity in addition to ecological and environmental significance of the Dictyotaceae family's metabolites. Drawing from relevant studies on this algae family, we delve into aspects of its chemical ecology in terms of life cycles and reproduction along with abiotic factors (such as light, temperature, and hydrodynamics). Additionally, we describe the molecules involved in these processes and emphasize their biotechnological potential as significant ecosystem services.

KEYWORDS: Macroalgae, Chemical Interactions, Abiotic Factors influence, Dictyotales-Phaeophyta

CONTENTS

CONTENTS

CHAPTER 1

MARINE MACROALGAE: DICTYOTALES AND THEIR TAXONOMIC AND PHYLOGENETIC CONTEXTS

The ocean is home to various marine organisms with diverse physiologies and adaptations. Both macro and microalgae include between 30,000 and one million different species, all of which exhibit a vast array of shapes and sizes (Akram et al. 2022). Most algae inhabit aquatic environments and possess unicellular gametangia and a thallus as vegetative bodies (Driss, 2021). The term “algae” includes both prokaryotic organisms (cyanobacteria) and eukaryotic organisms that form a combined polyphyletic group. Thus, “algae” is essentially an ecological term that applies to organisms of various origins (Gololobova and Belyakova, 2022). Currently, numerous uncertainties are present regarding which organisms should be classified as algae and whether a species may encompass two different phyla and classes thus rendering algae evolutionarily diverse. Such diversity means that algae do not represent a single taxonomic entity as seen in the case of vascular plants. Recognizing the challenges in the systematics of these organisms, recent years have witnessed extensive efforts to generate a more precise estimate of the number of algal species (Cavalier-Smith, 2016; Menaa et al., 2020; Guiry and Guiry, 2023). Presently, depending on their systematics and molecular phylogeny, algae are classified into approximately four kingdoms: (1) Kingdom Plantae (for instance, Chlorophytes, such as green algae, and Rhodophytes, such as red algae); (2) Kingdom Protozoa (formerly Protista; for example, Euglenozoa, formerly Euglenophytes); (3) Kingdom Chromista (for instance, Phaeophytes, such as brown algae, encompassing dinoflagellates and diatoms); and (4) Kingdom Eubacteria (cyanophytes, also known as blue-green algae) as described by Adl et al., (2005). It is essential to clarify that the term “algae” for cyanobacteria is considered erroneous by many authors in biology because algae should strictly refer to eukaryotic organisms. However, some definitions of algae also include prokaryotic organisms (Gololobova and Belyakova, 2022) as shown in Figure 1.

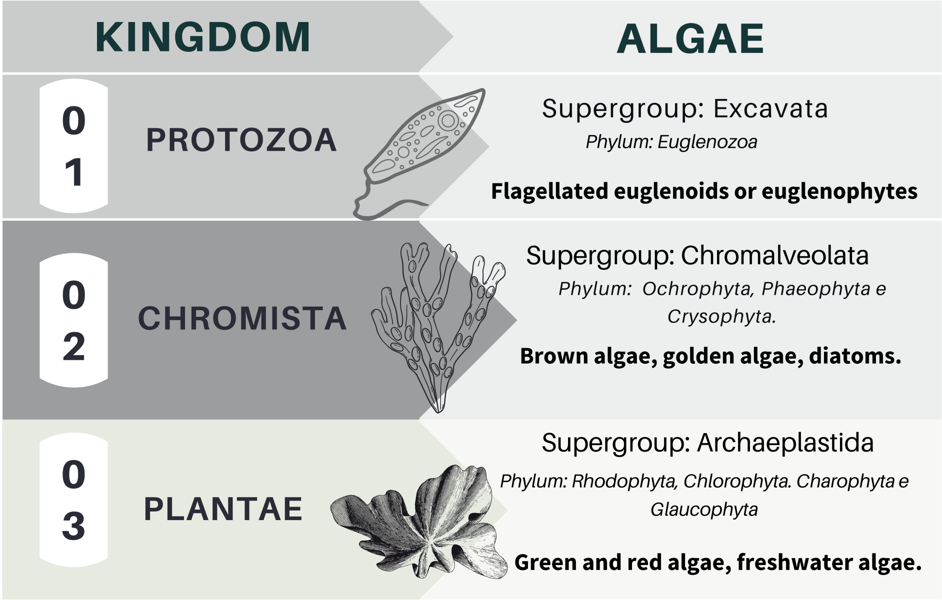


Figure 1. Classifying seaweed into kingdoms (Gololobova and Belyakova, 2022).

Algae are best defined as oxygenic photosynthetic organisms that are not terrestrial embryophyte plants (Cavalier-Smith, 2016). Specifically, marine macroalgae are macroscopic aquatic organisms (capable of measuring up to 65 m in length) that naturally inhabit predominantly rocky coastlines. A solid attachment point is crucial for their survival, although they can also float. Species of marine algae are found in aquatic systems that contain certain levels of salinity (above 3 practical salinity unit [PSU]) and sunlight for photosynthesis, both of which are environmental conditions that govern their ecology (García-Poza et al., 2022; Cotas et al., 2023). Seaweeds, as primary producers, form the foundation of the marine food chain thus fulfilling a crucial ecological role.

Seaweeds contribute significantly to oxygen production, offer habitat to diverse marine species, and serve as a vital food source for various herbivores, including invertebrates, such as certain sea urchins and gastropods and vertebrates, such as herbivorous fish.

Additionally, seaweeds provide shelter from predators and by doing so, enhance marine ecosystems' overall biodiversity and stability (Randall et al., 2020). The active and interesting metabolism of marine macroalgae makes these organisms producers of many chemical molecules that mediate each of their interactions with their natural environment thus forming an essential key in the trophic chain of the marine complex. On the other hand, seaweeds' biomass and diversity provide several ecosystem services (ES). ES are the human gains obtained from ecosystems and are divided into four categories: (1) support, (2) provisioning, (3) regulatory, and (4) cultural services according to the Millennium Ecosystem Assessment and the Common International Classification of Ecosystem Services (MEA and CICES, respectively). This perspective is reinforced by the fact that seaweed and humanity have been interconnected since the beginning of time, since humans in coastal communities have always used seaweed as a source of food, fiber, biochemicals, natural medicine, ornamental resources, artistic inspiration, and aesthetic values (Cotas et al., 2023). Most of the seaweed supply to humans (97.1%) is obtained from coastal water agriculture (Buschmann et al., 2017). In recent decades, seaweed cultivation has rapidly expanded. Seaweed cultivation represents 51.3% (34.7 MMT, wet weight) of total global marine aquaculture for which China and eight other Asian countries lead production (Troell et al., 2023; Chopin and Tacon, 2021). Seaweed is currently being studied in different areas, such as green carbon, carbon sequestration, and as a possible source of ingredients for the biomedical, cosmetic, and pharmaceutical sectors (Cotas et al., 2023).

Based on their pigment profile in addition to morphological, anatomical, and reproductive structures, marine macroalgae are generally categorized into three taxonomic groups: (1) Chlorophyceae (green algae), (2) Phaeophyceae (brown algae), and (3) Rhodophyceae (red algae). Based on the group, algae contain large amounts of carbohydrates (4% to 70% of their dry matter), lipids (1% to 20% of their dry matter), proteins (7% to 47% of their dry matter), and many other valuable chemicals (Abdel-Kareem and ElSaied, 2022). Brown algae (Phaeophyceae) are a group of multicellular heterokonts (or Stramenopiles) that are widely distributed in the oceans and play fundamental roles in the functioning of coastal marine ecosystems, a role that extends to the Arctic and tropical regions. Large brown algae, particularly those in the orders Laminariales, Tilopteridales, Fucales, and Desmarestiales, act as ecosystem engineers (Teagle et al., 2017; Bringloe et al., 2020). Approximately 2,000 species have been described for this group, and they are one of the few lineages of eukaryotic algae that have developed complex multicellularity (Charrier et al., 2008). These seaweeds form underwater forests that provide structural complexity to marine ecosystems (Bringloe et al., 2020).

Phylogenetically, the photosynthetic heterokonts share a common endosymbiotic event, namely phagocytosis of red alga from which the heterokonts' plastids evolved. In other words, the chloroplasts of brown algae evolved through a secondary endosymbiosis in which the red algae were absorbed by a non-photosynthetic eukaryote (Keeling, 2010), which formed the Ochrophyta, a lineage of mainly unicellular and mainly photosynthetic lineages (such as diatoms, chrysophytes, sinurophytes, and xanthophytes). Thus, brown algae, which belong to the Phaeophyceae class, independently evolved complex multicellularity in the heterokonte lineage (Terauchi et al., 2017). They evolved as a separate lineage from groups possessing a primary plastid, such as green algae, land plants, rhodophytes, and glaucophytes (Dorrell et al., 2017).

The class Phaeophyceae currently has around 2120 species distributed in around 350 genera (Guiry and Guiry, 2024) that are divided into four subclasses: (1) Discosporangiophycidae, (2) Dictyotophycidae, (3) Fucophycidae, and (4) Ishigeophycidae (Silberfeld et al., 2014). The subclass Dictyotophycidae encompasses the orders Sphacelariales, Syringodermatales, Dictyotales, and Onslowiales (Silberfeld et al., 2014). This subclass is quite heterogeneous but can be characterized by terminal polycystic growth (from a single or a group of cells, which form a meristem), cells with many discoid plastids, absence of pyrenoids, isomorphic life cycle, and isogamy, except Dictyotales, which presents oogamy (Silberfeld et al., 2010; Silberfeld et al., 2014). The order Dictyotales is highly diverse among brown algae and has a global distribution. Although cooler regions harbor the greatest diversity and are dominant in the Northern Hemisphere, tropical and subtropical areas are also important habitats for these algae. Traditionally, the classification of brown algae has relied on factors, such as thallus morphology, life history traits, spore and gamete types, and cytoskeletal features. However, the advent of DNA sequencing is reshaping our understanding of brown algae relationships and leading to new perspectives in classification. Molecular data (such as the molecular markers, 18S, 5.8S, 28S, atp B, psb A, psa B, psa A, rbc L, psb C, cox 1, cox 3, and nad) indicate that the global phylogenetic structure of brown algae presents two orders that resulted from early divergence events: (1) a large clade composed of four orders (Sphacelariales, Syringodermatales, Dictyotales, and Onslowiales, coined the SSDO clade) and (2) a large and initially poorly resolved clade comprising all remaining orders of brown algae, which are referred to as brown algal crown radiation (BACR). Ectocarpales with 756 species, Fucales with 570, Dictyotales with 363, and Laminariales with 126 species, represent the most abundant orders of brown algae (Bringloe et al., 2020; Guiry and Guiry, 2024).

The Dictyotales emerged from an early divergence event in the evolution of brown algae as they originated in the tropical southern Tethys during the Middle Jurassic period. Their current peak species diversity is found in the tropical Indo-Pacific region. This diversity is primarily attributed to two significant bursts of diversification in *Lobophora* and *Dictyota*, particularly in tropical regions. Today, genera such as *Dictyota*, *Lobophora*, and *Padina* play crucial roles as benthic components in tropical and subtropical reef ecosystems (Vieira, 2020; Vieira et al., 2021) (Figure 2). Traditional taxonomic treatments recognized three families: (1) Dictyotopsidaceae Allender (1980), (2) Scoresbyellaceae Womersley (1987), and (3) Dictyotaceae Lamouroux ex Dumortier (1822), the latter being divided into two tribes: (a) Dictyoteae Greville (1830) and (b) Zonarieae De Toni (1895). Recent molecular investigations have revealed that several genera within the Dictyotaceae do not form distinct monophyletic clades. Consequently, the subdivision into two tribes is most likely irrelevant (De Clerck et al., 2006; Bittner et al., 2008). Thus, the Dictyotales currently comprise a single family Dictyotaceae J.V. Lamouroux, which includes 21 genera and about 350 species (Guiry and Guiry, 2024). In this family, morphological plasticity is quite pronounced, which explains why its species are complex in taxonomy, especially in the genus *Dictyota* Lamouroux, which is quite sensitive to human impact, which can often lead to population reduction or local extinction (De Paula et al., 2020).

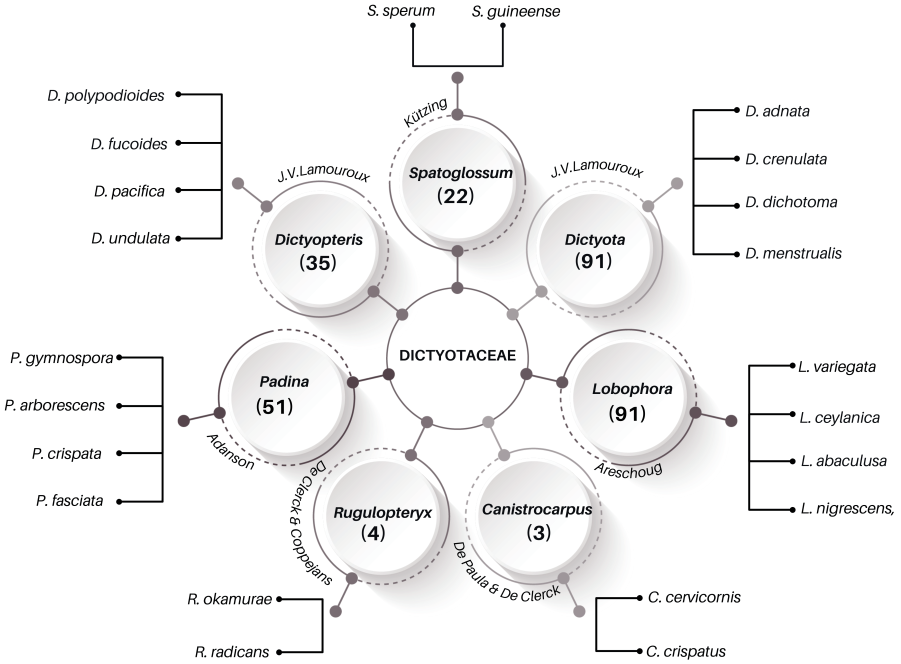


Figure 2. Illustrates the most representative genera of the Dictyotaceae family: *Dictyota* (91), *Lobophora* (91) *Dictyopteris* (35) *Padina* (51), *Spatoglossum* (22), *Rugulopteryx* (4), *Canistrocarpus* (3) (Gury an Gury 2024).

The genus *Dictyota* consists of parenchymal algae that occur predominantly in tropical to warm temperate waters. The species typically grows in intertidal rock pools and subtidal areas. The thallus is characterized by one or more lenticular apical cells that are divided into layers of cortical and medullary cells. These algae are parenchymal with flat, ribbon-like axes that grow from well-defined apical meristems that differentiate into an outer cortical layer and an inner medullary layer. Thallus branching in *Dictyota* occurs through dichotomous primary branching and is driven by longitudinal cell divisions of apical meristem cells. Additionally, adventitial branching can occur in which cortical cells or other cortical differentiations, such as male paraphyses and dedifferentiated reproductive cells, undergo dedifferentiation to facilitate branching (Bogaert, Delva and De Clerck, 2020). Species are recognized by discontinuities in morphological characters, but the inability to distinguish morphological plasticity from diagnostic features that separate the various species is evident. However, the use of molecular markers has made it possible to clarify intra- and inter-specific relationships, which has resulted in identification of several new species (Lozano-Orozco et al., 2015). However, the lack of genomic information for Dictyotales still limits our understanding of the taxonomic status and evolution of this group.

The genus *Lobophora* is a pantropical–temperate genus that commonly occurs in tropical and subtropical seas and has been previously documented in the Atlantic (including the Gulf of Mexico), the Indian and Pacific oceans, and in both hemispheres (Vieira et al., 2016). Its species are found in a multitude of habitats, including shallow and deep-water coral reefs, rocky coasts, mangroves, seagrass beds, and rhodolite beds (Camacho et al., 2019). They typically feature a procumbent, decumbent, or erect stem and form clusters of leaves that may resemble a rosette. The fronds widen at the apex and gradually tape towards the base. They exhibit a fan-shaped or lobed appearance with a smooth surface that contains concentric rings, which form distinctive zones. Stalks divide and give rise to irregular branches, while tangled rhizoids assist in anchoring; these rhizoids can be filamentous or moniliform. Frond margins are complete with a thickness of 6–9 layers. The intermediate portion consists of cells ranging from large squares to rectangles. A single central layer of cells is surrounded by rows of uniformly sized cells in the cortical portion with one pair of peripheral cells per cortical cell. Sori, which are dispersed on both surfaces, lack paraphyses and are arranged in concentric zones (Aisha and Shameel, 2012). Recent molecular studies have shown that the biodiversity of this genus has been greatly underestimated. Vieira et al. (2017) applied several algorithmic methods to delimit species in a mitochondrial dataset consisting of 598 specimens and arrived at an estimate of 98–121 species. This diversity exceeds traditional estimates based solely on morphological data.

The genus *Padina* has a global distribution in warm temperate and tropical waters and can be found in intertidal and subtidal zones to a depth of 110 meters (N'yeurt and Payri, 2010). It is one of the only two calcareous generates of brown algae, the other being Newhousia (Kraft et al., 2004). The thalli are generally fan-shaped and have a curled margin surrounding a marginal meristem from which growth is initiated. However, in some species, prostate rhizomes, the so-called Vaughaniella stages, develop from a single apical cell from which new erect thalli subsequently arise and become several cells thick (Win et al., 2013). Species of *Padina* are traditionally delineated based on the following morphological characteristics: (1) gross morphology, (2) thallus calcification, (3) number of cell layers, (4) presence or absence of Vaughaniella stage, (5) position and arrangement of hairs, (6) position and arrangement of tetra sporangial sori relative to the hairline, and (7) presence or absence of an indusium, which is a hyaline covering over tetra sporangial sori) (Huisman and Abbott, 2004; Win et al., 2013).

Even in the presence of several morphological characters in a specific specimen, identification becomes challenging due to subtle morphological differences and morphological plasticity that appear under the influence of certain environmental factors, such as grazing and intertidal stress. The global diversity of species and their distribution ranges remains largely unknown. In recent years, species-level diversity has been re-evaluated using DNA-based algorithmic delineation techniques with cox3 and rbcL sequence data from 221 global specimens. This new evaluation has led to estimates of 39 to 61 evolutionarily significant units (ESUs) of species. Subsequently, these units have been assigned to 31 known species and six unknown species, labeled as *Padina* spp. 1-6 (Silberfeld et al., 2013). Four of these six species were later assigned to *P. moffittiana*, *P. calcarea*, *P. ogasawaraensis,* and *P. boryana* (Ni-Ni-Win et al., 2018). Hanyuda and colleagues (2021) have substantially expanded information on the diversity of *Padina* species based on the combination of DNA sequences and worldwide morphological data. Forty-three known species and 13 unknown lineages are likely independent taxa, indicating the probable existence of at least 56 *Padina* species.

The genus *Dictyopteris* exhibits a wide distribution across oceans in tropical, subtropical, and temperate regions. Its species feature flattened thalli that typically branch dichotomously and feature a prominent central vein. Thalli are anchored by a tangled rhizoid support, which can extend up to 60 cm in length. Branching occurs subdichotomously with lateral branches that range from 0.5 to 25 mm wide. Growth is facilitated by a row of meristematic cells located within a shallow depression at the branch apex (Zatelli et al., 2018). The presence of a multilayered midrib is the sole generic feature distinguishing *Dictyopteris* from all other genera of Dictyotales. *Dictyopteris*' midrib is formed by derivatives of central apical cells that continue dividing considerably behind the apex (Phillips, 2000). Taxonomic classification within Dictyotales is challenging due to its morphological variability (Tronholm et al., 2010). In addition,the taxonomic classification and global species diversity within the genus *Dictyopteris* pose significant challenges due to its morphological variability as seen in other genera in the family. It is anticipated that the utilization of molecular markers will aid in clarifying intra- and inter-specific relationships, potentially leading to the identification of numerous new species. However, a notable research gap exists due to limited studies addressing hypotheses concerning the biogeography of this genus. Some characteristics of the four previously described genera are shown in Figure 3. These characteristics offer valuable insights into their morphology, reproductive strategies, and ecological roles within marine ecosystems.

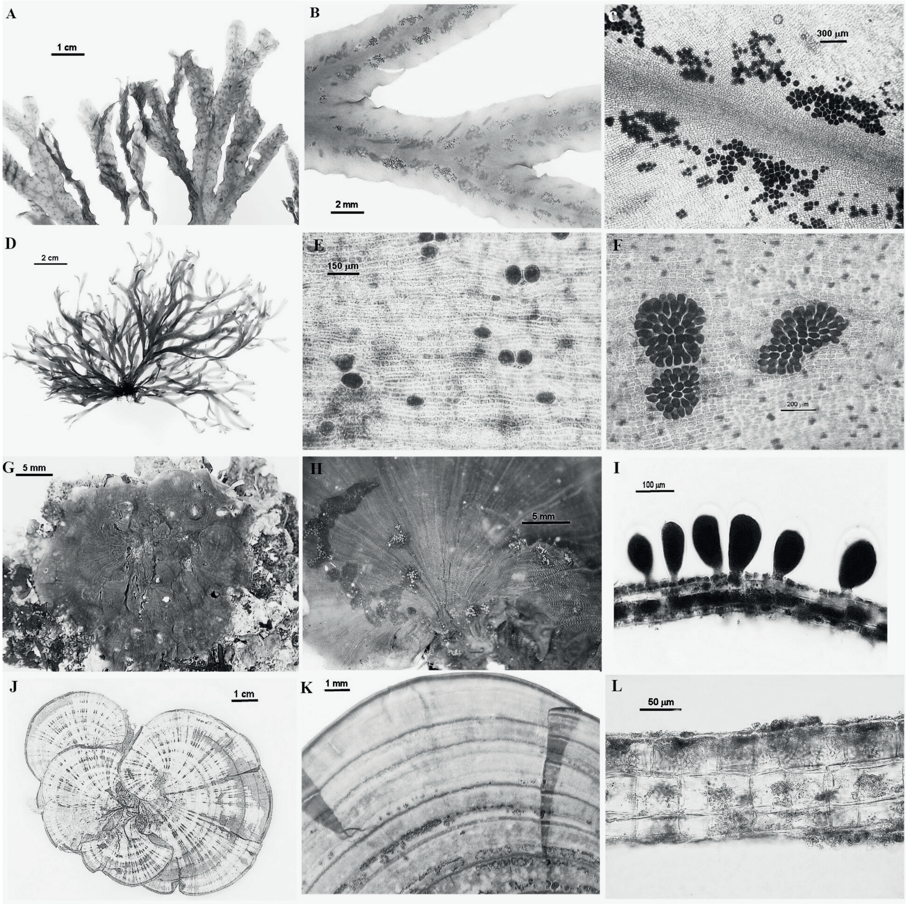


Figure 3. Images of representative species of the four genera of the Dictyotacea family. (1) Detail of the distal portions of *Dictyopteris polypodioide*s (A. P. De Candolle) J. V. Lamouroux; (2) Fronds with sporocystic buttons; (3) Sporocytes details, (4) Appearance of *Dictyota dichotoma* (Hudson) J. V. Lamouroux, (5) Mainly isolated sporocysts, (6) Sori on the oogonium, (7) Appearance of the thallus of *Lobophora variegata* (J. V. Lamouroux) Womersley ex E. C. Oliveira, (8) Sporocystic Sori., (9) Radial longitudinal section at the level of the sporocyst sori, (10) Herbarium specimen of *Padina pavonica* (Linnaeus) Thivy, (11) Detail of the marginal area, and (12) Radial longitudinal section in the middle area of the foliage. https://www.sma.unifi.it/upload/sub/catalogo_alghe/

CHAPTER 2

LIFE CYCLES, CHEMISTRY, AND REPRODUCTIVE BEHAVIOR IN THE DICTYOTACEAE

Life cycles of Dictyotaceae

The haplo–diplontic isomorphic life cycle of species in the order Dictyotales was theorized over a century ago (Williams, 1904), based on studies of *Dictyota dichotom*a (Hudson) Lamouroux, as well as affirmed later by Hoyt (1910) in the same species and by Wolfe (1918–1919) in *Padina vickersiae* Hoyt. Subsequently, this life cycle was acknowledged as a common characteristic across all taxa within the order Dictyotales. Thus, the life cycle of algae in the family Dictyotaceae may vary among different genera and species within the family, but the general pattern remains similar. It is important to note that algae life cycles are often complex and can be influenced by environmental factors, such as water temperature, sunlight, and nutrient availability.

In many species of Dictyotales, sexual individuals are much rarer than sporophytes, and in some cases, these species are unknown (Garreta et al., 2007). Specifically, sexual reproduction is always oogamous, and male gametes are generally uniflagellated, except in some species of *Zonaria*, which are characterized by biflagellated spermatozoids (Phillips, 1997). The diploid sporophyte typically produces unilocular sporangia with four non-flagellated meiospores (tetraspores), but some genera produce eight aplanospores per sporangium (such as *Lobophora* and *Zonaria*), a characteristic that is considered primitive. The gametophyte plants of most species are dioecious with the exception of a few species that have been studied as monoecious individuals (such as *P. pavonica* [Linneaus] Thivy) as described by Garreta et al. (2007).

The genus *Dictyota* exhibits the capacity for propagation through fragmentation (Herren, Walters and Beach, 2006). This capability enables the species to maintain biomass even under high grazing pressures and plays a crucial ecological role in benthic communities within subtropical and temperate ecosystems. Their capability to propagate via fragmentation makes them particularly valuable for suspension cultures. Specifically, the life cycle is isomorphic and diplo-haplontic and involves alternating between haploid gametophytes and diploid sporophytes. In other words, two free-living phases occur: (1) haploid (gametophyte) and (2) diploid (sporophyte).

Meiosis takes place during the formation of spores (Figure 4). The gametophytes of *Dictyota* are dioecious. Their reproductive structures are tetrasporangia, oogonial sori, and spermatangial sori, which are located on the sporophyte, female gametophyte, and male gametophyte, respectively. Female and male individuals can be easily distinguished by the presence of oogonia and antheridia, respectively, on the thallus surface, but they do not exhibit sexual dimorphisms beyond the reproductive structures. Similarly, the life cycle is isomorphic and differs morphologically only in terms of the reproductive structures (Bogaert, Beeckman and De Clerck, 2016).

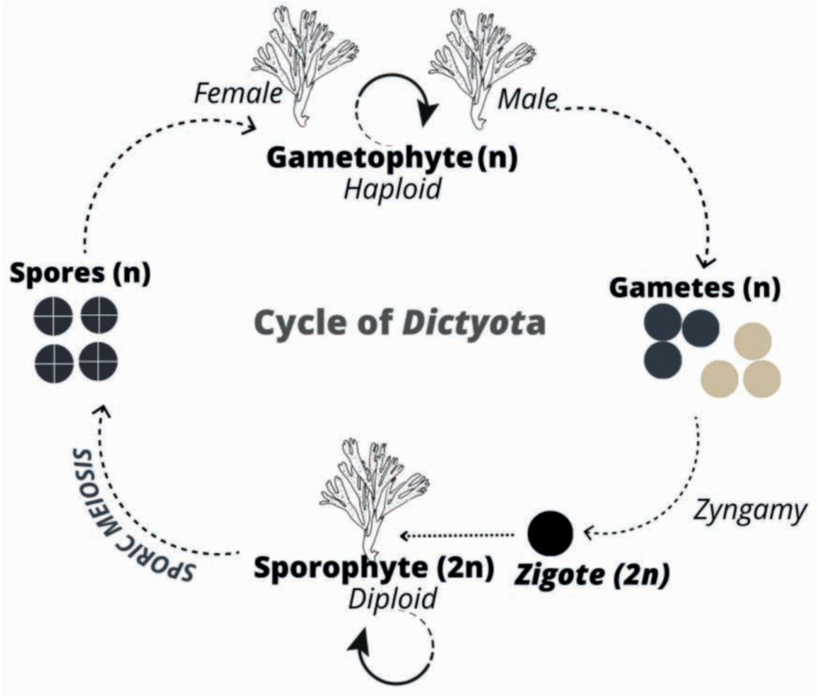


Figure 4. Schematic representation of the life cycle of algae of the genus D*ictyota*.

The Chemistry of Dictyotaceae and their ecological implications

Specialized metabolites participate in a diverse range of ecological functions in macroalgae, particularly in chemical communication with other marine organisms. However, the underlying sources of variation and the mechanisms regulating these metabolites remain largely unknown. Currently, studying metabolomic variations on the inter- and intra-specific scales, including across space and time, is crucial for understanding species ecology, community structure, and ecosystem functioning (Reverter et al., 2018). Tropical and subtropical benthic marine algae are richest in the production of these substances.

Tropical macroalgae exhibit a rich diversity of metabolites, such as halogenated compounds, phenolics, terpenoids, and acetogenins, which are small molecules that are regulated by genetic, developmental, and environmental factors. These metabolites evolved under natural selection and have adaptive roles in macroalgae, including chemical communication and various ecological activities. In addition to deterring competitors and herbivores, they act as a defense against pathogens (bacteria, fungi, viruses) and epibionts, offer protection from ultraviolet (UV) radiation, and even behave as sexual pheromones. These compounds also play a role in competition for space with other benthic organisms by adapting to the different physicochemical pressures of the marine environment (Wink et al., 2003; Kooke and Keurentjes, 2011; Gaubert et al., 2019).

The concentration of these metabolites in macroalgae varies within and among species due to environmental factors. However, many studies focus on specific compound families and neglect other crucial metabolites for ecological functions. Understanding natural parameters shaping macroalgae metabolomes is crucial for predicting ecological success in a changing ocean. Alterations in defensive metabolite production will significantly impact biological interactions and global marine ecosystems. Current studies addressing macroalgae's chemical composition and spatial environmental changes should focus on bioactivities associated with specific compounds.

Chemotaxis of Dictyotaceae Gametes

Sexual reproduction in brown algae encompasses three forms: (1) isogamy, (2) anisogamy, and (3) oogamy (Wynne and Loiseaux, 1976). The swimming by male gametes in all three forms is facilitated by two heterokont flagella, known as the anterior) and the posterior flagella (AF and PF, respectively). Dictyotales sperm lack a PF. Typically, the AF exhibits a sinusoidal waveform and moves rhythmically. In response to chemical (chemotaxis) and light (phototaxis) signals, these heterogeneous flagella in male gametes or sperm are crucial for reproductive success (Kinoshita, Nagasato and Motomura, 2017).

Male gametophytes of brown algae are attracted by chemical signals released by female gametes. In oogamous species, such as Dictyotales, Laminariales, and Fucales, eggs begin to secrete sexual pheromones shortly after being released from the oogonium. Once spermatozoids fuse with these eggs, the zygotes settle on the substrate and initiate development (Kinoshita, Nagasato and Motomura, 2017).

Compounds such as unfunctionalized, acyclic, and/or alicyclic unsaturated hydrocarbons have been studied in this biological function derived from the aliphatic terminal of C20 polyunsaturated fatty acids (PUFAs) by oxidative cleavage. Several functions have frequently been described for these molecules: (1) synchronized mating of male and female cells by the controlled release of male spermatozoa, (2) increased mating efficiency by attraction, and (3) chemical defense of the plant due to the presence of large quantities of pheromones that are released from the stalk into the environment (Boland, 1995)

The first marine pheromone isolated was from the cultivation of fertile female gametophytes of the brown alga *Ectocarpus siliculosus*. The biological function of this pheromone is to enhance mating efficiency by attracting flagellated and motile males. The chemical structure of the signaling compound was established as 6-(1Z)-(butenyl)cyclohepta-1,4-diene, also known as ectocarpene (1) as described by several researchers (Boland et al., 1983; Rui and Boland, 2010). The occurrence of ectocarpene was first confirmed in the fragrant essential oils of *D. prolifera* and *D. undulata*. Furthermore, the "ocean smell" of the essential oils from both species consisted mainly of non-isoprenoid C11 hydrocarbons called dictyopterenes A (2) and B (3). It has been demonstrated that the eggs of the species *D. dichotoma* produce n-butyl-cyclohepta-2,5-diene, referred to as dictyotene (4), as an attractant for pheromones/spermatozoa (Muller et al., 1981; Phillips et al., 2000). These volatile compounds have been primarily reported in *D. diemensi*s, *D. dichotoma*, *D. membranacea*, and *D. delicatula* (Rathod Bhushan and Mantri, 2023). The alkylbenzenes, (1-ethylnonyl)-benzene (5), (1-methyldecyl)-benzene (6), and (1-pentylheptyl) benzene (7), have been detected in *P. pavonica* and may play a role as pheromones in these species and other brown algae (El Shoubaky and Salem, 2014). Some of the molecules involved in reproduction processes are presented in Figure 5.

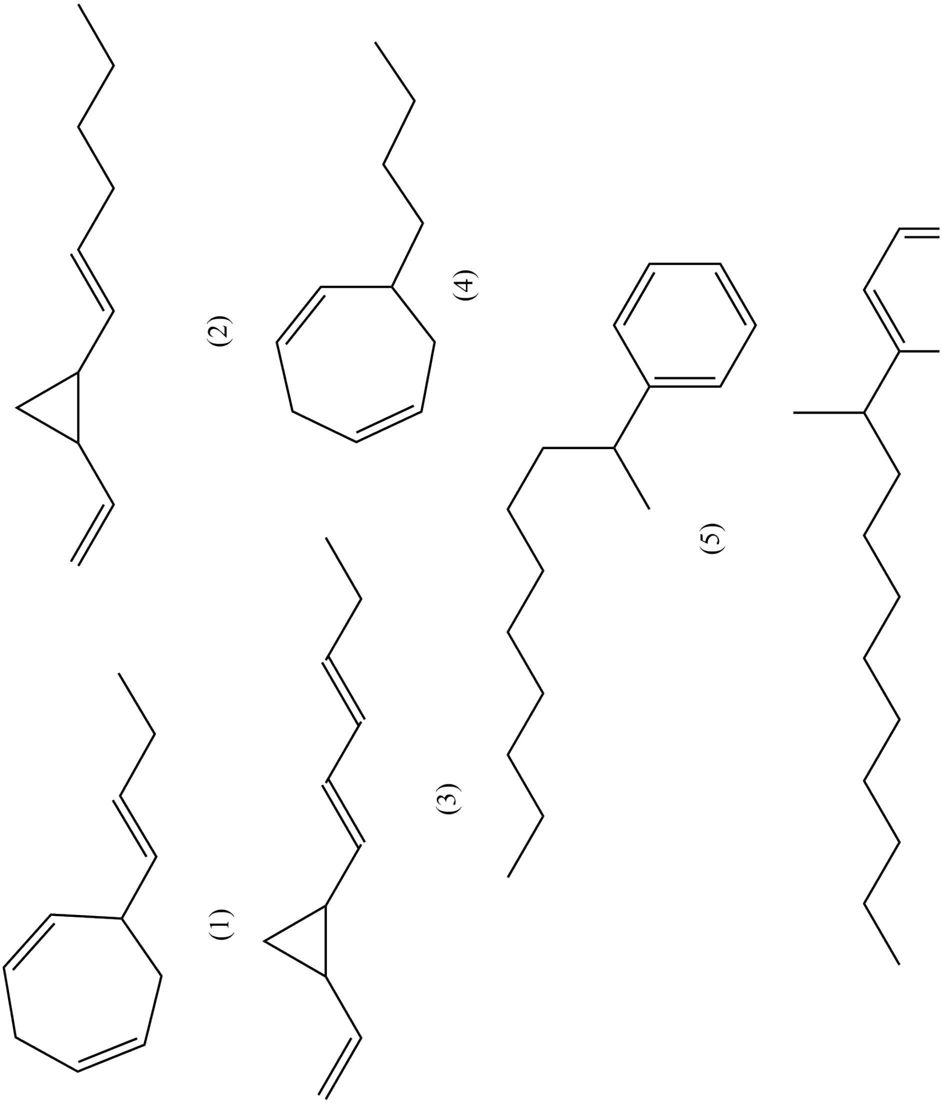


Figure 5. Pheromones accountable for gametic orientation within species of the Dictyotaceae family.

CHAPTER 3

CHEMICAL MEDIATORS IN PHYSICAL INTERACTIONS IN THE MARINE ENVIRONMENT

In the natural environment, seaweeds are constantly exposed to variations in biotic (such as herbivory, competition) and abiotic (such as temperature, irradiance, UV radiation, nutrients, air exposure) conditions in an air–water ecosystem interface imposed by the influence of tidal fluctuations. At the upper limit of the intertidal zone, physical factors, such as temperature, irradiance, and UV radiation can determine algal distribution, while the lower limits are generally defined by biological interactions, such as herbivory and competition (Urrea et al., 2020).

Hydrodynamics as a selective pressure for adaptive metabolite production

The vast majority of marine macroalgae reside firmly attached to substrates in coastal areas in which environments are notably variable. The hydrodynamics of the sea, which focuses on the movement of water in oceans and seas, explores phenomena, such as tides, waves, and currents, and plays a crucial role in the dynamics and behavior of macroalgae populations. The adaptations of these algae to coastal hydrodynamics are remarkable as they optimize their attachment to the substrate to leverage water dynamics and ensure sufficient exposure to the sunlight, which is necessary for photosynthesis (Lalegerie et al., 2020). Hydrodynamic variations occur not only between areas with different wave exposures but also along depth gradients within the same area. Generally, increasing depth leads to a reduction in turbulence and light availability. These differences in hydrodynamics along depth gradients can influence both macrophytes and their epiphytic communities. Such variations can appear on various spatial scales and range from meters within different sectors of a rocky shore (mesoscale) to kilometers across different beaches (Jacobucci et al., 2018)

Nutrient absorption is also influenced by marine currents and can impact both algae growth and distribution. These characteristics, both individually and collectively, affect the production of primary and secondary metabolites, which are essential for their adaptation to different conditions. Some species of macroalgae inhabit intertidal zones and emerge from the water during certain periods of the day, while others remain submerged in the subtidal zone or in tide pools and are affected by significant changes in abiotic factors during tidal cycles. This cycle of alternating between immersion and emersion expose macroalgae to important variations in abiotic parameters, such as light, temperature, and salinity, in addition to biotic factors, such as grazing, fouling, and pathogens. During high tide, submerged macroalgae face suitable environmental conditions; however, during low tide, these species may be exposed to high UV radiation and desiccation, which leads to an overproduction of reactive oxygen species (ROS) that causes oxidative stress (Lalegerie et al., 2020).

Recent studies have investigated how some metabolites found in algae from the Dictyotaceae family undergo changes in their concentration when exposed to hydrodynamic-related changes. Rodrigues et al. (2020) investigated the antioxidant activity and its relation to local tide variations (low and high tide) in three species: (1) *Canistrocarpus cervicornis*, (2) *D. delicatula*, and (3) *L. variegate*, all retrieved from two beaches on the northeastern coast of Brazil. They assayed and analyzed the extract yield in relation to phenolic content and noted that the aqueous extracts of *C. cervicornis* from Jaguaribe (with 3.47% dry mass) likely contained other water-soluble compounds, such as alginic acid and fucoidans, in addition to the phenolics from the cellular matrix of these algae (sulfated polysaccharides). This content resulted in lower antioxidant potentials due to lower phenolic content compared to extracts of *C. cervicornis* from Ponta de Pedras (with 1.97% dry mass). On the other hand, the results from the extracts of *D. delicatula* and *L. variegata* may correlate with the intrinsic characteristics of their variable chemical compositions and their respective antioxidant defense strategies. However, it is important to highlight that interpretations are challenging, so the authors therefore recommend carrying out additional studies to reach more definitive conclusions. These tropical reef species are interesting biological study models that can be useful when attempting to understand responses to stressful conditions as they are subject to large variations during tidal fluctuations. The biomass of these algae can be considered a potential source of raw material for obtaining natural products with antioxidant properties. This finding is based on evidence suggesting that the evolution of these algae helped develop an effective antioxidant defense system, probably as an adaptive response to more intense sun exposure.

Researchers measured the antioxidant and antimicrobial activities of 26 species in ten intertidal zones in eastern Guangdong, China. For the first time, they demonstrated the effect of abiotic factors caused by emersion on the antioxidant and antimicrobial activities of intertidal seaweeds. Higher antioxidant capacity was reported for brown algae that is found in low-tide zones, among which two representatives of the

Dictyotaceae family stood out. The first, *P. arborescens*, exhibited a high content of phenolic compounds (102.6 ± 3.6 mg gallic acid equivalent [GAE]/g dry extract) and good antioxidant activity followed by *Pachydictyon coriaceum* (54.0 ± 2.2 mg GAE/g dry extract). However, an analysis of the three groups of algae collected in low-tide belts revealed higher antibacterial activity than antioxidant activities similar to those collected in high or mid-tide belts (Xu et al., 2018). In this way, high UV-B radiation always leads to a rapid accumulation of phenols and pigments in seaweeds, which is related to their strong antioxidant protective capabilities (Fariman et al., 2016). The authors also discuss how nutrient availability can result in variations in phenol concentrations in some seaweeds after observing in seaweeds living in high-tide zones that were exposed to more extreme stresses, including high irradiance levels, desiccation, lower nutrition, and fluctuations in air temperature and salinity when compared with those living in low-tide zones.

In these studies, phenolic compounds took center stage as the primary focus. These molecules are prevalent in marine algae, particularly within the brown algae group, because of their significant role and contribution to organismal growth and survival. These compounds can be synthesized using the pentose phosphate, shikimate, or phenylpropanoid pathways (Figure 6). Regarding their chemical structure, all phenolic compounds comprise at least one aromatic phenolic ring with one or more hydroxyl substituents that gives them the capability of capturing free radicals, ROS, and chelated metal ions. Phenolic compounds that have more than one phenolic ring in their structure are known as polyphenols.

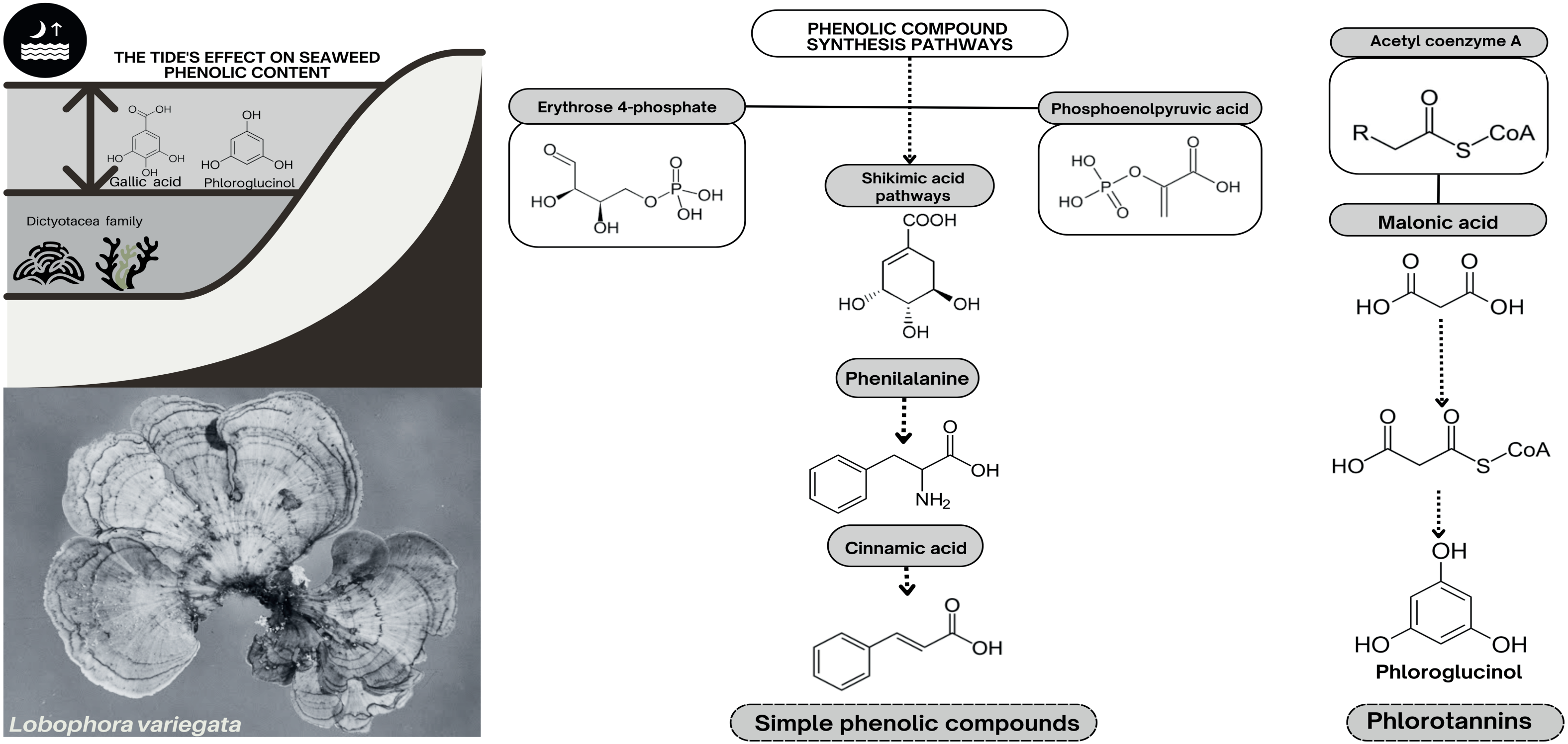
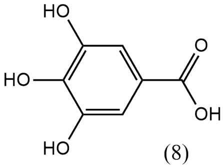


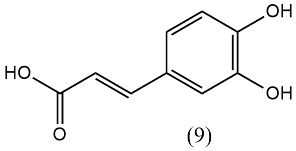
Figure 6. Impact of tidal cycles on the production of phenolic compounds in algae. Photo *Lobofora variegata* source: http://southafrseaweeds.uct.ac.za/descriptions/brown/lobophora_variegata.php.

The different classes and subclasses of polyphenols are generally based on the number of phenolic rings they possess and the structural elements attached to these rings. In this context, the main groups of phenolic compounds are: phenolic acids, coumarins, flavonoids, stilbenes, tannins, lignans, and lignin (Jimenez-Lopez, 2021). The discovery of secondary cell walls and lignin within the cells of the intertidal red algae *Calliarthron cheilosporioides* has been reported. Until now, these specialized cell walls in development have only been described in vascular plants (Martone et al., 2009). Of particular note are phlorotannins, which are exclusively found in algae, particularly in brown algae. Chemically defined as polymers of phloroglucinol (1,3,5-trihydroxybenzene), they are synthesized in algae through the acetate–malonate pathway (also known as the polyketide pathway) to yield compounds with a wide range of molecular sizes (126–650 kDa) as described by Agregán et al. (2017). The total content of phenolic compounds is quantified using colorimetric methods, such as the Folin–Ciocalteu, Folin–Denis, and Prussian Blue assays. However, these assays mask the chemical diversity of individual compounds present as they are based on colorimetric reactions that detect structurally related molecules. The lack of more sophisticated analysis methods has led to significant gaps in the differentiation of phenolic compound types and has made it challenging to establish a specific and suitable standard for quantification. Currently, phenolic content is expressed in results in milligrams of some standard compounds, such as GAE, phloroglucinol equivalents (PGE), pyrocatechol equivalents (PCE), phlorotannin content (PTC), and catechin equivalents (CE), which are based on dry algae extracts or dry algae weight (Subbiah et al., 2023)

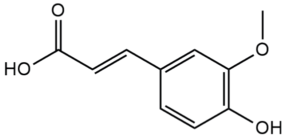
Gallic (8), caffeic (9) and ferulic acids (10) are phenolic carboxylic acids that were identified in *P. boergesenii* (Figure 7). In addition, using high-performance liquid chromatography/diode array detector (HPLC/DAD) chromatography, this research detected the presence of rutin (11) and quercetin (12) in the methanolic extract of this alga (Rajamani and Thirugnanasambandan 2018), although the presence of flavonoids in macroalgae is often questioned. It is important to highlight that the standards and colorimetric techniques used to detect phenolic metabolites still require refinement so as to provide conclusive data regarding the presence and characterization of these and other groups of phenolic compounds. Additionally, ferulic acid (10) was reported for *D. dichotoma* (Generalić et al., 2018) along with other derivatives of dihydroxybenzoic acid (13) as reported by Castillo et al. (2023). For *Z. tournefortii*, Acylphloroglucinol derivatives 1 (14) were reported (Hamiche et al., 2021) in addition to Spiralisones A (15) for the alga *Z. spiralis*. Many halogenated compounds, such as bromophenols, have been detected in members of the *Padina* genus.



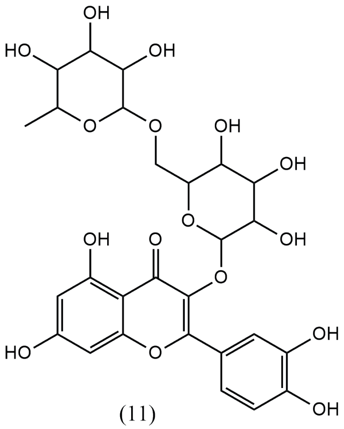
(8)



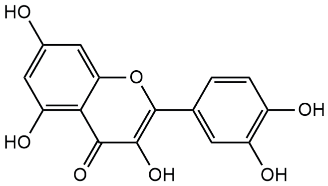
(9)



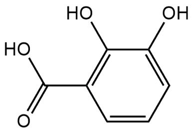
(10)



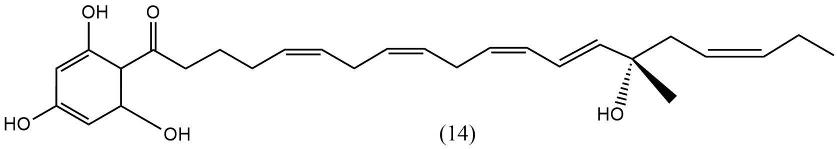
(11)



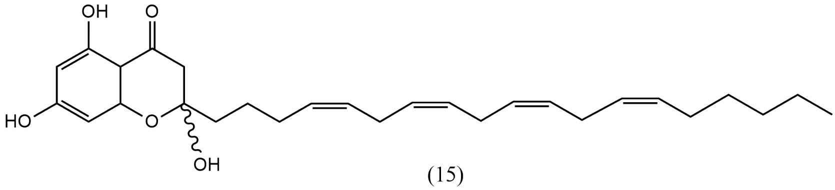
(12)



(13)



(14)



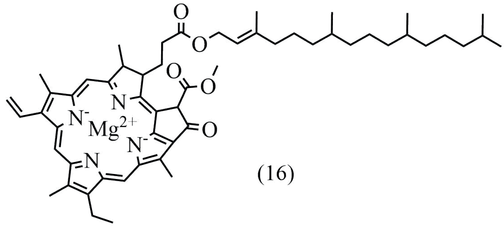
(15)

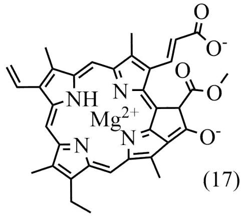
Figure 7. Phenolic Compounds in Species of the Dictyotaceae Family.

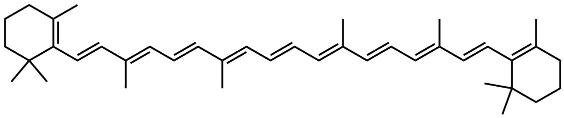
Irradiance and and the biosynthesis of protective metabolites

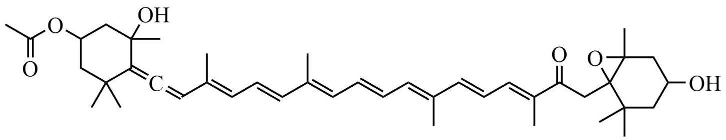
A significant source of stress for algae is solar radiation. Both high and low levels of radiation can negatively impact the performance of these organisms (Gómez, Orostegui and Huovinen, 2007). The reduction in light availability significantly affects the energy balance of algae in addition to the amount of carbon available for vital processes and production of defensive metabolites (Pavia and Toth, 2000). In particular, excessive solar radiation can cause DNA damage via formation of pyrimidine dimers, lipid peroxidation, photodamage, and delayed mitosis. Such daily underwater radiation, consisting of both photosynthetically active radiation and ultraviolet radiation (PAR and UVR, respectively) is affected by oceanographic conditions, which are determined by the amount of dissolved and particulate material in the water column that affects both the quality and intensity of irradiance (Schmitz et al., 2018).

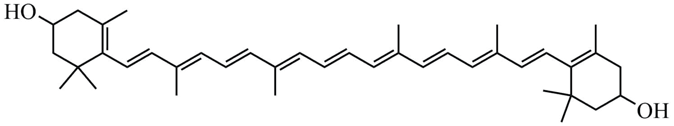
Macroalgae have developed various adaptive strategies to mitigate the effects of radiation control, including vertical movement in the water column, mechanisms to repair damage caused by photoreactivation, and synthesis and accumulation of compounds that absorb UV radiation. Among the brown algae of the Dictyotaceae family, several metabolites, including phenolic compounds and pigments, such as chlorophyll a (16), chlorophyll c (17), carotenoid like β-carotene (18), and fucoxanthin (19), have been investigated (Cikoš et al., 2022). Furthermore, xanthophyll group metabolites, such as zeaxanthin (20), antheraxanthin (21), violaxanthin (22) and amino acids similar to mycosporines (MAAs), such as MAA porphyra-334 (23), have been identified (Hegazi, 2002; Uhrmacher, Hanelt and Nultsch., 1995, Gröniger et al., 2020) as shown in Figure 8. Additionally, brown algae are known to be sources of laminarin and/or mannitol, which are the most abundant compounds in these macroalgae and whose synthesis is directly or indirectly related to solar radiation levels (Zubia et al., 2009; Schmitz et al., 2018).

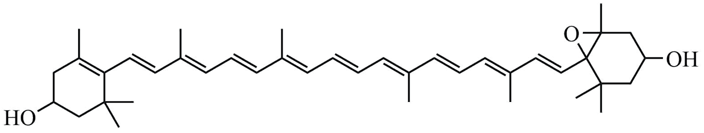

(16)

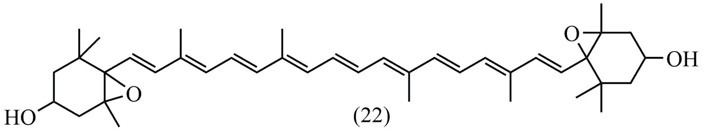

(17)


(18)


(19)


(20)


(21)


(22)

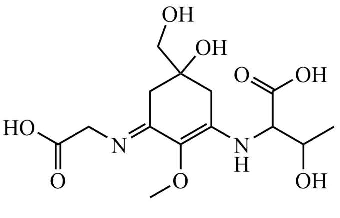

(23)

Figure 8. Key molecules involved in the ability of algae to tolerate the effects of stress caused by irradiance and light.

In 1992, Peckol and Ramus made a significant contribution to the literature by performing an *in situ* evaluation of the photosynthetic performance and dark respiration rates of abundant macroalgae found between 27 and 49 meters deep. Their results highlight species belonging to the family Dictyotaceae, which are predominantly present in all deep-water areas with *S. zonale* being the most prevalent species. Under extremely low irradiance conditions (< 0.01 maximum Io), all species showed net photosynthesis. However, *L. variegata* exhibited low productivity across all irradiance ranges.

On the other hand, *Dictyota* spp. (*D. bartayresii*, *D. dichotom*a, *D. divaricata*) and *S. zonale* demonstrated a high photosynthetic capacity of approximately 400 µmol O_2 gdw^{-1} h^{-1}, without showing light saturation even at higher ambient irradiance levels (300 µE m^{-1}s^{-1}). The fucoxanthin:chlorophyll-a ratio for all species measured in this study was approximately 0.7. This observation suggests an inverse correlation between irradiance and fucoxanthin concentration, indicating that even under low light conditions, similar proportions of these pigments in acclimated algae emphasize the importance of fucoxanthin in light capture. Furthermore, this relationship suggests the existence of an optimal concentration of fucoxanthin in the Dictyotales algae that inhabit deep water.

One aspect worth highlighting is the superior photosynthetic performance of species, such as *Dictyota* spp. and *Stypopodium*, which have thin and flat thalli that are characterized by a high ratio of surface area (SA) to volume (V) across all levels of ambient irradiance. This advantage can be attributed to the thallus structure since the highly branched thalli of *Dictyota* species has only three cell layers in their cross-section (< 150 µm), while the lobed thallus of *Lobophora* is thicker and usually has up to seven cell layers when sectioned (up to 300 µm). The recurrent presence and photosynthetic efficiency of these species in subtropical and tropical habitats of deep waters underscore their successful adaptation to environments with low light and scarce nutrients (Peckol and Ramus, 1992).

As mentioned earlier, intertidal macroalgae have developed protective mechanisms against high UV-B radiation in their habitats thus allowing for their survival. Studying the effects of this increased radiation on algae can provide insights into their defense strategies against solar stress. Some recent studies have investigated the profile of photoprotective compounds present in brown algae based on the hypothesis that the most significant amounts of these compounds are found in tropical areas with higher solar radiation incidence when compared with meridional latitudes along the Brazilian coast (Schmitz et al., 2018).

Species from the family Dictyotaceae, including *Canistrocarpus cervicornis*, *D.s delicatula*, *D. justii*, *D. plagiogramma*, *D. ciliolata*, *L. variegata*, *P. boergesenii*, and *P. gymnospora*, generally exhibit variations in the quantities of UV and PAR-absorbing compounds. In this study, seven main peaks were identified in the absorption spectrum of marine brown algae extracts that were characterized by high concentrations of phenolic compounds in the UV region and represent up to 30% of their dry weight. Specifically, two bands in the absorbance spectrum of phenolic-pholorotannins were described. One was between 240 and 280 nm. The other one was between 358 and 377 nm and contained coumarin. Additionally, other regions and peaks of absorbance, such as those of chlorophylls, carotenoids, and an absorption peak that could be attributed to amino acids similar to mycosporines were detected, even though finding these compounds in large quantities in brown algae is rare (Harker et al., 1999; Schmitz et al., 2018).

On the other hand, it is important to emphasize the xanthophyll cycle, which is a key metabolic pathway found in brown algae and plays a fundamental role in photoprotection regulation and adaptation to light stress. This cycle involves a series of biochemical reactions involving the reversible conversion of xanthophylls, which are carotenoid pigments present in algae, into different forms with photoprotective properties. Under conditions of high light intensity, brown algae face increased oxidative stress due to excessive absorption of light energy. To mitigate these effects, the xanthophyll cycle becomes active and involves the conversion of the xanthophylls, zeaxanthin and violaxanthin, into different forms that adjust the efficiency of the photosynthetic apparatus and dissipate the excess absorbed energy (Gevaert et al., 2002). Photoinhibition of photosynthesis in the brown alga *D. dichotoma* was investigated by analyzing changes in photosystem II fluorescence, oxygen production, and the xanthophyll pool (zeaxanthin, antheraxanthin, and violaxanthin) as shown in Figure 9. After photoinhibition, a reversible increase in zeaxanthin content and a concomitant reversible decrease in violaxanthin content were reported in *D. dichotoma* (Uhrmacher, Hanelt and Nultsch, 1995).

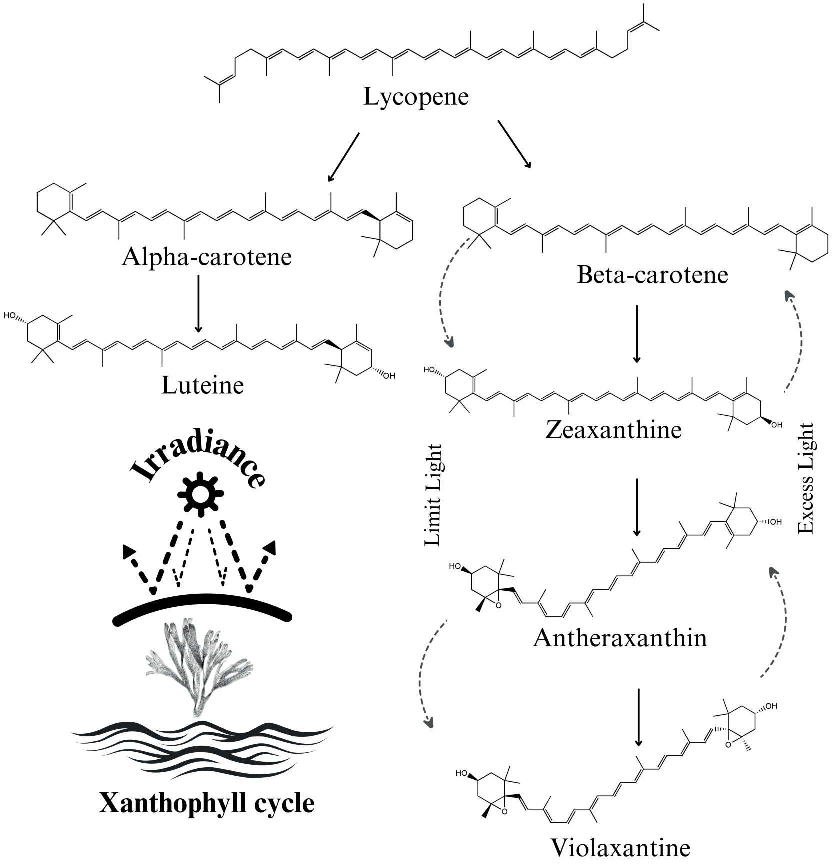


Figure 9. Schematic representation illustrating the synthesis pathway from lycopene to carotenoids such as α-carotene, lutein, β-carotene, and zeaxanthin, alongside the interconversions of zeaxanthin, antheraxanthin, and violaxanthin within the xanthophyll cycle (adapted by Krings et al., 2007).

Nutrient availability and the production of adaptive Metabolites

Several previous studies focused on understanding the influence of nutrient availability (nitrogen, phosphorus, and carbon) on the growth and biochemical quality of marine algae (Xu et al., 2024; Wang et al., 2018; Yu et al., 2022). Generally, nitrogen availability primarily affects the biosynthesis of amino acids and proteins (Yu et al., 2022). However, the presence of these nutrients can lead to increased levels of other biotechnologically relevant metabolites, such as pigments, sterols, phenolic compounds, and others (Mukherjee et al., 2020; Xu et al., 2024). This increase is related to an adaptive characteristic of algae in which the turgor pressure necessary to maintain ionic balance during osmotic stress induced by high nutrient availability is enhanced (Kumar et al., 2010; Mukherjee et al., 2020).

Recently, the influence of nutrient enrichment in laboratory cultivation systems on the diterpenoid profile of the species *D. menstrualis* and *C. cervicornis* using sterilized seawater enriched with Provasoli/2 as the medium was studied (Obando et al., 2023). It is noteworthy that the Provasoli culture medium is adequately enriched to support the growth of a wide variety of algae; hence, it has been applied in a broad range of studies (Obando et al., 2022a). The production of the compound fucosterol in *D. menstrualis* was favored in enriched medium with a relative abundance of 40.12% ± 1.52% after 56 days of cultivation; the results draw attention to fucosterol as one of the most abundant metabolites among brown algae. On the other hand, in a medium containing only sterilized seawater, the investigation revealed an abundance of 24.19% ± 1.16% (Obando et al., 2023). Obando et al. (2022b) recorded an increase in the relative abundance of sterols compared to diterpenes after 90 days of cultivation in sterilized seawater. Considering that steroids and terpenes share the common precursor, farnesyl diphosphate, in the metabolic pathway, the production of these metabolites may vary due to the metabolic needs of the algae (Obando et al., 2022b; Vallin et al., 2005).

The production of a guanine prenylated skeleton and xenia diterpenes in this species was favored in the non-enriched medium. The compound, pachydictyol A (24), was detected with higher relative abundance after 14 days (38.30% ± 3.48%) in sterilized seawater medium. For the macroalga, *C. cervicornis*, no significant differences were observed in terms of the relative abundances of key diterpenes, including acetoxy isolinearol (26), 4,7 diacetoxi-14-hidroxidolastano-1,8-dieno (27), and 4-acetoxi-9,14-diidroxi-1,9-dolastano-1,9-dieno (28) over the 21-day experimental period. It is noteworthy that compound 28 exhibited the highest abundance levels during the cultivation period with an abundance of 29.57% ± 2.92% after seven days in the medium enriched with Provasoli/2.

The diterpenes produced by the species *D. menstrualis* and *C. cervicornis* have demonstrated several important biological activities: (1) antiviral activity (Human Immunodeficiency Virus [HIV], Zika, Dengue, Chikungunya, and Herpes) as described by several researchers (Cirne-Santos et al., 2019; Cirne-Santos et al., 2020a; Cirne-Santos et al., 2020b), (2) antioxidant activity (Santos et al., 2024), (3) antifungal activity (Santos et al., 2024), (4) anticoagulant activity (Camara et al., 2011), (5) anti-inflammatory activity (Ávila et al., 2019), and (6) others. The biosynthetic pathway for diterpene production proposed for the Dictyotaceae family indicates the formation of three skeletons: (1) prenylated guaiane (group I), (2) dolastanes and secodolastanes (group II), and (3) xeniane and dichotomane (group III) as described by Vallim et al. (2005). Below are some compounds identified in *D. menstrualis* and *C. cervicornis* (Figure 10).

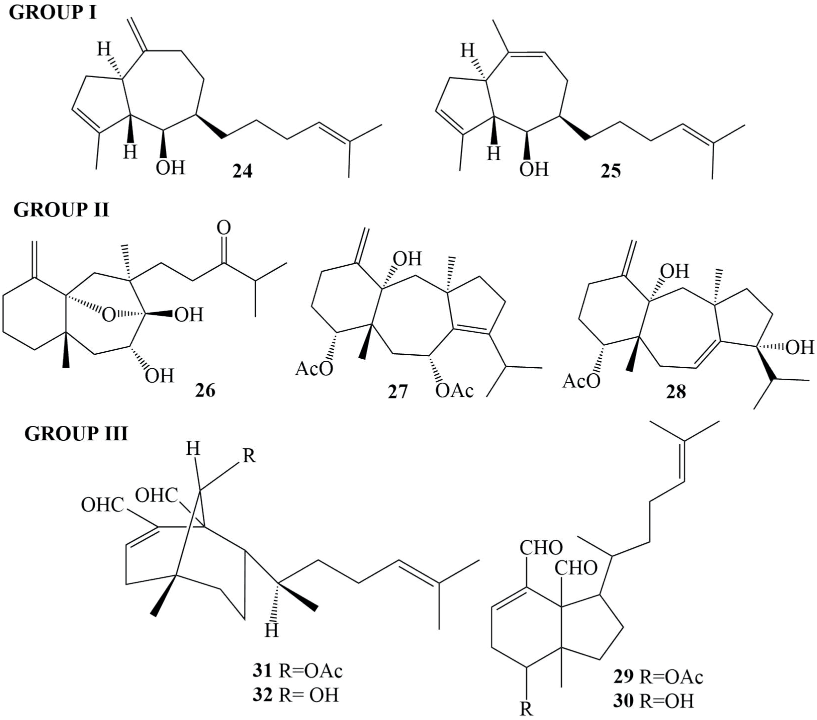


Figure 10. Diterpenes identified in *Dictyota menstrualis* and *Canistrocarpus cervircornis* under laboratory cultivation conditions with and without added nutrients (Obando et al., 2022b; Obando et al., 2023).

Biochemical modulation in the algae after the addition of carbon via the process of CO_2 aeration and nitrogen (NO^{3-}) addition in Von Stock medium in *D. menstrualis* bioreactor cultures and its influence on the fatty acid profile was investigated by Martins, Yokoya and Colepicolo (2016). Palmitic acid was the main fatty acid found in the *D. menstrualis* biomass after all treatments. For monounsaturated fatty acids, the concentration of C16:1 was higher in treatments containing added NO_{3-} without CO_2. The PUFA was stearidonic acid (C18:4) followed by arachidonic acid (C20:4). Overall, the concentration of PUFAs was higher when NO^{3-} had been added.

It should be noted that PUFAs, especially omega-3 and -6 (Figure 11), are precursors to important metabolites and hormones related to human health. These PUFAs play a crucial role in the regulation of inflammation (Santos et al., 2023; Wall et al., 2010). Therefore, they have a very high market value that exceeds $35 billion (Martins, Yokoya, and Colepicolo, 2016). Moreover, these products can be applied for various biotechnological purposes, including biofuel production (Gosch et al., 2012). In summary, it is evident that variations in nutrient availability interfere with the production of primary and secondary metabolites in the Dictyotaceae family. Thus, research focusing on understanding this biochemical modulation based on cultivation techniques is essential for comprehending ecological aspects but also for understanding the bioprospecting of commercially valuable compounds.

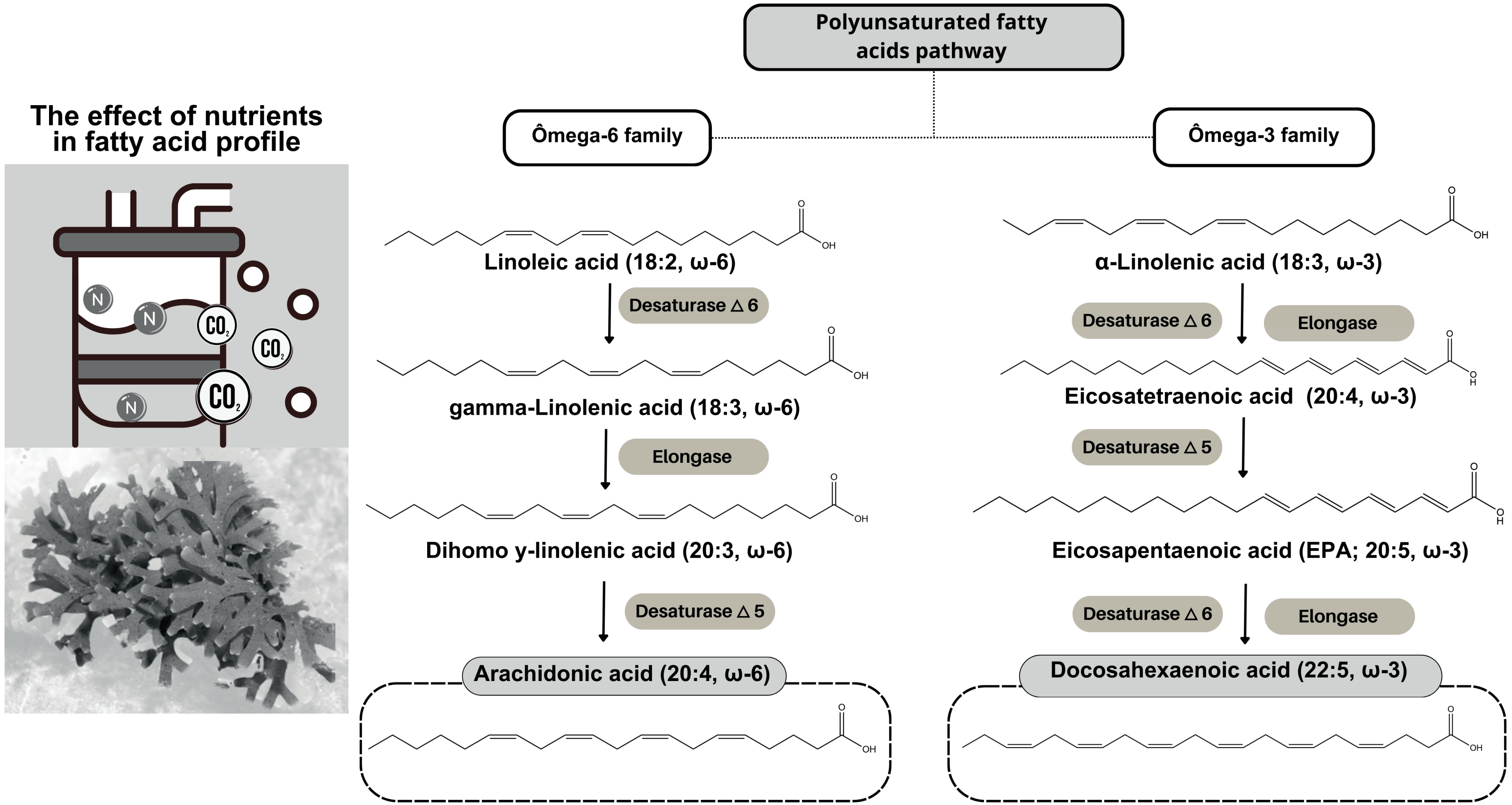


Figure 11. Impact of nutrients on the production of fatty acids (Martins, Yokoya and Colepicolo, 2016) and general pathway of omega-3 and omega-6 fatty acids synthesis (Misurcova et al., 2011).

Temperature as a regulator of adaptive metabolite production

Temperature is an important environmental factor that affects the growth, development, and productivity of macroalgae. Additionally, temperature is a key factor that controls the biogeography and reproductive capacity of seaweeds through its effects on metabolic rates. Moreover, changes in metabolic pathways can contribute to the tolerance and adaptability of seaweeds to high-temperature stress. Studies have indicated that the chemical composition of algae varies with temperature and other environmental stressors (Hamid et al., 2018). For instance, a reduction in the number of secondary metabolites was observed in seaweeds found in urban environments along the southern coast of Brazil compared to more pristine environments (Martins et al., 2014). This difference further underscores the relevance of the metabolic profile of aquatic plants as sensitive indicators of climate change (Betancor et al., 2014).

Some studies concerning brown algae have indicated that thermal stress suppresses chlorophyll content with a concurrent and significant alteration in a total of 31 metabolites in *Sargassum fusiforme* that was exposed to thermal stress at 27 °C compared to the control. Eighty metabolites were found to be significantly altered when the plants were subject to thermal stress at 32 °C. Strong modulation of various metabolic pathways, including organic acids, amino acids, sugars, sugar alcohols, esters, and amines, was also observed (Liu and Lin, 2020). Another study using the same brown algae model evaluated the algae's physiological vulnerability and sensitivity after exposure to five different temperatures by analyzing photosynthetic performance and chemical composition related to carbon and nitrogen metabolism. Photosynthetic pigments (carotenoid content) are a key point in algae adaptation to thermal stress (Urrea-Victori et al., 2020).

Regarding algae of the Dictyotaceae family, an ongoing and important study is assessing spatial and temperature variations in the composition of total fatty acids (TFA) in the species *D. bartayresii* and *D. australis* in Australia. The results demonstrate a general seasonal pattern in total fatty acid (TFA) content as *Dictyota* had its highest TFA content in summer when water temperature and light availability were at their annual maximu. In contrast, *Dictyopteris* had a higher TFA content during the same winter sampling period when water temperature and light availability were at their annual minimum. *D. bartayresii* consistently had a higher proportion of PUFA (n-3) and a less saturated fatty acid composition during winter, a result that suggests that the elevated PUFA (n-3) content in winter could be a physiological response to cooler water temperature and lower light availability (Gosch et al., 2015). The same study group clearly identified seasonal variations in TFA content and composition related to morphology and extensive seasonal changes in water temperature in the species *Spatoglossum macrodontum* (Gosch et al., 2014).

Tropical marine calcified macroalgae play an important role as primary producers in the marine food chain through photosynthesis. The production of calcium carbonate ($CaCO_3$) through calcification leads to an increase in reef sediment formation, promotion of accretion and stability, and facilitates coral larvae recruitment. Elevated temperatures associated with global climate change significantly impact various aspects of these calcified macroalgae, including photosynthesis, calcification, growth, and biochemical processes. Buapet and Sinutok (2023) showed that stress responses were primarily induced by high temperatures, which could be observed as reduced rates of photosynthetic carbon uptake, photoinhibition, and decreased calcification rates in the macroalga *P. boryana*. The extreme temperature of 42 °C also led to $CaCO_3$ dissolution and a reduction in antioxidant capacity (Buapet and Sinutok, 2023). Thus, high temperatures promote a decline in calcified macroalgae coverage, reef accretion, and net ecosystem calcification on reefs, all of which pose a potential threat to macroalgae health. Findings regarding high temperatures, metabolites, and climate change contribute valuable information toward conservation and management of coastal ecosystems and emphasize the need to address the impacts of climate change on macroalgae.

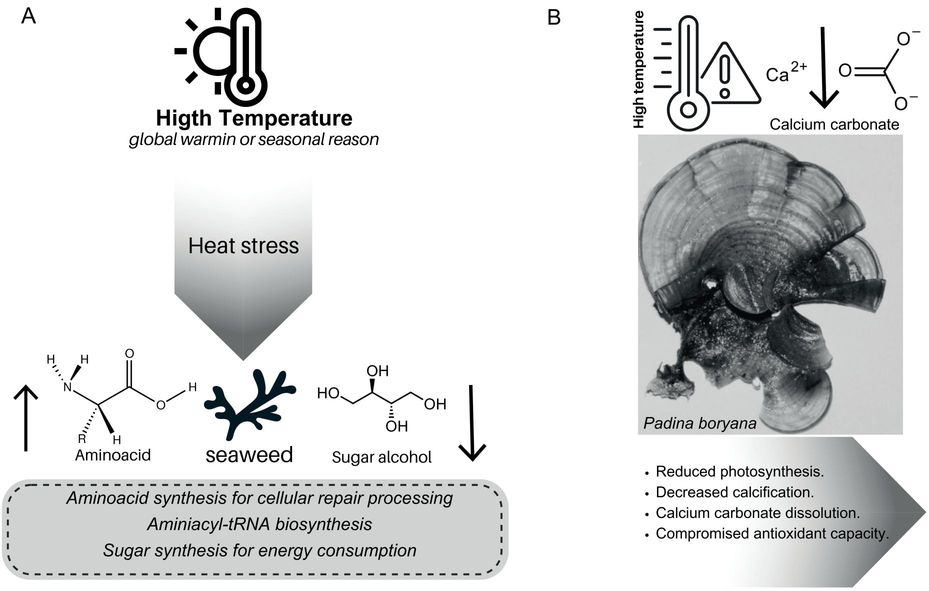


Figure 12. Influence of temperature. A) Diagram representing the responses of marine algae at high temperature adapted from Park et al 2023 (Liu and Lin, 2020; Urrea-Victoria et al., 2020) B) High temperatures in the calcification processes of *Padina boryana* (Buapet and Sinutok, 2023)

Other abiotic affecting the chemical profiles

In addition to the factors addressed throughout this chapter, other abiotic parameters such as salinity, seasonality, and pH, can affect the production of metabolites in macroalgae of the Dictyotaceae family (Čagalj et al., 2022; Deyab et al., 2017; Gaubert et al., 2019; Praiboon et al., 2018). Čagalj et al. 's study (2022) with the species *P. pavonica* evaluated the effect of seasonal variations on the chemical composition and antioxidant activity aiming at its application as a functional film. The highest content of total phenolics (26.69 ± 1.86 mg GAE equivalent/g) and antioxidant activity were found for the hydroethanolic extract of P. pavonica algae collected in June. Additionally, fatty acids such as oleic acid, stearidonic acid, and eicospenaenoic acid (EPA) were detected.

The effects of metabolomic variations over time and space were evaluated for four species of Lobophora (*L. monticola*, *L. obscura*, *L. rosacea*, and *L. sonderii*) as described by Gaubert et al. (2019). The authors managed to identify nine chemomarkers that belonged to the classes of fatty acids and polyolefins, which varied over the course of the 13-month investigation. Additionally, a significant correlation between variations and with temperature and salinity was found. The algae's metabolome adapted and evolved to fit a dynamic environment. Overall, the authors indicate that seasonality influences the variation of metabolites produced by macroalgae that highlight greater diversity during certain times of the year (Praiboon et al., 2018).

The world's oceans are becoming more acidic due to anthropogenic CO_2 emissions, which have produced multiple physiological and ecological responses (Dupont, Moya and Bailly, 2012). Seaweeds exhibit various responses to ocean acidification with some species benefiting from higher levels of CO_2, which enhance their growth (Riebesell et al., 2007). However, certain algae possess skeletal mineralogy that readily dissolves at predicted levels of calcium carbonate saturation (Martin and Gattuso, 2009).

Betancor et al. (2014) assessed the natural acidification effect from volcanic eruption that can affect the production of phenolic compounds and antioxidant activities of the brown algae *P. pavonica* and *L. variegata.* The increase in CO_2 concentrations due to a chemical equilibrium reaction leads to the release of carbonic acid, which produces a decrease in the pH of the surrounding water (Figure 13). The study revealed that this CO_2 release led to a decrease in the number of phenolic compounds in the studied species. Overall, it was observed that the content of phenolic compounds can be severely reduced in an acidic scenario (Arnold et al., 2012).

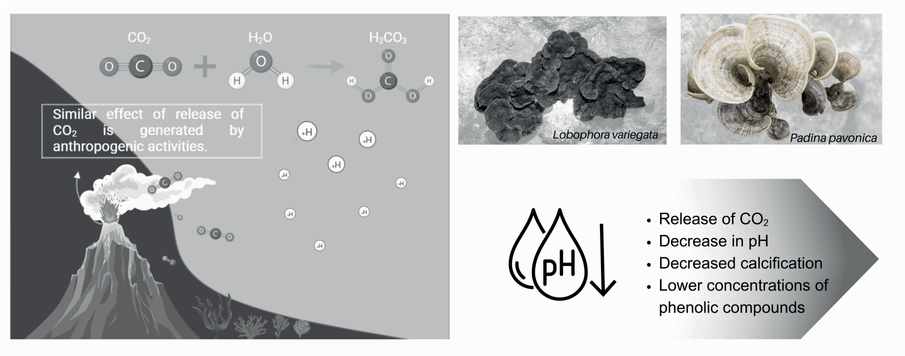


Figure 13. Diagram representing the responses of CO_2 release into the ocean. The reaction of water (H_2O) and carbon dioxide (CO_2) forms carbonic acid (H_2CO_3) which dissociates in the sea, forming carbonate (CO_3^{-2}) and hydrogen (H^+) ions, leading to a decrease in pH. Low pH in the phenolic compounds production of *P. pavonica* and *L. variegata* (Betancor et al 2014)

Due to the distribution of Dictyotaceae species, they have developed different strategies to survive in adverse environments and changes in salinity (Andrade et al., 2006; Muñoz et al., 2023a; 2023b). However, the relationship of this parameter with the algae's metabolome in this family is still unknown. Nevertheless, the literature indicates that an excess of Na^+ and Cl^- ions in the extracellular environment can cause cellular dehydration, disruption of ion exchange, and overproduction of ROS (Kumar et al., 2014). This phenomenon can cause the macroalgae to produce metabolites, especially phenolic compounds, with antioxidant properties that are known to protect against abiotic stressors, such as UV radiation and salinity (van Hees et al., 2017).

CONCLUSION

The e-book discussion of marine biology focuses on the exploration of the Dictyotaceae family, highlighting genera, such as *Dictyota*, *Dictyopteris*, *Padina*, *Lobophora*, and *Canistrocarpu*s. Offering an updated perspective on the taxonomy, diversity, and ecological significance of metabolites in the Dictyotaceae family, the findings we discuss reaffirm brown algae as pivotal constituents that are thriving within marine ecosystems. Their remarkable array of primary and secondary metabolites, including terpenes, polyphenols, steroids, fatty acids, and pigments, underscores their metabolic intricacies. The effects of these compounds are intricately entwined with the algae's metabolism and their interactions with diverse biotic factors, such as light, temperature, hydrodynamics, and nutrients in marine habitats. This intrinsic chemical diversity not only emphasizes the ecological indispensability of these algae but also plays a critical role in modulating crucial aspects of their life cycles, including reproduction and survival.

While many of the studies discussed are prompted by the search for fundamental insights into algae's ecological dynamics, a notable trend has emerged, investigating abiotic factors and metabolites with the aim of extracting biotechnologically relevant bioactive molecules, This trend underscores a dual purpose as it broadens our comprehension of algae's ecological relationships and also accentuates their pivotal role in providing ecosystem services through the production of valuable bioactive compounds.

REFERENCES

Abdel-Kareem MS, ElSaied AA. *Global seaweeds diversity*. Handbook of Algal Biofuels. Elsevier, 2022.

Adl SM, Simpson AG, Farmer MA, Andersen RA, Anderson OR, Barta JR, Bowser SS, Brugerolle G, Fensome RA, Fredericq S, James TY, Karpov S, Kugrens P, Krug J, Lane CE, Lewis LA, Lodge J, Lynn DH, Mann DG, Mccourt RM, Mendoza L, Moestrup O, Mozley-Standridge SE, Nerad TA, Shearer CA, Smirnov AV, Spiegel FW, Taylor MFJR. The New Higher Level Classification of Eukaryotes with Emphasis on the Taxonomy of Protists. *J. Eucarioto. Microbiol.*(2005) 52(5):399–451.

Agregan R, Munekata PE, Franco D, Dominguez R, Carballo J, Lorenzo JM. Phenolic compounds from three brown seaweed species using LC-DAD–ESI-MS/MS. *Food Research International* (2017) 99 (part 3):979-985.

Akram, A., & Suleria, H. A. R. (2022). Functional and nutraceutical significance of macro and micro algae. In *Bioactive compounds from multifarious natural foods for human health* (pp. 119-159). Apple Academic Press.

Aisha K, Shameel MUSTAFA. Occurrence of the genus *Lobophora* (Dictyophyceae, Phaeophycota) in the coastal waters of Karachi. *Pak. J. Bot* (2012) 44(2):837-840.

Allender, B. M. *Dictyotopsis* propagulifera (Phaeophyta)–an algal enigma. *Phycologia* (1980) 19(3):234-236.

Andrade S, Medina MH, Moffett JW, Correa JA. Cadmium– copper antagonism in seaweeds inhabiting coastal areas affected by copper mine waste disposals. *Environmental science & technology* (2006) 40(14):4382-4387.

Hanyuda T, Kato A, Shimabukuro, H, Uchimura M, Kawai H, Tokeshi M. Global diversity and geographic distributions of *Padina species* (Dictyotales, Phaeophyceae): new insights based on molecular and morphological analyses. *Journal of Phycology* (2021) 57(2), 454-472.

Arnold T, Mealey C, Leahey H, Miller AW, Hall-Spencer JM, Milazzo M, Maers K. Ocean acidification and the loss of phenolic substances in marine plants. *PLoS one* (2012) *7*(4): e35107.

Ávila FN, da Silva LGS, de Macedo PBC, Santos FA, Sasahara GL, Marinho JDBF, Araújo AJ, Barros AB, Monteiro NKV, Silveira ER, Pessoa ODL. Diterpenóides antiinflamatórios da alga brasileira *Dictyota menstrualis*. *Algas. Res.* (2019) 44:101695.

REFERENCES

Betancor S, Tuya F, Gil-Díaz T, Figueroa FL, Haroun R. Effects of a submarine eruption on the performance of two brown seaweeds. *Journal of Sea Research* (2014) 87:68-78.

Bittner L, Payri CE, Couloux A, Cruaud C, de Reviers B, Rousseau F. Molecular phylogeny of the Dictyotales and their position within the Phaeophyceae, based on nuclear, plastid and mitochondrial DNA sequence data. *Molecular phylogenetics and evolution* (2008) *49*(1):211-226.

Bogaert K, Beeckman T, De Clerck O. Abiotic regulation of growth and fertility in the sporophyte of *Dictyota dichotoma* (Hudson) JV Lamouroux (Dictyotales, Phaeophyceae). *Journal of applied Phycology* (2016) 28(5):2915-2924.

Bogaert KA, Delva S, De Clerck O. Concise review of the genus Dictyota JV Lamouroux. *Journal of Applied Phycology* (2020) 32(3):1521-1543.

Boland W. The chemistry of gamete attraction: chemical structures, biosynthesis, and (a) biotic degradation of algal pheromones. *Proceedings of the National Academy of Sciences* (1995) 92(1):37-43.

Boland W, Marner FJ, Jaenicke L, Muller DG, Folster E. Comparative receptor study in gamete chemotaxis of the seaweeds *Ectocarpus siliculosus* and *Cutleria multifida:* an approach to interspecific communication of algal gametes. *European Journal of Biochemistry* (1983) 134(1):97-103.

Bringloe TT, Starko S, Wade RM, Vieira C, Kawai H, De Clerck O, Cock JM, Coelho SM, Destombar C, Valero M, Neiva J, Pearson GA, Faugeron S, Serrão EA, Verbruggen H. Phylogeny and evolution of the brown algae. *Critical Reviews in Plant Sciences* (2020) 39(4):281-321.

Buapet P, Sinutok S. Physiological responses to increased temperature and irradiance in the calcifying macroalgae, *Halimeda macroloba*, *Halimeda opuntia* and *Padina boryana*. *Applied Ecology & Environmental Research* (2023) 21:(5).

Buschmann AH, Camus C, Infante J, Neori A, Israel Á, Hernández-González MC, Pereda SV, Gomez-Pinchetti JL, Golberg A, Tadmor-Shalev N, Critchley AT. Seaweed production: overview of the global state of exploitation, farming and emerging research activity. *European Journal of Phycology* (2017) 52(4):391-406.

REFERENCES

Čagalj M, Fras Zemljič L, Kraševac TG, Mežnar E, Sterniša M, Smole SM, Razola-Díaz MC, Šimat V. Seasonal changes in chemical profile and antioxidant activity of *Padina pavonica* extracts and their application in the development of bioactive chitosan/PLA bilayer film. *Foods* (2022) 11(23):3847.

Camacho O, Fernández-García C, Vieira C, Gurgel CFD, Norris JN, Freshwater DW, Fredericq S. The systematics of Lobophora (Dictyotales, Phaeophyceae) in the western Atlantic and eastern Pacific oceans: eight new species. *Journal of Phycology* (2019) *55*(3):611-624.

Camara RBG, Costa LS, Fidelis GP, Nobre LTDB, Dantas-Santos N, Cordeiro SL, Costa MSSP, Alves LG, Rocha HAO. Heterofucanos da alga marrom *Canistrocarpus cervicornis* com atividades anticoagulante e antioxidante. *Marine Drugs* (2011) 9:124–138.

Castillo A, Celeiro M, Lores M, Grgić K, Banožić M, Jerković I, Jokić S. Bioprospecting of Targeted Phenolic Compounds of *Dictyota dichotoma, Gongolaria barbata, Ericaria amentacea, Sargassum hornschuchii* and *Ellisolandia elongata* from the Adriatic Sea Extracted by Two Green Methods. *Marine drugs* (2023) 21(2):97.

Cavalcanti MIL, Gonzalez PMS, Fujii MT. Comparison of the diversity and biomass of beach-cast seaweeds from Ne and Se Brazil. *European Journal of Phycology* (2022) *57*(3):367-376.

Cavalier-Smith T. Higher Classification and Phylogeny of Euglenozoa. *European Journal of Protistology* (2016) 56:250–276.

Charrier B, Coelho SM, Le Bail A, Tonon T, Michel G, Potin, P, Kloareg B, Boyen C, Peters AF, Cock JM. Development and physiology of the brown alga *Ectocarpus siliculosus*: two centuries of research. *New Phytologist* (2008) 177(2):319-332.

Chopin T, Tacon AG. Importance of seaweeds and extractive species in global aquaculture production. *Reviews in Fisheries Science & Aquaculture* (2021) 29(2):139-148.

Cikoš AM, Šubarić D, Roje M, Babić J, Jerković I, Jokić S. Recent advances on macroalgal pigments and their biological activities (2016–2021). *Algal research* (2022) 65:102748.

Cirne-Santos CC, Barros CDS, Gomes MWL, Gomes R, Cavalcanti DN, Obando JM, Ramos CJB,Villaça RC, Teixeira VL, Paixão ICNP. Atividade antiviral in vitro contra o vírus zika a partir de um produto natural da alga marrom brasileira *Dictyota menstrualis* . *Nat. Prod. Comum* (2019) 14 (7):1–7.

REFERENCES

Cirne-Santos CC, de Souza Barros C, de Oliveira MC, Rabelo VWH, Azevedo RC, Teixeira V, Ferreira DF, Paixão ICNP. Estudos in vitro sobre a inibição da replicação dos vírus zika e chikungunya pelo dolastano isolado da alga marinha *Canistrocarpus cervicornis*. *Science Rep.* (2020a) 10 (1):1–10.

Cirne-Santos CC, de Souza Barros C, Esteves PO, Gomes MWL, Gomes R, Cavalcanti DN, Obando JMC, Ramos C, Villaça R, Teixeira VL, Paixão ICNP. Atividade antiviral contra o vírus chikungunya de diterpenos da alga marinha *Dictyota menstrualis*. *Revista Brasileira de Farmacognosia.* (2020b) 30(5):709–714.

Cotas J, Gomes L, Pacheco D, Pereira L. Ecosystem Services Provided by Seaweeds. *Hydrobiology* (2023) 2(1):75-96.

Deyab MA, El-Katony TM, El-Adl MF, Ward FM. Temporal variation in chemical composition of *Dictyota dichotoma* (Hudson) JV Lamouroux (Dictyotales, Phaeophyceae) from Red Sea Coast Egypt. *Journal of Coastal Life Medicine* (2017) 5(4):149-155.

De Clerck O, Leliaert F, Verbruggen H, Lane CE, De Paula JC, Payo DA, Coppejans E. A revised classification of the dictyotaceae (dictyotales, phaeophyceae) based on rbcl and 26s ribosomal dna sequence analyses 1. *Journal of phycology* (2006) 42(6):1271-1288.

De Paula JC, Lopes-Filho EAP, de Carvalho WF, de Souza Coracao AC, Yoneshigue-Valentin Y. Long-term changes in macroalgae assemblages reveal a gradual biodiversity loss over the last 200 years in the hypereutrophic Guanabara Bay. *Marine Environmental Research* (2020) 162: 105153.

De Ramon N'Yeurt, A, & Payri CE. Marine algal flora of French Polynesia III. Rhodophyta, with additions to the Phaeophyceae and Chlorophyta. Cryptogamie, Algologie (2010) 31(1): 3-205.

De Toni GB. *Sylloge algarum omnium hucusque cognitarum: Fucoideae* (Vol. 3). Sumptibus auctoris, 1895.

Dorrell RG, Gile G, McCallum G, Méheust R, Bapteste EP, Klinger CM, Brillet-Guéguen L, Freeman KD, Richter DJ, Bowler C. Chimeric origins of ochrophytes and haptophytes revealed through an ancient plastid proteome. *eLife* (2017) 6: e23717.

REFERENCES

Driss E. The seawater environment and ecological adaptations. In: Elements of Marine Ecology. *Butterworth-Heinemann* (2021) 37-151.

Dumortier BC. *Commentationes botanicae: Observations botaniques*. Tournay: Imprimerie de Ch. Casterman-Dieu, Rue de pont No. 10., 1822 .pp. [i], [1]-116 .

Dupont S, Moya A, Bailly X. Stable photosymbiotic relationship under CO2-induced acidification in the acoel worm *Symsagittifera roscoffensis*. *PLoS One* (2012) 7(1):e29568.

El Shoubaky GA, Salem EA. Terpenes and sterols composition of marine brown algae *Padina pavonica* (Dictyotales) and Hormophysa triquetra (Fucales). *International Journal of Pharmacognosy and Phytochemical Research* (2014) *6*(4):894-900.

Fariman GA, Shastan SJ, Zahedi MM. Seasonal variation of total lipid, fatty acids, fucoxanthin content, and antioxidant properties of two tropical brown algae (*Nizamuddinia zanardinii* and *Cystoseira indica*) from Iran. *Journal of Applied Phycology* (2016) 28(2):1323-1331.

García-Poza S, Pacheco D, Cotas J, Marques JC, Pereira L, Gonçalves AMM. Marine macroalgae as a feasible and complete resource to address and promote Sustainable Development Goals (SDGs). *Integrated Environmental Assessment Management* (2022) 18(5):1148–1161.

Garreta AG, Lluch JR, Martí MCB, Siguan MAR. On the presence of fertile gametophytes of *Padina pavonica* (Dictyotales, Phaeophyceae) from the Iberian coasts. *Anales del Jardín Botánico de Madrid* (2007) 64(1):27-33.

Gaubert J, Payri CE, Vieira C, Solanki H, Thomas OP. High metabolic variation for seaweeds in response to environmental changes: a case study of the brown algae *Lobophora* in coral reefs. *Scientific reports* (2019) 9(1):993.

Generalić MI, Šimat V, Botić V, Crnjac A, Smoljo M, Soldo B, Ljubenkov I, Cagalj M, Skroza, D. Bioactive phenolic metabolites from Adriatic brown algae *Dictyota dichotoma* and *Padina pavonica* (Dictyotaceae). *Foods* (2021) 10(6):1187.

Gevaert F, Creach A, Davoult D, Holl AC, Seuront L, Lemoine Y. Photo-inhibition and seasonal photosynthetic performance of the seaweed *Laminaria saccharina* during a simulated tidal cycle: chlorophyll fluorescence measurements and pigment analysis. *Plant, Cell & Environment* (2002) 25(7):859-872.

REFERENCES

Gololobova MA, Belyakova GA. Position of Algae on the Tree of Life. *Doklady Biological Sciences* (2022) 507(1):312-326.

Gómez I, Orostegui M, Huovinen P. Morpho-functional patterns of photosynthesis in the south pacific kelp lessonia nigrescens: effects of uv radiation on 14c fixation and primary photochemical reactions. *Journal of Phycology* (2007) 43(1):55-64.

Gröniger A, Sinha RP, Klisch M, Häder DP. Photoprotective compounds in cyanobacteria, phytoplankton and macroalgae—a database. *Journal of Photochemistry and Photobiology B: Biology* (2000) 58(2-3):115-122.

Gosch BJ, Magnusson M, Paul NA, Nys R. Total lipid and fatty acid composition of seaweeds for the selection of species for oil-based biofuel and bioproducts. *GCB Bioenergy* (2012) 4(6):919–930.

Gosch BJ, Paul NA, De Nys R, Magnusson M. Spatial, seasonal, and within-plant variation in total fatty acid content and composition in the brown seaweeds *Dictyota bartayresii* and *Dictyopteris australis* (Dictyotales, Phaeophyceae). *Journal of Applied Phycology* (2015) 27(1):1607-1622.

Gosch BJ, Paul NA, de Nys R, Magnusson M. Seasonal and within-plant variation in fatty acid content and composition in the brown seaweed *Spatoglossum macrodontum* (Dictyotales, Phaeophyceae). *Journal of Applied Phycology* (2015), 27: 387-398.

Greville RK. *Algae britannicae: or, Descriptions of the marine and other inarticulated plants of the British Islands, belonging to the order Algae*. Edinburgh and London: Maclachlan & Stewart, 1830.

Guiry MD, Guiry GM. 2023. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. https://www.algaebase.org; searched on 29 de novembro de 2023.

Guiry MD, Guiry GM. 2024. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. https://www.algaebase.org; searched on 02 de Janeiro de 2024.

Hamiche S, Bensouici C, Messaoudi A, Gali L, Khelouia L, Rateb ME, Akkal S, Badis A, Hattab ME. Antioxidant and structure–activity relationship of acylphloroglucinol derivatives from the brown alga *Zonaria tournefortii*. *Monatshefte für Chemie-Chemical Monthly* (2021) 152:431-440.

REFERENCES

Hamid SS, Wakayama M, Soga T, Tomita M. Drying and extraction effects on three edible brown seaweeds for metabolomics. *Journal of applied phycology* (2018) 30(6):3335-3350.

Harker M, Berkaloff C, Lemoine Y, Britton G, Young AJ, Duval JC, Nour-Eddine R, Rousseau B. Effects of high light and desiccation on the operation of the xanthophyll cycle in two marine brown algae. *European Journal of Phycology* (1999) 34(1):35-42.

Hegazi MM. Separation, identification and quantification of photosynthetic pigments from three red sea seaweeds using reversed-phase high-performance liquid chromatography. *Egypt J Bio* (2002) 4:1–6.

Herren LW, Walters LJ, Beach KS. Fragment generation, survival, and attachment of *Dictyota spp.* at Conch Reef in the Florida Keys, USA. *Coral Reefs* (2006) 25(2):287-295.

Huisman JM, Abbott, IA, Smith CM. Hawaiian reef plants. Honolulu: A publication of the University of Hawai'i Sea Grant College Program, 2007.

Jacobucci GB, Vieira EA, Leite FPP. Influence of a narrow depth gradient on the spatial structure of Sargassum peracarid assemblages in Southeastern Brazil. *Marine Biodiversity* (2018) 49(2):1-11.

Jimenez-Lopez C, Pereira AG, Lourenço-Lopes C, García-Oliveira P, Cassani L, Fraga-Corral M, Prieto MA, Simal-Gandara J. Main bioactive phenolic compounds in marine algae and their mechanisms of action supporting potential health benefits. *Food chemistry* (2021) 341(part 2):128262.

Keeling PJ. The endosymbiotic origin, diversification and fate of plastids. *Philosophical Transactions of the Royal Society B: Biological Sciences* (2010) 365(1541):729-748.

Kinoshita N, Nagasato C, Motomura T. Phototaxis and chemotaxis of brown algal swarmers. *Journal of plant research* (2017) 130(3):443-453.

Kraft GT, Saunders GW, Abbott IA, Haroun RJ. A Uniquely Calcified Brown Alga From Hawaii Newhousia imbricata gen. et. sp. Nov.(Dictyotales, Phaeophyceae) 1. *Journal of phycology* (2004) 40(2):383-94.

REFERENCES

Krings M, Klavins SD, Barthel M, Lausberg S, Serbet R, Taylor TN, Taylor EL. Perissothallus, a new genus for Late Pennsylvanian–Early Permian noncalcareous algae conventionally assigned to Schizopteris (aphleboid foliage). *Botanical Journal of the Linnean Society* (2007) 153(4):477-488.

Kumar M, Kumari P, Gupta V, Reddy CRK, Jha, B. Biochemical responses of red alga *Gracilaria corticata* (Gracilariales, Rhodophyta) to salinity induced oxidative stress. *Journal of Experimental Marine Biology and Ecology* (2010) 391(1-2):27-34.

Kumar M, Kumari P, Reddy C, Jha B. *Salinity and desiccation induced oxidative stress acclimation in seaweeds*. In: Sea Plants. Adv. Bot. Res., 2014 vol. 7, 1st edition, pp. 91-123.

Lalegerie F, Gager L, Stiger-Pouvreau V, Connan S. The stressful life of red and brown seaweeds on the temperate intertidal zone: Effect of abiotic and biotic parameters on the physiology of macroalgae and content variability of particular metabolites. *Advances in botanical research,* 2020 vol. 95, pp. 247-287.

Liu L., Lin L. Effect of heat stress on *Sargassum fusiforme* leaf metabolome. *Journal of plant biology* (2020) 63(3):229-241.

Lozano-Orozco JG, Sentíes A, De Clerck O, Dreckmann KM, Díaz-Larrea J. Two new species of the genus *Dictyota* (Phaeophyceae: Dictyotales) from the Mexican Caribbean. *American Journal of Plant Sciences* (2009) 6(15):2492.

Martin S, Gattuso JP. Response of Mediterranean coralline algae to ocean acidification and elevated temperature. *Global Change Biology* (2009) 15(8):2089-2100.

Martins CDL, Lhullier C, Ramlov F, Simonassi JC, Gouvea LP, Noernberg M, Maraschin M, Colepicolo P, Hall-Spencer JM, Horta PA. Seaweed chemical diversity: An additional and efficient tool for coastal evaluation. *Journal of Applied Phycology* (2014) 26(5):2037–2045.

Martins AP, Yokoya NS, Colepicolo P. Biochemical modulation by carbon and nitrogen addition in cultures of *Dictyota menstrualis* (Dictyotales, Phaeophyceae) to generate oil-based bioproducts. *Marine biotechnology* (2016) 18(3):314-326.

Martone PT, Estevez JM, Lu F, Ruel K, Denny MW, Somerville C, Ralph J. Discovery of lignin in seaweed reveals convergent evolution of cell-wall architecture. *Current biology*, *19*(2), 169-175.

REFERENCES

Menaa F, Wijesinghe PAUI, Thiripuranathar G, Uzair B, Iqbal H, Khan BA, Menaa B. Ecological and industrial implications of dynamic seaweed-associated microbiota interactions. *Marine drugs* (2020) 18(12):641.

Mišurcová L, Ambrožová J, Samek D. Seaweed lipids as nutraceuticals. *Advances in food and nutrition research* (2011), 64: 339-355.

Mukherjee P, Gorain PC, Paul I, Bose R, Bhadoria PBS, Pal R. Investigation on the effects of nitrate and salinity stress on the antioxidant properties of green algae with special reference to the use of processed biomass as potent fish feed ingredient. *Aquaculture International* (2020) 28(1):211-234.

Müller DG, Gassmann G, Boland W, Marner F, Jaenicke L. *Dictyota dichotoma* (Phaeophyceae): identification of the sperm attractant. *Science* (1981) 212(4498):1040-1041.

Muñoz PT, Rodríguez-Rojas F, Celis-Plá PSM, López-Marras A, Blanco-Murillo F, Sola I, Lavergne C, Valenzuela F, Orrego R, Sánchez-Lizaso JL, Sáez CA. Desalination effects on macroalgae (part b): transplantation experiments at brine-impacted sites with *Dictyota spp.* from the pacific ocean and Mediterranean Sea. *Front. Mar. Sci*. (2023B) 10:1042799.

Muñoz PT, Rodríguez-Rojas F, Celis-Plá PSM, López-Marras A, Blanco-Murillo F, Sola I, Lavergne C, Valenzuela F, Orrego R, Sánchez-Lizaso JL, Sáez CA.Desalination effects on macroalgae (part A): Laboratory-controlled experiments with Dictyota spp. from the Pacific Ocean and Mediterranean Sea. *Frontiers in Marine Science* (2023a) 10:1042782.

Ni-Ni-Win W, Hanyuda T, Kato A, Kawai H. Two new species of *Padina* (Dictyotales, Phaeophyceae) from southern Japan, *P. ogasawaraensis sp. nov.* and *P. reniformis sp. nov.*, based on morphology and molecular markers. *Phycologia* (2018) 57(1):20-31.

Park E, Yu H, Lim, JH, Choi, JH, Park KJ, & Lee J. Seaweed metabolomics: A review on its nutrients, bioactive compounds and changes in climate change. *Food Research International* (2023) 163: 112221.

Pavia H, Toth GB. Influence of light and nitrogen on the phlorotannin content of the brown seaweeds *Ascophyllum nodosum* and *Fucus vesiculosus. Hydrobiologia* (2000) 440(1):299-305.

REFERENCES

Peckol P, Ramus J. Photosynthetic performance of deep-water macroalgae (Phaeophyta, Dictyotales) off Bermuda. *Hydrobiologia* (1992) 231:93-98.

Phillips JA Systematics of the Australian species of *Dictyopteris* (Dictyotales, Phaeophyceae). *Australian systematic botany* (2000) 13(2):283-324.

Praiboon J, Palakas S, Noiraksa T, Miyashita K. Seasonal variation in nutritional composition and anti-proliferative activity of brown seaweed, *Sargassum oligocystum*. *Journal of Applied Phycology* (2018) 30(1):101-111.

Obando JMC, dos Santos TC, Fortes RDR, Bernardes M, Nascimento N, Villaça RC, Teixeira VL, Barbarino E, Cavalcanti DN. Influence of laboratory conditions on two species Dictyotaceae family (Phaeophyceae): Diterpenoid profile and physiological response. *Frontiers in Marine Science* (2023) 10:1150719.

Obando JMC, dos Santos TC, Bernardes M, Nascimento N, Villaça RC, Teixeira V L. Chemical variation and analysis of diterpenes from seaweed *Dictyota menstrualis* under controlled conditions. *Algal. Res.* (2022b) 62:102637.

Obando JMC, dos Santos TC, Martins RCC, Teixeira VL, Barbarino E, Cavalcanti DN. Current and promising applications of seaweed culture in laboratory conditions. *Aquaculture* (2022a) 560:738596.

Rajamani, K., & Thirugnanasambandan, S. S. (2018). Polyphenols from brown alga, Padina boergesenii (Allendar & Kraft) decelerates renal cancer growth involving cell cycle arrest and induction of apoptosis in renal carcinoma cells. *Environmental toxicology*, *33*(11), 1135-1142.

Rathod SG, Bhushan S, Mantri VA. Phytohormones and Pheromones in the Phycology Literature: Benchmarking of Data-Set and Developing Critical Tools of Biotechnological Implications for Commercial Aquaculture Industry. *Phycology* (2003), *4*(1):1-36.

Reverter M, Tribalat MA, Pérez T, Thomas OP. Metabolome variability for two Mediterranean sponge species of the genus Haliclona: specificity, time, and space. *Metabolomics* (2018) 14(9):114.

REFERENCES

Riebesell U, Schulz KG, Bellerby RGJ, Botros M, Fritsche P, Meyerhöfer M, Neill C, Nondal G, Oschlies A, Wohlers J, Zöllner E. Enhanced biological carbon consumption in a high CO2 ocean. *Nature* (2007) 450(7169):545-548.

Rodrigues S, Harb TB, Falcão EPDS, Pereira SMB, Chow, F. Antioxidant activity of dictyotales from tropical reefs of Brazil. *Applied Biochemistry and Biotechnology* (2020) 192(2):665-679.

Rui F, Boland W. Algal pheromone biosynthesis: stereochemical analysis and mechanistic implications in gametes of *Ectocarpus siliculosus*. *The Journal of Organic Chemistry* (2010) 75(12):3958-3964.

Santos TC, Obando JMC, Martins RCC, Alves MA, Villaça RC, Machado LP, Gasparoto MCG, Cavalcanti DN. Perfil Químico por CLUE-EMAR e Atividade Antifúngica e Antioxidante da Macroalga Marinha *Dictyota menstrualis. Revista Virtual de Química* (2024) 16(1).

Santos TC, Vale TM, Cavalcanti DN, Machado LP, Barbarino E, Martins RC, Obando JM. Metabólitos Bioativos e Aplicações Biotecnológicas de Macroalgas do Gênero *Sargassum*: Uma Revisão. *Revista Virtual de Química* (2023) 15(4):1-18.

Schmitz C, Ramlov F, de Lucena LAF, Uarrota V, Batista MB, Sissini MN, Oliveira I, Briani B, Martins CDL, Nunes JMC, Rorig L, Horta, PA, Figueroa FL, Korbee N, Maraschin M, Bonomi-Barufi J. UVR and PAR absorbing compounds of marine brown macroalgae along a latitudinal gradient of the Brazilian coast. *Journal of Photochemistry and Photobiology B: Biology* (2018) 178:165-174.

Silberfeld T, Bittner L, Fernández-García C, Cruaud C, Rousseau F, De Reviers B, Leliaert F, Payri CE, De Clerck O. Species diversity, phylogeny and large scale biogeographic patterns of the genus Padina (Phaeophyceae, Dictyotales). *Journal of phycology* (2013) 49(1):130-142.

Silberfeld T, Leigh JW, Verbruggen H, Cruaud C, De Reviers B, Rousseau F. A multi-locus time-calibrated phylogeny of the brown algae (Heterokonta, Ochrophyta, Phaeophyceae): Investigating the evolutionary nature of the "brown algal crown radiation". *Molecular phylogenetics and evolution* (2010) 56(2):659-674.

Silberfeld T, Rousseau F, de Reviers B. An updated classification of brown algae (Ochrophyta, Phaeophyceae). *Cryptogamie, Algologie* (2014) *35*(2):117-156.

REFERENCES

Subbiah V, Xie C, Dunshea FR, Barrow CJ, Suleria HA. The quest for phenolic compounds from seaweed: Nutrition, biological activities and applications. *Food Reviews International* (2023) 39(8):5786-5813.

Teagle H, Hawkins SJ, Moore PJ, Smale DA. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology* (2017) 492:81-98.

Terauchi M, Yamagishi T, Hanyuda T, Kawai H. Genome-wide computational analysis of the secretome of brown algae (Phaeophyceae). *Marine Genomics* (2017) 32:49-59.

Troell M, Henriksson PJ, Buschmann AH, Chopin T, Quahe S. Farming the ocean–seaweeds as a quick fix for the climate?. *Reviews in Fisheries Science & Aquaculture* (2023) 31(3):285-295.

Tronholm A, Steen F, Tyberghein L, Leliaert F, Verbruggen H, Antonia Ribera Siguan M, De Clerck O. Species delimitation, taxonomy, and biogeography of Dictyota in Europe (Dictyotales, Phaeophyceae). *Journal of phycology* (2010) 46(6):1301-1321.

Uhrmacher S, Hanelt D, Nultsch W. Zeaxanthin content and the degree of photoinhibition are linearly correlated in the brown alga *Dictyota dichotoma*. *Marine Biology* (1995) 123:159-165.

Urrea-Victoria V, Nardelli AE, Floh EI, Chow F. *Sargassum stenophyllum* (Fucales, Ochrophyta) responses to temperature short-term exposure: photosynthesis and chemical composition. *Brazilian Journal of Botany* (2020) 43(4):733-745.

Vallim MA, De Paula JC, Pereira RC, Teixeira VL. The diterpenes from Dictyotacean marine brown algae in the Tropical Atlantic American region. *Biochemical Systematics and Ecology* (2005) 33(1):1-16.

van Hees DH, Olsen YS, Wernberg T, Van Alstyne KL, Kendrick GA. Phenolic concentrations of brown seaweeds and relationships to nearshore environmental gradients in Western Australia. *Marine biology* (2017) 164(4)*:*1-13.

Vieira, C. Lobophora–coral interactions and phase shifts: summary of current knowledge and future directions. *Aquatic ecology* (2020) *54*(1):1-20.

REFERENCES

Vieira C, Camacho O, Wynne MJ, Mattio L, Anderson RJ, Bolton JJ, Sansón M, D'hondt S, Leliaert F, Fredericq S, Payri C, De Clerck O. Shedding new light on old algae: matching names and sequences in the brown algal genus Lobophora (Dictyotales, Phaeophyceae). *Taxon* (2016) *65*(4):689-707.

Vieira C, Steen F, D'hondt S, Bafort Q, Tyberghein L, Fernandez-García C, Wysor B, Tronholm A, Mattio L, Payri C, Kwai H, Saunders G, Leliaert F, Verbruggen H, De Clerck O. Global biogeography and diversification of a group of brown seaweeds (Phaeophyceae) driven by clade-specific evolutionary processes. *Journal of Biogeography* (2021) 48(4):703-715.

Wall R, Ross RP, Fitzgerald GF, Stanton C. Fatty acids from fish: the anti-inflammatory potential of long-chain omega-3 fatty acids. *Nutr. Rev.* (2010) 68(5):280–289

WangY, Feng Y, Liu X, Zhong M, Chen W, Wang F, Du H. Response of *Gracilaria lemaneiformis* to nitrogen deprivation. *Algal research* (2018) 34:82-96.

Williams JL. *Studies in the Dictyotaceae. II. The cytology of the gametophyte generation*. In: Proceedings of the Linnean Society of New South Wales. Sydney Linnean Society of New South Wales: Annals of Botany, 1904 vol. 18, number 70, pp. 183-204.

Win NN, Hanyuda T, Draisma SG, Lim PE, Phang SM, Kawai H. Taxonomy of the genus *Padina* (Dictyotales, Phaeophyceae) based on morphological and molecular evidences, with key to species identification. In: Taxonomy of Southeast Asian Seaweeds II. University of Malaya Press: *Taxonomy of Southeast Asian Seaweeds II,* 2013 p. 119.

Wink M. Evolution of secondary metabolites from an ecological and molecular phylogenetic perspective. *Phytochemistry* (2003) 64(1):3–19.

Womersley HBS. The marine benthic flora of Southern Australia, Part II. Adelaide. *Government Printer* (1987)

Wynne MJ, Loiseaux S. Recent advances in life history studies of the Phaeophyta. *Phycologia* (1976) *15*(3-4):435-452.

Xu P, Tan H, Jin W, Li Y, Santhoshkumar C, Li P, Liu W. Antioxidative and antimicrobial activities of intertidal seaweeds and possible effects of abiotic factors on these bioactivities. *Journal of oceanology and limnology* (2018) 36(6):2243-2256.

REFERENCES

Xu N, Xu K, Xu Y, Ji D, Wang W, Xie C. Interactions between nitrogen and phosphorus modulate the food quality of the marine crop *Pyropia haitanensis* (TJ Chang & BF Zheng) N. Kikuchi & M. Miyata (Porphyra haitanensis). *Food Chemistry* (2024) 138973.

Yu D, Yin J, Wang Y, Lu A, He Y, Shen S. Nitrogen assimilation-associated enzymes and nitrogen use efficiency of *Pyropia yezoensis* (Rhodophyta) in nitrate-sufficient conditions. *Algal Research* (2022) 64:102682.

Zatelli GA, Philippus AC, Falkenberg M. An overview of odoriferous marine seaweeds of the *Dictyopteris* genus: insights into their chemical diversity, biological potential and ecological roles. *Revista Brasileira de Farmacognosia* (2018) 28(2):243-260.

Zubia M, Fabre MS, Kerjean V, Le Lann K, Stiger-Pouvreau V, Fauchon M, Deslandes E. Antioxidant and antitumoural activities of some Phaeophyta from Brittany coasts. *Food chemistry* (2009) 116(3):693-701.

AUTHORS

JOHANA MARCELA CONCHA OBANDO: Seallg. Solutions, Innovation, and Products, Startup. Bioeconomy Living Lab and Science and Technology-Based Startup Incubators in the Ribeira Valley (Aquário de Ideias), Registro, SP, Brazil
National Institute of Science and Technology (INCT) in Nanotechnology for Sustainable Agriculture (INCTNanoAgro), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Sorocaba, Brazil.
ORCID: https://orcid.org/0000-0001-5351-2219

THALISIA CUNHA DOS SANTOS: Seallg. Solutions, Innovation, and Products, Startup. Bioeconomy Living Lab and Science and Technology-Based Startup Incubators in the Ribeira Valley (Aquário de Ideias), Registro, SP, Brazil
Chemistry of Natural Products Postgraduate Program, Institute of Research in Natural Products, Federal University of Rio de Janeiro, Rio de Janeiro, RJ, Brazil
ORCID: https://orcid.org/0000-0002-2043-4805

CLARA LOPES DOS SANTOS: Laboratory of Natural Products from Marine Algae (ALGAMAR), Department of Marine Biology, Institute of Biology, Fluminense Federal University, Niterói, RJ, Brazil

MARIA VITÓRIA RAUPP SEBASTIÃO: São Paulo State University (UNESP), School of Agricultural Sciences, Department of Fisheries Resources and Aquaculture, Constituinte of Advanced Marine Studies (IEAMar), Registro, SP, Brazil
ORCID: https://orcid.org/0009-0005-6227-153X

GUILHERME WOLFF BUENO: National Institute of Science and Technology (INCT) in Nanotechnology for Sustainable Agriculture (INCTNanoAgro), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Sorocaba, Brazil
São Paulo State University (UNESP), School of Agricultural Sciences, Department of Fisheries Resources and Aquaculture, Institute of Advanced Marine Studies (IEAMar), Registro, SP, Brazil
Aquaculture Center of UNESP - Caunesp, Jaboticabal, SP, Brazil
ORCID: https://orcid.org/0000-0002-1160-020X

AUTHORS

LEVI POMPERMAYER MACHADO: National Institute of Science and Technology (INCT) in Nanotechnology for Sustainable Agriculture (INCTNanoAgro), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Sorocaba, Brazil
São Paulo State University (UNESP), School of Agricultural Sciences, Department of Fisheries Resources and Aquaculture, Institute of Advanced Marine Studies (IEAMar), Registro, SP, Brazil
ORCID: https://orcid.org/0000-0002-6035-851X

VALÉRIA LANEUVILLE TEIXEIRA: Graduate Program in Neotropical Biodiversity, Laboratory of Algal Biology and Taxonomy, Institute of Biosciences, Rio de Janeiro, RJ, Brazil
Laboratory of Natural Products from Marine Algae (ALGAMAR), Department of Marine Biology, Institute of Biology, Fluminense Federal University, Niterói, RJ, Brazil
ORCID: https://orcid.org/0000-0003-4962-6912

DIANA NEGRÃO CAVALCANTI: Laboratory of Natural Products from Marine Algae (ALGAMAR), Department of Marine Biology, Institute of Biology, Fluminense Federal University, Niterói, RJ, Brazil
ORCID: https://orcid.org/0000-0001-6013-9889

THE INVISIBLE WORLD OF BROWN SEAWEEDS

How the Dictyotaceae Family Defends Itself and Interacts in the Ocean

www.atenaeditora.com.br
contato@atenaeditora.com.br
@atenaeditora
www.facebook.com/atenaeditora.com.br

Atena Editora
Ano 2025

SÃO PAULO GOVERNO DO ESTADO
unesp
Sealg
FAPESP
uff

THE INVISIBLE WORLD OF BROWN SEAWEEDS

How the Dictyotaceae Family Defends Itself and Interacts in the Ocean

www.atenaeditora.com.br
contato@atenaeditora.com.br
@atenaeditora
www.facebook.com/atenaeditora.com.br

Atena Editora
Ano 2025

SÃO PAULO
GOVERNO DO ESTADO
unesp
Sealig
FAPESP
uff